Permian gastropod faunas from Thailand – taxonomy, diversity and palaeobiogeography

Dissertation zur Erlangung des Doktorgrades
an der Fakultät für Geowissenschaften
der Ludwig-Maximilians-Universität München

Vorgelegt von
Chatchalerm Ketwetsuriya

München, 20. März 2020

Erstgutachter: Prof. Dr. Alexander Nützel

Zweitgutachter: Prof. Dr. Oliver Rauhut

Tag der mündlichen Prüfung: 13.05.2020

Statutory declaration and statement

I hereby confirm that my thesis entitled **"Permian gastropod faunas from Thailand – taxonomy, diversity and palaeobiogeography"**, is the result of my own original work. Furthermore, I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the Ludwig-Maximilians-University Munich.

Munich, 13.05.2020	Chatchalerm Ketwetsuriya
Place, date	Signature

Abstract

Gastropods form one of the most diverse invertebrate groups in marine habitats during the Permian period. It was a major component of marine faunas and was broadly distributed in all seas of the world. Permian carbonates are widely distributed throughout Thailand, and have yielded numerous marine invertebrate fossils e.g., brachiopods, fusulinids, corals, bryozoans, ostracods, bivalves and gastropods. Unlike for instance brachiopods, Permian gastropods had been largely unstudied until recently. Several newly discovered Early and Middle Permian gastropod faunas from Thailand are presented in this thesis to supplement our knowledge of Permian gastropod diversity and palaeobiogeography in Southeast Asia and also at a global scale. The main aim of this thesis is to investigate the diversity and structure of Permian gastropod faunas from two different continental terranes of Thailand, namely the Sibumasu Terrane in the west and the Indochina Terrane in the east. In this thesis, Permian gastropod faunas from Thailand are represented by at least 100 species, including twenty-two newly described species and one new genus, from two newly discovered occurrences in Thailand. Therefore, the Permian gastropod fauna of Thailand is one of the richest of Asia. The newly discovered Permian gastropod faunas from Thailand reveal palaeobiogeographic relationships to Permian gastropod faunas from the eastern Palaeo-Tethys, especially South China.

From the Sibumasu Terrane, thirty-four new silicified gastropod species are described, 17 nominate species and 17 in open nomenclature, from the Middle Permian (Wordian) Ratburi Group exposed at Khao Phrik, Ratchaburi Province, Central Thailand. Nine species are erected as new species: *Retispira khaophrikensis*, *Amaurotoma*? *multispirata*, *Eoplatyzona ratchaburiensis*, *Hesperiella cyrtocostata*, *Worthenia*? *waterhousei*, *Stegocoelia centrosinuata*, *Procerithium*? *inaequetuberculata*, *Chlorozyga asiatica* and *Hyphantozyga*? *khaophrikensis*. This gastropod fauna is reported from the Sibumasu Terrane of Thailand for the first time. The gastropod assemblage is strongly dominated by bellerophontids (especially *Warthia* and *Retispira*).

Forty-four Middle Permian (Roadian) gastropod species are reported from the Khao Khad Formation, Saraburi Group of the Indochina Terrane, (Lopburi Province, Central Thailand). Thirteen new species and one new genus are erected. The new genus is *Altotomaria*. The new species are *Bellerophon erawanensis*, *Biarmeaspira mazaevi*, *Apachella thailandensis*, *Gosseletina microstriata*, *Worthenia humiligrada*, *Altotomaria reticulata*, *Yunnania inflata*, *Trachydomia suwanneeae*, *Trachyspira eleganta*, *Heterosubulites longusapertura*, *Platyzona gradata*, *Trypanocochlea lopburiensis* and *Streptacis*? *khaokhadensis*. Most species of this assemblage belong to vetigastropods and caenogastropods.

An unusual Early Permian (Kungurian) microbial-fusulinid limestones with large gastropods is also reported from the Khao Khad Formation, Saraburi Province, Central Thailand. The gastropods contribute most to the rock volume. With a height of more than 6 cm, they are amongst the largest Early Permian gastropods ever reported.

Regarding to Permian gastropod diversity from Thailand, quantitative data sets are analyzed for the first time from assemblages of the Middle Permian (Wordian) Tak Fa Limestone of the Saraburi Group. This gastropod assemblage is strongly dominated by the vetigastropod, *Anomphalus* sp..

All studied faunas come from shallow water carbonates that are rich in fusulinids, followed by e.g., gastropods, ostracods, bivalves and brachiopods. Most of the studied gastropod species belong to Late Palaeozoic cosmopolitan genera such as *Bellerophon*, *Warthia*, *Worthenia*, *Naticopsis*, *Meekospira*, *Protostylus* and *Streptacis*. The comparison between the taxonomic compositions (at the species level) of these three Permian gastropod assemblages suggests that the gastropod faunas from two different terranes differ strongly from each other, they share only a single species. The Indochina Terrane fauna (Khao Khad Formation and Tak Fa Formation) is dominated by Caenogastropoda and Vetigastropoda. This contrasts with the gastropod faunas from the Sibumasu Terrane (Ratburi Limestone) in which bellerophontids are the most abundant group.

In addition, Permian gastropod faunas from Asia (Thailand, Malaysia, East Timor and Japan) are compared regarding their diversity. Rarefaction, diversity indices and rank-abundance distributions suggest that the diversity of the gastropod fauna from the Middle Permian Tak Fa Limestone is distinctly lower than that of others Middle Permian assemblages, in descending order, that from Perak, Malaysia, the Akasaka Limestone, Japan and from Timor. This could suggest an inverse diversity gradient, a latitudinal decline in species diversity towards the Palaeoequator, in the Palaeo-Tethys.

The gastropod fauna from the Indochina Terrane is similar to the Late Permian gastropod faunas from South China of the Palaeo-Tethys. This suggests that the Indochina Terrane was not located far from South China. In addition, the gastropod fauna from the Sibumasu Terrane shows relationships to Late Palaeozoic gastropod faunas from the eastern Palaeo-Tethys, such as those of Australia and Malaysia. These results facilitate a better understanding of the tectonic evolution and palaeobiogeography of this region. However, the high number of Formation singletons (pseudoendemic) shows that beta-diversity is high in the Permian of Thailand and sampling is still insufficient.

Contents

STATUTORY DECLARATION AND STATEMENT II
ABSTRACT III
CONTENTS V
1 INTRODUCTION
1.1 Introduction 1
1.2 General geology of Thailand 3
1.3 Previous knowledge of Permian gastropods from Thailand and Southeast Asia 7
1.4 Distribution of Permian gastropods in Southeast Asia and East Asia 8
1.5 Objectives of the dissertation 10
1.6 Overview of manuscripts 11
1.7 References 13
2 PERMIAN GASTROPODS FROM THE RATBURI LIMESTONE, KHAO PHRIK, CENTRAL THAILAND
2.1 Abstract 21
2.2 Introduction 21
2.3 Geological setting and age 22
2.4 Materials and methods 23
2.5 Systematic palaeontology 24
2.6 Discussion and conclusion 59
2.7 Acknowledgements 60
2.8 References 60
3 MIDDLE PERMIAN (ROADIAN) GASTROPODS FROM THE KHAO KHAD FORMATION, CENTRAL THAILAND: IMPLICATIONS FOR PALAEOGEOGRAPHY OF THE INDOCHINA TERRANE
3.1 Abstract 68
3.2 Introduction 68
3.3 Geological setting 69
3.4 Materials and methods 71
3.5 Results 71
3.6 Systematic palaeontology 75
3.7 Acknowledgements 128
3.8 References 129

4 DIVERSITY PATTERNS OF MIDDLE PERMIAN GASTROPOD ASSEMBLAGES FROM THE TAK FA FORMATION, CENTRAL THAILAND

4.1 Abstract 138
4.2 Introduction 138
4.3 Location and geological setting 140
4.4 Materials and methods 141
4.5 Results 142
4.6 Discussion 150
4.7 Acknowledgements 160
4.8 References 164

5 MICROBIAL-, FUSULINID LIMESTONES WITH LARGE GASTROPODS AND CALCAREOUS ALGAE – AN UNUSUAL FACIES FROM THE EARLY PERMIAN KHAO KHAD FORMATION OF CENTRAL THAILAND

5.1 Abstract 169
5.2 Introduction 169
5.3 Geological setting 170
5.4 Materials and methods 174
5.5 Results 175
5.6 Discussion 190
5.7 Conclusions 192
5.8 Acknowledgements 193
5.9 References 193

6 CONCLUSION

6.1 Conclusion 199

ACKNOWLEDGMENTS 202

1

Introduction

The present thesis comprises four contributions about Permian gastropods from Thailand (two published, two submitted (reviews require minor revisions), all to ISI-listed journals). Two of those are alpha taxonomic descriptions of newly discovered gastropod faunas from different terranes, one is a comparative diversity analysis and one is a microfacies analysis of an unusual mass occurrence of rather large gastropods. The investigations started almost from zero and it was the question whether there are Permian gastropod faunas in Thailand, and if so, what taxa are present, how diverse are they and what are the relationships of gastropod faunas from the various terranes of the Eastern Tethys.

Gastropods are one of the most diverse groups of animals and represent the largest class of molluscs. They appeared in the fossil record in the early Cambrian (Parkhaev 2007) and have radiated throughout their long evolutionary history until the present. They are diverse in size, shell morphology, habitats and are globally distributed.

The knowledge of Late Palaeozoic gastropod faunas has been available mostly from the U.S.A. (e.g., Hall 1858; Knight 1930, 1931a, b; Moore 1941; Chronic 1952; Batten 1958, 1964, 1989; Hoare and Sturgeon 1978, 1980; Erwin 1988a, b, c; Bandel et al. 2002), Europe (e.g., Gemmellaro 1887; Hollingworth and Pettigrew 1988; Clapham and Bottjer 2007; Posenato 2009), Russia (e.g., Mazaev 2002, 2006, 2011, 2015), China (e.g., Pan and Yu 1993; Nützel et al. 2002; Pan and Erwin 2002; Pan and Shen 2008), Japan (e.g., Hayasaka 1995; Isozaki and Kase 2014; Nützel and Nakazawa 2012) and Australia (e.g., Dickins 1963; Waterhouse 1963; Yoo 1988, 1994). However, until the start of our research program (Ketwetsuriya 2016; Ketwetsuriya et al. 2016, published master thesis of author), gastropods have been scarcely known from Southeast Asia, especially from Thailand which is the mainland of this region.

Thailand is composed of at least two continental terranes which are the Indochina Terrane located at nearly 10º south of the Palaeo-Equator (Tabakh and Utha-Aroon 1998; Thambunya et al. 2007; Metcalfe 2013) and the Sibumasu Terrane which was a part of the Cimmerian continental strip (Sengör 1984; Metcalfe 1984, 1988) in the eastern Palaeo-Tethys during the Permian period. The study of Permian gastropod faunas from Thailand regarding their composition, diversity and distributions from these two terranes facilitate a better understanding of the tectonic evolution and palaeobiogeography of this region.

Late Palaeozoic sedimentary rocks are extensively distributed in Thailand. They form an important source of industrial raw material and have been proven as a potential oil and gas reservoir (Booth and Sattayarak 2011; Khin Zaw et al. 2014; Warren et al. 2014). Therefore, these rocks have become targets for geological studies including palaeontological studies. They yield numerous marine invertebrate fossils (Ueno and Charoentitirat 2011) such as foraminifers (e.g., Sakagami 1969; Yanagida, 1988; Ingavat-Helmcke 1993), corals (e.g., Fontaine 1986, 1988), brachiopods (e.g., Waterhouse and Piyasin 1970; Yanagida 1970; Grant 1976), bivalves, echinoderms (e.g., Recey et al. 1994), ostracods (e.g., Chitnarin et al. 2012, 2017), sponges, conodonts and gastropods. However, until recently the knowledge of the Permian gastropod fauna from Thailand has been scarce, including a single nominate species (Sone 2010) and a few mentions of gastropod occurrences (e.g., Grant 1976; Waterhouse 1982).

In this contribution, newly discovered Permian gastropod faunas from Thailand are presented. They derive from two terranes, the Indochina and the Sibumasu terranes, which formed the core of Sundaland (Metcalfe 2002, 2011). These faunas are studied regarding diversity and composition. Permian gastropod faunas were collected from the Ratburi Limestone (Middle Permian, Ketwetsuriya et al. 2020b) of the Sibumasu Terrane on the west and the Saraburi Limestone (Khao Khad Formation and Tak Fa Formation) (Middle Permian, Ketwetsuriya et al. 2020b, c) of the Indochina Terrane on the east (Fig. 1.1). Apart from that, a mass occurrence of rather large Early Permian gastropods (> 6 cm) has been discovered and analyzed using microfacies analysis (Ketwetsuriya et al. 2020d). Furthermore, Permian gastropod faunas from Asia (Thailand, Malaysia, East Timor and Japan) are compared quantitatively to investigate their diversity by using rarefaction, diversity indices and rank-abundance distributions (Ketwetsuriya et al. 2020c). In summary, this study focuses on systematics, diversity, palaeoecology and palaeobiogeography of these Permian gastropod faunas from Thailand.

1.2 General geology of Thailand

The geology and geotectonic evolution of Thailand as a mainland of Southeast Asia (Sundaland) has been extensively studied in various aspects (see Ridd et al. 2011). Most of Thailand consists of two major continental blocks (terranes), namely the Sibumasu (previously Shan-Thai) Terrane in the west and the Indochina Terrane in the east (Figs 1.1, 1.2), which collided during the closing stage of Palaeo-Tethys Ocean (late Palaeozoic to early Mesozoic) (Sone and Metcalfe 2008; Khin Zaw et al. 2014). In addition, there are two sub-parallel suture zones between the Sibumasu Terrane and the Indochina Terrane, that is, the Inthanon Suture Zone and the Sukhothai Terrane (Barr and Macdonald 1991; Sone and Metcalfe 2008).

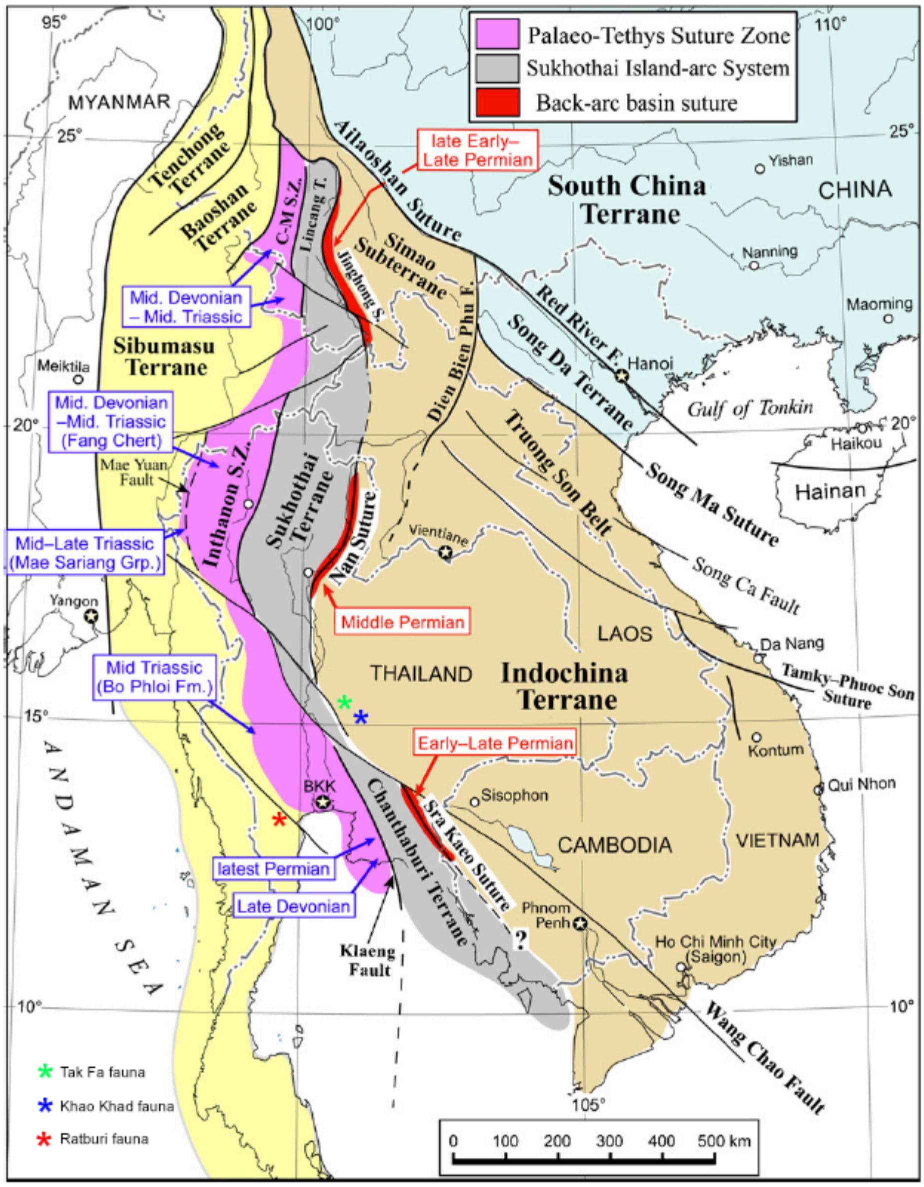

Figure 1.1 Tectonic subdivision of mainland Southeast Asia, showing the Sibumasu Terrane and the Indochina Terrane including the Palaeo-Tethys Suture Zone (the Inthanon Suture) Zone and back-arc sutures (the Sukhothai Terrane) (Sone and Metcalfe 2008).

The Sibumasu (previously termed as Shan–Thai) Terrane (Metcalfe 1984, 1988) was a part of the eastern elongate Cimmerian continental strip (Sengör 1984). This terrane is characterized by Late Palaeozoic Gondwana biotas and Late Carboniferous–Early Permian glacial-marine diamictites (Metcalfe 1984). The Sibumasu Terrane was at large distance to the palaeo-equatorial Tethyan domain (Ueno 2003). This terrane forms Northern Thailand, the western part of Central Thailand and Peninsular Thailand (Fig. 1.1).

The Ratburi Group (from which a new gastropod fauna is described (Ketwetsuriya et al. 2020a)) comprises Permian carbonate-dominated deposits of Western and Peninsular Thailand including massive to bedded carbonates, locally recrystallized and dolomitized, with chert nodules. The lithology of the Ratburi Limestone from which another gastropod fauna is described (Chapter 2) represents platform carbonates deposited on a shelf of the Sibumasu Terrane (Fig. 1.2). It is known for its highly diverse Permian marine invertebrate fauna, including foraminifers (e.g., Sakagami 1969; Brönnimann et al. 1978; Ingavat-Helmcke 1993), corals (e.g., Fontaine 1986, 1988), algae (Fontaine and Salyapongse 2001), echinoderms (Recey et al. 1994), brachiopods (e.g., Waterhouse and Piyasin 1970; Yanagida 1970; Grant 1976) and bryozoans (e.g., Sakagami 1965, 1970, 1973), whereas gastropods have been largely neglected so far. The fossils indicate that the Ratburi Limestone ranges from the latest Early Permian to the Late Permian (Ueno 2003).

The Indochina Terrane has derived from Gondwana by the opening of the Palaeo-Tethys ocean in the Early Devonian (Metcalfe 1998, 2002, 2005, 2011). The Late Palaeozoic faunas and floras of this terrane are warm-water, equatorial Tethyan/Cathaysian Province biotas (Metcalfe 1998, 1999). This terrane covers NE Thailand and the eastern part of SE Thailand, including the eastern side of central Thailand (Fig. 1.1). Various fossils have been reported from the Indochina Terrane, especially from its western margin where Upper Palaeozoic outcrops are widespread. These exposures mainly consist of carbonate sequences with minor clastic sedimentary rocks (Fig. 1.3). Many studies indicate that the sedimentary rocks along these areas were deposited in two carbonate platforms (the Pha Nok Khao Platform to the east and the Khao Khwang Platform to the west) with a basin (the Nam Duk Basin) in between (e.g., Wielchowsky and Young 1985; Ueno and Charoentitirat 2011; Morley et al. 2013).

The Saraburi Group of the Khao Khwang Platform ranging from Late Pennsylvanian–Permian is one of the most interesting limestone complexes of Thailand regarding palaeontology, sedimentology, structural geology and tectonics because it yields several groups of fossils such as fusulinids (e.g., Toriyama and Sugi 1959; Toriyama et al. 1974; Toriyama and Kanmera 1977, 1979; Hinthong 1981; Dawson 1993), bivalves (e.g., Udchachon et al. 2007), corals (e.g., Yanagida 1988; Fontaine et al. 1996, 1999), conodonts (Metcalfe and Sone 2008), brachiopods (e.g., Yanagida 1964, 1988; Yanagida and Nakornsri 1999; Sone et al. 2009), bryozoans (Sakagami 1975, 1999; Yanagida 1988), calcareous algae (Fontaine et al. 1999), ostracods (e.g., Chitnarin et al. 2012, 2017) and gastropods (Sone 2010; Ketwetsuriya et al. 2014, 2016). The Saraburi Group is exposed along the eastern side of the lower Chao Phraya Central Plain from Nakhon Sawan to Saraburi provinces. It is composed of several formations which have been assigned to different stages of the Permian (ranging from Asselian to Capitanian, see Ueno and Charoentitirat 2011), and which comprise different lithologies and have different distribution areas: the Khao Khwang Formation, the Nong Pong Formation, the Pang Asok Formation, the Khao Khad Formation (the present studied gastropod faunas are investigated (Ketwetsuriya et al. 2020b, d)) and the Tak Fa Formation (in which quantitative data sets of Permian gastropods are analyzed for the first time (Ketwetsuriya et al. 2020c)). They consist mainly of shallow marine carbonates.

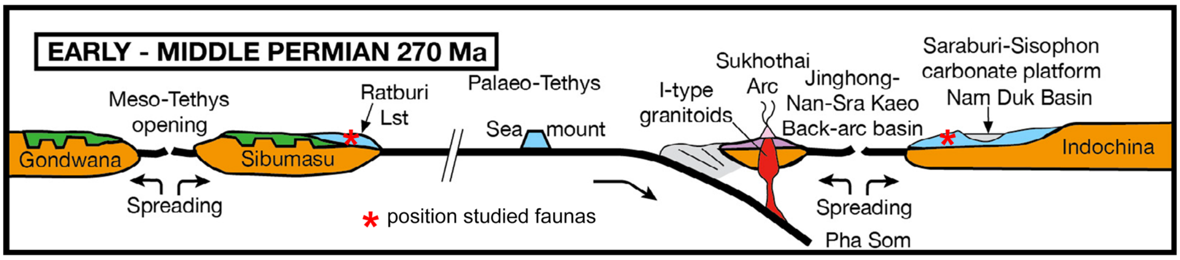

Figure 1.2 Model showing the tectonic evolution of Thailand during Early–Middle Permian times (after Metcalfe 2013, 2017).

The Inthanon Suture represents the main Palaeo-Tethys Ocean (Metcalfe 2011). This suture contains Carboniferous–Permian shallow-marine limestones with Cathaysian faunas deposited on intra-oceanic volcanic edifices and it is interpreted as Palaeo–Tethyan sea mounts now incorporated into the Palaeo-Tethyan Suture Zone (Metcalfe 2005; Wakita and Metcalfe 2005; Feng et al. 2008).

The Sukhothai Arc System was interpreted as being derived from the margin of South China–Indochina–East Malaya by back-arc spreading in the Late Carboniferous–Early Permian (Sone and Metcalfe 2008). This arc terrane is situated in Central Thailand and is composed of granitic batholiths and mafic-intermediate-felsic volcanic rocks including pyroclastic and carbonate sediments. This zone is devoid of marine invertebrate faunas.

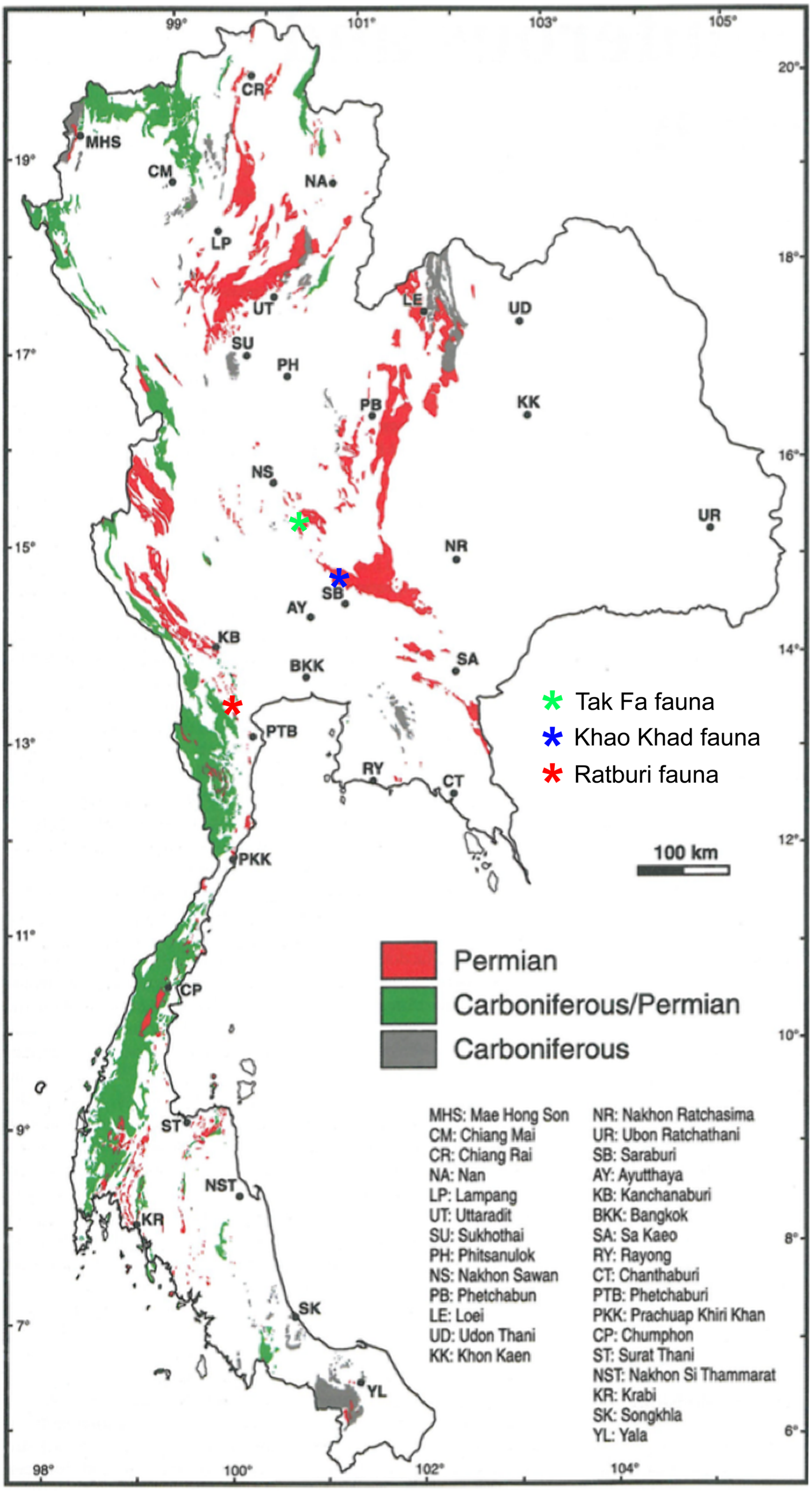

Figure 1.3 Map showing generalized distribution of Carboniferous and Permian strata in Thailand (Ueno and Charoentitirat 2011).

1.3 Previous knowledge of Permian gastropods from Thailand

Palaeontological studies over the last two decades from both, the Sibumasu Terrane and the Indochina Terrane of Thailand have provided abundant information about Permian marine invertebrate fossils. However, very few information on Permian gastropods has previously been available. Until the Master thesis of the author (Ketwetsuriya 2016; Ketwetsuriya et al. 2016) was published, only a single Permian nominate species had been reported from Thailand: *Magnicapitatus huazhangae* Sone, 2010 (Fig. 1.4) from the Khao Taa Ngog Formation (Capitanian, Middle Permian) of East Thailand (southern margin of the Indochina Terrane). This naticiform species is preserved as an internal mold and represents the first record of this Permo–Triassic genus outside South China (Wang and Xi 1980) and from the Capitanian. The Khao Taa Ngok Formation is the Thai equivalent of the Sisophon Limestone of western Cambodia, and together they form a continuous Guadalupian carbonate platform over the Thai-Cambodia border.

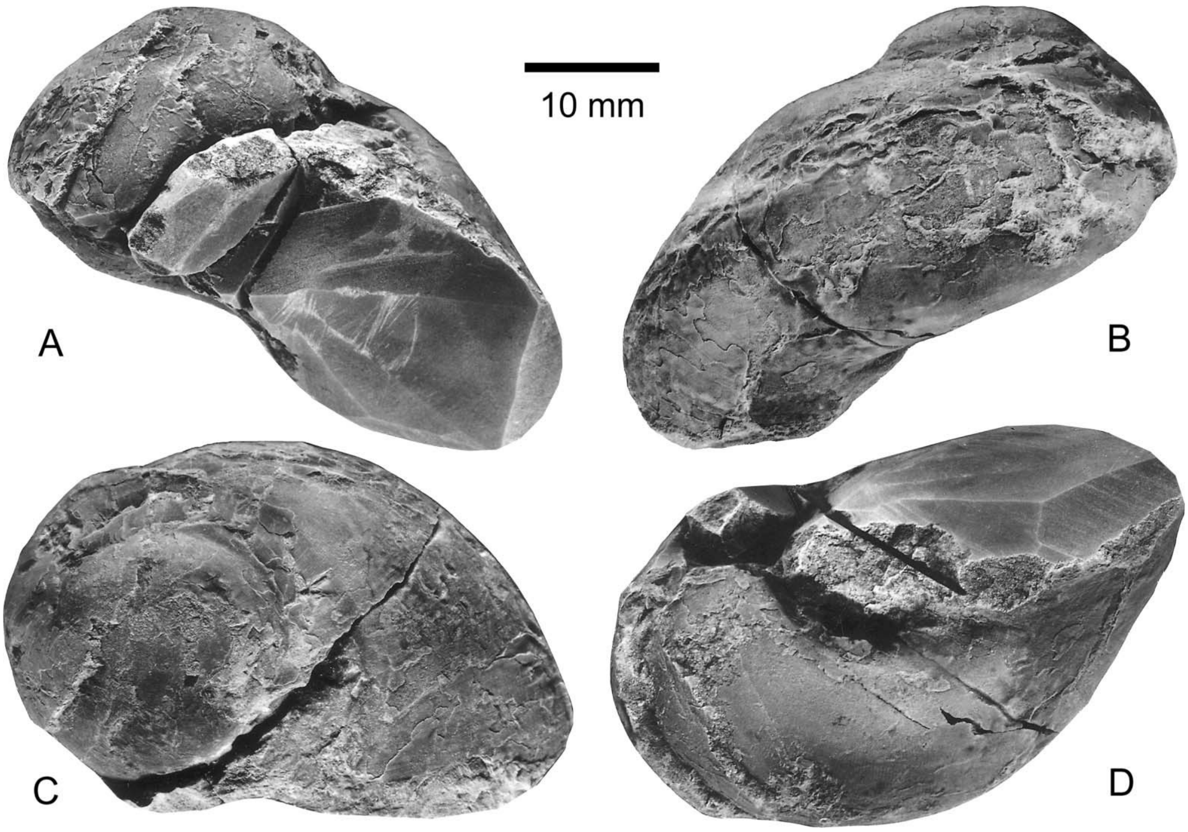

Figure 1.4 *Magnicapitatus huazhangae* Sone, 2010 from a limestone bed at Khao Makha (Capitanian, Middle Permian), East Thailand. A–D, apertural, ventral, apical and basal views respectively.

The most diverse Permian gastropod fauna of Thailand has been described from the Tak Fa Limestone of the Saraburi Group, Nakhonsawan Province, central Thailand as result of the master thesis of the author and colleagues (Ketwetsuriya et al. 2014, 2016). This gastropod fauna consists of typical Late Palaeozoic genera and comprises forty species, especially Bellerophontidae, Pleurotomarioidea, Meekospiridae and Goniasmatidae. Twelve species and one genus (*Takfaia*), are new to science (Fig. 1.5). The Tak Fa Formation is a part of Saraburi Group that is exposed along the western margin of the Indochina Terrane. In addition, there are some reports of Permian gastropods from Southern Thailand but they lack descriptions, illustrations and detailed systematic assignments. Grant (1976) investigated brachiopods from the Ratburi Limestone of southern Thailand and mentioned the presence platyceratids and pleurotomarioids. Waterhouse (1982) studied the early Permian fauna from the Kaeng Krachan Group at the Tong Lang Bay and Ko Phi Phi Island, Southern Thailand. He reported the occurrence of a single species (*Peruvispira* sp.) from this locality. These two reports were from the Permian Ratburi Limestone of the Sibumasu Terrane.

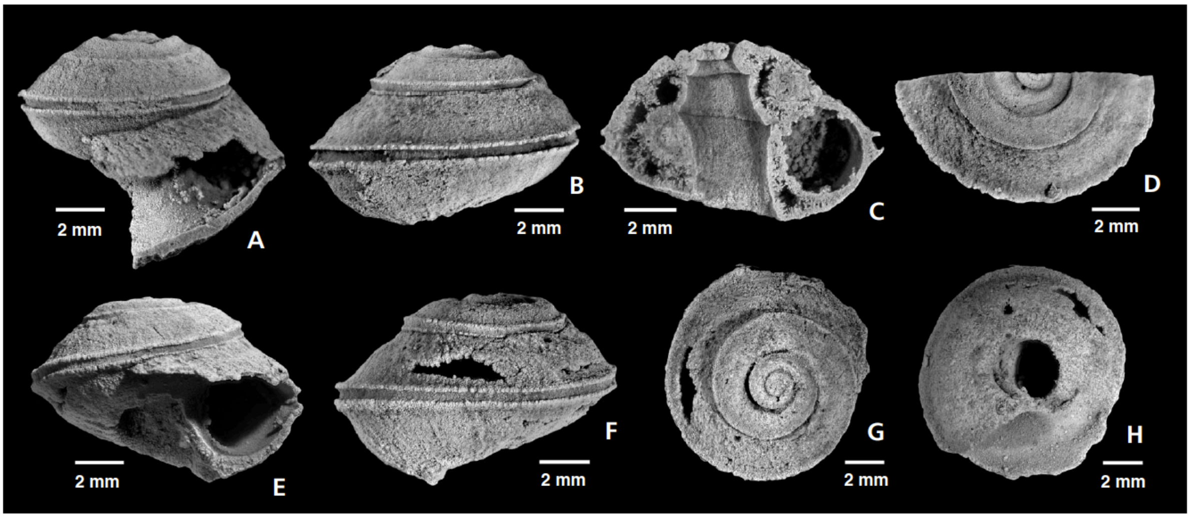

Figure 1.5 The new genus *Takfaia kuesi* sp. et gen. nov. Nützel and Ketwetsuriya, 2016 in Ketwetsuriya et al. (2016) from the Tak Fa Formation, Nakhon Sawan Province, northern Central Thailand.

1.4 Distribution of Permian gastropods in Southeast Asia and East Asia

Except from the studied fauna from Thailand, Permian gastropods from Southeast Asia have been reported only from three areas: Cambodia, East Timor and Malaysia. The first diverse Permian gastropod fauna was described from the Sisophon Limestone of Cambodia by Mansuy (1913), who reported about 30 species from this limestone. Seven gastropod species from the Permian limestone of Laos were reported by Mansuy (1912). Delpey (1940, 1941, 1942) revised the gastropod fauna from the Sisophon Limestone of Cambodia and reported 62 species including, several new genera and species. The Sisophon Limestone is situated at the southern margin of the Indochina Terrane.

Batten (1972, 1979, 1985) reported 93 Permian gastropod species from limestones at Lee Mine, Perak, Malaysia which derived from the Sibumasu Terrane (Tsegab et al. 2017). This gastropod fauna yielded bellerophontids, euomphalids, pleurotomarians, trochids, patellids, neritids, murchisoniids, cerithiids, loxonematids and subulitids. The age of this limestone is late Early Permian (Kungurian). This gastropod assemblage is dominated by the high-spired caenogastropods of which *Omphaloptychia paleozoica* is the most abundant gastropod species. Vetigastropods are as diverse as caenogastropods. The genera *Glabrocingulum*, *Anomphalus* and *Apachella* are the most abundant vetigastropods. The bellerophontoideans comprise mostly the typical Middle to Late Palaeozoic genus *Bellerophon*. Neritimorpha are the mostly present with the genus *Trachydomia*. The gastropod fauna from Perak, Malaysia is very diverse and has major implications for the palaeobiogeography at the margin of the eastern Palaeo-Tethys.

Wanner (1941) reported 67 species of Permian gastropods from Timor with planispiral shells of the euomphalid species *Schizostoma pusilliforme* being the most abundant, followed by *Schizostoma pusilliforme* var. *weiensi*., both contribute almost 30% of the total abundance. Bellerophontoideans make up the second most abundant group in Timor and are dominated by the genus *Bellerophon*. In addition, typical Late Palaeozoic genera such as *Naticopsis*, *Trachydomia* and *Soleniscus* are rare in the fauna from Timor.

Rich Permian gastropod faunas have been reported from Japan and China. Nützel and Nakazawa (2012) studied a very diverse Permian (Capitanian) gastropod fauna from the Akasaka Limestone (Gifu Prefecture, Japan) – a fauna that has yielded some of the largest gastropod species from the Permian and the entire Palaeozoic, with specimens as large as 40 cm. This fauna comprises at least 74 species. The Akasaka limestone is dominated by packstones with dark grey colour that were deposited in an open shallow marine environment (Ozawa and Nishiwaki 1992). The invertebrate fauna is strongly dominated by gastropods and bivalves (Nakazawa 2007; Nützel and Nakazawa 2012). Caenogastropoda are the most abundant and diverse group among the gastropods. The Akasaka gastropod fauna shows relationships to faunas from China, Malaysia, and Vietnam but contains also many formation singletons at species level.

Permian gastropods have been described from various localities of South China. Mansuy (1914) reported 7 species from the Permian limestone of Yunnan. Pan (1978, 1983a, b, 1985) reported a total of 19 Early Permian species and 10 Late Permian species. Yu et al. (1985) reported 4 Early Permian species and 5 Late Permian species. Wang and Xi (1980) studied one of the most diverse Permian gastropod faunas yielding 94 species representing 51 genera. Wang (1982) recorded 14 species from the Heshan Formation of Guangxi Province. Pan and Yu (1993) described 47 species from China such as from Sichuan, Guizhou, Yunnan and Xizang Autonomous Region. Pan and Erwin (2002) reported a diverse Permian gastropod fauna from the Heshan Formation of Guangxi, Ninglang and Yunnan provinces, South China, which yielded a total of 73 species including numerous new taxa. The position of the South China Terrane was close to the Indochina Terrane during the Permian period (Metcalfe 2011, 2013). The Permian faunas from this geographic province play a significant role for understanding palaeobiogeographic relationships in the Palaeo-Tethys.

1.5 Objectives of the thesis

The main aim of this study is to provide new information on the Permian gastropods from Thailand which derive from the Indochina Terrane and Sibumasu Terrane and to compare the diversity and composition of Permian gastropod assemblages from both terranes of Thailand as well as with assemblages from adjacent areas i.e., Malaysia, Cambodia, Laos, South China, Timor and Japan. This facilitates a better understanding of gastropod diversity and palaeobiogeography during the Permian in the eastern Palaeo-Tethys. It integrates taxonomic studies and quantitative analyses to answer the question how gastropods were distributed during the Permian. The more specific goals of this thesis include the following:

1. First documentation of systematic taxonomy and description of Permian gastropods from the Sibumasu Terrane of Thailand (Ketwetsuriya et al. 2020a).
2. Documentation of systematic taxonomy and description of Permian gastropods from the Indochina Terrane of Thailand and comparison of the species compositions with the other Permian gastropod faunas from Thailand and adjacent areas (Ketwetsuriya et al. 2020b).
3. Evaluation of diversity of the Permian gastropod faunas of Thailand including comparison with the other Permian gastropods from the eastern Palaeo-Tethys (Ketwetsuriya et al. 2020c).
4. Description of an unusual facies with large gastropods play an important role in this facies and their associated organisms (Ketwetsuriya et al. 2020d).

These topics are treated in the next four chapters (Chapter 2–5) of this thesis. Each of these chapters was written to stand on its own as an independent publication but are nevertheless related to each other and complement each other.

1.6 Overview of manuscripts

Chapter 2 provides the first taxonomic study of a new silicified Middle Permian gastropod fauna from the Sibumasu Terrane of Thailand collected from the Middle Permian (Wordian) Ratburi Limestone exposed at the Khao Phrik hill, Ratchaburi Province, Central Thailand. Thirty-four gastropod species are described, 17 nominate species and 17 in open nomenclature, of which nine species are new to science. This gastropod assemblage is strongly dominated by bellerophontids (especially *Warthia* and *Retispira*). The fauna reveals relationships to Late Palaeozoic gastropod faunas from the Palaeo-Tethys, such as those of Australia and Malaysia. On the other hand, the fauna shares only one species with faunas from other Permian deposits from Thailand: the Tak Fa Limestone and the Ratburi Limestone.

Chapter 3 describes 44 gastropod species, including one new genus: *Altotomaria* and thirteen new species from the Permian Khao Khad Formation, Saraburi Group, Central Thailand of the Indochina Terrane. The gastropod fauna represents another diverse Permian gastropod known from Thailand. Most species of the studied assemblage are represented by vetigastropods and caenogastropods and most represent Late Palaeozoic cosmopolitan genera. The species composition is compared with the gastropod assemblages from other Permian Formations in Thailand, the Tak Fa Limestone and the Ratburi Limestone, suggesting that it shares no species with these faunas. However, it is similar to the Late Permian gastropod faunas from South China of the Palaeo-Tethys, therefore it supports the hypothesis that the Indochina Terrane was close to the South China Terrane.

Chapter 4 focuses on diversity analyses of Permian gastropod assemblages from the Middle Permian Tak Fa Limestone of the Indochina Terrane and other Permian gastropod assemblages from Asia (Malaysia, East Timor and Japan). This study presents the first detailed quantitative analysis of Permian gastropod diversity using rarefaction, diversity indices and rank-abundance distributions. The results suggest that the diversity of the studied fauna from Thailand is distinctly lower than that of other faunas of the eastern Tethys despite coming from similar depositional environments. This is surprising because the Tak Fa gastropods lived at lower latitudes (close to the Palaeo-equator) than the others. This could suggest an inverse diversity gradient in the Palaeo-Tethys.

Chapter 5 reveals unusual microbial-fusulinid limestones with large gastropods which contribute most to the rock volume. At least four gastropods species are present; they belong probably to undescribed taxa with a height of more than 6 cm. The gastropods are amongst the largest Early Permian gastropods ever reported. The studied fauna comes from the Early Permian (Kungurian) Khao Khad Formation of Central Thailand on the western margin of the

Indochina Terrane. Besides gastropods, fusulinids, large dasycladaceans, intraclasts and thick microbial-cyanobacterial coatings and reticulate microbial patches as well as thick inter- and intragranular radial fibrous cement crusts are also present. The carbonate is interpreted as product of shallow water, non-metazoan-reefal platform community with a high productivity providing the large gastropod with sufficient food. However, conditions were too eutrophic for sessile filter feeders such as brachiopods, bryozoans, bivalves, corals and sponges which are rare or entirely absent.

Author contributions

Chapter 2: **Chatchalerm Ketwetsuriya**, Alex G. Cook and Alexander Nützel: Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand.

CK drafted the manuscript and prepared all figures. **CK** and AN conceptualized the study, analyzed the results, revised and wrote the final manuscript. AC provided the studied materials.

Contribution Percentage: **CK 70%;** AN 20%; AC 10%.

Manuscript published in *Paläontologische Zeitschrift* 94: doi:10.1007/s12542-019-00463-0.

Chapter 3 **Chatchalerm Ketwetsuriya**, Baran Karapunar, Thasinee Charoentitirat and Alexander Nützel: Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: implications for palaeogeography of the Indochina Terrane.

CK collected and prepared, and identified the specimens, drafted the manuscript, conducted the analyses and prepared all figures. BK contributed with the identification of Pleurotomariida. TC identified the fusulinids for age determination. **CK** and AN wrote the final manuscript. AN acquired the funding for field work.

Contribution Percentage: **CK 70%;** BK 15%; TC 5%; AN 10%.

Manuscript published in *Zootaxa* 4766(1): doi:10.11646/zootaxa.4766.1.1

Chapter 4 **Chatchalerm Ketwetsuriya**, Imelda M. Hausmann and Alexander Nützel: Diversity patterns of Middle Permian gastropod assemblages from the Tak Fa Formation, Central Thailand.

CK designed and drafted the manuscript, prepared figures, identified specimens and conducted the analyses. IH performed rank-abundance analysis. **All authors** interpreted the data, **CK** and AN contributed to discussions and the final manuscript.

Contribution Percentage: **CK 70%;** AN 10%; IH 20%.

Manuscript in revision in *Palaeodiversity and Palaeoenvironment*.

Chapter 5 **Chatchalerm Ketwetsuriya**, Matin Nose, Thasinee Charoentitirat and Alexander Nützel: Microbial-, fusulinid limestones with large gastropods and calcareous algae – an unusual facies from the Early Permian Khao Khad Formation of Central Thailand.

CK collected the rock samples, carried out point counting and drafted the manuscript. **CK** and MN interpreted the data, wrote the manuscript and prepared all figures. MN contributed with the identification of algae, microbes and prepare some rock slabs. TC identified the fusulinids for age determination. **CK** and AN provided the information on gastropods.

Contribution Percentage: **CK 60%;** MN 30%; AN 5%; TC 5%.

Manuscript in revision in *Facies*.

1.7 References

Bandel, K., Nützel, A. and Yancey, T.E. 2002. Larval shells and shell microstructures of especially well-preserved Late Carboniferous gastropods from the Buckhorn Asphalt deposit (Oklahoma, USA). *Senckenbergiana Lethaea* 82(2), 639–689.

Barr, S.M. and Macdonald A.S. 1991. Towards a Late Paleozoic–Early Mesozoic tectonic model for Thailand. *Journal of Thai Geosciences* 1, 11–22.

Batten, R.L. 1958. Permian Gastropoda of the southwestern United States. 2. Pleurotomariacea: Portlockiellidae, Phymatopleuridae, and Eotomariidae. *Bulletin of the American Museum of Natural History* 114(2), 153–246.

Batten, R.L. 1964. Some Permian Gastropoda from eastern Arizona. *American Museum Novitates* 2165, 1–16.

Batten, R.L. 1972. Permian gastropods and chitons from Perak, Malaysia. Part 1. Chitons, bellerophontids, euomphalids and pleurotomarians. *Bulletin of the American Museum of Natural History* 147, 1–44.

Batten, R. L. 1979. Permian gastropods from Perak, Malaysia. Part 2. The trochids, patellids, and neritids. *American Museum Novitates*, 2685, 1–26.

Batten, R.L. 1985. Permian gastropods from Perak, Malaysia. Part 3. The murchisoniids, cerithiids, loxonematids, and subulitids. *American Museum Novitates* 2829, 1–40.

Batten, R.L. 1989. Permian Gastropoda of the southwestern United States. 7. Pleurotomariacea: Eotomariidae, Lophospiriidae, Gosseletinidae. *American Museum Novitates* 2958, 1–64.

Booth, J. and Sattayarak, N. 2011. Subsurface Carboniferous–Cretaceous of NE Thailand. In *The geology of Thailand*, eds. Ridd, M.F., Barber, A.J. and Crow, M.J., 185–222. London: Geological Society.

Brönnimann, P., Whittaker, J.E. and Zaninetti, L. 1978. Shanita, a new pillared miliolacean foraminifer from the Late Permian of Burma and Thailand. *Rivista Italiana di Paleontologia e Stratigrafia* 84, 63–92.

Chitnarin, A., Crasquin, S., Charoentitirat, T., Tepnarong, P. and Thanee, N. 2012. Ostracods (Crustacea) of the Early–Middle Permian from Central Thailand (Indochina Block): part I, Order Palaeocopida. *Geodivesitas* 34(4), 801–835.

Chitnarin, A., Crasquin, S., Forel, M.-B. and Tepnarong, P. 2017. Ostracods (Crustacea) of the Early–Middle Permian (Cisarulian–Guadalupian) from Central Thailand (Indochina Block): part II, Orders Podocopida, Platycopida and Myodocopida. *Geodivesitas* 39, 651–690.

Chronic, H. 1952. Molluscan Fauna from the Permian Kaibab Formation, Walnut Canon, Arizona. *Bulletin of the Geological Society of America* 63, 95–166.

Clapham M.E. and Bottjer, D.J. 2007. Permian marine paleoecology and its implications for large-scale decoupling of brachiopod and bivalve abundance and diversity during the Lopingian (Late Permian). *Palaeogeography, Palaeoclimatology, Palaeoecology* 249, 283–301.

Dawson, O. 1993. Fusiline foraminiferal biostratigraphy and carbonate facies of the Permian Ratburi Limestone, Saraburi, central Thailand. *Journal of Micropalaeontology* 12, 9–33

Delpey, G. 1940. Les Gastéropodes permiens du Cambodge. *Journal de Conchyliologie* 84, 255–278.

Delpey, G. 1941. Les Gastéropodes permiens du Cambodge. Journal de Conchyliologie 84, 345–369.

Delpey, G. 1942. Les Gastéropodes permiens du Cambodge. Journal de Conchyliologie 85, 50–83.

Dickins, J.M. 1963. Permian pelecypods and gastropods from western Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics* 63, 1–203.

Erwin, D.H. 1988a. Permian Gastropoda of the Southwestern United States: Cerithiacea, Acteonacea, and Pyramidellacea. *Journal of Paleontology* 62, 566–575.

Erwin, D.H. 1988b. Permian Gastropoda of the Southwestern United States: Subulitacea. *Journal of Paleontology* 62, 56–69.

Erwin, D.H. 1988c.The genus *Glyptospira* (Gastropoda: Trochacea) from the Permian of the southwestern United States. *Journal of Paleontology* 62(6), 868–879.

Feng, Q.L., Yang W.Q., Shen S.Y., Chonglakmani, C. and Malila, K. 2008. The Permian seamount stratigraphic sequence in Chiang Mai, North Thailand and its tectogeographic significance Science. *China Series D: Earth Sciences* 51, 1768–1775.

Fontaine, H. 1986. The permian of Southeast Asia. *CCOP Technical Bulletin* 18, 1–111.

Fontaine, H. 1988. Permian corals of West Thailand. *CCOP Technical Bulletin* 20, 112–127.

Fontaine, H., Salyapongse, S., Suteethorn, V., Tansuwan. V. and Vachard, D. 1996. Recent biostratigraphic discoveries in Thailand: A preliminary report. *CCOP Newsletter* 21(2), 14–15.

Fontaine, H., Salyapongse, S. and Vachard, D. 1999. Fossils from Khao Sak and the adjacent hills, Amphoe Chon Daen, central Thailand. *CCOP Newsletter* 24(1), 9–14.

Fontaine, H. and Salyapongse, S. 2001. Permian corals of peninsular Thailand and other associated fossils. *CCOP Newletter* 26(3/4), 14–19.

Gemmellaro, G.G. 1887. La Fauna dei Calcari con Fusulina della Valle del Fiume Sosio nella Provincia di Palermo, Fasc. 1 - Ammonoidea. *Giornale di Scienze Naturali e Economiche* 19, 1–106.

Grant, R.E. 1976. Permian brachiopods from southern Thailand. *Paleontological Society Memoir* 9, 1–269.

Hall, J. 1858. Description of new species and fossils from the Carboniferous limestones of Indiana and Illinois. *Transactions of the Albany Institute*, 4 1–36.

Hayasaka, I. 1995. A New Permian Species of *Porcellia* from Japan. *Journal of the Faculty of Science, Hokkaido University. Series 4, Geology and mineralogy* 9(1), 21–24.

Hoare, R.D. and Sturgeon, M.T. 1978. The Pennyslvanian gastropod genera Cyclozyga and Helminthozyga and the classification of the Pseudozygopleuridae. *Journal of Paleontology* 52(4), 850–858.

Hoare, R.D. and Sturgeon, M.T. 1980. The Pennsylvanian pseudozygopleurid gastropod genus Gamizyga n. gen. from Ohio and West Virginia. *Journal of Paleontology* 54(1), 159–187.

Hinthong, C. 1981. Geology and Mineral Resources of Changwat Phra Nakhon Si Ayutthaya (ND 47–8), Scale 1:250,000. Department of Mineral Resources, Geological Survey Report, No. 4, 1–105. (in Thai with English summary)

Hollingworth, N. and Pettigrew, T. 1988. Zechstein reef fossils and their palaeoecology. *Palaeontological Association Field Guides to Fossils* 3, 1–75.

Ingavat-Helmcke, R. 1993. Contribution to the Permian fusulinacean faunas of Peninsular Thailand. *Journal of Southeast Asian Earth Sciences* 8, 67–75.

Isozaki, Y. and Kase, T. 2014. The occurrence of the large gastropod "Pleurotomaria" yokoyamai Hayasaka from the Capitanian (Permian) Iwaizaki Limestone in northeast Japan. *Paleontological Research* 18, 250–257.

Ketwetsuriya, C. 2016. *Biosystematics of Gastropoda fossil from Permian Tak Fa Formation, Amphoe Tak Fa and Amphoe Takhli, Changwat Nakhon Sawan*. Master thesis, Chulalongkorn University, Bangkok.

Ketwetsuriya, C., Nützel, A. and Kanjanapayont, P. 2014. A new Permian gastropod fauna from the Tak Fa Limestone, Nakhonsawan, Northern Thailand—a report of preliminary results. *Zitteliana A* 54, 137–146.

Ketwetsuriya, C., Nützel, A. and Kanjanapayont, P. 2016. Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. *Bulletin of Geosciences* 91, 481–513.

Ketwetsuriya, C., Cook, A.G. and Nützel, A. 2020a. Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand. *Paläontologische Zeitschrift* 94, 53–77. https://doi:10.1007/s12542-019-00463-0

Ketwetsuriya, C., Karapunar, B., Charoentitirat, T. and Nützel, A. 2020b. Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: implications for palaeogeography of the Indochina Terrane. *Zootaxa* 4766(1), 1–47.

Ketwetsuriya, C., Hausmann, I.M. and Nützel, A. 2020c. Diversity of a diverse Middle Permian gastropods assemblage from the Tak Fa Formation at Nakhonsawan Province, Central Thailand. (Manuscript in revision)

Ketwetsuriya, C., Nose, M., Charoentitirat, T. and Nützel, A. 2020d. Microbial-, fusulinid limestones with large gastropods and calcareous algae – an unusual facies from the Early Permian Khao Khad Formation of Central Thailand. (Manuscript in revision)

Khin Zaw, Meffre, S., Lai, C.K., Burrett, C., Santosh, M., Graham, I., Manaka, T., Salam, A., Kamvong, T. and Cromie, P. 2014. Tectonics and metallogeny of mainland Southeast Asia – A review and contribution. *Gondowana Research* 26, 5–30.

Knight, J.B. 1930. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: the Pseudozygopleurinae. *Journal of Paleontology Memoir* 4(4), 1–88.

Knight, J.B. 1931a. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: Aclisina and Streptacis. *Journal of Paleontology* 5(1),1–15.

Knight, J.B. 1931b. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: the Subulitidae. *Journal of Paleontology* 5(3), 177–229.

Mansuy, H. 1912. Mission du Laos. 1. - Géologie des environs de Luang-Prabang. *Memoires du Service de l'Géologique Indochine* 1(4), 33–52.

Mansuy, H. 1913. Faunes des calcaires a Productus de l'Indochine. Indochina. *Mémoires du Service Géologiques de l'Indochine* 2(4), 1–104.

Mansuy, H. 1914. Nouvelle contribution à la paléontologie du Yunnan. *Mémoires du Service Géologiques de l'Indochine* 1(3), 1–190.

Mazaev, A.V. 2002. Some murchisoniid gastropods from the Middle and Upper Carboniferous of the central part of the Russian Plate. *Ruthenica* 12(2), 89–106

Mazaev, A.V. 2006. Permian gastropods from the Kulogory Formation of the northern Moscow Syneclise. *Paleontological Journal* 40(4), 391–403.

Mazaev, A.V. 2011. Pennsylvanian gastropods of the suborders Murchisoniina Cox et Knight, 1960 and Sinuspirina Mazaev subordo nov. from the central regions of the Russian Platform: Morphology, taxonomy, and phylogeny. *Paleontological Journal* 45(12), 1533–1599.

Mazaev, A.V. 2016. Evolution of the genus Baylea (Gastropoda) in the Kazan paleobasin (Middle Permian, Volga-Ural Region). *Paleontological Journal* 50(6), 585–600.

Metcalfe, I. 1984. Stratigraphy, palaeontology and palaeogeography of the Carboniferous of Southeast Asia. *Mem. Soc. Geol. France* 147, 107–118.

Metcalfe, I. 1985. Lower Permian conodonts from the Terbat Formation, Sarawak. *Warta Geologi* 11, 1–4.

Metcalfe, I. 1986. Late Palaeozoic palaeogeography of Southeast Asia: some stratigraphical, palaeontological and palaeomagnetic constraints. *Geological Society of Malaysia Bulletin* 19, 153–164.

Metcalfe, I. 1988. Origin and assembly of Southeast Asian continental terranes. In *Gondwana and Tethys*, Special Publication, eds. Audley-Charles, M.G. and Hallam, A., 101–118. London: Geological Society of London.

Metcalfe, I. 1998. Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. In: *Biogeography and Geological Evolution of SE* Asia, eds. Hall, R., Holloway, J.D., 25–41. Amsterdam: Backhuys Publishers, The Netherlands.

Metcalfe, I. 1999. Gondwana dispersion and Asian accretion: an overview. In *Gondwana dispersion and Asian accretion, Final Results Volume for IGCP Project* 321, ed. Metcalfe, I., 9–28. Rotterdam: A.A. Balkema.

Metcalfe, I. 2002. Permian tectonic framework and palaeogeography of SE Asia. *Journal Asian Earth Science* 20, 551–566.

Metcalfe, I. 2005. Asia: South-East. In *Encyclopedia of Geology*, vol. 1, eds. Selley, R.C., Cocks, L.R.M. and Plimer, I.R., 169–198. Oxford: Elsevier.

Metcalfe, I. 2011. Tectonic framework and Phanerozoic evolution of Sundaland. *Gondwana Research* 19, 3–21.

Metcalfe, I. 2013. Tectonic evolution of the Malay Peninsula. *Journal of Asian Earth Sciences* 76, 195–213.

Metcalfe, I. 2017. Tectonic evolution of Sundaland. *Bulletin of the Geological Society of Malaysia* 63, 27–60.

Moore, R.C. 1941. Upper Pennsylvanian gastropods from Kansas. *State Geological Survey of Kansas Bulletin* 38(4), 121–162.

Morley, C.K., Ampaiwan, P., Thanudamrong, S., Kuenphan, N., Warren, J. 2013. Development of the Khao Khwang Fold and Thrust Belt: implications for the geodynamic setting of Thailand and Cambodia during the Indosinian Orogeny. Journal of Asian Earth Science 62, 705–719.

Nakazawa, K. (2007). Minute bivalve fossils from the Permian Akasaka Limestone, Central Japan: (Appendix) Description of a new species of Pernopecten. *Earth Science* 61, 187–201 [in Japanese with English abstract and English description of new species].

Nützel, A. and Nakazawa, K. 2012. Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). *Journal of Systematic Palaeontology* 10, 103–169.

Nützel, A., Pan, H.Z. and Erwin, D.H. 2002. New taxa and some taxonomic changes of latest Permian gastropod fauna from China. *Documenta Naturae* 145, 1–7.

Ozawa, T. and Nishiwaki, N. 1992. Permian Tethyan biota and sedimentary facies of the Akasaka Limestone Group. Field Trip Guidebook of 29th International Geological Congress, B13, 189–195.

Pan, Y.T. 1978. Gastropod fossils from Carboniferous to Mesozoic. In *Atlas of fossils in southwest China, Sichuan Volume Pt. 2*, 403-428. Sichuan Institute of Geological Sciences, SW China.

Pan, Y.T. 1983a. Four fossil gastropods from Permian of Sichuan and Yunnan Provinces. *Contribution to Geology of Qinghai-Xizang Plateau* 11, 243–353.

Pan, Y.T. 1983b. Permian Gastropoda of Southwestern China. *Memoir of the Institute of Geology, Academia Sinica* 2, 12–20.

Pan, Y.T. 1985. Fossil Gastropoda from the Permian of Sichuan, Guizhou, Yunnan, and Gaungxi. *Acta Palaeontologica Sinica* 24 (1), 29–37.

Pan, Y.T. and Yu, W. Z. 1993. *Permian Gastropoda of China*. Beijing: Ocean Press, 68 pp.

Pan, H.Z. and Erwin, D.H. 2002. Gastropods from the Permian of Guangxi and Yunnan provinces, South China. *Journal of Paleontology* 78, 1–49.

Pan, H.Z. and Shen, S.Z. 2008. Late Permian (Lopingian) Gastropods from the Qubuerga Formation at the Qubu Section in the Mt. Everest (Qomolangma) Region, Southern Tibet (Xizang), China. *Journal of Paleontology* 82(5), 1038–1042.

Parkhaev, P.Y. 2007. The Cambrian 'basement' of gastropod evolution. In *The Rise and Fall of the Ediacaran Biota"*, Special publications, eds. Vickers-Rich, P. and Komarower, P., 415–421. London: Geological Society.

Posenato, R. 2009. Survival patterns of macrobenthic marine assemblages during the end-Permian mass extinction in the western Tethys (Dolomites, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 280, 150–167.

Recey, A., Smith, A.B. and Dawson, O. 1994. Permian echinoderms from Peninsular Thailand. In *Proceedings of the International Symposium on Stratigraphic Correlation of Southeast Asia (IGCP306)*, eds. Angsuwathana, P., Wongwanich, T., Tansathien, W., Wongsomsak, S. and Tulyatid, J., 106–114. Bangkok: Department of Mineral Resources.

Ridd, M.F., Barber, A.J. and Crow, A.J. 2011. The geology of Thailand. London: Geological Society.

Sakagami, S. 1965. Three Carboniferous species of Bryozoa from Khao Noi, central Thailand. *Japanese Journal of Geology and Geography* 36(2–4), 143–147.

Sakagami, S. 1969. Fusulinacean fossils from Thailand, Part IV. On some Permian fusulinaceans from peninsular Thailand. In *Geology and Palaeontology of Southeast Asia, vol. 6*, eds. Kobayashi, T. and Toriyama, R., 265–275. Tokyo: University of Tokyo Press.

Sakagami, S. 1970. Addition to the Permian Bryozoa from Ko Muk, peninsular Thailand. In *Geology and Palaeontology of Southeast Asia, vol. 8*, eds. Kobayashi, T. and Toriyama, R., 43–68. Tokyo: University of Tokyo Press.

Sakagami, S. 1973. Permian bryozoa from Khao Raen, near Rat Buri, Thailand. In *Geology and Palaeontology of Southeast Asia, vol.12*, eds. Kobayashi, T. and Toriyama, R., 75–89. Tokyo: University of Tokyo Press.

Sakagami, S. 1975. Permian bryozoa from Khao Hin Kling, near Phetchabun, North-central Thailand. In *Geology and Palaeontology of Southeast Asia, vol.16*, eds. Kobayashi, T. and Toriyama, R., 33–43. Tokyo: University of Tokyo Press.

Sakagami, S. 1999. Permian bryozoans from some localities in the Khao Hin Kling area near Phetchabun, North-central Thailand. *Bulletin of the Kitakyushu Museum of Natural History* 18, 77–103.

Sengör, A.M.C. 1984. The Cimmeride orogenic system and the tectonics of Eurasia. *Geological Society of America Special Paper* 195. 82 pp.

Sone, M. 2010. A new species of the rare neritopsid gastropod *Magnicapitatus* from the Guadalupian (Middle Permian) of East Thailand (the Indochina Terrane). *Alcheringa* 34, 1–6.

Sone, M. and Metcalfe, I. 2008. Parallel Tethyan sutures in mainland Southeast Asia: New insights for Palaeo-Tethys closure and implications for the Indosinian orogeny. *Comptes Rendus Geosciences* 340(2), 166–179.

Sone, M. Chonglakmani, C and Chitnarin, A. 2009. Middle Permian productidine brachiopods from central Thailand (The Indochina Terrane) with paleobiogeographical implications. *Journal of Paleontology* 83, 804–810.

Tabakh, M.E. and Utha-Aroon, C. 1998. Evolution of a Permian carbonate platform to siliciclastic basin: Indochina plate, Thailand. *Sed Geol* 121, 97–119.

Thambunya, S., Pisutha-Arnond, V., Khantaprab, C. 2007 Depositional environments of Permian rocks of the Khao Khad Formation in central Thailand. *Science Asia* 33, 371–381.

Toriyama, R. and Sugi, T. 1959. Permian fusulinids from Central Thailand. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology* 9, 17–32.

Toriyama, R., Kanmera, K., Kaewbaidhoon, S., Hongnusonthi, A. 1974. Biostratigraphic zonation of the Rat Buri Limestone in the Khao Phlong Phrab area, Sara Buri, Central Thailand. In *Geology and Palaeontology of Southeast Asia, Volume 14*, eds. Kobayashi, T. and Toriyama, R., 25–48. Tokyo: University of Tokyo Press.

Toriyama, R. and Kanmera, K. 1977. Fusuline fossils from Thailand, Part X. The Permian fusulines from the limestone conglomerate formation in the Khao Phlong Phrab area, Sara Buri, Central Thailand. In *Geology and Palaeontology of Southeast Asia, Volume 18*, eds. Kobayashi, T., Toriyama, R. and Hashimoto, W., 1–27. Tokyo: University of Tokyo Press.

Toriyama, R. and Kanmera, K. 1979. Fusuline fossils from Thailand, Part XII. Permian fusulines from the Ratburi Limestone in the Khao Khao area, Sara Buri, Central Thailand. In: *Geology and Palaeontology of Southeast Asia, Volume 20*, eds. Kobayashi, T., Toriyama, R. and Hashimoto, W., 43–61. Tokyo: University of Tokyo Press.

Tsegab, H., Sum, C.W., Yuriy, G.A., Hunter, A.W., Abtalib, J. and Kassa, S. 2017. Higher-resolution biostratigraphy for the Kinta Limestone and an implication for 1 continuous sedimentation in the Paleo-Tethys, Western Belt of Peninsular Malaysia. *Turkish Journal of Earth Sciences* 26 (5), 377–394.

Udchachon, M., Chonglakmani, C., Campbell, H., Thanee, N. 2007. Late Middle Permian alatoconchid-bearing limestones from the south of the Khao Khwang Platform, Central Thailand. In: *Proceedings of the International Conference on Geology of Thailand (GEOTHAI'07): Towards Sustainable Development and Sufficiency Economy*, ed. Tantiwanit, W. 169–176. Bangkok.

Ueno, K. 2003. The Permian fusulinoidean faunas of the Sibumasu and Baoshan blocks: Their implications for the paleogeographic and paleoclimatologic reconstruction of the Cimmerian Continent. *Palaeogeography, Palaeoclimatology, Palaeoecology* 193, 1–24.

Ueno, K. and Charoentitirat, T. 2011. Carboniferous and Permian. In *The geology of Thailand*, eds. Ridd, M.F., Barber, A.J. and Crow, M.J., 71–135. London: Geological Society.

Wakita, K. and Metcalfe, I. 2005. Ocean Plate Stratigraphy in East and Southeast Asia. *Journal of Asian Earth Sciences* 24, 679–702.

Wang, H.J. 1982. Late Permian gastropods from Heshan of Laibin, Guangxi Province. *Acta Palaeontologica Sinica* 21, 491–496.

Wang, H.J. and Xi, Y.H. 1980. Late Permian to Early Triassic gastropods from Western Guizhou Province. *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formation in Western Guizhou and Eastern Yunnan*, 195–240.

Warren, J., Morley, C.K., Charoentitirat, T., Cartwright, I., Ampaiwan, P., Khositchaisri, P., Mirzaloo, M., Yingyuen, J. 2014. Structural and fluid evolution of Saraburi Group sedimentary carbonates, central Thailand: A tectonically driven fluid system. *Marine and Petroleum Geology* 55, 100–121.

Waterhouse, J.B. 1963. Permian gastropods of New Zealand, New Zealand. *Journal of Geology and Geophysics* 6(4), 587–622.

Waterhouse, J.B. 1982. An Early Permian cool-water fauna from pebbly mudstones in south Thailand. *Geological Magazine* 119, 337–354.

Waterhouse, J.B., and Piyasin, S. 1970. Mid Permian Brachiopods from Khao Phrik, Thailand. *Paleontographica (A: Paläozoologie, Stratigraphie)* 135, 83–197.

Wieldchowsky, C.C. and Young, J.D., 1985. Regional facies variation in Permian rocks of the Phetchabun Fold and Thrust Belt, Thailand. In *Procedings on Geology and Mineral Resources Development of Northeastern Thailand*, eds. Thanvarachorn, P., Hokjaroen, S., Youngme, W., 41–55. Khon Kaen: Khon Kaen University, Thailand.

Yanagida, J. 1964. Permian brachiopods from central Thailand. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology* 15, 1–22.

Yanagida, J. 1970. Permian brachiopods from Khao Phrik, near Rat Buri, Thailand. In *Geology and palaeontology of Southeast Asia*, vol. 14, eds. Kobayashi, T. and Toriyama, R., 7–23. Tokyo: University of Tokyo Press.

Yanagida, J. 1988. *Biostratigraphic Study of Paleozoic and Mesozoic Groups in Central and Northern Thailand – An Interim Report*. Department of Geology, Faculty of Science, Kyushu University, Fukuoka.

Yanagida, J. and Nakornsri, N. 1999. Permian brachiopods from the Khao Hin Kling area near Petchabun, North-central Thailand. *Bulletin of the Kitakyushu Museum of Natural History* 18, 105–136.

Yoo, E.K. 1988. Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales. *Records of the Australian Museum* 40(3), 233–264.

Yoo, E.K. 1994. Carboniferous Mollusca from the Tamworth Belt, New South Wales, Australia. *Records of the Australia Museum* 46(2), 63–120.

Yu, W., Pan, H.Z. and Wang, H.J. 1985. Fossil gastropods from E. Xizang, W. Sichuan and W. Yunnan. In *Stratigraphy and Palaeontology. In W. Sichuan and E. Xizang, China, Pt. 3*, 151–181. Edited by Rigional Geological Survey Team, Sichuan Province.

2

Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand

By **Ketwetsuriya C., Cook A. G. and Nützel A.** Published in *Paläontologische Zeitschrift*, 94, 53–77. doi:10.1007/s12542-019-00463-0.

2.1 Abstract

A new silicified Middle Permian gastropod fauna is reported from Central Thailand. It is the first diverse Permian gastropod assemblage described from the Sibumasu terrane. The gastropod fauna comes from fore-reef shallow water carbonates of the Middle Permian (Wordian) limestones of the Ratburi Group exposed at Khao Phrik, Ratchaburi Province. Thirty-four gastropod species are reported, 17 nominate species and 17 in open nomenclature. Nine species are new to science: *Retispira khaophrikensis*, *Amaurotoma*? *multispirata*, *Eoplatyzona ratchaburiensis*, *Hesperiella cyrtocostata*, *Worthenia*? *waterhousei*, *Stegocoelia centrosinuata*, *Procerithium*? *inaequetuberculata*, *Chlorozyga asiatica* and *Hyphantozyga*? *khaophrikensis*. The gastropod assemblage is strongly dominated by bellerophontids (especially *Warthia* and *Retispira*). The fauna shares only a few species with faunas from other Permian deposits in Thailand and elsewhere, namely the previously described gastropod fauna of the Tak Fa Limestone. The fauna shows relationships to Late Palaeozoic gastropod faunas from the Palaeo-Tethys, such as those of Australia and Malaysia.

2.2 Introduction

Permian gastropods from Southeast Asia are poorly known, including in Thailand, which is part of the mainland of Southeast Asia. There are only a few publications on the Permian gastropod fauna of Thailand. The earliest mention was provided by Grant (1976) from South Thailand. Waterhouse (1982) recorded the presence of the gastropod genus *Peruvispira* at Koh Phi Phi, South Thailand. Sone (2010) described a single gastropod genus and species, *Magnicapitatus huazhangae*, from the Middle Permian (Guadalupian) of East Thailand. Ketwetsuriya et al. (2014, 2016) reported a silicified gastropod fauna from the Middle Permian Tak Fa Limestone, North-Central Thailand. This gastropod fauna is one of the most diverse known from Southeast Asia (Indochina terrane), yielding 40 species.

The present paper describes the Permian silicified gastropod fauna from the Ratburi Limestone, exposed at Khao (Hill) Phrik, Ratchaburi Province, Central Thailand. Waterhouse and Piyasin (1970) previously reported and described the brachiopod fauna from this locality. However, the gastropods from this location have not yet been studied. The present contribution represents the first systematical treatment of a Permian gastropod fauna from the Sibumasu terrane and also the first report of a diverse gastropod assemblage from the Ratburi Limestone Group.

2.3 Geological setting and age

Khao Phrik is a small limestone hill in the Mueang Ratchaburi district, located about 13 km east of Ratchaburi city, Central Thailand (Fig. 1). This hill, extending 0.3 km in an east–west direction and approximately 1.5 km in a north–south direction, consists predominantly of shallow marine limestones of the Ratburi Group (informally known as Ratburi Limestone) and is underlain by sandstones, siltstones and pebbly mudstones of the Kaeng Krachan Group. Geotectonically, the Ratburi Limestone has been recognized as a part of the Sibumasu terrane (Ueno and Charoentitirat 2011) and is considered to have a latest Early Permian to Late Permian age (Bolorian to Wuchiapingian). These limestones are widely distributed in Western and Peninsular Thailand and normally occur as isolated small hills consisting predominantly of massive limestone. The Ratburi Limestone comprises massive to bedded carbonates, locally recrystallized and dolomitized, with chert nodules. It is known for its highly diverse Permian marine invertebrate fauna, including foraminifers (e.g., Sakagami 1969; Brönnimann et al. 1978; Ingavat-Helmcke 1993), corals (e.g., Fontaine 1986, 1988), algae (Fontaine and Salyapongse 2001), echinoderms (Recey et al. 1994), brachiopods (e.g., Waterhouse and Piyasin 1970; Yanagida 1970; Grant 1976) and bryozoans (e.g., Sakagami 1965, 1970, 1973), whereas gastropods have been largely neglected so far.

Sakagami (1969) and Yanagida (1970) suggested that the Ratburi Limestone at Khao Phrik is of an Artinskian age. Waterhouse and Piyasin (1970) reported the presence of 35 brachiopod species from Khao Phrik and assigned a Kazanian (= Wordian) age to them. Grant (1976) collected the block samples from Permian Ratburi Limestone in the Ratchaburi area consisting of 37 species of brachiopods. Therefore, the gastropods from Khao Phrik studied here are regarded to have a Wordian age.

The fossiliferous limestone of Khao Phrik yielding the studied gastropods is rich in brachiopods. It consists of a muddy pale limestone and a black limestone that left a very large residue of carbonaceous black clay after leaching in dilute hydrochloric acid (Waterhouse and Piyasin 1970) and dilute acetic acid. Brachiopods, gastropods, bryozoa, some fusulinids, sponges and corals are found. The depositional environment of the Ratburi Limestone of Khao Phrik was interpreted as a fore-reef setting with access to the open sea (Waterhouse and Piyasin 1970).

2.4 Materials and methods

The limestone samples from Khao Phrik were collected from limestone beds in February 1964 by Waterhouse (who conducted extensive work on Permian brachiopod faunas) and the staff of the Geological Survey, Department of Mineral Resources, Thailand (Waterhouse and Piyasin 1970). The limestone samples were etched with HCl acid to retrieve the silicified fossils. Several blocks of limestone were etched in dilute acetic acid. Most of the gastropod shells are small with abundant individuals, forming the predominant share of the fossilized community, which is also diverse in brachiopods and bivalves. The fauna has also yielded numerous bryozoans, some fusulinids, sponges and corals. Most gastropod specimens are poorly preserved due to coarse silicification. Thus, identification is difficult or impossible in many cases. However, quite a number of gastropod specimens are sufficiently preserved for species or generic identification including characterization of some new taxa. As mentioned, the brachiopods from this collection were studied by Waterhouse and Piyasin (1970); this was the main purpose for this collection. We have received Waterhouse's collection of silicified gastropods and some bivalve specimens in 2017. These gastropods were sorted, and representatives of each species were photographed. The gastropod specimens were coated with ammonium-chloride prior to photography. The gastropod species and genera were classified according to Bouchet et al. (2017).

All type and figured specimens are housed in the Queensland Museum, Brisbane under the repository numbers QMF 39083–39133 and 39350–39400.

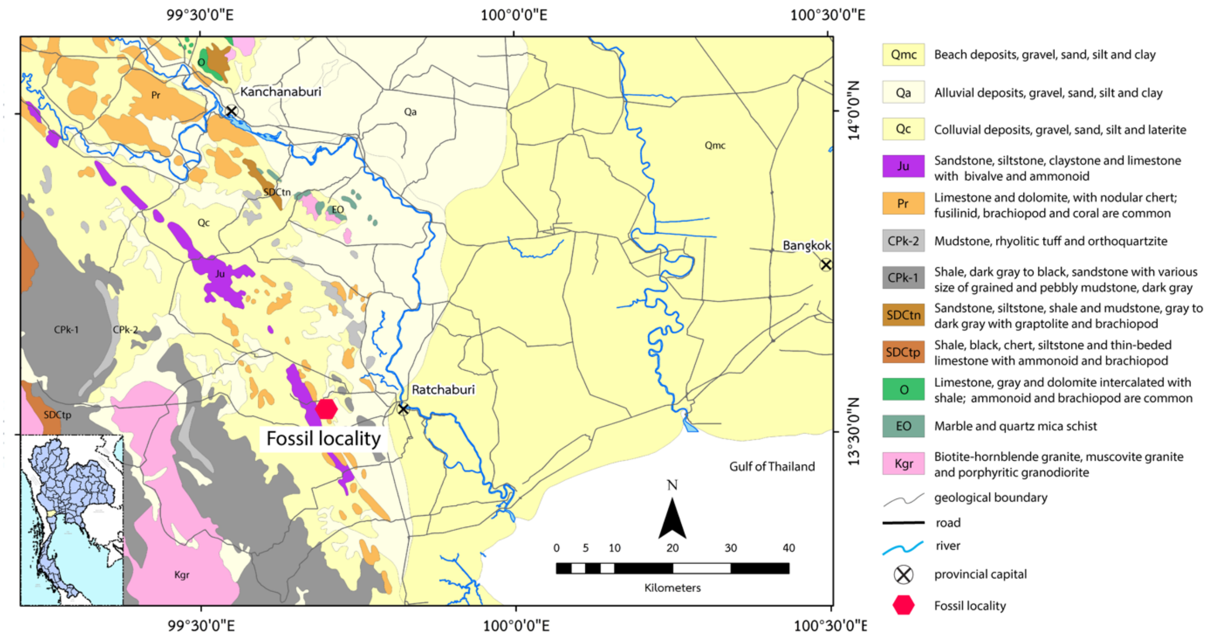

Figure 2.1: Geological map showing the sampling localities that produced the silicified gastropods at Khao Phrik hill, Ratchaburi district, Ratchaburi Province, Central Thailand.

2.5 Systematic palaeontology

Subclass Amphigastropoda Simroth, 1906

Order Bellerophontida Ulrich and Scofield, 1897

Superfamily Bellerophontoidea McCoy, 1852

Family Euphemitidae Knight, 1956

Subfamily Euphemitinae Knight, 1956

Genus *Euphemites* Warthin, 1930

Type species. *Bellerophon urii* Fleming, 1828, Carboniferous, Great Britain.

Euphemites sp.

Figure 2.2a, b

Material. One specimen, QMF 39083.

Description. Bellerophontoid, subglobular shell; specimen 13.0 mm long, 14.8 mm wide, 11.4 mm high; whorl surface ornamented with approximately ten sharp, strong spiral lirae; interspaces wider than spiral lirae; umbilical area rounded convex with narrow, distinct and deep umbilicus; aperture kidney-shaped.

Remarks. This specimen is a typical representative of the genus *Euphemites*. It has the typical spiral lirae on the dorsum. Yochelson (1960) illustrated various *Euphemites* species from the Permian of the Southwestern USA that resemble the present material, for instance, *E. batteni* Yochelson, 1960, *E. crenulatus* Yochelson, 1960, *E. aequisulcatus* Chronic, 1952 and especially *E. sparciliratus* Yochelson, 1960 in having strong, coarse, spiral lirae separated by wide interspaces, but differs from the present specimen by lacking an umbilicus and having fewer spiral lirae. However, it is unclear whether the present specimen is fully grown and the umbilicus could be closed at later growth stages. *Euphemites graffhami* Moore, 1941, is the only *Euphemites* species which has been reported from Thailand by Ketwetsuriya et al. (2016) from the Permian Tak Fa Limestone. However, this species has much deeper and wider umbilici and has a geniculate outline in lateral view.

Genus *Warthia* Waagen, 1880

Type species. *Warthia brevisinuata* Waagen, 1880, Permian, Pakistan.

Warthia cf. *saundersi* Yochelson, 1960
Figure 2.2f–q

cf. 1960 *Warthia saundersi* Yochelson: p. 259, pl. 49, figs. 9–13.

Material. QMF 39084, 39085, 39086, 39087.

Description. Shell involute, longer than wide; anomphalous; largest specimen 9.4 mm long, 9.4 mm wide, 5.7 mm high; whorl profile and dorsum evenly rounded; whorls smooth without visible ornament; aperture strongly bent to triangular, crescent-shaped in the transverse section with central U-shaped indentation; anterior lip rounded; lateral lips steep, joining anterior lips at an angle of nearly 90°.

Remarks. Several smooth involute shells representing the genus *Warthia* are present in this collection, which is widespread and diverse in the Late Palaeozoic (e.g., Nützel and Nakazawa 2012; Ketwetsuriya et al. 2016). The preservation of the material at hand is insufficient for specific identification. Yochelson (1960) reported numerous *Warthia* species from the Permian of the Southwestern USA that resemble the present material. The compressed and smooth shell is similar to *W. fissus* Yochelson, 1960 and *W. angustior* Yochelson, 1960, but the slit is much deeper in these two species than in the present specimens that have also a more rounded dorsum. *W. saundersi* Yochelson, 1960 is the most similar species although the slit of this species is much shorter. As noted by Yochelson (1960), *W.* saundersi is also similar to *W. welleri*, *W. crassus* and *W. waageni*. However, these species can be distinguished by the shape of the dorsum, the dimension of the sinus and the curve of the lateral slope.

Family Bellerophontidae McCoy, 1852
Subfamily Bellerophontinae McCoy, 1852

Genus *Bellerophon* de Montfort, 1808
Type species. *Bellerophon vasulites* de Montfort, 1808, Devonian, Germany.

Bellerophon? sp.
Figure 2.2c–e

Material. One specimen, QMF 39088.

Remarks. This smooth-shelled, anomphalous bellerophontoid shows very faint traces of growth lines withcrescent-shaped aperture in the transverse section. The anterior lip is rounded and seems to have a thick inductura. It is 8.1 mm long, 8.7 mm wide and 6.9 mm high. It could represent *Bellerophon* or *Warthia*. However, the presence of growth lines or ribs is suggestive of *Bellerophon* rather than *Warthia*. The preservation is too poor for further identification.

Subfamily Knightitinae Knight, 1956

Genus *Retispira* Knight, 1945
Type species. *Retispira bellireticulata* Knight, 1945, Middle Permian, Texas, USA.

Retispira khaophrikensis sp. nov.
Figure 2.2r–w

LSID. urn:lsid:zoobank.org:act:ED5DB8B6-AE6E-46F1-99E6-FCB4AB10A450.

Etymology. After the Khao Phrik hill at which the studied gastropod material was found.

Holotype. QMF 39089.
Paratypes. QMF 39090–39093.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell relatively large, bellerophontiform, globose in side view but wider than long in the transverse section; narrowly phaneromphalous; holotype 10.0 mm long, 10.8 mm wide and 8.0 mm thick; dorsum rounded, somewhat flattened; whorl surface largely smooth, ornamented by weak traces of transverse undulations and faint spiral lirae; selenizone slightly elevated; aperture broad, kidney-shaped; inner edges of lateral lips reflexed close to umbilicus; winglike turnout of lateral lips (see Mazaev 2015) wide, parallel to coiling axis, almost covering narrow umbilicus; inductura thin and unornamented; anterior lip and sinus not well preserved; lateral slopes strongly curved.

Remarks. *Retispira khaophrikensis* sp. nov. is placed in the genus *Retispira* based on having expanded lateral lips of the aperture, a depressed selenizone and an ornament of weak transverse undulations as well as fine spiral lirae. This species resembles *Retispira fragilis* Yochelson, 1960 from the Permian of the Southwestern, USA in lacking a strong ornament (a few specimens showing faint spiral lirae) and by being phaneromphalous (see also Kulas and Batten 1997). However, *R. fragilis* has distinct growth lines and differs from *Retispira khaophrikensis* sp. nov. in lacking transverse undulations, by having a more expanded aperture and a narrower umbilicus. *Retispira khaophrikensis* sp. nov. is also similar to *R. modesta* (Girty, 1909) from the Permian of the USA, but the latter species has numerous fine spiral threads.

Yochelson (1960) and Kulas and Batten (1997) mentioned that *R. fragilis* resembles *R. modesta* in having a rounded shell, but they differ from each other by their lateral lips and the umbilicus—the latter species has a wider umbilicus and develops low, transverse undulations. The depth of the slit and sinus are unknown due to preservation.

Retispira lyelli (Gemmellaro, 1890)
Figure 2.2x–ac

*1890 *Bellerophon* (*Bucania*) *lyelli* sp. nov. Gemmellaro— Gemmellaro: p. 178, pl. 16, figs. 13–15.
1922 *Bucania lyelli* Gemmellaro—Wanner: p. 18, pl. 151, fig. 7a–c.
1942 *Bellerophon* (*Bucania*) *lyelli* Gemmellaro—Delpey: p. 348, fig. 23.
1972 *Retispira lyelli* (Gemmellaro)—Batten: p. 13, fig. 6a, b.
v 2016 *Retispira lyelli* (Gemmellaro, 1890)—Ketwetsuriya et al.: p. 490, fig. 8a–c.

Material. Three specimens, QMF 39094–39096.

Description. Shell relatively small bellerophontiform, narrowly phaneromphalous; largest specimen 6.9 mm long, 7.5 mm wide, 5.8 mm thick; inductura thin; whorls ornamented by numerous closely spaced spiral threads and indistinct growth lines forming reticulation; slightly raised selenizone; aperture equally expanding, kidney-shaped; wing-like turnout of lateral lips (see Mazaev 2015) covering large parts of umbilicus; anterior lip very thin, having a narrow slit.

Remarks. According to the relatively characteristic shell morphology of the present specimens, we assign them to *Retispira lyelli* (Gemmellaro, 1890) that was first described from the Permian of Italy (Sicily). Wanner (1922) reported it from Timor. Delpey (1942), Batten (1972) and Ketwetsuriya et al. (2016) also reported this species from SE Asia although these specimens seem to have a narrower umbilicus and have two orders of fine spiral threads. *Knightites* (*Retispira*) *girtyi* Yochelson, 1960 from the Permian of the Southwestern, USA is also similar in having the lower part of the lateral slopes falling into the umbilici and consisting of two orders of ornament (stronger and weaker). However, *Retispira lyelli* has a much more bent aperture in the transverse section and a wider umbilicus.

Basal Gastropoda, unassigned to subclass and order
Superfamily Trochonematoidea von Zittel, 1895
Family Trochonematidae von Zittel, 1895

Genus *Amaurotoma* Knight, 1945
Type species. *Pleurotomaria subsinuata* Meek and Worthen, 1861, Pennsylvanian, USA.

Amaurotoma? *multispirata* sp. nov.
Figure 2.3a–g

LSID. urn:lsid:zoobank.org:act:EBF8B0E-A2DC-4391-ACD4-1D83ECD17457.

Etymology. Latin, for having many spiral cords.

Holotype. QMF 39097.
Paratypes. QMF 39098–39102.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell turbiniform, moderately high-spired, with gradate spire; larger specimen consisting of ca. five whorls (apex missing), 12.0 mm high, 11.5 mm wide with an apical angle of about 60°; early teleoconch whorls evenly convex; later whorls slightly angulated at about mid-whorl and somewhat above middle of spire whorls slightly convex to flat ramp; ramp dipping from upper suture at an angle of 30°; whorl face subvertical to markedly convex below

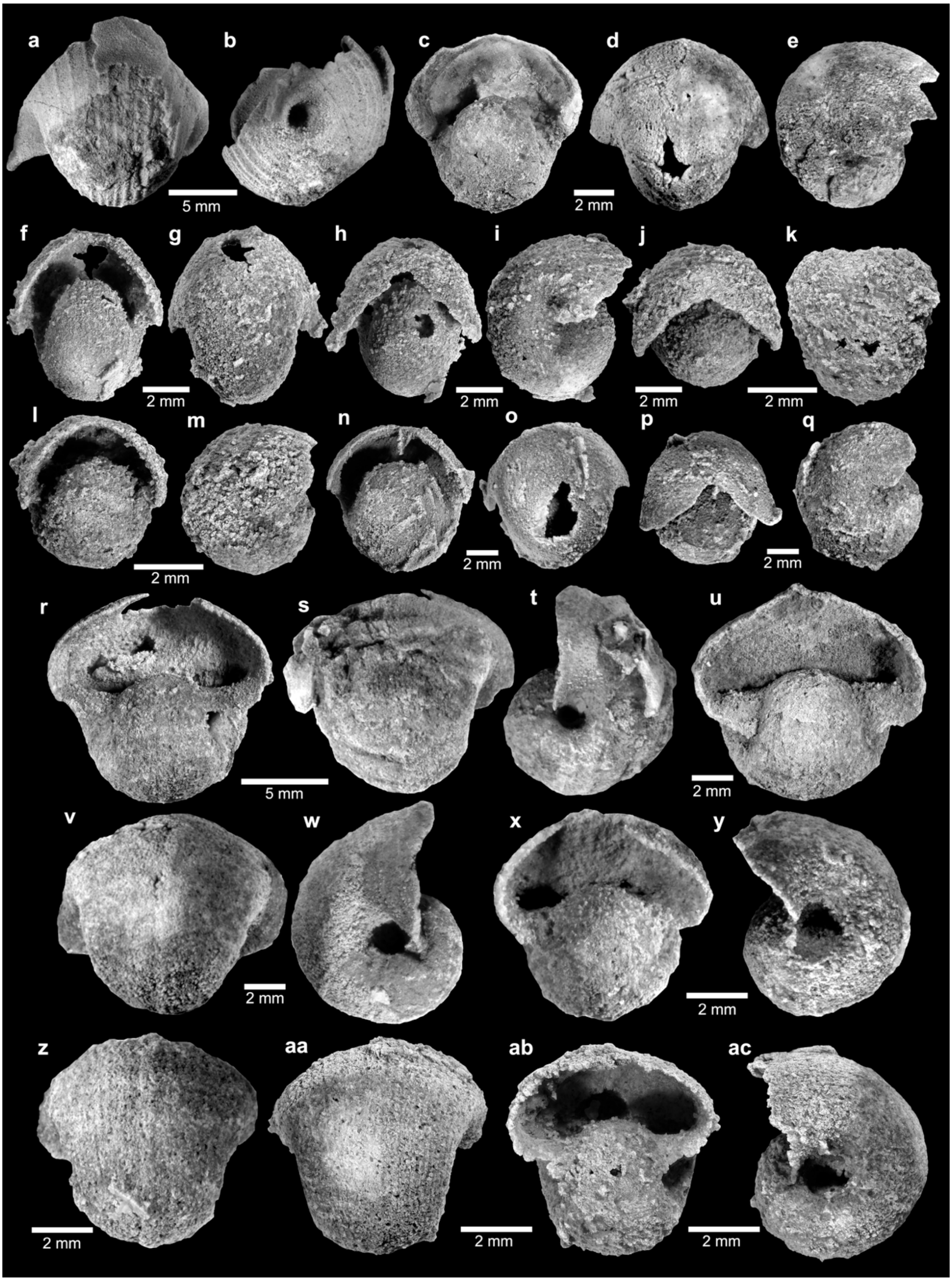

Figure 2.2: a, b *Euphemites* sp., QMF 39083. c–e *Bellerophon*? sp., QMF 39088. f–j *Warthia* cf. *saundersi* Yochelson, 1960, QMF 39084. k–m *Warthia* cf. *saundersi* Yochelson, 1960, QMF 39085. n–q *Warthia* cf. *saundersi* Yochelson, 1960, QMF 39086. r–t *Retispira khaophrikensis* sp. nov., paratype, QMF 39090. u–w *Retispira khaophrikensis* sp. nov., holotype, QMF 39089. x–z *Retispira lyelli* (Gemmellaro, 1890), QMF 39094. aa–ac *Retispira lyelli* (Gemmellaro, 1890), QMF 39095.

angulation; two to three faint spiral cords and several weaker axial ribs on ramp; intersections of axial ribs and spiral cords slightly nodular; abapical portion of whorls ornamented by three widely spaced spiral cords; second spiral cord strongest and forming periphery above lower suture; outer whorl face of body whorl ornamented with five to six distinct spiral cords; base evenly convex with rounded transition to whorl face, phaneromphalous, with several weak spiral cords; suture distinct, moderately impressed; aperture evenly circular.

Remarks. The growth lines are indistinct due to preservation; they seem to curve backward on the ramp. The present specimens resemble *Amaurotoma humerosa* (Meek and Hayden, 1858) as described and illustrated by Knight (1945) and Kues and Batten (2001) from the Pennsylvanian of the USA in respect to ornamentation and other diagnostic characters. However, *A*. *humerosa* has a much more distinctly angulated whorl profile and stronger spiral cords. The present specimens are also similar to *Knightinella ornata* Nützel and Ketwetsuriya, 2016 (in Ketwetsuriya et al.) from the Middle Permian of Thailand, but this species has a broader ramp and much stronger spiral cords, especially in the abapical portion of the whorls. *Amaurotoma multispirata* sp. nov. resembles species of the genera *Baylea* and *Biarmeaspira* but we found no clear evidence of a selenizone and hence place it tentatively in *Amaurotoma*.

Superfamily Trochonematoidea von Zittel, 1895
Family Lophospiridae Wenz, 1938

Genus *Worthenia* de Koninck, 1883
Type species. *Turbo tabulatus* Conrad, 1835, Carboniferous, Pennsylvania, USA.

Worthenia? *waterhousei* sp. nov.
Figure 2.3h–l

LSID. urn:lsid:zoobank.org:act:C5E3AD0E-2FF2-42D5-A8E0-EB08C72A032D.

Etymology. After Waterhouse who collected the present material and for his work on Late Palaeozoic faunas.

Holotype. QMF 39103, the only specimen.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell small, turbiniform, 3.0 mm high, 2.7 mm wide with an apical angle of about 100°; apex low-spired, dome-shaped; early whorls (first 2.5 whorls) convex, seemingly smooth; later whorls convex with an angulation situated at about mid-whorl separating slightly concave to straight sloping ramp and subvertical, slightly convex abapical portion of whorl; whorls densely ornamented with collabral axial ribs, numbering up to 40 per whorl; ribs forming sinus at angulation of whorl face, opisthocline and sinuous below it and prosocline on ramp; sinus shallow in penultimate whorls; last preserved whorl; whorl face of spire whorls ornamented with three spiral cords placed just below adapical suture at the angulation where the sinus of the ribs culminates and in between both; spiral cords are knobby at intersections with axial ribs; spiral cord 2 is strongest on last whorl suture and above lower suture; fourth spiral cord emerges from abapical suture; last whorl inflated, convex with three pronounced spiral cords, adapical spiral cord weakest located close to upper suture; sinus becoming selenizone at mid-whorl; selenizone widely concave with backward curving lunulae and bordered by two strong spiral cords; whorl surface above upper border of selenizone ornamented by prosocline axial ribs and opisthocline, prosocyrt axial rip on whorl face below lower border of selenizone; intersection of spiral cords and axial ribs distinctly nodular; suture distinct; base evenly rounded with rounded angular transition to whorl face and ornamented with ca. 60 axial ribs; base narrowly phaneromphalous; aperture circular, ca. 1.4 mm high, 1.7 mm wide; inner lip arcuate, outer lip thin.

Remarks. Due to the strong and dense axial ornament and the concave selenizone, this species is only tentatively assigned to *Worthenia*. This single shell resembles *Worthenia* sp. as illustrated by Yoo (1994: pl. 9, fig. 10) from the Early Carboniferous of New South Wales, Australia in shell shape and ornamentation, but it differs from that species in having more closely spaced axial ribs. *Worthenia crenilunula* Yoo, 1994, also from the Early Carboniferous of Australia, has a similar ornament. However, this species is more high-spired, the axial ribs are not as strong and it has spiral cords on the base, whereas the present specimen has only axial ribs on the base.

Worthenia cf. *crenulunula* Yoo, 1994
Figure 2.3m–p

cf. * 1994 *Worthenia crenulunula* sp. nov. Yoo—Yoo: p. 80, pl. 8, figs. 11–14, pl. 9, figs. 5–8.

Material. One specimen, QMF 39104.

Description. Moderately high-spired shell, turbiniform, approximately four whorls (protoconch missing), 7.3 mm high, 6.9 mm wide; teleoconch whorls sharply angulated slightly below mid-whorl, angulation forms periphery; whorl face with concave ramp and concave portion below angulation approximately parallel to shell axis; selenizone situated at angulation, elevated, convex, ornamented by lunulae, bordered by two spiral crests; whorls ornamented with two nodular spiral cords, a weaker one somewhat below adapical suture and a stronger one near abapical suture; suture shallow; base evenly rounded; transition to base angular; seemingly ornamented by several faint spiral cords; narrowly phaneromphalous; aperture circular, ca. 3.3 mm high, 4.0 mm wide.

Remarks. This shell closely resembles the Early Carboniferous species *Worthenia crenulunula* Yoo, 1994 (p. 80, pl. 8, figs. 11–14, pl. 9, figs. 5–8). However, it is not sufficiently well-preserved for a definitive identification.

Subclass Vetigastropoda von Salvini-Plawen, 1980
Order Pleurotomariida Cox and Knight in Knight et al., 1960
Superfamily Eotomarioidea Wenz, 1938
Family Eotomariidae Wenz, 1938
Subfamily Eotomariinae Wenz, 1938

Genus *Ananias* Knight, 1945
Type species. *Phanerotrema*? *welleri* Newell, 1935, Carboniferous, Kansas, USA.

Ananias sp.
Figures 2.3q–t, 2.4a–d

Material. QMF 39105–39114.

Description. Shell trochiform with gradate spire; larger specimen consisting of ca. 4.5 whorls, 8.3 mm high, 7.2 mm wide with an apical angle about 80°; whorls angulated at about mid-whorl; whorls slightly convex above angulation, forming sloping ramp; whorl face below angulation straight, to slightly concave, almost parallel to shell axis; selenizone situated at angulation at about mid-whorl; selenizone narrow, concave, somewhat elevated, bordered by pair of spiral threads, lower spiral thread forming angular periphery; whorl face above selenizone ornamented with prosocline elongated nodes or ribs and fine spiral threads; base minutely phaneromphalous, with faint spiral threads, convex and evenly rounded without angulation at transition to whorl face; suture distinct; aperture simple.

Remarks. This species has a distinct ornament on the ramp and the selenizone situated at about mid-whorl; it seems to be a typical representative of the genus *Ananias*, which is widespread in the late Palaeozoic. *Ananias permianus* Batten, 1989 (p. 21, pl. 4, figs. 8–19) from the Permian of the Southwestern United States is the most similar species in shape, in having well developed selenizone margins and subsutural nodes or riblets and a fine spiral ornament. In addition, the base this species has exclusively spiral ornament on its base, which seems to be the case in some of our specimens as well. However, *A. permianus* is more highspired than our specimens. The present species also resembles *A. labrectus* Batten, 1989 (p. 20, pl. 3, figs. 11–18, pl.4, figs. 1–7), but it differs from this species in having an elevated selenizone and by having a markedly concave upper whorl face immediately adjacent to the upper selenizone margin. The genus *Glabrocingulum* holds similar species having axially elongated nodes above the selenizone. However, *Glabrocingulum* is more depressed and its selenizone is situated close to the lower suture.

Subfamily Neilsoniinae Knight, 1956

Genus *Peruvispira* Chronic, 1949
Type species. *Peruvispira delicata* Chronic, 1949, Late Permian, Peru.

Peruvispira sp.
Figure 2.4e–g

Material. QMF 39115.

Description. Shell small, turbinate, moderately high-spired; single specimen consisting of ca. 4.5 whorls (apex missing), 3.1 mm high, 2.4 mm wide, apical angle about 72°; early teleoconch whorls (first preserved two whorls) smooth, convex; later whorls slightly angulated at about mid-whorl at lower border of selenizone that forms periphery; selenizone situated at mid-whorl, slightly concave and bordered by two strong spiral cords; adapical portion of whorls forming a distinctly concave ramp with faint prosocline growth lines; abapical portion of whorl face below margin of selenizone subvertical to concave, without visible ornament; base rounded with weak narrowly spaced spiral threads, minutely phaneromphalous; suture indistinct; aperture round, as wide as high.

Remarks. This single specimen resembles *Peruvispira gundyensis* Yoo, 1988 from the Early Carboniferous of New South Wales, Australia in shell shape and in the position of the selenizone at about mid-whorl. However, this species has a convex, not a concave, ramp and distinct sharp axial threads. *Neilsonia nuda* Mazaev, 2015 from the Middle Permian of the Volga-Urals Region, Russia is also similar in whorl profile and position of selenizone, but it differs from this specimen in having a broader shape, a wider selenizone and in having a deeper suture (Mazaev 2015, pl. 4, figs. 4–8). *Apachella turbiniformis* Winters, 1963 sensu Batten (1989: p. 28, pl. 6, figs. 13–15) is also similar, but it is broader and lacks a strongly concave ramp. The specimens representing *A. turbiniformis* as illustrated by Winters (1963: p. 29, pl. 6, figs. 22–24, Permian, USA) differ considerably from both, Batten's (1989) material and the present species. *A. glabra* Batten, 1989 resembles the present specimen in having a rounded base with very fine spiral threads. However, the upper whorl surface is evenly rounded and slightly convexoconcave in *A. glabra* but distinctly concave in the present specimen.

Family Gosseletinidae Wenz, 1938

Genus *Eoplatyzona* Frýda, 1998
Type species. *Eoplatyzona pulchra* Frýda, 1998, Devonian, Czech Republic.

Eoplatyzona ratchaburiensis sp. nov.
Figure 2.4h–k

LSID. urn:lsid:zoobank.org:act:BD88C5E1-8D82-4819-AE88-1966701D2730.

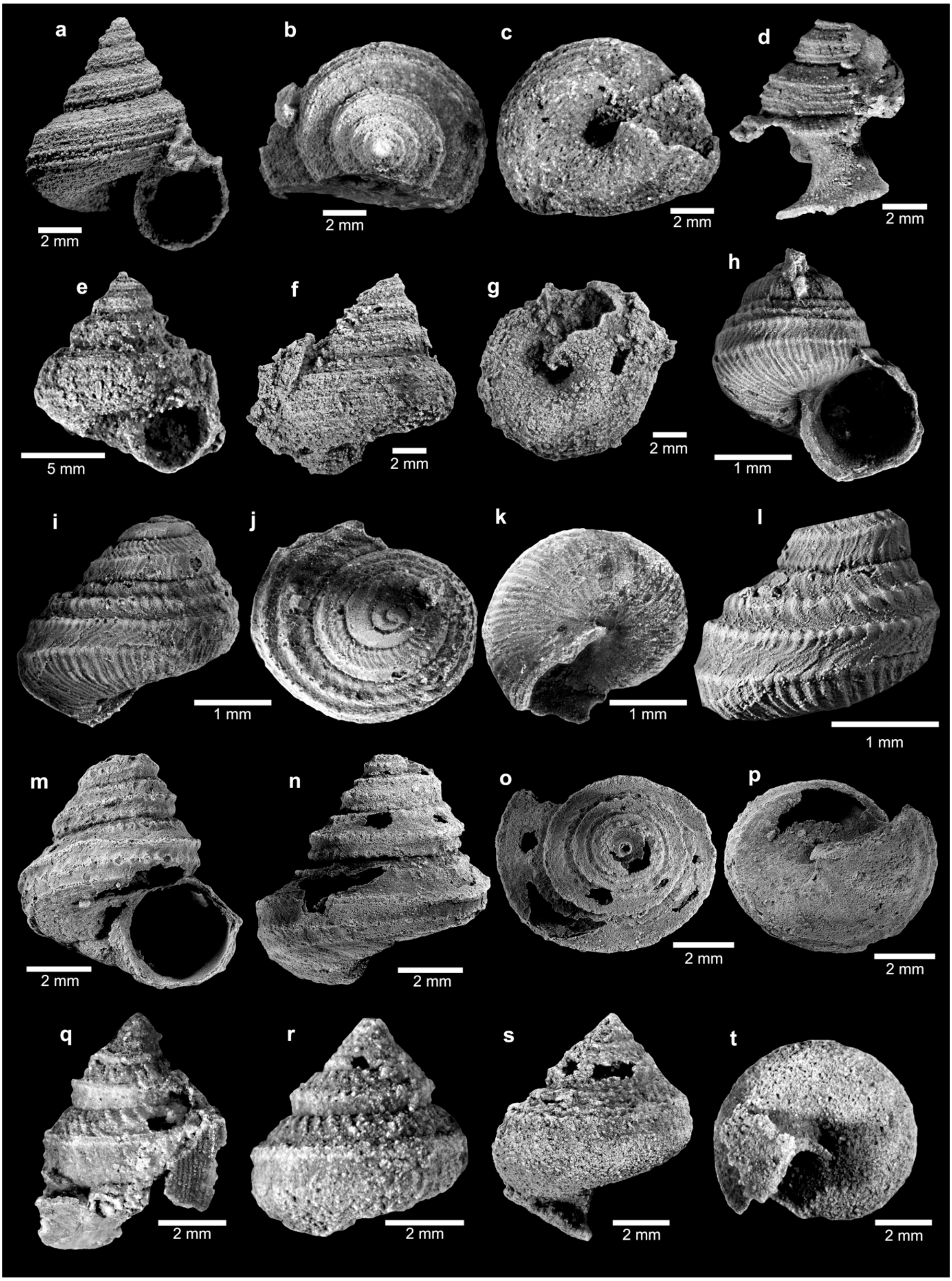

Figure 2.3: a–c *Amaurotoma*? *multispirata* sp. nov., holotype, QMF 39097. d *Amaurotoma*? *multispirata* sp. nov., paratype, QMF 39099. e–g *Amaurotoma*? *multispirata* sp. nov., paratype, QMF 39098. h–*l Worthenia*? *waterhousei* sp. nov., holotype, QMF 39103. m–p *Worthenia* cf. *crenulunula* Yoo, 1994, QMF 39104. q *Ananias* sp., QMF 39105. r *Ananias* sp., QMF 39106. s, t *Ananias* sp., QMF 39107.

Etymology. After the Province of Ratchaburi where the species occurs.

Holotype. QMF 39116, the only specimen.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell low-spired, turbiniform, consisting of ca. three whorls (apex missing), 3.8 mm high, 6.2 mm wide; body whorl broad, with slightly convex whorl face; whorl ornamented by distinct prosocline, widely and regularly spaced, sharp axial ribs (up to 60 ribs per whorl) above selenizone; ribs orthocline to prosocyrt below selenizone; selenizone immediately above suture, forming periphery, bordered by prominent spiral crests; selenizone concave, smooth, parallel to shell axis; base flatly convex with radial axial threads representing continuation of the axial ribs on whorl face; base either narrowly phaneromphalous or anomphalous.

Remarks. *Eoplatyzona ratchaburiensis* sp. nov. resembles *Eotomaria umbilicata* Yoo, 1994 from the Early Carboniferous of Australia (which also could be included in *Eoplatyzona*) in shell shape, the position of the selenizone and the ornamentation of sharp prosocline axial ribs. However, *E. umbilicata* differs from the present species in having distinct lunulae on the selenizone, in being distinctly phaneromphalous and in having S-shaped ribs below the selenizone, whereas they are orthocline to prosocyrt in the new species. The genus Eotomaria, based on an Ordovician type species, lacks axial ribs and has a coeloconoid shape but is otherwise similar to the present species. *Eoplatyzona pulchra* Frýda, 1998, the Devonian type species from the Czech Republic, is more high-spired, has a wider selenizone with distinct lunulae and more convex whorls.

Superfamily Porcellioidea Koken, 1895
Family Porcelliidae Koken, 1895
Subfamily Agnesiinae Knight, 1956

Genus *Hesperiella* Holzapfel, 1889
Type species. *Pleurotomaria contraria* de Koninck, 1842, Early Carboniferous, Belgium.

Hesperiella cyrtocostata sp. nov.
Figure 2.4l–t

LSID. urn:lsid:zoobank.org:act:C23C96A1-97BF-474D-8025-3E40F075C21E.

Etymology. Latin, for the arched axial ribs.

Holotype. QMF 39117.

Paratype. QMF 39118.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell small, sinistral, conical with blunt apex; larger specimen consisting of ca. 4.5 whorls, 3.6 mm high, 3.6 mm wide with an apical angle about 70°; early whorls depressed, dextral, smooth, coiling inward and covered by later whorl; early whorls umbilicated and thus apex has funnel like chimney; teleoconch whorls slightly convex to straight, ornamented with strongly opisthocline, widely spaced axial ribs, numbering more than 20 per whorl; ribs become more oblique and more strongly prosocyrt during ontogeny; suture distinct; selenizone located below lower suture, visible only on last whorl, narrow with distinct lunulae; base hemiomphalous, flat with rounded angular transition to whorl face; aperture unknown.

Remarks. *Hesperiella elongata* Yoo, 1994 from the Early Carboniferous of Australia closely resembles the new species. However, the axial ribs are much more prosocyrt (more convex) in doubt because the illustration of de Koninck shows a specimen with much more convex whorls and differs in this respect from the present species. *Hesperiella permiana* and *H. wordensis*, both described by Batten (1989) from the Permian of the southwestern USA, differ from the present species in having the selenizone much higher on the whorl and in being more high-spired. *Hesperiella karabolkensis* Licharev, 1975 from the Pennsylvanian of Russia is more slender and the selenizone is in a distinctly suprasutural position.

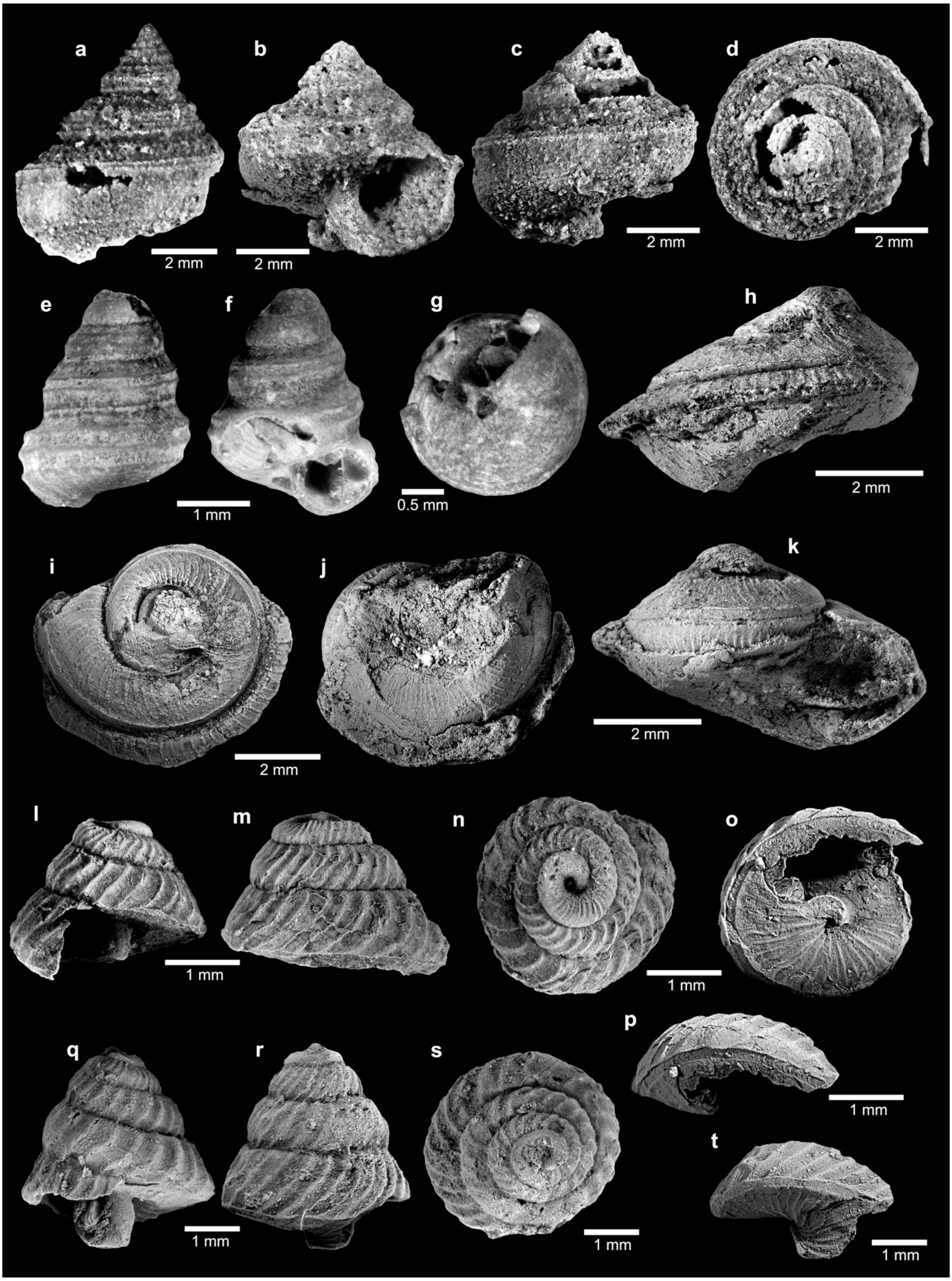

Figure 2.4: a *Ananias* sp., QMF 39108. b–d *Ananias* sp., QMF 39109. e–g *Peruvispira* sp., QMF 39115. h–k *Eoplatyzona ratchaburiensis* sp. nov., holotype, QMF 39116. Arrow marks position of selenizone. l–p *Hesperiella cyrtocostata* sp. nov., paratype, QMF 39118. Arrow marks position of selenizone. q–t *Hesperiella cyrtocostata* sp. nov., holotype, QMF 39117.

Order Seguenziida
Superfamily Seguenzioidea Verrill, 1884
Family Eucyclidae Koken, 1897

Genus *Eucycloscala* Cossmann, 1895
Type species. *Trochus binodosus* Münster, 1841, Late Triassic, northern Italy.

Eucycloscala? sp.
Figure 2.5a–d

Material. QMF 39119.

Description. Shell small, moderately high-spired, teleoconch fragment of three whorls; whorl face angular with angulation below mid-whorl; strong spiral cord on angulation; ramp wide, straight to slightly concave with one or two indistinct fine spiral threads; lower part of whorl face narrow and distinctly concave inclined inward, bearing a spiral cord somewhat above suture; a further spiral cord marks edge at base; about seven or eight varices or axial folds developed on the upper whorl surface at the shoulder, forming wavy upper whorl surface, shoulder and outer whorl face; whorl embraces at basal marginal cord; base flatly convex, anomphalous; suture shallow.

Remarks. *Eucycloscala asiatica* Batten, 1985 from the Permian of Perak, Malaysia is the most comparable Permian species, but differs from the present specimen in having coarser varices forming strong nodes on the periphery and in being more high-spired. Moreover, *E. asiatica* has strong spiral cords on the base whereas our specimen shows only a faint ornament on the base. The assignment of both, *Eucycloscala asiatica* Batten, 1985 and the present species, to the largely Mesozoic genus Eucycloscala needs confirmation.

Family Trochidae Rafinesque, 1815

Genus *Coeloconulus* Nützel, 2012
Type species. *Coeloconulus panae* Nützel in Nützel and Nakazawa, 2012, Middle Permian, Japan.

Coeloconulus panae Nützel, 2012
Figure 2.5e–g

v * 2012 *Coeloconulus panae* sp. nov. Nützel—Nützel and Nakazawa: p. 118, figs. 10i–p, 11a.

Material. QMF 39120.

Description. Shell small with coeloconoid profile; comprising about seven preserved whorls, earliest whorls missing; whorls low; whorl face flat; suture shallow and indistinct; surface seemingly smooth but strongly corroded; base flat, distinctly phaneromphalous.

Remarks. Due to the coarse silicification, the shell is poorly preserved but closely resembles the Permian type specimens of *C. panae* from Japan as reported by Nützel and Nakazawa (2012).

Subclass Neritimorpha Koken, 1896
Order Cycloneritimorpha Frýda, 1998
Superfamily Naticopsoidea Waagen, 1880
Family Naticopsidae Waagen, 1880
Genus *Naticopsis* McCoy, 1844
Type species. *Naticopsis philippsii* McCoy, 1844, Early Carboniferous, Ireland.

Naticopsis sp.
Figure 2.5h–j

Material. QMF 39121.

Description. Small shell, low spired, naticiform with about three whorls, 2.3 mm high and wide; apical angle about 104°; whorls smooth, distinctly convex, rounded; body whorl inflated, much higher than spire; spire distinctly elevated; suture shallow but distinct; aperture higher than wide, columellar lip curved, seemingly with callus.

Remarks. The preservation of the aperture is insufficient for specific identification. However, this naticiform smooth shell resembles species of the genus *Naticopsis*, which is diverse and widespread in the Late Palaeozoic. For instance, *Naticopsis minuta* Yoo, 1994 (p. 82, pl. 14, figs. 9–12) is similar in shell shape, but that species is smaller and has fine collabral threads. *Naticopsis hologyroides* Mansuy, 1914 from the Productus Limestone of Cambodgia has less convex whorls and a straight columellar lip.

Subclass Caenogastropoda Cox in Knight et al., 1960
Superfamily Orthonematoidea Nützel and Bandel, 2000
Family Goniasmatidae Nützel and Bandel, 2000

Genus *Goniasma* Tomlin, 1930
Type species. *Murchisonia lasallensis* Worthen, 1890, Pennsylvanian, USA.

Goniasma sp.
Figure 2.5k–m

Material. QMF 39122–39124.

Description. Shell medium-sized, turritelliform, high-spired; whorls regularly increasing; largest specimen consisting of ca. 3.5 whorls (apex and body whorl missing), 11.8 mm high, 7.5 mm wide; whorls without distinct ornament; periphery angulated at about mid-whorl in earlier whorls and well below mid-whorl in latest preserved whorl; selenizone not well visible but probably convex on angulation; upper whorl face above selenizone forming straight to gently concave ramp; whorl face below selenizone concave, inclined inward to suture; base flatly convex, anomphalous; aperture subovate (outer lip broken off); columellar lip nearly straight; siphonal groove well-developed.

Remarks. The present specimens probably belong to the genus *Goniasma*, which however usually has the angulation lower on the whorls. The selenizone is not visible due to the coarse silicification, but is probably situated on the angulation. The present specimens also resemble species of the subgenus *Murchisonia* (*Donaldospira*) Batten, 1966 in being high-spired and in having angulated whorls. However, *Donaldospira* has the angulation at mid-whorl throughout, whereas in Goniasma the angulation moves from a middle position to a position low on the whorls, and this is also the case in the present species. However, the limits of *Donaldospira* and *Goniasma* are not entirely clear. The present material resembles the Permian species *Murchisonia* (*Donaldospira*) *malaysia* Batten, 1985 from Perak, Malaysia in shape, in having angulated whorls and in having a siphonal groove. However, *M*. (*D*.) *malaysia* differs from it in having finer spiral cords on the whorls above and below the selenizone and in having the angulation higher on the whorls.

Genus *Stegocoelia* Donald, 1889
Type species. *Murchisonia* (*Stegocoelia*) *compacta* Donald, 1889, Early Carboniferous, Scotland.

Remarks. Some of the taxa present in our collection do also fit the subgenus *Stegocoelia* (*Hypergonia*) Donald, 1892, but *Hypergonia* has been treated as junior synonym of *Stegocoelia* by Mazaev (2001).

Stegocoelia? sp. 1
Figure 2.5n–s

Material. QMF 39125–39130.

Description. Moderately high-spired shell, comprising about five whorls (apex missing); larger specimen consisting of ca. 5.5 whorls, 7.9 mm high, 4.6 mm, apical angle about 62°; whorls low, strongly convex and somewhat angulated at mid-whorl; whorls ornamented with two median spiral cords at periphery of whorls; two weaker spiral cords somewhat below and above suture; suture distinctly impressed; aperture subcircular, in larger specimen 2.0 mm high, 2.1 mm wide; base flatly rounded, anomphalous.

Remarks. All the specimens are too poorly preserved for a safe identification. Assuming it had a selenizone or sinus in the outer lip, it would represent the genus *Stegocoelia*. There is resemblance to *Goniasma* sp. 1 as reported by Chronic (1949, in Newell et al.) from the Permian of Peru, but this species has a stronger angulation of the whorl face. *Stegocoelia akasakaensis* Nützel, 2012 from the Permian of Japan is also similar, but its spiral cords are more pronounced.

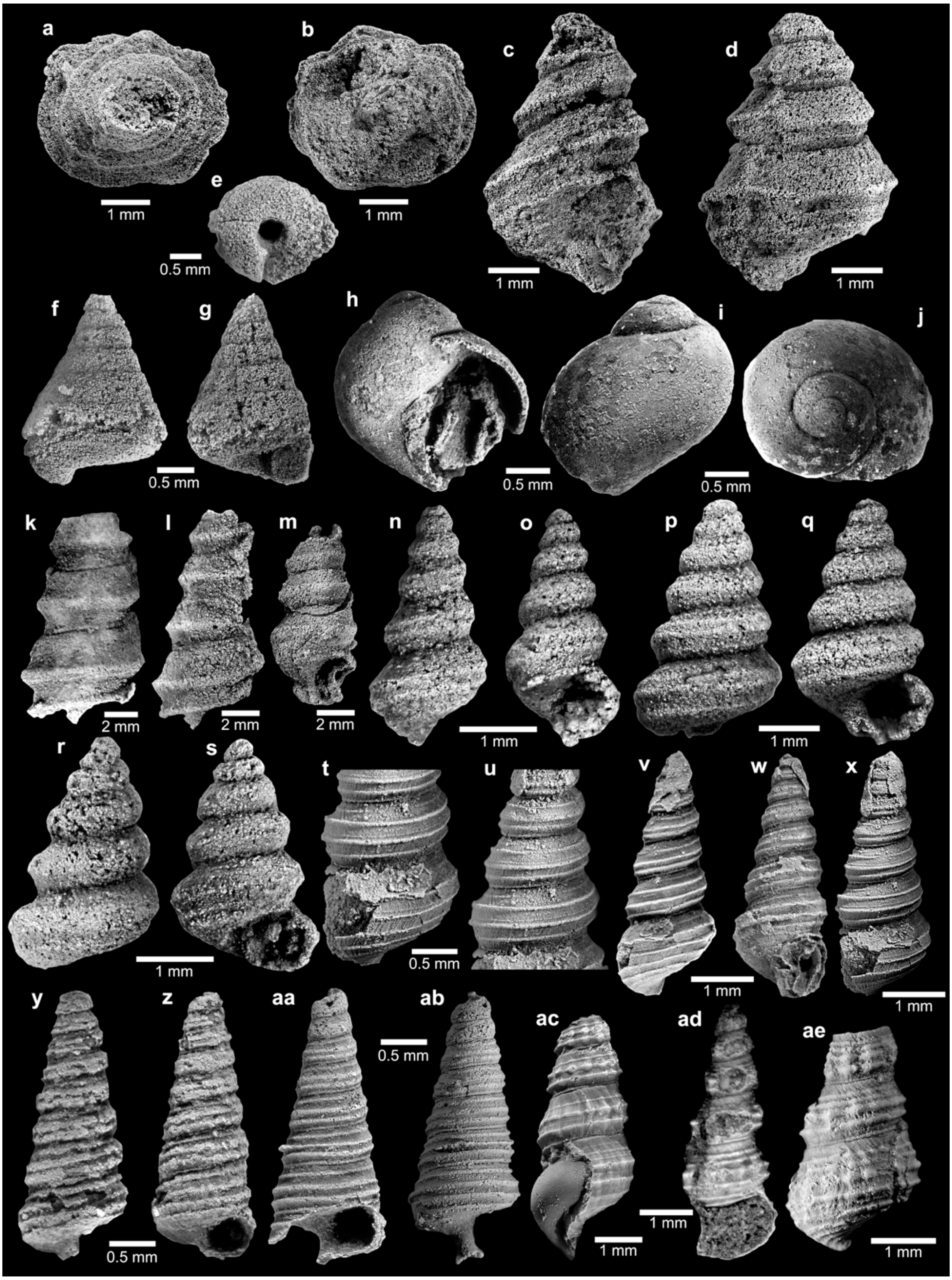

Figure 2.5: a–d *Eucycloscala*? sp., QMF 39119. e–g *Coeloconulus panae* Nützel, 2012, QMF 39120. h–j *Naticopsis* sp., QMF 39121. k *Goniasma* sp., QMF 39122. l *Goniasma* sp., QMF 39123. M *Goniasma* sp., QMF 39124. n, o Stegocoelia? sp. 1, QMF 39125. p, q *Stegocoelia*? sp. 1, QMF 39126. r, s *Stegocoelia*? sp. 1, QMF 39127. t–x *Stegocoelia centrosinuata* sp. nov., holotype, QMF 39131. Arrow marks position of selenizone. y, z *Stegocoelia*? sp. 2, QMF 39132. aa, ab *Stegocoelia*? sp. 2, QMF 39133. ac *Procerithium*? *inaequetuberculata* sp. nov., holotype, QMF 39350. ad, ae *Procerithium*? *inaequetuberculata* sp. nov., paratype, QMF 39351.

Stegocoelia centrosinuata sp. nov.
Figure 2.5t–x

LSID. urn:lsid:zoobank.org:act:54D2BD62-FA5A-4BE8-9881-16F1FC96096B.

Etymology. Latin, for having a sinus (selenizone) at about mid-whorl.

Holotype. QMF 39131.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell high-spired, slender, murchisoniform; specimen consists of seven whorls, 4.0 mm high, 1.0 mm wide with an apical angle of about 40°; whorls distinctly convex ornamented with four widely spaced spiral cords; first spiral cord weakest, located somewhat below adapical suture; second spiral cord somewhat above mid-whorl; third spiral cord strongest, forming periphery somewhat below mid-whorl, fourth spiral cord situated somewhat above abapical suture; fifth weak spiral cord emerging from abapical suture; selenizone (or pronounced sinus) broad, situated at mid-whorl, bordered by spiral cord 2 and 3; selenizone with faint spiral thread near abapical border; suture impressed and distinct; aperture elongated subovate, 2.0 mm high, 2.1 mm wide; base rounded with two revolving cords, anomphalous, growth lines prosocyrt.

Remarks. *Stegocoelia centrosinuata* sp. nov. has the selenizone (or a distinct sinus) at about mid-whorl whereas in other species of the genus *Stegocoelia*, it is situated high on the whorls. The present species resembles *Stegocoelia acutiformis* Mazaev, 2001 and *S. acuta* Mazaev, 2001 from the Middle and Upper Carboniferous of Russia in shell shape and ornamentation. However, these species have the selenizone situated high on the whorls. Both have higher whorls and differ in details of the ornamentation.

Stegocoelia? sp. 2
Figure 2.5y–ab

Material. QMF 39132–39133.

Description. Shell small, high-spired, slender, consisting of approximately eight whorls (apex missing), 2.9 mm high, 1.3 mm wide with an apical angle of 34°; whorls slightly convex, rather flat; whorls expand slowly and gradually; whorls ornamented with four distinct spiral cords; first spiral cord placed below upper suture; second and third spiral lirae stronger; spiral 2 at about mid-whorl, spiral 3 halfway between spiral 2 and abapical suture; fourth spiral lira weakest, emerging from abapical suture; whorl face between spiral cords markedly concave; sutures distinct; aperture subcircular; growth lines obscure due to preservation; base flattened, anomphalous.

Remarks. Growth lines could not be observed in the present material, and thus it is unclear whether this species represents *Stegocoelia* or *Orthonema*. There are a number of Late Palaeozoic species which are very similar, but the perseveration of our material is too poor to establish species identity: *Stegocoelia alta* Licharev, 1975 (p. 10, 7–9) from the Carboniferous of Russia is very similar to our material but seems to differ in its rather variable arrangement of the spiral cords. *Orthonema borovskensis* Mazaev, 2002 from the Carboniferous of Russia closely resembles our shells, but this species has less convex whorls and its spiral cords have the same strength instead of having a weaker adapical cord. The present material resembles *Stegocoelia* (*Hypergonia*) *elongata* Yoo, 1988 (p. 245, figs. 73–75) from the Early Carboniferous of Australia in shell shape and principal ornamentation. However, spiral cords are weaker in *S.* (*H.*) *elongata*, and as a consequence, interspaces are not as markedly concave.

Superfamily uncertain
Family Procerithiidae Cossmann, 1906

Genus Procerithium Cossmann, 1902 (in Chartron and Cossmann)
Type species. *Procerithium quinquegranosum* Cossmann, 1902, Jurassic, France.

Procerithium? *inaequetuberculata* sp. nov.
Figure 2.5ac–ae

LSID. urn:lsid:zoobank.org:act:C772DCD7-2D6D-478E-BE35-FDD6C8C93882.

Etymology. Latin, for the nodes being of unequal strength on the various spiral cords.

Holotype. QMF 39350.

Paratype. QMF 39351.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell high-spired, turritelliform; larger specimen consisting of ca. 4 whorls, 5.2 mm high, 2.4 mm wide with; apical angle about 40°; upper whorls convex; whorl face ornamented with three to four spiral cords and an additional cord emerging form abapical suture; adapical spiral cords weak; two abapical spiral cords strong, first (spiral 3) one forming periphery at about mid-whorl; spiral cords are irregularly undulating and knobby; knobs especially pronounced on spiral cords 3 at periphery, weaker and spirally elongated at spiral cord 4; whorl face between two main spiral cords concave; suture distinct; opisthocyrt growth lines; transition to base angular; base flatly rounded to rounded with up to five distinct spiral cords; apex not preserved and aperture unknown.

Remarks. Due to the ornament of knobby spiral cords, the high-spired shell shape and the opisthocyrt growth lines the present shells resemble Mesozoic shells belonging to the diverse and often abundant families Procerithiidae or Cryptaulacidae. Such shells are rare in the Late Palaeozoic, e.g., *Plicacerithium*? sp. as reported by Nützel and Nakazawa (2012) from the Permian of Japan, but this shell differs distinctly from the present ones, for instance, in having strong varix-like axial ribs. The assignment of the present species to *Procerithium* is tentative because the early whorls could not be observed. There are similar species of the vetigastropod family Eucyclidae. However, the opisthocyrt growth line pattern of the present material points more to Caenogastropoda. The specimens at hand have a different mode of preservation than the other material studied herein—they are obviously not silicified. It seems to be possible that they derive from a different rock unit.

Superfamily Peruneloidea Frýda and Bandel, 1997

Family Imoglobidae Nützel and Cook, 2002

Genus *Chlorozyga* Nützel and Cook, 2002

Type species. *Hemizyga decussata* Yoo, 1988, Early Carboniferous, Australia.

Chlorozyga asiatica sp. nov.

Figure 2.6a, b

LSID. urn:lsid:zoobank.org:act:519CC436-4522-48CF-9C06-E1DE49DAA818.

Etymology. After the Asian continent.

Holotype. QMF 39352.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell minute, fusiform; consisting of ca. five whorls (apex missing), 3.5 mm high, 2.0 mm wide with an apical angle about 50°; spire relatively low, whorls distinctly rounded and convex, ornamented with distinct, densely spaced axial ribs numbering about 35 per whorl or more; axial ribs slightly prosocline prosocyrt; ribs continue onto base but become weaker; last whorl inflated; sutures impressed; base anomphalous rounded, convex; aperture elongated subovate; columellar lip reflected.

Remarks. The single present specimen is very similar to *Chlorozyga decussata* (Yoo, 1988) from the Early Carboniferous of Australia as illustrated by Yoo (1988: figs. 88–91) in shell shape and in the ornament of axial ribs. However, *C. decussata* has adpressed teleoconch whorls which are less convex than in *C. asiatica* sp. nov. (see also Nützel and Cook 2002); the suture is less impressed in *C. decussata*. The specimens that were illustrated as *C. decussata* by Yoo (1994: p. 85, pl. 16, figs. 12–14) resemble our specimen more closely in these respects, but the species identification of these specimens from the Early Carboniferous of Australia is doubtful. The type species of *Chlorozyga* has a very characteristic reticulate ornament on the larval shell (Yoo 1988; Nützel and Cook 2002). However, the protoconch of the present specimen is not preserved. *Hemizyga* Girty, 1915 has distinctly prosocline axial ribs that become weaker during ontogeny (Hoare and Sturgeon 1980a: pl. 1, fig. 1). The Devonian genera *Nanochilina* Frýda, 1998 and *Balbiniconcha* Frýda, 2001 have a similar teleoconch morphology and could be related to *Chlorozyga*. *Globozyga* Thein and Nitecki, 1974 with the type species *G. tenuistriata* from the Mississippian of the Illinois Basin is also very similar, but has less convex whorls, the axial ribs are weaker and orthocline for the most part except a weak subsutural sinus. The larval shell of *Globozyga* is unknown and if it has the same type as *Chlorozyga*, these genera could be synonyms.

Superfamily Pseudozygopleuroideae Knight, 1930
Family Pseudozygopleuridae Knight, 1930

Genus Hyphantozyga Knight, 1930
Type species. *Hemizyga* (*Hyphantozyga*) *gracilis* Knight, 1930, Pennsylvanian, USA.

Remarks. *Hyphantozyga* was introduced as a subgenus of *Hemizyga* by Knight (1930). It was then considered a subgenus of *Gamizyga* by Hoare and Sturgeon (1980a) and of *Plocezyga* Knight, 1930 by Hoare and Sturgeon (1980b). Nützel (1998) and Mazaev (2015) treated it as genus.

Hyphantozyga? *khaophrikensis* sp. nov.
Figure 2.6c–f

LSID. urn:lsid:zoobank.org:act:52A52471-41DA-4842-B986-1CE2969F2FA7.

Etymology. After the type location.

Holotype. QMF 39353.

Locality and horizon. Khao Phrik hill, Mueang Ratchaburi district, Eastern Ratchaburi Province, about 13 km east of Ratchaburi city, Central Thailand (Fig. 1), Ratburi Group, Middle Permian, Wordian.

Description. Shell high-spired, slender; specimen consisting of ca. five whorls (apex missing), 3.8 mm high, 1.9 mm wide; whorls rather convex; adapical portion of whorl forming steeply sloping, gently convex to straight ramp, inclined at 50°; abapical whorl face subvertical, slightly convex; abapical half of whorl face ornamented by three equally strong spiral cords (four spiral cords on last whorl), adapical spiral cord placed at mid-whorl forming periphery, third spiral cord close to lower suture; spiral cords separated by equally wide, concave interspaces; whorl face ornamented with numerous fine, sharp axial ribs that are much weaker than spiral cords; axial ribs parasigmoidal, opisthocyrt on ramp, prosocyrt on abapical portion of whorl face; spiral cords and axial ribs forming reticulate sculpture on abapical half of whorl face with intersections being not nodular; suture impressed; base flatly convex, anomphalous.

Remarks. The cancellate ornamentation suggests this single shell could represent the pseudozygopleurid genus *Hyphantozyga*. However, unlike in this genus, the spiral cords are much stronger than the axial ornament and are restricted to the abapical half of the whorl face in *Hyphantozyga*? *khaophrikensis* sp. nov. Therefore, we place *H.*? *khaophrikensis* sp. nov. only tentatively in this genus—it probably represents a new genus.

Superfamily Subulitoidea Lindström, 1884
Family Subulitidae Lindström, 1884

Genus *Leptoptygma* Knight, 1936
Type species. *Auriptygma virgatum* Knight, 1931a, Pennsylvanian, USA.

Leptoptygma sp.
Figure 2.6g–i

Material. QMF 39354, 39,355.

Description. Shell turbiniform; larger specimen consisting of four whorls (apex missing), 5.4 mm high, 4.0 mm wide with an apical angle about 70°; whorls smooth and distinctly convex; last whorl inflated; whorls embrace low on the preceding whorl at rounded periphery at transition to base; base rounded, convex, phaneromphalous; inner lip developing single columellar fold; suture impressed.

Remarks. The aperture of the present specimens is broken, but the whorl profile and the presence of a columellar fold suggest them to represent Subulitoidea in a wider sense (see Nützel et al.

2000; Nützel and Pan 2005). The present specimens resemble *Leptoptygma subtilistriatum* Knight, 1931 (p. 225, pl. 25, fig. 1a) from the Pennsylvanian of the US, but they are too poorly preserved to establish species identity. *Leptoptygma gremechaensis* Mazaev, 2015 (p. 974, pl. 36, fig. 10) from the Middle Permian of the Volga-Urals region, Russia is also similar but has less convex whorls. *Soleniscus girtyi* (Erwin, 1988) as reported by Mazaev (2015: p. 969, pl. 36, figs. 3–7) from the Permian of Russia is similar but this species has more convex whorls and according to Erwin (1988) the illustrated holotype of this species from the Permian of the US has a more distinct columellar fold. *Strobeus dongluoensis* (Pan Y.T. and Yu, 1993) as reported by Pan and Erwin (2002: p. 32, figs. 15.14–15) from the Permian of China differs in having a shallower suture and a more elongated shape.

Superfamily Soleniscoidea Knight, 1931a
Family Soleniscidae Knight, 1931a

Genus *Soleniscus* Meek and Worthen, 1861
Type species. *Soleniscus typicus* Meek and Worthen, 1861, Carboniferous, USA.

Soleniscus sp. 1
Figure 2.6o–t

Material. QMF 39356–39358.

Description. Shell moderately high-spired with conical spire, conical; whorls smooth, slightly convex; larger specimen consisting of seven whorls, 8.4 mm high, 4.9 mm wide with an apical angle of about 50–60°; last whorl inflated; whorls embrace at rounded periphery at transition to base; base rounded, anomphalous; aperture subovate, outer lip somewhat thickened, inner lip with columellar fold; base anomphalous; suture shallow but distinct; apex acutely conical.

Remarks. Similar smooth shells with distinct columellar fold have been reported from the Late Palaeozoic all over the world. For example, *Soleniscus girtyi* (Erwin, 1988) (USA and Russia) as illustrated by Mazaev (2015: p. 969, pl. 36, figs. 3–7) is similar but this species has a weakly concave depression on the upper part of the whorls and a smaller pleural angle. *Soleniscus callosus* Yoo, 1988 (see also Yoo 1994) is also similar, but it has fine transverse lirae on the teleoconch whorls.

Soleniscus? sp. 2
Figure 2.6k–n

Material. QMF 39359–39360.

Description. Shell fusiform, distinctly higher than wide, with last portion of last whorl slightly constricted; larger specimen consisting of six whorls, 9.3 mm high, 4.7 mm wide with an apical angle of about 50°; whorls smooth, slightly convex; periphery at mid-whorl; whorl embracing below periphery; base rounded, convex, anomphalous; aperture subovate, elongated, 2.8 mm high and 2.4 wide; inner and outer lip thin; suture shallow; apex acutely conical.
Remarks. These poorly preserved specimens resemble *Soleniscus* species, but a columellar fold is not visible. They resemble for instance *Soleniscus pactus* Pan and Erwin, 2002 (p. 32, figs. 15.16–19) from the Permian of South China but the shape of the aperture of the present specimens is more ovate.

Family Meekospiridae Knight, 1956

Genus *Meekospira* Ulrich in Ulrich and Scofield, 1897
Type species. *Eulima peracuta* Meek and Worthen, 1861, Carboniferous, USA.

Meekospira? sp. 1
Figure 2.6u, v

Material. QMF 39361.

Remarks. This moderately slender shell with slightly convex, smooth whorls consists of at least five whorls, is 2.9 mm high (apex missing), 1.4 mm wide and has an apical angle of about 40°. The suture is shallow and indistinct. Details of the aperture and the base are not observed. This poorly preserved specimen could represent the widespread Late Palaeozoic genus *Meekospira*.

Meekospira? sp. 2
Figure 2.6w, x

Material. QMF 39362.

Description. Shell high-spired, consisting of at least six whorls (apex missing), 3.0 mm high, 1.6 mm wide with an apical angle of about 30°; whorl face smooth; whorls flat to slightly convex; whorl embrace low at periphery of preceding whorl at rounded transition to base; Base flatly convex, anomphalous; suture shallow but distinct; last whorl slightly inflated.

Remarks. This single meekospiriform, smooth specimen resembles *Bellazona polita* Gordon and Yochelson, 1987 (p. 81, pl. 9, figs. 22–25) from the Early Carboniferous of the USA, but *Bellazona* has a selenizone, and there is no indication that this is the case in our specimen, although the preservation does not really allow statements about the growth line pattern. It also resembles various other species that have been assigned to *Meekospira*; most of these are more slender, however, and have higher whorls (e.g., Erwin 1988; Nützel et al. 2000). Similar shells are also found among Permian species that have been assigned to the genus *Protostylus* Mansuy, 1914 (e.g., Batten 1985; Nützel and Nakazawa 2012).

Superfamily uncertain
Family Coelostylinidae Cossmann, 1908

Genus *Protostylus* Mansuy, 1914
Type species. *Protostylus lantenoisi* Mansuy, 1914, Carboniferous, Yunnan, China.

Protostylus sp.
Figure 2.6y–ab

Material. Two specimens, QMF 39363, 39364.

Description. Shell high-spired, slender; larger specimen with regularly increasing whorls (apex missing), 11.1 mm high, 3.6 mm wide; whorl face flattened; suture shallow and indistinct; surface smooth; base rounded-convex, lacking umbilicus; aperture ovate, outer lip thin, arched, columellar lip short with posterior angle, well developed anterior siphonal notch.

Remarks. *Protostylus* is a problematic genus of high-spired, smooth gastropods originally described from the Late Palaeozoic of South China. As outlined by Nützel (in Nützel and Nakazawa 2012), its type species was based on poorly preserved and documented type material.

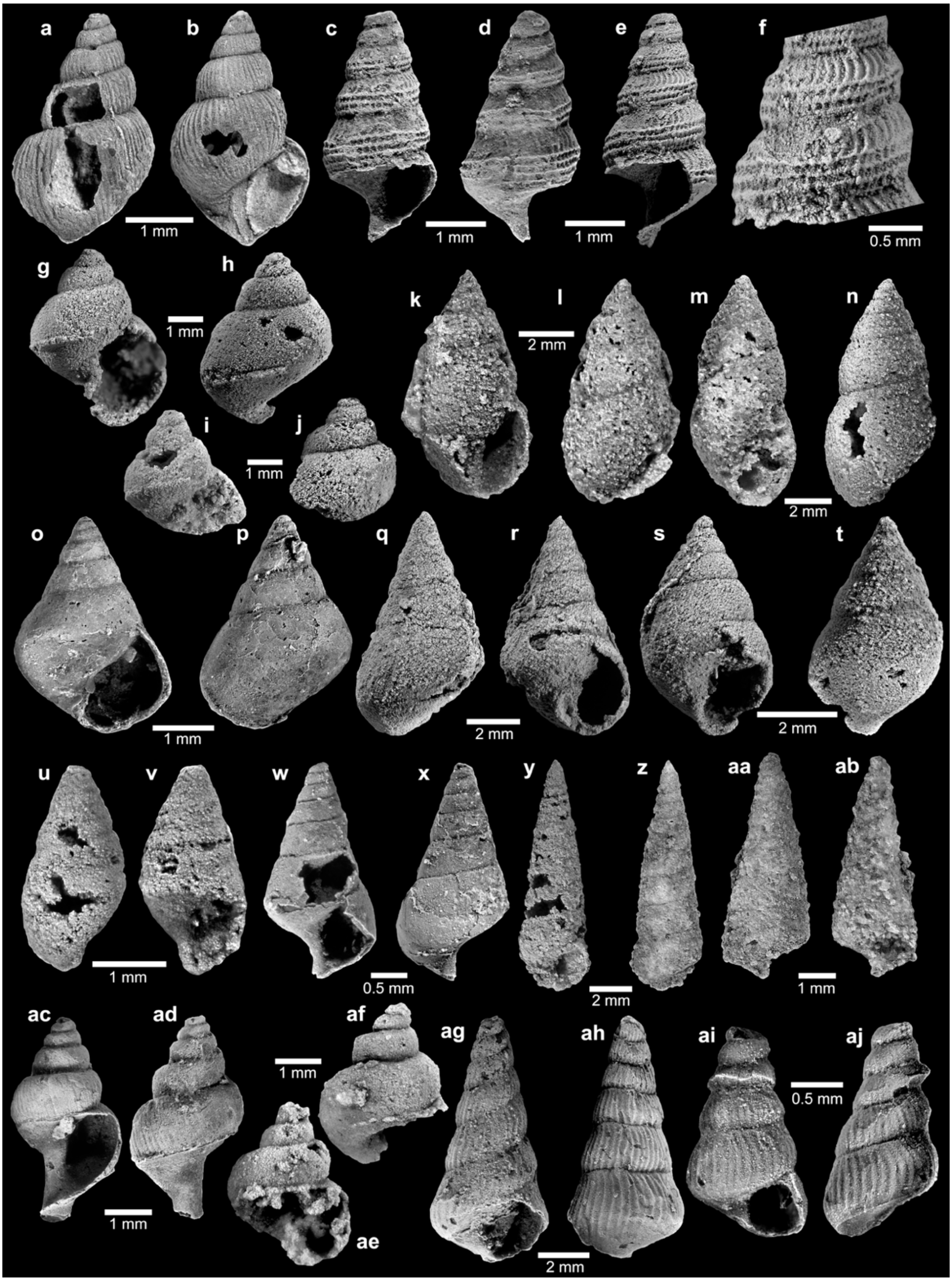

Figure 2.6: a, b *Chlorozyga asiatica* sp. nov., holotype, QMF 39352. c–f *Hyphantozyga*? *khaophrikensis* sp. nov., holotype, QMF 39353. g, h *Leptoptygma* sp., QMF 39354. i, j *Leptoptygma* sp., QMF 39355. k, l *Soleniscus*? sp. 2, QMF 39359. m, n *Soleniscus*? sp. 2, QMF 39360. o, p *Soleniscus* sp. 1, QMF 39356. q, r *Soleniscus* sp. 1. s, t *Soleniscus* sp. 1, QMF 39358. u, v *Meekospira*? sp. 1, QMF 39361. w, x *Meekospira*? sp. 2, QMF 39362. y, z *Protostylus* sp. aa, ab *Protostylus* sp., QMF 39364. ac, ad *Kimina* sp., ae, af *Kimina* sp., QMF 39366. ag, ah *Palaeozygopleura* cf. *obesa* Yoo, 1994, QMF 39367. ai, aj *Palaeozygopleura* cf. *obesa* Yoo, 1994, QMF 39368.

Batten (1985) identified specimens from the Permian of Malaysia as *P. lantenoisi* Mansuy, 1914, i.e., the type species of Protostylus. He placed the genus in Procerithiidae together with Palaeostylus mainly because of the presence of an anterior siphonal notch. A placement in Palaeostylidae is preferable because Procerithiidae is essentially a Mesozoic family and *Procerithium* differs widely from *Protostylus*. However, firm ground regarding its placement is only reached if the type species of *Protostylus* becomes better known, especially its aperture and protoconch (Nützel and Nakazawa 2012). *Omphaloptychia paleozoica* Batten, 1985 from the Permian of Perak, Malaysia is similar, but is broader and has higher whorls.

Superfamily and family uncertain

Genus Kimina Yoo, 1994
Type species. *Kimina globosa* Yoo, 1994, Carboniferous, Australia.

Kimina sp.
Figure 2.6ac–af

Material. QMF 39365, 39366.

Description. Shell moderately high-spired with gradate spire; larger specimen consisting of ca. five whorls (apex missing), 4.3 mm high, 2.3 mm wide, with an apical angle of about 50°–60°; whorls evenly convex ornamented with slightly prosocline prosocyrt, strengthened growth lines; base convex; suture deep, impressed.

Remarks. The present specimen resembles *Kimina australis* Yoo, 1994 (p. 91, pl. 19, figs. 1–4) from the Early Carboniferous of the Tamworth Belt, New South Wales, Australia, in shape and in having markedly convex whorls. However, the present material has much more distinct growth lines and higher whorls.

Subclass uncertain
Superfamily Loxonematoidea Koken, 1889
Family Palaeozygopleuridae Horný, 1955

Genus *Palaeozygopleura* Horný, 1955

Type species. *Zygopleura alinae* Perner, 1907, Devonian, Czech Republic.

Palaeozygopleura cf. *obesa* Yoo, 1994

Figure 2.6 ag–aj

cf. * 1994 *Palaeozygopleura obesa* sp. nov. Yoo—Yoo: p.84, pl. 16, figs. 1–4.

Material. QMF 39367–39368.

Description. Shell high-spired, small; apical angle nearly 40°; protoconch missing; specimen with six preserved regularly increasing whorls; larger specimen consisting of about six whorls, 9.5 mm high, 4.4 mm wide with an apical angle about 45°; whorls sloping, gently convex with periphery low on whorl so that whorl profile is pending; whorls embrace below; whorl face ornamented with slightly opisthocyrt prominent, closely spaced axial ribs numbering about 28–32 per whorl; ribs nearly as wide as interspaces; suture distinct; base flatly convex with rounded transition to whorl face; ribs continue onto base but cease rapidly; aperture as high as wide, rounded subquadrangular with almost straight parietal lip.

Remarks. Both specimens at hand strongly resemble *Palaeozygopleura obesa* Yoo, 1994 from the Early Carboniferous of Australia in shell size, shape, whorl profile and ornamentation. There are also other similar species of the genus *Palaeozygopleura*. A similar teleoconch morphology also occurs in Pseudozygopleuridae and in the genus *Chlorozyga* Nützel and Cook, 2002. However, the knowledge of the protoconch morphology would be needed for a correct placement of the present material. *Pseudozygopleura* (*Pseudozygopleura*)? *lauta* Gordon and Yochelson, 1987 from the Late Mississippian of Utah is also similar, but the present specimens have finer axial ribs. Gordon and Yochelson (1987) mentioned that their specimens of *P*. (*P*.)? *lauta* lack the early whorls including the protoconch and hence the assignment to *Pseudozygopleura* (*Pseudozygopleura*) is questionable. *Pseudozygopleura* (*P*.) *convexus* Batten, 1985 from the Permian of Malaysia has fewer, straighter and broader axial ribs. *Palaeozygopleura kushnarae* Licharev, 1968 from the Late Palaeozoic of Russia is similar to the present specimens, but this species has straighter ribs.

Subclass Heterobranchia Burmeister, 1837

Superfamily Streptacidoidea Knight, 1931b

Family Streptacididae Knight, 1931b

Genus *Streptacis* Meek, 1871

Type species. *Streptacis whitfieldi* Meek, 1871, Carboniferous, USA.

Streptacis? sp.

Figure 2.7a–f

Material. QMF 39369–39372.

Description. Shell high-spired, minute, slender (apex missing), consisting of about nine whorls; largest specimen 5.9 mm high, 1.8 mm wide with an apical angle of about 20°; protoconch unknown; whorls regularly increasing, smooth and strongly convex; suture distinctly impressed; body whorl rounded-convex; base evenly rounded, anomphalous.

Remarks. The present specimens are too poorly preserved—protoconch and early teleoconch are missing. These small, high-spired shells without ornamentation might resemble the widespread genus *Streptacis* as it has been reported from Thailand (Ketwetsuriya et al. 2016) and Japan (Nützel and Nakazawa 2012). The specimen number 70 and 71 are similar to *Streptacis inflata* Erwin, 1988b from the Permian of the Southwestern, USA in being turritelliform with strongly arched whorls and lacking ornaments. *Streptacis subgracilis* (Netchaev, 1894) from the Permian of Russia is also very similar (Mazaev 2018).

Family Donaldinidae Bandel, 1994

Genus *Yoospira* Bandel, 2002

Type species. *Donaldina minutissima* Yoo, 1994, Early Carboniferous, New South Wales, Australia.

Yoospira? sp. 1

Figure 2.7g–k

Material. QMF 39373–39375.

Description. Shell small, high-spired, slender, turriculate consisting of at least seven slowly increasing whorls (apex missing); largest specimen 4.4 mm high, 1.4 mm wide with an apical angle about 50°; whorls distinctly convex, ornamented with four to six prominent spiral cords; adapical spiral cord located near upper suture, weakest; other cords of about the same strength; abapical spiral cord just above abapical suture; suture impressed and distinct; aperture oval, slightly higher than wide; base rounded, anomphalous.

Remarks. The present shells closely resemble *Yoospira*, but are only tentatively assigned to that genus because they lack the protoconch. They resemble *Yoospira minutissima* (Yoo, 1994) (p. 93, pl. 21, figs. 1–6) from the Early Carboniferous of Australia. However, *Y. minutissima* has more convex whorls and its spiral cords are weaker. *Donaldina filosa* Yoo, 1988 (p. 248, figs. 104–109) from the Early Carboniferous, New South Wales, Australia is also similar to the present material. However, *D. filosa* has a strong opisthocline collabral ornamentation and *Donaldina* in general lacks spiral cords in the adapical portion of the whorls. *Pseudoaclisina microspirulata* Yoo, 1994 has many more spiral cords (22 fine spiral cords).

Yoospira? sp. 2
Figure 2.7l, m

Material. QMF 39376.

Description. Shell small, high-spired, very slender, turriculate consisting of at least seven slowly increasing whorls (apex missing); specimen 4.6 mm high, 1.1 mm wide with an apical angle about 34°; whorls flatly convex, with periphery low on the whorls; whorls ornamented with several faint spiral striae; aperture circular, 0.5 mm high, 0.6 mm wide; base flatly rounded.

Remarks. This specimen is more slender and has less convex whorls than *Yoospira*? sp. 1. It is questionable whether *Yoospira*? sp. 1 and *Yoospira*? sp. 2 are congeneric. The specimen illustrated here (Fig. 7l, m) closely resembles *Donaldina gracilis* Erwin, 1988 from the Wolfcampian Hueco Formation of West Texas, but preservation is too poor for an identification. *Yoospira morgantownensis* Bandel, 2002 from the Pennsylvanian of Ohio is similar bit its spiral cords are finer.

Problematic uncoiled sinistral taxon

Figure 2.7n, o

Material. QMF 39377.

Description. Shell sinistral, vermiform; consisting of ca. four whorls (apex missing), 3.3 mm high, 1.1 mm wide; whorls disjunct, round, convex and smooth; aperture subcircular, 1.8 mm high, 1.4 mm wide; protoconch not preserved.

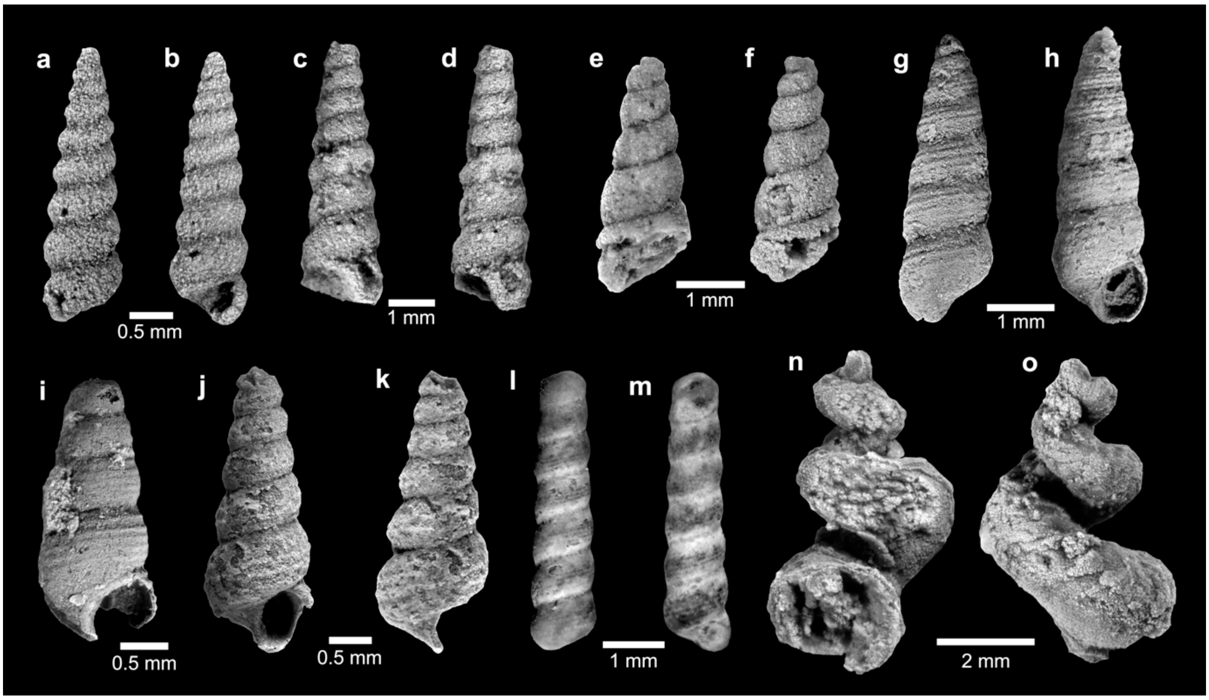

Figure 2.7: a, b *Streptacis*? sp., QMF 39369. c, d *Streptacis*? sp., QMF 39370. e, f *Streptacis*? sp., QMF 39371. g, h *Yoospira*? sp. 1, QMF 39373. i *Yoospira*? sp. 1, QMF 39374. j, k *Yoospira*? sp. 1, QMF 39375. l, m *Yoospira*? sp. 2, QMF 39376. n, o Problematic uncoiled sinistral taxon, QMF 39377.

Remarks. The single present shell probably represents an undescribed new taxon, but it is too poorly preserved for a taxonomic assignment. This shell is unique in that it has sinistral uncoiled whorls. It is similar to the Late Permian *Laxella* Pan and Erwin, 2002 in having an uncoiled, vermiform shell. However, *Laxella* has a dextral teleoconch. The protoconch is not preserved in our material. The possibility that this specimen is a steinkern of a sinistral taxon cannot be ruled out entirely. However, the aperture seems to indicate that this is not the case, as it seems to represent a replaced shell.

2.6 Discussion and conclusion

The studied Wordian materials derived from the Ratburi Limestone at Khao Phrik, Ratchaburi Province, Central Thailand, represent the first silicified Permian gastropod fauna known from the Sibumasu terrane of Thailand. This fossiliferous limestone produced abundant brachiopods together with gastropods, bryozoa, some fusulinids, sponges and corals. The presence of these fossils suggests that the depositional environment of the Ratburi Limestone of Khao Phrik was shallow water, probably from a fore-reef setting with access to the open sea.

The studied gastropod assemblage from this location is diverse and encompasses 34 species comprising 17 nominate species and 17 species in open nomenclature. The generally poor preservation due to the coarse silicification resulted in extensive use of open nomenclature. Nine new species are described herein: *Retispira khaophrikensis*, *Amaurotoma*? *multispirata*, *Eoplatyzona ratchaburiensis*, *Hesperiella cyrtocostata*, *Worthenia*? *waterhousei*, *Stegocoelia centrosinuata*, *Procerithium*? *inaequetuberculata*, *Chlorozyga asiatica* and *Hyphantozyga*? *khaophrikensis*. There are a number of typical Late Palaeozoic cosmopolitan genera in the present collection including as *Euphemites*, *Warthia*, *Ananias*, *Worthenia*, *Meekospira* and *Stegocoelia*. Some of these widespread genera are reported from Thailand for the first time (*Ananias* and *Worthenia*). Bellerophontids are the most abundant group, with *Warthia* and *Retispira* being especially abundant. With five species and four genera, bellerophontoids are also diverse. Vetigastropoda are diverse and abundant in this assemblage as well. The typical Late Palaeozoic genus *Ananias* is reported for the first time from Thailand. Heterobranchia seem to be diverse and important in this fauna. However, heterostrophic protoconchs are not preserved, and therefore the attribution of the species in question remains doubtful given that Heterobranchia and Caenogastropoda commonly have similar teleoconch morphologies.

The Permian gastropod fauna from the Ratburi Limestone of Khao Phrik shares only a single species with the diverse Permian gastropod fauna from the Tak Fa Limestone (Ketwetsuryia et al. 2016): *Retispira lyelli* (Gemmellaro, 1890). Moreover, several taxa treated in open nomenclature, such as *Naticopsis* sp., *Meekospira*? sp., *Protostylus* sp. and *Streptacis*? sp., are present in both faunas. Thus, although the gastropod faunas from the Ratburi Limestone and the Tak Fa Limestone have approximately the same age (Middle Permian) and come from the Palaeo-Tethys, their species composition differs strongly. This suggests that they belong to different biogeographic provinces. The Tak Fa fauna derives from the Indochina terrane, which had an equatorial position, whereas the Khao Phrik fauna belongs to the Sibumasu terrane, which was situated at lower latitudes (Ueno and Charoentitirat 2011).

In addition, the gastropods described herein display relationships to several other Late Palaeozoic gastropod faunas from the Palaeo-Tethys. *Retispira lyelli* (Gemmellaro, 1890) is the only species that was also reported from the Permian gastropod fauna from Perak, Malaysia (Batten 1972), and the only species that has been reported from all terranes of the Palaeo-Tethys. Several other species closely resemble species from Malaysia (Batten 1972, 1985), such as *Palaeozygopleura* cf. *obesa* Yoo, 1994, *Eucycloscala*? sp., *Protostylus* sp. and *Goniasma* sp. Moreover, several Khao Phrik species resemble species from the Early Carboniferous of Australia (Yoo 1988, 1994) as discussed above, including *Eoplatyzona ratchaburiensis* sp. nov., *Chlorozyga asiatica* sp. nov., *Worthenia* cf. *crenulunula* Yoo, 1994, *Worthenia*? *waterhousei* sp. nov., *Hesperiella cyrtocostata* sp. nov., *Palaeozygopleura* cf. *obesa* Yoo, 1994, *Kimina* sp., *Peruvispira* sp., *Stegocoelia*? sp. 2 and *Yoospira* sp. However, the large difference in age (Early Carboniferous vs. Middle Permian) makes it unlikely that species are actually identical. This underlines the fact that the studied fauna from Thailand has a typical Late Palaeozoic character. Several taxa are also shared with the Permian gastropod fauna from the Akasaka Limestone, Japan (Nützel and Nakazawa 2012) and South China (Pan and Erwin 2002). These faunas may have been related in the Palaeo-Tethys. However, additional systematic and quantitative studies of the gastropod faunas from the Palaeo-Tethys are needed to infer diversity dynamics and palaeobiogeographical distributions of Permian gastropods from Southeast and East Asia.

2.7 Acknowledgements

The first author thanks the Royal Thai Government who provided funding for a scholarship within the framework of the Development and Promotion of Science and Technology Talented Project. We thank Alexey Mazaev for critical remarks on an earlier draft of the manuscript. We thank Andrzej Kaim and Sven N. Nielsen for reviewing this article.

2.8 References

Bandel, K. 1994. Comparison of Upper Triassic and Lower Jurassic gastropods from the Peruvian Andes (Pucara Group) and the Alps (Cassian Formation). *Palaeontographica (A: Paläozoologie, Stratigraphie)* 233: 127–160.

Bandel, K. 2002. About the Heterostropha (Gastropoda) from the Carboniferous and Permian. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 86: 45–80.

Batten, R.L. 1966. The Lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset. Part II. *Palaeontographical Society Monographs* 119: 53–109.

Batten, R.L. 1972. Permian gastropods and chitons from Perak, Malaysia. Part 1. Chitons, bellerophontids, euomphalids and pleurotomarians. *Bulletin of the American Museum of Natural History* 147: 1–44.

Batten, R.L. 1985. Permian gastropods from Perak, Malaysia. Part 3. The murchisoniids, cerithiids, loxonematids, and subulitids. *American Museum Novitates* 2829: 1–40.

Batten, R.L. 1989. Permian Gastropoda of the Southwestern United States. 7. Pleurotomariacea: Eotomariidae, Lophospiriidae, Gosseletinidae. *American Museum Novitates* 2958: 1–64.

Bouchet, P., J.-P. Rocroi, B. Hausdorf, A. Kaim, Y. Kano, A. Nützel, P. Parkhaev, M. Schrödl, and E.E. Strong. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61: 1–526.

Brönnimann, P., J.E. Whittaker, and L. Zaninetti. 1978. Shanita, a new pillared miliolacean foraminifer from the Late Permian of Burma and Thailand. *Rivista Italiana di Paleontologia e Stratigrafia* 84: 63–92.

Burmeister, H. 1837. *Handbuch der Naturgeschichte, Zoologie*, vol. 2, 369–858. Berlin: Enslin.

Chartron, C., and M. Cossmann. 1902. Note sur l'infralias de la Vendée et spécialement sur un gisement situé dans la commune du Simon-la-Vineuse. *Bulletin de la Société Géologique de France, quatrième série* 2(2): 163–203.

Chronic, B.J. 1949. Invertebrate paleontology (excepting fusulinids and corals). In *Upper Paleozoic of Peru II*, eds. N.D. Newell, B.J. Chronic, and J. Roberts, 46–173. New York: Columbia University Press.

Chronic, H. 1952. Molluscan Fauna from the Permian Kaibab Formation, Walnut Canon, Arizona. *Bulletin of the Geological Society of America* 63: 95–166.

Conrad, T.A. 1835. Description of five new species of fossil shells in the collection presented by Mr. Edward Miller to the Geological Society. *Transactions of the Geological Society of Pennsylvania* 1(1): 267–270.

Cossmann, M. 1895. *Essais de Paléoconchologie comparée 1*. Paris: chez l'auteur and Deslis Frères.

Cossmann, M. 1906. *Essais de paléoconchologie comparée 7*. Paris: chez l'auteur and Deslis Frères.

Cossmann, M. 1908. Système silurien du centre de la Bohème, 1ère partie. Recherches paléontologiques. Vol IV: Gastropodes, T. II, par J. Perner. *Revue Critique de Paléozoologie* 12(2): 91–95.

Cuvier, G. 1795. Second mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordres, lu à la Société d'histoire naturelle de Paris, le 11 Prairial, an troisième [30 May 1795]. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts 1795 [1. Année]* 2: 433–449.

Delpey, G. 1942. Les Gastéropodes permiens du Cambodge. *Journal de Conchyologie* 85: 50–83.

Donald, J. 1889. Descriptions of new species of Carboniferous gastropods. *Quarterly Journal of the Geological Society of London* 45: 619–625.

Donald, J. 1892. Notes on some new and little known species of Carboniferous Murchisonia. *Quarterly Journal of the Geological Society of London* 68: 562–575.

Erwin, D.H. 1988. Permian Gastropoda of the Southwestern United States: Subulitacea. *Journal of Paleontology* 62: 56–69.

Fleming, J. 1828. *A history of british animals exhibiting the descriptive characters and systematical arrangements of the genera and species of quadrupeds, birds, reptiles, fishes, mollusca and radiata of the United Kingdom.* Edinburgh: Bell & Bradfute.

Fontaine, H. 1986. The permian of Southeast Asia. *CCOP Technical Bulletin* 18: 1–111.

Fontaine, H. 1988. Permian corals of West Thailand. *CCOP Technical Bulletin* 20: 112–127.

Fontaine, H., and S. Salyapongse. 2001. Permian corals of peninsular Thailand and other associated fossils. *CCOP Newletter* 26(3/4): 14–19.

Frýda, J. 1998. Some new and better recognized Devonian gastropods from the Prague Basin (Bohemia). *Bulletin of the Czech Geological Survey* 73(1): 41–49.

Frýda, J. 2001. Discovery of a larval shell in Middle Paleozoic subulitoidean gastropods with description of two new species from the Early Devonian of Bohemia. *Věstník Českého Geologického Ústavu* 76(1): 29–37.

Frýda, J., and K. Bandel. 1997. New Early Devonian gastropods from the *Plectonotus* (*Boucotonotus*)—*Palaeozygopleura* community in the Prague Basin (Bohemia). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 80: 1–57.

Gemmellaro, G.G. 1890. La Fauna dei calcari con Fusulina della valle del fiume Sosio nella Provincia di Palermo. *Giornale di Science Naturali ed Economiche* 20: 97–182.

Girty, G.H. 1909. Paleontology of the Manzano group. In *The Manzano group of the Rio Grande Valley, New Mexico*, eds. W.T. Lee and G.H. Girty. *Bulletin of the U. S. Geological Survey* 389: 40–141.

Girty, G.H. 1915. Fauna of the Wewoka formation of Oklahoma. *Bulletin of the United States Geological Survey* 544: 1–353.

Gordon, M., and E.L. Yochelson. 1987. Late Mississippian gastropods of the Chainman Shale, West-Central Utah. *United States Geological Survey. Professional Paper* 1368: 1–112.

Grant, R.E. 1976. Permian brachiopods from southern Thailand. *Paleontological Society Memoir* 9: 1–269.

Hoare, R.D., and M.T. Sturgeon. 1980a. The Pennsylvanian pseudozygopleurid gastropod genus *Gamizyga* n. gen. from Ohio and West Virginia. *Journal of Paleontology* 54: 159–187.

Hoare, R.D., and M.T. Sturgeon. 1980b. *Gamizyga*, a correction. *Journal of Paleontology* 54: 1101.

Holzapfel, E. 1889. Die Cephalopoden-führenden Kalke des unteren Carbon von Erdbach-Breitscheid bei Herborn. *Paläontologische Abhandlungen* 5: 1–74.

Horný, R.J. 1955. Palaeozygopleuridae nov. fam. (Gastropoda) ze stredoceskeho devonu. *Sbornik Ustredního Ústavuu Geologického oddíl Paleontologicky* 21(1): 17–74.

Ingavat-Helmcke, R. 1993. Contribution to the Permian fusulinacean faunas of Peninsular Thailand. *Journal of Southeast Asian Earth Sciences* 8: 67–75.

Ketwetsuriya, C., A. Nützel, and P. Kanjanapayont. 2014. A new Permian gastropod fauna from the Tak Fa Limestone, Nakhonsawan, Northern Thailand—a report of preliminary results. *Zitteliana A* 54: 137–146.

Ketwetsuriya, C., A. Nützel, and P. Kanjanapayont. 2016. Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. *Bulletin of Geosciences* 91: 481–513.

Knight, J.B. 1930. The gastropods of the St. Pseudozygopleurinae. *Journal of Paleontology* 4 (supplement 1): 1–89.

Knight, J.B. 1931a. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: the Subulitidae. *Journal of Paleontology* 5: 177–229.

Knight, J.B. 1931b. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: Aclisina and Streptacis. *Journal of Paleontology* 5: 1–15.

Knight, J.B. 1936. Notes on Paleozoic Gastropoda. *Journal of Paleontology* 10(6): 520–534.

Knight, J.B. 1945. Some new genera of Paleozoic Gastropoda. *Journal of Paleontology* 19: 573–587.

Knight, J.B. 1956. New families of Gastropoda. *Journal of the Washington Academy of Sciences* 46: 41–42.

Knight, J.B., L.R. Cox, A.M. Keen, R.L. Batten, E.L. Yochelson, and R. Robertson. 1960. Systematic descriptions. In *Treatise on invertebrate paleontology, Part I, Mollusca 1*, ed. R.C. Moore, I169–I310. Lawrence, Kans: University of Kansas Press and Boulder, Colo.: Geological Society of America.

Koken, E. 1889. Ueber die Entwicklung der Gastropoden vom Cambrium bis zur Trias. *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie, Beilage-Band* 6: 305–484.

Koken, E. 1896. Die Gastropoden der Trias um Hallstadt. *Jahrbuch der kaiserlich-königlichen Geologischen Reichsanstalt* 46: 37–126.

Koken, E. 1897. Die Gastropoden der Trias um Hallstadt. *Abhandlungen der kaiserlich-königlichen Geologischen Reichsanstalt* 17: 112.

Koninck, L.G. de. 1842. *Description des animaux fossiles quie se trouvent dans le terrain carbonifère de Belgique*. Paris: H. Dessein.

Koninck, L.G. de. 1883. Faune du calcaire carbonifère de la Belgique. Quatrième partie, Gastéropodes (suite et fin). *Annales du Musée Royal d'Histoire naturelle de Belgique* 8: 1–240.

Kues, B.S., and R.L. Batten. 2001. Middle Pennsylvanian gastropods from the Flechado Formation, north-central New Mexico. *Journal of Paleontology* 75 (supplement 1): 1–95.

Kulas, H.A., and R.L. Batten. 1997. Silicified gastropods from the Permian Phosphoria rock complex of Wyoming. *Contributions to Geology, University of Wyoming* 31: 33–58.

Licharev, B.K. 1968. *Skafopody i gastropody verkhnego karbona i nizhnei permi yuzhnoi Fergany (Scaphopods and gastropods from the Upper Carboniferous and Lower Permian of Southern Fergana)*, 1–118. Moscow: Nedra Press. (in Russian).

Licharev, B.K. 1975. Carboniferous gastropods from the region of the River Kavabolka. *Trudy Vsesoyuznogo nauchoissledovatel'skogo geologo-razvedochnogo instituta* 206: 5–183. (in Russian).

Lindström, G. 1884. The Silurian Gastropoda and Pteropoda of Gotland. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 19: 1–250.

Mansuy, H. 1914. Nouvelle contribution à la paléontologie du Yunnan. *Mémoires du Service Géologique de l'Indochine* 3(2): 1–190.

Mazaev, A.V. 2001. The gastropod genus *Stegocoelia* Donald, 1889 (Murchisoniidae) from Middle and Upper Carboniferous of the Central part of Russian Plate. *Ruthenica* 11: 137–151.

Mazaev, A.V. 2002. Some murchisoniid gastropods from the Middle and Upper Carboniferous of the central part of the Russian Plate. *Ruthenica* 12(2): 89–106.

Mazaev, A.V. 2015. Upper Kazanian (Middle Permian) gastropods of the Volga-Urals Region. *Paleontological Journal* 49: 869–986.

Mazaev, A.V. 2018. Early Kazanian (Middle Permian) gastropods. *Paleontological Journal* 52: 796–827.

McCoy, F. 1844. *A synopsis of the characters of Carboniferous Limestone Fossils of Ireland*. Dublin: McGloshan and Gill.

McCoy, F. 1852, *A synopsis of the classification of the British Palaeozoic rocks [by the Rev. Adam Sedgwick] with a systematic description of the British Palaeozoic fossils in the Geological Museum of the University of Cambridge [by Frederick McCoy] with figures of the new and imperfectly known species*. London: Parker & Son.

Meek, F.B. 1871. Descriptions of new species of fossils from Ohio and other western states and territories. *Proceedings of the Academy of Natural Sciences of Philadelphia* 23: 159–184.

Meek, F.B., and F.V. Hayden. 1858. Remarks on the Lower Cretaceous beds of Kansas and Nebraska, together with descriptions of some new species of Carboniferous fossils from the valley of Kansas River. *Proceedings of the Academy of Natural Sciences of Philadelphia* 10: 256–264.

Meek, F.B., and A.H. Worthen. 1861. Descriptions of new Carboniferous fossils from Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia* 12: 447–472.

Montfort, P.D. de. 1808. *Conchyliologie systématique et classification méthodique de coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Coquilles univalves, cloisonnées 1*. Paris: F. Schoell.

Moore, R.C. 1941. Upper Pennsylvanian gastropods from Kansas. *State Geological Survey Kansas, Bulletin* 38: 121–164.

Münster, G.G. zu. 1841. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. In *Beiträge zur Geognosie und Petrefacten-Kunde des südstlichen Tirol's vorzüglich der Schichten von St. Cassian*, H.L. Wissmann, and G. Graf zu Münster. *Beiträge zur Petrefacten-Kunde* 4: 25–152

Nechaev, A.V. 1894. Fauna of the Permian beds of the eastern part of European Russia. *Trudy Obshchestva estestvoispytatelei pri Imperatorskom Kazanskom universitete* 27(4): 1–503.

Newell, N.D. 1935. Some Mid-Pennsylvanian invertebrates from Kansas and Oklahoma. II. Stromatoporoidea, Anthozoa, and Gastropoda. *Journal of Paleontology* 9(3): 341–355.

Nützel, A. 1998. Über die Stammesgeschichte der Ptenoglossa (Gastropoda). *Berliner Geowissenschaftliche Abhandlungen (E: Paläobiologie)* 26: 1–229.

Nützel, A., and K. Bandel. 2000. Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2000(9): 557–569.

Nützel, A., and A.G. Cook. 2002. Chlorozyga, a new caenogastropod genus from the Early Carboniferous of Australia. *Alcheringa* 26(2): 151–157.

Nützel, A., and K. Nakazawa. 2012. Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). *Journal of Systematic Palaeontology* 10: 103–169.

Nützel, A., and H-Z Pan. 2005. Late Paleozoic evolution of the Caenogastropoda: larval shell morphology and implications for the Permian/Triassic mass extinction event. *Journal of Paleontology* 79: 1175–1188.

Nützel, A., D.H. Erwin, and R.H. Mapes. 2000. Identity and phylogeny of the late Paleozoic Subulitoidea (Gastropoda). *Journal of Paleontology* 74: 575–598.

Pan, H-Z, and D.H. Erwin. 2002. Gastropods from the Permian of Guangxi and Yunnan provinces, South China. *Journal of Paleontology* 78 (supplement 1): 1–49. (= The Paleontological Society, Memoir 56).

Pan, Y-T, and Y. Wen. 1993. *Permian Gastropoda of China*. Beijing: Ocean Press.

Perner, J. 1907. *Système silurien du centre de la Bohême Partie 1. Recherches paléontologiques. Volume 4, Gastéropodes, (2)*. Prague.

Rafinesque, C.S. 1815. *Analyse de la nature, ou tableau de l'univers et des corps organisées*. Palerme: Jean Barravecchia.

Recey, A., A.B. Smith, and O. Dawson. 1994. Permian echinoderms from Peninsular Thailand. In *Proceedings of the International Symposium on Stratigraphic Correlation of Southeast Asia (IGCP306)*, eds. P. Angsuwathana, T. Wongwanich, W. Tansathien, S. Wongsomsak, and J. Tulyatid, 106–114. Bangkok: Department of Mineral Resources.

Sakagami, S. 1965. Three Carboniferous species of Bryozoa from Khao Noi, central Thailand. *Japanese Journal of Geology and Geography* 36(2–4): 143–147.

Sakagami, S. 1969. Fusulinacean fossils from Thailand, Part IV. On some Permian fusulinaceans from peninsular Thailand. In *Geology and Palaeontology of Southeast Asia, vol. 6*, ed. T. Kobayashi and R. Toriyama, 265–275. Tokyo: University of Tokyo Press.

Sakagami, S. 1970. Addition to the Permian Bryozoa from Ko Muk, peninsular Thailand. In *Geology and Palaeontology of Southeast Asia, vol. 8*, eds. T. Kobayashi and R. Toriyama, 43–68. Tokyo: University of Tokyo Press.

Sakagami, S. 1973. Permian bryozoa from Khao Raen, near Rat Buri, Thailand. In *Geology and Palaeontology of Southeast Asia, vol. 12*, eds. T. Kobayashi and R. Toriyama, 75–89. Tokyo: University of Tokyo Press.

Salvini-Plawen, L. von. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* 19: 249–278.

Simroth, H. 1906. Versuch einer neuen Deutung der Bellerophontidae. *Sitzungsberichte der Natuforschenden Gesellschaft zu Leipzig* 32(1905): 3–8.

Sone, M. 2010. A new species of the rare neritopsid gastropod *Magnicapitatus* from the Guadalupian (Middle Permian) of East Thailand (the Indochina Terrane). *Alcheringa* 34: 1–6.

Thein, M.L., and M.H. Nitecki. 1974. Chesterian (Upper Mississippian) Gastropoda of the Illinois basin. *Fieldiana* 34: 1–238.

Thomas, E.G. 1940. Revision of the Scottish Carboniferous Pleurotomariidae. *Geological Society of Glasgow Transactions* 20: 30–72.

Tomlin, J.R.B. le. 1930. Some preoccupied generic names. II. *Proceedings of the Malacological Society of London* 19: 22–24.

Ueno, K., and T. Charoentitirat. 2011. Carboniferous and Permian. In *The geology of Thailand*, eds. M.F. Rido, A.J. Barber, and M.J. Crow, 71–135. London: Geological Society.

Ulrich, E.O., and W.H. Scofield. 1897. Chapter X: the lower Silurian Gastropoda of Minnesota. In *The geology of Minnesota, part 2 of the final report: paleontology, vol. 3*, eds. E.O. Ulrich, W.H. Scofield, J.M. Clarke, and N.H. Winchell, 813–1081. Minneapolis: Harrison & Smith.

Verrill, A.E. 1884. Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent part of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Arts and Sciences* 6(1): 139–194.

Waagen, W. 1880. Salt-Range Fossils. I. productus limestone fossils. 2. Pisces-Cephalopoda: supplement Gasteropoda. *Memoirs of the Geological Survey of India (Palaeontologia Indica)* 13: 1–183.

Wanner, C. 1922. Die Gastropoden und Lamellibranchiaten der Dyas von Timor. *Paläontologie von Timor* 18: 1–82.

Warthin, A.S. 1930. Micropaleontology of the Wetumka, Wewoka and Holdenville formations. *Oklahoma Geological Survey Bulletin* 53: 5–94.

Waterhouse, J.B. 1982. An Early Permian cool-water fauna from pebbly mudstones in south Thailand. *Geological Magazine* 119: 337–354.

Waterhouse, J.B., and S. Piyasin. 1970. Mid Permian Brachiopods from Khao Phrik, Thailand. *Paleontographica (A: Paläozoologie, Stratigraphie)* 135: 83–197.

Wenz, W. 1938. Gastropoda Teil 1: Allgemeiner Teil und Prosobranchia. In *Handbuch der Paläozoologie, vol. 6*, ed. O.H. Schindewolf, 1–1639. Berlin: Borntraeger.

Winters, S.S. 1963. Supai Formation (Permian) of eastern Arizona. *Geological Society of America Memoir* 89: 1–99.

Worthen, A.H. 1890. Descriptions of fossil invertebrates. *Illinois Geological Survey Bulletin* 8: 69–154.

Yanagida, J. 1970. Permian brachiopods from Khao Phrik, near Rat Buri, Thailand. In *Geology and palaeontology of Southeast Asia, vol. 14*, eds. T. Kobayashi and R. Toriyama, 7–23. Tokyo: University of Tokyo Press.

Yochelson, E.L. 1960. Permian Gastropoda of the southwestern United States. *Bulletin of the American Museum of Natural History* 119: 205–294.

Yoo, E.K. 1988. Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales. *Records of the Australian Museum* 40(3): 233–264.

Yoo, E.K. 1994. Carboniferous Mollusca from the Tamworth Belt, New South Wales. Australia. *Records of the Australia Museum* 46(2): 63–120.

Zittel, K.A. von. 1895. *Grundzüge der Paläontologie (Paläozoologie), Abt. I, Invertebrata*, 1–971. München & Leipzig: Oldenburg.

3

Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: implication for paleaogeography of the Indochina Terrane

By **Ketwetsuriya C., Karapunar B., Charoentitirat T. and Nützel A.** Published in *Zootaxa*, 4766(1), 1–47. doi:10.11646/zootaxa.4766.1.1

3.1 Abstract

A new Permian gastropod assemblage from the Roadian (Middle Permian) Khao Khad Formation, Saraburi Group (Lopburi Province, Central Thailand) which is part of the Indochina Terrane, has yielded one of the most diverse Permian gastropod faunas known from Thailand. A total of 44 gastropod species belonging to 30 genera are described herein, including thirteen new species and one new genus. The new genus is *Altotomaria*. The new species are *Bellerophon erawanensis*, *Biarmeaspira mazaevi*, *Apachella thailandensis*, *Gosseletina microstriata*, *Worthenia humiligrada*, *Altotomaria reticulata*, *Yunnania inflata*, *Trachydomia suwanneeae*, *Trachyspira eleganta*, *Heterosubulites longusapertura*, *Platyzona gradata*, *Trypanocochlea lopburiensis* and *Streptacis*? *khaokhadensis*. Most of the species in the studied assemblage represent vetigastropods (35.6%) and caenogastropods (26.7%) and most of the species belong to Late Palaeozoic cosmopolitan genera. The studied faunas come from shallow water carbonates that are rich in fusulinids, followed by gastropods, ostracods, bivalves and brachiopods. The gastropod assemblage from the Khao Khad Formation shares no species in common with the gastropod assemblages from other Permian Formations in Thailand, from the Tak Fa Limestone and the Ratburi Limestone. However, it is very similar to the Late Permian gastropod faunas from South China of the Palaeo-Tethys, therefore it suggests that the Indochina Terrane was not located far from the South China.

3.2 Introduction

Permian marine invertebrate faunas from the Indochina Terrane of Thailand have been intensively studied over the past decade (e.g., fusulinids, brachiopods, bryozoan, corals and ostracods). The knowledge on the fauna together with the previous stratigraphic and sedimentological studies suggest the existence of a carbonate platform along the western edge of the Indochina Terrane during the Permian. Although gastropods are a major benthic invertebrate component in the limestones from the Indochina Terrane of Thailand, their taxonomy and diversity have been rarely studied until recently. Permian gastropod faunas from Thailand have been studied in detail only during the last 6 years by Ketwetsuriya *et al*. (2014, 2016), who provided the first detailed study of the Middle Permian gastropods form the Tak Fa Limestone (Saraburi Group) of the Indochina Terrane and by Ketwetsuriya *et al*. (2019), who studied gastropods from the Ratburi Limestone of the Sibumasu Terrane. These studies reported numerous new species mostly representing typical Late Palaeozoic gastropod genera. Prior to these studies, only a few reports mentioned the presence of Permian gastropods from Thailand (Grant 1976; Waterhouse 1982; Sone 2010) without providing a detailed study.

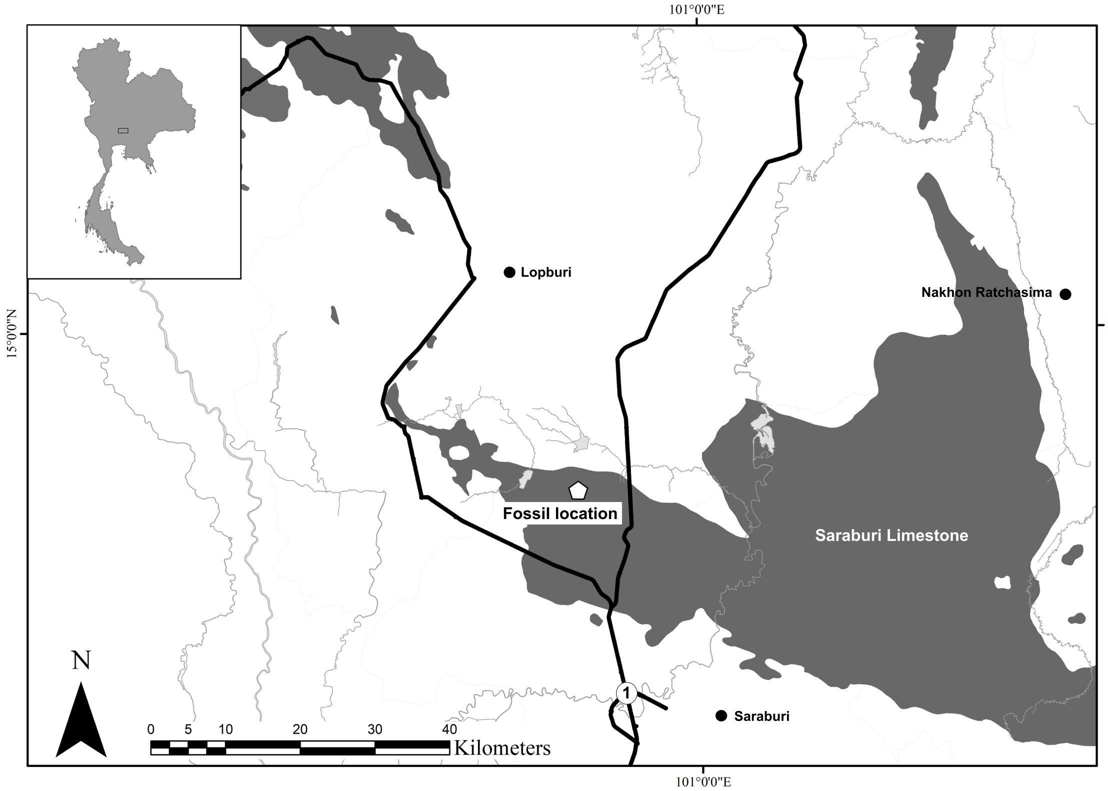

Figure 3.1: Geological map of the study location at Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand.

The present study describes a new Permian gastropod fauna from the Khao Khad Formation (Saraburi Group) at Erawan Hill, Lopburi Province, Central Thailand of the Indochina Terrane. The outcrops of the Khao Khad Limestone at Erawan Hill have yielded several species of the Permian marine invertebrate fossils including fusulinids, brachiopods, bryozoans, bivalves, ostracods and especially gastropods which form the most diverse group in this fauna. The studied gastropod assemblage represents one of the richest and most diverse Permian gastropod assemblages known from Thailand and provides important information on the distribution of Permian gastropods in the Palaeo-Tethys. Some species and genera suggest that the assemblage is related to the Late Permian gastropod faunas from South China, the Permian faunas from Cambodia and Japan and the Pennsylvanian and Permian faunas of the USA.

3.3 Geological setting

The Permian sedimentary rocks extending in central Thailand along the north–south orientation on the eastern side of the Chao Phraya Central Plain have been assigned to the Saraburi Group (informally known as Saraburi Limestone) (Nakornsri 1976, 1981; Bunopas 1981) which consists of widely exposed carbonate rocks along the western margin of the Indochina Terrane (Hinthong *et al*. 1985).

The Permian limestone in the study area is a part of the Khao Khad Formation of the Saraburi Group (Fig. 3.1). The Khao Khad Formation was initially erected by Hinthong (1981) for the carbonate rocks that exposed in an almost WNW–ESE direction in the Saraburi area through southern Lopburi area. It mainly comprises thin- to very thick-bedded limestone and locally interbedded with argillaceous limestone and clastic sedimentary rocks, i.e., shale, siltstone, sandstone and conglomerate. The bioclastic limestone lithology together with abundant marine invertebrate faunas suggests shallow-marine deposition in a carbonate platform. The presence of several invertebrate groups has been reported in this formation, e.g., fusulinids, brachiopods, gastropods, ostracods, bivalves, corals and ammonoids. However, only fusulinids have been investigated in detail, which indicate the age ranging from Early to Middle Permian (Pitakpaivan 1965; Toriyama *et al*. 1974; Toriyama & Kanmera 1977, 1979; Dawson 1993). The studied limestone samples yield numerous fusulinids of *Verbeekina* sp. (Fig. 3.2A, B) that indicate Kubergandian (=Roadian, Middle Permian) age based on Charoentitirat's identification.

The faunas described herein were collected from the weathered limestone surface exposed at Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1). The samples were taken from several limestone outcrops that exposed as the lapies (Fig. 3.3A, C) of 10 acres near the road No. 3334 at the west foot hill of Erawan Hill (GPS N21°56'24.5" and E96°30'11.2"). The outcrops composed predominantly of shallow marine limestone consisting generally of black to light gray limestone or recrystallized argillaceous limestone (Fig. 3.2C, D).

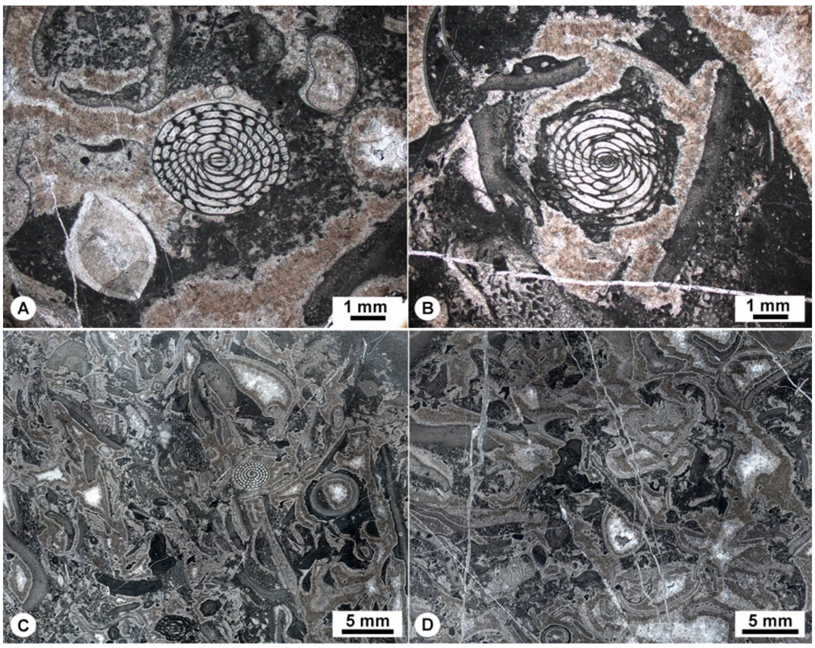

Figure 3.2: Photomicrographs of thin-sections of the studied fossiliferous limestone 0f the Khao Khad Formation at Erawan Hill, Lopburi Province, Central Thailand. A–B, the index taxa *Verbeekina* sp. C–D, Bioclastic packstone with gastropods, fusulinids, brachiopods, bivalves and dasyclad algae.

3.4 Material and methods

The present fossil material was obtained by surface collection from weathered out material at the surface of massive hard limestone blocks (Fig. 3.3B, D). Fossils could not be obtained from the unweathered parts of the hard, massive fossiliferous limestones. Sampling was performed in March 2017 and May 2018. In addition to collection of fossils in the field, 5 kg of weathered-out scree sediments from six different exposures near the limestone block. Laboratory work was done at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany. The sediments were wet sieved at mesh sizes of 0.2 mm, 0.5 mm and 5 mm and the residues were dried at the 40 degrees Celsius for one day. All fossils were picked from the residues under a microscope. Fossils were sorted according to species and selected specimens were documented aided by microphotography (mostly whitened with ammonium chloride) or with SEM. Finally, gastropods were identified as far as possible. In addition, thin sections of rock samples were prepared for sedimentological analysis.

Repository. All type specimens of gastropods are housed in the Department of Earth Sciences, Faculty of Science, Kasetsart University (Bangkok, Thailand) under the general repository number ESKU-19-LP 1–221.

Classification. The classification used in this article follows Knight *et al*. (1960) and Bouchet *et al*. (2017). Bellerophontids are classified as subclass of gastropods (Amphigastropoda). A recent discussion of the systematic placement of bellerophontids was given by Harper (2018). Euomphaloidea are classified as “Basal taxa that are certainly Gastropoda” (subclass incertae sedis according to Harper 2018) because it is sure that they represent Palaeozoic Gastropoda but their phylogenetic/systematic position is disputed e.g., Bandel & Frýda (1998): subclass Euomphalomorpha, and Nützel (2002): subclass Vetigastropoda.

3.5 Results

The studied samples have yielded 221 gastropods representing 44 species belonging to 30 genera. Gastropoda is the most abundant and diverse group. As mentioned above, the stratigrapy of the studied gastropod fauna is based on the fusulinids identified by T. Charoentitirat. Numerous fusulinids representing *Verbeekina* sp. (Fig. 3.2A, B) indicate an Kubergandian (= Roadian, Middle Permian) age. As in many other Permian faunas from Japan and Southeast Asia, the preservation of the gastropods is commonly poor and shells are strongly and coarsely recrystallized (coarsely silicified). However, a number of specimens provided sufficient morphological characters for an identification or characterization of new taxa.

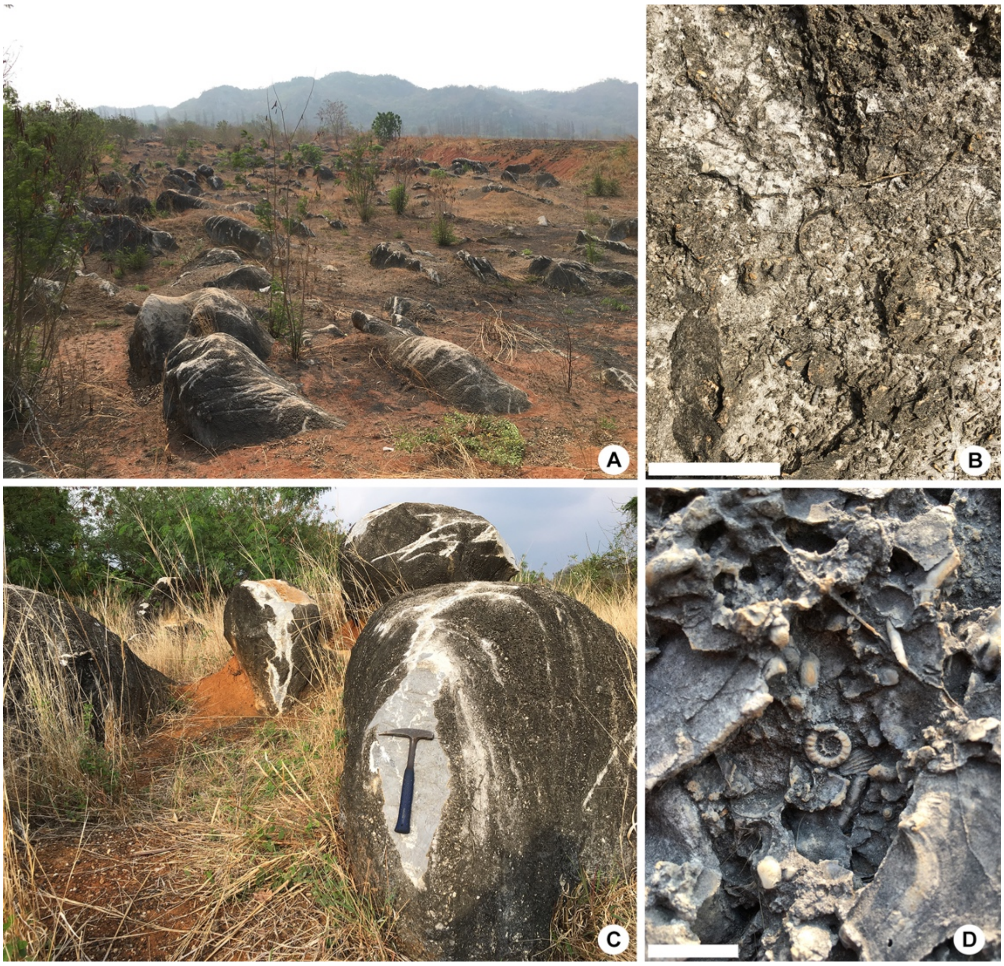

Figure 3.3: A, C, Limestone outcrops exposed as the lapies at the west foot hill of Erawan hill; hammer in the right side for scale (C). B, D, Weathered surface limestones represented by bioclastic packstone as an example for preservation that the studied materials were collected; scale bars represent: 10 cm (B); 2 cm (D).

The present gastropod assemblage from the Middle Permian of the Khao Khad Formation of Saraburi Group at Erawan Hill, Lopburi Province represents the most diverse Permian gastropod fauna known from Thailand. This fossiliferous limestone is rich in fusulinids and yields abundant gastropods together with ostracods, brachiopods, bivalves and some crinoids. Gastropods are the most diverse clade in this assemblage. The studied material comes from the shallow-marine carbonate platform of the Khao Kwang platform of the Indochina Terrane which is widely distributed in central and northeastern Thailand.

A total of 44 gastropod species have been described here, thirteen of which are new: namely *Bellerophon erawanensis*, *Biarmeaspira mazaevi*, *Apachella thailandensis*, *Gosseletina microstriata*, *Worthenia humiligrada*, *Altotomaria reticulata*, *Yunnania inflata*, *Trachydomia suwanneeae*, *Trachyspira eleganta*, *Heterosubulites longusapertura*, *Platyzona gradata*, *Trypanocochlea lopburiensis* and *Streptacis*? *khaokhadensis*. The assemblage consists of several typical, cosmopolitan Late Palaeozoic genera such as *Bellerophon*, *Warthia*, *Worthenia*, *Anomphalus*, *Naticopsis*, *Trachydomia*, *Palaeostylus* and *Protostylus*.

The clade proportions of the gastropod faunas that have been reported from Thailand so far differ considerably from each other (Fig. 3.4). The clade proportion of the present gastropod fauna (Fig. 3.4A) shows that it is dominated by Vetigastropoda which comprise of 16 species (35.6%). Pleurotomariida is the most diverse group of Vetigastropoda and most of the new species belong to this group. High-spired caenogastropods are present with 11 species (24.4%) including several species of the superfamily Orthonematoidea. Neritimorpha are represented by at least 8 species (17.8%) containing various species of the genera *Naticopsis* and *Trachydomia* and followed by Bellerophontida at 11.1%. Only a single species (2.2%) of Euomphalina and Heterobranchia is present this assemblage.

The Permian gastropod assemblages from the Tak Fa Limestone of the Saraburi Group reported by Ketwetsuriya *et al*. (2014, 2016) consists of 40 species and the relative quantitative data have been analyzed by Ketwetsuriya *et al*. (in prep.) from the Tak Fa Formation of the Nakhonsawan area, which is also located at the western margin of the Indochina Terrane (Sone & Metcalfe 2008). In contrast to the assemblage studied herein, Vetigastropoda is as diverse as Caenogastropoda in the Tak Fa assemblage (Fig. 3.4B) and both contribute 32.5% of the total species diversity each - with *Anomphalus* sp. being most abundant. Although, the gastropod faunas from the Khao Khad Formation and the Tak Fa Formation come from the Indochina Terrane of the eastern Palaeo-Tethys, there is no species in common and thus their species composition differs distinctly from each other as discussed above. However, at the genus level, there are several typical Late Palaeozoic cosmopolitan genera shared between the two localities i.e., *Warthia*, *Bellerophon*, *Euomphalus*, *Anomphalus*, *Yunnania*, *Microdoma*, *Naticopsis*, *Trachydomia*, *Strobeus*, *Pseudozygopleura*, *Protostylus* and *Streptacis*. This result shows that there are great variations in the diversity and composition of Permian gastropod assemblages in the Saraburi Limestone of the Indochina Terrane which probably reflects different environmental conditions within the carbonate platform of the Indochina Terrane.

The gastropod fauna from the Permian Ratburi Limestone, Ratchaburi Province, Central Thailand, represents the first silicified Permian gastropod fauna known from the Sibumasu Terrane (Ketwetsuriya *et al*. 2019). It consists of 34 species. Caenogastropoda are the most diverse clade in this assemblage (44.1% of the total species; Fig. 3.4C), followed by Vetigastropoda that encompass 26.5% of the total number of species. Euomphalina are absent in the Ratburi Limestone. The studied assemblage from the Khao Khad Formation of the Indochina Terrane has no shared species and its species content differs strongly from the gastropod assemblage from the Ratburi Limestone. However, there are several typical Late

Palaeozoic genera also shared between these two assemblages: *Warthia*, *Bellerophon*, *Peruvispira*, *Worthenia*, *Naticopsis*, *Pseudozygopleura*, *Protostylus* and *Streptacis*.

Caenogastropoda and Vetigastropoda contribute most to the species diversity of the Permian gastropods in Thailand. Neritimorpha and Bellerophontida are mainly represented by generally cosmopolitan genera. On the other hand, Heterobranchia and Euomphalina played a very minor role among the Permian gastropods from Thailand. However, the Permian gastropod fauna from the Khao Khad Formation of Erawan Hill studied herein shares no species with the gastropod faunas from the Tak Fa Limestone and the Ratburi Limestone. This suggests a high beta-diversity in this region and also that the Permian gastropod fauna of Thailand is still insufficiently studied. On the genus level, many more taxa are shared between those three known faunas: *Warthia*, *Bellerophon*, *Peruvispira*, *Worthenia*, *Naticopsis*, *Pseudozygopleura*, *Protostylus* and *Streptacis* which are present in all faunas from Thailand but also have a cosmopolitan distribution. Several widespread Permian genera are recorded for the first time from the Permian in Thailand herein: *Porcellia*, *Araeonema*, *Biarmeaspira*, *Trachyspira*, *Platyzona* and *Knightella*.

The comparison of the studied fauna and the other Permian eastern Palaeo-Tethys faunas suggests that the gastropods from the Khao Khad Formation of Erawan Hill are closely related to the Late Permian gastropod faunas from South China (Wang & Xi 1980; Wang 1982; Pan 1985; Pan & Yu 1993; Pan & Erwin 2002). The studied gastropod assemblage seems to have a connection with the faunas from South China, particularly the Guangxi and Yunnan provinces in South China. The presence of the species *Euomphalus* cf. *pronodocarinatus*, *Porcellia magninodosa*, *Naticopsis* cf. *heshanensis* and *Anomphalus* cf. *vanescens* further supports that the palaeogeographic positions of the Indochina Terrane and the South China Platform during the Permian period were palaeogeographically close to each other.

The studied gastropod fauna from the Khao Khad Formation of Erawan Hill (Middle Permian) is older than those of the South China (Late Permian). This could suggest that the gastropod faunas of South China migrated from the Indochina Terrane of Thailand to South China. Some species, e.g. *Worthenia* cf. *pagoda*, are commonly found from the Permian gastropod fauna of Cambodia (Mansuy 1914; Delpey 1941). The Permian gastropod fauna of the USA (Yochelson 1956, 1960; Batten 1989) and the Permian gastropod fauna of Japan (Nützel & Nakazawa 2012) also share some taxa with the present assemblage such as *Warthia* cf. *welleri*, *Anomphalus* cf. *vanescens*, *Anomphalus*? *blancus*, *Microdoma conicum* and *Trachydomia* cf. *nodosum*. However, the taxa reported from the richest known Permian gastropod fauna from Perak, Malaysia (Batten 1972, 1979, 1985) do rarely occur in the studied assemblage. The presence of several common taxa, especially on the genus level, in gastropod faunas from South China, Cambodia, Japan and the USA suggest a faunal connection and widespread palaeogeographic distribution of gastropods in the Palaeo-Tethys during the Permian.

In conclusion, the present Permian gastropod fauna from the Khao Khad Formation of Lopburi area has yielded about 44 species and represents one of the most diverse Permian gastropod faunas known from Southeast Asia. One genus (*Altotomaria*) and almost 30 % of the species described here are new. Vetigastropoda and Caenogastropoda are the most diverse groups in this fauna. This assemblage has no species in common with other Permian gastropod faunas in Thailand. However, a few taxa are shared with the Permian gastropod faunas from South China, Cambodia, Japan and the USA, especially with the Late Permian gastropod faunas from South China.

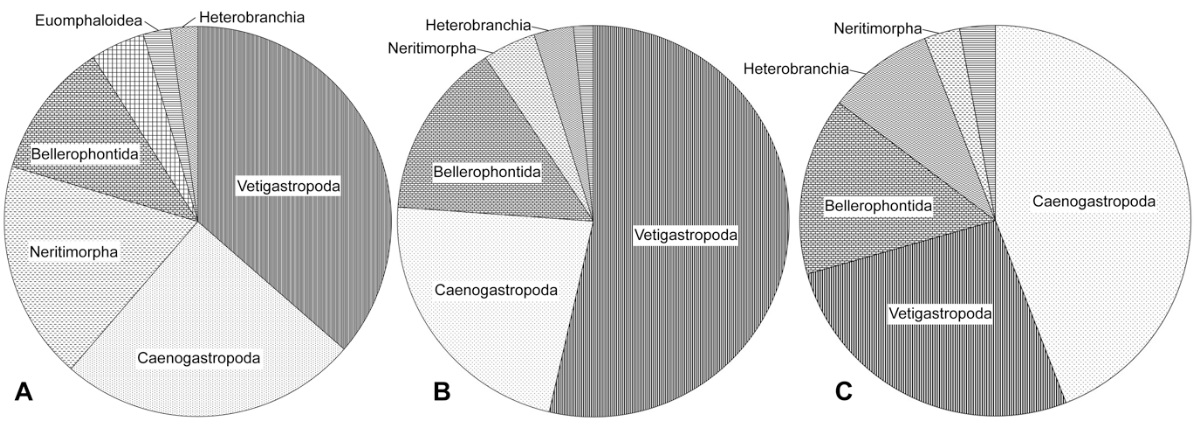

Figure 3.4: Relative species abundances of major clades of Middle Permian gastropod faunas in Thailand. The gastropod faunas from the Khao Khad Formation (this study), Lopburi province (A) from the Tak Fa Formation, Nakhonsawan province (B) as well as from the Ratburi Limestone, Ratchaburi province (C).

3.6 Systematic palaeontology

Class Gastropoda Cuvier, 1795

Subclass Amphigastropoda Simroth, 1906

Order Bellerophontida Ulrich & Scofield, 1897

Superfamily Bellerophontoidea McCoy, 1852

Family Euphemitidae Knight, 1956

Subfamily Euphemitinae Knight, 1956

Warthia Waagen, 1880

Type species. *Warthia brevisinuata* Waagen, 1880, Permian, Pakistan.

Warthia cf. *welleri* Yochelson, 1960

(Fig. 3.5A–D)

cf. *Warthia welleri* Yochelson, 1960: 255–256, pl. 48, figs 20–26.

Material. One specimen: ESKU-19-LP 24.

Dimensions (mm): ESKU-19-LP 24: height = 6.5; width = 6.5; thickness = 6.6.

Description. Involute, globose and inflated shell; minutely phaneromphalous; dorsum moderately arched; inductura thick, smooth; whorls smooth with a distinct slit, approximately 20 percent of body-whorl circumference; lips thin; lateral lips gently curved joining anterior lips smoothly; anterior lips evenly straight and slightly curved back forming a slit; aperture gently expanded, kidney-shaped in transverse section with U-shaped indentation.

Remarks. This specimen has a smooth involute shell with a slit representing the genus *Warthia.* This specimen is the most similar to *Warthia welleri* Yochelson, 1960 from the Permian of the Southwestern USA in shape and having a short slit, but the aperture of *W. welleri* is more arcuate than in the present material. The present specimen has a wing-like turnout of lateral lips (see Mazaev 2015) covering large parts of the umbilicus, which differs from *W. welleri* with gently sickle-shaped lateral lips.

Warthia sp. 1

(Fig. 3.5E–G)

Material. One specimen: ESKU-19-LP 20.

Dimensions (mm): ESKU-19-LP 20: height = 6.2; width = 4.9; thickness = 5.4.

Description. Compressed involute bellerophontiform shape, longer than wide; dorsum rounded; whorl seemingly geniculate in lateral view; whorls smooth without visible ornament, slit not observed; anomphalous; inductura smooth and thick; aperture kidney-shaped in transverse section but not broad; lateral lips gently sickle-shaped and thick, joining anterior lips at an angle of nearly 100 degrees; anterior lip curved and thin.

Remarks. This bellerophontiform shell is a typical representative of the genus *Warthia*, which is widespread and diverse in the Late Palaeozoic and has been reported from the Middle Permian of Thailand (e.g., Ketwetsuriya *et al*. 2016, 2019). However, the preservation of the material at hand is insufficient for species identification.

Warthia? sp. 2
(Fig. 3.5H–J)

Material. One specimen: ESKU-19-LP 57.
Dimensions (mm): ESKU-19-LP 57: height = 11.1; width = 11.1; thickness = 8.9.

Remarks. This smooth bellerophontoid seems to be a representative of the genus *Warthia,* but the poor preservation prevents a certain generic assignment. The species can be differentiated from *Warthia* cf. *welleri* by being anomphalous and by the absence of an indentation on the aperture. It differs from *Warthia* sp. 1 by a more inflated shape and a wider aperture.

Family Bellerophontidae McCoy, 1852

Bellerophon de Montfort, 1808
Type species. *Bellerophon vasulites* de Montfort, 1808, Devonian, Germany.

Bellerophon erawanensis sp. nov.
(Fig. 3.6A–G)

Etymology. After the Erawan Hill at which the studied gastropod material was found.
Holotype. ESKU-19-LP 55.
Paratypes. Three specimens, ESKU-19-LP 54, 56, 59.
Dimensions (mm): ESKU-19-LP 59: height = *c*. 11.7; width = 13.1; thickness = 10.6. ESKU-19-LP 55: height = 9.9; width = 8.1; thickness = 8.0. ESKU-19-LP 54: height = 9.5; width = *c*. 9.4; thickness = 7.1.

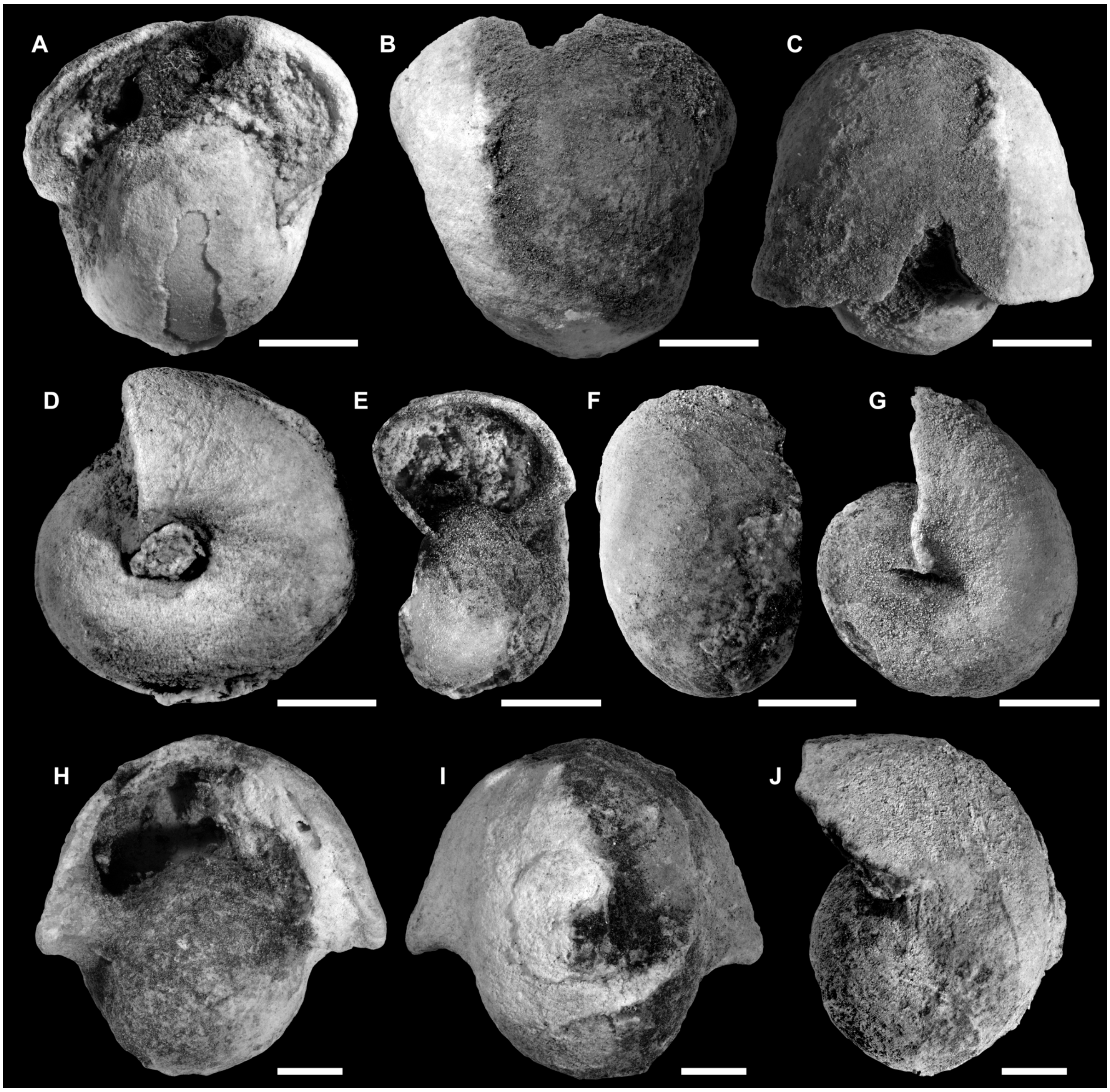

Figure 3.5: A–D, Warthia cf. welleri Yochelson, 1960, ESKU-19-LP 24. E–G, Warthia sp. 1, ESKU-19-LP 20. H–J, Warthia? sp. 2, ESKU-19-LP 57. All scale bars represent 2 mm.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Bellerophontiform, subglobular and slightly compressed shell, higher than wide; anomphalous, umbilical region covered by distinct callus; dorsum evenly rounded; whorls with a distinct slit; slit narrow and rather shallow; whorls covered by numerous closely arranged strengthened growth lines forming almost ribs, growth lines slightly curved backwards towards selenizone at an angle of about 70 degrees; inductura thin, ornamented with several growth lines developed continuing from whorl face; selenizone at periphery, narrow (*c.* 0.3 mm wide), marked by short curved transverse lunulae, at almost the same distance as of growth lines;

aperture reniform in transverse section, tiny V-shaped indentation at crest; lateral lip arched, somewhat angulated after wing-like turnout of lateral lips and smoothly joining anterior lips; outer lip sickle-shaped as suggested by course of growth lines.

Remarks. *Bellerophon* has previously been reported from the Middle Permian of Thailand (Ketwetsuriya *et al*. 2016, 2019) but it has been treated in open nomenclature because the preservation of that material is too poor for identification. *Bellerophon erawanensis* sp. nov. closely resembles *B. jonesianus* de Koninck, 1863 from the Permian of Pakistan (Chideru), which was also reported from the Permian of Pakistan (Salt Range) by Waagen (1880) and from the Permian of Japan (Akasaka Limestone) by Nützel & Nakazawa (2012). *Bellerophon jonesianus* has a similar ornamentation of pronounced growth lines, a narrow slit and a slightly elevated selenizone. However, *B. erawanensis* sp. nov. differs from *B. jonesianus* in having a less inflated shell, a narrower selenizone, a considerably higher number of fine threads formed by strengthened growth lines.

B. (*Bellerophon*) *sowerbyi*? d'Orbigny, 1840 as illustrated by Rollins (1975) from the Lower Mississippian of Southeastern Iowa is similar but this species has stronger growth lines and a slightly narrower selenizone. *B*. (*B*.) *kingorum* Yochelson, 1960 from the Permian of the Southwestern USA is also similar but has a more globular shape, thicker inductura and deeper slit. *B*. (*B*.) *huecoensis* Yochelson, 1960 can be differentiated by a deeper slit, a much more elevated selenizone, reflexed lateral lips and a very large size.

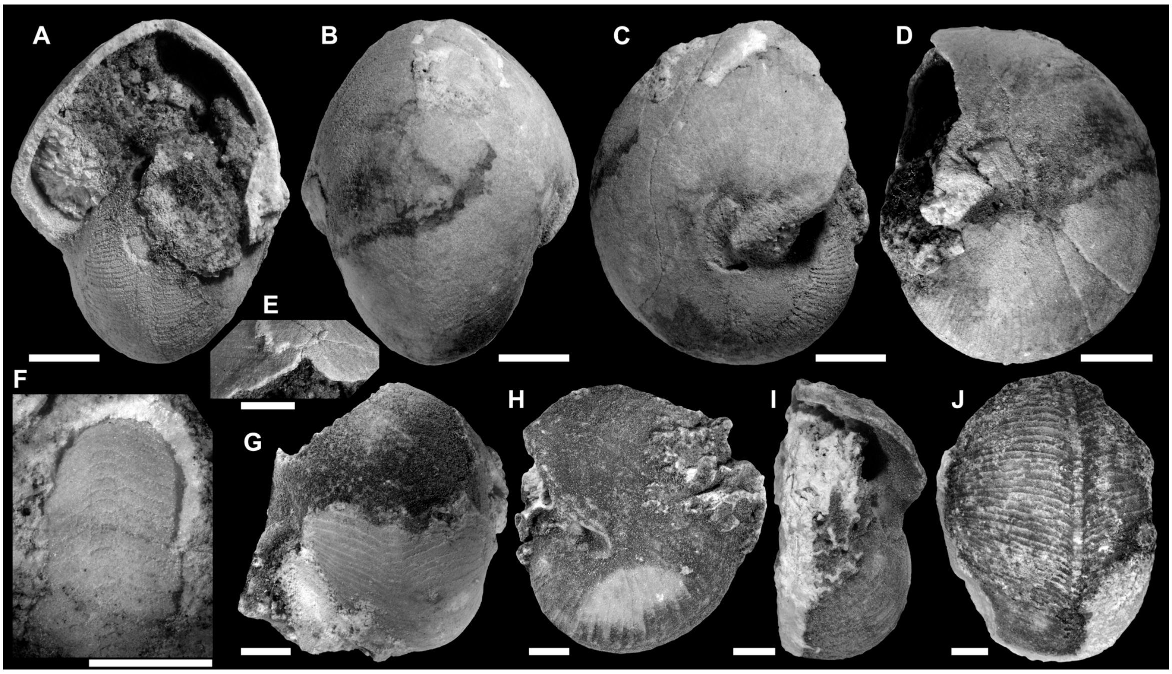

Figure 3.6: A–G, *Bellerophon erawanensis* sp. nov. A–E, ESKU-19-LP 55, holotype; E, shell showing V-shaped slit at crest. F, ESKU-19-LP 54, paratype; shell showing growth lines and position of selenizone. G, ESKU-19-LP 56, paratype. H–J, *Bellerophon* sp. H–I, ESKU-19-LP 58. J, ESKU-19-LP 59, shell fragment showing growth lines and position of selenizone. All scale bars represent 2 mm.

Bellerophon sp.
(Fig. 3.6H–J)

Material. ESKU-19-LP 58.
Dimensions (mm): ESKU-19-LP 58: height = 13.3; width (half) = 6.6; thickness = 12.1.

Remarks. A single anomphalous bellerophontiform shell and a fragment show strengthened, thread-like growth lines and a distinct selenizone with slightly straight short lunulae, which are the general characteristics of the genus *Bellerophon*. The involute shell is slightly elongated and inflated and the whorl profile is moderately well rounded. The present specimens resemble *Bellerophon jonesianus* de Koninck, 1863. The specimens assigned as *B*. cf. *jonesianus* by Mansuy (1913*a*, p.103, pl.11, figs 1–2) from the Permian of Laos is the most similar form. The specimens assigned to *B. jonesianus* by Delpey (1941, p.346, figs 21–22) from the Permian of Cambodia, by Waagen (1880, p.135, pl.8, figs 1–2) from the Permian of Pakistan and by Nützel & Nakazawa (2012, p.109, fig. 8A–H) from the Permian of Japan also resemble the present specimens. The present specimens resemble *B. erawanensis* sp. nov. they have a more elongated shape, more distinct selenizone, stronger growth lines and wider interspaces between the thread-like growth lines.

Basal taxa that are certainly Gastropoda
(subclass and order incertae sedis)

Superfamily Euomphaloidea White, 1877
Family Euomphalidae White, 1877

Euomphalus Sowerby, 1814
Type species. *Euomphalus pentangulatus* Sowerby, 1814, Carboniferous, Great Britain.

Euomphalus cf. *pronodocarinatus* Pan & Yu, 1993
(Fig. 3.7)

cf. *Euomphalus pronodocarinatus* Pan & Yu, 1993: p. 36, pl. 2, fig. 4.

Material. Two specimens: ESKU-19-LP 61, 95.

Dimensions (mm): ESKU-19-LP 61: height = 1.7; width = 7.8. ESKU-19-LP 61: height = 2.0; width = 7.6.

Description. Small anisostropic, discoidal shell; whorls rounded, convex, circular in transverse section, with the periphery at mid-whorl; whorls slowly increasing in diameter, only slightly embracing; suture deep; widely phaneromphalous with basal umbilicus deeper; whorl surface smooth with very faint and dense orthocline growth lines; rounded angulation on upper whorl surface at transition to upper umbilicus; base rounded; aperture subcircular, inner lip straight to somewhat concave.

Remarks. The present specimens closely resemble *Euomphalus pronodocarinatus* Pan & Yu, 1993 from the Lower Permian of Qixia Formation in Shangpingchuan, China in having a discoidal shape, a deep suture and numerous dense growth lines. However, the holotype of *E. pronodocarinatus* has nodes which are especially characteristic for this species that are absent in the studied material. *Straparollus* (*Straparollus*) *planorbiformis* de Koninck, 1881 as illustrated by Batten (1966*a*, p. 15, pl. 2, figs 12–14) from the Lower Carboniferous of the Hotwells Limestone, England is also similar in having rounded whorls with well-developed growth lines but it differs in being more high spired. Another similar species is *S.* (*Leptomphalus*) *micidus* Yochelson, 1956 (p. 220, pl. 12, figs 1–4) from the Middle Permian of Southwestern USA which is discoidal and has a weaker upper angulation. However, *S.* (*L.*) *micidus* differs in having a sinus on the angulation of the upper whorl surface. There are other Permian euomphalid species which were reported from Southeast Asia such as *Discotropis* sp. from the Tak Fa Limestone of Thailand (Ketwetsuriya *et al*. 2016), *S.* (*Euomphalus*) sp. from Perak, Malaysia (Batten 1972), *E. khmerianus* Mansuy, 1912 from the Sisophon limestone of Cambodia (Mansuy 1912; Delpey 1941) and *E. subcircularis* Mansuy, 1912 (pl. 7, figs 7–8). In addition, the present species also resembles *S.* (*E.*) *alaskensis* Yochelson & Dutro, 1960 from the Permian Siksikpuk Formation, USA, but the present specimens lack an upper angulation on whorl and the former species is larger in size. The studied specimens might represent a new species of the genus *Euomphalus* but the present material too poorly preserved to characterize it sufficiently.

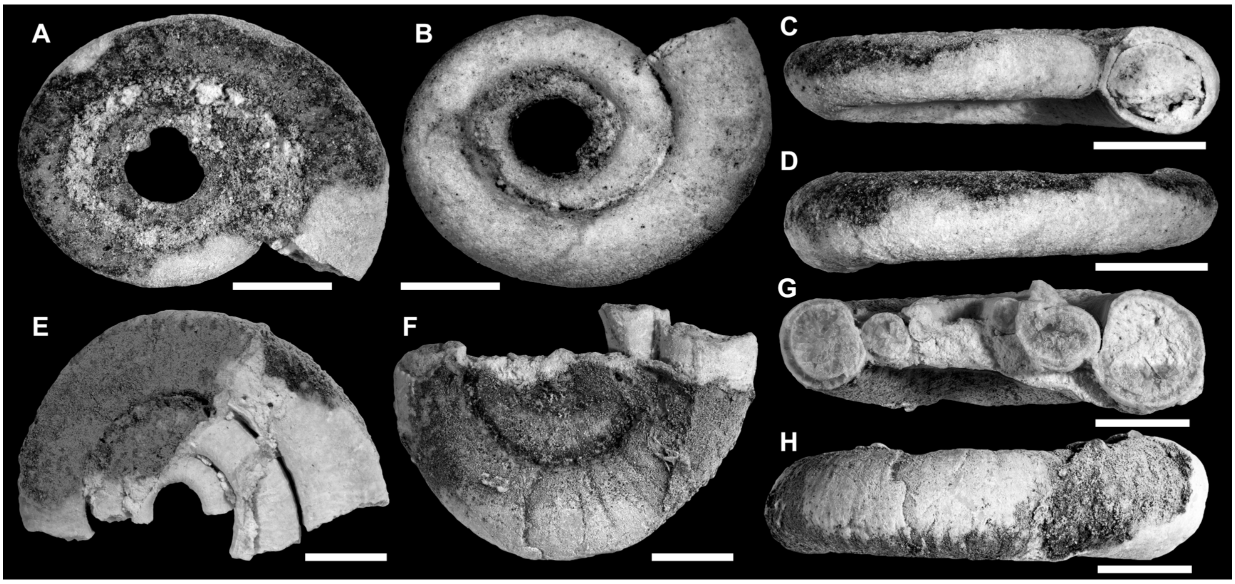

Figure 3.7: Euomphalus cf. pronodocarinatus Pan & Yu, 1993, A–D, ESKU-19-LP 61. E–H, ESKU-19-LP 95. All scale bars represent 2 mm.

Subclass Vetigastropoda Salvini-Plawen, 1980

Order uncertain

Superfamily uncertain

Family Holopeidae Cossmann, 1908

Holopea Hall, 1847

Type species. *Holopea symmetrica* Hall, 1847, Middle Ordovician, USA.

Holopea? sp.

(Fig. 3.8)

Material. Two specimens: ESKU-19-LP 2, 3.

Dimensions (mm): ESKU-19-LP 2: height = *c*. 3.8; width = 3.6. ESKU-19-LP 3: height = *c*. 6.3; width = 4.8.

Description. Turbiniform to naticiform, moderately high-spired shell consisting of three to four whorls (apex missing); whorls rapidly increasing strongly convex, rounded, embracing below periphery; whorl surface ornamented by prosocyrt, prosocline collabral ribs; ribs irregularly pace of unequal strength; suture impressed; base evenly convex; minutely phaneromphalous; aperture seemingly circular, columellar lip somewhat straight.

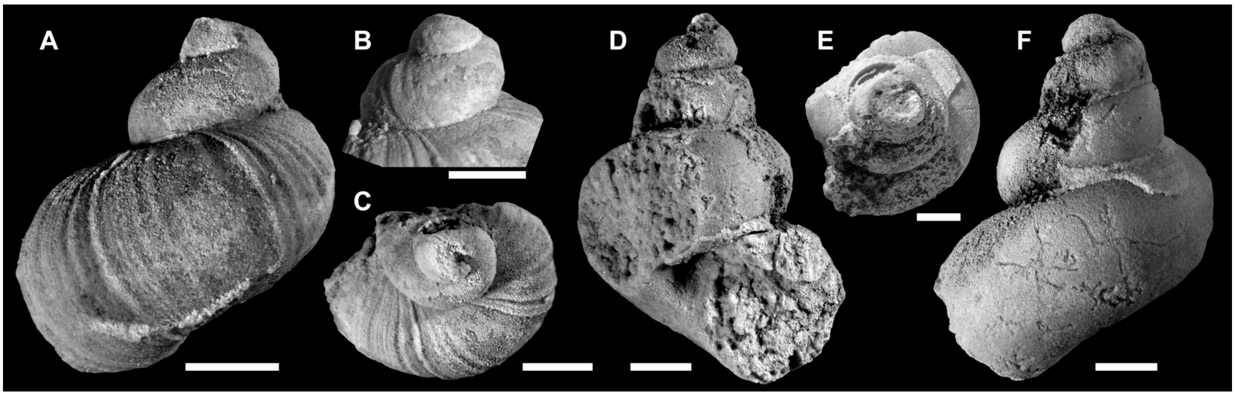

Figure 3.8: Holopea? sp., A–C, ESKU-19-LP 2. D–F, ESKU-19-LP 3. All scale bars represent 1 mm.

Remarks. These two incomplete specimens with deep suture, rounded whorls that bear collabral axial ribs resemble the Ordovician genus *Holopea* which has never been reported from the Permian of Thailand. However, similar shell morphologies have been reported frequently from Palaeozoic and Mesozoic strata and were assigned to various other genera. For instance, *Coelostylina costata* Batten & Stoke, 1986, a putative representative of the basically Mesozoic genus *Coelostylina* from the Early Triassic of the U. S. is quite similar to our specimens. *H. bacca* Pan & Erwin, 2002 (p. 13, fig. 8.5–8.11) from the Permian of South China resembles the present specimens the most in general features. The coiling direction of the protoconch is important for species assignment and it is slightly oblique to the axis in *H. bacca*. The coiling direction of the protoconch in the studied specimens is poorly preserved, therefore the species treated in open nomenclature.

Order Pleurotomariida Cox & Knight, 1960
Superfamily Porcellioidea Koken in von Zittel, 1895
Family Porcelliidae Koken in von Zittel, 1895
Subfamily Porcelliinae Koken in von Zittel, 1895

Porcellia Léveillé, 1835
Type species. *Porcellia puzo* de Koninck, 1883, Carboniferous, Belgium, original designation.

Porcellia magninodosa Pan, 1985
(Fig. 3.9)

Porcellia magninodosa Pan, 1985: p. 35, pl. 2, fig. 10; Pan & Yu, 1993: 43, pl. 6, figs 1–4.

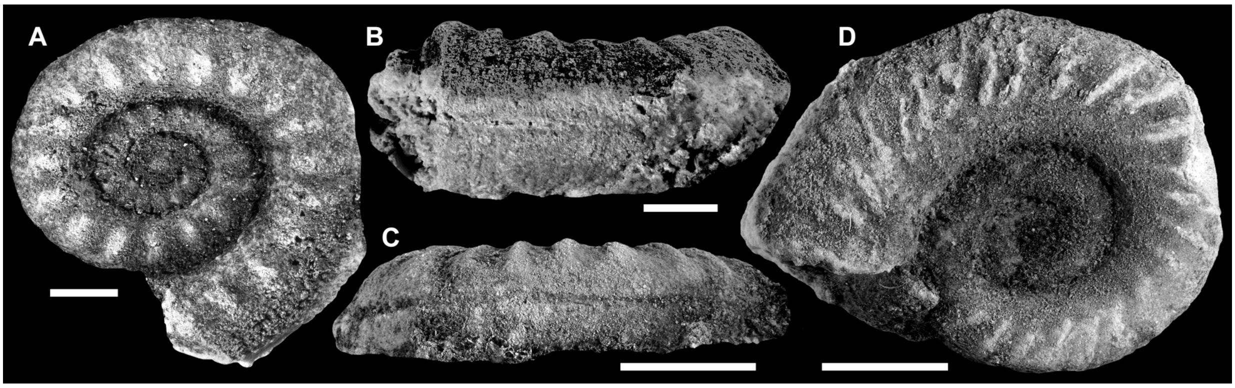

Figure 3.9: *Porcellia magninodosa* Pan, 1985, A–B, ESKU-19-LP 91. C, ESKU-19-LP 126. D, ESKU-19-LP 125. All scale bars represent 2 mm.

Material. Two specimens: ESKU-19-LP 91, 125, 126.

Dimensions (mm): ESKU-19-LP 91: height = 4.0; width = 11.7. ESKU-19-LP 125: height = 3.0; width = 7.4. ESKU-19-LP 126: height = 2.0; width = 9.4.

Description. Shell discoidal, pseudo-isostrophic, with 5 whorls; whorls well rounded; first whorl dextrally coiled, slightly elevated; later whorls planispirally coiled, expanding moderately; slit deep, extends one third of the whorl; selenizone narrow, concave, situated approximately at mid-whorl; selenizone bordered by two spiral lirae, representing periphery; upper and lower whorl face ornamented with *c*. 24 to 26 prominent, regularly spaced nodes or obliquely elongated (opisthocyrt) costae; suture deep and impressed; aperture subcircular.

Remarks. The present species is a typical representative of the genus *Porcellia* with its slightly elevated first whorls and nearly planispiral, dextrally coiled later whorls, with deep slit and very narrow selenizone. The present specimens closely resemble the type specimen of *Porcellia magninodosa* Pan, 1985 (p. 35, pl. 2, fig. 10) in shape, size and ornaments as well as those assigned to *P. magninodosa* by Pan & Yu (1993, p. 43, pl. 6, figs 1–4) from the Late Permian of the Changxing Formation, China. Other similar species are *Porcellia paucituberculata* Pan & Erwin, 2002 (p. 10, fig. 5.10–13) from the Permian of Guangxi and Yunnan Provinces, South China and *P. nodosa* Hall, 1859. The latter was also reported from the Lower Permian Sisophon Formation, Cambodia (Delpey 1941, p. 365, fig. 39). *P. nodosa* differs from *P. magninodosa* in having a rectangular whorl profile and fewer costae. In *P. paucituberculata*, the nodes and the interspaces are wider and it has fewer costae compared to *P. magninodosa*.

This is the first known occurrence of the genus *Porcellia* in Thailand and the earliest occurrence of *P. magninodosa*. Our report extends the range of the species to the Middle Permian and expands its geographical range to further south in the Palaeo-Tethys.

The *Porcellia* species that have been recorded from the North America (e.g., Thein & Nitecki 1974; Kues 1984) and Europe (Haughton 1859; Batten 1966*a*) are from the Carboniferous of Panthalassa and the western Palaeo-Tethys, respectively. The *Porcellia* species reported from Asia are from the Permian of the eastern Palaeo-Tethys, e.g., *P. nodosa* Hall, 1859 from Cambodia (Delpey 1941), *P. puzoidea* Hayasaka, 1955 from Japan, *P. lingshuiensis* Pan, 1985 from China, *P. magninodosa* Pan, 1985 from China and Thailand and *P. paucituberculata* Pan & Erwin, 2002 from South China. Our report further fills the biogeographic gap between these Carboniferous and Permian occurrences.

Superfamily Eotomarioidea Wenz, 1938
Family Eotomariidae Wenz, 1938

Biarmeaspira Mazaev, 2006
Type species. *Biarmeaspira verideclinata* Mazaev, 2006, Permian, Russia.

Remarks. When Mazaev (2006) erected the genus *Biarmeaspira*, he tentatively placed it within the family Phymatopleuridae Batten, 1956 (see also Mazaev 2015). However, the characters regarding the selenizone suggest a placement within the family Eotomariidae. The members of Eotomariidae are characterized by a concave selenizone and the lower edge of their selenizone represents the shell periphery. The early shell development of genus *Biarmeaspira* as documented by Mazaev (2015) shares these characteristics with other Eotomariidae. As suggested by Mazaev (2006, 2015), *Biarmeaspira* probably derived from the eotomariid genus *Baylea*. This further supports its placement in the family Eotomariidae.

Biarmeaspira mazaevi sp. nov.
(Fig. 3.10)

Etymology. After Alexey Mazaev for his work on the Late Palaeozoic gastropods and establishment of this genus.
Holotype. One specimen: ESKU-19-LP 1.
Dimensions (mm): ESKU-19-LP 1: height = 11.0; width = *c*. 9.5; apical angle = 100°.

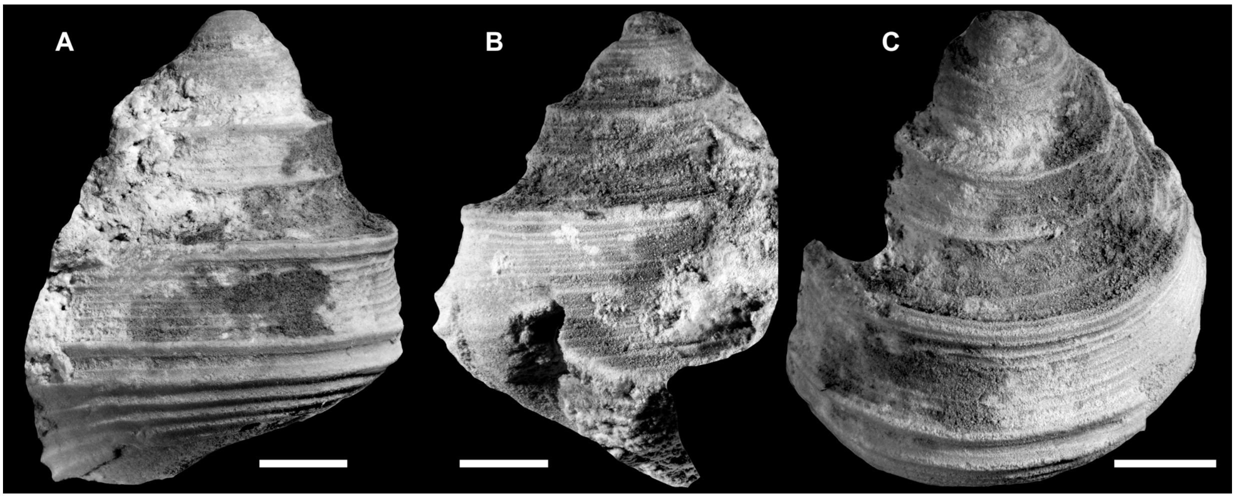

Figure 3.10: *Biarmeaspira mazaevi* sp. nov. ESKU-19-LP 1, holotype. All scale bars represent 2 mm.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell moderately high-spired, turbiniform, earliest whorls missing, 4 whorls preserved; early teleoconch whorls convex, ornamented by up to four spiral lirae; later spire whorls with sharp angulation at mid whorl face; upper whorl face above angulation develops a concave subsutural ramp; ramp ornamented with several spiral threads; selenizone narrow, angulated, situated at middle angulation, ornamented with obscure lunulae, bordered by two distinct spiral cords; lower whorl face flat to concave, subvertical inclined about 10 degrees from axis, ornamented with up to eight widely spaced fine spiral lirae; lower whorl face twice as wide as upper whorl face; suture shallow and indistinct; lower part of the lower whorl face ornamented by two strongest spiral cords, representing periphery, interspace between the two cords markedly concave, wide and ornamented with additional 2 fine spiral lirae, lowest cord represents the basal edge; profile near basal edge swollen; base convex, ornamented by numerous widely spaced fine spiral cords that are stronger and more widely spaced than those on ramp and lower whorl face; aperture unknown.

Remarks. This single specimen is placed in the genus *Biarmeaspira* due to the presence of an angular selenizone and a strong spiral ornament. The early teleoconch is absent and the growth lines and the aperture are poorly preserved so that this generic assignment is not entirely beyond doubt. Another genus having a prominent spiral ornament, a swollen basal edge and an angular selenizone is the Triassic genus *Sisenna*. *Sisenna* has a lower spire compared to *Biarmeaspira* and it possesses an angulation on the early whorl face which later turns into selenizone during ontogeny, a characteristic that is absent in *Biarmeaspira.*

Biarmeaspira mazaevi sp. nov. can be differentiated from other *Biarmeaspira* species by its ornamentation and by having a swollen basal edge. *B*.? *loatienensis* (Mansuy, 1914) from the Carboniferous of Loatien, Yunnan is very similar in shape, but is ornamented with more prominent spiral ribs on the upper and lateral whorl face. *B*.? *choueitangensis* (Mansuy, 1912, pl. 18, fig. 12) shows a similar whorl morphology and might be closely related.

Subfamily Neilsoniinae Knight, 1956

Apachella Winters, 1956
Type species. *Apachella translirata* Winters, 1956, Permian, USA.

Apachella thailandensis sp. nov.
(Fig. 3.11)

Etymology. After the country of Thailand.
Holotype. ESKU-19-LP 62.
Paratypes. Four specimens: ESKU-19-LP 25, 60, 89, 100.
Dimensions (mm): ESKU-19-LP 25: height = *c*. 9.4; width = 5.5; apical angle = 75^{O}. ESKU-19-LP 62: height = 8.5; width = 5.2; apical angle = 60^{O}. ESKU-19-LP 60: height = *c*. 4.6; width = *c*. 4.6. ESKU-19-LP 89: height = *c*. 7.1; width = *c*. 4.1; apical angle = 66^{O}. ESKU-19-LP 100: height = *c*. 6.5; width = *c*. 4.8.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell high-spired, consisting of 8 whorls, first whorl planispiral; first two teleoconch whorls smooth, rounded, third whorl ornamented with spiral threads; selenizone starts within the 4th whorl; suture slightly impressed; subsutural ramp slightly convex, ornamented with 3–4 spiral ribs that are ornamented with nodes; selenizone concave, ornamented with very faint lunulae, bordered by two straight spiral ribs; lower rib forms periphery; lower whorl face twice as wide as the upper whorl face; lower whorl face slightly

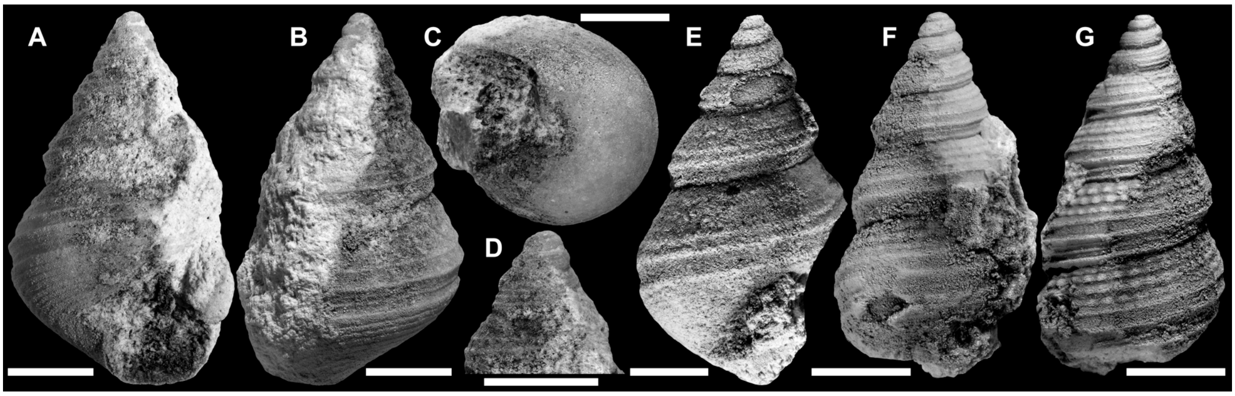

Figure 3.11: *Apachella thailandensis* sp. nov. A–D, ESKU-19-LP 62, holotype. E, ESKU-19-LP 25, paratype. F–G, ESKU-19-LP 89, paratype. All scale bars represent 2 mm.

convex, ornamented with one spiral rib just above suture, equal in strength to spiral rib bordering the lower edge of selenizone; lower whorl face further ornamented with two spiral threads between two spiral ribs; base convex, ornamented with several evenly spaced spiral ribs of same strength as ribs on lower whorl face; base convex, anomphalous; aperture unknown.

Remarks. *Apachella thailandensis* sp. nov. has a wider upper whorl face (above selenizone) than other species of *Apachella*. The ratio of the height of the upper and the lower whorl face of *A. thailandensis* sp. nov. is similar to that of *A. alimillana* (Girty, 1909). However, the latter lacks spiral ribs on upper whorl face. *A. powwowensis* Battten, 1995 has a wider selenizone, a median spiral lira on its selenizone and only one spiral rib on its upper whorl face. *A. franciscana* (Chronic, 1952) differs by having two faint spiral ribs on the upper whorl face adjacent to the suture, more prominent ribs bordering the selenizone, a stepped whorl profile and a higher whorl expansion rate.

Peruvispira Chronic, 1949
Type species. *Peruvispira delicata* Chronic, 1949, Permian, Peru.

Peruvispira sp.
(Fig. 3.12)

Material. Two specimens: ESKU-19-LP 10, 68.
Dimensions (mm): ESKU-19-LP 10: height = *c*. 2.7; width = *c*. 2.0. ESKU-19-LP 68: height = *c*. 3.3; width = 3.1.

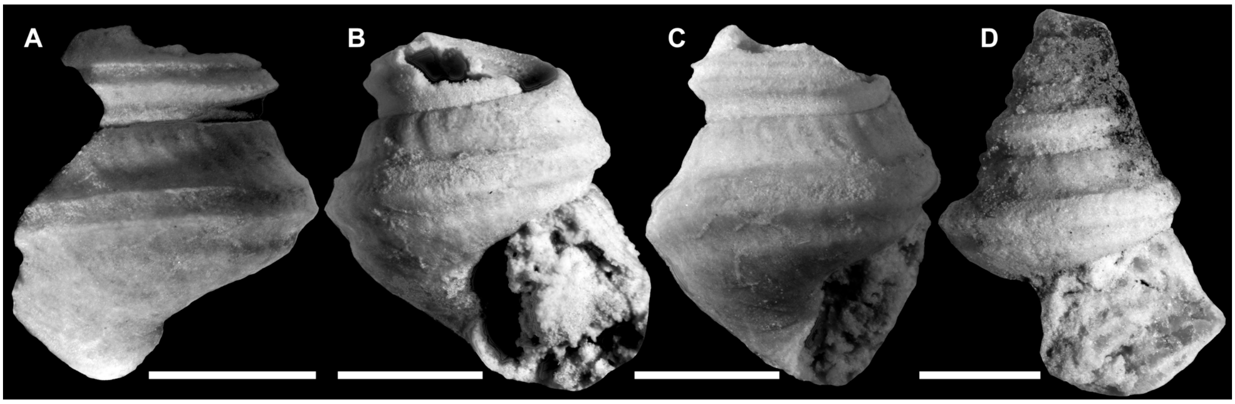

Figure 3.12: *Peruvispira* sp., A–C, ESKU-19-LP 10. D, ESKU-19-LP 68. All scale bars represent 1 mm.

Description. Shell small, conical, moderately high-spired; suture distinct, situated just below basal edge; whorl face above selenizone slightly convex near suture, concave above selenizone, ornamented with very faint, obliquely elongated, prosocline/prosocyrt subsutural nodes; upper whorl face three times as wide as the lower whorl face; selenizone wide, concave, slightly raised, situated at lower half of whorl face, bordered above and below by pronounced spiral cords; lower cord forms periphery; the whorl face below selenizone concave, smooth; basal edge rounded; base convex, smooth; aperture subovate, outer lip convex angular, basal lip convex, lower half of the columellar lip slightly reflexed; base anomphalous.

Remarks. The whorl profile is very similar to that of *Peruvispira turrita* Yu, 1980 from the Permian of Guizhou, but it is not clear whether the latter species has subsutural nodes or not. *P. allandalensis* Fletcher, 1958 and *P. trifilata* (Dana, 1847) from the Permian of Australia are other similar species but they differ in having collabral threads and a rather convex upper and lower whorl face.

Family Gosseletinidae Wenz, 1938

Gosseletina Fischer, 1885

Type species. *Pleurotomaria callosa* de Koninck, 1843, Carboniferous, Belgium.

Gosseletina microstriata sp. nov.

(Fig. 3.13)

Etymology. From Latin micro, meaning small, and Latin stria, meaning furrow, referring the tiny spiral ornaments.

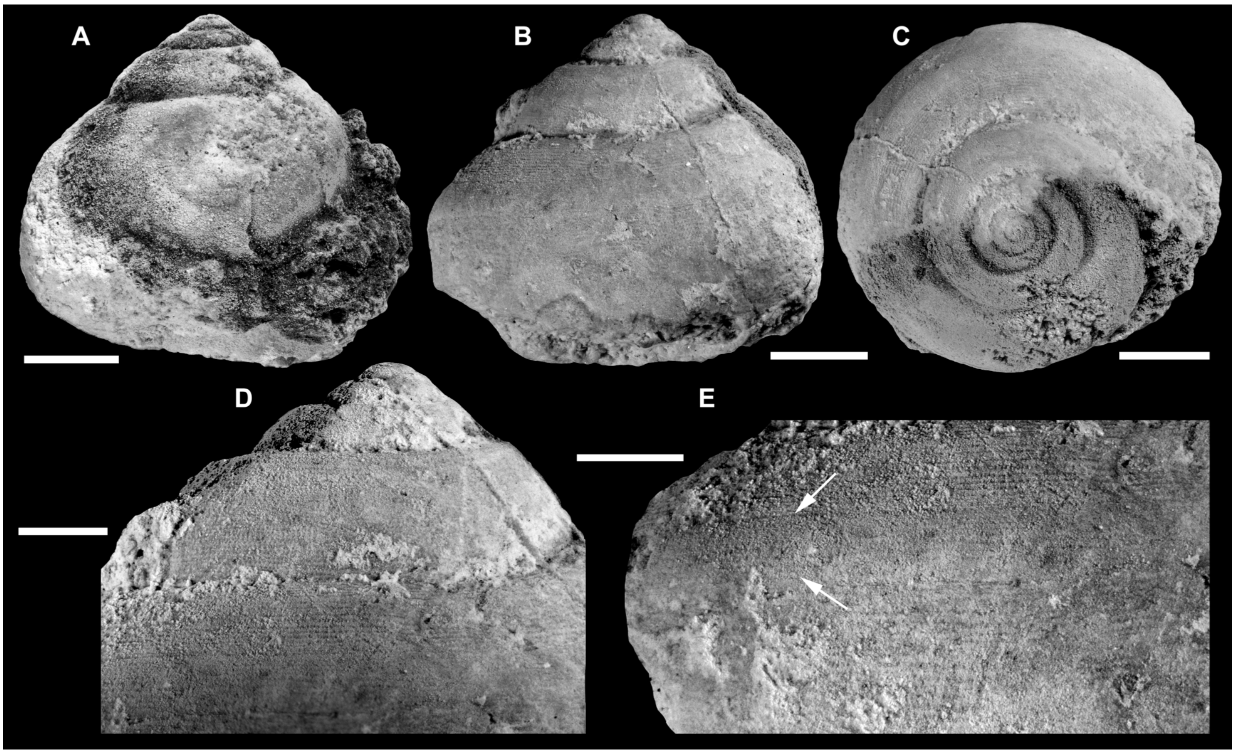

Figure 3.13: *Gosseletina microstriata* sp. nov., A–E, ESKU-19-LP 29, holotype. Scale bars represent: 2 mm (A–C); 1 mm (D–E). Arrows indicate the presence of selenizone.

Holotype. ESKU-19-LP 29.

Paratypes. Two specimens: ESKU-19-LP 5, 14.

Dimensions (mm): ESKU-19-LP 5: height = *c*. 3.8; width = *c*. 4.4. ESKU-19-LP 14: height = 2.2; width = 2.2. ESKU-19-LP 29: height = 7.3; width = 8.3.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Low-spired, globose shell, medium-sized, comprising *c*. 4.5 whorls; apex obtuse; spire distinctly elevated; body-whorl broad and inflated, covering approximately 80% of the entire height; whorls rapidly increasing; whorls distinctly convex; whorl surface with numerous very thin, faint spiral threads; whorls embracing at periphery; selenizone broad, situated high on whorl, above periphery, flush with whorl surface or very slightly convex, ornamented as on whorl face; suture impressed but shallow; base rounded; aperture unknown.

Remarks. *Gosseletina microstriata* sp. nov. differs from other *Gosseletina* species in several aspects. *G. aspeniana* (Girty, 1927) (Early Carboniferous, USA) is with faint spiral threads but differs by its whorl profile with distinctly convex whorl face above selenizone. *G. permiana*

Batten, 1989 (Permian, USA) has a coarser spiral ornament and deeper sutures. *G. nodosa* Batten, 1966*a* (Early Carboniferous, England) has subsutural axial riblets and lacks a spiral micro-striation. *G. portlockiana* (de Koninck, 1843) (Early Carboniferous, Europe) has a stronger spiral striation (Batten 1966*a*). *G. johnsoni* Thein & Nitecki, 1974 is more slender and has a cancellate ornament in subsutural position. *G. callosa* (de Koninck, 1843) (Carboniferous, Belgium), the type species of *Gosseletina*, lacks spiral ornament (Knight 1941). *G. persimplex* (Girty, 1915) (Pennsylvanian, USA) lacks spiral ornament and is more low-spired (Hoare 1961). *G. subglobosa* (Hall in Miller, 1877) (Early Carboniferous, USA) has a coarser spiral ornament. *G. spironema* (Meek & Worthen, 1866) (Pennsylvanian, USA) has a coarser spiral ornament and prosocyrt folds on whorl face above selenizone (Kues & Batten 2001).

Superfamily Pleurotomarioidea Swainson, 1840
Family Phymatopleuridae Batten, 1956

Worthenia de Koninck, 1883
Type species. *Turbo tabulatus* Conrad, 1835, Carboniferous, Pennsylvania.

Worthenia humiligrada sp. nov.
(Fig. 3.14A–I)

Etymology. From Latin humilis, meaning low, and Latin gradus, meaning step, referring to the low-stepped whorl profile.
Holotype. ESKU-19-LP 22.
Paratypes. ESKU-19-LP 23, 33, 34, 35, 74
Dimensions (mm): ESKU-19-LP 22: height = 6.8; width = 7.0; apical angle = 98^{O}. ESKU-19-LP 23: height = 10.5; width = 12.7. ESKU-19-LP 33: height = *c*. 16.0; width = 13.8; apical angle = 92^{O}. ESKU-19-LP 34: height = *c*. 9.0; width = 11.3; apical angle = 110^{O}. ESKU-19-LP 35: height = *c*. 10.9; width = 13.6; apical angle = 110^{O}. ESKU-19-LP 74: height = *c*. 1.7; width = *c*. 3.1.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell low-spired for genus, gradate, trochiform; first whorl planispiral; early teleoconch whorls (about first two or three whorls) low-spired, smooth, convex, rounded; second and third whorls with fine spiral and axial ribs; suture distinct and impressed; later whorls sharply angulated at about mid-whorl face, the middle angulation separates subsutural ramp from subvertical lower whorl face; subsutural ramp slightly convex near adapical suture to concave on the remaining part; ramp inclining at an angle of 35–50°; subsutural ramp ornamented with up to eight spiral ribs and equally spaced prosocyrt fine collabral ribs or strengthened growth lines; spiral ribs and collabral ribs form nodes at intersections, forming fine reticulate pattern; ornamentation more prominent near adapical suture; lower whorl face subvertical, concave, ornamented with up to six strong spiral cords and numerous faint prosocyrt collabral threads or growth lines; mid angulation forms crest-like periphery of whorl where selenizone situated; selenizone sharply angular covered by v-shaped lunulae; lunulae form nodes when intersecting with angulation; selenizone bordered with fine spiral ribs, upper rib represents lowest spiral rib of subsutural ramp, while lower rib represents uppermost spiral rib of the subvertical lower whorl face; intersections of lunulae and angulation nodular; basal edge sharply angulated; base convex, ornamented by several evenly spaced spiral ribs and very weak opisthocyrt collabral threads; suture shallow, indistinct; narrowly phaneromphalous; aperture unknown.

Remarks. The convex early teleoconch whorls, the position and the ornamentation pattern of the selenizone suggest that this species belongs to the genus *Worthenia* de Koninck, 1883. The distinguishing characters of *Worthenia humiligrada* sp. nov. are the relatively low spire, wide umbilicus, weak subsutural convexity of the ramp, sharp angulation at the basal edge and nodular selenizone. The combination of these characters distinguishes *W. humiligrada* sp. nov. from the other species belonging to the genus *Worthenia*.

There are some similar Permian species in Southeast Asia which have been assigned to *Worthenia*, for instance *W. multicarinata* (Mansuy, 1912) from the Carboniferous of Yunnan, China (Mansuy 1912) and the Permian of Cambodia (Delpey 1941) and Malaysia (Batten 1972, p. 32, figs 36–38) is very similar in shape but it has more prominent subsutural nodes on the upper whorl face, a distinctly impressed suture and its basal edge is rounded angular and ornamented with nodes. The type specimens of *W. schirjaevensis* (Stuckenberg, 1905) from the Upper Carboniferous of Samara, Russia and the specimens assigned to *W. schirjaevensis* from the Permian of Cambodia (Delpey 1941, fig. 27) has a very similar whorl profile and ornamentation but they differ from *W. humiligrada* sp. nov. by having a higher spire. According to Batten (1972, fig. 38), *W. schirjaevensis* (Stuckenberg, 1905) lacks nodes on the selenizone. *W. arizonensis* Winters, 1963 from the Permian of Arizona is another species with planispiral early whorl but differs from *W. humiligrada* sp. nov. by having a narrower upper whorl face, a very prominent subsutural convexity, by lacking the sharp angulation at the basal edge and by having a very narrow or no umbilicus. *W. crenulata* Batten, 1989 from the Permian of southwestern United States, with steeper upper whorl face and more prominent nodes on its selenizone. The specimens assigned to *W. corrugata* Chronic, 1952 by Batten (1989) differ from *W. humiligrada* by having a stronger spiral ornament, a sharper collabral ornament and by the presence of axial folds on its upper whorl face. The specimens assigned to *W. corrugata* by Kulas & Batten (1997) from the Permian of Wyoming differ by having a narrow umbilicus and faint lunulae.

Worthenia cf. *pagoda* Mansuy, 1912
(Fig. 3.14J–N)

cf. *Worthenia pagoda* Mansuy, 1912: 39, pl. 7, fig. 6; Delpey, 1941: 353, fig. 26.

Material. Two specimens: ESKU-19-LP 17, 66.
Dimensions (mm): ESKU-19-LP 17: height = *c*. 6.6; width = 4.9. ESKU-19-LP 66: height = 5.5; width = *c*. 5.0; apical angle = 75°.

Description. Shell moderately high-spired, trochiform, consisting of 6 whorls; first three teleoconch whorls smooth, convex, rounded; mid angulation develops starting from the 4th whorl onward; the last quarter of the last whorl slightly deflected; suture slightly impressed; subsutural ramp with faint subsutural convexity, slightly concave on remaining part; ramp inclining at an angle of about 45–60°; subsutural ramp ornamented with three spiral ribs starting from 4th whorl and almost straight prosocline growth lines; spiral ribs ornamented with equally spaced nodes; mid-angulation forms periphery where selenizone situated; selenizone prominent, wide, comprising about 1/7 of the whole whorl face of 5th whorl, ornamented with equally spaced strong nodes, bordered by fine spiral ribs; lower whorl face facing abapically, concave, ornamented with two nodular spiral ribs; lowest spiral rib stronger, situated at angulation, forming basal edge; base convex, ornamented by several evenly spaced nodular spiral ribs, narrowly phaneromphalous; aperture unknown.

Remarks. We tentatively assign the studied specimens to *Worthenia pagoda*, based on the whorl profile, the presence of three nodular spiral ribs on the upper whorl face and the nodular selenizone. Species with a similar whorl profile belonging to *Worthenia* are more common in the Triassic e.g., *W. annamensis* Mansuy, 1913*b* from Tonkin, Vietnam but are very rare in the Permian. *W.*? *psiche* (Gemmellaro, 1889) from the Permian of Italy has a similar shape but have only two spiral ribs on the upper whorl face.

Worthenia sp.
(Fig. 3.14O–S)

Material. One specimen: ESKU-19-LP 88.
Dimensions (mm): ESKU-19-LP 88: height = 6.4; width = 4.8; apical angle = 74°.

Description. Shell moderately high-spired, trochiform, consisting of at least 6 whorls; first two teleoconch whorls smooth, convex, rounded; third whorl ornamented with fine spiral threads; mid angulation develops starting from the 4th whorl; suture slightly impressed; subsutural ramp slightly convex, becoming concave just above selenizone; ramp inclining at an angle about 45–55°; subsutural ramp ornamented with four spiral ribs, uppermost two ribs ornamented with weak nodes, lowest one represents upper border of selenizone; mid angulation represents periphery where selenizone is situated; selenizone prominent, ornamented with equally spaced small nodes; lower whorl face concave just below the selenizone, slightly convex otherwise, ornamented with three spiral ribs, uppermost spiral rib represents lower border of selenizone; spiral ribs on lower whorl face stronger than ribs on ramp; suture situated between lowermost two ribs; base convex, ornamented with several evenly spaced, prominent spiral ribs of about same strength as ribs on lower whorl face; base anomphalous; aperture unknown.

Remarks. *Worthenia* sp. differs from *Worthenia* cf. *pagoda* in ornamentation pattern and has a narrower and less ornamented selenizone. The whorl profile of *Worthenia* sp. is similar to that of *W.*? *constantini* (Mansuy, 1912) from the Carboniferous of Yunnan, but the latter without nodular spiral ribs.

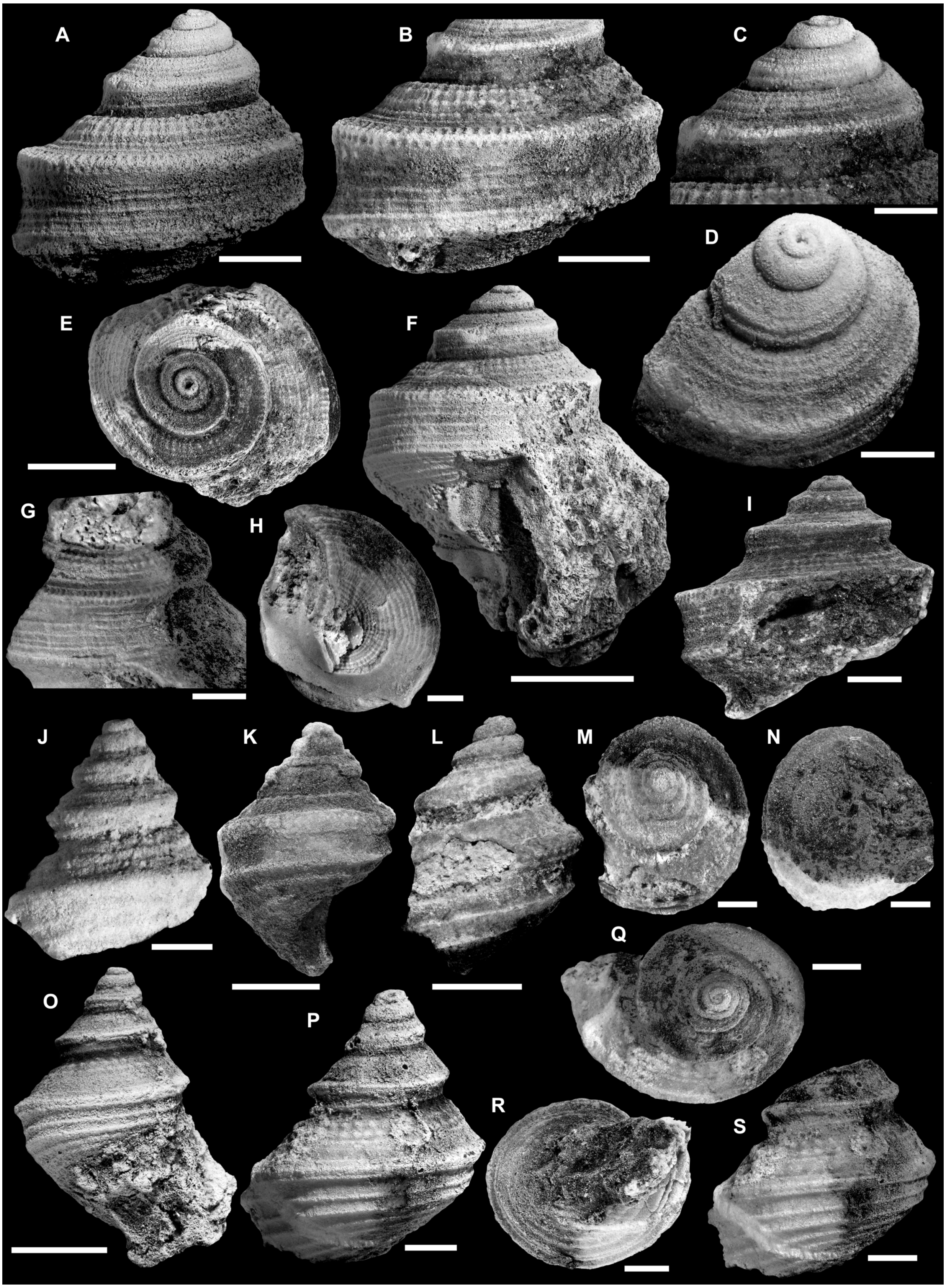

Figure 3.14: A–I, *Worthenia humiligrada* sp. nov. A–D, ESKU-19-LP 22. E–F, ESKU-19-LP 33. G–H, ESKU-19-LP 23. I, ESKU-19-LP 34. J–N, *Worthenia* cf. *pagoda* Mansuy, 1912, J, ESKU-19-LP 17. K–N, ESKU-19-LP 66. O–S, *Worthenia* sp., ESKU-19-LP 88. Scale bars represent: 2 mm (A, B, G, H, I, K, L, O); 1 mm (C, D, J, M, N, P–S); 5 mm (E, F).

Altotomaria gen. nov.

Type species. *Altotomaria reticulata* sp. nov.

Etymology. From Latin alto, meaning high, referring both the high spire and the high position of the selenizone; -tomaria refers to the genus name *Pleurotomaria*, typical of the group Pleurotomarioidea to which the new genus belongs; gender feminine.

Diagnosis. Shell relatively high-spired; whorl face strongly ornamented with widely spaced spiral cords and narrowly spaced axial ribs or threads forming reticulate pattern; spiral cords more prominent than the axial ribs; periphery low on whorls in mature whorls, formed by strong spiral cord; selenizone above mid-whorl face, flush with the whorl face, bordered by two spiral cords, ornamented with widely spaced lunulae and median spiral thread; base anomphalous.

Remarks. Differences to other genera are discussed below.

Altotomaria reticulata sp. nov.

(Fig. 3.15)

Etymology. From Latin reticulata, meaning net-like, referring the reticulated ornament.

Holotype. Only specimen: ESKU-19-LP 83.

Dimensions (mm): Height = *c*. 5.8; width = 4.4.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

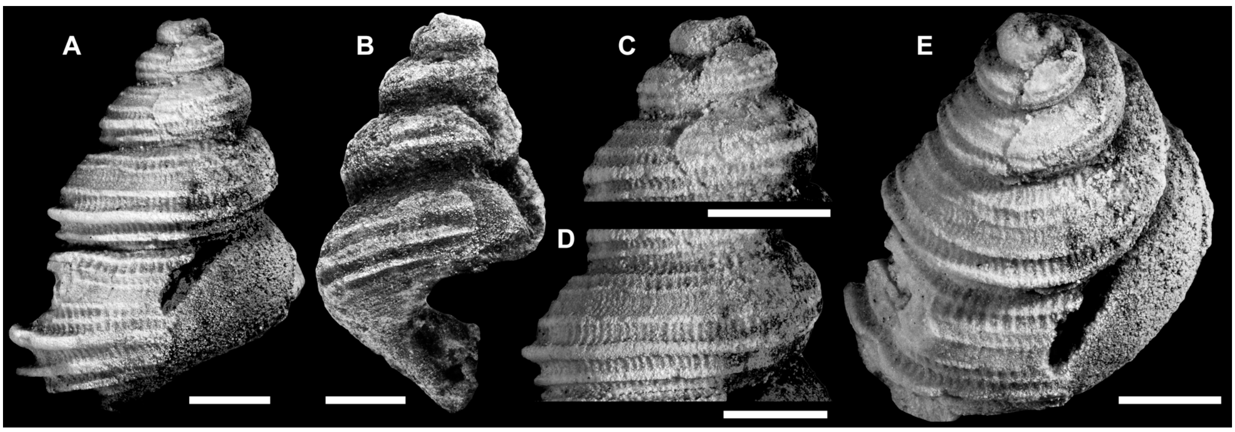

Figure 3.15: *Altotomaria reticulata* sp. nov. A–E, ESKU-19-LP 83, holotype. All scale bars represent 1 mm.

Description. Shell relatively high-spired, consisting of about 5 preserved whorls, whorls convex with periphery low on the whorl face; periphery in late teleoconch whorl with strong spiral cord angulating whorl face, first whorl(s) missing; first preserved whorl seemingly smooth (corroded), rounded; second whorl ornamented with spiral threads; whorl face above selenizone convex, narrow, ornamented with nearly orthocline regular axial threads and 2 spiral ribs, lower one bordering selenizone; selenizone situated above mid-whorl, flush with whorl face, ornamented regular with distinct lunulae and a median thread; selenizone bordered by two spiral cords; slit depth about 1/6 of last whorl; lower whorl face twice as wide as the upper whorl face; lower whorl face convex, ornamented with regularly spaced axial threads and 3 prominent, broad spiral cords, uppermost cord bordering selenizone; middle spiral cord strongest, representing periphery, interspace between spiral cords concave; suture slightly impressed, situated just below the lowermost spiral band; base convex, anomphalous, ornamented with axial threads and evenly spaced spiral cords of about same strength as those on upper whorl face; aperture unknown.

Remarks. The general whorl profile of *Altotomaria reticulata* sp. nov. is similar to that of species and genera of the subfamily Neilsoniinae but in *Altotomaria*, the lower edge of the selenizone does not represent the periphery and the selenizone is not raised above rest of the shell surface and as prominent as in neilsoniins. Median thread on selenizone has never been reported in Neilsoniinae. The reticulate ornament with stronger spiral cords, the relatively wide selenizone that is flush with the whorl face and bordered by two cords, the widely spaced regular lunulae that are in the same strength with the spiral ornaments, the presence of median thread on the selenizone suggest its affinity to the Triassic genera *Euryalox* Cossmann, 1897 and *Eymerella* Cossmann, 1897, therefore we tentatively place the new genus *Altotomaria* to Phymatopleuridae. The difference of the new genus from the latter two genera is the higher position of the selenizone. The position of the selenizone was regarded as informative for taxonomy and phylogeny (e.g., Knight *et al*. 1960). However, the position of the selenizone can differ among the species of the same genus (e.g., *Kokenella*, *Stuorella*) and may also change during ontogeny (e.g. *Pleurotomaria*, *Eirlysia*). *A*. *reticulata* sp. nov. resembles the neilsoniin species *Apachella exaggerata* Batten, 1989 (pl. 6, figs 3–10) from the Permian southwestern USA. Apart from the above discussed features that distinguish *Altotomaria* from the neilsoniin genera, *A*. *exaggerata* has less prominent spiral ornaments, sharper axial ornaments and differs in selenizone position.

Superfamily Seguenzioidea Verrill, 1884

Family Eucyclidae Koken, 1896

Ampezzalina Bandel, 1993

Type species. *Pleurotomaria calcar* Münster, 1841, Cassian Formation, Late Triassic, Carnian, Italy; original designation.

Ampezzalina? sp.

(Fig. 3.16)

Material. One specimen: ESKU-19-LP 36.

Dimensions (mm): ESKU-19-LP 36: height = 8.9; width = 11.7.

Description. Shell trochiform, consisting of at least 2.5 whorl (apex missing); whorl face straight to slightly convex; whorl surface ornamented with at least seven spiral cords and equally spaced opisthocyrt fine collabral threads or strengthened growth lines; intersections between spiral cords and collabral threads forming a weak reticulate pattern with tiny nodes at intersections; six of the spiral cords equally strong; suprasutural spiral cord most prominent, representing shell periphery, with several coarse broken-off hollow spines; spines open in apertural direction, rounded convex in abapertural direction; base flatly convex, ornamented with spiral cords separated by concave interspace; the five strongest spiral cords situated at outer half of base; suture situated at outermost basal cord; basal cords evenly decreasing in prominence and more closely spaced toward umbilical area; minutely phaneromphalous; aperture not well-preserved but seemingly oblique.

Remarks. The single present shell probably represents a new species, but due to the state of preservation we refrain from erecting a new species. This shell is unique in that it has a well-developed spiny cord just above abapical suture. Spine-forming cords are known from Mesozoic vetigastropods e.g., in the family Eucyclidae (e.g., *Bandelastraea* Nützel & Kaim, 2014, *Ampezzalina* Bandel, 1993). *Ampezzalina* Bandel, 1993 and *Bandelastraea* Nützel & Kaim, 2014 might represent synonyms and their type species should be restudied. The single specimen has prominent suprasutural spines similar to type species of *Ampezzalina*; therefore, placed in *Ampezzalina* instead of *Bandelastraea*. *Ampezzalina* is so far only known from the Triassic.

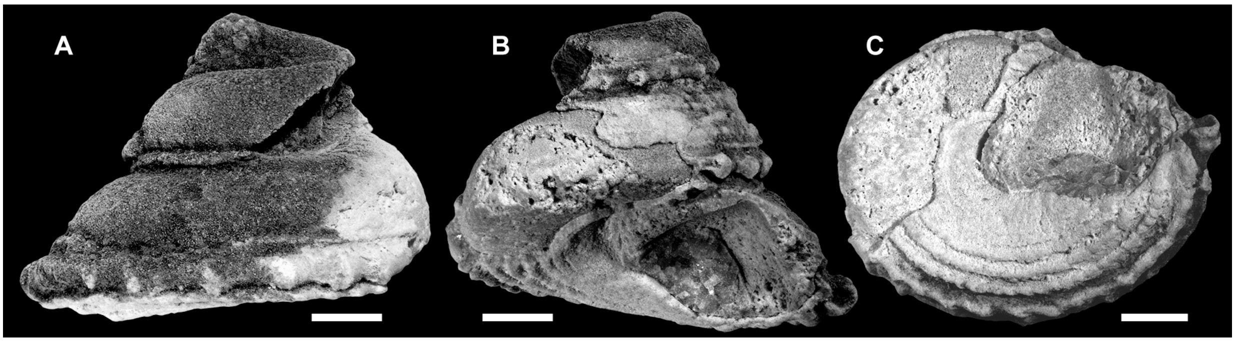

Figure 3.16: *Ampezzalina*? sp., A–C, ESKU-19-LP 36. All scale bars represent 2 mm.

It is possible that the abapical spiny spiral cord of the present specimen is a selenizone and in that case it would represent a new genus. However, the preservation is insufficient to be sure.

Order Trochida Cox & Knight, 1960

Superfamily Trochoidea Rafinesque, 1815

Family Anomphalidae Wenz, 1938

Anomphalus Meek & Worthen, 1866

Type species. *Anomphalus rotulus* Meek & Worthen, 1867, Carboniferous, USA.

Anomphalus cf. *vanescens* Yochelson, 1956

(Fig. 3.17A–E)

cf. *Anomphalus vanescens* Yochelson, 1956: 253, pl. 22, figs 19–22; Pan & Yu, 1993: 46, pl. 9, fig. 3.

Material. Three specimens: ESKU-19-LP 30, 31, 50.

Dimensions (mm): ESKU-19-LP 30: height = 4.4; width = 7.7. ESKU-19-LP 31: height = *c.* 4.1; width = 6.7. ESKU-19-LP 50: height = 3.7; width = 5.5.

Description. Shell small, low-spired, rotelliform comprising about three whorls; whorls smooth, convex. embracing at periphery; whorls ornamented by numerous fine and dense prosocline collabral threads; upper whorl face somewhat flattened with convex periphery at mid-whorl; suture shallowly impressed, distinct; base flatly convex, narrowly phaneromphalous; umbilicus deep; aperture not certainly known.

Remarks. *Anomphalus vanescens* Yochelson, 1956 from the Permian of the Southwestern USA and from the Early Permian of China (Pan & Yu 1993, p. 46, pl. 9, fig. 3) is similar but has a flatter spire, whorls embrace above periphery and whorls are lower. *A. studiosus* Yochelson, 1956 (p. 254, pl. 22, figs 25–28) is also similar in shell shape as well as the rate of whorl expansion but has smaller size, a narrower umbilicus has a flatter spire and its whorls embrace above periphery. *A. fusuiensis* Pan & Erwin, 2002 from the Late Permian of South China is also similar but has lower, more rounded whorls, a wider umbilicus and a deeper suture. The Middle Permian species *A. lateumbilicatus* Nützel & Ketwetsuriya, 2016 from the Tak Fa Limestone of Thailand has a very wide umbilicus and consists of more whorls compared to the *A.* cf. *vanescens* at comparable size. *Anomphalus* sp. which is reported from the Tak Fa Limestone is also similar but has a wider umbilicus and a flatter spire. *Anomphalus* sp. from the Permian of Malaysia as reported by Batten (1979, p. 8, figs 10–11) is higher spired. The present specimens also resemble *A. japonicus* Nützel *in* Nützel & Nakazawa, 2012 from the Middle Permian of Japan but the latter has a wider umbilicus and a small umbilical ridge. The present species is probably undescribed but the preservation of the material is too poor for a safe species assignment, especially the aperture and the collabral threads is hardly visible in the studied specimens.

Anomphalus? *blancus* Kues & Batten, 2001
(Fig. 3.17F–L)

Anomphalus? *blancus* Kues & Batten, 2001: 44, figs 8.23–8.28.

Material. Two specimens: ESKU-19-LP 67, 96.
Dimensions (mm): ESKU-19-LP 67: height = 2.5; width = 3.0; apical angle = 124°. ESKU-19-LP 96: height = 2.3; width = 2.6; apical angle = 125°.

Description. Shell small, low-spired but spire clearly elevated, last whorl much higher than spire, turbiniform to naticiform, consisting of two to four whorls; whorls smooth, rounded, convex; whorls embrace at or slightly below periphery at mid-whorl; suture shallow but distinct; aperture somewhat circular, columellar lip straight to gently arched joining outer lip; base convex, minutely phaneromphalous.

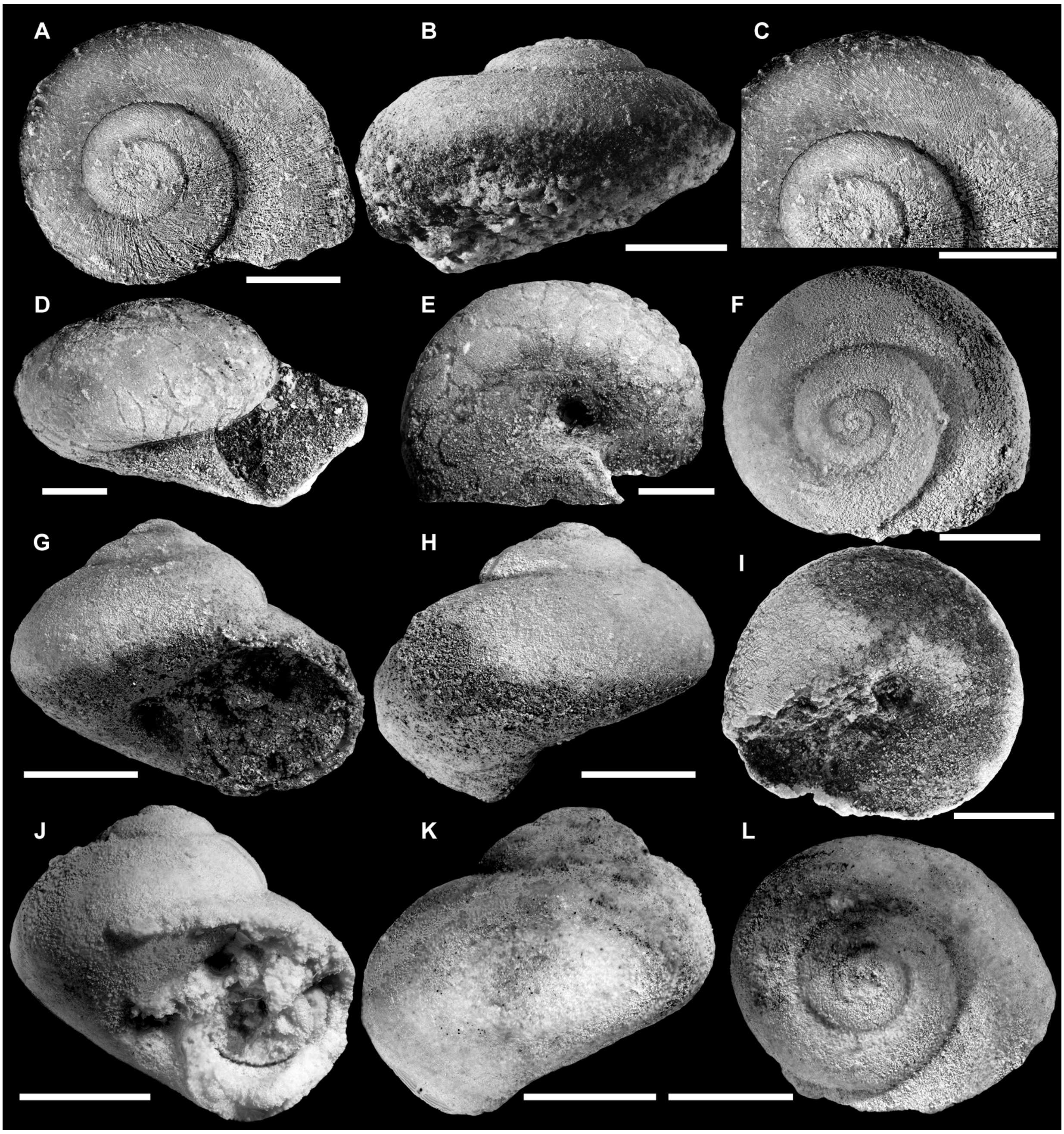

Figure 3.17: A–E, *Anomphalus* cf. *vanescens* Yochelson, 1956, A–C, ESKU-19-LP 30. D–E, ESKU-19-LP 50. F–L, *Anomphalus*? *blancus* Kues & Batten, 2001, F–I, ESKU-19-LP 67. J–L, ESKU-19-LP 96. Scale bars represent: 2 mm (A–C); 1 mm (D–L).

Remarks. These specimens are very similar to the illustrations of *Anomphalus*? *blancus* Kues & Batten, 2001 (p. 44, fig. 8.23–8.28) from the Middle Pennsylvanian of New Mexico in shell shape and the whorl expansion rate. Kues & Batten (2001) assigned *A.*? *blancus* questionably to the genus *Anomphalus* due to its higher spired and more inflated shell which differs from typical species of *Anomphalus* in these respects that have low-spired or planispiral shells. The studied specimens also resemble the specimens assigned to *Anomphalus* sp. from the Permian of Malaysia by Batten (1979, p. 8, figs 10–11). However, the present specimens are more high-spired. Batten (1979) and Kues & Batten (2001) discussed that their specimens closely resemble the genus *Turbinilopsis* in shell shape and proportions of the shell, but *Turbinilopsis* is distinguished in having an obvious callus within the umbilicus. Other species of *Turbinilopsis* which have been reported from the Permian of Southeast Asia differ distinctly from the present material. *T. rotundus* Delpey, 1941 (p. 276, fig. 18) from Cambodia (see also Batten 1979) has a much more straight whorl face and a blunt apex. The specimens assigned to *Turbinilopsis*? sp. by Mansuy (1914, pl. 4, fig. 11) have a lower spire and hence a greater apical angle. The present specimens are placed tentatively in the genus *Anomphalus.* They are rather high-spired for this genus and hence become similar to the genus *Anematina* which generally is even more high-spired.

Family Araeonematidae Nützel *in* Nützel & Nakazawa, 2012

Remarks. *Yunnania*, *Araeonema* and *Rhabdotocochlis* were previously placed in Gyronematidae by Knight *et al*. (1960) but were placed in Araeonematidae by Nützel (2012) because these genera lack angulations.

Yunnania Mansuy, 1912
Type species. *Yunnania termieri* Mansuy, 1912, Late Carboniferous, China.

Yunnania inflata sp. nov.
(Fig. 3.18A–J)

Etymology. From Latin inflata, for having *swollen, inflated whorl.*
Holotype. ESKU-19-LP 9.
Paratypes. ESKU-19-LP 8, 16, 21, 38, 65, 98, two juvenile specimens: ESKU-19-LP 205, 212.
Dimensions (mm): ESKU-19-LP 8: height = 4.3; width = 3.9; apical angle = 87^{O}. ESKU-19-LP 9: height = 5.0; width = 4.1; apical angle = 85^{O}. ESKU-19-LP 16: height = 3.2; width = 2.8; apical angle = 80^{O}. ESKU-19-LP 21: height = 8.9; width = 5.6; apical angle = 75^{O}. ESKU-19-LP 38: height = 4.9; width = 3.9; apical angle = 87^{O}. ESKU-19-LP 65: height = 5.4; width = 4.9; apical angle = 85^{O}. ESKU-19-LP 98: height = 4.5; width = 4.6; apical angle = 87^{O}. ESKU-19-LP 205: height = *c*. 1.9; width = *c*. 1.9; apical angle = 90^{O}. ESKU-19-LP 212: height = *c*. 1.8; width = *c*. 1.9; apical angle = 96^{O}.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell small, turbiniform, cyrtoconoid with strong reticulate ornament; holotype comprising *c*. 5 whorls; first three to four whorls slightly convex, evenly rounded and low-spired, dome-shaped, without ornament or ornamented by very faint spiral threads; later whorls distinctly convex and inflated; periphery at about mid-whorl; suture impressed; whorls convex, embracing at about mid-whorl, slightly below periphery; whorls ornamented with about 10 evenly spaced spiral cords and numerous weaker collabral axial ribs; axial ribs proscline slightly prosocyrt; spiral cords and axial ribs forming reticulate ornament with slightly nodular intersections; nodes strongest near upper suture; base convex with evenly rounded transition to whorl face, ornamented with up to 10 strong equally spaced spiral cords; base convex, anomphalous; aperture approximately circular; columellar lip straight.

Remarks. *Yunnania inflata* sp. nov. closely resembles *Yunnania meridionalis* Mansuy, 1914 (p. 41, pl. 4, fig. 10a–c) from the Permian Productus Limestone of Cambodia in shell shape, size and ornament on whorl face and base but *Y. meridionalis* has a deeper suture, its spiral cords are more pronounced and the axial ribs are less pronounced and less numerous *Y. meridionalis* has also been reported from another Permian deposits of Cambodia by Delpey (1941) and from the Permian of Malaysia (Batten 1979). *Y. inflata* sp. nov. also resembles *Y. pulchra* Nützel & Ketwetsuriya, 2016 from the Middle Permian of the Tak Fa Limestone from Thailand (Ketwetsuriya *et al*. 2016, p. 499, fig. 16A–H) in shell shape and ornamentation but *Y. pulchra* has fewer but stronger spiral cords, the axial ribbing is denser, axial ribs are sharper, it has more convex and inflated whorls as well as the axial ribs of *Y. pulchra* are more distinct, dense and thinner. *Y. inflata* sp. nov. has much more inflated whorls than *Y. meridionalis* and *Y. pulchra. Y. inflata* sp. nov., improves our knowledge on the distribution of Yunnania in this region of the Indochina Terrane.

Araeonema Knight, 1933*a*
Type species. *Araeonema virgatum* Knight, 1933*a*, Pennsylvanian, USA.

Araeonema cf. *tenuistriata* (Netchaev, 1894)
(Fig. 3.18K)

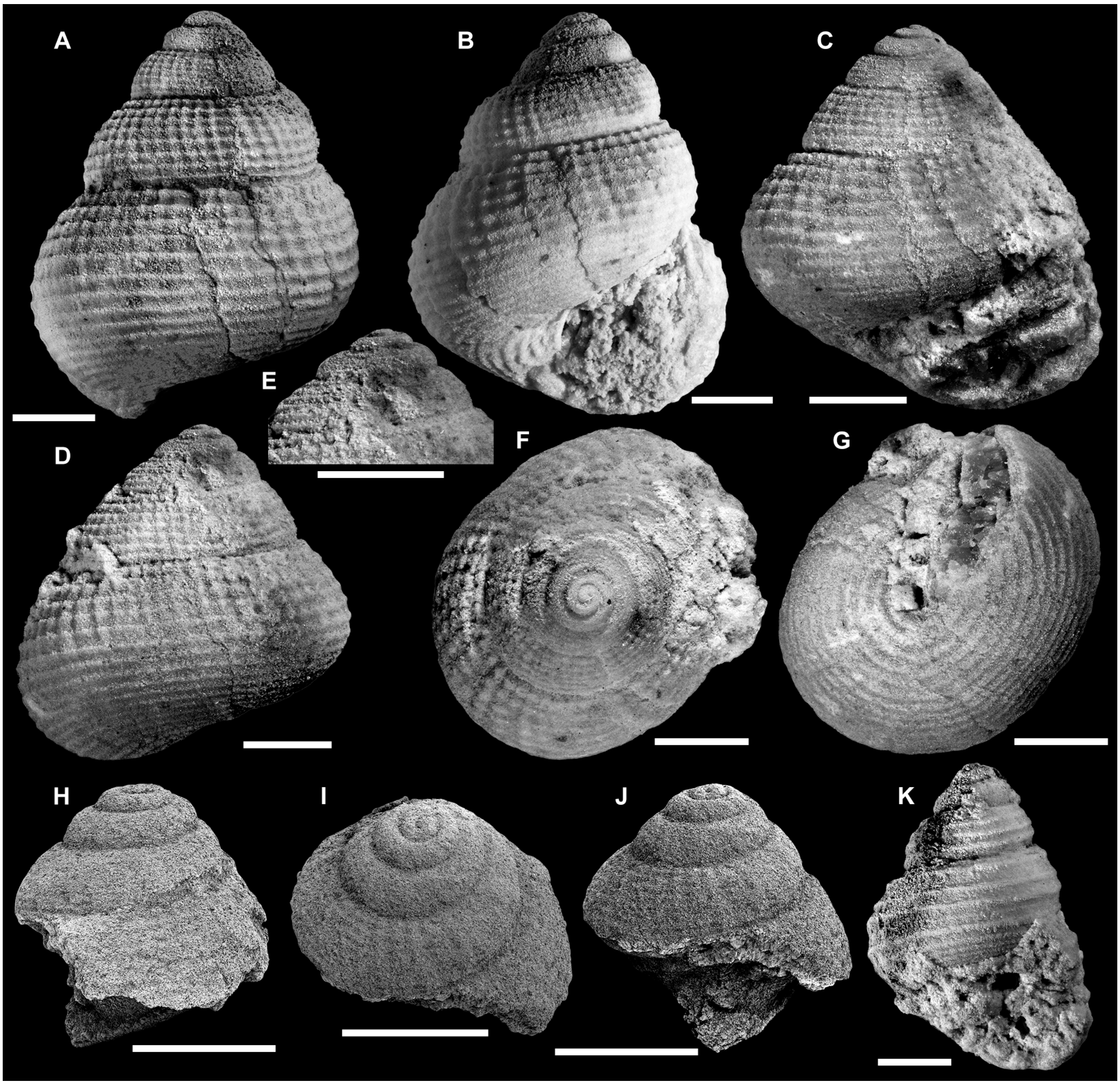

Figure 3.18: A–J, *Yunnania inflata* sp. nov. A–B, ESKU-19-LP 9, holotype; C–G, ESKU-19-LP 65, paratype. H–J, juvenile specimens, H–I, ESKU-19-LP 205. J, ESKU-19-LP 215. K, *Araeonema* cf. *tenuistriata* (Netchaev, 1894), ESKU-19-LP 99. All scale bars represent 1 mm.

cf. *Turbo tenuistriata* Netchaev, 1894; 349, pl. 11, fig 17.

cf. *Araeonema tenuistriata* (Netchaev, 1894); Mazaev 2015: 954, pl. 31, figs 1–8.

Material. One specimen: ESKU-19-LP 99.

Dimensions (mm): ESKU-19-LP 99: height = 4.2; width = 2.9; apical angle = 80^{O}.

Description. Shell small, turbiniform; blunt apex; whorls weakly convex, evenly rounded; whorls ornamented by 4 strong spiral cords, and fifth emerging at abapical suture; spiral cords equally spaced with concave interspaces; base convex with rounded transition to whorl face, bordered by a strong spiral cord; base ornamented with 12 narrowly spaced spiral cords; sutures deep, distinct; aperture seemingly circular.

Remarks. The single specimen at hand closely resembles *Araeonema tenuistriata* (Netchaev, 1894) as reported by Mazaev (2015, p. 954, pl. 31, figs 1–8) from the Middle Permian of the Volga-Ural Region, Russia in shell shape, size and principal ornamentation. However, *A. tenuistriata* has a broader shell, more and weaker spiral cords and more convex whorls. *A. tenuistriata* is narrowly phaneromphalous but the umbilical area is not visible in the specimen at hand. *A. tenuistriata* is similar to *A. panthalassica* Nützel *in* Nützel & Nakazawa, 2012 from the Upper Middle Permian Akasaka Limestone, Japan but *A. panthalassica* is smaller, weaker spiral cords and a flatter apex. *A. virgatum* Knight, 1933*a* (p. 52, pl. 9, fig. 3) from the Pennsylvanian of the Labette Shale, Missouri, USA has more and much finer spiral cords and its whorl are less convex. Both, *A. novamexicanum* Kues, 2004 from the Laborcita Formation, New Mexico and *A. microspirulata* Yoo, 1994 from the Early Carboniferous of Australia are similar to the present specimen but those species are broader and have very fine and many more spiral cords. *A. problematicum* Wang *in* Wang & Xi, 1980 from the Permian of China is similar in shell shape but the ornamentation cannot be compared meaningfully because of its poor preservation. *A.* cf. *tenuistriata* resemble *Amaurotoma*? sp. as illustrated by Ketwetsuriya *et al.* (2016, p. 494, fig. 12A–C) from the Middle Permian Tak Fa Limestone, Thailand in having strong spiral cords, but differs in having a higher spire, steeper ramp and an angulated whorl profile. This is the first species which is referred to the genus *Araeonema* from Thailand and Southeast Asia.

Family Microdomatidae Wenz, 1938

Microdoma Meek & Worthen, 1867
Type species. *Microdoma conicum* Meek & Worthen, 1867, Pennsylvanian, USA.

Microdoma conicum Meek & Worthen, 1867
(Fig. 3.19A–C)

Microdoma conicum Meek & Worthen, 1867: 269, pl. 9, fig. 1; Knight 1933*a*: 48–49, pl. 9, fig. 1; Batten 1995: 25, fig. 34.

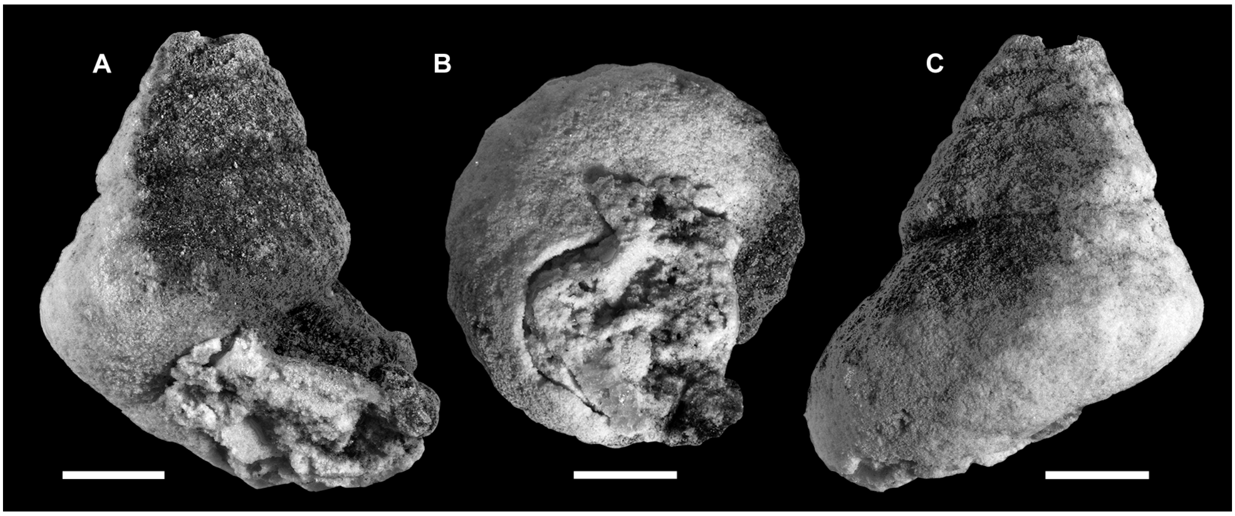

Figure 3.19: A–C, *Microdoma conicum* Meek & Worthen, 1867, ESKU-19-LP 69. All scale bars represent 1 mm.

Material. One specimen: ESKU-19-LP 69.

Dimensions (mm): ESKU-19-LP 69: height = 4.5; width = 3.9.

Description. Shell conical, turbiniform consisting of *c*. 3 whorls (apex and early teleoconch whorls missing); whorl face nearly straight to slightly convex; periphery low on whorl just above suture; whorls ornamented by several collabral ribs which are separated in three rows of coarse nodes by two spiral grooves; suture shallow; base rounded and convex without ornament; seemingly minutely phaneromphalous; aperture sub-oval.

Remarks. The present material is very close to *Microdoma conicum* Meek & Worthen, 1867 as illustrated by Knight (1933*a*) from the Pennsylvanian of Missouri and by Batten (1995) from the Pennsylvanian of Texas, USA. The feature of ornamentation in the later whorls is identical with this species, although the present material lacks the early whorls. This species has been known only from the Pennsylvanian of USA. This is the first report of this species in the Palaeo-Tethys.

Subclass Neritimorpha Koken, 1896

Superfamily Naticopsoidea Waagen, 1880

Family Naticopsidae Waagen, 1880

Subfamily Naticopsinae Waagen, 1880

Naticopsis McCoy, 1844

Type species. *Naticopsis philippsii* McCoy, 1844, Early Carboniferous, Ireland.

Naticopsis sp. 1
(Fig. 3.20A–C)

Material. One specimen: ESKU-19-LP 47.
Dimensions (mm): ESKU-19-LP 47: height = *c*. 8.3; width = 11.3; apical angle = 115^{O}.

Remarks. The present specimen at hand shows 3 teleoconch whorls that are inflated and rapidly increasing. The shell is low-spired. Whorls are convex and the whorl profile is quite elongated. The surface of whorls is smooth. The suture is impressed and embraces the upper whorl surface. The aperture is broken, but it seems to be ovate with distinctly thickened callus on the parietal area. Judging from a single shell exhibiting the spire and half of the last body-whorl, the whorl profile of the studied specimen is similar to *Naticopsis khurensis* Waagen, 1880 (p. 100, pl. 9, fig. 10) from the Permian of Pakistan (Salt Range) but the latter differs in the absence of a callus. In contrast to the type specimen, the specimens illustrated and described as *N. khurensis* by Batten (1979, p. 13, fig. 15) from the Permian of Perak, Malaysia exhibits a callus. Nevertheless, the present specimen differs from the Malaysian specimen in having a more swollen upper whorl surface of the body-whorl. The specimens identified as *Neritina khurensis* by Delpey (1941, p. 271, fig. 13) from the Permian of Cambodia has a lower spire and its upper whorl surface is less inflated. Batten (1979) discussed that the degree of whorl curvature is highly variable in *N. khurensis*, so we cannot completely rule out the possibility that the studied specimen is conspecific to *Naticopsis khurensis*.

Naticopsis sp. 2
(Fig. 3.20D–F)

Material. One specimen: ESKU-19-LP 46.
Dimensions (mm): ESKU-19-LP 46: height = 9.3; width = 10.3; apical angle = 112^{O}; apertural height = 7.5; apertural width = 7.7.

Description. Moderately low-spired shell, naticiform, consisting of three rapidly expanding whorls; whorls smooth, strongly convex, rounded, embracing at periphery; spire low but distinctly elevated; body-whorl inflated, very large and much higher than spire with height about 90% of total height; periphery at about mid-whorl; base convex; suture shallow but impressed; anomphalous; aperture evenly rounded in cross section, lip thin, inner lip arched.

Remarks. *Naticopsis* sp. 2 differs from *Naticopsis* sp. 1 in having more flattened upper whorl surface, lacking callus, having a higher whorl expansion rate and a rounded aperture. It resembles *Naticopsis subovata* Worthen *in* Meek & Worthen (1873) as illustrated by Knight (1933*b*, p. 379, pl. 43, fig. 2a–j) in size, shell shape and pleural angle. *N. wortheni* Knight, 1933*b* (p. 377, pl. 43, fig. 3a–k) is also similar. Knight (1933*b*) mentioned that these two species, *N. subovata* and *N. wortheni,* are very close to each other but *N. subovata* can be differentiated from *N. wortheni* in having a swelling just above the mid-whorl height, and by the shape of the columellar lip, which is evenly crescent-shaped in *N. subovata* while it is slightly angled in *N. wortheni*. Although the parietal area of the present specimen is obscure it seems closer to *N. subovata*. The present specimen is also similar to the specimens illustrated and described as *N. praealta* Wanner, 1922 by Batten (1979; p. 14, fig. 16a–b) from the Permian of Perak, Malaysia but the latter specimens are more slender and relatively high-spired.

Naticopsis? sp. 3
(Fig. 3.20G–I)

Material. One specimen: ESKU-19-LP 32.
Dimensions (mm): ESKU-19-LP 32: height = 5.3; width = 7.8; apical angle = 108^{O}.

Description. Shell flatly turbiniform to naticiform with about three whorls (apex missing); spire elevated; rate of whorl expansion rapidly increasing; body-whorl broad, approximately 70% of the entire height; whorls rounded, strongly convex, with undulating, irregular axial ribs; base rounded; aperture unknown.

Remarks. The undulating, irregular axial ribs on the whorl surface and the broader body-whorl distinguish *Naticopsis* sp. 3 from the others present in this fauna. It might represent a new species, but the poor preservation prevents a further taxonomic assignment.

Naticopsis? sp. 4
(Fig. 3.20J)

Material. One specimen: ESKU-19-LP 52.
Dimensions (mm): ESKU-19-LP 52: height = 6.0; width = 8.0; apical angle = 126^{O}; apertural height = 4.2; apertural width = 5.2.

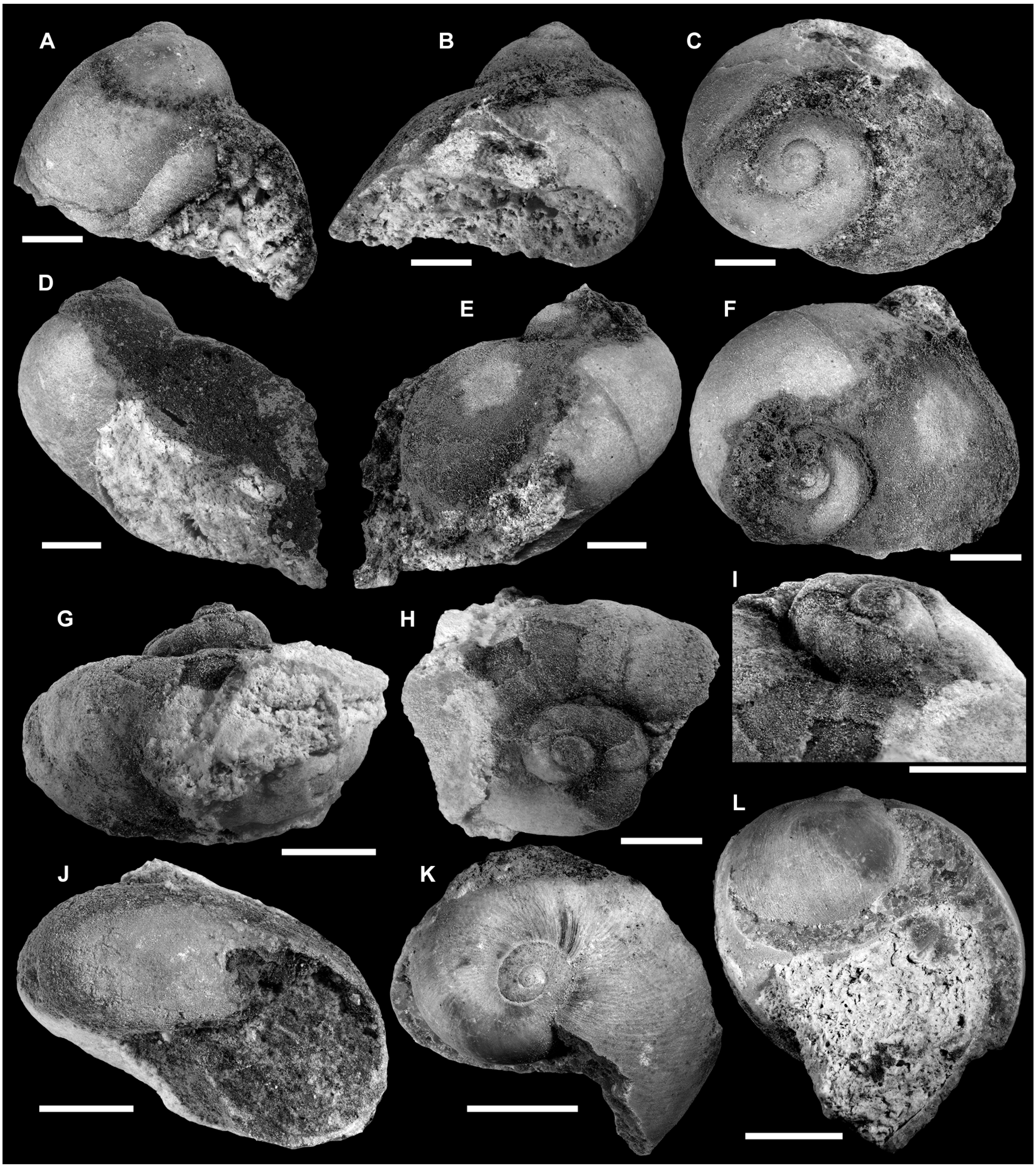

Figure 3.20: A–C, *Naticopsis* sp. 1, ESKU-19-LP 47. D–F, *Naticopsis* sp. 2, ESKU-19-LP 46. G–I, *Naticopsis*? sp. 3, ESKU-19-LP 32. J, *Naticopsis*? sp. 4, ESKU-19-LP 52. K–L, *Naticopsis* cf. *heshanensis* Pan & Erwin, 2002, ESKU-19-LP 44. Scale bars represent: 2 mm (A–J); 5 mm (K–L).

Remarks. The present specimen is low-spired with the spire only somewhat protruding, consisting of three smooth rapidly increasing whorls. The body-whorl is very inflated, the height of the last whorl is about 90% of the total shell height. The aperture is broad with a thick inductura and seems to develop a columellar fold which has never been observed in *Naticopsis*. However, the preservation of the aperture is insufficient to be sure that a fold is really present.

Naticopsis cf. *heshanensis* Pan & Erwin, 2002
(Fig. 3.20K–L)

cf. *Naticopsis* (*Naticopsis*) *heshanensis* Pan & Erwin, 2002: 21, fig. 11.12–11.17.

Material. One specimen: ESKU-19-LP 44.
Dimensions (mm): ESKU-19-LP 44: height = 19.0; width = 16.2; apical angle = 124°.

Description. Subglobose shell, very low-spired, medium-sized, comprising *c*. 3.5 whorls; apex obtuse; whorls rapidly increasing; body-whorl large and inflated, with flatly convex periphery; whorls embracing on preceding whorl, well above periphery; whorl surface with numerous fine, prosocyrt, distinct growth lines; suture adpressed; base convex; aperture unknown.

Remarks. This single globose shell with distinct, dense growth-lines resembles *Naticopsis* (*Naticopsis*) *heshanensis* Pan & Erwin, 2002 (p. 21, fig. 11.12–11.17) as reported from the Permian of Guangxi Provinces, South China, although the present specimen has a much lower spire than the holotype of *N.* (*N.*) *heshanensis*. The Permian species *N. permica* Netchaev, 1894 as illustrated by Mazaev (2015, p. 959, pl. 33, figs 1–5) from the Middle Permian of Volga Region, Russia is similar but has a higher spire, more convex whorls and less distinct growth lines.

Family Trachyspiridae Nützel, Frýda, Yancey & Anderson, 2007

Trachydomia Meek & Worthen, 1866
Type species. *Naticopsis nodosa* Meek & Worthen, 1860, Carboniferous, USA.

Trachydomia suwanneeae sp. nov.
(Fig. 3.21A–D)

Etymology. In honor of Suwannee Phomprasith for her work in biodiversity in Thailand.
Holotype. ESKU-19-LP 26.
Paratypes. ESKU-19-LP 27, 94.
Dimensions (mm): ESKU-19-LP 26: height = 12.1; width = 9.2; apical angle = 82°. ESKU-19-LP 27: height = 6.4; width = 5.7. ESKU-19-LP 94: height = 5.4; width = 4.2.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell naticiform to turbiniform; spire acute; whorls round, convex; body whorl distinctly higher than spire; whorls ornamented with distinct small nodes which are especially well-developed on the body whorl and weak or absent on the earliest preserved whorls; nodes roughly arranged in opistocline arranged nodes; distance between nodes exceeds diameter of nodes; suture distinct; whorls convex with periphery at mid-whorl of body whorl but below mid-whorl of whorl face of spire whorls, with narrow subsutural ramp; base convex with gradually embracing of body whorl at transition below the periphery; aperture unknown; anomphalous.

Remarks. Based on the shell characters of the studied specimens such as having a naticiform shell and pustules on whorl face, the present material represents undoubtedly the genus *Trachydomia*. *Trachydomia suwanneeae* sp. nov. resembles most closely *T. dussaulti* Mansuy, 1913*a* (p. 101, pl. 11, fig. 5a–b) from the Permian Productus Limestone of Laos in shape and ornaments that was also reported by Batten (1979, p. 17, fig. 20) from the Permian of Perak, Malaysia and by Delpey (1941, p. 268, fig. 10) from the Permian of Cambodia. However, *T. dussaulti* is not as high-spired and hence its spire is not as acute. *T. dussaulti* has more nodes and the nodes are more densely spaced. The specimen illustrated as *T. dussaulti* Mansuy, 1913*a* by Delpey (1941) has a more distinctly inflated body whorl, a blunter spire and finer nodes, whereas the specimens assigned to *T. nodusum* (Meek & Worthen, 1866) by Delpey (1941, p. 268, fig. 9) is more similar to the present specimens in having an acute spire and a rather elongated shape. Knight (1933*b*) has reported several specimens of *T. nodusum* from the Pennsylvanian, USA (from which this species was originally described) differs distinctly from the studied specimens in having a lower spire, a broader and more pronounced ramp, stronger and coarser nodes and more inflated body whorl. *T. suwanneeae* sp. nov. also resembles *T. whitei* Knight, 1933*b*, both in having small and widely spaced nodes and a similar whorl profile but *T. whitei* differs from *T. suwanneeae* sp. nov. by its wider, more pronounced subsutural ramp, by being broader and by having stronger nodes. *T. suwanneeae* sp. nov. is also similar to *T. takhliensis* Nützel & Ketwetsuriya, 2016 (Ketwetsuriya *et al*. 2016, p. 502, fig. 19J–M) from the Middle Permian of the Tak Fa Limestone, Thailand. However, the shell of *T. takhliensis* is broader, its spire is less acute and it has more inflated body whorl. *T. takhliensis* has more densely spaced, somewhat coarser and more protruded nodes and a more pronounced ramp.

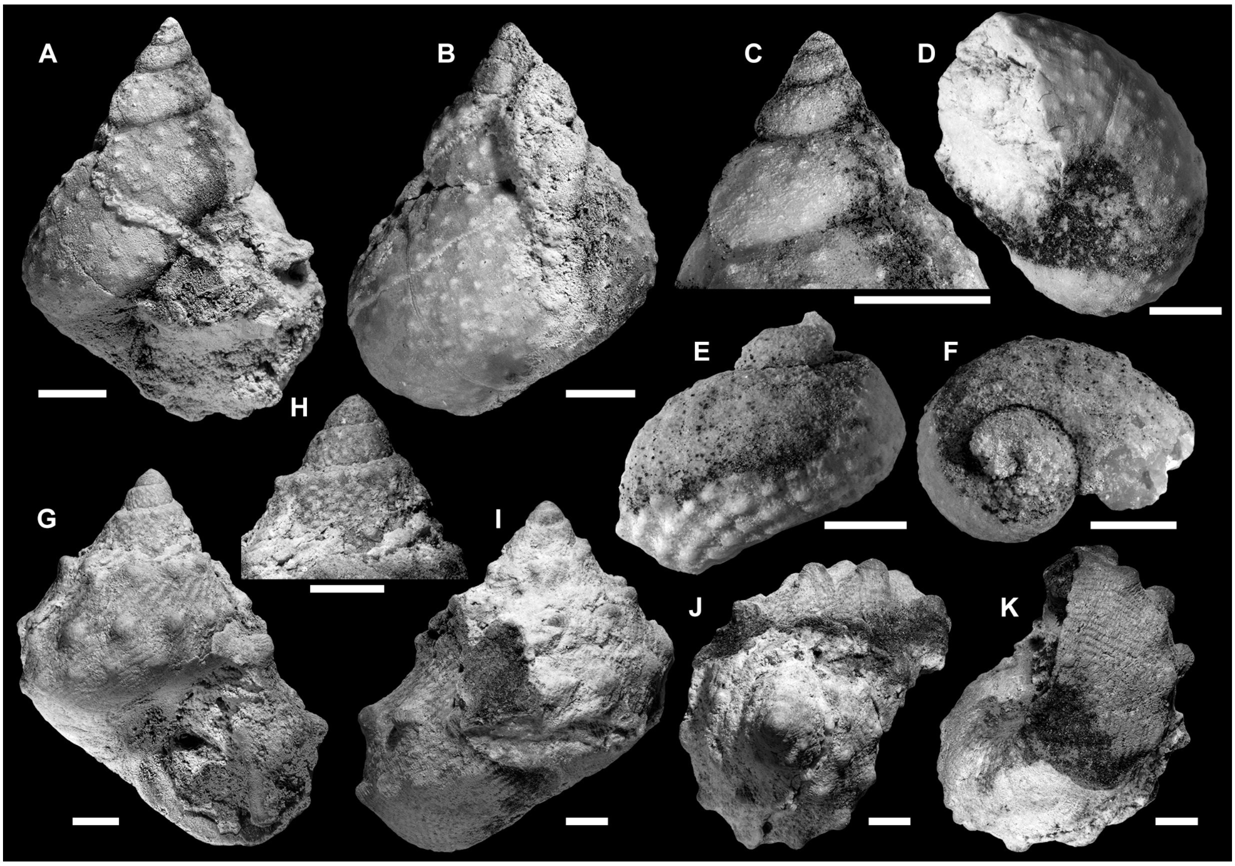

Figure 3.21: A–D, *Trachydomia suwanneeae* sp. nov., ESKU-19-LP 26, holotype. E–F, *Trachydomia* cf. *nodusum* (Meek & Worthen, 1866), ESKU-19-LP 92. G–K, *Trachyspira eleganta* sp. nov., ESKU-19-LP 28, holotype. Scale bars represent: 2 mm (A–D, G–K); 1 mm (E–F).

Trachydomia cf. *nodosum* (Meek & Worthen, 1866)
(Fig. 3.21E–F)

cf. *Trachydomia nodosum* (Meek & Worthen, 1866); Knight 1933: 383, pl. 45, fig. 2a–i.

Material. One specimen: ESKU-19-LP 92.
Dimensions (mm): ESKU-19-LP 92: height = *c*. 2.9; width = 3.2.

Remarks. The single specimen at hand represents has the general characteristics of the genus *Trachydomia*. It is naticiform, ornamented with distinct nodes on whorl face and has a rather deep suture. It seems to resemble *Trachydomia nodusum* (Meek & Worthen, 1866) as illustrated by Knight (1933*b*) from the Pennsylvanian of the U.S.A. This specimen can be differentiated from *T*. cf. *dussaulti* as described above in having coarser and denser nodes, an impressed suture, a subsutural ramp and a distinctly broader body whorl. The present specimen is too poorly preserved for a safe identification.

Trachyspira Gemmellaro, 1889

Type species. *Trachyspira delphinuloides* Gemmellaro, 1889, Permian, Italy; subsequent designation by Cossmann 1916.

Trachyspira eleganta sp. nov.

(Fig. 3.21G–K)

Etymology. From Latin, meaning elegant, beautiful.

Holotype. Only one specimen ESKU-19-LP 28.

Dimensions (mm): ESKU-19-LP 28: height = 17.6; width = 13.3; apical angle = 75°.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Medium-size, moderately high-spired shell, conical , subturbiniform, consisting of approximately 5 whorls; apex acute, spire angle 75°; body whorl height about 80 percent of the total height; suture adpressed; earliest two whorls without visible ornament (preservation?), convex; following whorl with fine pustules and narrow shoulder; last two preserved whorls ornamented with two categories of nodes, large nodes arranged in spiral rows and fine, densely spaced nodes arranged in opisthocline rows tending to fuse to opisthocline ribs; body whorl with three rows of nodes,10–14 nodes per row; uppermost nodular row near adapical suture, forming edge of narrow ramp; middle row of nodes strongest, situated near abapical suture; third row with weakest nodes, situated on base; whorl angulated at nodular rows; whorl face concave between nodular rows; base rounded, anomphalous, ornamented with numerous spiral cords consisting of small pustules representing continuations of opisthocline rows on whorl face; aperture acute adapically, outer and anterior lip evenly rounded.

Remarks. This single specimen at hand is assigned to the genus *Trachyspira* Gemmellaro, 1889 which is characterized by having two different size-categories of nodes: numerous small pustules, aligned in opisthocline rows and few large nodes arranged in spiral rows (Knight *et al.* 1960). It is the first report of this genus from Thailand.

Trachyspira eleganta sp. nov. from the Khao Khad Limestone resembles the specimens illustrated and described as *T. obliquinodula* Wang, 1982 by Pan & Erwin (2002) from the

Permian of Guangxi and Yunnan Provinces, South China. The type material of this species as illustrated by Wang (1982) is poorly preserved and not well-documented. However, these specimens as well as those illustrated by Pan & Erwin (2002) are much broader and stouter and hence have a larger apical angle (> 90°) and the nodules are much coarser.

The type species *T. delphinuloides* Gemmellaro, 1889 as illustrated by Batten (1979, p. 21, figs 29–31) from North Africa and Malaysia is also similar to *T. eleganta* sp. nov. in having three principal rows of nodes with the second row dominant but Batten's (1979) specimen have a larger apical angle and the second order pustules are larger in the African specimen. However, the original illustration of *T. delphinuloides* given by Gemmellaro (1889) shows a specimen with relatively small first order nodules that are spirally elongated. Knight (1941, pl. 56) figured a specimen form the type series that differs considerably from Gemmellaro's (1889) figure. Nevertheless, Knight (1941) identified this specimen as possible holotype. This specimen (probably the one used for the drawing in the Treatise, Knight et al. 1960, fig. 182/6) differs from our specimen in having a broader ramp, finer second order and stronger first order nodes, especially the adapical ones. *T. heshanensis* Pan & Erwin, 2002 (p. 25, fig. 12.11–12.14) from the Late Permian of China has a larger apical angle (close to 90°), the first order nodes are weaker at comparable growth stages and it lacks a third row of first order nodes on the base. *T. quangxiensis* Pan & Erwin, 2002 (p. 25, fig. 12.9–12.10) from the Late Permian of China has more convex whorls, a wider ramp and three instead of two rows of first order nodes on the whorl face.

Subclass Caenogastropoda Cox *in* Knight *et al.*, 1960
Superfamily Soleniscoidea Knight, 1931*a*
Family Soleniscidae Knight, 1931*a*
Subfamily Soleniscinae Knight, 1931*a*

Strobeus de Koninck, 1881
Type species. *Strobeus ventricosus* de Koninck, 1881, Mississippian, Belgium.

Strobeus? sp. 1
(Fig. 3.22A–C)

Material. Two specimens: ESKU-19-LP 49, 90.

Dimensions (mm): ESKU-19-LP 49: height = *c*. 10.4; width = *c*. 10.9; apical angle = 90^{O}. ESKU-19-LP 90: height = 6.5; width = 5.9; apical angle = 82^{O}.

Description. Subglobose, broad, low-spired shell with elevated, acute spire; approximately four whorls; whorl embracing above periphery; whorls smooth; spire-whorls very slightly convex; periphery convex. Rounded; body-whorl very inflated, strongly convex, rounded; suture shallow; base evenly rounded, inductura seemingly thick; aperture acute adapically, broken abapically.

Remarks. The incomplete specimens resemble *Strobeus welleri* Knight, 1931*a* (p. 219, pl. 23, fig. 1) from the Desmoinesian (Pennsylvanian) Labette Shale of Missouri, USA. This species has also been reported from the Permian of Cambodia (Delpey, 1941; p. 61, fig. 54), the Middle Pennsylvanian of New Mexico (Kues & Batten, 2001; p. 85, fig. 16.30) and the Permian of Mexico (Sour-Tovar *et al*. 2005). The present specimens also resemble several other Late species representing *Strobeus* but it more low-spired than most of them. However, the broken aperture prevents an identification; presence or absence of columellar folds are important characters that cannot be seen in the present material.

Strobeus? sp. 2
(Fig. 3.22D–E)

Material. Two specimens: ESKU-19-LP 217, 220.
Dimensions (mm): ESKU-19-LP 217: height = 1.4; width = 1.0; apical angle = 76^{O}. ESKU-19-LP 220: height = 1.3; width = 1.0; apical angle = 78^{O}.

Description. Shell fusiform, distinctly higher than wide with about three whorls (apex missing); periphery evenly rounded, convex; whorls embracing at or slightly above periphery; spire whorls slightly convex; whorls smooth; body-whorl inflated; suture shallow; base rounded, convex; anomphalous; aperture unknown.

Remarks. The two specimens resemble *Strobeus dongluoensis* (Pan & Yu, 1993) from the Upper Permian Changxing Formation, China (see also Pan & Erwin 2002; Nützel & Nakazawa 2012). The identification of the present specimens remains doubtful due to insufficient preservation.

Family Meekospiridae Knight, 1956

Girtyspira Knight, 1936

Type species. *Bulimella canaliculata* Hall, 1856, Carboniferous, USA.

Girtyspira? sp.

(Fig. 3.22F)

Material. One specimen: ESKU-19-LP 222.

Dimensions (mm): ESKU-19-LP 222: height = *c*. 1.0; width = 0.6.

Remarks. This very small single specimen is smooth and has slightly convex whorl with blunt apex and possess triangular-shaped aperture. It resembles *Girtyspira yodai* Erwin, 1988 from the Permian Cathedral Mountains Formation of West Texas. However, *Girtyspira yodai* species has much more slender shell and impressed suture.

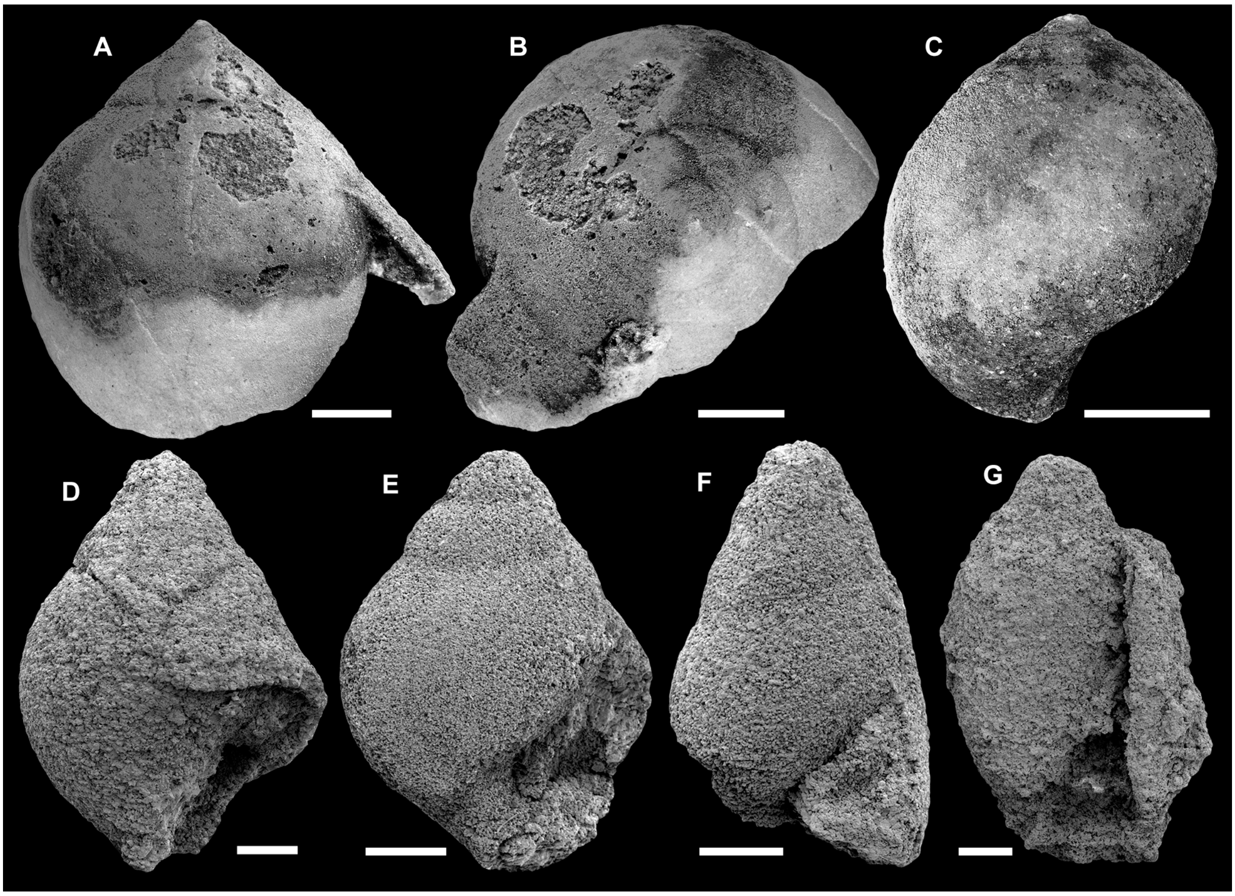

Figure 3.22: A–C, *Strobeus*? sp. 1, A–B, ESKU-19-LP 49. C, ESKU-19-LP 90. D–E, *Strobeus*? sp. 2, D, ESKU-19-LP 217. E, ESKU-19-LP 220. F, *Girtyspira*? sp., ESKU-19-LP 222. G, *Heterosubulites longusapertura* sp. nov. ESKU-19-LP 215, holotype. Scale bars represent: 2 mm (A–C); 200 μm (D–G).

Heterosubulites Bandel, 2002*a*

Type species. *Ceraunocochlis blatta* Knight, 1931*a*, Pennsylvanian, USA.

Heterosubulites longusapertura sp. nov.

(Fig. 3.22G)

Etymology. Latin, because of the long-shape aperture.

Holotype. Only one specimen: ESKU-19-LP 215.

Dimensions (mm): ESKU-19-LP 215: height = 1.6; width = 0.9; apical angle = 82^{O}.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell very small, fusiform; whorls smooth; whorls embracing high on the whorls; whorls evenly convex with periphery above mid-whorl; spire whorls only slightly convex; spire small, blunt, rounded; body-whorl inflated, much higher than spire with height about 90% of total height; sutures indistinct; base flat; aperture elongated, narrow, with wide and short anterior siphonal canal; outer lip almost straight.

Remarks. *Heterosubulites longusapertura* sp. nov. is very close to the type species *H. blatta* (Knight, 1931*a*, p. 203–204, pl. 21, fig. 2a–d) (see also Bandel 2002*a*) from the Pennsylvanian of Missouri, USA in shape, size and shell proportions, but *H. longusapertura* n. sp. differs from *H. blatta* having a narrower aperture, a much broader anterior siphonal canal and a much more arched outer lip. *H. fusiformis* Nützel, 2012 from the Middle Permian Akasaka Limestone, Japan is also similar but its shell is larger, the shell is more slender, whorls embrace lower on preceding whorl, its aperture is wider and its anterior siphonal canal is narrower.

Superfamily Palaeostyloidea Wenz, 1938

Family Pithodeidae Wenz, 1938

Platyzona Knight, 1945

Type species. *Platyzona trilineata* (Hall, 1856), Carboniferous, USA.

Remarks. Nützel *in* Nützel & Nakazawa (2012) placed *Platyzona* in Caenogastropoda because Pan & Erwin (2002) reported the presence of caenogastropod larval shell of this genus from the latest Permian of South China.

Platyzona gradata sp. nov.
(Fig. 3.23)

Etymology. From Latin gradata, because of the gradate spire.
Holotype. Only one specimen: ESKU-19-LP 11.
Dimensions (mm): ESKU-19-LP 11: height = 11.6; width = 8.3; apical angle = *c*. 72^{O}.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Moderately high-spired, turbiniform shell consisting of 6 whorls (apex missing) with a step-like whorl profile; early teleoconch whorls (first three whorls) rounded, convex, with an ornament of faint spiral threads (maybe due to preservation); upper whorl surface of later whorls developing wide, steeply inclined ramp; ramp slightly convex to straight ornamented by *c*. 8 to 10 equally spaced spiral threads; selenizone wide and flat, approximately 0.8 mm wide, covering almost half of whorl height of body-whorl, situated below ramp; adapical border of ramp at about mid-whorl, forming also angulated border of ramp; outer whorl surface of selenizone almost straight, parallel to shell axis, bordered by two spiral threads followed by strong spiral cords; selenizone with curved transverse lunulae; adapical spiral rib forming periphery; abapical spiral somewhat above lower suture; whorls embracing somewhat below abapical spiral rib; suture distinctly impressed; base flatly convex with numerous evenly spaced spiral threads, shallowly phaneromphalous; aperture not well-preserved, seemingly with straight columellar lip.

Remarks. *Platyzona* is reported from Thailand for the first time. Several species of this genus have been reported from other Permian assemblages from Asia e.g., from Cambodia (Mansuy 1913*a*; Delpey 1941), Perak, Malaysia (Batten 1972), South China (Pan & Erwin 2002) and from the Akasaka Limestone, Japan (Nützel & Nakazawa 2012). It has also been reported from the USA (Batten 1989).

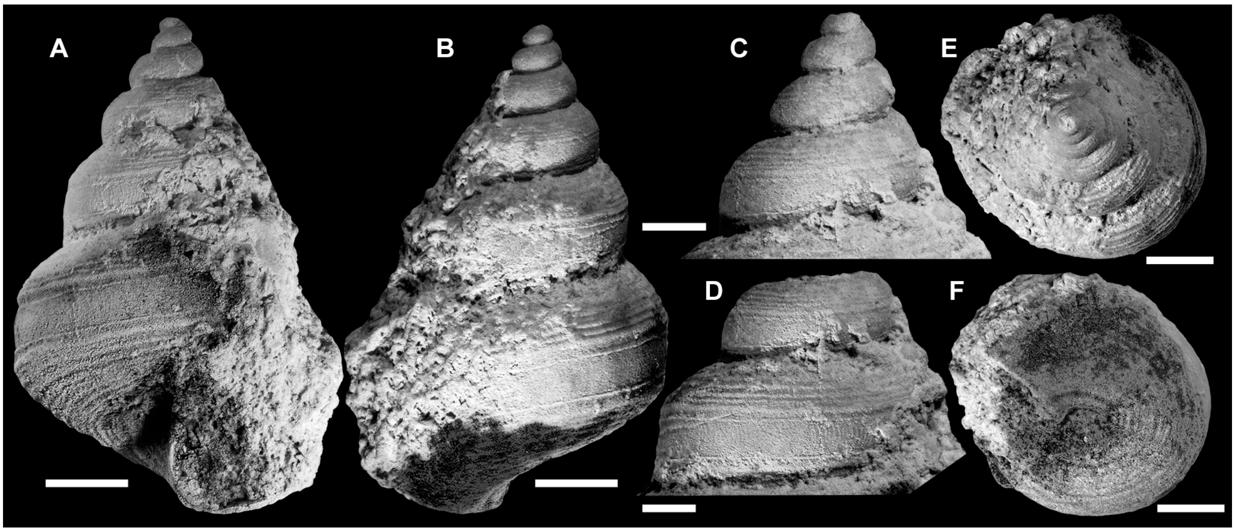

Figure 3.23: *Platyzona gradata* sp. nov., A–F, ESKU-19-LP 11, holotype. Scale bars represent: 2 mm (A–B, E–F); 1 mm (C–D).

The single specimen at hand resembles the paratype of *Platyzona dongluoensis* (Pan & Yu, 1993) from the Upper Permian Changxing Formation of south China (Pan & Yu 1993, pl. 8, fig. 3a–c). However, the holotype of this species differs considerably from the paratype and from the present specimen in having a narrow selenizone at mid-whorl and in other characters (Pan & Yu 1993, pl. 8, fig. 2a–b). The paratype of *P. dongluoensis* represents the genus *Platyzona* but the holotype and hence the species itself does not, the species reported by Pan & Erwin (2002) as of *P. dongluoensis* from the Late Permian of China resembles the misidentified paratypes of this species and *P. gradata* sp. nov. and could be conspecific.

P. nodohumerosa Batten, 1972 from the Permian of Malaysia resembles *P. gradata* sp. nov. but has a nodular ornament and distinct spiral cords or lirae on the selenizone. *P. eulkaiensis* (Reed, 1927) as illustrated by Batten (1972) from the Permian of Malaysia and by Nützel & Nakazawa (2012) form the Permian of Japan is also similar but has a narrower selenizone that is lower on the whorls (just above the suture) and a weaker spiral ornament.

Three Late Permian species from South China have been assigned to *Platyzona* by Pan & Erwin (2002): *P. pulchella* Pan & Erwin, 2002 lacks spiral cords and has more pronounced growth-lines. *P. nitella* Pan & Erwin, 2002 is broader and has more pronounced lunulae. *P. luculenta* Pan & Erwin, 2002 is based on an early juvenile specimen (protoconch and 1.5 teleoconch whorls). In contrast to *P. gradate* sp. nov., it has strong spiral cords on the earliest teleoconch and the selenizone is higher on the whorls.

Four Permian species from SW USA have been assigned to *Platyzona* by Batten (1989): *P. rotunda* Batten, 1989 is broader and has entirely rounded whorls. *P. cancellata* Batten, 1989 has a much narrower selenizone and a cancellate ornament. *P. pagoda* Batten, 1989 is more slender and has a concave selenizone and has entirely rounded whorls. *P. anguispira* Batten, has uncoiled whorls.

Family Palaeostylidae Wenz, 1938
Subfamily Palaeostylinae Wenz, 1938

Palaeostylus Mansuy, 1914
Type species. *Palaeostylus pupoides* Mansuy, 1914, Permian, Cambodia.

Palaeostylus sp.
(Fig. 3.24A–B)

Material. One specimen: ESKU-2019-LP 7.
Dimensions (mm): ESKU-19-LP 7: height = 3.6; width = 2.2; apical angle = 84^{O}.

Remarks. This small, high-spired, cyrtoconoid, shell has a straight whorl face that is ornamented by slightly opisthocline axial ribs, forming node-like extensions situated immediately adjacent to the adapical suture. The whorls are low as is typical for the genus *Palaeoestylus*. Similar shells do also occur in the genera *Pseudozygopleura* Knight, 1930 and *Zygopleura* Koken, 1892. The present specimen is too fragmentary for an identification.

Superfamily Pseudozygopleuroidea Knight, 1930
Family Pseudozygopleuridae Knight, 1930

Pseudozygopleura Knight, 1930
Type species. *Loxonema semicostatum* Meek, 1971, Carboniferous, USA.

Pseudozygopleura? sp.
(Fig. 3.24C–D)

Material. One specimen: ESKU-19-LP 63.
Dimensions (mm): ESKU-19-LP 63: height = *c*. 9.2; width = 2.6.

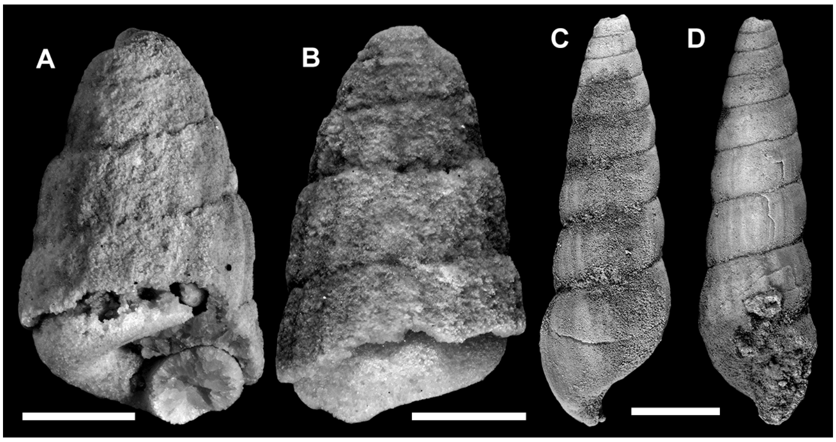

Figure 3.24: A–B, *Palaeostylus* sp., ESKU-19-LP 7. C–D, *Pseudozygopleura*? sp., ESKU-19-LP 63. Scale bars represent: 1 mm (A–B); 2 mm (C–D).

Description. Shell high-spired, slender, turritelliform, slightly cyrtoconoid comprising at least 8 whorls with apex missing; whorls twice as wide as high; whorls gently convex, ornamented by straight faint collabral ribs numbering about 10 to 14 per whorl; ribs presumably reduced on last preserved whorl; sutures shallow but distinct; transition to base gradually convex; base rounded; anomphalous; aperture elongated suboval (higher than wide) with indistinct siphonal notch, columellar lip nearly straight.

Remarks. This single specimen resembles several species from the Pennsylvanian of the USA (Knight 1930; Hoare & Sturgeon 1985) but the preservation is insufficient for an identification. Pseudozygoppleuridae have a typical larval shell and hence knowledge of the protoconch is needed for a save family and genus assignment. Similar shells as the present one may also occur in Palaeostylidae and other groups. Several species that have been recorded from the Permian of the Palaeo-Tethys from Thailand (Ketwetsuriya *et al*. 2016) and Malaysia (Batten 1985) have been reported but those species have a more distinct axial ornament.

Superfamily Orthonematoidea Nützel & Bandel, 2000

Family Orthonematidae Nützel & Bandel, 2000

Donaldospira Batten, 1966*b*

Type species. *Murchisonia pertusa* de Koninck, 1883, Early Carboniferous, Europe

Donaldospira? sp.

(Fig. 3.25A)

Material. One specimen: ESKU-19-LP 85.
Dimensions (mm): ESKU-19-LP 85: height = 10.4; width = 3.1.

Description. Turritelliform, high-spired, slender shell, comprising about five whorl (apex missing); whorls gradually increasing; whorls generally gently convex with median angulation; whorls with two fine spiral cords new near upper and lower suture; third cord strongest, situated at mid-whorl, forming crest-like periphery; upper whorl face forming evenly concave ramp; lower whorl face slightly concave, inwardly sloping from angulation to suture; suture distinct; base evenly rounded; anomphalous; aperture elongated suboval in shape with thin lip, columellar lip nearly straight.

Remarks. Due to the preservation a possibly present selenizone on the angulation at mid-whorl, this specimen can only be assigned to *Donaldospira* tentatively. The Permian species *Murchisonia* (*Donaldospira*) *malaysia* Batten, 1985 from Perak, Malaysia is similar but has a straighter whorl face and finer spiral cords on the whorls above and below the selenizone. *M. gubleri* Delpey, 1941 (p. 367, fig. 41) from the Lower Permian Sisophon Formation, Cambodia is similar but it has a much more protruding peripheral carina and lacks spiral cords near the sutures. *M. fischeri* Stuckenberg, 1905 as illustrated by Delpey (1941) is much similar in whorl profile but it develops selenizone at the periphery which is bordered by two spiral ribs.

Knightella Longstaff, 1933
Type species. *Knightella irregularis* (Longstaff, 1933), Carboniferous, Scotland.

Knightella irregularis (Longstaff, 1933)
(Fig. 3.25B–E)

Knightia irregularis Longstaff, 1933: 118, pl. 12, figs 4–5; Knight, 1941: 164, pl. 49, fig. 6a–b.

Material. Two specimens: ESKU-19-LP 41, 84.
Dimensions (mm): ESKU-19-LP 41: height = *c*. 16.6; width = 6.1. ESKU-19-LP 84: height = 8.9; width = 4.0; apical angle = 42°.

Description. Shell high-spired, slender; largest specimen consisting of 10 whorls; protoconch smooth, seemingly about two orthostrophic whorls; whorls low, gently increasing; whorls smooth; whorl face evenly convex or somewhat pendent with periphery at mid-whorl or somewhat below; sutures moderately deep, distinct; base evenly convex, rounded; anomphalous; aperture unknown.

Remarks. The present specimens closely resemble the type species, *Knightella irregularis* (Longstaff, 1933) from the Carboniferous, Scotland as re-described and illustrated by Knight (1941, p.165, pl. 49, fig. 6a–b), although the present specimens are much larger. The general features of this species (i.e., high spire, sharply rounded and somewhat pendent whorl profile, a body whorl which is two-fifths of the total height, rounded base, anomphalous shell and slightly protruding protoconch) are obviously identical with the present specimens. Other similar species are *K. hydrobiformis* Nützel, 2012 and *Knightella* sp. from the Middle Permian Akasaka Limestone of Japan (Nützel & Nakazawa, 2012) and also several *Knightella* species which have been reported by Nützel (1998) from the Pennsylvanian of the USA. However, these species are smaller and have less convex whorls. *Loxonema karabolkensis* Licharev, 1975 (p. 78, pl. 13, figs 5–8) from the Pennsylvanian of Russia is similar but it differs in having a dense spiral ornament on the whorls. The present specimens are also similar to *Protostylus*; however, this genus has flatter whorls. This is the first known member of the genus *Knightella* in Thailand which extends the range of this species and genus to the Middle Permian and expands its distribution to the eastern Palaeo-Tethys.

Protostylus Mansuy, 1914
Type species. *Protostylus lantenoisi* Mansuy, 1914, Carboniferous, SE Asia.

Protostylus sp.
(Fig. 3.25F–H)

Material. Two specimens: ESKU-19-LP 39, 64.
Dimensions (mm): ESKU-19-LP 39: height = *c*. 16.8; width = 7.8. ESKU-19-LP 64: height = *c*. 6.9; width = 2.9.

Description. Shell high-spired, slender, consisting of approximately 7 whorls (apex missing); whorls smooth; whorls slightly convex to almost straight, periphery somewhat below mid-whorl; base evenly rounded, convex; anomphalous; sutures shallow but distinct; aperture unknown.

Remarks. These unornamented high-spired shells resemble several Permian *Protostylus* species e.g. from the Middle Permian Tak Fa Limestone from Thailand (Ketwetsuriya *et al*. 2016) but the body-whorl of the present specimens seems to be more inflated. The Japanese *Protostylus* species from the Middle Permian Akasaka Limestone (Nützel & Nakazawa 2012) are much smaller. *Protostylus* sp. from the Permian of Ratburi Limestone, Thailand (Ketwetsuriya *et al*. 2019) is more slender in shape. The type species, *Protostylus lantenoisi* Mansuy, 1914 from the Carboniferous of South China (Yunnan) and the specimens illustrated by Batten (1985) from the Permian of Malaysia, differ from the present specimens in being more slender smaller and having lower whorls. The Permian Malaysian species *Omphaloptychia paleozoica* Batten, 1985 is similar in having high whorls, but it has a moderately high-spired turbiniform shape and a more step-like whorl profile. The studied specimens are also similar to *Knightella irregularis* (Longstaff, 1933) but its whorls are somewhat lower and less convex, and it has shallower sutures.

Family Goniasmatidae Nützel & Bandel, 2000

Trypanocochlea Tomlin, 1931
Type species. *Trypanocochlea cerithioides* (Koken,1896), Late Triassic, Carnian.

Trypanocochlea lopburiensis sp. nov.
(Fig. 3.25I–N)

Etymology. After the Lopburi Province in which the studied gastropod material was found.
Holotype. ESKU-19-LP 210
Paratypes. ESKU-19-LP 201, 203, 204, 206, 211, 218, 221.
Dimensions (mm): ESKU-19-LP 201: height = *c*. 1.1; width = 0.6. ESKU-19-LP 203: height = *c*. 1.1; width = 0.5. ESKU-19-LP 204: height = *c*. 1.0; width = 0.5. ESKU-19-LP 206: height = *c*. 1.9; width = 0.8. ESKU-19-LP 210: height = 1.5; width = 0.6. ESKU-19-LP 211: height = *c*. 1.1; width = 0.6. ESKU-19-LP 218: height = 1.3; width = 0.5. ESKU-19-LP 221: height = *c*. 0.7; width = *c*. 0.4.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

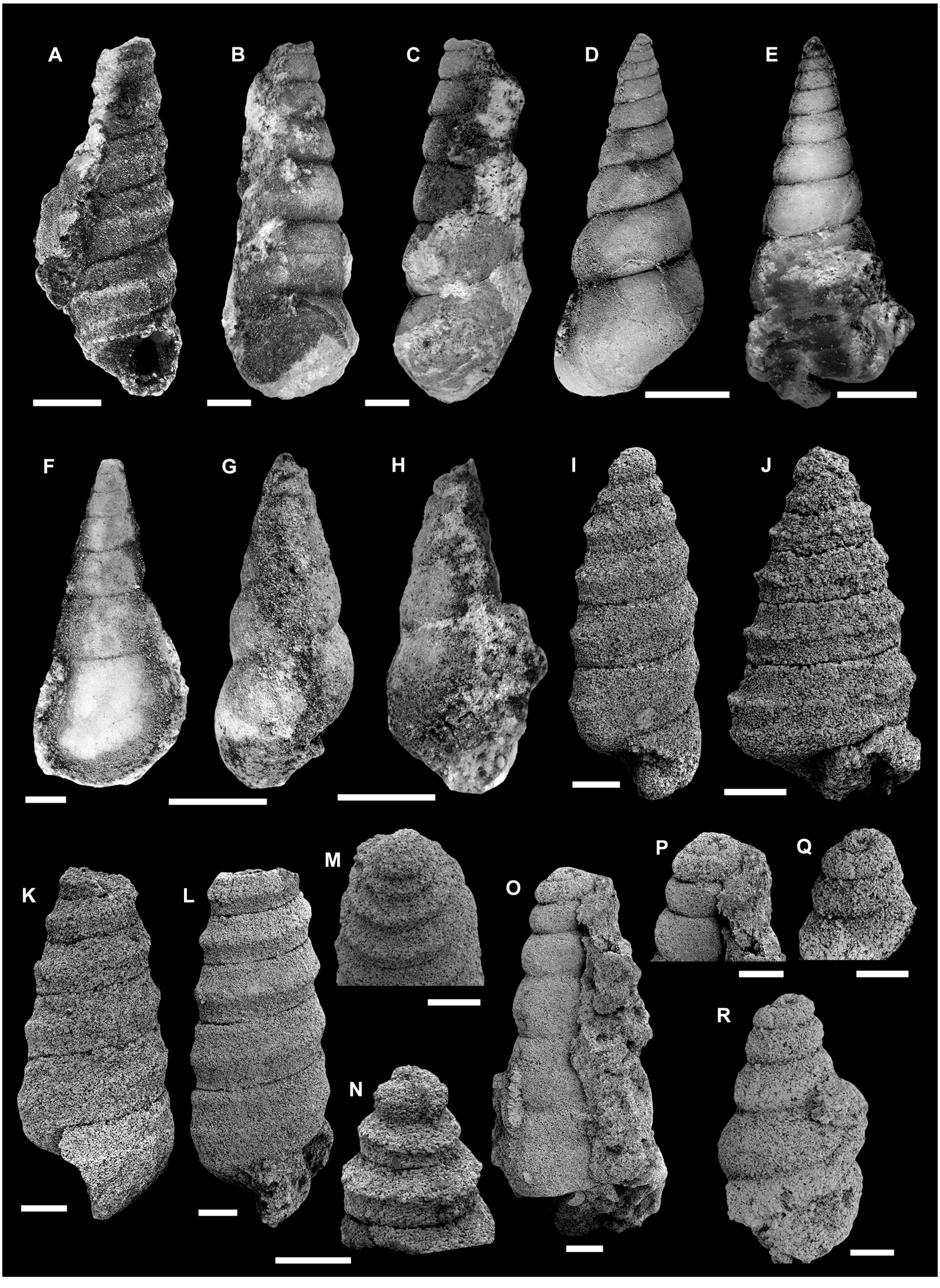

Figure 3.25: A, *Donaldospira* sp., ESKU-19-LP 85. B–E, *Knightella irregularis* (Longstaff, 1933), B–C, ESKU-19-LP 41. D–E, ESKU-19-LP 84. F–H, *Protostylus* sp., F, ESKU-19-LP 39. G–H, ESKU-19-LP 64. I–N, *Trypanocochlea lopburiensis* sp. nov. I, M, ESKU-19-LP 210, holotype; oblique view of early whorls to show protoconch. J, ESKU-19-LP 201, paratype. K, ESKU-19-LP 203, paratype. L, ESKU-19-LP 206, paratype; lateral view of early whorls to show protoconch. N, ESKU-19-LP 221, paratype. O–R, *Streptacis*? *khaokhadensis* sp. nov., O–P, ESKU-19-LP 214, holotype. Q–R, ESKU-19-LP 213, paratype. Scale bars represent: 2 mm (A–H); 200 µm (I–R).

Description. Shell very small, high-spired, turritelliform, slightly cyrtoconoid comprising about six whorls; earliest two whorls (probably protoconch) convex, without visible ornament, somewhat mammilated; suture distinct; whorls low with evenly increasing whorl expansion after early first whorl, angulated at about mid-whorl with concave subsutural ramp; lower whorl below angulation concave; strong spiral cord located at mid-whorl at angulation forming periphery, with numerous small nodules (crenulated); additional weak spiral threads situated at subsutural position and second spiral thread located emerging from lower suture; whorl face on ramp and lower whorl smooth without visible ornament; base flatly convex without ornament; shallowly minutely phaneromphalous or anomphalous; aperture not well-preserved, seemingly circular with short slit.

Remarks. These tiny shells are assigned to the genus *Trypanocochlea* due to their high spire and the nodular spiral keel which is situated at the mid-whorl. However, due to preservation it is unclear whether a selenizone is present on the keel in the present specimens. *Trypanocochlea parva* Nützel, 2012 from the Akasaka Limestone, Japan is the only other Permian nominate species; it has much larger nodes on the keel, the keel is more pronounced, it is not cyrtoconoid but conical. Both species share a mammilate protoconch probably representing a larval shell of the caenogastropod type. The genus *Donaldospira* holds similar species but this genus lack nodes on the median keel. *Donaldospira taosensis* Kues & Batten (2001, fig. 9.30) from the Middle Pennsylvanian of New Mexico is similar but has higher whorls and several spiral threads above and below the carina (that lacks crenulation), which are not present in the present specimens. *D. carinata* Bandel, 2002*b* from the East Mount Shale, Pennsylvanian of Texas, USA has a much more protruding peripheral carina. The present specimens are much smaller than the other Permian *Donaldospira* species and the spiral cord at mid-whorl is weaker in the other species and the carina is not crenulated. *Trypanocochlea lopburiensis* is established as a new species that yields approximately 10 specimens in the present collection.

Subclass Heterobranchia Burmeister, 1837
Superfamily Streptacidoidea Knight, 1931b
Family Streptacididae Knight, 1931b

Streptacis Meek, 1871
Type species. *Streptacis whitfieldi* Meek, 1871, Carboniferous, USA.

Streptacis? *khaokhadensis* sp. nov.
(Fig. 3.25O–R)

Etymology. After the Khao Khad Formation in which the studied gastropod material was found.
Holotype. ESKU-19-LP 213.
Paratype. ESKU-19-LP 214.
Dimensions (mm): ESKU-19-LP 213: height = *c*. 2.4; width = *c*. 0.8. ESKU-19-LP 214: height = *c*. 1.3; width = *c*. 0.7.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 3.1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell very small, high-spired, slender, largest specimen consisting of 7 whorls; protoconch smooth, seemingly coaxially heterostrophic; whorls low, smooth; earliest teleoconch whorls low, markedly convex with periphery at mid-whorl; later whorls higher, less convex; sutures deep; base and aperture unknown.

Remarks. Both specimens at hand are close to the Permian Japanese species *Knightella hydrobiformis* Nützel, 2012 from the Akasaka Limestone as reported by Nützel & Nakazawa (2012) in shell shape and size. However, in *K. hydrobiformis* convexity of the whorl face and height of the whorl does not change during ontogeny in contrast to the specimens at hand. The protoconch of the present material shows coaxial heterostrophy as does a specimen representing *K.* aff. *hydrobiformis* illustrated by Nützel & Nakazawa (2012, fig. 20N, O). However, the holotype of *K. hydrobiformis* does not display heterostrophy (maybe due to preservation) and was hence assigned to the caenogastropod genus *Knightella* (see Nützel 1998). *Streptacis* is characterized by transaxial heterostrophy i.e., the protoconch axis is more or less perpendicular to the shell axis of the teleoconch. However, *Streptacis*? *khaokhadensis* sp. nov. shows coaxial heterostrophy as does for instance the Jurassic genus *Usedomella* Gründel, 1998 and the Pennsylvanian *Mapesella* Bandel, 2002*a*. However, in *Usedomella* the width of the protoconch exceeds that of the early teleoconch and *Mapesella* has axial threads on the teleoconch whorls, both is not the case in *S.*? *khaokhadensis* sp. nov.. Therfore we tentaively place *S.*? *khaokhadensis* sp. nov. in *Streptacis*. *S.*? *khaokhadensis* sp. nov. differs from *K. irregularis* (Longstaff, 1933) in whorl profile that is somewhat pendent and in being larger.

Genus and species indeterminate 1
(Fig. 3.26A–C)

Material. One specimen: ESKU-19-LP 4.
Dimensions (mm): ESKU-19-LP 4: height = 3.9; width = 3.1; apical angle = 82^{O}.

Remarks. This small, moderately high-spired, barrel-shaped shell has a prominent ornament of three spiral cords on convex whorl face, a forth emerging at the lower and flattened, planispiral early whorls (with earliest whorls missing). It represents clearly a distinct species in the present collection. However, the present specimen is too poorly preserved for a safe identification. It resembles the genus *Stegocoelia* Donald, 1889 but this genus has no flattened early whorls and it is unclear whether the present specimen has a selenizone. Otherwise, it resembles several Late Palaeozoic species, for instance *Stegocoelia akasakaensis* Nützel, 2012 from the Middle Permian Akasaka Limestone of Japan but its spiral cords are much more prominent. It is also similar to some species from the Middle Pennsylvanian of New Mexico as described by Kues & Batten (2001).

Genus and Species indeterminate 2
(Fig. 3.26D)

Material. One specimen: ESKU-19-LP 207.
Dimensions (mm): ESKU-19-LP 207: height = *c*. 1.0; width = 0.9.

Remarks. This tiny incomplete specimen has several coarse orthocline ribs on whorl face and one spiral rib at abapical suture. is similar to *Hemizyga* (*Plocezyga*) sp. 1 as illustrated and described by Kues & Batten (2001) from the Middle Pennsylvania of New Mexico but the studied specimen differs in having a spiral rib at lower suture. The present specimen could represent a trochid or a caenogastropod but is too poorly preserved for an identification.

3.7 Acknowledgements

The first author would like to thank the Royal Thai Government who provided funding for a scholarship in the frame of the Development and Promotion of Science and Technology Talented Project. We thank Alex Cook and an anonymous reviewer for reviewing this article.

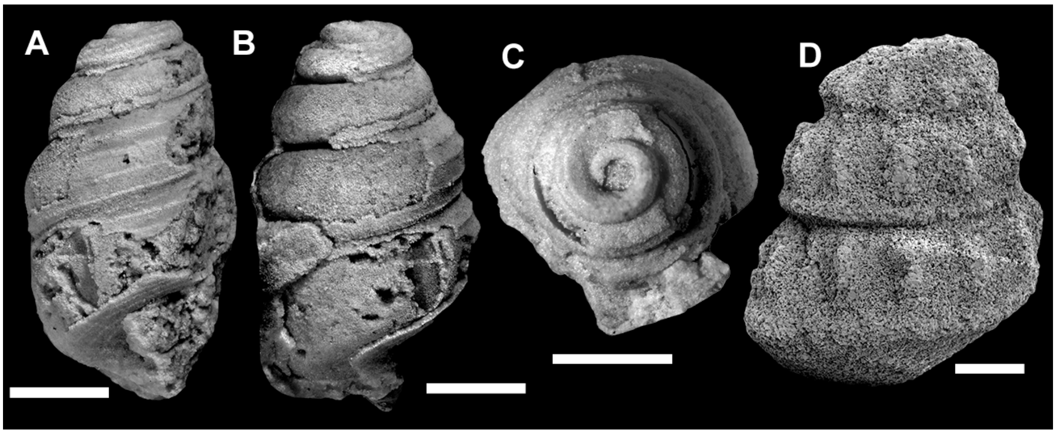

Figure 3.26: A–C, Genus and Species indeterminate 1, ESKU-19-LP 4. D, Genus and Species indeterminate 2, ESKU-19-LP 207. Scale bars represent: 2 mm (A–C); 200 μm (D).

We are grateful to Somchai Nakapadungrat and Pitsanupong Kanjanapayont for their information on thegeology of Thailand. Sasimook Chokchai and students from Department of Geology, Faculty of Science, Chulalongkorn University are kindly acknowledged for their help to the first author in field sampling. Bayerische Staatssammlung für Paläontologie und Geologie is thanked for financial support to the first author for the field work in Thailand.

3.8 References

Bandel, K. (1993) Trochomorpha (Archaeogastropoda) aus den St. Cassian-Schichten (Dolomiten, Mittlere Trias). *Annalen des Naturhistorischen Museums Wien, Reihe A*, 95, 1–99.

Bandel, K. (2002*a*) About the Heterostropha (Gastropoda) from the Carboniferous and Permian. *Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg*, 86, 45–80.

Bandel, K. (2002*b*) Reevaluation and classification of Carboniferous and Permian Gastropoda belonging to the Caenogastropoda and their relation. *Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg*, 86, 81–188.

Bandel, K. & Frýda, J. (1998) The systematic position of the Euomphalidae. *Senckenbergiana lethaea*, 78, 103–131.

Batten, R.L. & Stokes, W.L. (1986) Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah. *American Museum Novitates*, 2864, 1–33.

Batten, R.L. (1956) Some new pleurotomarian gastropods from the Permian of west Texas. *Journal of the Washington Academy of Sciences*, 46 (1), 42–44.

Batten, R.L. (1966*a*) The Lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset. Part I. *Palaeontographical Society Monographs*, 119, 1–52.

Batten, R.L. (1966*b*) The Lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset. Part II. *Palaeontographical Society Monographs*, 119, 53–109.

Batten, R.L. (1972) Permian gastropods and chitons from Perak, Malaysia. Part 1. Chitons, bellerophontids, euomphalids and pleurotomarians. *Bulletin of the American Museum of Natural History*, 147, 1–44.

Batten, R.L. (1979) Permian gastropods from Perak, Malaysia. Part 2. The trochids, patellids, and neritids. *American Museum Novitates*, 2685, 1–26.

Batten, R.L. (1985) Permian gastropods from Perak, Malaysia. Part 3. The murchisoniids, cerithiids, loxonematids, and subulitids. *American Museum Novitates*, 2829, 1–40.

Batten, R.L. (1989) Permian Gastropoda of the Southwestern United States. 7. Pleurotomariacea: Eotomariidae, Lophospiriidae, Gosseletinidae. *American Museum Novitates*, 2958, 1–64.

Batten, R.L. (1995) Pennsylvanina (Morrowan) gastropods from the Magdalena Formation of the Hueco Mountains, Texas. *American Museum Novitates*, 3122, 1–46.

Bouchet, P., Rocroi, R.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E. E. (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, 61, 1–526.

Burmeister, H. (1837) *Handbuch der Naturgeschichte, vol. 2., Zoologie*. Enslin, Berlin, pp. 369–858.

Bunopas, S. (1981) *Paleogeographic history of Western Thailand and Adjacent Parts of South-east Asia - A plate tectonics interpretation*. PhD thesis, Victoria University of Wellington, New Zealand, 810 pp. (Reprinted 1982 as Geological Survey Division, Department of Mineral Resources, Thailand, Geological Paper. No. 5, Special Issue).

Chronic, B.J. (1949) Invertebrate paleontology (excepting fuslinids and corals). *Upper Paleozoic of Peru*. 46–173.

Chronic, H. (1952) Molluscan fauna from the Permian Kaibab Formation, Walnut Canyon, Arizona. *Geological Society America Bulletin*, 63 (2), 95–166.

Conrad, T.A. (1835) Description of five new species of fossil shells in the collection presented by Mr. Edward Miller to the Geological Society. *Transactions of the Geological Society of Pennsylvania*, 1, 267–270.

Cossmann, M. (1897) Die Gastropoden der Trias um Hallstatt. Von E. Koken (1). *Revue critique Paléozoologie*, 1, 139–143.

Cossmann, M. (1908) [Review of] Système silurien du centre de la Bohème, 1ère partie. *Recherches paléontologiques. Vol. IV: Gastropodes, T. II, par J. Perner. Revue Critique de Paléozoologie,* 12 (2), 91–95.

Cox, L.R. & Knight, J.B. (1960) Suborders of the Archaeogastropoda. *Proceedings of the Malacological Society of London*, 33, 262–264.

Cuvier, G. (1795) Second mémoire sur l'rorganisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordres, lu à la Société d'histoire naturelle de Paris, le 11 Prairial, an 3. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 2, 433–449.

Dana, J.D. (1847) Descriptions of fossil shells of the collections of the exploring expedition under the command of Charles Wilkes, USN, obtained in Australia, from the lower layers of the coal formation in Illawarra, and from a deposit probably of nearly the same age at Harper's Hill, Valley of the Hunter. *American Journal of Science and Arts*, *Second Series*, 4, 151–160.

Dawson, O. (1993) Fusuline foraminifera1 biostratigraphy and carbonate facies of the Permian Ratburi Limestone, Saraburi, central Thailand. *Journal of Micropalaeontology*, 12, 9–33.

Delpey, G. (1941) Les Gastéropodes permiens du Cambodge. *Journal de Conchyologie*, 84, 255–278, 345–369.

Delpey, G. (1942) Les Gastéropodes permiens du Cambodge. *Journal de Conchyologie*, 85, 50–83.

Donald, J. (1889) Descriptions of new species of Carboniferous gastropods. *Quarterly Journal of the Geological Society of London*, 45, 619–625.

Erwin, D.H. (1988) Permian Gastropoda of the Southwestern United States: Cerithiacea, Acteonacea, and Pyramidellacea. *Journal of Paleontology*, 62, 566–575.

Fischer, P. (1885) *Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des molluscques vivants et fossils*, 8, 1–1369.

Fletcher, H.O. (1958) The Permian gastropods of New South Wales. *Records of the Australian Museum*, 24 (10), 115–164.

Gemmellaro, G.G. (1889) La Fauna dei Calcari Con Fusulina della Valle del Fiume Sosio nella Provincia di Palermo, Fasc 2. Nautiloidea e Gastropoda. *Giornale di Scienze Naturali e Economiche*, 20, 97–182.

Girty, G.H. (1909) Paleontology of the Manzano group. *In*: Lee, W.T. and Girty, G.H. (Eds.), *The Manzano group of the Rio Grande Valley, New Mexico*. Bulletin of the U. S. Geological Survey, Government Printing Office, Washington, pp. 40–141.

Girty, G.H. (1915) The fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1–353.

Girty, G.H. (1927) Descriptions of new species of Carboniferous and Triassic fossils (from southeastern Idaho). *United States Geological Survey Professional Paper*, 152, 411–446.

Grant, R.E. (1976) Permian brachiopods from southern Thailand. *Paleontological Society Memoir*, 9, 1–269.

Gründel, J. (1998) Heterostropha (Gastropoda) aus dem Dogger Norddeutschlands und Nordpolens. II. Weitere Allogastropoda. *Freiberger Forschungsheft C 474, Paläontologie, Stratigraphie, Fazies*, 6, 1–37.

Hall, J. (1847) Containing descriptions of the organic remains of the lower division of the New York system (equivalent of the Lower Silurian rocks of Europe). *Paleontology of New York*, 1, 1–338.

Hall, J. (1856) Description of new species of fossils from the Carboniferous limestones of Indiana and Illinois. *Transactions of the Albany Institute*, 4, 1–36.

Hall, J. (1859) Contributions to the palaeontology of Iowa; being descriptions of new species of Crinoidea and other fossils. *Iowa Geological Survey*, 1 (2), 1–92.

Harper, J.A. (2018) Gastropods from the Gilmore City Formation (Lower Mississippian) of North-Central Iowa: Part 1, geology and systematics of Bellerophontoidea and Euomphaloidea. *Annals of the Carnegie Museum*, 85, 61–90.

Haughton, S. (1859) On some fossil Pyramidellidae from Carboniferous Limestone of Cork and Clonmel. *Proceedings of the Dublin University Zoology and Botany Association*, 1, 281–283.

Hayasaka, I. (1955) A new Permian species of Porcellia from Japan. *Journal of the Faculty of Science, Hokkaido University, Series 4, Geology and Mineralogy*, 9, 21–24.

Hinthong, C. (1981) *Geology and mineral resources of the Changwat Phranakorn Sri Ayutthaya (Map ND 47–8), scale 1:250,000*. Department of Mineral Resources, Geological Survey Report no. 4, Bangkok, Thailand, 1–105. [in Thai, English summary]

Hinthong, C., Chuaviroj, S., Kaewyana, W., Srisukh, S., Pholprasit, C. & Pholachan, S. (1985) *Geological map of Changwat Phranakorn Sri Ayutthaya, Thailand 1: 250 000 (ND 47–8)*. Geological Survey Division of the Department of Mineral Resources, Bangkok, Thailand. [in Thai]

Hoare, R.D. (1961) Desmoinesian Brachiopoda and Mollusca from southwest Missouri. *Missouri University Studies*, 36, 1–262.

Hoare, R.D. & Sturgeon, M.T. (1985) The Pennsylvanian gastropod *Pseudozygopleura* (Pseudozygopleura) from the Appalachian Basin: II. *Journal of Paleontology*, 59 (1), 60–78.

Ketwetsuriya, C., Nützel, A. & Kanjanapayont, P. (2014) A new Permian gastropod fauna from the Tak Fa Limestone, Nakhonsawan, Northern Thailand—a report of preliminary results. *Zitteliana A*, 54, 137–146.

Ketwetsuriya, C., Nützel, A. & Kanjanapayont, P. (2016) Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. *Bulletin of Geosciences*, 91, 481–513.

Ketwetsuriya, C., Cook, A.G. & Nützel, A. (2020a) Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand. *Paläontologische Zeitschrift*, 94, 53–77. https://doi:10.1007/s12542-019-00463-0

Ketwetsuriya, C., Karapunar, B., Charoentitirat, T. & Nützel, A. (2020b) Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: implications for palaeogeography of the Indochina Terrane. *Zootaxa* 4766(1), 1–47.

Knight, J.B. (1930) The gastropods of the St. Pseudozygopleurinae. *Journal of Paleontology*, 4 (1), 1–89.

Knight, J.B. (1931*a*) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: the Subulitidae. *Journal of Paleontology*, 5 (3), 177–229.

Knight, J.B. (1931*b*) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: *Aclisina* and *Streptacis*. Journal of Paleontology, 5, 1–15.

Knight, J.B. (1933*a*) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: V. The Trocho-Turbinidae. *Journal of Paleontology*, 7 (1), 30–58.

Knight, J.B. (1933*b*) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: VI. The Neritidae. *Journal of Paleontology*, 7 (4), 359–392.

Knight, J.B. (1936) Notes on Paleozoic Gastropoda. *Journal of Paleontology*, 10 (6), 520-534.

Knight, J.B. (1941) Paleozoic gastropod genotypes. *Geological Society of America Special Paper*, 32, 1–510.

Knight, J.B. (1945) Some new genera of the Bellerophontacea. *Journal of Paleontology*, 19, 333–340.

Knight, J.B. (1956) New families of Gastropoda. *Journal of the Washington Academy of Sciences*, 46, 41–42.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. (1960) Systematic descriptions. *In* Moore, R.C. (ed.), *Treatise on invertebrate paleontology. Part I. Mollusca 1*. Geological Society of America & University of Kansas Press, pp. I169–I310.

Koken, E. (1892) Ueber die Gastropoden der rothen Schlernschichten nebst Bemerkungen über Verbreitung und Herkunft einiger triassischer Gattungen. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 1892, 25–36.

Koken, E. (1896) Die Gastropoden der Trias um Hallstadt. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt*, 46, 37–126.

Koninck, L.G. de (1843) *Précis élément, de géologie*, 1–600.

Koninck, L.G. de (1863) *Mémoire sur les Fossiles Paléozoiques Recueillis dans l'Inde par M. le Docteur Fleming*. H. Dessaain, Liège, 44 pp.

Koninck, L.G. de (1881) Faune du calcaire carbonifère de la Belgique, 3e partie, Gastéropodes. *Annales du Musée Royal d'Histoire Naturelle de Belgique, serie Paleontologie*, 6, 1–170.

Koninck, L.G. de (1883) Faune du calcaire carbonifére de la Belgique. 4. Gastéropodes (suite en fin). *Annales du Musée Royale d'Historie Naturelle Belgique*, 8, 1–240.

Kues, B.S. (1984) Pennsylvanian stratigraphy and paleontology of the Taos area, north-central New Mexico. *Rio Grande Rift: Northern New Mexico. New Mexico Geological Society Guidebook*, 35, 107–114.

Kues, B.S. (2004) Stratigraphy and brachiopod and molluscan paleontology of the Red Tanks Formation (Madera Group) near the Pennsylvanian–Permian boundary, Lucero uplift, west-central New Mexico. *Carboniferous–Permian transition at Carrizo Arroyo, central New Mexico*, 25, 143–210.

Kues, B.S. & Batten, R.L. (2001) Middle Pennsylvanian gastropods from the Flechado Formation, north-central New Mexico. *Journal of Paleontology*, 75 (supplement 1), 1–95.

Kulas, H.A. & Batten, R.L. (1997) Silicified gastropods from the Permian Phosphoria rock complex of Wyoming. *Contributions to Geology, University of Wyoming*, 31 (2), 33–58.

Léveillé, C. (1835) A perçu géologique de quelques localités très riches en coquilles sur les frontiers de France et de Belgique. *Mémoires de la Société géologique de France*, 2 (1), 29–40.

Licharev, B.K. (1975) Carboniferous gastropods from the region of the River Karabolka. *Trudy Vsesoyuzniei Navcho-Issledovatelbskii Geologicheskii Institut*, 206, 5–183.

Longstaff, J.D. (1933) A revision of the British Carboniferous Loxonematidae, with descriptions of new forms. *Quarterly Journal of the Geological Society of London*, 89 (2), 87–124.

Mansuy, H. (1912) Paléontologie. *In*: Mansuy, H. & Deprat, J. (Eds.), *Etude géologique du Yun-Nan oriental. Actes de la Société Géologique de l'Indo-Chine 1(2)*, pp. 1–146.

Mansuy, H. (1913*a*) Faunes des calcaires à Productus de l'Indochine. *Mémoires du Service Géologique de l'Indochine*, 2 (4), 1–133.

Mansuy, H. (1913*b*) Paléontologie de L'Annam et du Tonkin. *Mémoires du Service Géologique de L`Indochine*, 2 (3), 1–48.

Mansuy, H. (1914) Nouvelle contribution à la paléontologie du Yunnan. *Mémoires du Service Géologique de l'Indochine*, 3 (2), 1–190.

Mazaev, A.V. (2006) Permian gastropods from the Kulogory Formation of the northern Moscow Syneclise. *Paleontological Journal*, 40, 391–403.

Mazaev, A.V. (2015) Upper Kazanian (Middle Permian) gastropods of the Volga-Urals Region. *Paleontological Journal*, 49, 869–986.

McCoy, F. (1844) *A Synopsis of the Characters of Carboniferous Limestone fossils of Ireland*. McGloshan & Gill, Dublin, 274 pp.

McCoy, F. (1852) *A synopsis of the classification of the British Palaeozoic rocks [by the Rev. Adam Sedgwick] with a systematic description of the British Palaeozoic fossils in the Geological Museum of the University of Cambridge [by Frederick McCoy] with figures of the new and imperfectly known species*. Parker & Son, London, 661 pp.

Meek, F.B. (1871) Descriptions of new species of invertebrate fossils from Ohio and other western states and territories. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 23, 159–184.

Meek, F.B. & Worthen, A.H. (1860) Description of new Carboniferous fossils from Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 12, 447–472.

Meek, F.B. & Worthen, A.H. (1866) Descriptions of invertebrates from the Carboniferous system. *Geological Survey of Illinois 2, Palaeontology*, 143–411.

Meek, F.B. & Worthen, A.H. (1867) Contributions to the paleontology of Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 18, 251–275.

Meek, F.B. & Worthen, A.H. (1873) Descriptions of invertebrates from the Carboniferous System. *Illinois Geological Survey*, 5 (2), 321–619.

Montfort, P.D. de (1808) *Conchyliologie systématique et classification méthodique de coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Coquilles univalves, cloisonnées 1*. F. Schoell, Paris.

Miller. S.A. (1877) *The American Palaeozoic fossils: a catologue of the genera and species. 2nd ed.* Published by author, Ohio, 334 pp.

Münster, G. zu (1841) Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. *In*: Wissmann, H.L., Münster, G. zu & Braun, K. F. (Eds.), *Beiträge zur Geognosie und Petrefacten-Kunde des SÜdöstlichen Tirol's vorzüglich der Schichten von St. Cassian. Heft 4*. Buchner, Bayreuth, pp. 25–152.

Nakornsri, N. (1976) *Geological Map of Ban Mi Sheet ND 47–4, Scale 1:250,000*. Geological Survey Division. Department of Mineral Resources, Bangkok, Thailand. [in Thai]

Nakornsri, N. (1981) *Geology and Mineral Resources of Amphoe Ban Mi (ND 47–4)*. Department of Mineral Resources, Geological Survey Report no. 3, Bangkok, Thailand. [in Thai]

Netchaev, A.V. (1894) Fauna from the Permian beds of the eastern band of European Russia. *Tr. Ob-va Estestvoispyt. Kazan. Imp. University*, 27 (4), 1–503.

Nützel, A. (1998) Über die Stammesgeschichte der Ptenoglossa (Gastropoda). *Berliner Geowissenschaftliche Abhandlungen, Serie E, Palaeobiologie*, 26, 1–229.

Nützel, A. & Bandel, K. (2000) Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 2000 (9), 557–569.

Nützel, A. (2002) An evaluation of the recently proposed Palaeozoic gastropod subclass Euomphalomorpha. *Palaeontology*, 45, 259–266.

Nützel, A., Frýda, J., Yancey, T.E. & Anderson, J.R. (2007) Larval shells of Late Palaeozoic naticopsis gastropods (Neritopsoidea: Neritimorpha) with a discussion of the early neritimorph evolution. *Palaeontologische Zeitschrift*, 81 (3), 213–228.

Nützel, A. & Nakazawa, K. (2012) Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). *Journal of Systematic Palaeontology*, 10, 103–169.

Nützel, A. & Kaim, A. (2014) Diversity, palaeoecology and systematics of a marine fossil assemblage from the Late Triassic Cassian Formation at Settsass Scharte, N Italy. *Paläontologische Zeitschrift*, 88, 405–431.

Orbigny, A. d' (1840) Chapter on *Bellerophon*. *In*: Ferussac, A. de & Orbigny, A.d' (Eds.), *Histoire naturelle generale et particuliere des cephalopods acetabuliferes vivants et fossiles*, 1, pp. 180–218.

Pan, H.-Z. & Erwin, D.H. (2002) Gastropods from the Permian of Guangxi and Yunnan provinces, South China. *Journal of Paleontology,* 78(S56), 1–49.

Pan, Y.-T. (1985) Fossil Gastropoda from the Permian of Sichuan, Guizhou, Yunnan, and Gaungxi. *Acta Palaeontologica Sinica*, 24 (1), 29–37

Pan, Y.-T. & Yu, W. Z. (1993) *Permian Gastropoda of China*. Ocean Press, Beijing, 68 pp.

Pitakpaivan, K. (1965) Fusulines of the Rat Buri Limestone of Thailand. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology*, 17, 3–69.

Rafinesque, C.S. (1815) Analyse de la nature, ou tableau de l'univers et des corps organisées. Jean Barravecchia, Palerme. 223 pp.
https://doi.org/10.5962/bhl.title.106607

Reed Cowper, F.R. (1927) Upper Carboniferous fossils from Argentina. *Carnegie Institute of Washington*, 381, 129–158.

Rollins, H.B. (1975) Gastropods from the Lower Mississippian Wassonville Limestone in Southeastern Iowa. *American Museum Novitates*, 2579, 1–35.

Salvini-Plawen, L. von (1980) A consideration of systematics in the Mollusca (Phylogeny and higher classification). *Malacologia*, 19, 249–278.

Simroth, H. (1906) Versuch einer neuen Deutung der Bellerophontidae. *Sitzungsberichte der Natuforschenden Gesellschaft zu Leipzig*, 32, 3–8. [dated 1905]

Sone, M. (2010) A new species of the rare neritopsid gastropod *Magnicapitatus* from the Guadalupian (Middle Permian) of East Thailand (the Indochina Terrane). *Alcheringa*, 34, 1–6.

Sone, M. & Metcalfe, I. (2008) Parallel Tethyan sutures in mainland Southeast Asia: New insights for Palaeo-Tethys closure and implications for the Indosinian orogeny. *Comptes Rendus Geosciences*, 340 (2), 166–179.

Sour-tovar, F., Alvarez, F. & Chacon, M. L. M. (2005) Lower Mississippian (Osagean) spire-bearing brachiopods from Canon de la Peregrina, north of Ciudad Victoria, Tamaulipas, northeastern Mexico. *Journal of Paleontology*, 79 (3), 469–485.

Sowerby, J. (1812–1822) *The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the Earth*. Benjamin Meredith, London. 803 pp.

Stuckenberg, A. (1905) Die Fauna der obercarbonischen Suite des Wolgadurchbruches bei Samara. *Geologie Kommitte Trudy Memoir*, 23, 1–115.

Swainson, W. (1840) *A treatise on malacology or shells and shell-fish*. Longman, London, viii + 419 pp.

Thein, M. L. & Nitecki, M.H. (1974) Chesterian (Upper Mississippian) Gastropoda of the Illinois basin. *Fieldiana: Geology, New Series*, 34, 1–238.

Tomlin, J.R.B. (1931) Some preoccupied generic names. III. *Proceedings of the Malacological Society of London*, 19, 174–175.

Toriyama, R. & Kanmera, K. (1977) Fusuline fossils from Thailand, Part X. The Permian fusulines from the Limestone Conglomerate Formation in the Khao Phlong Phrab area, Sara Buri, Central Thailand. *In*: Kobayashi, T., Toriyama, R. & Hashimoto, W. (Eds.), *Geology and Palaeontology of Southeast Asia*. University of Tokyo Press, Tokyo, 18, 1–27.

Toriyama, R. & Kanmera, K. (1979) Fusuline fossils from Thailand, Part XII. Permian fusulines from the Ratburi Limestone in the Khao Khao area, Sara Buri, Central Thailand. *In*: Kobayashi, T., Toriyama, R. & Hashimoto, W. (Eds.), *Geology and Palaeontology of Southeast Asia*. University of Tokyo Press, Tokyo, 20, 43–61.

Toriyama, R., Kanmera, K., Kaewbaidhoam, S. & Hongnusonthi, A. (1974) Biostratigraphic zonation of the Rat Buri Limestone in the Khao Phlong Phrab area, Sara Buri, Central Thailand. *In*: Kobayashi, T. and Toriyama, R. (Eds.), *Geology and Palaeontology of Southeast Asia*. University of Tokyo Press, Tokyo, 14, 25–48.

Ulrich, E.O. & Scofield, W.H. (1897) Chapter X: the lower Silurian Gastropoda of Minnesota. *In*: Ulrich, E.O., Scofield, W.H., Clarke J. M., & Winchell, N. H. (Eds.), *The geology of Minnesota, part 2 of the final report: paleontology, vol. 3*. Harrison & Smith, Minneapolis, pp. 813–1081.

Verrill, A.E. (1884) Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent part of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Arts and Sciences*, 6 (1), 139–194.

Waagen, W. (1880) Salt-Range Fossils. I. Productus Limestone fossils. 2. Pisces-Cephalopoda: supplement Gasteropoda. *Memoirs of the Geological Survey of India (Palaeontologia Indica)*, 13, 1–183.

Wang, H.J. (1982) Late Permian gastropods from Heshan of Laibin, Guangxi Province. *Acta Palaeontologica Sinica*, 21, 491–496.

Wang, H.J. and Xi, Y.H. (1980) Late Permian to Early Triassic gastropods from Western Guizhou Province. *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formation in Western Guizhou and Eastern Yunnan*, 195–240.

Wanner, C. (1922) Die Gastropoden und Lamellibranchiaten der Dyas von Timor. *Palaontologie von Timor*, 11, 1–82.

Waterhouse, J.B. (1982) An Early Permian cool-water fauna from pebbly mudstones in south Thailand. *Geological Magazine*, 119, 337–354. https://doi.org/10.1017/S0016756800026261

Wenz, W. (1938–1944) Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. *In*: Schindewolf, O.H. (ed.), *Handbuch der Paläozoologie. 6. Gastropoda*. Borntraeger, Berlin, 1639 pp.

White, C.A. (1877) Report upon the invertebrate fossils collected in portions of Nevada, Utah, Colorado, New Mexico, and Arizona, by parties of the expeditions of 1871, 1872, 1873, and 1874. *Report upon United States geographical surveys west of the one hundredth meridian, Paleontology*. Government Printing Office, Washington. 4, 1–219.

Winters, S.S. (1956) New Permian gastropod genera from eastern Arizona. *Journal of the Washington Academy of Sciences*, 46 (2), 44–45.

Winters, S.S. (1963) Supai Formation (Permian) of eastern Arizona. *Geological Society of America Memoir*, 89, 1–99.

Yochelson, E.L. (1956) Permian Gastropoda of the southwestern United States. 1. Euomphalacea, Trochonematacea, Anomphalacea, Craspedostomatacea, and Platyceratacea. *Bulletin of the American Museum of Natural History*, 110, 179–275.

Yochelson, E.L. (1960) Permian Gastropoda of the southwestern United States. *Bulletin of the American Museum of Natural History*, 119, 205–294.

Yochelson, E.L. & Dutro, J.T. Jr. (1960) Late Paleozoic Gastropoda from Northern Alaska. *U.S. Geological Survey Professional Paper* 334-D, 111–147.

Yoo, E.K. (1994) Carboniferous Mollusca from the Tamworth Belt, New South Wales, Australia. *Records of the Australia Museum*, 46 (2), 63–120.

Yu, W.Z. (1980) Taxonomic names, in Late Permian to Early Triassic gastropods from Western Guizhou Province. *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formation in Western Guizhou and Eastern Yunnan, China*. 195–232.

Zittel, K.A. von (1895) *Grundzüge der Paläontologie (Paläozoologie), Abt. I, Invertebrata*. München & Leipzig, Oldenburg, 1–971.

4

Diversity patterns of Middle Permian gastropod assemblages from the Tak Fa Formation, Central Thailand

By **Ketwetsuriya C., Hausmann I.M. and Nützel A.** In revision in *Palaeobiodiversity and Palaeoenvironment*. Manuscript number: PBPE-D-20-00028

4.1 Abstract

Middle Permian marine invertebrate assemblages from Central Thailand are strongly dominated by gastropods. Two gastropod assemblages from the Tak Fa Limestone at Khao Noi and Khao Chao Thong of the Nakhonsawan area are the first Permian ones from Thailand that are analyzed regarding diversity and composition based on quantitative data. Both gastropod assemblages, comprising 40 species in total, are dominated by the gastropods *Anomphalus* sp., *Warthia* cf. *brevisinuata* and *Glabrocingulum magnum*; the genus *Anomphalus* is especially abundant which is unusual for Permian assemblages. Both studied gastropod assemblages have a similar taxonomic composition and diversity including the same values of diversity indices that indicate a moderate diversity. In addition, rarefaction analyses and rank-abundance distributions also suggest that diversity and structure of both assemblages are the same. The studied assemblage is compared with other Permian gastropod assemblages from Asia (Malaysia, East Timor and Japan). Rarefaction, diversity indices and rank-abundance distributions suggest that the diversity of the studied fauna is distinctly lower than that of the others despite coming from similar depositional environments. This is surprising because the Tak Fa gastropods lived at lower latitudes than the others. This could suggest an inverse diversity gradient in the Palaeo-Tethys but more evidence is needed to substantiate this assumption. Several Late Palaeozoic and Early Mesozoic fossil assemblages are dominated by gastropods e.g., those from the Pennsylvanian Buckhorn Asphalt deposit, the Permian from Japan and Malaysia, as well as the Late Triassic Cassian Formation. This shows that at least locally, gastropods dominance is not restricted to the modern faunas.

Keywords Gastropoda, Permian, Thailand, Tak Fa Formation, diversity

4.2 Introduction

In the last years, several new Permian gastropod faunas from Thailand were discovered (Ketwetsuriya et al. 2014–2020). Virtually nothing had been known about Permian gastropods from Thailand before. The most diverse of these gastropod faunas is that from the Tak Fa Formation (Ketwetsuriya et al. 2014, 2016). This silicified invertebrate fauna is strongly dominated by gastropods. It was retrieved by bulk sampling and etching from the calcareous rocks and therefore this collection is quantitative. This offers the possibility of a meaningful comparison, regarding its diversity and composition, with other gastropod faunas from Southeast Asia, for which relative abundances are known. The analyzed assemblages of the Tak Fa Formation come from two localities in the Nakhonsawan Province, Central Thailand:

1) Khao Noi hill – this fauna has been monographed by Ketwetsuriya et al. (2016) and 2) a newly retrieved assemblage from Khao Chai Thong hill. Both localities are 2 km apart (Fig. 4.1) and have a similar species composition. However, relative abundances differ. The aim of this contribution is to expand the understanding of Permian gastropod diversity of Thailand and adjacent areas by comparing the quantitative data set of the two localities of the Tak Fa Formation at Khao Noi hill and Khao Chai Thong hill. This study also presents a detailed quantitative analysis of gastropod diversity, which is the most abundant group in the studied samples using diversity indices, rarefaction analysis and rank-abundance distributions. The studied Permian gastropod assemblage from Thailand is compared by means of diversity to other gastropod faunas from Asia for which quantitative data were published for instance to the Permian gastropod fauna from Perak, Malaysia, East Timor and the Akasaka Limestone, Japan to enhance our knowledge on the Permian gastropod diversity and palaeobiogeography.

The Tak Fa Formation, consists of shallow water carbonate deposits (fusulinid limestones) and crops out along the western margin of the Indochina Terrane (Wielchowsky and Young 1985; Metcalfe and Sone 2008) in the Phetchabun Province, Lop Buri Province and Nakhonsawan Province, Central Thailand. It yields one of the most extensively studied Permian marine invertebrate faunas of Thailand. Gastropods are one of its most important components. However, until recently the Permian gastropod fauna from Thailand has hardly been studied. The presence of gastropods was just mentioned in treatments of other groups e.g. brachiopods (Grant 1976; Waterhouse 1982; Sone 2010). Recently, Ketwetsuriya et al. (2014, 2016) produced the first systematic study on the Middle Permian gastropod fauna from the Tak Fa Formation, Nakhonsawan Province, Central Thailand. Gastropods comprise 72.7 % of the species and 88.4 % of the specimens in the analyzed samples (excluding fusulinids which are highly abundant). Around 40 species gastropod fauna were reported, 17 nominate species and 23 species in open nomenclature, with one new genus and twelve new species. However, a quantitative census of the Permian gastropods from Thailand and also from Southeast Asia, has rarely been reported (from Perak, Malaysia: Batten 1972,1979,1985 and from East Timor: Wanner, 1941). An investigation of Permian gastropod diversity facilitates a better understanding of the regional palaeobiogeography of this region.

4.3 Location and geological setting

The studied gastropod assemblages come from two isolated limestone hills, Khao Noi hill (15º18’50” N, 100º26’10” E) and Khao Chai Thong hill (15º17’59” N, 100º26’51” E) in Tak Fa District, Nakhonsawan Province, Central Thailand, forming part of a hill chain, which extends for approximately 6 km in northwest-southeast direction, and is surrounded by unconsolidated Quaternary alluvial deposits at an average elevation of 300 m above mean sea level (Fig. 4.1). The distance between the two sampling spots is approximately 2 km. The fauna from Khao Noi was treated systematically by Ketwetsuriya et al. (2016) who also provided data about diversity and relative abundances. The fauna from the second sampling spot (Khao Chai Thong) was retrieved later and had not been included in the mentioned monograph.

The limestone deposits in the study area are assigned to the Tak Fa Formation (informally known as Tak Fa Limestone), which is a part of Saraburi Group (Nakornsri 1976, 1981). The Tak Fa Formation is distributed over the Phetchabun, Lop Buri and Nakhon Sawan provinces (Nakornsri 1976) and consists mainly of bedded fossiliferous limestones, massive limestones and subordinate siliciclastic rocks (Yanagida 1988). The marine invertebrate fauna of the Tak Fa Limestone has been studied by various authors, and comprises fusulinid foraminifers (Pitakpaivan 1965; Igo 1972, 1992), brachiopods (Yanagida 1988; Sone et al. 2009), conodonts (Metcalfe and Sone 2008; Chitnarin et al. 2012, 2017), corals (Yanagida, 1988), calcareous algae (Fontaine et al. 1999), bryozoans (Sakagami 1975, 1999) and gastropods (Ketwetsuriya et al. 2014, 2016). The unit formed during the Early to late Middle Permian (Chonglakmani and Fontaine 1992; Igo 1992), and has its type area at Tak Fa in southeastern Nakhonsawan Province. During the Permian, the area in which the Tak Fa Formation is exposed was situated in the Palaeo-Tethys, at an equatorial position in the Equatorial Warm Water Province (Metcalfe and Sone 2008)

The age estimates of the Tak Fa Formation range from the latest Carboniferous to middle or late Middle Permian (Ueno and Charoentitirat 2011), based on biostratigraphy (e.g. fusulinid foraminifers, conodonts, brachiopods and bryozoans). The age of the Tak Fa Formation of the study area is based on the fusulinid foraminifers *Verbeekina verbeeki* and *Parafusulina* sp., which indicate a Middle Permian age (Middle Wordian to Middle Capitanian) (Napradit 2005; Jaiboon 2001). Chitnarin et al. (2012) noted that the Ta khli section of the Tak Fa Limestone in Nakhonsawan and Lopburi provinces which is related to the studied localities, has a Middle Permian (Wordian) age based on fusulinid foraminifers. Chitnarin et al. (2017) re-assigned this section to the Early Permian (Artinskian) due to the discovery of the fusulinid foraminifers *Pamirina* sp. and *Pseudofusulina* sp..

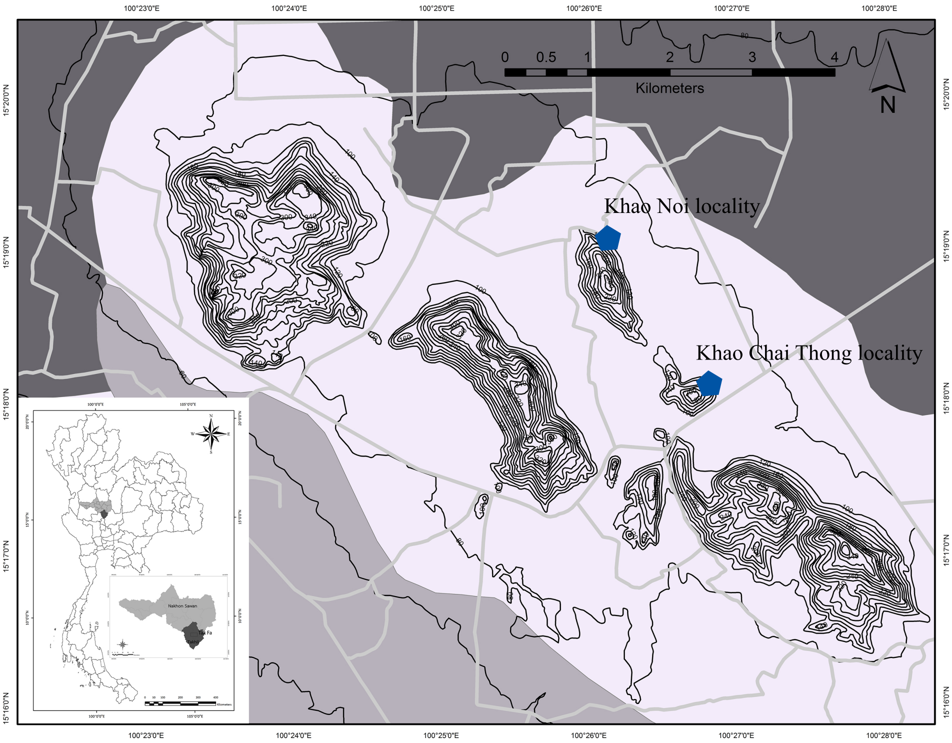

Figure 4.1: Geological map of the study area showing the positions of the studied samples at Khao Noi hill (15º 18’ 50” N, 100º 26’ 10” E) and Khao Chai Thong hill (15º 17’ 59” N, 100º 26’ 51” E), Tak Fa District, Nakhonsawan Province, Central Thailand. Contour lines are indicated in meters.

4.4 Materials and methods

The limestone samples were taken by the first author in 2010, 2013 and 2015 where weathered silicified gastropods were visible on the surface of the carbonate rock on two isolated limestone hills (Khao Noi and Khao Chai Thong) in Tak Fa District, Nakhonsawan Province, Central Thailand (Fig. 4.1). The limestone block samples (approximately 100 kg) were dissolved in formic acid at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany. After dissolving, the residue was wet sieved at a mesh size of 0.5 mm. All determinable fossils were picked from the washed residues. Most fossil material consists of fragmented shell hash, but more or less complete specimens were also present. Gastropods were classified at species-level in the course of taxonomic study by Ketwetsuriya et al. (2016). The specimens of each species were counted, including other fossils e.g. bivalves, brachiopods and algae. Rarefaction analyses and calculation of diversity indices (Shannon-Wiener and Simpson) were performed using the PAST software package (Hammer et al. 2001). Rank-abundance distributions and model fit were calculated in R (R Core Team 2017) using the packages vegan (Oksanen et al. 2018) and sads (Prado et al. 2018). For the diversity analysis, fusulinids were excluded.

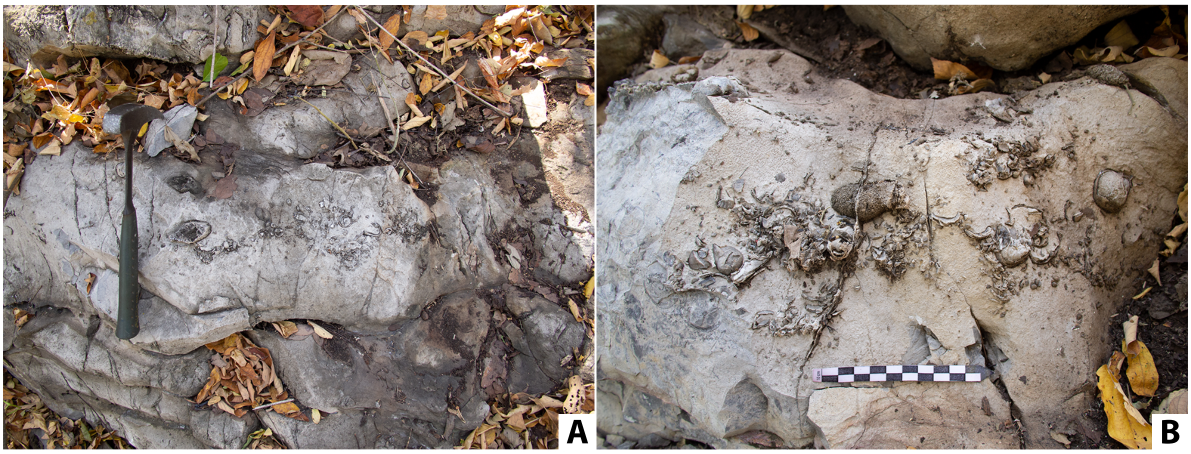

Figure 4.2: Field photographs. A Fossiliferous limestone from the middle part of Khao Noi hill predominately containing gastropods. B Fossiliferous limestone from Khao Chai Thong hill yielding mainly gastropod fragments.

The majority of the fossil material is housed in the Bayerische Staatssammlung für Paläontologie und Geologie (Bavarian State Collection for Palaeontology and Geology) in Munich, Germany (SNSB-BSPG 2014 XI). Some specimens are housed in the Chulalongkorn University, Museum of Zoology, Bangkok, Thailand (CUMZ).

4.5 Results

The samples from the Tak Fa Formation produced a rich silicified fossil assemblage. Besides a high amount of unidentifiable shell fragments, the washed residues yielded gastropod shells, fusulinids, bryozoan fragments, sponge spicules, bivalve shells and brachiopods. Due to the coarse silicification and fragmentation, not all fossils could be determined at species level. Molluscs, especially gastropods, are the most abundant and diverse group in both fossil assemblages, yielding 72.7 % of the species and 88.4 % of the specimens. The strong dominance of gastropods in terms of species richness and abundance is remarkable, but it must be taken into account that gastropod-rich rocks were sampled preferentially in the field.

Gastropod fauna of the studied samples

Taxonomic composition

The gastropod assemblage from Khao Noi comprises 579 specimens which represent 40 species (Fig. 4.3), i.e. 17 nominate species and 23 species in open nomenclature. At the species level, the vetigastropod *Anomphalus* sp. is the most abundant species (34.1%), followed by the bellerophontid *Warthia* cf. *brevisinuata* (8.7%), eotomariid *Glabrocingulum magnum* (8.0%) and the high-spired orthonematid *Protostylus* sp. (7.6%).

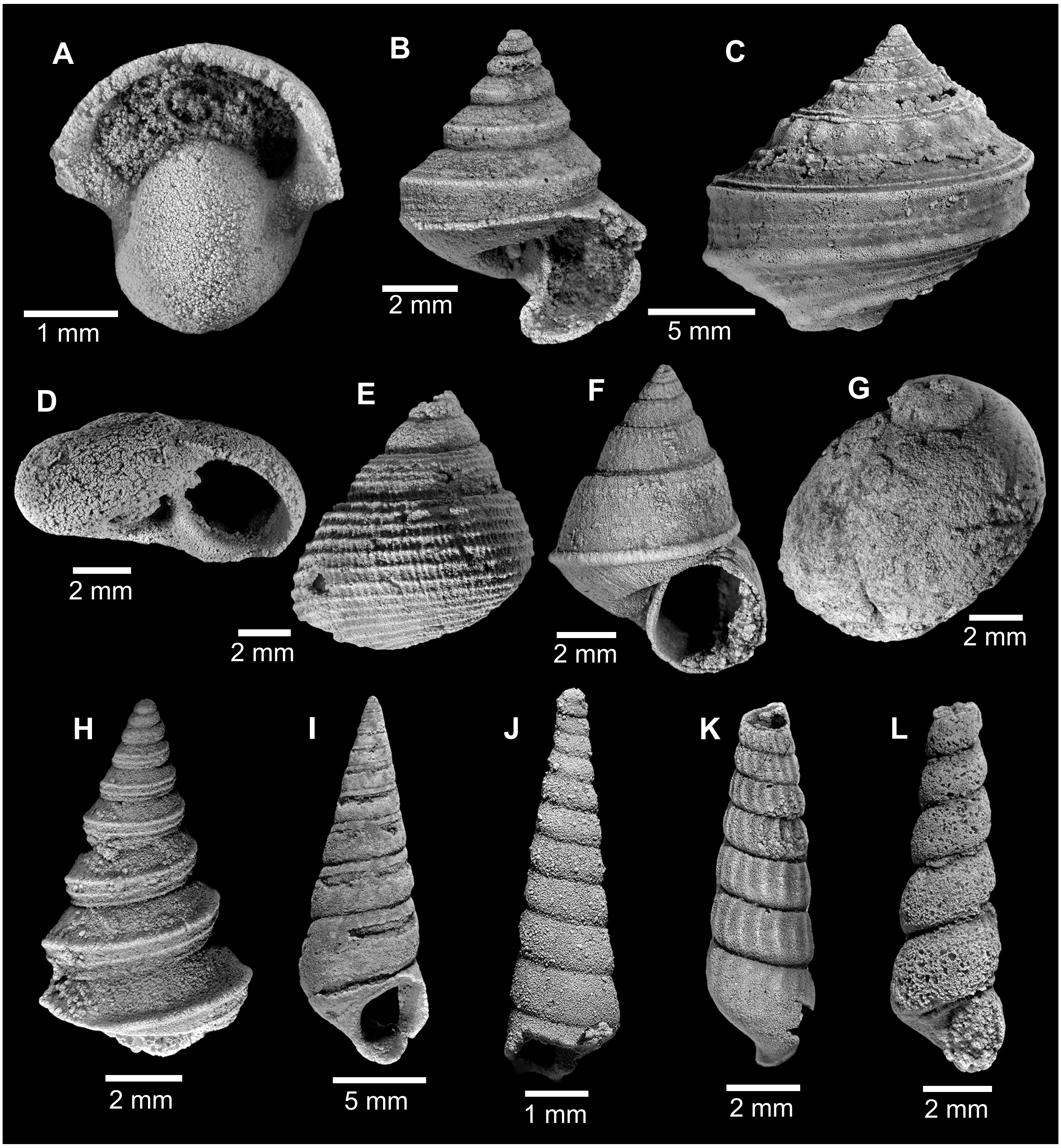

Figure 4.3: The twelve most abundant gastropod species from the Tak Fa Limestone at Nakhonsawan area; A Bellerophontoidean, *Warthia* cf. *brevisinuata* Waagen, 1880, SNSB-BSPG 2014 XI 2. B–F Vetigastropoda, B *Baylea*? *umbilicata* Nützel and Ketwetsuriya, 2016, SNSB-BSPG 2014 XI 13. C *Glabrocingulum thailandensis* Nützel and Ketwetsuriya, 2016, SNSB-BSPG 2014 XI 48. D *Anomphalus* sp., SNSB-BSPG 2014 XI 28. E *Yunnania pulchra* Nützel and Ketwetsuriya, 2016, SNSB-BSPG 2014 XI 34. F *Microdoma carinata* Nützel and Ketwetsuriya, 2016, SNSB-BSPG 2014 XI 47. G Neritimorpha, *Naticopsis* sp., SNSB-BSPG 2014 XI 95. H–L Caenogastropoda, H *Goniasma tricarinata* Nützel and Ketwetsuriya, 2016, SNSB-BSPG 2014 XI 45. I *Protostylus* sp., SNSB-BSPG 2014 XI 56. J *Cambodgia acuminate* Nützel and Ketwetsuriya, 2016, SNSB-BSPG 2014 XI 117. K *Trepsipleura chordanodosa* Kues, 2002, SNSB-BSPG 2014 XI 1. L *Streptacis*? sp., SNSB-BSPG 2014 XI 51.

In comparison, the gastropod assemblage from Khao Chai Thong yielded 402 specimens representing 34 species, i.e. 14 nominate species and 20 species in open nomenclature. The three most abundant species are the same as in the Khao Noi assemblage. *Anomphalus* sp. (32.5%) is the most abundant species again, followed by *Warthia* cf. *brevisinuata* (7.2%). *Glabrocingulum* *magnum* and meekospirid *Cambodgia acuminata* are equally abundant with 6.0% each, as are naticopsid *Naticopsis* spp. and microdomatid *Microdoma carinata* dealing with 4.7% each. Six taxa from the Khao Noi assemblage were not observed in the Khao Chai Thong assemblage; these are, in descending order, the euphemitid *Euphemites graffhami* (0.5%), the trochonematid *Knightinella ornata* (0.5%), the bellerophontid *Khumerspira thailandensis* (0.3%), the trochonematid *Amaurotoma? sp*. (0.3%), the soleniscid *Cylindritopsis spheroides* (0.2%) and the meekospirid *Ceraunocochlis* sp. (0.2%). These taxa are rare at Khao Noi. Almost half of the total number of gastropod species is only represented by one to three specimens. All species of two gastropod assemblages and their abundances are listed in Table 4.1.

Diversity

The diversity of both gastropod assemblages is practically the same. The Simpson indices of the Khao Noi (0.86) and Khao Chai Thong samples (0.87) are identical when considering the relative error intervals. The Shannon-Wiener Index is 2.7 for both assemblages, indicating a moderate diversity.

Rank-abundance distributions confirm these results. The shape of the Khao Noi and Khao Chai Thong distributions are almost the same (Fig. 4.4). When trying to fit models to both rank-abundance distributions, a lognormal model fits best to both assemblages (Table 4.2). However, AIC (Akaike Information Criterion) values indicate that the gastropod assemblage from Khao Noi also fits well to the Zipf model, since the values are almost identical (lognormal 181.21 vs. Zipf 181.39). Both assemblages have a similar diversity and ecological complexity. The evenness is moderate as is indicated by the chosen model (e.g. Magurran 2004).

Rarefaction analysis suggests that the sample sizes of the gastropod assemblages from Khao Noi and Khao Chai Thong are sufficient to estimate diversity, because the rarefaction curves are saturated at approximately 400 specimens (Fig. 4.5). The curves further suggest that two assemblages are almost identical regarding diversity. The similarity of both curves as well as the other mentioned diversity metrics suggest a similar original diversity of biota.

In addition, both studied assemblages closely resemble each other in taxonomic composition and relative abundances with the gastropods *Anomphalus* sp., *Warthia* cf. *brevisinuata* and *Glabrocingulum magnum* being most abundant at both localities, suggesting that they come from the same environmental setting. The similarity both with regard to diversity and composition justifies that these two samples from the Tak Fa Limestone can be pooled to represent a single gastropod assemblage, for further comparisons with other Permian gastropod assemblages from Southeast Asia and adjacent areas.

Table 4.1: Species and their abundances of the studied gastropod assemblages, Khao Noi hill and Khao Chai Thong hill, from the Tak Fa Limestone, Nakhonsawan.

Groups	Species	Number of specimens	
		Khao Noi	Khao Chai tong
Bellerophontoidean	*Euphemites graffhami*	3	0
	Warthia cf. *brevisinuata*	50	29
	Warthia sp.	12	4
	Bellerophon sp.	5	4
	Bellerophon? sp.	2	6
	Pharkidonotus khaonoiensis	11	8
	Khumerspira thailandensis	2	0
	Retispira lyelli	5	2
Euomphalina	*Discotropis*? sp.	1	1
	Euomphalid	5	7
Vetigastropoda	*Baylea*? *umbilicata*	14	11
	Knightinella ornata	3	0
	Knightinella sp.	2	3
	Amaurotoma? sp.	2	0
	Takfaia kuesi	7	9
	Glabrocingulum magnum	46	24
	Anomphalus lateumbilicatus	2	5
	Anomphalus sp.	197	131
	Yunnania pulchra	12	15
	Anticonulus? sp.	3	1
	Coeloconulus panae	1	1
	Eocalliostoma sp.	6	2
	Microdoma carinata	10	19
Neritimorpha	*Naticopsis* spp.	14	19
	Trachydomia takhliensis	9	1
Caenogastropoda	*Goniasma tricarinata*	22	14
	Stegocoelia sp. 1	5	1
	Stegocoelia sp. 2	5	7
	Orthonema sp.	2	2
	Protostylus sp.	44	17
	Soleniscus sp.	5	5
	Strobeus sp.	1	2
	Cylindritopsis spheroides	1	0
	Meekospira sp.	5	8
	Ceraunocochlis sp.	1	0
	Cambodgia acuminata	20	24
	Trepsipleura chordanodosa	21	7
	Pseudozygopleura? sp.	1	1
Heterobranchia	*Streptacis*? sp.	21	11

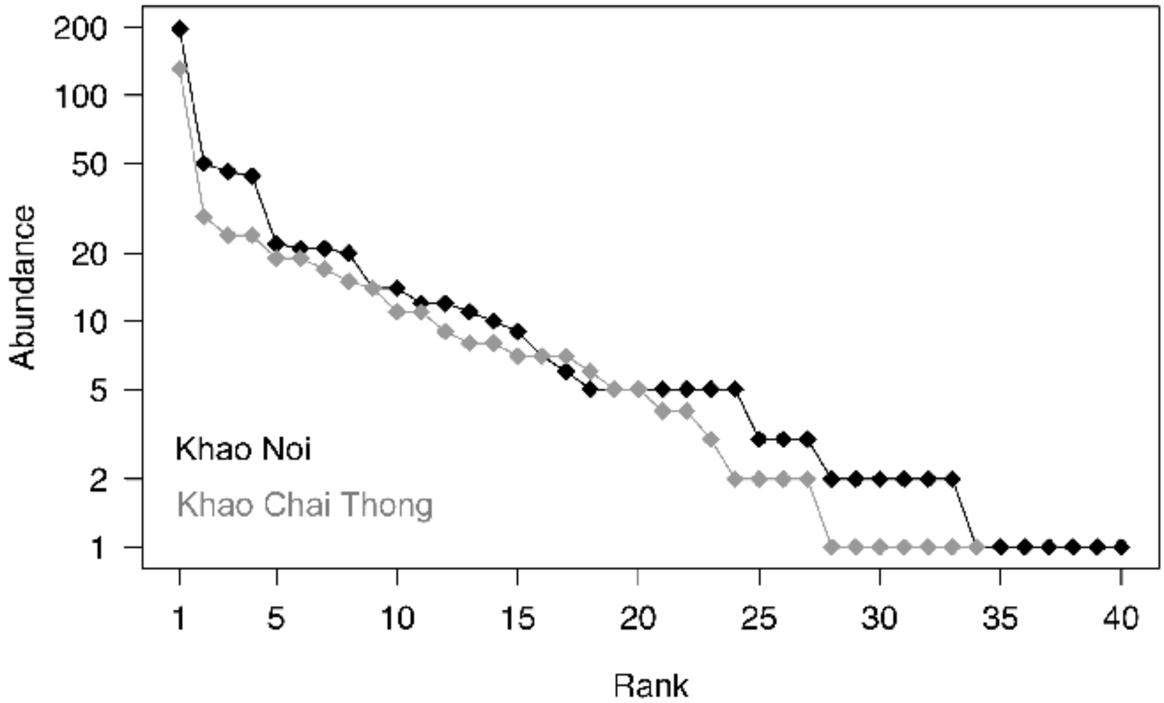

Figure 4.4: Rank abundance diagram of the two studied Middle Permian gastropod assemblages of the Tak Fa Limestone from Khao Noi hill and Khao Chai Thong hill, Tak Fa District, Nakhonsawan Province, Central Thailand.

Table 4.2: Model fit for rank-abundance distributions of the Tak Fa assemblages. Best model fit is shown in bold.

Tak Fa assemblages	Models	AIC
Khao Noi	Brokenstick	413.15
	Preemption	334.06
	Lognormal	**181.21**
	Zipf	181.39
	Zipf-Mandelbrot	183.39
Khao Chai Thong	Brokenstick	243.67
	Preemption	237.82
	Lognormal	**157.83**
	Zipf	163.88
	Zipf-Mandelbrot	165.88

Diversity in specific gastropod groups

Combined from the two sampling localities, the studied gastropod fauna comprises 981 specimens representing 40 species (Fig. 4.6), and is clearly dominated by Vetigastropoda (Fig. 4.7). 526 specimens or 53.6% of the gastropod specimens belong to the Vetigastropoda, which is also the most diverse group (13 species). *Anomphalus* sp. is the most abundant species (33.4%), followed by four “endemic” species, so far only known from the Tak Fa Limestone:

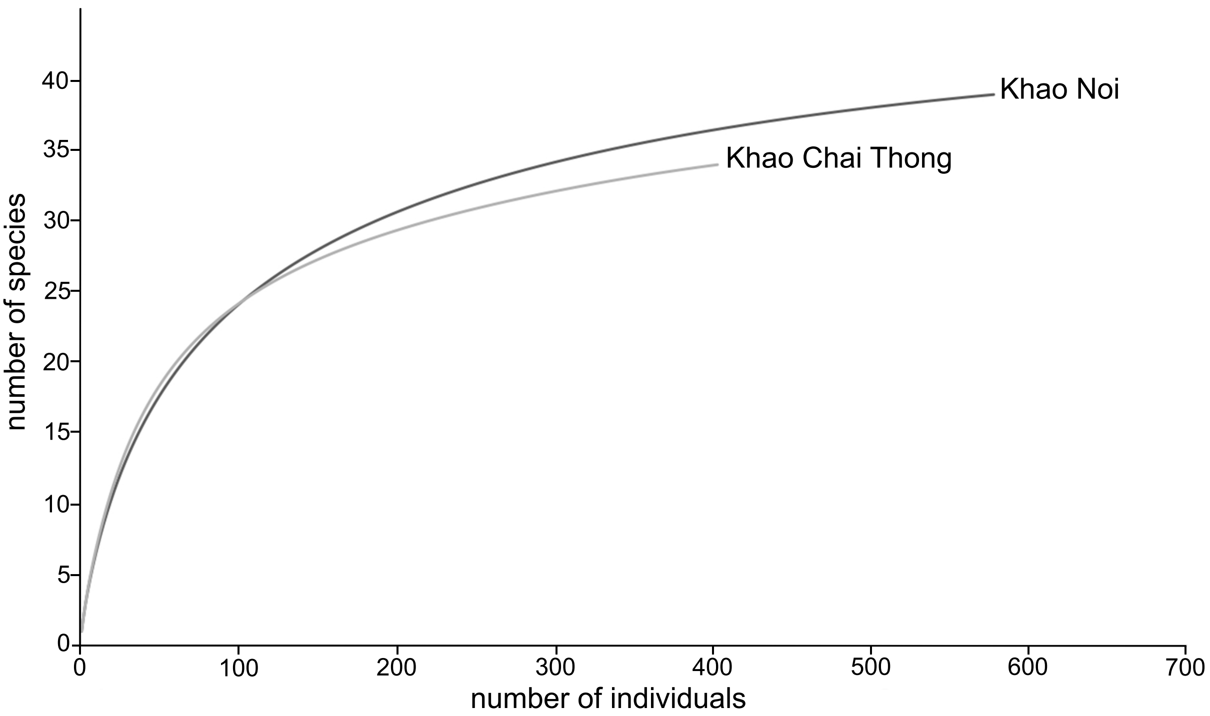

Figure 4.5: Rarefaction curves for the two studied Middle Permian gastropod assemblages of the Tak Fa Limestone from Khao Noi hill and Khao Chai Thong hill, Tak Fa District, Nakhonsawan Province, Central Thailand.

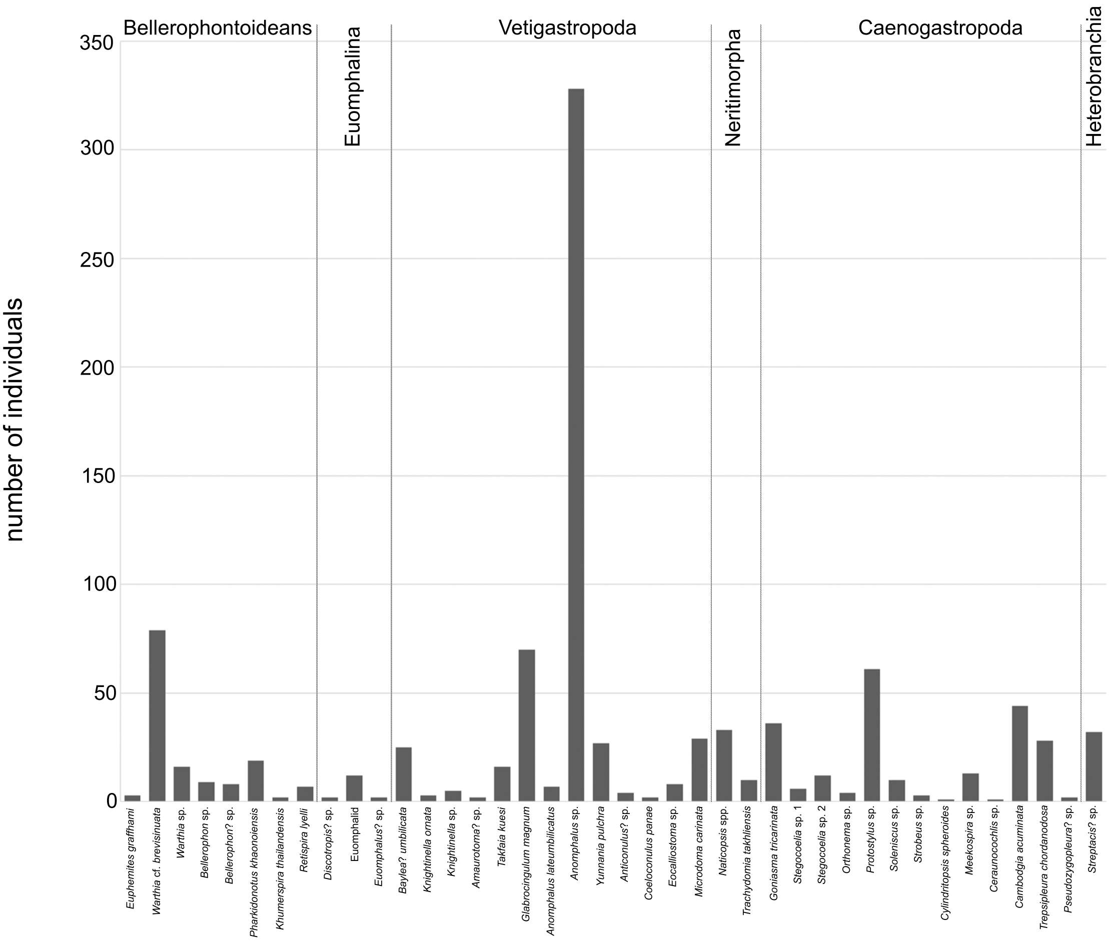

Figure 4.6: Distribution of species abundances (number of specimens) showing a strong dominance and diverse of Vetigastropoda and a diverse of Caenogastropoda in the studied gastropod assemblage of the Tak Fa Limestone, Nakhonsawan.

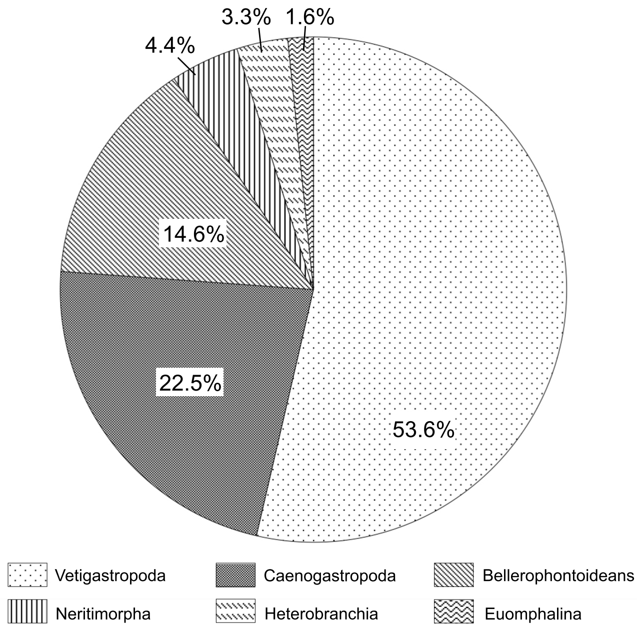

Figure 4.7: Pie chart of gastropod group composition showing the high abundance of Vetigastropoda in the studied gastropod assemblage of the Tak Fa Limestone, Nakhonsawan.

Glabrocingulum magnum (7.1%), *Microdoma carinata* (3.0%), *Yunnania pulchra* (2.8%) and *Baylea*? *umbilicata* (2.5%). The high-spired Caenogastropoda are also important and represent the second most abundant group with 221 specimens (22.5%).

With 13 species, caenogastropods are as species-rich as Vetigastropoda. *Protostylus* sp. (6.2%) is the most abundant caenogastropod, followed by *Cambodgia acuminata* (4.5%), *Goniasma tricarinata* (3.7%) and *Trepsipleura chordanodosa* (2.9%).

The bellerophontoideans are present with 8 species and 143 specimens (14.6%). *Warthia* cf. *brevisinuata* is most abundant in this group (8.1%), followed by *Pharkidonotus khaonoiensis* (1.9%) and *Warthia* sp. (1.6%). The typical cosmopolitan genera *Bellerophon*, *Warthia*, *Euphemites* and *Retispira* are also present in this assemblage. The bellerophontoid species *Pharkidonotus khaonoiensis* and *Khumerspira thailandensis* were newly described from this fauna.

Neritimorpha are present with two typical Late Palaeozoic genera with 43 specimens (4.4%). Of those, *Naticopsis* is more abundant (3.4%), followed by *Trachydomia takhliensis* (1.0%).

Planispiral shells of Euomphalina are only a minor part of the assemblage, comprising 3 species and 16 specimens (1.0%). All species in this group are left in open nomenclature because the specimens are too poorly preserved.

Heterobranchia is represented by a single species, *Streptacis*? sp., with 32 specimens (3.3%). However, it must be noted that protoconchs would be needed to diagnose

Heterobranchia with certainty, but are not preserved in the studied assemblages. Accordingly, the generic and higher assignments remain tentative. It should be noted, though, that *Streptacis* has been commonly reported from Late Palaeozoic deposits.

The significant number of species only known from the Tak Fa Limestone in the analyzed assemblages suggests that Permian Paleo-tethyan gastropod faunas are poorly known and that additional sampling of new fossil sites will result in the finding of new species.

Faunal compositions of the Tak Fa Limestone at Nakhonsawan area

The present collection from the two fossil assemblages from the Tak Fa Limestone in the Nakhonsawan area comprises ca. 1,110 invertebrate fossil specimens, and is characterized by a moderate diversity (moderate species richness and moderate evenness). The analyzed collections comprise a total of 55 species. The assemblage is strongly dominated by gastropods (Fig. 4.8), which account for 88.5% of all specimens (981 gastropod specimens) and 40 species (75.5% of the species), mostly representing widespread Late Palaeozoic genera such as *Warthia*, *Bellerophon*, *Glabrocingulum*, *Anomphalus, Solensicus, Naticopsis* and *Stegocoelia*. The samples also yield three species of bivalves (a small nuculoid bivalve and two indetermined bivalves). Bivalves are the second most diverse group (5.7%). Articulate brachiopods are represented by two small species accounting for 0.4% of the number of specimens. One scaphopod specimen and a polyplacophoran plate are present in the studied samples. Calcareous algae contribute 4.7% of the specimens (fragments) representing two species, a codiaceaen and the dasycladacean *Mitzia* sp.. The samples also yielded large sclerites probably deriving from sponges, counted as a single species and specimen for our analyses. Two species of rugose corals, one solitary and one colonial form, are present. In addition, two species of bryozoans and one crinoid species (crinoid ossicles) are present in the samples from both localities.

The presence of conjoined valves of bivalves, ostracods and brachiopods indicate that the fauna is predominantly autochthonous. Moreover, the presence of the algae and of foraminifera suggests a tropical shallow water environment. Many of the gastropods are strongly fragmented and the complete shells lie in various directions what may suggest deposition in a high-energy environment. However, the presence of complete large shells and articulated shells of bivalves and ostracods suggest that this assemblage is autochthonous or parautochthonous.

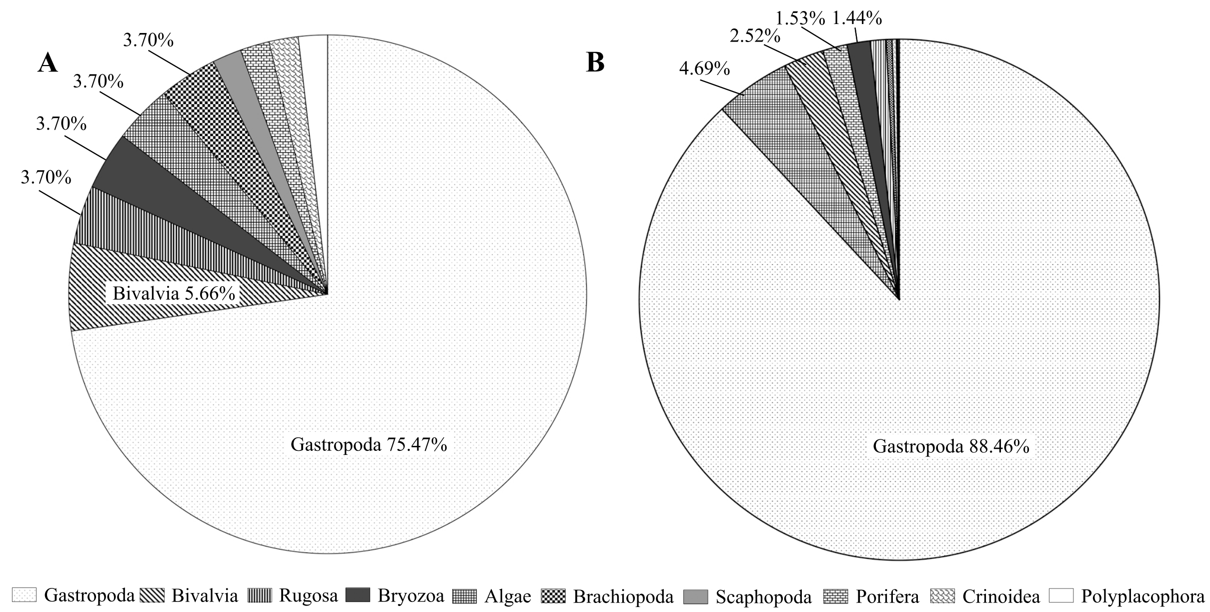

Figure 4.8: Pie chart of species composition (A) and abundance distributions (B) of the studied samples, showing a strong dominance of gastropods.

4.6 Discussion

Gastropods are one of the most diverse marine invertebrate groups of the Late Palaeozoic. They were also widespread in the tropical carbonate platforms in the Paleo-thethys. However, quantitative analyses of the Permian gastropods from East and Southeast Asia have never been conducted and few data sets providing relative abundances have been published so far i.e. from only four areas: Malaysia, East Timor, Japan and the studied gastropod assemblage from Thailand.

When we started our study of Permian gastropods from Thailand, a single nominate gastropod species had been known: *Magnicapitatus huazhangae* Sone, 2010. Meanwhile 44 nominate species and 64 genera have been reported from three locations (Table 4.3), 34 as new species and also two new genera (Ketwetsuriya et al. 2016, 2020a,b). Still, compared to brachiopod taxa reported from Southeast Asia (see Shi and Shuzhong Shen 2000), the number of gastropod occurrences is low. The high proportion of newly discovered species in these gastropod assemblages reflects the poor sampling and given the vast amount of Permian calcareous rocks in Thailand and other areas of Southeast Asia, many of them lacking any paleontological study, we anticipate many new discoveries in this region. In addition, 73 species have been reported in open nomenclature, reflecting the preservation of these gastropods – probably many of them could have been described as new if the preservation was sufficient. Most of the genera present in the Permian of Thailand are typical Late Paleozoic genera with a widespread or even cosmopolitan distribution.

Table 4.3: A list of all Thailand gastropod species and their occurrences from three locations, the Tak Fa Formation, the Ratburi Limestone and the Khao Khad Formation (see Ketwetsuriya et al. 2016, 2020a,b).

Species	Tak Fa	Ratburi	Khao Khad
Euphemites graffhami	●		
Euphemites sp.		●	
Warthia cf. *brevisinuata*	●		
Warthia cf. *saundersi*		●	
Warthia cf. *welleri*			●
Warthia sp. 1	●		
Warthia sp. *2*			●
Warthia? sp. 3			●
Bellerophon erawanensis			●
Bellerophon sp. 1	●		
Bellerophon sp. 2			●
Bellerophon? sp. 1	●		
Bellerophon? sp. 2		●	
Pharkidonotus khaonoiensis	●		
Khumerspira thailandensis	●		
Retispira khaophrikensis		●	
Retispira lyelli	●	●	
Discotropis? sp.	●		
Euomphalus cf. *pronodocarinatus*			●
Euomphalus? sp.	●		
Holopea? sp.			●
Porcellia magninodosa			●
Biarmeaspira mazaevi			●
Apachella thailandensis			●
Baylea? *umbilicata*	●		
Worthenia? *waterhousei*		●	
Worthenia cf. *crenulunula*		●	
Worthenia humiligrada			●
Worthenia cf. *pagoda*			●
Worthenia sp.			●
Altotomaria reticulata			●
Peruvispira sp. 1			●
Peruvispira sp. 2		●	
Gosseletina microstriata			●
Eoplatyzona ratchaburiensis		●	
Knightinella ornata	●		
Knightinella sp.	●		
Amaurotoma? *multispirata*		●	

Table 4.3 (continued)

Species	Tak Fa	Ratburi	Khao Khad
Amaurotoma? sp.	●		
Hesperiella cyrtocostata		●	
Takfaia kuesi	●		
Ananias sp.		●	
Glabrocingulum magnum	●		
Ampezzalina? sp.			●
Anomphalus lateumbilicatus	●		
Anomphalus cf. *vanescens*			●
Anomphalus? *blancus*			●
Anomphalus sp.	●		
Yunnania pulchra	●		
Yunnania inflata			●
Anticonulus? sp.	●		
Coeloconulus panae	●		
Araeonema cf. *tenuistriata*			●
Eucycloscala cf. *asiatica*		●	
Eocalliostoma sp.	●		
Microdoma carinata	●		
Microdoma conicum			●
Coeloconulus panae		●	
Naticopsis spp.	●		
Naticopsis sp. 1		●	
Naticopsis sp. 2			●
Naticopsis sp. 3			●
Naticopsis? sp. 4			●
Naticopsis? sp. 5			●
Naticopsis cf. *heshanensis*			●
Trachydomia takhliensis	●		
Trachydomia suwanneei			●
Trachydomia cf. *nodosum*			●
Trachyspira eleganta			●
Platyzona gradata			●
Goniasma tricarinata	●		
Goniasma sp.		●	
Stegocoelia centrosinuata		●	
Stegocoelia sp. 1	●		
Stegocoelia sp. 2	●		
Stegocoelia? sp. 3		●	
Stegocoelia? sp. 4		●	

Table 4.3 (continued)

Species	Tak Fa	Ratburi	Khao Khad
Procerithium? *Inaequetuberculata*		●	
Orthonema sp.	●		
Trypanocochlea lopburiensis			●
Chlorozyga asiatica		●	
Hyphantozyga? *khaophrikensis*		●	
Leptoptygma sp.		●	
Soleniscus sp. 1	●		
Soleniscus sp. 2		●	
Soleniscus? sp. 3		●	
Strobeus sp. 1	●		
Strobeus? sp. 2			●
Strobeus? sp. 3			●
Girtyspira? sp.			●
Heterosubulites longusapertura			●
Cylindritopsis spheroides	●		
Meekospira sp. 1	●		
Meekospira? sp. 2		●	
Meekospira? sp. 3		●	
Protostylus sp. 1	●		
Protostylus sp. 2		●	
Protostylus sp. 3			●
Knightella irregularis			●
Kimina sp.		●	
Ceraunocochlis sp.	●		
Cambodgia acuminata	●		
Palaeostylus sp.			●
Palaeozygopleura cf. *obesa*		●	
Pseudozygopleura? sp. 1			●
Pseudozygopleura? sp. 2	●		
Trepsipleura chordanodosa	●		
Donaldospira? sp.			●
Streptacis? *khaokhadensis*			●
Streptacis? sp. 1	●		
Streptacis? sp. 2		●	
Yoospira? sp. 1		●	
Yoospira? sp. 2		●	
Problematic uncoiled sinistral taxon		●	
Gen. indet. sp. Indet. 1			●
Gen. indet. sp. Indet. 2			●

With 40 species, the studied gastropod assemblage from the Tak Fa Limestone in the Nakhonsawan area, Central Thailand is relatively rich when compared with other Permian gastropod faunas from Southeast and East Asia. Vetigastropoda are the most abundant and diverse group among the assemblage with the strong dominance of the species *Anomphalus* sp.. This limestone was situated in the Equatorial Warm Water Province of the Palaeo-Tethys (Metcalfe and Sone 2008) and the depositional environment was interpreted as a tropical shallow marine environment in the back-reef on a restricted carbonate platform (Wielchowsky and Young 1985; Jaiboon 2001; Ketwetsuriya 2016).

Batten (1972, 1979, 1985) reported 93 Permian gastropod species from limestones at Lee Mine, Perak, Malaysia which derived from the Sibumasu Terrane (Tsegab et al. 2017). This gastropod fauna yielded bellerophontids, euomphalids, pleurotomarians, trochids, patellids, neritids, murchisoniids, cerithiids, loxonematids and subulitids. The age of this limestone is late Early Permian (Kungurian). This gastropod assemblage is dominated by the high-spired caenogastropods of which *Omphaloptychia paleozoica* is the most abundant species. Vetigastropods are as diverse as caenogastropods. The genera *Glabrocingulum*, *Anomphalus* and *Apachella* are the most abundant vetigastropods. The bellerophontoideans comprise mostly the typical Middle to Late Palaeozoic genus *Bellerophon*. Neritimorpha are the mostly present with the genus *Trachydomia*. The gastropod fauna from Perak, Malaysia is very diverse and has major implications for the palaeobiogeography at the margin of the eastern Palaeo-Tethys.

Wanner (1941) reported 67 species of Permian gastropods from East Timor with planispiral euomphalid shells being the most abundant. Bellerophontoideans make up the second most abundant group and are dominated by the genus *Bellerophon*. Other typical Late Palaeozoic genera such as *Naticopsis*, *Trachydomia* and *Soleniscus* are rare in the Timor fauna. This limestone was deposited in an open shallow marine environment in the Palaeo-Tethys.

Rich Permian gastropod fauna have been reported from Japan. Nützel and Nakazawa (2012) studied a very diverse Permian (Capitanian) gastropod fauna from the Akasaka Limestone (Gifu Prefecture, Japan). The Akasaka gastropod fauna comprises at least 74 species. The Akasaka limestone is dominated by packstones with dark grey colour that were deposited in an open shallow marine environment on a palaeo-seamount in the Panthalassa Ocean (Ozawa and Nishiwaki 1992). The invertebrate fauna is strongly dominated by gastropods and bivalves (Koizumi 1995; Nakazawa 2007; Nützel and Nakazawa 2012). Caenogastropoda are the most abundant and diverse group among the gastropods. The Akasaka gastropod fauna shows relationships to faunas from China, Malaysia, and Vietnam but contains also many formation singletons at species level.

The gastropod faunas from Malaysia, Japan and Thailand derive from fossil assemblages from tropical fusulinid limestones and hence were deposited under similar conditions as the Tak Fa fauna, which is tropical shallow carbonate platforms. In all three cases, gastropods are dominating the macro-fauna (Batten 1972; Koizumi 1995; Nützel and Nakazawa 2012). Therefore, in all these cases gastropod diversity represents a comparable proxy for the diversity of entire macro-fauna.

The comparison of the present Tak Fa fauna with three other reported gastropod assemblages in Asia shows that the diversity of the Tak Fa fauna is relatively low and distinctly less diverse than the gastropod fauna from Malaysia, Timor and Japan according to rarefaction curves (Fig. 4.9) and diversity indices (Table 4.4). The Perak fauna has the highest diversity; diversity measures such as the Simpson index of 0.97 (close to 1) and Shannon-Wiener Index of 3.98 (Table 4.4) indicate a very high diversity. Rarefaction analysis and diversity indices indicate that the Akasaka fauna is as diverse as the Timor fauna and that both significantly exceed the diversity of the studied Tak Fa fauna. Rarefaction curves of both assemblages are not yet fully saturated, therefore additional sampling would result in finding additional taxa.

When fitting models to the rank-abundance distributions of Perak (Malaysia), Akasaka (Japan) and Timor (East Timor) (Fig. 4.10), they all fit best to the Zipf-Mandelbrot model (Table 4.5). In contrast, the Tak Fa fauna resembles mostly the lognormal distribution. This indicates differences in ecological processes (e.g., Wilson 1991; Magurran 2004) effective in the Tak Fa fauna compared to the other investigated Asian gastropod assemblages. Assemblages fitting the Zipf-Mandelbrot model are assumed to be shaped by ecological processes operating successively, whereas assemblages fitting best a lognormal distribution are thought to be characterized by simultaneously operating processes (e.g. Frontier 1985; Wilson 1991; Magurran 2004). For example, species interactions are one of the ecological processes and play together with physical pre-conditions a significant role in structuring successional stages of an assemblage that is described by the Zipf-Mandelbrot model; pioneer species and species which arrive later in a habitat are characterized by different requirements, resulting in a rare abundance of later immigrating species compared to pioneer species (e.g., Frontier 1985, 1987; Wilson 1991). However, since the ecological applicability of rank-abundance models is controversial and the question arises if model assumptions fit for all kind of assemblages (for instance, plants, invertebrates, vertebrates), an ecological interpretation should be drawn with caution (e.g., Magurran 2004). The shape of the rank-abundance distributions shows that the Perak assemblage has the highest evenness of all four assemblages. The second-most even assemblage

– following rank-abundance shape – is that from Akasaka (Japan). The assemblage with the lowest evenness is the one from the Tak Fa Limestone.

In terms of taxonomic composition, the Perak fauna (Malaysia) is dominated by caenogastropods. This is in contrast to the Tak Fa fauna in which vetigastropods form the most abundant group. *Anomphalus* sp., the most abundant gastropod from the Tak Fa fauna, is also present at Perak, and only a single species, *Retispira lyelli* (Gemmellaro, 1890), is shared. Several typical Late Palaeozoic genera such as *Bellerophon*, *Anomphalus*, *Glabrocingulum*, *Naticopsis*, *Trachydomia*, *Goniasma*, *Pseudozygopleura*?, *Meekospira*?, *Orthonema*, *Soleniscus*, *Cylindritopsis* and *Streptacis* are present in both faunas. The genus *Takfaia* from the Tak Fa Limestone resembles the genus *Ambozone* Batten, 1972 from Perak, Malaysia and both genera are probably closely related to each other.

The Akasaka fauna from Japan, high-spired caenogastropods play an important role in this fauna. Moreover, *Coeloconulus panae*, one of the most abundant species from the Akasaka Limestone is present with a single specimen in the Tak Fa assemblage. The Akasaka fauna differs considerably in taxonomic composition from the Tak Fa fauna from Thailand. The vertigastropod *Anomphalus* sp. contributes 33.4% of the abundance of the Tak Fa fauna, conversely it accounts for only 1.6% of the Akasaka fauna.

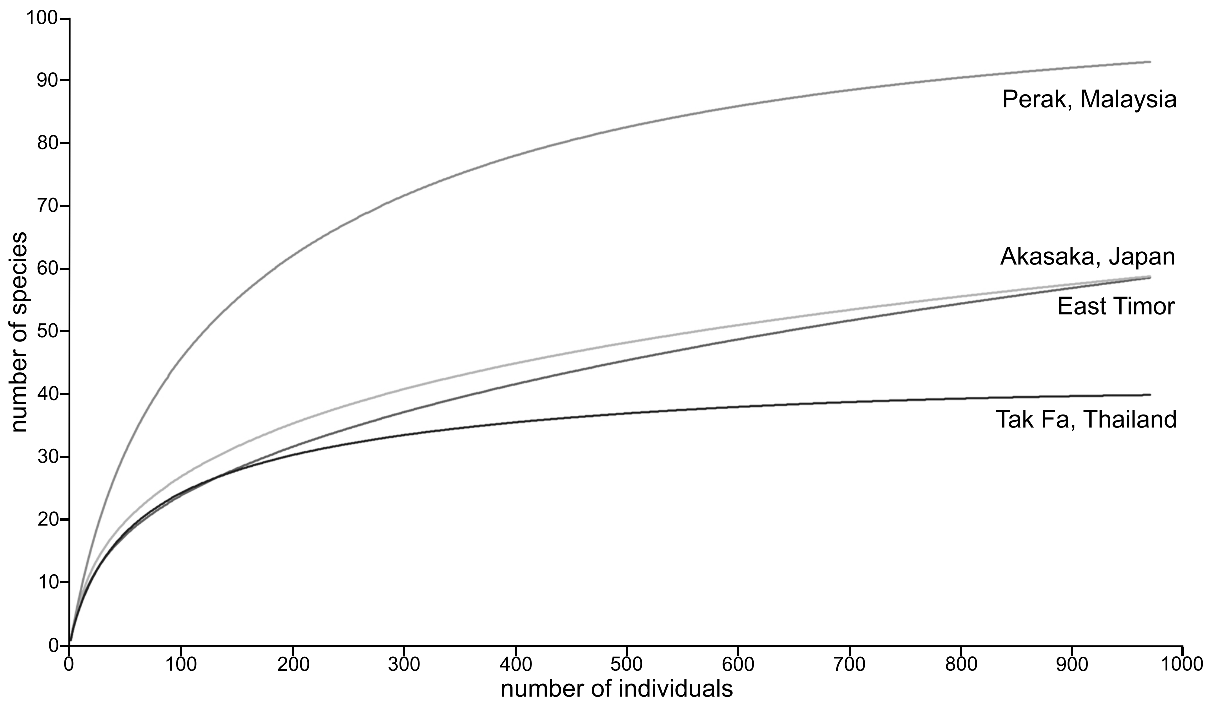

Figure 4.9: Rarefaction curves of the studied Middle Permian gastropod assemblage from the Tak Fa Limestone, Thailand, the Middle Permian gastropod assemblage from Perak, Malaysia (Batten 1972, 1979, 1985), the Middle Permian gastropod fauna from the Akasaka Limestone, Japan (Nützel and Nakazawa 2012) and the Permian gastropod fauna from Timor (Wanner 1941).

Table 4.4: Comparison of the diversity indices between the studied gastropod assemblage from the Tak Fa Limestone, Thailand, the gastropod assemblage from Perak, Malaysia (Batten 1972,1979,1985), the gastropod fauna from the Akasaka Limestone, Japan (Nützel and Nakazawa 2012) and the gastropod fauna from Timor (Wanner 1941).

Samples	Species	Specimens	Simpson	Shannon Wiener
Tak Fa, Thailand	40	981	0.86	2.72
Perak, Malaysia	93	970	0.97	3.98
Akasaka, Japan	74	2263	0.93	3.13
Timor	67	1396	0.90	2.86

Table. 4.5: Model fit for rank-abundance distributions of the Asian assemblages. Best model fit is shown in bold. Both Tak Fa assemblages are pooled in this analysis

Asian assemblages	Models	AIC
Tak Fa, Thailand	Brokenstick	570.59
	Preemption	473.38
	Lognormal	**225.33**
	Zipf	239.35
	Zipf-Mandelbrot	241.35
Perak, Malaysia	Brokenstick	390.13
	Preemption	374.80
	Lognormal	368.10
	Zipf	474.13
	Zipf-Mandelbrot	**355.57**
Akasaka, Japan	Brokenstick	1539.06
	Preemption	430.78
	Lognormal	576.31
	Zipf	922.08
	Zipf-Mandelbrot	**312.15**
Timor, East Timor	Brokenstick	1276.78
	Preemption	480.55
	Lognormal	325.98
	Zipf	444.97
	Zipf-Mandelbrot	**278.37**

The Permian gastropod from East Timor is dominated by planispiral shells of an euomphalid species which contribute almost 30% to the total assemblage, but they are absent in the Tak Fa fauna. Bellerophontoideans make up the second most abundant group in Timor and are dominated by the genus *Bellerophon*, whereas *Warthia* is the most abundant bellerophontoid in the Tak Fa assemblage. The vetigastropod *Anomphalus* sp. is the most abundant gastropod of the Tak Fa fauna, but *Anomphalus* is present with only a single specimen in the Timor fauna. In addition, typical Late Palaeozoic genera are rare in the Timor fauna but abundant in Thailand.

High-spired caenogastropods are the most diverse and abundant group in the Akasaka Limestone as well as in the Perak fauna. Euomphalids are of minor importance in the mentioned Permian gastropod assemblages from Akasaka and Perak, but are abundant in the Timor fauna. Although, rarefaction analysis (Fig. 4.9) and diversity indices of the Timor fauna (Table 4.4) reveal the same curve patterns and the same diversity indices as the Akasaka fauna, the Timor fauna differs strongly in taxonomic composition (there are no shared species and few genera are shared). The taxonomic composition of the gastropod fauna from Timor differs also significantly from those of the Akasaka fauna (Japan), from the Tak Fa fauna (Thailand) and from the Perak fauna (Malaysia). Heterobranchia seems to be less important in all assemblages of Asia. However, protoconch preservation is needed to substantiate heterostrophy and this preservation is either absent or rare in the compared assemblages due to insufficient preservation.

The gastropod fauna of the Tak Fa Limestone shares several taxa with Permian gastropod faunas from China, e.g. from Guangxi and Yunnan provinces, South China (Pan and Erwin 2002) and from Cambodia, e.g. the Permian *Productus* Limestone (Mansuy 1914) and the Permian of Cambodia (Delpey 1941) (Table 4.5). Moreover, some taxa resemble those from the Permian of the USA (cf. Moore 1941; Hall 1858; Chronic 1952; Erwin 1988a,b). However, these shared taxa are rather on generic than species level.

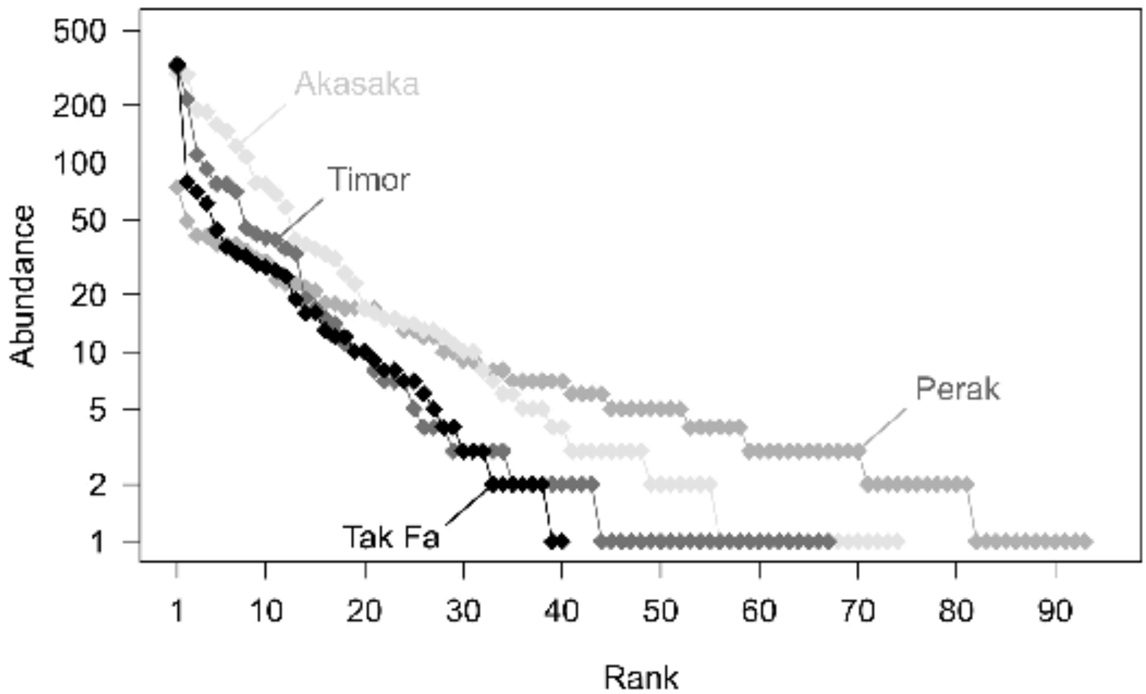

Figure 4.10: Rank abundance diagram of the studied Middle Permian gastropod assemblage from the Tak Fa Limestone, Thailand, and other Permian gastropod assemblages from Asia.

For the mentioned Late Palaeozoic examples including those from Southeast Asia, typical Late Palaeozoic gastropod genera such as *Bellerophon*, *Anomphalus*, *Glabrocingulum*, *Naticopsis*, *Trachydomia*, *Goniasma* and *Meekospira* are present throughout. Others of course are formation singletons, *Takfaia* (Thailand), *Asamiella*, *Akasakiella*, *Costataenia*, *Yochelsonistylus*, *Permocerithium* (Akasaka), *Loxisonia*, *Acrospira*, *Sinuozyga* (Perak, Malaysia), and have not been reported from the diverse and well-studied Permian gastropods faunas of the North American Continent or the western Tethys. They may indicate the presence of the eastern Tethys/western Panthalassa gastropod faunal provinces. The diversity and preservation of these gastropods from Thailand, collected from only a few spots, show the potential for further discoveries in the area.

The differences in diversity and species composition between the mentioned Permian gastropod assemblages from Asia result probably from differences in latitude (Fig. 4.11), in depositional environment, in age and also in sampling methods. Although, these fossil assemblages were deposited under similar conditions, considering that all assemblages derived from tropical shallow marine carbonate platforms of the eastern Palaeo-Tethys during the Permian period, but variations in environmental factors, such as temperature, salinity, oxygenation, or sediment characteristics (Roden et al. 2020) may be linked to the differences in composition. However, it is remarkable that the Perak fauna is significantly more diverse than that of the Tak Fa fauna although the latter lived at lower, palaeo-latitudes, more or less at the palaeo-equator (see Metcalfe and Sone 2008). The Tak Fa fauna lived in a back-reef environment of a restricted carbonate platform of the Indochina Terrane situated closely to volcanic arc. This may have had a limiting impact on its diversity. However, other faunas lived in an open shallow marine environment. The comparison of the Tak Fa assemblage (close to palaeo-equator) with assemblage from higher latitudes could suggest an inverse diversity gradient of Permian gastropods in the Palaeo-Tethys i.e., diversity declines towards the equator. Powell (2009) found a shift of peak brachiopod diversity from South to North during the Phanerozoic; during the Late Palaeozoic, he observed maximum brachiopod diversity at about the palaeo-equator but a slight shift to higher latitudes has occurred during Middle to Late Permian times.

The strong gastropod dominance of the Tak Fa fossil assemblage is remarkable because mollusk and gastropod dominance have been identified as being typical of the Modern Evolutionary Fauna but molluscs were by far not as important in the Palaeozoic (e.g., Sepkoski 1981). However, Clapham & Bottjer (2007) showed that relative abundances of molluscs including gastropods increased considerably during the Permian (analyzed data from the U.S.A., Greece and China). Gastropods are the most abundant and most diverse group of invertebrates in the Permian faunas from Asia (Malaysia, Japan and Thailand) discussed herein. Batten (1985) mentioned that gastropods dominate the fossil assemblage from Perak, Malaysia, although abundances and species richness of the non-gastropods were not reported. Yancey & Stevens (1981) reported communities that are strongly dominated by gastropods from the Early Permian of Nevada and Utah. For the Middle Permian Akasaka Limestone, Japan, Koizumi (1995), Nakazawa (2007) and Nützel and Nakazawa (2012) reported that approximately 55 % of the species belong to Gastropoda. In the Permian faunas from Thailand, gastropods form the most diverse and abundant constituent. Seuss et al. (2008) showed that the fauna of the Pennsylvanian Buckhorn Asphalt Deposit (Pennsylvanian, U.S.A.) – one of the very few Palaeozoic assemblages with aragonitic shell material preserved – is dominated by gastropods.

These examples show that Late Palaeozoic faunas can be dominated by gastropods, although of course not all faunas are dominated by gastropods. Generally, gastropod dominance occurred earlier than previously assumed. For the Late Triassic Cassian Formation, Hausmann and Nützel (2015) and Roden et al. (2020) showed a pronounced mollusk dominance with gastropod being the most abundant and diverse group. This study and our results suggest that mollusk and gastropod dominance date back at least to the Late Palaeozoic/Early Mesozoic and that the apparent lack or scarcity of mollusks in many fossil assemblages are commonly result of taphonomic bias such as strong lithification or aragonite dissolution.

4.7 Acknowledgements

The first author was supported by the Royal Thai Government who provided funding for a scholarship in the frame of the Development and Promotion of Science and Technology Talented Project. We thank Simon Schneider (Cambridge) and Andrzej Kaim (Warszawa) for reviewing this article and for their helpful comments. We are grateful to Pitsanupong Kanjanapayont for information on the geology of Thailand and for his support during the preparation of fieldwork. We would also like to thank Suwannee Phomprasith, Chawisa Phujareanchaiwon, Chittchon Chittpayak, Watcharapol Seeyangnok and students from Department of Geology, Faculty of Science, Chulalongkorn University for their help with field sampling. SNSB-Bayerische Staatssammlung für Paläontologie und Geologie is thanked for financial support.

Table 4.6: A list of all Thailand Permian gastropod genera and their distribution in the Palaeo-Tethys.

Genera	Thailand			Malaysia	Cambodia		Yunnan	South China			Japan	Timor
	A	B	C	D	E	F	G	H	I	J	K	L
Euphemites	●	●							●	●		●
Warthia	●	●	●				●			●	●	
Bellerophon	●	?	●	●	●	●	●	●	●	●	●	●
Pharkidonotus	●											
Khumerspira	●											
Retispira	●	●		●				●	●	●		
Euomphalus	●		●	●	●	●	●		●			●
Discotropis	?											
Holopea			?					●				
Porcellia			●			●	●	●	●			
Baylea	?				●				●	●		
Biarmeaspira			●									
Apachella			●	●					●	●		
Knightinella	●											
Amaurotoma	?	?										
Peruvispira		●	●					●		●		
Gosseletina			●									
Worthenia		●	●	●	●	●	●			●	●	●
Altotomaria			●									
Takfaia	●											
Worthenia		●	●	●	●	●	●			●	●	●
Altotomaria			●									

Table 4.6 (continued)

Genera	Thailand			Malaysia	Cambodia		Yunnan	South China			Japan	Timor
	A	B	C	D	E	F	G	H	I	J	K	L
Takfaia	●											
Ananias		●						●	●			
Glabrocingulum	●			●					●		●	
Ampezzalina			?									
Eoplatyzona		●										
Hesperiella		●										
Eucycloscala		●		●							●	
Anomphalus	●		●	●				●	●		●	?
Yunnania	●		●	●	●	●	●					
Araeonema			●							●	●	
Anticonulus	?											
Coeloconulus	●	●									●	
Eocalliostoma	●											
Microdoma	●		●	●			●					
Naticopsis	●	●	●	●	●	●	●	●	●	●	●	●
Trachydomia	●		●	●	●	●		●			●	●
Trachyspira			●	●				●	●		●	
Strobeus	●		?	●				●			●	
Soleniscus	●	●		●	●	●	●	●		●	●	●
Cylindritopsis	●			●				●	●	●		
Leptoptygma		●						●	●			
Girtyspira			?					●		●		
Heterosubulites			●								●	

Table 4.6 (continued)

Genera	Thailand			Malaysia	Cambodia		Yunnan	South China			Japan	Timor
	A	B	C	D	E	F	G		A	B	C	D
Platyzona			●	●				●			●	
Palaeostylus			●	●	●	●		●	●	●	●	
Palaeozygopleura		●										
Pseudozygopleura	?		?	●				●		●		
Goniasma	●	●		●				●		●	●	
Stegocoelia	●	?		●				●			●	
Orthonema	●			●	●	●				●	●	
Procerithium		?										
Hyphantozyga		?										
Chlorozyga		●										
Cambodgia	●				●	●						
Meekospira	●	?		●				●				
Trepsipleura	●											
Ceraunocochlis	●			●							●	
Kimina												
Donaldospira			?	●								
Knightella			●							●	●	
Protostylus	●	●	●	●	●					●	●	
Trypanocochlea			●								●	
Streptacis	?	?	?	●				●			●	
Yoospira		?										

● present; ? uncertain generic placement. Locations: A, the Tak Fa Formation, Thailand, Middle Permian (Ketwetsuriya et al. 2016); B, Ratburi Limestone, Ratchaburi, Thailand, Middle Permian (Ketwetsuriya et al. 2020a); C, the Khao Khad Formation, Lopburi, Thailand, Middle Permian (Ketwetsuriya et al. 2020b); D, Perak, Malaysia, Middle Permian (Batten 1972, 1979, 1985); E, Cambodia, Middle Permian (Mansuy 1914); F, Sisophon Formation, Cambodia, Middle Permian (Delpey 1941); G, Yunnan, South China, Middle Permian (Mansuy 1912); H, Guangxi and Yunan, South China, Early–Late Permian (Pan & Erwin 2002); I, China, Early–Late Permian (Pan & Yu 1993); J, Western Guizhou, South China, Late Permian (Wang & Xi 1980); K, Akasaka Limestone, Japan (Nützel & Nakazawa 2012); L, Timor, Middle Permian (Wanner 1941)

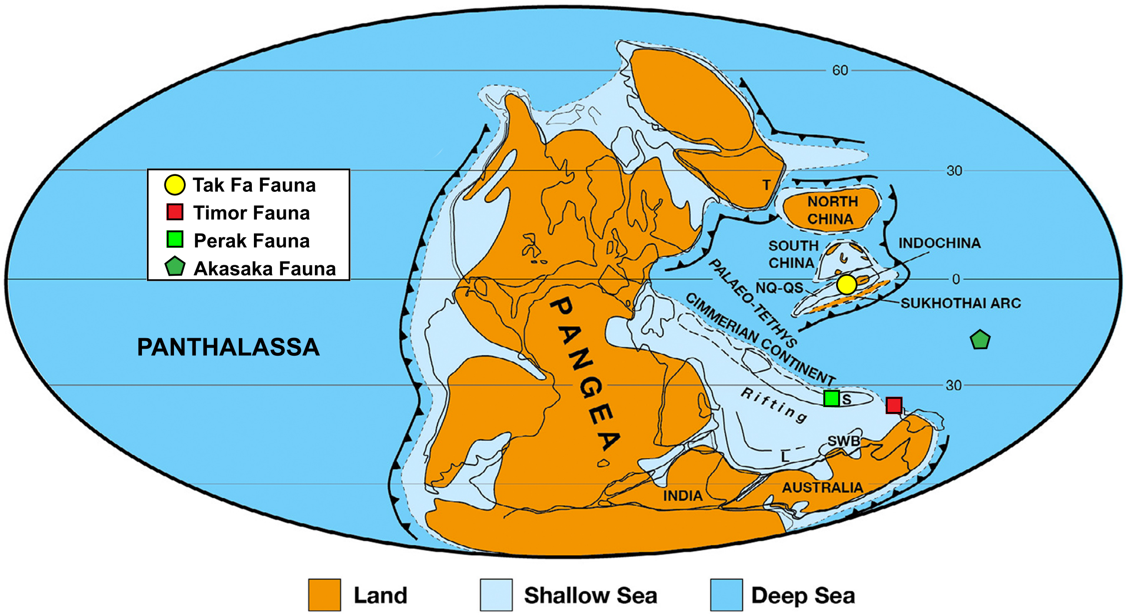

Figure 4.11: Palaeogeographic map for the Middle Permian showing the geographic distribution of Middle Permian gastropods on the Indochina Terrane and the Cimmerian Continent during the Permian. S, Sibumasu; SWB, Borneo; NQ-QS = North Qiangtang-Qamdao-Simao. (Modified from Metcalfe 2013)

4.8 Reference

Batten, R. L. (1972). Permian gastropods and chitons from Perak, Malaysia. Part 1. Chitons, bellerophontids, euomphalids and pleurotomarians. *Bulletin of the American Museum of Natural History*, 147, 1–44.

Batten, R. L. (1979). Permian gastropods from Perak, Malaysia. Part 2. The trochids, patellids, and neritids. *American Museum Novitates*, 2685, 1–26.

Batten, R. L. (1985). Permian gastropods from Perak, Malaysia. Part 3. The murchisoniids, cerithiids, loxonematids, and subulitids. *American Museum Novitates*, 2829, 1–40.

Chitnarin, A., Crasquin, S., Charoentitirat, T., Tepnarong, P. & Thanee, N. (2012). Ostracods (Crustacea) of the Early- Middle Permian from Central Thailand (Indochina block). Part I. Order Palaeocopida. *Geodiversitas*, 34(4), 801–835.

Chitnarin, A., Crasquin, S., Forel, M. -B. & Tepnarong P. (2017). Ostracods (Crustacea) of the Early-Middle Permian (Cisarulian-Guadalupian) from Central Thailand (Indochina Block): Part II, Orders Podocopida, Platycopida and Myodocopida. *Geodiversitas*, 39(4), 651–690.

Chonglakmani, C. & Fontaine, H. (1992). The Lam Narai-Phetchabun region: A platform of Early Carboniferous to Late Permian age. In P. Charusiri, s. Jarupongsakul & V, Pisutha-arnond (Eds.), *Proceeding of the Technical Conference on Development of Geology for Thailand into the year 2000* (pp. 39–98). Bangkok: Chulalongkorn University, Thailand.

Chronic, H. (1952). Molluscan Fauna from the Permian Kaibab Formation, Walnut Canon, Arizona. *Bulletin of the Geological Society of America*, 63, 95–166.

Clapham, M.E. & Bottjer, D. (2007). Permian marine paleoecology and its implications for large-scale decoupling of brachiopod and bivalve abundance and diversity during the Lopingian (Late Permian). Palaeogeography, Palaeoclimatology, Palaeoecology, 249, 283–301.

Delpey, G. (1941). Les Gastéropodes permiens du Cambodge. *Journal de Conchyologie*, 84, 255–278, 345–369.

Erwin, D. H. (1988a). Permian Gastropoda of the Southwestern United States: Cerithiacea, Acteonacea, and Pyramidellacea. *Journal of Paleontology*, 62, 566–575.

Erwin, D. H. (1988b). Permian Gastropoda of the Southwestern United States: Subulitacea. *Journal of Paleontology*, 62, 56–69.

Fontaine, H. Salyapongse, S. & Vachard, D. (1999). Fossils from Khao Sak and the adjacent hills, Amphoe Chon Daen, central Thailand. *CCOP Newsletter*, 24(1), 9–14.

Frontier, S. (1985). Diversity and structure in aquatic ecosystems. In M. Barnes (Ed.), *Oceanography and Marine Biology – An Annual Review* (pp. 253–312). Aberdeen: Aberdeen University Press.

Frontier, S. (1987). Applications of Fractal Theory to Ecology. In: P. Legendre & L. Legendre (Eds) *Develoments in Numerical Ecology. NATO ASI Series (Series G: Ecological Sciences)*, vol 14. (pp. 335–378). Berlin, Heidelberg: Springer.

Gemmellaro, G. G. (1890). La Fauna dei calcari con Fusulina della valle del fiume Sosio nella Provincia di Palermo. *Giornale di Science Naturali ed Economiche*, 20, 97–182.

Grant, R. E. (1976). Permian brachiopods from southern Thailand. *Paleontological Society Memoir*, 9, 1–269.

Hall, J. (1858). Description of new species and fossils from the Carboniferous limestones of Indiana and Illinois. *Transactions of the Albany Institute*, 4, 1–36.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. (2001). PAST: Palaeontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1), 1–9.

Hausmann, I. & Nützel, A. (2015). Diversity and palaeoecology of a highly diverse Late Triassic marine biota from the Cassian Formation at the Stuores Wiesen (North Italy, Dolomites). *Lethaia*, 48, 235–255.

Igo, H. (1972). Fusulinacean fossils from Thailand. Part VI. Fusulinacean fossils from North Thailand. In T. Kobayashi & R. Toriyama (Eds.), *Geology and Palaeontology of Southeast Asia* (pp. 63–116). Tokyo: University of Tokyo Press.

Igo, H. (1992). *Orientoschwagerina* (Fusulinacea) from Khao Tham Rusi, south of Lom Sak, central Thailand. Annual Report of the Institute of Geoscience, University of Tsukuba, No. 18, 43-47.

Jaiboon, T. (2001). *Biostratigraphy of Tak Fa Formation at Khao Wong and Khao Chakkachan, Amphoe Hong Muang, Changwat Lop Buri with reference to Fusulinids*. Master Thesis, Department of Geology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand.

Ketwetsuriya, C., Nützel, A. & Kanjanapayont, P. (2014). A new Permian gastropod fauna from the Tak Fa Limestone, Nakhonsawan, Northern Thailand – a report of preliminary results. *Zitteliana A*, 54, 137–146.

Ketwetsuriya, C., Nützel, A. & Kanjanapayont, P. (2016). Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. *Bulletin of Geosciences*, 91, 481–513.

Ketwetsuriya, C., Cook, A. G. & Nützel, A. (2020a). Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand. *Paläontologische Zeitschrift*, 94, 53–77. https://doi.org/10.1007/s12542-019-00463-0

Ketwetsuriya, C., Karapunar, B., Charoentitirat, T. & Nützel, A. (2020b). Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: implications for palaeogeography of the Indochina Terrane. *Zootaxa* 4766(1), 1–47.

Koizumi, S. (1995). Gastropoda. In K Hachiya (Ed.), *The illustrated collections of Asami Fossil Museum, Fossils of Kinsyozan. Asami Fossil Museum, Gifu* (pp. 95–169). [in Japanese]

Mansuy, H. (1914). Nouvelle contribution à la paléontologie du Yunnan. *Mémoires du Service Géologique de l'Indochine*, 3(2), 1–190.

Magurran, A. E. (2004). *Measuring Biological Diversity*. Malden, MA: Blackwell Publishing

Metcalfe, I. & Sone, M. (2008). Biostratigraphy and palaeobiogeography of Lower Permian (lower Kungurian) conodonts from the Tak Fa Formation (Saraburi Limestone), Thailand. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 257, 139–151.

Moore, R. C. (1941). Upper Pennsylvanian gastropods from Kansas. *State Geological Survey Kansas, Bulletin*, 38, 121–164.

Nakazawa, K. (2007). Minute bivalve fossils from the Permian Akasaka Limestone, Central Japan: (Appendix) Description of a new species of Pernopecten. *Earth Science*, 61, 187–201 [in Japanese with English abstract and English description of new species].

Nakornsri, N. (1976). *Geological Map of Ban Mi Sheet ND 47-4, Scale 1:250,000, Geological Survey Division*. Bangkok: Department of Mineral Resources, Thailand.

Nakornsri, N. (1981). *Geology and Mineral Resources of Amphoe Ban Mi (ND 47-4), Geological Survey Report Number 3*. Bangkok: Department of Mineral Resources, Thailand.

Napradit, T. (2005). *Permian Fusulinoidean Limestones from East of Changwat Nakhon Sawan*. Master Thesis, Department of Geology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand.

Nützel, A. & Nakazawa, K. (2012). Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). *Journal of Systematic Palaeontology*, 10, 103–169.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. & Wagner, H. (2018). vegan: Community Ecology Package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan.

Pan, H. -Z. & Erwin, D. H. (2002). Gastropods from the Permian of Guangxi and Yunnan provinces, South China. *Journal of Paleontology*, 78, Supplement to No 1*, The Paleontological Society Memoir*, 56, 1–49.

Pitakpaivan, K. (1965). Fusulines of the Rat Buri limestone of Thailand. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology*, 17, 3–69.

Powell, M. (2009). The Latitudinal Diversity Gradient of Brachiopods over the Past 530 Million Years. *The Journal of Geology*, 117(6), 585–594

Prado, P. I., Miranda, M. D. & Chalom, A. (2018). sads: Maximum Likelihood Models for Species Abundance Distributions. R package version 0.4.2. https://CRAN.R-project.org/package=sads.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Roden, V. J., Hausmann, I. M., Nützel, A., Seuss, B., Reich, M., Urlichs, M., Hagdorn. H. & Kiessling, W. (2020). Fossil liberation: a model to explain high biodiversity in the Triassic Cassian Formation. *Palaeontology*, 63, 85–102.

Sakagami, S. (1975). Permian bryozoan from Khao Hin Kling, near Phetchabun, North-central Thailand. In T. Kobayashi & R. Toriyama (Eds), *Geology and Palaeontology of Southeast Asia. V.16* (pp. 33–43). Tokyo: University of Tokyo Press.

Sakagami, S. (1999). Permian bryozoans from some localities in the Khao Hin Kling area near Phetchabun, North-central Thailand. *Bulletin of the Kitakyushu Museum of Natural History*, 18, 77–103.

Seuss, B., Nützel, A., Mapes, R. H. & Yancey, T. E. (2009). Facies and fauna of the Pennsylvanian Buckhorn Asphalt Quarry deposit: a review and new data on an important Palaeozoic fossil Lagerstätte with aragonite preservation. *Facies*, 55, 609–645.

Shi, G.R. and Shuzhong Shen. (2000). Asian-Western Pacific Permian brachiopoda in space and time: biogeography and extinction patterns. In: Yin Hongfu, J.M. Dickins, G.R. Shi & Tong Jinnan (Eds.), *Permian-Triassic Evolution of Tethys and Western Circum-Pacific* (pp. 327–352). Developments in Palaeontology and Stratigraphy.

Sone, M. (2010). A new species of the rare neritopsid gastropod *Magnicapitatus* from the Guadalupian (Middle Permian) of East Thailand (the Indochina Terrane). *Alcheringa*, 34, 1–6.

Sone, M., Chonglakmani, C. & Chitnarin, A. (2009). Middle Permian Productidine Brachiopods from Central Thailand (the Indochina Terrane) with Paleobiogeographic Implications. *Journal of Paleontology*, 83(5), 804–810.

Tsegab, H., Sum, C.W., Yuriy, G.A., Hunter, A.W., Abtalib, J. and Kassa, S. (2017). Higherresolution biostratigraphy for the Kinta Limestone and an implication for 1 continuous sedimentation in the Paleo-Tethys, Western Belt of Peninsular Malaysia. *Turkish Journal of Earth Sciences* 26 (5), 377–394.

Ueno, K., & Charoentitirat, T. (2011). Carboniferous and Permian. In M. F. Rido, A. J. Barber and M. J. Crow (Eds.), *The Geology of Thailand* (pp. 71–135). London: Geological Society.

Wanner, C. (1941). Neue Beiträge zur Gastropoden fauna des Perm von Timor. In *Geological Expedition to the Lesser Sunda Islands* Under the leadership of H. A. Brouwer, Professor of Geology at the University of Amsterdam. Vol. 4. *Nieuw Verbond Noord-Hollandsche Uitgevers Maatschappij* (pp.1–71). Amsterdam.

Waterhouse, J. B. (1982). An Early Permian cool-water fauna from pebbly mudstones in south Thailand. *Geological Magazine*, 119, 337–354.

Wielchowsky, C. C. & Young, J. D. (1985). Regional facies variations in Permian rocks of the Phetchabun fold and thrust belt, Thailand. *Conference on the Geology and Mineral Resource Development of NE Thailand*, 41–55.

Wilson, J. B. (1991). Methods for fitting dominance/diversity curves. *Journal of Vegetation Science*, 2, 35–46.

Yanagida, J. (1988). Biostratigraphic Study of Paleozoic and Mesozoic Groups in central and northern Thailand. In J. Yanagida (Ed.), *An Interim Report by the Research Group* (pp. 1–47). Fukuoka: Department of Geology, Faculty of Science, Kyushu University.

Yancey, T. E. & Stevens, C. H. (1981) Early Permian fossil communities in northwestern Nevada and northeastern Utah. In C. Gray, A. J. Boucot & W. B. N. Berry (Eds.), *Communities of the past* (pp. 243–269). Hutchinson: Stroudsburg.

5

Microbial-, fusulinid limestones with large gastropods and calcareous algae – an unusual facies from the Early Permian Khao Khad Formation of Central Thailand

By **Ketwetsuriya C., Nose M., Charoentitirat T. and Nützel A.** In revision in *Facies*. Manuscript number: FACI-D-20-00015

5.1 Abstract

The Early Permian (Kungurian) Khao Khad Formation of Central Thailand consists mostly of carbonates deposited on the western margin of the Indochina Terrane. This formation has yielded unusual microbial-fusulinid limestones with large gastropods which contribute most to the rock volume. With a height of more than 6 cm the gastropods are amongst the largest Early Permian gastropods ever reported. Gastropods as major rock formers are rare in the Palaeozoic. This, and other recently reported invertebrate faunas from Thailand shows that gastropods may dominate Permian fossil assemblages not only in diversity but also regarding abundance and in some cases also regarding biomass. Besides gastropods, fusulinids, various calcareous algae, intraclasts and thick microbial-cyanobacterial (*Girvanella* and *Archaeolithoporella*) coatings and reticulate microbial patches as well as thick inter- and intragranular radial fibrous cement crusts are present. The gastropods represent at least four species and belong probably to undescribed taxa. The fusulinid *Misellina* (*M.*) *termieri* and *Pseudofusulina* sp. are reported form the Khao Khad Formation for the first time and indicate a Bolorian age. Calcareous algae are dominated by dasyclads followed by gymnocodiaceans and solenoporaceans. The studied limestone almost completely lacks metazoan reef builders such as corals and sponges. Likewise, brachiopods and bivalves are absent in the studied samples and echinoderms are very scarce. The carbonate is interpreted as product of shallow water, back-reef lagoonal platform community with a high productivity providing the large gastropods with sufficient food. However, conditions were too eutrophic for sessile filter feeders including metazoan reef builders.

Keywords Khao Khad Formation, large gastropods, Saraburi Group, dasyclads, microbialites, Permian

5.2 Introduction

The role of gastropods – one of the major marine invertebrate clades – in the vast Late Palaeozoic deposits of Southeast Asia has been poorly known until recently. Even the other invertebrate fauna from that region is not particularly well studied. This hinders analyses of faunal distributions and diversity patterns in an area that was likely a diversity hotspot during that time, situated at low latitudes at the Eastern margin of the Tethys Ocean. It also hinders a global picture of marine faunas prior to the end-Permian mass extinction event. Also, the evolutionary history of gastropods remains insufficiently known if data from vast areas are missing. There is evidence that the gastropod contribution to diversity and relative abundance has been underestimated until recently and that gastropods may even represent the most diverse and abundant group in many Late Palaeozoic fossil assemblages (Clapham & Bottjer 2007; Seuss et al. 2008; Ketwetsuriya in press) although global generic gastropod richness rarely exceeds 15% of all invertebrate genera (Roden et al. 2020, fig 4).

The present paper reports and interprets an unusual Permian carbonate facies from Thailand that is rich in large, high-spired gastropods, fusulinids, dasyclads and microbes. Until recently, the Permian of Thailand was *terra incognita* regarding gastropods. A single nominate species had been reported until we started to explore Permian gastropod faunas from Thailand (Ketwetsuriya et al. 2014–2020). Several diverse silicified and non-silicified assemblages were discovered and some of the fossil assemblages are dominated by gastropods. The calcareous rocks of the Khao Khad Formation are at least locally rich in large, undescribed gastropods showing that this group was an important part of the Permian carbonate platform biota. Herein we describe a new unusual coarse grained rudstone facies from the Khao Khad Formation at Khao Wong Hill, Phra Phutthabat district, Saraburi Province, *Central Thailand,* characterized by large gastropods, fusuline foraminifers, calcareous algae, intraclasts, thick microbial-cyanobacterial coatings, microbialites as well as thick inter- and intragranular radial fibrous cement crusts. In this work, microbes, algae and gastropods are described and analyzed as well as the fusuline foraminifers that are used for age determination. The results of microfacies analysis and a comparison with previous relevant microfacies studies from Thailand and adjacent countries provide new insights into carbonate sedimentology of the Late Palaeozoic of Thailand.

5.3 Geological setting

Permian limestones have an extensive distribution on the margin of the Indochina Terrane (Tabakh and Utha-Aroon 1998; Sone and Metcalfe 2008; Udchachon et al. 2014). The Permian of central Thailand has long been part of intensive research focusing on stratigraphy, sedimentology and tectonic evolution along the western margin of the Indochina Terrane (e.g., Wieldchowsky and Young 1985; Chonglakmani 2001; Udchachon et al. 2014; Dew et al. 2017). It is characterised by a complex reef-bearing carbonate platform and basin development during the Late Pennsylvanian to Guadalupian (Hinthong 1981; Fontain et al. 1996, 1999; Assavapatchara et al. 2006; Udchachon et al. 2007; Sone and Metcalfe 2008) prior to the Indosinian Orogeny (Morley et al. 2013; Dew et al. 2017), resulting in complex tectonic patterns with several fold-and-thrust belts.

The Saraburi Limestone (Saraburi Group) of the Khao Khwang platform of the Indochina Terrane extensively exposes as numerous limestone hills, ridges and occasionally as mounds in central Thailand especially in the Saraburi region situated on the eastern side of the Chao Phraya Central Plain and the western margin of the Khorat Plateau (Ueno and Charoentitirat 2011). Numerous studies of the Saraburi Limestone have been conducted covering various aspects of geology and palaeontology (e.g., Dawson and Racey 1993; Chitnarin et al. 2012, 2017; Ketwetsuriya et al. 2014, 2016).

The Khao Khad Formation of the Saraburi Group, which is a part of the Khao Khwang platform, generally developed through the Early–Middle Permian on a marine shelf with a broad range of environments ranging from peritidal, low-energy lagoonal, high-energy middle platform to back-reef, algal reef to outer shelf fore slope settings (Thambunya et al. 2007; Dew et al. 2017).

Thailand is composed of at least two continental lithospheric terranes and was formed by their collision during latest Palaeozoic–early Mesozoic time (Metcalfe 2002, 2006, 2011; Ueno and Charoentitirat 2011). The Indochina Terrane, which is a distinct terrane in the east of Thailand, derived from Gondwana during the Early Devonian (Metcalfe 1999, 2002*, 2017*) and located at nearly 10º south of the palaeoequator (Tabakh and Utha-Aroon 1998; Thambunya et al. 2007; Metcalfe 2013) in the eastern Palaeotethys during the Permian period. Permian sedimentary rocks are exposed extensively as carbonates at the western margin of the Indochina Terrane (Sone and Metcalfe 2008; Ueno and Charoentitirat 2011; Ueno et al. 2012; Warren et al. 2014; Udchachon et al 2014). In terms of palaeogeography, these Permian rocks consist of three major elements: the Khao Khwang Platform in the west, the Pha Nok Khao Platform in the east and the Nam Duk Basin located in the middle of the Loei–Petchabun Fold Belt in central Thailand covering the Saraburi and Petchabun region (Wieldchowsky and Young 1985). The sedimentary successions of these platforms are part of the Saraburi Group (or Saraburi Limestone) and were deposited on a tropical shallow-marine carbonate platform developed from the Asselian to Capitanian (Altermann 1989; Fontaine 2002; Ueno and Charoentitirat 2011). During the Indosinian Orogeny (Early–Late Triassic), the Khao Khwang Platform was deformed within the Khao Khwang Fold–Thrust Belt (Morley et al. 2013; Arboit et al. 2014, 2016, 2017; Zaw et al. 2014).

The rocks studied herein were collected from a 50 cm thick layer exposed in a quarry, which is located at the Khao Wong hill (GPS position 14°40′16″N, 100°49′32″E) in Phra Phutthabat district about 20 km north-east of Saraburi Province (Fig. 5.1). This layer consists of a grey fossiliferous limestone yielding abundant large gastropods, microbes, algae and fusulines

(Figs. 5.2, 5.3) while the other layers are not apparently as rich in gastropods. The investigated Permian carbonate belongs to the Khao Khad Formation of the Saraburi Group, which is a part of the Khao Khwang Platform (Ueno and Charoentitirat 2011; Warren et al. 2014). The structural and fluid evolution of this area was studied by Warren et al. (2014) that was part of the fold and thrust belt which developed during the Indosinian Orogeny (Sone and Metcalfe 2008; Morley et al. 2013) and resulted in steeply inclined bedding, normal and thrust faults as well as folds.

The Khao Khad Formation was named by Hinthong (1981). It is composed mainly of thin- to very thick-bedded limestone with chert nodules and interbedded argillites, dolomitic shales, siltstones, sandstones and conglomerates in the Saraburi area. This formation commonly yields fusulines, brachiopods, gastropods and some ammonoids assemblages. The fauna and the bioclastic lithology suggests that the Khao Khad Formation was deposited in a shallow marine carbonate platform environment (Thumbunya et al. 2007; Ueno and Charoentitirat 2011; Dew et al. 2017). Facies analyses of the Khao Khad Formation have been performed at some localities (e.g., Thumbunya et al. 2007; Warren et al. 2014)

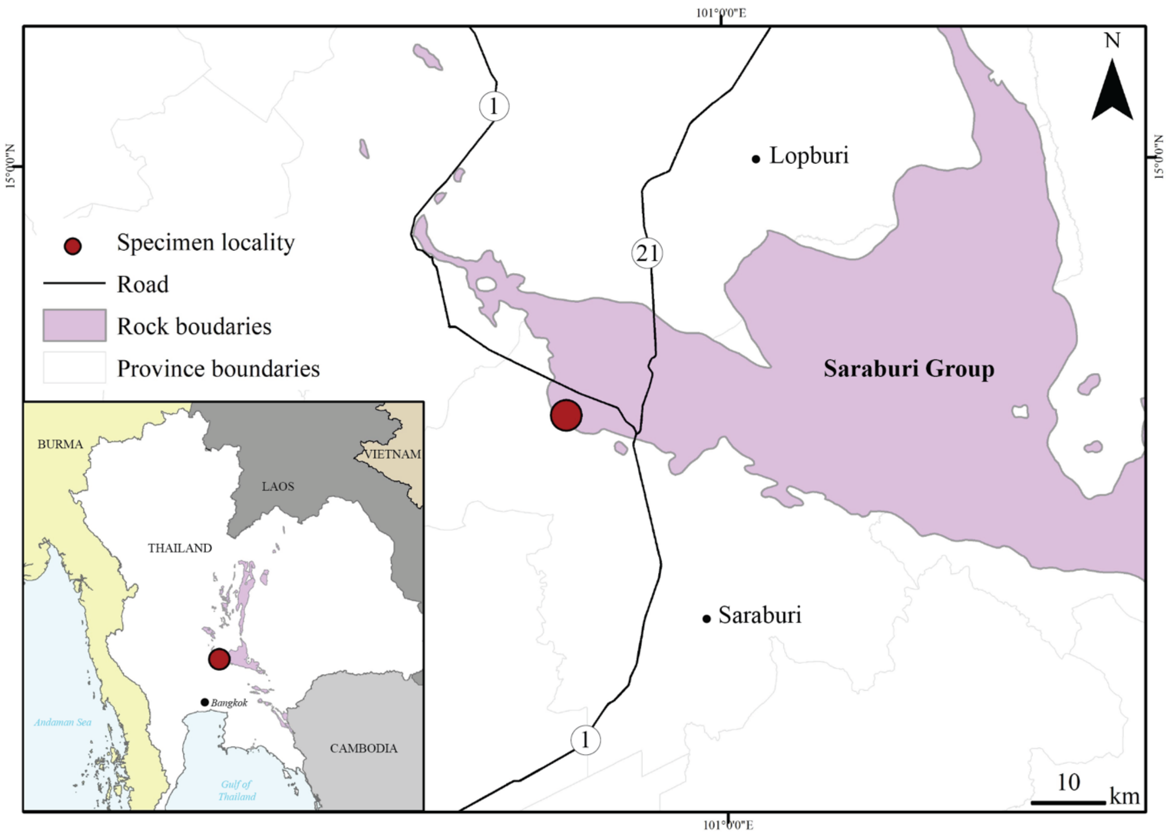

Figure 5.1: Simplified geologic map of the Saraburi Group in Saraburi Province, Central Thailand. The investigated locality is situated at Khao Wong hill, Saraburi Province which is a part of the Khao Khad Formation of the Saraburi Group.

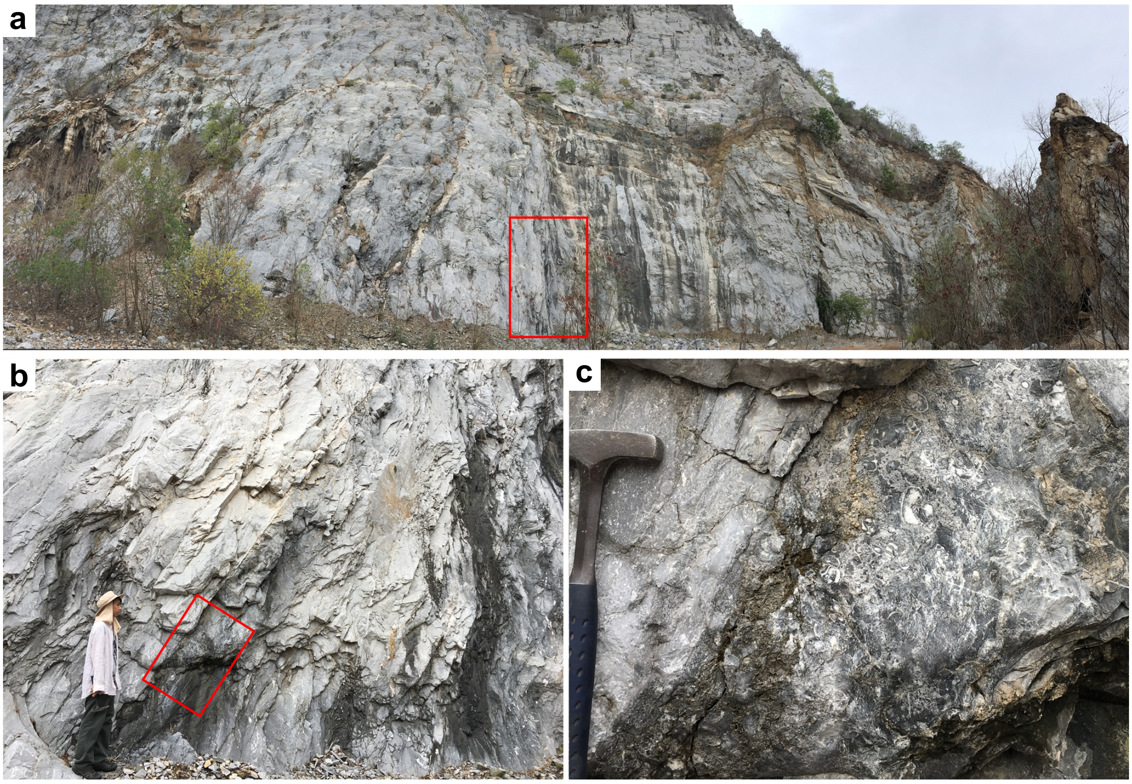

Figure 5.2: Outcrop photographs of the studied layers. a Outcrop panorama of the Khao Khad Formation at Khao Wong hill, Saraburi Province. b showing a position of the studied shell bed in the outcrop (marked by red square). c Bioclastic-packstone composed mainly of large gastropods.

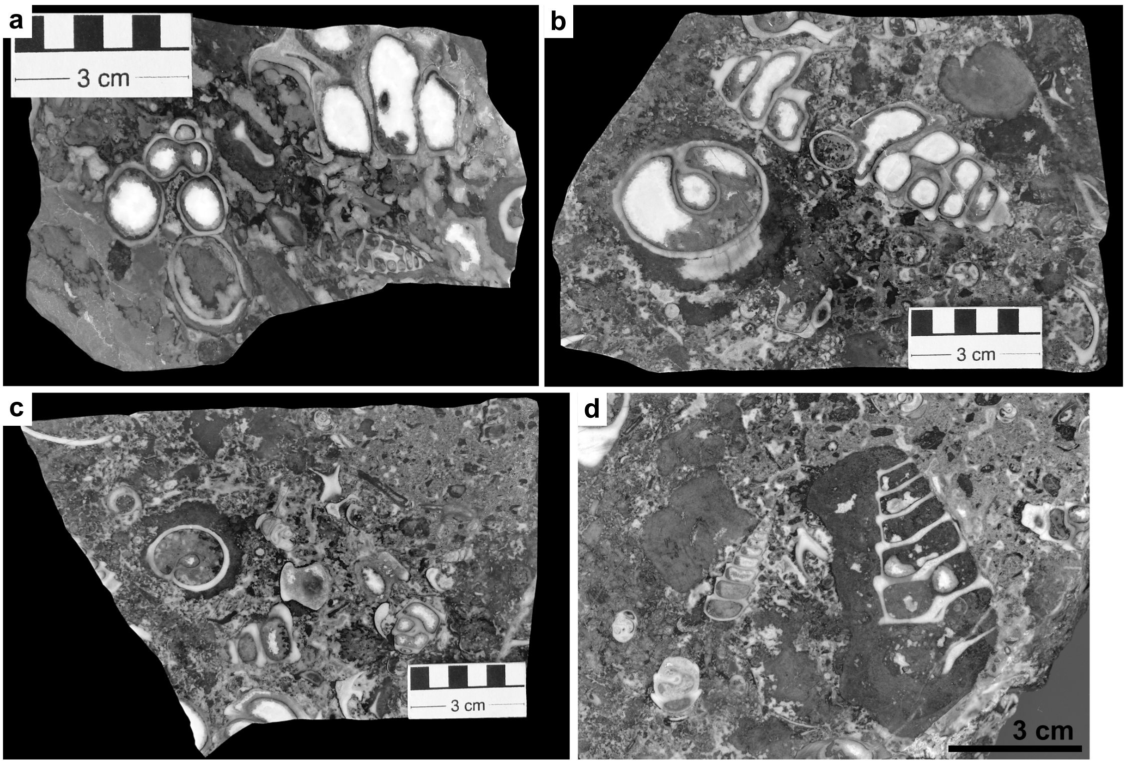

Figure 5.3: Polished slabs of the studied limestone samples. a Poorly sorted coated-grain rudstone with large gastropods and oncoids. sample no. KW-3-01. b–c Poorly sorted packstone containing large gastropods, fusuline foraminifers, solenoporaceans, dasyclads and non-skeletal microbialitic structures. b sample no. KW-3-04; c sample no. KW-3-06. d Coarse-grained intraclast packstone. sample no. KW-3-03.

According to the fusuline foraminifers, the Khao Khad Formation developed from the Early to Middle Permian (Sakmarian–Murgabian or possibly Midian) (Toriyama and Sugi 1959; Toriyama et al. 1974, Toriyama 1975; Toriyama and Kanmera 1977, 1979; Dawson 1993; Charoentitirat 2002; Ueno and Charoentitirat 2011). However, the presence of fusuline foraminifers in the studied limestone samples from the Khao Wong Hill, including *Pseudofusulina* sp. (Fig. 5.4a,b) and *Misellina* (*M.*) *termieri* (Fig. 5.4c,d) shows the certain age constraints. *Misellina* (*M.*) *termieri* is indicative and one of common fusuline fauna widely distributed from Turkey to Japan (Ingavat et al., 1980). It has been reported from *Misellina otai*-*M.*cf. *termieri* Zone of Saraburi Limestone in the Khao Phlong Phrab of Saraburi area and from *Misellina* (*M.*) *termieri* Zone of Pha Nok Khao platform in Loei area (Charoentitirat, 2002). Therefore, the carbonate succession represented by this zone can be correlated within Bolorian Stage of the Tethyan standard zonation for the Permian (=latest Kungurian, Early Permian).

5.4 Materials and Methods

Limestone block samples that yielded abundant gastropods were collected from a 50-cm-thick layer that yielded abundant gastropods collected in the quarry at the Khao Wong hill (Fig. 5.2a), Phra Phutthabat district, Saraburi Province. Microfacies characteristics including biota were analyzed based on 7 large thin-sections of sizes 14 x 9 cm and 10 x 7 cm that were made at Friedrich-Alexander-University Erlangen. The petrographic descriptions were performed according to Flügel (2004) and carbonate rocks were classified after Dunham (1962). In addition, the proportion of components was calculated through point counting on thin sections. For each section, approximately 10,000 points were considered as adequate for quantitative characterization (Dual point counting, see Flügel 2004). The fusuline content was investigated in order to determine the age of the studied material.

The material under investigation (thin sections, polished slabs, raw material) and illustrated within the manuscript is deposited at the Bavarian State Collection of Palaeontology and Geology in Munich, Germany (no. SNSB-BSPG 2020 LV).

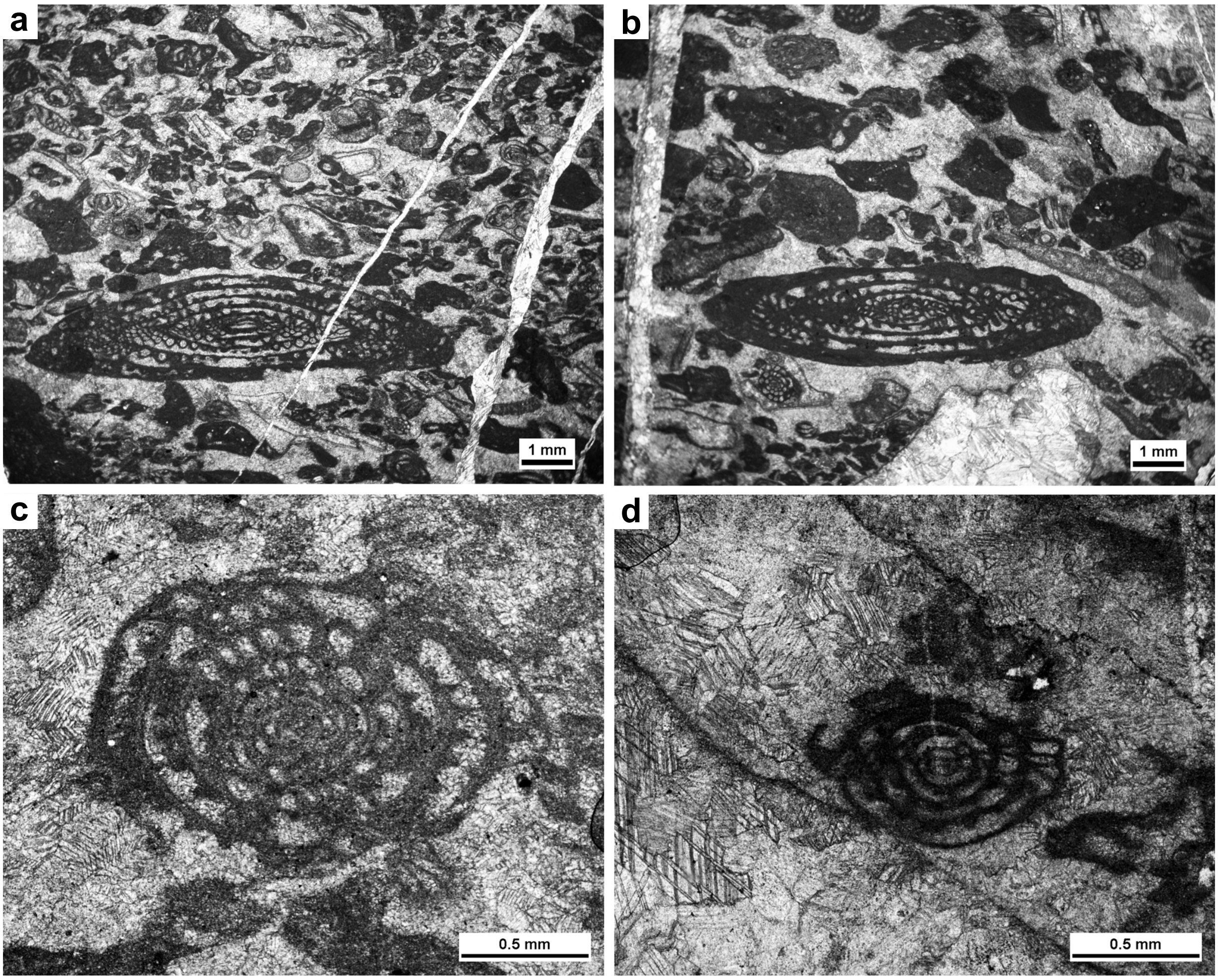

Figure 5.4: Photomicrographs of fusuline foraminifers of the studied limestone samples. **a,b** *Pseudofusulina* sp. **c,d** *Misellina* (*M.*) *termieri*.

5.5 Results

Microfacies description

The carbonates of the studied material are rudstones, floatstones, grainstones and bindstones with abundant large gastropods, microbes, microbialites, calcareous algae and fusulines as well as oncoids and intraclasts.

Two subfacies types (A and B) are differentiated based on their biotic composition obtained by point counting represented by bar graph (Fig. 5.5). The bar graph shows the main components for each microfacies which mainly consist of gastropod shell fragments and micrite as well as sparry cement.

Microfacies A: large gastropod-calcareous alga-fusuline pack- to rudstone/bindstone (Fig. 5.6)

Microfacies A is the predominating facies in the studied samples. It is composed of numerous bioclastic constituents which are mainly large gastropods (21.5%), calcareous algae (3.5%) and fusulines (1.0%). Microproblematic organisms include *Irregularina* sp., a putative lobose amoebozoan, and accessory *Tubiphytes* sp. Irregular meshes of thin micritic threads occur locally and might represent sphinctozoid sponges with affinities to *Uvanella* (see below). Non skeletal constituents comprise various-sized intraclasts and lumps (7.2 %) with microbialitic, micritic or bioclastic composition. In rare cases large gastropods occur within large intraclasts (up to 6 cm). Among calcareous algae, algal remains constitute several transverse sections of various dasyclad algae including large *Macroporella* sp. (2.6%, ca. 2-3, up to 10 mm diameter), solenoporaceans (*ca*. 20-30 mm diameter) as well as cm-sized cluster of "phylloid algae" (mainly *Eugonophyllum*). Microbialites (10.8%) encompass skeletal (e.g., anastomosing filaments of *Girvanella* cf. *magna*) and non-skeletal microbial encrustations on gastropods and other biomorphic remains as well as non-skeletal microbialites within the groundmass like reticular microbial patches (see below). The groundmass consists of micrite (30.4%) and interparticular sparry calcite cements (25.6%).

Microfacies B: large gastropod-oncoid rudstone (Fig. 5.7)

In the outcrop this microfacies occurs at the upper part of the limestone layer (approximately 5 cm-thick) and is again composed mainly of large gastropods (29.2%). However, this facies

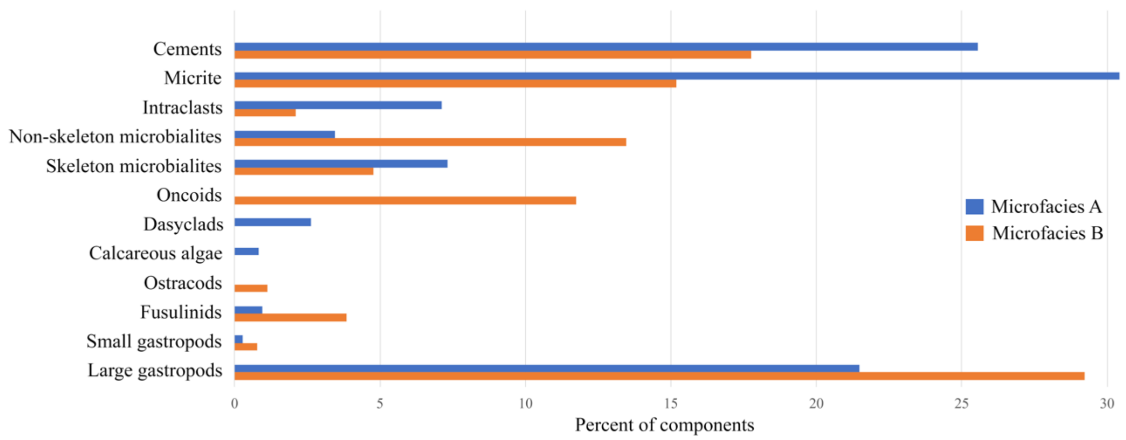

Figure 5.5: Bar graph showing relative abundance of components of two subfacies types (Microfacies A and Microfacies B)

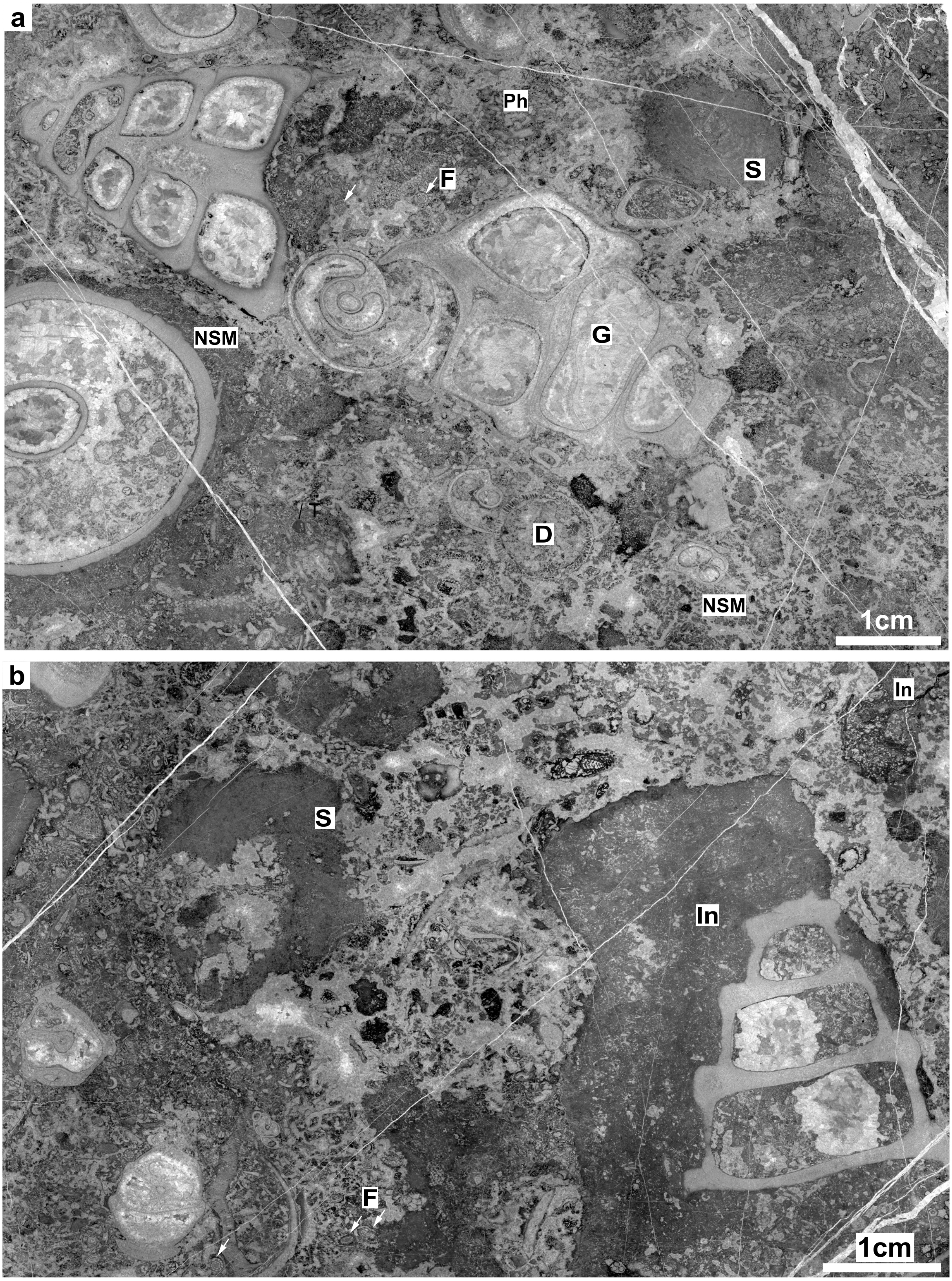

Figure 5.6: Photomicrographs of Microfacies A: large gastropod-calcareous alga-fusuline pack- to rudstone/bindstone. a Poorly sorted packstone containing large gastropods (G), fusuline foraminifers (F, white arrows), solenoporacean (S), dasyclad (D), phylloid algae (Ph), non-skeletal microbialitic structures (NSM). b Coarse-grained intraclast packstone. Intraclast (In), solenoporacean (S), fusulinids (F, white arrows).

is distinguished from microfacies A by the occurrence of large oncoids with ellipsoidal shape, partly controlled by the shape of the biomorphic cores (11.8%, variable width between 10.0-17.5 mm). Frequently, the oncoids are encrusted by thick enigmatic *Archaeolithoporella* sp. crusts. Besides oncoids non-skeletal constituents include irregular microbial or micritic intraclasts (2.1%). Skeletal constituents (excluding large gastropods) are fusuline foraminifers (3.8%), ostracods (1.1%) and small gastropods (0.8%) as well as other shell fragments and rare crinoid stem fragments. Calcareous algae are scarce in this subfacies. The groundmass is composed of sparry interparticular calcite (18.9%) and micrite (15.2%).

Remarks on diagenesis

The coarse-grained facies described herein reveals a complex diagenetic history. Thin sections analysis revealed early diagenetic isopachous radialfibrous interparticular cements and late diagenetic blocky calcite thin sections analysis show several features of neomorphic overprint. Gastropod shells are strongly recrystallized (with ghost structures). Moreover, aggrading neomorphism (pseudospar) of original fine-grained matrix (micrite), asymmetric dripstone-like cement crusts on mollusc shells and vadose silt as geopetal void fillings were observed. Hence, multiple subaerial exposures and/or meteoric phreatic and vadose diagenetic overprint is very likely. Since diagenesis is out of the focus of this study and needs much more detailed structural and geochemical analyses we refer to a separate investigation.

Facies interpretation

Microfacies A: The composition of the large gastropod-calcareous alga-fusuline facies type described herein with its abundance of calcareous algae (mainly dasycladaceans and solenoporaceans), and skeletal as well as non-skeletal microbialites is indicative for a well-lit mesotroph shallow water environment. The coarse grained relatively micrite-poor packstone/grainstone/rudstones fabrics developed in agitated water. The usually well-preserved gastropods and the fusulinids were part of the living community together with algae and microbes, the latter of which were frequently prone to degradation and parauthochthonous resedimentation. The presence of abundant calcareous algae supports the attribution of this subfacies type to a shallow water environment in the platform interior (cf. Flügel 2004). Gastropods are also considered to be tolerant to high temperature and salinity variations which point to at least some or temporary environmental restriction (Wagner and Van der Togt 1973;

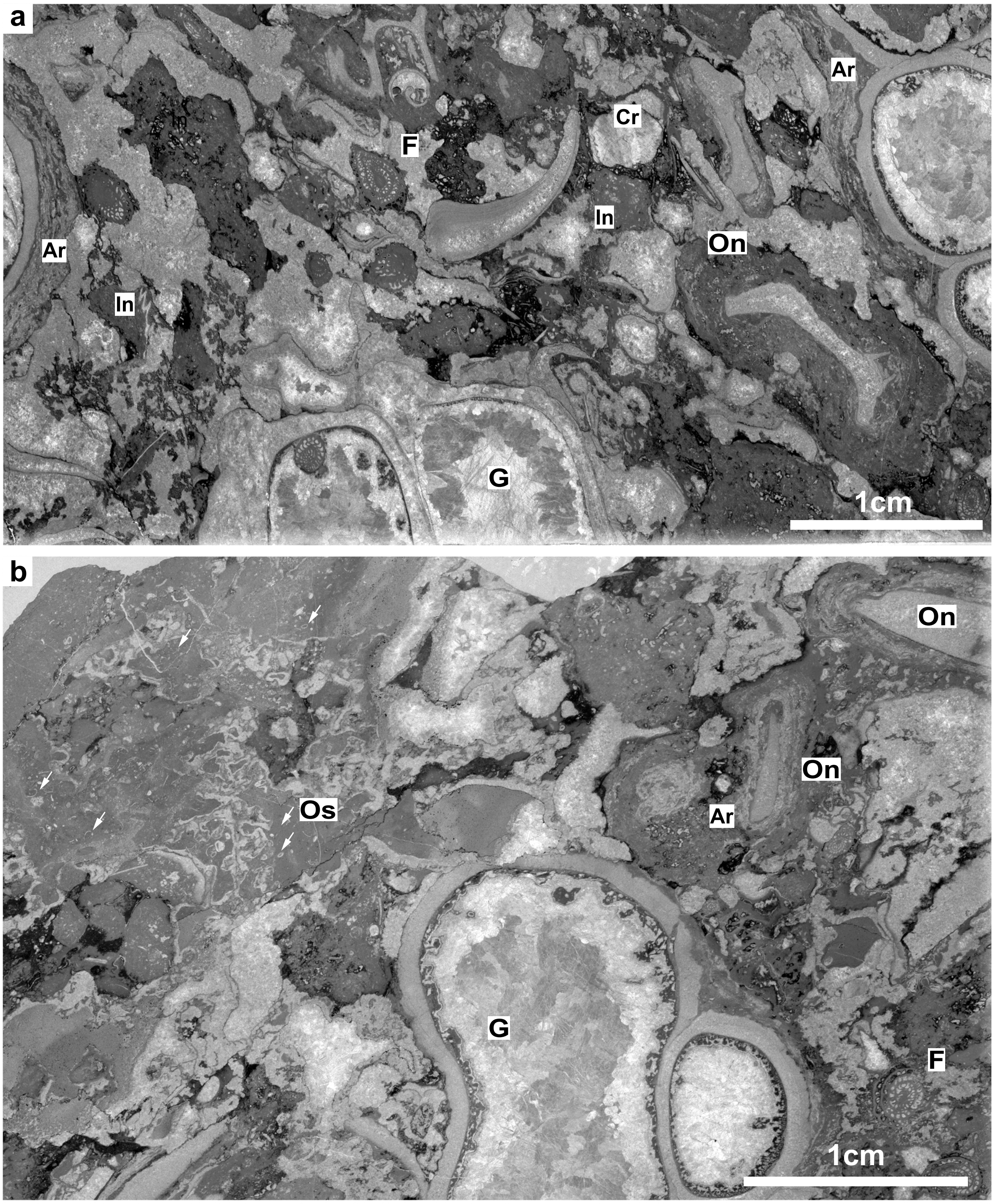

Figure 5.7: Photomicrographs of Microfacies B: large gastropod-oncoid rudstone. a Poorly sorted coated-grain rudstone composed of abundant large oncoids (On) with encrusting *Archaeolithoporella* (Ar), large gastropods (G), fusulinids (F), intraclast (In), and less crinoid remains (Cr). b Microfacies B showing large oncoids (On), *Archaeolithoporella* (Ar), large gastropods (G), fusulines (F) and ostracods (Os, white arrows) in fine-grain micrite.

Tucker and Wright 1990; Riegl et al. 2010; Peybernes et al. 2016). Intraclasts, some of them quite large and yielding also large gastropods, indicate resedimentation and a considerable topography and finally proximate deposition.

Microfacies B: Oncoid-rich rudstone sedimentation, forming a subfacies type, developed in an agitated shallow marine environment resembling that of microfacies A. High water energy can be deduced from the almost even thickness of oncoidal coatings, which points to frequent overturning, and the irregular intraclasts derived from intra-environmental resedimentation. In contrast to microfacies A, the formation of spherical oncoids suggests bidirectional currents within a tidal regime (?channel) or constant water agitation on the wave-affected shoreface. A highly agitated depositional environment is also consistent with the interpretation of Early Permian oncolites from the South China Platform (Shi and Chen 2006).

Diversity and abundance of biota

The fossil assemblage is diverse not only with regard to the abundant large gastropods but also to the calcareous algae and fusuline foraminifers, the latter of which are used to determine the age of the studied samples. The diagenetic overprints of the limestone and the bioclast is considerable. The gastropods were most probably originally aragonitic and was entirely replaced by sparry calcite cements.

Gastropods

Gastropods are particularly abundant in the studied facies and form a considerable part of the rock volume. They can be distinctly observed on the surface in the studied outcrop (Fig. 5.2c,5.3). Most of the gastropods are high-spired to conical with small to large sizes (up to 60 mm). Gastropods are the dominant constituent (30–40% of the rock volume) of this fossiliferous limestone. The gastropods could not be isolated from the rock due to strong lithification and recrystallization. A proper identification is therefore not possible. However, at least four different taxa are present according to their shapes in the studied thin sections.

Gastropod indeterminate A (Fig. 5.8a–g) has conical, high-spired shells with prominent peripheral shoulder and flange immediately below the suture producing a step-like outline; the whorl face is nearly straight and somewhat inclined or parallel to the shell axis below the suture. The whorls are rounded rectangular in transverse section and the columellar is massive. This species is distinct in the present collection and represents the most abundant form. The largest specimen is up to 25 mm wide, 60 mm high with about 6 preserved whorls and the apex broken off. Complete specimens have certainly reached a size > 60 mm and are thus rather large (category “rather large” according to Wenz 1938–44: 50–70 mm). This species probably belongs to the subclass Caenogastropoda in having typical characteristics: high-spired shell with numerous whorls. However, since protoconch, growth lines and aperture could not be observed, any taxonomic assignment remains speculative. The characteristic telescope-shape with the pronounced shoulder and flange combined with the large size has not been reported from Late Palaeozoic gastropods and this form probably represents an undescribed species and genus. Similar shapes are present in the Late Palaeozoic gastropod genera *Orthonema* (e.g., Mazaev 2002) or similar forms but detail about the growth-line pattern would be needed to propose a relationship.

Gastropod indeterminate B (Fig. 5.8h–i) has high-spired shells; the largest specimen consists of about 7 whorls, is 4.2 mm high and 1.8 mm wide; the suture is distinct; the whorls are strongly convex and rounded. This form could be related to Late Palaeozoic caenogastropods e.g., it resembles *Loxonema*? sp. from the Permian Productus Limestone of Cambodia (Mansuy 1914) or the heterobranch *Streptacis*? sp. from the Middle Permian Tak Fa (Ketwetsuriya et al. 2016) and Khao Khad formations (Ketwetsuriya et al. 2020b).

Gastropod indeterminate C (Fig. 5.8j–k) has trochiform shells; the largest specimen comprises about 5 whorls, is 32 mm high, 27 mm wide; the suture is distinct but shallow; the whorl face is straight with a pronounced spiral cord at low on the whorls forming the periphery. This species might belong to Platyceratacea.

Gastropod indeterminate D (Fig. 5.8l) shows a relatively large turbiniform shell with rounded whorls and a wide, open umbilicus (35 mm high, 30 mm wide). The last whorls show a thinning or outage of the shell which indicates the presence of a shell slit. Therefore, this shell represents a member of Pleurotomariida.

Fusuline foraminifers

The fusulines *Chalaroschwagerina* (indicative of Early Permian age) and *Neoschwagerina* and *Pseudodoliolina* (indicative of Middle Permian age), have been reported from this locality (Warren et al. 2014). Moreover, the fusuline fauna of the studied limestone samples yields *Pseudofusulina* sp. (Fig. 5.4a,b) and *Misellina* (*M.*) *termieri* (Fig. 5.4c,d), which suggest a Bolorian age (=latest Kungurian, Early Permian). The presence of these species has never been documented from the Khao Khad Formation of the Saraburi Group and supports the stratigraphic range of the Khao Khad Formation.

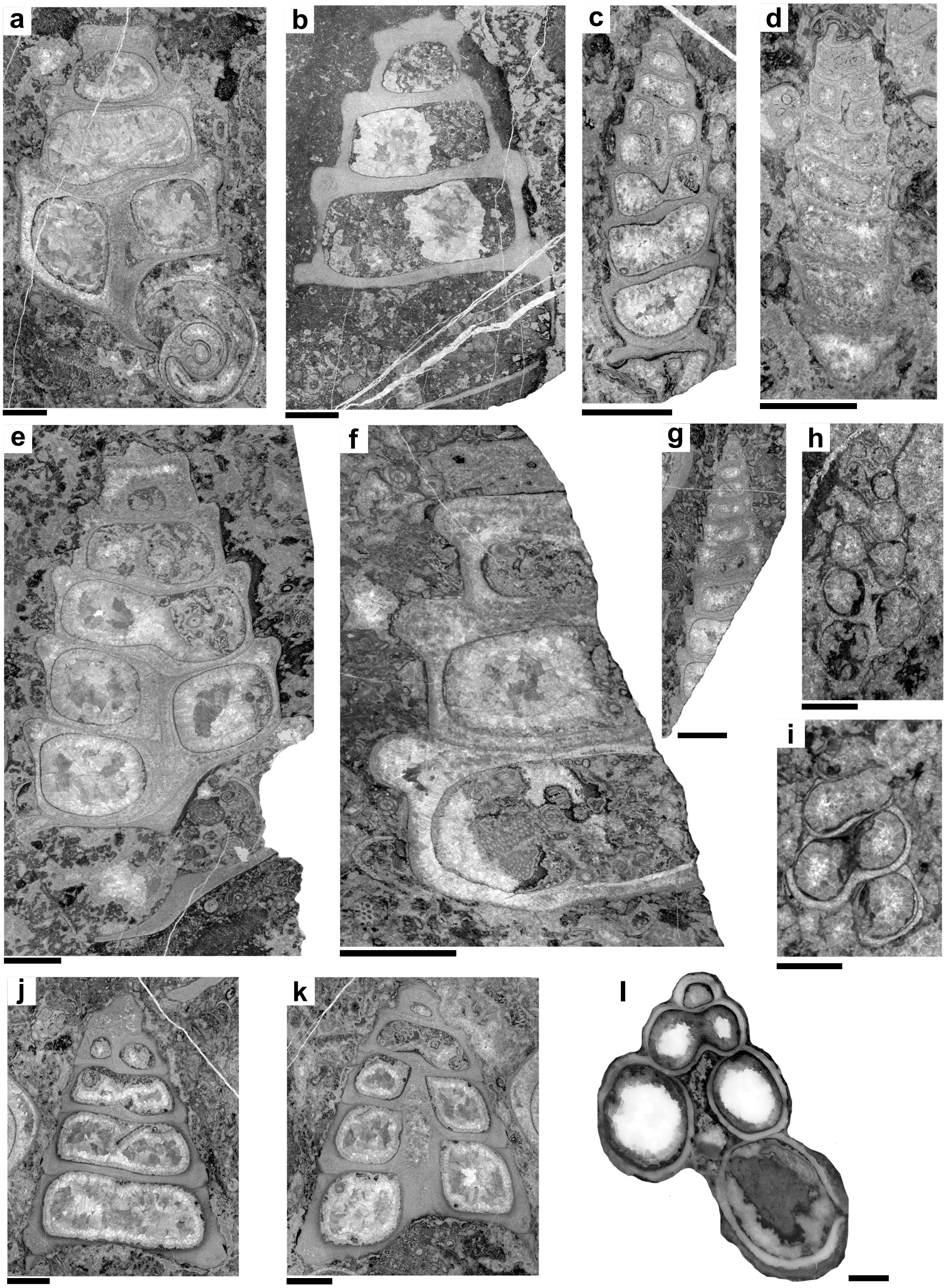

Figure 5.8: Photomicrographs of gastropod fauna from the Khao Khad Formation at Khao Wong hill, Saraburi Province. a–g Gastropod indeterminate A. h–i Gastropod indeterminate B. j–k Gastropod indeterminate C. l Gastropod indeterminate D. Scale bars represent: 5 mm (a–g, j–l); 1 mm (h–i).

Ostracods

Numerous ostracods were found in thin-sections (Fig. 5.7b) representing microfacies B. The valves are averagely 800–1,000 µm wide and 400–600 µm high and without ornamentation. They cannot be identified based on thin-sections only.

Sponges

Potentially reef building metazoans like corals and coralline sponges are extremely scarce, except for one biogenic structure that is tentatively assigned to the sphinctozoan sponges. Those structures form irregular meshes of thin micritic threads usually associated with non-skeletal microbialitic crusts. The sparitic cavities in between the threads also exhibit an irregular morphology, in rare cases circular to tubular forms are visible. Connecting pores of variable size (0.1–0.5 mm) exist. The thickness of the walls varies between 0.05 to 0.1 mm. The finer micritic threads (0.025 mm) partly resemble vesiculae of sphinctozoid sponges. The size of whole individuals might reach 2–3 cm. They occur as encrustations on biogenic hard substrates like mollusc shells or microbial crusts (Fig. 5.9c) or as encrusting masses between calcareous algae (e.g., phylloid algae) or other biogenic constituents. The structures show similarities to the bacinelloid *Vangia telleri* (Flügel in Flügel et al. 1984) from the Permian of Iran (Senowbari-Daryan & Rashidi 2011) but differs in wall thicknesses and the existence of connecting pores. We tentatively suggest a sphinctozoid sponge, probably *Uvanella* sp. although this taxon to date seems to occur not before the Mid-Triassic (for discussion see Senowbari-Daryan & Rashidi 2011).

Microbialites, cyanobacteria and calcareous algae

Calcimicrobes and non-skeletal microbialites

The coarse grained rudstones/grainstone gastropod facies reveals a diverse variety of skeletal microbial organisms as well as non-skeletal microbialitic structures that occur in form of encrustations on gastropods shells or on other bioclasts, as microbial lumps/intraclasts and as oncoidal coatings.

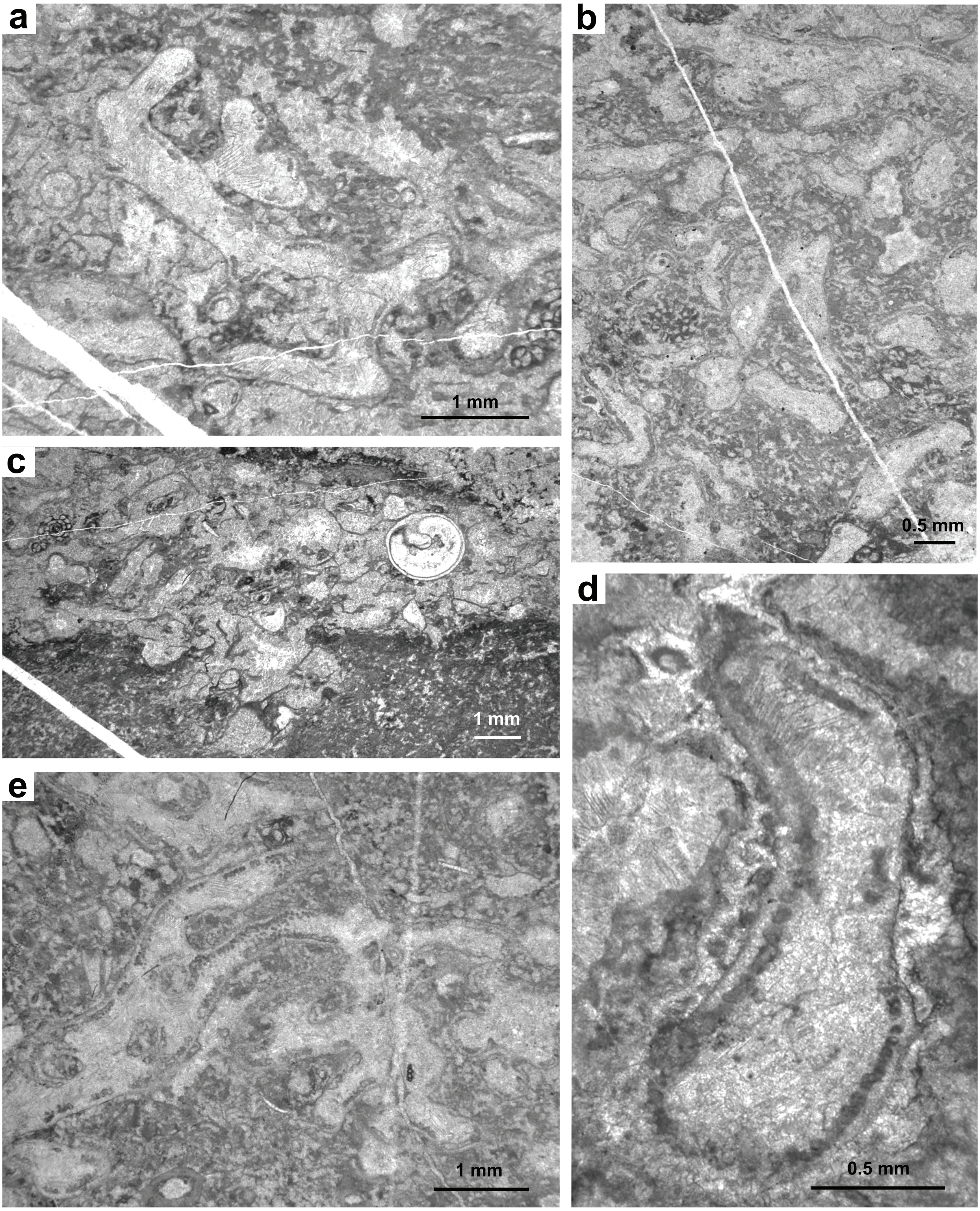

Figure 5.9: a–d "Phylloid algae" and sphinctozoid sponge, Khao Khad formation, Khao Wong hill, Saraburi Province. a, b, e *Eugonophyllum* cf. *huecoense* Wray, 1961. Note marginal circular and/or ellipsoid cells of the thallus. c putative sphinctozoid sponge, probably *Uvanella*? sp. Note fine irregular micritic threads and sparitic cavities with connecting pores. d *Neoanchicodium* sp.

Cyanobacteria

Coarse twisted tubes with well-defined walls form a loose structure. The inner diameter of the tubes ranges from 25 to 35 µm, the variable wall thickness is 20–25 µm which suggest an assignment to the porostromate cyanobacterium *Girvanella* cf. *magna* Johnson. *Girvanella* occurs preferentially in thick (several millimetres) microbial encrustations on biogenic constituents like gastropod shells (Fig. 5.10a). *Girvanella* tubes also occur within oncoids, frequently associated with enigmatic *Archaeolithoporella* (Fig. 5.10f; see below). In larger abundances such oncoids might form a subfacies type B (large gastropod-oncoid floatstones/rudstones).

Non-skeletal microbialites

Microbialitic structures lacking skeletal remains of bacteria are a common element in the gastropod-rich grainstones/rudstones. In most cases they form encrustations with variable thicknesses not only on gastropods but also on other bioclastic constituents like brachiopod and bivalve shells. Non-skeletal microbialites frequently occur also as poorly sorted intraclasts and lumps. In rare cases they form patches between biogenic components leading to a bindstone character of the otherwise allochthonous bioclastic carbonates. The fabric of non-skeletal microbialites reveal a clotted peloidal micritic structure indicative for a thrombolitic texture often resembling a reticular microbialitic fabric in the sense of Nakazawa et al. (2015) (Fig. 5.10b–d). Remarkably, the sparitic intraparticular cavities within the large gastropods sometimes reveal minute dark micritic encrustations with a fractal geometry along the inner surface of the gastropods (?cryptic microbialites).

Calcareous Algae

Dasyclad green algae are a common floral element in the allochthonous coarse grained carbonates of the Khao Wong hill, which is in accordance with the general composition of the algal flora of the Permian, that is strongly dominated by dasyclads (cf. Flügel 1990; Parvizi et al. 2013). Quite a few taxa occur, which are briefly described here. Aspondyl forms with phloiophor branches belong either to *Mizzia* sp. or *Gyroporella* sp. (Fig. 5.11a,b,f,g). The thallus of *Gyroporella* sp. shows no or only weak annulation whereas the thallus of *Mizzia* sp. is characterised by spherical or ovoid segments joined end to end. Thallus diameter for both taxa

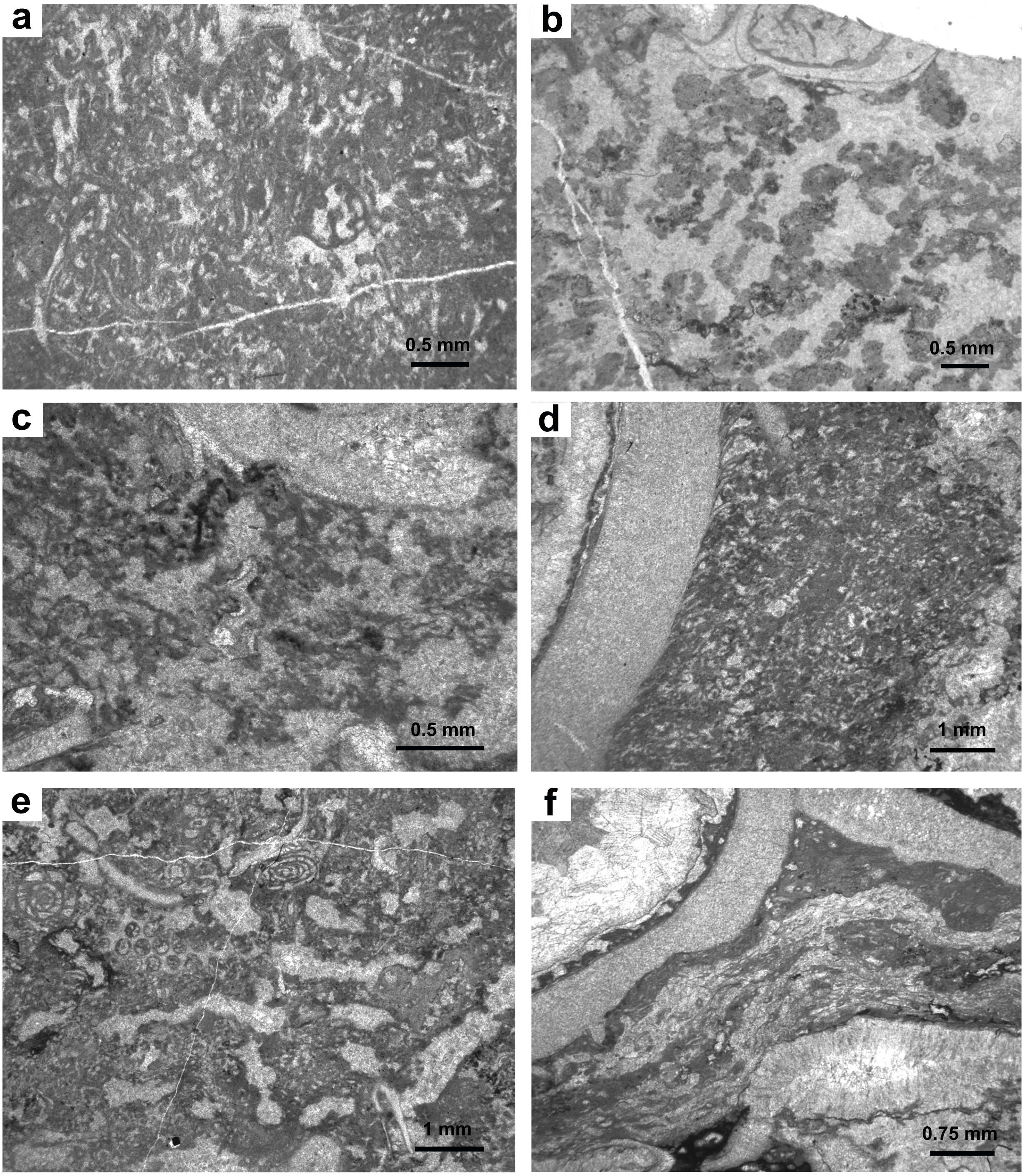

Figure 5.10: a–d skeletal and non skeletal microbialites, e, f microproblematica. a cyanobacterium *Girvanella* cf. *magna* Johnson. Note scattered tubes in an open microbialitic mesh. sample no. KW-3-03. b non skeletal microbial crust with clotted peloidal fabric. Note alignment of irregular shaped microbial peloids and lumps. Sample no. KW-3-04. c, d non skeletal microbialites growing on mollusk shells. Peloidal crusts form a irregular mesh resembling a reticular microbialitic fabric described by Nakazawa et al. (2015). sample nos. KW-3-1821, KW-3-04. e *Irregularina* Bykova, 1955, a putative lobose amoebozoan with psammobiotic lifestyle (cf. Schlagintweit et al. 2013). sample no. KW-3-1821. f microproblematicum *Archaeolithoporella* sp., tentatively assigned to algae (cf. Flügel et al. 1981, 1984). sample no. KW-3-01.

range between 2–3 mm, wall thickness is 0.15–0.25 mm and the pores diameter is 0.1–0.2 mm. A few sections of very large cylindrical aspondyl thalli reveal external diameters of 7.0–10.0 mm. The internal diameter is about 8.0 mm, the pores range between 0.15–0.2 mm. The measurements and the overall morphology allow for the assignment to *Macroporella* cf. *maxima* (Endo) (Fig. 5.11c). Euspondyl articulated forms belong to the genus *Clavaporella* sp., the remains of which are relatively scarce in the rock samples (Fig. 5.11d,e). The length of the thalli is between 2–3 mm, their diameters are 1.5 mm. The diameter of the pores is between 0.08–0.1 mm.

Gymnocodiacean algae are mainly represented by *Permocalculus* cf. *plumosus* Elliott (Fig. 5.11h). They are less abundant than dasyclad green algae. A number of oblique sections occur in the thin sections characterised by a well preserved cortical zone with fine filaments (diameter: 0.02–0.025 mm) revealing common ramification. The medullar zone is usually not preserved.

Solenoporacean algae are common constituents in the allochthonous rudstone facies. They exhibit an overall nodular, sometimes hemispherical morphology. The variable size ranges between 0.6–0.8 cm and 2.0–3.0 cm. Based on microstructure two taxa can be identified. *Parachaetetes lamellatus* Konishi reveal pronounced parallel layers in vertical sections composed of very fine cells (diameter about 0.02–0.03 mm; Fig. 5.12a,b). *Solenopora* sp. is characterized by somewhat larger cells (0.03–0.04 mm) and a faint horizontal lamination (Fig. 5.12c,d).

The informal group of the “Phylloid algae” are represented by *Neoanchicodium* sp. and *Eugonopyhllum* cf. *huecoense* Konishi & Wray, the latter of which reveal irregular undulating blades several centimeteres in length and width with sporadic circular or oval perforations (Fig. 5.9a,b,e). The thallus of *Neoanchicodium* sp. exhibit a non-undulating cylindrical, partly blade-like morphology and lack perforations (Fig. 5.9d). Typically, both taxa show a recrystallized central (“medular”) zone and a peripheral (“cortical”) zone. The latter is characterised by circular to ellipsoid cells (diameter: 0.05 mm) appearing as a “string of pearls” in transverse sections. “Phylloid algae” occur frequently but only in moderate quantities in the samples.

Microproblematica

Microorganisms with to date uncertain affinities include *Tubiphytes* sp. and *Archaeolithoporella* sp. The latter often forms thick crusts on various hard substrates like e.g. gastropod or other mollusc shells. *Archaeolithoporella* sp. is frequently developed in oncoids, where it might dominate the encrusting biota. The microstructure of *Archaeolithoporella* is characterised by alternating couplets of thin micritic and thicker sparitic irregular layers (Fig. 5.10f). Sometimes micritic layers are disturbed or tend to vertical orientation resulting in isolated sparitic bodies. *Archaeolithoporella* is a common constituent in Permian subtidal reefs (e.g., Wang et al. 2019) where it might form rapidly lithifying rigid wave-resistant frameworks together with syngenetic aragonitic cements. However, it occurs in various settings including shelf edge, platform margin and fore reef as well as upper slope settings (cf. Flügel et al. 1984; Flügel 2004). Remarkably, *Tubiphytes* sp. is very rare. Only a few transverse sections occur in thin sections with a central tube and an irregular, quite homogenous dense micritic coating. The systematic position of *Tubiphytes* is still a matter of debate (?cyanophycean, foraminifera, porifera; see Senowbari-Daryan 2013 for discussion).

Another enigmatic organism developed as irregular, sometimes interconnected sparitic tubes within intra-bioclastic groundmass. Sometimes an irregular dark micritic margin ("lining") is developed. The resulting fabric often resembles an anorganic laminoid fenestral fabric (LF-B) in the sense of Flügel (2004). But, because of the patchy occurrence of these structures, this interpretation seems unlikely (see also Nose et al. 2014). The morphological characters allow for the assignment to *Irregularina* Bykova, an enigmatic microorganism, usually classified as parathuramminid foraminfer (e.g., Bykova 1955; Loeblich and Tappan 1987; Fig. 5.10e). In accordance with the observations of Schlagintweit et al. (2013), we suggest a lobose amoebozoan organism with a psammobiotic lifestyle being the producer of those structures. In literature, the stratigraphic range of *Irregularina* is indicated as Middle Devonian (Givetian, possibly Eifelian) to Lower Carboniferous (Tournaisian). Remarkably, this is the first report from the Lower Permian.

Absent organisms

The studied samples lack metazoan reef builders such as corals and sponges (except rare individuals of a putative sphinctozoid sponge, probably *Uvanella*? sp.). Likewise brachiopods, bryozoans, and bivalves were absent in the studied samples. Echinoderms are represented by a single ossicle (Fig. 5.7a). Hence the guild of sessile filter feeders is almost absent in the studied samples.

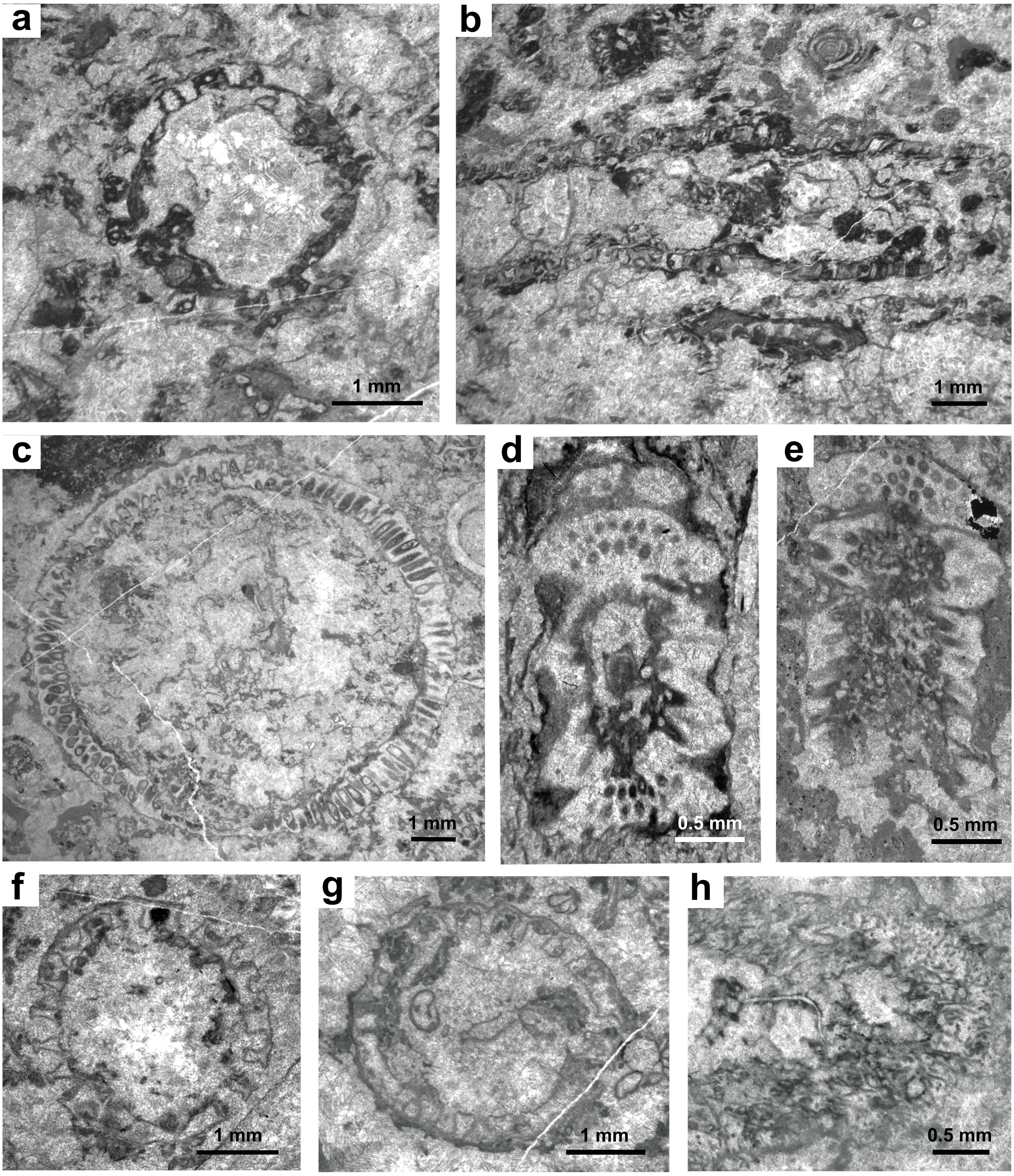

Figure 5.11: a–g dasycladacean and h gymnocodiacean algae, Khao Khad formation, Khao Wong hill, Saraburi Province. a *Gyroporella* sp. cross section. sample no. KW-3-02. b *Gyroporella* sp. longitudinal section. sample no. KW-3-02. c *Macroporella* cf. *maxima* Endo, 1952. sample no. KW-3-04. d, e *Clavaporella* sp. Note euspondyl pore configuration and thallus articulation. sample nos. KW-3-02, KW-3-1821. f, g *Mizzia* sp. sample nos. KW-3-02, KW-3-04. h *Permocalculus* cf. *plumosus* Elliott, 1955. sample no. KW-3-05/06.

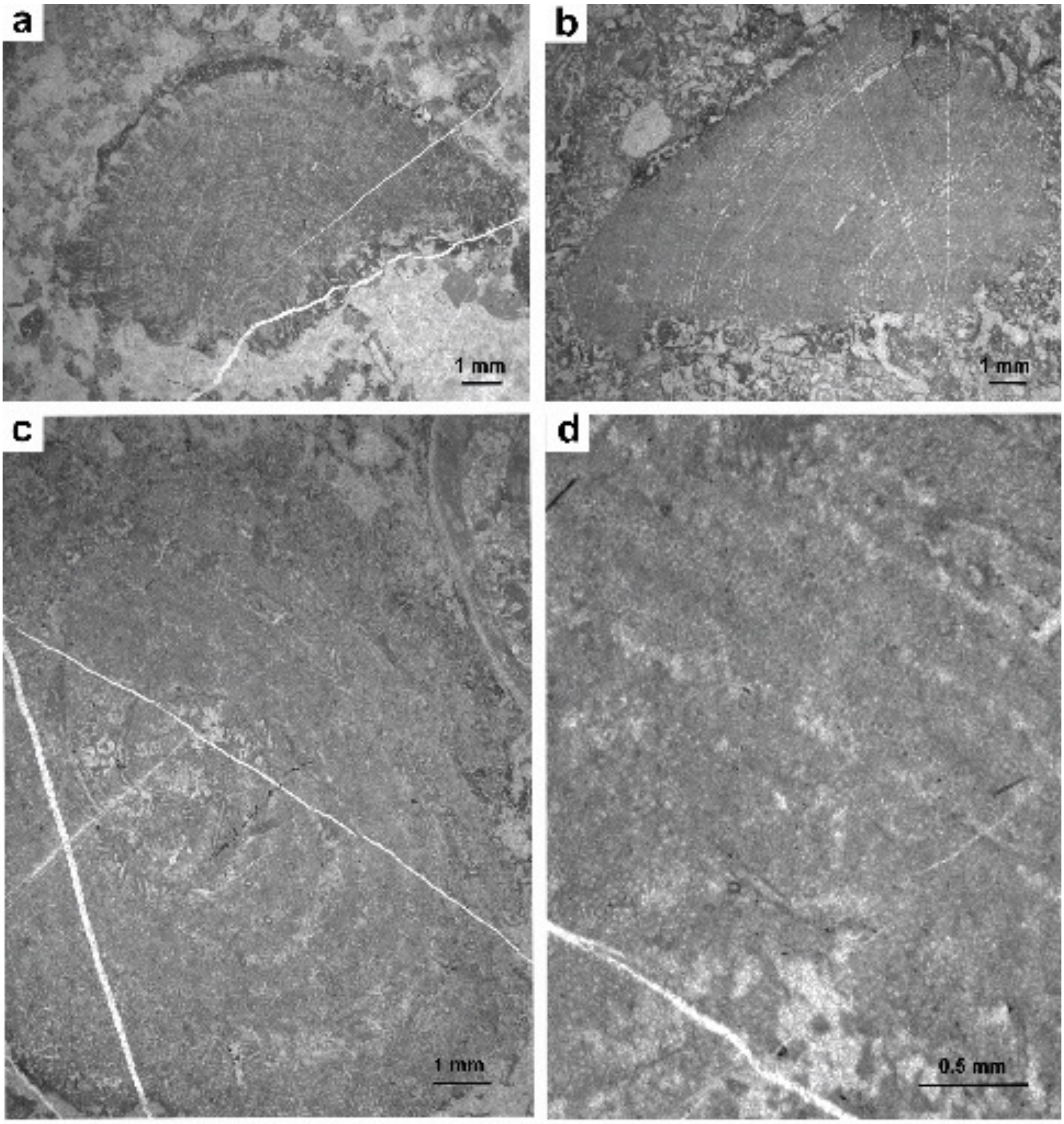

Figure 5.12: a–d solenoporacean algae, Khao Khad formation, Khao Wong hill, Saraburi Province. a, b *Parachaetetes lamellatus* Konishi, 1954. sample no. KW-3-03. c *Solenopora* sp. d detail of c revealing polygonal transverse sections of tubes. sample no. KW-3-04.

5.6 Discussion

Comparison with other localities of the Khao Khad Formation

Microbial precipitation of calcium carbonate plays an important role in the development of carbonate platforms throughout the Phanerozoic (see Flügel 2010). In terms of platform geometries in the Lower Permian to Early Middle Permian of Thailand, no reef rimmed margins developed. Rather, boundstones formed small biostromal reef bodies situated within a fusuline-dasyclad platform margin shoal complex (Dawson et al. 1993). According to Dawson & Racey (1993) reefs are usually characterized by a lack or subordinate occurrence of reef-building metazoans (sponges, corals, bryozoans) and abundant encrusting algae, bacteria and microproblematica (e.g., enigmatic *Archaeolithoporella*, *Tubiphytes*). This interpretation is backed up by Dew et al. (2017) stating that instead of reef building metazoans the marginal platform is characterized by small algal biostromes and the back-reef area by fusuline packstone/grainstone sedimentation showing similarities with the subtidal lagoon environment (Unit A: calcilutite with nodular chert) described by Thambunya et al. (2007). Wang et al. (2019) reported *Archaeolithoporella*- *Tubiphytes* dominated reefs or build-ups rich in micrite from the Middle Permian of China. All this is in good accordance with the faunal composition of the subfacies types described herein. Moreover, it seems that the facies of Khao Wonk Hill reflects to some extent also the overall compositional character of the Lower Permian with the dominance of phylloid algae, *Palaeoaplysina* and dasyclad reefal communities just before the late Early Permian faunal turnover with abundant algal cement reefs, sponge reefs and coral reefs (Wahlmann 2002; Weidlich 2002). However, the putative occurrence of putative sphinctozoan sponges indicate at least some importance of reef building/binding metazoans. More field work is required to clarify whether the studied carbonate bodies from Thailand formed elevated structures qualifying as reefs as was for instance shown for Middle Permian *Archaeolithoporella*-*Tubiphytes*-micrite dominated carbonates from South China (Wang et al. 2019).

Remarks on the large gastropods of this facies

Until we started our exploration on Permian gastropods of Thailand, a single nominate gastropod taxon had been known. Since then Ketwetsuriya et al. (2016, 2020a,b) have reported 116 species and representing 64 genera from the Middle Permian of Thailand. None of these gastropods match the characteristic morphology of the gastropods from the present samples and we assume that these taxa are undescribed. None of these gastropods reach sizes over 60 mm unlike those form the samples studied herein. Despite their high diversity, gastropods do not belong to the classical rock formers in Earth History. Locally, gastropods are main rock formers for instance the late Mesozoic *Nerinea* and *Actaeonella* Limestones (Waite et al. 2008), the Early Triassic Gastropod Oolite (Nützel & Schulbert 2005), or the Late Triassic *Anulifera* mass occurrence (Zapfe 1962; Nützel et al. 2012). The studied gastropod facies resembles the Late Jurassic nerinean gastropod facies from the Holy Cross Mts of Poland (Wieczorek 1979), where large accumulations of nerinean shells occur. External surfaces of the nerinean are commonly encrusted by serpulids and hydrozoans which differ from the studied Permian gastropods encrusted mainly by microbes. Also, the studied Permian gastropods are not nerineans which represent a Jurassic/Cretaceous clade; they lack the complex internal folds typical of that group. However, Late Palaeozoic gastropod mass accumulations are rare (e.g., Fletcher 1958 reported slabs with numerous gastropods from the Early Permian of Australia).

High-spired gastropods with rather large sizes (*ca*. 20–60 mm high) are the predominant faunal elements in the fossil-rich facies types described herein. They are amongst the largest Early Permian gastropods ever reported (Payne 2005 fig. 4 reported 65 mm as maximum height for Early Permian gastropods). Previously, Sone (2010) reported the neritopsid *Magnicapitatus huazhangae* which is preserved as a steinkern (42 mm wide, 36 mm high) from the Middle Permian of East Thailand (Khao Taa Ngog Formation). Ketwetsuriya et al. (2016) described 40 gastropod species from the Middle Permian Tak Fa Formation of Thailand. With up to 40 mm in height and width, *Glabrocingulum magnum* is the largest representative of this assemblage.

Hayasaka and Hayasaka (1953) documented unusually large molluscan assemblages from the Middle Permian of Japan, especially gastropods (*ca*. 40–130 mm high), e.g., *Bellerophon*, "*Murchisonia*", *Naticopsis* and *Trachydomia*. *Akasakiella yabei* (Hayasaka, 1943) from the Akasaka Limestone with the shell height of up to 40 cm is probably the largest Permian (and Palaeozoic?) gastropod ever reported (Koizumi 1995; Nützel & Nakazawa 2012). *Nipponomaria yokoyamai* (Hayasaka, 1943), also from the Akasaka Limestone is up to 20 cm high and 25 cm wide (Asato et al. 2016). Payne (2005) suggested that gastropod size is increased due to the local ecological factors, especially nutrient availability. Gastropod feeding has generally involved grazing of algae from rocks. The facies of the studied limestone with abundant primary producers such as algae and probably cyanobacteria suggest that abundant food was present for the gastropods.

5.7 Conclusions

This contribution documents an – to date unknown – unusual fusuline-bearing facies with large gastropods, various calcareous algae and microbialitic structures from the Early Permian Khao Khad Formation of Thailand. In particular:

1. Two coarse-grained, mainly grain-supported subfacies types have been recognized composed of large gastropods, fusuline foraminifers, calcareous algae (dasycladaceans, gymnocodiaceans, "phylloid algae", solenoporaceans) and various non-skeletal constituents (e.g., intraclasts, oncoids).

2. The fusulines *Misellina* (*M.*) *termieri* and *Pseudofusulina* sp. (first report for the Khao Khad Fm.) are indicative of a Bolorian age (=latest Kungurian, Early Permian) of the studied samples from the Khao Khad Formation. Thus, the stratigraphic range of the Khao Khad Formation is firmly ascribed from Early Permian to Middle Permian.
3. All faunas and floras present in this facies including microbialites, cyanobacteria and calcareous algae together with the structural characteristics point to an agitated, well-lit and mesotrophic to eutrophic shallow water environment.
4. Numerous large high-spired gastropods make this facies exceptional and different from all other shallow water carbonate deposits known from the Permian of Thailand.
5. The gastropods are amongst the largest ever reported from the Early Permian suggesting nutrient availability and high primary production present in the habitat of these gastropods.
6. The carbonate is interpreted as product of shallow water, back-reef lagoonal platform community with a high productivity providing the large gastropod with sufficient food. Conditions were too eutrophic for sessile filter feeders including metazoan reef builders.

5.8 Acknowledgement

SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, is thanked for financial support to the first author for doing the field work in Thailand. First author is also thankful to the Royal Thai Government who provided funding for a scholarship in the frame of the Development and Promotion of Science and Technology Talented Project. The reviewers William Foster and Andrzej Kaim are thanked for reviewing this article and their helpful comments. Nartmongkhol Songserm, Panut Rakkasikorn and Pitchaya Hotarapavanond are kindly acknowledged for their help to the first author in field sampling. We would like to thank B. Leipner-Mata, Erlangen for preparing thin-sections.

5.9 References

Altermann W (1989) Facies development in the Permian Petchabun basin, central Thailand. Verlag Für Wissenschaft und Bildung, Berlin, p. 235

Arboit F, Collins AS, King R, Morley CK, Hansberry R (2014) Structure of the Sibumasu–Indochina collision, central Thailand: A section through the Khao Khwang fold and thrust belt. Journal of Asian Earth Sciences 95:182–191

Arboit F, Collins AS, Morley CK, King R, Amrouch K (2016) Detrital zircon analysis of the southwest Indochina terrane, central Thailand: Unravelling the Indosinian orogeny. Geological Society of America Bulletin 128:1024–1043

Arboit F, Amrouch K, Morley C, Collins AS, King R (2017) Palaeostress magnitudes in the Khao Khwang fold–thrust belt, new insights into the tectonic evolution of the Indosinian orogeny in central Thailand. Tectonophysics 710:266–276

Asato K, Kase T, Ono T, Sashida K, Agenatsu S (2016) *Nipponomaria*, a new pleurotomarioidean gastropod genus (Mollusca) from the Permian Akasaka Limestone, central Japan. Paleontological Research 20: 385–393

Assavapatchara S, Charusiri P, Charoentitirat T, Chutakositkanon V, Hisada K, Ueno K (2006) On the lithostratigraphy of Permian rocks in Thailand: implications for depositional environments and tectonic settings. Journal of the Geological Society of Thailand 2006:27–48

Bykova EV (1955) Devonian foraminifers and radiolarians of the Volga-Ural region and Central Devonian field, and their significance for stratigraphy. In: Bykova EV, Polenova EN (eds.) Devonian foraminifers, radiolarians and ostracods of the Volga-Ural region (in Russian). Trudy Vsesoyuz Neft Nauchno-Issled Geol Inst (VNIGRI) ns 87:5–190 [in Russian].

Charoentitirat T (2002) Permian Fusulinoidean Biostratigraphy and Carbonate Development in the Indochina Block of Thailand with Their Paleogeographic Implication. Phd thesis, University of Tsukuba, Tsukuba.

Chitnarin A, Crasquin S, Charoentitirat T, Tepnarong P, Thanee N (2012) Ostracods (Crustacea) of the Early–Middle Permian from Central Thailand (Indochina Block): part I, Order Palaeocopida. Geodivesitas 34(4): 801–835

Chitnarin A, Crasquin S, Forel M-B, Tepnarong P (2017) Ostracods (Crustacea) of the Early–Middle Permian (Cisarulian-Guadalupian) from Central Thailand (Indochina Block): part II, Orders Podocopida, Platycopida and Myodocopida. Geodivesitas 39:651–690

Chonglakmani C (2001) The Saraburi Group of north–central Thailand: implication for geotectonic evolution. Gondwana Research 4:597–598

Dawson O (1993) Fusiline foraminiferal biostratigraphy and carbonate facies of the Permian Ratburi Limestone, Saraburi, central Thailand. Journal of Micropalaeontology 12:9–33

Dawson O, Racey A (1993) Fusuline-caleareous algal biofacies of the Permian Ratburi Limestone, Saraburi, Central Thailand. Journal of Southeast Asia Earth Sciences 8:49–65

Dawson O, Baird A, Bosence D (1993) No reef-rimmed margins to Permian carbonate platforms of Thailand. Journal of Southeast Asia Earth Sciences 8:181–186

Dew REC, King R, Collins AS, Morley CK, Arboit F, Glorie S (2017) Stratigraphy of deformed Permian carbonate reefs in Saraburi Province, Thailand. Journal of the Geological Society 175(1):163–175

Dunham RJ (1962) Classification of carbonate rocks according to depositional texture. In: American Association of Petroleum Geologists Memoir, v. 1. AAPG special volumes, pp. 108–121

Endo R (1952) Stratigraphical and Paleontological Studies of the Later Paleozoic Calcareous Algae in Japan. III. A few species from the Maiya section, Maiyamachi, Tomegun, Miyagiken. Sei Rep Saitama Univ B v 1 p 23–28

Fletcher HO (1958) The Permian gastropods of New South Wales. Records of the Australian Museum 24:115–164

Flügel E (1981) Lower Permian *Tubiphytes/Archaeolithoporella* buildups in the Southern Alps (Austria and Italy). Soc Econ Paleont Min Spec Publ 30:143–160.

Flügel E (1990) “Einschnitte” in der Entwicklung permischer Kalkalgen. Mitteilungen naturwiss Ver Steiermark 120:99-124.

Flügel E (2004) Microfacies of Carbonate Rocks: Analysis, Interpretation and Application. 976 pp., Berlin-

Heidelberg (Springer)

Flügel E (2010) Microfacies of Carbonate Rocks: Analysis, Interpretation and Application 2nd Edition. 976 pp., Berlin-Heidelberg (Springer-Verlag)

Flügel E, Kochansky-Devidé V, Ramovs A (1984) A Middle Permian Calcisponge/Algal/Cement Reef: Straza near Bled, Slovenia. Facies 10:179–256

Fontaine H (2002) Permian of Southeast Asia: an overview. J Asian Earth Sci 20:567–588

Fontain H, Salyapongse S, Suteethorn V, Tansuwan V, Vachard D (1996) Recent biostratigraphic discoveries in Thailand: A preliminary report. CCOP Newsletter 21(2):14–15

Fontain H, Salyapongse S, Vachard D (1999) New Carboniferous fossils found in Ban Bo Nam area, Central Thailand. In: Khantaprab C (ed.) Proceedings of Symposium on Mineral, Energy, and Water Resources of Thailand: Towards the Year 2000. Bangkok, 28–29 October 1999:210–211

Hayasaka, I. 1943. On some Permian gastropods from Kinsyozan, Akasaka-Mati, Gihu Prefecture. Memoirs of the Faculty of Science, Taihoku Imperial University, Series 3, 1:23–48

Hayasaka I, Hayasaka S (1953) Fossil Assemblages of Molluscs and Brachiopods of unusually large sizes from the Permian of Japan. Trans Proc Palaeont Soc Japan 10:37–44

Hinthong C (1981) Geology and Mineral Resources of Changwat Phra Nakhon Si Ayutthaya (ND 47–8), Scale 1:250,000. Department of Mineral Resources, Geological Suevey Report, No. 4, 1–105 (in Thai with English summary)

Ketwetsuriya C, Nützel A, Kanjanapayont P (2014) A new Permian gastropod fauna from the Tak Fa Limestone, Nakhonsawan, Northern Thailand – a report of preliminary results. Zitteliana A 54:137–146

Ketwetsuriya C, Nützel A, Kanjanapayont P (2016) Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. Bulletin of Geosciences 91:481–513

Ketwetsuriya C, Cook AG, Nützel A (2020a) Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand. Paläontologische Zeitschrift 94: 53–77

Ketwetsuriya C, Kampunar B, Charoentitirat T, Nützel A (2020b) Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. *Zootaxa* 4766(1): 1–47

Koizumi S (1995) Gastropoda. In: Hachiya K (ed.) The illustrated collections of Asami Fossil Museum, Fossils of Kinsyozan. Asami Fossil Museum, Gifu, pp. 95–169 [in Japanese]

Konishi K, Wray JL (1961) *Eugonophyllum*, a new Pennsylvanian and Permian genus. Journal of Paleontology 35:659–666

Loeblich AR, Tappan H (1987) Foraminiferal genera and their classification. 2 volumes, 970 pp, New York (van Nostrand Reinhold).

Mansuy S (1914) Nouvelle contribution à la paléontologie du Yunnan. Mémoires du Service Géologique de l'Indochine 3(2):1–190

Mazaev AV (2002) Some murchisoniid gastropods from the Middle and Upper Carboniferous of the central part of the Russian Plate. Ruthenica 12(2):89–106

Metcalfe I (1999) Gondwana dispersion and Asian accretion: an overview. In: Metcalfe I. (ed.) Gondwana dispersion and Asian accretion, Final Results Volume for IGCP Project 321. A.A. Balkema, Rotterdam, pp. 9–28

Metcalfe I (2002) Permian tectonic framework and palaeogeography of SE Asia. Journal of Asian Earth Sciences 20:551–566

Metcalfe I (2006) Palaeozoic and Mesozoic tectonic evolution and palaeogeography of East Asian crustal fragments: the Korean Peninsula in context. Gondwana Research 9:24–46

Metcalfe I (2011) Tectonic framework and Phanerozoic evolution of Sundaland. Gondwana Research 19:3–21

Metcalfe I (2013) Tectonic evolution of the Malay Peninsula. Journal of Asian Earth Sciences 76:195–213

Metcalfe I (2017) Tectonic evolution of Sundaland. Bulletin of the Geological Society of Malaysia 63:27–60

Morley CK, Ampaiwan P, Thanudamrong S, Kuenphan N, Warren J (2013) Development of the Khao Khwang Fold and Thrust Belt: implications for the geodynamic setting of Thailand and Cambodia during the Indosinian Orogeny. Journal of Asian Earth Science 62:705–719

Nakazawa T, Igawa T, Ueno K, Fujikawa M (2015) Middle Permian sponge-microencruster reefal facies in the mid-Panthalassan Akiyoshi atoll carbonates: observations on a limestone slab. Facies 61:15

Nose M, Schlagintweit F, Hladil J (2014) Sediment-dwelling organisms mimicking laminoid fenestral fabrics in shallow water carbonates. 19th International Sedimentological Congress (IAS), abstracts book, p. 525, Geneva.

Nützel A, Schulbert C (2005) Facies of two important Early Triassic gastropod lagerstätten: implications for diversity patterns in the aftermath of the end-Permian mass extinction. Facies 51:495–515

Nützel A, Nakazawa K (2012) Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). Journal of Systematic Palaeontology 10:103–169

Nützel A, Aghababalou B, Senowbari-Daryan B (2012) Gastropods from the Norian (Late Triassic) Nayband Formation near Natanz (Iran). Bulletin of Geosciences 87:53–65

Peybernes C, Chablais J, Onoue T (2016) Mid-oceanic shallow-water carbonates of the Panthalassa domain: new microfacies data from the Sambosan Accretionary Complex, Shikoku Island, Japan. Facies 62:24

Parvizi T, Rashidi K, Vachard D (2013) Midle Permian calcareous algae and microproblematica (Dalan Formation, Dena Mountain, High Zagros, SW Iran). Facies 59:149–177

Payne JL (2005) Evolutionary dynamics of gastropod size across the end-Permian extinction and through the Triassic recovery interval. Paleobiology 31:269–290

Riegl B, Poiriez A, Janson X, Bergman KL (2010) The gulf: facies belts, physical, chemical, and biological parameters of sedimentation on a carbonate ramp. Carbonate depositional systems: assessing dimensions and controlling parameters. Springer, New York, pp 145–213

Schlagintweit F, Hladil J, Nose M (2013) New observations and interpretations of the enigmatic poorly known Late Palaeozoic *Irregularina* Bykova, 1955. Acta Paleontologica Romaniae 9:3–22

Senowbari-Daryan B (2013) *Tubiphytes* Maslov, 1956 and description of similar organisms from Triassic reefs of the Tethys. Facies 59:75–112

Senowbari-Daryan B, Rashidi K (2011) *Lercaritubus problematicus* Flügel, Senowbari-Daryan & Di Stefano and *Vangia telleri* (Flügel): two problematic organisms from the Permian Jamal Formation of Shotori mountains, Northeast Iran. Rivista Italiana di Paleontologia e Stratigrafia, 117(1):105–114

Shi GR, Chen ZQ (2006) Lower Permian oncolites from South China: Implications for equatorial sea-level responses to Late Palaeozoic Gondwana glaciation. Journal of Asian Earth Sciences 26:424–436

Sone M (2010) A new species of the rare neritopsid gastropod *Magnicapitatus* from the Guadalupian (Middle Permian) of East Thailand (the Indochina Terrane). Alcheringa 34:1–6

Sone M, Metcalfe I (2008) Parallel Tethyan sutures in mainland Southeast Asia: new insights for Palaeo-Tethys closure and implications for the Indosinian orogeny. Compte Rendus Geoscience 340:166–179

Tabakh ME, Utha-Aroon C (1998) Evolution of a Permian carbonate platform to siliciclastic basin: Indochina plate, Thailand. Sed Geol 121:97–119

Thambunya S, Pisutha-Arnond V, Khantaprab C (2007) Depositional environments of Permian rocks of the Khao Khad Formation in central Thailand. Science Asia 33:371–381

Toriyama R (1975) Fusuline fossils from Thailand, Part IX. Permian fusulines from the Rat Buri Limestone in the Khao Phlong Phrab area, Sara Buri, Central Thailand. Memoirs of the Faculty of Science, Kyushu University, Series D, Geology 23:1–116

Toriyama R, Sugi T (1959) Permian fusulinids from Central Thailand. Memoirs of the Faculty of Science, Kyushu University, Series D, Geology 9:17–32

Toriyama R, Kanmera K, Kaewbaidhoon S, Hongnusonthi A (1974) Biostratigraphic zonation of the Rat Buri Limestone in the Khao Phlong Phrab area, Sara Buri, Central Thailand. In: Kobayashi T, Toriyama R (eds) Geology and Palaeontology of Southeast Asia, Volume 14. University of Tokyo Press, Tokyo, 25–48

Toriyama R, Kanmera K (1977) Fusuline fossils from Thailand, Part X. The Permian fusulines from the limestone conglomerate formation in the Khao Phlong Phrab area, Sara Buri, Central Thailand. In: Kobayashi T, Toriyama R, Hashimoto W (eds) Geology and Palaeontology of Southeast Asia, Volume 18. University of Tokyo Press, Tokyo, 1–27

Toriyama R, Kanmera K (1979) Fusuline fossils from Thailand, Part XII. Permian fusulines from the Ratburi Limestone in the Khao Khao area, Sara Buri, Central Thailand. In: Kobayashi T, Toriyama R, Hashimoto W (eds) Geology and Palaeontology of Southeast Asia, Volume 20. University of Tokyo Press, Tokyo, 43–61

Tucker ME, Wright P (1990) Carbonate sedimentology. Blackwell Publishers Ltd, Oxford

Udchachon M, Chonglakmani C, Campbell H, Thanee N (2007) Late Middle Permian alatoconchid-bearing limestones from the south of the Khao Khwang Platform, Central Thailand. In: Tantiwanit W (ed.) Proceedings of the International Conference on Geology of Thailand (GEOTHAI'07): Towards Sustainable Development and Sufficiency Economy. Bangkok, 21–22 November 2007:169–176

Udchachon M, Burrett C, Thassanapak H, Chonglakmani C, Campbell H, Feng Q (2014) Depositional setting and paleoenvironment of an alatoconchid-bearing Middle Permian carbonate ramp sequence in the Indochina Terrane. Journal of Asian Earth Sciences 87:37–55

Ueno K, Charoentitirat T (2011) Carboniferous and Permian. In: Ridd MF, Barber, AJ, Crow MJ (eds.) The geology of Thailand. London, Geological Society, pp. 71–135

Ueno K, Miyahigashi A, Kamata Y, Kato M, Charoentitirat T, Limruk S (2012) Geotectonic implications of Permian and Triassic carbonate successions in the Central Plain of Thailand. Journal of Asian Earth Sciences 61:33–50

Wahlmann GP (2002) Upper Carboniferous-Lower Permian (Bashkirian-Kungurian) mounds and reefs. In: Kiessling W, Flügel E, Golonka J (eds.) Phanerozoic Reef Patterns, SEPM Special Publication 72:271–338.

Wagner CW, Van der Togt C (1973) Holocene sediment types and their distribution in the southern Persian Gulf. The Persian Gulf. Springer, New York, pp 123–155

Waite R, Wetzel A, Meyer CA, Strasser A (2008) The paleoecological significance of nerineoid mass accumulations from the Kimmeridgian of the Swiss Jura Mountains. Palaios 23: 548–558

Wang X, Foster WJ, Yan J, Li A, Mutti M (2019) Delayed recovery of metazoan reefs on the Laibin-Heshan platform margin following the Middle Permian (Capitanian) mass extinction. Global and Planetary Change 180: 1–15

Warren J, Morley CK, Charoentitirat T, Cartwright I, Ampaiwan P, Khositchaisri P, Mirzaloo M, Yingyuen J (2014) Structural and fluid evolution of Saraburi Group sedimentary carbonates, central Thailand: A tectonically driven fluid system. Marine and Petroleum Geology 55:100–121

Weidlich O (2002) Middle and Late Permian Reefs – distributional patterns and reservoir potential. In: Kiessling W, Flügel E, Golonka J (eds.) Phanerozoic Reef Patterns, SEPM Special Publication 72:339–390

Wenz W (1938–1944) Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. In: Schindewolf OH (ed.) Handbuch der Paläozoologie, Band 6, Gastropoda. Berlin, Borntraeger

Wieczorek J (1979) Upper Jurassic nerineacean gastropods from the Holy Cross Mts (Poland). *Acta Palaeontologica Polonica* 24(3):299–350

Wieldchowsky CC, Young JD (1985) Regional facies variation in Permian rocks of the Phetchabun Fold and Thrust Belt, Thailand. In: Thanvarachorn P, Hokjaroen S, Youngme W. (eds.) Procedings on Geology and Mineral Resources Development of Northeastern Thailand. Khon Kaen University, Thailand, pp. 41–55

Zapfe H (1962) Beiträge zur Paläontologie der nordalpinen Riffe. Ein Massenvorkommen von Gastropoden im Dachsteinkalk des Tennengebirges, Salzburg. Annalen des Naturhistorischen Museum Wiens 65: 57–69

Zaw K, Meffre S, Lai C-K, Burrett C, Santosh M, Graham I, Manaka T, Salam A, Kamvong T, Cromie P (2014) Tectonics and metallogeny of mainland Southeast Asia—A review and contribution. Gondwana Research 26:5–30

6

Conclusion

The previous chapters demonstrate that the discovery of Permian gastropod faunas from several localities in Thailand sheds new light on the diversity and distribution of Permian gastropods of the eastern Palaeo-Tethys, before the mainland of Thailand were formed. The present thesis reviews and greatly supplements the current knowledge of Permian gastropod faunas from two continental terranes, the Sibumasu and the Indochina terranes, of Thailand. Prior to this thesis, Sone (2010) reported a single nominate species and the author (Ketwetsuriya et al. 2016) reported 40 species in his published master thesis (17 nominate, 23 open nomenclature). The gastropod faunas from the Ratburi Limestone and the Khao Khad Formation presented in this thesis yielded about 80 additional species of which 30 are new. To date, a total of 117 Permian gastropod species (44 nominate species, 73 species in open nomenclature) belonging to 64 genera have been reported from both terranes of Thailand. All Permian gastropod assemblages from Thailand differ strongly from each other in taxonomic composition. Most of the present genera are cosmopolitan and typical of the Late Palaeozoic, encompassing genera such as *Euphemites*, *Bellerophon*, *Glabrocingulum*, *Worthenia*, *Anomphalus*, *Yunnania*, *Microdoma*, *Trachydomia, Goniasma* and others.

From the Sibumasu Terrane, a Permian gastropod fauna has been previously reported from Perak, Malaysia (Batten 1972, 1979, 1985). The studied assemblage from the Middle Permian Ratburi Group at Khao Phrik, Ratchaburi Province, Central Thailand, is the first diverse Permian gastropod fauna from the Sibumasu Terrane of Thailand (Chapter 2). Thirty-four gastropod species are described, nine species are new to science: *Retispira khaophrikensis*, *Amaurotoma*? *multispirata*, *Eoplatyzona ratchaburiensis*, *Hesperiella cyrtocostata*, *Worthenia*? *waterhousei*, *Stegocoelia centrosinuata*, *Procerithium*? *inaequetuberculata*, *Chlorozyga* *asiatica* and *Hyphantozyga*? *khaophrikensis*. The gastropod assemblage is strongly dominated by bellerophontids.

From the Indochina Terrane, 44 Roadian gastropod species are described from the Khao Khad Formation, Lopburi Province, Central Thailand (Chapter 3). This is the first time that Permian gastropods have been reported from this formation. Of those one new genus: *Altotomaria*, and thirteen new species: *Bellerophon erawanensis*, *Biarmeaspira mazaevi*, *Apachella thailandensis*, *Gosseletina microstriata*, *Worthenia humiligrada*, *Altotomaria reticulata*, *Yunnania inflata*, *Trachydomia suwanneeae*, *Trachyspira eleganta*, *Heterosubulites longusapertura*, *Platyzona gradata*, *Trypanocochlea lopburiensis* and *Streptacis*? *khaokhadensis* are erected. The studied assemblage is dominated by vetigastropods and caenogastropods. This assemblage represents one of the most diverse Permian gastropod faunas known from Thailand and Southeast Asia. This fauna and that of the Tak Fa Formation (Thailand) and the Sisophon Limestone (western Cambodia) show that the Permian marine deposits from this terrane yield a very diverse gastropod fauna, especially given the low number of shared species amongst the known occurrences which suggest high beta- and gamma diversity as well as still insufficient sampling.

Diversity analyses of Permian gastropod from the Tak Fa Formation (Middle Permian (Wordian), the Indochina Terrane) (Chapter 4) suggest that the studied fauna is of moderate diversity. This fauna shares no species with faunas from other the two Permian deposits of Thailand which are treated above. The clade proportions of the known gastropod faunas from Thailand differ considerably from each other. The gastropod faunas from the Indochina Terrane is dominated by vetigastropods and high-spired caenogastropods. By contrast, the assemblage from the Sibumasu Terrane is strongly dominated by bellerophontids. These faunas were separated by a geographical barrier, the Sukhothai volcanic arc (Fig. 6.1) which may explain this differentiation regarding taxonomic composition and diversity the studies assemblages.

Moreover, the comparative diversity analysis of Permian gastropod from Thailand, Malaysia, Timor and Japan of the eastern Palaeo-Tethys based on rarefaction, diversity indices and rank-abundance distributions showed that the Permian gastropod fauna of Perak, Malaysia has the highest diversity, while the faunas from Thailand are distinctly less diverse. It is noteworthy that gastropods are the most diverse and abundant group in the studied examples although gastropod dominance is generally seen as a modern trait.

An unusual mass occurrence of large gastropods in a microbial-fusulinid limestone facies from the Early Permian Khao Khad Formation is reported in Chapter 5. This formation has yielded with *at least four species* large gastropods (up to 6 cm height) which contribute most to the rock volume. These are amongst the largest Early Permian gastropods ever reported. Besides gastropods, fusulinids, large dasycladaceans and thick microbial-cyanobacterial coatings are present. The carbonate is interpreted as product of shallow water, non-reefal platform community with a high productivity providing the large gastropod with sufficient food. This contribution shows that gastropods are not only among the most diverse and abundant groups in Permian marine faunas of Southeast Asia but also were rock formers and important contributors to the total biomass at least locally.

Permian gastropods were widespread on carbonate platforms of the eastern Palaeo-Tethys (Fig. 6.1) from the Palaeo-equator (e.g. South China Terrane and Indochina Terrane) to higher latitude of the Cimmerian Continent (Sibumasu Terrane) as well as a paleo-*seamount* in the Panthalassa Ocean (Akasaka Limestone). These gastropod faunas show moderate to very high diversity and a significant variation of taxonomic compositions. The gastropod faunas from the Sibumasu Terrane of Thailand reveals relationships to Late Palaeozoic gastropod faunas from the eastern Palaeo-Tethys, such as those of Australia and Malaysia. The Permian gastropod assemblages from the Indochina Terrane of Thailand have relationships to those from the South China Terrane – both were situated close to the Palaeo-equator during the Permian period.

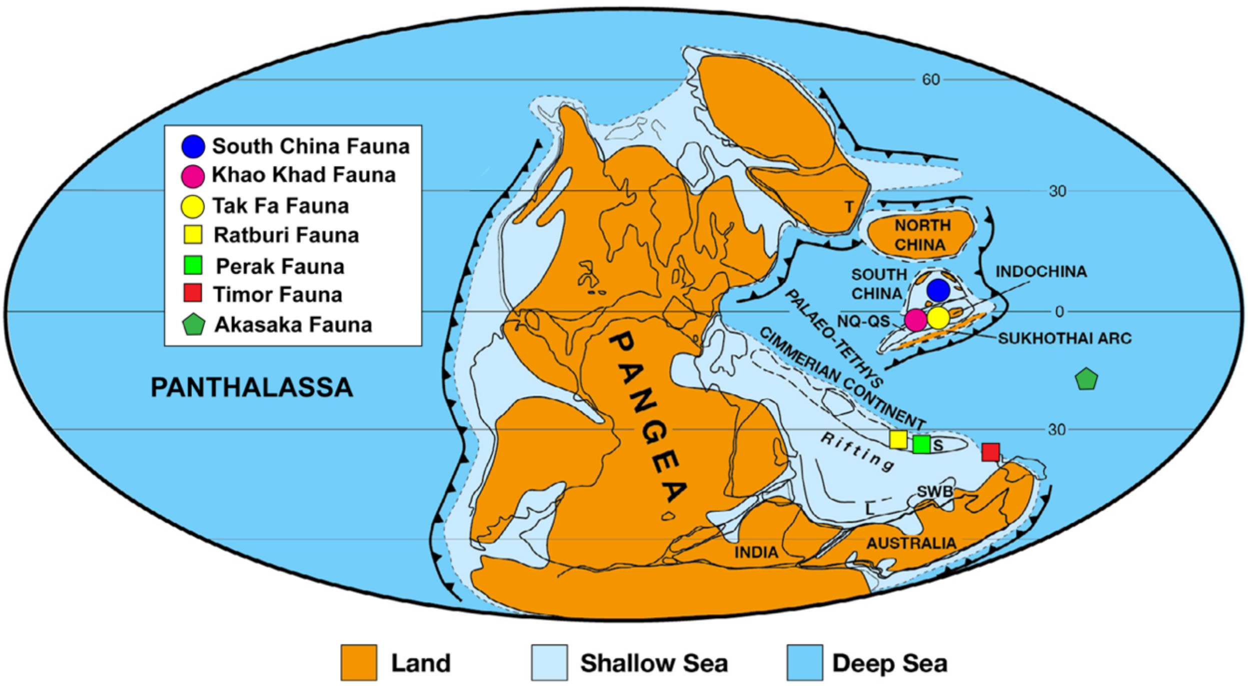

Fig. 6.1: Palaeogeographic reconstructions of the Tethyan region for the Permian (Kungurian) showing relative positions of the East and SE Asian terranes and biogeographic distribution of the Permian gastropod faunas on South China Terrane, Indochina Terrane and Cimmerian Continent in the Permian (modified from Metcalfe 2013).

Acknowledgements

I would like to acknowledge to my supervisor, Professor Dr. Alexander Nützel, who introduced me to the world of Gastropoda since I was an undergraduate student as well as for his invaluable advices and suggestion of my work. I am really grateful for his care and his kind support. This means a lot to me. I would like to express my deepest gratitude to all my co-authors, Dr. Martin Nose of Bayerische Staatssammlung für Paläontologie and Geologie, München, Germany, Associate Professor Dr. Thasinee Charoentitirat of Department of Geology, Faculty of Science, Chulalongkorn University, Thailand and Dr. Alex Cook from the Queensland Museum, Brisbane, Australia for their valuable information in the manuscripts.

I sincerely thank my colleagues and friends, the members of gastropod group, Imelda Hausmann and Baran Karapunar, for their contribution as co-authors in our manuscripts and of course for their enormous guidance and fruitful discussions about a PhD student life. I also thank the members of the BSPG, for technical support during my study in Munich.

I am also especially thankful to Professor Dr. Pitsanupong Kanjanapayont, Professor Dr. Punya Charusiri and Dr. Kantapon Suraprasit of Department of Geology, Faculty of Science, Chulalongkorn University, Thailand, Assistant Professor Dr. Anisong Chitnarin of School of Geotechnology, Institute of Engineering, Suranaree University of Technology, Thailand and Dr. Apsorn Sardsud of Department of Mineral Resources, Thailand for the information in geology and palaeontology of Thailand.

Special thanks go to my family, Suntari Ketwetsuriya, Chatchai Ketwetsuriya, Srirat Ketwetsuriya, Kaew Ketwetsuriya and Prommin Sriskuljarus for their encouragement and support, including my good friends in Munich and Thailand.

Finally, I am also indebted to the Royal Thai Government who provided funding for a scholarship within the framework of the Development and Promotion of Science and Technology Talented Project and Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany that support my Ph.D. study and my scientific work in Munich, Germany.

Vielen Dank – ขอบคุณครับ