# **Chapter 13 Flora of the Late Triassic**

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**Abstract** The Triassic was a time of diversification of the global floras following the mass-extinction event at the close of the Permian, with floras of low-diversity and somewhat uniform aspect in the Early Triassic developing into complex vegetation by the Late Triassic. The Earth experienced generally hothouse conditions with low equator-to-pole temperature gradients through the Late Triassic. This was also the time of peak amalgamation of the continents to form Pangea. Consequently, many plant families and genera were widely distributed in the Late Triassic. Nevertheless,

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two major floristic provinces are recognizable during this interval-one in the Southern Hemisphere (Gondwana) and another in the Northern Hemisphere (Laurussia); these being largely separated by the Tethys Ocean and a palaeotropical arid belt. Regional variations in topography, climate and light regime imposed further constraints on the distribution of plant groups in the Late Triassic such that two floristic sub-provinces are recognizable within Gondwana, and nine within Laurussia based on the plant macrofossil and dispersed spore-pollen records. In a broad sense, the Late Triassic saw the diversification of several plant groups that would become important components of younger Mesozoic floras (e.g., Bennettitales. Czekanowskiales, Gnetales and several modern fern and conifer families). The representation of these groups varied not only geographically, but waxed and waned through time in response to climatic pulses, such as the Carnian Pluvial Event. Significant turnovers are apparent in both macrofossil- and palyno-floras across the Triassic-Jurassic boundary, especially in the North Atlantic and Gondwanan regions. The geographic and temporal variations in the floras have necessitated the establishment of numerous regional palynozonation schemes that are tentatively correlated in this study. Major plant macrofossil assemblages of the Late Triassic world are also placed in a stratigraphic context for the first time. The Late Triassic floras also record the re-diversification of insect faunas based on a broad array of damage types preserved on leaves and wood. By the Late Triassic, all modern terrestrial arthropod functional feeding groups were established, and several very specialized feeding traits and egg-laying strategies had developed. Although age constraints on various fossil assemblages need to be improved, this study provides the first global overview of the temporal and geographic distributions of Late Triassic floras, and establishes a basis for future targeted research on Triassic phytogeography and phytostratigraphy.

**Keywords** Non-marine ecosystems • Palaeoclimate • Plant fossils • Palynomorphs • Palaeo-provinces • Mass-extinction • Plant-animal interactions

#### 13.1 Introduction

The Triassic, spanning the interval from 252 to 201 million years (Myr) ago, was a crucial period in the evolution of non-marine ecosystems. It witnessed the recovery of terrestrial ecosystems following the end-Permian mass extinction and saw a proliferation of new fern and gymnosperm families and genera that peaked in the Late Triassic before another global biotic crisis at the end of the period (Anderson et al. 1999; Willis and McElwain 2002; Vajda and Bercovici 2014). The continents reached their maximum phase of amalgamation, forming the supercontinent Pangaea (Fig. 13.1), which began to break up towards the end of the Triassic when rifting started in the North Atlantic region. The continued northward drift of the Cimmerian continental blocks progressively closed the Palaeotethys Ocean and opened the Neotethys Ocean at this time. The most significant Late Triassic convergent event, the Indosinian orogeny, occurred as a result of the consolidation of the South China and North China blocks, and the opening of the so-called





Mongol-Okhotsk Ocean (Golonka 2007). The climate was warm with no polar icecaps, although the variation in photoperiod regime imposed some latitudinal constraints on the composition of vegetation belts, and the equable conditions were interrupted by several global and regional climate perturbations (Preto et al. 2010 and references therein). Moreover, the Triassic in general was a period of exceptional sea-level lowstand in comparison with the Palaeozoic.

The Triassic is delineated by two of the five major mass extinctions in Earth history, the end-Permian Event (EPE) and the end-Triassic Event (ETE), owing to which the Triassic flora differs markedly from preceding and succeeding floras. Thus, it was a time of transition and of great changes in the composition of the global flora although our understanding of this transformation of plant communities is challenged by the scattered palaeontological record.

Past phytogeographic studies of the Triassic have used a diverse range of terms to denote floristic regions. In this chapter, we aim to rationalize the nomenclature applied to these regions and better define the relationships between areas based on shared taxa. We apply the term 'assemblage' to a suite of fossils derived from a particular bed. Thus, several assemblages constitute a local 'flora', multiple floras from related areas comprise a floristic 'subprovince', and two or more subprovinces make up a floristic 'province', the last of these categories being of continental or pancontinental scale. Available space constrains us from documenting the finer details of every studied Triassic flora. Nevertheless, we provide the first summary of the succession of Late Triassic plant assemblages globally (Tables 13.1 and 13.2) in order to elucidate phytostratigraphic patterns that might be related to variations in palaeoclimate and/or evolutionary processes. Although this contribution focuses on the macrofloral record, brief details on the complementary dispersed spore-pollen successions are also included because palynology provides the basis for the biostratigraphical framework of many of the continental successions. Pollen and spores also provide insights into the vegetation and climatic signals owing to their abundant presence in near-shore marine successions. This review is a first step towards a better understanding of the composition and distribution of the Late Triassic floras through time.

#### 13.2 Late Triassic Floras of North America

Late Triassic plant fossils occur in five widely separated parts of North America: in a string of narrow rift basins along the eastern seaboard of the United States, adjacent parts of Canada, the desert southwest of the United States and on some of the Arctic islands of Canada and in northwestern and northeastern Mexico (Figs. 13.1 and 13.2, Table 13.1). The known floras are restricted to the Carnian and early Norian stages, whereas Rhaetian floral assemblages are unknown in North America. Since the Late Triassic flora of Greenland is more closely related palaeogeographically to the Late Triassic floras of northern Europe, it is discussed within the European section of this chapter, whereas the floras of the Canadian Arctic are discussed here. The nomenclature of the Upper Triassic strata in eastern North America that is used here follows that recently proposed by Weems, et al., 2016 and approved by the U.S. Geological Survey.

	Age	Chinle/Dockum	Arctic Canada - N.	Western Tethyan	Siberian - Middle	Northern E Asian Subarov	Southern E Asian Subprov	Ipswich Flora	Onslow Flora
	201.3		Bjuv Mbr		Central Pamir			Raceview Fm	Parsora Fm
	±0.2		Kap Stewart Grp Schilfsandstein fl.		& Afghanistan floras		Yangbaichong Fm Sanqiutian Fm	Aberdare Cgl	
	Rhaetian		Valläkra Mbr Tatra Mts flora Seinstedt flora		Nayband Fm Novorayskaya Fm	Dongfeng flora	Wenbinshan flora Tonkin flora	Callide C.M.	La Temera & El Puquen floras
			Bayreuth flora east-central Axel Heiherd		Aktash and Tashkutan fms				
	c. 208.5	10	Ørsted Dal Mbr		Aghdarband flora				Los Colorados Fm
			Sverdrup Basin fl.			Malugou Fm	Dakeng Fm		
SIC					Protopivskaya Fm		Badong Fm		
SAIЯT			Seefeld flora	0	Nemtsov Fm	Primorye floras	Nariwa flora	l aich Craak C M	Tiki Fm McKelvev Mhr
<b>TAA</b>	Norlan		Contraction of the second	Filettino floras	Kozyrevskaya Fm	Amba Fm	Anyuan Fm	(Telford Basin)	(Flagstone Bench Fm)
			upper ollesiali flora				Daging Fm		
		Dockum Grp flora Chinle Fm flora	Flatsalen Fm				Hsuchiaho Fm		Cacheuta Fm
		Lockatong Fm flore	-			Imalinovo flora			
	c. 227	Zanta Clara Fm fl.	De Geerdalen Fm	Bergamasc	Chelyabinsk Basin			Tarong C.M. Lashly, Falla,	Ischigualasto Fm
		Stockton Fm flora		Alps flora	flora		Momonoki and	Section Peak fms Blackstone Fm	Guilacoya Mbr Santa Maria Fm
			Lunz flora Neuewelt flora	Monte Pora, Dogna & Raibl	Nikolaevka flora	Sad-Gorod Fm	Aso fms	Red Cliff C.M. Bradv Fm	Potrerillos Fm
	Carnian	Doswell Fm flora	Krasiejów flora	floras Karavanke Mts	eastern Urais floras		Indonesian floras Daqiaodi Fm	Molteno Fm	Cortaderita Fm Barreal Fm
	c. 237			Heiligkreuz Fm Rio del Lago Fm	Madygen flora		Jiuligang Fm Jiapeila Fm	Tivoli Fm	





Pable 13.2 Tentative correlation of selected Late Triassic palynozonation schemes erected within the major phytogeographic subprovinces recognized in this study Data sourced from numerous studies: Chinle/Dockum–Newark subprovinces (Cornet 1977a; Litwin et al. 1991; Reichgelt et al. 2013); Arctic Canada–North Subprovince (Roghi et al. 2010); Siberian-Middle Asian subprovinces (Odintsova 1977; Romanovskaya and Vasilieva 1990; Ghavidel-Syooki et al. 2015); Atlantic/Central European subprovinces (Lund 1977; Kürschner and Herngreen 2010; Vigran et al. 2014; Paterson and Mangerud 2015); Western Tethyan Northern East Asian Subprovince (Peng et al. 2017b); Southern East Asian Subprovince (Wang et al. 2010); South Gondwana (Helby et al. 1987; de Jersey and Raine 1990); North Gondwana (Helby et al. 1987; Tripathi et al. 2005)



Fig. 13.2 Areas with major Upper Triassic plant assemblages in Arctic Canada, the US and northern Mexico

### 13.2.1 Carnian Floras of North America

The Carnian floras of North America occur in the basal coal-bearing Doswell Formation of the Newark Supergroup in the Richmond rift basin in Virginia, in a clay quarry excavated into the Stockton Formation in the Chatham Basin of North Carolina and in the Gettysburg Basin in Pennsylvania (Wanner and Fontaine, in Ward 1900). The plant fossils associated with the coal deposits in the Doswell Formation soon began to attract attention after they were first reported by William MacClure (1817). However, the fossils were not systematically investigated until William Fontaine began his work on them in the early 1880s. Subsequently, he (Fontaine 1883) described 18 genera in the Doswell flora including several ferns (*Acrostichides, Lonchopteris* [*Cynepteris*], *Mertensides*), conifers (*Cheirolepis*), bennettitaleans (*Ctenophyllum, Pterophyllum, Sphenozamites*) and ginkgophytes (*Baiera*).



Plate 13.1 Upper Triassic plants from North America. (a) *Cynepteris lasiophora*, Petrified Forest National Park, Arizona, Norian. (b) *Samaropsis* sp., Fort Wingate, New Mexico, Norian. (c) *Sanmiguelia lewisii*, Petrified Forest National Park, Arizona, Norian. (d) *Palodurophyton quanahensis*, Palo Duro Canyon, Texas, Norian. (e) *Pagiophyllum* sp., Fort Wingate, New Mexico, Norian. (f) *Fraxinopsis patharrisiae*, Palo Duro Canyon, Texas, Norian. (g) *Neocalamites* sp., Petrified Forest National Park, Arizona, Norian. (h) *Ginkgoites watsoniae*, Petrified Forest National Park, Arizona, Norian. (j) *Dechellyia gormanii*, Canyon de Chelly, Arizona, Norian. (k) *Dinophyton spinosus*, Petrified Forest National Park, Arizona, Norian.

In contrast to the plant assemblage preserved in the underlying Doswell Formation, the Stockton flora is not associated with coal deposits although cuticles are preserved on some specimens. The flora that occurs in the Stockton Formation was discovered in the Gettysburg Basin, Pennsylvania in the late nineteenth century and first described by Wanner and Fontaine (in Ward 1900). Much later additional Carnian-age plant assemblages were collected from the same rift basin by several workers including Wilhelm Bock (1969), Bruce Cornet (1977b) and Brian Axsmith (1989). Most of the taxa these workers found commonly occur in the Newark Supergroup at other localities and included the conifers Cheirolepis, Glyptolepis, Pagiophyllum, Palissya and Podozamites, the cycads/bennettitaleans Cycadospadix, Eoginkgoites, Nilssonia and Zamites, and the enigmatic gymnosperm *Dinophyton* (Plate 13.1k). A new era in the study of the Carnian flora really began when a report on the plant fossils in the Stockton Formation in the Chatham Basin was published by Hope and Patterson in 1969. Other workers who soon joined Hope in the study of this flora were Ted Delevoryas (Delevoryas and Hope 1971, 1975, 1981, 1987), Brian Axsmith and Tom Taylor (see Axsmith et al. 1995 for more details). An unpublished review of the Stockton flora from the Chatham Basin (Mickle et al. 2000) lists 25 taxa. Since then, two additional genera have been described (Axsmith et al. 2001; Pott and Axsmith 2015) so that the known diversity of the assemblage now includes 27 genera, eight of which seem to be restricted to that deposit (e.g., Leptocycas, Metridiostrobus, Pekinopteris), the rest are relatively common in other Upper Triassic floras.

It is currently uncertain exactly how many genera are present in the Carnian successions of the Richmond, Chatham and Gettysburg basins, since Fontaine's and Wanner's identifications have never been critically re-evaluated. However, a quick comparison between the fossil lists in each plant assemblage suggests that nearly all of the genera in the Doswell Formation also occur in the overlying Stockton Formation, so it is probable that the Carnian flora of the Newark Supergroup consists of about 30 genera. Sphenophytes (*Equisetites, Neocalamites*) and ferns (*Clathropteris, Danaeopsis, Lonchopteris* [= *Cynepteris*], *Mertensides, Pekinopteris, Phlebopteris*) are particularly well represented in the flora, whereas the cycads/bennettitaleans (*Cycadospadix, Leptocycas, Otozamites, Williamsonia, Zamites*) and conifers (*Compsostrobus, Metridiostrobus, Pagiophyllum, Voltzia*) are abundant. Collectively, the Carnian flora of North America appears to closely resemble the succeeding Norian flora of that continent.

The age of the plant fossils found in the Santa Clara Formation in Sonora (northwestern Mexico) is somewhat uncertain, ranging as it does from ?Carnian to Norian (see Weber 1995, 1996, 1999). Most of the fossil plants are typical Late Triassic sphenophytes (*Equisetites, Neocalamites*), ferns (*Asterotheca*), cycads/bennettitaleans (*Laurozamites, Pterophyllum, Ctenophyllum*), ginkgophytes and conifers. Some additional plants in this flora are of uncertain relationship, such as *Marcouia*, or putative angiosperm precursors, such as *Scoresbya* and *Sonoraphyllum*.

The palynoflora in the Carnian succession in the Chatham Basin in the eastern United States is rich and well preserved (e.g., Schultz and Hope 1973; Cornet 1977a; Dunay and Fisher, 1979; Fisher and Dunay 1984; Cornet and Olsen 1985; Traverse 1986; Litwin et al. 1991; Litwin and Ash 1993) and has been subdivided in two palynozones: the Chatham-Taylorsville palynofloral Zone and the overlying New Oxford-Lockatong palynofloral Zone (Cornet 1977a; Cornet and Olsen 1985); in the Chinle Formation to the informal palynomorph zones I and II sensu Litwin et al. (1991). Patinasporites densus and Vallasporites ignacii dominate the Carnian palynofloras. The informal palynomorph zone I sensu Litwin et al. (1991) is characterized by abundant taeniate bisaccate taxa (Litwin et al. 1991). The Chatham-Taylorsville palynofloral Zone is characterized by the overlapping ranges of **Patinasporites** densus. *Striatoabieites* aytugii, Triadispora verrucata. Protodiploxypinus doubingeri, Plicatisaccus badius and Lagenella martinii. The informal palynomorph zone II includes the more diverse and abundant palynological assemblages, and is characterized by the FOs (first occurrences) of Camerosporites rudis, Enzonalasporites vigens, Heliosaccus dimorphus, Ovalipollis ovalis, Pseudoenzonalasporites summus and other taxa (e.g., Alisporites spp., Cycadopites stonei, Guthoerlisporites cancellosus). The coeval New Oxford-Lockatong palynoflora Zone is dominated by Patinasporites densus, Vallisporites ignacii, Alisporites parvus and Triadispora spp. Most of the palynomorphs correlate with taxa in Carnian assemblages in Western Europe and Australia (Litwin et al. 1991).

#### 13.2.2 Norian Floras of North America

Plant macrofossils of Norian age occur in the lower part of the Newark Supergroup in both the Chatham and Danville rift basins along the eastern seaboard of the United States as well as in the lower part of the Chinle-Dockum beds in the desert southwest of the United States. They were first described from what is now called the Passaic Formation in the Chatham rift basin by Ebenezer Emmons (1856, 1857) who reported that they came from coal prospects "...many hundreds of feet..." above the coal-bearing strata in the Carnian Doswell Formation from which Fontaine was to later (1883) make his collections. Eventually, Fontaine (in Ward 1900) redescribed Emmons' collection and reported that the Passaic flora includes 24 genera including sphenophytes (Equisetites), ferns (Laccopteris [=Phlebopteris], Lonchopteris [=Cynepteris], Pseudodaneosis, Sphenopteris), conifers (Abietites, Cephalotaxopsis, Pagiophyllum; Plate 13.1e), cycads/bennettitaleans (Anomozamites, Ctenophyllum, Otozamites) and ginkgophytes (Baiera).

Starting in the late 1970s, important collections of Norian plant fossils, insects and fish remains were described by Fraser et al. (1996) and Axsmith et al. (1997, 2013) from the Lockatong Formation in the Solite clay quarry in the Danville rift basin on the border between North Carolina and Virginia. A floral list published by Fraser et al. (1996) indicated that the Lockatong flora included about 30 genera (including at least 10 new taxa), such as sphenophytes (*Neocalamites*, Plate 13.1g), ferns (*Cynepteris*, *Dictyophyllum*, *Wingatea*), ginkgophytes (*Sphenobaiera*, Plate 13.1h, *Metreophyllum*), cycads/bennettitaleans (*Otozamites*, *Pterophyllum*, *Zamiostrobus*, *Zamites*), together with many conifers (*Cheirolepis*, *Palissya*, *Podozamites*) and several enigmatic forms (*Brunswickia*, *Dinophyton*, *Edenia*, *Fraxinopsis* Plate 13.1f, *Pannaulika*). Several (*Edenia*, *Pannaulika*) seem to occur only at this locality.

The Norian plant fossils that occur in the desert southwest of the United States occur principally in the lower one-third of the Chinle Formation (Shinarump and Blue Mesa Members) and the Dockum Group (Garita Creek and Trujillo formations: Chinle Group of some authors), although it is noted that the basal units of both the Chinle and Dockum are considered Carnian if the 'short' Norian time scale is accepted (cf. Lucas et al. 2012). The fossil assemblages, here referred to as the Chinle-Dockum flora, were not documented until 1941 when Lyman Daugherty (Daugherty 1941) described more than 40 genera based on compressed leaves, stems, and reproductive structures of lycophytes, sphenophytes, ferns, conifers and cycads/ bennettitaleans that mostly came from the Chinle Formation in Petrified Forest National Park, Arizona. Since then elements of the Chinle-Dockum flora have been found at several dozen localities in northern Arizona, southern Utah, northern New Mexico and west Texas. Probably the most well-known of all these localities are still those in Petrified Forest National Park where literally hundreds, if not thousands of highly coloured silicified conifer (pycnoxylic) logs (up to 40 m in length and 2 m in diameter) are exposed on the surface of the desert (Ash 2005; Sadler et al. 2015). In addition, amber, charcoal, and burned logs have been found in the park, together with a rich palynoflora (Litwin and Ash 1991; Reichgelt et al. 2013).

Most genera in the Chinle-Dockum flora are represented by a single species; only the common form genera, such as Cladophlebis and Pagiophvllum (Plate 13.1e), seem to be represented by more than one species (Ash 1989). The components of this flora represent all major groups of vascular land plants except the angiosperms. Given the abundance of petrified conifer (pycnoxylic) logs found in the Chinle-Dockum beds, it is not especially surprising that about one-third of the compressed flora is coniferous (Agathoxylon, Elatocladus, Pagiophyllum, Pelourdea). The cycads/bennettitaleans are next in order of abundance with about 13 genera (Nilssonia, Nilssoniopteris, Williamsonia, Weltrichia, Zamites) followed by the ferns with about eight genera (Clathropteris Plate 13.1i, Cynepteris Plate 13.1a, Phlebopteris, Todites; Ash 1969, 1975; Ash et al. 1982). Although there are only five sphenophyte genera (Neocalamites, Equisetites, Schizoneura) in the flora, their remains, especially stem casts, are very common and more widely distributed than most other taxa in the flora suggesting generalist ecological niches in a wide range of habitats. Other plant groups, such as the ginkgophytes and gnetopsids are represented only by two to three genera each (Ginkgoites and Dechellyia; Plate 13.1j) and several seed plants were represented by dispersed seeds (Plate 13.1b) and cones (Plate 13.1d) of uncertain relationships.

Some of the plant macrofossils are so unusual and/or incomplete that they are difficult to classify with any assurance. One of the most contentious of these is *Sanmiguelia* (Plate 13.1c), a monopodial plant that was a little less than a metre tall and bore large, palm-like, pleated leaves on its non-woody stem. Apparently, it grew extensively along the shores of rivers and lakes throughout the desert southwest during the Norian and Rhaetian ages of the Late Triassic and during the Hettangian age of the Early Jurassic in southwestern Utah (Ash and Hasiotis 2013). Another genus that is difficult to classify is *Dechellyia*. It consists of a leafy shoot bearing long, narrow, opposite, decussate leaves and winged seeds with a narrowly elliptical wing that are borne in pairs at the ends of short stalks attached to the base of the main

rachis of the leaf. The opposite-decussate leaves and the characters of the associated pollen are shared with all extant Gnetales, whereas winged seeds are present only in *Welwitschia* (Crane 1985). Until more material is found, it will be impossible to determine the systematic relationships of these enigmatic plants. At present, the Chinle-Dockum plant assemblage includes approximately 60 well-defined genera incorporating about 70 species based on plant megafossils, i.e., compressed leaves, leafy shoots, and reproductive structures and permineralized axes (Ash 1989, and personal observations).

The Chinle-Dockum (Carnian-Norian) and the Newark (Carnian-Norian) floras share many genera and species. However, each flora also contains a few distinctive genera, such as Dechellyia and Sanmiguelia that occur only in the Chinle-Dockum flora, and Edenia and Leptocycas that are restricted to the Newark flora (Axsmith et al. 2013; Delevoryas and Hope 1971). The presence of *Fraxinopsis* in both the Chinle-Dockum and the Newark floras (Axsmith et al. 1997; Ash 2011) and Schizoneura in the Chinle-Dockum floras (Ash 1986) suggest that there was some floral interchange between North America, Europe and Gondwana during the Late Triassic or earlier. It appears that the Newark flora generally grew in a more humid climate than the Chinle flora, since minable coal deposits occur in the Carnian and the lower part of the Norian beds of the Newark Supergroup but not in the Chinle-Dockum beds. Furthermore, many of the leaves in the Newark Supergroup are much larger than those of the same genera in the Chinle-Dockum flora. This is particularly true for the ferns (e.g., Clathropteris, Phleboteris) and some of the bennettitaleans (e.g., Sphenozamites). Consequently, it appears that the climate was much more humid along what is now the eastern seaboard of North America. Although the climatic changes along the eastern seaboard of North America were due to continental drift, the changes in the desert southwest were probably caused by orogeny and elevation changes in eastern California (Nordt et al. 2015).

The Norian portion of the Newark Supergroup found in the rift basins along the eastern seaboard of North America contains a moderately diverse palynoflora (Cornet 1977a; Cornet and Olsen 1985; Litwin et al. 1991). The Norian is divided into two main palynozones, separated from the Carnian palynofloras by a transitional zone (Cornet 1977a; Weems et al. 2016), i.e., the Lower Passaic-Heidlersburg Zone and the Manassas-Upper Passaic Zone (Cornet and Olsen 1985). The former zone is distinguished by the presence of *Camerosporites verrucosus* together with abundant large and varied pollen grains including *Alisporites opii*, *Patinasporites densus*, *Vallasporites ignacii* and *Triadispora* spp. The Manassas-Upper Passai Zone is characterized by the first occurrence of *Corollina torosus* and *Granuloperculatispollis rudis* in combination with the ongoing presence of the previously appeared pollen (Cornet and Olsen 1985).

The Norian (and Rhaetian?) corresponds in the Chinle Formation to parts of the informal palynomorph zones II and III, divided by a transitional zone. The informal palynomorph zone III has lately been divided into two subzones, IIIa and IIIb (Reichgelt et al. 2013). The palynoflora of the Norian is generally rich and diverse with more than 100 species (Dunay and Traverse 1971; Fisher and Dunay 1984; Litwin et al. 1991; Lucas et al. 2012). Zone II has a high diversity but low spore

abundance, high dominance of bisaccates and with Cordaitina minor, Protodiploxypinus spp. and Angustisaccus reniformis as characteristic elements (Reichgelt et al. 2013). In zone IIIa palynofloral diversity drops significantly and several pollen types disappear from the record. The spores increase in abundance and diversity (Osmundacidites, Todisporites, Dictyophyllidites, Froelichsporites). Characteristic elements of this zone are Klausipollenites gouldii, Pretricolpipollenites bharadwajii, Araucariacites sp., Todisporites major and Dictyophyllidites harrisii. The abundance of *Klausipollenites gouldii* remains high also in the zone IIIb (>50%), the general pollen diversity increases again (Klausipollenites, Patinasporites, Colpectopollis, Cordaitina, Protodiploxypinus) and the spore abundance drops. Patinasporites densus also becomes abundant. Additional characteristic elements of this zone are Froelichsporites traverse and Colpectopollis ellipsoideus (Litwin et al. 1991; Reichgelt et al. 2013). Thus, these two Norian palynofloras not surprisingly reflect the change in climate that occurred in the desert southwest of North America as a consequence of strong orogenic activity in eastern California (Nordt et al. 2015).

The late Norian flora of the Sverdrup Basin (eastern Canadian Arctic Archipelago) reflects a high-latitude vegetation that lived close to the border with Europe and Siberia and contains elements of both regions. The flora includes 25 genera of plant macrofossils from 11 localities. The diversity at most of the localities is relatively low (only a few species). In total, the flora is characterized by abundant sphenophytes (Equisetites, Neocalamites) and ferns (Camptopteris, Cladophlebis, Clathropteris, Marattiopsis, Phlebopteris, Todites) and less abundant bennettitale-Pterophyllum, Ptilophyllum), ginkgophytes (Ginkgo, ans (Anomozamites, Sphenobaiera), Czekanowskiales (Czekanowskia) and conifers (Pelourdea, Swedenborgia), Podozamites, Stachyotaxus, together with tree trunks (Araucarioxylon, Mesembrioxylon). The floral composition (large horsetails, ginkgophytes, *Camptopteris* and *Clathropteris*) and the presence of coal beds indicate that the plants grew in a relatively warm climate with abundant rainfall and welldeveloped seasons (well-developed growth rings; Ash and Basinger 1991). Also from Canada is the Norian flora of east-central Axel Heiberg Island. This flora is dominated by bennettitalean leaves (Anomozamites, Pterophyllum, Vardekloeftia) and conifer shoots (Podozamites) with only a few sphenophyte (Neocalamites), fern (Dictyophyllum, Todites), seed fern (Lepidopteris), Czekanowskiales (Czekanowskia) and ginkgophyte (Ginkgoites) remains, suggesting a drier climate and/or palaeoenvironment than proposed on studies of the Norian floras of Axel Heiberg and Ellesmere islands (Vavrek et al. 2007). Alternatively, a Rhaetian age might be considered for this flora.

#### 13.3 Late Triassic Floras of Europe and Greenland

Late Triassic floras are widely distributed in Europe and Greenland (these two landmasses being juxtaposed as part of northern Pangea at that time) and they have been grouped historically into three sectors, the Central European Basin (known also as



Fig. 13.3 Areas with major Upper Triassic plant assemblages in Europe, Svalbard and Greenland

the Germanic Basin) and the northern Alpine belt, the Southern Alps and the higher latitude Scandinavia-Greenland area (Figs. 13.1 and 13.3, Table 13.1). These sectors host floras with subtly different compositions. This area also includes the type section for the Triassic–Jurassic boundary, at the Kuhjoch Section in the Karwendel Mountains (Northern Calcareous Alps, Austria; e.g., Ogg et al. 2008). The Triassic– Jurassic boundary is dated radiometrically to  $201.3 \pm 0.2$  Ma, and is defined on the First Appearance Datum (FAD) of the ammonite *Psiloceras spelae tirolicum*. In the continental realm, this coincides with the FAD of the gymnosperm pollen-taxon *Cerebropollenites thiergarthii* (Kürschner et al. 2007; Ogg et al. 2008; Von Hillebrandt et al. 2008).

The most famous floras of the Central European Basin (mostly Germany) are the Schilfsandstein flora and the Germanic Basin 'Rhaeto-Liassic' flora (e.g., Schenk 1867; Gothan 1914; Frentzen 1922; Weber 1968; Kirchner 1992; Kelber and Hansch 1995; Kelber 1998, 2000; Pott et al. 2016a). The Alpine floras host plant assemblages of all stages of the Late Triassic (e.g., Schenk 1866–1867; Stur 1868, 1885; Leuthardt 1903; Kräusel and Leschik 1955; Kräusel and Schaarschmidt 1966; Dobruskina 1993, 1994; Pott 2007; Pott et al. 2007d, 2008a; Pott and Krings 2010;



Plate 13.2 Upper Triassic plants from Europe. (a) Equisetites arenaceus, Lunz, Austria, Carnian.
(b) Asterotheca merianii, Lunz, Austria, Carnian. (c) Pterophyllum filicoides, Lunz, Austria, Carnian. (d, e) Ginkgoites sp., Edgeøya, Svalbard, Carnian. (f) Voltzia sp., Seefeld, Austria, Norian.
(g) Elatocladus sp., Rögla, Sweden, Rhaetian. (h) Nilssonia pterophylloides, Bjuv, Sweden, Rhaetian. (i) Voltzia coburgensis, Ziegelanger, Germany, Rhaetian. (j) Dictyophyllum exile, Rögla, Sweden, Rhaetian. (k) Thaumatopteris schenkii, Stabbarp, Sweden, Hettangian. (l) Wielandiella angustifolia, Jameson Land, Greenland, Rhaetian. (m) Wielandiella angustifolia, Jameson Land, Greenland, Rhaetian. (m) Wielandiella angustifolia, Jameson Land, Greenland, Rhaetian. Scale bar = 10 mm in each image

Kustatscher et al. 2011; Petti et al. 2013; Dalla Vecchia 2000) including historically famous plant suites, such as the Lunz, Neuewelt and Raibl plant assemblages. Additional Carnian floras occur in Slovenia (Dobruskina 2001) and Poland (Pacyna 2014), Norian floras in Poland (Barbacka et al. 2012; Pacyna 2014) and the Apennines (Dalla Vecchia 2000), and Rhaetian floras in France (Lozere: de Saporta

1873–1891; Depape and Doubinger 1963), England (Worchstershire and Bristol: Harris 1938, 1957) and Poland (Schmidt 1928). The Late Triassic floras of the Scandinavia–Greenland sector are documented from relatively few areas but host rich and highly diverse plant assemblages, that reflect extensive wetland systems developed in narrow basins that opened up during initial rifting across the North Atlantic region (e.g., Svalbard, southern Sweden, Greenland; Harris 1931a, 1932a, b, 1935, 1937; Pott and McLoughlin 2009, 2011; Pott 2014a, b).

#### 13.3.1 Carnian Floras of Europe

The Carnian floras of Europe (Lunz, Neuewelt, Monte Pora, Raibl, several localities in Germany, Svalbard) are diverse and reflect generally humid conditions and swampy fluvial to deltaic depositional environments (e.g., Dobruskina 1994; Kelber and Hansch 1995; Pott et al. 2008b). The Carnian flora of Lunz is one of the most diverse Late Triassic floras currently known from the Northern Hemisphere (Pott and Krings 2010). The swampy depositional environment is reflected by coals and carbonaceous shales hosting abundant plant fossils referable to a great diversity of species belonging to numerous plant groups. Ferns (including Matoniaceae, Gleicheniaceae, Marattiaceae; Plate 13.2b), cycads/bennettitaleans (Nilssonia, Nilssoniopteris, Pseudoctenis, Pterophyllum; Plate 13.2c) are very abundant, whereas sphenophytes (Equisetites, Neocalamites; Plate 13.2a), conifers (Elatocladus) and putative ginkgophytes (Arberophyllum, Ginkgoites) are less common (e.g., Dobruskina 1994, 1998; Pott et al. 2007a, b, c, d, 2008a, b, c, in press; Pott and Krings 2010 and references therein). The Lunz flora is especially well known for its abundant and diverse bennettitaleans that are among the earliest representatives of that group. The material includes excellently preserved reproductive structures that play a key role in understanding the phylogeny of the group (Pott 2016; Pott et al. 2017).

The flora of Neuewelt in Basel (Switzerland; Kräusel and Leschik 1955; Kräusel and Schaarschmidt 1966) is slightly less diverse but incorporates abundant sphenophytes, ferns and bennettitaleans, whereas conifers are scarce. The Schilfsandstein flora (Germany) is dominated by sphenophytes (*Equisetites, Neocalamites*) and ferns (*Asterotheca, Cladophlebis*); conifers (*Swedenborgia, Voltzia*) and bennettitaleans (*Pterophyllum*) are rare. The succession hosting this flora incorporates multiple palaeosol layers with successive generations of horsetail (*Equisetites*) shoots and roots; the roots of one generation cut through the plant remains of the previous (underlying) generation (Kelber and Hansch 1995). The plant assemblages from Lunz and the Germanic Basin are considered autochthonous or parautochthonous based on the presence of abundant large, randomly oriented and well-preserved leaves, the presence of extensive, monotypic accumulations of ferns, and the occurrence of *in situ* sphenophyte rhizomes (Kelber and Hansch 1995; Pott et al. 2008a, b). Monotypic associations of ferns and sphenophytes, together with palynological signatures, suggest that these floras grew in a humid environment (e.g., Pott et al. 2008a, b; Mueller et al. 2016a).

Some other Alpine floras differ noticeably in composition from the Lunz assemblages suggesting important local to regional environmental influences on the composition of the fossil assemblages. These include plant assemblages of the Italian Mount Pora (Bergamasc Alps), Dogna and Raibl (Julian Prealps), which are not as diverse as the better known coeval floras of the northern Alps and the Central European Basin and are dominated by gymnosperms (*Pterophyllum*, *Ptilozamites*, Sagenopteris, Voltzia; Plate 13.2f), although various sphenophytes (Equisetites) and ferns (Chiropteris, Danaeopsis) are also preserved, together with enigmatic plant remains, such as Phylladelphia (Schenk 1866–1867; Stur 1868, 1885; Dobruskina 2001; Kustatscher and Van Konijnenburg-van Cittert 2008). The Raibl and Dogna floras are dominated by conifers but, in the former, they belong to the voltzialeans (Voltzia, Bronn 1858; Stur 1885; Dobruskina 2001), whereas in the latter they are attributable to the cheirolepidiaceans (Roghi et al. 2006a). Brachyphyllum and Pelourdea are the most abundant taxa in the Monte Pora plant assemblages. This might reflect a palaeovegetation adapted to less humid environments and/or a taphonomic bias owing to longer transport distances before deposition of the plant remains. A small Carnian plant assemblage from the Karavanke Mountains (Slovenia) has yielded a few conifer remains (Desmiophyllum, Voltzia; Dobruskina 2001). The fossil flora of the Carnian Prealps is dominated by Brachyphyllum, Pagiophyllum and Pelourdea (Dalla Vecchia 2000, 2012), and that of the Bergamasc Alps by unidentified conifer shoots (Andrea Tintori, pers. comm. 2016). The plant assemblages from the famous Carnian Krasiejów fossiliferous locality (southwestern Poland) are generally poor in species and consist mainly of poorly studied leaves, leafy shoots, seeds and cone scales of conifers (Desmiophyllum, Glyptolepis, Pachylepis, Pseudohirmerella, Voltzia) and rare remains of ferns (Sphenopteris) and bennettitaleans (Pterophyllum; Dzik and Sulej 2007; Pacyna 2014).

Carnian strata of Europe have also yielded important amber discoveries. These derive mostly from the Heiligkreuz Formation in the eastern Dolomites and from the Rio del Lago Formation in the Julian Alps (Koken 1913; Zardini 1973; Wendt and Fürsich 1980; Gianolla et al. 1998; Roghi et al. 2005, 2006b) but amber has been found also in the Schilfsandstein of Switzerland and Germany (Soom 1984; Kelber 1990; Schönborn et al. 1999), the Raibler Schichten and the Lunz flora of Austria (Pichler 1868; Sigmund 1937; Vávra 1984) and the Sándorhegy Formation of Hungary (Budai et al. 1999). This unusually high abundance of amber in the fossil record has been linked to the environmental stresses imposed on the plants by the Carnian Pluvial Event (Gianolla et al. 1998; Roghi et al. 2006b).

The Carnian palynological record in Europe expresses a major floristic change characterised by a significant increase in the Circumpolles-group. Circumpolles is an interesting group that increased in abundance and diversity around the Ladinian–Carnian boundary and includes taxa such as *Duplicisporites*, *Paracirculina* and *Camerosporites*, all having supposed cheirolepidiaceous affinities (Zavialova and

Roghi 2005). The group is of great interest to evolutionary palaeontologists as it seems to have diversified through the Late Triassic to produce pollen grains of varied morphologies, and especially so during the Carnian. Its radiation coincides with an arid phase during the early Carnian. The early Carnian palynological assemblages are dominated by xeromorphic elements including taeniate bisaccate pollen and Triadispora (Kürschner and Herngreen 2010). The FADs of several characteristic sporomorphs, including *Camerosporites secatus*, *Enzonalasporites vigens*, Triadispora verrucata and Vallasporites ignacii are recorded during this period. The palynoflora registers a maximum in diversity and a dominance of spores (Leschikisporis, Calamospora, Deltoidospora, Dictyophyllidites) during the middle Carnian, in correspondence with the Carnian Pluvial Event (e.g., Simms and Ruffel 1989, 1990; Olsen and Kent 2000; Hochuli and Frank 2000; Roghi 2004; Breda et al. 2009; Kozur and Bachmann 2010; Preto et al. 2010; Arche and Lopez-Gomez 2014; Dal Corso et al. 2015; Mueller et al. 2016b). During the late Carnian, diversity began to decline and cheirolepidiacean pollen experienced further diversification. The entire Carnian was assigned to the Camerosporites secatus Zone by Herngreen (2005) and Kürschner and Herngreen (2010); this biozone is defined by the FADs of Camerosporites secatus, Enzonalasporites vigens, Triadispora verrucata and Vallasporites ignacii and the first common occurrence of Ovalipollis pseudoalatus. The lower part of this zone is assigned to the Triadispora vertucata Subzone, which corresponds to zones 12 and 13 of Heunisch (1999), the Porcellispora longdonensis Zone of Orłowska-Zwolińska (1984) and the Concentricisporites bianulatus assemblage of Roghi (2004). The middle part of the Camerosporites secatus Zone is named Aulisporites astigmosus Subzone; it correlates to zone 14 of Heunisch (1999), the Aulisporites astigmosus Zone of Orłowska-Zwolińska (1984), the Aulisporites astigmosus assemblage and the Lagenella martinii Assemblage of Roghi et al. (2010). The upper Carnian, is represented by zone 15 of Heunisch (1999), the lower part of the Corollina meyeriana Zone of Orłowska-Zwolińska (1984) and the Granuloperculatipollis rudis Assemblage of Roghi et al. (2010). This interval was not assigned to any subzone by Herngreen (2005) and Kürschner and Herngreen (2010).

Carnian floras of the Scandinavia-Greenland region are known from Svalbard and the Barents Sea (Figs. 13.1 and 13.3, Table 13.1). Svalbard comprises an archipelago of nine main islands with extensive exposures of Upper Triassic successions, including fossiliferous sandstones, siltstones and shales (Vajda and Wigforss-Lange 2009; Vigran et al. 2014). The most extensive Upper Triassic successions hosting plant remains are attributed to the Carnian De Geerdalen Formation and are represented by non-marine delta plain deposits (Klausen and Mørk 2014). Detailed palynological studies through the Upper Triassic successions have revealed variations in the miospore/dinoflagellate cyst ratios that were responses to variations in climate and sea-level. The assemblages document increased marine influences during the Late Triassic in this region (Hochuli and Vigran 2010; Vigran et al. 2014). The Svalbard flora is dominated by ferns (Asterotheca, Cladophlebis, Clathropteris, Phlebopteris, Sphenopteris), bennettitaleans Danaeopsis. Dictyophyllum, (Nilssoniopteris, Pterophyllum) and seed ferns (Paratatarina, Ptilozamites, Sagenopteris) but sphenophytes (Equisetites, Neocalamites) and ginkgophytes are also well represented. Pott and Launis (2015), McLoughlin and Strullu-Derrien (2016), Pott (2016) and Pott et al. (2016b) identified 26 species in the late Carnian (to possibly early Norian) flora of Svalbard, Vassilevskaja (1972) reported a similar flora from Franz Josef Land. Common genera include the sphenophyte *Neocalamites*, the osmundaceous fern Asterotheca, possible peltasperms Paratatarina and Glossophyllum, ginkgophytes Arberophyllum, Ginkgoites (Plate 13.2d, e) and Sphenobaiera, and several species of the bennettitalean foliage Pterophyllum. Dipteridaceae occur only in the uppermost fossiliferous beds. Gothan (1910) reported woods with indistinct growth rings from the Svalbard flora, suggesting only weakly seasonal growth conditions.

Vassilevskaja (1972) argued that there were strong similarities between the Svalbard Carnian flora and assemblages of the Alpine region but notable differences from the coeval floras of central Europe and the slightly younger floras of Sweden and Greenland. Recent studies of the Late Triassic floras of the Svalbard Archipelago have partially supported these interpretations, with several taxa shared between the Svalbard, Lunz and Neuewelt floras (Launis et al. 2014; Pott 2014b). Pott (2014b) argued that the distinctive floristic North Atlantic Subprovince hypothesized for Rhaetian floras (Pott and McLoughlin 2009, 2011) within Dobruskina's (1994) Siberian and European-Sinean palaeofloral areas, was already established by the Carnian.

Extensive palynostratigraphic studies both onshore and, in recent years, from subsurface strata of the Barents Sea have established four Upper Triassic palynoassemblage zones that document the existence of a succession of four distinct, highdiversity palynofloras in this region (Vigran et al. 2014; Paterson and Mangerud 2015). Svalbard Carnian assemblages are represented by the Aulisporites astigmosus Composite Assemblage Zone of early to mid-Carnian age (Table 13.2). Assemblages attributable to this zone are typified by the high relative abundance of the trilete spores Aulisporites astigmosus and Deltoidospora toralis and the acme of monolete spores including Leschikisporis aduncus. The zone is further defined on the FADs of Ricciisporites tuberculatus and Camarozonosporites rudis (Vigran et al. 2014). The succeeding Rhaetogonyaulax spp. Composite Assemblage Zone (Table 13.2) has been dated to late Carnian-early Norian. This zone is defined within nearshore marine deposits and is characterized by a high relative abundance of the dinoflagellate cyst Rhaetogonyaulax rhaetica, together with abundant spores and bisaccate pollen, such as Protodiploxypinus and Ovalipollis pseudoalatus. Taxa defining the zone include a combination of dinoflagellate cysts and pollen, with key FADs of the dinoflagellates R. rhaetica and R. arctica and last occurrence datums (LADs) of several bisaccate pollen taxa, such as Protodiploxypinus gracilis and Staurosaccites quadrifidus.

#### 13.3.2 Norian Floras of Europe

Exposures of Norian strata yielding plant fossils are known from the Alps (Bergamasc Prealps, Carnian Prealps; Northern Calcareous Alps), Apennines (Italy) and Silesia (Poland) (Figs. 13.1 and 13.3, Table 13.1). Norian floras in Europe generally have low taxonomic diversity and are dominated by conifers (reaching 80-90% of the assemblages: Dobruskina 1993, 1994; Dalla Vecchia 2000; Dalla Vecchia and Selden 2013; Pacyna 2014; Kustatscher et al. 2017), whereas cycads/ bennettitaleans, lycophytes, sphenophytes and seed ferns are rare (Dobruskina 1993). The Seefeld flora is dominated by conifers of both voltzialean and cheirolepidiacean affinity (Plate 13.2e), in association with probable cycads (*Taeniopteris*) and lycophytes (e.g., Lepacyclotes; Dobruskina 1993, 1994; Kustatscher et al. 2017). The two small plant assemblages from the Appenines, i.e., Giffoni (Salerno) and Filettino (Frosinone), have yielded bennettitaleans (Pterophyllum) and conifers (Araucarites, Brachyphyllum, Podozamites, Voltzia; Dalla Vecchia 2000). The Upper Silesian flora (Poland) is dominated by conifers (Brachyphyllum) associated with sparse horsetails (Equisetites), ferns (Cladophlebis, Clathropteris), bennettitaleans (Pterophyllum) and Czekanowskiales (Pacyna 2014). In some localities, Pachylepis-type seed scales, matching the cuticles of the Brachyphyllum shoots, and putative fragments of *Czekanowskia* and ginkgophyte leaves are also preserved. Even a liverwort, Palaeohepatica, was described but never figured from this flora (Pacyna 2014).

The fragmentary nature of most of the Norian plant remains and the preservation of the cuticles in the Seefeld flora suggest that, in most cases, the plant remains were subjected to extensive transport. The thick cuticle and the sunken stomata protected by papillae suggest that the plants grew in stressed environments, such as small carbonate islands with thin soils and low groundwater levels and/or under arid conditions (Kustatscher et al. 2017). This may be true for most of the Norian plant assemblages of Europe with the exception of the Polish flora, which incorporates various ferns and a putative bryophyte, both considered hygrophytic plant groups. This suggests that the Polish flora grew under moister environmental conditions favoured by Poland's higher palaeolatitude, and/or the Polish assemblages were subjected to shorter transport before deposition.

During the Norian, the Circumpolles-producers became progressively more prominent in the vegetation, which is reflected in their high abundance. Generally, the palynofloral diversity decreases by about 50% between the early Carnian and the Norian (Kürschner and Herngreen 2010). Carnian hold-overs (*Duplicisporites* spp., Enzonalasporites spp. and *Camerozonosporites* spp.) remain common in lower Norian successions (Cirilli 2010). Difficulties assessing the Norian palynological record include the absence of continental deposits that can be readily correlated with marine successions and also the fact that Norian and lower Rhaetian assemblages are generally rather homogeneous. Owing to the incomplete Norian palynological record, considerable uncertainty exists about the ranges of so-called 'typical' Rhaetian sporomorphs (e.g., *Cornutisporites* spp., *Limbosporites lundbladii*, *Perinosporites thuringiacus, Rhaetipollis germanicus, Semiretisporis* spp., *Triancoraesporites* spp. and *Zebrasporites* spp.), for which a late Norian appear-

ance cannot be excluded (Kürschner and Herngreen 2010). The Norian successions are attributed by Herngreen (2005) to the *Granuloperculatipollis rudis* Zone, based on the FAD of the marker species and the abundance of *Classopollis meyeriana* and *C. zwolinskae*. This zone corresponds to zones 16–17 of Heunisch (1999), the middle–upper part of the *Corollina meyeriana* Zone of Orłowska-Zwolińska (1984) and the upper part of the *Granuloperculatipollis rudis* assemblage of Roghi et al. (2010).

In Svalbard, the Norian Flatsalen Formation incorporates predominantly shallow marine deposits and, consequently, does not preserve abundant plant macrofossils. However, well-preserved Norian palynological assemblages from this unit are assigned to the Limbosporites lundbladii Composite Assemblage Zone (Vigran et al. 2014; Table 13.2), which is typified by a dominance of spores (especially spikes of Annulispora spp. and Deltoidospora spp.), together with diverse representatives of the fern spore Kyrtomisporis. This zone is defined by the FADs of Limbosporites lundbladii and Rogalskaisporites barentzii, and the regular occurrence of Ricciisporites umbonatus, Cingulizonates rhaeticus, Granuloperculatipollis rudis and Quadraeculina anellaeformis. Owing to the nearshore marine depositional setting of the Flatsalen Formation, the palynoassemblages include dinoflagellates, mainly Heibergella spp., H. asymmetrica and Rhaetogonyaulax rhaetica, which aid regional correlation. Palynostratigraphic studies have also noted the inception of cheirolepidiacean conifers (commonly an indicator of drier and/or saline influences) and a relative increase in the abundance of gymnosperms producing bisaccate pollen in this interval (Paterson and Mangerud 2015).

Strata of this age in southern Sweden are assigned to the Kågeröd Formation and occur mostly in the subsurface as red-beds devoid of plant material. Similarly, the Norian–lower Rhaetian Ørsted Dal Member (Fleming Fjord Formation) of East Greenland consists of fluvial and lacustrine red, marly mudstones, grey sandstones and carbonates that lack plant fossils (Surlyk 2003). In the Alpine area, the Norian succession is characterized by dolomitic strata that are also poor in palynomorphs.

#### 13.3.3 Rhaetian Floras of Europe and Greenland

Several of the most important latest Triassic assemblages (Fig. 13.3, Table 13.1) were assigned historically to 'Rhaeto-Liassic' floras because, in early studies, the distinctions between the Rhaetian and Early Jurassic successions were difficult to resolve. A more detailed stratigraphic resolution of the Triassic–Jurassic transition in continental successions of Europe and Greenland has been achieved in recent years utilizing palynofloral (e.g., Lindström and Erlström 2006; Larsson 2009; Vajda et al. 2013; Vigran et al. 2014; Lindström et al. 2017), macrofloral (e.g., McElwain et al. 2009; Pott and McLoughlin 2009, 2011; Pott et al. 2016b), stable isotope (e.g., Hesselbo et al. 2002) and magnetostratigraphic data (e.g., Lord et al. 2014), and this has facilitated a better understanding of the significant changes in the vegetation across this boundary.

The Bayreuth flora (Oberfranken, Germany) includes one of the most famous 'Rhaeto-Liassic' floras (Weber 1968). The richest Rhaetian plant assemblage restudied recently is that from Wüstenwelsberg (e.g., Kelber and Van Konijnenburgvan Cittert 1997; Bonis et al. 2010; Zavialova and Van Konijnenburg-van Cittert 2011; Van Konijnenburg-van Cittert et al. 2014, 2016; Pott et al. 2016a). The sandstone quarry at Wüstenwelsberg is well known for its rich and diverse flora, including lycophytes (Selaginellites), sphenophytes (Equisetites), ferns (e.g., Cladophlebis, Clathropteris, Dictyophyllum, Marattia, Phlebopteris, Todites, Thaumatopteris), seed ferns (Ctenozamites, Lepidopteris, Pachypteris, Ptilozamites, Rhapidopteris), cycads/bennettitaleans (Anomozamites, Ctenis, Nilssonia, Nilssoniopteris, Pseudoctenis, Pterophyllum), ginkgophytes (Ginkgoites, Schmeissneria) and conifers (Desmiophyllum, Elatocladus, Palissva, Stachytaxus, Schizolepis, Voltzia; Plate 13.2i). Cycads/bennettitaleans are very abundant but *Voltzia* is apparently absent; so too is *Hirmerella*, one of the most prominent taxa of the 'Rhaeto-Liassic flora of Bavreuth' (Gothan 1914; Kirchner 1992; Bonis et al. 2010). The Rhaetian Seinstedt plant assemblage is also a diverse and hygrophytic flora (Barth et al. 2014).

The Polish Rhaetian flora of Upper Silesia and the Tatra Mountains is of low diversity and consists mostly of fragments of sphenophytes (*Neocalamites*), ferns (*Cladophlebis, Clathropteris*), seed ferns (*Lepidopteris, Peltaspermum*), cycads/ bennettitaleans (*Pterophyllum, Taeniopteris*), Czekanowskiales (*Czekanowskia*), ginkgophytes (*Ginkgoites*) and conifers (*Brachyphyllum, Pagiophyllum, Palissya, Widdringtonites*, Cheirolepidiaceae) (Barbacka 1991; Reymanówna and Barbacka 1981; Wawrzyniak and Ziaja 2009; Pacyna 2014).

Rhaetian and Early Jurassic floras in Skåne (southern Sweden) derive from the coal-rich Bjuv Member (upper Rhaetian) and Helsingborg Member (Hettangian) of the Höganäs Formation, but a few plants have also been recovered from the underlying Vallåkra Member (lower Rhaetian). The plant remains are abundant and exceptionally well preserved. A wealth of fossils has been collected and curated over the past century in association with bituminous coal mining (more than 28,000 specimens are curated in the collections of the Swedish Museum of Natural History alone). Rhaetian-Hettangian plant assemblages of southern Sweden, similarly to the Rhaeto-Liassic floras of the Central European Basin, were treated as a single flora in many early taxonomic studies because the uppermost Triassic and lowermost Jurassic successions were difficult to distinguish lithologically, problematic to trace laterally, and the depositional environment was represented by relatively consistent floodplain settings across the boundary interval. A consistent lithostratigraphic framework did not develop for the region until the mid-twentieth century (Troedsson 1943, 1950, 1951). The floras are preserved in deltaic and coastal plain deposits that locally also host fossils of fishes, amphibians and dinosaur trackways (Nilsson 1946; Troedsson 1951; Vajda et al. 2013). This wealth of fossil plant material has been the subject of numerous taxonomic studies over the past two centuries (Nilsson 1820; Nathorst 1876a, b, 1878a, b, c, 1879, 1880, 1886, 1888, 1902, 1909a, b, 1913; Halle 1908; Johansson 1922; Lundblad 1949, 1950, 1959a, b; Pott and McLoughlin 2009, 2011; Pott 2014a).

Although around 445 taxa have been recorded from the Rhaetian–Early Jurassic floras of Skåne, accurate measures of diversity are difficult to obtain without wholesale revision of the historical fossil collections because various authors have adopted different approaches to the delimitation of taxa. For example, Lundblad (1959a) re-assessed the taxonomy of several *Ginkgo* taxa described by Nathorst (1878c, 1886), synonymizing some forms, and emphasized that morphological characteristics for taxonomical delinations of Ginkgo species need to be combined with cuticular analyses. Further, Pott and McLoughlin (2009), in an analysis of bennettitalean foliage from the various Scanian localities, reduced the around 50 taxa of this group reported previously to just 10 clearly demarcated species attributable to Pterophyllum and Anomozamites, of which only five were recorded with confidence from Rhaetian strata. Overall, the Skåne Rhaetian floras include a diverse array of plant groups including bryophytes, lycophytes, sphenophytes (Equisetites, Neocalamites), ferns (Camptopteris, Dictyophyllum Plate 13.2j, Phlebopteris, Thaumatopteris Plate 13.2k, Todites), bennettitaleans (Anomozamites, Pterophyllum), cycads (Nilssonia; Plate 13.2h), seed ferns (Lepidopteris, Ptilozamites, Sagenopteris), ginkgophytes (Baiera, Ginkgo, Ginkgoites, Sphenobaiera) and conifers (Cyparissidium, *Elatocladus* Plate 13.2g, *Stachyotaxus*, *Palissya*). Ouantitatively, sphenophyte stems and foliage of ferns, conifers and bennettitaleans tend to dominate the Rhaetian assemblages of Skåne (Pott and McLoughlin 2009, 2011). The overall composition of the flora suggests a multi-storey vegetation with ferns, sphenophytes and lycophytes dominating the under-storey, conifers and ginkgoaleans the upperstorey, and a range of bennettitaleans, cycads and seed-ferns constituting plants of intermediate stature.

Many of the genera and species in the Skåne deposits are shared with the Rhaetian flora of Jameson Land (East Greenland), and Lundblad (1950, 1959a) noted a disjunction in Skåne between the composition of latest Triassic assemblages (assigned to the Lepidopteris Zone) of the Bjuv Member and the succeeding earliest Jurassic assemblages of the Helsingborg Member (assigned to the Thaumatopteris Zone) that is matched in the Greenland succession. The first appearances of several fern and gymnosperm species, notably Thaumatopteris schenkii (Plate 13.2k), Pterophyllum subequale, Anomozamites gracilis, Dictyophyllum nilssonii, Sagenopteris nilssoniana, Ginkgoites marginatus, Baiera taeniata, Czekanowskia rigida, Podozamites distans, and Palissya braunii characterize basal Jurassic strata in Skåne and signify an important change in the flora. Further, a stratigraphic interval of a few metres in the uppermost Rhaetian strata is typified by great abundances of the enigmatic gymnosperm pollen Ricciisporites tuberculatus. This taxon ranges from the Norian to the Sinemurian but has a pronounced acme in the upper Rhaetian of Northwest Europe (Kürschner et al. 2014; Peterffy et al. 2016). The acme provides a useful biostratigraphic marker for the end-Triassic biotic crisis interval in both the East Greenland and Skåne successions (Pedersen and Lund 1980; Mander et al. 2013; Vajda et al. 2013). The Ricciisporites-rich zone is succeeded by a short interval dominated by fern (mainly Deltoidospora) spores. In Skåne, as in East Greenland, this stratigraphic package is identified as a transitional interval (Larsson 2009; Vajda et al. 2013) that possibly incorporates fossils of the recovery vegetation following the end-Triassic crisis.

Fossiliferous strata in Jameson Land and nearby Traill Island (East Greenland) were first mentioned by William Scoresby Jnr. The coal layers were first considered to be Carboniferous (Jameson 1823), later Cenozoic (Heer 1868) and finally Rhaetian in age (Hartz 1896). Harris (1926, 1931a, 1932a, b, 1935, 1937, 1946) undertook the most intensive studies of the Primulaely Formation floras (Kap Stewart Group) from the Hurry Inlet and Klitdal areas (Pedersen 1976; Surlyk 2003; McElwain et al. 2007). Harris described around 200 species of fossil plants, many of them represented by specimens with excellent preservation yielding cuticular details (Plate 13.2l, m). As in Skåne, Harris (1937) recognized two stratigraphically distinct floras in this region, a lower Lepidopteris flora, and an upper Thaumatopteris flora. Only a few species are common to both floras but there are great similarities at family level (McElwain et al. 2009). Bennettitales, cycads, ginkgophytes and conifers dominate both floras. The transition from the Rhaetian to the Lower Jurassic is marked by the inception of several fern and gymnosperm taxa, especially Thaumatopteris schenkii, Pterophyllum subequale, Anomozamites gracilis, Dictyophyllum nilssonii, Sagenopteris nilssoniana, Ginkgoites marginatus, Baiera taeniata, Czekanowskia rigida, Podozamites distans and Palissya braunii.

Harris (1937) assigned the Lepidopteris Zone to the Rhaetian and Thaumatopteris Zone to the Early Jurassic based on correlations with the fossil floras of southern Sweden and southern Germany (e.g., the Grenzschichten flora). These ages were later confirmed by palynostratigraphy and stable isotope signatures (Pedersen and Lund 1980; Hesselbo et al. 2002). These palynological studies have provided more detailed insights into the floristic transition in East Greenland; the most important of these being the study by Pedersen and Lund (1980) who identified well-preserved and rich miospore assemblages dominated by gymnosperm pollen in the Rhaetian and Hettangian siliciclastic successions exposed along Hurry Inlet. In general terms, these assemblages matched the composition of the macrofloras documented by Harris in the 1930s. Pedersen and Lund (1980) grouped the assemblages into two 'microflora zones' (Microflora Zone 1 and Zone 2), which essentially are equivalent to the Lepidopteris (Rhaetian) and Thaumatopteris (Hettangian) macrofloral zones of Harris (1937), respectively. Zone 1 is characterized by abundant Ricciisporites tuberculatus, and the presence of Limbosporites lundbladii, Rhaetipollis germanicus, Heliosporites altmarkensis, Ovalipollis ovalis and Apiculatisporis parvispinosus. It is correlated to the northwest European Rhaetipollis-Limbosporites Zone of early Rhaetian age (Lund 1977), the Rhaetipollis germanicus Zone of Herngreen (2005), zones 18-20 of Heunisch (1999) and the Ricciisporites tuberculatus Composite Assemblage Zone of Vigran et al. (2014) and Orłowska-Zwolińska (1984) (Table 13.2). The latter is defined mainly on the high relative abundance of L. lundbladii and Cingulizonates rhaeticus, together with Chasmatosporites spp. and R. tuberculatus. Several of these taxa, e.g., L. lundbladii and R. tuberculatus, together with the dinoflagellate cysts Rhaetogonyaulax rhaetica, Suessia swabiana and S. mutabilis, also have their LADs within this zone.

Pedersen and Lund (1980) subdivided Microfloral Zone 1 into three sub-zones (Lower, Middle and Upper). 'Zone 1 Lower' is distinguished from the succeeding subzones mainly by the presence of '*Vesicaspora' fuscus* and more common



Fig. 13.4 Areas with major Upper Triassic plant assemblages in easternmost Europe and Asia (except India)

*Ovalipollis ovalis.* 'Zone 1 Middle' is defined by the acme of *Limbosporiteslundbladii*, includes the dominance of *Deltoidospora toralis* and *Uvaesporites reissingeri*, and the presence of *Polypodiisporites polymicroforatus*, *Araucariacites* spp. and a spike of *R. tuberculatus* in the upper part of this sub-zone. The coeval*R. tuberculatus* Composite Assemblage Zone in Svalbard (Fig. 13.4) is also characterized by a high abundance of the nominal taxon. 'Zone 1 Upper' is distinguished from the preceding sub-zones based on the occurrence of *Vesicaspora fuscus* and the common presence of *Ovalipollis ovalis*. This sub-zone is also characterized by a highly diverse miospore assemblage with high relative abundances of *Deltoidospora toralis*, *Baculatisporites comaumensis*, *Vitreisporites bjuvensis*, *Araucariacites* spp., *Classopollis* spp. and *Ricciisporites tuberculatus*. At the Triassic–Jurassic transition, palynofloral diversity declines by about 20%, mainly as a result of a decrease in the number of spore species (Kürschner and Herngreen 2010). The Hettangian Miospore Zone 2 palynomorph species richness is similar to that prior to the Rhaetian. Zone 2 is characterized by the absence (or rarity) of some taxa diagnostic

of Zone 1, and the appearance of various gymnosperm pollen, and fern and lycophyte spores, such as *Cerebropollenites thiergartii*, *Heliosporitesaltmarkensis*, *Trachysporites asper*, *Lycodopiumsporites semimuris*, *Deltoidospora crassexina*, *Iraquispora laevigata* and *Schismatosporites ovalis*.

The end-Triassic biotic crisis has an ambiguous palynofloral signal in Europe and Greenland. Some studies indicate only minor changes in the palynoflora (Lund 1977; Achilles 1981; Batten and Koppelhus 1996; Bonis et al. 2009a, b; Kürschner and Herngreen 2010; Götz et al. 2011). Others (Pedersen and Lund 1980; Lindström and Erlström 2006; Van de Schootbrugge et al. 2007; Larsson 2009; Vajda et al. 2013; Lindström 2016) have indicated a significant floral turnover and a spike in the pollen Ricciisporites tuberculatus across the Triassic-Jurassic transition. Although some floristic modifications and  $\delta^{13}$ C isotope excursions might be related to facies changes around the boundary (Brenner 1986; Heunisch 1999), the significant turnover in palynomorph taxa in correspondence with changes in the plant macrofossil assemblages (Harris 1937; Lundblad 1959b; McElwain et al. 2009) and a spike in R. tuberculatus, matching equivalent surges in disaster taxa during other Earth crises (Visscher et al. 1996; Vajda et al. 2001; Vajda and McLoughlin 2004, 2007; Vajda and Bercovici 2014), suggests a marked disruption to the vegetation, at least in the North Atlantic sector. High-resolution palynological studies in widely separated basins will be necessary to obtain a clear picture of the regional patterns of floristic turnover across this boundary.

Silicified and sideritized fossil wood is preserved in both the East Greenland and the Skåne floras (Clemmensen 1976; S. McLoughlin pers. obs.). Despite the apparently wide distribution of fossil woods in the region, few palaeoxylological studies have been undertaken. One exception is a silicified (permineralized) peat block recovered from the island of Hopen (Svalbard Archipelago), which has yielded a remarkable array of three-dimensionally preserved autochthonous roots and stems of lycophytes and bennettitaleans, and parautochthonous sporangia, spores, pollen and leaves from various pteridophytes and gymnosperms (Selling 1944, 1945; Strullu-Derrien et al. 2012; McLoughlin and Strullu-Derrien 2016). Future studies on fossil woods from the Late Triassic of these regions offer considerable opportunities for analysis of biotic interactions (arthropod borers and fungal damage) and palaeoclimates (via growth-ring analysis) that can be compared and contrasted with equivalent parameters from the Early Jurassic of the same areas (Vajda et al. 2016; McLoughlin and Bomfleur 2016).

## 13.4 Late Triassic Floras of Easternmost Europe and Asia (Except China and Eastern Asia)

The major regions hosting Upper Triassic fossiliferous strata in easternmost Europe and Asia lie in the territory of the former Soviet Union (Figs. 13.1 and 13.4, Table 13.1), attributed by Dobruskina (1994) to the Middle Asian and East Asian sectors (Middle Asian and East Asian floristic subprovinces). The East Asian

Subprovince includes the Donets Basin, Fore-Caucasus, Kazakhstan and Southern Fergana, Southern Urals and Caspian Depression, whereas the Middle Asian Subprovince comprises the Pechora Basin, eastern Urals, and eastern and northern Siberia (Fig. 13.6). Floras of the Middle Asian floristic Subprovince are characterized by a dominance of peltasperms, the presence of marattiacean ferns, rare cycadocarpidiacean conifers and a lack of Dipteridaceae. The East Asian Subprovince (Primorye included) is characterized by numerous dipteridacean ferns and cycadocarpidiacean conifers whereas marattiacean ferns and peltasperms are virtually absent.

Palynological studies of Upper Triassic deposits in the territory of the former Soviet Union are scattered and no synthetic palynozonation scheme has been established. The best-studied miospore assemblages derive from the European part of Russia, Donetsk Basin, Western Caucasus and Siberia. No palynological studies have been carried out on the Upper Trassic strata of Primorye.

## 13.4.1 Carnian Floras of Easternmost Europe and Asia (Except China and Eastern Asia)

Carnian floras are well represented across easternmost Europe and north and central Asia (Figs. 13.1 and 13.3, Table 13.1). The richest and best-studied Carnian floras from this region derive from the lower part of the Protopivskaya Formation of the Donets Basin (Stanislavsky 1965, 1971, 1973, 1976), Kalachevskaya Formation of the Pechora Basin (Kirichkova 2011; Kirichkova and Esenina 2014), eastern Urals (Vladimirovich 1959, 1965, 1967; Kirichkova 1990), southern Fergana and Kazakhstan (Turutanova-Ketova 1931; Brick 1941; Sixtel 1960; Dobruskina 1995) and southern Primorye (Kryshtofovich 1912; Srebrodolskaya 1960; Shorokhova 1975a; Shorokhova and Srebrodolskaya 1979; Volynets and Shorokhova 2007; Volynets et al. 2008).

Peltasperms (e.g., Lepidopteris, Peltaspermum, Scytophyllum; Plate 13.3h) reach their maximum abundance and diversity in the Middle Asian Subprovince during this interval, especially in assemblages close to the Urals. The floras of the Donbass, Urals and Central Asia are composed of up to 30% peltasperm remains. Apart from various spore-producing plants (Plate 13.3b), the Madygen flora also contains seed ferns (Peltaspermum, Ptilozamites, Scytophyllum, Vittaephyllum; Plate 13.3c) among its most common elements (Dobruskina 1995; Moisan et al. 2011; Moisan and Voigt 2013). The Carnian assemblages of the western and eastern part of the Urals contain Scytophyllum-type leaves suggesting that the Ural Mountains were not an impassable barrier for peltasperms during the Late Triassic (Dobruskina 1994), whereas the floras of the East Asian Subprovince lack peltasperms. Glossophyllum-type leaves are the common element in the Carnian floras of the Central European and Middle Asian subprovinces. Dobruskina (1994) referred her lanceolate leaves of Glossophyllum to the ginkgophytes, but at least some of them may alternatively belong to pteridosperms. Czekanowskiales are restricted to northern latitudes. They may have radiated from the mountains of the Ural-Tien Shan region to Primorye, Japan and Mongolia during the Carnian and to the eastern side of the Urals during the Norian (Dobruskina 1994; Volynets and Shorokhova 2007).

Marattiacean ferns (e.g., Danaeopsis, Marattiopsis, Rhinipteris) were important during the Carnian in the Urals, Caucasus and Central Asia, but were absent from the eastern Urals, Taimyr and Primorye. Dobruskina (1994) related this distribution to the migration of families from the west of Eurasia, up to the geographic barrier posed by the Ural Mountains. Dipteridaceae spread at lower latitudes of the East Asian Subprovince, being represented in such deposits as the Sad-Gorod Formation of the Primorye (Volynets and Shorokhova 2007), whereas they are rare or absent in the continental interior. The fact that one of the oldest Northern Hemisphere records comes from the Ladinian deposits of Japan (Dictyophyllum; Plate 13.3a) might indicate that the family originated in and spread from the East Asian sector. Sphenophytes are numerous but taxonomically monotonous; they are represented by three genera only (Neocalamites, Annulariopsis, Schizoneura) and occupy a subordinate position in relation to other plant groups in the southern latitudes of the Central European and Middle Asian Subprovince. However, they constitute a significant component of several assemblages in the northern part of the Chelyabinsk Basin and the Southern Urals (Kirichkova 1969) and in the Bukobay Formation of the Ilek River Basin (Brick 1952). Bryophytes (Muscites, Ricciopsis) and lycophytes (Annalepis, Ferganodendron, Isoetites, Mesenteriophyllum, Pleuromeiopsis) are rare, although Moisan et al. (2012b) and Moisan and Voigt (2013) described a few new taxa from the Madygen locality of South Fergana. The peculiar composition of this flora has been attributed to its special palaeoenvironmental setting; the plants grew in rather humid environments of alluvial plains, delta plains and shallow lacustrine environments near the northern limits of the Tethys Ocean during the Carnian (Kochnev 1934; Brick 1936; Sixtel 1961, 1962; Dobruskina 1995; Moisan et al. 2011).

Conifers constitute a subordinate component of most northern and central Asian Carnian floras, and only at Nikolaevka (Donets Basin) do they reach more than 30% of all plant remains (Stanislavsky 1976). Primitive voltzialean conifers were gradually replaced by more advanced groups (e.g., *Pachylepis, Schizolepis, Stachyotaxus*; Dobruskina 1994). Conifers (*Cycadocarpidium, Podozamites*; Plate 13.3f) were widely distributed in the southern latitudes of the East Asian sector. The dominance of coniferous genera changes from west to east and is probably linked to the provincialism of the Carnian floras (Dobruskina 1994). The relative abundance of cycads/bennettitaleans increased towards the south; they are the most abundant group in the Carnian flora of Primorye (up to 50%; Volynets and Shorokhova 2007). This is mainly a consequence of the great abundance of *Taeniopteris* remains, whereas *Otozamites* and *Pseudoctenis* leaves (Plate 13.3d) are rare. Moisan et al. (2011) noted the first occurrence of *Pseudoctenis* and *Pterophyllum* (Plate 13.3e) from central Asia (Madygen flora).

A rich and well-preserved palynological assemblage was first described by Yaroshenko (1978) from marine deposits of Western Ciscaucasia containing bivalves, ammonoids and brachiopods of Carnian age. The assemblage is characterized by a high relative abundance of *Camerosporites secatus*, *Alisporites australis* 



Plate 13.3 Upper Triassic plants from Asia. (a) *Dictyophyllum kryshtofovichii*, Razdol'naya River basin, Primorye, Russia, Norian. (b) *Cladophlebis* sp., Madygen, Kyrgyzstan, Carnian. (c) *Vittaephyllum hirsutum*, Madygen, Kyrgyzstan, Carnian. (d) *Pseudoctenis mongugaica*, Filipovka River basin, Primorye, Russia, Carnian. (e) *Pterophyllum* sp., Madygen, Kyrgyzstan, Carnian. (f) *Podozamites* sp., Madygen, Kyrgyzstan, Carnian. (g) *Gleichenites* sp., Dharbid Khun, Iran, Rhaetian. (h) *Lepidopteris ottonis*, Apuntal, Iran, Rhaetian. (i) *Baiera muensteriana*, Dharbid Khun, Iran, Rhaetian. (j) *Anomozamites polymorpha*, Aghusbin, Iran, Rhaetian. (k) *Pterophyllum nathorstii*, Apuntal, Iran, Rhaetian. Scale bar = 10 mm in each image

and *Dictyophyllidites* spp., and the FAD of *Auritulinasporites scanicus* and *Granosaccus tkhachensis*. Ilyina and Egorov (2016) noted that the continental strata of the transitional continental-marine deposits of northern Middle Siberia were characterized by a significant representation of *Ovalipollis, Ricciisporites* and *Minutosaccus* pollen grains, and *Kyrtomisporis, Tigrisporites* and *Limbosporites* 

spores (Romanovskaya and Vasilieva 1990). Carnian pollen assemblages differ significantly from those of the western and eastern slopes of the Ural Mountains of the Middle Asian Subprovince. The pollen assemblages from the Protopivskaya Formation of the Donetsk Basin are characterized by *Tigrisporites*, *Limbosporites*, Aratrisporites, Minutosaccus, Ovalipollis and Ricciisporites (Semenova 1970, 1973; Gluzbar 1973). It is noteworthy that the Carnian assemblage of the Donetsk Basin is poorly correlated with coeval assemblages of the eastern part of the Pechora Basin (Chalyshev and Variukhina 1966; Variukhina 1971), West Siberia (Malyavkina 1964), Franz-Josef Land (Fefilova 2005) and Kazakhstan (Sakulina 1973) but are similar to the Middle Keuper assemblages of Western Europe (Gluzbar 1973). A review of the palynological assemblages from the territory of former Soviet Union identified the Ovalipollis-Dictyophyllidites-Enzonalasporites-Porcellispora longdonensis assemblage as characteristic for the Carnian of the East European platform and Southern Kazakhstan (Romanovskaya and Vasilieva 1990). Romanovskaya and Vasilieva (1990) also proposed several regional assemblages (Table 13.2): the Aratrisporites-Disaccites-Dictyophyllidites-Ovalipollis association for the Pechora Basin. the Disaccites-Osmundacidites-Aratrisporites-Dictyophyllidites-Punctatosporites walkomi-Striatites association for the Chelyabinsk Basin, the Duplexisporites-Lycopodiacidites kuepperi-Cingulizonates delicatus-Chasmatosporites association for eastern Taymir and the Dictyophyllidites-*Osmundacidites-Chasmatosporites-Cingulizonates* delicatus-Neoraistrickia taylorii association for the Arctic regions.

## 13.4.2 Norian–Rhaetian Floras of Asia (Except China and Eastern Asia)

Norian and Rhaetian floras of easternmost Europe and northern and central Asia (Figs. 13.1 and 13.4, Table 13.1) are discussed together, because, in most cases, the continental deposits of these ages are difficult to correlate with well-dated marine sequences (Dobruskina 1980; Markevich and Zakharov 2004). Norian continental deposits are common in many regions of easternmost Europe and northern and central Asia, especially from Primorye (Shorokhova 1975b; Shorokhova and Srebrodolskaya 1979; Volynets and Shorokhova 2007). They are preserved in the upper part of the Protopivskaya Formation of the Donets Basin (Stanislavsky 1976), the upper part of the Nemtsov Formation of central Siberia, the Kozyrevskaya Formation of the eastern Urals and the Amba Formation of Primorye (Kirichkova 1962, 1969, 2011; Volynets and Shorokhova 2007). Rhaetian continental facies with plant remains are completely absent from some areas. Rhaetian plant assemblages are interpreted to be present in the Novorayskaya Formation of the Donets Basin (Stanislavsky 1971) and the Aktash and Tashkutan formations of central Asia (Genkina 1964; Gomolitzky 1993; Sixtel 1960).

The Norian–Rhaetian was a time of optimum development of cycads and bennettitaleans. Cycad/bennettitalean remains typically constitute 35–50% of specimens in leaf-dominated assemblages of this sector and are particularly rich in the Rhaetian Novorayskaya Formation of the Donbass region. Volynets et al. (2008) also noted that the Imalinovo plant assemblage (early Norian) of Primorye is rich in *Otozamites, Pseudoctenis* and many remains of *Ctenis, Drepanozamites, Nilssonia* and *Pterophyllum.* An especially large number of cycads/bennettitaleans is known from the Rhaetian Novorayskaya Formation of Donbass.

There are almost no ferns of Palaeozoic aspect in the Norian–Rhaetian floras. However, Mesophytic marattialean fern families, Osmundaceae (*Todites*), Matoniaceae (*Phlebopteris*) and Dipteridaceae (e.g., *Camptopteris*, *Clathropteris*, *Dictyophyllum*) are widely distributed in the Novorayskaya Formation of Donbass (Stanislavsky 1971), in the Eastern Caucasus (Vakhrameev et al. 1977) and in Central Asia (Issyk-Kul and Kavak-Tau) (Turutanova-Ketova 1931). Primorye is known for its unusual occurrences of endemic fern species attributable to *Acrostichopteris* (Shorokhova 1975a).

Ginkgoales and Czekanowskiales are geographically widespread in central and northern Asia during this time. Ginkgoales are represented by *Allicospermum*, *Baiera*, *Ginkgoites*, *Sphenobaiera* and leaves of Umaltolepidiaceae (*Pseudotorellia*), which are also typical of the Early Jurassic assemblages. New conifer genera (e.g., *Fraxinopsis*, *Palaeotaxus*, *Palissya*, *Storgaardia*) appeared in the Rhaetian and coexisted with forms that appeared earlier in the Norian. Peltasperms decrease in abundance, and in Central Asia are they virtually absent. Only *Ctenozamites*, *Ptilozamites* and *Lepidopteris* are found on the eastern slope of the Polar Urals (Dobruskina 1994). Leaves of *Thinnfeldia* and the endemic pteridosperms *Imania* and *Tudovakia* were described from Primorye (Volynets et al. 2008; Krassilov and Shorokhova 1970). The species diversity and relative abundance of sphenophytes decreases in the Norian–Rhaetian floras of central and northern Asia.

Rhaetian plant assemblages are also known from localities in central Pamir and Afghanistan (Prynada 1934; Sixtel 1960; Vakhrameev et al. 1978). These consist mainly of cycads and bennettitaleans (Anomozamites, Nilssonia, Otozamites, Pterophyllum, Taeniopteris), conifers (Pelourdea) and ferns (Clathropteris, Dictyophyllum, Thaumatopteris). The Nayband Formation of Central-East Iran has also yielded 19 genera (31 species) of sphenophytes (Equisetites), ferns (Cladophlebis, Clathropteris, Dictvophyllum, Gleichenites Plate 13.3g. Phlebopteris, Todites), seed ferns (Scytophyllum, Lepidopteris; Plate 13.3h), cycads/ bennettitaleans (Androstrobus, Dictvozamites, Nilssonia, Nilssoniopteris, Pterophyllum Plate 13.3k, Anomozamites Plate 13.3j, Weltrichia, Williamsonia), ginkgophytes (Ginkgoites, Baiera; Plate 13.3i) and conifers (Elatocladus, Krasser 1891; Kilpper 1964, 1971; Fakhr 1977; Schweitzer 1977, 1978; Schweitzer and Kirchner 1995, 1996, 1998, 2003; Schweitzer et al. 1997, 2000, 2009; Vaez-Javadi 2012, 2013a, b). The Norian–Rhaetian flora from Aghdarband (northeast Iran) is dominated by cycads/bennettitaleans (Pterophyllum, Taeniopteris) and conifers (Pagiophyllum, Podozamites, Stachytaxus) with a few horsetails (Neocalamites), ferns (*Cladophlebis*) and ginkgophytes (*Sphenobaiera*) (Boersma and Van Konijnenburg–van Cittert 1991).

Extensive palynostratigraphic studies of Norian and Rhaetian marine deposits have been undertaken in Western Caucasia. Yaroshenko (2007) noted strong similarities between the Rhaetian palynofloras of this region and the Rhaetipollis germanicus-Ricciisporites tuberculatus Zone of Western Europe, particularly in the abundance of Ricciisporites tuberculatus (87%) with abundant Rhaetipollis germanicus. The palynoflora from the Salgir Formation of the Crimean Peninsula (Bolotov et al. 2004) closely resembles that of western and eastern Ciscaucasia (Yaroshenko 2007). The Triassic deposits of southern Kazakhstan have yielded *Deltoidospora* spp., Dictyophyllidites spp., *Kyrtomisporites* speciosus, Chasmatosporites among others (Table 13.2) but lack the characteristic Rhaetian taxa Riccisporites tuberculatus and Rhaetipollis germanicus (Vinogradova and Tsaturova 2005).

The *Thuringiatriletes* Assemblage Zone (Table 13.2) typifies the Norian deposits of the Siberian Platform. This assemblage is characterized by the high abundance of Thuringiatriletes microverrucatus and Zebrasporites laevigatus and its cooccurrence with Cingulatisporites bulbifera and Camptotriletes echinatus (Odintsova 1977). The Rhaetian strata of the Donets Basin are characterized by Triancoraesporites ancorae, *Cornutisporites* seebergensis, Т. reticulatus. Zebrasporites laevigatus, Z. interscriptus, Cingulatizonates insignis, Ricciisporites tuberculatus and Limbosporites spp. (Semenova 1970, 1973). The most typical forms in the Norian and Rhaetian assemblages of Siberia are representatives of typical European genera. such as Cingulatizonates, Chasmatosporites, Lycopodiumsporites, Ovalipollis, Tigrisporites, Zebrasporites, Aratrisporites, and Triancoraesporites ancorae, along with numerous saccate pollen grains of gymnosperms (Odintsova 1977; Yaroshenko 2007).

Romanovskaya and Vasilieva (1990) proposed two miospore associations for the European sector of Russia (Table 13.2). The lower miospore assemblage includes *Circulina* spp., *Punctatosporites walkomii, Dictyophyllidites* spp., *Cingulizonates* spp., *Camarozonotriletes rudis*, whereas the upper assemblage includes *Dictyophyllidites* spp., *Ricciisporites tuberculatus*, *Chasmatosporites* spp. and *Triancoraesporites*.

#### 13.5 Late Triassic Floras of China and Eastern Asia

The first studies of Late Triassic floras from this region were carried out by European scholars, such as Schenk (1883, 1884) and von Richthofen (1882), working on the Upper Triassic Xujiahe (=Hsuchiaho) Formation in Guangyuan (northern Sichuan Basin). In the early to mid-twentieth century, Sze (1933) and Sze and Lee (1952) published on the fossil flora of the Sichuan Basin, followed later by Yang (1978) and Hsü et al. (1979).

The Late Triassic floras of China (Figs. 13.1 and 13.4, Table 13.1) can be segregated into Southern-type floras (=Southern East Asia Subprovince; i.e.,

Dictyophyllum-Clathropteris flora) and Northern-type floras (=Northern East Asia Subprovince; i.e., *Danaeopsis-Bernouillia* [=Symopteris] flora), which correspond to the southern and northern China tectonic regions, respectively. Floras of the Southern East Asia Subprovince are widely distributed in South China, extending south to Indonesia and north to a small area of eastern northeast China. This subprovince is mainly represented by the Xujiahe (Hsuchiaho) flora (Li 1964; Ye and Liu 1986) and Baoding flora of Sichuan (Hsü et al. 1979), the Shaqiao flora of Hunan (Zhou 1989) and the Tiangiaoling flora of Jilin (Sun 1993). The Southern East Asia Subprovince can be divided into three suites based on their distinctive floristic characters (see below) with age constraints provided by associated marine fossil faunas. The Northern East Asia Subprovince is widely distributed in North China, southern Northeast China and northern Northwest China. The floras are represented by the Yenchang (Yanchang) flora of northern Shaanxi (P'an 1936; Sze 1956a; Huang et al. 1980) and the Xiaohekou flora of Hunjiang (Jilin: Mi 1977), among others (Table 13.1). Unfortunately, it has so far been impossible to assign these floras to different stages with confidence. The boundary between the two floristic subprovinces follows a rough line from Kuga in Xinjiang to Nanzhang in Hubei (Li et al. 1991). Mixed assemblages characterized by elements of both the Southern East Asia Subprovince and Northern East Asia Subprovince exist close to this line.

High-resolution stratigraphical schemes are presently lacking for the Chinese terrestrial successions. This is mainly due to the enormous thicknesses of strata, making detailed palynostratigraphy an expensive and time-consuming task. However, pollen and spore assemblages have been employed for broad-scale stratigraphic and palaeoenvironmental reconstructions. A general feature of the Carnian and Norian assemblages is the abundant occurrence of *Dictyophyllidites harrisii*, *Alisporites* spp., *Cyclogranisporites* spp. and in places *Aratrisporites* spp. (Peng et al. 2017b).

No reliably dated Late Triassic plants have yet been found in southern Tibet, although some poor coal layers are present in the Norian Langjixue Group of Xiukang, south of the Yarlung Zangbo River (Sun 1993). However, Peng et al. (2017a) recovered Upper Triassic palynoassemblages from mostly marine strata at Tulong, Nyalam County, southern Xizang (Tibet), that are referable to three Middle to Late Triassic zones more characteristic of the Gondwanan Onslow Subprovince: viz., the Staurosaccites quadrifidus Assemblage Zone (late Anisian to early Norian), the Dictyophyllidites harrisii Assemblage Zone (early Norian), and the Craterisporites rotundus Assemblage Zone (middle to late Norian). This region of southern Tibet was part of Gondwana during the Late Triassic. The local palynoflora reveals a marked rise of Classopollis (Cheirolepidiace) pollen in the Rhaetian that might reflect a more xeric vegetation under a torrid and arid (or subarid) climate in this region compared with other parts of China. Adjacent regions of southern Tibet (Lhasa Block) and central Tibet (Qiangtang Block) belong to the Cimmerian terranes but have not yet yielded productive Late Triassic palynofloras. Further studies will be required to assess whether their phytogeographic affinities lie more closely with Gondwana or with the Southern East Asian terranes.



Plate 13.4 Upper Triassic plants from China. (a) *Clathropteris platyphylla*, Zigui, Hubei, China, Carnian. (b) *Gleichenites* sp. cf. *G. nitida*, Nanzhang, Hubei, China, Carnian. (c) *Anthrophyopsis* sp., Guangyuan, Sichuan, China, Norian. (d) *Symopteris (Bernoullia) zeilleri*, Jimusaer, Xinjiang, China, Carnian. (e) *Clathropteris meniscioides*, Hechuan, Chongqing, China, Norian. (f) *Dictyophyllum* sp. cf. *D. nathorstii*, Lufeng, Yunnan, China, Norian. (g) *Symopteris (Bernoullia)* sp., Jimusaer, Xinjiang, China, Carnian. (h) *Danaeopsis fecunda*, Jimusaer, Xinjiang, China, Carnian. Scale bar = 10 mm in each image

Also of Late Triassic age, although not more precisely dated, are some remains of *Leptostrobus* from the Amisan Formation and wood remains (*Agathoxylon*, *Cedroxylon*, *Phyllocladoxylon*, *Xenoxylon*) from the Nampo Group of Korea. The Daedong flora of Korea includes rich assemblages of sphenophytes (*Neocalamites*), ferns (*Clathropteris*, *Dictyophyllum*, *Hausmannia*, *Todites*), seed ferns (*Ctenozamites*), cycads/bennettitaleans (*Anomozamites*, *Ctenis*, *Nilssonia*, *Otozamites*, *Pseudoctenis*, *Pterophyllum*, *Taeniopteris*), ginkgophytes (*Baiera*, *Sphenobaiera*), Czekanowskiales (*Czekanowskia*) and conifers (*Cycadocarpidium*, *Elatocladus*, *Podozamites*) (Yabe 1905; Kawasaki 1925, 1926, 1939; Kimura and Kim 1984, 1988, 1989; Kim and Kimura 1988; Kim 1989, 1993; Kim et al. 2002, 2005).

#### 13.5.1 Carnian Floras of China and Eastern Asia

Carnian deposits of the Southern East Asia Subprovince (Figs. 13.4 and 13.6, Table 13.1) host plant assemblages attributed to the *Abropteris-Pterophyllum longi-folium* Flora ('Assemblage'). This flora incorporates plant assemblages from the Daqiaodi Formation of Yongren, Yunnan and Yunnan-Sichuan border area, the Jiuligang Formation of Nanzhang, Hubei, and the Jiapeila Formation of Tibet (Zhou and Zhou 1983; Meng 1983, 1990). The flora includes the sphenophyte *Equisetites*, the ferns *Abropteris, Yungjenophyllum, Asterotheca, Miscopteris, Stenopteris, Angiopteris Clathropteris* (Plate 13.4a) and *Danaeopsis* (Plate 13.4h), the seed ferns *Sagenopteris, Thinnfeldia* and *Ctenozamites*, and the cycads/bennettitaleans *Pterophyllum* and *Paradrepanozamites*. The assemblage bears some resemblance to the Carnian Schilfsandstein flora of Western Europe (Zhou and Zhou 1983).

The Indonesian Carnian flora is dominated by sphenophytes (Kon'no 1972; Vakhrameev et al. 1978; Annulariopsis, Neocalamites, Neocalamostachys), ferns (Clathropteris, Dictyophyllum, Cladophlebis, Todites) and cycads/bennettitaleans (Dictyozamites, Otozamites). Carnian floras are also known from Japan; i.e., the Yamaguti plant assemblages from the Momonoki and Aso formations of the Mine Group (Ôishi 1932a, b, 1940; Ôishi and Takahashi 1936; Takahashi 1951). The ferns (Cladophlebis, Clathropteris, Todites), conifers (Podozamites) and cycads/ bennettitaleans (Cycadocarpidium, Nilssonia, Taeniopteris) are the most abundant groups, whereas sphenophytes (Neocalamites, Equisetites, Equisetostachys) are rare (Volynets and Shorokhova 2007).

## 13.5.2 Norian Floras of China and Eastern Asia

Norian deposits of the East Asia Subprovince (Figs. 13.1, 13.4, and 13.6, Table 13.1) host the Dictyophyllum-Drepanozamites flora ('Assemblage') or the Dictyophyllum-Cycadocarpidium flora ('Assemblage') (Sun 1987). These floras are represented mainly by the fossil assemblages of the Hsuchiaho (Xujiahe) Formation of Sichuan, the Daqing Formation of the Sichuan-Yunnan border area, the Anyuan Formation of Hunan and Jiangxi, the Badong Formation of eastern Tibet, the Dakeng Formation of Fujian and the Malugou Formation of Tianqiaoiin (Jilin) (Sun 1987). The main elements of the flora are ferns (e.g., Clathropteris Plate 13.4e, Dictyophyllum Plate 13.4f, Hausmannia, Reteophlebis, Gleichenites Plate 13.4b), cycads/bennettitaleans Cycadocarpidium, Doratophyllum, (e.g., Anomozamites, Drepanozamites, *Pterophyllum*) and conifers (e.g., *Podozamites*). The bennettitaleans are particularly diverse and, among the ferns, Dipteridaceae is especially abundant. Sphenophytes are also abundant but of low diversity. Conifers are rare and represented mainly by large-leafed taxa (e.g., Ferganiella and Podozamites). Ginkgophytes are represented by some species of Glossophyllum and the Czekanowskiales by Czekanowskia (Wang et al. 2010).
These Norian floras closely resemble the Nariwa flora of Japan and some coeval floras of Eurasia (Zhou and Zhou 1983; Volynets and Shorokhova 2007). The Nariwa flora includes abundant ferns (*Cladophlebis, Goeppertella, Marattiopsis, Thaumatopteris*) and cycads/bennettitaleans (*Nilssonia, Otozamites, Pterophyllum, Taeniopteris*); sphenophytes (*Annulariopsis, Neocalamites*), ginkgophytes (*Baiera, Ginkgoites, Sphenobaiera*), seed ferns (*Ptilozamites, Sagenopteris*), conifers (*Pityophyllum, Elatocladus, Pityophyllum, Podozamites*) and Czekanowskiales (*Ixostrobus*) are rare (Ôishi 1932a; Ôishi and Takahashi 1936; Volynets and Shorokhova 2007).

## 13.5.3 Rhaetian Floras of China and Eastern Asia

Rhaetian successions of eastern Asia are typified by the Ptilozamites-Anthrophyopsis flora ('Assemblage') from the Yangbaichong Formation of Shaqiao (Hunan; Zhou 1989), which contains mainly Clathropteris, Cycadocarpidium, Nilssoniopteris, Pterophyllum, Ptilozamites, Podozamites, Stalagma and Todites (Figs. 13.1, 13.4, and 13.6, Table 13.1). This flora resembles closely that of the Lepidopteris Zone of eastern Greenland and Germany. The Sanqiutian Formation flora of the Anyuan Group (Jiangxi) and the Wenbinshan flora of Fujian also have similar content (Zhou 1978). Recently, some plants were found from the Dongfeng area (Jilin) in which Anthrophyopsis (Plate 13.4c) occurs associated with Neocalamites and Cycadocarpidium; these fossils may represent a Rhaetian assemblage. Floras of the Northern East Asia Subprovince cannot be attributed confidently to any stage. They contain more than 100 species belonging to about 50 genera whose main representatives are the sphenophyte Equisetites, the ferns Danaeopsis, Bernouillia (=Symopteris) and Todites, the seed fern Thinnfeldia, the ginkgophytes Glossophyllum, Ginkgoidium and Ginkgoites and the cycads/bennettitaleans Sinozamites and Sphenozamites (Zhou and Zhou 1983).

Rich Rhaetian floras with abundant sphenophytes (*Annulariopsis, Equisetites, Neocalamites*), ferns (*Cladophlebis, Clathropteris, Dictyophyllum, Marattiopsis, Sphenopteris, Todites*), seed ferns (*Sagenopteris*), cycads/bennettitaleans (*Ctenis, Nilssonia, Pterophyllum, Taeniopteris*), ginkgophytes (*Baiera*) and conifers (*Cycadocarpidium, Elatocladus, Podozamites*) were also described from Tonkin, Vietnam (Zeiller 1903; Akagi 1954) and Japan (Ôishi 1930, 1931, 1932a, b; Ôishi and Takahashi 1936). The cycads/bennettitaleans and conifers in these assemblages closely resemble those of the middle Norian flora of the Primorye region (Volynets and Shorokhova 2007).

Based on palynology of the Junggar Basin, Northwestern China (Sha et al. 2011, 2015), the Triassic–Jurassic boundary is placed at the last appearance datum of the pollen taxon *Lunatisporites rhaeticus*. The transition is characterized by a turnover from a vegetation dominated by lycophytes (*Aratrisporites*-producers) and seed ferns (*Alisporites*-producers) to an Early Jurassic flora dominated by *Lycopodiumsporites*-producers, Taxodiaceae (*Perinopollenites*) and Pinaceae (*Pinuspollenites*).

## 13.6 Late Triassic Floras of the Southern Hemisphere

The Late Triassic floras of those southern landmasses (Figs. 13.1, 13.5, and 13.6, Table 13.1) that were formerly united into the supercontinent Gondwana are characterized by broad compositional similarities at generic and, in some cases, specific level (Retallack 1987; Srivastava and Manik 1991; Anderson et al. 1999; Hill et al. 1999; Artabe et al. 2003; Escapa et al. 2011; and references therein). The Late Triassic saw the climax of the Dicroidium-dominated flora of Gondwana-a floristic association that had essentially supplanted the *Glossopteris* flora in diversity and geographic extent across the middle and high latitudes of the Southern Hemisphere after the end-Permian mass extinction (McLoughlin 2001, 2011). Despite the wide distribution and richness of austral Late Triassic floras (Figs. 13.1 and 13.6, Table 13.1), most data comes from a few well-studied assemblages that are widely separated within the former supercontinent. Moreover, the scarcity of marine strata and radiometrically dated ash beds intercalated with the plant-bearing intervals in Gondwana has greatly hindered precise dating of many Late Triassic plant assemblages in that region. This overview of the Gondwanan Late Triassic floras outlines the general representation of plant groups and broad-scale geographic and temporal variations in the palaeovegetation. Foremost among the sources of data for this overview is the series of monographs dealing with the Molteno Formation flora of South Africa produced by Anderson and Anderson (1983, 1985, 1989, 2003, 2008), which also incorporates data from other southern continents.

## 13.6.1 Carnian Floras of the Southern Hemisphere

Carnian floras are well represented across Gondwana, although in some areas they have been inadequately studied. By far the richest and best-studied Gondwanan Carnian flora is that of the Molteno Formation of the Karoo Basin, South Africa, from which some 30,000 catalogued rock slabs have been recovered from around 100 assemblages. From this vast collection, Anderson and Anderson (1983, 1985, 1989, 2003, 2008, in press) have documented over 200 species of vegetative organs. Based on a generalized inverse Gaussian-Poison distribution of fossil records, they estimated that the identified fossil diversity equates to an original vegetation containing over 2000 species of plants. Foremost among the constituents of the Molteno Formation flora are the remains of Umkomasiales (=Corystospermales), particularly the foliage attributed to various species of *Dicroidium* (Plate 13.5c-e). Of the 21 species of *Dicroidium* recognized throughout the Triassic of Gondwana, at least seven occur in the Carnian of the Karoo Basin. Remains of these species typically constitute more than 90% of specimens in leaf-dominated assemblages. Moreover, leaves attributed to several other taxa across Gondwana (viz., Johnstonia, Dicroidiopsis, Diplasiophyllum, Zuberia, Xylopteris, Tetraptilon and Hoegia) undoubtedly belong in *Dicroidium* on the basis of consistency in leaf architecture,



Plate 13.5 Upper Triassic plants from Gondwana. (a) Rissikia media, Mount Bumstead, Antarctica, Late Triassic. (b) Heidiphyllum elongatum, leaf with arthropod piercing-and-sucking damage (arrowed), Transantarctic Mountains, Antarctica, Late Triassic. (c) Dicroidium dutoitii, Allan Nunatak, Australia, Late Triassic. (d) Dicroidium odontopteroides, Dinmore, Ipswich Basin, Australia Carnian-Norian. (e) Dicroidium elongatum, Birds River, Karoo Basin, South Africa, Carnian. (f) Scytophyllum neuburgianum, Argentina, El Tranquilo Group, Carnian. (g) Rochipteris etheridgei, Leigh Creek Coal Measures, Telford Basin, Australia, ?Carnian. (h) Equisetites sp., Birds River, Karoo Basin, South Africa, Carnian. (i) Dictyophyllum rugosum, Ipswich Basin, Australia, Carnian–Norian. (i) Lepidopteris stormbergensis Birds River, Karoo Basin, South Africa, Carnian. (k) Thalloid liverwort (Hepaticopsida); Barbers Mine, Fingal, Tasmania, Late Triassic. (l) Sphenobaiera schenkii, Birds River, Karoo Basin, South Africa, Carnian. (m) Linguifolium tenisonwoodsi, Dinmore, Ipswich Basin, Australia, Carnian-Norian. (n) Taeniopteris lentriculiformis, Dinmore, Ipswich Basin, Australia, Carnian-Norian. (o) Seed of Fanerotheca papilioformis, Birds River, Karoo Basin, South Africa, Carnian. (p) Umkomasia simmondsii, Dinmore, Ipswich Basin, Australia, Carnian–Norian. (q) Pteruchus minor Slacks Creek, Ipswich Basin, Australia, Carnian– Norian. (r) Single cupule of Hamshawvia longipedunculata, Denmark Hill, Ipswich Basin, Australia, Carnian-Norian. (s) Fredlindia moretonensis, Denmark Hill, Ipswich Basin, Australia, Carnian-Norian. (t) Asterotheca sp., Dinmore, Ipswich Basin, Australia, Carnian-Norian. (u) Antevsia mazenodensis, Dinmore, Ipswich Basin, Australia, Carnian–Norian. Scale bar = 10 mm in each image



Fig. 13.5 Areas with major Upper Triassic plant assemblages in the Southern Hemisphere and India (Gondwana)

venation style, cuticular micromorphology and examples of hybridism (Anderson and Anderson 1983). Such examples of taxonomic inflation may account for relatively high apparent generic diversity in some Late Triassic Gondwanan assemblages (Colombi and Parrish 2008; Pattemore 2016a, b).

Among other gymnosperms that co-dominate or are important components of the Molteno Formation flora in terms of relative abundance are Peltaspermales (Lepidopteris: Plate 13.5), Ginkgoales/Hamshawviales (Ginkgo, Sphenobaiera: Plate 13.51), voltzialean and pinalean conifers (Heidiphyllum and associated genera: Plate 13.5b), and Matatiellales (*Dejerseya* and possibly *Linguifolium*: Plate 13.5m). Various other enigmatic seed fern families (e.g., Petriellales Plate 13.5g, Alexiales, Hlatimbiales), putative podocarp and pinalean conifers (e.g., Pagiophyllum, Rissikia: Plate 13.5a), Bennettitales (Halleyoctenis), Pentoxylales (Taeniopteris: Plate 13.5n), Gnetopsida (Gontriglossa, Yabeiella and related taxa) and Cycadales (Pseudoctenis, Jeanjacquesia) represent subordinate gymnospermous components of the Carnian flora. Extensive and detailed documentation of physical attachments and organ associations has enabled confident linkages between the various dispersed sterile and fertile parts (Plate 13.50-u) belonging to many of the plant groups represented in this flora (Anderson and Anderson 1989, 2003). Sphenophytes are represented by eight genera and 23 species of fertile and sterile organs (mostly schizoneurid and equisetacean genera; Plate 13.5h) in the Molteno Formation flora. They are locally abundant, especially in lake-margin and floodplain wetland facies. Ferns are represented by around 16 genera and 37 species in this flora (dominantly members of Osmundaceae and Dipteridaceae; Plate 13.5i, t) and represent rare to moderately common elements of the Carnian understorey vegetation. Bryophytes



nofloras (after Foster et al. 1994; Césari and Colombi 2013). Note: NEA and SEA are commonly referred to as Northern and Southern Floristic Region of Fig. 13.6 Palaeogeographic map showing floral zonation in the Late Triassic. Distribution of Onslow Subprovince and Ipswich Subprovince based on paly-China, respectively. Basemap: PALEOMAP Project, C. R. Scotese, Arlington, Texas, USA

(Plate 13.5k) and lycophytes are rare components of this fossil flora, although this may be an artefact of poor preservational potential owing to their diminutive size and soft tissues.

Elsewhere in Gondwana, Carnian plant assemblages show strong similarities to the Molteno Formation flora in terms of taxonomic representation (at least at generic level) and relative group abundance. Any deviations appear to be linked mostly to differences in depositional environment and less intense sampling. In Argentina, Spalletti et al. (1999) assigned the bulk of Carnian-age plant assemblages to their Yabeiella brackebuschiana-Scytophyllum neuburgianum-Rhexoxylon piatnitzkyi (BNP) Biozone. This biozone differed little in generic representation and relative abundance from the preceding (Middle Triassic) flora, but its inception was marked by the turnover in key species of Scytophyllum (Peltaspermales; Plate 13.5f) and Yabeiella (?Gnetales) (Morel et al. 2003). Key Gondwanan floras of this age outside South Africa include those of the Blackstone Formation and Red Cliff Coal Measures in Australia (Walkom 1917; Jones and de Jersey 1947; Flint and Gould 1975) and Brady Formation and New Town Coal Measures in Tasmania (Johnston 1886, 1887, 1894, 1896). In Argentina, Carnian floras are known from the Barreal and Cortaderita formations in the Barreal Basin (Bonetti 1963), the Ischigualasto Formation in the Ischigualasto Basin (Archangelsky 1968), the Potrerillos Formation in the Cuyo Basin (Jain and Delevoryas 1967; Spalletti et al. 2005) and the El Tranquilo Group in southern Argentina (Jalfin and Herbst 1995; Crisafulli and Herbst 2011). Additional Carnian floras in South America come from the Quilacoya Member in Chile (Nielsen 2005) and the Santa Maria Formation (Paraná Basin) in Brazil (Barboni and Dutra 2015; Barboni et al. 2016). In Antarctica, the Lashly, Falla and Section Peak formations all possibly extend from the Carnian to the Norian or Rhaetian (Bomfleur et al. 2011b, 2012, 2013a, b, 2014a, b; Escapa et al. 2011).

Palynology is the main tool for dating the Upper Triassic continental successions and half a century of intensive palynological investigations related mainly to hydrocarbon prospecting have resulted in the development of detailed palynostratigraphical schemes particularly for Australia (De Jersey 1975; Helby et al. 1987; Price 1997). As a consequence of the initiation of Pangean break-up and more latitudinally differentiated climate regimes, floristic provincialism became more pronounced in the Late Triassic resulting in two Gondwanan palynofloral provinces and a zone of intermediate or transitional assemblages (Table 13.2). The so-called Ipswich 'Microflora' represents the Late Triassic southern polar vegetation; these temperate floras spanning present-day eastern Australia, New Zealand and most of Antarctica (de Jersey and Raine 1990; Farabee et al. 1990; Zhang and Grant-Mackie 2001). The warm temperate Carnian floras belong to the Onslow 'Microflora' represented and extending across northern Australia (including Timor), along the western Tethys coasts, to westernmost Gondwana. The Onslow Microflora is distinguished by its higher diversity and a greater number of species shared with the Tethyan region. Consequently, different palynostratigraphical zonation schemes exist for these subprovinces (Table 13.2). Importantly, some Australian Carnian successions incorporate shallow marine strata allowing correlation with dinoflagellate, conodont and ammonite zones (Helby et al. 1987).

The Carnian successions in Western Australia are represented by the *Samaropollenites speciosus* Oppel Zone (Helby et al. 1987; Fig. 13.4) and dominated by the *Falcisporites* pollen complex, probably produced by *Dicroidium* (Umkomasiales [=Corystospermales]) plants. This zone is correlated with the *Craterisporites rotundus* Zone (Table 13.2) in deposits of eastern and southern Australia, New Zealand and parts of India and China. The latter zone is defined on the FAD of the nominal taxon and characterised by the high relative abundances of the bisaccate pollen *Falcisporites australis* and the fern spore taxon *Striatella seebergensis*.

Argentinean Carnian continental deposits are world renowned for hosting important vertebrate fossils and a need for accurate dating has spurred interest in palynological studies of these successions. The Paso Flores and Comallo formations in northern Patagonia host assemblages of late Carnian-early Norian age, which are coeval with those of the Craterisporites rotundus Oppel Zone of eastern Australia (Zavattieri et al. 1994; Zavattieri and Mego 2008). These assemblages are characterized by the absence of typical Tethyan taxa otherwise present in the Onslow Microflora. However, in the light of new results from the Ischigualasto Formation, this might be re-evaluated by future high-resolution studies. The Ischigualasto Formation is one of the few South American continental Triassic units constrained by reliable radioisotopic dating. Dated beds from near the base and top of the unit yield ages of ~231.4 and ~225.9 Ma, respectively (Rogers et al. 1993; Martínez et al. 2011), placing the formation in the upper Carnian to lower Norian (Fig. 13.3). New palynological results from the Ischigualasto Formation (Césari and Colombi 2016) reveal the presence of typical Tethyan taxa showing that spore-pollen suites from westernmost Gondwana belong to the warm temperate Onslow palynoflora and not to the Ipswich palynoflora (Césari and Colombi 2013). This assignment is evidenced by the presence of pollen and spores previously found only outside *Cadargasporites* granulatus, Argentina, such as *Cycadopites* stonei, Enzonalasporites vigens, Ovalipollis pseudoalatus, O. ovalis, Patinasporites densus, Quadraeculina anellaeformis, Samaropollenites speciosus and Staurosaccites quadrifidus.

## 13.6.2 Norian Floras of the Southern Hemisphere

Although the Norian spans more than 18 million years on the current international chronostratigraphic chart (Cohen et al. 2013), surprisingly few macrofloras of this age have been documented from Gondwana (Table 13.1). In part, this may be a consequence of poor age constraints on many of the assemblages, such that any newly discovered macroflora having broad similarities to that of the Molteno Formation is automatically assigned to the Carnian. Exceptions to this are the macrofloras of the Cacheuta Formation in Argentina (Cuyo Basin: Frenguelli 1948, Morel et al. 2011), the Tiki Formation in India (Maheshwari et al. 1978, Srivastava and Pal 1983; Pal 1984), and the Flagstone Bench Formation in East Antarctica (Cantrill et al. 1995; McLoughlin and Drinnan 1997; McLoughlin et al. 1997). It is possible that part of

the well-studied Blackstone Formation of the Ipswich Basin, eastern Australia, also extends to the Norian based on palynostratigraphic data (de Jersey 1975; Helby et al. 1987). However, Pattemore (2016b) has argued that one of the key assemblages from the Ipswich Basin (the Dinmore assemblage) traditionally assigned to the Blackstone Formation may instead derive from the underlying Tivoli Formation (Carnian). Other plant-rich units across Gondwana may also be of Norian age, based on palynostratigraphic dating, but their macrofossil floras have not yet been investigated in detail. Examples of these include portions of the Leigh Creek Coal Measures preserved within the Copley and Telford basins of central South Australia (Barone-Nugent et al. 2003), the upper part of the Tarong Coal Measures of southern Queensland (Jell 2013; Pattemore 2016a), and the lower part of the Callide Coal Measures of central Queensland (Australia: Jell and McKellar 2013).

Norian macrofossil floras from Gondwana, like those of the Carnian, are dominated by the remains of Umkomasiales and voltzialean conifers. A broad range of accessary gymnosperms, ferns and sphenophytes are also present in these floras. Clubmosses remain scarce as macrofossils, but diverse assemblages of megaspores in strata of this age attest to a rich but cryptic representation of herbaceous heterosporous lycophytes (Dettmann 1961; Cantrill and Drinnan 1994) that, as a group, persisted into the Jurassic as subsidiary elements of the vegetation (McLoughlin et al. 2014). In Argentina, the *Dicroidium odontopteroides-D. lancifolium* (OL) Biozone of Spalletti et al. (1999) probably equates to the Norian. The nominal species reach their acme in this biozone, whereas other Umkomasiales, and most other seed-plants, become subordinate, with the exception of *Yabeiella*, which persisted with equivalent abundance from the preceding biozone (Morel et al. 2003).

The most studied Norian palynological assemblages in Gondwana are those of Australia. There, detailed and well-dated spore-pollen zonation schemes have been tied to dinoflagellate zonations. In eastern Australia, Norian palynofloras are represented by the '*Aratrisporites* Assemblage' which includes the *Polycingulatisporites crenulatus* Zone in its upper part, the same zone that represents this interval in New Zealand (Table 13.2). The base of the *P. crenulatus* Oppel Zone is characterized by the FAD of *P. crenulatus* and a decline in abundance of the previously dominant bisaccate *Falcisporites*, together with a significant increase in *Classopollis* species. In Western Australia, the Norian warm temperate Onslow flora is represented by the *Minutosaccus crenulatus* Oppel Zone (Table 13.2) characterized by a decline in typical Tethyan taxa, such as *Enzonalasporites vigens* and *Samaropollenites speciosus*.

#### 13.6.3 Rhaetian Floras of the Southern Hemisphere

Rhaetian floras are poorly documented from the Gondwanan continents (Table 13.1). Spalletti et al. (1999) attributed latest Triassic floras (Los Colorados Formation and equivalents) of Argentina to their *Dictyophyllum tenuiserratum-Linguifolium arctum-Protocircoporoxylon marianaensis* (DLM) Biozone. They noted the importance of *Linguifolium* and voltzialean conifers associated with the last occurrences of *Dicroidium* in this zone. They also reported initial sporadic occurrences of

cheirolepid conifers, together with osmundacean and dipteridacean ferns of Jurassic aspect in this interval. Other plant fossil assemblages possibly of Rhaetian age occur in Chile (La Ternera and El Puquen floras: Solms-Laubach 1899; Brüggen 1918; Herbst and Troncoso 2000), India (Parsora Formation: Bose 1974; Pal 1985; Ghosh et al. 2016), and eastern Australia (Raceview Formation and Aberdare Conglomerate: Jell 2013; Jell et al. 2013), but precise age constraints are scarce. In general, these floras are consistent with the Argentine assemblages in hosting the last representation of *Dicroidium* and *Linguifolium* before an influx of cheirolepid conifers and bennettitaleans at the Triassic–Jurassic transition. The upper part of the Callide Coal Measures in eastern Australia apparently hosts a rich Rhaetian flora but, to date, only a few species (e.g., *Dicroidium feistmantelii, Taeniopteris taeniopteroides*) have been documented (Pattemore 2016b).

Some regions, such as New Zealand and New Caledonia, possibly host Rhaetian floras that are potentially important for understanding the structure of the maritimeinfluenced vegetation along the Panthalassan margin at the end of the Triassic. However, these floras remain poorly studied and dated. The few Triassic plant remains recorded from New Caledonia are mostly represented by coniferous/pteridospermous fossil woods from the Moindou and Baie de St. Vincent regions (Loubiere 1936; Lanteaume 1950; Boureau 1954, 1955, 1957; Salard 1968; Vozenin-Serra and Salard-Cheboldaeff 1992). The ages of these fossil woods are poorly constrained, although some from the Moindou region are probably Carnian-Norian rather than Rhaetian in age. Others, previously considered Triassic, may be as old as Permian (Vozenin-Serra and Salard-Cheboldaeff 1992). Retallack (1985) described Smithian to Rhaetian floras of the Murihiku Supergroup from the Southland Syncline (Southland) and the Kawhia Syncline (North Island). These constitute mostly fragmentary foliage impressions preserved in marine sediments, but are otherwise similar to coeval assemblages from eastern Australia. A total of 54 plant macrofossil taxa have been identified from the New Zealand Triassic and, as in other Gondwanan regions, the makeup of individual assemblages appears to be strongly influenced by local sedimentary facies and the environmental setting of the parent flora within regional-scale depositional tracts (Retallack 1987).

This dearth of studies on Gondwanan Rhaetian floras is unfortunate given their importance in assessing floristic changes across the Triassic–Jurassic boundary. Palynological data provide the best insights into changes in the vegetation at the close of the Triassic.

Australian and New Zealand Rhaetian palynofloral successions are dominated by *Falcisporites* species and *Densoisporites psilatus* together with a range of ornate trilete spores (Zhang and Grant-Mackie 2001; Akikuni et al. 2010). The appearance of *Classopollis* in the lower part of the local New Zealand stage Otapirian has, traditionally, been used to correlate this stage to the Rhaetian (Marwick 1953). This feature is consistent with the increase in relative abundance in the Circumpolles Group, and specifically *Classopollis*, in the Northern Hemisphere, while many of the characteristic Triassic palynotaxa declined dramatically across the T–J boundary in the New Zealand succession (de Jersey and Raine 1990) as they do globally. The Triassic–Jurassic transition in both Australia and in New Zealand is character-

ized by a marked increase in the proportion of Classopollis and Perinopollenites pollen and a great decline of Falcisporites suggesting that Umkomasiaceae were replaced by Cheirolepidiaceae and Cupressaceae as the dominant arborescent components of the vegetation (Helby et al. 1987; Burger 1994; de Jersey and Raine 1990; Akikuni et al. 2010; de Jersey and McKellar 2013). There were also significant changes in the understorey components of the vegetation evidenced by the loss of several key Triassic fern/bryophyte spore taxa and the replacement among the lycophytes of Densoisporites by Retitriletes (de Jersey and Raine 1990; Zhang and Grant-Mackie 2001; Akikuni et al. 2010). The regional Rhaetian palynological zonations differ in that the Western Australian zonation scheme includes the transitional Triassic-Jurassic boundary Ashmoripollis reducta Oppel Zone (extending through the basal Hettangian; Table 13.2) characterized by the consistent presence of the very distinctive nominal taxon and the FAD of Zebrasporites interscriptus. In eastern Australia, the equivalent interval is represented by the upper part of the Polycingulatisporites crenulatus Zone and in New Zealand by the Foveosporites moretonensis Zone (Table 13.2), representing the local Otapirian stage, and followed by the Hettangian Retitriletes austroclavatidites Zone. In both Australian provinces, most of the Hettangian is represented by the *Classopollis torosus* Zone and the differences between New Zealand and Australia are probably due mainly to alternative taxonomic approaches by the palynologists working on the respective floras because the palynofloras from the Hettangian onwards are very similar in Australia and New Zealand and consistently include both Classopollis and Retitriletes species (Vivi Vajda pers. obs.).

As yet, no study has undertaken a detailed assessment of the contemporaneous plant macrofossil turnover at the T–J transition in Gondwana but, on a broad scale, the dominant elements of the Late Triassic flora (viz., *Dicroidium, Lepidopteris, Heidiphyllum, Linguifolium, Dejerseya, Yabeiella*) are entirely absent from the Early Jurassic floras (Hill et al. 1999; Anderson et al. 1999). They are replaced in the Early Jurassic by floras dominated by scale-leafed cheirolepid and araucarian conifers, Bennettitales, Caytoniales and Pentoxylales (Gould 1975; Tidwell et al. 1987; McLoughlin and Hill 1996; Bromfield et al. 2007; McLoughlin and Pott 2009; Bomfleur et al. 2011a; Pattemore 2016b). This change attests to a major extinction and reorganization of plant communities around the Triassic–Jurassic boundary, a change also apparent in the palynofloras (Helby et al. 1987). From this time onwards until the rapid fragmentation of Gondwana in the Cretaceous, a world emerges with a more homogenous (cosmopolitan) flora.

## 13.7 Discussion

# 13.7.1 Climate Considerations

The climate of the Triassic in a general sense was warm with dry continental interiors and no polar icecaps. The aggregation of the Pangaean supercontinent (Figs. 13.1 and 13.6), which was completed during the Triassic, gave rise to a strong global monsoon regime (e.g., Robinson 1973; Mutti and Weissert 1995; Loope et al. 2004; Wang 2009). This generated three broad climatic regions with ill-defined latitudinal distributions. The tropical belt spanning the western margin of the Tethys Ocean and the central part of Pangaea, together with the horse latitudes (those atmospheric zones typified by subtropical highs) were characterized by a broad arid belt with dry conditions persisting throughout the entire year (Preto et al. 2010). The coasts of eastern Laurussia, Gondwana and the western coasts of Pangaea would have been subjected to seasonally wet and dry periods (Parrish and Peterson 1988; Dubiel et al. 1991; Mutti and Weissert 1995) and the more polar areas by warm and wet climates (evidenced by palaeosols and fossil floras up to 85°N and S; Robinson 1973; Taylor 1989; Retallack 1999; Kidder and Worsley 2004). However, other authors have suggested a more pronounced zonal climatic pattern with a narrow equatorial humid zone, an arid belt extending up to 30° and, beyond that, northwards and southwards humid temperate climates (e.g., Kent and Olsen 2000; Olsen and Kent 2000).

Climatic oscillations were superimposed on the general climate belts during the 50 million years of the Triassic. Humid episodes were experienced throughout the Triassic with the most pronounced documented during the Carnian. The increase in rainfall during the 'Carnian Pluvial Event' (CPE), documented worldwide, constitutes the most distinctive climate change within the Triassic (Gianolla et al. 1998; Hochuli and Frank 2000; Preto and Hinnov 2003; Hornung and Brandner 2005; Hochuli and Vigran 2010). This contributed to a suite of environmental changes and biotic turnover (Simms and Ruffel 1989, 1990; Simms et al. 1995) including an increase in deposition of coarse siliciclastics in the western Tethys (e.g., Schilfsandstein) and the development of coal seams (e.g., Lunz, Svalbard, Skåne, Australia, South Africa; e.g., Köppen and Wegener 1924). The different hypotheses providing a causal mechanism for this event include changes in atmospheric or oceanic circulation driven by plate tectonics (Hornung and Brandner 2005), a peak of the global monsoon due to maximum continental aggregation (Parrish 1993; Colombi and Parrish 2008) or triggering by the eruption of a large igneous province (e.g., Furin et al. 2006; Greene et al. 2009a, b; Preto et al. 2010 and ref. therein). The remainder of the Late Triassic seems to have been climatically stable. The trend from humid to arid observed, for example, in the Newark Basin, has been attributed to the northwards drift of the North American continent (Smoot and Olsen 1988; Kent and Olsen 2000; Olsen and Kent 2000). In contrast, the abrupt change from a humid climate to an arid climate in the desert southwest of the United States during the lower Norian Stage is thought by some to be the result of orogeny and elevation changes brought about by the uplift of the Cordilleran magmatic arc in eastern California (Nordt et al. in). However, some other indications exist for minor or regional climatic changes. This includes the shift from red-beds rich in gypsum or other aridity indices to plant-rich and coal-bearing paralic sediments in the early to mid-Rhaetian (Hallam 1985) as well as small late Carnian (Mazza et al. 2010; Tanner and Lucas 2007) and late Norian climate changes (Berra et al. 2010; Haas et al. 2012). The end-Triassic biotic crisis appears to have occurred at a time of relatively high humidity, especially in the northern Tethyan realm (Preto et al. 2010), in northern Europe (Vajda and Wigforss-Lange 2009) and in southern Gondwana based on the distribution of fluvial and paludal strata (Turner et al. 2009).

## 13.7.2 Floristic Provincialism

The Permian world initiating at the peak of the Late Palaeozoic Ice Age and terminating with marked global warming (Fielding et al. 2008) was characterized by strong floristic provincialism (Meyen 1987). That provincialism apparently became less pronounced after the end-Permian mass extinction. Essentially two floral provinces remained (Fig. 13.6), the Gondwana Province encompassing all regions in the Southern Hemisphere (together with at least part of the Cimmerian rifted terranes), and the Laurussian Province spanning the continental masses of the Northern Hemisphere, e.g. North America, Europe and Asia including China (Dobruskina 1994; Vakhrameev et al. 1970, 1978). An equatorial belt encompassing the northern regions of Gondwana (i.e., northern South America, North Africa and Arabia; Fig. 13.6) has yielded very little data with respect to Late Triassic plant macrofossils. This region provides considerable scope for future palaeobotanical research that will have a strong bearing on our understanding of the degree of taxonomic mixing between the two major floristic provinces of the Late Triassic.

The Late Triassic floras of the southern landmasses are rather uniform (see above), whereas the vegetation in the Northern Hemisphere was less homogeneous. Consequently, several floristic subprovinces are apparent in the latter region (Fig. 13.6), although linked by broad areas hosting mixed or 'transitional' floras. A North Atlantic sub-province was proposed for the coastal plains of southern Sweden (Skåne), eastern Greenland (Jameson Land) and northern central Europe (Poland: Reymanówna 1963; Harris 1926, 1931b; Pott and McLoughlin 2009; Pott 2014a). This subprovince was originally recognized based on Rhaetian floras, but was probably already established during the Carnian (Pott 2014b).

Vakhrameev et al. (1970, 1978) and Krassilov and Shorokhova (1975) divided Eurasia into two palaeolatitudinally distinct Late Triassic floristic regions that became more distinct during the Norian–Rhaetian. The northern area (Siberian palaeoprovince or Arctotriassic geoflora = Siberian Subprovince herein) was characterized by an extra-tropical, temperate climate and dominated by *Phoenicopsis*. The more southern, subtropical areas (historically referred to the European-Sinian palaeoprovince or Mediotriassic geoflora) were dominated by *Lepidopteris* and *Goeppertella*. Dobruskina (1994) proposed dividing these two floristic subprovinces into three zones or sectors delimited by longitude: (i) European (=North Atlantic/Central European Subprovince), (ii) Middle Asian (=Middle Asian Subprovince) and (iii) East Asian (=East Asian Subprovince) sectors. She considered these sectors to be centres of dominance or emergence and spread of the most important Late Triassic plant groups. The Middle-Asian Subprovince includes the Donets Basin, Fore-Caucasus, Kazakhstan and Southern Fergana, Southern Urals and Caspian Depression (Fig. 13.6) and is characterized by the dominance of peltasperms, presence of marattiacean ferns and Cycadocarpidiaceae and a lack of Dipteridaceae. The Siberian Subprovince (Fig. 13.6) comprises the Pechora Basin, Eastern Urals, and Eastern and Northern Siberia (Dobruskina 1994). The Northern and Southern East Asian subprovinces (Primorye included; Fig. 13.6) are characterized by numerous dipteridacean ferns and cycadocarpidiacean conifers during the Carnian; marattiacean ferns and peltaspermalean seed ferns are virtually absent from the East Asian sector. The North American continent is divided into the Chinle/Dockum Subprovince, the Arctic Canada Subprovince (with some shared characters with the Siberian floras), and the floras of the Newark Supergroup Subprovince (Fig. 13.6), which have characteristics shared with both the North Atlantic/Central European Subprovince and the Chinle/Dockum Subprovince.

Sun (1987, 1993) divided China into three Late Triassic floristic subprovinces based on the taxonomic composition and palaeogeographic position of the various floras. The Northern Floristic Region (=Northern East Asia Subprovince) corresponds to vegetation (Danaeopsis-Bernouillia [=Symopteris] flora) occupying the subtropical-temperate zone or the coastal temperate zone with a warm and humid climate. It comprises floras from more than 20 localities in northern China, including Yanchang of Shaanxi, Tianzhu of Gansu (Sze 1960), Muriof Oinghai (He 1980), Xiaoquangou (Hu and Gu 1987), Manas and Haojiagou of Xinjiang (Sze 1956b; Deng et al. 2001), and Xiaohekou of Jilin. Typical Northern East Asia Subprovince plants are *Glossophyllum*, *Danaeopsis*, *Bernouillia* (=*Symopteris* Plate 13.4d, g) and Sphenobaiera. The boundary with the Southern East Asia Subprovince lies roughly along the line of the South Tianshan Oinling-Dabie Mountains (Fig. 13.6). The Southern East Asia Subprovince covers almost the entirety of southern China (except for southern Tibet) and southern Northwest China. More than 30 localities have yielded floras of this type in southern China, including Baoding and Xujiahe in Sichuan, Yipinglang in Yunnan (Li et al. 1976), Baqen-Amdo in eastern Tibet (Wu and Pu 1982), Shazhengxi in Hubei (Wu et al. 1980), Shaqiao in Hunan (Zhou 1989), Dakeng-Wenbinshan in Fujian (Zhou 1978), Jieza in Yushu (Qinghai: He 1980) and the Tianqiaoling flora of Jilin (Sun 1979, 1981, 1993). The Tianqiaoling flora closely resembles the Nariwa and Yamaguchi floras of Japan (Norian or Carnian-Norian), and the Mongugai flora of Primorye, Russia (Carnian-Norian). This may be related to the fact that it was palaeogeographically close to the Japanese localities during the Triassic (Wang et al. 1986; Zhang 1990; Shao et al. 1992; Yin and Ling 1986; Sun 1979, 1981, 1987, 1990, 1993) but later became separated and drifted northwards. The plant remains of the Southern East Asia Subprovince (Dictyophyllum-Clathropteris flora) reflect a rich tropical-subtropical vegetation (more than 80 genera and 160 species), although there are some differences in the composition of assemblages between the eastern and western parts of the region. This flora is dominated by cycads/bennettitaleans (Anomozamites, Anthrophyopsis, Ctenozamites, Cycadocarpidium, Drepanozamites, Doratophyllum, Ctenis, Nilssonia, Nilssoniopteris, Otozamites, Pseudoctenis, Pterophyllum) and dipteri-Dictyophyllum, dacean ferns (Abropteris, Clathropteris, Goeppertella, Thaumatopteris, Yungjenophyllum). Seed ferns (e.g., Ptilozamites) are rare.

The Yarlung-Zangbo-River Subprovince (Fig. 13.6) is represented by plant assemblages from the coal-beds of the Norian Lanjixue Group of Xiukang near Lhasa, south of the Yarlung Zangbo River (Sun 1993). Palaeogeographically, this area belonged to the Gondwanan Province during the Late Triassic (24.3°S), and the plant remains are affiliated with Gondwanan assemblages dominated by Pagiophyllum, Elatocladus and Dicroidium (Sukh-Dev 1987). In the transition zone between the Northern East Asia Subprovince and Southern East Asia Subprovince there is also a belt of mixed floras, such as the Xiaoquangou flora of Xinjiang, the Xujiahe, Baoding and Wolunggang floras and the Nanzhang flora of western Hubei (Hu 1986; Hu and Gu 1987). These floras contain a mixture of 'Northern-type' elements, such as Asterotheca, Bernouillia (= Symopteris), Danaeopsis, Glossophyllum, Neocalamites, Thinnfeldia and Todites, and 'Southern-type' elements, such as Dictyophyllum and Hausmannia (Meng 1983, 1992; Chen et al. 1979a, b, c, 1985). The existence of these mixed floras suggests that northern China was probably connected with southern China from the early Late Triassic onwards. The Tethys Ocean probably remained only to the south of the western Qinling Mountains, and regressed by the end of Late Triassic, giving origin to huge tracts of exposed land facilitating the migration and mixing of plants from the Northern and Southern East Asia subprovinces.

Two Late Triassic palynofloral provinces have been defined for China; the North and South China provinces, first defined by Qu et al. (1983) and subsequently described by many authors (see Peng et al. 2017b and references therein). The South China province is characterized by the presence of key taxa, such as *Ovalipollis*, *Rhaetipollis* and *Camerosporites*. The North China Province is typified by Late Triassic cosmopolitan taxa, such as *Apiculatisporis* and *Striatella seebergensis* along with *Ovalipollis* and *Kyrtomisporites* (Peng et al. 2017b). The presence of *Ricciisporites* has been claimed for both Provinces but, so far, no illustrations have been presented.

During the Late Triassic, Pangea began its initial fragmentation segregating the Northern and Southern Hemisphere landmasses divided by the broad Tethys Ocean. In addition, the broad latitudinal spread of the landmasses by the Carnian, imposed significant floral provincialism (Buratti and Cirilli 2007). The Gondwana Province is generally divided in two subprovinces (Fig. 13.6), based mostly on differences in palynomorph assemblages. This Late Triassic provincialism has necessitated the establishment of separate palynological zonation schemes in Western and eastern Australia (Table 13.2): the southeastern Australian 'Ipswich-type' (=Ipswich Subprovince) and northwestern Australian 'Onslow-type' (=Onslow Subprovince) floras (Dolby and Balme 1976) with a few intervening 'mixed' or 'intermediate' palynofloras (Foster et al. 1994). The Onslow Subprovince generally has a slightly higher diversity and includes a greater proportion of equatorial (European) taxa. The lower-diversity Ipswich Subprovince is dominated by Falcisporites (Umkomasiales) species. These two subprovinces can be traced across Gondwana and appear to have been constrained by palaeolatitude (Dolby and Balme 1976; Césari and Colombi 2013). The Ipswich Subprovince is distributed from about 90° to 40°S palaeolatitude, whereas the Onslow Subprovince flanked the Tethyan margin of Gondwana, extending to central South America at palaeolatitudes of around 45° to 20°S (Fig. 13.6). The contrasting compositions of the palynofloristic subprovinces probably reflect the Onslow Subprovince's proximity to the Laurussian Province (facilitating floristic interchange) and warmer climates supporting higher plant diversity. The Ipswich Subprovince appears to have hosted cooler and perhaps more humid climates supporting umkomasialean-dominated deciduous-forest biomes. Although this latitudinally defined provincialism is marked in the palyno-floras, no such distinct variations have yet been recognized in the plant macrofossil floras.

However, it is possible that the contrasting opinions concerning the age of some Gondwanan fossil floras, e.g., that of the Parsora Formation of central India treated as Early Jurassic by Mukherjee et al. (2012) but Norian-Rhaetian by Ghosh et al. (2015, 2016), relate to equatorial influences endowing the composition of the flora with an apparently younger aspect than its true age. Within the Triassic Gondwanan Province, local palaeoenvironmental changes also imposed significant influences on the vegetation structure and, together with taphonomic sorting, played an important role in determining the composition of individual plant fossil assemblages (Retallack 1977; Cairncross et al. 1995; Anderson et al. 1998; Spalletti et al. 2005). Retallack (1977) noted several contrasting plant-community associations in the Triassic of eastern Australia that potentially obscure straightforward biostratigraphic signals based on taxon ranges in the plant fossil assemblages. Moreover, Spalletti et al. (2005) recognized 16 macrofloral taphocenoses representing diverse combinations of gymnosperm and pteridophyte taxa with various taphonomic influences within the continental Upper Triassic Potrerillos Formation of Argentina. In a similar manner, Cairncross et al. (1995) linked fossil faunal and floral associations with sedimentological data to interpret palaeoenvironmental settings that were eventually developed into seven habitat (mostly plant community) reconstructions for the Molteno Formation (South African) biotas (Anderson et al. 1998). These habitats ranged from riparian forests and sandbar meadows to floodplain woodlands and marsh communities. Given the taxonomic similarities evident in plant macrofossil assemblages across the Southern Hemisphere, equivalent discrete palaeocommunities to those of the Molteno Formation biotas were probably represented throughout Gondwana during the Late Triassic.

# 13.7.3 Animal-Plant Interactions

The study of arthropod-plant-fungal interactions has become a burgeoning field of research in recent years. Consequently, many more examples of biotic linkages in Triassic continental fossil assemblages are likely to be forthcoming in the near future. Prior to the 1980s there were few reports of feeding damage or oviposition scars on Triassic plants from Gondwana. Subsequent reports, have come from all major regions of the supercontinent (Wappler et al. 2015). By the Late Triassic, insect faunas appear to have recovered from the end-Permian mass extinction, with a major expansion of herbivory in Gondwana. Preliminary results indicate that the Late Triassic radiation of arthropod herbivores targeted a broad range of plants

including ferns, seed ferns, cycads/bennettitaleans, ginkgophytes, gnetaleans and conifers and was essential in the trophic modernization of terrestrial plant-animal interactions especially in external foliage feeding, piercing-and-sucking, galling, leaf mining and seed predation (Labandeira 2006). For terrestrial ecosystems, most of the functional feeding groups (FFG) had been established by the Pennsylvanian but all were clearly present in the early Late Triassic, when the herbivores of land plants became trophically modern (Labandeira 2006). Key evidence of interactions has come from the Molteno Formation (Carnian, South Africa), where 79 damage types were identified on around 220 plant taxa including liverworts, lycophytes, sphenophytes, ferns, peltasperms, umkomasialeans, hamshawvialeans, ginkgophytes, cycads, bennettitaleans, voltzialean conifers and gnetaleans (Anderson and Anderson 1983, 1985, 2003; Scott et al. 2004; Labandeira and Anderson 2005). Other fossil floras have provided evidence of specialized feeding traits or egg-laying strategies. For example, galls and oviposition damage have been reported on a range of ferns, conifers, Umkomasiales and cycads/bennettitaleans from the Blackstone Formation (Carnian) of Australia (Tillyard 1922; Webb 1982), La Ternera and Las Breas formations (probable Rhaetian) of Chile (Gallego et al. 2003, 2004; Gnaedinger et al. 2007, 2008, 2014) and the Parsora Formation (Rhaetian) of India (Ghosh et al. 2015). Adami-Rodrigues et al. (2008) reported various complex herbivory patterns of fossil leaves from the Laguna Colorado Formation (Norian) of Argentina. Rozefelds and Sobbe (1987) and McLoughlin (2013) illustrated early mining traces on Heidiphyllum (conifer) and Ginkgoites leaves from the Blackstone or Tivoli Formation of Australia. Archangelsky and Brett (1961) identified putative arthropod boring traces and frass within Rhexoxylon (Umkomasiales) wood from the Ischigualasto Formation of Argentina. Finally, we illustrate (Plate 13.5b) an additional form of probable piercing-and-sucking damage on Heidiphyllum (conifer) leaves from an unspecified Upper Triassic deposit in the Transantarctic Mountains, Antarctica. Many of these same feeding and egg-laying strategies persisted beyond the end-Triassic mass extinction into the Jurassic of the Southern Hemisphere, albeit associated with new plant groups in many cases (McLoughlin et al. 2015). In addition, various forms of interactions between seed-plants and fungi have been detected in Middle to Late Triassic woods and leaves from Antarctica (Stubblefield and Taylor 1986; Bomfleur et al. 2013a; Harper et al. 2016).

Evidence of Late Triassic plant-animal interactions are not restricted to the Southern Hemisphere, although they are less well described from Northern Hemisphere assemblages. In North America, only a few plant fossil assemblages of the Chinle Formation (Norian) in the desert southwest of the United States have yielded plant-insect interactions. This evidence consists of empty and frass-filled tunnels and chambers in petrified wood (Walker 1938; Ash 2000; Creber and Ash 2004; Lucas et al. 2010) and several types of leaf damage, including marginal and non-marginal feeding traces and leaf galls (Ash 1997, 1999, 2000, 2001, 2014; Ash and Savidge 2004). Several more irregular patterns of degradation in these woods were generated by fungal degradation (Tanner and Lucas 2013).

Few Late Triassic plant assemblages of Europe have been analysed for plantanimal interactions. One of these few examples is the deposition of insect (probable odonatan) eggs and ovipositional damage on bennettitalean leaves from the Carnian flora of Lunz, accompanied by mining-structures, and marginal and non-marginal feeding traces on *Nilssoniopteris* leaves (Pott et al. 2008c; Meller et al. 2011; Wappler et al. 2015). Borings in *Dadoxylon* woods and possible oviposition scars on *Equisetites* have been mentioned from the Carnian of Germany (Linck 1949; Roselt 1954; Grauvogel-Stamm and Kelber 1996; Wappler et al. 2015). Possible oviposition scars on *Podozamites* were also indicated from the Rhaetian of Sweden (Nathorst 1876a, 1878b; Wappler et al. 2015). A very special type of plant-animal interaction is represented by the arthropods (nematoceran fly and mites) and microorganisms that were discovered in the Carnian amber of the Dolomites (Roghi et al. 2005; Schmidt et al. 2006, 2012) and of Germany (Schönborn et al. 1999).

Few studies have been carried out on arthropod-plant-fungal interactions in the Late Triassic fossil biotas of the North Atlantic sector (Greenland, Sweden and Svalbard). Pott and McLoughlin (2009) reported indentations in the adaxial cuticle of Anomozamites angustifolium leaves from the Rhaetian of Skåne that might represent wound callouses of piercing-and-sucking insects. Steinthorsdottir et al. (2015) documented putative odonatan endophytic oviposition scars referable to the ichnogenus Paleoovoidus on ginkgoalean (Ginkgoites, Sphenobaiera, Baiera) leaves across the Triassic-Jurassic transition in East Greenland. They noted that examples of such leaf damage are more abundant below than above the Triassic-Jurassic transition, possibly reflecting a turnover in insect faunas at the close of the Triassic. McLoughlin and Strullu-Derrien (2016) documented interactions of chytrid fungi and bacteria infecting some parenchymatous bennettitalean root cells in a silicified peat from Hopen, Svalbard. Various other fungi and fungi-like remains are scattered through the detrital matrix of this peat. Cavities excavated through some roots (especially cortical cells) and through patches of compacted plant detritus contain abundant coprolites that were probably produced by sapro-xylophagous oribatid mites (Strullu-Derrien et al. 2012). A few larger coprolites containing leaf fragments attest to the presence of unidentified invertebrate folivores in the Carnian ecosystem of Hopen (McLoughlin and Strullu-Derrien 2016).

Vasilenko (2009) reported an assemblage of damaged leaves and stems from the Madygen flora of southern Fergana. The assemblage includes leaf mines, traces of feeding on leaf tissues (margin feeding), and traces of damage of ambiguous nature (some of them may be insect-eggs). The author considered the diversity of damage types at Madygen similar to known associations of damage traces from the Triassic of Germany and South Africa (Vasilenko 2009). Moisan et al. (2012a) identified and illustrated odonatan (dragonfly) oviposition scars on leaves of two lycopsid species of *Isoetites* from Madygen. Plant-animal interactions in the Late Triassic floras of China are rare but crescentic bite marks on *Mixopteris* and intense skeletonization of *Dictyophyllum* fronds were described from the Late Triassic strata of Yunnan Province (Hsü et al. 1974; Feng et al. 2014). The plant-animal interactions documented so far indicate that the diversity in damage types was vastly greater than had been described in the twentieth century, and was probably higher than that recognized for the Permian and Early Jurassic (Vasilenko 2009; Wappler et al. 2015).

#### 13.8 Concluding Remarks

The transition from palaeophytic plant assemblages (Korvunchana/Pleuromeia flora) to mesophytic ones (*Scytophyllum*, *Lepidopteris* and *Thaumatopteris* floras) occurred during the Ladinian and Carnian in many areas (Kryshtofovich 1957; Meyen 1970; Dobruskina 1988). Indeed, several Palaeozoic *bauplans*, such as the arborescent sphenophytes (*Equisetites*) and the winged seeds (*Fraxinopsis*, *Samaropsis*) are still represented in the Late Triassic plant assemblages. Key plant groups, such as the Bennettitales, Gnetales and modern fern and conifer (Pinaceae, Taxodiaceae, Araucariaceae, Cheirolepidiaceae) families, originated during this span of time. Further, some enigmatic plants putatively related to angiosperms (e.g., *Furcula, Imania, Marcouia, Phylladelphia, Sanmiguelia*) developed during the Late Triassic although superficially angiosperm-like pollen grains have been described from strata as old as the Middle Triassic (Hochuli and Feist-Burkhardt 2013; Herendeen et al. 2017).

Although the Late Triassic saw important evolutionary innovations and plant diversification, our understanding of floristic change is constrained by the geographically and stratigraphically irregular distribution of fossil assemblages. Norian floras, for example, are rare and relatively uniform in Europe but floras of this age are the best-represented of the Late Triassic floras in North America. Rhaetian floras, on the other hand, are apparently absent from North America but are widespread and host diverse taxa in Europe and Greenland. In several areas, such as Russia and Gondwana, it is difficult to distinguish between Norian and Rhaetian floras with confidence. Our understanding of the change in diversity and composition of the plant communities through the Late Triassic, thus, remains at an early stage of development and great opportunities exist for future researchers to document additional fossil assemblages from poorly sampled regions and stratigraphic intervals, and to integrate the available data into regional syntheses of plant evolution, phytogeography and palaeoclimatology. The composition of the various fossil assemblages show that the Triassic floras are indeed much more homogeneous than those of the Permian on a global scale. Although several floristic provinces and subprovinces have been recognized by various authors, our global analysis identifies just two major provinces: Gondwana and Laurussia (Fig. 13.6). Within these provinces, variations in taxonomic representation and group abundance were mainly imposed by climatic and regional environmental conditions, and these define several floristic subprovinces (Fig. 13.6, Table 13.1), typically with diffuse boundaries. Similar regional variations are evident in the palynofloras (Table 13.2) and, together with diachronous inceptions of some key taxa, this has necessitated the establishment of numerous regional palynostratigraphic schemes (Table 13.2).

Finally, we note that many plant families and genera were widely distributed in the Late Triassic, at least in the respective hemispheres. The fact that it is still difficult to distinguish between Norian and Rhaetian floras (e.g., within Asia and Gondwana) based on family- or genus-level floral composition, that the Chinle-Dockum (Carnian) flora and the Newark (Carnian–Norian) flora share many taxa, and that the Primorye flora is very similar to the floras of Tonkin, Japan and the German Keuper shows how closely related the regions are at higher taxonomic levels. A clearer picture of phytogeographic relationships and levels of endemism will likely emerge with improved systematic appraisal of the floras and when area relationships are analysed at species-level.

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