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Research Paper

Late Triassic floras from Guangdong, South China: Biostratigraphical context and palaeoenvironmental implications ☆

Xiaoqing Zhang [a,d], Yongdong Wang [a,*], Chong Dong [a], Xiaoming Lin [b], Jianhua Jin [c]

[a] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China
[b] Guangdong Geologic Survey Institute, Guangzhou 510080, China
[c] School of Life Sciences, Sun Yat-Sen University, Guangzhou 510275, China
[d] Department of Earth and Environmental Sciences, Wesleyan University, Middletown 06459, USA

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ABSTRACT

Triassic-Jurassic deposits are well developed in Guangdong Province, South China. In particular, the Upper Triassic coal-bearing strata which alternate between marine and terrestrial deposits yield diverse and abundant fossil plants, ammonites and bivalves. These strata provide a significant reference for the study of palaeoenvironmental variations in the lower latitude regions. In this paper, we review the major progress on Late Triassic floral studies in this area. Specifically, we compare the regional plant assemblages from different fossil sites in central and northern Guangdong which have been dated with marine fauna. 155 species belonging to 56 genera of fossil plants have been reported so far in northern and central Guangdong. The Late Triassic floras in Guangdong are mainly composed of Bennettitales and ferns, followed by horsetails, seed ferns, cycads, ginkgos and conifers. In ascending order, four regional plant fossil assemblages can be recognized in the Late Triassic deposits, namely the *Pachypteris-Lindleycladus* Assemblage (Julian), the *Pterophyllum-Baiera* Assemblage (late Julian), the *Clathropteris-Otozamites* Assemblage (Tuvalian), and the *Danaeopsis-Anomozamites* Assemblage (Rhaetian). In general, the Late Triassic climate in the Guangdong region was mainly humid and warm and either tropical or subtropical. The fossil plants corroborate palaeomagnetic evidence that the central and northern Guangdong region was located at approximately the same latitude as it is today and formed the southern coastline of the South China Block during the Late Triassic. Palaeogeographically, the transgression started at the end of the Julian and the south coastal terrane consisted of a western bay, a peninsula and an eastern bay. During the regression period, post-Rhaetian, the bays evolved into a gulf coastal plain.

1. Introduction

The Triassic-Jurassic Boundary (TJB; 201.3 Ma) represents one of the largest mass extinction events in the Phanerozoic. The TJB is marked by a series of geological and environmental changes such as increased CO_2 and accompanying extreme global warming, floral and faunal turnovers as well as more frequent wildfire activities. These changes probably resulted from the massive volcanism in the Central Atlantic Magmatic Province (CAMP) (McElwain et al., 1999; Beerling and Berner, 2005; Belcher et al., 2010; Petersen and Lindström, 2012).

The deposits of the T-J transition are well developed in China. In recent decades, studies on TJB community composition and turnover and palaeoenvironmental changes have been reported in some notable T-J sections such as in the higher latitude Junggar Basin with terrestrial facies (Ashraf et al., 2010; Deng et al., 2010; Sha et al., 2011, 2015) and in the middle-low latitude Sichuan Basin, with alternating marine and terrestrial facies (Wang et al., 2010; Li et al., 2020). Marine deposits of the Late Triassic in China are mainly developed in southern Tibet, eastern Heilongjiang and southeastern Guangdong up to Hunan and Jiangxi. In the low latitude area of central and northern Guangdong, the early Mesozoic coal-bearing series are represented by alternating marine and terrestrial facies such as in the Upper Triassic Xiaoping, Hongweikeng, Xiaoshui and Toumuchong formations. These formations are well-developed, yielding rich and diverse terrestrial and marine fossils such as ammonites, bivalves (Niu et al., 2013; Zhang et al., 2014), ostracods (Fang and Xu, 1978), insects (Lin, 1989), and abundant plants (Ao, 1956; Tsao, 1965; Wang, 1991, 1993; Zhang, 1930). These formations thus show great potential

☆ Corresponding editor: Evelyn Kustatscher.
* Corresponding author.
E-mail address: ydwang@nigpas.ac.cn (Y. Wang).

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for investigating the ecosystems and geological events prior to the T-J transition.

The fossil plants of the Late Triassic have been recorded in central and northern Guangdong since the 1930′s. Zhang (1930) first reported plant fossils from the Xiaoping Fm. in the Guangzhou area. Subsequently, a variety of plant fossils from central Guangdong were described focusing on fossil morphology, chronology, stratigraphic subdivisions and correlations (Ao, 1956; Tsao, 1965). In northern Guangdong, many studies have reported fossil plants collected by the geological survey or coal geologists during 1942 to 1988, however, only one study has been published (Liu, 1979). In the 1990′s, Wang (1993) summarized and supplemented the Late Triassic flora from northern Guangdong describing the floral composition of each horizon. However, the geographic scope of the study was limited. Therefore, in this paper, we provide a synthesis of Triassic northern and central Guangdong plant diversity (including published materials and new collections), with an emphasis on community composition palaeoclimate and palaeoenvironmental variations in Guangdong and adjoining areas (i.e. Hunan), so as to provide an overview and perspective for further investigations in this region.

2. Geological and stratigraphical settings

Tectonically, Guangdong is one of the most complex areas of southern China. Within this area, due to the subduction of the Pacific Plate and frequent volcanic activity, the sedimentary strata from different periods have been faulted and tilted. Uplifted crust formed Late Triassic topographic features in the region such as the intermountain basin facies in western Guangdong, the littoral and swamp facies in central and northern Guangdong and the neritic facies in eastern Guangdong (BGMRGP, 1988; Fig. 1).

The fossil-rich Upper Triassic strata from central and northern Guangdong are dominated by alternating marine and terrestrial facies and are known as the Genkou Group. The Genkou Group in northern Guangdong includes many localities such as Shaoguan, Yingde and Heyuan (Fig. 1). Abundant brackish/marine fossils are recorded in northern Guangdong including bivalves and ammonites. Stratigraphically, the Upper Triassic Genkou Group has been divided into three lithological units (in ascending order; Fig. 2): the Hongweikeng Fm., the Xiaoshui Fm. and the Toumuchong Fm. In northern Guangdong, the "Xiaoping Fm." was previously used locally before 1970's but is now treated as the Hongweikeng Fm. The Xiaoping Fm. in central Guangdong and Hongweikeng Fm. in northern Guangdong are lithologically similar. After the names of the Hongweikeng, Xiaoshui and Toumuchong formations were established, the name of Xiaoping Formation in northern Guangdong was no longer used. The Hongweikeng Fm. is located near the border of Guangdong and Hunan provinces and characterized by alternating coal-bearing clastic rocks, marine and terrestrial facies (BGMRGP, 1988; Figs. 1, 2), yielding fossil plants and brackish water bivalves.

The Hongweikeng Fm. unconformably overlaps the Tongziyan Fm. (Middle Permian) or other underlying strata and is conformably overlaid by the Upper Triassic Xiaoshui Fm. (Nan and Zhou, 2012). The Hongweikeng Fm. was divided into two members. The lower Shezhu Mb. is characterized by a series of gray-purple conglomerates and sandstones, intercalated with shale, sandy shale and coal bed (or coal seams). The upper Niugudun Mb. is dominated by sandstone and shale and contains fossil bivalves such as *Nanlingella* Rui et Sheng, *Gervillia* Defrance, *Bakevellia* King, *Bakevelloides* Tokuyama, *Guangdongella* Li et Li and *Myophoriopsis* Wöhrmann. The Hongweikeng Fm. is regarded as early Carnian in age based on the fossil bivalve *Guangdongella-Bakevellia* Assemblage (Chen, 1983; Niu et al., 2013; Fig. 3).

The Xiaoshui Fm. is conformably deposited in between the Hongweikeng Fm. and the Toumuchong Fm. It is characterized by a series of off-white to dark-gray siltstones, sandy mudstones, a fine-sandstone and a dark gray mudstone which includes siderite concretions (Nan and Zhou, 2012). It contains marine bivalve fossils such as *Trigonucula* Ichikawa, *Tosapecten* Kobayashi et Ichikawa, *Palaeopharus* Kittl, *Bakevelloides* Tokuyama, *Bakevellia* King, *Oxytoma* Meek, *Palaeopharus* Agassiz, and *Pleuromya* Agassiz (Wang, 1993, Niu et al., 2013) and ammonites (*Choristoceras* Hauer, *Rhacophyllites* Zittel). This formation is dated as middle Carnian to early Norian based on the fossil bivalve *Palaeopharus-Trigonucula* Assemblage Zone (Niu et al., 2013). In addition, the new records of ammonites (*Choristoceras* and *Rhacophyllites*) from the top of the Xiaoshui Fm. are index fossils of Rhaetian age. Thus, the age of the Xiaoshui Fm. is probably from Tuvalian to early Rhaetian based on a combination of the previously recorded fossil invertebrates and our new records of ammonites (Fig. 3).

The Toumuchong Fm. lies conformably between the Xiaoshui Fm. and Jinji Fm. (Early Jurassic). It is characterized by a grey-white quartz sandstone, interbedded with siltstone, carbonaceous mudstone, coal seams and coal beds (Nan and Zhou, 2012). The formation yields the fossil bivalves *Jiangxiella* Liu and *Myophoriopsis* Wöhrmann. They are important components of the fossil bivalve *Waagenoperna* Assemblage (Chen, 1983) and *Trigonodus*? *liuyangensis* Assemblage (Xiong and Wang, 1987). Thus, the Toumuchong Fm. is regarded as Late Norian to Rhaetian (Fig. 3).

The Xiaoping Fm. is mainly exposed in the central area of Guangdong with some limited areas of western Guangdong including Guangzhou, Gaoyao, Gaoming, and Meixian. The base of the Xiaoping Fm. is not exposed and unconformably overlaps the Lower Carboniferous through Lower Triassic deposits. Previously, the Xiaoping Fm. was subdivided into three members including the Luoke Mb., Fenggang Mb. and Ma'an Mb. (Nan and Zhou, 2012). The Luoke Mb. and Ma'an Mb. are characterized by a set of coal-bearing clastic rocks, including interbedded grey-white sandstone and black shale with thin coal seams. These two members are coevel to the Hongweikeng Fm. and the Toumuchong Fm., respectively, in northern Guangdong. The type sections of the Fenggang Mb. mainly outcrop in Gaoming and Foshan in central Guangdong, thinning out gradually to the east, characterized by grey-white siltstone, mudstone and black shale, which stratigraphically corresponds to the Xiaoshui Fm. These three members show a complete transgression-regressive sequence. The Xiaoping Fm. from the Gaoming section contains the fossil bivalves *Bakevelloides* Tokuyama and *Palaeopharus* Kittl (Nan and Zhou, 2012) which indicate a marine environment (Sepkoski, 2002). We also found some fossil bivalves such as *Unionites* Wissman in the town of Tanbu, Guangzhou which show a brackish water environment in the middle portion of the Xiaoping Fm. It can be compared with the *Unionites*? *emeiensis* Assemblage in northern Guangdong of Norian age (Xiong and Wang, 1987). Recently, we also found more localities along the border region of Guangdong and Hunan (also called the Nanling region) with diverse plant fossils (Fig. 3). Based on the marine and terrestrial fossils from the Xiaoping Fm., the deposits in these localities are assigned to Carnian to Rhaetian in age (Zhang, 2017; Figs. 3, 4; Table S1, Appendix A).

3. Material and methods

The fossil plant materials used in this study consist of all records relating to the Late Triassic flora in Guangdong since 1923, including published monographs, research papers, reports and theses. Some important taxa from our recently collected specimens are also examined. They came from the Xiaoping Fm. of

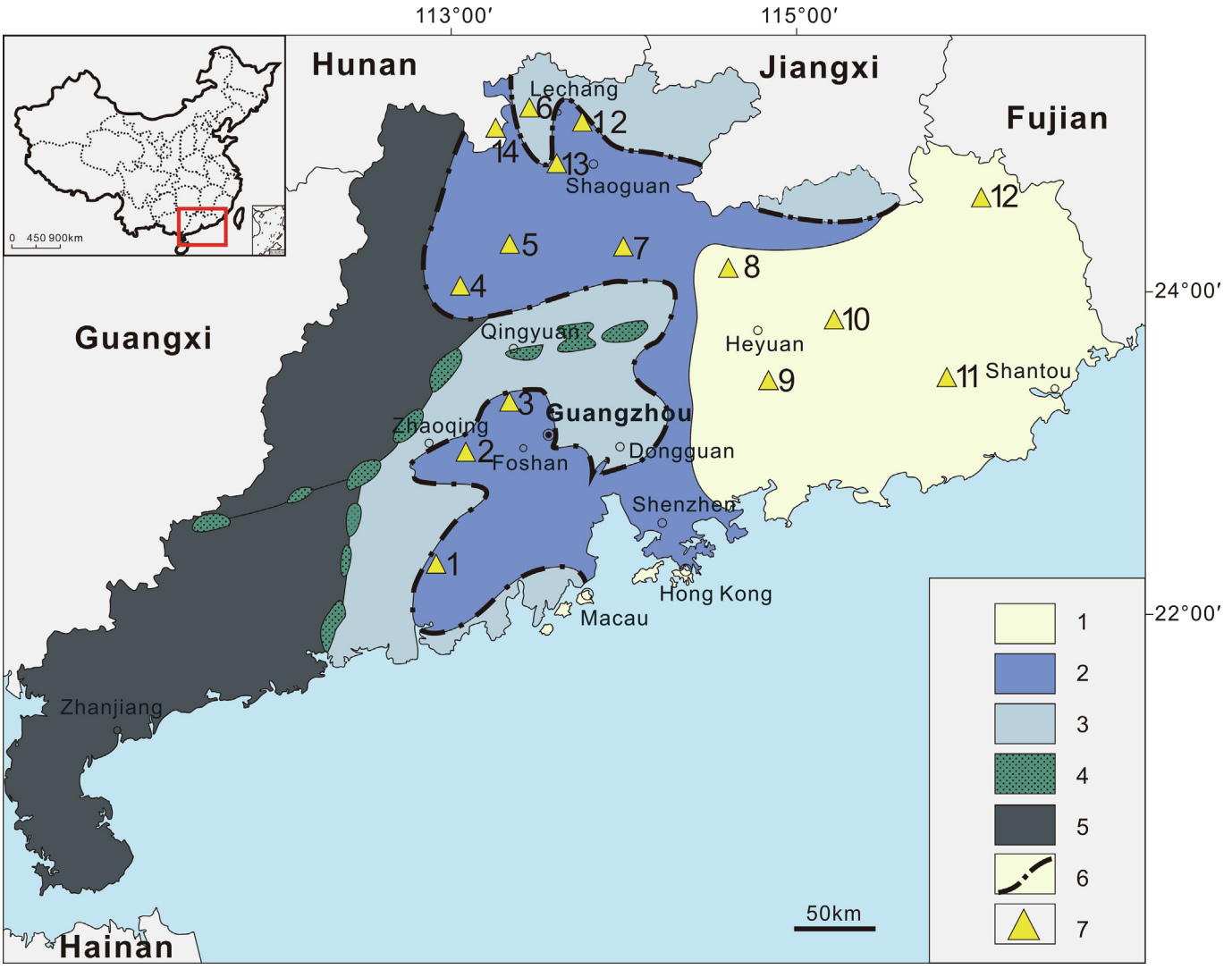

Fig. 1. Simplified lithofacies palaeogeographic map showing the localities of previous Late Triassic fossil records in the Guangdong region of China (modified after BGMRGP, 1988). Facies: 1, Shallow Marine facies; 2, Alternating marine and terrestrial facies; 3, Littoral and swamp facies; 4, Intermountain basin facies; 5, Mountain facies; 6, Maximum transgressive boundary; 7, Upper Triassic sections. Localities (△): 1, Jinji, Kaiping; 2, Gaoming, Foshan; 3, Huadu, Guangzhou; 4, Qingyuan; 5, Yingde; 6, Lechang; 7, Wengcheng, Shaoguan; 8, Xinfeng, Shaoguan; 9, Zijin, Heyuan; 10, Huangcun, Heyuan; 11, Huizhai, Jiexi; 12, Gaosi, Jiaoling; 13, Gouyadong, Chenzhou, Hunan province; 14, Longgui, Shaoguan.

Guangzhou, the Hongweikeng Fm. in Nanling and the Xiaoshui Fm. of Xinfeng in northern Guangdong. Some of the collections from Guangzhou are housed at the Natural Resources Bureau of Huadu District (NRBHD) of Guangzhou and others are housed in the Palaeobotany Collection at the Nanjing Institute of Geology and Palaeontology, CAS (NIGPAS, PB). In addition, the catalogued specimens from the Gaoming section (Tsao, 1965) housed in the Palaeobotany Collection in NIGPAS have been re-examined and re-photographed. The dataset on occurrences, localities and horizons of these fossil plants have been compiled. The representative taxa of the Late Triassic fossil plants from Guangdong are illustrated in Figs. 5–10.

The fossil specimens were photographed with a Sony ILCE-6000 camera equipped with a micro lens and Nikon Z7 digital single-lens relex camera equipped with an 24-70/4S zoom lens. Specimens' details were observed and photographed under a Zeiss SteREO Discovery V20 Stereo microscope. Multifocal photography was employed for fossils with three-dimensional preservation. All multifocal images of a fossil specimen were combined using depth-of-field compositing in the Adobe Photoshop.

4. Results

4.1. Diversity of plant fossils

The Late Triassic deposits of Guangdong yield a very high diversity of fossil plants. To date, 155 species representing 56 genera of fossil plants have been reported from the Upper Triassic strata in this province. These fossils are mostly documented from the Hongweikeng and Toumuchong formations in northern Guangdong. Sparse previous studies and collections from the Xiaoping Fm. in the central part of the province gave the appearance of lower species richness compared to the northern region. Recently, we made additional field surveys in central Guangdong where we collected more fossil plant genera and species, which are currently under investigation.

4.1.1. The Genkou Group

Various fossil plants, totaling to 92 species in 40 genera have been recognized from the Genkou Group (Hongweikeng, Xiaoshui

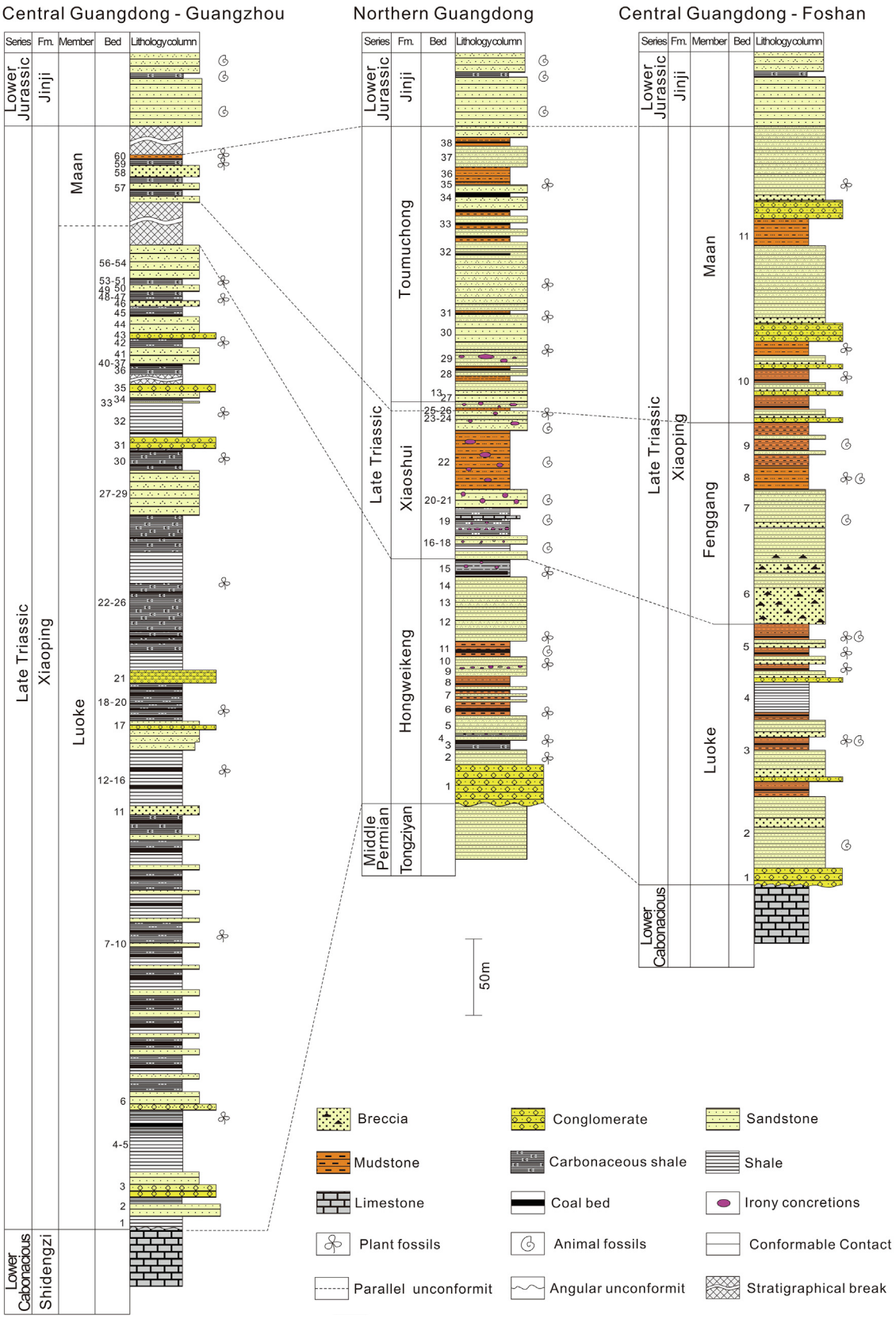

Fig. 2. Stratigraphic correlation diagram of Genkou Group of the Upper Triassic in the Guangdong area (according to BGMRGP, 1988 and Tsao, 1965).

Region	Fm.	Member	Age	Location	Bivalves	Ammonites	Plants (Details see Table 1 and Appendix Table 1)	References
Northern Guangdong	Toumuchong		late Norian-Rhaetian	Tianmenao, Shaoguan; Xiaoshui, Lechang, Shaoguan;	*Jiangtiella* Liu, *Myophoriopsis* Wöhrmann		**Horstails:** *Equisetites* **Ferns:** *Phlebopteris* , *Danaeopsis* , *Dictyophyllum, Clathropteris* , *Thaumatopteris* , *Gleichenites* , *Symopteris* **Seed ferns:** *Pachypteris* , *Sagenopteris* **Bennettitales:** *Otozamites* , *Pterophyllum* **Conifers:** *Cycadocarpidium*	Bivalves (Chen, 1983; Xiong and Wang, 1987) Plants (Nan and Zhou, 1996; Internal data from XiAn Coal Research Institute, 1973)
	Xiaoshui		late Julian, Carnian to ? Rhaetian	Xinfeng, Shaoguan	*Trigonucula* Ichikawa, *Tosapecten* Kobayashi and Ichikawa, *Palaeopharus* Kittl, *Bakevelloides* Tokuyama, *Bakevellia* King, *Oxytoma* Meek, *Palaeopharus* Agassiz, *Pleuromya* Agassiz	*Choristoceras* cf. *marshi* Hauer, *Rhacophyllites* sp.	**Ferns:** *Dictyophyllum* , *Clathropteris, Cladophlebis, Gleichenites* , *Symopteris* **Bennettitales:** *Otozamites* , *Pterophyllum* **Ginkgos:** *Baiera*	Bivalves (Wang, 1993, Niu et al., 2013) Ammonites (our data) Plants (our collections)
	Hongweikeng	Niugudun	Julian, Carnian	Hongweikeng, Longgui, Shaoguan; Guanchun, Lechang, Shaoguan; Ankou, Lechang, Shaoguan; Gouyadong, Yizhang, Chenzhou; Xinfeng, Shaoguan	*Nanlingella* Rui et Sheng, *Gervillia* Defrance, *Bakevellia* King, *Bakevelloides* Tokuyama, *Guangdongella* Li et Li, *Myophoriopsis* Wöhrmann		**Horstails:** *Equisetites* , *Annulariopsis* , *Neocalamites* **Ferns:** *Todites* , *Dictyophyllum, Clathropteris* , *Thaumatopteris* , *Cladophlebis* **Seed ferns:** *Pachypteris* , *Ptilozamites* , *Xinlongophyllum* **Bennettitales:** *Pterophyllum* , *Ptilophyllum* , *Anomozamites* , *Otozamites* , *Sinoctenis* , *Cycadolepis* , *Vardekloftia* , *Tyrmia* , *Dictyozamites* , *Anthrophyopsis* **Cycads:** *Nilssonia* , *Pseudoctenis* , *Drepanozamites* , *Doratophyllum* **Ginkgos:** *Ginkgoites* , *Glossophyllum* , *Stenorachis* , *Baiera* , *Sphenobaiera* **Conifers:** *Lindleycladus* , *Cycadocarpidium* , *Podozamites* , *Ferganiella* , *Stachyotaxus* **Incertae Sedis:** *Taeniopteris*	Bivalves (Chen, 1983; Niu et al., 2013) Plants (Nan and Zhou, 1996; Internal data from XiAn Coal Research Institute, 1973; our collections)
		Shezhu	Julian, Carnian					
Central Guangdong	Xiaoping	Maan	late Norian-Rhaetian	Chini, Huadu, Guangzhou Gaoming, Foshan Huadu, Guangzhou (D2003, D1028 upper, D1035, D1039, D1115, D1116)			**Horstails:** *Equisetites* , *Neocalamites* **Ferns:** *Danaeopsis* , *Phlebopteris* , *Gleichenites* , *Dictyophyllum* , *Clathropteris* , *Thaumatopteris* , *Cladophlebis, Todites* , *Sphenopteris* , *Todites* , *Spiropteris* **Seed ferns:** *Ptilozamites* , *Protoblechnum* , *Pachypteris* , *Ctenozamites* , *Sagenopteris* **Bennettitales:** *Pterophyllum* , *Anomozamites* , *Sinoctenis* , *Tyrmia* , *Wielandiella* , *Otozamites* **Cycads:** *Ctenis* , *Nilssonia* **Conifers:** *Podozamites* , *Lindleycladus* **Incertae Sedis:** *Umkomasia* , *Taeniopteris*	Plants (Chen, 1949; Cao, 1965; our collections)
		Fenggang	late Julian, Carnian to ? early Norian	Gaoming, Foshan	*Bakevelloides* Tokuyama, *Palaeopharus* Kittl, *Unionites* Wissman			Bivalves (Nan and Zhou, 1996)
		Luoke	Julian, Carnian	Xiaoping, Guangzhou Huadu, Guangzhou (D1028 lower, D1128, D1324)	*Unionites* Wissman		**Horstails:** *Equisetites, Neocalamites, Phyllotheca* **Ferns:** *Phlebopteris* , *Stachypteris* , *Clathropteris, Dictyophyllum, Thaumatopteris, Hausmannia, Goeppertella, Cladophlebis, Todites, Spiropteris, Sphenopteris* **Seed ferns:** *Pachypteris, Ptilozamites, Caytonia* **Bennettitales:** *Pterophyllum, Ptilophyllum, Otozamites, Sinoctenis, Cycadolepis, Dictyozamites* **Cycads:** *Ctenis, Nilssonia* **Ginkgos:** *Ginkgoites, Baiera* , *Czekanowskia* , *Stenorachis* **Conifers:** *Podozamites* **Incertae Sedis:** *Taeniopteris, Carpolithus*	Bivalves (our collections) Plants (Zhang, 1930; Ao, 1956; our collections)

Fig. 3. Late Triassic strata and plant fossil assemblage composition in Guangdong.

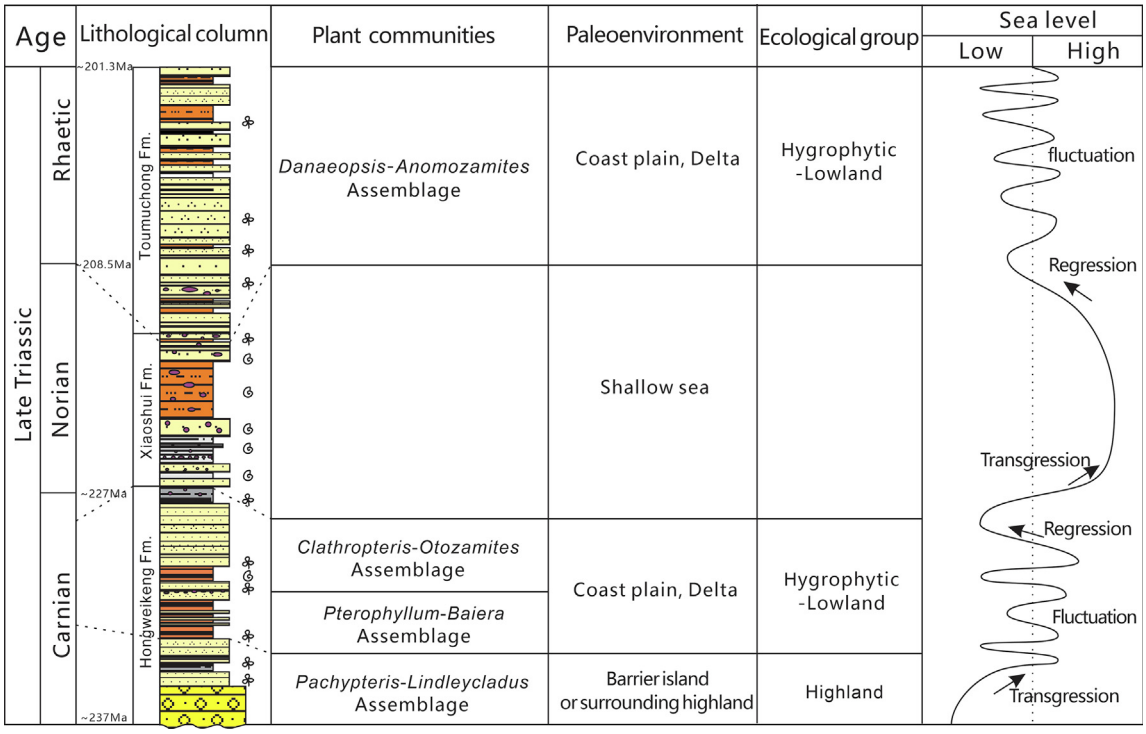

Fig. 4. Diagram of the Late Triassic palaeovegetation and palaeoenviromental changes in Guangdong and adjacent area. Lithological column based on northern Guangdong strata; right column showing schematic sea level variations.

and Toumuchong formations) in northern Guangdong, include horsetails (Equisetales), ferns (Filicales), seed ferns (Pteridospermae), Caytoniales, Bennettitales, cycads (Cycadales), ginkgos (Ginkgoales), conifers (Coniferales) as well as fructifications, incertae sedis and fossil woods (Table S1, Appendix A).

The fossil plant diversity is extremely high (86 species, 36 genera) in the Hongweikeng Fm. (Wang, 1993; Fig. 3; Table S1, Appendix A). Horsetails like *Equisetites* Sternberg is abundant in some beds. The seed fern genus *Pachypteris* (Brongniart) Harris (Fig. 5 (A, B)) has low species diversity but is very abundant throughout the formation. Bennettitalean plants like *Pterophyllum* Brongniart (Fig. 5(C, D)) and *Tyrmia* Prynada (Fig. 5(E, F)) are very abundant, especially *Pterophyllum* which is the taxon with the highest species richness in this formation. Ginkgos, including *Baiera* Braun (Fig. 5 (G)) and *Ginkgoites* Seward emend. Florin, are somewhat rare in the Late Triassic strata. However, they mostly co-occur with vari-

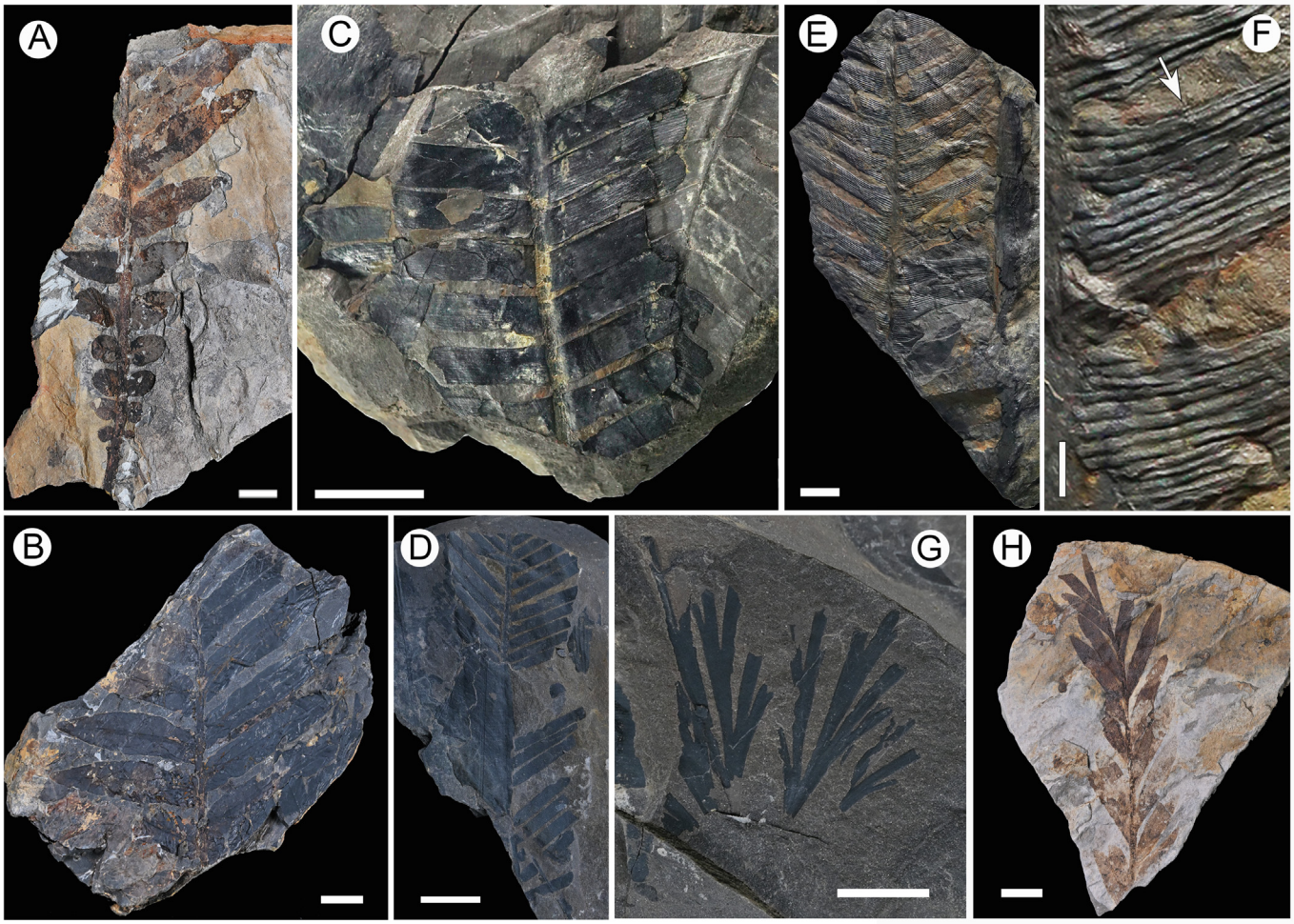

Fig. 5. Representative plant fossil taxa collected from the Hongweikeng Formation in northern Guangdong. **A.** *Pachypteris xiaoshuiensis* Feng, D1003, Gouyadong, Chenzhou, PB200515. **B.** *Pachypteris xiaoshuiensis* Feng, D1004, Gouyadong, Chenzhou, PB200516. **C.** *Pterophyllum kochi* Harris, D1001, Gouyadong, Chenzhou, PB200518. **D.** *Pterophyllum ptilum* Harris, D2003, Gouyadong, Chenzhou, PB200519. **E, F.** *Tyrmia furcata* (Chow et Tsao) Wang, Ankou, Lechang, PB200520. **F.** Inset of Fig. 5(E) showing curling leaf margin (white arrow). **G.** *Baiera* cf. *müensteriana* (Presl) Heer, D2003, Gouyadong, Chenzhou, PB200524. **H.** *Lindleycladus lanceolatus* Harris, D1003, Gouyadong, Chenzhou, PB200525. Scale bars: 1 cm (A-E, G, H), 2 mm (F).

ous *Pterophyllum* leaves. Conifers like *Podozamites* Braun, *Lindleycladus* Harris (Fig. 5(H)) are also common in this stratum.

The plant diversity of the Xiaoshui Fm. is comparatively low (8 species, 8 genera) due to the transition between brackish water conditions to extensive marine transgression conditions during the Norian. Recently, new specimens were collected from the coal seams of the top part of the Xiaoshui Fm. They consist of *Cladophlebis* Brongniart, *Dictyophyllum* Lindley et Hutton, *Clathropteris* Brongniart, *Symopteris* Xu, *Gleichenites* Seward, and *Pterophyllum* (Fig. 3; Table 1; Table S1, Appendix A). Almost all of these fossils can be found in the Toumuchong Fm.

In the Toumuchong Fm., the plant diversity begins to increase, with 16 species belonging to 15 genera. The main taxa are *Equisetites*, *Danaeopsis* Heer, *Phlebopteris* Brongniart, *Clathropteris*, *Dictyophyllum*, *Thaumatopteris* (Goeppert) Nathorst, *Marattiopsis* Schimper, *Gleichenites*, *Ptilozamites* Nathorst, *Sagenopteris* Presl, *Pterophyllum*, *Otozamites* Braun, *Nilssonia* Brongniart, *Ginkgoites* Seward emend. Florin and *Cycadocarpidium* Nathorst (Wang, 1993; Fig. 3; Table 1; Table S1, Appendix A).

4.1.2. The Xiaoping Formation

A previous report (Tsao, 1965) indicated that in the Gaoming section of Foshan, there were about 38 species across 20 genera of plant fossils. The major fossil taxa include *Equisetites* (Fig. 6(A–D)), *Neocalamites* (Fig. 6(E, F)), *Danaeopsis*, *Phlebopteris* (Fig. 6(G)), *Dictyophyllum* (Fig. 6(H)), *Thaumatopteris*, *Clathropteris* (Fig. 6(I)), *Gleichenites* (Fig. 6(J)), *Cladophlebis*, *Protoblechnum* Lesq., *Pachypteris* (formerly *Thinnfeldia*), *Ptilozamites* (Fig. 7(A)), *Pterophyllum* (Fig. 7(B)), *Anomozamites* Schimper, *Nilssonia* (Fig. 7(C)), *Ctenis* Lindley et Hutton (Fig. 7(D–F)), *Taeniopteris* Brongniart (Fig. 7(G)), *Podozamites*, *Lindleycladus* (Fig. 7(H)), and *Carpolithus* Wallerius (Fig. 3; Table S1, Appendix A). The existence of representative plant taxa from the Toumuchong Fm. in Nanling like *Danaeopsis* and *Gleichenites*, shows that the Xiaoping and Toumuchong formations are probably coeval.

Previously, over 20 species from 16 genera have been reported from the type section of the Xiaoping Fm. which is located at the Xiaoping Station, Guangzhou (Zhang, 1930; Ao, 1956). In recent years, we have made more palaeobotanical field surveys in Tanbu Town, Huadu District, Guangzhou. Based on previous studies (Zhang, 1930; Ao, 1956) and our new collected specimens, about 90 species ascribed to 44 genera have been recognized from this region, including horsetails (*Equisetites*, *Neocalamites*, *Radicites* Potonie and *Phyllotheca* Brongiart; Fig. 8(A)), ferns (*Danaeopsis* (Fig. 8(B)), *Phlebopteris* (Fig. 8(C)), *Gleichenites*, *Stachypteris* Pomel (Fig. 8(D, E)), *Todites* Seward, *Dictyophyllum*, *Clathropteris* (Fig. 8(F, G)), *Thaumatopteris* (Fig. 8(H)), *Hausmannia* Dunker, *Goeppertella* Ôishi et Yamasita, *Spiropteris* Schimper, *Cladophlebis* and *Sphenopteris* (Brogniart) Sternberg), seed ferns (*Pachypteris* (Fig. 9(A)), *Ptilozamites* (Fig. 9(B)), *Protoblechnum* Lesquereux (Fig. 9(C)),

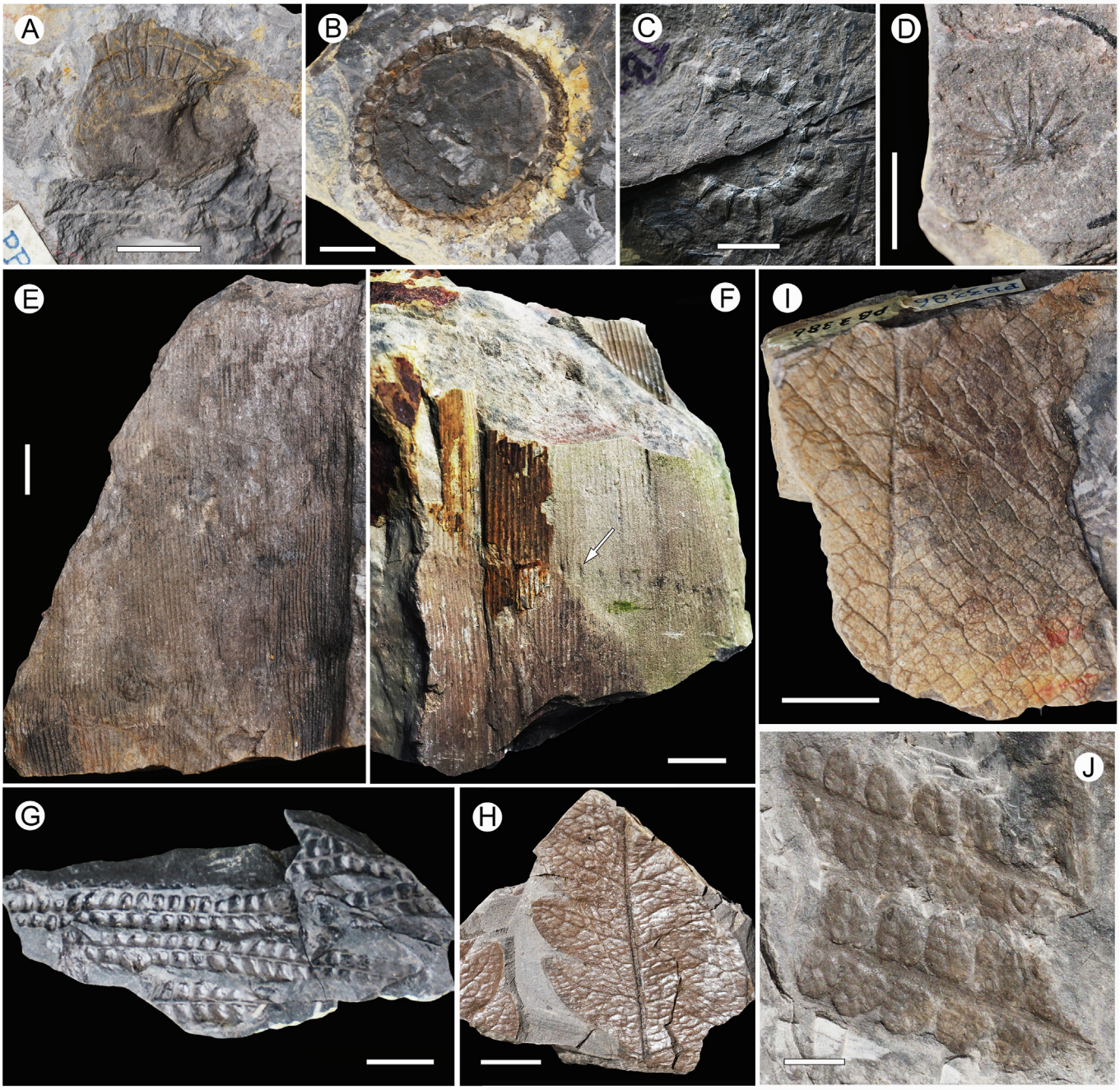

Fig. 6. Representative taxa collected from the Xiaoping Formation in the Gaoming section, central Guangdong. **A.** *Equisetites* sp., Gaoming, Foshan, PB3373 (after Tsao, 1965). **B.** *Equisetites kaomingensis* Tsao, Gaoming, Foshan, PB3370 (after Tsao, 1965). **C.** Leaf-sheath of an equisetaceous plant, D1028, Huadu, Guangzhou, PB200509. **D.** Leaf-sheath of an equisetaceous plant, Gaoming, Foshan, PB3374. **E.** *Neocalamites carrerei* (Zeiller) Halle, Gaoming, Foshan, PB3375 (after Tsao, 1965). **F.** *Neocalamites carrerei* (Zeiller) Halle, D1028Y, Huadu, Guangzhou, NRBHD-D1028Y-01. **G.** *Phlebopteris angustiloba* (Presl) Hirmer et Hörhammer, Gaoming, Foshan, PB3377 (after Tsao, 1965). **H.** *Dictyophyllum nathorsti* Zeiller, Gaoming, Foshan, PB3384 (after Tsao, 1965). **I.** *Clathropteris meniscioides* Brongniart, Gaoming, Foshan, PB3386 (after Tsao, 1965). **J.** *Gleichenites yipinglangensis* Li and Cao, Gaoming, Foshan, PB3381 (after Tsao, 1965). Scale bars: 1 cm (A-C, E, F, H, I), 5 mm (D, G, J).

Sagenopteris (Ao, 1956 misidentified these specimens as a new genus *Hexaphyllum*) and *Caytonia* Reid et Chandler), Bennetitales (*Pterophyllum* (Fig. 9(D)), *Ptilophyllum* Morris, *Anomozamites* (Fig. 9(E)), *Otozamites* (Fig. 9(F)), *Sinoctenis* Sze (Fig. 9(G)), *Cycadolepis* Saporta, *Dictyozamites* Oldham, *Tyrmia* Prynada and *Wielandiella* Nathorst (Fig. 9(H))), cycads (*Nilssonia* and *Ctenis*), ginkgos (*Ginkgoites* (Fig. 10(A)), *Baiera* (Fig. 10(B–D)), *Czekanowskia* Heer (Fig. 10(E)) and *Stenorachis* Saporta (Fig. 10(F))), conifers (*Podozamites* (Fig. 10(G)), *Lindleycladus* (Fig. 10(H)) and *Voltzia* Brongniart) and some incertain sedis (*Taeniopteris* (Fig. 10(I)), *Umkomasia* Thomas and *Carpolithus*). The plant assemblages based on northern Guangdong fossil collections support that the Xiaoping Fm. is Carnian to Rhaetian in age (Zhang, 2017; Fig. 3; Table S1, Appendix A).

4.2. Fossil plant assemblages and biostratigraphy

From the 1930′s to 1990′s geological survey teams and palaeobotanical researchers worked on several Xiaoping Fm. sections for coal mining purposes. They found that the fossil plant orders in

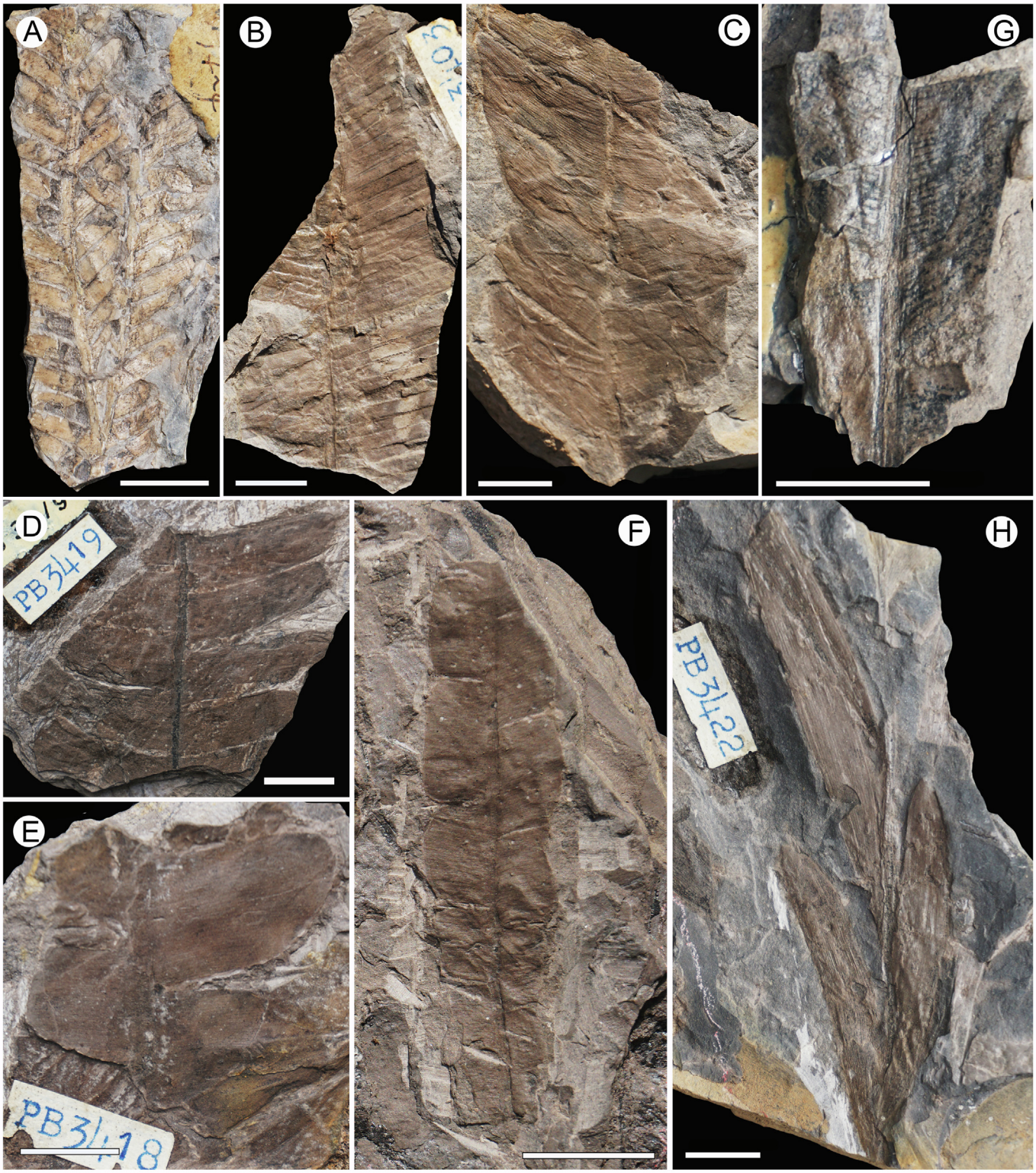

Fig. 7. Representative plant fossil taxa collected from the Xiaoping Formation in the Gaoming section, central Guangdong. **A.** *Ptilozamites chinensis* Hsü, Gaoming, Foshan, PB3395. **B.** *Pterophyllum bavieri* Zeiller, Gaoming, Foshan, PB3403 (Cao, 1965: pl. 4–8). **C.** *Nilssonia* sp., Gaoming, Foshan, PB3417 (after Tsao, 1965). **D.** *Ctenis* sp., Gaoming, Foshan, PB3419 (after Tsao, 1965). **E.** *Ctenis chaoi* Sze, Gaoming, Foshan, PB3418 (after Tsao, 1965). **F.** *Ctenis gracilis* Tsao, Gaoming, Foshan, PB3420 (after Tsao, 1965). **G.** *Taeniopteris* sp., Gaoming, Foshan, PB3421 (after Tsao, 1965). **H.** *Lindleycladus lanceolatus* Harris, Gaoming, Foshan, PB3422 (after Tsao, 1965). Scale bars: 1 cm.

the Guangdong and Nanling regions of southern China during the Late Triassic were different from other Late Triassic localities in China and around the World, which might be related to plant distribution history and geological movement. Thus, further research about the regional plant assemblage characters and the evolution of how they form assemblages is very important.

Most of the Late Triassic plant specimens in the Guangdong region were collected from fossil localities that yield no continuous

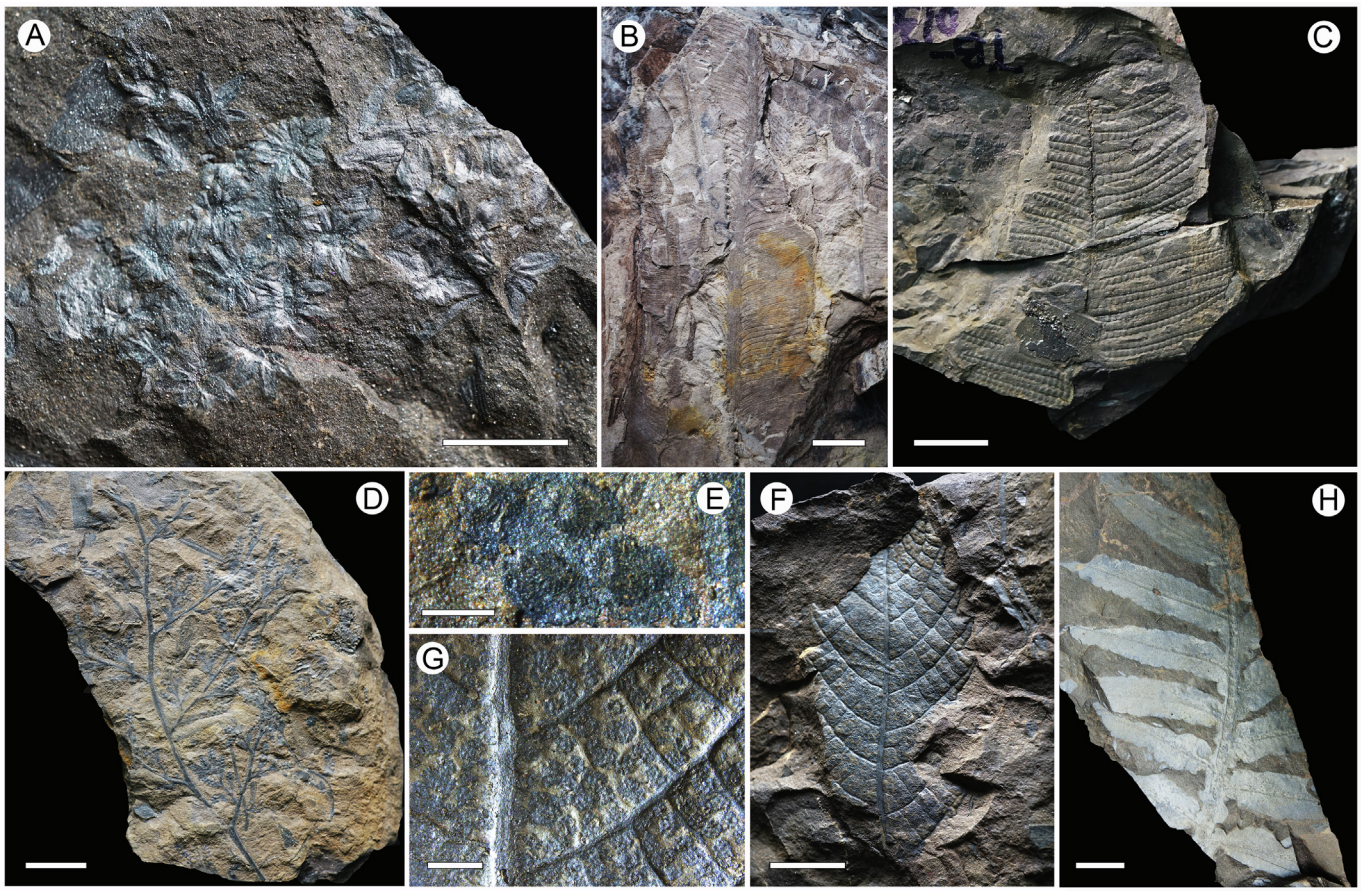

Fig. 8. Representative plant fossil taxa collected from the Xiaoping Formation in the Huadu section, central Guangdong. **A.**?*Phyllotheca* sp., D1028, Huadu, Guangzhou, PB200510. **B.** *Danaeopsis fecunda* Halle, D1028, Huadu, Guangzhou, NRBHD-D1028-N07. **C.** *Phlebopteris angustiloba* (Presl) Hirmer et Hörhammer, D1028, Huadu, Guangzhou, PB200512. **D, E.** *Stachypteris spicans* (Pomel) Harris, D1028, Huadu, Guangzhou, PB200511. **F.** *Clathropteris obovata* Ôishi, D1028, Huadu, Guangzhou, PB200513. **G.** Showing the sporangia for Fig. 8(F). **H.** *Thaumatopteris remauryi* (Zeill.) Ôishi et. Yam, D1028, Huadu, Guangzhou, PB200514. Scale bars: 1 cm (A-D, F, H), 0.5 mm (E), 2 mm (G).

sections (Fig. 3; Table S1, Appendix A). Thus, the chronological setting of these sections is mainly based on plant fossils and brackish-marine animal fossils from the localities of central and northern Guangdong (Fig. 2). However, the Late Triassic brackish-marine fossil assemblage zones from northern Guangdong and adjacent provinces have been thoroughly investigated (Chen, 1983; Xiong and Wang, 1987; Niu et al., 2013). Therefore, according to the stratigraphic sequence indicated by these fossil faunas, four plant fossil assemblages can be distinguished from the Late Triassic deposits in Guangdong, covering the ages from Carnian to Rhaetian of the Late Triassic (Fig. 4).

Three plant assemblages have been recognized from the Carnian age. The *Pachypteris–Lindleycladus* Assemblage and *Pterophyllum-Baiera* Assemblage were assigned to the early Carnian because of the co-occurrence of bivalve assemblage zones (*Guangdongella-Bakevellia* Assemblage Zone and *Bakeveloides hekiensis-Palaeopharus oblongatus* Assemblage Zone; Chen, 1983; Niu et al., 2013).

4.2.1. Pachypteris–Lindleycladus Assemblage

The *Pachypteris–Lindleycladus* Assemblage can be found in Gouyadong, Chenzhou in southern Hunan Province and Tanbu Town, Guangzhou. This floral assemblage is characterized by the abundant presence of the seed fern *Pachypteris xiaoshuiensis* Feng and conifer *Lindleycladus* cf. *lanceolatus* (L. et H.) Harris with a relatively small number of Bennettitales *Pterophyllum* sp. This assemblage starts from Bed 2 of the Lower Mb. of Hongweikeng Fm. and ends at Bed 9 from the Gouyadong section in the northern Guangdong region (Fig. 2).

4.2.2. Pterophyllum-Baiera Assemblage

The *Pterophyllum-Baiera* Assemblage is based on fossils from Dawo Village in Guangzhou and Gouyadong in Chenzhou (Fig. 3; Table S1, Appendix A). It is dominated by the high diversity of *Pterophyllum*, including *Pterophyllum aequale* (Brongn.) Nathorst, *Pt. ptilum* Harris, *Pt. ctenoides* Ôishi, *Pt. schenki* Zeiller, *Pt. sinense* P. Lee, *Pt. xinanense* Yang and *Pt. kochi* Harris; horsetails like *Equisetites sarrani* (Zeiller) Harris, *Neocalamites carrerei* (Zeiller) Halle and ginkgos like *Ginkgoites sibiricus* (Heer) Seward, *Baiera elegans* Ôishi, *B. multipartita* Sze et Lee and *B. müensteriana* (Presl) Heer. The Dipteridaceae fronds, like *Clathropteris meniscioides* Brongniart, *C. obovata* Ôishi, *Dictyophyllum nathorsti* Zeiller, *Thaumatopteris contracta* Li et Tsao and *T. remauryi* (Zeiller) Ôishi et Yamasita are also common in this group. These plant fossils were collected from black to dark grey shales. The presence of horsetails demonstrates a lowland to wetland plant community (Cao, 1992; Abbink et al., 2004; Deng, 2007). This assemblage yields the most abundant plant fossils. It starts from Bed 10 of the Hongweikeng Fm. and ends at Bed 12 from the Gouyadong, Guanchun, Lechang, and Longgui sections in northern Guangdong (Fig. 2). They are also preserved in Beds 7–42 from the Luoke Mb. of the Xiaoping Fm. from the Huadu section in central Guangdong (Fig. 2).

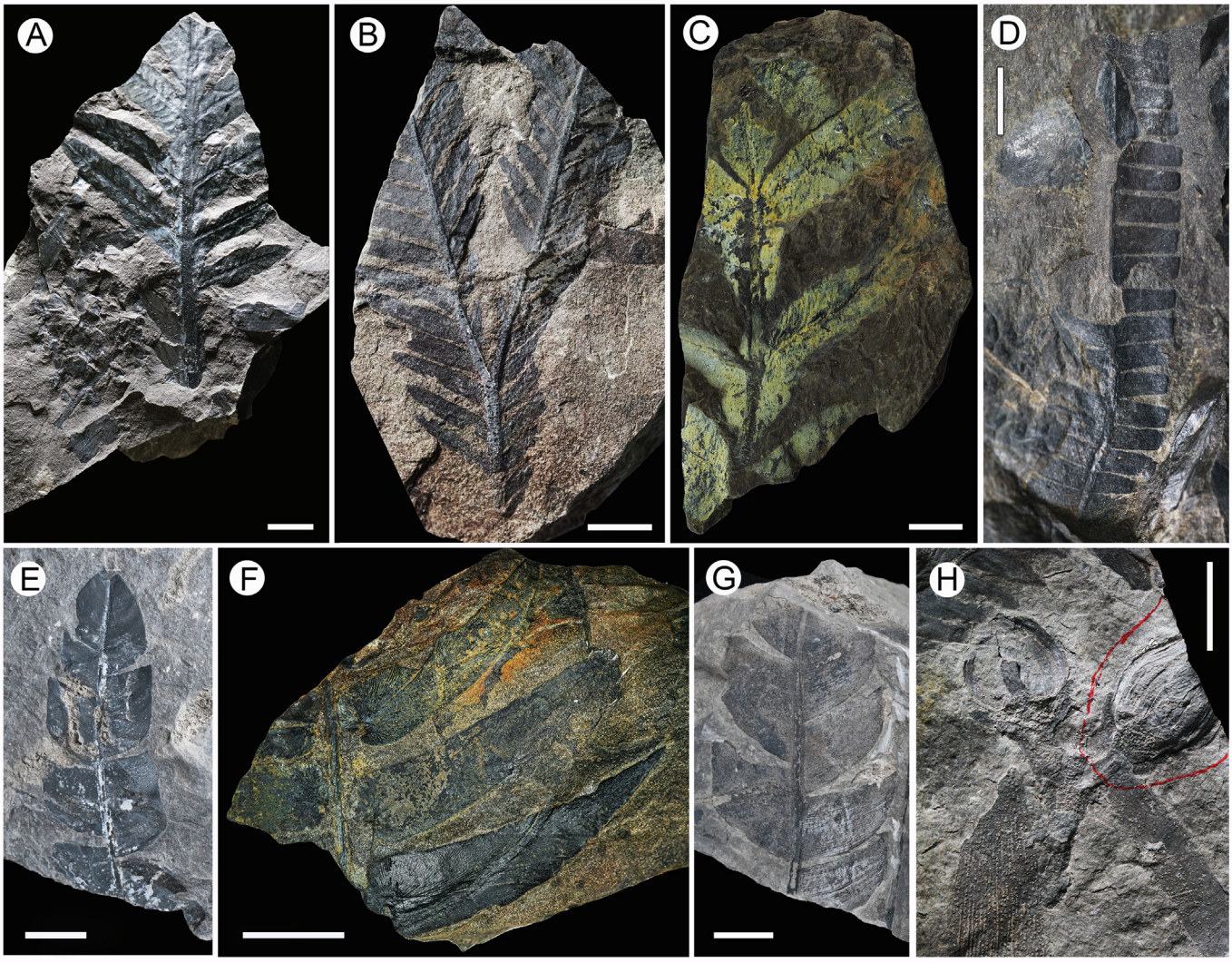

Fig. 9. Representative plant fossil taxa collected from the Xiaoping Formation in the Huadu section, central Guangdong. **A.** *Pachypteris xiaoshuiensis* Feng, D0003, Huadu, Guangzhou, NRBHD-D0003-16. **B.** *Ptilozamites chinensis* Hsü, D1039, Huadu, Guangzhou, NRBHD-D1039-25. **C.**?*Protoblechnum hughesi* (Feist) Halle, D0003, Huadu, Guangzhou, NRBHD-D0003-11. **D.** *Pterophyllum aequale* (Brongn.) Nathorst, D1324, Huadu, Guangzhou, PB200517. **E.** *Anomozamites minor* (Brongn.) Nathorst, D1039, Huadu, Guangzhou, PB200522. **F.** *Otozamites* cf. *hsiangchiensis* Sze, D1324, Huadu, Guangzhou, NRBHD-D1324-03. **G.** *Sinoctenis calophylla* Wu et Lih, D1039, Huadu, Guangzhou, PB200521. **H.** *Wielandiella* sp., D1039, Huadu, Guangzhou, NRBHD-D1039-29. Scale bars: 1 cm (A-E, G, H), 2 cm (F).

4.2.3. Clathropteris-Otozamites Assemblage

The third assemblage is defined by *Clathropteris* and *Otozamites*. It is based on plant fossils in the Hongweikeng Fm. and Luoke Mb. of the Xiaoping Fm. from Xinfeng, Shaoguan and Huanshan Villages in Guangzhou. This assemblage is represented by high amounts of Dipteridaceae leaves, such as *Clathropteris meniscioides* Brongniart, *Cl. platyphylla* Goeppert, *Cl. obovata* Ôishi, and *Dictyophyllum nathorsti* Zeiller, as well as the Bennettitales *Otozamites* cf. *hsiangchiensis* Sze and *Pterophyllum aequale* (Brongn.) Nathorst, *Pt. bavieri* Zeiller, and *Pt. jaegeri* Brongniart. It persists from Bed 15 of the Lower Mb. of Hongweikeng Fm. in the Xinfeng section of northern Guangdong and in Beds 47–51 from the Luoke Mb. of the Xiaoping Fm. in the Huadu section in central Guangdong (Fig. 2).

4.2.4. Danaeopsis-Anomozamites Assemblage

The fourth, *Danaeopsis-Anomozamites* Assemblage was assigned a Rhaetian age based on ammonites (*Choristoceras* cf. *marshi* Hauer and *Rhacophyllites* sp.) found above the strata and the co-occurrence of the bivalve *Unionites*? *emeiensis–Yunnanophorus* Assemblage Zone. This assemblage is recognized based on fossil collections from the Toumuchong Fm. in Shaoguan and Ma'an Mb. of the Xiaoping Fm. in Gaoming, Foshan and Dawo Village in Guangzhou (D1028 upper) (Table S1, Appendix A). It is characterized by abundant ferns such as *Danaeopsis fecunda* Halle, *Symopteris* sp., *Gleichenites yipinglangensis* Li et Tsao, *Todites denticulata* (Brongn.) Krasser, *Cl. meniscioides* Brongniart, *Cl. mongugaica* Srebrodolskaya; seed ferns such as *Protoblechnum hughesi* (Feist.) Halle as well as Bennettitales *Anomozamites* cf. *major* (Brongniart) Nathorst and *A. minor* (Brongniart) Nathorst. This assemblage occurs in Beds 25 to 38, from the top of the Xiaoshui Fm. through the Toumuchong Fm. in the Zhangtiankeng, Tianmenao, Xiaoshui and Tangcun sections of northern Guangdong. It is also found in Beds 57–60 in the Ma'an Mb. in the Xiaoping Fm. in the Gaoming and Huadu sections in central Guangdong (Fig. 2).

5. Discussions

5.1. Remarks on taxa with biostratigraphic significance

According to the fossil record, there were no obvious floral changes on the order and family levels though some variations

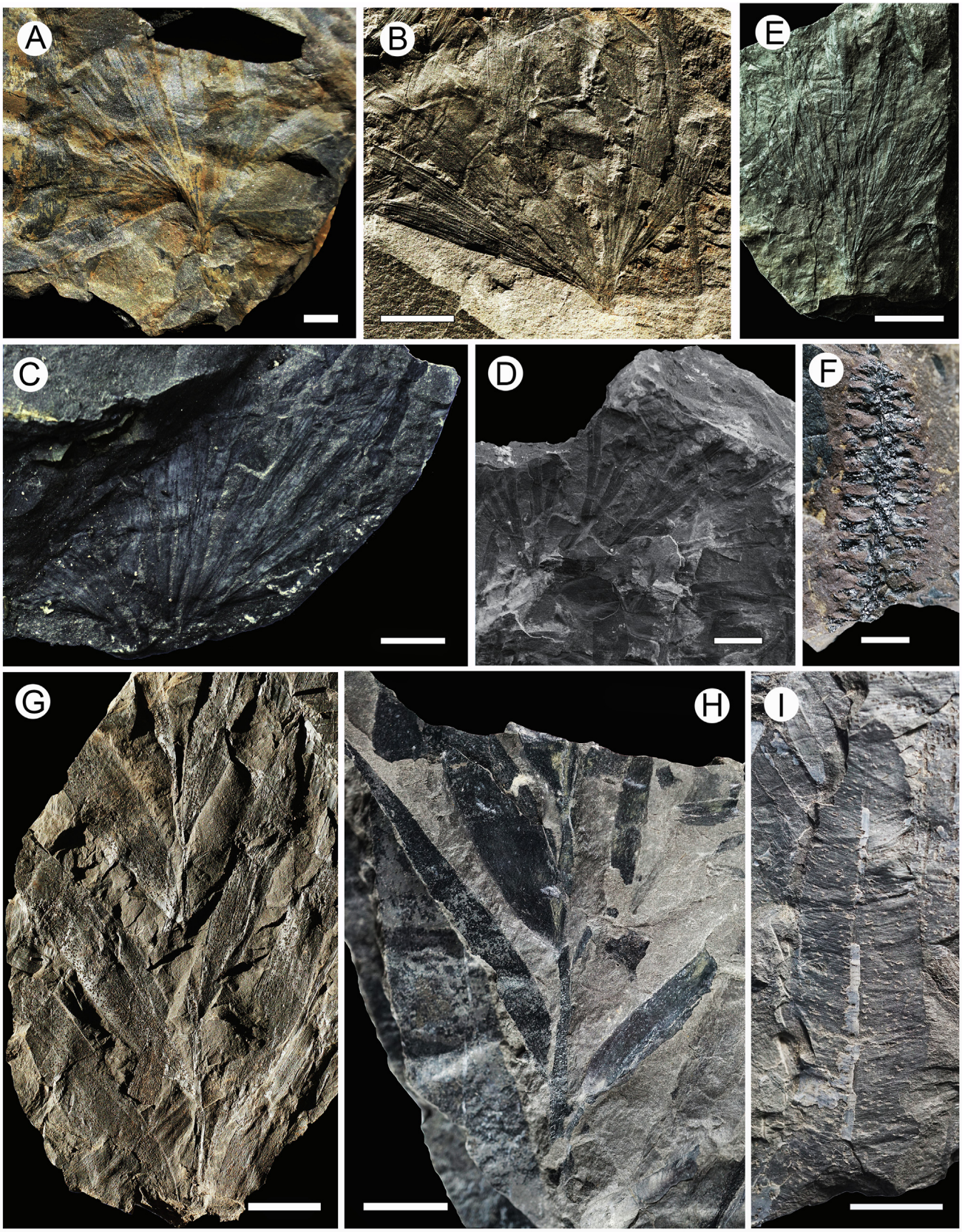

Fig. 10. Representative fossil plant taxa collected from the Xiaoping Formation in the Huadu section, central Guangdong. **A.** *Ginkgoites* cf. *sibiricus* (Heer) Seward, D1028, Huadu, Guangzhou, NRBHD-D1028-41. **B.** *Baiera elegans* Ôishi, D1028, Huadu, Guangzhou, D1028Y-15. **C.** *Baiera multipartita* Sze et Lee, D1028, Huadu, Guangzhou, NRBHD-D1028-37. **D.** *Baiera* cf. *müensteriana* (Presl) Heer, Huadu, Guangzhou, NRBHD-D1028-238. **E.** *Czekanowskia rigida* Heer, D1028, Huadu, Guangzhou, NRBHD-D1028-39. **F.** *Stenorachis* sp., D1028, Huadu, Guangzhou, PB200523. **G.** *Podozamites giganteus* Sun, D1039, Huadu, Guangzhou, NRBHD-D1039-09. **H.** *Lindleycladus lanceolatus* Harris, D1035, Huadu, Guangzhou, NRBHD-D1035-06. **I.** *Taeniopteris* sp., D1028, Huadu, Guangzhou, NRBHD-D1028Y-02. Scale bars: 1 cm (A-D, H, I), 2 cm (E, G), 5 mm (F).

Table 1
Stratigraphic ranges of plant megafossil genera from Upper Triassic strata in Guangdong. See Table S1 (Appendix A) for details.

Locality	Central Guangdong			Northern Guangdong		
Formation/Member	Xiaoping Fm.			Hongweikeng Fm.	Xiaoshui Fm.	Toumuchong Fm.
Genus	Luoke Mb. (species)	Fenggang Mb. (species)	Maan Mb. (species)			
Equisetites	1		2+	3		1
Annulariopsis				1		
Neocalamites	1		1	2		
Phyllotheca	1					
Danaeopsis			1			1
Symopteris					1	
Phlebopteris	1		1			1
Stachypteris	1					
Todites	1		3	3		
Gleichenites			1		1	
Dictyophyllum	1		1	1	1	
Clathropteris	4		3	4	1	1
Thaumatopteris	1		1	2		
Hausmannia	1					
Goeppertella	1					
Spiropteris			1			
Cladophlebis	4		3	4	1	
Sphenopteris	1					
Pachypteris	4			2+		
Xinlongophyllum				1		
Ptilozamites	1		3	4		
Protoblechnum			1			
Sagenopteris			1			1
Caytonia	1					
Pterophyllum	5		5	17	1	1
Ptilophyllum	1			2		
Anomozamites			3	1		
Otozamites	4			3		1
Sinoctenis	1		2	2		
Cycadolepis	2			3		
Dictyozamites	1			1		
Tyrmia			1	1		
Anthrophyopsis				3		
Wielandiella			1			
Nilssonia	2		1	5		
Pseudoctenis				1		
Doratophyllum				1		
Drepanozamites				1		
Ctenis	1		1	1		
Ginkgoites	1			2		
Glossophyllum				1		
Baiera	3			3		
Czekanowskia	1					
Sphenobaiera				2		
Stenorachis	1			1		
Lindleycladus			1	1		1
Podozamites			3	1		1
Ferganiella				1		
Cycadocarpidium				1		1
Stachyotaxus				1		
Taeniopteris	2			1		
Umkomasia			1			
Carpolithus	1					

were observed at the genus and species level in these fossil assemblages (Fig. 3). However, some taxa may show distinct biostratigraphic differences.

For example, *Daneopsis* fronds were widely distributed in Middle-Upper Triassic sediments (Kustatscher et al., 2012). In China, *Daneopsis fecunda* became a dominant element in the Northern Floristic Region characterized by *Danaeopsis–Symopteris* Assemblage Zone during the Carnian age (Sun et al., 1995, 2010). It is also common in the Norian in Yunnan Province, China (An et al., 2022). While in Guangdong, they are only preserved in Rhaetian sediments.

Anthrophyopsis was a representative genus of the Late Triassic and apparently reached its peak abundance in Rhaetian sequences worldwide (Sun et al., 1995; Kustatscher et al., 2018). Among all *Anthrophyopsis* records in China, they were mainly distributed in Carnian sediments such as in the Hongweikeng Fm. at Lechang in Guangdong (Wang, 1993) and the Zijiachong and Sanqiutian formations in Liuyang of Hunan. This may represent the oldest record of *Anthrophyopsis* in China (Xu et al., 2021).

Thaumatopteris was treated as a distinct biostratigraphic indicator of the early Mesozoic. The *Thaumatopteris* Zone was regarded as the onset of the Jurassic in Greenland (Harris, 1931). However, in China the genus *Thaumatopteris* was widely distributed in the Sorthern Floristic Province (SFP) during the Late Triassic and was particularly diverse in Sichuan, Yunnan, Hunan, Jiangxi, Guangdong and Tibet, with fewer records from the Early Jurassic. This

indicates the fossil records of *Thaumatopteris* are geochronologically concentrated from the Late Triassic through Early Jurassic in China (Lu et al., 2020).

Tidwell (1998) believed that the genus *Pterophyllum* persists through many stratigraphic levels, with unclear stratigraphic significance. In Guangdong, *Pterophyllum* reached its highest species richness in the *Pterophyllum-Baiera* Assemblage during the Carnian (i.e., the Hongweikeng Fm.). This may be related to Carnian Pluvial Event (CPE), showing some potential as a stratigraphic indicator of the Carnian stage.

Northern Guangdong Group Geologic Team from Xi'an Coal Research Institute analyzed the spores and pollen from Late Triassic strata in northern Guangdong in 1973, and record in their internal document. This unpublished material mentions the occurrence and identification of fossil spores and pollen, however, without illustrations or descriptions. In order to investigate the Late Triassic palynological records in northern Guangdong, we have collected new spore and pollen samples for further studies and the results will be published separately.

5.2. Palaeoclimate significance

Both floras from the Genkou Group and the Xiaoping Fm. indicate that the Late Triassic vegetation in the Guangdong area was characterized by the predominance of gymnosperms with abundant ferns. Ferns were represented by Dipteridaceae, Osmundaceae and Marattiaceae. Bennettitales, cycads, conifers and ginkgos were also well preserved. These taxa show a warm and humid environment.

Specifically, living horsetails (genus *Equisetum*) usually live along riverbanks and marshes. It is the same scenario in fossil horsetails, like *Neocalamites*, *Equisetites* and related organ genera. They could co-occur with lacustrine fauna such as bivalves and ostracods. The plants of this group are more abundant in warm and humid climates and are shade-tolerant. Thus, the majority of Mesozoic ferns, including Osmundaceae, Marattiaceae, Matoniaceae, Gleicheniaceae and Dipteridaceae, have always been interpreted as living under warm, humid and moist conditions, with limited sunlight, often probably as the understory in forests either along riverbanks or in freshwater marshes (Wang, 2002, Deng, 2007). Extant species are mainly distributed in warm conditions in moist environments in tropical-subtropical zones and very few species appear in temperate zones (Deng, 2007; Guignard et al., 2009; Li and Wang, 2016; Van Konijnenburg-Van Cittert, 2002; Wang, 2002; Wang et al., 2005, 2009a,b; Wang and Mei, 1999; Wang and Zhang, 2010; Zhou et al., 2015). The habitats that *Danaeopsis* occupied were warm and humid with rarely semiarid conditions (Kustatscher et al., 2012; An et al., 2022). *Anthrophyopsis* also usually existed in warm and humid environments (Xu et al., 2021). The living Dipteridaceae genus *Dipteris* Reinward includes eight species and are restricted to moist rocky slopes in tropical and warm-temperate regions (Kramer, 1990). During the Mesozoic, they were represented by 6 genera including *Clathropteris*, *Dictyophyllum*, *Hausmannia*, *Thaumatopteris*, *Goeppertella*, and *Camtopteris* Presl (Ôishi and Yamashita, 1936; Zhou et al., 2015). Except for *Camtopteris*, the other five genera are found in and co-exist in some Carnian and Rhaetian sediments in Guangdong, showing warm and humid environments as well.

The palaeobotanical and palynological records from typical Carnian coal-bearing strata in Italy and Austria (Roghi, 2004; Roghi et al., 2006a, 2006b; Pott et al., 2008; Roghi et al., 2010, 2022; Dal Corso et al., 2011, 2020; Preto et al., 2019) show that strata are dominated by humid environment taxa. Carnian coal beds were also found in Antarctica, South America, India, and Australia (Retallack et al., 1996; McLoughlin et al., 1997; Awatar et al., 2014). Among them, Mesozoic gymnosperms are the abundant and highly diverse Bennettitales like *Pterophyllum* and *Ptilophyllum* from the Carnian which may represent a hot and humid climate and can be related to the CPE event (Zhang, 2021). Cycads usually indicate a hot and semiarid-arid environment in tropical-subtropical zones (Wang et al., 2005; Deng, 2007). They are rare from the Upper Triassic in Guangdong. Moreover, most of the gingkos are generally thought to inhabit humid temperate zones (Deng, 2007; Abbink et al., 2004). The conifers thrive in a wide range of habitats from relatively dry areas to tropical, subtropical and temperate regions (Couper, 1960; Miller, 1977; Alvin, 1982; Deng, 2007). During the Mesozoic, some conifers like *Podozamites* and *Lindleycladus* were common in peat swamp facies, representing a warm and humid environment (Pole et al., 2016).

Based on these associations, we speculate that the Guangdong region was located in tropical-subtropical zone during the Late Triassic. The palaeoclimate is generally characterized by humid and warm conditions. On the other hand, the record of the fossil wood taxa *Protophyllocaldoxylon lechangense* Wang and *Xenoxylon ellipticum* Schultze-Motel collected from the Hongweikeng Fm. in Guanchun, Hongweikeng area in Shaoguan (Wang, 1991, 1993) may indicate cool and/or wet climatic conditions (Oh et al., 2015; Tian et al., 2016; Boonchai et al., 2020) and interspersed, seasonal variations.

5.3. Palaeogeographical significance

Geographically situated in the coastal region in the Late Triassic, the central and northern Guangdong regions share similar lithofacies and fossil plant associations. It may imply the regions were at approximately the same latitude in the tropical-subtropical zone. According to palaeomagnetic evidence, during the Late Triassic the palaeolatitude of Guangzhou was 7.2 ± 2.6°N, which is lower than the modern location (GPS: 23.1°N, 113.3°E). From the Late Triassic through the Early Cretaceous, the South China Block kept moving northward with counterclockwise rotation (≈43°; Wu et al., 1994). The palaeomagnetic evidence supports the view that both central and northern Guangdong regions were located at approximately the same latitude and formed the southern coastline of the South China Block during the Late Triassic interval.

The fossil plant assemblages change from highland type (*Pachypteris-Lindleycladus* Assemblage) to hygrophytic-lowland type (*Pterophyllum-Baiera* Assemblage) in the Hongweikeng Fm., showing that transgression happened during this period. In the Ma'an and Luoke members of the Xiaoping Fm. in central Guangdong as well as the Hongweikeng and Toumuchong formations in northern Guangdong, the fossil plants and brackish water fauna indicate a clear sea level fluctuation phenomenon. The Xiaoshui Fm. exposed in Xinfeng, Shaoguan and the Fenggang Mb. of the Xiaoping Fm. in Foshan are both marine deposits as indicated by marine bivalves and ammonites, however, there were barely any brackish lithofacies and no marine lithofacies developed from the Xiaoping Fm. in Guangzhou. Instead, they are dominated by peat-mire deposition. During the biggest transgression period in the Late Triassic, the south coastal terrane was a combination of a western and eastern bay with a peninsula in the center. At the end of Norian, regression started and the bays changed to gulf coastal plain (Figs. 1, 4).

6. Conclusions

The Upper Triassic in the Guangdong and Nanling region contains a rich and highly diverse fossil plant record. To date, about 155 species corresponding to 56 genera have been reported. Four assemblages can be recognized in the Late Triassic deposits (in ascending order): *Pachypteris-Lindleycladus* Assemblage (Julian),

Pterophyllum-Baiera Assemblage (late Julian), *Clathropteris-Otozamites* Assemblage (Tuvalian), and *Danaeopsis-Anomozamites* Assemblage (Rhaetian).

The Late Triassic floras in Guangdong shows a predominance of Bennettitales and ferns, followed by seed ferns, cycads, ginkgos and conifers. There are few horsetails and Caytoniales. The Guangdong region is mainly located in the tropical-subtropical zone. The Late Triassic climate of the Guangdong region was characterized as generally humid and warm, maybe accompanied by short cooling and drying events.

Previous studies on Late Triassic flora from Guangdong have revealed a general outline of plant diversity in the Late Triassic during the past 80 years. However, better understanding of the Late Triassic flora and biodiversity change will depend on further investigations on systematic taxonomy. Due to preservation limitations, we did not find specimens suitable for cuticles preparations for several Guangdong localities. However, recently, we have collected new plant fossil specimens with perfect cuticle and epidermal details from the gray-purple to dark grey shale layers of the Hongweikeng Fm. in the adjacent regions of northern Guangdong and Chenzhou in southern Hunan Province. The cuticles are well preserved in taxa such as *Pachypteris xiaoshuiensis*, *Anthrophyopsis crassinervis*, *Pterophyllum kochi*, *P. ptilum*, *P. xinanense*, *Ptilophyllum lechangense*, *Ginkgoites* cf. *sibiricus*, and *Baiera müensteriana*. This not only helps further systematic palaeobotany investigations, but also shows potential for plant carbon isotope analysis and palaeo-CO_2 reconstruction. The new collection of fasciated propagative female organs of *Wielandiella* (Fig. 9(H)) and *Stachypteris spicans* (Fig. 6(B, C)) with clear sporangia and potential in-situ spores are particularly notable.

In addition, an integration of multiple methods such as palynology, coal petrology, wide fire activity, leaf morphology and organic carbon isotope analysis will create the potential for revealing climate fluctuations during the Late Triassic. The change of dominant taxa, for instance Dipteridaceae and other environmentally sensitive families, are firsthand evidence to indicate climate variation and events. Moreover, due to the exceptional advantages of alternating facies of marine and terrestrial coal-bearing strata, the Late Triassic deposits of the Guangdong region are abundant in marine and non-marine faunas, such as ammonites, bivalves, and insects. These fossil organisms also contribute to global stratigraphic correlation and palaeoenvironment reconstruction for the Late Triassic ecosystem.

CRediT authorship contribution statement

Xiaoqing Zhang: Data collection, Conceptualization, Original draft, Methodology, Review and edit, Funding acquisition. **Yongdong Wang:** Conceptualization, Writing – review & editing, Supervision, Resources, Funding acquisition. **Chong Dong:** Data collection, Writing – review & editing. **Xiaoming Lin:** Data collection, Writing – review & editing. **Jianhua Jin:** Data collection, Writing original draft, Review and & editing.

Data availability

No data was used for the research described in the article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary information (including Table S1) associated with this article can be found online at https://doi.org/10.1016/j.geobios.2023.12.003.

References

Abbink, O.A., Van Konijnenburg-Van Cittert, J.H.A., Visscher, H., 2004. A sporomorph ecogroup model for the Northwest European Jurassic-Lower Cretaceous I: Concepts and framework. Netherlands Journal of Geosciences-Geologie En Mijnbouw 83, 17–38.

Alvin, K.L., 1982. Cheirolepidiaceae: Biology, structure and palaeoecology. Review of Palaeobotany and Palynology 37, 71–98.

An, P.C., Lu, N., Li, Y., Wang, Y.D., Zhu, Y.B., Li, L.Q., 2022. New material of marattialean fern (*Danaeopsis fecunda*) from the Late Triassic in China with considerations on the tempo-spatial distribution pattern of *Danaeopsis*. Geobios 71, 13–26.

Ao, Z.K., 1956. A pilot study of Rhaetic flora in Xiaoping coal series in Guangzhou, Guangdong. Institute Report of Central-South Institute of Mining and Metallurgy, 18–32 (in Chinese).

Ashraf, A.R., Sun, Y.W., Sun, G., Uhl, D., Mosbrugger, V., Li, J., Herrmann, M., 2010. Triassic and Jurassic palaeoclimate development in the Jungger Basin, Xinjiang, Northwest China-a view and additional lithological data. Palaeobio Palaeoenv 90, 187–201.

Awatar, R., Tewari, R., Agnihotri, D., Chatterjee, S., Pillai, S.S.K., Meena, K.L., 2014. Late Permian and Triassic palynomorphs from the Allan Hills, central Transantarctic Mountains, South Victoria Land, Antarctica. Current Science 106, 988–996.

Beerling, D.J., Berner, R.A., 2005. Feedbacks and the coevolution of plants and atmospheric CO_2. Proceedings of the National Academy of Sciences of the United States of America 102, 1302–1305.

Belcher, C.M., Mander, L., Rein, G., Jervis, F.X., Haworth, M., Hesselbo, S.P., McElwain, J.C., 2010. Increased fire activity at the Triassic/Jurassic boundary in Greenland due to climate-driven floral change. Nature Geoscience 3, 426–429.

Bureau of Geology and Mineral Resources of Guangdong Province (BGMRGP), 1988. Regional geology of Guangdong Province. Beijing: Geological Publishing House 177-191 (in Chinese).

Boonchai, N., Suteethorn, S., Sereeprasirt, W., Suriyonghanphong, C., Amiot, R., Cuny, G., Legrand, J., Thévenard, F., Philippe, M., 2020. *Xenoxylon*, a boreal fossil wood in the Mesozoic redbeds of Southeast Asia: Potential for the stratigraphy of the Khorat group and the palinspatic reconstruction of Southeast Asia. Journal of Asian Earth Sciences 189, 104153.

Cao, H.S., 1992. A study of stratigraphy and flora of Late Triassic in Western Guizhou. Geology of Guizhou 9, 26–40 (in Chinese, with English abstract).

Chen, J.H., 1983. Late Triassic and Early Jurassic bivalve assemblages and palaeogeography of Southeast China, with a bivalve division in China. In: Lu, Y.H. (Ed.), Palaeobiogeography Provinces of China. Science Press, Beijing, pp. 100–120 (in Chinese).

Couper, R.A., 1960. Southern Hemisphere Mesozoic and Tertiary Podocarpaceae and Fagaceae and their palaeogeographic significance. Proceedings of the Royal Society of London, Series B, Biological Sciences 152, 491–500.

Dal Corso, J., Preto, N., Kustatscher, E., Mietto, P., Roghi, G., Jenkyns, H.C., 2011. Carbon-isotope Variability of Triassic Amber, as Compared with Wood and Leaves (Southern Alps, Italy). Palaeogeography Palaeoclimatology Palaeoecology 302, 187–193.

Dal Corso, J., Bernardi, M., Sun, Y., Song, H., Seyfullah, L.J., Preto, N., Gianolla, P., Ruffell, A., Kustatscher, E., Roghi, G., Merico, A., Hohn, S., Schmidt, A.R., Marzoli, A., Newton, R.J., Wignall, P.B., Benton, M.J., 2020. The Carnian Pluvial Episode: extinction and dawn of the modern world. Science Advances 6, eaba0099.
Deng, S.H., 2007. Palaeoclimatic implications of main fossil plants of the Mesozoic. Journal of Palaeogeography 9, 559–574 (in Chinese).
Deng, S.H., Lu, Y.Z., Fan, R., Pan, Y.H., Cheng, X.S., Wang, Q.F., Pan, H.Z., Shen, Y.B., Wang, Y.Q., Duan, W.Z., Zhang, H.C., Jia, C.K., Fang, L.H., 2010. The Jurassic system of Northern Xinjiang, China. University of Science and Technology of China Publishing House, Hefei, China.
Fang, J.T., Xu, M.Y., 1978. Upper Triassic ostracods of Hunan, Jiangxi and Northern Guangdong. Acta Palaeontologica Sinica 17, 131–148 (in Chinese with English abstract).
Guignard, G., Wang, Y.D., Ni, Q., Tian, N., Jiang, Z.K., 2009. A dipteridaceous fern with in situ spores from the Lower Jurassic in Hubei, China. Review of Palaeobotany and Palynology 156, 104–115.
Kustatscher, E., Kelber, K.P., van Konijnenburg-van Cittert, J.H., 2012. *Danaeopsis* Heer ex Schimper 1869 and its European Triassic species. Review of Palaeobotany and Palynology 183, 32–49.
Harris, T.M., 1931. The fossil flora of Scoresby Sound, East Greenland. Meddelelser OM. Grønland 85, 1–102.
Kustatscher, E., Ash, S.R., Karasev, E., Pott, C., Vajda, V., Yu, J.X., McLoughlin, S., 2018. Flora of the Late Triassic. In: Tanner, L.H. (Ed.), The Late Triassic World: Earth in a Time of Transition. Springer International Publishing AG, Heidelberg, pp. 545–622.
Li, L.Q., Wang, Y.D., 2016. Late Triassic palynofloras in the Sichuan Basin, South China: Synthesis and perspective. Palaeoworld 25, 212–238.
Li, L.Q., Wang, Y.D., Wolfram, W.M., Ruhl, M., Vajda, V., 2020. Palaeovegetation and palaeoclimate changes across the Triassic-Jurassic transition in the Sichuan Basin, China. Palaeogeography Palaeoclimatology Palaeoecology 556, 109891.
Lin, Q.B., 1989. On insects from the Upper Triassic Xiaoping Formation, Guangzhou, China. Acta Palaeontologica Sinica 28, 598–603 (in Chinese with English abstract).
Liu, M., 1979. Nature, age and correlation of the Late Triassic flora in northern Guangdong. Journal of Changchun College of Geology 3, 100–113 (in Chinese).
Lu, N., Li, Y., Wang, Y.D., Xu, Y.Y., Zhou, N., 2020. Fossil dipterid fern Thaumatopteris in China: new insights of systematics, diversity and tempo-spatial distribution patterns. Historical Biology 33, 2316–2329.
McElwain, J.C., Beerling, D.J., Woodward, F.I., 1999. Fossil plants and global warming at the Triassic-Jurassic boundary. Science 285, 1386–1390.
McLoughlin, S., Lindstrom, S., Drinnan, A.N., 1997. Gondwanan floristic and sedimentological trends during the Permian-Triassic transition: New evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica. Antarctic Science 9, 281–298.
Miller, C.N., 1977. Mesozoic conifers. The Botanical Review 43, 217–280.
Nan, G., Zhou, G.Q., 2012. Lithostratigraphy of Guangdong Province. China University of Geoscience Press, Wuhan (in Chinese).
Niu, Y.Z., Jiang, B.Y., Zhang, Y.W., 2013. Late Triassic and Early Jurassic bivalve fossils from Eastern South China and their biostratigraphic implication. Acta Palaeontologica Sinica 52, 352–376 (in Chinese with English abstract).
Oh, C., Philippe, M., Kim, K., 2015. *Xenoxylon* synecology and palaeoclimatic implications for the Mesozoic of Eurasia. Acta Palaeontologica Polonica 60, 245–256.
Ôishi, S., Yamasita, K., 1936. On the fossil Dipteridaceae. Journal of the Faculty of Science of the Hokkaido Imperial University Ser 3, 135–184.
Petersen, H.I., Lindstrom, S., 2012. Synchronous wildfire activity rise and mire deforestation at the Triassic-Jurassic Boundary. PLoS One 7, e47236.
Pole, M., Wang, Y.D., Bugdaeva, E.V., Dong, C., Tian, N., Li, L.Q., Zhou, N., 2016. The rise and demise of Podozamites in East Asia – An extinct conifer life style. Palaeogeography Palaeoclimatology Palaeoecology 464, 97–109.
Pott, C., Krings, M., Kerp, H., 2008. The Carnian (Late Triassic) flora from Lunz in Lower Austria: Palaeoecological considerations. Palaeoworld 17, 172–182.
Preto, N., Bernardi, M., Dal Corso, J., Gianolla, P., Kustatscher, E., Roghi, G., Rigo, M., 2019. The Carnian Pluvial Episode in Italy: History of the research and perspectives. Bollettino della Società Paleontologica Italiana 58, 35–49.
Retallack, G.J., Veevers, J.J., Morante, R., 1996. Global coal gap between Permian-Triassic extinction and Middle Triassic recovery of peat-forming plants. Geological Society of America Bulletin 108, 195–207.
Roghi, G., 2004. Palynological investigations in the Carnian of the Cave del Predil area (Julian Alps, NE Italy). Review of Palaeobotany and Palynology 132, 1–35.
Roghi, G., Ragazzi, E., Gianolla, P., 2006a. Triassic Amber of the Southern Alps (Italy). Palaios 21, 143–154.
Roghi, G., Kustatscher, E., van Konijnenburg-van Cittert, J.H.A., 2006b. Late Triassic Plants from Julian Alps (Italy). Bollettino della Società Paleontologica Italiana 45, 133–140.
Roghi, G., Gianolla, P., Minarelli, L., Pilati, C., Preto, N., 2010. Palynological correlation of Carnian humid pulses throughout western Tethys. Palaeogeography Palaeoclimatology Palaeoecology 290, 89–106.
Roghi, G., Gianolla, P., Kustatscher, E., Schmidt, A.R., Seyfullah, L.J., 2022. An exceptionally preserved terrestrial record of LIP effects on plants in the Carnian (Upper Triassic) amber-bearing section of the Dolomites, Italy. Frontiers of Earth Sciences 10, 900586.
Sepkoski, J.J., 2002. A compendium of fossil marine animal genera. Bulletins of American Palaeontology. Palaeontological Research Institution, New York 363, 1–560.
Sha, J.G., Vajda, V., Pan, Y.H., Larsson, L., Yao, X.G., Zhang, X.L., Wang, Y.Q., Cheng, X. S., Jiang, B.Y., Deng, S.H., Chen, S.W., Peng, B., 2011. Stratigraphy of the Triassic-Jurassic Boundary Successions of the Southern Margin of the Junggar Basin, Northwestern China. Acta Geoloica Sinica - English Edition 85, 421–436.
Sha, J.G., Olsen, P.E., Pan, Y.H., Xu, D.Y., Wang, Y.Q., Zhang, X.L., Yao, X.G., Vajda, V., 2015. Triassic-Jurassic Climate in Continental High-Latitude Asia Was Dominated by Obliquity-Paced Variations (junggar Basin, Urumqi, China). Proceedings of the National Academy of Sciences 112, 3624–3629.
Sun, G., Meng, F.S., Qian, L.J., Ouyang, S., 1995. Late Triassic Flora. In: Lee, H.H., Zhou, Z.Y., Cai, C.Y., Sun, G., Ou, Y.S., Deng, L.H. (Eds.), Fossil Floras of China through the Geological Ages. Guangdong Science and Technology Press, Guangzhou, pp. 241–246 (in Chinese).
Sun, G., Miao, Y., Mosbrugger, V., Ashraf, A.R., 2010. The Upper Triassic to Middle Jurassic strata and floras of the Junggar Basin, Xinjiang, Northwest China. Palaeobiodiversity Palaeoenvironments 90, 203–214.
Tian, N., Wang, Y.D., Philippe, M., Li, L.Q., Xie, X.P., Jiang, Z.K., 2016. New record of fossil wood *Xenoxylon* from the Late Triassic in the Sichuan Basin, southern China and its palaeoclimatic implications. Palaeogeography Palaeoclimatology Palaeoecology 464, 65–75.
Tidwell, W.D., 1998. Common fossil plants of western North America,. Smithsonian Institution Press, Washington, D. C.
Tsao, C.Y., 1965. Fossil plants from the Siaoping Series in Kaoming Kwangtung. Acta Palaeontologica Sinica 6, 510–528 (in Chinese with English abstract).
Van Konijnenburg-Van Cittert, J.H.A., 2002. Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. Review of Palaeobotany and Palynology 119, 113–124.
Wang, S.J., 1991. A new permineralized wood of Later Triassic from Northern Guangdong province. Acta Sicientiarum Naturalium Universitatis Sunyatseni 30, 66–69 (in Chinese, with English abstract).
Wang, S.J., 1993. Late Triassic plant fossils of Northern Guangdong. Song Yet-Sen University Press, Guangzhou (in Chinese).
Wang, Y.D., 2002. Fern ecological implications from the Lower Jurassic in Western Hubei, China. Review of Palaeobotany and Palynology 119, 125–141.
Wang, Y.D., Mei, S.W., 1999. Fertile organs and in situ spores of a matoniaceous fern from the Lower Jurassic of West Hubei. Chinese Science Bulletin 44, 1333–1337.
Wang, Y.D., Zhang, H., 2010. Fertile organs and *in situ* spores of a new dipteridaceous fern *Hausmannia* sinensis from the Jurassic of northern China. Proceedings of the Royal Society B 277, 311–320.
Wang, Y.D., Mosbrugger, V., Zhang, H., 2005. Early to Middle Jurassic vegetation and climatic events in the Qaidam Basin, Northwest China. Palaeogeography Palaeoclimatology Palaeoecology 224, 200–216.
Wang, Y.D., Tian, N., Jiang, Z.K., Mei, S.W., 2009a. Recent progresses on the studies of fossil ferns from the Early Jurassic Hsiangchi flora in western Hubei. China. Acta Palaeontologica Sinica 48, 527–540 (in Chinese, with English abstract).
Wang, Y.D., Yang, X.J., Guignard, G., Deng, S.H., Tian, N., Jiang, Z.K., 2009b. The fossil Gleicheniaceous ferns of China: Biodiversity, systematics, spore ultrastructure and evolution. Review of Palaeobotany and Palynology 156, 139–156.
Wang, Y.D., Fu, B.H., Xie, X.P., Huang, Q.S., Li, K., Li, G., Liu, Z.S., Yu, J.X., Pan, Y.H., Tian, N., Jiang, Z.K., 2010. The terrestrial Triassic and Jurassic Systems in the Sichuan Basin. China University of Science & Technology of China Press.
Wu, N.Y., GE, T.M., Liu, J., Fan, L.M., Li, L.P., Li, X.S., 1994. Paleomagnetic research of Late Triassic Xiaoping Formation in Huanan Block and its tectonic significance. Geological Research of South China Sea 6, 51–61 (in Chinese with English abstract)。
Xiong, C.W. and Wang, S.Y., 1987. Mesozoic coal-bearing strata in southern China. Coal Industry Press, Beijing (In Chinese).
Xu, Y.Y., Popa, M.E., Lu, N., Zhang, T.S., Zeng, J.L., Zhang, X.Q., Li, L.Q., Wang, Y.D., 2021. Re–appraisal of Anthrophyopsis (Gymnospermae): global fossil records with newly collected materials from China. Review of Palaeobotany and Palynology 292, 104475.
Zhang, X.T., 1930. Plant fossils identification of the Xiaoping series. Geological Survey of Kwangtung and Kwangsi 7, 1–29 (in Chinese).
Zhang, Y.W., Jiang, B.Y., Niu, Y.Z., 2014. Upper Triassic-Lower Jurassic bivalve biostratigraphy and Triassic-Jurassic Boundary of Nanling region. Geological Journal of China Universities 20, 570–581 (in Chinese).
Zhang, X.Q., 2021. Late Triassic flora of Guangdong Province, southern China and palaeoenviromental significance. Ph.D. Thesis, University of Science and Technology of China, 169 p. (unpubl.; in Chinese, with English abstract).
Zhou, N., Wang, Y.D., Li, L.Q., Zhang, X.Q., 2015. Diversity variation and tempo-spatial distribution of the Dipteridaceae ferns in the Mesozoic of China. Palaeoworld 25, 263–286.