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Fossil insects in Gondwana – localities and palaeodiversity trends

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Abstract. The faunal history of insects in the various fragments of Gondwana is presented. The first part of the paper summarizes the current knowledge of its insect-bearing localities, particularly their stratigraphy and fossil content, emphasizing the record of the higher systematic groups. The second part discusses some trends of their palaeobiodiversity as evidenced from the above mentioned sites. Generally, the knowledge of the fossil Gondwanan insect faunae is still much lower than that of the Laurasian ones, but has considerably increased over the last decade. Altogether about 85 localities are known from Gondwana, with a maximum of sites in Permian and a minimum in Jurassic times. Best represented is South America. Fossil insects of Gondwana are probably less known than those of Laurasia due to inadequate exploration rather than unfavourable conditions for the formation of deposits.

Key words: insects, palaeofauna, Gondwana, Phanerozoic, biodiversity.

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I. INTRODUCTION

It is the aim of this paper to compile an inventory of insect-bearing localities in Gondwana and to review and summarize the current knowledge of their stratigraphy and fossil content, with emphasis on the record of higher systematic groups, and to interpret some trends of their palaeodiversity. Although the geological history of insects is generally still based mostly on discoveries in the northern hemisphere (or Laurasia), since the last summarizing report on Gondwanan insects (SCHLÜTER 1990) the available data on new localities and the systematic analysis of the already known faunae have tremendously increased.

It is therefore and also due to the methodology developed by ANDERSON et al. (1996) now much more reasonable to present some general remarks on trends of their palaeodiversity that have occurred in the Gondwanan insect history. However, it has still to be pointed out that the distribution of insect-bearing sites in the particular continental fragments of Gondwana in space and time is still quite uneven: South America has yielded a number of localities from Upper Carboniferous through Pleistocene. In Africa – apart from its southern part – only a few and isolated localities are known. Australia is comparatively well endowed throughout Paleozoic to Cenozoic times. During the last years some new, especially Paleozoic localities, have been discovered in India. Antarctica has due to its remoteness only yielded a few and isolated localities.

A c k n o w l e d g e m e n t s. I have to thank all those palaeoentomologists, who throughout the past 20 years have sent me their papers on Gondwanan insects, or provided other information on this subject. It is my sincere hope that exchange of ideas and papers may also continue in future in similar ways.

II. REVIEW OF STRATA AND LOCALITIES

Figs 1, 2; Table I

II. 1. Devonian and Lower Carboniferous

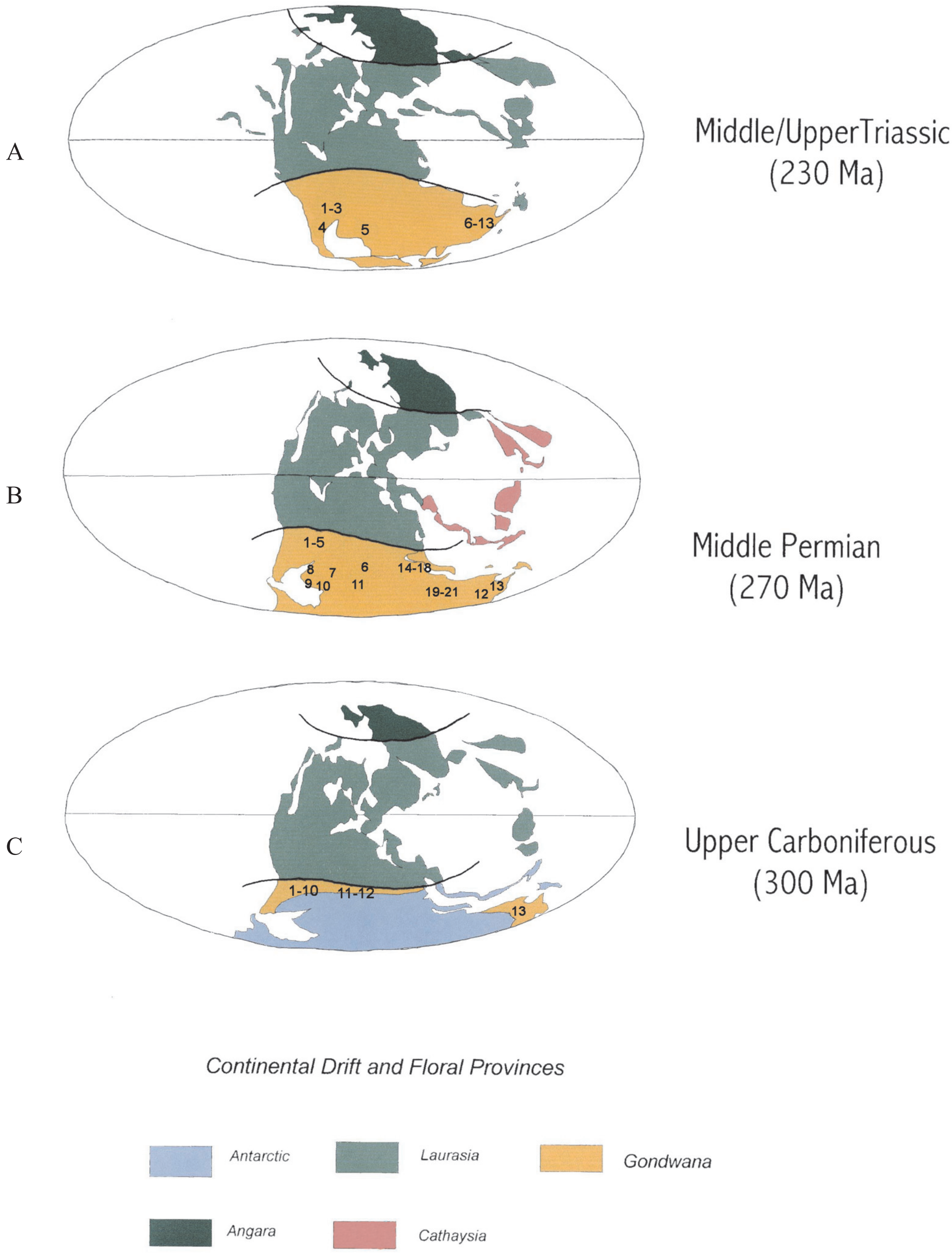
The Lower to Middle Devonian strata provide the first adequate glimpse of terrestrial ecosystems from numerous sites around the world (TILLYARD 1928; BEHRENSMEYER et al. 1992), but although most of the continental land surface was in the southern hemisphere, altogether only a few faunal fossiliferous deposits are known, of which in Gondwana none has yet yielded fossil insects. Also from the Upper Devonian through the Lower Carboniferous only very few terrestrial animal assemblages containing arthropods have yet been discovered, with no evidence at all from the southern continents. It has, however, to be assumed that insect diversification had already occurred during this period, as indirectly indicated by the various winged insect groups evidenced in Namurian strata.

II. 2. Upper Carboniferous

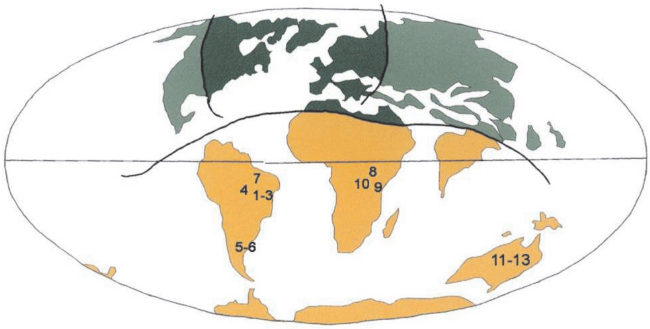
(Fig. 1A, Table I)

Insects have a substantial fossil record in Westphalian and Stephanian deposits of Laurasia and were sometimes highly diversified, thus playing similar roles as today in being predators, detritivores and herbivores in a large ecological spectrum. However, comparatively few insect-bearing localities are known from Upper Carboniferous strata of Gondwana. This scarcity of fossil insects may be related to the wide glaciation of the Southern Hemisphere during late Paleozoic times. The record of this glaciation can be correlated with the movement of the Gondwana fragments across the South Pole: During Ordovician the Saharan region was widely glaciated, when North Africa lay near the pole. By Silurian to Lower Devonian central South America arrived over the pole causing minor glacial activity there. Eastern Antarctica had moved over the pole in late Carboniferous, when the maximum glacial activity gave rise to several ice sheets scattered across South America,

Fig. 1. Fossil insect bearing localities in Gondwana, marked on palaeocontinental maps of various ages, including to show the respective predominant floral provinces (modified after ANDERSON et al. 1999, and SCOTESE, 1997). **A.** Palaeogeography of the Upper Carboniferous (with Gondwanan insect bearing sites of the Upper Carboniferous). 1. Arroyo Genoa, central Patagonia; 2. La Rioja, Sierra de los Llanos; 3. Bajo de Veliz, San Luis Province; 4. Betancourt, central Patagonia; 5. Durasnal, Rio Grande do SulState; 6. Anitapolis, Santa Catarina State; 7. Boituva City, Praca da Bandeira; 8. Teixeira Soares 1, Parana State; 9. Teixeira Soares 2, Parana State; 10. Monte-Mor county, Sao Paulo; 11. Matabola Flats, Zimbabwe; 12. Mavonono River, Madagascar; 13. Hellyer Gorge, Tasmania. **B.** Palaeogeography of the Middle Permian (with Gondwanan insect bearing sites of the Permian). 1. San Luis Province, Argentina; 2. Sao Gabriel, Brazil; 3. Minas do Leao, Brazil; 4. Piracicaba, Brazil; 5. Falkland/Malvinas Islands; 6. Lukuga Beds, Congo (DRC); 7. Madziwadzido, Zimbabwe; 8. Hammanskral, South Africa; 9. Kenmore Quarry, South Africa; 10. Mombasa, Kenya; 11. Drakensberg in Natal, South Africa; 12. Belmont and Warner's Bay area, New South Wales; 13. Coal Measures, New South Wales; 14. Kashmir; 15. Daltongunj Coalfield, India; 16. Raja Colliery, India; 17. Risin Spur, Srinagar, Kashmir; 18. Baliarpatti Spur, Kashmir; 19. Theron Mountains, Filchner Ice Shelf, Antarctica; 20. Sentinel Mountains, Polarstar Peak, Antarctica; 21. Leaia Ledge, Ohio Range, Antarctica. **C.** Palaeogeography of the Middle/Upper Triassic (with Gondwanan insect bearing sites of the Triassic). 1. Minas de Petroleo and Cacheuta, northern Argentina; 2. Mendoza, northern Argentina; 3. Ischigualastro Basin, northern Argentina; 4. Rio Grande do Sul, Brazil; 5. Molteno Formation of the Karoo Basin, South Africa; 6. Brookvale, New South Wales; 7. Wianamatta Shales near Sydney; 8. Mt. Crosby, Queensland; 9. Danmark Hill, Queensland; 10. Hill River, Western Australia; 11. Hobart, Tasmania; 12. Barber's Colliery, Tasmania; 13. Awakino-Mahoenui, southern Auckland, New Zealand.

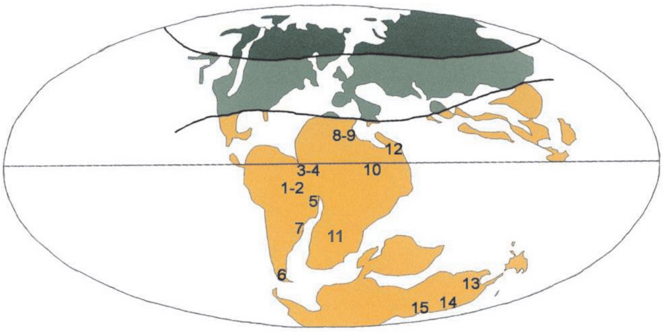

A
Middle/UpperTriassic
(230 Ma)
1-3
4
5
6-13
B
Middle Permian
(270 Ma)
1-5
8
7
6
14-18
9
10
11
19-21
12
13
C
Upper Carboniferous
(300 Ma)
1-10
11-12
13
Continental Drift and Floral Provinces
Antarctic
Laurasia
Gondwana
Angara
Cathaysia

D



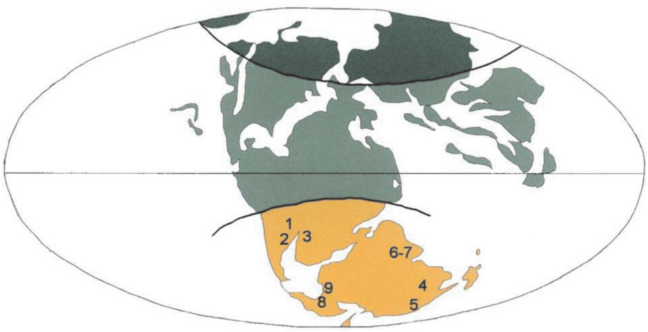
Paleogene (Eocene)
(50 Ma)

E



Lower Cretaceous
(120 Ma)

F



Middle Jurassic
(160 Ma)

Fig. 1 (left). Fossil insect bearing localities in Gondwana, marked on palaeocontinental maps of various ages, including to show the respective predominant floral provinces (modified after ANDERSON et al. 1999, and SCOTESE, 1997).
D. Palaeogeography of the Middle Jurassic (with Gondwanan insect bearing sites of the Jurassic). 1. Laguno de Molino, Argentina; 2. Estancia Malacara, Bahia Lauro, Argentina; 3. Chinguba River, Lunda, Angola; 4. Talbragar River, New South Wales; 5. Unnamed locality, New Zealand; 6. Pranhita-Godavari Basin, Andhra Pradesh, India; 7. Chanda District, Bombay; 8. Carapace Nunatuk, Antarctica; 9. Mount Flora, Grahamland, Antarctica; 10; Phra Wihan Formation, northern Thailand. **E.** Palaeogeography of the Lower Cretaceous (with Gondwanan insect bearing sites of the Cretaceous). 1. Bajo Grande, Argentina; 2. Sierra del Gigante, Argentina; 3. Uchoa, northern Brazil; 4. Sanfranciscan Basin, Brazil; 5. Santana Formation of the Araripe Plateau, northern Brazil; 6. Cerro Guido, southern Chile; 7. Nueva Palmira, southern Uruguay; 8. Brezina and Toulouala, northern Algeria; 9. Saida District, Algeria; 10. Abu Ballas Formation, southwestern Egypt; 11. Orapa, Botswana; 12. Levantine Amber Belt (various sites in Lebanon, Jordan, Syria and Israel); 13. Flinders River, northern Queensland, 14. Koonwarra, south of Melbourne; 15. Hawkes Bay, New Zealand. **F**. Palaeogeography of the Paleogene (Eocene) (with Gondwanan insect bearing sites of the Tertiary and Quaternary). 1. Unnamed locality in Minais Gerais State, southern Brazil; 2. Taubate Basin, Brazil; 3. Various localities in Sao Paulo State, Brazil; 4. Sunchal, northwestern Argentina; 5. Laguna del Hunco, southern Argentina; 6. Pichileufu, southern Argentina; 7. Paraopeba River, Brazil; 8. Rusinga and Mfwanganu Islands, Kenya; 9. Semliki Plain, Uganda; 10. Copal deposits in East Africa, Madagascar, West Africa and Congo; 11. Redbank Plains Series and Dinmore, southern Queensland; 12. Vegetable Creek near Emmaville, northern New South Wales; 13. Duaringa, Queensland.

	Carboniferous	*Permian*	*Triassic*	*Jurassic*	*Cretaceous*
Collembola		●			●
Diaphanopterodea	■				
Ephemeroptera			●		● ■ ▲
Megasecoptera	■	● ■			
Odonata		▲ ■	● ■ ▲	◆	● ■ ▲
Palaeodictyoptera		■			
Protodonata	■		●		
Blattodea	■	● ■ ◎	● ■ ▲	◎	● ■ ▲
Isoptera					● ■
Mantodea			●		
Orthoptera		●	● ■ ▲		● ■ ▲
Phasmatodea			▲		
Plecoptera		● ▲	● ■ ▲		■ ▲
Protelyroptera		● ▲			
Protorthoptera	● ▲	● ▲ ◆	● ■ ▲		
Hemiptera		● ■ ▲ ◆	● ■ ▲	● ▲	● ■ ▲
Psocoptera		▲			● ▲
Thysanoptera					●
Coleoptera		● ■ ▲	● ■ ▲ ◆	● ■ ▲ ◎	● ■ ▲
Diptera			▲	◎	● ■ ▲
Glosselytrodea		▲	● ▲		
Hymenoptera			● ▲		● ■ ▲
Lepidoptera					●
Mecoptera		● ■ ▲	● ▲		▲
Neuroptera		● ■ ▲	● ■		● ■
Rhaphidioptera				◎	■
Siphonaptera					▲
Trichoptera		▲	▲		▲
Miomoptera		●			

● Africa ▲ Australia ◎ India

■ South America ◆ Antartica

Fig. 2. Insect orders recorded in the respective Gondwanan fragments.

Table I

Number of insect-bearing localities in the respective Gondwanan fragments through time

	South America	Africa	Australia	India	Antarctica	
Tertiary	7	3	3	–	–	13**
Cretaceous	7	5	3	–	–	15
Jurassic	2	1	2	2	2	9*
Triassic	4	1	8	–	–	13
Permian	5	6	2	5	3	21
Upper Carboniferous	10	2	1	–	–	13
	35	18	19	7	5	**84**

southern Africa and Antarctica. By Permian Gondwana had moved westwards so that Australia and Antarctica were glaciated, but the ice centres had generally diminished or already disappeared, for instance in Africa and South America. The first species of the *Glossopteris* land plants evolved in Gondwana during later stages of the Carboniferous. The geographical distribution of *Glossopteris* associations is larger than that of the glacial deposits. Clearly the stimuli provided by the cold climate favoured the growth of this unique flora (ANDERSON et al. 1999).

South America

The knowledge of the South American Paleozoic insects has recently been summarized by PINTO & ADAMI-RODRIGUES (1999) and WÜRDIG et al. (1999), on whose papers the report here presented is mainly based. Till now, the 10 known sites of Upper Carboniferous and 5 of Permian insects in South America are all located in Argentina and Brazil.

Argentina:

1. Piedra Shotle Formation at Arroyo Genoa, Chubut Province, central Patagonia. Fine-laminated olive-grey sediments between two coal-bearing horizons have yielded a few insects, which were described by PINTO (1992, 1994) and determined as Palaeodictyoptera (*Breyeria brauckmanni* and *Archaemegaptilus ferreirai*). The stratigraphic age of the deposit was originally indicated as Permian, due to the associated plants and spores, but the insect families Breyeridae and Archaemegaptilidae are otherwise only known from Upper Carboniferous strata and the deposit has therefore been assigned to this age.

2. La Rioja, Cuestitia de la Herradura, Sierra de los Llanos, La Rioja. From this lacustrine turbidite sequence three species of fossil insects have been described (RIEK & KUKALOVÁ-PECK 1984; PINTO 1986), which after some dispute are now referred due to the associated macropalaeobotanical fossils either to the latest Namurian or the early Westphalian (BRAUCKMANN et al. 1996). The three insect species are each represented by a single specimen and belong to the orders Meganisoptera (two species of the family Eugereopteridae) and the Megasecoptera (family Xenopteridae).

3. Bajo de Veliz, Pallero Member, San Luis Province. PINTO & ORNELLAS (1978a, 1980a) described from this locality of probably Stephanian age a few isolated wings of the orders Diaphanopterodea and Protorthoptera. An almost completely preserved representative of the Megasecoptera, *Sphecocorydalis lucchesei*, was subsequently recorded by PINTO (1995).

4. Betancourt at Nueva Lubecka, Chubut Province, central Patagonia. This deposit of greenish and dark grey lutites has yielded the blattoid *Archangelskyblatta vishniakovae*, together with plant remains of the genus *Gangamopteris*, and has been assigned to the latest Carboniferous or the earliest Permian (PINTO & ADAMI-RODRIGUES 1999).

Brazil:

5. Durasnal, Cacapava do Sul, Rio Grande do Sul State. In a bed of the Budo Formation, a rose to grey sandstone deposit, a representative of the Protorthoptera has been recorded and described by PINTO & ADAMI-RODRIGUES (1999).

6. Anitapolis, at Fazenda do Juca, about 14 km from the city of Anitapolis, Santa Catarina State. A well-preserved wing of a representative of the Paraplecoptera was described by PINTO (1990) from this locality, where strata of the Itarare Suggroup of probably Stephanian age are outcropping.

7. Boituva City, a core sample drilled at Praca da Bandeira, Boituva City, at 206 m, containing grey rhythmites with plant remains. PINTO & ADAMI-RODRIGUES (1995) described a representative of the Protorthoptera: Cacurgidae from this deposit, which has been assigned to the Upper Carboniferous.

8. Teixeira Soares 1. This is a site in a ravine about 1km east of Teixeira Soares county in the Parana State, embedded in dark grey sediments 45 m below a yellow sandstone with pebbles and a thin bed of plants, also belonging to the Itarare Subgroup.

9. Teixeira Soares 2. Dark grey shales crop out at about 2 km east of the Teixeira Soares railroad station, Teixeira county in the Parana State. Several Blattodea and Protorthoptera have been described from the latter two localities (CARPENTER 1930; PETRI 1945; MEZZALIRA 1948; PINTO & ORNELLAS 1978c, PINTO & PURPER 1979; PINTO 1990). There was considerable conflict over the age of the Itarare Subgroup, which by palaeobotanists has been assigned to the Lower Permian, whereas the insects seem to indicate a clear Upper Carboniferous age (PINTO 1995).

10. Monte-Mor county. Argiliceous siltic sediments of the Monte-Mor Formation 4 m below the floor of the old coal mine at Sitio da Mina in Sao Paulo are mentioned by PINTO & ADAMI-RODRIGUES (1999) as additional insect-bearing strata of the Itarare Subgroup.

Africa

1. Matabola Flats, Zimbabwe. RIEK (1974a) recorded and described a representative of the Protorthoptera (originally assigned to the Paraplecoptera), *Hadentomoides dwykensis*, recovered from a borehole core drilled in a depth of about 250 m at the top of the Dwyka Series (probably Upper Carboniferous) of Zimbabwe.

2. Mavonono River, Madagascar. Two representatives of the order Protorthoptera, *Appertia besaire*i, and a doubtful species of the genus *Narkemina* sp. were recorded from plant-bearing layers along the right side of the River Mavonono in Madagascar by PAULIAN (1965), who assigned these beds to either the Upper Carboniferous or the Lower Permian. The deposit was subsequently by PINTO et al. (1980) referred to the Upper Carboniferous.

Australia

1. Wynyard Tillite at Hellyer Gorge, Tasmania, Australia. RIEK (1973, 1976a) described *Psychroptilus burrettae*, a well-preserved representative of the Megasecoptera, for which he established the new suborder Neosecoptera, since this species combines ancestral characters of both the orders Megasecoptera and Palaeodictyoptera in having a very simple wing venation with reduced cross veins and lacking paratergal processes on the pronotum. The fossil was found in an ancient tillite of the Hellyer Gorge of northwest Tasmania. It is preserved in varve-like sediments deposited at the margins of a small shallow lake adjacent to or in association with glacial moraines, indicating cold conditions during deposition. The microfloral association of this site and the occurrence of the plant fossil *Botrychiopsis plantiana* are indicative for an Upper Carboniferous (or possibly earliest Permian = Asselian) age of this deposit.

II. 3. Permian

(Fig. 1B, Table I)

Generally, the record of Permian hexapods reveals continued diversification of herbivorous insects and evolution or expansion of a number of major groups (BEHRENSMEYER et al. 1992). By the earliest Permian, as the Gondwanan glacials continued their retreat, sparse faunas are encountered in all the Gondwana continents excepting Antarctica. In the Late Permian, two top faunas with diverse assemblages, have been sampled: one from a suite of localities in the Estcourt Formation of the Karoo Basin in South Africa, and another from the single Belmont locality in the Sydney Basin of New South Wales in Australia.

South America

1. San Luis Province, Argentina. FOSSA-MANZINI (1941) reported three undescribed insect wings of unknown systematic affinities.

2. Sao Gabriel, an outcrop on the right bank of the Santa Maria River, Passo de Sao Borja, Sao Gabriel, Rio Grande do Sul State, Brazil. Grey limestone lens of the Irati Formation of the Passa Dois Group of Upper Permian age (PINTO & ADAMI-RODRIGUES 1999).

3. Minas do Leao, at the left side of a cutting along the road Porto Alegre to Uruguiana, Brazil. Yellow, silty shales of the Irati/Estrado Nova Formation of the Passa Dois Group of Upper Permian age (PINTO & ADAMI-RODRIGUES 1999).

4. Piracicaba, a natural outcrop at Pedreira de Mineracao Amaral Machado at the left side along the road Tiete to Piracicabo, Brazil. Silty shales of the Irati Formation of the Passa Dois Group of Upper Permian age. The last three mentioned sites, all located in the Parana Basin, have yielded a number of different insect species, distributed over the following orders: Odonata, Blattodea, Homoptera, Neuroptera, Mecoptera and Coleoptera (PINTO 1972b; PINTO & ORNELLAS 1980b; 1981; RÖSLER et al. 1981).

5. Falkland/Malvinas Islands. From the probably Upper Permian Gondwana Series of the Falkland/Malvinas Islands HALLE (1911) reported a well-preserved wing of the Blattodea. TILLYARD (1928) described a representative of the Odonata, *Protagrion falklandicu*m, and FOSSA-MANZINI (1941) reported a single wing of a representative of the Palaeodictyoptera from the same islands.

Africa

1. Lukuga Beds at Kivu, Democratic Republic of Congo. An isolated representative of the Protorthoptera, *Boutakovia saleei*, was already described by PRUVOST in 1934.

2. Madziwadzido along the Serami River, Sebungu District, Zimbabwe. A single Blattodea, *Rhodesiomylacris bondi*, was described by ZEUNER (1955) from the Lower Beaufort (= Upper Permian) Karoo System.

3. Hammanskral near Pretoria, South Africa. From carbonaceous shales of the Middle Ecca (= Lower Permian) RIEK (1976b, d) described a few representatives of the orders Collembola (*Permobrya mirabilis*), Paraplecoptera (*Thaumatophora pronotalis*) and Blattodea (*Sysciophlebia euglyptica*)

4. Kenmore quarry, about 20 km southeast of Worcester, and Willowmore in the Western Cape Province, South Africa. From the Whitehill Formation, previously known as White Band Formation, which is Lower Ecca in age (= Lower Permian), in the western part of the Karoo Basin, PINTO & ORNELLAS (1978b) and GEERTSEMA & VAN DEN HEEVER (1996) described representatives of the Mecoptera (*Afrochoristella maclachlani*), Paraplecoptera (*Sharovia permiafricana*) and Coleoptera (*Afrocupes firmae*), respectively.

5. Cores of borehole drillings in the Maji ya Chumvi Formation about 60 km west of Mombasa, Kenya. These samples of probably Upper Permian age yielded one, not yet in detail described repre-

sentative of the Blattodea: Mesoblattinidae and a few other undetermined insect specimens (MILLER 1952; SCHLÜTER 1997b).

6. Estcourt Formation with about 25 sites strung along a 200 km arc of country within the midlands below the Natal Drakensberg in South Africa. These localities of the Beaufort Group (= Upper Permian) have yielded a flora and insect fauna of global significance. Some 70 species, strongly dominated by the Homoptera, have been recognised, including representatives of the Megasecoptera, Protorthoptera, Blattodea, Orthoptera, Miomoptera, Protelytroptera, Hemiptera, Trichoptera, Mecoptera and Neuroptera (VAN DIJK 1997; VAN DIJK & GEERTSEMA 1998; VAN DIJK et al. 1978).

Australia

1. Coal measures at Belmont and Warner's Bay area north of Sydney in New South Wales. Fossil insects are preserved in a hard fine-grained chert, associated with phyllopod crustaceans, fish scales and a *Glossopteris* flora, indicating an Upper Permian age. The insect fauna consists mainly of Mecoptera, Neuroptera, Homoptera and Psocoptera. Protelytroptera (KUKALOVÁ 1966) and Coleoptera are moderately well-preserved (TILLYARD 1926a). Mecoptera with dipterological venation are also recorded (TILLYARD 1929, 1937), which subsequently by WILLMANN (1989) – in contrast to most other dipterologists – had been assigned to the Diptera. Each of the other orders is recorded by only one or two specimens, sometimes too fragmentary for specific determination. The fauna is curiously unbalanced as compared with other faunas of similar age. The absence of Blattodea and almost complete absence of orthopteroid orders is surprising, especially as the Blattodea and the Paraplecoptera were so abundant in extra-Australian regions at this time and even earlier in the Lower Permian. There are a few Plecoptera, an order in which the nymphs are almost invariably aquatic. The Palaeoptera are represented only by one Odonata (TILLYARD 1935) and a fragment of the wing of a Meganisoptera (RIEK 1968b). The Trichoptera, and possibly the Megaloptera, orders in which the immature stages are all or mostly aquatic, are also present.

2. From the roof of the Coal Measures of the Sydney Harbour Colliery, New South Wales, an Orthoptera: Elcanidae, *Elcanopsis sydneiensi*, was already described by TILLYARD (1918) and its age may either be assigned to the Upper Permian or the Lower Triassic.

India

1. *Gangamopteris* Beds of Kashmir. HANDLIRSCH (1906-1908), BANA (1964) and VERMA (1968) described a few Blattodea from these deposits of the Lower Gondwana Sequence, which are either of Upper Carboniferous or more probably of Lower Permian age.

2. Daltongunj Coalfield in Bihar. From the probably lowermost Permian Talchir Formation DUTT (1977) reported an isolated wing of a representative of the Blattodea, which was recovered from a borehole core.

3. Raja Colliery, West Raniganj Coalfield. From the Barakar Formation of probably Middle Permian age. SRIVASTAVA (1987a, b, 1988) mentioned a few Blattodea and Homoptera, partially later described in detail by PINTO et al. (1992).

4. Risin Spur, about 10.5 km southeast of Srinagar. Kashmir Basin. From the Mamal Formation of probably Lower Permian age PINTO et al. (1992) described a few Blattodea.

5. Baliarpatti Spur, Kashmir Basin. From tuffaceous shales of the Mamal Formation of Lower Permian age KAPOOR et al. (1992) and PINTO et al. (1992) described an isolated, but partially preserved body fossil of the Blattodea.

Antarctica

1. Theron Mountains near Filchner Ice Shelf, Antaractica. A single but well-preserved wing of a representative of the Homoptera was found during the Trans-Antarctic Expedition of 1955-1958 (CARPENTER 1970), which, however, got lost before a detailed study. It was assigned to a Permo-Carboniferous age.

2. Sentinel Mountains on the eastern slope of Polarstar Peak. From the Polarstar Formation of probably Permian age an isolated wing of a possible Homoptera was reported by TASCH & RIEK (1969) and subsequently by CARPENTER (1970).

3. Leaia Ledge, Mercer Ridge, Ohio Range, Antarctica. From a small piece of a carbonaceous shale the single specimen of *Uralonympha schopfi*, an immature insect of unknown affinities, was described by CARPENTER (1970).

II. 4. Triassic

(Fig. 1C, Table I)

The general appearance of the Mesozoic insect faunae is relatively modern in character from the Triassic onwards, forwarded by an abrupt floral replacement during the Norian, when the *Dicroidium* flora in the southern hemisphere was replaced by a worldwide dominance of Coniferae-Bennettitales, which may have led to the extinction and appearance of various associated insect taxa.

South America

1. Minas de Petroleo and Cacheuta, Cacheuta Basin, Mendoza Province, northern Argentina. From lacustrine sediments of the Upper Triassic (= Carnian) Cacheuta Formation a few specimens of the orders Plecoptera, Orthoptera, Homoptera and Trichoptera have been collected (PINTO & PURPER 1978).

2. Five, probably closely related localities in the vicinity of Mendoza in the Cacheuta Basin, Mendoza Province, northern Argentina. The Potrerillos Formation lays conformably below the Cacheuta Formation and is characterized by claystones and limonitic volcanic shales, which have yielded representatives of the orders Odonata, Plecoptera, Blattodea, Orthoptera, Miomoptera, Homoptera and Coleoptera (GALLEGO & MARTINS-NETO 1999).

3. Ischigualasto Basin, San Juan and La Rioja Province, northern Argentina. From the Los Rastros Formation of Upper Triassic (= Carnian) age a few species of the following orders have been recorded: Blattodea, Orthoptera, Homoptera, Mecoptera and Coleoptera. These are preserved in grey to dark claystones.

4. Santa Maria Formation, Rio Grande do Sul, Brazil. Red or brownish argillaceous siltstones of the lower part of the Santa Maria Formation have yielded a few representatives of the Blattodea, Homoptera and Coleoptera. Their stratigraphic age is probably the top of the Middle Triassic (Upper Ladinian - Lower Carnian) (PINTO 1956).

Africa

1. Molteno Formation, Karoo Basin, South Africa. The lacustrine/riverine taphocoenoses of the Upper Triassic (Carnian) Molteno Formation in South Africa have yielded by far the richest insect lagerstaette in Africa. Altogether approximately 3,000 insect specimens from about 43 localities have yet been collected. Generally among the insects of the Molteno Formation, herbivores clearly demonstrate dominance over the carnivores, both in abundance and in diversity. Blattodea, Coleoptera and Homoptera count for a high proportion of specimens. Less important are representatives of the Odonata, Orthoptera, Neuroptera, Mecoptera, Paraplecoptera, Plecoptera and the so-called "Paratrichoptera". Only isolated specimens of the Ephemeroptera, Meganisoptera, Glosselytrodea and Hymenoptera were found. Surprisingly, Diptera are apparently absent in the yet available material (ANDERSON et al. 1998, RIEK 1974b, 1976a, b; SCHLÜTER 1997a, 2000; WAPPLER 1999, 2001; ZEUNER 1961). Fig. 3 shows a reconstruction of the Molteno biocenosis, including representatives of the Odonata, Blattodea, "Paratrichoptera", Plecoptera, Coleoptera and Hymenoptera.

2. It is not quite clear if the few fossil insects already mentioned by HAUGHTON (1924) from the Stormberg Series of the Karoo Basin may also represent part of the same biocenosis as those of the Molteno Formation.

Fig. 3. Reconstruction of a palaeobiocenosis in the Upper Triassic Molteno Formation, South Africa, showing some typical plants and representatives of the Odonata, Plecoptera, Blattodea, Hemiptera, “Paratrichoptera”, Coleoptera and Hymenoptera.

Australia and New Zealand

1. Brookvale, New South Wales. Fossil insects occur in a lenticular shale in the Hawkesbury Sandstone Series of Middle Triassic age at Beacon Hill, Brookvale, near Manly. Relatively few specimens are recorded from this horizon, and most are wings of larger insects. The fauna consists mainly of orthopteroid insects and Homoptera. There are two species of the Blattodea and a single species of the Mecoptera. Protorthoptera, Paraplecoptera and Plecoptera are also recorded (RIEK 1950, 1953; TILLYARD 1925).

2. Wianamatta Shales. These shales are situated about 100-130 m above the top of the Hawkesbury Sandstone Series and are considered to be of Upper Triassic age. Insect remains have been obtained from three localities within this series, which are named St. Peters, near Sydney, Narellan and Glenlee. The most productive site is Glenlee, where several beetle elytra, one mecopteron, fragments of a cockroach, and the apex of a homopterous wing have been collected (RIEK 1970a).

3. Mt. Crosby, Queensland. This deposit, at the base of the Ipswich Series of Upper Triassic age, has yielded more than a thousand recognizable insect fossils (RIEK 1970a; TILLYARD 1936). Blattodea dominate the fauna with about half of the fossils referred to this order. Mecoptera, Neuroptera, Trichoptera, Diptera and Homoptera constitute the other main components of the fauna by adding about 40% to the total of specimens (TILLYARD 1917, 1922). There are smaller numbers of Coleoptera and Orthoptera (RIEK 1955; ROZEFELDS 1985). Each of the orders Hymenoptera, Plecoptera, Odonata and Paraplecoptera is represented by one or two specimens. There is a surprisingly poor representation of most aquatic orders (TINDALE 1946). In this locality the oldest Diptera of Australia were found (EVANS 1971, KOVALEV 1983, BLAGODEROV 1999, LUKASHEVICH & SHCHERBAKOV 1999).

4. Denmark Hill, Queensland. The fossil insects of this assemblage are found on the top of the Upper Triassic Ipswich Series, but its composition is very different from that of Mt. Crosby. About half of the Denmark Hill fossils are Coleoptera, while Homoptera and Blattodea constitute other important components. There are a few Odonata, Mecoptera, Neuroptera and Orthoptera. Each of the

orders Plecoptera, Phasmatodea, Trichoptera, Paraplecoptera and Glosselytrodea is represented by one or two specimens (TILLYARD & DUNSTAN 1923; RIEK 1970a; ROZEFELDS & SOBBE 1987).

5. Hill River, western Australia. The only well-preserved insect fossils in a small collection from this area are beetle elytra. One representative of the Mesoblattinidae has also been recorded (RIEK 1968a, 1970a).

6. Hobart, Tasmania. A few fossil insects have been obtained from a plant-bearing horizon in the New Town Coal Measures at Hobart, including the wing of a Blattodea and of a large scytinopterid Homoptera (RIEK 1962).

7. Barber's Colliery, Mt. Nicholas Coal Measures at Fingal, Tasmania. This locality has only yielded the fore wing of a Blattodea of the genus *Triassoblatta* (RIEK 1967).

8. Hokonui System, Awakino-Mahoenui area, southwest Auckland, New Zealand. GRANT-MACKIE (1958), quoted in CRAW & WATT (1987), reported an isolated beetle elytron fragment from this locality of Triassic age.

II. 5. Jurassic

(Fig. 1D, Table I)

With all the continental areas of the world broadly connected at the beginning of the Jurassic, it is expected that the plant and animal inhabitants would be substantially alike across the land, a certain amount of geographic variation in the faunal distribution not withstanding. Whereas the Jurassic of the northern hemisphere since the 19th century has commonly been assigned as a period with rich occurrences of fossil insects (CARPENTER 1992; HENNIG 1981), Jurassic strata of Gondwana have yielded up to date only a few and mostly isolated findings. Major discoveries apart from those given in the review by SCHLÜTER (1990) are only reported from India.

South America

1. Laguno de Molino, Argentina. A representative of the Coleoptera has been reported from probable Jurassic deposits at Laguno de Molino (FERUGLIO 1949).

2. Estancia Malacara of Bahia Lauro, Argentina. A possible representative of the Hemiptera has been reported from probable Jurassic deposits of Estancia Malacara (TASCH 1970).

Africa

1. Chinguba River near Lunda, Angola. From red argillaceous strata of late Karoo age in Angola, TEIXEIRA (1974) has described *Coptolavia* (sic!) *africana*, a genus possibly related to Jurassic or Cretaceous hydrophagous beetle larvae (Coptoclavidae), which are otherwise well-known from several - sometimes contemporaneous - localities in Laurasia. However, age determination and systematic assignment of this single specimen from Angola are still tentative.

Australia and New Zealand

1. Talbragar River near Mudgee, New South Wales. From this deposit of probably Upper Jurassic age RIEK (1970a) has mentioned the isolated finding of a representative of the Cercopoidea (Hemiptera), which apparently has not yet been described in detail.

2. From an unnamed locality of Jurassic age in New Zealand CRAW & WATT (1987) reported the finding of the wing of a prophalangopsid locust.

India

1. Kota-Maleri Beds, Kota Formation, Pranhita-Godavari Basin, Andhra Pradesh. These deposits were first mentioned already by HISLOP (1861) as being insect-bearing. RAO & SHAH (1959) reported a few isolated wings and elytra of Blattodea, Coleoptera and Hemiptera from these localities, which were stratigraphically assigned to the Upper Gondwana Formation (= Rhaeto/Liassic?). Subsequently TASCH (1987) reported additional Blattodea, Coleoptera, Heteroptera, Homoptera, Neu-

roptera and Ephemeroptera from the same formation. MOSTOVSKI & JARZEMBOWSKI (2000) also mentioned representatives of the Orthoptera, Raphidioptera and Hymenoptera, but excluded the Ephemeroptera. They also described two species of brachycerous Diptera, *Taschigatra bharataja* and *T. tulyabhijana*.

2. Other reports of fossil insects of possibly Jurassic age in India include the old quotations of MURRAY (1860) from the Intertrappan beds of Takli, Nagpur. More recent contributions (SAHNI & TRIVEDI 1943; MANI 1946; SUKESWALA 1954) pertain mostly to some fossil insects found in the Salt Range of Pakistan and the Intertrappan beds of Bombay State. Their stratigraphic age is, however, still uncertain.

Antarctica

1. Carapace Nunatuk. CARPENTER (1970) has described the dragonfly *Caraphlebia antarctica* from volcanic deposits of the Mawson Tillite on Carapace Nunatuk.

2. Mount Flora, Hope Bay, Grahamland. ZEUNER (1959) reported two beetles, *Grahamelytron crofti* and *Ademosynoides antarctica*, from a deposit on Mount Flora, Hope Bay, Grahamland, at the northern tip of the Antarctic peninsula. Subsequently TASCH (1970, 1973) has pointed to the palaeogeographic significance of these beetle discoveries in the context of continental drifting.

Other Sites

1. Phra Wihan Formation, between Phrae and Nan Provinces, northern Thailand. A small fauna of middle Jurassic age in northern Thailand (HEGGEMANN et al. 1990), which yielded among some freshwater arthropods also a few representatives of the Blattodea and Hemiptera, may tentatively be allocated to a peri-Gondwanan fragment.

2. In the same context some of the insect findings listed by FUJIYAMA (1973) from the Jurassic of China and South Korea may also be considered.

II. 6. Cretaceous

(Fig. 1E, Table I)

Until the 1970s fossil insects of Cretaceous age were reported from only a few localities worldwide. These sporadic occurrences have now been supplemented by many additional sites, both in Laurasia and Gondwana. During Cretaceous times fossiliferous resins (amber) are becoming increasingly important in palaeoentomology. So far, the oldest fossil resin containing arthropod inclusions is the so-called Levantine Amber, which has been found in Libanon, Syria, Jordan and Israel. This region is here considered as belonging to the northeastern flank of the African part of Gondwana.

South America

1. Bajo Grande, Santa Cruz Province, Argentina. From the Lower Cretaceous (Aptian) Baquero Formation PINTO (1990) has described a single species of the Blattodea, *Blattulopsis popovi*.

2. Sierra del Gigante, San Luis Province, Argentina. From the Lower Cretaceous Cantera Formation two species of the Hemiptera were described, Canteronecta trajae MAZZONI 1985 and *Rhomboidella popovi* MAZZONI 1987.

3. Uchoa, Barra do Corda, Maranhao Basin, northern Brazil. From the Lower Cretaceous (Aptian) Coda Formation PINTO & ORNELLAS (1975) have described two species of the Homoptera, *Pricecoris beckerae* and *Latiscutella santosi.*

4. Sanfranciscana Basin, Brazil. From the Lower Cretaceous (Aptian) Areado Formation MARTINS-NETO (1996, 2000) has described two species of the Coleoptera, *Saucrolus silvai* and *S. ribeiroi.*

5. Araripe Plateau, along the southern border of Ceara, northeastern Brazil. The Crato Member is the lowest of the Aptian-Albian Santana Formation and has yielded more than 3,000 insect speci-

mens, which are distributed over 18 orders and about 200 species. Representatives of the following orders have been recorded: Ephemeroptera, Odonata (BECHLY 1998), Plecoptera, Dermaptera, Psocoptera Isoptera, Orthoptera (MARTINS-NETO 1987a, b, 1989, 1990), Phasmatodea, Blattodea, Homoptera, Heteroptera, Planipennia (MARTINS-NETO 2000), Raphidioptera, Coleoptera, Hymenoptera, Diptera (VULCANO et al. 1981; RIBEIRO & KRZEMIŃSKI 2000), Trichoptera and Lepidoptera (GRIMALDI 1990 – see there many additional references). The palaeoenvironment of the deposit was lacustrine, with two distinct sub-environments: black shales and laminated carbonates represent the deeper lake centre, while algal shales, carbonates and evaporites represent the marginal environment. The well-bedded unit rich in organic matter, possibly originating from algal filaments and fishes, is the one with many insect fossils.

6. Cerro Guido, Ultima Esperanza, Magellanes, southern Chile. From the uppermost Cretaceous (Maastrichtian) Dorothea Formation KUSCHEL (1959) has described a single weevil (Coleoptera), *Dorotheus guidensis.*

7. Nueva Palmira, southwest Uruguay. From palaeosols preserved in the Ascencio Formation, ROSELLI (1938) was the first palaeontologist in South America who described various ichnocenoses of fossil bees and dung beetles, which were later evaluated by MARTINEZ (1982), SCHLÜTER (1984), GENISE & BROWN (1996) and finally GENISE (1998). The stratigraphic age of these ichnofossils has been assigned to the Upper Cretaceous or early Tertiary.

Africa and Middle East

1. Brezina and Toulouala, northern Algeria. From probably Aptian/Albian strata of this area ZHERIKHIN (1978) reported some Ephemeroptera, Odonata, Blattodea, Hemiptera and Coleoptera.

2. Saida District, Algeria. From the Lower Cretaceous of this area SINITSHENKOVA (1975) described *Hexemeropsis africanus*, the larva of an Ephemeroptera.

3. Abu Ballas Formation, southwestern desert, Egypt. From Lower Cretaceous strata of the Abu Ballas Formation various insects of the orders Odonata, Blattodea, Hemiptera, possible Isoptera, Orthoptera and Coleoptera have been reported (SCHLÜTER 1981), of which two Odonata (*Aegyptidium aburasiensis* and *Gondvanogomphus bartheli*) (SCHLÜTER & HARTUNG 1982) and one Orthoptera (*Locustopsis africanus*) (ANSORGE 1991) were subsequently described in detail. This site has a great potential for further discoveries, but is very difficult to approach.

4. Orapa, Botswana. Epiclastic sediments overlying a diamondiferous kimberlite in central Botswana have yielded a unique assemblage of fossils, including flowering plants and whole-bodied insects. Their deposition has been dated as middle Cretaceous (Cenomanian-Coniacian). The crater lake waters were apparently poisonous or inhospitable, with the insects dying soon after landing on the surface of this lake. About 3,000 specimens have yet been collected (MCKAY & RAYNER 1986; BROTHERS 1992), including representatives of the following orders: Orthoptera, Blattodea, Dermaptera, Hemiptera, Coleoptera, Diptera and Hymenoptera. No aquatic insects have yet been recovered. The fauna is overwhelmingly dominated in both diversity and abundance by the Coleoptera. The Blattodea fall second in abundance, with Diptera and Hymenoptera joint third. A reconstruction of the palaeoenvironment of the Orapa crater lake is shown in Fig. 4.

5. Levantine Amber Belt. Fossiliferous resins ranging in age from early to middle Cretaceous have been found at several places in the Lebanon, Jordan, Syria and Israel. The most productive sites are in the southern Lebanon, but in Jordan also localities with insect inclusions occur (BANDEL et al. 1997), whereas the amber found in Syria and Israel has not yet yielded any insect remains. Representatives of the following orders have been recognized: Collembola, Thysanura, Archaeognatha, Orthoptera, Psocoptera, Thysanoptera (ZUR STRASSEN 1973), Heteroptera, Homoptera (SCHLEE 1970), Isoptera, Neuroptera (WHALLEY 1980), Coleoptera, Hymenopetra, Lepidoptera (WHALLEY 1977, 1978) and Diptera (HENNIG 1970, 1971, 1972; SCHLEE 1972, GRIMALDI 1996 – see there many additional references). Ecologically it has been concluded that the environment of these insects was characterized by a hilly landscape and a warm, tropical climate, where lakes and rivers were also well distributed (SCHLÜTER, in press). Some of the well-preserved specimens of the

Fig. 4. Reconstruction of a palaeobiocenosis in the Upper Cretaceous volcanic/kimberlitic site of Orapa, Botswana, showing a profile through an anoxic crater lake with some typical plants and representatives of the Blattodea, Hemiptera, Coleoptera, Hymenoptera and Diptera.

Levantine Amber Belt are shown in Fig. 5 (Diptera Nematocera, Diptera Brachycera, Neuroptera Planipennia, Lepidoptera, Homoptera Sternorrhyncha, Thysanoptera, Araneae, Acari and Millipeds; all from Lebanese sites) (modified after HENNIG 1972, SCHLEE 1970, WHALLEY 1980, ZUR STRASSEN 1973 and GRIMALDI 1996).

Australia and New Zealand

1. Flinders River, northern Queensland. A single species of an anisopteran Odonata, *Aeschnidiopsis flindersiensis*, has been recorded from marine limestones of the Flinders River Bed of northern Queensland (RIEK 1954).

2. Koonwarra, Gippsland Basin, southeast of Melbourne, 2.5 km west of Tarwin in Victoria. The Lower Cretaceous Koonwarra Fossil Bed, encountered in a road cutting south of Leongatha on the South Gippsland Highway, yielded more than 70 insect species in 13 orders of several thousand specimens. The fauna is dominated in diversity by Hemiptera, Coleoptera and Diptera, but numerically by aquatic immature Ephemeroptera and Diptera. Lesser components are representatives of the Odonata, Blattodea, Plecoptera, Orthoptera, Psocoptera, Mecoptera, Trichoptera, Hymenoptera and Siphonaptera, the latter representing the oldest evidence of this order. The Koonwarra fauna is also remarkable because of its predominance of immature stages of insects (CAROLL 1962; JELL & DUNCAN 1986 – see there many additional references). A reconstruction of the former biocenosis is shown in Fig. 6.

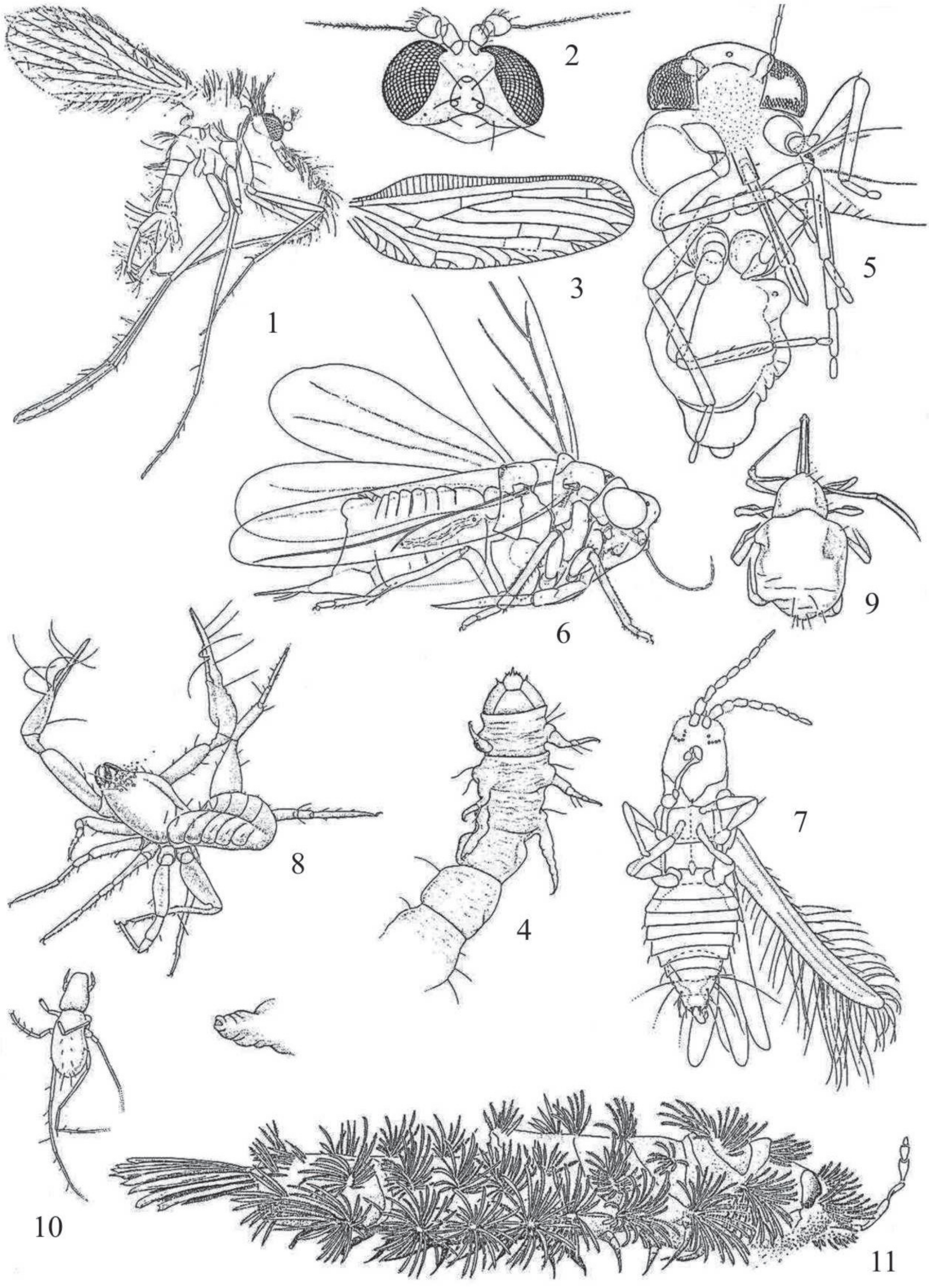


Fig. 5. Representatives of insect inclusions found in the Lower Cretaceous resins of the Levantine Amber Belt, Middle East. 1: Diptera, Nematocera; 2: Diptera, Brachycera; 3: Neuroptera, Planipennia; 4: Lepidoptera; 5: Heteroptera, Homoptera; 6: Heteroptera, Homoptera; 7: Thysanoptera; 8: Araneae; 9: Acari; 10: Acari; 11: Millipeds.

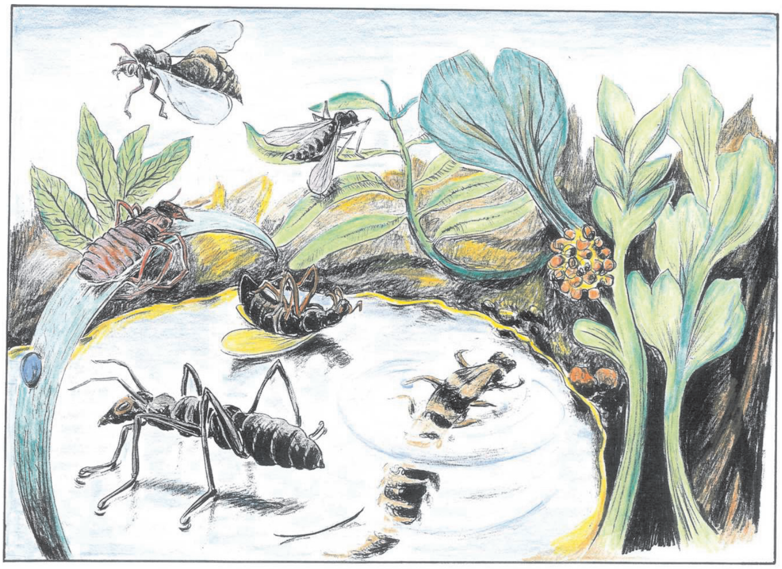


Fig. 6. Reconstruction of the palaeobiocenosis of the Lower Cretaceous Koonwarra Lake Beds, Australia, showing some typical plants and representatives of the Ephemeroptera, Plecoptera, Hymenoptera, Diptera, Coleoptera and Siphonaptera.

3. Hawkes Bay, New Zealand. From Upper Cretaceous (Campanian - Maastrichtian) strata of the Mangahouanga Stream, inland Hawkes Bay, a buprestid or chrysomelid Coleoptera elytron was recovered, preserved in a marine-derived concretion (CRAW & WATT 1987).

II. 7. Tertiary and Quaternary

(Fig. 1F, Table I)

In the pre-ceding summarizing report on fossil insects in Gondwana (SCHLÜTER 1990), it was stated that there are many Cenozoic localities thus making it very difficult to cross check and to evaluate them all. This is apparently not true. From most of the recent Gondwanan fragments only a few sites of Cenozoic insects are known. In Late Pleistocene and Holocene deposits sometimes archaeological findings associated with various insect assemblages have been recorded (especially in the northern hemisphere), which in this report are not considered.

South America

1. Unnamed locality in the Minais Gerais State, southeast Brazil. From Oligocene strata EMERSON (1965) described a species of the Isoptera, *Spargotermes costalimai.*

2. Taubate Basin, Brazil. From the Oligocene Pirassununga Formation MARTINS-NETO (1989) described a species of the Hemiptera, *Parafitopterix duarteae.*

3. Various localities in Sao Paulo State, Brazil. From the Oligocene Tremembe Formation representatives of the following insect orders have been recorded: Hemiptera, Coleoptera, Diptera, Trichoptera, Lepidoptera and Hymenoptera PETRULEVICIUS & MARTINS-NETO 2000).

4. Sunchal, La Mendieta, Jujuy Province, northwest Argentina. From the late Paleocene Maiz Gordo Formation 38 species of the following orders have been recorded: Odonata, Orthoptera, Dermaptera, Hemiptera, Coleoptera and Trichoptera. The fauna is in diversity dominated by the Coleoptera, which constitute more than 30 species (COCKERELL 1936, PETRULEVICIUS & MARTINS-NETO 2000).

5. Laguna del Hunco, Chubut Province, southern Argentina. From the Paleocene-Eocene Laguna del Hunco Formation a single species of the Hymenoptera, *Urocerus patagonicus*, has been described (FIDALGO & SMITH 1987).

6. Pichileufu, Confluencia, Rio Negro Province, southern Argentina. From the Paleocene-Eocene Ventana Formation two species of the Hymenoptera, *Ameghinoia pianitzkyi*, and *Polanskiella smekali*, have been recorded (VIANA & HAEDO ROSSI 1957; ROSSI DE GARCIA 1983).

7. Paraopeba River, Minais Gerais State, Brazil. From the Pleistocene Rio das Velhas Series PINTO (1991) described a single species of the Blattodea, *Amazonina purperae.*

8. Late Tertiary, Pleistocene or Holocene Copal deposits have been reported from Colombia, Chile and Brazil (SCHLÜTER 1987), but these localities were mostly cited from quotations of the 19^{th} century and it is not clear if insect inclusions have been found in the respective copal samples.

Africa

1. Albertine Rift Valley, Uganda. From the Upper Miocene Nkondo Formation NEL (1994) reported various ichnofossils of xylophagous insects (Coleoptera, Isoptera and Hymenoptera) preserved in fossil wood.

2. Mfwanganu and Ruzinga Islands, Lake Victoria, western Kenya. From Miocene volcaniclastic sediments of these two islands LEAKEY (1952) reported some exceptionally well-preserved fossil arthropods, including a few caterpillars of Lepidoptera. Subsequently WILSON & TAYLOR (1964) described a partly preserved fossil ant colony from Mfwanganu Island. THACKRAY (1994) described a fossil nest of sweat bees (Halictinae) from Ruzinga Island. The fauna of about 120 collected specimens including various Coleoptera, Heteroptera and Lepidoptera has not yet been described in detail and has also the potential of a lagerstaette.

3. Laetoli, northern Tanzania. From the Pliocene Laetoli Beds of this famous hominid-bearing locality different types of insect trace fossils have been recorded, including fossilized casts of soil-working Isoptera (SANDS 1987), radially arranged grooves covering bone surfaces, which were probably also produced by termites (KAISER 2000), and bee brood cells of Hymenoptera (RITCHIE 1987).

4. Fossil mounds of Neogene age caused by termites have been reported by CROSSLEY (1984, 1986) from the Malawi Rift Valley.

5. Makapangsgat, near Potgietersrus, in the Pretoria area, South Africa. From this classic hominid-bearing cave of Plio/Pleistocene age KITCHING (1980) reported various insect findings, mostly pupae of flies and beetle dung ball casts.

6. Copal has been reported from various places in Africa, and sometimes some of its inclusions have been systematically described. Most famous is probably the East African copal, which was found along the East African coast (Kenya, Tanzania, Mozambique) and has yielded an abundance of different insect species. However, only a few of those have yet been described, among them representatives of the Embioptera, Psocoptera, Blattodea, Isoptera, Hemiptera, Coleoptera, Hymenoptera, Lepidoptera and Diptera. Another well-known site for copal is Madagascar, but also from West Africa various localities are known (e. g. Ghana, Guinea, Sierra Leone, Gabon, Angola) (SCHLÜTER 1987). However, similarly as mentioned for South America, most of these quotations are cited from sources of the 19^{th} or early 20^{th} century and may therefore not always be reliable.

7. Etosha Salt Pan, Namibia. An actuopalaeontological example for the preservation of mostly larger insects under hyper-saline conditions during the Holocene has been presented by STEFFAN & MURSCH (1998).

Australia and New Zealand

1. Redbank Plains Series and Dinmore, southeastern Queensland. From these two lake deposits of Lower Tertiary age representatives of the Coleoptera, Homoptera, Diptera, Mecoptera, Neuroptera, Blattodea, Hemiptera, Odonata and Isoptera have been reported (RIEK 1970a).

2. Vegetable Creek near Emmaville in northern New South Wales. The fossil insects of this locality occur in the youngest Tertiary stanniferous lead of the tin-field, representing well-preserved nymphs and larvae of aquatic insects, including some Ephemeroptera, chironomid Diptera and dytiscid Coleoptera (RIEK 1970a).

3. Duaringa, about 100 km west of Rockhampton in Queensland. Two zygopterid Odonata nymphs have been obtained from a borehole core, probably of Tertiary age (RIEK 1970a)

4. Anglesea, southern Victoria. ROZEFELDS (1988) reported Eocene insect leaf mines, which were probably produced by various Lepidoptera and possibly a representative of the Diptera.

5. Glencoe area, central Queensland. Silicified Kalotermitidae frass in conifer wood of mid-Tertiary age has been reported by ROZEFELDS & DE BAAR (1991).

6. Copal is well-known from deposits in New Zealand, ranging in age from early Tertiary to Recent (THOMAS 1968). The source plant is the Araucariaceae-genus *Agathis*. Insect inclusions have sometimes been reported, but not yet been described in detail (SCHLÜTER 1987). Another locality is at Allendale, Victoria, in southern Australia, from where some isolated insect inclusions have been described (HILLS 1957; KOHRING & SCHLÜTER 2000).

India

1. Copal deposits of unknown localities in India were already mentioned by DALMAN (1825) and later by KLEBS (1910).

III. PALAEODIVERSITY TRENDS

In palaeontology, species diversity can be expressed at four successive levels of inclusiveness: described, observed (known), preserved and existed (ANDERSON 1999). From the basis of available data (i. e. the number of sampled [= observed] species at a certain locality) with the help of derived statistical techniques (generalised Inverse Gaussian-Poisson Distribution [IGPD]) the ratio of the potentially available number of species (= preserved) and finally of the existing species at this locality can be concluded. This procedure has for instance been carried out with the amount of fossils collected in the Upper Triassic Molteno Formation (ANDERSON et al. 1996; see there also for mathematical handling of the data). Some specific observations considering the taxonomic richness of both fossil plants and fossil insects of the Molteno Formation are remarkable. There are more than 300 different insect species distributed over approximately 3,000 specimens, whilst there are more than 30,000 slabs collected with about 300,000 specimens of vegetative plants, but the latter hardly comprising altogether more than 200 known plant species. Applying the above mentioned IGPD method, from a starting tally of about 200 observed species of vegetative plants, a projected 876 preserved species and a total of about 2,000 plant species is estimated to have existed in the Molteno Formation, whilst with a record of more than 300 known insect species, a projected 8,000 preserved and a total of about 20,000 insect species may have existed in the Molteno Formation. This calculation indicates that the number of species of the palaeoentomofauna was apparently ten times more diverse than that of the palaeoflora. It is also intriguing to compare the insect/plant diversity ratio arrived at for the Molteno Formation with that assumed for the extant world. Though there persists always the problem of equivalence of species of insects and plants, a near 10:1 ratio emerges also in case of the globally existing species of both taxonomic categories (about 3-4 million extant insect species compared to about 300,000 extant vegetative plant species). From the basis of “projected” and “existing” biodiversity ratios of insects and plants in the Molteno Formation and their comparison with the biodiversity ratio of the globally extant species of both groups a correspondent proportion is clearly recognizable. The question thus arising is if this 10:1 ratio may be a near constant persisting since the earliest arrival of both groups on land, or if this trend has developed sometimes later.

It was generally concluded by LABANDEIRA & SEPKOSKI (1993) that the origination rates of new families from the Triassic onwards were not higher than during Palaeozoic times, but since Triassic times the extinction rates are apparently much lower (Fig. 7). The taphocoenoses of Tertiary insects are composed almost exclusively of living families, and even during mid-Cretaceous times (Cenomanian) more than 80% of the global palaeoentomofauna consisted of extant families (JARZEMBOWSKI 1989). Only till the Jurassic extinct families constituted the majority of the global diversity pattern of insects, which contrasts dramatically with that of the terrestrial Tetrapoda, in which fewer than 10% of the extant families are present at the Jurassic/Cretaceous boundary. Additionally remarkable is the fact that the post-Paleozoic radiation of many families commenced more than 100 million years before the ascendancy of the Angiosperms in the fossil record during Aptian/Albian.

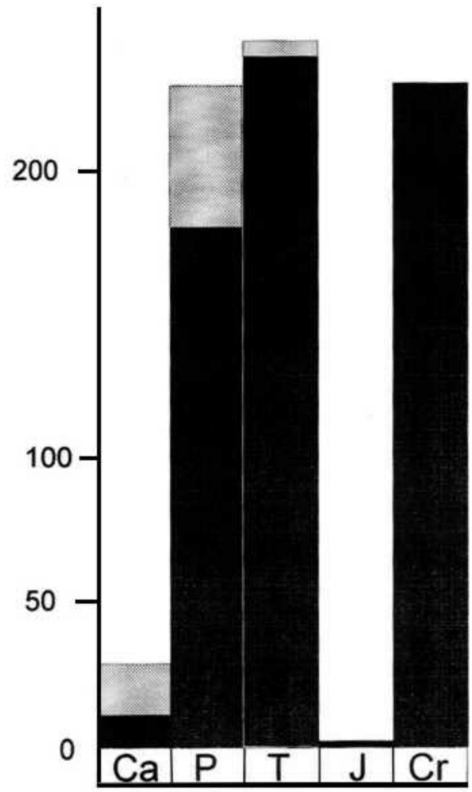
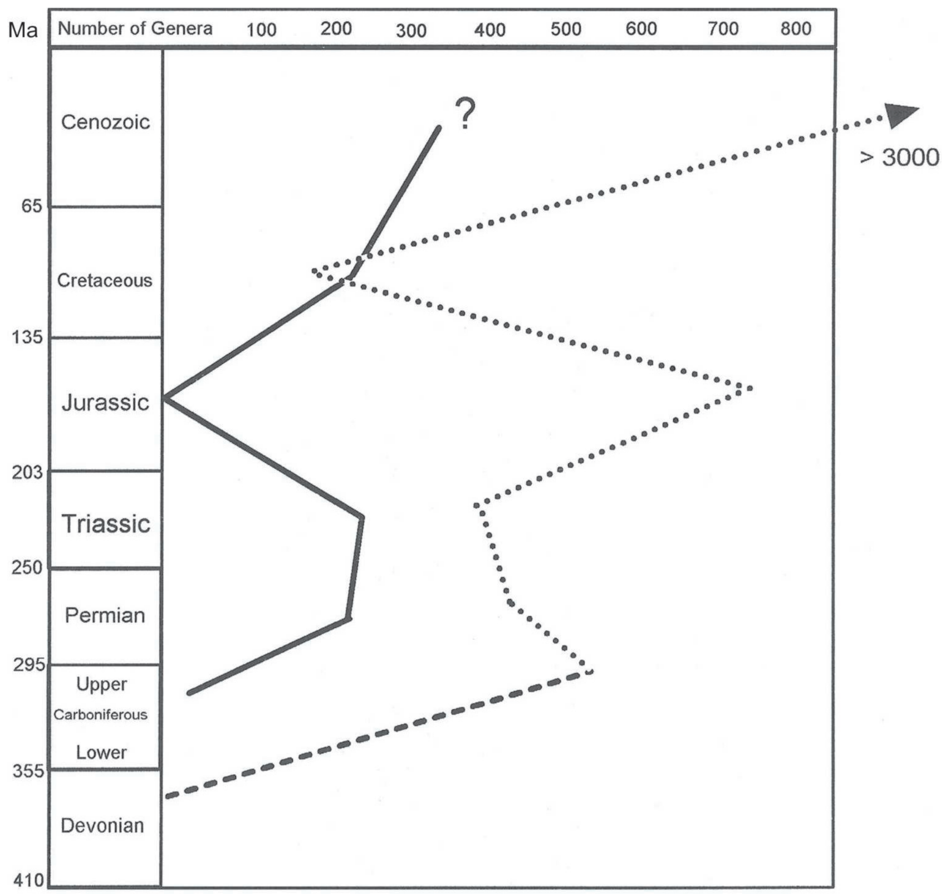


Fig. 7. Approximate number of the known species of insects in Gondwana from Upper Carboniferous through Cretaceous. Grey: Species belonging to extinct orders. Black: Species belonging to extant orders (modified after SCHLÜTER 1990).

Concerning specifically the diversity trends of fossil insects in Gondwana (Fig. 8), it has to be considered that there are till now comparatively few localities that allow to project from the number of described species the number of potentially available and then the number of existing species. From the Gondwanan sites mentioned above there are only Estcourt in South Africa and Belmont in Australia for the Permian, Molteno from southern Africa and Ipswich from Australia for the Triassic, and Santana from Brazil, Orapa from Botswana, the Levantine Amber Belt and Koonwarra from Australia for the Cretaceous yielding comprehensively known faunas for the determination of diversity trends. Most other localities have to date yielded only very few specimens. Additionally, it should also be pointed out that the faunal history of insects during Permian and Triassic mainly derives from key formations yielding a range of localities, whereas diversity trends during Cretaceous and Cenozoic are essentially based on isolated lagerstaetten.



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