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FOSSIL BIODIVERSITY IN THE LIMESTONES OF THAILAND: A CORNUCOPIA OF INFORMATION ABOUT THE HISTORY OF LIFE

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ABSTRACT

In Thailand, fossils are common and diverse. They come from both terrestrial and marine environments. They belong to many time periods beginning with the Cambrian, thus spanning more than 500 million years (the Phanerozoic eon). This rich past emerges from extensive published data and is still very interesting to explore.

This publication concerns only fossils included in limestone deposited in the seas of the past. Limestone is widespread in Thailand and of various ages. Marine floras (algae) and faunas are in abundance at many limestone exposures and their skeletons are an important component of the limestone. They give a deep-time perspective on the evolution of the life in the seas of the past.

The limestones of Thailand are not restricted to the widespread exposures visible on the land. They have been found by hydrocarbon exploration at varied depths and in different areas. Permian limestone has been reached by wells under the Khorat Plateau and its extent has been determined by seismic interpretation; it is widespread (for instance, see MOURET, 1994). This publication is concerned only with limestones exposed at ground surface. Limestone is a general term for diverse types of rocks, deposited in different environments. Before describing their biodiversity, we discuss the origin of the limestones of Thailand.

Key words: Diversity, fossils, limestone, mass extinctions, paleogeography, stratigraphy, Thailand

LIMESTONES OF THAILAND

In Thailand, limestone (*Hin Pun* in Thai language) is a rock very widespread at the surface of the land all over the country. It makes up small to very large hills, which are locally numerous, for instance north of Saraburi between Lopburi and Muak Lek. Beautiful landscapes have been carved by erosion, producing a marvellous castellated topography. Caves are common. In addition to the prominent hills, small limestone outcrops are scattered at ground surface. They are not visible in the topography, but easily seen in the banks of the rivers as well as in ponds or other holes dug by farmers.

Limestone is known by everybody and many hills are called Khao Hin Pun or simply Khao Pun (= Limestone Hill). In other places, the names show the imagination of the local people; they describe the peculiar topography of the limestone (karst topography; see Figs. 1, 4 to 6). Many hills are called Khao Tham or Khao Khuha (= Hill with a Cave). A qualifier may be added because of an underground river (Khao Tham Nam Lot), a peculiar

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feature (Khao Suwana Khuha = Hill of the Gold Cave), or the size (Khao Tham Yai or Khao Tham Luang = Hill of the Large Cave). Khao Laem indicates a pointed hill. Phu Tum means a bud shape; it is a common name in Loei Province. Doi Sam Sao (Hill of the Three Triangles), between Chiang Dao and Phrao, displays 3 angular points of limestone standing out from its top. Limestone hills are commonly steep-sided; Khao Pha Daeng is a hill with a red cliff, Khao Pha Dam is a hill with a black cliff, Khao Pha Lat is a hill with an inclined cliff, Khao Lak is a hill surrounded by cliffs and showing a milestone shape. Khao Wong is a hill with a sinkhole at its centre. When the limestone is clearly bedded, it is compared to a pile of folded clothes (Khao Phap Pha). Khao Phap Pha is a common name in Surat Thani Province (see Fig. 3).

The names of other hills are focussed on the flora or the fauna of the hills: Khao Ruak (Hill of a small kind of bamboo), Khao Phrik (Hill of the Red Pepper), Khao Pha Fai (Hill with a cliff and cotton), Khao Kwang (Hill of the Deer), Khao Tham Ikea (Hill of the Cave of the Bats), Khao Lan (Bald Hill, without vegetation). Many species live in karst topography at the surface of the hills or in the caves which are common in limestone hills.

Types of Limestone

Limestone is commonly grey to black, but locally it may be white, yellow or red. It is massive or thinly to thickly bedded (Figs. 1 to 6). It is fine- to coarse-grained. From a chemical point of view, it is almost pure carbonate of calcium deposited in a clean environment; this is the case at many localities of Thailand. However, this is not the rule; clay and even sand locally occur in the limestone, occasionally in such a quantity that the appropriate names of the rocks become calcareous shale or calcareous sandstone. Limestones are polygenetic; they were deposited in differing environments which will be described below. In these different types of rocks, fossils are commonly well preserved. Their abundance distributions and their diversities reflect the images of ancient living communities, with some fidelity.

After its deposition, limestone has been transformed by different diagenetic processes which were destructive or constructive. It may have been dolomitized; then, it displays a fair content of magnesium. In the field, dolomitic limestone is easy to recognize because its surface is not smooth, but looks like elephant skin. Dolomitization commonly destroys the fossils and precise identifications are impossible. When limestone has been heated by intrusion of igneous rocks, it is recrystallized and the fossils are again largely or entirely destroyed. In dolomitized and recrystallized limestones, the original characters are obscured or erased. These rocks are not helpful in reconstructing life of the past and they are locally difficult to date. They are fortunately restricted to small areas of Thailand.

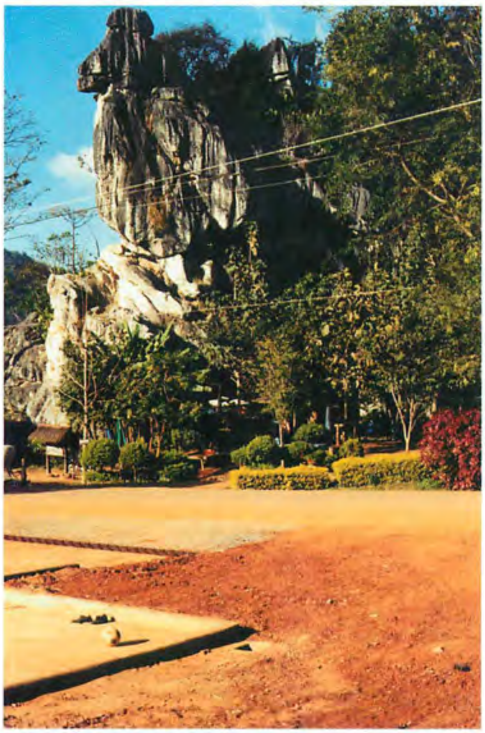
Depositional Environments

Limestone has been deposited almost everywhere in Thailand in marine environments, and commonly in distinct subenvironments of shallow seas. An exception has been recognized (IWAI, 1972 and 1973), a few limestone beds at the base of the Khorat Group in Northeast Thailand have been considered lake deposits; they are thin, less than 10 cm thick, with the exception of a bed reaching 2 m in thickness. This limestone is practically barren of fossils. Lacustrine faunas are commonly of low diversity. Such deposits are

Figure 1. Limestone hills near Nam Piyang Din Waterfall south of Wang Saphung in Loei Province, northeastern Thailand. The limestone, Early Permian in age, contains many foraminifera (smaller foraminifera and fusulinaceans). It is also rich in calcispheres and *Tubiphytes* fragments; corals are rare (FONTAINE *ET AL.*, 2002, and in preparation).

Figure 2. Bedded limestone at Ko Si Chang near Vashiravut Bridge. Ko Si Chang is an island of the northeastern part of the Gulf of Thailand. The limestone is partly recrystallized and poor in fossils (SALYAPONGSE *ET AL.*, 2002); it is considered Ordovician in age.

Figures 3. Bedded limestones at two different hills. a: Permian limestone hill of Surat Thani Province in Peninsular Thailand. The limestone is clearly bedded. It is compared to a pile of folded clothes (Phap Pha) and called Khao Phap Pha (Hill of the Folded Clothes). It is locally rich in fossils, but of a low diversity. b: Khao Pha Wak, a hill south of the road from Tak to Mae Sot. The limestone is poor in fossils. This hill has a cave and is historically interesting; it was a hiding place for soldiers during World War II.



Figures 4. Limestone hills at a Buddhist temple before arriving at the Nam Piyang Din Waterfall. a: Thickly bedded limestone at a hill near the temple. b: The same limestone, eroded, at the entrance of the temple.

Figure 5. Khao Tham Krachaeng, hill of Ban Nang Sata area in southernmost Thailand, with an underground tunnel followed by a river. The limestone is massive and recrystallized.

Figure 6. Doi Pha Chu (18°23'15"N, 100°48'55"E) in Na Noi area of Nan Province. Massive limestone containing fossils in moderate quantity: algae, fasciculate corals, sponges, bryozoans and bivalves (FONTAINE *ET AL.*, 2001).

known in lakes of North America, occurring under different sets of circumstances. In addition to the limestone of the Khorat Group, caliche, travertine and tufa can be mentioned. They are terrestrial calcareous materials of secondary accumulation, known at many localities of Thailand; they are too small in space and too restricted in time to be very interesting. However, this type of rock has recently attracted attention at Khao Si Siet, a hill built up by unconsolidated pebbly alluvial deposits, north of Amphoe Lao Kwan in the northern part of Kanchanaburi Province. Polished fragments of carbonate material formed in these deposits give beautiful pieces of marble, occasionally containing land snails. In addition to that, fissure fillings are common at the limestone hills of Thailand; they locally contain fossils such as skeletons of Quaternary terrestrial vertebrates (for instance, see CHAIMANEE *ET AL.*, 1996, fossils from Khao Sam Ngam near Ratburi).

In the geologic record, limestone is commonly absent from deep sea deposits. However, it is occasionally represented by thin turbidite beds, called allodapic limestone. Fossils are not in their original place, they were transported from shallow areas and transferred to bathyal depths. In Central Thailand, this type of rock (Nam Duk Formation) has been described along the road from Lom Sak to Chumphae, especially near milestone 17.2 km (HELMCKE & KRAIKHONG, 1982); it contains a poor allochthonous fusulinacean fauna.

Shallow water marine limestone is extensive in Thailand. It has been commonly deposited in well oxygenated water, illuminated by day-light, at suitable salinity and temperature. Great numbers of fossils with high diversity suggest favourable environments. The shallow depth of the water is indicated by the occurrence of green algae at many localities. Warm water is suggested by the abundance of large compound corals at many Devonian to Jurassic localities.

Some limestone formations are thick; they were continuously deposited during a long time, in the same environment. They consist of accumulations of skeletal material as well as organically induced accumulations of other types of carbonate material. Some organisms encrust or attach to one another; they locally built up a rigid mass even before fossilization.

The environment was locally energetic, with strong waves increasing the supply of food and oxygen. Many organisms could thrive easily. But after their death, their skeletons were often broken by the turbulent water, but commonly in not too small fragments, thus allowing good identification. In some places, the fossils and their debris were accumulated in detrital mounds, later on consolidated by inorganic cementation. Reefs were commonly wave-resistant. The limestone produced in energetic environments is formed mainly of grains and skeletal debris. However, modern sea-grass is regarded as protecting lime-mud buildups; the size of the grain must not be always considered according to the water turbulence.

Environment was more or less quiet in other areas. Limestone is fine-grained. It is locally ultrafine-grained, clay-sized carbonate and it is called micstone. Fossils are better preserved, but they are commonly less diverse and less abundant. They may be almost absent where water was confined to an undisturbed environment, poorly aerated and almost deprived of oxygen. In lagoons, salinity can become low with influx of fresh water, or become high with evaporation during dry seasons. High evaporation has produced the deposition of gypsum in several areas of Thailand.

In addition to the limestone displaying castellated topographic relief, other formations consist of shale, siltstone, sandstone and limestone interbeds or lenses, with less impressive topographic features. The limestone is commonly not visible in the topography, but it may be of great interest in the search for fossils. In Loei Province, some Middle Carboniferous limestone lenses are algal mounds very rich in algae associated with other fossils (FONTAINE *ET AL.*, in preparation).

Ages

The limestones of Thailand belong to different ages. They are prominent from Ordovician to Middle Jurassic, or from 490 to 150 million years (Ma) ago. During the Cretaceous and the Tertiary (from 135 to 5 Ma), there was no actual sea on the present land of Thailand and there is no marine limestone of these ages. During Late Tertiary and Quaternary, marine influence sporadically extended to low parts of Thailand, without important deposition of limestone.

In Krabi Province of Peninsular Thailand, calcareous mudstone is exposed at Phra Nang Bay 16 km from Krabi town. It overlies Late Eocene coal beds. Very rich in gastropods, it is an enchantment for tourists. The gastropods belong to a few species of fresh water molluscs, according to identifications made in 1949 (PITAKPAIVAN *ET AL.*, 1969).

During the Jurassic (206 to 143 Ma), sea covered only the western part of Thailand, from Mae Hong Son to Peninsular Thailand, while the eastern-northeastern part of Thailand, especially the Khorat Plateau, was a plain with meandering rivers and roaming dinosaurs. Jurassic limestone is present only in the western part of the country. It looks fresher than the older limestones. It builds up large hills in Mae Sot and Umphang areas. It is locally present in Kanchanaburi and Mae Hong Son areas. At many localities, it is rich in diverse fossils; algae, foraminifera, corals, brachiopods, gastropods, bivalves and ammonites have been noticed and occasionally described.

Triassic (248 to 205 Ma) limestone is presently known in many areas of Thailand, from the peninsula to northern and eastern Thailand. Because Triassic limestone is not different from the Permian limestone at a first glance, it was assigned to Permian in the past in some areas of central, eastern and southern Thailand. Because it is rich in diverse fossils, it has been possible to ascertain the exact age of the Triassic limestone of several areas during recent paleontological research (FONTAINE & VACHARD, 1981; FONTAINE *ET AL.*, 1993; AMPORNMAHA, 1995; FONTAINE *ET AL.*, 2001 and 2003). In the Lampang Basin of northern Thailand, the Triassic sequences are more than 3000 m thick and have been known for a long time (PITAKPAIVAN, 1955). They contain significant carbonate facies of different lithologic types. The limestone approximately corresponds to a fourth of the total section. Its fauna (bivalves, brachiopods, and ammonites) has been described. It belongs to Lower (Upper Griesbachian or the lower part of the Lower Triassic), Middle (Lower and Upper Anisian) and Upper (Middle Carnian) Triassic (CHONGLAKMANI, 1981; CHONGLAKMANI & OUDOMUGSORN, unpublished report: 14 p.).

Permian limestone (290 to 247 Ma) is very widespread all over the country, even after the correction of the ages of some limestone outcrops erroneously assigned to the "Permian Ratburi Limestone" in the past. The Permian limestone mainly belongs to Lower and Middle Permian. Upper Permian limestone is rare and does not build thick formations; it is known at a few localities in Lampang and Nan in North Thailand, in the Klaeng area in East Thailand, and from Phangnga and a few other localities (only lower part of Upper Permian) in Peninsular Thailand. The Upper Permian limestone is not diverse in fossils; it announces the great mass extinction of the end of the Permian. It is associated with shale

Table 1. Divisions of the Mesozoic. Times are the beginning of the periods in Ma.

Tertiary			65Ma
Cretaceous	Upper		99Ma
	Lower		144Ma
		Tithonian	151Ma
	Upper = Malm	Kimmeridgian	154Ma
		Oxfordian	159Ma
		Callovian	164Ma
		Bathonian	169Ma
Jurassic	Middle = Dogger	Bajocian	176Ma
		Aalenian	180Ma
		Toarcian	190Ma
		Pliensbachian	195Ma
	Lower = Liassic	Sinemurian	202Ma
		Hettangian	206Ma
	Upper	Norian	221Ma
		Carnian	227Ma
Triassic	Middle	Ladinian	234Ma
		Anisian	242Ma
	Lower	Olenekian	245Ma
		Induan	248Ma

containing peculiar brachiopods, the Lyttoniidae. Lower and Middle Permian limestones are commonly very rich in diverse fossils with prominent assemblages of fusulinaceans and corals. The Lower Permian, known for a long time at Khao Tham Nam Maholan in Loei Province, extends south to the Nam Piyang Din Waterfall area according to new findings (FONTAINE *ET AL.*, 2002; new data).

Carboniferous (354 to 289 Ma) and Devonian (417 to 355 Ma) limestones are rare in Peninsular and West Thailand. In Loei region in Northeast Thailand, they are widely exposed at many localities (FONTAINE *ET AL.* in preparation).

Carboniferous limestones are less widespread than the Permian limestones. They are in evidence in Eastern Thailand (Klaeng, Sa Kaeo and Kabinburi areas), in Central Thailand (Ban Bo Nam area east of Lam Narai, Noen Maprang and Chon Daen areas west and southwest of Petchabun), in Northeastern Thailand (at many localities of Loei Province), in Northwestern Thailand (between Mae Hong Son and Chiang Dao as well as north of Chiang Dao), in Western Thailand (northwest of Kanchanaburi) and in the southern part of Peninsular Thailand. *Fusulinella* has been very recently discovered in a limestone lens included in shale near Nam Piyang Din Waterfall (new data). Accordingly, this new locality (17°03'21"N, 101°44'45"E) belongs to an age corresponding to upper Middle Carboniferous; the Carboniferous was previously unknown in that area. In Thailand, Lower Carboniferous is known at a greater number of localities than Middle and Upper Carboniferous. Lower Carboniferous fossils have been collected from limestone in Peninsular Thailand as early

Table 2. Divisions of the Paleozoic

Permian	Upper = Lopingian	Changhsingian	252Ma
		Wuchiapingian	256Ma
	Middle = Guadalupian	Midian	259Ma
		Murgabian	262Ma
		Kubergandian	264Ma
	Lower = Cisuralian	Kungurian	266Ma
		Artinskian	269Ma
		Sakmarian	282Ma
		Asselian	290Ma
Carboniferous	Upper =Upper Pennsylvanian	Gshelian	296Ma
		Kasimovian	303Ma
	Middle=Lower Pennsylvanian	Moscovian	311Ma
		Bashkirian	323Ma
	Lower = Mississippian	Serpukhovian	327Ma
		Visean	342Ma
		Tournaisian	354Ma
Devorian	Upper	Famennian	364Ma
		Frasnian	370Ma
	Middle	Givetian	380Ma
		Eifelian	391Ma
	Lower	Emsian	400Ma
		Pragian	412Ma
		Lochkovian	417Ma
Silurian		Pridoli	419Ma
		Ludlow	423Ma
		Wenlock	428Ma
		Llandovery	443Ma
Ordovician		Ashgill	449Ma
		Caradoc	458Ma
		Llandeilo	464Ma
		Llanvirn	470Ma
		Arenig	485Ma
		Tremadoc	490Ma
Cambrian	Upper		
	Middle		
	Lower		543Ma

as 1899. Since then, other localities have provided Lower Carboniferous fossils, but Middle and Upper Carboniferous limestones remain unknown in this part of the country.

In 1969, it was believed that no definite Devonian fossil had been found in Thailand (PITAKPAIVAN *ET AL.*, 1969). In fact, a single fossil had been mentioned in 1961 (FONTAINE, 1961, p. 216); it was at a locality in Nong Bua Lamphu Province. Since 1980, diverse Devonian fossils have been collected from limestone widespread in the Loei region (Loei and Nong Bua Lamphu Provinces). They consist primarily of corals and stromatoporoids (FONTAINE *ET AL.*, 1981; FONTAINE & TANTIWANIT, 1987; FONTAINE *ET AL.*, 1990). Devonian limestone is less important and widespread in West Thailand from Chiang Mai to Satun and it does not contain the diverse faunas of the Loei region. Devonian conodonts have been reported in Mae Sariang area where they are associated with fishes. West of Thoen, Devonian limestone has been described in Mae Ping National Park (BURRETT *ET AL.*, 1986). Devonian trilobites and conodonts have been collected from limestone of Satun Province (LONG & BURRETT, 1975), trilobites and tentaculites (HAHN & SIEBENHUNER 1982) as well as conodonts (SAVAGE & SARDSUD, 2003) from calcareous rocks of Thong Pha Phum area in Kanchanaburi Province, tentaculites from a limestone lens along Huai Song Song in the National Park north of Thong Pha Phum (FONTAINE *ET AL.*, 1988).

Silurian (443 to 418 Ma) is of relatively short duration. Limestone is not prominent in the Silurian sequences of Thailand. It has been mentioned in Northeast, West and Peninsular Thailand. In 1969, Silurian fossils were known only in shale (PITAKPAIVAN *ET AL.*, 1969).

Ordovician (490 to 444 Ma) limestone is widespread in western Thailand, from Mae Hong Son to the Malaysian border. It has provided diverse fossils. In 1969, cephalopods, gastropods, brachiopods and trilobites were already reported in the Ordovician of southern Thailand (PITAKPAIVAN *ET AL.*, 1969). Later on, Lower to Middle Ordovician limestone with argillaceous layers has provided a diverse fauna in Satun Province, Thailand; the fauna included trilobites, nautiloids, gastropods, brachiopods and ostracods. The limestone had been deposited in peritidal to deeper waters (WONGWANICH *ET AL.*, 1990). Other localities have been described.

The ages indicated in Tables 1 and 2 are those of the bases of the stages. They are average ages, based on slightly different results obtained from different isotopic systems. Paleontological investigations are focussed on well-preserved sediments, and absolute ages are obtained from volcanic ashes or layers. Nevertheless, results from the same geologic horizons can provide a better understanding of the rapidity of the evolution of the living world. Additional research on radiometric dating of volcanic layers is continuously improving the precision of the ages.

BIODIVERSITY

Disturbance of present environments can reduce the biodiversity of the present-day ecosystems and become a challenging problem of more than academic interest. At a few localities of Thailand, geologists and other scientists have observed the negative results of mangrove destruction, leading to seashore erosion and loss of land for farmers, loss of habitat for some species and loss of reproduction area for other species. Mangroves are a type of vegetation growing under the stress of complex tidal movements. They are well-known in present-day tropical zones, but are geographically restricted. They are difficult to recognize in sediments older than the Cenozoic because they are easily destroyed. In Singapore, loss of habitat by anthropogenic changes has produced a wide range of local extinctions (BROOK *ET AL.*, 2003). Fish stocks are declining, at least in some seas, partly but not entirely, due to overfishing. In some areas, fish stocks have failed to recover when fisheries were closed. In 2002 off the Oregon coast, the upwelling of water poor in oxygen killed great quantities of crabs and fishes (GRANTHAM *ET AL.*, 2004). Some species of deer and birds (moa of New Zealand, dodo of Mauritius) have disappeared. The worldwide decline of coral reefs calls for an improved understanding of the ecological processes that underlie reef resilience (BELLWOOD *ET AL.*, 2004). About 70% of North American large mammal species were lost at the end of the Pleistocene, a response to climate change (GUTHRIE, 2003). Vegetation locally changes in composition. Increasing carbon dioxide in the atmosphere gives a competitive advantage to fast growing plant species at the expense of the native vegetation. Scientists have discovered that knapweed grown in a sterile liquid secretes a chemical (catechin) from its roots that kills other plants, allowing this species to invade the American West (ACHENBACH, 2004). In 1982, an imported alga (*Caulerpa taxifolia*) started to invade the Mediterranean sea bottom south of France and reached Italian and Spanish coasts by 1992. Highly toxic, it does not interest herbivores. It disperses rapidly, eliminating many other plant and animal species (MEINESZ, 1999). A scenario for 2050 foresees important shifts in the distribution and abundance of species because of climate fluctuation (THOMAS *ET AL.*, 2004). Highly endangered species will be most vulnerable to loss of their environments. Natural mechanisms can change productivity and population dynamics and ecosystems are vulnerable to fluctuations. Wildlife conservation becomes a complex problem, especially when it spreads from one country into another (SRIKOSAMATARA & SUTEETHORN, 1994). The present-day ecologists can test how the organisms are affected by each other and by their environments. They can measure and evaluate the physical factors controlling the environments. They can map patterns of biodiversity. Paleontologists lack that luxury; their analysis is a more imprecise art. Their conclusions are partly based on comparisons with present-day analogous examples; as elsewhere in geology, the present is the key to the past. For instance, it is difficult to know with a great precision the complete food web of an ecosystem of the past. However, our understanding of the evolution of the living world has increased and our vision of paleoecology has progressed.

Studies of the remote past show successions of floras and faunas on a time scale of millions of years. They give a deep-time perspective on biological events. All the limestones of Thailand were not deposited in exactly the same environments. Biodiversity has multiple facets. In order to give a general picture of this biodiversity, information will be given on the diversity of the fossils, their stratigraphic ranges, the changes in their populations with geographic distribution, and the dramatic events of their history.

The Fossils

The first important discoveries of fossils in Thailand date back to 1899. A few molluscs and a foraminifer were found in Chon Daen area in Central Thailand by an officer of the Forest Department; they were studied by the British Museum and were assigned to Carboniferous. They actually belong to Lower Permian. The report of this first discovery was published in the *Bangkok Times Weekly Mail* of 7 August 1900 and was forgotten. In 1924, N. B. Garrett, interested in old newspapers, found the report and suggested that it be reprinted in the *Journal of the Siam Society* (vol. 18: 63–64). Also in 1899, Lower Carboniferous fossils (cephalopods, bivalves, brachiopods, trilobites and a fragment of Tabulata) were collected from Phatthalung area by a Cambridge expedition; later on, they were described (REED, 1920).

The great majority of paleontological studies have been carried out during the last 50 years. They have established the biostratigraphy of Thailand and allowed international correlations over very long distances. Among Thai geologists involved in the first paleontological studies, K. Pitakpaivan is well known in particular because of his publications on fusulinaceans. In 1966, he described fusulinids collected prior to 1957 and mentioned "the future possibility of using fusulines in distinguishing faunal zones in the differentiation of the Rat Buri limestone" (PITAKPAIVAN, 1966, p. 4). Other geologists have been partly forgotten, although they strongly stimulated paleontological research in the 1950s and 1960s, for instance V. Sethaput, S. Buravas, M. Veeraburas, D. Bunnak, S. Kaewbaidhoon and A. Hongnusonthi.

The aim of this paper is not to give long boring lists of the fossils found so far in Thailand, but to illustrate the diversity of the fossils with occasional mention of the names of particular fossils.

Algae

Algae are locally in great abundance. They are more common than indicated in the published literature, because they have been studied only occasionally. Green algae (Dasycladaceae) indicate a shallow water environment because they need strong light to survive. Some algae are good stratigraphical markers. *Tubiphytes* is a problematical type difficult to assign to a systematic group; it is sometimes regarded as an alga. It is widespread and in abundance in Carboniferous and Permian limestones of Thailand. It occasionally acts as an incrusting and binding organism. It is prominent at many localities. *Renalcis*, another problematical form, has been found in Devonian limestone at two localities of Ban Chok Chai area in Northeast Thailand (FONTAINE *ET AL.*, 1990). It is common in the Devonian of Western Australia and is known in Europe and Canada.

A Jurassic alga, *Holosporella siamensis* Pia, was described as early as 1930; it had been collected at the Burmese border near Mae Sot from a bed supposed to be of Upper Triassic age (PIA, 1930), an age not confirmed by recent studies. Later on, this alga was found at Jurassic localities in Thailand and other countries. It mainly belongs to Middle Jurassic; it has been rarely mentioned in Upper Jurassic (BASSOULLET, 1988).

Algae are widespread in the Triassic limestones of different areas of Thailand, from Peninsular Thailand to East and Central Thailand. They belong to several genera (VACHARD, 1988; ADACHI *ET AL.*, 1993; FONTAINE *ET AL.*, 1996).

Algae have recently been discovered at Khao Ma (14°09'00"N, 99°07'40"E; samples T8540 to T8547), a limestone hill 186 m in elevation 5 km northwest of Amphoe Sai Yok and the new Mahidol University campus. They are locally the dominant framework constituent of the limestone of this hill. They apparently belong to a single species. They are not associated with foraminifera in the material which has been collected so far; see Figure 10d (preliminary information before the detailed study).

Permian algae are diverse and abundant at many localities. They have been studied in detail in Saraburi where 64 species have been described (ENDO, 1969), but they occur all over Thailand and have been mentioned in many publications, occasionally with precise identifications and photographs. *Mizzia* is a green alga found at many Permian localities of Thailand.

In Middle Carboniferous rocks in the Loei area, algae (*Beresella* and others) are very abundant and are the dominant framework constituent of the limestone. During their life, they grew erect and probably looked like a meadow of sea grass. Some are presently still in their living positions. Most have been broken and the debris have accumulated to form algal mounds (Fontaine et al. in preparation). The alga *Koninckopora* has been found in Northeast, East, Central and Northwest Thailand. It has a quite narrow stratigraphical range, belonging to the upper part of Lower Carboniferous, mainly Middle-Upper Visean.

In the Lower Devonian of Ban Muang in Nong Bua Lamphu Province, green algae (*Lancicula*) are locally in abundance. This type of algae is not very widespread in the Devonian of the world, but is known in several countries from Austria to Australia.

Radiolarians

Devonian, Carboniferous, Permian and Triassic radiolarians have been extracted from chert and siliceous shale at several localities of northern, northeastern and southern Thailand. Studies of radiolarians from limestone are rare exceptions.

Radiolarians have been recovered from a thin-bedded limestone at Khao Chiak near Phatthalung, southern Thailand. They were well-preserved, associated with conodonts (SASHIDA & IGO, 1992); they indicate an age ranging from Lower Triassic (latest Olenekian) to the lowermost Middle Triassic (earliest Anisian). Lower Triassic radiolarians have also been found at another limestone locality of Phatthalung area (SASHIDA *ET AL.*, 1998).

Foraminifera

This group of protozoans is so diverse that it is difficult to give a complete information about them. They rank high in terms of usefulness for age determination. They have been studied by several paleontologists and have been described in a large number of papers; the main authors are: Pitakpaivan, Toriyama, Igo, Ingavat, Vachard, Bassoullet, Ueno, Charoentitirat. Permian foraminifera, including smaller foraminifera and fusulinaceans, have been extensively studied in Central Thailand and also in other parts of Thailand. Carboniferous, Triassic and Jurassic foraminifera are known in a much smaller number of publications. Foraminifera of other ages are almost unknown. In the Lower Paleozoic all over the world, they are actually not diverse and are mostly simple tubular or globular forms. In Middle-Upper Devonian, they show a first radiation. No important assemblage has been noticed so far in the Devonian of Thailand. Calcispheres are a group of microfossils that have been described as "single-chambered foraminifera"; they are widespread in the Carboniferous and Permian limestones of Thailand.

Jurassic foraminifera were described for the first time in Thailand in 1976. They were included in limestone samples collected from the northern part of Kanchanaburi Province (HAGEN & KEMPER, 1976; KEMPER, 1976). Later on, Jurassic foraminifera were discovered in Mae Sot and Umphang areas (BASSOULLET, 1988 and 1994). These foraminifera belong to the following genera: *Gutnicella, Haurania, Mesoendothyra, Timidonella, Bosniella, Spiraloconulus* and other less important genera. They suggest Lower–Middle Jurassic ages. *Timidonella* has also been mentioned in Jurassic limestone of Mae Hong Son area.

Triassic foraminifera are small and cannot be easily noticed in the field. Because of that, they have not been considered valuable for many years. Their recent discovery at several localities of Thailand has changed our ideas about these fossils. They have been found near Nan (FONTAINE *ET AL.*, 2001), in Kanchanaburi Province (KEMPER *ET AL.*, 1976), in Uthai Thani area of Central Thailand (FONTAINE *ET AL.*, 2000), in Klaeng area (FONTAINE & VACHARD, 1981) and near the Cambodian border in East Thailand (FONTAINE *ET AL.*, 1996), at several localities (southwest of Songkhla, in Trang, Phatthalung, Phangnga and Chumphon areas) of southern Thailand (FONTAINE *ET AL.*, 1993).

Permian foraminifera are widely distributed in Thailand. They are very diverse and they are good index fossils. They have been described in many papers published during the last 40 years. As early as 1969, 41 species of fusulinaceans were already known in Thailand (PITAKPAIVAN *ET AL.*, 1969). In contrast with other foraminifera which are small, some fusulinaceans are easy to see in the field with the naked eye. When limestone is polished, they may adorn some pieces of beautiful marble. In Peninsular and West Thailand, Permian fusulinaceans are not diverse and are distributed in only a part of the Permian. Elsewhere, they are present in all the Permian, especially from Asselian to Midian (Lower Midian is more widespread than Upper Midian), and display a high diversity. They provide a precise biostratigraphic zonation of the Permian. They are common in the Lower Permian of Central, Northeast, North and Northwest Thailand. They are abundant in the Middle Permian all over Thailand. A very good section, rich in fusulinaceans ranging from the upper part of the Lower Permian (*Misellina* horizons) to almost the end of the Middle Permian (*Colania douvillei* horizon), has been described from the Saraburi area, mainly at Khao Prong Prab and partly at Khao Khao and Khao Imot (see table 4 in the following paragraph on the stratigraphic ranges of the fossils); eleven biozones have been reported (TORIYAMA, 1976; TORIYAMA & KANMERA, 1979; TORIYAMA, 1984). The top of Middle Permian (Upper Midian) contains *Lepidolina*, a genus found at several localities of Sakaeo Province (PITAKPAIVAN & INGAVAT, 1980) and at Khao Tham Yai east of Lomsak in Northeast Thailand (FONTAINE *ET AL.*, 2002). During Upper Permian, fusulinaceans are known only in a few small areas of North and East Thailand; they are small. Outside the fusulinaceans group, a small foraminifera, recently described as *Sphairionia* Nguyen 1989 and widespread in Thailand, deserves special mention because it indicates a high horizon of the Permian near the boundary between Middle and Upper Permian. In March 2003 between Kanchanaburi and Thong Pha Phum, this genus was found in the bedded limestone of Khao Yai at Wat Tham Phrommalok (sample T8514; 14°13'05"N, 99°08'15"E; new data) in the area of Mahidol University campus. It is associated with *Tubiphytes*. At the top of a limestone hill (14°05'42"N, 99°16'09"E; samples T8519 and T8520; new data) near the Buddhist Temple of Ban Phu Plu along the road from Kanchanaburi to Thong Pha Phum, the limestone beds are packed with *Rectostipulina*, a small elongated foraminifer which indicates an Upper Permian (Wuchiapingian) age, but is not perfectly preserved. At the foot of the same hill about 30 m below the *Rectostipulina* horizon, limestone beds are rich in fusulinaceans including *Eopolydiexodina* (FONTAINE *ET AL.*, 1988, p. 35–36). Genus *Rectostipulina* Jenny-Deshusses 1985 is a very peculiar foraminifer (FONTAINE & NGUYEN, 1989). It has been found at five localities of the Sai Yok – Thong Pha Phum area; it has also been collected from Khao Khan Ban Dai northeast of Prachuabkhirikhan, where it is associated with other important foraminifers: *Hemigordiopsis, Codonofusiella, Dagmarita* and *Paradagmarita.*

Publications on the Carboniferous foraminifera of Thailand are fewer than publications on Permian foraminifera. They start in 1972 with a description of Middle–Upper Carboniferous foraminifera found in limestones of the Wang Saphung area in Loei Province (IGO, 1972; see Table 3 in the following lines of this text). Later on, Middle–Upper Carboniferous foraminifera were found at many other localities of Loei Province as well as Lower Carboniferous foraminifera; 40 species have been reported in the lower part of Middle Carboniferous: Upper Bashkirian (VACHARD, 1990; FONTAINE *ET AL.*, in preparation). Lower, Middle and Upper Carboniferous foraminifera have been discovered at many localities between Mae Hong Son and Chiang Dao as well as north of Chiang Dao. Foraminifera, associated with corals and belonging to the upper part of Lower Carboniferous (Visean), occur north of Klaeng in East Thailand. Only Lower Carboniferous foraminifera have been found in Peninsular and West Thailand. Foraminifera (chernyshinellid) belonging to the lower part of Lower Carboniferous (Tournaisian) have been collected from a locality in a national park north of Kanchanaburi (FONTAINE & VACHARD, 1987).

Corals

Corals are in abundance at many limestone exposures in Thailand. They are locally contributors to the building of topographic prominences or reefs, for instance in the Devonian of Northeast Thailand. In other areas, they are restricted to limestone beds, for instance the Middle Carboniferous bed of Ban Na Charoen in Northeast Thailand rich in *Lublinophyllum* and some Permian limestone beds along the road from Saraburi to Lam Narai (near Km 10). At other localities, they are scattered in the limestone. Their distribution in time and space has been presented in a recent paper (FONTAINE *ET AL.*, 2003).

In the past, corals of the Atlantic were rarely considered endemic to this ocean; they were said to belong to the same lineages as the corals of the Pacific because of morphological similarities. Analyses of mitochondrial and nuclear genes have shown that this assumption was incorrect; many Atlantic corals belong to a previously unrecognized lineage (FUKAMI *ET AL.*, 2004). The microstructures of coral skeletons actually substantiates this conclusion. Fossil corals must be studied according to their morphology, but also according to their microstructure without forgetting possible diagenetic changes.

Jurassic corals are in great abundance at some localities of the Mae Sot and Umphang areas; they locally reach 1 m in diameter (BEAUVAIS, 1988; BEAUVAIS & FONTAINE, 1993). They have been studied by L. Beauvais, especially in a major publication of 1988; 49 species have been described. They were collected from a fine-grained limestone, characteristic of a moderately quiet environment.

Triassic corals have been found from Peninsular to northern Thailand. In North Thailand, three species have been recorded from the Kang Pla Limestone at the Ban Pha Khan antimony mine in Phrae Province (PITAKPAIVAN *ET AL.*, 1969). Triassic corals are abundant and diverse at some localities near Uthai Thani in central Thailand (FONTAINE *ET AL.*, 2000), of Nan area in northern Thailand (FONTAINE *ET AL.*, 2001) and of Sakaeo Province near the Cambodian border (FONTAINE & SALYAPONGSE, 1997). From Khao Phanom Wang, about 9 km northwest of Phatthalung in Peninsular Thailand, solitary, fasciculate and massive corals have been considered important builders of an Upper Triassic (Carnian) limestone (ADACHI *ET AL.*, 1993).

Permian corals have been found all over Thailand and have been observed at more than 100 localities. They are abundant and diverse at many localities of Central, Northwest, North, Northeast and Southeast Thailand. They locally consist of large fasciculate or massive colonies, reaching 1 m in diameter (FONTAINE *ET AL.*, 1994; FONTAINE, 1999). They are less diverse in Peninsular Thailand (FONTAINE, 1989). Outside Peninsular Thailand where corals are unknown in Lower Permian, they range from Lower to Upper Permian with a decline after the end of Middle Permian. More than 90 species of Tabulata and Rugosa have been identified.

Carboniferous corals are locally in abundance. They consist of dendroid Tabulata and solitary, fasciculate, and massive Rugosa. They are known in limestones ranging from Lower to Upper Carboniferous in the Loei region (FONTAINE *ET AL.*, 1991, 1995). They occur in Lower Carboniferous of Central Thailand (west and southwest of Phetchabun), of East Thailand (Klaeng and Kabinburi areas) and of Northwest Thailand (Amphoe Pang Mapha and Ban Na Wai areas). One group of corals is easy to recognize; it belongs mainly to *Hexaphyllia*, a genus indicating the upper part of Lower Carboniferous. Middle-Upper Carboniferous limestone lenses have also provided corals east of Lam Narai in Central Thailand.

In the Loei region (Loei and Nong Bua Lamphu Provinces) of Northeast Thailand, Devonian limestone is widespread and builds up many hills. It contains diverse coral faunas belonging mainly to Lower and Middle Devonian. These corals consist of branching (*Thamnopora, Cladopora*, etc.) and massive (*Favosites, Alveolites, Heliolites*, etc.) Tabulata, solitary (*Solipetra, Sinospongophyllum*, etc.), branching (*Dendrostella, Thamnophyllum*, etc.) and massive (Phillipsastraeidae, *Endophyllum* and others) Rugosa (FONTAINE *ET AL.*, 1981; FONTAINE *ET AL.*, 1990). They are associated with stromatoporoids which are in abundance at many localities.

In Northeast Thailand, Silurian corals (Tabulata and solitary Rugosa) have been reported from two localities north of Nam Som: 5 km south of Ban Nong and near Ban Na Tum 33 km south of Ban Nong (SAKAGAMI & NAKORNSRI, 1987).

A few coral specimens have been reported in Middle–Late Ordovician of Chiang Mai area (HAHN & SIEBENHUNER, 1982). Corals associated with trilobites and brachiopods have been mentioned in an Upper Ordovician limestone of Thong Pha Phum area (HAGEN *ET AL.*, 1976).

Sponges

Sponges are important and widespread organisms of the present-day seas, with an estimated 10,000 species alive today. They were also abundant in the past. According to their present systematics, they include Stromatoporoidea.

Calcareous sponges are common in many limestone exposures of Thailand. Some authors consider that Chaetetidae (in the past assigned to the Tabulata: corals) and *Solenopora* (red alga in many old publications) are sponges (for instance, see RIDING, 2004). In Thailand, Chaetetidae have been described at many localities belonging to Devonian and Carboniferous. *Solenopora*, as originally defined, is known only in the Ordovician and possibly the Lower Silurian. The "*Solenopora*" specimens found in Thailand are apparently not authentic

Solenopora. They belong to ages younger than Silurian; they have been found at several Triassic localities. They may actually be red algae; they need to be re-identified.

Many kinds of calcareous sponges have been noticed, especially in the study of thin sections from limestone samples of Thailand. They have been cursorily mentioned in diverse publications, without detailed study. They are abundant in some limestones and because of that, some authors have described "sponge limestones", for instance in the Triassic of Phatthalung area (ADACHI *ET AL.*, 1993). A sponge species (*Cladocoropsis mirabilis*) has been reported at a few Jurassic limestone exposures south of Umphang (BEAUVAIS, 1988). Several species of Upper Permian sponges have been discriminated at a limestone locality of Phrae Province in North Thailand and the limestone has been considered "reefal" (SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1993). The sponges were associated with foraminifera including *Colaniella*, bryozoans, gastropods and echinoderms.

Stromatoporoids are very abundant and diverse in the Devonian limestone of the Loei region; they are important framework builders of the Devonian reefal structures of this region. They are dendroid or massive. Where they occur, they provide precise information on the age of the limestone exposures (FONTAINE *ET AL.*, 1990). The local abundance of the slender stick-like Amphipora suggests the presence of dense "*Amphipora* meadows". In addition, stromatoporoids have been mentioned at several Ordovician localities of Peninsular Thailand (WONGWANICH & BURRETT, 1983; BURRETT & STAIT, 1985). Stromatoporoids have been considered to be the main reef-building organisms in the Devonian of Central Europe.

Bryozoans

Bryozoans are common fossils at many localities. The fan-shaped Fenestellidae are easy to recognize in the field; they appeared in Middle Ordovician and disappeared at the end of the Permian.

Carboniferous and especially Permian bryozoans of Thailand were actively studied between 1964 and 1980. They were collected from shale, siliceous rock, calcareous rocks and occasionally limestone, especially of Peninsular Thailand (for instance, see SAKAGAMI, 1968; PITAKPAIVAN *ET AL.*, 1969). Bryozoans occurring in calcareous facies are commonly associated with brachiopods and crinoids; they are less strongly associated with fusulinaceans (SAKAGAMI, 1976).

Brachiopods

Brachiopods are mainly inhabitants of the shallow sea bottom. They are important fossils of Thailand, but they have been collected more often from clastic rocks than from limestone (see Fig. 8). Because of that, they are mentioned only briefly in this paper. Brachiopod spines have been noticed in many limestone thin sections from different Paleozoic localities.

Jurassic brachiopods are especially abundant in marly limestones and limestones of Umphang area (MEESOOK, 1994).

Lyttoniidae are an interesting group of brachiopods that have been found in the Upper Permian of North and East Thailand, but in shales close to Upper Permian (Changhsingian) containing *Palaeofusulina*, a fusuline indicative of the top of the Permian. Brachiopods

Figure 7. Ko Si Chang. Fossils visible at the surface of a limestone exposure, but difficult to extract.

Figure 8. Near Khao Than in Sawi District of Chumphon Province, along the sea shore (10°10'25"N, 99°10'53"E). Brachiopods are easy to see and collect in the shale and calcareous shale.

9a

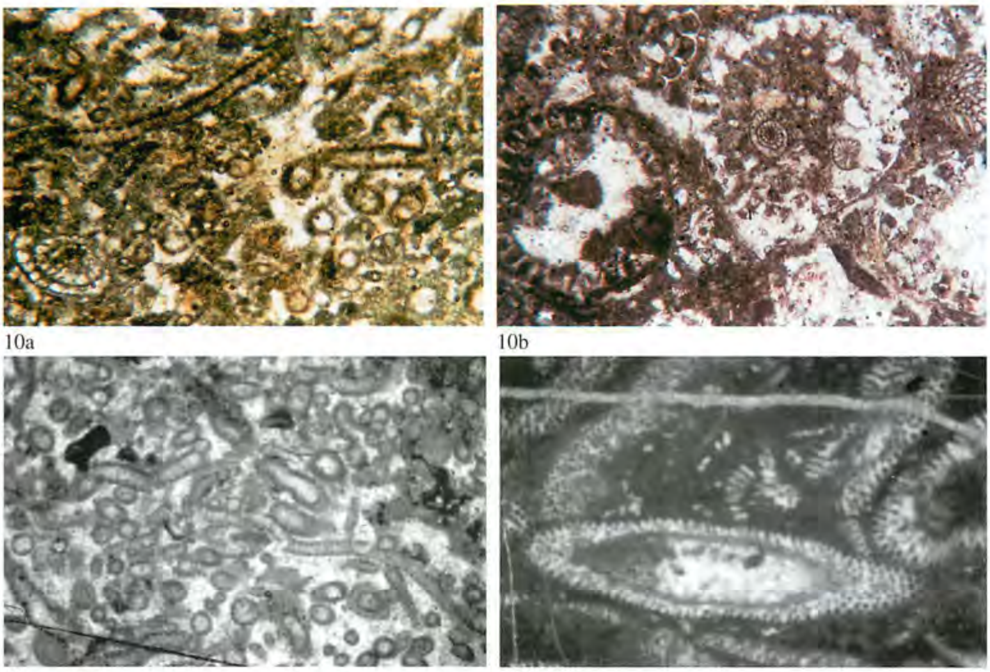
9b

9c

Figures 9. Corals seen in the field at the surface of limestone exposures. a: hornshaped solitary coral. b: branching coral. c: massive coral; corallites are prismatic, septa and columella are clearly visible.

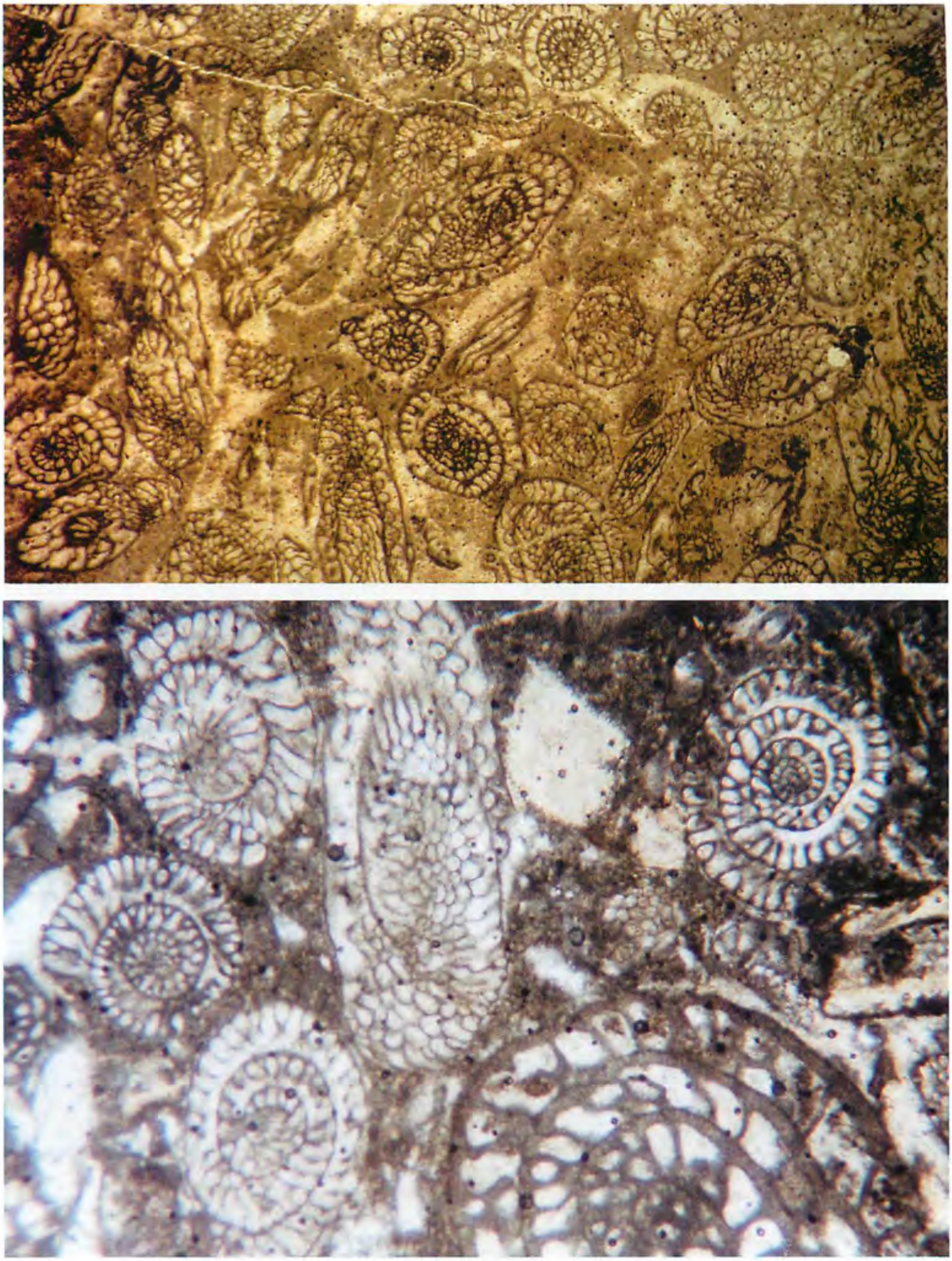
very peculiar in shape with an elongate bilobate outline and an anterior incision have been found in shale north of Nan in North Thailand (MEESOOK & WANAPEERA, 1983). They belong to *Permianella*, an Upper Permian genus known from Japan to Iran. This group of brachiopods has been assigned to Lyttonioidea since its first discovery in Afghanistan. Middle Permian brachiopods have been discovered in a calcareous mudstone south-southwest of Phetchabun (YANAGIDA, 1964). In Peninsular Thailand, Early Permian brachiopods have been found in pebbly mudstones at several localities; they have also been collected from sandstone 21 km north of Chumphon. From a general point of view, brachiopods have provided information on the ages of rock exposures of Peninsular Thailand. Their diversity is low in this part of the country and they show strong affinities with Gondwana faunas, indicating that they thrived in a cool temperate environment (SHI & ARCHBOLD, 1995). Middle Carboniferous brachiopods of Loei area in Northeast Thailand have been collected from shales and tuffaceous shales. Middle Ordovician brachiopods have been described in calcareous shale from Satun Province.

Brachiopods from some Permian limestone outcrops of Peninsular Thailand have received some attention with four papers devoted to systematic studies, for instance the limestone of Khao Phrik in Ratburi area (YANAGIDA, 1970; see the overview of WATERHOUSE, 1981). A rich brachiopod fauna has been described from Khao Tham Nam Maholan in Loei Province (YANAGIDA, 1967). Middle Permian and Lower Devonian brachiopods have been found in limestones of Thong Pha Phum area (HAGEN & KEMPER, 1976).



10a 10b 10c 10d

Figures 10. Abundant algae occasionally associated with a few fusulines. a: Beresellid algae (longitudinal and transverse sections) belonging to the Middle Carboniferous limestone of Loei Province. Sample T7644 from Phu Bo Bit (17°30'14"N, 101°46'11"E). b: Algae (Dasycladaceans; transverse sections) in a limestone belonging to the top of Middle Permian. Sample T6260 from Khao Tham Yai (16°56'41"N, 101°30'50"E) between Lomsak and Nam Nao. c: Middle Carboniferous algae of a limestone cropping out 1 km south of Ban Saat (17°39'09"N, 101°50'27"E; sample T7816) in Loei Province. d: Algae in a bedded limestone of the top of Khao Ma in the area of Mahidol University campus (14°09'00"N, 99°07'40"E; sample T8542).



Figures 11. Limestones packed with fusulines. This type of limestone very rich in fusulines is common in Thailand. a: The fusulines include *Ruzhencevites* and indicate a Lower Permian (Asselian) age. Thin section from sample T7542 collected from Phu Sam Pha (17°04'37"N, 101°59'57"E). b: Limestone rich in fusulines including a great number of *Dunbarula* specimens and belonging to the top of Middle Permian (Upper Midian). Thin section from sample T6261 collected from Khao Tham Yai (16°56'41"N, 101°30'50"E) between Lomsak and Nam Nao. See FONTAINE *ET AL.* (2002).

Mollusca

Mollusca presently live in a great variety of environments: sea, streams, lakes, ponds and even land. They are common fossils, but they are more easily studied in shale than in limestone. They have been mentioned at many limestone outcrops of Thailand, but often without identification.

Gastropods: They occur at many limestone localities, but they are not easy to extract from this type of rock. They occur, for instance, in the Jurassic of Klo Tho (BASSOULLET, 1994), in the Triassic near the Cambodian border and in Uthai Thani area (FONTAINE *ET AL.*, 1996) and the Triassic of Phatthalung area (ADACHI *ET AL.*, 1993), in the Permian of Chon Daen area (CHONGLAKMANI & FONTAINE, 1992), in the Ordovician of Thong Pha Phum (HAHN & SIEBENHUNER, 1982), in Ordovician black calcareous shale of Satun Province (PITAKPAIVAN *ET AL.*, 1969). An Early Ordovician Gondwana snail (*Peelerophon*) is very common in the Shan-Thai Block. Gastropods are commonly more difficult to use for stratigraphy than other fossils such as the foraminifera.

Bivalves: Unbroken bivalves shells, conjoined or disjointed, are well-preserved at some localities. They have been recognized as good index fossils, especially for the Triassic and the Jurassic, but they have been collected commonly from rocks other than limestone. *Claraia* and *Halobia* are well known fossils of the Lower (*Claraia*) and the Upper (*Halobia*) Triassic. In the Jurassic of Thailand, they are abundant and diverse; 39 bivalve species have been identified, from Mae Hong Son to Nakhon Si Thammarat (MEESOOK, 1994). In Mae Hong Son area, 20 species have been found at the same locality of Ban Pa Lan whereas 17 species have been reported 3 km east of Ban Klo Tho. In Peninsular Thailand, a few Jurassic bivalves have been found at Chumphon River mouth in a calcareous sandstone. South of Nakhon Si Thammarat, rare Jurassic bivalves were collected from interbedded sandstone and mudstone. Bivalves occur in some Jurassic limestones, for instance in Mae Sot area.

Cephalopods: These fossils are an important element of marine faunas since the Ordovician. They are good index fossils, but they are commonly difficult to collect from limestone even though they occur in this type of rocks. Nautiloids are useful fossils throughout the Ordovician carbonates of Peninsular, western and northwestern Thailand. As early as 1958, they have been reported in southern Peninsular Thailand (KOBAYASHI, 1958; PITAKPAIVAN *ET AL.*, 1969; WONGWANICH & BURRETT, 1983). The Ordovician was a period of rapid and great differentiation for nautiloids. Ammonoids have been described at many localities of Thailand; they have been collected mainly from shale, siltstone and calcareous shale or calcareous siltstone. They will be briefly mentioned in this paper because some specimens have been found in calcareous rocks, argillaceous limestone, and exceptionally pure limestone. Jurassic ammonites have been found in the Mae Sot area, mainly in calcareous shale (SATO, 1961; BRAUN & JORDAN, 1976). An ammonite belonging to *Dumortieria* has been collected from a Jurassic calcareous bed 3 km southeast of Klo Tho (BASSOULLET, 1994). Later on, Jurassic ammonites have been more systematically collected from many localities of Mae Hong Son, Mae Sot, Umphang and Chumphon (Khao Lak) areas; they have been identified to generic level (MEESOOK, 1994). Upper Permian ammonoids have been described at Doi Pha Phlung in North Thailand while other Permian ammonoids have been found in Loei and Muak Lek areas. Eight upper Lower to lower Middle Permian species of ammonoids have been reported in limestone at Khao

Nong Hoi, a hill near Ban Hua Krok and 3 km north-northeast of Amphoe Muak Lek (GLENISTER *ET AL.*, 1990; LIENGJARERN & ZHOU, 2002). Carboniferous ammonoids have been reported in Northwest (Ban Mae Lana) and Northeast (Loei) Thailand (ISHIBASHI *ET AL.*, 1997). Lower Carboniferous ammonoids were collected from limestone of Peninsular Thailand as early as 1899; later on, they were described (REED, 1920).

Belemnites, cephalopods belonging to Mesozoic, remain practically unknown in Thailand. "The reason why belemnites have not yet been found in the Jurassic of Thailand is that the Thai Jurassic ranges from Toarcian to Early Bajocian and during this period belemnites were not abundant in Southeast Asia and Australasia" (MEESOOK, 1994, p. 163).

Arthropods

Arthropods are invertebrates of highly varied forms. Their stratigraphical range is not homogeneous. It may be short to some extent; it may be long extending from Cambrian to present. They include groups very interesting for paleontology and stratigraphy.

Ostracods occur at many limestone localities. These fossils are minute bivalved crustaceans, ranging from Lower Ordovician to present. They are benthic faunas, still common in the present-day seas. They are quite good indicators of the differing marine environments. They have been rarely identified in Thailand. A few ostracods have been mentioned in the Permian of Nan Province, at Carboniferous–Permian localities of Northwest Thailand, at a probably Carboniferous locality north of Ban Tha Rua, at a Lower Carboniferous locality of Thong Pha Phum area, at a probably Late Devonian–Early Carboniferous locality east of Ban Tha Song Yang (HAHN & SIEBENHUNER, 1982). The assemblages are poor, restricted to 1 or 2 genera. In many papers concerning other localities, they have been mentioned without identification in limestones of different ages. Near Chon Daen at the top of Khao Sak (western end of Khao Sap Laeng), ostracodes are in abundance in Lower Permian beds (FONTAINE *ET AL.*, 1999). Well-preserved ostracods have been recently extracted from Permian limestones of the Loei–Phetchabun region. They have been identified; they belong to seven genera (CHITNARIN *ET AL.*, 2003).

Trilobites include good index fossils. They range from Cambrian to the end of the Permian and have been found at many localities of Thailand. They have been noticed in Permian limestone. They have been collected from Middle–Upper Carboniferous shales of Loei area and a new genus (*Thaiaspis*) was described as early as 1961 by T. Kobayashi. Lower Carboniferous trilobites have been reported in Phatthalung area (REED, 1920). Early Devonian (probably Emsian) trilobites were collected from a fine grained limestone in Satun Province (FORTEY, 1989). A Silurian trilobite has been collected from a calcareous mudstone northwest of Nam Som in Loei region (KOBAYASHI & SAKAGAMI, 1989). Trilobites have been described in Middle Ordovician bedded limestone of Satun Province, in Upper Cambrian sandstone of Tarutao Island (KOBAYASHI & HAMADA, 1984).

Insects started to colonize the land during the Devonian and perhaps earlier. For Carboniferous and Lower Permian continental deposits, they have been considered good stratigraphic markers and interesting for correlations between continents because they could fly very far. In Thailand, they are known as fossils in a black shale at Ban Khuan Kun between Krabi and Trang. They are common, but in a continental Mesozoic (Jurassic) rock. Insects are terrestrial organisms and are unknown so far in the limestones of Thailand.

Echinoderms

Echinoderms are exclusively marine animals. Many of them are attached to the sea bottom; others are free-moving animals.

Urchins are armoured by an external box-like skeleton, often of exceptional beauty, but easily broken by waves. Their fossils are generally reduced to small fragments and are practically impossible to study. However, strong movable spines may be present on the outside of the skeleton; such spines are common in the Middle Carboniferous of Loei Province. They are well preserved, but have not been studied yet. Urchin spines have also been mentioned in Triassic limestone near the Cambodian border (FONTAINE *ET AL.*, 1996).

Crinoids (or sea lilies) are very common in the limestones of Thailand. Fragments of their stems are even the main constituent of some limestones, then called "crinoidal limestones". They have contributed large and important quantities of lime carbonate. From a stratigraphical point of view, they are not very interesting or easy to use.

Graptolites

Graptolites are commonly known in shales, but occasionally occur in limestone. Graptolite morphology was described in 1890 after etching undistorted specimens out of limestone. They ranged from Cambrian to Lower Carboniferous and reached their climax during Ordovician and Silurian. They have been mentioned at several localities of Thailand.

Conodonts

Conodont remains are very small, tooth-like and plate-like. They cannot be seen in the field with the naked eye. They consist mostly of calcium phosphate and they may be better preserved than other fossils. They are very valuable for dating the rocks in which they occur. They went through phases of rapid evolution and are good index fossils. They are widespread in layers ranging from Upper Cambrian to the end of the Triassic, that is to say from 500 to 203 million years ago. In Thailand, conodonts have been identified or described at many localities belonging to different geological intervals.

Conodonts have been extracted from limestones of several areas of Thailand, from the peninsula to the north. Ordovician, Silurian, Devonian, Carboniferous, Permian and Triassic conodonts have been mentioned at many localities of North Thailand. They belong to many species; 22 Lower Devonian species have been identified at the same locality of Chiang Mai area (HAHN & SIEBENHUNER, 1982; CAREY *ET AL.*, 1995). In Northeast Thailand, conodonts have been collected from the Upper Carboniferous–Lower Permian limestone of Khao Tham Nam Maholan in Loei Province (IGO, 1974). In Northwest Thailand, Upper Silurian conodonts have been found in limestone outcropping between Tat Sador Waterfall and Ko Luong Waterfall, west of Thoen (BURRETT *ET AL.*, 1986). Upper Devonian (Late Famennian) conodonts have been obtained from thin limestone beds along the road from Mae Sariang to Ban Mae Sam Laep (LONG, 1993).

In Kanchanaburi Province at two localities (6 km west of Si Sawat and between Bo Ngam and Sake), limestone has yielded a Middle Triassic (Anisian) conodont assemblage (KEMPER *ET AL.*, 1976). In Thong Pha Phum area, a sequence containing conodonts is continuous from the Upper Devonian into the Carboniferous (HAGEN & KEMPER, 1976).

It has recently yielded Upper Frasnian conodonts (SAVAGE & SARDSUD, 2003). Upper Silurian and Lower Ordovician conodonts were also found in Thong Pha Phum area (HAGEN & KEMPER, 1976). Northeast of Amphoe Sang Klaburi, 16 species of Tournaisian (Lower Carboniferous) conodonts have been identified at the same locality (HAHN & SIEBENHUNER, 1982).

Conodonts have been obtained from a limestone in Satun Province; they indicate an Early Devonian age (LONG & BURRETT, 1989). In Phatthalung area, Triassic conodonts were recovered from several localities; they indicated Early to Late Triassic ages (IGO *ET AL.*, 1989; AMPORNMAHA, 1995).

Fishes

Fragments of fishes skeletons have been noticed at several localities of Thailand. They have been studied only occasionally; for instance, some fragments have been recently observed in Permian limestone of the Phetchabun area, but not studied.

In Loei Province, a single tooth (bradyodont) has been found in Lower Carboniferous limestone of Pha Chom Nang on the side of the road from Chiang Khan to Pak Chom (INGAVAT & JANVIER, 1981). Two teeth (bradyodont and shark) have been extracted from the Middle–Upper Carboniferous (considered Permian in the past) limestone of Ban Na Charoen (JANVIER, 1981).

At road cuttings (near km 27) along the road south of Mae Sariang to Ban Mae Sam Laep on the Burmese border, abundant vertebrate and conodont assemblages have been found in bluish-grey Devonian (Emsian and Famennian) bedded limestones. They are dominated by small chondrichthyan (shark) remains, but include also other fish remains; they contain cosmopolitan and endemic elements. They suggest a proximity to the western margin of east Gondwana (BURRETT, 1989; LONG & INGAVAT, 1989; LONG, 1990 and 1993).

Other Vertebrates

In 1988, an ichthyosaur was discovered by C. Chonglakmani in a weathered dolomitic limestone at Khao Thong 14 km north of Phatthalung. It was associated with poorly preserved ammonites. The limestone belongs to Lower Triassic. Primitive ichthyosaurs have been rarely found in the world. The specimen of Thailand has been described as a new genus and a new species: *Thaisaurus chonglakmanii* (MAZIN *ET AL.*, 1991).

Limestone has not yielded so far other vertebrates than fishes and ichthyosaurs, but diverse vertebrates are known at several localities of the continental Mesozoic Khorat Group of Northeast Thailand and *Dicynodon* has been found in Upper Permian sandstone near Luang Prabang (Laos), a similar Permian terrestrial sequence occurring northwest of Loei in Northeast Thailand.

STRATIGRAPHIC RANGES OF THE FOSSILS

Many groups of plants and animals lived only for a short time on the geologic time scale. Their evolutionary development has had an important significance in the geological

Table 3. Biozonation of the Middle-Upper Carboniferous of Wang Saphung area

Huai Kap Tin	Huai Luang	Ban Pha Noi	Tham Nam Maholan
			Triticites ozawai/ Paraschwagerina yanagidai
		Protriticites tethydis	
	Fusulina pulchella		
Hemifusulina thaiensis			
Beedeina paradistenta			
Profusulinella prisca timanica			
Profusulinella parva			

Table 4. Biozonation of the Permian north of Saraburi

Khao Prong Prab	Khao Khao	Khao Imot
		Colania douvillei
	Neoschwagerina haydeni	
	Afghanella schencki	
Presumatrina schellwieni	*Presumatrina schellwieni*	
Neoschwagerina simplex	*Neoschwagerina simplex*	
Maklaya sethaputi		
Maklaya pamirica		
Maklaya saraburiensis		
Misellina confragaspira		
Misellina otai/M. cf. *termieri*		
Monodiexodina shiptoni		

history of the world. They provide keys to decipher the history of the deposition of the sediments. There are very good stratigraphic markers at the genus and even the species levels because they indicate immediately the age of the rock in which they are included. Foraminifera, brachiopods, trilobites, conodonts and others are well known for that. In addition, some organisms could live in different environments and their fossils therefore occur in many rock outcrops over the world. They allow precise biozonations of sedimentary sequences (see Tables 3 and 4 for examples) as well as interbasinal to interregional correlations. Some important events, of different origins, have punctuated the organisms evolution.

The initial flowering of animal life on the earth occurred during the Cambrian, a period moderately known in Thailand because rocks of this age are exposed only in very small areas. Fossils have been found mainly in clastic rocks.

Ordovician and Silurian limestones have provided fossils at several localities of Thailand; see the paragraph on "The Fossils". In Peninsular Thailand, biozonation is more detailed. Limestones have been referred to Tremadoc and Arenig in Tarutao Island. On the mainland in Satun Province, a succession of limestones and clastic rocks ranges from Middle Ordovician (Caradoc) to Silurian (WONGWANICH *ET AL.*, 1990); it is conformably overlain by a Devonian sequence of carbonates and clastic rocks. Fossils are diverse and belong to trilobites, graptolites, nautiloids, brachiopods, gastropods and ostracodes. A thick Siluro-Devonian limestone sequence has been described west of Thoen in Northwest Thailand (BURRETT *ET AL.*, 1986).

In the Loei region, Devonian limestone is rich in diverse fossils, indicating Early and Middle Devonian ages and probably extending to the lower part (Frasnian) of the Upper Devonian. A sharp change in the environment after the Frasnian led to the disappearance of limestone deposition and the extinction of diverse faunas, probably because of the Kellwasser Crisis, a prominent perturbation observed in many countries. In West Thailand, shaly limestone has yielded Frasnian conodonts, but the search for Famennian conodonts has been so far without results (SAVAGE & SARDSUD, 2003).

The history of the Carboniferous of Loei region is complex, with sharp changes in the environments. The Tournaisian consists of chert, shale, sandstone and conglomerate. Chert has yielded Famennian to Tournaisian radiolarians. During the Visean, limestone was deposited with its diverse and rich marine fossil assemblages. After the Visean, the water disappeared because of a lowering of sea level. Continental plants developed and their imprints presently occur in shale and siltstone belonging to the boundary between Lower and Middle Carboniferous. Coal is locally present, but not in very large quantity. Gypsum occurs in other areas of Loei region. During the late part of the Bashkirian, sea invaded again the Loei region and was inhabited by diverse floras and faunas, until the end of the Carboniferous (FONTAINE *ET AL.*, 1995 and in preparation). In Moscow Basin, a sharp sea-level drop has also been observed during the Bashkirian and has been considered a response to Gondwanan glaciation (ALEKSEEV *ET AL.*, 2004). Biozonation ranging from Moscovian to Gshelian (IGO, 1972 and other recent publications). The Carboniferous strata of Loei region do not build prominent and sharp topography as the Permian limestone of the same region.

In Northwest Thailand, the Carboniferous is complete. It is largely similar to that of the Loei region.

The Permian of the world is divided into about 30 fusulinacean, ammonoid or conodont biozones (JIN *ET AL.*, 1994); the division of the Carboniferous is similar. In Thailand, fusulinaceans have been studied more extensively than ammonoids and conodonts. Other fossils were restricted to particular environments; they cannot be used for global correlations. Corals, for instance, needed warm water to thrive; they are useful only for the parts of the world which were not too far from the equator at the studied period. Permian limestone is widespread in Thailand and belongs to different parts of the Permian. It is locally packed with fusulines; see figs. 11a-b as well as the following table 4.Biozonation ranging from the upper part of Lower Permian to Lower Midian (TORIYAMA, 1984). Khao Khao and Khao Imot are two hills near Khao Prong Prab. The 3 hills are about 20 km from Saraburi, and belong to a series of hills with strong karstic topography, called the "Khao Khad Formation" and extending from Lopburi to Pak Chong.

Some fossils are very simple and do not receive the detailed study they deserve. Their study is more difficult; it must be based on oriented sections and on well preserved specimens. If the differences between the specimens are not noticed, the fossils are considered to belong to very long periods. An exception to that is a very simple fossil known at many Permian localities of Thailand; it is easy to recognize in different types of sections. Called *Sphairionia*, it has been described for the first time only in 1989 (NGUYEN, 1989). It is a globular form, small in size (0.5 to 1.5 mm in diameter), consisting of a single chamber, with bottleneck-shaped openings. At first known only in Southeast Asia, it has been discovered in other parts of the world and has a wide geographic distribution. It is presently known at several localities of Cambodia, Thailand, Malaysia, Pamir, Transcaucasia and Turkey; it has been considered a marker of the Lower Midian, belonging to the upper part of Middle Permian (PRONINA, 1996).

The oldest fossils of a group are commonly more simple than the younger ones; evolution leads to more complex structures. However, empirical data do not always follow this principle. In 1912 (C R Acad Sc. 154: 1548–1550), Deprat studied the fusulinaceans of Vietnam, Laos and Yunnan, and found some "primitive" fusulines. He established the new Genus *Palaeofusulina* and assigned it to Early Carboniferous because it looked primitive. Now, we know that this genus is the youngest, belonging to the top of the Permian and corresponding to a period of decline of the fusulines before the great mass extinction of the end of the Permian.

The first Triassic fossils found in Thailand were discovered 8 km southeast of Chiang Rai; they were identified as early as 1923. In 1952, Triassic fossils were found in shale in Lampang Province (PITAKPAIVAN, 1955). This new discovery stimulated new research in that area; highly fossiliferous limestone was found. After 1960, Triassic sediments, largely marine, became evident in many parts of Thailand. They have yielded diverse faunas (foraminifera, corals, brachiopods, bivalves and ammonites) associated with algae; they range from Lower Triassic to Carnian, locally to Lower Norian. They have been divided into several formations. Carbonate facies are common.

The Jurassic is divided into formations ranging from Upper Hettangian to Callovian (top of Middle Jurassic), with the Toarcian and the Aalenian more widespread than the other parts of the Jurassic (MEESOOK, 1994). The occurrence of Upper Jurassic remains very doubtful and, if true, has a strongly limited geographic distribution.

PALEOGEOGRAPHY

Since the 1970s, the geological history of Southeast Asia has been reviewed in the context of the plate-tectonic theory (METCALFE 2002). Thailand is presently considered to be made up of an amalgamation of at least 2 main blocks derived from Gondwanaland at different periods: the Shan-Thai Block derived in the late Early Permian and the Indochina Block derived in the Devonian. The position of the boundary between these two blocks is still the subject of controversy.

The Shan–Thai Block has been supposed to be part of the Gondwanaland until its rifting at the end of the Early Permian. It consists of Peninsular Thailand and extends to the north into Myanmar (and even to the Baoshan Block of west Yunnan in southwest China; see for instance WANG *ET AL.*, 2001) and to the south into Peninsular Malaysia. Its faunas are very different from those of the Indochina Block especially those of the Carboniferous and the Permian. Cold water environments have been found in the Lower Permian and are well documented (see below). The "Shan–Thai" name was proposed by BUNOPAS & VELLA (1978) as the Shan–Thai Craton which extended through a large part of Thailand. They described the north-south trending geological structures of Thailand and tried to incorporate them into a new plate tectonics vision of Southeast Asia. Later on, it has been suggested to replace "Shan–Thai" by the name "Sibumasu", indicating more clearly the geographic extension of the block.

The Indochina Block (= Indosinian Craton of BUNOPAS & VELLA, 1978) includes the eastern part of Thailand and extends to Cambodia, Laos, Vietnam and the eastern part of Peninsular Malaysia. Its faunas indicate warm water environments throughout the Late Paleozoic. Limestone is widespread in the Carboniferous and the Permian exposures of the Indochina Block. It is unknown in the Middle–Upper Carboniferous as well as the lowest part of the Permian of the Shan–Thai Block.

In the past, the Permian limestone of Thailand was called the "Ratburi Limestone" all over the country (BROWN *ET AL.*, 1951). The term "Ratburi Limestone" is presently restricted to limestone exposures of Peninsular and West Thailand. Limestone of the other parts of Thailand is called "Saraburi Limestone" (BUNOPAS, 1981). The differences between these two limestones are easy to observe. Fusulinaceans may be in great number in the two limestones, but they consist of one or two species in the Ratburi limestone while they are much more diverse in the Saraburi Limestone. Corals occur in the two limestones, but their diversity is much lower in the peninsula. Among bryozoans, *Fistulipora* is quite common in Peninsular Thailand where it is represented by 12 species, some of which are known in Timor (SAKAGAMI, 1976). Permian corals of Peninsular Thailand are quite different from those of central and eastern Thailand (FONTAINE & SALYAPONGSE, 2001). Limestone is absent from the lower part of the Lower Permian in the peninsula; accordingly, it is impossible to find fusulinaceans and corals (in particular Kepingophyllidae) in the lowest part of the Permian. In addition to that, pebbly mudstones are extensive in this part of the Permian in the peninsula. They contain dropstones supposed to have been rafted by marine ice. The largest block is a granitic boulder, approximately 1 m in size, found in Phuket. A trondhjemite boulder of northwest Peninsular Malaysia has yielded a Precambrian age (STAUFFER & MANTAJIT, 1981; TANTIWANIT *ET AL.*, 1983). The pebbly mudstones have been considered glacial deposits. These beds contain cool-water fauna (WATERHOUSE, 1982). From a stratigraphical point of view, they are below the Ratburi Limestone. In Gondwanaland, a severe glaciation began at the end of Lower Carboniferous and reached its maximum near the Carboniferous–Permian boundary. In Thailand, traces of glaciation have been observed mainly at the base of the Permian. The upper part of the Carboniferous has not been clearly evidenced in Peninsular and West Thailand. The Ratburi Limestone corresponds to an improving climate. At the foot of a limestone hill in Chom Bung area, corals are few and display growth bands, whereas corals at the top of the hill are very common and devoid of bands (FONTAINE & JUNGYUSUK, 1997). The presence of growth bands appears to indicate a seasonal climate with cold and warm seasons in an older period of the Permian. The absence of growth bands suggests regular growth in a continuously warm climate at a younger time. The Shan–Thai climate became warmer after the rifting of this block from Gondwanaland and its rapid drifting northward. Provincialism is strongly indicated by a small foraminifera, *Shanita*, which has been reported at several upper

Middle to lower Upper Permian localities of Peninsular Thailand and is known to the north in eastern Myanmar up to western Yunnan. *Shanita* is unknown so far in the Indochina Block. Up to now, *Eopolydiexodina*, a fusulinid, has been reported only from Kanchanaburi Province. *Neoschwagerina, Colania, Verbeekina* and *Lepidolina* are fusulinid genera common in the Indochina Block, but apparently absent from the Shan–Thai Block. Corals such as *Ipciphyllum* and *Pseudohuangia*, widespread on the Indochina Block, are unknown in the Shan–Thai Block. The Permian of Australia is extensive; it locally offers complete marine sequences. It does not contain fusulinids or compound corals (Rugosa), but only smaller foraminifera (CRESPIN, 1958) and solitary Rugosa. During Middle and Upper Permian, the Shan–Thai Block is already far from Gondwanaland.

In Northwest Thailand, the discovery of widespread fossiliferous Carboniferous and Permian limestones has been unexpected (FONTAINE *ET AL.*, 1993); in the past, a few fossil identifications had been mentioned, but without paleogeographic conclusion. This part of Thailand was believed to belong to the Shan–Thai Block and its geology had to be compared to that of Peninsular Thailand. The newly discovered faunas were diverse. They showed similarities with the faunas of the Indochina Block. They indicated several horizons of the Carboniferous and of the Permian. Later on, fossils were collected and described from localities north of Chiang Dao, and they are again quite different from those reported from the Shan–Thai Block (UENO & IGO, 1997). A conclusion of all the paleontological studies carried out in Northwest Thailand appears very clear: limestone has been deposited almost continuously from Lower Carboniferous to the end of the Permian. This contrasts with Peninsular and West Thailand, where Middle and Upper Carboniferous limestone remains unknown as well as Early Permian limestone.

Ordovician fossils (nautiloids, gastropods, brachiopods, stromatoporoids) found in Thailand have suggested that the Shan–Thai Block was adjacent to Australia because of close faunal similarities, also noticed for fossils (trilobites) found in the Upper Cambrian of Thailand (BURRETT & STAIT, 1985). Lower–Middle Ordovician limestone is known in Peninsular Thailand. Upper Ordovician limestone has also been mentioned at few localities, but without strong evidence of this age; it is possibly absent as it is in Australia (METCALFE, 1992). Early Devonian conodonts of Satun Province of Peninsular Thailand include species only known in Australia and South China (LONG & BURRETT, 1975). Comparison of the Paleozoic paleontology and stratigraphy of the Shan–Thai Block with those of Australia shows remarkable similarities; some fossil genera have been found only in Shan–Thai Block and Australia. Shan–Thai and Australia were still in close proximity at the end of the Devonian (BURRETT *ET AL.*, 1990).

EXTINCTIONS

The history of life on the earth has been punctuated, at a global scale, by many episodes of rapid extinction and periods of more or less rapid origination of new forms. Extinction is a fundamental phenomenon of nature, involving the loss of entire groups. Some periods saw enormous radiation of animal diversity, but at other times, deterioration of conditions led to catastrophic extinctions. Biological recovery has sometimes been slow. Corals are poorly known in the Lower Triassic, during a period of five million years. After the important crisis of the end of the Permian (see below), the diversity of the faunas was restored by only about 5 million years later, apparently from refuges which sustained panchronic organisms as well as Lazarus taxa. Microbial mats, mostly of bacteria and algae, commonly become abundant on the sea bed after an extinction. They could thrive better without grazing pressure from multicellular organisms (for instance see SHEEHAN & HARRIS, 2004). Stromatolites are abundant at some Thai localities corresponding to the end of the Permian and the beginning of the Triassic. Data about fossils and information on modern ecosystems can lead to a better understanding of extinctions and their consequences.

A well-known mass extinction occurred at the end of the Cretaceous (65 million years ago) in both terrestrial and marine environments, with the expiry of the dinosaurs on land and the disappearance of the ammonites in the sea. In Thailand, there is no marine Cretaceous and no marine Tertiary deposits; the marine biotic crisis cannot be observed in the field.

At the Triassic-Jurassic boundary, 203 million years ago, a widespread mass extinction occurred also in marine and terrestrial environments. This catastrophic event is not easy to observe in detail in Thailand because marine Jurassic sediments are restricted to only a few areas of western Thailand. The transition from Triassic to Jurassic is not commonly exposed; but the lists of the fossils from different localities indicate strong changes from one period to the other period.

A mass extinction ended of the Permian about 250 million years ago, which was probably the most severe of all times and consisted of several phases. It eliminated almost 90 percent of all species. It caused more ravages in marine environments and especially affected the faunas of the shelf seas. The marine environments suffered bad changes in their ecosystems, with a large drop in sea level, higher salinity, important accumulations of organic matter during the Late Permian and anoxic conditions. Because the Triassic and Permian are well represented in Thailand, this dramatic event is easy to observe. It spanned a few million years. It was not a simple catastrophe, but at least a double catastrophe which can be studied in Thailand near the Cambodian border or in the northern part of the country. At the end of the Middle Permian (end of Midian or Capitanian), the large fusulinids and many massive Rugose corals died out because of their vulnerability to hostile environmental changes. The skeletal wall of the large fusulinids is peculiar; it is called a keriotheca. *Lepidolina*, the last large fusulinid, displayed abnormal growths before its extinction (FONTAINE *ET AL.*, 2002, pl. 8, fig. D). This is the first crisis very easy to observe in the field. The rest of the fusulinids and the corals disappeared only at the end of the Permian; these last fusulinids were small in size, without keriotheca. The trilobites are almost unknown in the Upper Permian of Thailand; they disappeared entirely from earth at the end of the Permian. This is the second crisis which has been very important, with the disappearance of many other groups. Some other animal groups survived, such as the conodonts which disappeared only at the end of the Triassic.

Other extinctions were less spectacular, although they were important and noticeable in the faunal successions of the Paleozoic. From the base of the Devonian (410 Ma) to the end of the Permian (250 Ma), 5 important extinctions occurred. The base of the Devonian is marked by the disappearance of the main Silurian faunas. During Upper Devonian at the end of the Frasnian (370 Ma; Kellwasser Crisis), many organisms living in shallow seas such as corals or stromatoporoids disappeared; this fact is easily visible in Loei Province. The end of Lower Carboniferous (320 Ma) is marked by rapid changes of faunas. At the end of Lower Permian, changes in the composition of the faunas are visible.

The number of extinctions and appearances of species, as seen in many sedimentary rock sequences, is commonly not spectacular. Extinctions are usually slow, but continuous. This fact has allowed us to establish stratigraphical scales, which become more and more precise after detailed paleontological studies.

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