Title

Late Cambrian (Furongian) and Lower Ordovician (Tremadocian) trilobites of Sibumasu

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Late Cambrian (Furongian) and Lower Ordovician (Tremadocian) trilobites of Sibumasu

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of the requirements for the degree of

Doctor of Philosophy

in

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by

Shelly Jean Wernette

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The text of this dissertation, in part and with minor revisions, is a reprint of the material as it appears in Journal of Paleontology, June 2020. The coauthor Nigel Hughes listed in that publication directed and supervised the research which forms the basis for this dissertation.

Coauthors contributing to chapters: Chapters 1–3: Nigel Hughes, Paul Myrow, and Apsorn Sardsud; Chapter 4: Nigel Hughes, Paul Myrow, and Aye Ko Aung. Nigel Hughes has been principle investigator on all aspects of this project. Paul Myrow has been responsible for the stratigraphic logs and assisted in fossil collecting. Apsorn Sardsud and Aye Ko Aung have provided logistic support in the field and helped with fossil collecting.

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DEDICATION

This dissertation is dedicated to my father, Gene Wernette, who introduced me to hiking, mapwork, and anything related to exploring the outdoors. Dad, you would have made an formidable field geologist if life had taken you down a different path.

ABSTRACT OF THE DISSERTATION

Late Cambrian (Furongian) and Lower Ordovician (Tremadocian) trilobites of Sibumasu

by

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Doctor of Philosophy, Graduate Program in Geological Sciences
University of California, Riverside, June, 2020
Dr. Nigel Hughes, Chairperson

Geochronologically calibrating the latest Cambrian and earliest Ordovician is critical for further investigations into the cycles of evolutionary diversifications and extinctions during this interval. The peri-Gondwanan terrane, Sibumasu (western Thailand, eastern Myanmar, northern Malaysia, and western Yunnan, China) is globally the only tectonic province known to have multiple zircon-bearing tuffs interbedded with fossiliferous strata from both the latest Cambrian and earliest Ordovician. The terrane thus has great potential for producing a geochronologically constrained biostratigraphic succession. Well-resolved taxonomy is foundational for reliable biostratigraphic correlations, without which absolute dates have limited value beyond the locality from which the dated material was collected. Trilobites are particularly useful fauna for correlations during this time interval as their diversity, environmental pervasiveness, and good preservation potential mean that they are found on most tectonic provinces and can be correlated with reasonably high precision. Hitherto the trilobites of Sibumasu have not been taxonomically well-resolved. This study uses field collections made during three excursions (2008, 2016, and 2018) to southern Shan State, Myanmar and Ko Tarutao, Thailand to revise Sibumasu's Cambro-Ordovician trilobite fauna. It is the first description and illustration of trilobites from Cambrian Myanmar and substantially expands the trilobite record of the fauna of Thailand's Tarutao Group. The latter, though the subject of three separate studies (1957–1988), had been left with most species in open nomenclature. Collections from both localities have tightly constrained stratigraphic context where possible. Detrital zircon and volcanic ash samples were collected at the same time as the fossils for use in dating and paleogeographic reconstructions. Three species, one of which is new, are recorded from Myanmar. 42 species were recovered from the Tarutao Group, 18 of which are new; following the most recent revision in 1988, only 18 species were recognized. Two new genera were also recovered from the Tarutao Group.

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Introductory Remarks

The latest Cambrian (late Furongian) was a dynamic time of widespread volcanism, shifting tectonic regimes, and relatively rapid cycles of biotic diversification and extinction (Palmer, 1984; Cawood and Buchan, 2007; McKenzie et al., 2014; Saltzman et al., 2015). These diversity and extinction cycles perturbed the net diversity (measured by genus-richness) plateau between the Cambrian Explosion and Great Ordovician Biodiversity Event (Sepkoski, 1981). This time interval offers clues about the Earth's physical controls on biological diversifications and extinctions through exploring the links between biological signatures and such physical factors as continental margin assembly and ocean and atmosphere perturbations (e.g. outgassing of CO_2 potentially causing early Paleozoic climate change and biodiversity cycles).

Palmer (1965, 1984) first noted late Cambrian cycles of extinction and diversification through detailed systematic work in Laurentia. He coined the term biomere to describe a cycle from one extinction horizon to the next (Palmer, 1965). Each biomere is bounded by two distinct extinction horizons. Initially biomeres were described as a Laurentian phenomenon with up to seven being recognizable in the trilobite record (Palmer, 1965, 1984; Westrop and Ludvigsen, 1987). Three of the extinctions were in the Furongian with one in the lower Tremadocian (Westrop, 2013). Later studies showed several extinction horizons to be global such as the extinction horizon that correlates with the onset of the Steptoan positive carbon isotope excursion (SPICE; Saltzman et al., 2000; Zhou and Zhen, 2008; Westrop, 2013). Plausible phenomena forcing these extinctions include the onset of marine anoxia, changes in thermohaline circulation causing increased coastal deep-water upwelling, and sea-level rise displacing continental shelf communities (Stitt, 1975; Palmer, 1984; Westrop and Ludvigsen, 1987; Saltzman et al., 2000; Westrop, 2013; Babcock et al., 2015).

Oddly, despite strong evidence for a global peak in felsic magmatism during the "late" Cambrian (McKenzie et al., 2014), possibly related to the extinction cycles, this late Cambrian interval is one of the three most sparsely geochronologically-dated intervals in the Phanerozoic (Schmitz, 2012). This is because felsic magmatism was concentrated around the equatorial Gondwana margin, much of which has been destroyed or obscured by subsequent collisional tectonics. The latest Cambrian and earliest Ordovician volcanic records outside of marginal Gondwana are sparse (Davidek et al., 1998; Landing et al., 2015; Normore et al., 2018), which prevents the acquisition of the geochronologic dates that are attainable from the interbedded volcanic and fossiliferous strata. The link between fossiliferous strata and volcanics is critical for merging relative and absolute dating methods. Geochronologic calibration of biostratigraphic units is necessary for understanding temporal correlations and patterns of the biomeres.

Collisional tectonics have not only compromised strata from which absolute dates might have been obtained but also led to poor resolution of lower Paleozoic Gondwanan marginal paleogeography. Just as resolving the late Cambrian geochronology is important for understanding the biomeres, reconstructing Gondwanan paleogeography is also important for understanding their spatial patterns; each Laurentian extinction horizon is linked with a redistribution or lateral homogenization of fauna (Westrop, 2013). How the fauna radiated or migrated through Gondwana cannot be traced without better paleogeographic reconstructions.

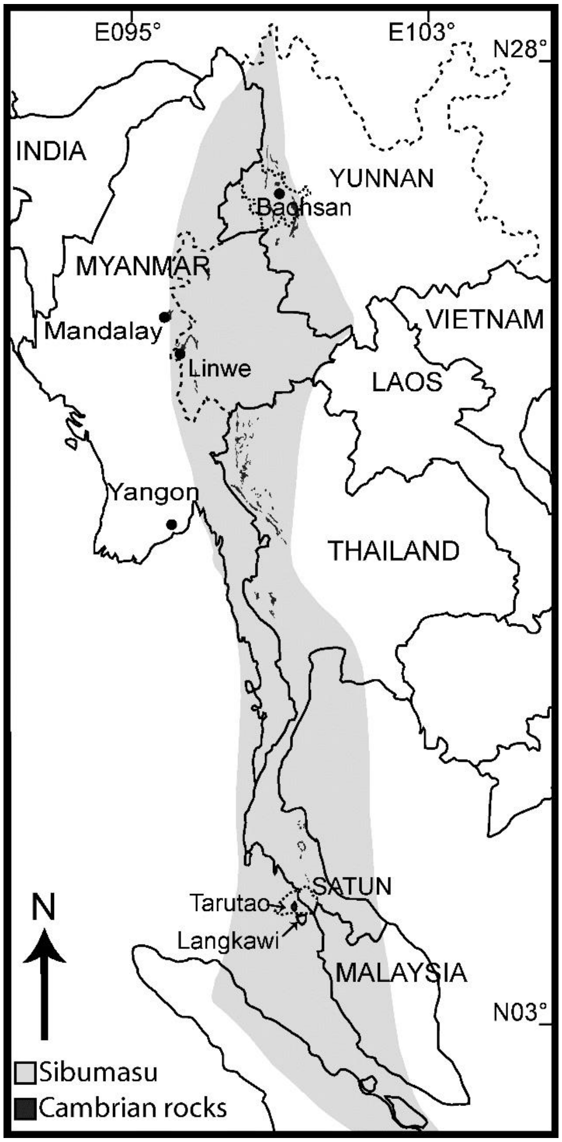


Figure 0:1 Modern map of Sibumasu. Modified from Wernette et al., 2020.

Sibumasu, a marginal Gondwanan terrane, is globally the only known area to have multiple "late" Cambrian and earliest Ordovician interbedded volcanic deposits within fossiliferous strata, spanning the latest Furongian and earliest Tremadocian strata. Furthermore its trilobite and detrital zircon records are important sources of information for reconstructing peri-Gondwanan paleogeography and projecting geochronologic information to associated terranes such as the North China Block, South China Block, and Australia. Despite this potential, to-date no geochronologic work and relatively little paleontological work has been completed in Sibumasu. This area thus offers the potential for filling a major gap in the global Phanerozoic geochronological record.

The Sibumasu terrane is comprised of western Thailand, western Baoshan in the Yunnan province of China, eastern Myanmar, northwestern Malaysia, and northern Sumatra (Fig. 0:1). The name is an acronym for its constituent regions: Si- Siam/Sino; Bu- Burma=Myanmar; Ma- Malaysia; Su- Sumatra (Metcalfe, 1984). In some areas, including Thailand, Sibumasu is better known as the Shan-Thai Block. Sibumasu has a rich late Cambrian stratigraphic record with trilobitic, detrital zircon-bearing sandstones interbedded with datable zircon-bearing rhyolitic ashes (Kobayashi, 1957; Mitchell et al., 2012; Shergold et al., 1988; Soe, 1983; Thein, 1973). Trilobite fossils are particularly useful in biostratigraphic correlation as many late Cambrian taxa are relatively short lived (Davidek et al., 1998; Choi and Kim, 2006). Nevertheless, despite the advantages of the Sibumasu record, serious attempts to reevaluate the fauna have been limited to three publications focused on the fauna of Ko Tarutao in southwest Thailand (Kobayashi, 1957; Stait et al., 1984; Shergold et al., 1988).

While fossils are useful tools for stratigraphic and geographic correlation, correlation accuracy and resolution are strongly dependent on the quality of the underlying systematic work. The Furongian (late Cambrian) and Tremadocian (earliest Ordovician) trilobite record of Sibumasu has not benefited from the same history of rigorous detailed systematic studies that have improved biostratigraphy and correlation in Australia (e.g. Shergold, 1972, 1975, 1980, 1991) and China (e.g. Sun, 1924, 1935; Lu et al., 1965). Baoshan’s fauna was described in 1979 by Xiang et al.; Malaysia’s fauna is strongly fragmented and has not been described to date; Myanmar’s fauna has never been formally illustrated or described though species occurrences have been suggested (Thein, 1973). Thailand’s fauna from the southern island, Ko Tarutao, is the best known of Sibumasu’s Cambro-Ordovician trilobites. Kobayashi described new species from several slabs in 1957; Stait et al. described Ordovician material in 1984; Shergold et al. (1988) expanded on Kobayashi’s descriptions of the Cambrian fauna but left all but three of the species unresolved. Unresolved species cannot be reliably used in biostratigraphic or paleogeographic correlations. Since that time no further investigations have been made.

In order to proceed with geochronologic and paleogeographic studies on Sibumasu, it is first necessary to extensively revise and expand the Cambro-Ordovician trilobite record from Sibumasu based on both re-evaluation of original type material and detailed additional collection on a bed-by-bed basis where possible. This faunal analysis focuses on Myanmar and Thailand, because they are the areas known to have both volcanic tuffs or “ash” beds and reasonably well-preserved fossils, making them potentially geochronologically valuable locations. This work was completed over a series of four excursions. A very short, preliminary excursion by Nigel Hughes, Paul Myrow, and Apsorn Sardsud in 2008 determined that Thailand’s fossil record on Ko Tarutao was accessible and of sufficient outcrop quality and fossil density to make further studies worthwhile. Initial geochronologic investigation suggested that the ashes were likely to yield well resolved dates. A second excursion in 2016 focused on stratigraphic logs and making collections of fossils, ash beds, and detrital zircons in both Thailand and Myanmar and to identify plausible locations for further study in Myanmar. A third excursion in 2018 focused more person-power on making extensive collections in Thailand from those localities that had previously yielded both ash samples and fossils and on improving sample density in those sections. A fourth excursion in 2020 brought more person-power to Myanmar in order to extensively sample those localities where fossils and ash beds had been found on the more exploratory 2016 excursion.

The revisions to the trilobites of Ko Tarutao, Thailand and southern Shan State, Myanmar that are described in the subsequent four chapters are based on material from the first three excursions. The material from the fourth excursion will be described in future studies. The fauna from Ko Tarutao, Thailand, is considerably more diverse than expected going into the study. The revised faunal list contains 43 discrete species, compared with the 18 species described by Kobayashi (1957), Stait et al. (1984) and Shergold et al. (1988) (as recognized following revisions by Shergold et al., 1988). Many of these species are endemic to Ko Tarutao, Thailand with 3 out of 35 genera and 17 out of 27 taxa resolved to the species level unknown outside of southern Thailand. Two genera and 14 species are new from this study. The collections made during the 2020 excursion to Myanmar also recovered a diverse assemblage exceeding previous expectations. Apart from three reasonably abundant or well-preserved species collected during the 2016 excursion to Myanmar, the remaining Myanmar material from the 2016 excursion has been left to be included with the larger collections from 2020 in order to ensure any species assignments or descriptions are based as many specimens and on as good of quality of material as possible. One new species, *Asioptychaspis lata*, is described from Myanmar based on abundant material.

The following chapters focus on systematics and do not present firm conclusions on the quantitative geochronology, biostratigraphic correlation, and paleogeographic correlation. This is for several reasons. Firstly, the extensive taxonomic work required to revise the entirety of Thailand's more diverse than expected Cambro-Ordovician trilobite assemblage in such a way that it may be reliably used in high-resolution faunal correlations delayed the application of the assemblage to such correlations. Secondly, the Covid-19 virus and the facilities closures it caused has delayed the labwork required for geochronology which collaborators in Hong Kong have only recently resumed. The collaborators at Princeton Universities have further delays before they may begin dating the samples. Thirdly, the nature of the measured sections from which the fauna was collected in both Thailand and Myanmar inhibit easy reconstruction of the biostratigraphic order of succession among separate sections. The sections are relatively short, are separated by extensive cover and faults (Shergold et al., 1988; Imsamut and Yathakam, 2011), and all of the Cambrian sections have similar fauna. While comparison with trilobite successions on other peri-Gondwanan terranes provides a general sense of the stratigraphic age, we await seeing whether the ash-bed geochronology is sufficient to resolve the stratigraphic order of sections from Ko Tarutao. Without a resolved order of sections on Ko Tarutao it is difficult to test whether correlations using methods like constrained optimization (CONOP; Sadler et al., 2003) are producing reasonable results from our data.

Currently correlation between Thailand's and Myanmar's middle of Cambrian Stage 10 fauna is feasible through their shared species, *Eosaukia buravasi*. Myanmar also shows evidence of an earlier, Jiangshanian fauna. As the extensive 2020 collections from Myanmar are described and analyzed, the fauna therein will be correlated against the fauna from Thailand to better constrain the regional Sibumasu biostratigraphic succession.

In the following paper, Chapter One is from a published paper, and *Satunarcus molaensis* Wernette and Hughes (2020) described therein is a valid genus and species name. Chapter 2 is in review, accepted with minor revisions, and *Prosaukia oculata* will be an invalid name until such time as it is published. Chapters 3 and 4 have not yet been submitted to journals and all new taxa described therein are invalid until such time as they are submitted and accepted.

Chapter 1. Satunarcus, a new late Cambrian trilobite genus from southernmost Thailand and a reevaluation of the subfamily Mansuyiinae Hupé, 1955

Introduction

Peninsular Thailand’s latest Cambrian strata comprise interbedded fossiliferous sandstones and rhyolitic ash beds, making this succession particularly important for resolving the geochronology of the Cambro-Ordovician boundary (Stait et al., 1984). Previous studies of Thailand’s Cambrian trilobites (Kobayashi, 1957; Shergold et al., 1988) recovered a mix of taxa both endemic to Thailand and shared with Australia, North China, or South China, and here we describe here the first of several recently collected taxa, new to Ko Tarutao, which will help further resolve the biostratigraphic succession of Thailand and its paleogeographic association with other Gondwanan terranes. *Satunarcus molaensis* n. gen., n. sp. is one such new taxon. *Satunarcus* belongs to Kaolishaniidae (Kobayashi, 1935) and, while morphologically distinctive, bears close resemblance to genera known from Australia, North China, and South China.

Trilobites of the corynexochid suborder Leiostegiina, particularly tsinaniids and kaolishaniids, are prevalent in the late Cambrian (Furongian) record from equatorial Gondwana. They occur in Sibumasu, South and North China, Bhutan, and Australia (Sun, 1924; Shergold, 1972; Shergold, 1975; Shergold et al., 1988; Shergold, 1991; Zhu et al., 2010; Hughes et al., 2011; Zhu et al., 2013; Park et al., 2014). The evolution and dispersal patterns of Kaolishaniidae Kobayashi (1935) and Tsnianiidae Kobayashi (1933) reflect Cambro-Ordovician paleogeography during the final accretion of Gondwana prior to its mid-Paleozoic breakup (Cawood et al., 2007). These trilobites are also useful index taxa for establishing Stage 10 biozones including the *Shergoldia nomas* Zone of Australia and the *Ptychaspis-Tsinania* and *Kaolishania pustulosa* zones of North China (Geyer and Shergold, 2000). The discovery of a new kaolishaniid genus, *Satunarcus*, from Thailand's Tarutao Group and its affinities with various genera traditionally classified as Mansuyiinae Hupé (1955) prompts a revision of this subfamily and its role in the evolution of Tsinaniidae from Kaolishaniidae.

Tsinaniids have been scrutinized in numerous studies on the origins of higher level taxa that became prominent during the Great Ordovician Biodiversification Event. They have alternatively been suggested as a sister taxon to Asaphida (Zhu et al., 2007) or as an early family in, or sister taxon to, the derived corynexochid suborder, Illaenina (Fortey, 1997; Adrain, 2011). The asaphid hypothesis has been strongly refuted (Park and Choi, 2009; Zhu et al., 2010) while the basal illaenid hypothesis is not well supported, although classification schemes listing Tsinaniidae as an illaenid remain current (Adrain, 2011). As a result of investigations into the potential role of Tsinaniidae as a sister taxon to more derived Ordovician groups, several different cladistics-based phylogenetic schemes have arisen for the emergence of Tsinaniidae with the general consensus being that the family is rooted in Kaolishaniidae (Zhu et al., 2013; Lei and Liu, 2014; Park et al., 2014). In each of these phylogenies, *Mansuyia* Sun (1924) is important in the split between Tsinaniidae and other kaolishaniids. In one cladistic analysis, *Mansuyia* resolved as a paraphyletic stem genus to Tsinaniidae (Park et al., 2014) with the holaspid retention of pygidial spines linking it to Kaolishaniidae and the ventral median suture and overall pygidial form excluding the spines linking it to Tsinaniidae. In another analysis, *Mansuyia* was made the outgroup to tsinaniids, thus providing no meaningful information on the relationship between Kaolishaniidae and Tsinaniidae while assuming a polarization of characters from *Mansuyia* to Tsinaniidae (Zhu et al., 2013). In yet a third study, the relationship between *Kaolishania* Kobayshi (1935), *Mansuyia*, and tsinaniids was an unresolved polytomy (Lei and Liu, 2014).

All three cladistic investigations into the tsinaniid-kaolishaniid link suffer from a lack of focus on the kaolishaniid taxa. Park et al. (2014) and Lei and Liu (2014) each used only a single kaolishaniid species apart from *Mansuyia* in the analysis; in Park et al. (2014) it is the outgroup, forcing a *Mansuyia*-Tsinaniidae connection. Additionally, no members of the taxa assumed to be *Mansuyia*'s closest relatives, the Mansuyiinae Hupé (1955) were included in any analysis. When considering the position of *Mansuyia* in regards to kaolishaniids and tsinaniids, the placement of taxa generally considered *Mansuyia*'s closest relatives, the other Mansuyiinae, must be considered. Mansuyiinae is vaguely characterized as "Mansuyia-like taxa" (Shergold, 1972). Because *Manusyia* is the type genus of Mansuyiinae, any questions of its affinity should also consider the affinities of the entire subfamily.

The discovery of a new kaolishaniid trilobite from the Ao Mo Lae Formation of the Tarutao Group of southernmost peninsular Thailand prompts a reevaluation of kaolishaniid and tsinaniid systematics with emphasis on the inclusion of a broader range of Mansuyiinae genera. The most similar previously published material comes from

Australia and was originally assigned to *Mansuyia* cf. *orientalis* due to its comparable pygidium (Shergold, 1975, 1991), but for both the Thai and Australian material *Mansuyia* cf. *orientalis* is an unsatisfactory designation. Specimens from both collections are more similar to Mansuyiinae genera other than *Mansuyia* itself, particularly in the large, flat preglabellar area. The cladistic analysis described herein was initially conducted to evaluate the generic placement of the Thai and Australian material, but it reveals new insight into kaolishaniid-*Mansuyia*-tsinaniid evolution by restricting Mansusyiinae as it is currently understood and revealing a previously unrecognized clade within Kaolishaniidae.

Geologic and stratigraphic context

Western Thailand, along with northern Malaysia, eastern Myanmar, and western Yunnan, China, is part of the peri-Gondwanan terrane known as Sibumasu (Metcalfe, 2002) or the Shan-Thai block (Bunopas, 1982). To date, the island Ko Tarutao (Fig. 1:1) has the best-studied Cambrian fossils from Sibumasu (Kobayashi, 1957; Stait et al., 1984; Shergold et al., 1988); they are found in the Tarutao Group (Javanaphet, 1969), a

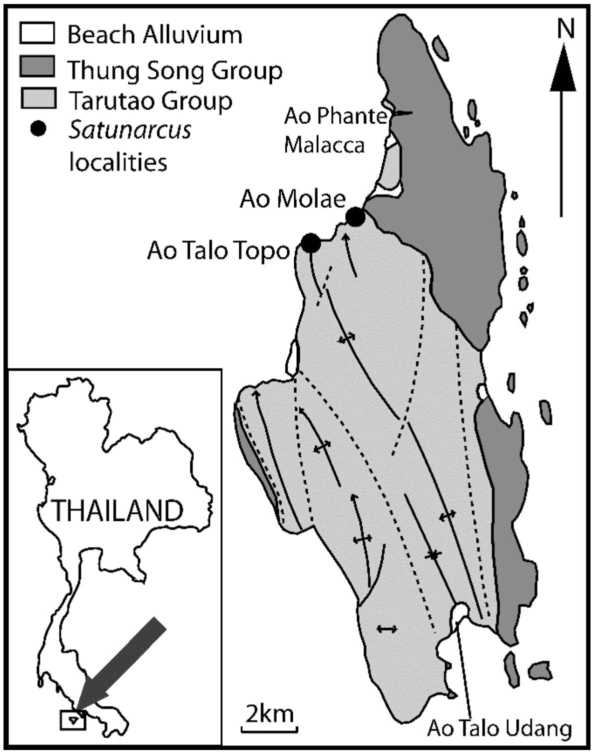


Figure 1:1 Geologic map of Ko Tarutao, Thailand with localities from which Satunarcus was discovered. (Modified from Shergold et al., 1988)

clastic unit dominated by sandstone that forms the base of the Paleozoic succession in western Thailand. The Tarutao Group contains a diverse latest Cambrian and earliest Ordovician faunal assemblage, including the newly discovered *Satunarcus molaensis* n. gen., n. sp. Its best exposed and accessible outcrops are on Ko Tarutao itself, Thailand’s southern-most island which is ~25 km off the west coast of Satun province and ~5 km north of Langkawi, Malaysia. There are some outcrops of the Tarutao Group on the mainland, but these are mainly quartzite, having experienced low-grade regional or contact metamorphism (Wongwanich et al., 2002); no fossils have been found outside of Ko Tarutao. The Machinchang Formation of Langkawi is the southern lithologic continuation of the Tarutao Group and does bear some fossils (Lee, 1983).

The Tarutao Group extends from the upper Furongian into the Tremadocian, where it transitions into the limestone of the Thung Song Group (Bunopas, 1981; Stait et al., 1984). The exact thickness of the Tarutao Group is difficult to estimate due to faulting; exposures occur only as isolated coastal headland outcrops in short sections separated by long covered intervals. Total thickness estimates range from 800 m (Bunopas et al., 1983) to 3,100 m (Teraoka et al., 1982). Shergold et al. (1988) accepted a conservative estimate of 850 m, which we consider more reasonable than estimates surpassing 1,000 m, because it better considers the faults and folds across the island. At present, we have collected Cambrian fossils from four localities: Ao Phante Malaca, Ao Molae, Ao Talo Topo, and Ao Talo Udang. *Satunarcus* has been found only at Ao Molae (06°40'13.68"N, 099°38'1.38"E) and Ao Talo Topo (06°40'8"N, 099°37'6.12"E) where it occurs in association with another genus first described from Ko Tarutao, the dikelocephalid *Thailandium* Kobayashi (1957). The fossil assemblages at these two localities suggest that they are from near the base of Cambrian Stage 10, and equivalent in age to the *Changia* trilobite zone of North China (Sun, 1924; Zhou and Zhen, 2008; Peng, 2009) and the *Sinosaukia impages* through *Shergoldia nomas* zones of Australia (Fig. 1:2), ~489 Ma (Shergold, 1972). The outcrops at Ao Talo Toppo and Ao Molae are from the Ao Mo Lae Formation, the stratigraphically lowest fossiliferous part of the Tarutao Group (Imsamut and Yathakam, 2011).

All specimens from Ao Talo Topo described herein were collected from a single horizon during our scouting expedition in 2008. Unfortunately the later excursion, during which the section was measured, failed to find *Satunarcus* at Ao Talo Topo though

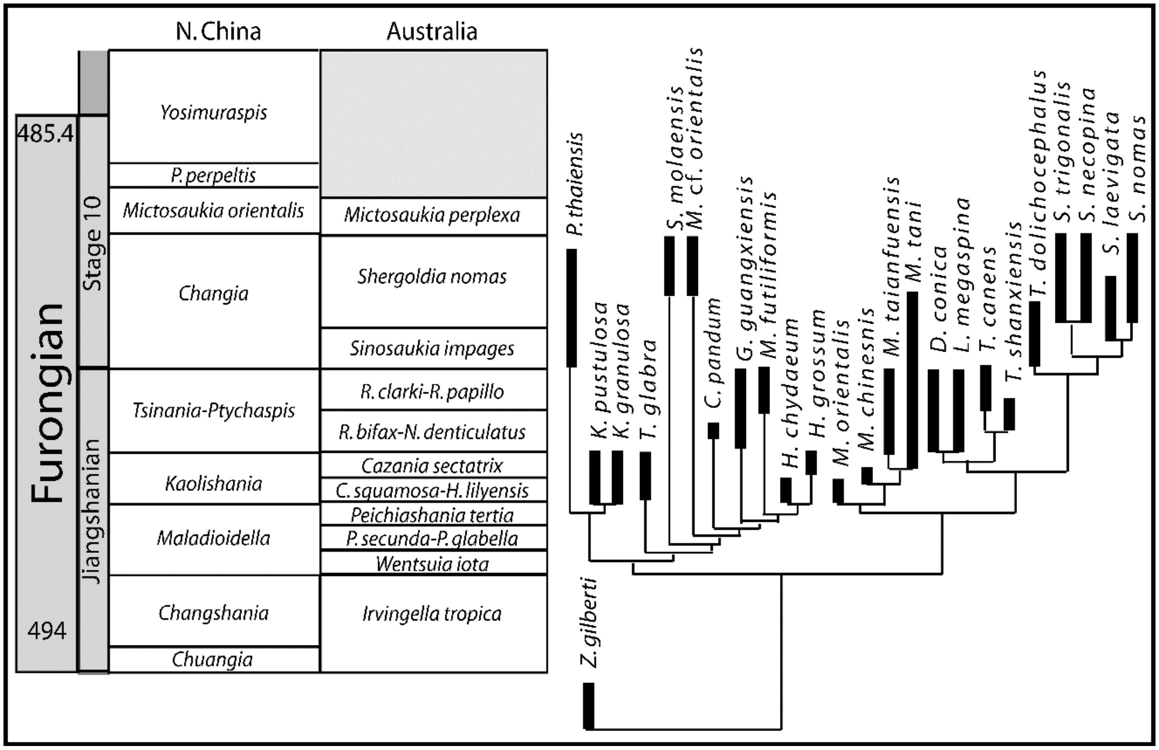


Figure 1:2 Trilobite biostratigraphic zones of North China and Australia and stratigraphic constraint of the tsinaniid and kaolishaniid cladogram. The taxa with abbreviated generic names are *Pseudokoldinioidia perpeltis*, *Rhaptagnostus clarki*, *Rhaptagnostus papillo*, *Rhaptagnostus bifax*, *Neagnostus denticulatus*, *Caznaia squamosa*, *Hapsidocare lilyensis*, *Peichiashania secunda*, and *Prochuangia glabella*. (Shergold, 1972, 1975, 1991; Geyer and Shergold, 2000; Shergold et al., 2007; Zhu et al., 2007; Peng et al., 2009; Zhu et al., 2010, 2013; Hughes et al., 2011; Park et al., 2012, 2014; Lei and Liu, 2014)

numerous other species were found. Without the recovery of at least some of the key species that co-occur with *Satunarcus*, such as *Thailandium* and *Pagodia*, it is not possible to place *Satunarcus w*ithin the section. The first fossils ever published from Ko Tarutao were from a lithologically and biostratigraphically comparable horizon of purple sandstones with *Thailandium*, though in a different section (Kobayashi, 1957; Shergold et al., 1988). Specimens from Ao Molae (horizons 1 and 2) were also collected at the time of the expedition to Ao Talo Topo, in addition to during a later visit in December 2016. Ao Molae has an ~11 m thick section through the Ao Mo Lae Formation with fossiliferous beds confined to the middle part (Fig. 1:3). *Satunarcus molaensis* itself has been recovered from only the upper half of the fossiliferous beds (4.71 m–6.01 m) of the Ao Molae section. When Ao Talo Topo and Ao Molae collections are considered together, *S. molaensis* co-exists with *Eosaukia buravasi* Kobayashi, 1957, *Thailandium solum* Kobayashi, 1957, *Quadraticephalus planulatus* (Kobayashi, 1957), *Hoytaspis*? *thanisi* Shergold et al.,

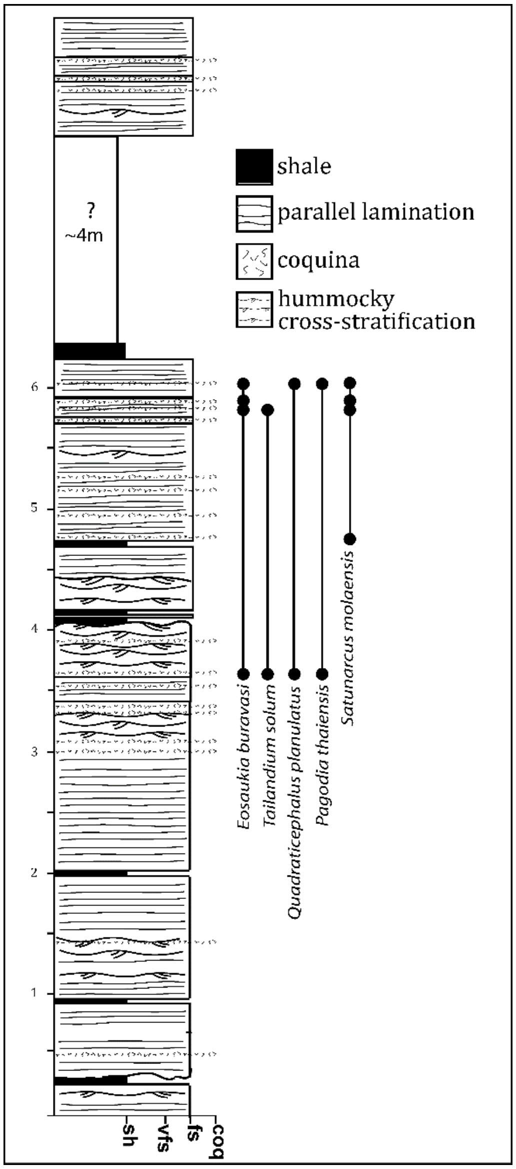


Figure 1:3 Ao Molae measured section and range chart. Section height is measured in meters.

1988, and *Lichengia*? *tarutaoensis* (Kobayashi, 1957). It is the recovery of *Eosaukia, Thailandium,* and *Quadraticephalus* that suggests stratigraphic equivalency with the *Sinosaukia impages* and *Changia* zones of Australia and North China respectively.

The Tarutao Group is primarily composed of hummocky, cross-bedded, and parallel-bedded fine-grained quartzarenite with a minor component of siltstone and shale and is interbedded with rhyolitic volcanic ash and breccia (Fig. 1:3). Fossils are primarily preserved as molds in coquina horizons within the sandstone beds (Fig. 1:4). Fossiliferous horizons are readily identitiable in cross section in the outcrop as thin (less than 1 cm), pitted horizons oriented parallel to bedding, from which internal and external molds can be retrieved. The sandstones are devoid of all carbonates includeing shell material which was lost during diagenesis. All *Satunarcus* n. gen. were recovered from such horizons, but a small number of other fossils including trilobites, brachiopods, and cephalopods are isolated within the sandstone and oriented obliquely to bedding. All fossils within the Tarutao Group are disarticulated, with the degree of fragmentation ranging from absent to unidentifiable scleritic hash. The molds forming the coquina horizons at Ao Talo Topo and Ao Molae are in some cases whitened by secondary silica

Figure 1:4 Photo of Ao Talo Topo bedding; the white arrow points to a pitted, fossiliferous shellbed horizon. Hammer with head ~18 cm long included for scale.

precipitation that partially infill the molds. Preservation as molds in fine-grained sandstone precludes the occurrence of early ontogenetic stages and only disarticulated holaspid sclerites have been recovered. For *Satunarcus*, pygidial and cranidial associations can be made with reasonable confidence on the basis of size, frequency of occurrence, and inferred taxonomic affinity, but no librigena, hypostomes, or thoracic segments have been found of the right size and morphology to make them a plausible match. This study's cladistic analysis is restricted to characters of mature holaspid cranidia and pygidia because this is the only information available for most tsinaniid and kaolishaniid taxa, including *Saturnarcus*.

Characters and taxa used in cladistic analysis

The cladistic analysis of Tsinaniidae and Kaolishaniidae presented herein uses a heuristic examination of 51 characters with a total of 91 character states across 24 ingroup taxa and one outgroup (Table 1:1). The ingroup taxa were chosen based on the following criteria: (1) taxonomic significance of species — type species such as *Mansuyia orientalis* Sun, 1924 and *Tsinania canens* (Walcott, 1905) were favored because their characteristics are central to evaluating their generic concepts; (2) use in recent tsinaniid phylogenetic studies (including Zhu et al., 2013; Lei and Liu, 2014; Park et al., 2014) — taxa used in these studies were favored in order to facilitate comparisons between the results of these different phylogenetic analyses; (3) quality of published figures — analysis was based primarily on figured specimens, and those with only low resolution or poor quality images from older publications are less useful in providing confident character state assignments; and (4) taxonomic breadth of coverage — we favored sampling a wide range of genera from within Mansuyiinae more than multiple species within a single genus. Exceptions were made for *Shergoldia* and *Tsinania* since the monophyly of these genera is particularly questionable.

Previous analyses of Kaolishaniidae and Tsinaniidae used *Kaolishania granulosa* Kobayashi, 1933, *Kaolishania pustulosa* Sun, 1924, or *Mansuyia orientalis* Sun, 1924 as outgroups, all of which belong to either Kaolishaniidae or Tsinaniidae (Zhu et al., 2013; Lei and Liu, 2014; Park et al., 2014). However, in order to evaluate the relationship between kaolishaniids and tsinaniids, it is important to use an outgroup that is not a member of either. Because the relationships between kaolishaniids and tsinaniids may have implications for the derivation of Illaeniina from Leiostegiina, we chose to use an outgroup from the third Corynexochida suborder, Corynexochina, which is stratigraphically older than either Illaeniina or Leiostegiina. *Zacanthoides gilberti* Young and Ludvigsen, 1989 is suitable as the outgroup because it is a well-known, stratigraphically older representative of Corynexochina.

Cladistic analysis used the following species. For measurements we used the noted specimens as they are relatively complete and unambiguous representatives of the species.

- *Zacanthoides gilberti* Young and Ludvigsen, 1989: two cranidia and two pygidia (Young and Ludvigsen, 1989, pl. 6, figs. 12, 13, 16 and pl. 7, fig. 2)
- *Ceronocare pandum* Shergold, 1975: two cranidia and one pygidium (Shergold, 1975. pl. 43, figs. 1, 7, 8)

- *Dictyella conica* Shergold et al., 2007: two cranidia and two pygidia (Shergold et al., 2007, figs. 27.a, 27.c, 27.j, 27.o, 27.r)
- *Guangxiaspis guangxiensis* Zhou, 1977: two cranidia and two pygidia (Zhu et al., 2010, fig. 5.9, 5.10)
- *Hapsidocare chydaeum* Shergold, 1975: one cranidium and three pygidia (Shergold, 1975, pl. 40, fig. 1, pl. 41, figs. 1–3)
- *Hapsidocare grossum* Shergold, 1975: one cranidium and one pygidium (Shergold, 1975, pl. 42, figs. 1, 5)
- *Kaolishania granulosa* Kobayashi, 1933: two crandidia and two pygidia (Park et al., 2012, fig. 8.a, 8.b, 8.y; Kobayashi, 1960, pl. 20, figs. 11, 12)
- *Kaolishania pustulosa* Sun, 1924: three cranidia and three pygidia (Sun, 1924, pl. 3., fig. 8.a, 8.e; Lu et al., 1965, pl. 81, figs. 1, 4; Qian, 1994, pl. 27, figs. 5, 8)
- *Lonchopygella megaspina* Zhou in Zhou et al., 1977: three cranidia and three pygidia (Zhou et al., 1977, pl. 55, figs. 11, 12; Zhu et al., 2013, figs. 2.22, 2.23, 3.30, 3.31)
- *Satunarcus molaensis* n. gen. n. sp.: nine cranidia and six pygidia (Figs 1:9 and 1:10)
- *Mansuyia chinensis* (Endo, 1939): two cranidia and two pygidia (Park et al., 2014, fig. 3.B, 3.H, 3.L, 3.N)
- *Mansuyia orientalis* Sun, 1924: three cranidia and two pygidia (Qian, 1994, pl. 32, figs. 5, 6, 11, pl. 33, figs. 1, 3)

- *Mansuyia* cf. *orientalis* (Sun, 1924; sensu Shergold, 1991, 1975): four cranidia and two pygidia (Shergold, 1975, pl. 38, figs. 6, 7; Shergold, 1991, pl. 2, figs. 2, 4, 5, 6)
- *Mansuyia taianfuensis* (Endo, 1939): two cranidia and two pygidia (Endo, 1939, pl. 2, figs. 21, 22; Park et al., 2014, fig. 6.f, 6.h)
- *Mansuyia tani* Sun, 1935: two cranidia and two pygidia (Park et al., 2014, fig. 5.b, 5.g, 5.l, 5.p)
- *Mansuyites futiliformis* Shergold, 1972: two cranidia and two pygidia (Shergold, 1972, pl. 13, figs. 1, 6, pl. 14, figs. 1, 4)
- *Pagodia thaiensis* Kobayashi, 1957: two cranidia and one pygidium (Kobayashi, 1957, pl. 4, figs. 5-7)
- *Shergoldia laevigata* Zhu et al., 2007: three cranidia and two pygidia (Zhu et al., 2007, figs. 2.c, 2.f, 3.e)
- *Shergoldia necopina* (Shergold, 1975): two cranidia and one pygidium (Shergold, 1975, pl. 48, figs. 2, 3, 5)
- *Shergoldia nomas* (Shergole, 1975): two cranidia and two pygidia (Shergold, 1975 pl. 47, figs. 1-3, 5)
- *Shergoldia trigonalis* (Shergold, 1975): one cranidium and two pygidia (Shergold, 1975, pl. 50, figs. 3, 7, 8)
- *Taipaikia glabra* (Endo in Endo and Resser, 1937): two cranidia and two pygidia (Endo and Resser, 1937, pl. 69, fig. 21; Hughes et al., 2011, figs. 9.e, 9.g, 10.c)

- *Tsinania canens* (Walcott, 1905): three cranidia and two pygidia (Park et al., 2014, fig. 7.a-7.c, 7.g, 7.j)
- *Tsinania dolichocephala* (Kobayashi, 1933): three cranidia and two pygidia (Lei and Liu, 2014, figs. 6.a-6.c, 6.g, 6.h)
- *Tsinania shanxiensis* (Zhang and Wang, 1985): two cranidia and two pygidia (Lei and Liu, 2014, figs. 3.d, 3.f, 5.m, 5.o)

Fifty-one characters of holaspid cranidia and pygidia were considered and possess a mix of binary and multi-state attributes. All quantitative character states are based on discrete breaks in character distributions. Characters that could not be coded for a species because of missing data or inapplicable features were coded as missing, indicated by "?". Characters inapplicable to the outgroup do not have an assigned state zero and are also indicated by "?" (as in Carlucci et al., 2010 and Wernette and Westrop, 2016). The characters and character states are:

1. Anterior border dorso-ventral convexity: (0) Convex, (1) Concave, (2) Flat
2. Anterior border furrow lateral condition – the appearance of the lateral part of the anterior border furrow: (0) Distinct, (1) Faint, (2) Effaced
3. Anterior border furrow medial condition — the appearance of the medial part of the anterior border furrow: (0) Distinct, (1) Faint, (2) Effaced
4. Anterior margin shape: (0) Evenly curved, (1) Triangular
5. Anterior margin angularity — the angularity of the triangular shaped anterior margin from character 4[1]: (1) Roundish, (2) Blunt, (3) Sharp, (4) Concave

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
Z. gilberti	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0	?	?	?	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0
C. pandum	1	1	1	1	4	1	1	0	0	1	3	1	3	1	2	1	0	0	1	1	0	1	1	1	0	2	1	1	1	1	1	0	2	1	1	1	1	0	1	1	0	0	0	1	1	0	1	1	0	1	2
D. conica	2	1	1	1	3	0	0	1	?	1	1	?	0	2	2	0	?	2	0	?	?	0	2	0	?	1	2	?	1	?	?	?	?	?	1	0	2	1	1	1	1	0	2	0	0	2	?	1	0	1	?
G. guangxiensis	1	1	1	1	4	0	1	0	0	1	3	1	0	1	0	1	0	0	1	1	0	0	1	1	0	2	?	?	0	0	1	0	2	2	1	0	1	0	1	1	0	0	1	1	1	1	?	1	1	1	1
H. chydaeum	1	0	1	1	2	0	1	0	0	1	3	1	0	0	1	1	0	0	0	1	1	0	1	1	0	2	1	1	1	1	1	0	2	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1
H. grossum	1	0	1	1	2	0	1	0	?	1	3	?	0	0	1	1	0	0	0	1	0	0	1	1	0	2	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	1	0	1	1
K. granulosa	0	0	0	0	?	0	0	0	1	0	2	1	0	0	0	0	?	0	0	1	0	1	1	0	0	1	1	1	?	1	0	1	2	1	3	1	1	0	0	0	0	0	0	0	1	0	2	1	1	1	1
K. pustulosa	0	0	0	0	?	0	0	0	1	0	2	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	0	1	0	1	2	1	1	1	1	0	0	0	0	0	0	1	1	0	2	1	1	2	1
L. megaspina	2	0	0	1	3	0	0	1	?	1	1	0	0	1	1	0	0	1	0	0	1	0	?	0	?	1	2	?	1	0	2	0	2	1	1	0	2	1	1	1	1	0	2	0	0	2	0	1	0	1	2
S. molaensis	2	2	2	0	?	1	1	0	1	1	3	1	0	1	0	1	0	0	0	1	0	1	1	1	0	2	1	1	?	?	0	1	2	1	1	1	1	0	1	0	0	0	0	1	1	1	1	0	1	2	1
M. cf. *orientalis*	0	1	2	1	2	1	1	0	1	1	3	1	0	1	1	1	0	0	0	1	0	1	2	1	0	2	1	1	0	0	0	0	2	1	1	1	1	0	1	0	0	0	0	1	1	0	1	0	1	1	1
M. chinensis	2	0	0	1	2	0	0	0	1	1	1	1	0	2	1	1	1	0	0	0	0	?	2	0	0	1	1	2	1	0	0	0	2	2	1	0	2	1	1	1	0	0	0	0	1	1	0	0	1	2	1
M. orientalis	0	0	0	1	1	0	?	0	0	1	3	1	0	0	1	1	1	0	0	0	0	0	2	0	0	1	1	2	1	1	0	0	2	2	1	0	2	1	1	1	0	0	0	0	1	1	0	0	1	2	1
M. taianfuensis	2	0	0	1	2	0	0	0	1	1	1	1	0	2	2	1	1	1	0	?	0	?	?	0	0	1	1	2	1	1	?	0	?	?	1	0	2	1	1	1	0	0	0	0	1	2	1	0	1	1	2
M. tani	2	0	0	1	2	0	0	0	1	1	2	1	0	2	1	1	1	1	0	0	0	1	2	0	0	1	1	2	1	0	1	0	2	2	1	0	2	1	1	1	0	0	0	0	1	2	1	0	1	1	2
M. futiliformis	0	1	1	1	2	0	1	0	0	1	3	1	0	0	1	1	0	0	1	1	0	0	2	1	0	2	1	1	0	0	1	0	2	1	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	1	1
P. thaiensis	0	0	0	0	?	0	0	1	?	0	0	?	0	0	0	0	0	0	0	?	0	1	0	0	0	1	1	1	?	1	1	1	1	?	1	0	1	1	0	?	1	0	?	0	0	2	1	1	0	1	1
S. laevigata	0	0	0	1	1	0	0	0	1	1	3	0	0	1	1	0	0	1	1	0	1	1	2	0	1	1	2	?	1	1	0	0	2	2	1	1	1	1	1	1	1	0	0	0	0	0	2	0	1	1	3
S. necopina	0	0	0	0	?	0	1	0	1	1	2	0	1	2	1	0	0	1	1	0	1	1	2	0	1	1	2	?	0	1	0	0	2	1	3	0	2	1	1	1	1	0	0	0	1	1	?	0	1	1	1
S. nomas	0	0	0	0	?	0	0	0	1	1	3	0	1	2	1	0	0	2	1	0	1	1	2	0	1	1	2	?	1	1	1	0	2	2	3	0	1	1	1	1	1	0	0	0	0	0	2	0	1	1	1
S. trigonalis	0	0	0	1	1	0	1	0	1	1	2	0	1	2	1	0	0	1	1	0	1	1	2	0	1	1	2	?	0	?	0	0	2	1	1	0	2	1	1	1	1	0	0	0	0	0	2	0	1	1	1
T. glabra	1	1	2	0	?	1	1	1	?	0	3	1	0	2	2	1	0	0	0	1	0	1	0	1	1	1	2	?	1	?	2	0	2	1	2	0	1	1	0	1	1	0	1	1	0	0	1	0	1	1	1
T. canens	0	1	1	1	1	0	0	1	?	1	1	0	0	2	1	0	0	1	0	0	0	0	?	0	1	1	2	?	1	1	1	0	2	2	1	0	2	1	1	1	1	0	0	0	0	2	1	1	0	1	2
T. dolichocephala	0	0	1	1	1	0	0	0	1	1	2	0	0	2	1	0	0	2	0	0	1	0	?	0	1	1	2	?	1	0	0	0	2	1	1	?	2	1	1	1	1	0	0	0	0	0	2	0	1	1	3
T. shanxiensis	0	0	0	1	1	?	0	1	?	1	1	?	0	1	1	0	0	1	0	0	0	0	2	0	1	1	2	?	1	1	0	0	2	2	1	0	2	1	1	1	1	0	0	0	0	2	1	1	0	1	2

Table 1:1 Matrix of character states for each taxon. See the in-text list of characters for the description of each numbered character and its states.

6. Anterior border lateral corner position: (0) Opposite preglabellar furrow, (1) Anterior to glabella

7. Preglabellar field: (0) Absent, (1) Present

8. Preocular facial suture orientation:(0) Divergent, (1) Convergent

9. Extent of preocular facial suture deflection — only applicable for taxa with character 8[0]: (0) >33°, (1) <33°

10. Facial suture and anterior margin intersection: (0) Lateral, (1) Axial — facial suture anterior branches fuse on dorsal surface

11. Maximum anterior area width (tr.) divided by preoccipital glabellar length (sag.): (0) <110%, (1) 110 – 129%, (2) 130–149%, (3) >150%

12. Widest (tr.) point on preocular cranidium: (0) On anterior border, (1) Posterior to anterior border
13. Plectrum: (0) Absent, (1) Present
14. Preglabellar furrow expression: (0) Incised, (1) Inflected — preglabellar border defined by a sharp change of slope, (2) Faint
15. Axial furrow expression: (0) Deep, (1) Shallow, (2) Effaced
16. Lateral glabellar furrow expression: (0) Distinct, (1) Faint, (2) Effaced
17. Preglabellar and anterior border furrow confluence: (0) Confluent, (1) Separate
18. Preglabellar and axial furrow junction: (0) Defined, (1) Continuous curve
19. Axial furrow bacculae: (0) Absent, (1) Present
20. Median glabellar ridge: (0) Present, (1) Absent
21. Posterior glabellar narrowing — posterior end of L1 distinctly narrower (tr.) than anterior: (0) Absent, (1) Present

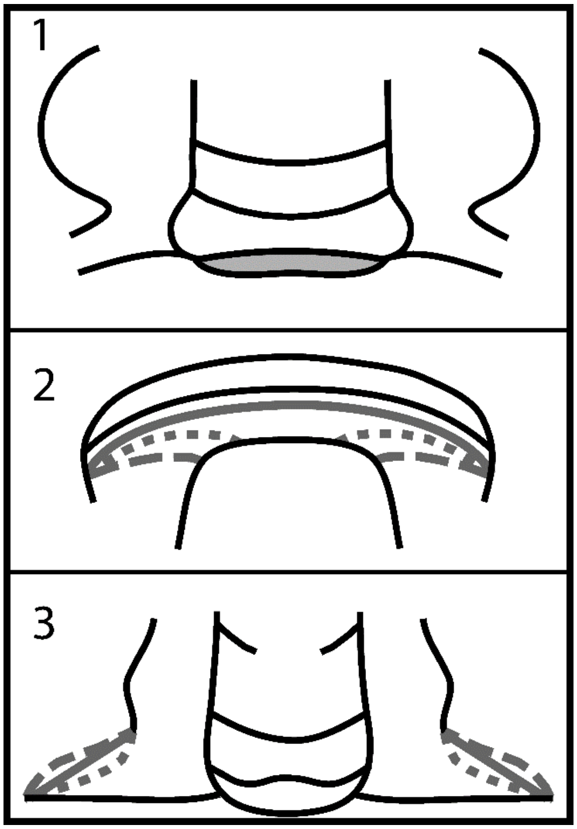


Figure 1:5 Explanatory illustrations of select characters. **(1)** post-occipital ridge 25[1]; **(2)** anterior termination position of inflated fixigenal areas: solid line 27[2], short dash 28[2], long dash 28[1]; **(3)** post ocular facial suture shape: long dash 35[1], solid line 35[2], short dash 35[3].

22. SO medial anterior bend: (0) Present, (1) Absent

23. LO width relative to L1: (0) Same, (1) LO narrower, (2) LO wider

24. LO termination at axial furrows: (0) Pinched — LO shortens (exsag.) as it approaches the axial furrows, (1) Blunt — LO truncates against axial furrows

25. Transverse postoccipital ridge — a flange or ridge on the posterior edge of the occipital ring: (0) Absent, (1) Present (Fig. 1:5.1)

26. Anterior fixigenal termination — the feature against which fixigena terminate anteriorly: (1) Anterior border — fixigena terminate against the anterior border furrow, (2) Preglabellar field — the preglabellar field separates the fixigena from the anterior border

27. Adaxial position of fixigenal termination — the position of the adaxial end of the line denoting the anterior edge of the fixigena: (1) Opposite glabella, (2) Anterior to glabella (Fig. 1:5.2)

28. Glabellar adaxial fixigenal termination — for taxa with character 27[1] the glabellar feature against which the anterior adaxial fixigenal corner terminates: (1) Anterior glabellar corner, (2) Preglabellar border (1:Fig. 5.2)

29. Palpebral lobe curvature — how strongly curved the adaxial edge of the palpebral lobe is: (0) Strong, (1) Weak

30. Palpebral lobe curvature evenness: (0) More curved posteriorly, (1) Evenly curved

31. Exsagittal position of palpebral lobe anterior point: (0) Anterior to S2, (1) Opposite S2, (2) Opposite L2

32. Palpebral lobe posterior position: (0) Posterior to S1, (1) Opposite S1

33. Eye ridge: (1) Absent, (2) Present

34. Eye ridge condition — only applies to taxa with character 33[2]: (1) Faint, (2) Distinct

35. Postocular facial suture shape: (1) Increasingly arched toward posterior, (2) Straight, (3) Increasingly arched abaxially (Fig. 1:5.3)

36. Cranidial posterior border shape: (0) nearly straight, (1) distinctly curved

37. Posterior border furrow length (exsag.): (1) Consistent length, (2) Abaxially lengthening

38. Anterior pygidial corner shape — the extent of rounding at the inflection where the anterior pygidial border joins the lateral pygidial border: (0) Rounded, (1) Angular

39. Anterior pygidial margin shape: (0) Straight, (1) Arched posterolaterally

40. Anteriormost pygidial segment length (exsag.): (0) Distally expanding, (1) Constant

41. Paired segment-related spines: (0) Present, (1) Absent

42. Paired pygidial border spines — the presence of pygidial spines extended from undifferentiated border rather than as extensions of segments: (0) Absent, (1) Present

43. Posterior pygidial margin shape: (0) Strongly curved, (1) Gently curved, (2) Triangular

44. Pygidial axial furrow shape: (0) Straight, (1) Curved

45. Macropleural pygidial segment: (0) Absent, (1) Present

46. Pygidial border width (sag. and exsag.): (0) Broad, (1) Narrow, (2) Absent

47. Pleural bands: (0) Continue to margin, (1) Fade out gradually before border, (2) Abrupt termination defining border

48. Pygidial border convexity: 0) Concave, 1) Convex

49. Posterior axial termination point: 0) Pygidial margin, 1) Before pygidial margin

50. Axial ring shape: 0) Medial posterior inflection, 1) Straight, 2) Medial anterior inflection

51. Number of pygidial rings: 0) Four, 1) Five-Seven, 2) Eight-Nine, 3) Ten or more

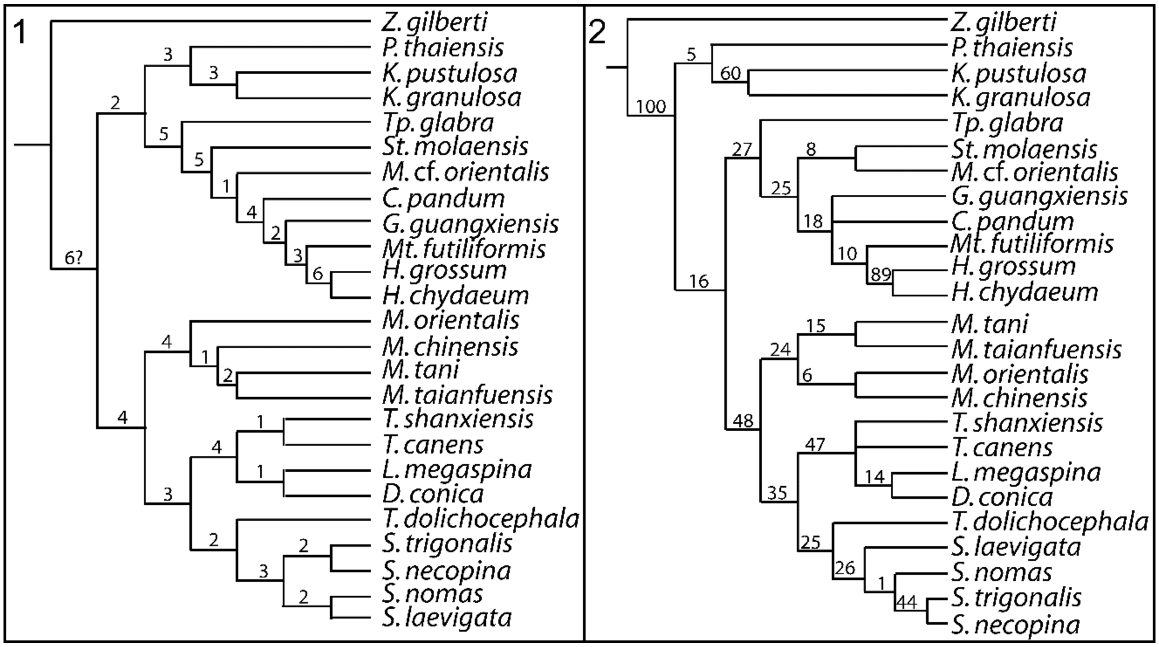


Figure 1:6 Most parsimonious and bootstrapped trees. **(1)** Bremer support for the most parsimonious tree, tree length 187; **(2)** Bootstrap results from 10000 replicates; numbers are given as percentages. To avoid confusion for genera starting with the same letter, the following scheme is applied: *M = Mansuyia; Mt = Mansuyites; S = Shergoldia; St = Satunarcus; Tp = Taipaikia; T = Tsinania.*

Results of cladistic analysis

We utilized Mesquite (Maddison, 2001) to build the matrix, Tree Analysis Using New Technology (TNT; Goloboff et al., 2008) to run the analysis, and Winclada (Nixon, 2002) to map characters and evaluate some support metrics. The heuristic analysis of the matrix of 25 taxa by 51 characters described above used Wagner trees with 100 random seeds and 1000 replications, saving up to 10 trees per replication. The analysis resulted in a single most parsimonious tree with length 187, CI 37, and RI 67 (Fig. 1:6). The general structure of the cladogram is two sided and follows the currently recognized systematics; kaolishaniids, including *Satunarcus*, are on one side and tsinaniids on the other. Exceptions to the traditional classification scheme are that *Mansuyia* Sun, 1924, generally accepted to be a kaolishaniid (Shergold, 1972), shows affinity with the tsinaniids, and *Taipaikia* Kobayashi (1960), generally accepted to be a tsinaniid (Kobayashi, 1960; Hughes et al., 2011), groups with the kaolishaniids. The unambiguous character supporting the grouping of *Mansuyia* with Tsinaniidae is 11[1], a preglabellar width that is 110–130% of the glabellar length (Fig. 1:7). Character 17[1], the presence of axial and preglabellar furrows that are smoothly continuous and undifferentiated, with the support of four additional ambiguous characters, supports *Mansuyia* as its own clade rooting at the base of Tsinaniidae with a Bremer index of four (Fig. 1:6.1). *Tsinania* is revealed to be a polyphyletic concept, its members forming a clade only with the inclusion of *Shergoldia*, *Dictyella*, and *Lonchopygella*. No unambiguous characters support the monophyly of *Shergoldia*, but its basal node has a Bremer support of three. *Dictyella* and *Lonchopygella* also fall within the clade encompassing *Tsinania* and

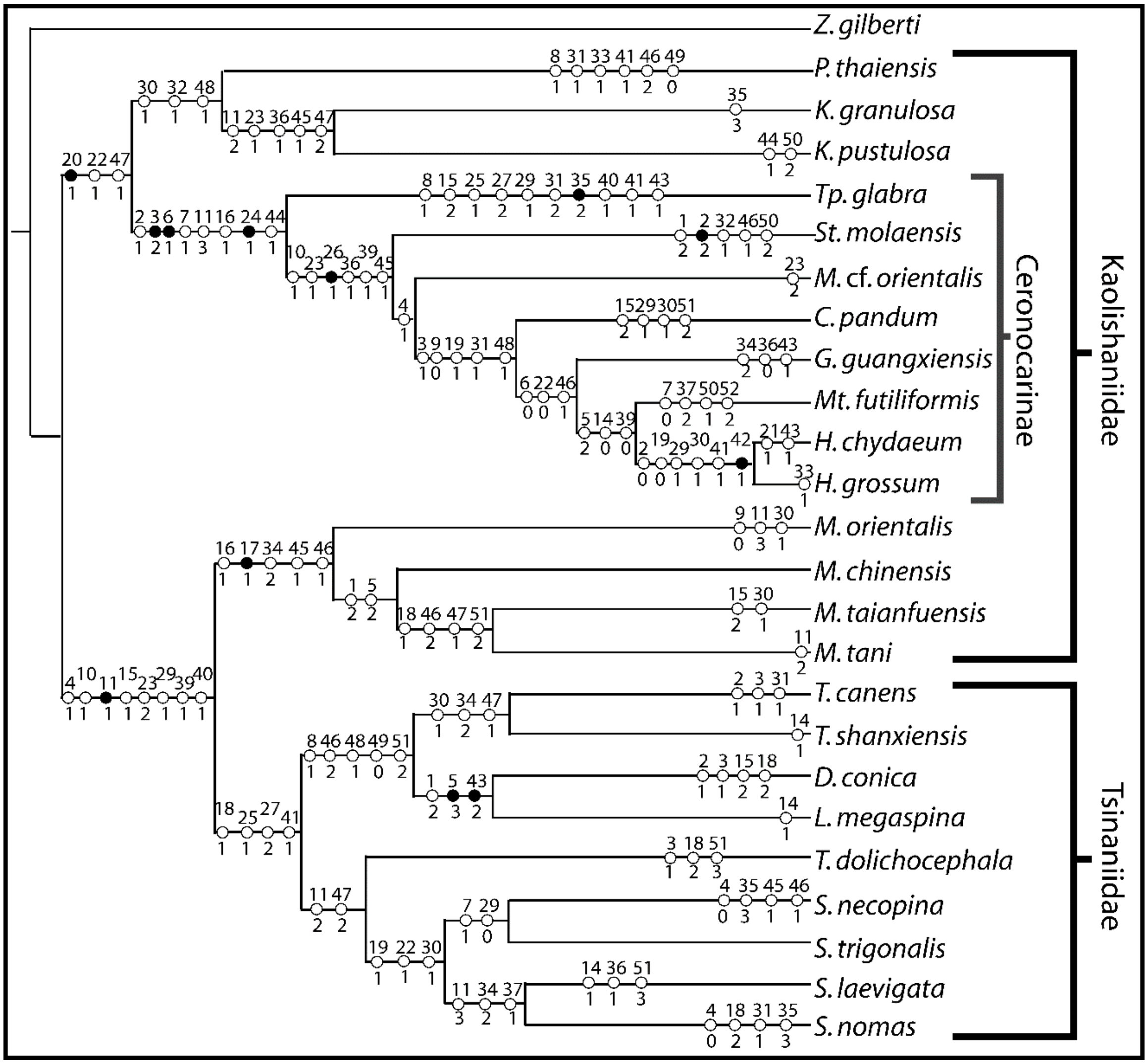


Figure 1:7 Character optimization for the most parsimonious tree. Numbers on top show the character number and numbers on bottom show the state for that character. Filled circles indicate those characters which are unambiguous. To avoid confusion for genera starting with the same letter, the following scheme is applied: *M = Mansuyia; Mt = Mansuyites; S = Shergoldia; St = Satunarcus; Tp = Taipaikia; T = Tsinania.*

Shergoldia. The node joining *Dictyella* and *Lonchopygella* is unambiguously supported by 5[3], a distinctly angular convexly triangular anterior margin, and 43[2], a sharply triangular pygidium.

Taipaikia's grouping within Kaolishaniidae, as opposed to Tsinaniidae, is as part of the clade containing *Satunarcus* and the genera formerly assigned to Mansuyiinae, excluding *Mansuyia.* This clade is supported by three unambiguous characters and a Bremer support index of five. The supporting unambiguous characters include a medially effaced anterior border furrow (3[2]), an anterior border entirely anterior to the glabella, as opposed to the anterior border's lateral corners extending back to opposite or posterior the anterior glabellar margin (6[1]), and an occipital lobe that truncates bluntly at the axial furrows rather than laterally pinching out (24[1]). Within this clade, an even tighter, similarly supported clade exists that includes *Satunarcus*, *Mansuyites*, *Ceronocare, Guangxiaspis*, *Hapsidocare,* and *Mansuyia* cf. *orientalis.* This clade is unambiguously supported by the fixigena anteriorly terminating against the broad preglabellar field as opposed to the anterior borders, 26[2]. The node joining the group has a Bremer support index of five.

Materials and methods

The specimens were prepared manually using a Dremel tool, blackened with India ink, whitened with ammonium chloride, and photographed with a Leica stereoscopic camera model MZ16. Apart from *Satunarcus molaensis* itself, the systematic analysis was based exclusively on figures from prior publications. The criteria used in the selection of species for analysis and which specimens were used for measurements is listed in the "Characters and taxa used in cladistic analysis" section above. All figures and plates were created using Adobe Photoshop CC2017 and Adobe Illustrator CS2.

Repositories and institutional abbreviations.—All *Satunarcus molaensis* illustrated in this paper are reposited in Thailand's Department of Mineral Resources' Geological

Referenced Sample Collection (DGSC); unfigured specimens are reposited in either DGSC or the Cincinnati Museum Center (CMC).

Systematic paleontology

The systematic paleontology section is authored by Wernette and Hughes.

Class TRILOBITA Walch, 1771

Order CORYNEXOCHIDA Kobayashi, 1935

Suborder LEIOSTEGIINA Bradley, 1925

Superfamily LEIOSTEGIOIDEA Bradley, 1925

Family KAOLISHANIIDAE Kobayashi, 1935

Subfamily CERONOCARINAE new subfamily

Type Genus.—*Ceronocare* Shergold, 1975

Type Species.—*Ceroncare pandum* Shergold, 1975

Diagnosis.—Ceronocarinae n. subfam. cranidium is distinguished by a long (sag.) frontal area comprising a depressed or flat elongated (sag.) preglabellar field with comparatively short (sag.) anterior border; a broad (tr.) frontal area that reaches maximum width on the anterior border; anterior border with lateral corners anterior to the preglabellar margin; prepalpebrally divergent anterior facial sutures that converge anteriorly to meet medially or are nearly convergent at the anterior cranidial margin; inflated palpebral areas that anteriorly terminate with a moderately strong to sharp inflection point opposite the preglabellar furrow and are separated from the anterior border by a wide (tr. & exsag.) preglabellar field; occipital ring that does not laterally narrow or pinch out at the axial furrows. Pygidia possess one pair of segmentally derived spines and an inflated posterior band on the anterior pygidial segment.

Remarks.— Ceronocarinae encompasses genera previously contained in Mansuyiinae with the exception of *Mansuyia* Sun, 1924. Shergold (1972) restricted Mansuyiinae to include only "*Mansuyia*-like" genera. However, the cladistic analysis herein reveals that these "*Mansuyia*-like" genera are not closely related to *Mansuyia*, rendering this conception of the subfamily polyphyletic and obsolete. *Ceronocare* Shergold, 1975, *Mansuyites* Shergold, 1972, *Guangxiaspis* Zhou, 1977, and *Hapsidocare* Shergold, 1975 are no longer assigned to Mansuyiinae and are hereby reassigned to Ceronocarinae which includes *Satunarcus* n. gen. This subfamily encompasses those taxa that have a particularly long preglabellar field and inflated palpebral areas anteriorly defined by a sharp inflection point (Fig. 1:6). *Ceronocare* displays the most exaggerated form of these characters. It is evident that the preglabellar field is lengthened here, not the anterior border, because an anterior border is visible in some genera including *Satunarcus*, *Ceronocare*, and *Hapsidocare*. Homologous depressions in the preglabellar area occur in *Tsinania* and *Mansuyia* as a merger between the anterior border and preglabellar furrows, but the condition is much more exaggerated in Ceronocarinae. Ceronocarinae are most diverse in Australia but also present in South China and Sibumasu. *Ceronocare* was chosen as the type genus because it best exemplifies the strongly inflated palpebral areas terminating sharply into a long, broad preglabellar field with a very short anterior border whose furrow is medially effaced.

Genus *Satunarcus* new genus

Type species.—*Satunarcus molaensis* n. sp.; by original designation; by monotypy.

Diagnosis.— As for the type species by monotypy.

Occurrence.—Ao Mo Lae Formation of the Tarutao Group of Ko Tarutao, Thailand. Furongian, Cambrian Stage 10, stratigraphically near the boundary between the *Sinosaukia impages* and *Shergoldia nomas* trilobite zones of Australia. Ao Talo Topo horizon 1 and Ao Molae horizons 4.71 m, 5.81 m, 5.84 m, and 6.01 m.

Etymology.—"Satun-" is in honor of Satun UNESCO Global Geopark where the type species is found. "-arcus" is in recognition of the particularly arched posterolateral projections, an unusual feature useful in distinguishing this genus.

Remarks.—Satunarcus is a member of Ceronocarinae that may have split from the rest of the subfamily early in its development (Fig. 1:2). Its general dimensions in terms of preglabellar area and glabellar width and length are similar to *Mansuyia* cf. *orientalis*, particularly to specimens from Australia's Pacoota Sandstone which are preserved under similar lithologic and taxonomic conditions (Shergold, 1991). Nevertheless, *M.* cf. *orientalis* is excluded from *Satunarcus* on account of its long, strongly curved palpebral lobes and narrow, weakly curving posterolateral projections.

Satunarcus molaensis new species

Figs 1:8–10

Holotype.—DGSC F0343 Figs 1:9.1–9.3; Ao Mo Lae Formation of the Tarutao Group; Furongian, Cambrian Stage 10; Ao Molae bed 5.81 m. Paratypes: DGSC F0358, F0351, F0356, F0337 Figs 1:9.8–9.11, 10.3, 10.5, 10.6.

Diagnosis.—Cranidium with long, broad, flat or slightly concave frontal area dominated by preglabellar field with indistinguishable or poorly differentiated anterior border; hourglass shaped glabella relatively narrow (tr.) and short (sag.); palpebral lobes short (exsag.), weakly curved; palpebral areas anteriorly terminate at broad preglabellar field; posterolateral projections broad and strongly posteriorly arched. Pygidium with broad, semielliptical

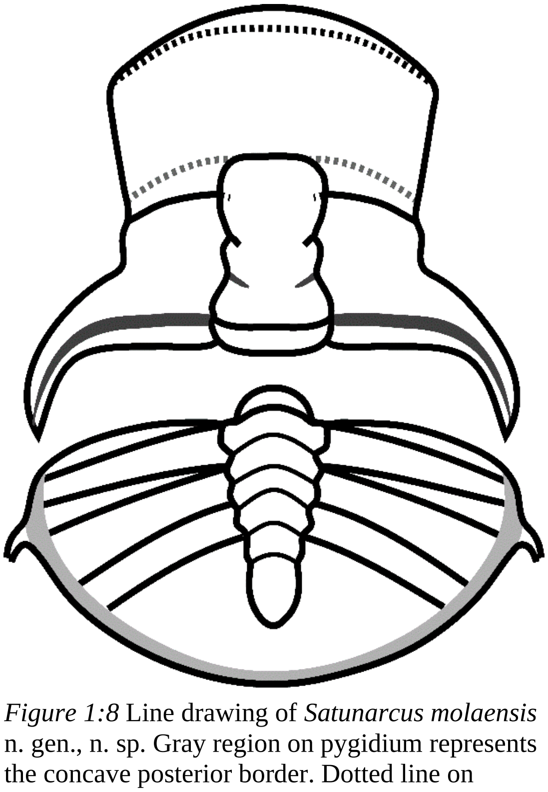


Figure 1:8 Line drawing of *Satunarcus molaensis* n. gen., n. sp. Gray region on pygidium represents the concave posterior border. Dotted line on preglabellar field is the often effaced anterior border furrow.

outline; five axial rings; axis terminating bluntly at posterior border; posterior border narrows medially.

Occurrence.—Ko Tarutao, Thailand at localities Ao Talo Topo, undetermined horizon, and Ao Molae horizons 4.71 m, 5.81 m, 5.84 m, and 6.01 m; Ao Mo Lae Formation, Tarutao Group; Furongian, Cambrian Stage 10.

Description.—Glabellar width at L1 35–40% cranidial width across palpebral areas; total glabellar length 55–60% of total cranidial length; anterior margin strongly curved; anterior border poorly differentiated to effaced; preglabellar area long (sag. and exsag.) and flat to slightly concave; preglabellar area maximum width 270–300% L1 glabellar width; anterior suture branches diverge ~15–20°; glabella hour-glass shape with rounded anterior margin; preglabellar furrow laterally deep and medially shallowing to effaced; glabella narrowest across L2; three pairs of short (tr.), firmly-incised lateral glabellar furrows angled obliquely toward posterior; S1 broadens (exsag.) abaxially; axial furrows weakly incised; S3 very short, nearly effaced; SO deep but slightly shallowing medially; LO short (sag.) and constant length (sag. and exsag.) across width (tr.); LO forms ontinuous band with posterior cranidial border but differentiated from rest of border by distinct axial furrows; LO width (tr.) slightly less than L1 width; palpebral areas moderately inflated, terminating anteriorly at preglabellar field with moderately sharp inflection; palpebral lobes narrow (tr.), straight, and short (exsag.), ~30–35% glabellar length; palpebral lobes angled 10–15° from sagittal axis, anteriorly palpebral lobe

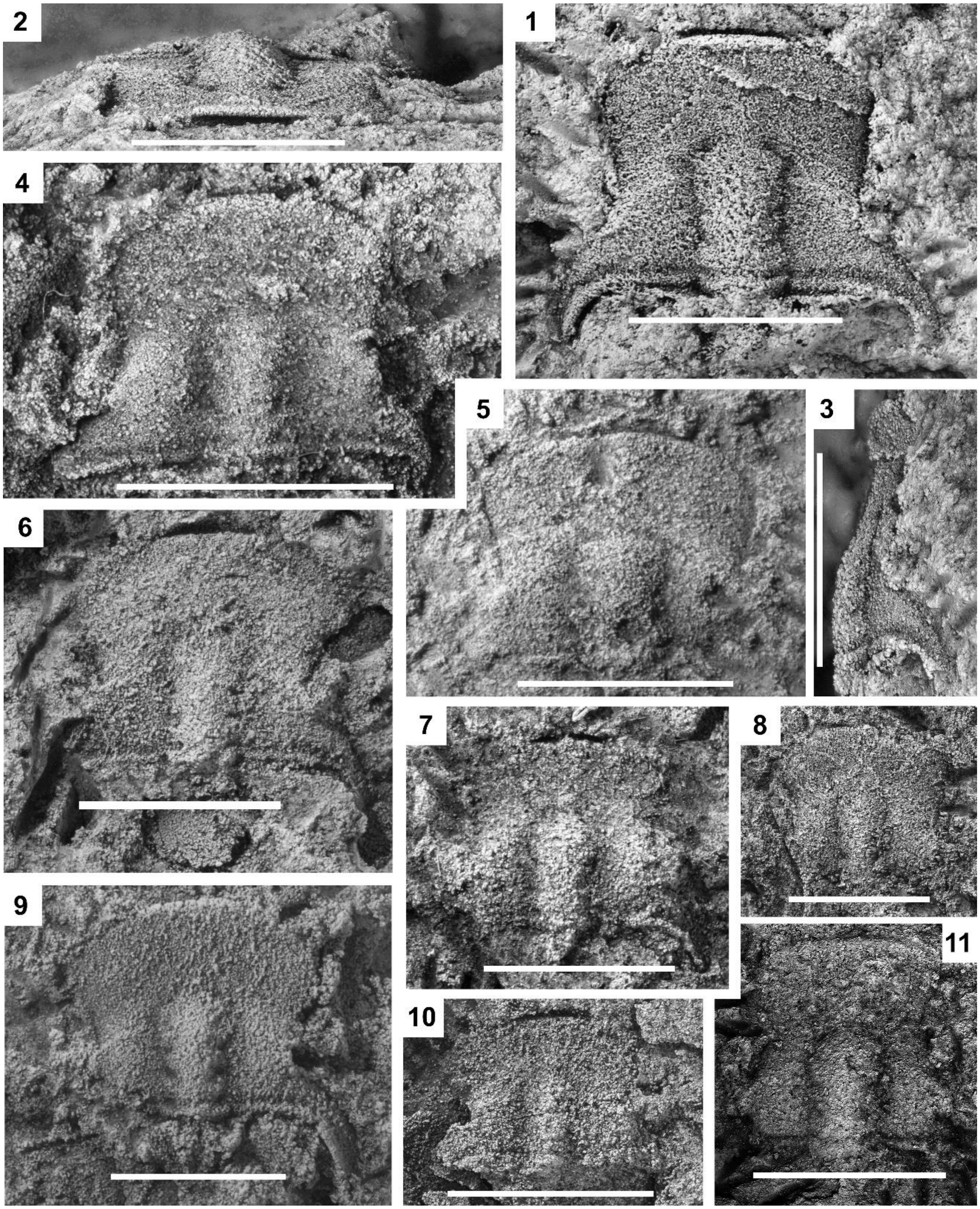


Figure 1:9 Satunarcus molaensis n. gen., n. sp., all cranidia. **(1–3)** Holotype: dorsal, anterior, and right lateral views respectively, DGSC F0343, Ao Molae horizon 5.81 m; **(4)** DGSC F0371, Ao Talo Topo; **(5)** DGSC F0383, Ao Talo Topo; **(6)** DGSC F0333, Ao Molae horizon 4.71 m; **(7)** DGSC F0363, Ao Molae horizon 5.84 m; **(8)** DGSC F0358, Ao Molae horizon 5.81 m; **(9)** DGSC F0351, Ao Molae horizon 5.81 m; **(10)** DGSC F0356, Ao Molae horizon 5.81 m; **(11)** DGSC F0337, Ao Molae horizon 5.81 m. Scale bars are 5 mm.

connected to S3 by short (exsag.) eye ridge; posterolateral projection broad (tr.) and long (exsag.) forming a curving triangular shape; posterolateral projection curves ~90° of arc, approaching resupinate condition; posterior border curves evenly parallel to posterior margin with broad (exsag.), firmly-incised posterior border furrow.

Pygidial width (tr.) ~175% of length (sag.); anterior margin gently curved and medially straight (tr.); posterior margin smoothly and strongly curved but for posterolateral spines; axial length 75–85% of pygidial length, terminating at evenly sloped posterior border; anterior axial width ~25% of maximum pygidial width; axial furrows straight, at 10–15° angle to sagittal axis; five axial segments excluding terminal piece; axial ring furrows weakly incised and medially arched anteriorly; pleural furrows

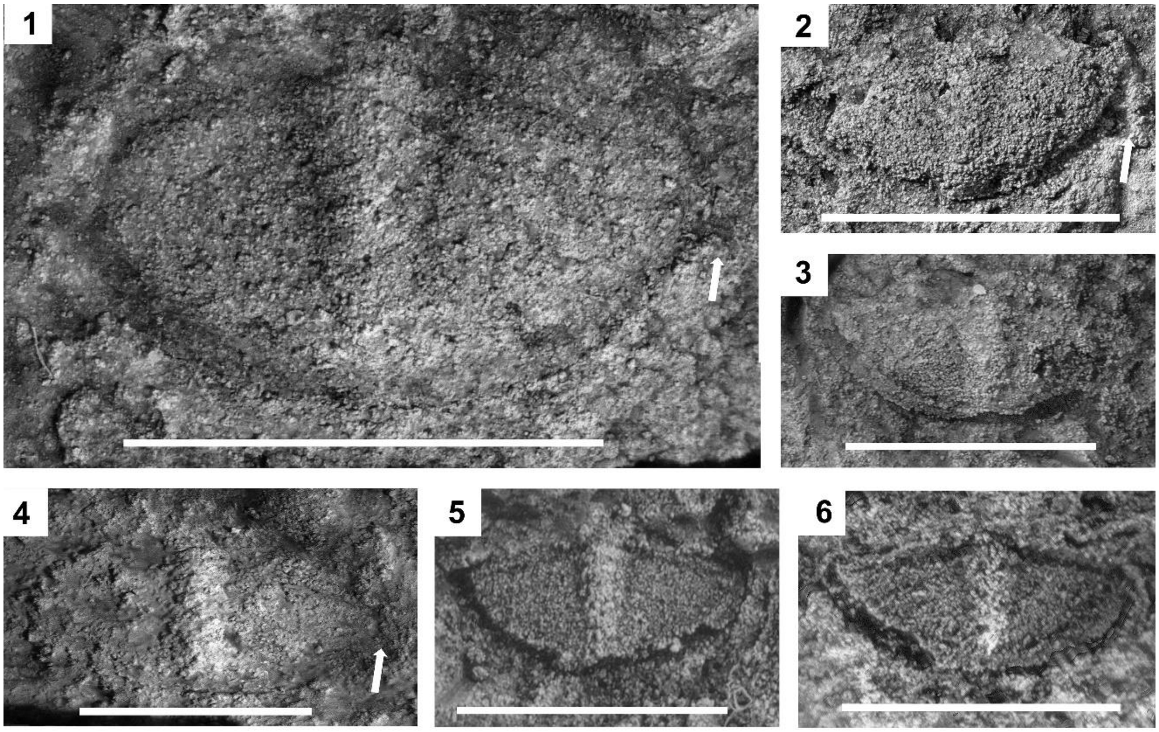


Figure 1:10 Satunarcus molaensis n. gen., n. sp., all pygidia. **(1)** DGSC F0381, Ao Talo Topo; **(2)** DGSC F0382, Ao Talo Topo; **(3)** DGSC F0341, Ao Molae horizon 5.81 m; **(4)** DGSC F0384, Ao Talo Topo; **(5)** DGSC F0360, Ao Molae horizon 5.81 m; **(6)** DGSC F0359, Ao Molae horizon 5.81 m. Arrows point to spine bases. Scale bars are 2.5 mm.

straight and nearly effaced; posterior band of anterior segment gently expanded; other pleural bands subequal; furrows become obsolete abruptly defining pygidial border; pygidial border narrow (tr., sag.), 15–20% of anterior pygidial width; border narrows sagittally, almost pinching out; one pair of lateral spines apparently related to the posterior band of the first pygidial segment; spine short and thin (tr., exsag., and dorsoventrally) and rarely preserved.

Etymology.—Named for the holotype locality Ao Molae and for the Ao Mo Lae Formation, the only geologic unit currently known to yield this species.

Materials.—Cranidia: From Ao Molae horizon 4.71 m, one figured (DGSC F0333); from Ao Molae horizon 5.81 m, five figured and two unfigured (DGSC F0337, F0343, F0351, F0352, F0356, F0358; CMC IP83136); from Ao Molae horizon 5.84 m, one figured (DGSC F0363); from Ao Molae horizon 6.01 m, two unfigured (CMC IP83154, IP83160); from Ao Molae horizon 2, one unfigured (CMC IP83165); from Ao Talo Topo, two figured and three unfigured (DGSC F0371, F0372, F0383, F0385, F0386); Pygidia: from Ao Molae horizon 5.81 m, three figured and 11 unfigured (DGSC F0341, F0344; F0353, F0359, F0360, F0361; CMC IP83129, IP83130, IP83135, IP83137–IP83139, IP83141, IP83142); from Ao Molae horizon 5.84 m, three unfigured (CMC IP83143–83145); from Ao Molae horizon 6.01 m, two unfigured (CMC IP83153, IP83161); from Ao Talo Topo, three figured and three unfigured (DGSC F0373, F0374, F0381, F0382, F0384, F0387). All specimens internal molds preserved in fine-grained sandstone except IP83136 which is an external mold in sandstone.

Remarks.—Satunarcus molaensis is a small species with cranidia rarely exceeding 5 mm in length. While ornamentation is easily distinguishable on both the cranidium and pygidium of *Mansuyia* cf. *orientalis* in its distinctive palpebral and posterolateral regions, in *S. molaensis* it is unknown due to their small size, sandstone preservation, and scarcity of external molds. The spines on the pygidium are exceptionally poorly preserved; they are typically preserved only as outward extensions of the impression left from the border in an otherwise smoothly rounded pygidial margin. Confidence that this is a spine rather than irregularity in the matrix comes from the marginal disruption consistently occurring in the same position on multiple specimens. *Satunarcus molaensis* is found at two separate but geographically close localities with similar lithofacies. At Ao Molae where the stratigraphy is better known and fossils more broadly sampled, *S. molaensis* is stratigraphically restricted to a range of less than a meter which may explain why it has not been recovered in previous analyses of the Tarutao fauna (Kobayashi, 1957; Shergold et al., 1988). Where it does occur, *S. molaensis* is moderately abundant.

Discussion

This is the first phylogenetic analysis of tsinaniids and kaolishaniids to include a variety of taxa from both groups. Previous studies, which were constrained in taxon diversity due to the inclusion of ontogenetic data, have used kaolishaniids only as an outgroup for evaluating the tsinaniids (Zhu et al., 2013) or included only a single supposed kaolishaniid genus, *Mansuyia*, to consider the relationship with tsinaniids (Lei and Liu, 2014; Park et al., 2014). The results herein indicate that if *Mansuyia* were excluded from Kaolishaniidae and reclassified as a tsinaniid, then Kaolishaniidae forms its own clade separate from Tsinaniidae. If *Mansuyia* is a member of Kaolishaniidae, then this family is paraphyletic with Tsinaniidae emerging out of it. As the nature of evolution inherently results in paraphyletic groupings, there is no reason to reassign *Mansuyia* based on these results. *Mansuyia* itself is a well-supported clade, contrary to Park et al.'s (2014) view of *Mansuyia* as a stem group to the Tsinaniidae. The other genera previously assigned to Mansuyiinae, excluding *Mansuyia*, form their own well-supported clade, herein designated Ceronocarinae within the Kaolishaniidae. As a polyphyletic taxon is incompatible with evolution-based taxonomy, Mansuyiinae is henceforth restricted to members of the genus *Mansuyia*. The Ceronocarinae are characterized by a long (sag.) and broad (tr.) frontal area consisting of an extended and nearly flat preglabellar field and short anterior border, prepalpebrally divergent anterior sutures that converge anteriorly to meet medially, inflated palpebral areas that terminate with a moderately strong to sharp inflection point opposite the preglabellar furrow, and a pygidium possessing one pair of segmentally derived spines and an inflated posterior band on the anterior pygidial segment.

Taipaikia has historically been included with Tsinaniidae which are generally characterized as large, effaced trilobites (Kobayashi, 1960; Jell and Adrain, 2002). However, this classification has previously been challenged by *Taipaikia*'s abaxial intersection between the facial suture sand the anterior margin (Zhu et al., 2007; Hughes et al., 2011). Zhu et al. (2013) presented a cladistic scheme that supports the classification of *Taipaikia* as a tsinaniid more closely related to *Tsinania* and *Shergoldia* than to *Mansuyia*, but that analysis did not test the relationship of *Taipaikia* to tsinaniids, for it assumed, *a priori*, *Mansuyia* as the outgroup. This forced the tree to be rooted on *Mansuyia* with *Taipaikia* ingroup to Tsinaniidae. The more comprehensive view of Kaolishaniidae provided herein resolves *Taipaikia* as part of Ceronocarinae, and as a kaolishaniid rather than as a tsinaniid (Figs 1:6, 7).

Based on the phylogenetic analysis presented here, it is clear that *Mansuyia* cf. *orientalis sensu* Shergold (1975) is not a member of *Mansuyia*, and is not closely comparable to *Mansuyia orientalis*. As part of Ceronocarinae its generic affiliation should be reevaluated following a comprehensive revision of the available material.

Conclusions

Satunarcus molaensis is a new species and genus from Ko Tarutao, Thailand. It belongs within the new subfamily Ceronocarinae, erected herein, which contains many of the genera previously assigned to Mansuyiinae. Cladistic analysis of Mansuyiinae, "*Mansuyia*-like" genera, and related members of Kaolishaniidae and Tsinaniidae reveals that *Mansuyia* and other genera assigned to Mansuyiinae (Shergold, 1972) are polyphyletic, hence the restriction of the subfamily Mansuyiinae to *Mansuyia* alone. The subfamily Ceronocarinae is erected to contain the genera formerly considered Mansuyiinae excluding *Mansuyia* itself.

Resolution of *Tsinania* and *Shergoldia*, the more derived tsinaniids, agrees with Park et al.'s (2014) and Zhu et al.'s (2013) conclusion that, as presently conceived, these genera are not monophyletic. In the previous two studies *Tsinania* is nested within *Shergoldia,* and in this analysis the opposite is true. Given the lower stratigraphic position of *Tsinania,* the latter analysis is a more stratigraphically consistent branching relationship (Fig. 1:2). While no non-reversable characters support the monophyly of *Shergoldia*, reversable supporting characters include the presence of bacculae, an anteriorly directed medial bend in the occipital furrow, and a curved anterior pygidial margin. This analysis additionally agrees with Park et al.'s (2014) view that *Lonchopygella* is part of the *Tsinania-Shergoldia* clade, not a sister taxon as depicted in Zhu et al. (2013). *Lonchopygella* is most closely related to *Dictyella* based on the overall effaced and triangular pygidial and cranidial morphology.

Chapter 2. The Furongian (late Cambrian) trilobite *Thailandium*'s endemicity reassessed along with a new species of *Prosaukia* from Ko Tarutao, Thailand

Introduction

The trilobite genera commonly referred to as "saukiid" are among the most diverse, abundant, and spatio-temporally important late Cambrian trilobite groups, but their taxonomy is not well-resolved. At a broad taxonomic level, there is little agreement on whether "saukiid" trilobites collectively are a clade, part of a clade, or are a polyphyletic assemblage within Dikelocephalidae (Adrain, 2011; Lee and Choi, 2011; Park and Kihm, 2015). At the genus level, some differential diagnoses are ambiguous between genera, resulting in some "saukiid" species being reassigned to several different genera after their initial description (e.g. *Eosaukia micropora* Qian, 1985; Lee and Choi, 2011). Rectifying "saukiid" relationships at both the genus and family levels is important, because "Saukiidae" encompasses numerous genera that are of great importance to late Cambrian (Furongian) biostratigraphy and paleogeography. As of 2002, Jell and Adrain recognized 30 distinct genera referred to as Saukiidae Ulrich and Resser (1930). Of these *Mictosaukia* Shergold (1975), *Sinosaukia* Sun (1935), *Eosaukia* Lu (1954), *Lophosaukia* Shergold (1972), *Saukia* Walcott (1914), and *Saukiella* Ulrich and Resser (1933) have all been used to characterize Cambrian Stage 10 trilobite biostratigraphic zones and subzones in Laurentia, Australia, Kazakhstan, South China, North China, and South Korea (Shergold and Geyer, 2003; Lee and Choi, 2011). *Caznaia* Shergold (1975) characterizes two middle Jiangshanian zones in Australia while *Saukia* and *Saukiella* define the uppermost Jiangshanian zones and subzones in Laurentia (Peng et al., 2012; Ogg et al., 2016). In addition to their biostratigraphic application, “saukiid” genera are also important for paleogeographic reconstruction: Gondwana contains a suite of “saukiid” genera unique to its terranes, including but not limited to *Lophosaukia*, *Mictosaukia*, and *Eosaukia*.

The taxonomic challenges associated with “saukiids” limit their current application to broader geologic questions. The characters differentiating many of the “saukiid” genera are not the discrete presence or absence of particular traits but rather the exaggeration or reduction of traits common to all “saukiids”. Some “saukiids” are

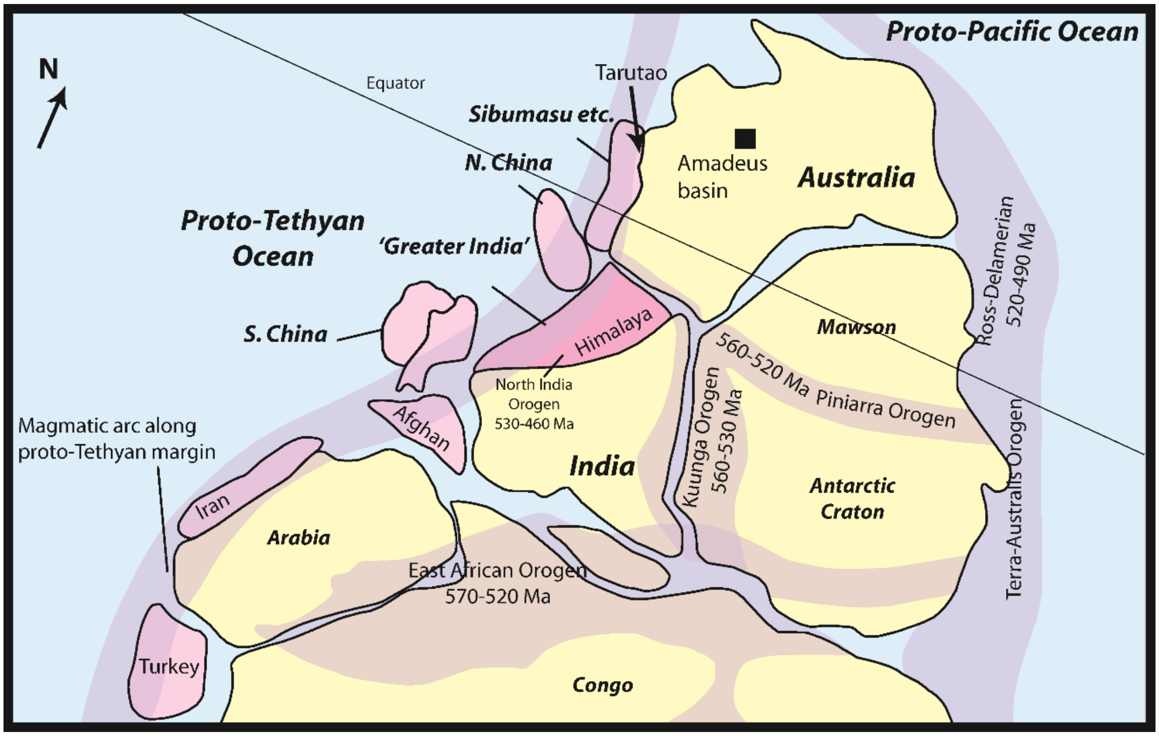


Figure 2:1 Cambro-Ordovician paleogeographic reconstruction of northern Gondwana. Locations of the Amadeus Basin and Tarutao are only approximations to indicate their relative locations and proximity. Modified from Hughes, 2016; orogenies from Cawood et al., 2007; equator from Cocks and Torsvik, 2013.

differentiated by the presence, length, or inflation of the preglabellar field (Ulrich and Resser, 1933; Ludvigsen and Westrop, 1983). Shergold (1991) recognized three morphological groupings of “saukiid” cranidia, the first of which comprises *Prosaukia*-like genera, including *Thailandium*, *Caznaia*, *Lichengia*, and *Saukiella*, which have a distinct preglabellar field fully distinguishable from the anterior border.

Within this group of “saukiids” with a distinct preglabellar field, *Thailandium* Kobayashi (1957) has an exceptionally long preglabellar field and strongly differentiated anterior border. This genus has been reported from two regions: Thailand’s Ko Tarutao (also called Tarutao Island) in Satun Global Geopark (Kobayashi, 1957) and Australia’s Amadeus Basin (Shergold, 1991). The type species, *Thailandium solum* Kobayashi (1957), was described from the Ao Mo Lae Formation of the Tarutao Group in the initial description of the fauna of Ko Tarutao. No further specimens of *Thailandium solum* were illustrated or discussed in the more extensive faunal analysis of Shergold et al. (1988). Specimens from the Pacoota Sandstone of the Amadeus Basin (Fig. 2:1), with a similarly long frontal area and defined anterior border, were

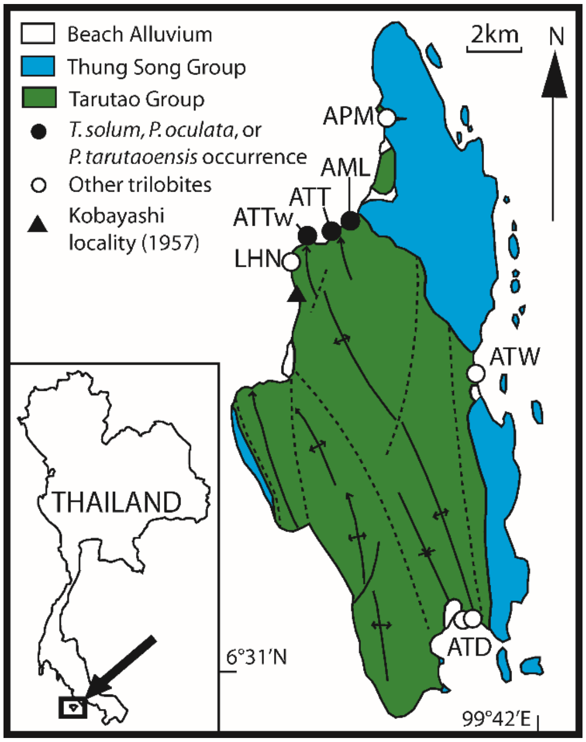


Figure 2:2 Trilobite occurrences on Ko Tarutao: AML = Ao Mo Lae; ATT = Ao Talo Topo; ATTw = Ao Talo Topo west; LHN = Laem Hin Ngam; ATD = Ao Talo Udang; APM = Ao Phante Malacca; ATW = Ao Talo Wao. Modified from Bunopas et al., 1983 and Wernette et al., 2020.

assigned by Shergold (1991) to *Thailandium* but as an undetermined species and with the caveat that it likely actually belongs to *Prosaukia*. Shergold (1991) suggested that the status of his Australian material could be meaningfully evaluated only after reevaluation of the *T. solum* type material with greater consideration of possible morphologic variation within it. A series of excursions from 2008 to 2018 have greatly expanded trilobite collections from Ko Tarutao (Fig. 2:2). This new material permits reevaluation of the cranidial morphology of *T. solum*. Species of *Prosaukia* found during the same excursions, *Prosaukia tarutaoensis* (Kobayashi,, 1957; *not Lichengia tarutaoensis* in Shergold et al., 1988) and *P. oculata* n. sp, suggested the need to reevaluate the generic assignment of *Thailandium* sp. undet. from Australia.

Landmark-based morphometric analysis is a useful tool for objectively considering morphological variation within and between groups. This tool was herein applied to *Thailandium solum, Prosaukia tarutaoensis*, and *Prosaukia oculata* from Ko Tarutao, the figured type material of *P. misa* (Hall, 1863), the *Prosaukia* type species, and the figured material of *Thailandium* sp. undet. from Australia in order to determine whether a meaningful difference exists between *Thailandium* and *Prosaukia* and, if so, to which genus *Thailandium* sp. undet. is best assigned. As demonstrated herein, the continued recovery of new species from poorly explored terranes like Sibumasu, offers material on which to refine definitions of existing genera like *Prosaukia* and *Thailandium.*

Tarutao localities

The Tarutao Group is the lowest Paleozoic unit in western Thailand. While the Tarutao Group cops out on both the mainland of southern Thailand and Ko Tarutao, only outcrops on Ko Tarutao are documented as containing identifiable fossils (Wangwanich et al. 2002). Ko Tarutao is sufficiently removed from the Bentaung Raub Suture Zone between Sibumasu and the East Malaysian Terrane to the east and from the Sumatran Fault Zone to the west that it represents a reasonably tectonically stable area, and the fossils show no evidence of tectonic deformation (Burrett et al., 2014). The Tarutao Group is a clastic succession of mostly very fine to fine-grained sandstones with interbedded silt stones, mud stones and rhyolitic tuffs. It is distinct from the overlying carbonate-rich Thung Song Group, the only other lithologic unit to occur on the island. Of the four formations that comprise the Tarutao Group (Ao Makham, Ao Tami, Ao Mo Lae, and Talo Wao), only the upper two, Ao Mo Lae and Talo Wao, have yielded trilobite fossils.

Of the five fossiliferous localities and six stratigraphic sections on which our team worked during visits made between 2008–2018 (Fig. 2:2) the materials of relevance to this paper are only found at Ao Talo Topo (ATT) (06°40’08”N, 099°37’46”E), Ao Talo Topo west (ATTw) (06°39’49”N, 099°37’08”E), and Ao Mo Lae (AML) (06°40’13”N, 099°38’02”E). ATTw is separated from ATT by a prominent bay. Both localities were mistakenly given the same name by the authors, but they are here differentiated. All stratigraphic measurements were completed at ATT, and only a single bed was sampled with little stratigraphic context at ATTw as part of the 2008 exploratory excursion; this is also the bed in which *Satunarcus molaensis* Wernette and Hughes (2020) was collected, so any references to ATT in that paper refer to ATTw.

All three localities with material considered in this paper consist exclusively of the Ao Mo Lae Formation, the second highest of the four formations included within the Tarutao Group (Imsamut and Yathakam, 2011). The entire formation, only a small portion of which is exposed at Ao Mo Lae, is estimated to be ~600m thick, but this estimate is speculative due to the prevalence of faults around the island and discontinuity of exposures (Imsamut and Yathakam, 2011). It primarily consists of purplish red and gray fine-grained quartzarenites. Rhyolitic tuff deposits occur mostly in the upper portions of this formation (Imsamut and Yathakam, 2011). Disarticulated, mildly fragmented fossils are concentrated into dense coquinas on some bedding surfaces. Fossil preservation is as molds which may appear white where silica has become concentrated as a thin staining on the surface of the mold but not enough to form a silicic cast.

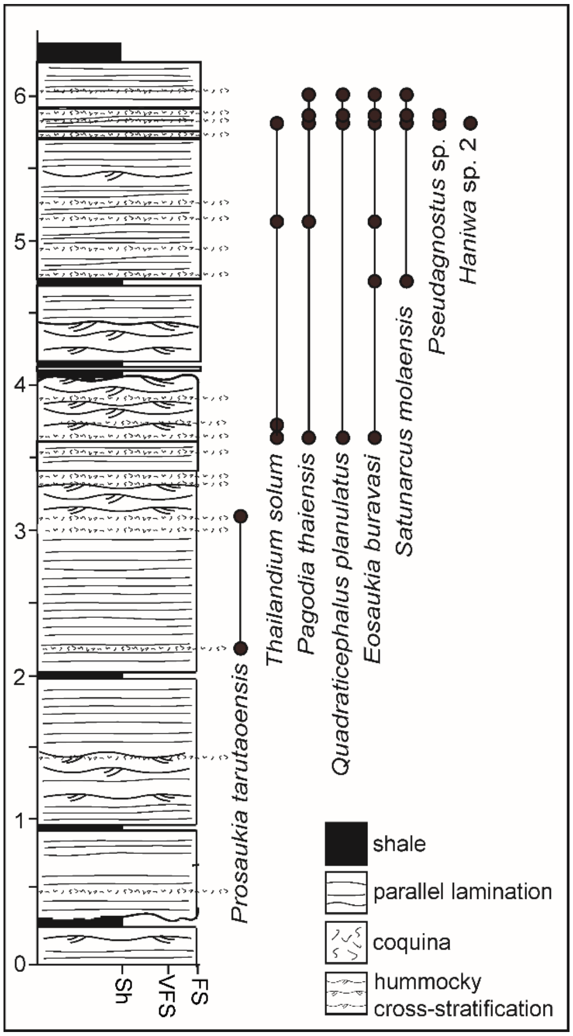


Figure 2:3 Measured lithostratigraphic section and faunal ranges for Ao Mo Lae (AML). Sh = shale; vfs = very fine sand; fs = fine sand; coq = coquina. Measurements are in meters.

The similarity of faunal content indicates that the Ao Mo Lae Formation is from Cambrian Stage 10, and the ATTw and AML fauna appear to be of nearly the same depositional age (see Fig 2:3 and following paragraph for faunal content); ATT (Fig. 2:4) may have a slightly different age than the other two. Based on the shallow northeastward dip evident at both ATT and AML, the latter may be slightly younger if these sections are in stratigraphic continuity, but they are separated by a small, sandy inlet which may conceal one of Ko Tarutao's many faults. The lithology of all three localities is similar except that ATT and ATTw contain several prominent horizons of rhyolitic tuffs. ATT has a slightly different faunal assemblage than the other two localities (Figs 2:3 and 4) with much of their shared fauna occurring only in poorly-located material in ATT or AML. These horizons, exclusive of those collected in 2008 as preliminary samples, have dubious stratigraphic context due to sampling errors caused by miscommunication in the field.

Collections of fossils with uncertain stratigraphic provenance are included here, because these collections are informative regarding the diversity of the Ao Mo Lae Formation and regarding taxon cooccurrences. Each of these stratigraphically poorly constrained collections contains specimens from a different bed. The single horizon at ATTw contains *Thailandium solum* Kobayashi (1957), *Prosaukia tarutaoensis* (Kobayashi, 1957), *Haniwa* sp. 1, *Pagodia thaiensis* Kobayashi (1957), *Quadraticephalus planulatus* (Kobayashi, 1957), *Satunarcus molaensis* (Wernette et al., *2020*), and *Eosaukia buravasi* Kobayashi (1957). One poorly localized horizon at Ao Talo Topo, henceforth referred to as ATT h1 contains *Koldinioidia* sp. and *Prosaukia*

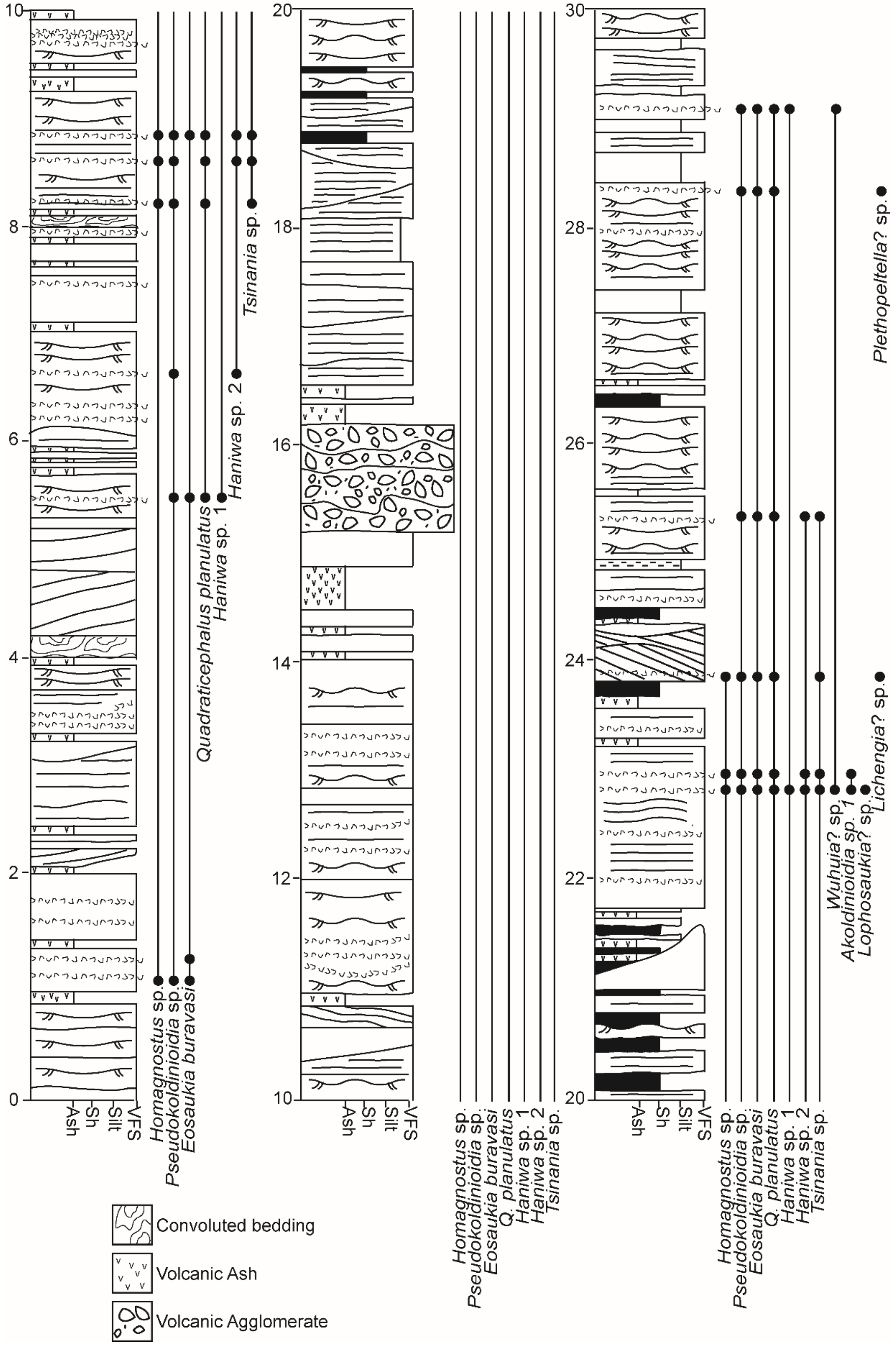

0
2
4
6
8
10
Ash
Sh
Silt
VFS
Homagnostus sp.
Pseudokoldinioidia sp.
Eosaukia buravasi
Quadraticephalus planulatus
Haniwa sp. 1
Haniwa sp. 2
Tsinania sp.
10
12
14
16
18
20
Ash
Sh
Silt
VFS
Homagnostus sp.
Pseudokoldinioidia sp.
Eosaukia buravasi
Q. planulatus
Haniwa sp. 1
Haniwa sp. 2
Tsinania sp.
20
22
24
26
28
30
Ash
Sh
Silt
VFS
Homagnostus sp.
Pseudokoldinioidia sp.
Eosaukia buravasi
Q. planulatus
Haniwa sp. 1
Haniwa sp. 2
Tsinania sp.
Wuhuia? sp.
Akoldinioidia sp. 1
Lophosaukia? sp.
Lichengia? sp.
Plethopeltella? sp.
Convoluted bedding
Volcanic Ash
Volcanic Agglomerate

Figure 2:4 (*Previous Page*) Measured lithostratigraphic section and faunal ranges for Ao Talo Topo (ATT). Measurements are in meters. See Fig. 4 for abbreviations and additional legend symbols.

oculata. Five poorly-localized horizons containing material described herein were sampled at AML, henceforth referred to as Ao Mo Lae horizons 1–5 (AML h1–AML h5). AML h1 and AML h2 correspond to horizons 1 and 2 from Wernette et al. (2020), but no further specimens from AML h1 are considered herein. AML h2 contains *Thailandium solum*, *Quadraticephalus planulatus*, *Satunarcus molaensis*, and *Eosaukia buravasi*; AML h3 contains *T. solum*, *P. tarutaoensis*, *P. thaiensis*, and *E. buravasi*; AML h4 contains *T. solum*, *Q. planulatus*, and *E. buravasi*; AML h5 contains *T. solum*, *E. buravasi*, and *Pacootasaukia*? sp. The fauna listed herein, excluding *P. tarutaoensis* and *P. oculata*, uses the names originally given by Kobayashi (1957), Shergold et al. (1988), or Wernette et al. (2020); previously undescribed species collected on the recent excursions (excluding those described herein) are listed by genus only. This paper is part of ongoing work to revise the Kobayashi (1957) and Shergold et al. (1988) material as well as to describe the new material (e.g. Wernette et al. 2020).

Materials and Methods

The following morphometric analysis is based on 22 discrete landmarks (Fig. 2:5) and 29 cranidia. Only specimens with sufficient preservation to distinguish all axial landmarks and at least one of each paired landmark were eligible for use in the analysis. 15 cranidia are of *Thailandium solum*, all from Ko Tarutao (DGSC F0419, F0435, F0568, F06569, F0570, F0574, F0583, F0595, F0601, F0606, F0607, F0609, F0543, F0544, and CMC IP87617). The holotype of *Thailandium*, though figured from a vinyl polysiloxane cast herein, was excluded from the analysis as the original figure (Kobayashi, 1957, pl. 4 fig. 9) lacks a clear posterior occipital margin and the cast is susceptible to slight distortion. Four cranidia are assigned to *Thailandium* sp. undet. from the Pacoota Sandstone in the Amadeus Basin of Australia (Shergold, 1991 pl. 4 figs 16–18, 21; CPC26805A, CPC26806, CPC26807, CPC26825). Two cranidia are of *Prosaukia misa* (Hall, 1863), the type species of *Prosaukia* Ulrich and Resser (1933 pl. 24 figs 3 and 7; USNM 84538, MPM 5968). Four cranidia are of *Prosaukia oculata* n. sp. (DGSC F0461, F0503, F0511, and F0512). Four cranidia are of *Prosaukia tarutaoensis* (Kobayashi, 1957, pl. 5 fig. 12 and three recently collected specimens; UMUT PA02298c, DGSC F0566, F0546, and F0545). The published figures of the *P. misa* type material (Ulrich and Resser, 1933), *Prosaukia tarutaoensis* (Kobayashi, 1957), and *Thailandium* undet. (Shergold, 1991) are of sufficient quality that landmarks could be mapped directly onto digitized copies of the original published illustrations. The size range for each taxon, measured by the length of the preoccipital glabella, is as follows: 2.47–16.53 mm for *Thailandium solum*, 4.57–8.37 mm for *Thailandium* sp. undet., 1.10–1.60 mm for *P. misa*, 2.31–6.34 mm for *P. oculata*, and 2.50–7.71 mm for *P. tarutaoensis*.

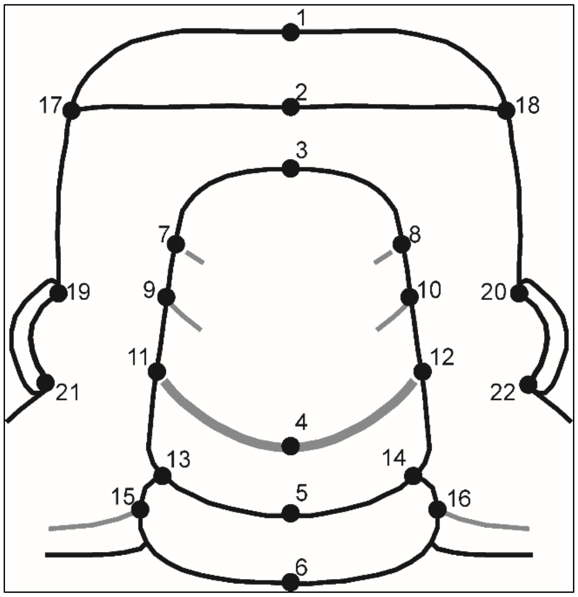


Figure 2:5 Landmark scheme showing the 22 landmarks used in the morphometric analysis of *Prosaukia* and *Thailandium*.

Thai specimens from the 2008, 2016, and 2018 excursions were prepared manually using a Dremel vibrotool, then blackened with India ink, whitened with ammonium chloride, and photographed with a Leica stereoscopic camera model MZ16 or M205C. All figures and plates were created using Adobe Illustrator CS2 and Adobe Photoshop CC2017. External molds were figured in positive relief by using the color inversion feature available in Photoshop CC2017. Molds of Kobayashi's (1957) type material were made using vinyl polysiloxane in the form of light bodied President Plus by Coltene.

Geometric morphometric analysis was conducted using the free software ImageJ and the Integrated Morphometrics Package (CoordGen8, BigFix8, Regress8, and PCAGen8), a set of compiled software tools for displaying and analyzing 2-D landmark-based geometric morphometric data (Webster and Sheets, 2010; http://www.filogenetica.org/cursos/Morfometria/IMP_installers/index.php). Landmarks were reflected and averaged across the sagittal axis so that any specimen with a full set of axial landmarks and at least one of each symmetrical pair of additional landmarks could be used for this study.

All figured specimens and select unfigured specimens from the 2008-2018 excursions are reposited at Thailand's Department of Mineral Resources' Geological Referenced Sample Collection (DGSC). Additional unfigured specimens are curated at the Cincinnati Museum Center (CMC). Type material from Kobayashi (1957) is reposited at the University of Tokyo University Museum (UMUT); one or more polysiloxane molds of each specimen in the Kobayashi (1957) collection at UMUT is also reposited in the plastotype collection at CMC. Additional specimens used in the morphometric analysis are curated in the Commonwealth Palaeontological Collection, Bureau of

Mineral Resources, Canberra (CPC) and the Smithsonian National Museum of Natural History (USNM), and the Milwaukee Public Museum (MPM).

Results and discussion

Sliding baseline registration (SBR) best displays the variation within the dataset and so is used consistently throughout the following discussion of morphometrics except where Procrustes superimposition in required for statistical calculations of group mean differences. The SBR distribution of landmarks (Fig. 2:6) indicates that *Thailandium*

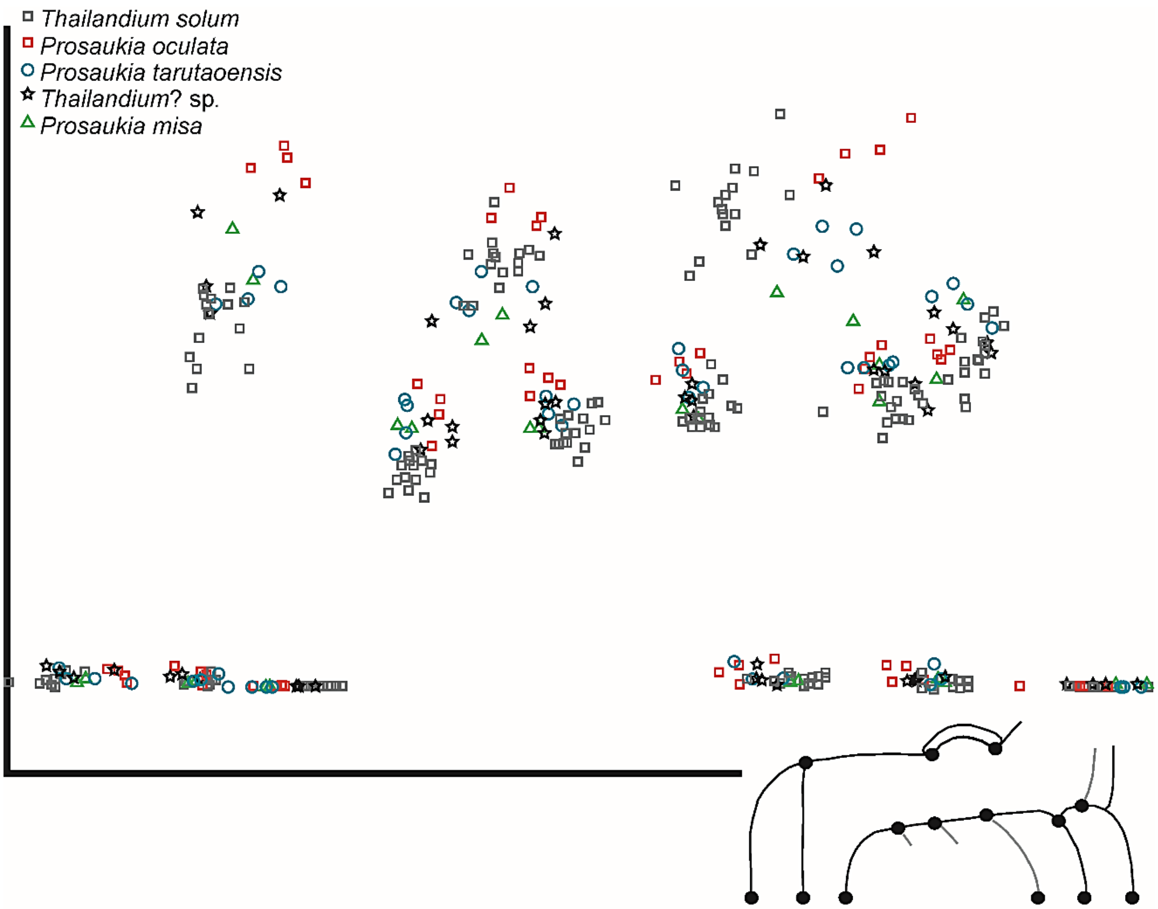


Figure 2:6 Sliding baseline registration of 22 landmarks across 28 cranidia of dikelocephalids. The baseline endpoints are 3 and 6. See figure 3 for landmark scheme. *Thailandium*? sp. is the taxon from Australia (Shergold, 1991) herein reassigned to *Prosaukia* sp.

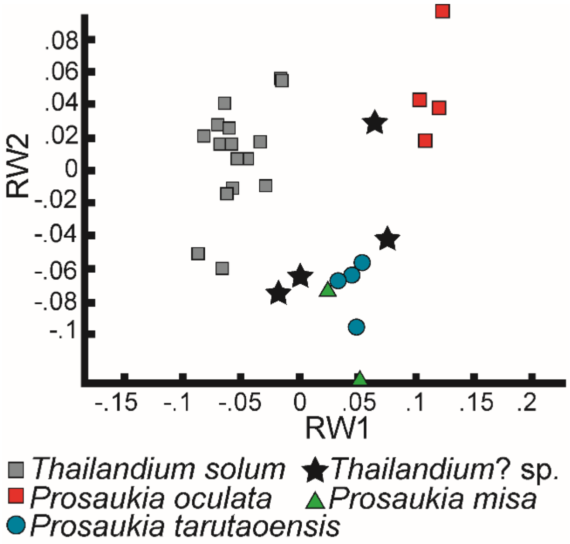


Figure 2:7 First two relative warps (RW1 and RW2), accounting for 43.019% and 20.944% of the variance respectively. *Thailandium*? sp. is the taxon from Australia (Shergold, 1991) herein reassigned to *Prosaukia* sp.

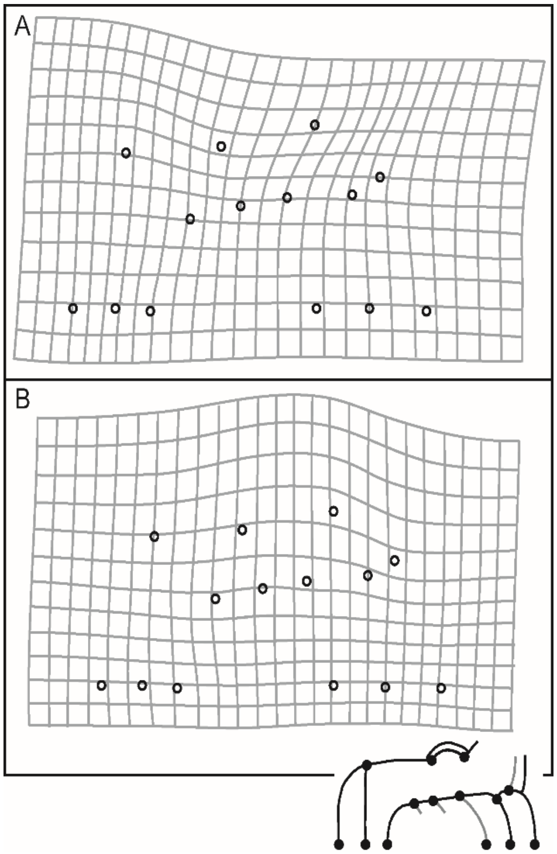


Figure 2:8 Relative warp grids using SBR superimposition for RW1 and RW2 for the 15 cranidial landmarks of all specimens of *Thailandium solum, Prosaukia misa, Prosaukia oculata, Prosaukia tarutaoensis,* and *Thailandium* sp. undet. (1) shape variation related to Relative Warp (RW) 1, 43.019% of total variance; (2) shape variation related to RW2, 20.944% of total variance.

solum and *Thailandium* sp. undet. (*sensu* Shergold, 1991) have similarly long frontal areas relative to glabellar length and similar division of the frontal area into preglabellar field and anterior border. With regard to the palpebral lobe position (Fig. 2:5, points 19–22), *T. solum*'s landmark positions align more with *Prosaukia oculata*; the eyes for these species are more abaxially placed than in the other species; the palpebral lobes of *P. oculata* are, however, longer with the posterior end extending further backwards. *Prosaukia misa*, *Prosaukia tarutaoensis*, and *Thailandium* sp. undet. have similarly long palpebral lobes that are more posteriorly centered than in *T. solum*. All five species have a similar longitudinal placement of the anterior end of the palpebral lobe, so it is the position of the posterior end that indicates differences in overall palpebral length. The lateral corner of the anterior border (Fig. 2:5, landmarks 17, 18) is similarly placed in *P. misa*, *P. tarutaoensis*, *T. solum*, and *Thailandium* sp. undet., but in *P. oculata* it is more posterolaterally positioned, attributable to the very short preglabellar field and wide-set fixigena. If isolated clusters of landmarks were to be required for generic distinction, no evident differences separate *Thailandium* from *Prosaukia*. However, the collective trend of the six lateral most landmarks (Fig. 2:5, landmarks 17–22) is different for *T. solum* than for the other four species. In *T. solum* the landmarks are aligned with an anteromedial trendline. In the other four species the anterior palpebral landmarks (Fig. 2:5, points 19, 20) are more medial than the posterior palpebral landmarks or lateral corners of the anterior border (Fig. 2:5, points 21, 22, 17, 18). In this way *T. solum* is distinct and *Thailandium* sp. undet. follows the same trend as the species of *Prosaukia*.

The first two relative warps (RW1 and RW2) account for 42.58% and 20.79% of the variance respectively; other relative warps account for less than 10% of variance each. The distribution of specimens along the first two relative warps, particularly RW1, further support the differentiation of *Thailandium solum* from the other four species discussed with a distinct group of *T. solum* and overlap among *P. misa*, *P. tarutaoensis*, *P. oculata*, and *Thailandium* sp. undet. The proximity of specimens of *Thailandium* sp. undet. to those of the three species of *Prosaukia* (Fig. 2:7) and its evident separation from the specimens of *T. solum* suggest that *Thailandium* sp. undet. should be reclassified as a species of *Prosaukia*.

The first two Relative Warps (RW1 and RW2) represent the first two principal components of the thin plate spline decomposition of shape variation within the sample (Fig. 2:8) (Bookstein 1991). RW1 largely captures differences in the lateral placement of the anterior border's lateral corner, the length of the frontal area, and the longitudinal placement of the palpebral lobe's posterior point. RW2 primarily captures the width of the fixigena and lateral position of the palpebral lobes. The differentiation of *Prosaukia* and *Thailandium* along RW1 (Fig. 2:7) supports the observations from the SBR landmark distribution (Fig. 2:6) that *Thailandium solum* differs from *Prosaukia*, including *Thailandium* sp. undet., in the anterior convergence of the anterior facial suture branches, shorter palpebral lobes, and a particularly long frontal area. *Thailandium solum* also has wider fixigena than is typical for *Prosaukia* as indicated by distribution along RW2, but this is not a reliably diagnostic character since *P. oculata* has fixigena of comparable width to *T. solum*. A reliable diagnosis for the difference in length and longitudinal position of the palpebral lobe of *Thailandium* versus *Prosaukia* is that the posterior end of the palpebral lobe is opposite S1 in *T. solum* but in all other species included herein it is opposite L1.

The separate clustering of *P. oculata* on RW1 and RW2 reflects its wide fixigena and short preglabellar field. The short preglabellar field is consistent with some other species of *Prosaukia* (e.g. *P. subaequalis* Ulrich and Resser, 1933). Broad fixigena are also known in other species of *Prosaukia* (e.g. *P. delecostata* Ulrich and Resser, 1933). Therefore, these characters do not suggest the need to establish a separate genus.

Systematic paleontology

The systematic paleontology section is by Shelly Wernette and Nigel Hughes. Measurements and species descriptions are based on internal molds unless otherwise specified. The abbreviations SO and S1–S3 refer to the occipital furrow and lateral glabellar furrows respectively; LO and L1-L3 refer to the occipital and glabellar lobes.

Superfamily DIKELOCEPHALOIDEA Miller, 1889

Family DIKELOCEPHALIDAE Miller, 1889

Remarks.—The dikelocephalid trilobites discussed herein are those historically assigned to Saukiidae Ulrich and Resser (1930) and still commonly referred to as "saukiid" trilobites. The taxonomic ranking or validity of the "saukiid" grouping has long been controversial. Saukiinae was initially established as a subfamily within Dikelocephalidae (Ulrich and Resser, 1930). Raasch (1951) elevated Saukiinae to the level of family, arguing for a closer link to Ptychaspidiidae Raymond (1924) than to other Dikelocephalids. This view quickly became widely accepted (e.g. Hupé, 1955; Lochman, 1956). However its taxonomic position has not been stable with Kobayashi (1960), Longacre (1970), Stitt (1971, 1977), and Taylor and Halley (1974) relegating it to a subfamily of Ptychaspididae and Ludvigsen and Westrop (1983) retaining the family designation but reassigning it to Dikelocephaloidea. Ludvigsen et al. (1989), due to the inability to establish synapomorphic characters for all of Saukiidae, later abandoned the use of this grouping, claiming that it is a paraphyletic and a junior synonym of Dikelocephalidae. This scheme has been widely accepted by Laurentian and Gondwanan trilobite workers (e.g. Adrain, 2011 and Lee and Choi, 2011), although some authors continue to use Saukiidae as a family-level designation within Dikelocephaloidea (e.g. Park and Kihm, 2015a; Shergold et al., 2007). Herein we follow the scheme assigning the "saukiid" trilobites to Dikelocephalidae but without strong opinion as to whether the existence of Saukiidae is supported by synapomorphies either as a paraphyletic or monophyletic group. It seems likely that *Prosaukia* contains sister taxa to all derived Dikelocephaloidea.

Genus *Thailandium* Kobayashi, 1957

Type species.—*Thailandium solum* Kobayashi, 1957 from the Ao Mo Lae Formation, Tarutao Group, Ko Tarutao (by original designation)

Emended diagnosis.—As for *Thailandium solum.*

Remarks: According to the results of the above landmark morphometric analysis and additional pygidial characteristics discussed in the *T. solum* species remarks below, *Thailandium* is a monospecific genus known only from Ko Tarutao, Thailand. *Thailandium* sp. undet. as reported from the Pacoota Sandstone of Australia (Shergold, 1991), is reassigned to *Prosaukia* Ulrich and Resser (1933).

Thailandium solum Kobayashi, 1957

Figs 2:9,10

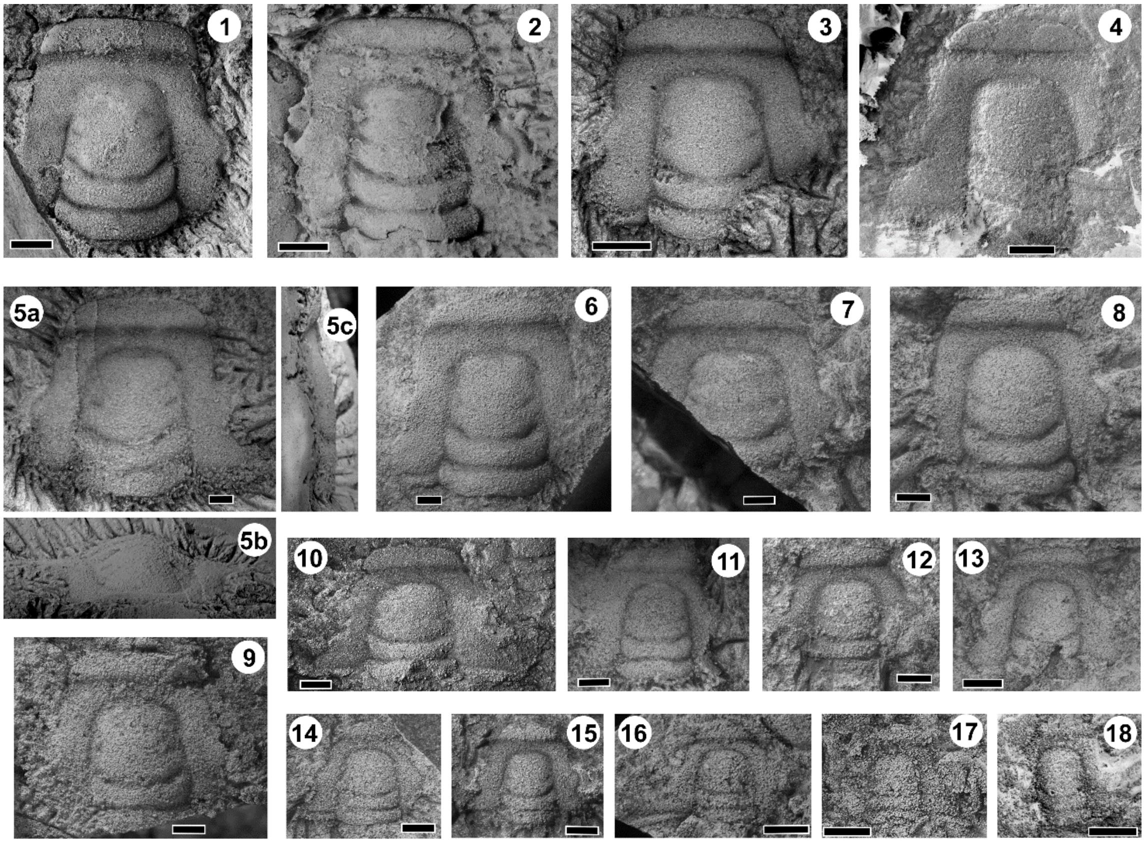
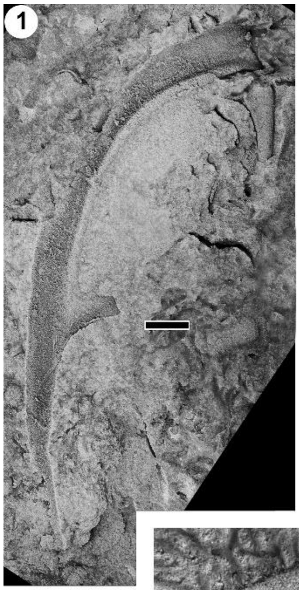


Figure 2:9 Thailandium solum Kobayashi, 1957 cranidia from Ko Tarutao. **(1)** DGSC F0570, Ao Mo Lae (AML) 3.72 m; **(2)** DGSC F0419, Ao Talo Topo west (ATTw); **(3)** DGSC F0609, AML 581 m; (4) CMC IP87037, vinyl polysiloxane cast, original of UMUT PA02299b-1, Kobayashi (1957) pl. 4 fig. 9, holotype; **(5a–c)** dorsal, anterior, and left lateral views respectively, DGSC F0607, AML 5.81 m; **(6)** DGSC F0568, AML 3.62 m; **(7)** DGSC F0602, AML 5.81 m; **(8)** DGSC F0601, AML 5.81 m; **(9)** DGSC F0596, AML 5.81 m; **(10)** DGSC F0435, ATTw; **(11)** DGSC F0583, AML 5.81 m; **(12)** DGSC F0576, AML 5.81 m; **(13)** DGSC F0598, AML 5.81 m; **(14)** DGSC F0595, AML 5.81 m; **(15)** DGSC F0544, AML h3; **(16)** DGSC F0569, AML 3.62 m; **(17)** DGSC F0574, AML 5.17 m; **(18)** DGSC F0591, AML 5.81 m. All internal molds except 18, external mold. Scale bars = 5mm for 10.1–10.4 and 2mm for 10.5–10.18.

1957. *Thailandium solum* Kobayashi p. 373, pl. 4 fig. 9,10; not figs 11,12 (*Quadraticephalus planulatus*).

1957. *Coreanocephalus planulatus* Kobayashi pl. 4 figs 16,17 only, not figs 13–15 (*Quadraticephalus planulatus*).

Diagnosis.—A *Prosaukia*-like species with low convexity, shallow furrows, anterior facial suture branches subparallel to anteriorly convergent outlining a trapezoidal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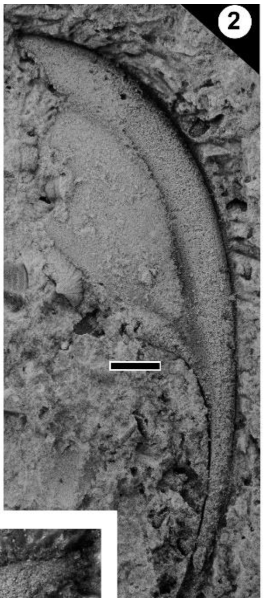
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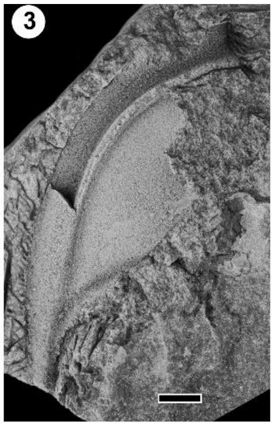
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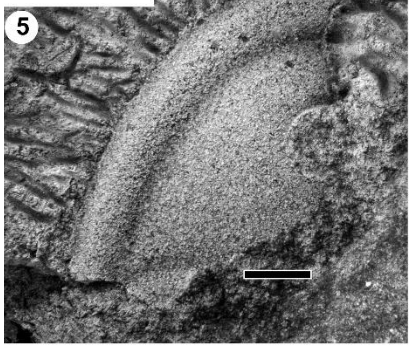
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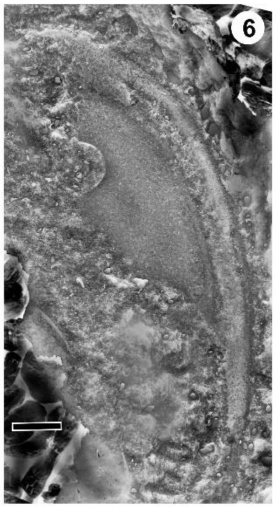
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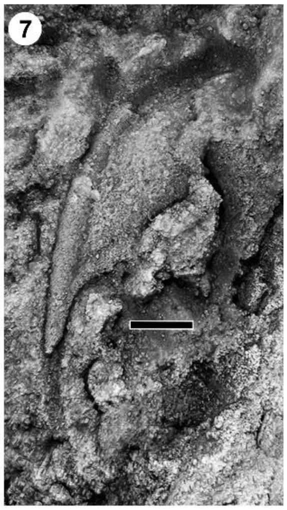
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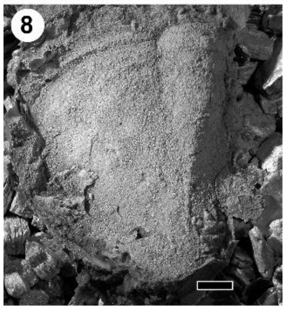
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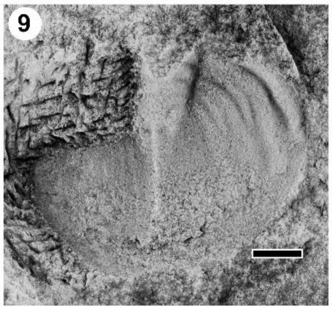
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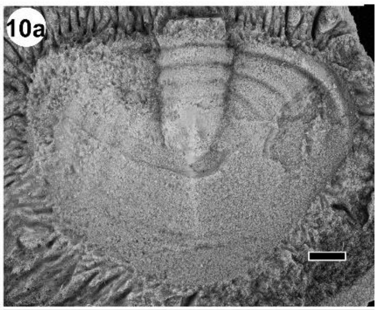
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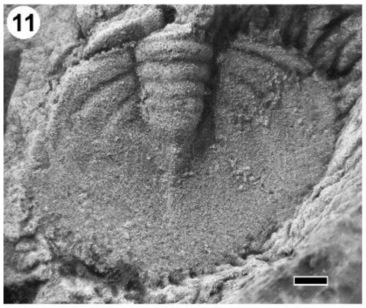
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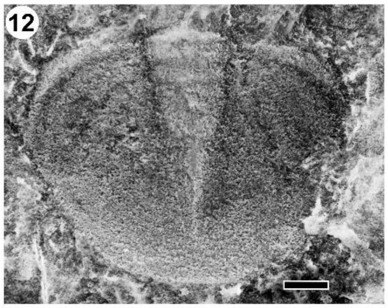
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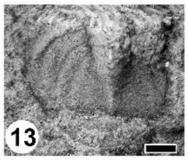
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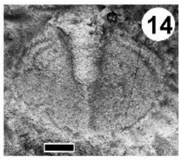
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Figure 2:10 (Previous Page) *Thailandium solum* Kobayashi, 1957 librigena (1–7) and pygidia (8–14) from Ko Tarutao. **(1)** DGSC F0621 Ao Mo Lae (AML) h2; **(2)** DGSC F0554, AML h3; **(3)** DGSC F0612, AML 5.81 m; **(4)** DGSC F0616, AML 5.81 m; **(5)** DDGSC F0631, AML 5.81 m; **(6)** CMC IP87039, vinyl polysiloxane cast, original of UMUT PA02299b-2, Kobayashi, 1957 pl. 4 fig. 10; **(7)** DGSC F0418, Ao Talo Topo west (ATTw); **(8)** CMC IP87046, vinyl polysiloxane cast, original of UMUT PA02299d-1, Kobayashi (1957) pl. 4 fig. 16; **(9)** DGSC F0610, AML 5.81 m; (**10a–c**) dorsal, right lateral, and posterior views respectively, DGSC F0611, AML 5.81m; **(11)** DGSC F0565 AML 2.2m; **(12)** DGSC F0583, AML 5.81m, external mold; **(13)** DGSC F0604, AML 5.81 m; **(14)** DGSC F0560, AMLh4. All internal molds except 5. Scale bars = 5mm for 1–3, 8–13 and 2mm for 4–7, 14.

cranidium; frontal area long (sag.) and equally to subequally divided into the anterior border and preglabellar field; palpebral lobes short (exsag.) with posterior point opposite S1. Pygidium subcircular to subtriangular, axis short with four axial rings and long post-axial ridge occupying about half the pygidial length (sag.), pleural field broad, effaced.

Occurrence.—Ao Mo Lae (AML) 3.62–5.81 m, AML horizons 3–5, and Ao Talo Topo west; Ao Mo Lae Formation of the Tarutao Group, Thailand; lower to middle of Cambrian Stage 10.

Emended Description.—Cranidium as described by Kobayashi (1957, p. 374) except that the entire dorsal surface is faintly granulose, not smooth. Occipital glabellar length (sag.) up to 1.6 cm.

Librigena moderately broad with smooth, gently sloping pleural area and firmly-incised posterior and lateral border furrows defining wide, inflated borders; posterior border furrow confluent with lateral border furrow, extending to posterior margin so as to fully separate lateral and posterior borders. Genal spine long with broad base and slow posterior tapering; uninterrupted extension of lateral border. Doublure same width (exsag. and tr.) as lateral border. Eye semi-circular.

Pygidium subtriangular, spatulate, with widest (tr.) point varying but typically with terminal piece; pygidial width (tr.) 125–130% of pygidial length (sag.); margin most strongly curved at widest point and medioposterior point. Axial width (tr.) at first ring ~25% pygidial width at widest (tr.) point; axial length 40–50% pygidial length (sag.); 4 axial rings; transverse axial furrows straight to slightly wavy; axial furrows sharp, straight, and slightly posteriorly convergent; terminal piece short; post axial ridge distinct but dissipating at ~2/3 distance from terminal piece and posterior margin. Pleural furrows proximally well-defined but distally effaced; interpleural furrows shallow and short (tr.), abaxially or completely effaced; anterior pleural band short (exsag.) and crescent-shaped, pinching out on pleural slope; posterior pleural band distally broadens. Broad, poorly defined border flat to concave with posterior curving upwards.

Material.—The new collections of *Thailandium solum* include 27 cranidia: 21 from Ao Mo Lae (AML) 3.62 m (DGSC F0568, F0569), 3.72 m (DGSC F0571, F0570), 5.17 m (DGSC F0574), 5.81 m (DGSC F0576, F0583, F0595, F0596, F0598, F0601, F0602, F0606, F0607, F0609, and CMC IP88617, IP88618), AML h3 (DGSC F0543, F0544), and AML h5 (DGSC F0591, F0618); six from Ao Talo Topo west (ATTw) (DGSC F0398, F0388, F0421, F0419, F0434, F0435). Eight librigenae: seven from AML 5.81 m (DGSC F0612, F0616 and CMC IP88612, IP88622, IP88623), AML h1 (DGSC F0554), and AML h4 (CMC IP88607); one from ATTw (DGSC F0418). 10 pygidia: eight from

AML 2.2 m (DGSC F0565), 5.81 m (DGSC F0583, F0584, F0604, F0610, F0611 and CMC IP88610), and AML h4 (DGSC F0560); 2 from ATTw (DGSC F0395, F0420).

Remarks.—The ontogeny of *Thailandium solum* is poorly understood, even with the larger sample size available in this study. The regression of partial Procrustes distances determines the extent to which shape change is related to size (Webster and Sheets, 2010). The same landmark configurations of the same 15 specimens of *T. solum* used in the shape analysis were regressed against the mean shape of the smallest 3 specimens in the sample and the partial Procrustes distance from the mean calculated. The result was a scatter of generalized Procrustes distance from the mean, with no significant trend associating size and shape change. Shape variance for all 15 specimens of *T. solum* was .0048 (bootstrapped by 1600 repetitions with a 95% confidence interval of 0.0031–0.0060). For comparison, a single specimen (Fig.2:9.3, DGSC F0609) was remounted, photographed, and marked for landmarks ten times; the variance for these ten images of a single specimen was 0.0008 over 1600 bootstraps.

When defining *Thailandium solum* Kobayashi (1957) tentatively assigned a relatively short and broad pygidium. That pygidium instead belongs to *Quadraticephalus planulatus* (Kobayashi, 1957 as *Coreanocephalus planulatus*; Shergold et al., 1988). Shergold et al. (1988) reassigned the pygidium initially assigned to *C. planulatus to Lichengia? tarutaoensis* Kobayashi, 1957; Shergold et al. (1998), recognizing it as “saukiid” in form and with a somewhat similar shape to the *Lichengia*? *tarutaoensis* pygidium (Shergold et al., 1988, fig. 5W). However, the pygidium herein assigned to *T. solum* has a notably broader pleural and postaxial region and is not easily confused with that of *L.*? *tarutaoensis*. Shergold et al. (1988) made the assumption that they had fossils from approximately the same collections as Kobayashi (1957) and inaccurately revised several of Kobayashi's taxa based on that assumption (e.g. *Pagodia thaiensis* as *Parakoldinioidia thaiensis* and *Saukiella tarutaoensis* as *Lichengia*? *tarutaoensis*; *S. tarutaoensis* instead is herein recognized as a species of *Prosaukia*). It is now clear that Kobayashi's (1957) collection represents a distinct interval from Shergold et al.'s (1988) and the only cooccurring taxa are those that are relatively long-lived in the Ao Mo Lae Formation, including *Eosaukia buravasi* Kobayashi (1957) and *Quadraticephalus planulatus* (Kobayashi, 1957). The pygidium initially assigned to *C. planulatus (*Kobayashi, 1957) and improperly synonymized with *Lichengia? tarutaoensis* (Shergold et al., 1988) belongs to *Thailandium* which was not in Shergold et al.'s collections (1988). The large pygidium is inconsistent with even the largest cranidia of any other species in either Kobayashi's (1957) collection or the collection presented herein excepting perhaps *Quadraticephalus planulatus* and *Eosaukia buravasi*; the shape and pleural divisions are notably "saukiid"-like, ruling out assignation to *Quadraticephalus*, and the broad pleural field is inconsistent with the lenticular shape of an *Eosaukia* pygidium which is otherwise well-documented in the Tarutao collections.

The cranidium of *Thailandium* is similar to that of *Prosaukia* Ulrich and Resser (1933) save for the angle of the anterior suture branches and length of the palpebral lobe. Likewise, the pygidium of *Thailandium* differs from that of *Prosaukia*, at least the type species, mainly by degree of axial length, post-axial length, and effacement of the pleural field.

The librigena of *Thailandium solum* is distinct from the librigena of similar genera, including *Prosaukia* and *Tellerina* Ulrich and Resser (1933) in that the posterior and lateral border furrows are firmly-incised and truly confluent. In both *Tellerina* and *Prosaukia* the joining of the furrows is marked by a continuous curve for the posterior border furrow and a bend, often sharply dog-legged, in the lateral border furrow. In *Prosaukia* the lateral furrow may become effaced with an inflated extension of the pleural field separating it from the posterior border furrow; this state is particularly well-developed on *Prosaukia misa* (Hall) and to a lesser extent on *Prosaukia oculata* n. sp.

Though cephalically distinct, particularly in the frontal area, *Thailandium* has a similar overall pygidial structure to *Tellerina* Ulrich and Resser (1933) and *Calvinella* Walcott, 1914. Similarities include a short axis, long postaxis, broad and poorly-defined flat to concave border without a border furrow. Some species of *Calvinella* (e.g. the type species, *C. spiniger*) have well-defined postaxial ridges; these are rare in *Tellerina*. In *C. spiniger* the pygidium is more circular or subellipsoidal than in *Thailandium,* but *Tellerina,* at least for the type species *Tellerina crassimargniata* (Whitfield, 1882) has a subtriangular to spatulate pygidium, like that of *Thailandium.* Of the three genera, *Thailandium* has the most effaced interpleural furrows and shortest (tr.) pleural furrows. All three genera grow to sizes larger than is typical for “saukiids” though not as large as some species of *Dekelocephalus* (e.g. *Dikelocephalus minnesotensis* Owen, 1852; see Hughes, 1994). *Dikelocephalus minnesotensis* has a similarly broad, poorly defined and flat border with a long postaxial area. The broad, flat, effaced border may reflect a convergence of all dikelocephalid trilobites that grow to be more than a few centimeters in total length.

Genus *Prosaukia* Ulrich and Resser, 1933

Type species.—Dikelocephalus misa Hall (1863)

Remarks.—The generic diagnosis of *Prosaukia* has been discussed thoroughly in previous work (Ulrich and Resser, 1933, Ludvigsen and Westrop, 1983), but the divergent anterior suture branches has not been noted as a diagnostic feature. This character is helpful in differentiating *Prosaukia* from *Thailandium* Kobayashi (1957) and also from *Hoytaspis* Ludvigsen and Westrop (1983).

Prosaukia tarutaoensis (Kobayashi, 1957)

Fig. 2:11

1957. *Saukiella tarutaoensis* Kobayashi, p. 378, pl. 5, fig. 12.

not 1988. *Lichengia*? *tarutaoensis* (Kobayashi) Shergold et al., p. 309, figs. 5S–W.

Emended diagnosis.—Species of *Prosaukia* with short (sag.) preglabellar field, long (sag.) and weakly bowed anterior border, strongly anteriorly tapering glabella, fine granulation, wide (tr.) LO, and narrow (tr.) pygidial axis.

Occurrence.—Ao Mo Lae (AML) 2.2–3.1 m, AML h3, and Ao Talo Topo west; Ao Mo Lae Formation of the Tarutao Group, Thailand; Furongian.

Emended description.—Cranidium subtrapezoidal; width across palpebral areas 90% of cranidial length in smallest holaspids to 105% of cranidial length in largest holaspids. Occipital glabellar length (sag.) up to 1.1cm; glabellar width across L1 60% width across palpebral areas in smaller holaspids and 70% in larger; length of glabella and LO 82–85% of cranidial length; glabella trunco-conical with low dorso-ventral relief; axial furrows straight or slightly pinched at S2, weakly incised; anterior glabellar margin transverse to gently curved; LO 15–20% wider than L1; SO gently posteromedially

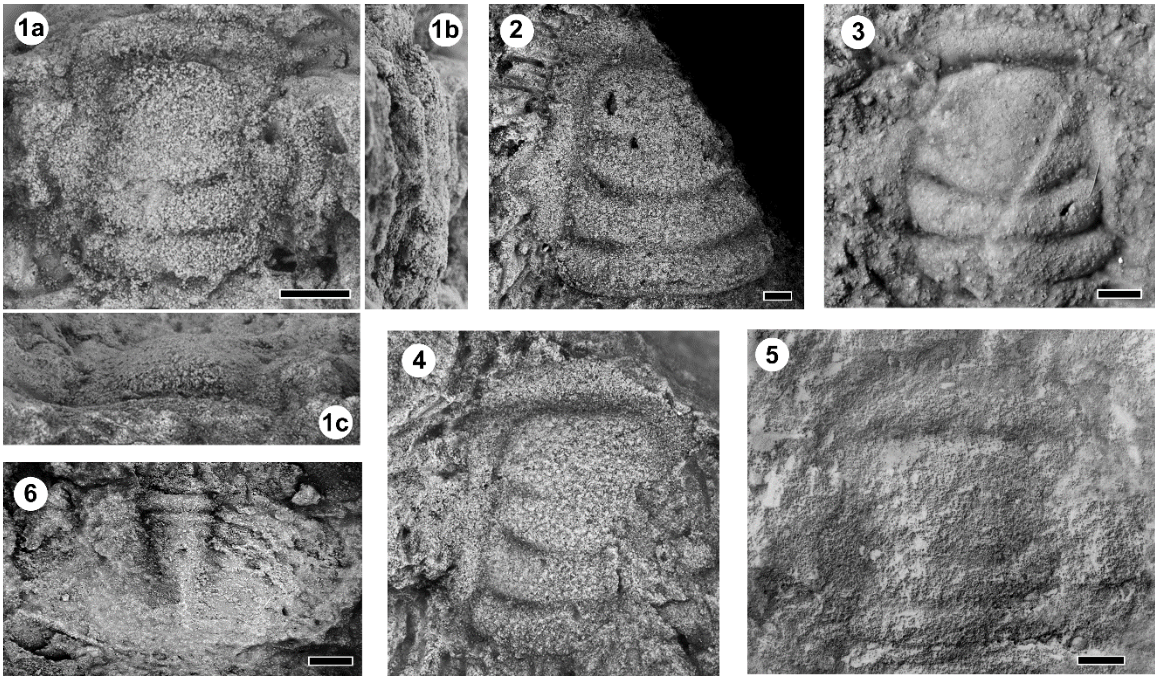


Figure 2:11 *Prosaukia tarutaoensis* n. sp. cranidia (1–6) and pygidium (7). **(1a–c)** dorsal, left lateral, and anterior views respectively, DGSC F0566, AML 2.2 m; **(2)** DGSC F0567, Ao Mo Lae (AML) 3.1 m; **(3)** DGSC F0414, Ao Talo Topo west (ATTw); **(4)** DGSC F0546, AML h3; **(5)** CMC IP87029, vinyl polysiloxane cast, holotype, original of UMUT PA02298c, Kobayashi, 1957, pl. 5, fig. 12; **(6)** DGSC F0453, ATTw. All internal molds. Scale bars = 2mm.

bowed, shallowing medially; S1 moderately to strongly posteromedially bowed, shallowing medially; S2 short (tr.) and well-defined, less posteromedially angled than S1; anteromedially angled S3 poorly-defined to effaced. Palpebral lobe moderately arched with greatest curvature in posterior part; widest palpebral point slightly anterior to S1 in smaller holaspids and slightly posterior in larger; palpebral lobe length (exsag.) 30% cranidial length (sag.) in smaller holaspids to 40% in larger; width (tr.) across anterior palpebral corners 80–90% width across posterior corners. Fixigena narrow (tr.) with moderately wide preocular areas; anterior suture branches anteriorly divergent from anterior palpebral corners, curving gently adaxially for rounded lateral margins of frontal area; frontal area widest (tr.) point slightly posterior to anterior border. Preglabellar field short, depressed; anterior border furrow gently anteromedially bowed; anterior border 15% cranidial length, weakly inflated, horizontally oriented. All surfaces densely granulated.

Pygidium subellipsoid to lenticular; width (tr.) twice length (sag.); axial width (tr.) at anterior-most ring 20% pygidial width at widest point; axial length (sag.) 65% pygidial length (sag.); four axial rings, only first three clearly defined; axial furrows converging at 15° from sagittal axis; terminal piece narrow and long; postaxial ridge short, not extending to pygidial margin. Pleural furrows poorly-defined and pleural field effaced.

Material.—Five cranidia from Ao Mo Lae (AML) 2.20 m (DGSC F0566), AML 3.1 m (DGSC F0567), AML h3 (DGSC F0545, F0546), and Ao Talo Topo west (ATTw) (DGSC F0414); one pygidium from ATTw (DGSC F0453); all internal molds.

Remarks.—*Prosaukia tarutaoensis* represents a typical species of *Prosaukia* in many ways; in the dimensions and shape of the glabella, length of the palpebral lobes, width of the fixigena, length of the anterior border, surface texture, and expression of furrows it clearly resembles the type species, *Prosaukia misa* (Hall, 1863). *Prosaukia tarutaoensis* differs cranidially from known species of *Prosaukia* primarily in the notably short (sag.) preglabellar field and wide (tr.) occipital lobe. In *Prosaukia misa* (Hall, 1863) and most other species of *Prosaukia* the occipital lobe is either slightly narrower than L1 as in *Prosaukia oculata* n. sp. or else the axial furrows flank the occipital lobe along the same path as the preoccipital glabella. In *P. tarutaoensis* the axial furrows curve sharply around the occipital lobe. The pygidium of *P. tarutaoensis* is distinct as it is the only known species of *Prosaukia* with a lenticular pygidium.

Shergold et al. (1988) considered the single specimen of *Prosaukia tarutaoensis* known at that time (Kobayashi, 1957; pl. 5 fig. 12, Fig. 11.5) to be synonymous with new material that they called *Lichengia*? *tarutaoensis* on account of the frontal area and palpebral lengths and positions. It is clear from the strong anteriorly narrowing glabella and medial discontinuity of the lateral glabellar furrows in the latter material that these specimens are not synonymous with *Prosaukia tarutaoensis*. Therefore *Lichengia*? *tarutaoensis* is excluded from Kobayshi's (1957) concept of the species. Additional specimens of *Lichengia tarutaoensis* (sensu Shergold et al., 1988) have been recovered from the Ao Mo Lae Formation, and revision of this species will appear in future work.

Prosaukia oculata n. sp.

Fig. 2:12

?1988 *Lichengia*? *tarutaoensis* (Kobayashi) Shergold et al., p. 309–310, fig. 5W only, *not* figs 5S–V = (*Lichengia*? *tarutaoensis*)

Type material.—Holotype, DGSC F0512 (Fig. 2:12.1a–b) from Ao Talo Topo 22.78 m; paratypes DGSC F0461, F0489, F0498, F0503, F0511, F0532, F0534; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Thailand; Furongian.

Occurrence.—Ao Talo Topo 22.78–22.88 m and horizon 1 (Figs 2, 5), Ao Mo Lae Formation of the Tarutao Group, Thailand; Furongian.

Diagnosis.—Species of *Prosaukia* with wide, flat fixigena, including palpebral areas, short (sag.) preglabellar field, and subcircular pygidium with strongly inflated posterior pleural bands and reduced but well-defined propleural bands.

Description.—Cranidium subrectangular; width across palpebral areas 120%–135% cranidial length (sag.). Occipital glabellar length (sag.) up to 0.9cm; glabellar width (tr.) across L1 50% width across palpebral areas; length of glabella and LO 85% cranidial length (sag.); glabella bullet-shaped with moderate dorso-ventral relief; axial furrows

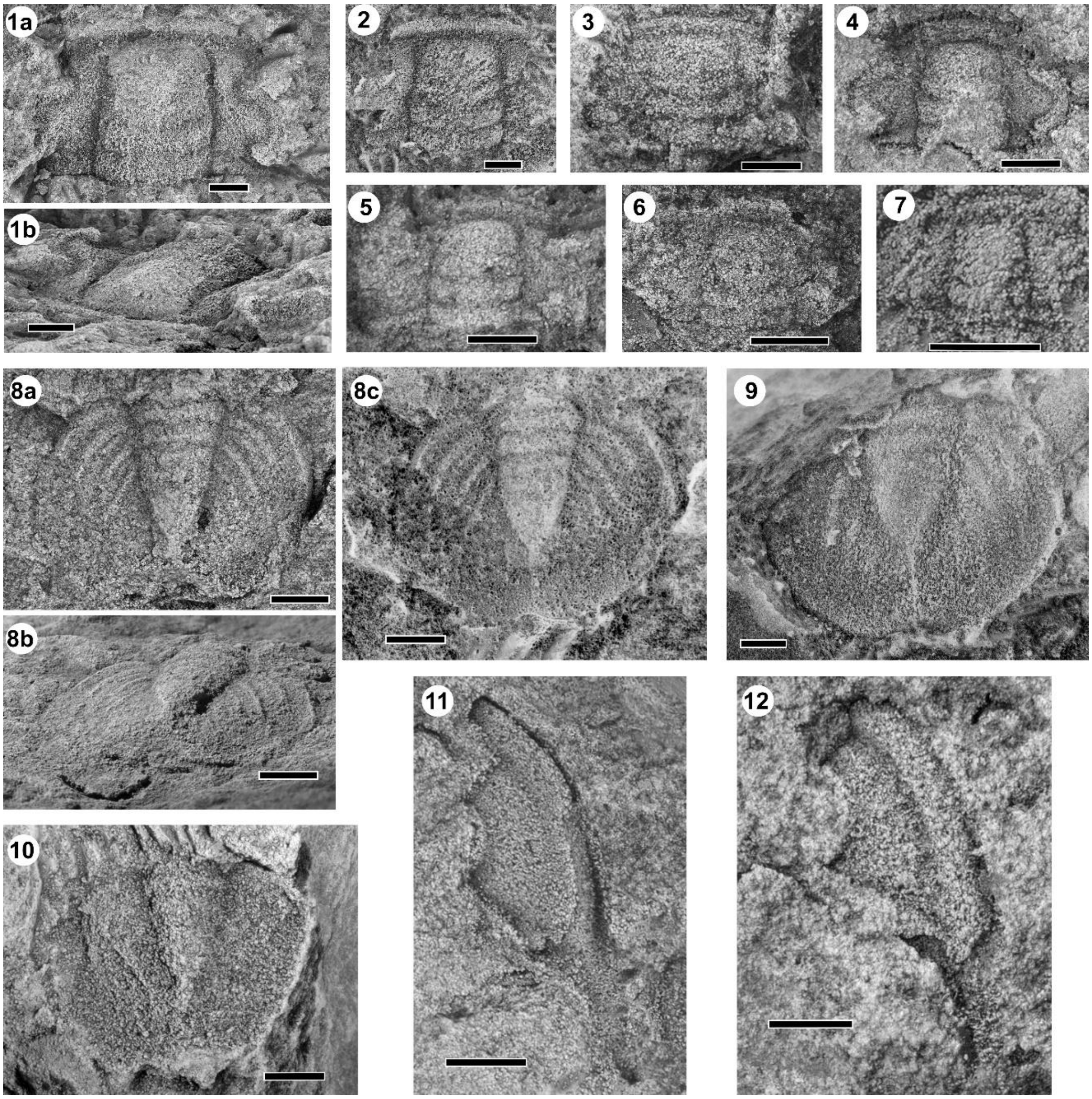


Figure 2:12 Prosaukia oculata n. sp. cranidia (1–7), pygidia (8–10), and librigena (11,12). **(1a–b)** dorsal and left anterolateral views respectively, holotype, DGSC F0512; **(2)** DGSC F0503; **(3)** DGSC F0498; **(4)** DGSC F0532; **(5)** DGSC F0511; **(6)** DGSC F0461; **(7)** DGSC F0534, Ao Talo Topo (ATT) 22.88 m; **(8a–c)** internal dorsal, internal right posterolateral oblique, and external dorsal views respectively, DGSC F0509, F0510; **(9)** DGSC F0470, external mold; **(10)** DGSC F0467; **(11)** DGSC F0488; **(6)** DGSC F0513. All from ATT 22.78 m except 7; all internal molds unless otherwise indicated. Scale bars = 2mm.

smoothly curved around glabella or slightly bowed at L1, well-defined; anterior glabellar margin transverse to gently curved; L1 slightly wider than LO; SO transverse or gently posteromedially bowed, shallowing medially; S1 slightly more strongly posteromedially bowed than SO, shallowing medially; S2 medially discontinuous and weakly to moderately well-defined, less posteromedially angled than S1; S3 poorly-defined to effaced, oriented slightly postermedially to transverse. Palpebral lobe strongly curved, nearly symmetric about the midpoint; palpebral midpoint opposite S1; palpebral lobe length (exsag.) 35%–40% cranidial length (sag.); width (tr.) across anterior palpebral corners equal or slightly less than width across posterior corners. Fixigena broad (tr.) with wide preocular areas only slightly narrower than palpebral areas; anterior suture branches anteriorly divergent 35–40° from sagittal, curving strongly adaxially at anterior border furrow. Preglabellar field very short to furrow-like, depressed; anterior border furrow gently anteromedially bowed; anterior border 15% cranidial length, strongly inflated, horizontally oriented. Weakly granulated surface sometimes effaced.

Librigena with narrow, gently convex genal field; lateral and posterior border furrows well-defined; lateral border furrow shallowing near junction with posterior border furrow; lateral border broad, nearly 75% genal field width measured orthogonally from cephalic margin to ocular suture.

Pygidium subcircular with slight posterior marginal embayment; length (sag.) 80% width (exsag.); widest (tr.) point of pygidium near pygidial mid-length (exsag.); axial width (tr.) at anterior-most ring 30%–35% pygidial width at widest point; axial length (sag.) 60%–70% pygidial length (sag.); 4 axial rings, only first 2 clearly defined;

axial furrows converging at 10°–15° from sagittal axis; terminal piece posteriorly angular; postaxial ridge distinct and extending to pygidial margin. Pleural furrows and interpleural furrows well-defined; anterior pleural bands narrow; posterior pleural bands strongly inflated; pleural furrows broader than interpleural furrows; all pleurae well-aligned with axial rings; all pleurae maintain width to edge of pleural field and become effaced where pleural field slopes into border; border flat without defined furrow; doublure short, not reaching terminal axial piece.

Etymology.—A fusion of ocula- and -lata, Latin for eye and wide respectively.

Material.—Seven cranidia (DGSC F0461, F0489, F0498, F0512, F0511, F0532 – internal molds, DGSC F0503 – external mold), 2 librigena (DGSC F0488, F0513 – internal molds), and 4 pygidia (DGSC F0510 – internal and external mold, F0430 – external mold, F0470 – external mold, F0467 – internal mold) all from Ao Talo Topo 22.78 m, one cranidium internal mold from Ao Talo Topo 24.1 m (DGSC F0534), and one cranidium from ATT h1 (DGSC F0459).

Remarks.—Prosaukia oculata, as its name suggests, has more widely set apart palpebral lobes than is typical for the genus. The greater distance between the eyes results from broader fixigena rather than a wider glabella. *Prosaukia delcostata* Ulrich and Resser (1933) also has relatively broad fixigena, but it differs from *P. oculata* by the former’s longer preglabellar field, broader lateral cephalic border, more rectangular anterior glabellar margin, and less circular pygidium. The preglabellar field of *P. oculata* is very short, nearly absent compared with most *Prosaukia*, but it is still clearly recognizable on some specimens (e.g. DGS F0532, Fig. 12.4), and this intraspecific variation proves the presence of the preglabellar field within the taxon.

Chapter 3. Trilobites of Thailand's Cambro-Ordovician Tarutao Group

Introduction

Sibumasu, the Shan-Thai block (Fig. 3:1), is important for Cambro-Ordovician geochronologic and paleogeographic studies as it is the only Gondwanan terrane known to have both latest Cambrian and earliest Ordovician ash beds (Thein, 1973; Stait et al., 1984; Shergold et al., 1988; Imsamut and Yathakam, 2011), and may share correlative faunal links with both North China and Australia. These may prove critical in constraining the dates of events in one of the three least well constrained intervals of Phanerozoic time – the "late" Cambrian. And yet, despite its global and regional significance, Sibumasu's earliest Paleozoic faunal record is critically under-studied. For geochronologic work to have maximum value it must integrate data from both absolute and relative dating methods with information on regional paleoenvironment. Accordingly, a well-

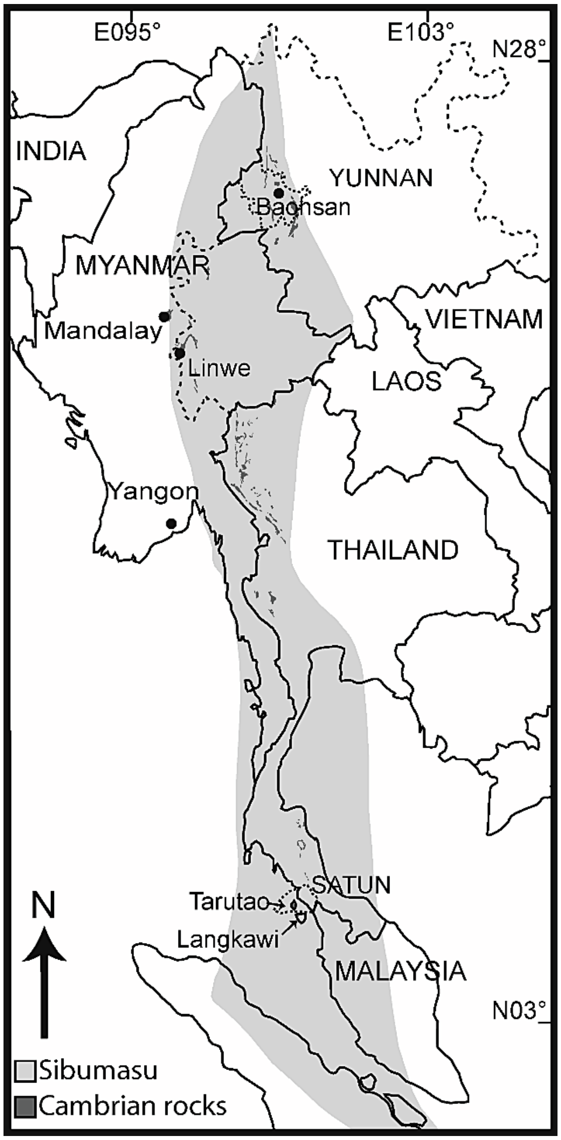


Figure 3:1 The modern extent of the Sibumasu terrane. Modified from Wernette et al., 2020.

resolved inventory of the fauna in detailed stratigraphic context is essential as reliable biostratigraphy is a key tool for correlating geochronologic information from this terrane to the rest of the world. Furthermore, although Sibumasu is most commonly represented as an “outboard” continental fragment located off northwestern Australia in recent reconstructions (e.g. Cocks and Torsvik, 2013; Domeier, 2018), its exact position is far from being firmly constrained. While the broad span of detrital zircon grain ages in the late Cambrian rocks of Ko Tarutao suggest connection to core Gondwana (e.g. McKenzie et al., 2014), the specific placement of Sibumasu is quite poorly constrained. No reliable paleomagnetic determinations have yet been made, and neither are biotic comparisons adequate.

Of the regions that make up Sibumasu, peninsular Thailand has the best studied Cambro-Ordovician faunal record. No descriptions or illustrations of Cambrian fossils have yet been published from Myanmar (Thein, 1973; Aung and Cocks, 2017), and no identifiable fossils have been discovered of in the tectonically altered Cambrian rocks of northern Thailand (Wongwanich, et al., 2002). The tectonically deformed mudstone fauna of Baoshan was described in a single publication (Sun and Xiang, 1979) but no recent work has reconsidered and extended that analysis. To date, three separate studies have addressed the Cambrian and Ordovician fauna from Ko Tarutao, Thailand in what is now the Satun UNESCO Global Geopark. Kobayashi (1957) described the fauna sent to him within six slabs collected from a single bed in the northwest of the island and assigned a late Cambrian age to the assemblage (Fig. 3:2). Stait et al. (1984) described the Ordovician fauna from Ao Phante Malacca (Fig. 3:2). Shergold et al. (1988) made a more extensive survey of the island and revised and expanded upon Kobayashi’s (1957) descriptions of the Cambrian fauna. However, these three studies on the fauna of Thailand did not provide a comprehensive inventory of the biota. Shergold et al. (1988), for example, left all but three species in open nomenclature, although they commonly provided addendums “aff.”, “cf.”, and “?” on the specific or generic assignments. Without better taxonomic resolution fauna has limited value for regional correlations and other geologic studies.

The study herein is part of an ongoing effort to describe and revise the latest Cambrian and earliest Ordovician fauna of all regions of Sibumasu (Wernette et al., 2020; Wernette et al., in review; Wernette et al., in prep). Work commenced on the Thai fauna from the Tarutao Group, because it is relatively well known with previously studied sections known to contain ash beds interbedded with fossils (Stait et al., 1984; Shergold et al., 1988). Studies of Thailand’s Cambrian and earliest Ordovician record, including this one, focus on outcrops from Ko Tarutao (Fig. 3:2), because the coastline of the island has well-exposed sections, and it is sufficiently distant from the effects of

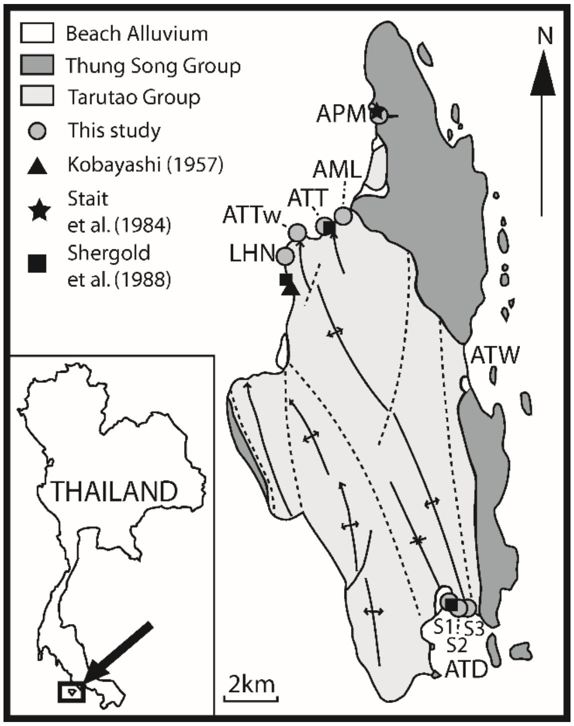


Figure 3:2 Map of Ko Tarutao. APM = Ao Phante Malacca; AML = Ao Mo Lae; ATT = Ao Talo Topo; ATTw = Ao Talo Topo west; LHN = Laem Hin Ngam; ATD = Ao Talo Udang; S1–S3 = ATD Sections 1–3; ATW = Ao Talo Wao. Modified from Bunopas et al., 1983 and Wernette et al., 2020.

tectonism that have rendered much of the Cambrian rock in mainland Thailand too deformed to yield identifiable fossils (Wongwanich et al. 2002). Over three excursions to Ko Tarutao fossils, ashes, and detrital zircons were collected from five localities, from all of which fossils had been described in the previous studies. Each fossiliferous bed sampled was treated as a unique collection and, with the exception of the first exploratory excursions and a few additional samples, each collection was located within a detailed stratigraphic log. These collections contain trilobites, brachiopods, cephalopods, and crinoids. Herein we focus on the trilobite fauna which is the best preserved and by far the most abundant and diverse. Following the faunal revisions by Shergold et al. (1988), 18 unique trilobite taxa were recognized from Thailand, but only eight of them resolved to species level. In this study we conservatively recognize at least 40 from the Tarutao Group, 29 of which have species-level resolution. Of the 40 taxa, 25 of are considered endemic to Thailand, including two new genera and 14 new species (Table 1). New material of all trilobite forms noted in previous studies was recovered in our work, with the possible exception of an indeterminate leiostegiid (Shergold et al., 1988). We use our improved understanding of the fauna to affirm previous interpretations of the faunas' age as latest Cambrian through Tremadocian (Stait et al., 1984; Shergold et al., 1988) with most of the Cambrian fossils coming from middle of Cambrian Stage 10. Similarities with the South Korean fauna at the species and genus level (Sohn and Choi, 2007; Park and Khim, 2015a, 2015b) suggest a strong geographic association with the far-eastern Sino-Korean or North China Block. Association with northwest and central Australia is supported by fauna at the genus level (Shergold, 1972, 1975, 1991).

This study	Kobayashi, 1957	Shergold et al., 1988	Stait et al., 1984
Homagnostus obesus	agnostid gen et sp. indet.		
Pseudagnostus sp.			
Geragnostus sp.			*Geragnostus* sp.
Tsinania sirindhornae n. sp.		*Tsinania* (*Tsinania*) cf. *nomas*	
Mansuyia oientalis?			
Satunarcus molaensis n. gen. et sp.			
Parakoldinioidia callosa		*Parakoldinioidia thaiensis,* in part	
Pseudokoldinioidia sardsudae n. sp.		*Parakoldinioidia thaiensis,* in part	
Pagodia thaiensis	*Pagodia thaiensis* n. sp.	? Leiostegiid gen. et sp. indet. not *Parakoldinioidia thaiensis*	
Pagodia? *uhleini* n. sp.		*Szechuanella*? cf. *damujingensis*	
Parapilekia bunopasi			*Rossaspis*? *bunopasi* n. sp.
Asaphellus charoenmiti n. sp.			*Asaphellus* sp.
Apatokephalus arcuatus n. sp.			
Yosimuraspis acufrons n. sp.			
Tarutaoia techawani n. gen. et sp.			
Jiia talowaois n. sp.			
Pseudokainella malakaensis			*Pseudokainella malakaensis* n. sp.
Haniwa mucronata			
Haniwa sosanensis			
Caznaia imsamuti n. sp.			
Caznaia? *undulata* n. sp.			
Eosaukia buravasi	*Eosaukia buravasi* n. sp.	*Eosaukia buravasi*	
Hoytaspis thanisi		*Hoytaspis*? *thanisi* n. sp.	
Lichengia simplex		*Lichengia*? *tarutaoensis*	
Lophosaukia nuchanongi n. sp.	?*Eosaukia buravasi*, in part	*Lophosaukia* cf. *jiangnanensis*	
Prosaukia tarutaoensis		*Saukiella tarutaoensis* n. sp.	
Prosaukia oculata n. sp.		?*Lichengia? tarutaoensis*, in part	
Prosaukia. sp. 1			
Prosaukia sp. 2		*Prosaukia*? cf. *nema*	
Prosaukia sp. 3			
Sinosaukia sp.			
Thailandium solum	*Thailandium solum* n. sp.		
Pacootasaukia sp.			
Wuhuia? sp.			
Corbinia perforata n. sp.			
Plethopeltella sp.			
Quadraticephalus planulatus	*Coreanocephalus planulatus* n. sp.	*Quadraticephalus planulatus*	
Parashumardia sp.			
Akoldinioidia lata		Shumardiid gen. et sp. Indet.	
Akoldinioidia sp.			
Koldinioidia choii			
Indet. harpiid			Harpiid fragments

Table 3:1 (*Previous page*) Trilobites of the Tarutao Group. A summary of the Tarutao Group's trilobite fauna from this and previous studies with "this study" being inclusive of recent publications that are part of this same project. In column 1,"n. sp." indicates new species described as part of this study; *Satunarcus molaensis* was first described in Wernette et al., 2020 and *Prosaukia oculata* in Wernette et al., in review. "n. sp." is used elsewhere to indicate the prior study in which the species was first described. Shaded taxa are those endemic species unknown outside of the Tarutao Group. Species are listed in the order in which

Geologic setting and regional stratigraphy

Western and peninsular Thailand are part of Sibumasu, also known as the Shan-Thai Block (Bunopas, 1981; Metcalfe, 1984). During the lowest Paleozoic, Sibumasu was one of several peri-Gondanan “outboard” terranes that bordered northern equatorial Gondwana. These terranes are thought to have accreted to core Gondwana during the Neoproterozoic and earliest Paleozoic (Meert, 2003; Boger and Miller, 2004; Cocks and Torsvik, 2013). A long subduction zone located along Gondwana’s northern margin facilitated this accretion, which was associated with widely distributed and voluminous felsic intrusions (LeFort et al., 1986; Zhu et al., 2012; Xu et al., 2014; Domeier, 2018) (Fig. 3:3). Sibumasu was part of this volcanic belt. Rhyolites and granites are known

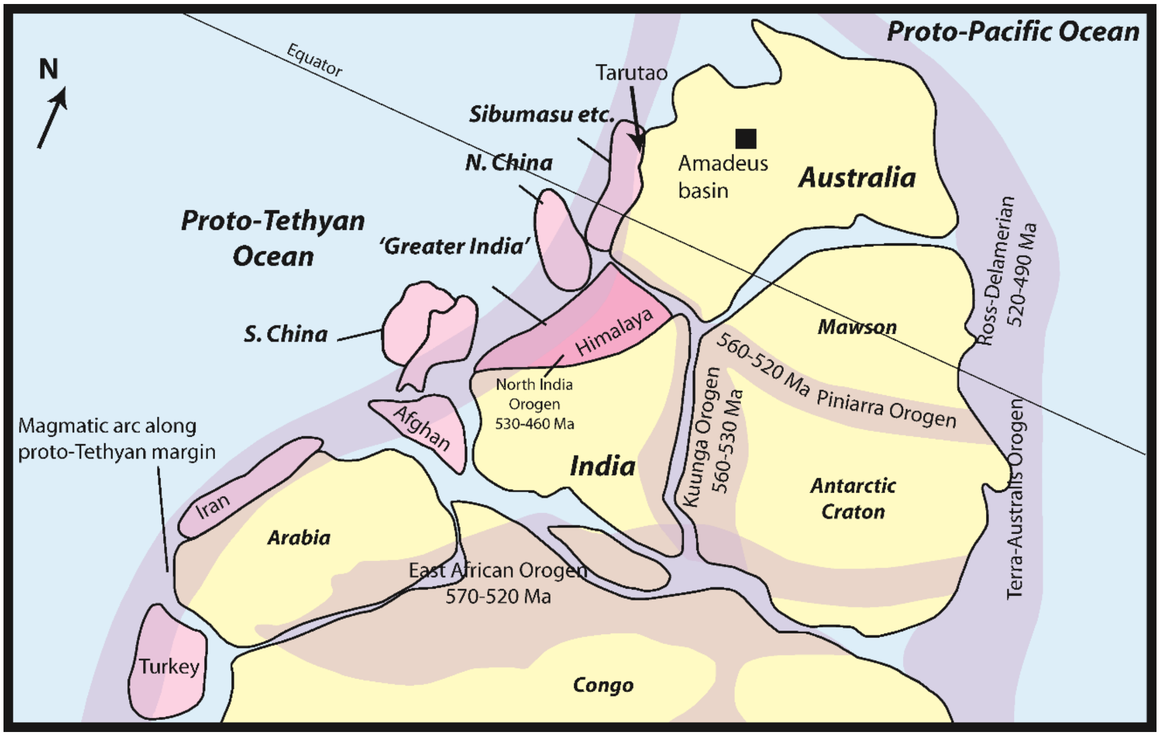
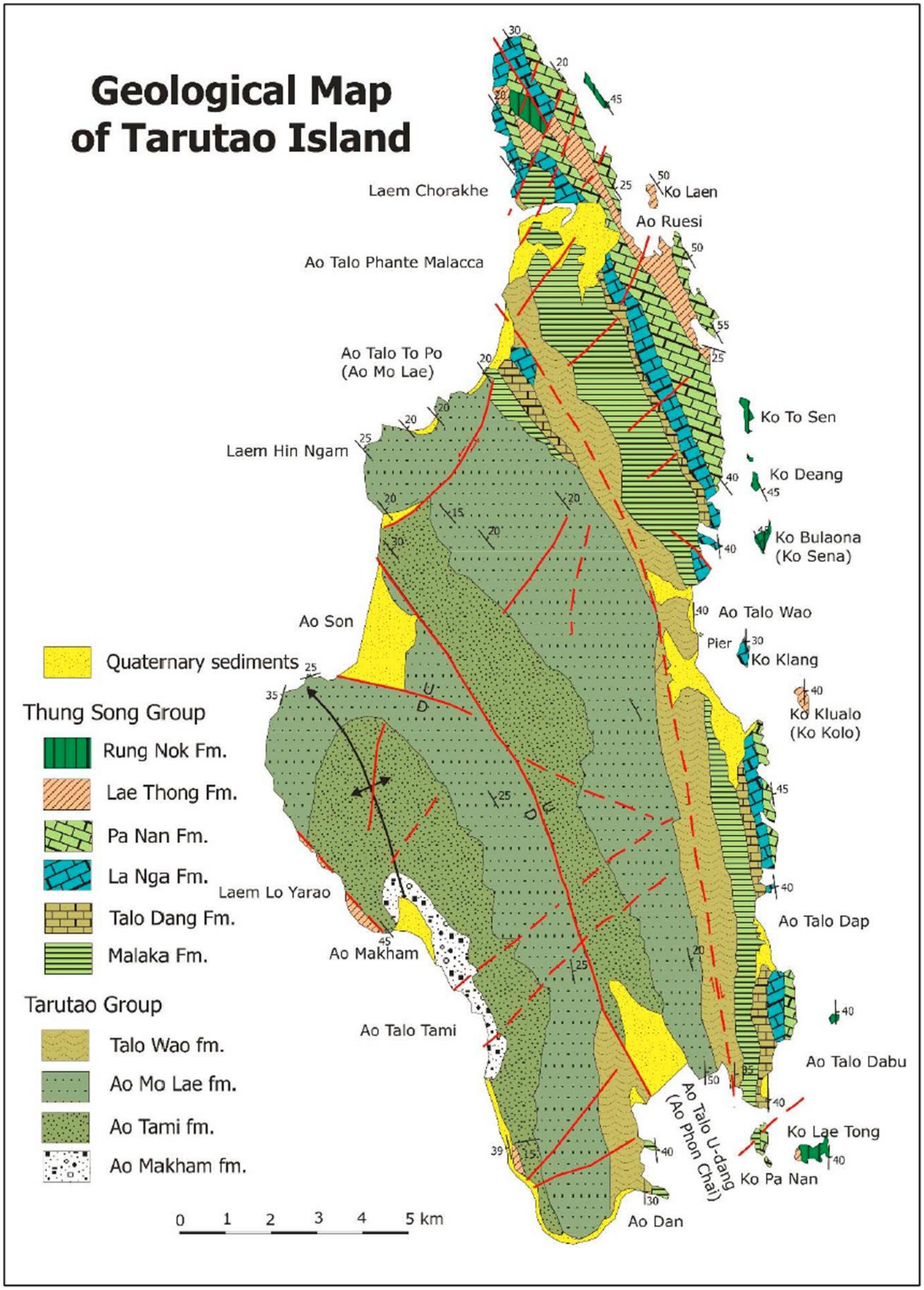


Figure 3:3 One of the plausible Cambro-Ordovician paleogeographic reconstructions of northern Gondwana. Locations of the Amadeus Basin and Tarutao are only approximations to indicate their relative locations and proximity. Modified from Hughes, 2016; orogenies from Cawood et al., 2007; equator from Cocks and Torsvik, 2013.

from the Bawdwin Mine area of Myanmar's northern Shan State (Brinkmann and Hinze, 1981; Bender, 1983), but these have not been radioisotopically dated using modern techniques. In southern Thailand, as in the southern Shan State of Myanmar, ash beds provide evidence of the Cambro-Ordovician volcanism (Stait et al., 1984; Shergold et al., 1988; Imsamut and Yathakam, 2011). In the southern Shan State of Myanmar the Furongian Molohein Group and Pangyun Formation sit unconformably on top of the Precambrian or earliest Cambrian Chaung Magyi Formation (Wolfart et al., 1984). There is also an unconformity between the Precambrian rocks of mainland Thailand and the Cambro-Ordovician Tarutao Group, but the Precambrian rocks are known only from the mainland where they and the immediately overlying Tarutao Group have been subjected to high-grade and low-grade regional metamorphism respectively (Wongwanich et al., 2002). On Ko Tarutao, the Tarutao Group is the oldest lithologic unit exposed, and there it is unmetamorphosed (Shergold et al., 1988).

The Tarutao Group is the lower of the two units on Ko Tarutao. It was named the Tarutao Group by Javanaphet (1969), but in most of the twentieth century literature it is referred to as the Tartuao Formation, the designation given to it in a report by Bunopas et al. (1983) who sought to combine it with the Thung Song Formation (presently the Thung Song Group) into the Langu Group. Either designation has been applied well into the twenty-first century, but as of 2011 the Tarutao Group has been subdivided into four named formations (Imsamut and Yathakam, 2011; Fig. 3:4). Prior to the formal establishment these formations, the Tarutao Group had been subdivided into three or four informal units depending on the preferences of individual authors. The four formations


Geological Map of Tarutao Island
Laem Chorakhe
Ko Laen
Ao Ruesi
Ao Talo Phante Malacca
Ao Talo To Po
(Ao Mo Lae)
Ko To Sen
Laem Hin Ngam
Ko Deang
Ko Bulaona
(Ko Sena)
Ao Son
Ao Talo Wao
Pier
Ko Klang
Ko Klualo
(Ko Kolo)
Laem Lo Yarao
Ao Makham
Ao Talo Dap
Ao Talo Tami
Ao Talo Dabu
Ao Talo U-dang
(Ao Phon Chai)
Ko Lae Tong
Ko Pa Nan
Ao Dan
U
D
U
D
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40
Quaternary sediments
Thung Song Group
Rung Nok Fm.
Lae Thong Fm.
Pa Nan Fm.
La Nga Fm.
Talo Dang Fm.
Malaka Fm.
Tarutao Group
Talo Wao fm.
Ao Mo Lae fm.
Ao Tami fm.
Ao Makham fm.
0 1 2 3 4 5 km

Figure 3:4 (Previous page) Detailed geologic map of Ko Tarutao. Reproduced from Burrett and Yathakam, 2020

now recognized, in ascending stratigraphic order, are the Ao Makham, Ao Tami, Ao Mo Lae, and Talo Wao formations. The lower and upper formations consistently correspond with the upper and lower units described in past literature, regardless of whether authors considered there to be three (e.g. Lee, 1983; Bunopas et al., 1983) or four (e.g. Teraoka et al., 1982) formation within the group. Imsamut and Yathakam's (2011) stratigraphy formalizes the four part division suggested informally by others.

Due to the dense forests and discontinuous exposure along the shoreline, coupled with the prevalence of both faults and folds, attempts to calculate the thickness of the Tarutao Group have only achieved rough estimates. Lee (1983) thought the group to be more than 3000 m thick (a 450 m+ lower unit, 1950 m+ middle unit, and a 575 m upper unit), but more recently, estimates have been little more than 1000 m thick. Here we follow the thickness estimates based on the official descriptions and formalization of the formation names by Imsamut and Yathakam (2011). The oldest unit, the Ao Makham Formation, is at least 100 m of thick-bedded brown to gray-brown siltstone and sandstones with minor pebbly conglomerates; the only fossils reproted are rare brachiopods preserved in thin shale units, and these do not yield significant biostratigraphic age constraint (Teraoka et al., 1982; Akerman, 1986; Imsamut and Yathakam, 2011). The next oldest unit, the Ao Tami Formation, is ~450m thick and consists of thick to very thick beds of strongly cross-bedded brown quartz arenite with interbedded gray-green shale (Wongwanich and Burrett, 1983); it is less fossiliferous than the immediately overlying Ao Mo Lae Formation, and both trilobites found in this unit, *Hoytaspis thanisi* Shergold et al., 1988 and *Prosaukia laemensis* n. sp. (=*Prosaukia*? cf. *nema* sensu Shergold et al., 1988), are also found in the succeeding formation (Imasamut and Yathakam, 2011). All Cambrian fauna included herein were collected from the Ao Mo Lae Formation. This formation is estimated to be ~600m thick and comprises purplish red and gray fine purplish red and gray fine to medium-grained quartz arenites with small amounts of interbedded shales. Imsamut and Yathakam (2011) suggested that rhyolitic tuffs were most common in the upper part of this formation, but provided no biostratigraphic or geochronologic evidence for this suggestion. The youngest unit of the Tarutao Group is the Talo Wao Formation which is ~250m thick and mostly consists of thin to medium beds of reddish brown to grayish brown fine-grained sandstone interbedded with micaceous siltstones and shales (Wongwanich and Burrett, 1983; Stait et al., 1984; Imsamut and Yathakam, 2011).

The Tarutao Group's abundance of quartz-rich sandstones with only minor components of shale or siltstone suggest a near-shore shelf depositional history. The Tarutao Group has been suggested to represent a prograding wave-dominated delta with associated barrier bar sands (Lee, 1983). Tabular cross-bedding in the upper part of the Tarutao succession has been interpreted to indicate paleocurrent flow eastward relative to the island's current orientation (i.e. the west side of Tarutao was landward; Bunopas, 1981; Teraoka et al., 1982). This is consistent with the interpretation of Sibumasu's orientation relative to core Gondwana depicted in Fig. 3:3. Shallowing as the delta prograded possibly may have resulted in shallow sub-tidal to intertidal and beach environments for the middle units of the Tarutao Group as indicated by bimodal or inconsistent crossbedding alternating with trough cross-bedding in the Ao Tami Fm. Some combination of sea level changes and subsidence resulted in the water level deepening in the Ao Mo Lae Formation, depositing this formation below wave base, but not below storm base as indicated by the abundant coquina horizons. Towards the top of the Tarutao Group, sediment influx slowed, likely as the location of inflow of clastic sources migrated further mainland. This allowed carbonates to start developing, eventually shifting the entire system to the carbonate platform recorded in the Thung Song Group (Lee, 1983).

Materials and methods

Field work

We made the collections described herein over the course of three separate excursions to Ko Tarutao: 2008, 2016, and 2018. Each excursion made collections of fossils, detrital zircons, and ash beds. Detailed stratigraphic logs were made to record the stratigraphic context of these collections during the 2016 and 2018 excursions, with each bed recorded on the log as a separate collection. During the 2008 excursion, the sampling of beds was haphazard, searching for any beds that might yield fossils. During the December 2016 attention focused on beds with obvious coquina horizons (Wernette et al., 2020) and those closest to ash beds. Many other beds were also sampled, some of which yielded fossils; any bed with fossils was collected to the greatest extent feasible by time, specimen density and quality, specimen diversity, and available sample bags and pack volume. At Ao Mo Lae, three collections were packed and removed from the site prior to recording their stratigraphic position. For this reason, the taxa within each collection may be treated as present within the section and co-occurrences within the collection, but are excluded from the faunal range chart (see Table 2 for each collections without stratigraphic context). The January 2018 excursion, in partnership with IGCP 668, again focused on collecting samples closest to ashes but also made intentional efforts to find fossiliferous horizons that might fill sampling gaps in sections from the 2016 excursion. The 2008 excursion made collections from Ao Talo Topo west (ATTw), Ao Mo Lae (AML), and Ao Talo Udang Section 2 (ATD S2). The 2016 excursion made collections from AML, Ao Phante Malacca (APM), and ATD S2 and S3. The 2018 excursion made collections from AML, Ao Talo Topo (ATT), APM, Laem Hin Ngam (LHN), and ATD S1 and S2. See the Localities section for more information about each. All fossils from Ko Tarutao are disarticulated.

Many fossiliferous beds on Ko Tarutao contain only highly fragmented specimens that are not taxonomically identifiable; all fossiliferous horizons within the sequence contain material that is at least partially fragmented. All fossils on Ko Tarutao occur as internal and external molds with the exception of some Ordovician material that is partially but weakly infilled with an orange oxide, presumed to be limonite. These infilled fossils stand out as orange, typically against a brown matrix. Some molds, especially in the deeply purple sandstones, have very thin coatings of silica, making the fossils stand out white against the purple matrix.

Sample preparation and analysis

The specimens were prepared manually using Dremel vibro and rotary tools, blackened with India ink, whitened with ammonium chloride, and photographed with a Leica stereoscopic camera model MZ16 or M205C. Broken or very fragile samples were glued or impregnated using butvar dissolved in acetone. Molds of each of Kobayashi's (1957) specimens, curated at the University of Tokyo University Museum (UMUT), were made using vinyl polysiloxane in the form of light bodied President Plus by Coltene. All figures and plates were created using Adobe Photoshop CC2017 and Adobe Illustrator CS2. Specimen measurements were taken from the photographs using the ruler tool in Adobe Photoshop CC 2017. External molds are figured in positive relief using image color inversion in Adobe Adobe Photoshop except where use of a latex cast is specified.

Landmark-based morphometric analysis used software created by H. David Sheets as part of the Integrated Morphometrics Package: CoordGen8, BigFix8, Regress8, and PCAGen8 (Webster and Sheets, 2010; available free of charge at http://www.filogenetica.org/cursos/Morfometria/IMP_installers/index.php).

In agreement with Thailand's Department of Mineral Resources, all figured material is reposited at Thailand's Department of Mineral Resources' Geological Referenced Sample Collection (DGSC). Unfigured material, excluding those specimens occurring on slabs with figured material, is reposited at the Cincinnati Museum Center (CMC). The vinyl polysiloxane casts of Kobayashi's (1957) material is reposited in the plastotype collection at CMC.

Localities

Ao Mo Lae (AML)

Ao Mo Lae is the most accessible of the Tarutao localities since a road exists to the beach camp grounds. It does not contain prominent ash beds. At the south end of Ao Mo Lae dark purple sandstones crop out of the pale beach sand with a strike and dip of ~325/25NE. These sandstones become progressively better exposed and more fossiliferous to the west until they form a high cliff at which point the section ends (06°40'13"N, 099°38'02"E), because it is not possible to progress on foot. Due to the geometry of the shoreline and the increasingly elevated beds, walking over the section traveling west proceeds up section.

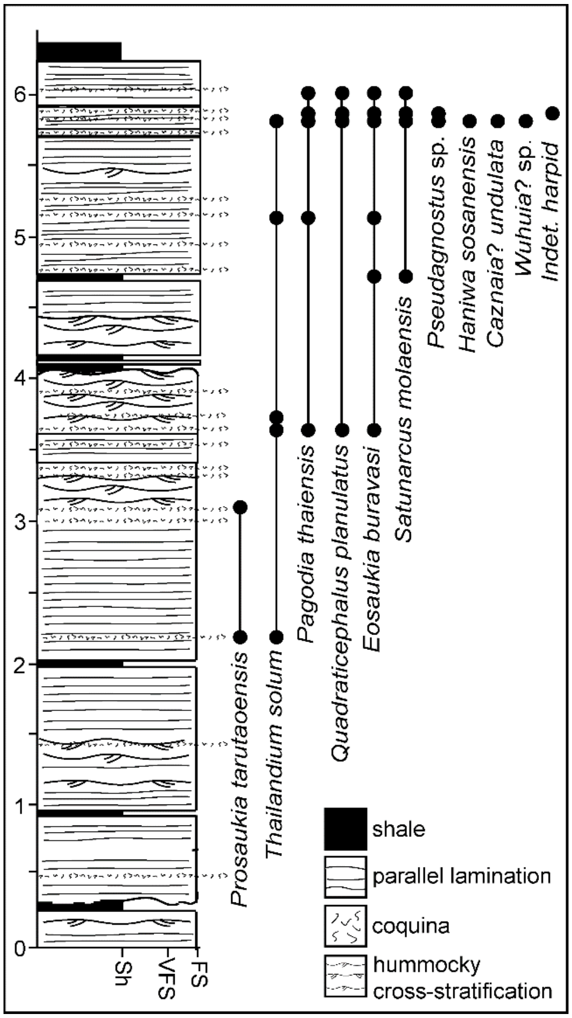


Figure 3:5 Measured section from Ao Mo Lae. Sh = shale; FVS = very fine-grained sand; FS = fine-grained sand. Fossil horizons are at 2.20 m, 3.10 m, 3.62 m, 3.82 m, 4.71 m, 5.17 m, 5.81 m, 5.84 m, and 6.01 m. Modified from Wernette et al., 2020.

The dominant lithology is a fine-grained quartz arenite that is purplish when fresh and dark purplish or reddish gray or brown when weathered. The color is produced by a combination of hematitic and silicic cements (Akerman, 1986). Bed forms are parallel lamination or hummocky cross stratification. Very thin shale beds are irregularly distributed throughout the section. Fossils occur as thin coquinas within the sandstones. The coquinas are identifiable in cross section as pitted horizons and may show bedding-parallel or low-angled cross-bedding. Sporadically secondary silicification of the voids appear white against the purple matrix but does not produce a natural cast. No datable ash beds of sufficient are known from this section. Despite its laterally long outcrop along the coast, the measured section for AML is relatively short, ~6m (Fig. 3:5).

Fossils from Ao Mo Lae are exclusively Cambrian, belonging to the Ao Mo Lae Formation. There are five poorly localized horizons from AML: two from 2008 (AML h1 and h2) and three from 2016 (AML h3–h5). AML h2 correspond to AML horizons 2 in

	AML					ATTw	ATT		ATD		
	h1	h2	h3	h4	h5	------	h1	h2	S2h1	S2h2	S3f
Pseudagnostus sp.						▨					
Tsinania sirindhornae									▨		
Satunarcus molaensis		▨				▨					
Pseudokoldinioidia sardsudae						▨	▨				▨
Pagodia thaiensis			▨			▨		▨			
Parapilekia bunopasi											▨
Asaphellus charoenmiti											▨
Yosimuraspis acufrons											▨
Pseudokainella malakaensis											▨
Haniwa mucronata						▨					
Caznaia ?undulata						▨	▨				
Eosaukia buravasi	▨	▨	▨	▨	▨	▨	▨	▨	▨		
Prosaukia tarutaoensis			▨			▨					
Prosaukia oculata							▨				
Prosaukia sp. 1										▨	
Prosaukia sp. 3			▨								
Sinosaukia sp.									▨		
Thailandium solum		▨	▨	▨	▨	▨					
Pacootasaukia sp.					▨					▨	
Wuhuia ? sp.	▨										
Corbinia perforata											▨
Quadraticephalus planulatus		▨	▨	▨		▨	▨			▨	
Koldinioidia choii							▨				

Table 3:2 Trilobite occurrences within horizons with poor stratigraphic provenance. AML = Ao Mo Lae; ATTw = Ao Talo Topo west; ATT = Ao Talo Topo; ATD = Ao Talo Udang. S1–S3 = sections 1–3 at ATD. S3f = float from ATD S3, not a single sampling horizon as for the other columns. Species are listed in the order in which they occur in the text.

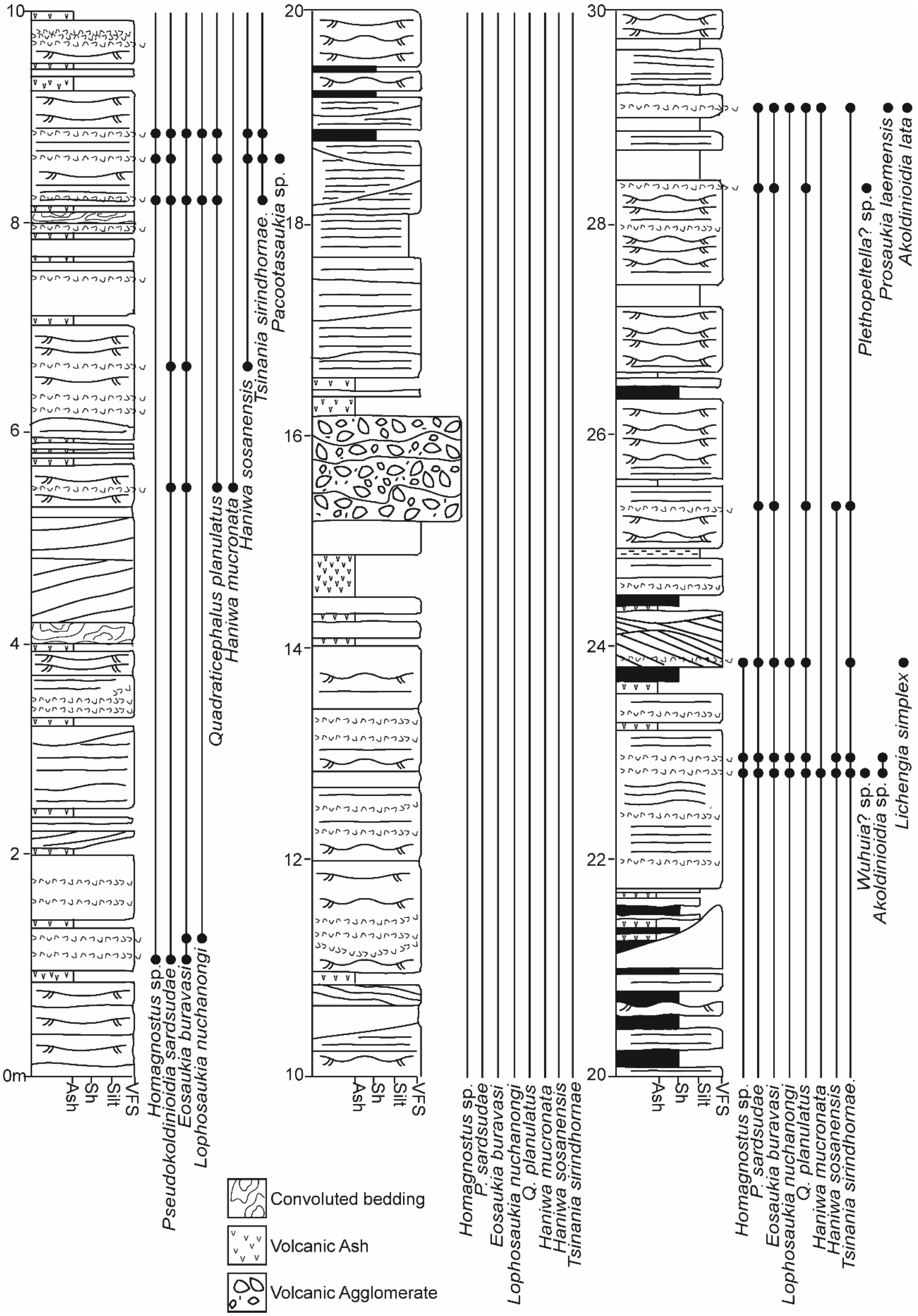
Wernette et al. (2020); AML h2–h5 correspond to horizons of the same name in Wernette et al. (in review). Their faunal assemblages are recorded in Table 2.

Ao Talo Topo (ATT)

Ao Talo Topo corresponds to Shergold et al.'s (1988) locality 6, the only locality from which the authors recorded multiple discrete fossil horizons. Like at Ao Mo Lae (AML), the Ao Talo Topo section of the Ao Mo Lae Formation is highly fossiliferous but also contains several ash beds. It is separated from Ao Mo Lae by only a small inlet with at least one clearly exposed fault between them. The fault recorded at the top of the ATT section strikes ~115°, projecting into the inlet. The dip of the section is consistent with that at Ao Mo Lae.

Despite the proximity of the ATT and AML, the cliffs that form the shoreline make accessing ATT by land immensely difficult. Access by boat is also subject to some difficulties. The boat may either pull up directly against the rock ledges that make up the section (06°40'08"N, 099°37'46"E) or pull up on the gravel and cobble-strewn strip of land between AML and ATT and walk some distance. Both options have moderate innate dangers. Accessing the section is therefore dependent on weather, tides, marine turbulence, and the risk-adverseness of the local boatmen. It is these limitations that prevented work from being done at Ao Talo Topo during the 2016 excursion. The 2008 and 2018 excursions referred to two different sets of outcrops as Ao Talo Topo. The 2008

Figure 3:6 (*Next Page*) Measured section from Ao Talo Topo. Sh = shale; FVS = very fine-grained sand. Fossil horizons are at 0.95 m, 1.10 m, 5.50 m, 6.65 m, 8.20 m, 8.60 m, 8.85 m, 22.78 m, 22.88 m, 23.33 m, 23.89 m, 25.34 m, 27.97 m, 28.37 m, and 29.17 m. See Fig. 5 for additional symbol codes. Modified from Wernette et al., in review.


0m
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4
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18
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22
24
26
28
30
Ash
Sh
Silt
VFS
Homagnostus sp.
Pseudokoldinioidia sardsudae
Eosaukia buravasi
Lophosaukia nuchanongi
Quadraticephalus planulatus
Haniwa mucronata
Haniwa sosanensis
Tsinania sirindhornae.
Pacootasaukia sp.
Homagnostus sp.
P. sardsudae
Eosaukia buravasi
Lophosaukia nuchanongi
Q. planulatus
Haniwa mucronata
Haniwa sosanensis
Tsinania sirindhornae
Homagnostus sp.
P. sardsudae
Eosaukia buravasi
Lophosaukia nuchanongi
Q. planulatus
Haniwa mucronata
Haniwa sosanensis
Tsinania sirindhornae.
Wuhuia? sp.
Akoldinioidia sp.
Lichengia simplex
Plethopeltella? sp.
Prosaukia laemensis
Akoldinioidia lata
Convoluted bedding
Volcanic Ash
Volcanic Agglomerate

locality was subsequently designated ATT west, and it is not considered part of the same section (see below).

Ao Talo Topo is a relatively long and continuous section of sandstone, siltstone, shale, and volcaniclastic deposits (Fig. 3:6). The sandstone has a similar color, texture, and hardness to that at AML, and the fossils occur in similar coquina horizons. ATT has more tabular and trough cross-bedded sandstones, mostly in the lower half, while AML is more dominated by hummocky and parallel laminated sandstones, which also occur at ATT. The bedding surfaces at ATT are often irregular or wavy. The top half of the section is finer grained with a higher proportion of silt stones and shales. The bottom third of the section has multiple convoluted beds. Volcanic tuffs occur throughout, but they are thickest in the middle of the section which also contains a thick volcanic agglomerate with irregular internal bedding suggesting at least three separate pulses of deposition.

This section terminates at a fault (06°40’09”N, 099°37’49”E) as in Shergold et al.’s (1988) stratigraphic log for locality 6. About 1.5m above this fault we collected a volcanic ash sample and two fossiliferous horizons (ATT h1 and ATT h2) but did not measure an additional section.

Ao Talo Topo west (ATTw)

The 2008 excursion sampled a single fossiliferous sandstone and an ash bed from Ao Talo Topo west (06°39’40”N, 099°37’04”E), a section of the Ao Mo Lae Formation. The ash did not yield a sufficient zircon sample to date, but the sandstone yielded a rich fossil assemblage. The lithology and faunal assemblage are most similar to the sections from Ao Talo Topo, and Ao Mo Lae. Like Ao Talo Topo, Ao Talo Topo west can only be reached by boat.

Laem Hin Ngam (LHN)

Laem Hin Ngam (06°39’19”N, 099°36’54”E) is a short distance south of Ao Talo Topo (ATT) west and also part of the Ao Mo Lae Formation. Like ATT and ATT west, it is only accessible by boat. The bottom half of this short section consists of laminated purple sandstones (Fig. 3:7). The top half has two thick ash beds interbedded with tabular and hummocky cross-stratification along irregular bedding planes. The sandstones are purplish brown rather than the deeper purple of ATT and Ao Mo Lae. Fossils are found in weakly developed coquina horizons in the bottom portion of the section. Higher concentrations of oxide minerals impart an orangish staining to some internal and external molds. The fossiliferous horizons at 1.54 m and 2.85 m contain very small specimens with the exception of a single large librigena fragment in the 2.85 m horizon.

Ao Talo Udang (ATD)

The Tarutao Group is exposed at the southeast end of Ko Tarutao in a bay called Ao Talo Udang (ATD). Both the Ao Mo Lae Formation and the Talo Wao Formation crop out at Ao Talo Udang. As between Ao Talo Topo and Ao Mo Lae, however, faults and covered shorelines split this locality up into shorter, discontinuous sections. There are three

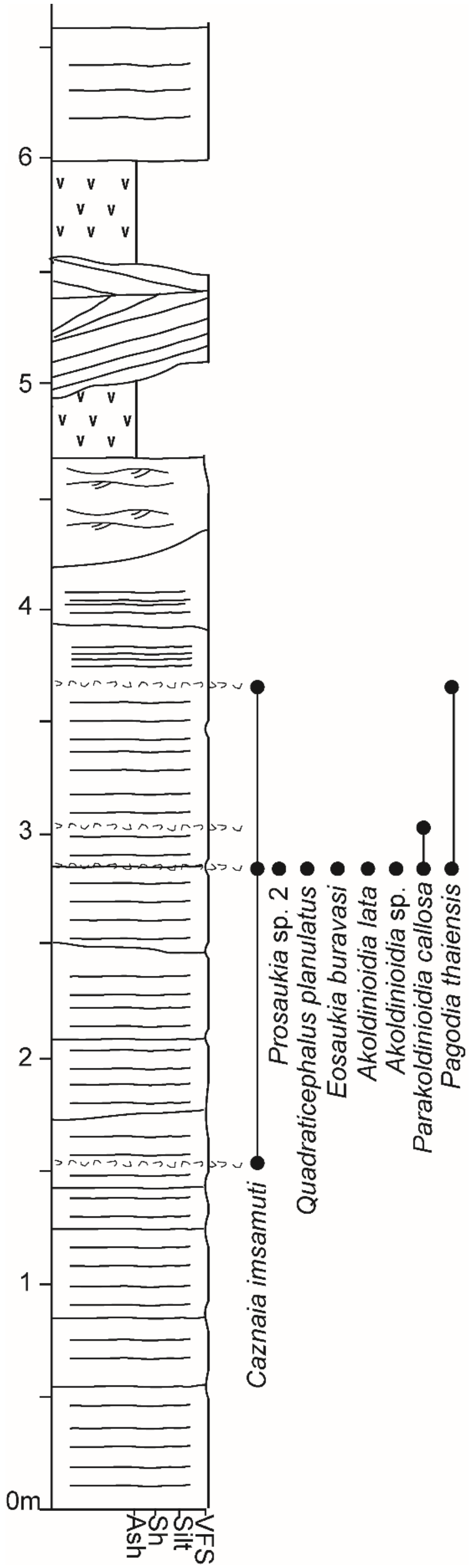


Figure 3:7 Measured section from Laem Hin Ngam. Sh = shale; FVS = very fine-grained sand. Fossil horizons are at 1.54 m, 2.85 m, 3.05 m, and 3.69 m. See Figs 4 and 5 for symbol codes.

sections (S1–S3 from west to east) at ATD: S1 and S2 are of the Ao Mo Lae Formation and are both Cambrian. S3 is from the Talo Wao Formation and is Ordovician.

ATD S1 (06°32’09”N, 099°40’47”E)

ATD S1, the westernmost section from Ao Talo Udang, is relatively long (20m) with abundant volcanic tuffs in the upper and lower portions and fossils only in the lower middle portion (Fig. 3:8). Due to a fault between this section and ATD S2, and the lack of evident correlative marker beds across the fault, its stratigraphic position relative to S2 can only be determined based on dating.

The base of this section is at the top of a thick (>5m) nearly homogeneous outcrop of thinly bedded, very fine to fine-grained purple sandstone. ATD S1 has more variety to the sandstone colors than at Ao Talo Topo, Ao Mo Lae, or Laem Hin Ngam, including red, brown,

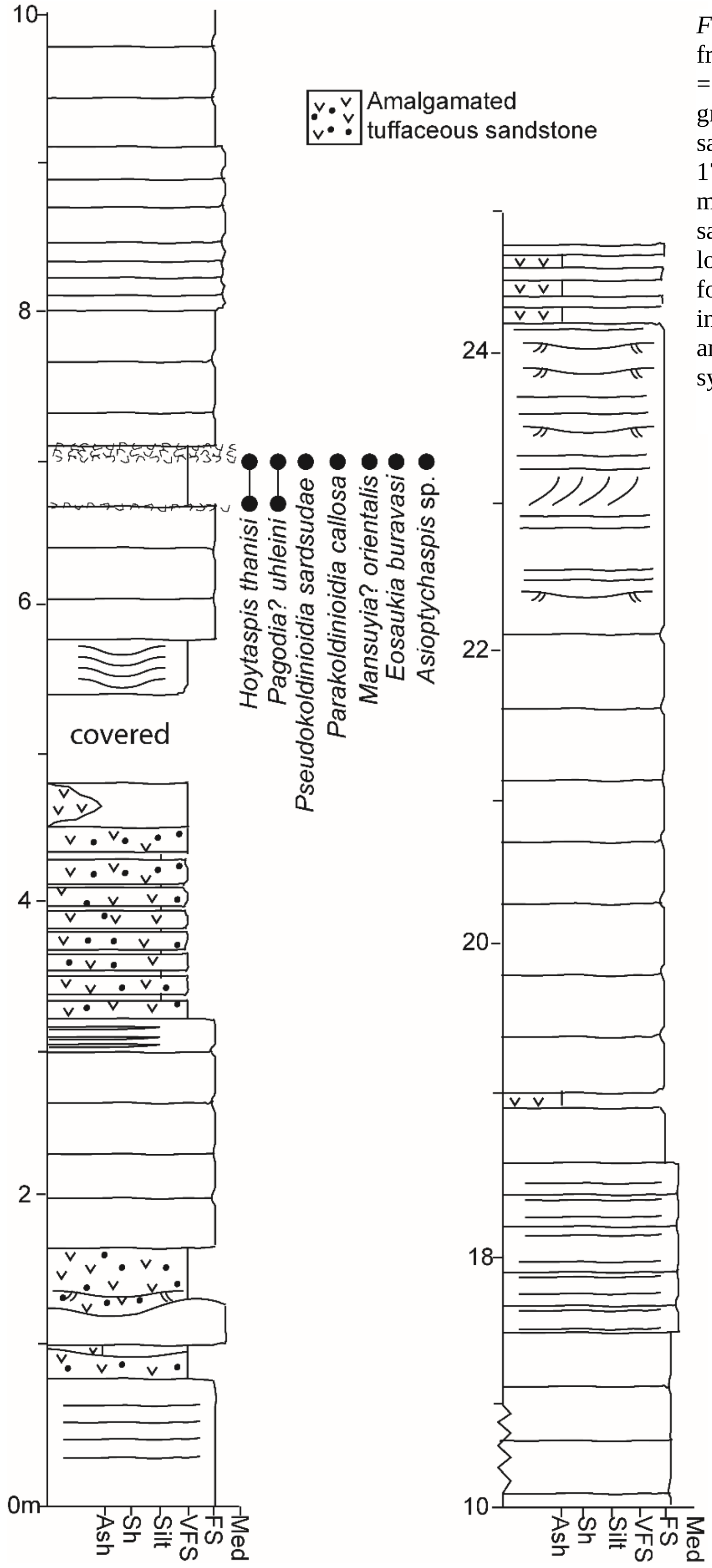


Figure 3:8 Measured section 1 (S1) from Ao Talo Udang. Sh = shale; FVS = very fine-grained sand; FS = fine-grained sand; Med = Medium-grained sand. The break in the scale from m to 17 m abbreviates an interval of massive medium-thick bedded sandstones, indistinguishable on this log from the units before or after; no fossils or ash beds were found in this interval. Fossil horizons are at 6.65 m and 7.00 m. See figs 4 and 5 for symbol codes.

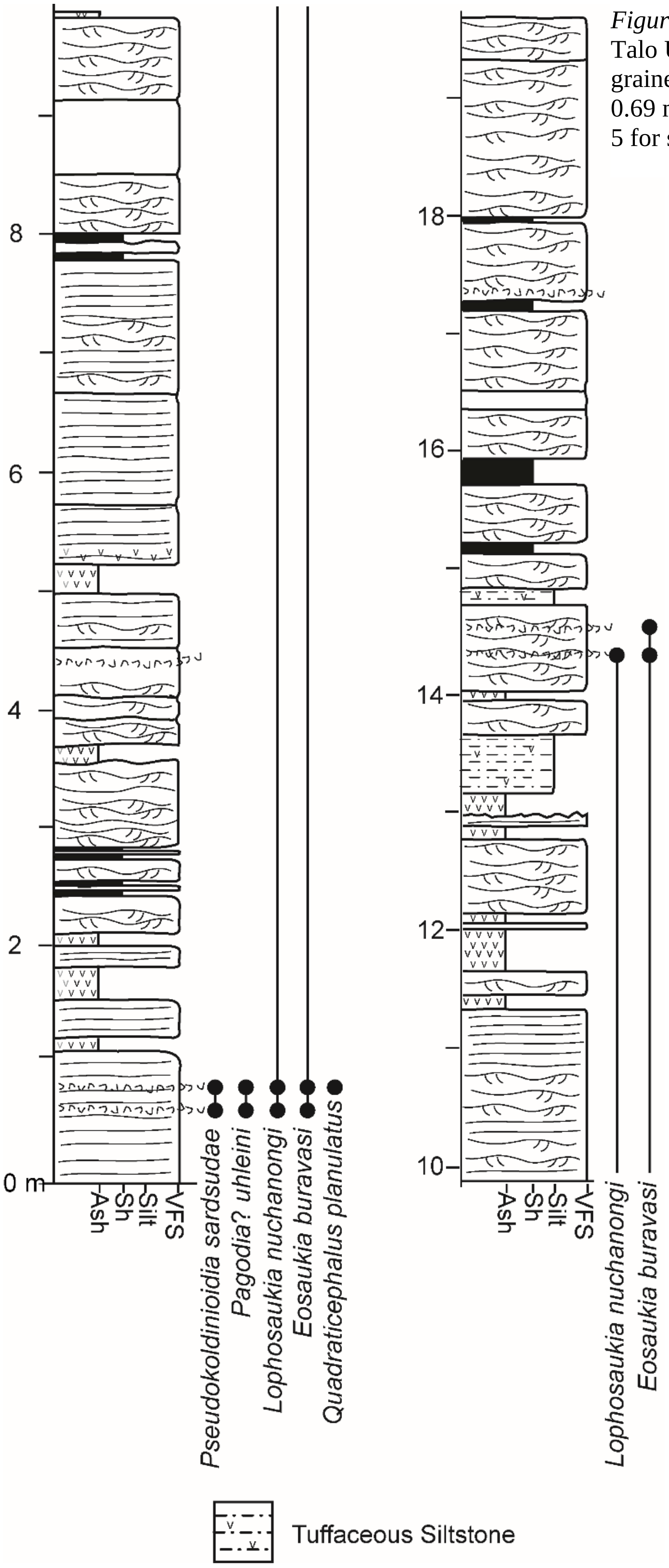


Figure 3:9 Measured section 2 (S2) from Ao Talo Udang. Sh = shale; VFS = very fine-grained sand. Fossil horizons are at 0.52 m, 0.69 m, 14.29 m, and 14.5 m. See Figs 4 and 5 for symbol codes.

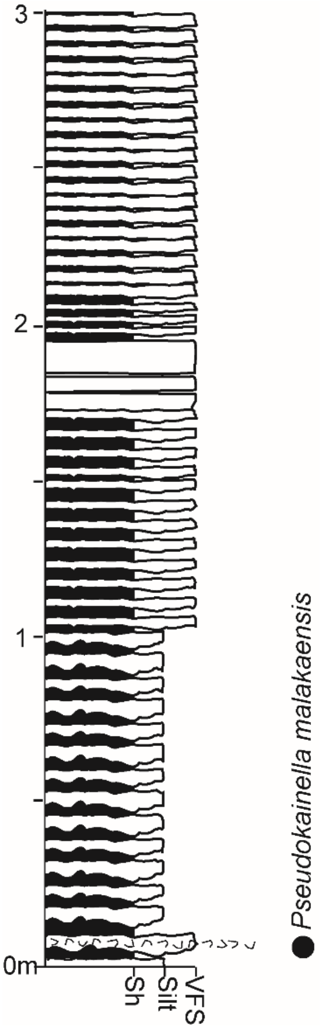


Figure 3:10 Measured section 2 (S2) from Ao Talo Udang. Sh = shale; VFS = very fine-grained sand.

or light purple. While sandstones may be massive and thickly bedded over long intervals, especially in the middle of the section, they may also be laminated, have hummocky cross-stratification, or be interbedded with thin siltstones or tuffs. Where this interbedding occurs, beds are often irregular and wavy with one or both lithologies being laterally discontinuous. Sandstones and ashes are so thinly laminated and of mixed lithology in some units, that the term amalgamated tuffaceous sandstone is used to refer to the whole interval.

There are only two fossiliferous beds known from ATD S1. The 6.65 m horizon is not as densely fossiliferous as coquinas at other localities; as at Laem Hin Ngam the fossils tend to be orange against a purplish brown or reddish matrix. The 7.00 m bed is unique relative to other fossiliferous beds from the Ao Mo Lae Formation, because the fossils are haphardly distributed throughout a brown, very fine grained, poorly cemented bed, occurring at various angles to bedding. This is the only horizon from the Ao Mo Lae Formation with relatively widespread distortion of fossils, though the deformation is not intense. At least part of the distortion is compressional; fossils at the highest angle to bedding are the most deformed. These fossils also have a more finely preserved texture than in most coquina horizons.

ATD S2 (06°32’07”N, 099°40’51”E)

ATD S2 is the next outcrop east of ATD S1. The section is mostly sandstones with some shales and volcanic tuffs (Fig. 3:9). Hummocky cross stratification is common in this section with short intervals of parallel laminated beds. The sandstones vary from light gray-purple to dark purple with the light color being more prevalent. The internal and external molds preserved in coquina horizons are often stained by a thin mineral film. In light purple sandstones this staining is most often orange from oxide minerals; in darker purple sandstones the staining is typically white from silica.

ATD S3 (06°32’06”N, 099°41’08”E)

ATD S3 is to the east of ATD S2, separated by a boulder strewn costal inlet with no rock exposure. It is part of the Talo Wao Formation, but the exposure and fossil yield is better at Ao Phante Malacca. The section is dominated by interbedded very fine sandstones and mudstones (Fig. 3:10). The only fossiliferous horizon is low in the section. It is a buff-colored very fine-grained sandstone with orange, oxidized staining on the fossils. This bed has very low trilobite diversity, yielding only a single type of librigena, and brachiopods. Despite the poor fossil quality of the *in situ* material during the 2016 excursion, float material in the area yields a much richer faunal assemblage of both Cambrian and Ordovician fossils (Table 2, ATD S3f). Float blocks are commonly ~30 cm in diameter and contain fossils heavily infilled with an orange oxide mineral, most likely limonite.

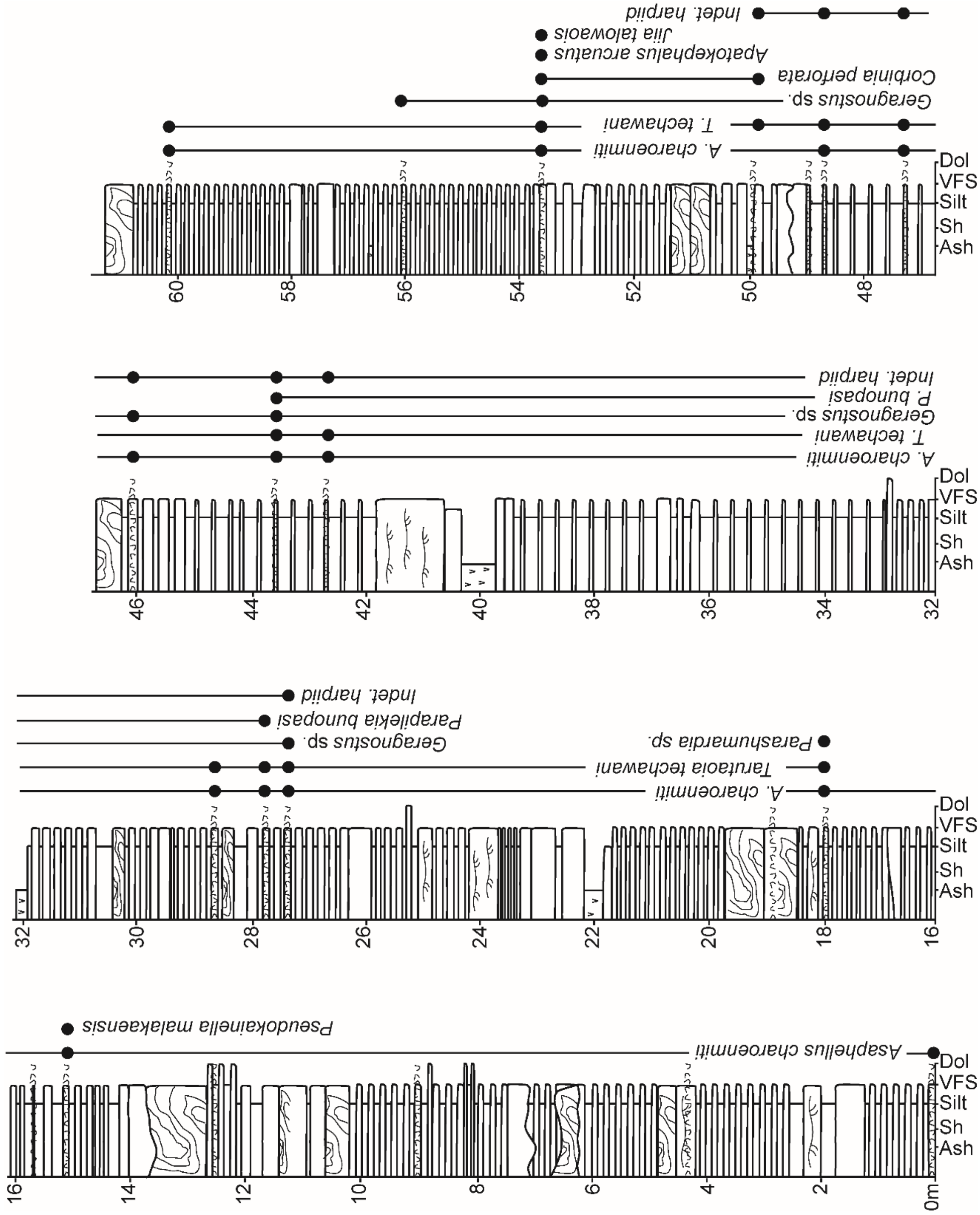

Indet. harpid
Jiia talowaois
Apatokephalus arcuatus
Corbinia perforata
Geragnostus sp.
T. techawani
A. charoenmiti
Dol
VFS
Silt
Sh
Ash
60
58
56
54
52
50
48
Indet. harpid
P. bunopasi
Geragnostus sp.
T. techawani
A. charoenmiti
46
44
42
40
38
36
34
32
Indet. harpid
Parapilekia bunopasi
Geragnostus sp.
Parashumardia sp.
Tarutaoia techawani
A. charoenmiti
30
28
26
24
22
20
18
16
Pseudokainella malakaensis
Asaphellus charoenmiti
14
12
10
8
6
4
2
0m

Figure 3:11 (*Previous page*) Measured section from Ao Phante Malacca. Sh = shale; VFS = very fine-grained sand; Dol = dolostone. The fossiliferous horizons are at 0.05 m, 15.10 m, 18.00 m, 27.35 m, 27.80 m, 28.70 m, 42.75 m, 43.40 m, 46.05 m, 47.30 m, 48.65 m, 49.90 m, 53.65, 56.00 m, and 60.20 m. See Figs 4,5, and 10 for symbol codes.

Ao Phante Malacca (APM)

Ao Phante Malacca is one of the longest, best exposed, and most accessible continuous sections on Ko Tarutao (06°42’14”N, 099°38’42”E). Most of the fossil record for the Talo Wao Formation comes from this locality as do the only known Ordovician ash beds. It is directly north of the inlet harboring the island’s main pier. There are small faults cross-cutting APM, but they have sufficiently small offset and there are sufficiently distinct marker beds to correlate strata that the section may be continued across faults.

Most of this section is comprised of thinly interbedded brownish gray sandstone and siltstone. The interbedded horizons are discreet, and the fossils are known only from the sandstone. Massive or hummocky cross-stratified sandstones may form thicker units. Prominent convoluted beds with ball-and-pillow structures occur periodically throughout the section as do calcareous beds. Carbonate lenses are common in the bottom quarter of the section, particularly around and within the thick convoluted unit at 13 m. Weathered exposures of these lenses reveal dense fossil hash, but both dissolution and manual preparation was unsuccessful in recovering the fossils. Sandstones at APM have calcareous cement which is rare elsewhere in the Tarutao Group.

Numerous thin ash horizons occur throughout the section, but the most prominent ashes are restricted to the middle portion of the section which yields Tremadocian fossils. The lower portion of the section has a poor fossil record, but fragments were found up to

14 m that suggest a possible saukiid assemblage. *Asaphellus* occurs from the lowest horizons upwards in the section. While a predominantly Ordovician genus that is unlikely to co-occur with saukiids, *Asaphellus* occurs in the Cambrian of China (Zhou and Zhen, 2008). Fossils throughout the section occur as internal and external molds with an orange, limonite film. In addition to the trilobite and brachiopod fauna, the top 30 m of this section contain abundant disarticulated, thin-walled crinoid columnals.

Biostratigraphic correlation

The Tarutao Group is late Furongian and Tremadocian. The discontinuous nature of the sections on Ko Tarutao inhibits constructing a consolidated range chart for all taxa and the establishment of trilobite zones for Sibumasu. Correlation with the trilobite successions of other northern Gondwanan terranes is currently only moderately well-resolved (Fig. 3:12). The endemism of the fauna offers additional correlation difficulties beyond the genus level; for many taxa the genus level is insufficient to differentiate biozones from late Jiangshanian through Late Stage 10 (e.g. *Prosaukia* Ulrich and Resser, 1933; Shergold, 1975). Geochronologically dating the volcanic tuffs found in each section and comparing the fauna with recent collections made from Myanmar will assist future endeavors to this goal.

There is no clear faunal succession within any succession, although recovered diversity does change among beds. There are general trend of fauna becoming more diverse (Ao Phante Malacca, Ao Talo Topo, Ao Mo Lae) or less diverse (Ao Talo Udang S2) over the course of a section. Laem Hin Ngam and Ao Mo Lae are short sections, but Ao Talo Topo is over 29 m with a prolonged, middle unfossiliferous interval across

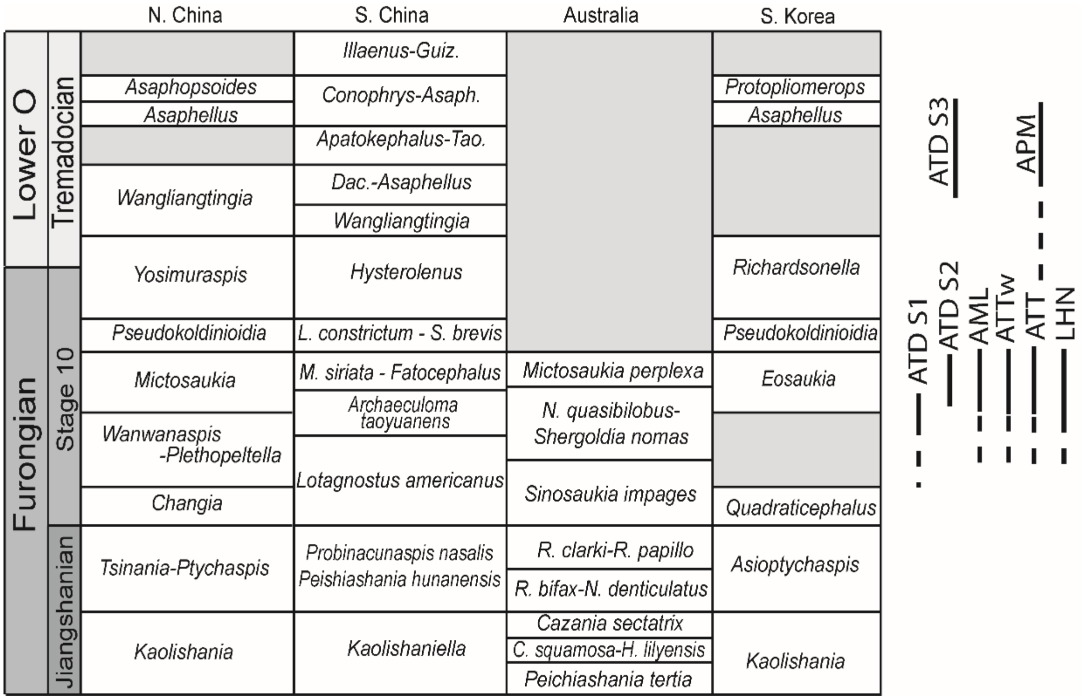


Figure 3:12 Trilobite zones from Cambro-Ordovician northern Gondwanan terranes. Some genera have been abbreviated in the chart for readability; the full names are: *Caznaia squamosa, Hapsidocare lilyiensis, Leiostegium constrictum, Mictosaukia striata, Neoagnostus denticulatus, Neoagnostus quasibilobus, Rhaptagnostus clarki, Rhaptagnostus papillo, Rhaptagnostus bifax, Shenjiania brevis, Dactyocephalus-Asaphellus, Apatokephalus-Taoyuania, Conophrys-Asaphopsoides, and Illaenus-Guizhouhystricus*. Vertical axis not to scale. The range given for each section is the possible range within which the section occurs; not the assumed duration of the section. ATT(w) = Ao Talo Topo (west); APM = Ao Phante Malacca; ATD = Ao Talo Udang; AML = Ao Mo Lae; LHN = Laem Hin Ngam. The South Korean biozones are for the Taebaek Group. Zone correlations are compiled from Choi et al., 2016 and

which there are no perceptible changes in fauna. Ao Talo Udang S1 is likely the oldest locality since *Mansuyia orientalis*? and *Hoytaspis thanisi* are not found at other localities, and *Hoytaspis* occurs in the underlying Ao Tami Formation (Imsamut and Yathakam, 2011). It is not, however, significantly younger, as it also contains species found in the other localities. Most of the sections (Laem Hin Ngam, Ao Talo Udang S2, Ao Mo Lae, Ao Talo Topo, and Ao Talo Topo west) have similar assemblages, and their relative ages cannot be determined without further data, such as from geochronology. Ao Talo Udang S3 correlates with the Ao Phante Malacca section based on fauna and lithology. These are indisputably the youngest sections as Ao Phante Malacca has fossils not found outside of the Tremadocian.

At each of Ao Mo Lae, Ao Talo Topo, Ao Talo Topo west, and Laem Hin Ngam the faunal assemblage is strongly suggestive of the middle of Cambrian Stage 10 (Fig 3:12). There are strong correlations with both the *Quadraticephalus* and *Eosaukia* zones of South Korea, but there is greater support for correlation with the latter. *Haniwa sosanensis* (pervasive through most of Ao Talo Topo and at the top of Ao Mo Lae) is known only from the *Quadraticephalus* Zone (Park and Choi, 2011), which is defined by the first occurrence of *Lophosaukia orientalis,* a different species of *Lophosaukia* than is found throughout the section at both Ao Talo Topo and Laem Hin Ngam. The *Quadraticephalus* zone also includes species of *Quadraticephalus*, *Koldinioidia*, and *Tsinania*. However, *Eosaukia buravasi* is pervasive in all Ao Mo Lae Formation localities, including where it cooccurs with *Haniwa sosanensis*, and, in Korea, *Eosaukia* is only known from the *Eosaukia* Zone (Choi et al., 2016). *Eosaukia* has a longer reorded range in north and south China, but is not known from the lower portion of Stage 10 (Zhou and Zhen, 2008). The *Eosaukia* Zone is also rich in other dikelocephalid trilobites, *Quadraticephalus*, and *Pagodia*. *Lichengia simplex*, which occurs at the top of Ao Talo Topo, is from the *Neoagnostus quasibilobus–Shergoldian nomas* Zone of Australia (Shergold, 1975). Its occurrence supports an age equivalent to Korea’s *Eosaukia* Zone as it is correlative with this Australian Zone. The occurrence of *Haniwa mucronata* throughout the Ao Talo Topo section provides another species-level correlation with the fauna of Australia’s *Shergoldia nomas* Zone (Shergold, 1975). The shared Thai and

Australian presence of *Lichengia simplex* links the Tarutao fauna to Australia's Pacoota Sandstone Assemblage 1 which is interpreted as mid to late Payntonian (Shergold, 1991). North China's *Parakoldinioidia callosa* Qian, 1985b, found at Ao Talo Udang S1 and Laem Hin Ngam, is also from the middle to upper Stage 10 interval and correlative with the *Shergoldia nomas* Zone. Given the strong association with this middle stage 10 interval, correlating with the *Mictosaukia* zones of north and south China, the *Shergoldia nomas* Zone of Australia, and the *Eosaukia* Zone of South Korea, we suggest this as the most likely age for the fossiliferous localities of the Ao Mo Lae Formation.

The biostratigraphic correlation of Ao Mo Lae, Ao Talo Topo, Ao Talo Topo west, Ao Talo Udang S1 and S2, and Laem Hin Ngam results in required extensions to the global ranges of *Haniwa sosanensis*, *Caznaia*, and *Akoldinioidia lata*, which are currently only known from the latest Jiangshanian (Shergold, 1975; Sohn and Choi, 2007; Park and Kihm, 2015a).

Ao Talo Udang S1 contains a unique "late" Cambrian assemblage relative to the previously noted localities. There is some overlap (*Eosaukia buravasi*, *Parakoldinioidia callosa*, and *Pseudokoldinioidia sardsudae*), that suggests the age cannot be significantly different, but the dominant species in this locality, *Hoytaspis thanisi*, *Mansuyia*? *orientalis*, and *Pagodia*? *uhlieni*, are not found in the other sections, excluding the base of Ao Talo Udang S2. *Hoytaspis thanisi* was one of two species also found in the underlying Ao Tami Formation (Imsamut and Yathakam, 2011), suggesting that Ao Talo Udang S1 may be the lowest section of the Ao Mo Lae Formation described herein. However, the other species that occurs in both formations, *Prosaukia* sp. 2, occurs at

Laem Hin Ngam and Ao Talo Topo but not Ao Talo Udang S1. Therefore one or the other of these species apparently has a relatively long range, assuming Ao Talo Udang S1 is a different age than the other sections, as indicated by biostratigraphic correlation with other terranes. *Hoytaspis* occurs in the early Sunwaptan (~Jiangshanian) of North America (Ludvigsen and Westrop, 1983), which led Shergold et al. (1988) to suggest it is older than the fauna in the other localities. *Mansuyia orientalis*'s occurrence in the *Kaolishania* Zone of North China (Park et al., 2014), is also significantly older than the age suggested by co-occurrent trilobites that occur in other Tarutao localities (*Eosaukia buravasi, Parakoldinioidia callosa,* and *Pseudokoldinioidia sardsudae*). If the somewhat tentative species assignment, *Mansuyia orientalis*? is correct, then it considerably extends this species' global range to the middle of Cambrian Stage 10. The occurrence of the endemic *Pagodia*? *uhlieini* and of *Asioptychaspis* sp. offer little stratigraphic constraint to Ao Talo Udang S1, because at the genus level both *Pagodia* and *Asioptychaspis* are known from the Jiangshanian onwards (Shergold, 1975; Park and Kihm, 2015). The conflict between the significantly older date suggested by *Mansuyia* and *Hoytaspis* and the correlation based on taxa shared with other localities from the Ao Mo Lae Formation will be addressed when dates from ash beds become available.

Though Ao Talo Udang S1 and S2 are not a continuous section, the presence of *Pagodia*? *uhleini* in the basal part of Ao Talo Udang S2 suggests that the unexposed region between the two sections may not contain a discontinuity that significantly effects stratigraphy. Apart from this species, the Ao Talo Udang S2 assemblage is similar to that at Ao Talo Topo, Ao Mo Lae, and Laem Hin Ngam.

The fauna at Ao Talo Udang S3 and Ao Phante Malacca are exclusively endemic at the species or genus level. The lowest occurring genera at Ao Phante Malacca (*Asaphellus, Pseudokainella*, and *Parapilekia*) may be either latest Cambrian or Ordovician (Zhou and Zhen, 2008). Field notes of saukiid fragments in this lower portion suggest that it is Cambrian, but no specimens confirm this. Only the genera in the upper portion of the section (*Jiia* and *Apatokephalus* are unreported outside the Tremadocian. *Jiia* is known only in the middle to upper Tremadocian (Zhou and Zhen, 2008). Therefore the uppermost Ao Phante Malacca section appears to be of middle to late Tremadocian age while the lower-most portion of the section is possibly latest Furongian. The conodont fauna of the Talo Wao Formation support this Tremaocian age (Teraoka et al., 1982) as do Tremadoc conodonts at the base of the conformably overlying Thung Song Group (Agematsu et al., 2008).

Systematic paleontology

The following descriptions use the morphological terminology outlined in Whittington and Kelly (1997). References to glabellar length exclude the occipital ring. Dorsal views of specimens were photographed with the palpebral lobes in the horizontal plane as feasible given the surrounding matrix and condition of the fossil (Whittington, 1997). The use of trilobite orders follows Adrain (2011) with the exception of treating Agnostida as a separate order (Paterson, 2019). Authorship of the systematics section and all new taxa is limited to Wernette and Hughes.

Order AGNOSTIDA Salter, 1864

Family AGNOSTIDAE M'Coy, 1849

Subfamily AGNOSTINAE M'Coy, 1849

Genus *Homagnostus* Howell, 1935

Type species.—Agnostus pisiformis obesus Belt, 1867 from the Lower Lingula Flags, Wales.

Remarks.—Homagnostus, Oncagnostus Whitehouse, 1936, *Micragnostus* Howell, 1935, and *Geragnostus* Howell, 1935 all share similar overall morphologies to the point that they have regularly been confused, misidentified, and variably considered subgenera of each other or *Agnostus* Brongniart, 1822 (Pratt, 1992; Shergold et al., 1990; Choi et al., 2004). Based on the definitions provided in the treatise (Shergold and Laurie, 1997), however, definable differences enable their consistent differentiation. *Micragnostus* is the only of these genera with a parallel-sided glabella and has a pygidial axis short enough that the pygidial acrolobe has little to no posterior tapering. *Homagnostus* is the only genus on this list with a preglabellar median furrow although it may be significantly reduced even to the point of near effacement or a vestigial nature as for *Homagnostus obesus* (Belt, 1867; Choi et al., 2004). F3 of *Geragnostus* is distinctly curved, leaving a subovate anterior lobe. *Oncagnostus* has no preglabellar median furrow, unlike *Homagnostus*, and a pygidial axis *terminating* against or near the posterior border furrow.

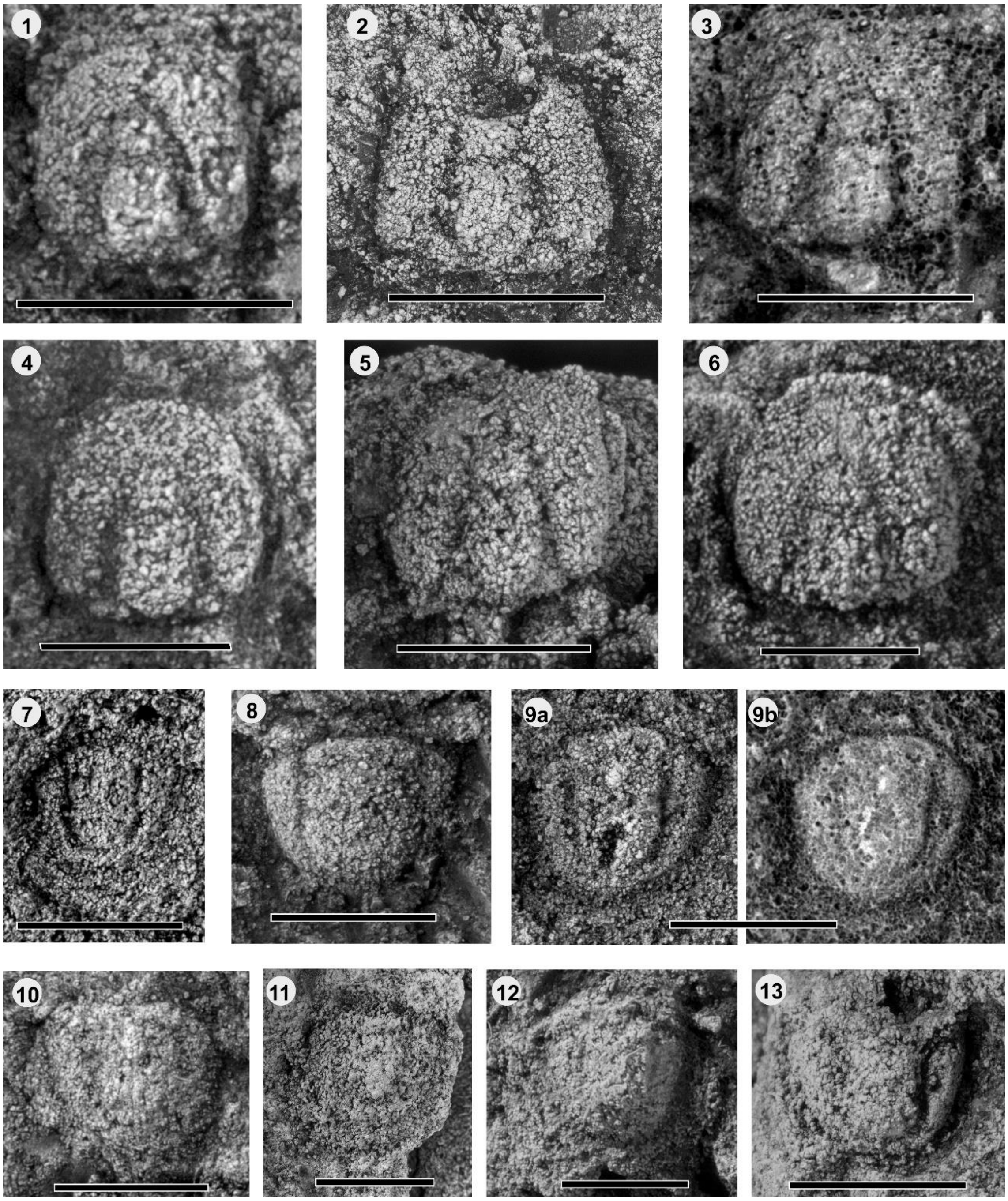


Figure 3:13 *Homagnostus obesus* (Belt, 1867). **(1)** _33, cephalon, ATT 22.78 m; **(2)** _13, cephalon, ATT 23.89 m; **(3)** _44, cephalon, ATT 22.88 m; **(4)** _2, cephalon, ATT 8.85 m; **(5)** _1, cephalon, ATT 0.95 m; **(6)** _86, cephalon, ATT 22.78 m; **(7)** _7, pygidium, ATT 22.78 m; **(8)** _9, pygidium, ATT 8.60 m; **(9)** _2, pygidium, internal (a) and external (b) molds, ATT 8.20 m; **(10)** _65, pygidium, ATT 22.88 m; **(11)** _96, pygidium, ATT 22.78 m; **(12)** _58, pygidium, ATT 22.88 m; **(13)** _42, pygidium, ATT 22.78 m. All internal molds unless otherwise indicated. Scale bars = 2 mm. ATT = Ao Talo Topo.

Homagnostus obesus (Belt, 1867)

Fig. 3:13

1867. *Agnostus pisiformis* var. *obesus* Belt, p. 295, pl. 12, fig. 4.

1877. *Agnostus tumidosus* Hall and Whitfield, p. 231, pl. 1, fig. 32.

1935b. *Homagnostus obesus* (Belt, 1867); Howell, p. 15, fig. 12.

?1957. agnostid gen. et sp. indet; Kobayashi p.380, pl. 4 fig. 8.

1958. *Agnostus* (*Homagnostus*) *obesus* Belt; Henningsmoen, p. 182, pl. 5, figs 13–16.

1988. *Micrgnostus* sp; Shergold et al. p. 305, fig. 3.a-d.

1992. *Homagnostus obesus* (Belt); Pratt, p. 27, pl. 1, figs 26–38 (for additional synonymy).

1994. *Connagnostus lubricus* Qian, p. 43, pl. 1, figs 5–8.

2004. *Homagnostus obesus* (Belt); Choi et al., p. 165, fig. 4.1–8 (for additional synonymy).

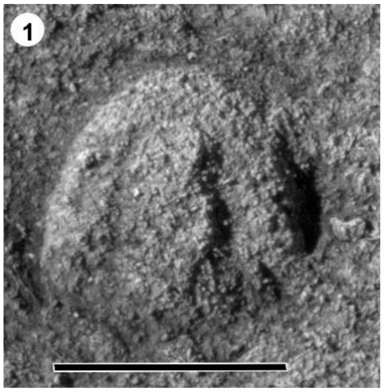
Occurrence.—Ao Talo Topo 0.95–23.89 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Cambrian Stage 10.

Material.— 15 cephala from Ao Talo Topo (ATT) 0.95 m (_1), 8.85m (_2), 22.78 m (_3, 33, 69, 86), 22.88 m (_20, 28, 41, 44, 48, 59, 61), and 23.78 m (_9, 13). Seven pygidia from ATT 8.20 m (_2 – internal and external mold), 8.60 m (_9), 22.78 m (_7, 42, 96), and 22.88 m (_58, 65). All internal molds unless otherwise indicated.

*Remarks.—*The agnostids collected from Ao Talo Topo 0.95–23.89 m are morphologically indistinguishable from those Shergold et al. (1988) described from locality 6 (Ao Talo Topo) and assigned by them to *Micragnostus* Howell (1935). The assignment to *Micragnostus* includes their caveat that these specimens belong to a subgroup of *Micragnostus* that has a posteriorly curving anterior glabellar furrow (F3), which is contrary to the description of *Micragnostus* given in Shergold and Laurie (1997); they state that *Micragnostus* has a straight F3. Even more problematic for a *Micragnostus* designation, the Tarutao specimens have a distinctly anteriorly tapering glabella while the *Micragnostus* glabella is parallel-sided. Also the pygidial axis reaches nearly to the posterior border furrow whereas *Micragnostus* is restricted to forms possessing a short axis. The genus *Micragnostus* has been extensively used to include numerous agnostids with anteriorly narrowing glabellae (e.g. Shergold, 1991), and it should be revised either to a broader definition or restricted to only those species with parallel-sided glabellae. Such revision is outside the scope of this paper.

Pratt (1992) revised *H. obesus* to encompass an array of intraspecific variation and provided an extensive synonymy list. The single diagnostic trait for the species is that the pygidium's anterior lateral axial furrows (F1) do not connect across the axis. The state of preservation of the Thai material makes it difficult to determine if there is a faint connection between the anterior pair of furrows, but if any median furrow segment exists it is significantly shallower than the lateral portions. The anterior lateral axial furrows are obliquely oriented, consistent with the condition in *Homagnostus obesus*, and the axial node sits just anterior to F2. This species is uncharacteristic of *Homagnostus* in that the median preglabellar furrow, while visible in some individuals, may be greatly reduced or absent in others. In this “vestigial” form of the furrow (Choi et al., 2004), it is visible only as a faint ‘v’ or impression at its most posterior end and lacks expression for most of its length. Specimens from the Tarutao Group, as well as those from Korea’s Machari Formation (Choi et al., 2004), tend to have an exceptionally reduced median preglabellar furrow. Another source of intraspecific variation is the relative width and length of the pygidial axis. While consistently longer than in *Micragnostus*, the axis may be distinctly separated from the pygidial border or nearly touching it. Only one specimen from Tarutao, found in Ao Talo Topo horizon 8.60m, displays the latter condition. The pygidial axis is so much wider and longer than the others, that it could easily be mistaken as a separate species if not for the more continuous intraspecific variation seen in other locations (e.g. the Rabbitkettle Formation; Pratt, 1992). Variation in axial dimension has no obvious connection to stratigraphy or size; specimens of the same size or from the same horizon may have either a wide or narrow axis (Pratt, 1992).

The indeterminate agnostid figured by Kobayashi (1957) is of insufficient preservational quality to confidently assign a species or even genus, but give its co-occurring taxa and apparent lack of median preglabellar furrow, it most likely is a specimen of *H. obesus*.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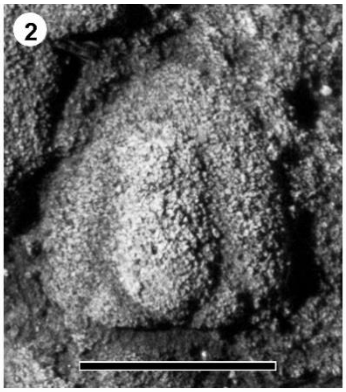
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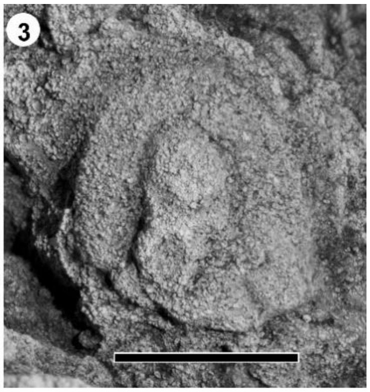
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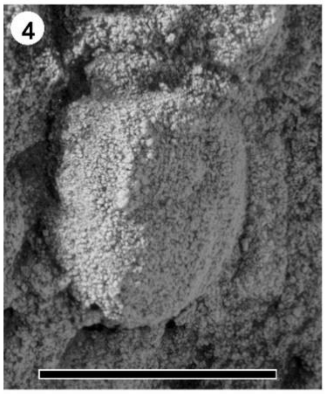
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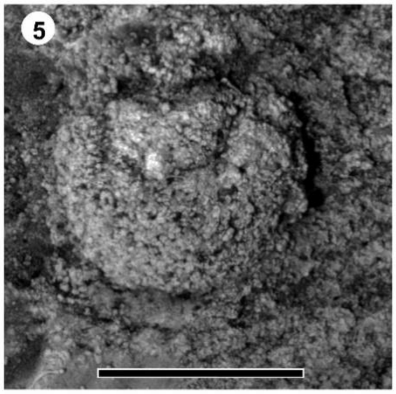
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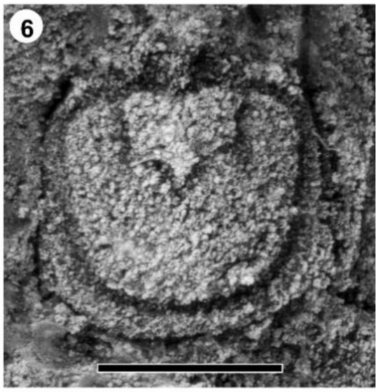
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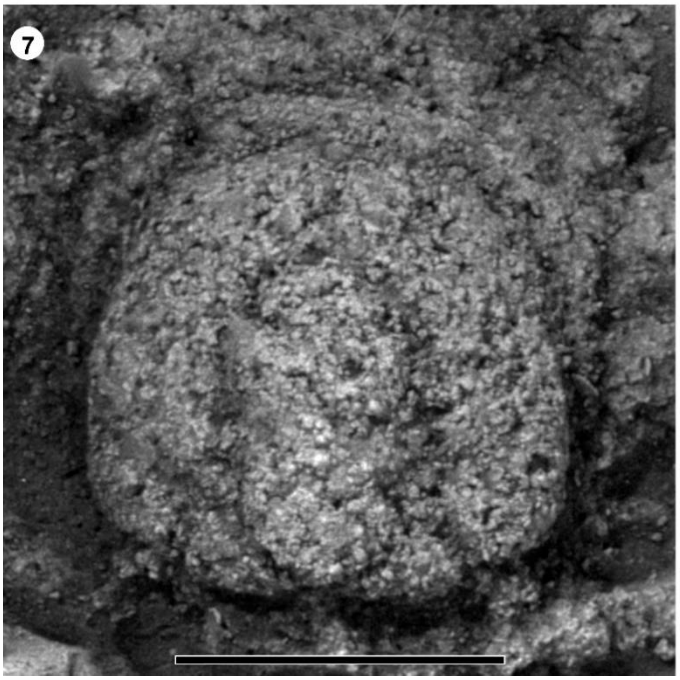
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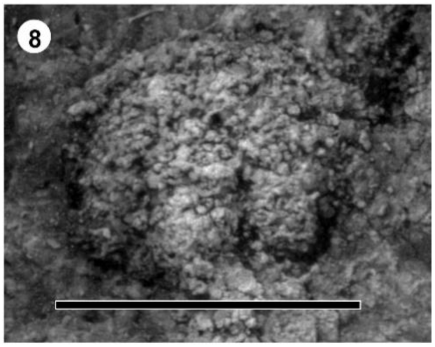
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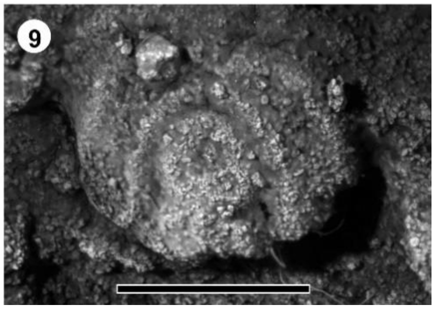
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Figure 3:14 (*Previous page*) *Geragnostus* sp. and *Pseduagnostus* sp. *Geragnostus* sp. 1–4. **(1)** _5, cephalon, APM 46.05 m; **(2)** _5, cephalon, APM 56.00 m; **(3)** _44, cephalon, APM 53.65 m; **(4)** _34, pygidium, APM 53.65 m. *Pseudagnostus* sp. 5–8,?9 **(5)** _23, pygidium, AML 5.84 m; **(6)** _64, pygidium, AML 5.81 m; **(7)** _4, cephalon, AML 5.84 m; **(8)** _193, cephalon, AML 5.81 m; **(9)** _5, cephalon, ATTw. All internal molds unless otherwise indicated. Scale bars = 2mm. APM = Ao Phante Malacca; AML = Ao Mo Lae; ATTw = Ao Talo Topo west.

Genus *Pseudagnostus* Jaekel, 1909

Type species.—Agnostus cyclopyge Tullberg, 1880 from the *Parabolina* Zone of Andrarum, Sweden.

Pseudagnostus sp.

Fig. 3:14.5–8,9?

Occurrence.—Ao Molae 5.81–5.84 m, ?Ao Talo Topo west; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Material.—Three cephala from Ao Mo Lae (AML) 5.81 m (_193) and 5.84 m (_4, 19); one? From Ao Talo Topo west (_5). Two pygidia from AML 5.81 m (_64) and 5.84 m (_23). All internal molds.

Remarks.—These specimens most resemble *Pseudagnostus josepha* (Hall, 1863) which is a much older species, dating to the *Glyptagnostus stolidus* Zone (Peng and Robison, 2000; Choi et al., 2016). Peng and Robison (2000) revised *Pseuagnostus josepha* based on the understanding that it encompasses broad morphological variation within and between populations. Their emended cephalic diagnosis includes a posteriorly angular glabella and straight or posteriorly bowed F3. The pygidium is somewhat more distinct with the axial furrow weakening or becoming effaced posterior to F2, axial constriction at M2, a tubercle posteriorly indenting F2, a strongly expanded posteroaxis, and a small pair of posterolateral border spines. Three cranidia and two pygidia from Ao Molae horizons 5.81 and 5.84m fit this diagnosis well. The cranidia particularly exemplify the shortened (sag.) anterior glabellar lobe common in *P. josepha*. The broad morphometric variation of *P. josepha* results in the diagnosis for that species encompassing forms that should be excluded such as *Pseudagnostus* sp. from Ko Tarutao. *Pseudagnostus* sp. has a post F2 axial furrows of the pygidium that is completely effaced, not extending as far as the axial tubercle, and the posteroaxis is not as laterally expanded as is common in most *P. josepha.*

Genus *Geragnostus* Howell, 1935

Type species.—Agnostus sidenbladhi Linnarson, 1869 from the Ceratopyge Limestone of Sweden.

Geragnostus sp.

Fig. 3:14.1–4

1984 *Geragnostus* sp. Stait et al., fig. 4.5.

Occurrence.—Ao Phante Malacca 27.35–56.00 m; Talo Wao Formation, Tarutao Group, Ko Tarutao, Thailand; middle to upper Tremadocian.

Material.— 11 cephala from Ao Phante Malacca (APM) 27.35 m (_2), 43.60 m (_9, 10, 73 – external mold, 75 – external mold, 94, 95, 105), 46.05 m (_5), 53.65 m (_44) , and 56.00 m (_5); six pygidia from 43.60 m (_1, 6, 32, 76 external mold, 81 – external mold) and 53.65 m (_34). All internal molds unless otherwise indicated.

Remarks.—The cephalon of *Geragnostus*. sp. is similar to that of *Homagnostus obesus*, also found in the Tarutao Group. An important distinguishing feature is that *Geragnostus* sp. has a strongly curved, subtriangular anterior margin. Stait et al. (1984) published a single agnostid cephalon with no description or remarks other than calling it *Geragnostus* sp. That specimen is not so strongly anteriorly curved as the specimens of *Geragnostus* sp. presented herein, but it is found in the same section at Ao Pante Malaka and is likely the same species. Both cephalon and pygidium are similar to those of *Geragnostus intermedius* Palmer, 1968, alternatively assigned to *Micragnostus* (e.g. as in Pratt, 1988), but *Geragnostus* sp. has wider (tr.) pygidial spine bases and a more strongly curved cranidial margin. The cranidial margin is narrower than in *G. tilcuyensis* (Kayser, 1876; *sensu* Harrington and Kay, 1951).

Class TRILOBITA Walch, 1771

Order CORYNEXOCHIDA Kobayashi, 1935

Suborder ILLAENINA Jaanusson, 1959

Family TSINANIIDAE Kobayashi, 1935

Remarks.—Wernette et al. (2020) demonstrated that the traditional view of the Mansuyiinae subfamily Hupé (1955) is polyphyletic and not collectively transitional between Kaolishaniidae Kobayashi, 1955 and Tsinaniidae. Mansuyiinae is restricted to only its type genus *Mansuyia* Sun, 1924. *Mansuyia* is a sister genus to the Tsinaniidae though not a stem group as suggested by Park et al., 2014. Based on the retention of *Mansuyia* within Kaolishaniidae, Tsinaniidae apparently originated with a paraphyletic Kaolishaniidae but the split that lead to Tsinaniidae came relatively early within the duration of that parataxon.

Genus *Tsinania* Walcott, 1914

Type species.—Illaenurus canens Walcott, 1905, p. 96 *nom. nud.*; 1913, p. 222–223, pl. 23, figs 3, 3a–c, from the Chaumitien Limestone of Tsinanan, Shantung, China; designated Walcott (1914, p. 43).

Tsinania sirindhornae n. sp.

Fig. 4:15

1988. *Tsinania* (*Tsinania*) cf. *nomas* Shergold; Shergold et al. p. 316 fig. 4A-G.

Type material.—Holotype: ATT8.85_8 (Fig. 4:15.3), Ao Talo Topo 8.85 m; Ao Mo Lae Formation, Tarutao Group; Ko

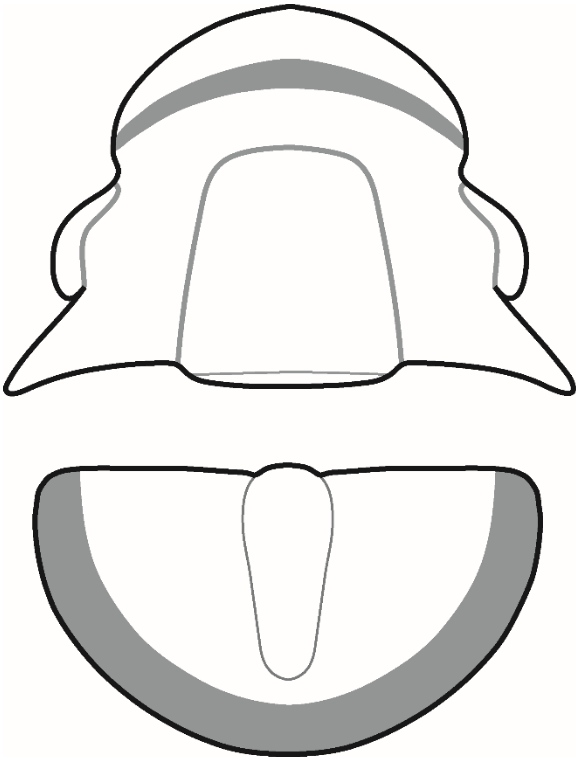


Figure 3:15 Tsinania sirindhornae n. sp. line drawing. The furrows, indicated by gray, are nearly effaced.

Tarutao, Thailand; Furongian, Cambrian Stage 10. Paratypes: ATT24.10_16, ATT24.70_16, ATT8.60_8, ATT24.00_9, ATT26.50_12, ATD1_1, ATT24.00_11, ATT24.00_9, ATT24.10_17, ATT24.10_62, ATT24.70_1, ATT24.70_20, ATT30.30_5, ATT30.30_53, and ATT30.30_68.

*Diagnosis.—*Cranidium with slightly angular anterior margin, long (sag., exsag.) anterior border, long (sag., exsag.) and medially shallowing anterior border furrow, effaced axial and glabellar furrows even on internal molds; pygidium wide (tr.) with long and broad (sag., exsag., tr.) border, low convexity, subtrangular pleural field, relatively long post-axial area (sag.), and effaced axial, ring, and pleural furrows.

*Occurrence.—*Ao Talo Topo 8.20–25.34 m and Ao Talo Udang S2 h1; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Cambrian Stage 10.

*Description.—*Cranidium subtriangular; width (tr.) across posterolateral projections ~1.5 times cranidial length (sag.), widening with growth; width (tr.) across palpebral lobes 80–90% width (tr.) across posterolateral projections; width (tr.) across anterior border 65–70% width (tr.) across posterolateral projections; anterior margin gently angular; low convexity. Glabellar length (sag., including LO) ~65% cranidial length; cranidial width (tr.) across palpebral lobes ~2.2 times glabellar width (tr.) on same line; preglabellar and axial furrows nearly completely effaced; transverse glabellar furrows and LO completely effaced; slight postoccipital tranverse ridge or flange (see remarks). Fixigena extend anterior to glabella, extending medially to separate preglabellar and anterior border

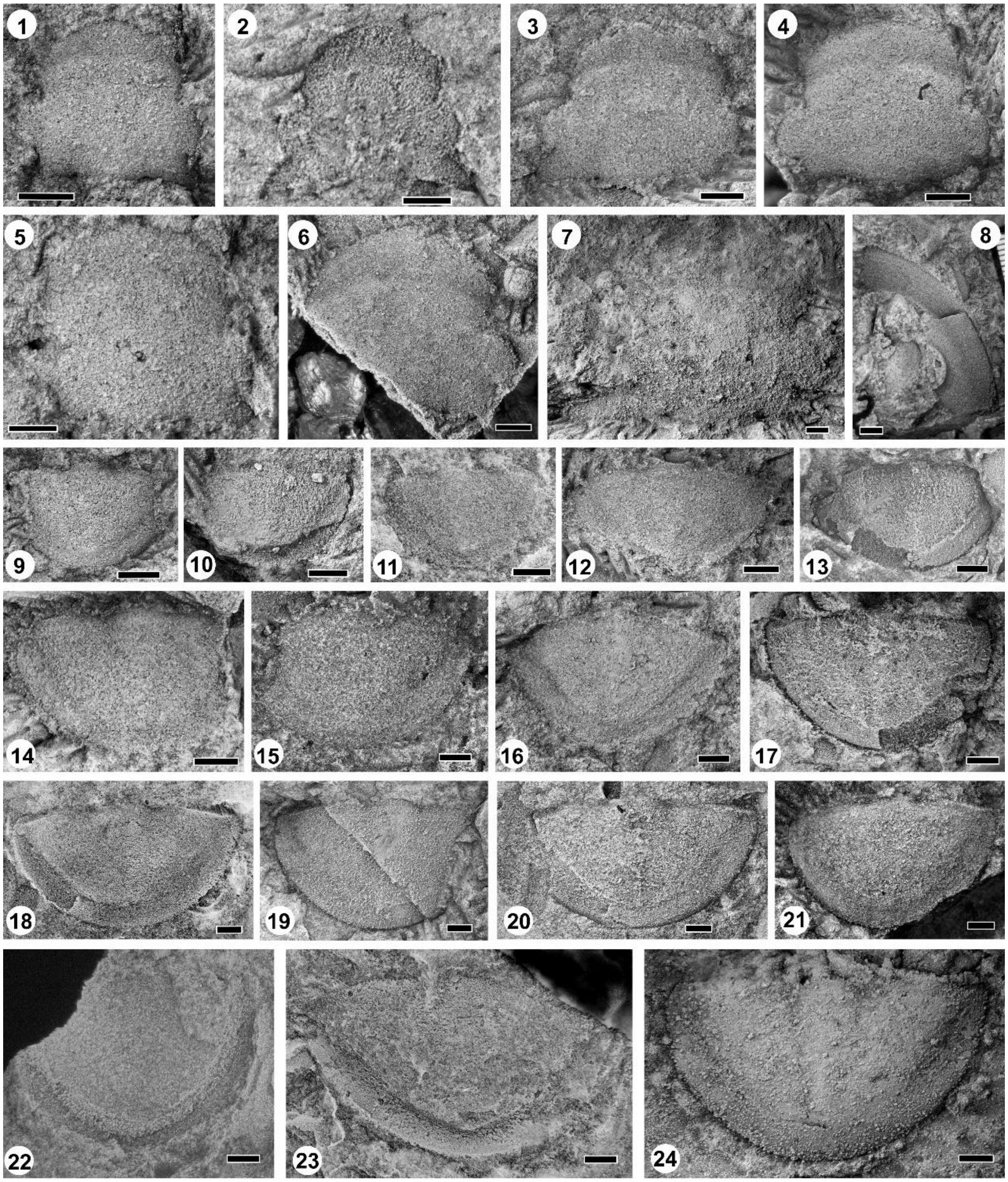


Figure 3:16 Tsinania sirindhornae n. sp. **(1)** _50, cranidium, ATT 29.14 m; **(2)** _9, cranidium, ATT 22.78 m; **(3)** _8, holotype, cranidium, ATT 8.85 m **(4)**_16, cranidium, ATT 23.89 m; **(5)** _16, cranidium, ATT 22.88 m; **(6)** _8, cranidium, ATT 8.60 m; **(7)** _7, cranidium, ATT 8.20 m; **(8)** _3, librigena, ATT 23.89 m; **(9)** _20, pygidium, ATT 23.89 m; **(10)** _40, pygidium, ATT 29.17 m; **(11)** _2, external mold, pygidium, ATT 22.78 m; **(12)** _9, pygidium, ATT 8.85 m; **(13)** _50, pygidium, ATT 29.17 m; **(14)** _11, pygidium, ATT 22.78 m; **(15)** _97, pygidium, ATT 22.78 m; **(16)** _17, pygidium, ATT 22.88 m; **(17)** _1, pygidium, ATT 3.89 m; **(18)** _54, pygidium, external mold, ATT 29.17 m; **(19)** _53, pygidium, ATT 29.17 m; **(20)** _68, pygidium, 29.17 m; **(21)** _62, pygidium, 22.88 m; **(22)** _91, pygidium, external mold, ATT 22.78 m; **(23)** _4, pygidium, external mold, ATT 8.60 m; **(24)** _1, pygidium, Ao Talo Udang Section 2 horizon 1. All internal molds unless otherwise indicated. Scale bars = 2mm. ATT = Ao Talo Topo.

furrows; anterior border furrow broad (sag.), medially shallowing, strongly curved, and well defined posteriorly but anteriorly sloping gently into anterior border; anterior border long (sag.), weakly inflated. Palpebral lobe length (exsag.) 25–30% cranidial length (sag.); midpoint of lobe opposite posterior 1/3 of cranidium (sag.); palpebral lobes strongly curved with greatest curvature in posterior half; anterior facial suture branches moderately abaxially deflected then strongly adaxially curving to meet medially on anterior margin; posterior facial suture branches extend nearly straight posterlaterally at angle 45–70° from exsag.; posterior border furrows effaced.

Librigena narrow, lateral border occupying ~half width (tr.); border furrow noted only by change in slope; doublure attached to librigena extends far anteriorly, lengthening (exsag.) as it nears axial midline; median ventral suture.

Pygidium semicircular with nearly straight (tr.) anterior margin and strongly curved posterior margin; pygidial width (tr.) across anterior margin 1.6–1.9 times pygidial length (sag.); low convexity. Axis narrow (tr.), ~25% pygidial width (tr.) across anterior margin; axial furrows nearly effaced; ring furrows, pleural furrows, and interpleural furrows completely effaced; pleural field subtriangular to semicircular. Border furrow weakly defined; posterior border long (sag., exsag., tr.); doublure same length (sag., exsag., tr.) as border, moderately convex.

Etymology.—Named in honor of Her Royal Highness Princess Maha Chakri Sirindhorn of Thailand in recognition of her support for science, particularly paleontology.

Material.—Nine cranidia from Ao Talo Topo (ATT) 8.20 m (_7), 8.60 m (_8), 8.85 m (_8), 22.78 m (_9), 22.88 m (_16), 23.89 m (_8, 16), and 25.34 m (_7 – external mold, 12). One librigena from ATT 23.89 m (_3). 17 pygidia: one from Ao Talo Udang S2 h1 (_1) and 16 from ATT 8.60 m (_4 – external mold), 8.85 m (_9), 22.78 m (_2 – external mold, 11, 65 – external mold, 91 – external mold,97), 22.88 m (_17, 62), 23.89 m (_1, 20), and 29.17 m (_40, 50, 53, 54 – external mold, 68). All internal molds unless otherwise indicated.

Remarks.—Shergold et al. (1988) initially assigned tsinaniid material from the Tarutao fauna to *Tsinania* cf. *nomas* with the only doubt given for its synonymy being a difference in the degree of effacement between the Tarutao specimens and the type material. With the larger sample size figured and discussed herein, we can identify additional differences between the Tarutao specimens and *T. nomas* Shergold, 1975 type material which suggest that they are a separate and new species, *T. sirindhornae*. *Tsinania sirindhornae* has a longer (sag.) anterior border than *T. nomas* with a less strongly incised anterior border furrow and less developed plectrum, though this structure is not well-developed in either species. The pygidium of *T. sirindhornae* has a noticeably wider (tr., sag., exsag.) border and more effaced axial and pleural furrows. The very slight postoccipital transverse ridge or flange that is discernible on some specimens of *T. sirindhornae* (e.g. Fig. 3:16.1) is better developed on *T. nomas* (e.g. Shergold, 1975, pl. 47, fig. 1).

Compared with *Tsinania canens* (Walcott, 1905), *T. sirindhornae* has a longer (sag.) cranidial anterior border, longer (sag.) pygidial posterior border, less developed plectrum and more effaced axial and lateral furrows on both the cranidium and pygidium. Compared with *Tsinania dolichocephala* (Kobayashi, 1933), *T. sirindhornae* is less convex with more effaced furrows and a less developed plectrum. *Tsinania antidictys* Shergold, 1975 has better defined axial furrows on the cranidium and a more convex axis on a shorter (sag.) pygidium.

The genera *Tsinania* and *Shergoldia* Zhang and Jell, 1987 are sufficiently similar that it is doubtful whether they are different genera. Two separate cladistic analyses using different sets of taxa and characters by Zhu et al. (2013) and Wernette et al. (2020) suggest that *Tsinania* as currently conceived is either polyphyletic or includes all species assigned to *Dictyella* Kobayashi, 1933, *Shergoldia*, and possibly *Lonchopygella* Sun and Xiang, 1979. *Shergoldia* is either polyphyletic or monophyletic and an early descendant of *Tsinania* (Wernette et al., 2020). Regardless of the status of *Shergoldia* as a genus, *T. sirindhornae* is easily recognizable as *Tsinania* by its advanced degree of effacement and lack of a developed plectrum.

The ventral median suture has historically been used to characterize tsinaniids as asaphid-like taxa (e.g. Moore, 1959), but increasing numbers of studies have shown that ventral median sutures evolved independently in numerous lineages (e.g. Zhu et al., 2007; Park, and Choi, 2010).

Suborder LEIOSTEGIINA Bradley, 1925

Superfamily LEIOSTEGIOIDEA Bradley, 1925

Family KAOLISHANIIDAE Kobayashi, 1935

Subfamily MANSUYIINAE Hupé, 1955

Remarks.—Mansuyiinae was restricted by Shergold (1972) to contain "*Mansuyia*-like" genera: *Mansuyia* (Grabau) Sun, 1924*, Paramansuyella* Endo (in Endo and Resser), 1937*, Kaolishaniella* Sun, 1935, and *Mansuyites* Shergold, 1972. However, cladistic consideration of relationships between tsinaniids and kaolishaniids suggests that Mansuyiinae is polyphyletic (Wernette et al., 2020). The use of Manusyiinae herein refers exclusively to *Mansuyia* with *Mansuyites* and like taxa considered belonging to Ceronocarinae.

Genus *Mansuyia* (Grabau) Sun, 1924

Type species.—*Mansuyia orientalis* (Grabau) Sun, 1924 from the Fengshan Stage in the Yehli Limestone, China.

Mansuyia orientalis? (Grabau) Sun, 1924

Fig. 3:17

?1924. *Mansuyia orientalis* (Grabau) Sun, p. 50–52, pl. 3, figs 7i–j, *non* figs a7–h.
?1935. *Mansuyia orientalis* (Grabau) Sun; Sun, p. 58, pl. 2, figs 20–24.
?1965. *Mansuyia orientalis* (Grabau) Sun; Lu et al., p. 416–417, pl. 79, figs 5–11.
?1994. *Mansuyia orientalis* (Grabau) Sun; Qian, p. 125, pl. 32, figs 5–12; pl. 33, figs 1–5.
?2014. *Mansuyia orientalis* (Grabau) Sun; Park et al., p. 272, fig. 3.

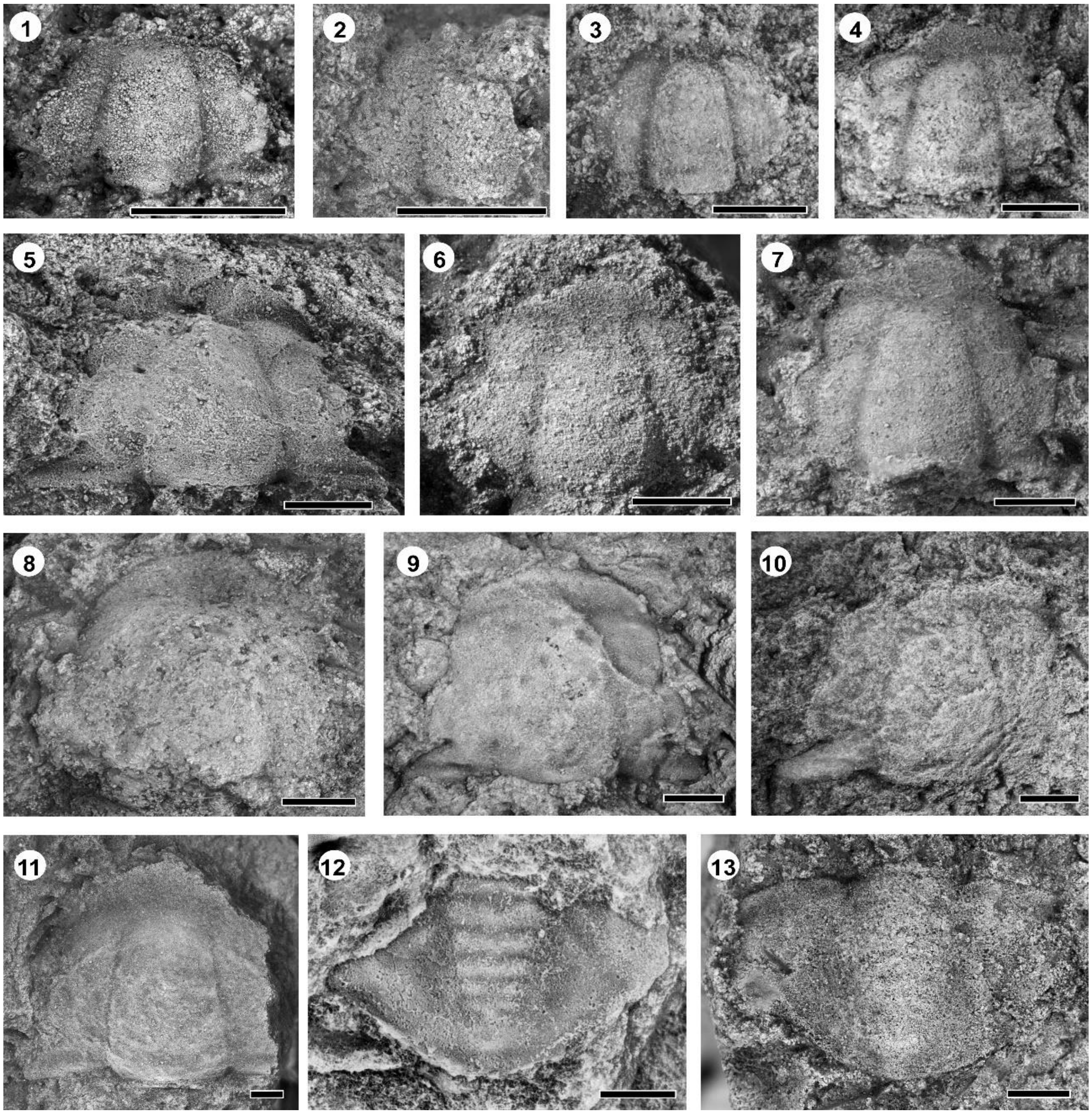


Figure 3:17 Mansuyia orientalis? (Grabau) Sun, 1924. **(1)** _217, cranidium; **(2)** _235, cranidium; **(3)** _181, cranidium; **(4)** _74, cranidium; **(5)** _244, cranidium; **(6)** _257, cranidium; **(7)** _86, cranidium; **(8)** _106, cranidium; **(9)** _4, cranidium; **(10)** _57, cranidium; **(11)** _229, cranidium; **(12)** _15, external mold, pygidium; **(13)** _187, pygidium. All internal molds unless otherwise indicated. All specimens from Ao Talo Udang Section 1 7.00 m. Scale bars = 2mm.

Occurrence.— Ao Talo Udang S1 7.00 m, Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand, Furongian, Cambrian Stage 10.

Material.—13 cranidia (_4, 57, 74, 86, 106, 165, 181, 217, 229, 235, 244, 257, 267) and two pygidia (_15, 187). All from Ao Talo Udang S1 7.00 m.

Remarks.—When first published by Sun (1924) the cranidia and pygidia assigned to *Mansuyia* were misassociated. Two of the pygidia were subsequently declared the type material and a new cranidial form was assigned (Sun, 1935), though the reassignments of the type material were handled in a confusing manner leaving some question as to which pygidia are retained in *M. orientalis* (Resser, 1942). Herein we follow the concept of *M. orientalis* adapted by Lu et al. (1965), Qian (1994), and Park et al. (2014).

Cranidia of *Mansuyia orientalis* are difficult to distinguish from those of *Mansuyia chinensis* (Endo, 1939)(Park et al., 2014). The latter is generally considered more effaced with a shorter (sag.) preglabellar field and some evidence of a plectrum, but all of these characters are variably expressed within collections. The material from Tarutao varies in its degree of effacement from the axial furrows being nearly effaced (e.g. Fig. 3:17.9) to the axial furrows being well defined (e.g. Fig. 3:17.3). These specimens consistently have a moderately long (sag.), depressed preglabellar area that is of equal length or longer than the anterior border. Despite the effacement of some specimens, this latter character suggests they belong to *M. orientalis* rather than *M. chinensis*.

Subfamily CERONOCARINAE Wernette and Hughes, 2020

Genus *Satunarcus* Wernette and Hughes, 2020

Satunarcus molaensis Wernette and Hughes, 2020

Fig. 3:18.1–3

2020. *Satunarcus molaensis* Wernette and Hughes; Wernette et al. p. 10–12, figs 8–10.

Occurrence.—Ao Talo Topo west and Ao Mo Lae (AML) 4.71–6.01 m and AML h2; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Cambrian Stage 10.

Material.—See Wernette et al., 2020. Additionally: nine cranidia from Ao Mo Lae (AML) 5.81 m, (_45, 75, 87, 95, 145), AML h2 (_40), and Ao Talo Topo west (ATTw) (_68, 69, 73); two librigenae from AML 5.81 m (_84) and ATTw (_39); 14 pygidia from AML 5.81 m (23, 44, 46, 47, 49, 52, 81, 90, 100, 127–external mold, 201, 209, 216), and ATTw (_99). All specimens internal molds unless otherwise indicated.

Remarks.—Wernette et al. (2020) recently discussed *S. molaensis* using material collected on the 2008 and 2016 excursions. At the time of publication, no librigenae had yet been identified for this species, but two have since been identified from the same sampling horizons (Fig 3:18.3). The exceptionally long preglabellar field and short, poorly defined anterior border is a unique character lending confidence to the assignment of the librigenae which have very long anterior suture branches extending through a broad genal field and a nearly effaced border furrow. Unfortunately, neither has a completely preserved anterior facial suture, so it is not possible to determine he anteromedial extent of the librigenal border, the presence of a rostrum or median suture, or whether the free cheeks were ventrally joined.

Family MISSISQUOIIDAE Hupé, 1955

Genus *Parakoldinioidia* Endo in Endo & Resser, 1937

Type species.—*Parakoldinioidia typicalis* Endo in Endo & Resser, 1937 from Liaoning Province, North China.

Remarks.—*Parakoldinioidia* has been variably interpreted since its first diagnosis by Endo (1937). Westrop and Adrain (2014) describe a parallel to anteriorly tapered glabella whereas the original diagnosis describes an anteriorly divergent glabella with a truncated frontal margin. A more fitting diagnosis would be that the glabella is nearly parallel-sided or slightly hour-glass shaped with smoothly curving axial furrows that reach their narrowest point at S2.

Parakoldinioidia callosa Qian, 1985b

Fig. 3:18.4–9

1985 *Parakoldinioidia callosa* Qian, p. 151, pl. 1, figs 12–13.

1988 *Parakoldinioidia thaiensis* Kobayashi; Shergold et al., p. 316 figs 3S,T only, not figs 3Q,R,U–X (*Pseudokoldinioidia sardsudae*).

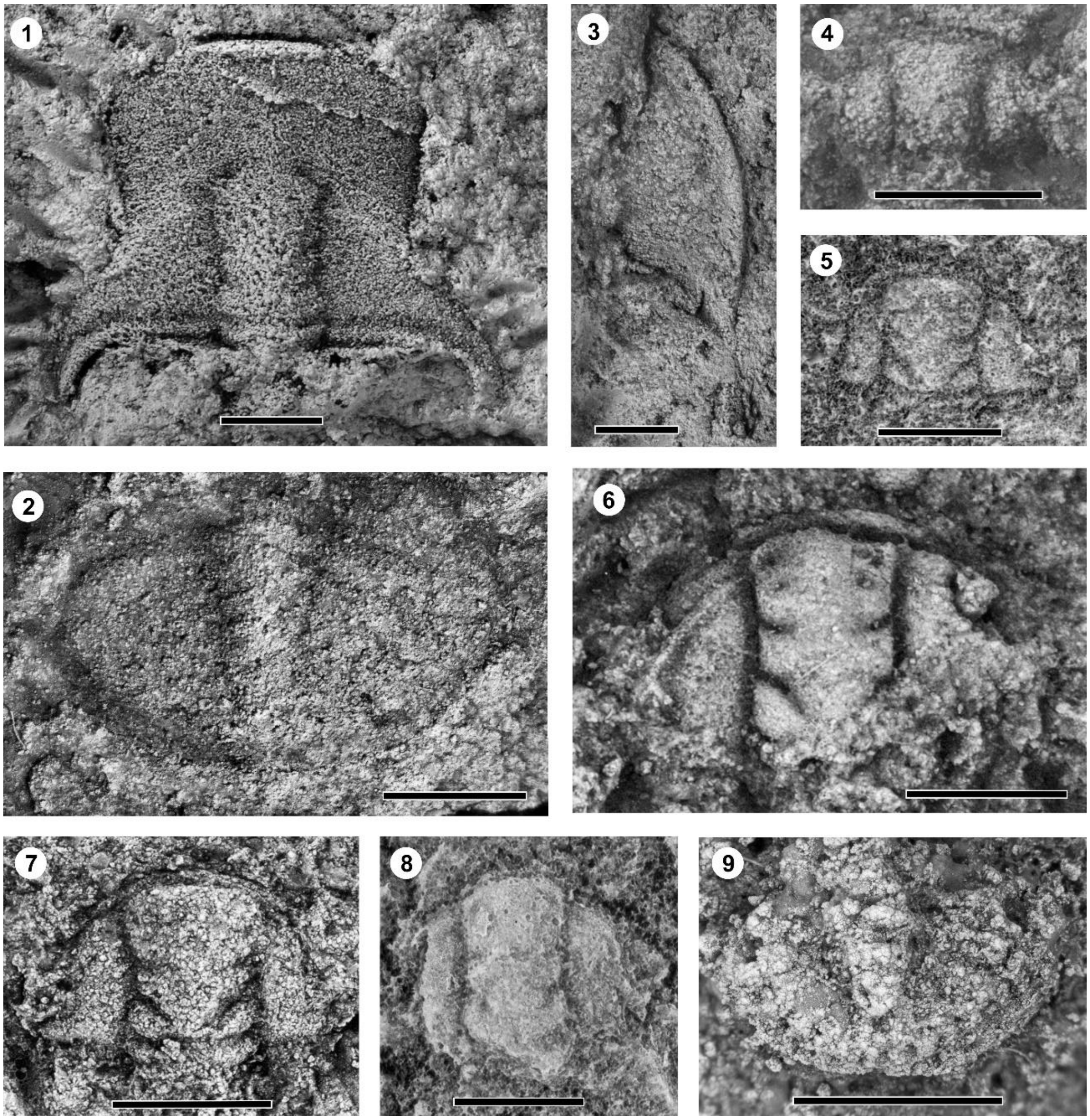


Figure 3:18 Satunarcus molaensis Wernette and Hughes, 2020 and *Parakoldinioidia callosa* Qian, 1985b. *Satunarcus molaensis* 1–3. **(1)** DGSC F0343, holotype, cranidium, Ao Mo Lae 5.81 m, refigured from Wernette and Hughes, 2020, Fig. 9.1; **(2)** DGSC F0381, pygidium, ATTw, refigured from Wernette and Hughes, 2020, Fig. 10.1; **(3)** _39, librigena, ATTw. *Parakoldinioidia callosa* 4–9. **(4)** _3, cranidium, LHN 3.05 m; **(5)** _24, cranidium, external mold, LHN 2.85 m; **(6)** _169, cranidium, ATD S1 7.00 m; **(7)** _34, cranidium, LHN 2.85 m; **(8)** _155, cranidium, ATD S1 7.00 m; **(9)** _272, pygidium, ATD S1 7.00 m. All internal molds unless otherwise indicated. ATTw = Ao Talo Topo west; ATD S1 = Ao Talo Udang section 1. Scale bars = 2 mm for 1–8 and =1 mm for 9.

Occurrence.—Ao Talo Udang S1, 7.00 m; Laem Hin Ngam 2.85–3.05 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Cambrian Stage 10.

Material.—Six cranidia from Ao Talo Udang (ATD) S1 7.00 m (155 – external mold, 169, 230) and Laem Hin Ngam 2.85 m (_24 – external mold, 34) and 3.05 m (_3). One pygidium from ATD S1 7.00 m (_272). All internal molds unless otherwise indicated.

Remarks.—Shergold et al. (1988) considered the Thai material now assigned to *P. callosa* to be synonymous with *Pagodia thaiensis* Kobayashi, 1957. The synonymy was established with a small sample size, and all morphological variation was attributed to size and preservation. The larger sample size in this study and the broader range of sampling horizons and localities allows us to recognize consistent differences between these two species and to recognize a third form also incorrectly synonymized with *P. thaiensis* by Shergold et al., herein designated *Pseudokoldinioida sardsudae*. The most immediately recognizable character distinguishing these forms is the anterior tapering of the glabella. In *Parakoldinioidia* the glabella is subrectangular without distinct tapering, in *Pseudokoldinioidia* the glabella expands anteriorly, and in *Pagodia* the glabella tapers anteriorly.

Parakoldinioidia callosa occurs at two separate localities on Ko Taruao, Ao Talo Udang and Laem Hin Ngam. The specimens from Ao Talo Udang tend to have less rounded anterior glabellar corners and a narrower glabella while the specimens from Laem Hin Ngam have a shorter, more robust looking glabella. It is not possible to determine whether these represent locality-specific differences, because the specimens from Laem Hin Ngam are all smaller than those from Ao Talo Udang and the sample size from both localities is very small. A tentative interpretation from this small sample is that the shape change seems to be dependent on size, suggesting ontogenetic variation rather than locality-based. As all Tarutao localities were likely geographically relatively continuous during the late Cambrian, stratigraphic age probably accounts for the biggest control of locality-based differences if they exist.

Compared with the type material of *P. callosa* collected from southern Anhui (Qian, 1985b), the Thai material differs only in having a less strongly rounded anterior glabellar margin. However, both collections contain only a few specimens and the intraspecific variation present within the Thai collection, ranging from a transverse to gently curved, suggests that this character is insufficiently stable to be of use in differentiating separate species. One specimen from Ao Talo Udang (Fig. 3:18.6) possesses prominent eye ridges; the eye ridges are either effaced or only very faint in all other known specimens, but this is as likely due to preservation. The granulation present on the material figured by Qian (1985) also occurs only inconsistently on the specimens of *P. callosa* from Tarutao. This too is likely preservational and its occurrence on some of the specimens (Figs 3:18.6,7) is sufficient to determine that the Tarutao material has this character in common with the *P. callosa* type material.

Genus *Pseudokoldinioidia Endo*, 1944

Type species.—Pseudokoldioidia granulosa Endo, 1944 from the *Tsinania canens* Zone of Liaoning Province, North China.

Pseudokoldinioidia sardsudae n. sp.

Figs 3:19–21

1988. *Parakoldinioidia thaiensis* Shergold et al. figs 3.Q,R,U–X only, not figs 3.S,T (*Parakoldinioidia callosa*).

Type material.—Holotype: ATT24.00_81 (Fig. 3:20.26), Ao Talo Topo 22.78 m; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian. Paratypes: Paratypes: ATT24.10_27, ATT0.95_3, ATT0.95_4, ATT0.95_8, ATT5.50_3, ATT6.65_2, ATT8.20_10, ATT8.60_6, ATT8.85_12, ATT24.00_6, ATT24.00_16, ATT24.00_17, ATT24.00_28, ATT24.00_30, ATT24.00_35, ATT24.00_38, ATT24.00_50, ATT24.00_54, ATT24.00_71, ATT24.00_76, ATT24.00_80, ATT24.10_2, ATT24.10_4, ATT24.10_7, ATT24.10_8, ATT24.10_10, ATT24.10_13, ATT24.10_18, ATT24.10_21, ATT24.10_25, ATT24.10_30, ATT24.10_31, ATT24.10_33, ATT24.10_35, ATT24.10_36, ATT24.10_38, ATT24.10_39, ATT24.10_40, ATT24.10_42, ATT24.10_49, ATT24.10_50, ATT24.10_66, ATT24.70_10, ATT24.70_17, ATT26.50_10, ATT29.50_13, ATT30.30_48, ATTF2_1].

Diagnosis.—Cranidium with glabella expanding anteriorly 35–40% of L1 width; excluding S0 and sometimes S1, lateral glabellar furrows poorly defined to effaced; eyes short (exsag.) and positioned anteriorly with midpoint opposite S2 to S3; posterolateral projections long (exsag.) and medially nearly transverse, curving strongly posteriorly only at distal tips. Pygidium long (sag.) and semielliptical with long axis reaching nearly to posterior margin; four axial rings and poorly defined terminal piece; axial furrows slightly posteromedially curved; pleura lengthen (exsag.) distally and shorten (exsag.) posteriorly with straight, moderately well-defined pleural furrows and effaced interpleural furrows.

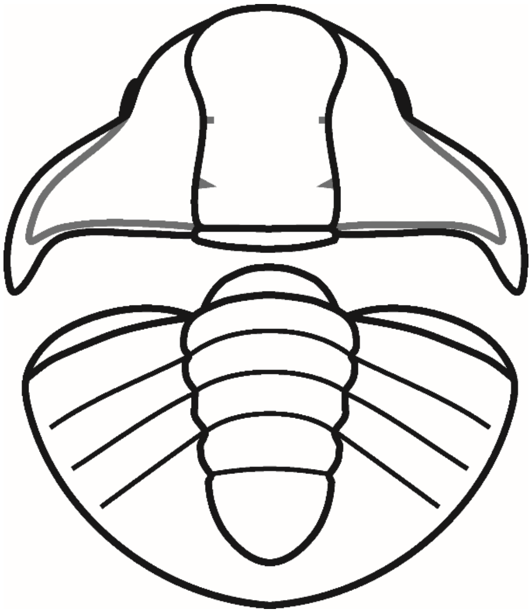
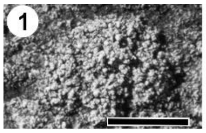


Figure 3:19 Pseudokoldinioidia sardsudae *n. sp. line drawing.*

Occurrence.—Ao Talo Topo 0.95 m–30.30 m and ATT h1; Ao Talo Udang S1 7.00 m, S2 0.52 m and 0.69 m, and S3 as float; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Description.—Cranidium subtrapezoidal to semicircular in outline; cranidial width (tr.) across midpoints of palpebral lobes ~1.1–1.4 times cranidial length (sag.); anterior margin strongly curved lacking anterior border and glabella occupying full cranidial length; anterior glabellar margin variably confluent with pre-ocular curvature of anterior suture branches or sutures dogleg at anterolateral glabellar corners to outline anteriorly protruding (sag., exsag.) glabella; glabella anteriorly widening (tr.) with anterior glabella 1.35–1.4 times width of L1; LO equal width or slightly broader than L1; axial furrows weakly to moderately incised and smoothly curved; S1 variably expressed from well-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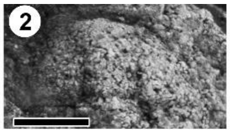
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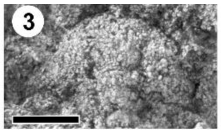
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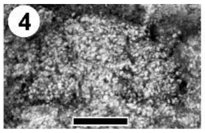
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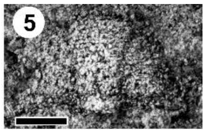
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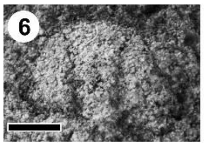
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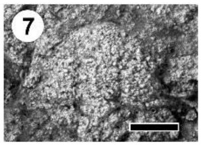
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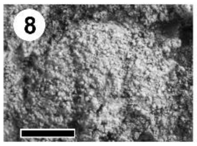
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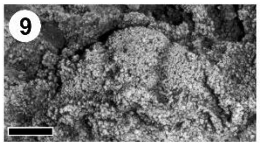
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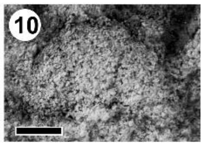
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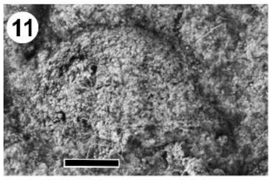
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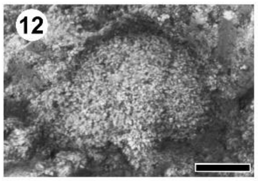
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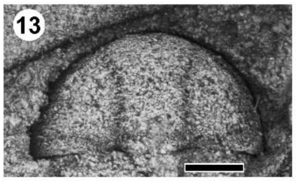
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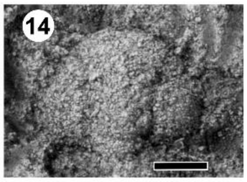
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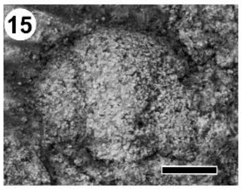
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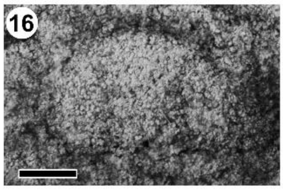
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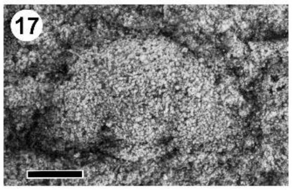
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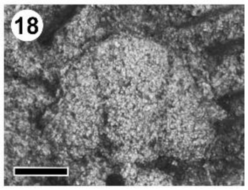
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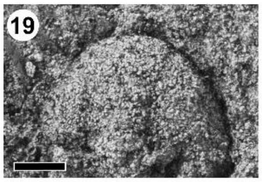
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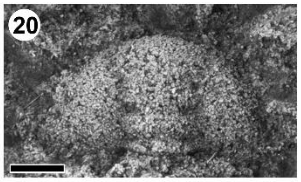
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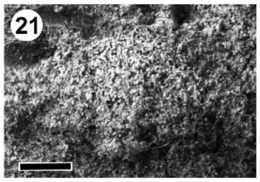
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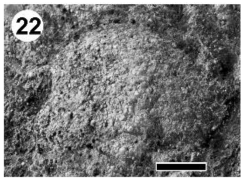
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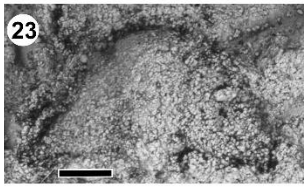
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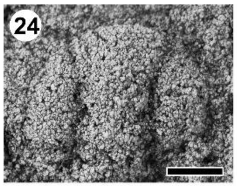
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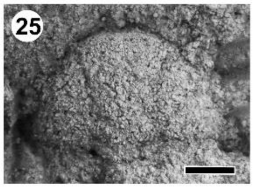
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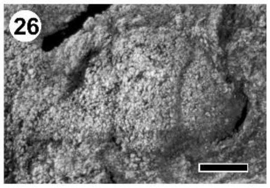
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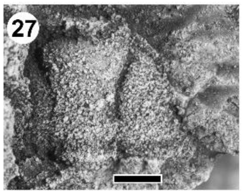
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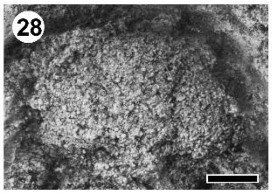
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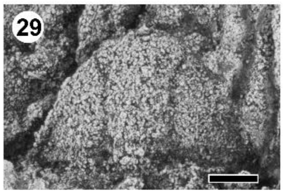
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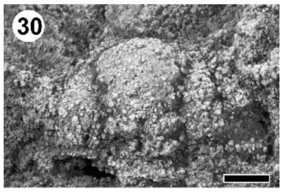
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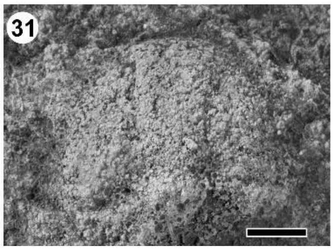
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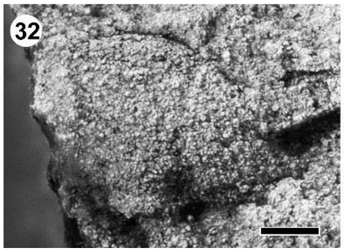
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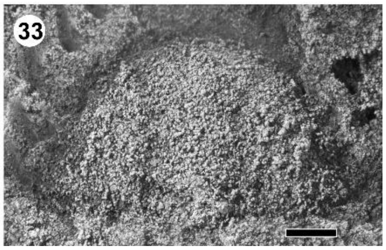
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Figure 3:20 (Previous Page) *Pseudokoldinioidia sardsudae* n. sp., all cranidia. **(1)** _7, ATT 22.88 m; **(2)** _17, ATT 23.89 m; **(3)** _10, ATT 22.88 m; **(4)** _80, ATT 22.88 m; **(5)** _71, ATT 22.78 m; **(6)** _36, ATT 22.88 m; **(7)** _21, ATT 22.88 m; **(8)** _25, ATT 22.88 m; **(9)** _3, ATT 0.95 m; **(10)** _38, ATT 22.88 m; **(11)** _39, ATT 22.88 m; **(12)** _4, ATT 22.88 m; **(13)** _48, ATT 29.17 m; **(14)** _66, ATT 22.88 m; **(15)** _10, ATT 23.89 m; **(16)** _30, ATT 22.88 m; **(17)** _ 10, ATT 8.20 m; **(18)** _12, ATT 8.85 m; **(19)** _8, ATT 22.88 m; **(20)** _6, ATT 8.60 m; **(21)** _31, ATT 22.88 m; **(22)** _42, ATT 22.88 m; **(23)** _17, ATT 22.78 m; **(24)** _8, ATT 0.95 m; **(25)** _27, ATT 22.88 m; **(26)** _81, holotype, ATT 22.78 m; **(27)** _10, ATT 25.34 m; **(28)** _18, ATT 22.88 m; **(29)** _2, ATT 6.65 m; **(30)** _13, Ao Talo Udang S2 0.69 m; **(31)** _50, ATT 22.88 m; **(32)** _15, ATT 22.88 m; **(33)** _6, ATT 22.78 m. All internal molds. ATT = Ao Talo Topo. Scale bars = 1 mm.

incised to faint and with transverse to gently posteriorly oblique orientation; S2 short and poorly defined to effaced; S3 and S4 nearly always effaced; SO straight (tr.) and moderately incised. Palpebral lobes short (exsag), angled strongly obliquely, and anteriorly positioned with midpoint opposite S2 to S3. Posterolateral projections long (exsag., tr.); posterior margin medially transverse to slightly posterolaterally deflected; curves strongly posteriorly near distal end; posterior border lengthens at distal end into fixigenal spine; posterior border furrow moderately to strongly incised.

Pygidium semielliptical with width (tr.) across anterior pleural band, the widest point, 1.35–1.55 times pygidial length (sag.); anterior margin gently anteriorly bowed; posterior margin strongly curved. Axial length 85–90% cranidial length (sag.); axial width across anterior most ring ~35% cranidial width (tr.) at widest point; axial furrows moderately to strongly incised with slight posteromedial curve; lateral axial ring furrows laterally well-defined but shallow medially, often becoming effaced; 4 axial rings and terminal piece with poorly defined posterior tip. Pleural bands not clearly aligned with axial rings; interpleural furrows effaced; pleural furrows straight and moderately incised to effaced; pleurae slightly laterally lengthening (tr.); pleural furrows terminate at lateral margin.

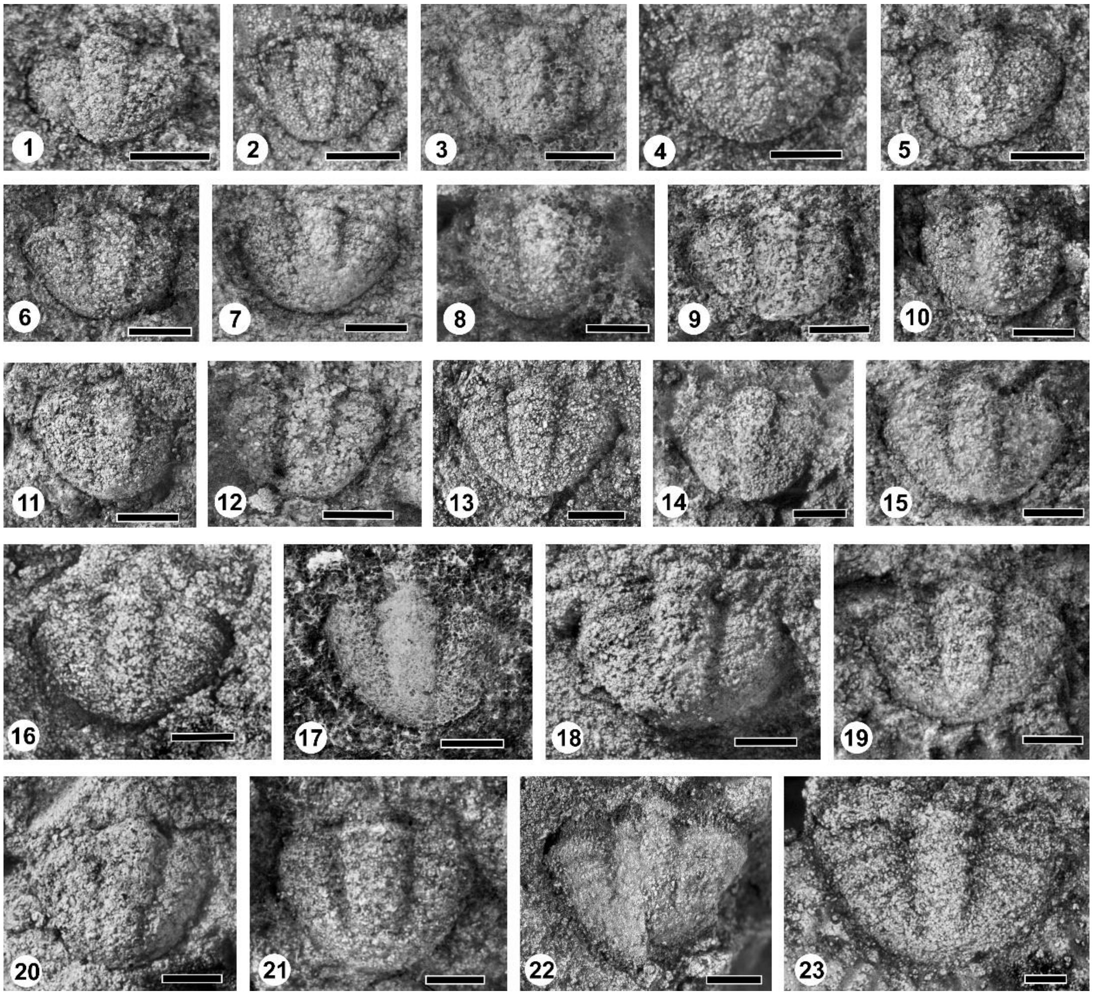


Figure 3:21 Pseudokoldinioidia sardsudae n. sp., all pygidia. **(1)** _63, ATT 29.17 m; **(2)** _12, ATT 29.17 m; **(3)** _23, ATT 22.78 m; **(4)** _56, ATT 22.78 m; **(5)** _12, ATT 8.20 m; **(6)** _5, ATT 22.78 m; **(7)** _51, ATT 29.17 m; **(8)** _43, ATT 22.88 m; **(9)** _33, ATT 22.88 m; **(10)** _3, ATT 22.88 m; **(11)** _19, ATT 22.88 m; **(12)** _14, ATT 23.89 m; **(13)** _14, ATT 22.88 m; **(14)** _1, ATT 22.88; **(15)** _34, ATT 22.88 m; **(16)** _3, ATT 8.85 m; **(17)** _15, external mold, ATT 23.89 m; **(18)** _41, ATT 29.17 m; **(19)** _93, ATT 22.78 m; **(20)** _29 ATT 22.88 m; **(21)** _45, ATT 22.88 m; **(22)** _16, ATT 29.17 m; **(23)** _2, ATT horizon 1. All internal molds. ATT = Ao Talo Topo. Scale bars = 1 mm.

Etymology.—Named in honor of Dr. Apsorn Sardsud, colleague and director at the Thai Department of Mineral Resources.

Material.—52 cranidia: 49 from Ao Talo Topo (ATT) 0.95 m (_3, 4, 8), 5.50 m (_3), 6.65 m (_2), 8.20 m (_10), 8.60 m (_6), 8.85 m (_12), 22.78 m (_6, 16, 17, 28, 30, 35, 38, 50, 54, 71, 76, 80, 81), 22.88 m (_2, 4, 7, 8, 10, 13, 18, 21, 25, 27, 30, 31, 33, 35, 36, 38, 39, 40, 42, 49, 50, 66), 23.89 m (_10,17), 25.34 m (_10), 28.37 m (_13), 29.17 m (_48), and ATT h1 (_1); three from Ao Talo Udang (ATD) S1 7.00 m (_236), S2 0.52 m (_27m) and 0.69 m (_13), and S3 float (_11). 40 pygidia: 37 from ATT 0.95 m (_5), 6.65 m (_5), 8.20 m (_8,12), 8.85 m (_3), 22.78 m (_13,22,36,78,93), 22.88 m (_1, 3, 5, 9, 12, 14, 19, 23, 29, 32, 34, 43, 45, 46, 51, 52, 56), 23.89 m (_14,15), 29.17 m (_12, 16, 39, 41, 51, 57, 63), and ATT h1 (_2); two from ATT west (_38, 53); one from ATD S3 float (_31). All internal molds.

*Remarks.—*The posterolateral projections of *P. sardsudae* are posteriorly curved as is typical for *Pseudokoldinioidia*, but the proximal portions of the posterolateral projection, including the posterior border, are sufficiently transverse in orientation that only those specimens with the distal part preserved show a clear posterior bend. This trait is somewhat variable with some specimens (e.g. Fig. 3:20.7) having a stronger curve and others (e.g. Fig. 3:20.26) being more medially transverse with only a curve in the most distal part. *Pseduokoldinioidia granulosa* Endo, 1944, *Pseudokoldinioidia perpetis* (Zhou and Zhang, 1985) and *Pseudokoldinioidia* sp. cf. *P. granulosa* (Park and Kihm, 2015) exhibit stronger posterior curvature than the most strongly curved specimens from Tarutao. The palpebral lobes of *P. sardsudae* are smaller relative to these other species, accommodating longer (exsag.) posterolateral projections.

The cranidial outline is variable with the eyes close to the glabella in some specimens (e.g. Fig. 3:20.7) such that there is a noticeable concavity to the cranidial outline but more distally set in others (e.g. Fig. 3:20.13) such that the palpebral lobes are almost confluent with the anterior margin and the transition between anterior and posterior facial sutures. This trait is not size dependent as the most distally set eyes occurs in one of the medium-sized specimens and both the largest and smallest specimens exhibit relatively narrowly set eyes. Likewise, the variation is not locality controlled as both extremes occur in the collection from Ao Talo Topo. It may be partially stratigraphically controlled as the specimen with the most wideset eyes occurs in the uppermost horizon; but if there was a strong stratigraphic trend, then the long gap in fossiliferous horizons at Ao Talo Topo from 8.85 m to 22.78 m should expose that difference in the collections from above and below the gap, but no such clear difference exists.

Family LEIOSTEGIIDAE Bradley, 1925

Subfamily PAGODIINAE Kobayashi, 1935

Remarks.—The relegation of Pagoniinae to a subfamily within Leiostegiidae follows Zhou and Zhen, 2008 and Adrain, 2011.

Genus *Pagodia* Walcott, 1905

Type species.—Pagodia lotos Walcott, 1905 from the *Tsinania* Zone of Shandong, North China; designated by Kobayashi, 1935.

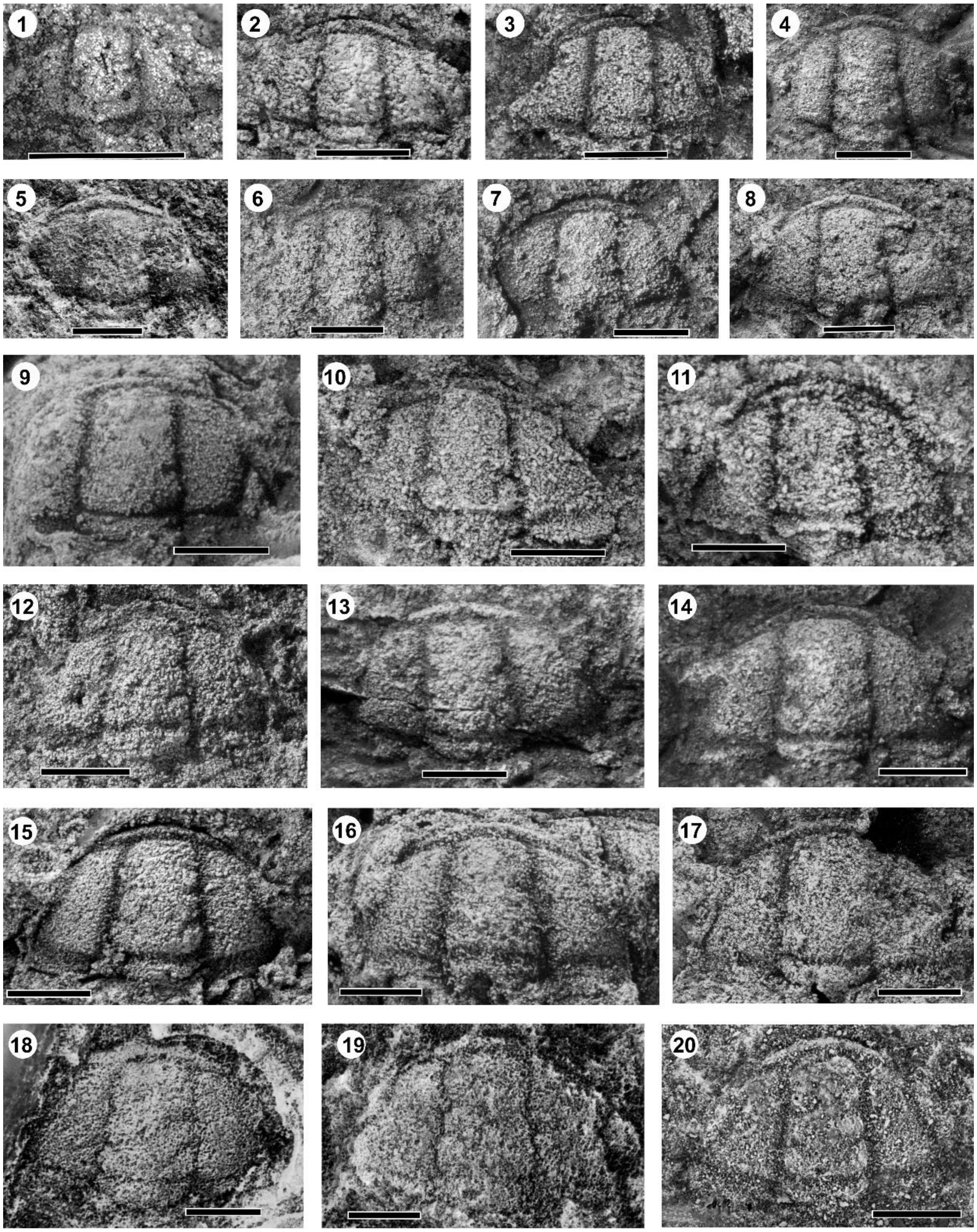


Figure 3:22 Pagodia thaiensis Kobayashi, 1957, all cranidia. **(1)** _10, Laem Hin Ngam 2.85 m; **(2)** _60, AML 5.81 m; **(3)** _13, AML 5.17 m; **(4)** _29, AML 5.81 m; **(5)** _16, external mold, AML 5.81m; **(6)** _219, AML 5.81 m; **(7)** _1, AML 6.01 m; **(8)** _143, AML 5.81 m; **(9)** _199, AML 5.81 m; **(10)** _155, AML 5.81 m; **(11)** _62, AML 5.81 m; **(12)** _19, AML 5.17 m; **(13)** _14, AML h3; **(14)** _20, AML 5.81 m; **(15)** _66, AML 5.81 m; **(16)** _156, AML 5.81 m; **(17)** _72, AML 5.81 m; **(18)** _195, external mold, AML 5.81 m; **(19)** _45, external mold, AML 5.17 m; **(20)** CMC IP87003, vinyl polysiloxane cast of UMUT PB 02294b-1, holotype, from Kobayashi, 1957, pl. 4 fig. 5. All internal molds unless otherwise indicated. AML = Ao Mo Lae. Scale bars = 2 mm for 2–20; = 1 mm for 1.

Pagodia thaiensis Kobayashi, 1957

Figs 3:22, 23

1957. *Pagodia thaiensis* Kobayashi p. 372, pl. 4 figs. 5–7, Figs 20.20, 21.8.

?1988. Leiostegiid gen. et sp. indet. Shergold et al., p. 314, fig. 3E.

Occurrence.—Laem Hin Ngam 2.85–3.69m, Ao Talo Topo west, Ao Talo Topo h2, and Ao Mo Lae 3.62–6.01m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Cambrian Stage 10.

Material.— 31 cranidia: one from Laem Hin Ngam (LHN) 2.85 m (_10); four from Ao Talo Topo (ATT) west (_13, 54, 102–external mold, 107); 26 from Ao Mo Lae (AML) 3.62 m (_3), 5.17 m (_13, 19, 20, 45–external mold), 5.81 m (_16 – external mold, 20, 24, 28, 29, 60, 62, 66, 72, 110, 143, 147–external mold, 155, 156, 170, 195–external mold, 199, 219), 5.84 m (_37), 6.01 m (_1), and h3 (_14). Nine pygidia: one from LHN 3.69 m (_3); one from ATT h2 (_2); seven from AML 5.17 m (_38, 47) and 5.81 m (_82, 101, 149, 161, 184). All internal molds unless otherwise indicated.

Remarks.—Shergold et al. (1988) reassigned the type material to *Parakoldinioidia* Endo, 1937, suggesting the two cranidia are synonymous with specimens illustrated in Shergold et al.'s 1988 publication. However, the collections made in 2008–2018 provide sufficient material to determine that the specimens figured in Shergold et al. (1988) and Kobayashi (1957) as *Parakoldinioidia thaiensis* and *Pagodia thaiensis,* respectively, represent three distinct species from three separate genera: *Parakoldinioidia*, *Pseudokoldinioidia* Endo, 1944, and *Pagodia*. New collections contain a reasonably large sample size of *Pseudokoldinioidia sardsudae* and *Pagodia thaiensis* with insufficient morphological overlap between these species to suggest they might be synonymous. Likewise, specimens of the rarer species *Parakoldinioidia callosa* Qian, 1985 do not morphologically grade into either species.

Kobayashi (1957) assigned a single pygidium to *Pagodia thaiensis* (PB02294b-2, pl. 4, fig. 7; Fig. 3:23.8) which looks similar to the narrower *P. sardsudae* in the published figure. Reexamining this material, however, shows that the pygidium is broad with a relatively narrower axis consistent with *Pagodia thaiensis*. The misleading appearance is due to shadow obscuring a large portion of the pleural field.

The specimen that Shergold et al. (1988) referred to leiostegiid gen. et sp. indet. (Shergold et al., 1988 fig. 3E) is more similar in size and overall morphology to *P. thaiensis* than to any other specimens found in the Tarutao Group. The two major points of differentiation are that the specimen figured by Shergold et al. (1988, fig. 3E). has a

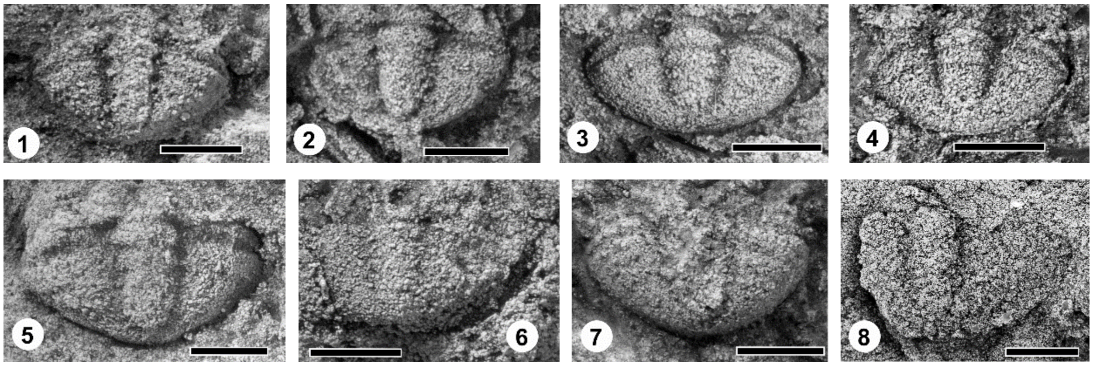


Figure 3:23 Pagodia thaiensis Kobayshi, 1957, all pygidia. **(1)** _161, AML 5.81 m; **(2)** _38, AML 5.17 m; **(3)** _82, AML 5.81 m; **(4)** _101, AML 5.81 m; **(5)** _47, AML 5.17 m; **(6)** _184, AML 5.81 m; **(7)** _149, AML 5.81 m; **(8)** CMC IP87003, vinyl polysiloxane cast of UMUT PB 02294b-2 from Kobayashi, 1957, pl. 4 fig. 7. All internal molds. AML = Ao Mo Lae. Scale bars = 2 mm.

convex glabellar outline rather than slightly concave lateral margin of *P. thaiensis*, and it also has narrow fixigenae. As to the first difference, *P. thaiensis* demonstrates intraspecific variability in this character with some specimens (e.g. Figs 3:22.1,9) approaching a similarly shaped glabellar outline. Addressing the second difference: *P. thaiensis* also shows variation in width of the fixigena; furthermore, the specimen figured by Shergold et al. (1988) is incomplete and thus the fixigena may be wider than they appear, particularly across the posterolateral projections. An important point of similarity is that the lateral furrows, though nearly effaced on the unidentified leiostegiid, have the same spacing and curvature as in *P. thaiensis*. For these reasons, the unidentified leiostegiid documented by Shergold et al. (1988) is herein tentatively assigned to *P. thaiensis*.

Pagodia? *uhleini* n. sp.

Figs 3:24–26

1988. *Szechuanella*? cf. *damujingensis* (Lo, 1974): Shergold et al., p. 313–314, figs 3F–N.

Type material.—Holotype: ATDB-7.0_2 (Fig. 3:25.21), Ao Talo Udang S1 7.00 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Cambrian Stage 10. Paratypes: ATDB-6.65_2, 3, 5, 6, 8, 9, ATDB-7.0_2, 3, 11, 14, 26, 27, 32, 35, 43, 45, 55, 56, 60, 62, 64, 69, 71, 79, 81, 85, 88, 91, 95, 97–99, 105, 107, 115, 118, 126, 128, 133, 136, 140, 142, 143, 150, 160, 163, 170, 171, 174, 179, 201, 204, 208, 209, 214, 223, 224, 225, 237, 238, 239,241, 247, 248, 251, 254, 255, 261, 263, 273, 274, 275, 276, ATDA_9, 29, ATDB_8, 24].

Diagnosis.—Cranidium with long, medially constricted, slightly anteriorly tapering glabella protruding anteriorly of fixigenae, faint to effaced lateral glabellar furrows, dorsally inflated occipital lobe, faint eye ridges, short and strongly curved anteriorly placed palpebral lobes, and faint granulation. Pygidium with long, strongly convex axis extending to posterior border with four to five axial rings and a long, bullet-shaped terminal piece; broad border defined by distinct border furrows; effaced interpleural furrows and straight, well-defined pleural furrows terminating at border furrow.

Occurrence.—Ao Talo Udang S1 6.65–7.00 m and S2 0.52–0.69 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Description.—Cranidium subtrapezoidal to subtriangular with cranidial width (tr.) across the palpebral lobes 1.15–1.45 times cranidial length (sag.); anterior margin strongly curved to subangular. Glabella long (sag.), protruding beyond anterior end of fixigenae; preglabellar furrow deeply incised; anterior

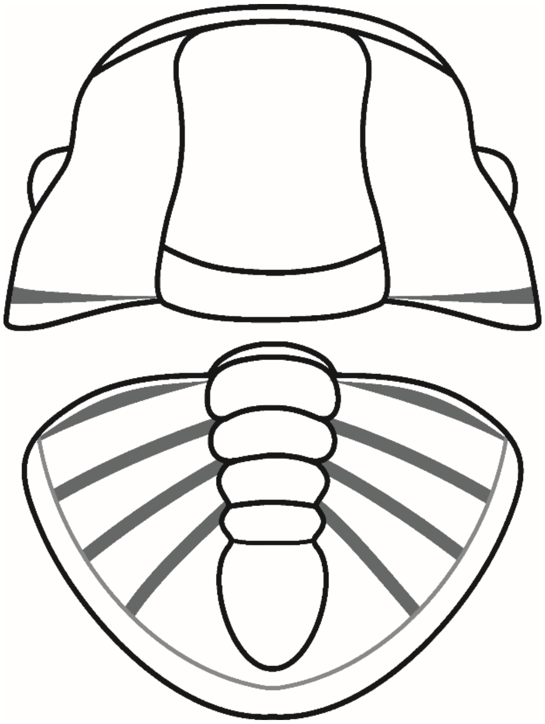


Figure 3:24 Pagodia? uhleini n. sp. line drawing

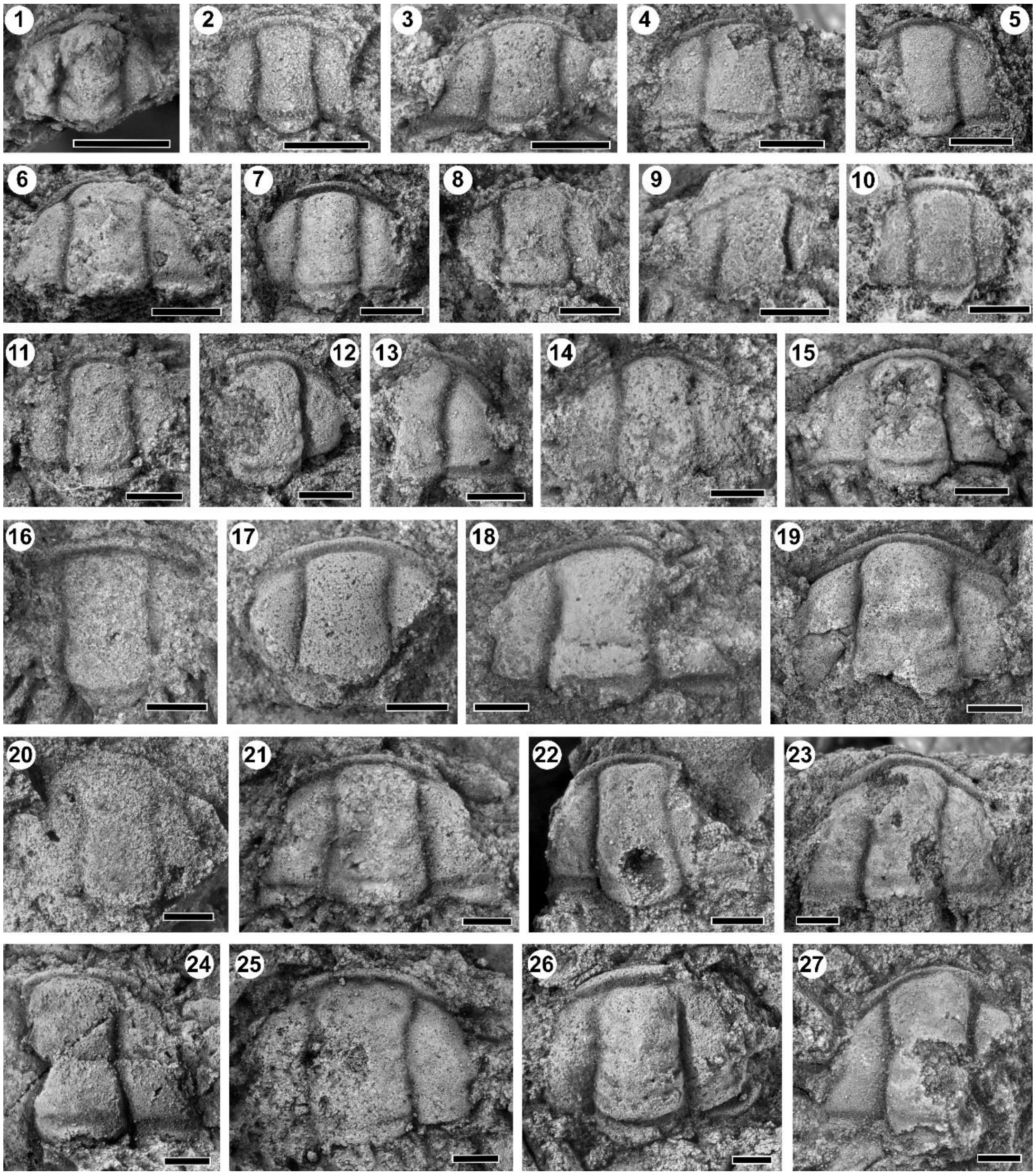


Figure 3:25 Pagodia? *uhleini* n. sp., all cranidia. **(1)** _99, ATD S1 7.00 m; **(2)** _150, ATD S1 7.00 m; **(3)** _2, ATD S1 6.65 m; **(4)** _275, ATD S1 7.00 m; **(5)** _62, ATD S1 7.00 m; **(6)** _56, ATD S1 7.00 m; **(7)** _85, ATD S1 7.00 m; **(8)** _254, ATD S1 7.00 m; **(9)** _128, ATD S1 7.00 m; **(10)** _238, external mold, ATD S1 7.00 m; **(11)** _241, ATD S1 7.00 m; **(12)** _142, ATD S1 7.00 m; **(13)** _255, ATD S1 7.00 m; **(14)** _239, ATD S1 7.00 m; **(15)** _3, ATD S1 7.00 m; **(16)** _179, ATD S1 7.00 m; **(17)** 208_, ATD S1 7.00 m; **(18)** _126, ATD S1 7.00 m; **(19)** _3, ATD S1 6.65 m; **(20)** _24, ATD S2 0.69 m; **(21)** _2, holotype, ATD S1 7.00 m; **(22)** _276, ATD S1 7.00 m; **(23)** _91, ATD S1 6.65 m; **(24)** _247, ATD S1 7.00 m; **(25)** _60, ATD S1 7.00 m; **(26)** _88, ATD S1 7.00 m; **(27)** _160, ATD S1 7.00 m. All internal molds unless otherwise indicated. ATD = Ao Talo Udang Sections 1 (S1) and 2 (S2). Scale bars = 2 mm.

glabellar margin moderately curved to strongly curved, frequently with medial cleft; axial furrows deeply incised; glabella gently anteriorly tapering (tr.) with anterior glabella 85–95% of L1; LO equal width or slightly broader (tr.) than L1; glabellar margin concave, weakly to strongly constricted at S2; lateral glabellar furrows nearly effaced with S1 and S2 faintly defined in some specimens; S1 short and curved posteriorly; S2 short and straight, slightly posteromedially oblique; SO posteriorly bowed and faint to well-incised; occipital ring lengthens (sag.) and becomes dorsally elevated medially with small occipital node. Palpebral lobes short (exsag), strongly and evenly curved, and positioned with midpoint oppositeL2; faint eye ridge present. Anterior suture branch anteriorly convergent to subparallel or even slightly divergent. Anterior border short (sag., exsag.); anterior border furrow strongly incised and confluent with preglabellar border furrow; anterior border strongly curved with medial portion more strongly curved than lateral. Posterolateral projections long (exsag.) and triangular; posterior margin medially transverse; posterior border furrow strongly incised; posterior border short and slightly laterally lengthening (exsag.).

Pygidium semielliptical with width (tr.) across anterior pleural band, the widest point, 1.4–1.6 times pygidial length (sag.); anterior margin gently anteriorly bowed; posterior margin strongly curved. Axial length 85–90% cranidial length (sag.); axial width across anterior most ring ~25% cranidial width (tr.) at widest point; axial furrows moderately to strongly incised, gently curved for concave axial outline; axial ring furrows straight (tr.); 4 axial rings clearly defined by well-incised furrows, one axial ring poorly defined, and strongly-posteriorly rounded terminal piece with a well-defined posterior axial furrow. Pleural bands of subequal length (exsag.) interpleural furrows effaced; pleural furrows straight and strongly incised; pleural furrows terminate at lateral margin. Pygidial border narrow but well-defined by sharp termination of pleural bands and gently incised border furrow; lateral and posterior border of constant thickness (tr., exsag., sag.).

Etymology.—Named in honor of Dr. Gabriel Uhlein in gratitude for him finding the bed in which this species occurs.

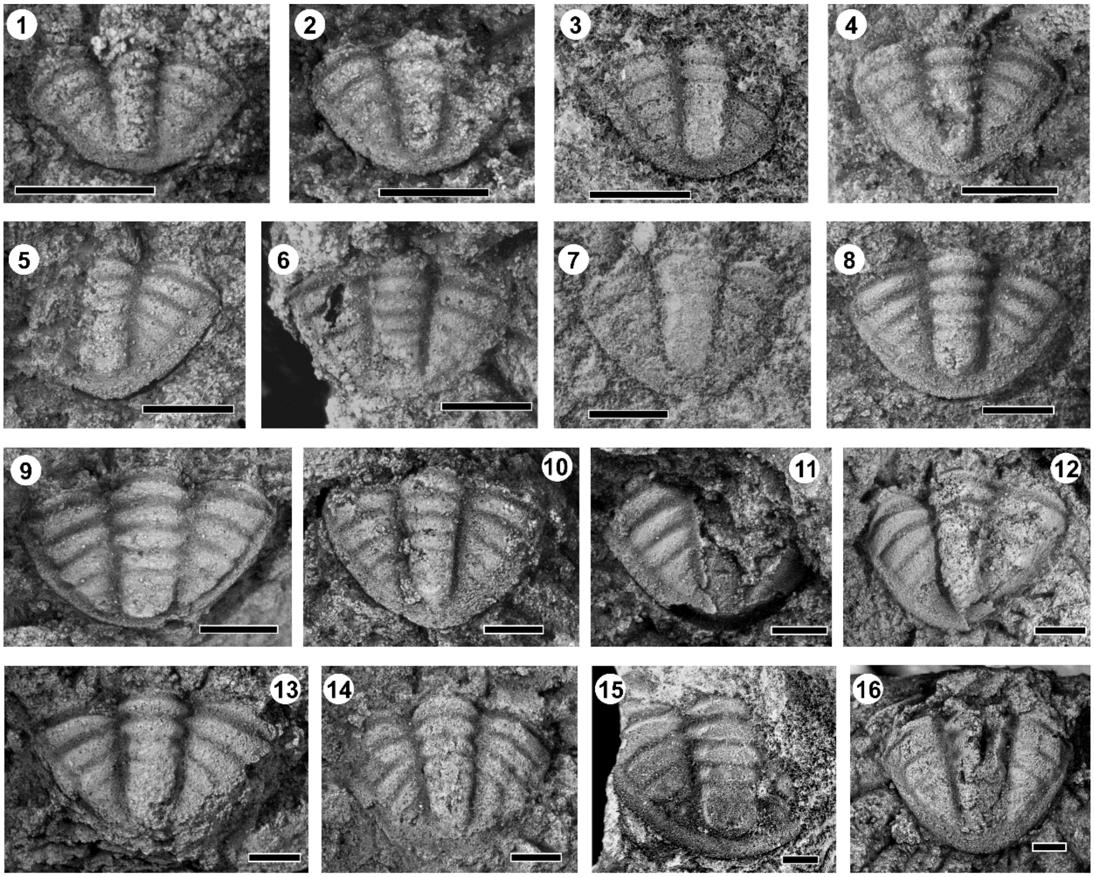


Figure 3:26 Pagodia? *uhleini* n. sp., all pygidia. **(1)** _8, ATD S1 6.65 m; **(2)** _170, ATD S1 7.00 m; **(3)** _107, external mold, ATD S1 7.00 m; **(4)** _251, ATD S1 7.00 m; **(5)** _9, ATD S1 6.65 m; **(6)** _214, ATD S1 7.00 m; **(7)** _273, external mold, ATD S1 7.00 m; **(8)** _6, ATD S1 6.65 m; **(9)** _171, ATD S1 7.00 m; **(10)** _81, ATD S1 7.00 m; **(11)** _26, ATD S1 7.00 m; **(12)** _14, ATD S1 7.00 m; **(13)** _225, ATD S1 7.00 m; **(14)** _5, ATD S1 6.65 m; **(15)** _105, external mold, ATD S1 7.00 m; **(16)** _237, ATD S1 7.00 m. All internal molds unless otherwise indicated. ATD = Ao Talo Udang Sections 1 (S1) and 2 (S2). Scale bars = 2 mm.

Material.—53 cranidia: four from Ao Talo Udang (ATD) S2 0.52 m (_9, 29) and 0.69 m (_8, 24); 49 from ATD S1 6.65 m (_2, 3) and 7.00 m (_2, 3, 11, 32, 35, 43, 45, 56, 60, 62, 64, 69 – external mold, 71 – external mold,79, 85, 88, 91, 95, 97 – external mold, 99, 115, 118, 126, 128, 133 – external mold, 136, 140, 142, 143, 150, 160, 174, 179, 204, 208, 209, 223, 238, 239, 241, 247, 248, 254, 255, 274, 275, 276). 24 pygidia from ATD S1 6.65 m (_5, 6, 8, 9) and 7.00 m (_14, 26, 27, 55 – external mold, 81, 98, 105, 107 – external mold, 163, 170, 171, 201, 214, 224, 225, 237, 251, 261,263,273 – external mold). All internal molds unless otherwise indicated.

Remarks.—The specimens herein assigned to *Pagodia*? *uhleini* are undifferentiable from the material assigned by Shergold et al. (1988) to *Szechuanella*? cf. *damujingensis* (Luo, 1974). Both collections are from Ao Talo Udang. When Shergold et al. (1988) assigned it to *Szechuanella* Zhang and Fan, 1960, they left it in open nomenclature, commenting that it could also be plausibly assigned to *Leiostegium* Raymond, 1913 but that *Szechuanella* was preferred because of pygidial similarities between of *Szechuanella szechuanensis* and the Thai material. The pygidial border furrow and well-defined pleural furrows of the Thai material are inconsistent with *Leiostegium.*

Pagodia is another viable generic assignment for this material. Several authors have remarked on the similarities between *Szechuanella* and *Pagodia* (e.g. Lu, 1975, Shergold et al., 1988). Lu (1975, p. 296) enumerated the differences between *Pagodia* and *Szechuanella* with the conclusion that *Pagodia*, exclusively described from the upper Cambrian, may be ancestral to *Szechuanella*, exclusively described from the

Tremadocian (with the exception of Shergold et al., 1988; Zhou and Zhou in Zhou and Zhen, 2008). These differences include the width of the fixigena, coarseness of granulation, acuteness of the edge of the frontal border, and orientation of the anterior facial branches. The most diagnostic character among these is that *Pagodia* has anteriorly convergent facial sutures while *Szechuanella* has anteriorly divergent sutures. The material presented herein has fine or no granulation and relatively narrow fixigena like *Szechuanella*, but the angularity of the anterior margin is variable and the anterior facial suture branches may be convergent or divergent. The lateral glabellar furrows of *Szechuanella* tend to be more effaced than in *Pagodia*, but the effacement of *Pagodia* is variable both among species (Kobayashi, 1933, pl. 11 figs 4–11) and within the same species (e.g. *Pagodia thaiensis* Kobayashi, 1957, fig. 10). The pygidium of *Szechuanella* cannot be reliably differentiated from that of *Pagodia* as both have long axes, well defined pleural furrows but effaced interpleural furrows, and a defined pygidial border and border furrow. Based on the anterior suture branches being anteriorly convergent more often than divergent and the clear expression of lateral glabellar furrows on numerous specimens at variable sizes, we herein tentatively assign the Thai material to *Pagodia* as *P.*? *uhleini*. *Pagodia*? *uhleini* is larger than a typical species of *Pagodia* with the largest specimen reaching a cranidial length of 8.7 mm compared to a maximum length of 5.3 mm for *Pagodia thaiensis*.

The decision to assign this Thai material to *Pagodia*? did not depend on stratigraphic criteria but is stratigraphically conservative. If the Thai material is *Szechuanella*, this would be the oldest and first non-Ordovician occurrence of that genus;

as *Pagodia* it is consistent with this genus' stratigraphic range known from elsewhere (Zhou and Zhen, 2008). This species may indicate the evolutionary relationship suggested by Lu, 1975 between the Cambrian *Pagodia* and the Ordovician *Szechuanella*, but a thorough phylogenetic analysis incorporating multiple species from both genera is required to test this hypothesis.

Rather than defining a species using the material then available, Shergold et al. (1988). made a comparative assignment to *Szechuanella* cf. *damujingensis*. The type material for *S. damujingensis* is a single mildly deformed cranidium and probably also deformed pygidium though whether the pygidium is naturally short or has been artificially shortened by deformation is not clear (Lo, 1974). Independent of this deformation, the palpebral lobes of *S. damujingensis* are too far posterior and the anterior border is too wide (tr.) to be the same species as the Thai material. Furthermore, the pleural furrows extend to the margin of the pygidium of *S. damujingensis* rather than leaving a distinct, unfurrowed pygidial border. As such, a new species is erected herein.

Order PHACOPIDA Salter, 1864

Suborder CHEIRURUINA Herrington and Leanza, 1957

Family PLIOMERIDAE Raymond, 1913

Genus *Parapilekia* Kobayashi, 1934

Type species.—*Calymene*? *speciosa* Dalman, 1827.

Parapilekia bunopasi Stait et al., 1984

Fig. 3:27

1984. *Rossaspis*? *bunopasi* Stait et al., p. 60–63, fig. 5.

Occurrence.—Ao Phante Malacca 27.80 m and 43.60 m and Ao Talo Udang S3 float; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian.

Material.—Two cranidia from Ao Phante Malacca (APM) 27.80 m (_10) and Ao Talo Udang S3 float (_16); one pygidium from APM 43.60 m (_93). All internal molds.

Remarks.— When Stait et al. (1984) tentatively assigned this species to *Rossaspis* Harrington (1957) they explicitly said that it likely belongs to a different genus such as *Parapilekia* or *Kanoshia* Harrington (1957). These genera as well as other pliomerids including *Koraipsis* Kobayashi (1934), *Teinfuia* Kuo et al. (1982), and *Protopliomerops* Kobayashi (1934) have long been considered poorly defined and in need of revision to delineate the differences between them (Fortey and Droser, 1996; Adrain and Karim, 2019). Such generic revisions require extensive work, including a phylogenetic analysis, and are beyond the scope of this paper.

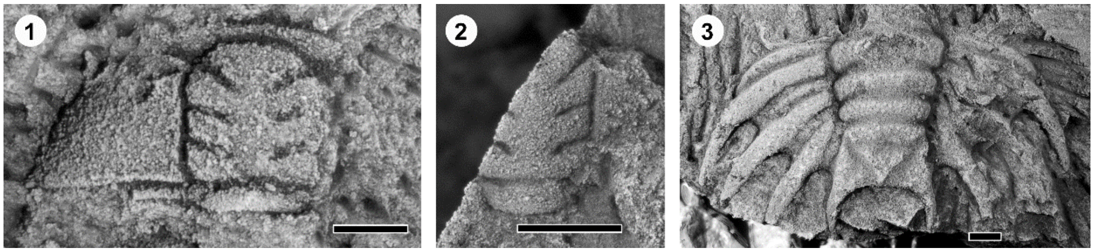


Figure 3:27 *Parapileikia bunopasi* Stait et al., 1984. **(1)** _16, cranidium, Ao Talo Udang S3 float; **(2)** _10, cranidium, APM 28.70 m; **(3)** _93, pygidium, 43.60 m. All internal molds. APM = Ao Phante Malacca. Scale bars = 2 mm.

Stait et al. (1984) chose to assign the species to *Rossaspis* on the grounds of the lack of preglabellar field, size of the anterior border, size and position of the eye ridges, and the position of the spines on the pygidium. They considered the generic assignment questionable due to the strength of the interpleural furrows and the presence of a spine on the posterolateral projection. We consider *Parapilekia* the better generic assignment, because it also has similarly sized and placed eyes, similar eye ridges, and pygidial spines formed by extensions of posterior pleural band. Furthermore, *Parapilekia* includes numerous species with short (exsag.) but well-defined anterior pleural bands, deeply incised interpleural furrows, and spines on the posterolateral projections (e.g. *Parapilekia olesnaensis* Ruzicka, 1935 and *Parapilekia ferrigena* Mergl, 1994).

Order ASAPHIDA Salter, 1864

Superfamily ASAPHOIDEA Burmeister, 1843

Family ASAPHIDAE Burmeister, 1843

Genus *Asaphellus* Callaway, 1877

Asaphellus charoenmiti n. sp.

Figs 3:28–30

1984. *Asaphellus* sp. Stait et al. p. 60, figs 4.1–3.

Type material.—Holotype: APMF_108 (Fig. 3:28.7), Ao Phante Malacca 43.60 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; uppermost Furongian–

Tremadocian. Paratypes: APMG_1, 2, 4, 5, 6, 13, 17, 19, 20, 27, 28, 29, 30, 31, 33, 35, 37, 39, 62, 68, 90, 93, APMB2.95_2, 3, 5, 6, APMB34_6, APMB35_1, 3, 6, 13, APMB1_1, 4, 10, 11, 18, 33, 43, 50, APME_7, 9, 14, 16, APMF_2, 12, 25, 27, 41, 42, 43, 44, 50, 58, 61, 69, 70, 82, 90, 91, 97, 104, 108, 111, 112, 113, 114, 115, 116, APM-B5.7_4, 16, 17, APM-B15.2_3, 4, 5, 7, 8, APM-B16.25_1, 2, 4, 5, 6, 9, 12, 13, 15, 17, 18, APM-B16.5_1, 2, APM-B48_2, 3, 7, 10, 11, 12, APMgam_1, 2, 3a, 7, 9, 11].

Diagnosis.—Long (sag.) medially constricted cranidium with medially constricted, strongly anteriorly rounded glabella; anterior margin broad (tr.) and smoothly but less strongly curved than the anterior glabellar margin; palpebral lobes short (exsag.) and strongly curved. Pygidium subelliptical with broad, depressed border, effaced pleural and interpleural furrows, seven or more axial rings, well-defined axial and post-axial furrows and inflated, broad (exsag.) articulating facets.

Occurrence.—Ao Phante Malacca 0.05–60.20 m and Ao Talo Udang S3 float; Talo Wao Formation, Tarutao Group, Ko Tarutao, Tremadocian.

Emended Description.—Cranidium of low convexity; cranidial length (sag.) 1.8–2.25 times cranidial width (tr.) at anterior corner of

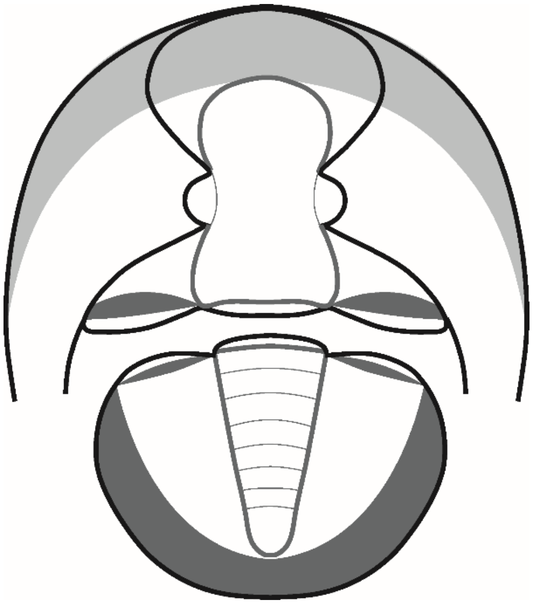
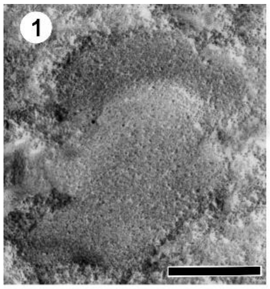


Figure 3:28 Asaphellus charoenmiti n. sp. line drawing.

palpebral lobe; width (tr.) across posterolateral projections nearly equal to cranidial length; width (tr.) across frontal area 1.5-1.75 times width (tr.) across anterior corner of palpebral lobes; anterior branches of facial sutures diverge at 35°–45°, reach widest point at lateral corners of anterior border and then converge to meet medially; curvature of anterior facial suture branches and anterior margin variable with angular anterior margin more common in larger specimens; posterior suture branches gently sigmoidal. Glabella 75–80% cranidial length, strongly anteriorly rounded; nearly straight, parallel to slightly anteriorly convergent axial furrows; axial furrows and preglabellar furrow faint; lateral glabellar furrows completely effaced; SO faint; LO short (sag., exsag.), lenticular, especially at larger sizes. Anterior border gently inflated ; separated from glabella by broad preglabellar field; anterior border furrow effaced. Palpebral areas narrow; palpebral lobes short, ~20% glabellar length including LO, adjacent to glabella, located at glabellar mid-length, and strongly curved. Posterolateral projections triangular with nearly blunt termination at facial sutures; posterior border furrow broad and distinct, outlining gently inflated posterior border.

Librigena broad and ~1/4 circle in outline; border and doublurebroad, narrowing posteriorly; lateral and posterior border furrow absent. Ocular surface sharply upturned, short (exsag.) and strongly rounded. Genal spine broad at base and weakly tapering. Doublure broad with faint, irregular ridges; median ventral suture.

Figure 3:29 (Next page) *Asaphellus charoenmiti n. sp.* **(1)** _18, cranidium, external mold, APM 53.65 m; **(2)** _50, cranidium, APM 43.60 m; **(3)** _9, cranidium, APM 27.80 m; **(4)** _69, cranidium, latex cast, APM 43.60 m; **(5)** _112, cranidium, APM 43.60 m; **(6)** _64, cranidium, APM 43.60 m; **(7)** _108, holotype, cranidium, APM 43.60 m; **(8)** _1, cranidium, APM 53.65 m; **(9)** _113, cranidium, APM 43.60 m; **(10)** _39, cranidium, APM 42.75 m; **(11)** _12, cranidium, APM 60.20 m; **(12)** _11, librigena, APM 15.10 m; **(13)** _36, APM 53.65 m. All internal molds unless otherwise indicated. APM = Ao Phante Malacca. Scale bars = 2 mm for 1–9; = 4 mm for 10–13.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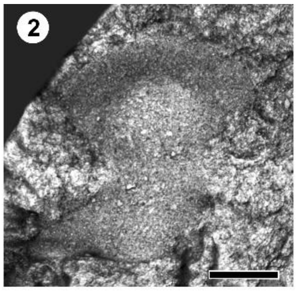
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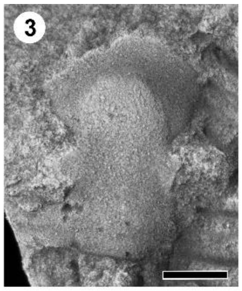
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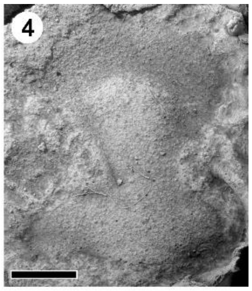
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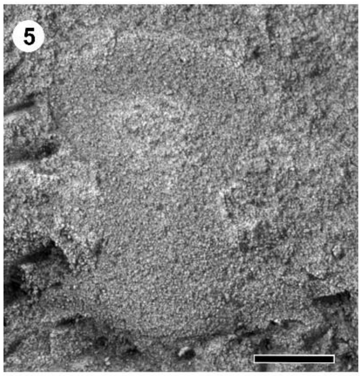
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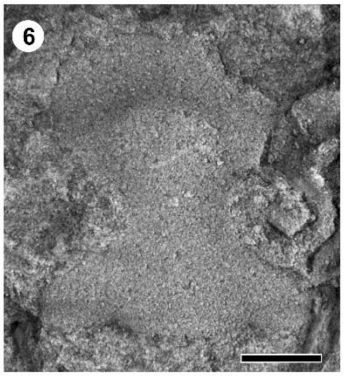
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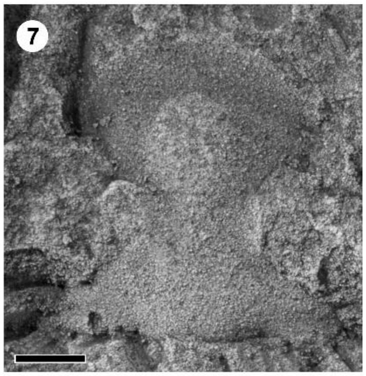
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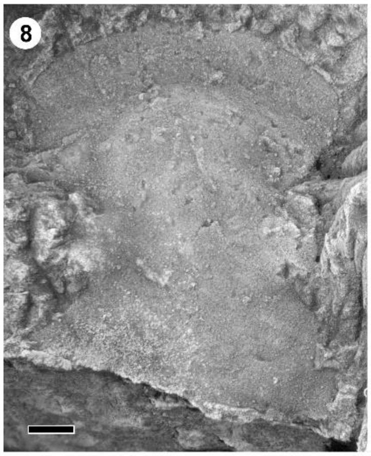
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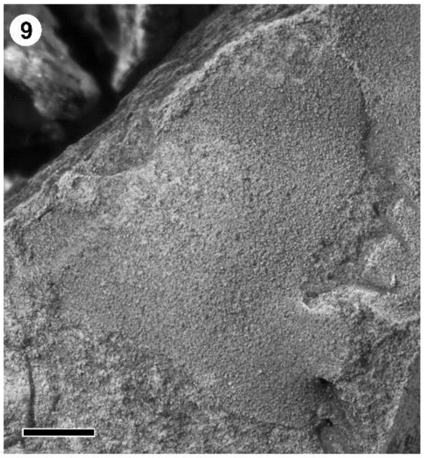
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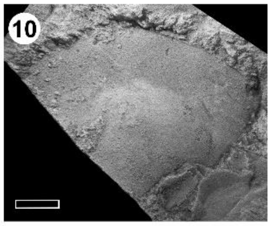
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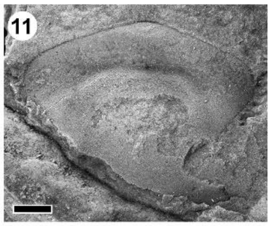
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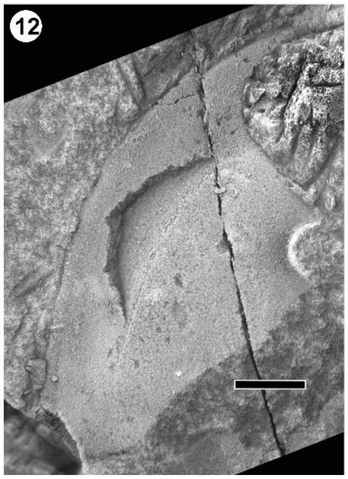
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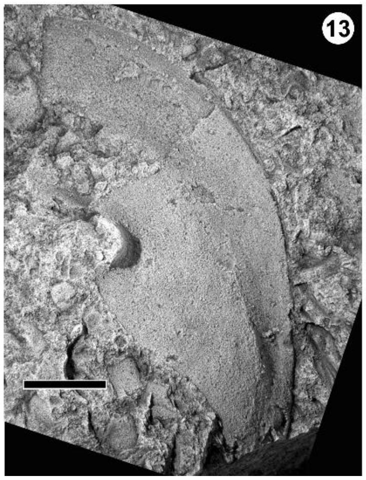
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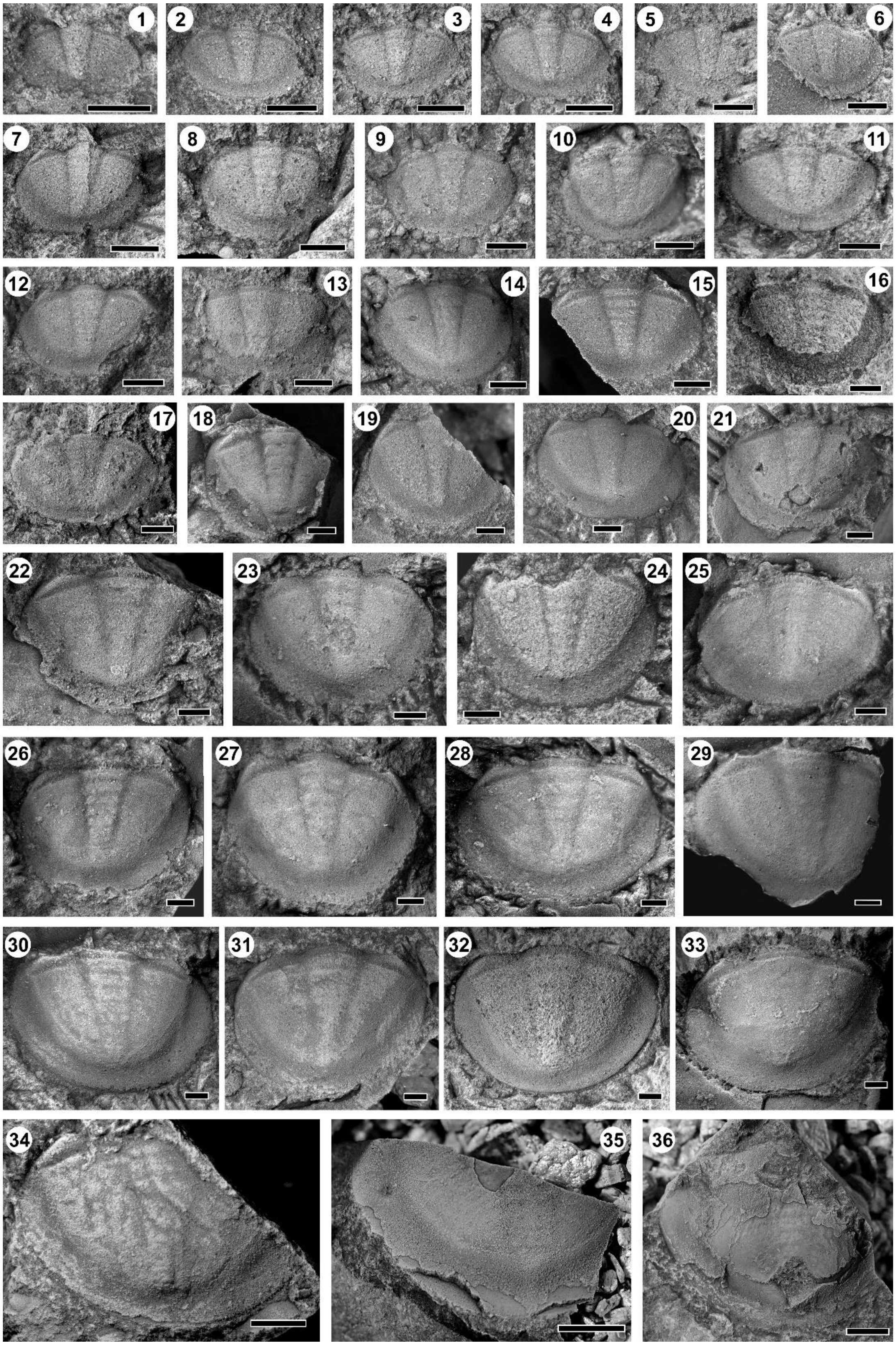
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Figure 3:30 (*Previous page*) *Asaphellus charoenmiti* n. sp., all pygidia. **(1)** _16, APM 48.65 m; **(2)** _1, APM 27.80 m; **(3)** _5, APM 29.35 m; **(4)** _15, APM 27.80 m; **(5)** _111, APM 43.60 m; **(6)** _3, APM 60.20 m; **(7)** _4, APM 27.80 m; **(8)** _4, APM 27.35 m; **(9)** _3, APM 27.35 m; **(10)** _41, APM 43.60 m; **(11)** _70, APM 43.60 m; **(12)** _18, APM 27.80 m; **(13)** _11, APM 53.65 m; **(14)** _12, APM 27.80 m; **(15)** _2, APM 27.80 m; **(16)** _10, ATD S3 float; **(17)** _33, APM 53.65 m; **(18)** _31, APM 42.75 m; **(19)** _91, APM 43.60 m; **(20)** _17, APM 27.80 m; **(21)** _116, APM 43.60 m; **(22)** _114, APM 43.60 m; **(23)** _90, APM 42.75 m; **(24)** _2, APM 43.60 m; **(25)** _29, APM 42.75 m; **(26)** _43, APM 43.60 m; **(27)** _42, APM 43.60 m; **(28)** _4, APM 42.75 m; **(29)** _62, latex cast, APM 42.75 m; **(30)** _27, APM 42.75 m; **(31)** _90, APM 43.60 m; **(32)** _19, ATD S3 float; **(33)** _68, APM 42.75 m; **(34)** _2, APM 42.75 m; **(35)** _2, APM 0.05 m; **(36)** _3, APM 0.05 m. All internal molds unless otherwise indicated. APM = Ao Phante Malacca; ATD S3 = Ao Talo Udang Section 3. Scale bars = 2mm for 1–33; = 4 mm for 34; = 8 mm for 35,36.

Pygidium subelliptical, width (tr.) at widest point 1.4–1.5 times length; strongly curved posterior margin. Axis long (sag.), 80–90% pygidial length; seven or more axial rings plus terminal piece; axial furrows straight, shallow. Flattened posterior border occupies entire postaxial glabella; border offset from pleural field by strong ventral slope; from posteromedial margin border broadens laterally and then narrows again toward the anterolateral margin. Pleural field effaced except for deep furrows differentiating lens-shaped, upturned flanges; interpleural furrows entirely effaced; where visible pleural furrows straight and subparallel.

Etymology.—Named in honor of Mr. Jirasak Charoenmit of the Thai department of Mineral Resources in recognition for his extensive help with fieldwork on Ko Tarutao.

Material.—27 cranidia from Ao Phante Malacca (APM) 18.00 m (_16), 27.35 m (_7), 27.80 m (_5, 9), 42.75 m (_30, 33, 39), 43.60 m (_25, 27 – external mold, 50, 61, 69 – external mold, 82, 97, 104, 108, 112, 113), 46.05 m (_6), 47.30 m (_3,6), 48.65 m (_9), 53.65 m (_1, 4, 10, 18 – external mold), and 60.20 m. 14 librigenae from APM horizons 15.10 m (_11), 18.00 m (_13), 27.80 m (_16), 28.70 m (_8), 42.75 m (_23 – external mold, 32 – external mold, 42 – external mold,91), 43.60 m (_72), 47.30 m (_14 – external mold), 48.65 m (_8, 18), and 53.65 m (_3, 36). 80 pygidia: 71 from APM 0.05 m (2, 3a,7, 9 – external mold, 11 – external mold), 15.10 m (_2, 3, 5, 6), 18.00 m (_4, 17 – external mold), 27.35 m (_3, 4, 5, 8), 27.80 m (_1 – internal and external mold, 2, 4, 6, 12, 13, 15, 17, 18), 28.70 m (_1 – internal and external mold, 2), 60.20 m (_2, 3, 7, 10, 11 – external mold), 42.75 m (_1 – external mold, 2, 4, 5, 6 – external mold, 13, 17 – external mold, 19, 20, 27, 28 – external mold, 29, 31, 35 – external mold, 37, 62 – external mold, 68, 90, 93), 43.60 m (_2, 12 – external mold, 41, 42, 43, 44, 58, 70, 90, 91, 111, 114, 115, 116), 48.65 m (_7, 14, 16), and 53.65 m (_11, 33, 43 – external mold, 50); nine from Ao Talo Udang S3 float (_1, 3, 10, 12, 13, 14, 19, 28 – external mold, 37 – external mold). All internal molds unless otherwise indicated.

Remarks.—The cranidium of *Asaphellus charoenmiti* is nearly indistinguishable from *Asaphellus acutulus* Zhou and Zhang, 1978 with the exception that the anterior border of the latter is slightly more strongly curved. The two species, however, are readily differentiated by the broader pygidium of *A. acutulus*. Compared with *Asaphellus homfrayi* (Zhang, 1989) and *Asaphellus trinodus* Zhang, 1989, *A. charoenmiti* has a broader (tr.) frontal area between consequently more strongly diverging anterior suture branches. *Asaphellus tomkolensis* Kobayashi, 1934 has a concave point to its anterior margin which distinguishes it from *A. charoenmiti* and other species of *Asaphellus*. *Asaphellus coreanicus* Kobayashi, 1934 is different from *A. charoenmiti* in the anterolateral sweep of the preocular anterior facial sutures and palpebral lobes that stick out farther than in other species of *Asaphellus*.

The occipital lobe described herein is considerably longer than that described by Stait et al. (1984). Stait et al. (1984) were able to distinguish only the occipital posterior band which is lenticular and evident in more specimens than the occipital lobe which is equal in length (exsag.) to the cranidium’s posterior border (e.g. Fig. 3:29.3).

During holaspid ontogeny the pygidium becomes relatively longer (sag.). This change may result from proarthrous growth in which segments continue to be added after the last segment has been released into the thorax (Hughes et al., 2006). However, the effacement of the axis in smaller specimens impedes further investigations into this ontogenetic issue.

Family REMOPLEURIDIDAE Hawle and Corda, 1847

Remarks.—Remopleurididae includes genera formerly belonging to Richardsonellidae Raymond in accordance with Adrain et al. (2009) which judged the Ordovician members of Richardsonellidae to be polyphyletic within Remopleurididae.

Pseudokainella malakaensis was previously the only remopleurid known from the Tarutao Group (Stait et al., 1984).

Genus *Apatokephalus* Brögger, 1896

Type species.—Trilobites serratus Boeck, 1838, p. 139; designated by Bassler, 1915.

Remarks.—Apatokephalus is distinguished by the combination of an urceolate glabella closely flanked by long (exsag.) arcuate palpebral lobes and a distinct preglabellar field (Brögger, 1896; Shergold, 1991). Some species (e.g. *A. hyotan* Kobayashi, 1953), have been assigned to *Apatokephalus* despite the lack of a preglabellar field, giving this genus considerable morphological overlap with *Fatocephalus* Duan and An (in Kuo et al., 1982) which is stratigraphically older, dating to Cambrian Stage 10 while *Apatokephalus* is most common in the middle to upper Tremadocian, though it has been reported from the Cambrian (Zhou and Zhen, 2008). Shergold (1991) did not discuss the potential for this overlap to reveal polyphyly or paraphyly between these genera, noting only that they can be delineated using the age difference. Age is not a criterion we consider valid in assessing systematic placement, and Remopleurididae would greatly benefit from an extensive phylogenetic analysis to help determine the nature and validity of its genera. Such analysis is outside the scope of this paper.

Apatokephalus arcuatus n. sp.

Figs 3:31,32.1

Type material.—Holotype: APMB1_46 (Fig. 3:32.1), Ao Phante Malacca 53.65 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian. *No available paratypes.*

Diagnosis.—Cranidium with firmly incised S1 and S2 pits, exsagitally long preglabellar field that shortens adaxially due to medially shallowing and posteromedially bowed anterior border furrow, long (sag.) anterior border.

Occurrence.—Ao Phante Malacca 53.65 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian.

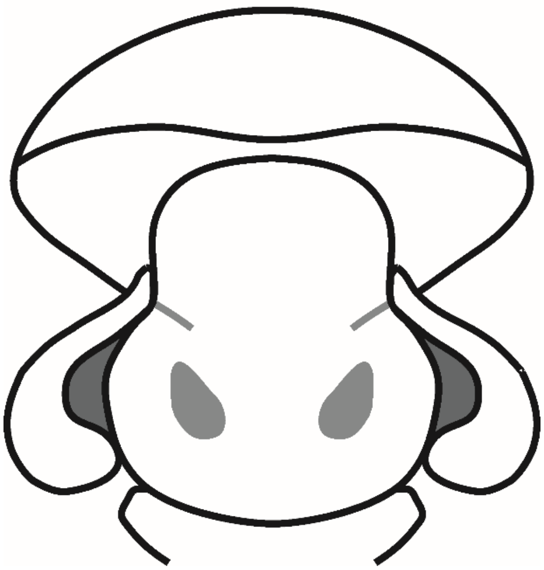
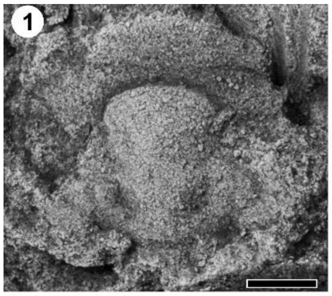


Figure 3:31 Apatokephalus arcuatus n. sp., line drawing.

Description.—Glabella urceolate, expanded (tr.) around firmly incised, posteromedially oriented S1 pit that is disconnected from axial furrow; glabellar width (tr.) at S2 equal to posterior-most and anterior-most glabellar widths; S2 firmly incised and posteromedially angled; anterior glabellar margin moderately curved. Palpebral lobes arcuate adjacent to glabella with no interpalpebral fixigena except depressed crescent-shaped palpebral area fully encompassed by axial furrow and palpebral lobe; palpebral lobe inflated and broad (tr.), extending almost from opposite LO to S2; palpebral lobe asymmetrically curved with posterior end more strongly curved. Axial furrow weakly incised preglabellar furrow strongly incised. Anterior suture branches slightly undercut anterior palpebral lobe, diverging moderately outward for broad preocular fixigena that are continuous with the depressed, broad (tr.) preglabellar field. Undulating anterior border furrow with distinct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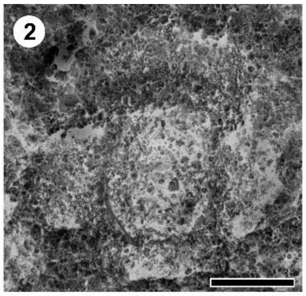
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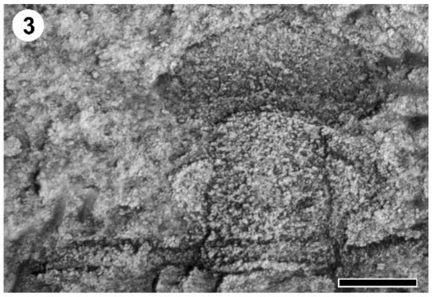
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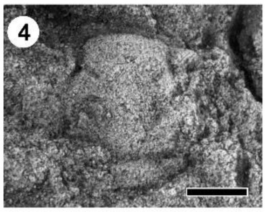
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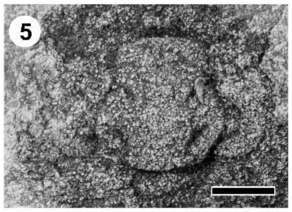
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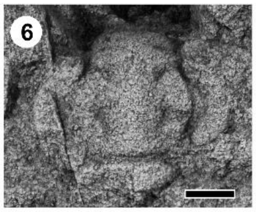
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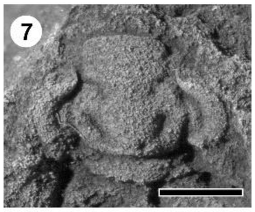
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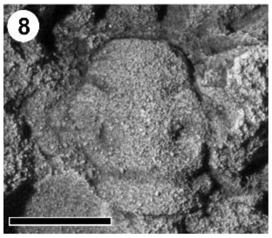
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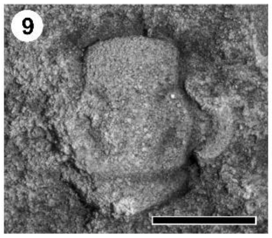
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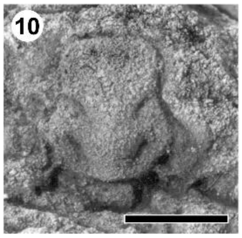
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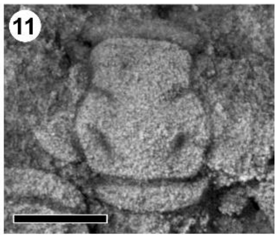
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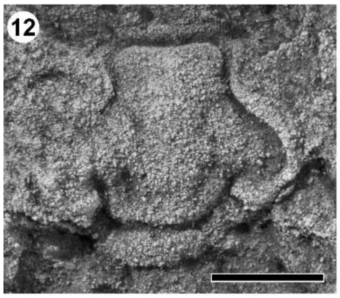
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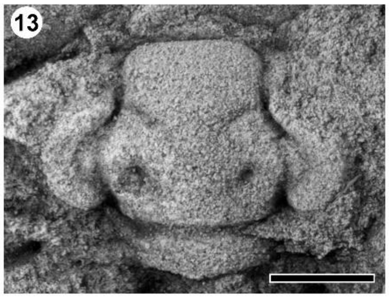
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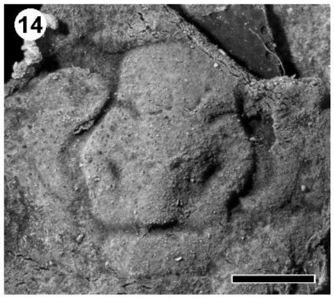
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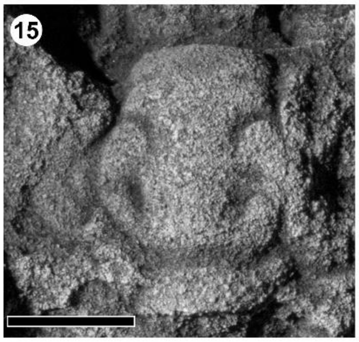
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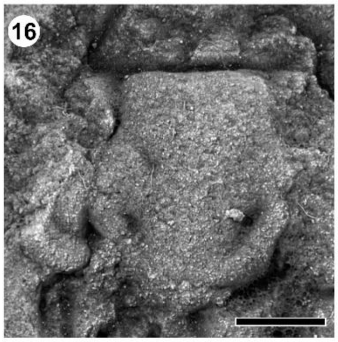
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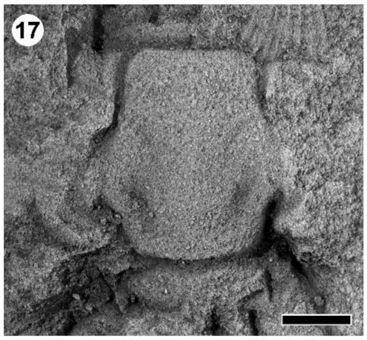
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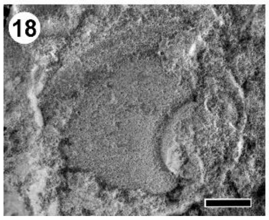
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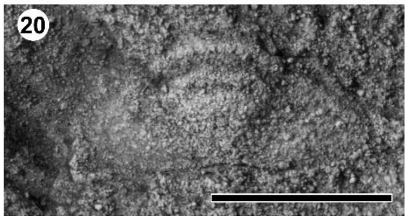
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Figure 3:32 (*Previous page*) *Apatokephalus arcuatus* n. sp., *Yosimuraspis acufrons* n. sp., and *Tarutaoia techawani* n. gen. et sp. **(1)** _46, *Apatokephalus arcuatus*, cranidium, APM 53.65 m; *Yosimuraspis acufrons* (2,3) **(2)** _5, holaspis, cranidium, external mold, ATD S3 float; **(3)** _15, holaspis, cranidium, ATD S3 float; *Tarutaoia techawani* (4–19) **(4)** _5, cranidium, APM 53.65 m; **(5)** _31, cranidium, APM 43.60 m; **(6)** _96, APM 43.60 m; **(7)** _5, cranidium, APM 47.30 m; **(8)** _2, cranidium, APM 47.30 m; **(9)** _7, cranidium, APM 53.65 m; **(10)** _29, cranidium, APM 53.65 m; **(11)** _102, cranidium, APM 43.60 m; **(12)** _109, cranidium, APM 43.60 m; **(13)** _49, holotype, cranidium, APM 53.65

posteromedial bend separates frontal area into medially long anterior border and short preglabellar field but exsagitally long preglabellar field and short anterior border.

Etymology.—Latin for arched, referring to the posteromedially bowed or arched anterior border furrow.

Material.—One cranidium from Ao Phante Malacca 53.65 m, internal mold.

Remarks.—Though it is known from only a single specimen, *Apatokephalus arcuatus* is distinct from all other species of *Apatokephalus* and should be considered a new species. The frontal area is atypically long and has a distinctly undulated or bowed anterior border furrow. A single specimen of *Apatokephalus latilimbatus* Peng, 1990 also displays a slight undulation to its anterior border (Park and Kihm, 2015b, fig. 5.R), not so striking as that of *A. arculatus*, but sufficiently distinct to demonstrate that this character occurs within *Apatokephalus* and a new genus is unnecessary. The two species additionally vary in *A. latilimbatus* possessing longer palpebral lobes and a shorter frontal area.

Genus *Yosimuraspis* Kobayashi, 1960

Type species.—*Yosimuraspis vulgaris* Kobayashi, 1960; from Bankoku Fm., South Korea; by original designation.

Remarks.—Yosimuraspis differs from *Apatokephalus* Brögger, 1896 in both its longer anterior border and preglabellar field and in its more subrectangular rather than urceolate glabella. The long preglabellar field also differentiates it from *Jiia* Zhou and Zhang, 1978 and *Fatocephalus* Duan and An (in Kuo et al.), 1982. The relatively shorter glabella, narrow (sag., exsag.) anterior border, and convex rather than concave preglabellar field differentiates it from *Apatokephalops* Lu, 1975.

Yosimuraspis acufrons n. sp.

Figs 3:32.2,3,19; 33

Type material.—Holotype: ATDGf_15 (Fig. 3:32.3), Ao Talo Udang S3 float; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian. Paratype: ATD Gf_5.

Diagnosis.— Subrectangular to gently urceolate ranidium with weakly pitted S1 and effaced S2, moderately long (sag.) preglabellar field, strongly elongated (sag.) anterior border with angular anterior margin.

Occurrence.—Ao Talo Udang S3 float and Ao Phante Malacca 43.60 m; Talo Wao Formation, Tarutao Group, Ko Tarutao, Tremadocian.

Description.—Glabella subrectangular to gently urceolate, expanded (tr.) around weakly pitted, posteromedially oriented S1 that is disconnected from axial furrow; glabellar width (tr.) at S2 slightly narrower than posterior-most and anterior-most glabellar widths; S2 effaced; LO short and wider than glabella at S1; SO straight (tr.); glabellar anterior moderately rounded. Palpebral lobes longitudinally symmetrically arcuate and adjacent to glabella with no fixigena excepting semicircular palpebral area fully encompassed by axial furrow and palpebral lobe; palpebral lobe extending from nearly opposite SO to anterior of S2, likely to S3. Axial and preglabellar furrows strongly incised. Anterior suture branches strongly anteriorly divergent; convex preglabellar field longer exsagitally than sagitally; anterior border furrow less strongly curved than preglabellar furrow and gently incised; anterior border subpentagongal and long, more than four times length (sag.) of preglabellar field; anterior margin angular. Posterolateral projections short (exsag.) and broad (tr.) with straight (tr.) posterior border furrow; posterior border occupies nearly entire length (exsag.) of posterolateral projections.

Pygidium lens-shaped; axis broad and short with one, possibly two axial rings; terminal piece broad, semicircular; transverse furrow firmly incised; pleural field effaced except first pleural furrow; posterior margin with regular serrations.

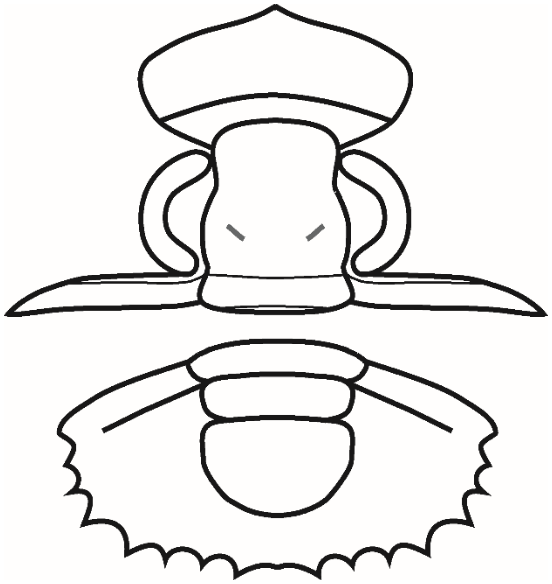

Figure 3:33 Yosimuraspis acufrons n. sp. line drawing; dentition on pygidium is estimated and may vary.

Etymology.—Latin for angular front.

Material.—Two cranidia from Ao Talo Udang S3 float (_15 – internal mold, 5 – external mold).

Remarks.—Yosimuraspis acufrons differs from *Yosimuraspis vulgaris* primarily in the length and angularity of the anterior border and also in the more strongly arched palpebral lobes. The length of the anterior border is most similar to that of *Yosimuraspis luna* Kuo et Duan, but *Y. luna* has longer glabella and less angular anterior margin.

The cranidium of *Y. acufrons* is only known from float at Ao Talo Udang section 3, but a *Yosimuraspis*-type pygidium occurs at Ao Phante Malacca (APMF_59, Fig. 3:32.19). The pleural field is effaced, unlike for *Apatokephalus*, and the axis is short and pauci-segmented, unlike for *Pseudokainella* and *Jiia* (Harringon and Leanz, 1957; Zhou and Zhang, 1987; Kim and Choi, 2000; Park and Kihm, 2015b). The only other potential match for this remopleurid pygidium is *Tarutaoia* n. gen. whose pygidium has not previously been described. It may more plausibly be *Y. acufrons*. A different lens-like pygidium, (APM16.5_7, Fig. 3:32.20) inconsistent with any of the other remopleurids or *Yosimuraspis* is assigned to *Tarutaoia*.

Genus *Tarutaoia* n. gen.

Type species.—Tarutaoia techawani n. sp.; by original designation; by monotypy.

Diagnosis.—As for the type species by monotypy.

Occurrence.—Ao Phante Malacca 18.00–60.20 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian.

Etymology.—Named for the Tarutao Group and Ko Tarutao.

Remarks.—Tarutaoia is similar to other remopleurids including *Apatokephalus* Brögger, 1896, *Apatokephalops* Lu, 1975, *Pseudokainella* Harrington, 1938 (= *Fatocephalus* Duan and An in Kuo et al., 1982; Jell, 1985), and *Yosimuraspis* Kobayashi, 1960 in possessing an urceolate glabella and long, strongly curved inflated palpebral lobes that touch the axial furrows. *Tarutaoia* lacks the preglabellar field present in *Yosimuraspis*, *Apatakephalops*, *Apatokephalus* and some species of *Pseudokainella*. *Jiia* Zhou and Zhang, 1978 and some species of *Pseudokainella*, including those previously assigned to *Fatocephalus*, are described as lacking a preglabellar field. However, in those taxa the preglabellar field is only absent medially where the otherwise discreet preglabellar and anterior border furrows become confluent over some distance (tr.). Laterally the fixigena wrap around the anterior glabellar corners to form a usually depressed exsagittal preglabellar field. In *Tarutaoia* the anterior border furrow is fully confluent with the entire preglabellar furrow such that there is no remnant of a preglabellar field. Furthermore the fixigena are inflated and form a well-incised furrow where they meet the anterior border. This furrow may follow the same orientation as the joint preglabellar and anterior border furrow (e.g. Fig. 3:32.16), or it may be oblique to the medial portion of the anterior border furrow (e.g. Fig. 3:32.14).

Tarutaoia techawani n. sp.

Fig. 3:32.4–18,20

1984. *Pseudokainella malakaensis* Stait et al. p. 56–59, figs 3.3,7 only; figs 3.1,2,4–6 = *Pseudokainella malakaensis.*

Type material.—Holotype: APMB1_49 (Fig. 3:32.13), Ao Phante Malacca 43.60 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian. Paratypes: APMB1_5, APMF_4, 5, 11, 13, 15, 18. 20, 21, 23, 28, 31, 38, 39, 46, 53, 79, 85, 96, 98, 102, 103, 106, 109, APMB35_2, 5, APMB1_7, 8, 14, 15, 16, 22, 25, 29, 40, APMB16.5_6, APMB16.25_11, 14.

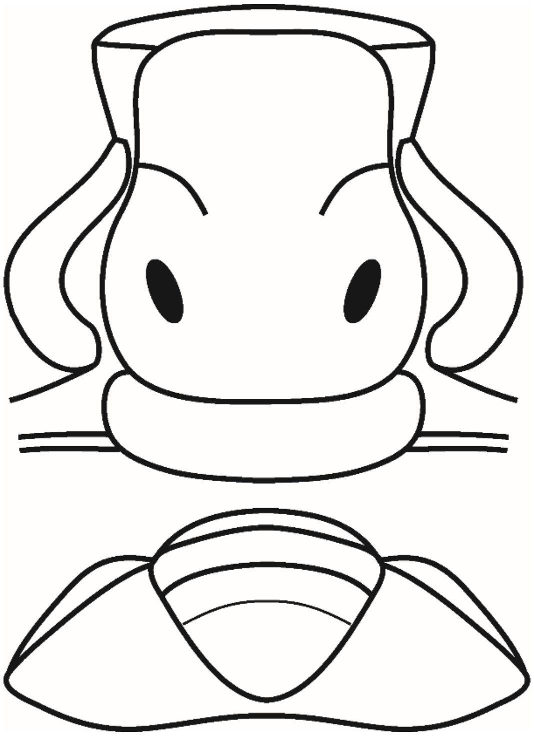
Figure 3:34 Tarutaoia techawani n. gen. et sp. line drawing

Diagnosis.—Cranidium with strongly urceolate glabella and no preglabellar field; S1 firmly incised and disconnected from axial furrows; S2 firmly incised and curved; strongly curved palpebral lobes touching axial furrows; preocular fixigena narrow and separated from anterior border by subtransverse or anterolaterally oblique furrow. Pygidium lenticular with broad, strongly tapering axis, two axial rings, short terminal piece, effaced pleural area except first pleural furrow, and smooth posterior margin.

Occurrence.—Ao Phante Malacca 18.00–60.20 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian.

Description.—Glabella urceolate (urn-shaped), expanded (tr.) around firmly incised, posteromedially oriented S1 pit that is disconnected from axial furrow; glabellar width (tr.) at S2 equal to posterior-most and anterior-most glabellar widths; S2 firmly incised and posteromedially arched; LO subequal in width (tr.) to posterior glabella and variably has obtuse spine node in some specimens; anterior glabellar margin variable including straight (tr.), gently convex, or gently concave. Palpebral lobes arcuate adjacent to glabella with no fixigena excepting narrow, inflated preocular strap and narrow, depressed crescent-shaped palpebral area fully encompassed by axial furrow and palpebral lobe; palpebral lobe inflated, broad (tr.), and long (exsag.) extending from posterior L1 to S2; palpebral lobe asymmetrically curved with anterior end slightly recurved into preocular areas and posterior end more strongly curved. Axial and preglabellar furrows strongly incised. No preglabellar field; anterior border furrow fully confluent with preglabellar furrow; well-incised furrow with oblique or subtransverse orientation separating inflated fixigena and anterior border. Anterior facial sutures gently divergent.

Librigena broad with narrow border, shallow border furrow and wide (tr.) genal field; anterior facial suture changes from anteriorly divergent to convergent sharply at border furrow.

Pygidium lenticular. Axis broad and strongly tapering, reaching posterior margin; axial furrows straight; two axial rings; first transverse axial furrow well-incised and broad (sag.); short terminal piece. Pleural field effaced except first pleural furrow. Posterior margin smooth.

Etymology.—Named in honor of Dr. Sommai Techawan, Director-General of Thai Department of Mineral Resources.

Material.—96 cranidia from Ao Phante Malacca (APM) 18.00 m (_9), 27.35 m (_1), 27.80 m (_11, 14), 28.70 m (_6, 9), 42.75 m (_38), 43.60 m (_3 – external mold, 4, 5, 7, 8, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 26, 28, 29, 31, 33, 34, 35, 38, 39, 40, 45, 46, 47, 51, 53, 54, 55, 57, 60, 74, 77, 78, 79, 83, 84, 85 – external mold, 86, 88, 89, 96, 98, 102, 103, 106, 109, 110), 47.30 m (_2, 5, 7, 10, 11), 48.65 m (_1 – external mold, 2, 5 – external mold, 11 – external mold, 13, 15, 17 – external mold, 19), 49.90 m (_4), 53.65 m (_5, 6, 7, 8, 14, 15,16, 17, 22, 24, 25, 27, 29, 35, 39, 40, 41, 42, 48, 49), and 60.20 m (_6). One pygidium from APM 27.80 m (_7).

Remarks.—Tarutaoia techawani is most distinguished from other remopleurids by its unique frontal area. However, even without a preserved frontal area it can be distinguished from the other remopleurids in the Talo Wao Formation by its deeply-incised, lateral glabellar furrows, particularly the strongly curved S2 which are straight and shallow or nearly effaced in *Yosimuraspis acufrons* n. sp., *Apatokephalus arcuatus* n. sp., and *Jiia talowaois* n. sp. On more effaced specimens of *T. techawani*, a distinction can also be made from *Y. acufrons* and *J. talowaois* based on the strongly urceolate glabellar outline.

A remopleurid-type pygidium is assigned to *Tarutaoia* based on its association with the cranidia at Ao Phante Malacca and its incompatibility with any of the other remopleurids in the Talo Wao Formation. It is too short for *Pseudokainella,* or *Jiia,* too effaced for *Apatokephalus,* and has a more strongly tapering, v-shaped axis than *Yosimuraspis* (Harrington and Leanza, 1957; Zhang and Jell, 1978; Choi and Kim, 2000; Park and Kihm, 2015b). Stait et al. (1984) found pygidia of this form (figs 3.3,3.7) and assigned it to their new species *Pseudokainella malakaensis*, the only remopleurid known from the Tarutao Group at that time. They remarked on the pauci-segmented form being more similar to *Elkanaspis* or another remopleurid than to other species of *Pseudokainella*.

Genus *Jiia* Zhou and Zhang, 1978

Type species.—Jiia ampuliformis Zhou and Zhang, 1978 from the Yehli Fm., Hebei, China; by original designation.

Jiia talowaois n. sp.

Figs 3:35, 36.1–7,?8

Type material.—Holotype: APMB1_19 (Fig. 3:36.1), Ao Phante Malacca 53.65 m; Talo Wao Formation, Tarutao Group, Tremadocian. Paratypes: APMB1_26, 21, 30, 31, 32, 45, 4.

Diagnosis.—Square cranidium with short, anteriorly tapering glabella, moderately curved fixigena adjacent to glabella, and medially confluent anterior border and preglabellar furrows resulting in medially absent but laterally remnant preglabellar field. Pygidium subelliptical with long axis reaching posterior border furrow, moderately incised pleural and interpleural furrows, and narrow, inflated posterior border.

Occurrence.—Ao Phante Malacca 53.65 m; Talo Wao Formation, Tarutao Group, Ko Tarutao, Tremadocian.

Description.—Cranidium subrectangular and short; width (tr.) across palpebral lobes subequal (95%–110%) cranidial length (sag.). Glabella gently anteriorly tapering; glabellar length (sag., including LO) 85–90% cranidial length; glabellar width (tr.) at S1 subequal (90%–105%) preoccipital glabellar length (sag.); anterior glabellar margin gently convex or straight (tr.); axial

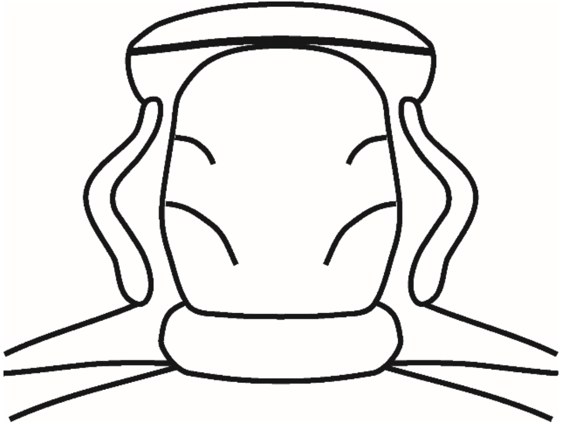

Figure 3:35 Jiia talowaois n. sp. line drawing.

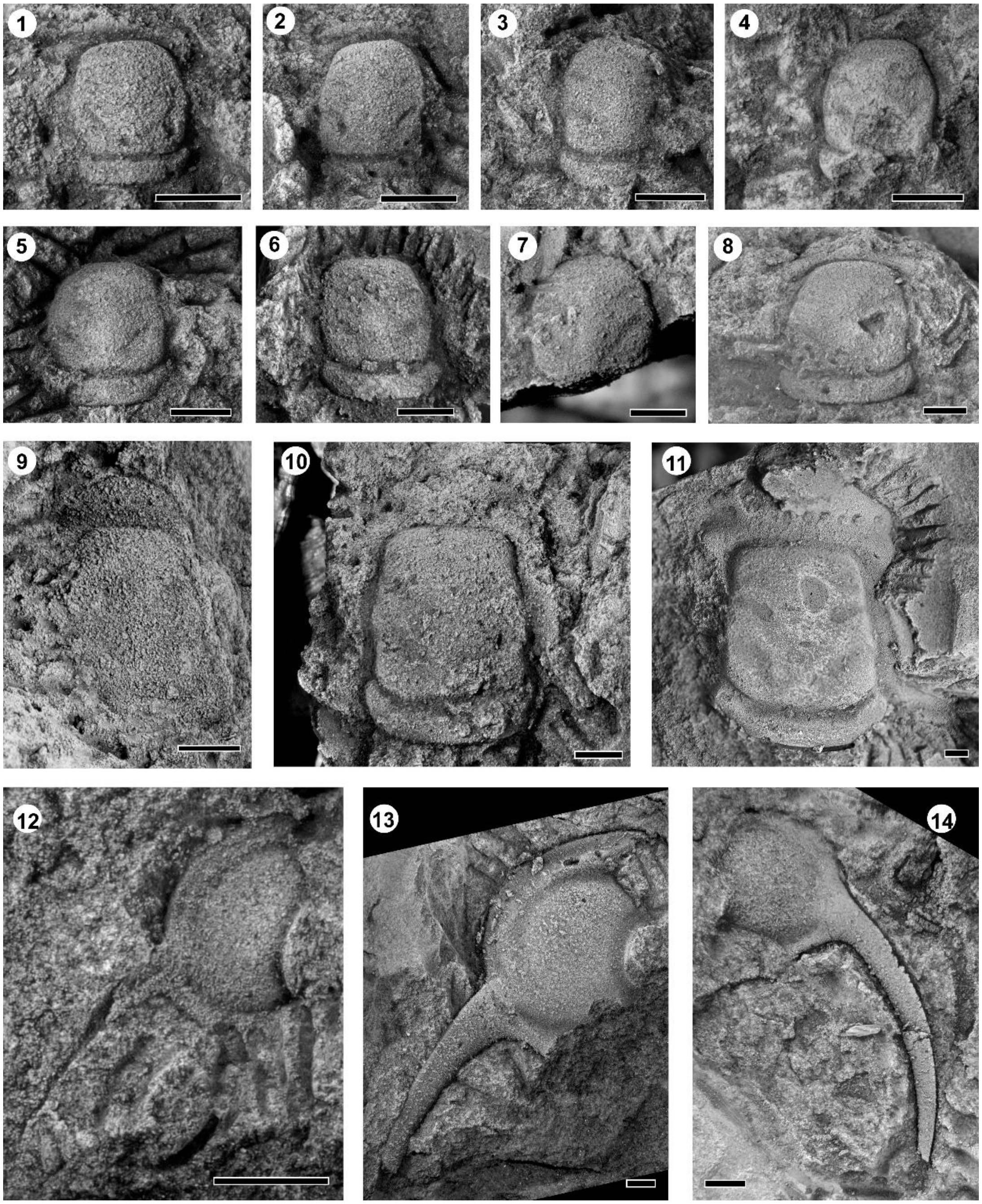

Figure 3:36 *Jiia talowaois* n. sp. and *Pseudokainella malakaensis* Stait et al., 1984. *Jiia talowaois* (1–7), all cranidia from APM 53.65 m; **(1)** _19; **(2)** _30; **(3)** _47; **(4)** _32; **(5)** _31; **(6)** _21; **(7)** _45. **(8)** _51, *Jiia talowaois*?, external mold, APM 53.65 m. **(9)** _3, *Pseudokainella malakaensis*?, cranidium, ATD S3 0.03 m. *Pseudokainella malakaensis* (10–14) **(10)** _9, cranidium, APM 15.10 m; **(11)** _1, cranidium, APM 15.10 m; **(12)** _11, librigena, APM 18.00 m; **(13)** _12, librigena, APM 15.10 m; **(14)** _33, librigena, ATD S3 float. All internal molds unless otherwise indicated. APM = Ao Phante Malacca; ATD = Ao Talo Udang. Scale bars = 2 mm.

furrows broad and deeply incised, gently curved; S1 posteromedially oblique, variably straight to strongly curved and effaced to deeply incised; S2 short, posteromedially oblique, weakly incised; SO firmly incised with posteromedial bow; LO wider (tr.) than L1 and thick (sag.), ~20% total glabellar length, with constant thickness sag. and exsag. Narrow (tr.) moderately arcuate palpebral lobes adjacent to broad axial furrows; palpebral lobes moderately long (exsag.), extending from posterior L1 to S2; anterior palpebral tip gently recurved; depressed but centrally gently inflated palpebral area fully encompassed by palpebral lobe and axial furrow. Anterior facial sutures diverge gently and then curve toward convergent at lateral corners of anterior border. Anterior border furrow medially confluent with but less strongly curved than preglabellar furrow; depressed preocular fixigena continuous with lateral preglabellar field; anterior border short (sag., exsag.). Long (exsag.), strap-like posterolateral projections with deep and broad (exsag.) posterior border furrow and inflated posterior border. Entire cranidium finely granulated.

Etymology.—Named for the Talo Wao Formation.

Material.—Nine cranidia from Ao Phante Malacca 53.65 m (_26, 19, 21, 30, 31, 32, 45, 47, 51), all internal molds.

Remarks.—This species adheres to Zhou and Zhang’s (1978) diagnosis of *Jiia* as having a relatively rapidly anteriorly narrowing glabella, short anterior facial sutures, a narrow and depressed preglabellar field, and a finely granulated surface. It differs from the type species, *J. ampuliformis* in having a less strongly anteriorly tapering glabella and correspondingly wider (tr.) frontal area. Furthermore, S1 and S2 are not so firmly incised.

The largest specimen herein of *J. talowaois*, APMB1_51 (Fig. 3:36.8), is assigned only questionably. Its anterior border is more angular, and the preglabellar and anterior border furrows are confluent along the entire anterior glabellar margin. Other than this frontal area, the morphology of this specimen is consistent with other specimens of *J. talowaois*. Because the only other two specimens with preserved frontal areas are the two smallest, APMB1_19,30 (Figs 3:36.1,2), it is unclear whether the difference in anterior border is ontogenetic with intermediate stages that have not been preserved or whether APMB1_51 belongs to a different taxon. The ontogeny of other species of *Jiia* is unknown. Preservation type is unlikely to be the source of variation. ATDB1_51 is the only external mold in the collection, and the others are internal molds. While differences in external and internal contouring may have resulted in some artificial divisions in trilobites (e.g. Zhu and Peng., 2006), the lateral corners of the anterior border in the *J. talowaois* type material are too anteriorly placed to have been contained within the more angular border of ATDB1_51.

Genus *Pseudokainella* Harrington, 1938

Type species.—Pseudokainella keidelli Harrington, 1938; from the Rupasca Shale, Argentina; by original designation.

Pseudokainella malakaensis Stait et al., 1984

Fig. 3:36.10–14,?9

1984. *Pseudokainella malakaensis* Stait et al., p. 56–59, fig. 3.1,2,4–6,8; *not* 3.3,7 = *Tarutaoia techawani* n. sp.

Occurrence.—Ao Phante Malacca 15.10(?0.05)–53.65m; Ao Talo Udang S3 0.03 m and float; Talo Wao Formation, Tarutao Group, Ko Tarutao, Tremadocian.

Material.—Three cranidia from Ao Phante Malacca (APM) 15.10 m (_1, 9) and Ao Talo Udang (ATD) S3 0.03 m (_3). 18 librigenae from APM 0.05 m (_4, 5, 6, 8, 10), 15.10 m (_12), 18.00 m (_11), and 53.65 m (_13) and ATD S3 0.03 m (_18, 22,31) and float (_4, 68, 21, 32, 33, 34). All internal molds.

Remarks.—When first describing *Pseudokainella malakaensis*, Stait et al. (1984) expressed uncertainty regarding the generic assignment of *Pseudokainella* due to questionable distinctions between *Pseudokainella* and *Elkanaspsis* Ludvigsen, 1982. As defined by Harrington (1938) *Pseduokainella* lacks a preglabellar field, but numerous species have since been added with a distinct preglabellar field (Harrington and Kay, 1951). *Pseduokainella* and *Elkanaspis* are now considered synonymous (Jell, 1985; Jell and Adrain, 2002), thus eliminating this source of uncertainty regarding the generic assignment of *P. malakaensis*.

The cranidium from Ao Talo Undang ATDG3 (Fig. 3:36.9) is much narrower (tr.) than the two cranidia from Ao Phante Malacca figured herein. ATDG3 is considerably smaller than the other two specimens; possible ontogenetic differences cannot be recognized based on the limited material presently available. This difference could be tectonic as both a fault and a fold axis run near to the Ao Talo Udang locality (Fig. 3:2), or perhaps it is due to localized compression. Alternatively, the specimen from Ao Talo Udang may represent a different species from that known at Ao Phante Malacca. Given this possibility the cranidium figured in Fig. 3:36.9 is only tentatively ascribed to *P. malakaensis.*

The *Pseudokainella* pygidial form, known from fully articulated specimens, has four or more segments, and is spiny (Harington and Leanza, 1957). The pygidium originally assigned to *Pseudokainella malakaensis* (Stait et al., 1984) is paucisegmented with a smooth posterior margin. It is herein reassigned to *Tarutaoia malakaensis* n. gen. et sp.

Genus *Haniwa* Kobayashi, 1933

Type species.—Haniwa sosanensis Kobayashi, 1933 from the *Tsinania* Zone of the Chosan (=Sosan) area, Korea.

Haniwa mucronata Shergold, 1975

Fig. 3:37.1–5,?27

1975. *Haniwa mucronata* Shergold, p. 164–167, fig. 53, pl. 33, figs 2–7, pl. 34, figs 1–7.

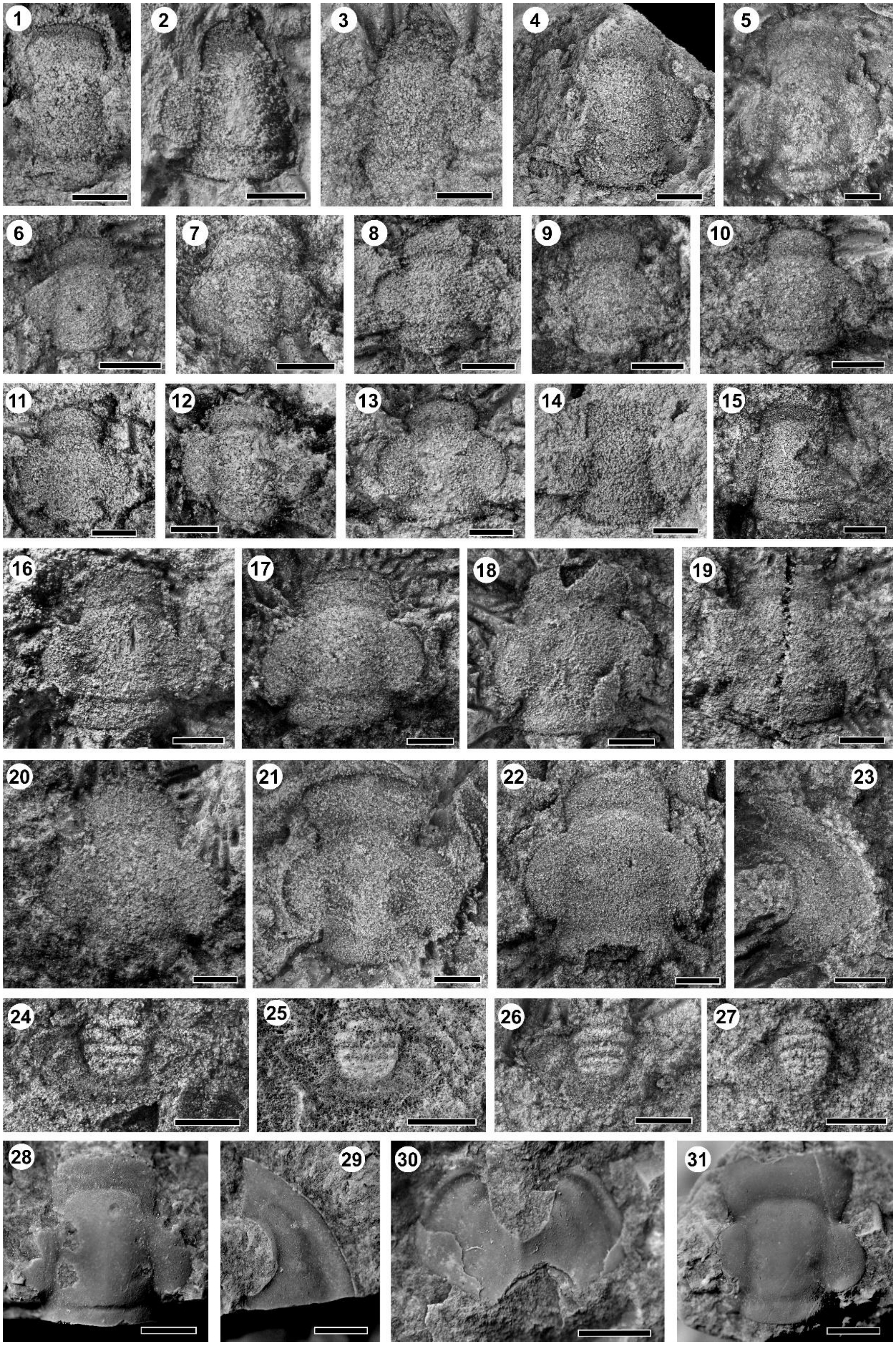
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Figure 3:37 Haniwa mucronata Shergold, 1975 and *Haniwa sosanensis* Kobyashi, 1933. *Haniwa mucronata* (1–5,?27), all cranidia **(1)** _2, ATT 5.50 m; **(2)** _43, ATT 29.17 m; **(3)** _53, ATT 22.78 m; **(4)** _75, ATT west; **(5)** _41, ATTw. *Haniwa sosanensis* (6-26) **(6)** _10, cranidium, ATT 8.85 m; **(7)** _60, cranidium, ATT 22.78 m; **(8)** _85, cranidium, ATT 22.78 m; **(9)** _77, cranidium, ATT 22.78 m; **(10)** _32, cranidium, ATT 22.78 m; **(11)** _56, cranidium, ATT 22.78 m; **(12)** _37, cranidium, ATT 22.78 m; **(13)** _64, cranidium, ATT 22.88 m; **(14)** _47, cranidium, ATT 22.78 m; **(15)** _1, cranidium, ATT 25.34 m; **(16)** _162, cranidium, AML 5.81 m; **(17)** _118, cranidium, AML 5.81 m; **(18)** _8, cranidium, ATT 25.34 m; **(19)** _182, cranidium, AML 5.81 m; **(20)** _175, cranidium, AML 5.81 m; **(21)** _3, cranidium, ATT 6.65 m; **(22)** _43, cranidium, ATT 22.78 m; **(23)** _217, librigena, AML 5.81 m; **(24)** _6, pygidium, ATT 22.88 m; **(25)** _15, pygidium, external mold, ATT 22.88 m; **(26)** _10, pygidium, ATT 22.78 m; **(27)** _24, *Haniwa mucronata*?, pygidium, ATT 24.88 m; **(28)** UMUT PA041, *Haniwa sosanensis*, lectotype, cranidium, original of Kobayashi, 1933 pl. 15, fig. 2; **(29)** UMUT PA0422, *Haniwa sosanensis*, librigena, original of Kobayashi, 1933 pl. 15, fig. 7; **(30)** UMUT PA0423, *Haniwa sosanensis* pygidium, original of Kobayashi, 1933, pl. 15, fig. 5; **(31)** UMUT PA0424, *Haniwa* quadrata, lectotype, cranidium, original of Kobayashi, 1933, pl. 15, fig. 7. All internal molds unless otherwise indicated. ATT = Ao Talo Topo; AML = Ao Mo Lae. Scale bars = 2 mm.

Occurrence.— Ao Talo Topo 5.50–29.17 m and Ao Talo Topo west; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—Seven cranidia from Ao Talo Topo 5.50 m (_2), 22.78 m (_8, 53), 29.17 m (_37, 43), and Ao Talo Topo west (_41, 75).

Remarks.—The differential diagnosis of *H. mucronata* is based on its possession of pygidial spines (Shergold, 1975). Of the *Haniwa*-type pygidia recovered from the Ao Mo Lae Formation, only ATT24.10_24 (Fig. 3:37.27) is a potential match, and its posterior margin is insufficiently preserved to determine whether it bore spines. However, comparisons of cranidial features lead to the reasonably confident assignment of Thai material to *H. mucronata*. Such features include the acutely anteriorly rounded glabella, palpebral lobes extending from SO to the anterolateral glabellar corners, gently anteriorly divergent facial sutures, faint glabellar furrows, and a preglabellar field separating the preglabellar and anterior border furrows. The length (sag.) of the preglabellar field is longer relative to the anterior border than in most other members of *Haniwa* though the quantitative range of this ratio is highly susceptible to dorso-ventral flattening and the angle of viewing the specimen. Additionally, the posterolateral projections are longer (exsag.) and less strap-like than in other species of *Haniwa.* While the relative length of the glabella is similar to that of *Haniwa elongata* Qian (in Qian et al.), 1985, *H. elongata* lacks a genal spine and well-defined anterior border furrow.

The other species of *Haniwa* found in the Ao Mo Lae Formation, *H. quadrata* Kobayashi, 1933 has a proximally nearly transverse anterior pygidial margin at all stages of development (Park and Choi, 2011). The pygidium of *H. mucronata* has a more strongly curved anterior margin. ATT24.10_6, ATT24.10_15, and ATT24.00_10 (Figs 3:37.24–26) are representative of the former condition whereas ATT24.10_24 (Fig. 3:37.27) has a more strongly curved margin ant is tentatively assigned to *H. mucronata*.

Haniwa sosanensis Kobayashi, 1933

Figs 3:37.6–26

1933. *Haniwa sosanensis* Kobayashi, p. 148–149, pl. 15, figs 1–4, *not* 5.

2007. *Haniwa sosanensis* Kobayashi; Sohn and Choi, p. 310, figs 6p–s.

?2011. *Haniwa quadrata* Kobayashi; Park and Choi, figs 6,10,11.

?2015. *Haniwa quadrata* Kobayashi; Park and Kihm, p. 191, fig. 9.

Occurrence.— Ao Mo Lae 5.81 m and Ao Talo Topo 6.65–25.34 m; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—33 Cranidia: four from Ao Mo Lae (AML) 5.81 m (_118, 162, 175, 182); 29 from Ao Talo Topo (ATT) 6.65 m (_3), 8.60 m (_2 – external mold), 8.85 m (_6, 10), 22.78 m (_5, 18, 31, 32, 34, 37, 43, 44, 47, 56, 60, 62 – external mold, 77, 79, 85, 87, 88, 94 – external mold,95 – external mold), 22.88 m (_22, 26, 63, 64), and 25.34 m (_1, 8). Two librigenae from AML 5.81 m (_217, 174). Five pygidia from ATT 22.78 m (_10, 25) and 22.88 m (_6, 15 – external mold, 24). All internal molds unless otherwise indicated.

Remarks.—When Kobayashi (1933) first established *Haniwa*, two new species were assigned to the genus: *H. sosanensis* and *H. quadrata*. Based on the lectotypes (UMUT PA0421, PA0424; Figs 3:37.28,31), these two species are readily distinguishable by the anteriorly tapered glabella and parallel anterior facial sutures of the former and parallel-sided glabella with anteriorly divergent facial sutures of the latter. When Sohn and Choi (2007) described specimens of *Haniwa* from the Taebaeksan Basin, they directly contrasted *H. sosanensis* with other species of *Haniwa* but not with *H. quadrata.* They assigned the specimens in their paper to *H. sosanensis* due to the undifferentiated frontal area, obsolete palpebral furrows, and nearly effaced glabella. The cranidia (Sohn and Choi, 2007, figs 6p–r) have anteriorly tapering glabellae, but only their fig. 6p has parallel or nearly parallel anterior suture branches, with the result that these specimens

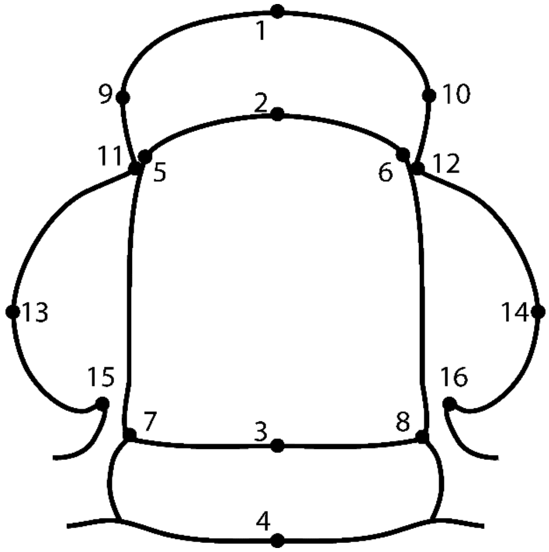


Figure 3:38 Haniwa landmark scheme

resemble *H. quadrata* in the divergence of the anterior sutures. Park and Choi (2011) focused on the anterior divergence of the suture branches to suggest a need for taxonomic revision, but Park and Kihm (2015a) indicated that Sohn and Choi's (2007) material is not synonymous with *H. quadrata* with the exception of SNUP4071 (Sohn and Choi, 2007, fig. 6s), a yoked librigena. The assignment of these free cheeks but not the associated cranidia to *H. quadrata* was based exclusively on the strong anterior divergence of the facial sutures. This was despite the fact that the genal spine base is more anteriorly placed in Sohn and Choi's (2007) specimen than in the librigenae of *H. quadrata* featured in Park and Choi (2011). In summary, recent species concepts for *H. sosanensis* and *H. quadrata* have relied on frontal area morphology without regard for the glabellar tapering that was considered important for the species distinction in the original description Kobayashi (1933).

At a minimum, the collection of *Haniwa* from the Ao Mo Lae Formation contains two distinct species: *H. sosanensis* and *H. mucronata* Shergold, 1975. *Haniwa mucronata* has a clearly differentiated, relatively narrow (tr.) frontal area, and a long, strongly tapering and anteriorly curved glabella. However, analysis of the collections herein assigned to *H. sosanensis* shows important morphological variation that casts doubt on a distinction between *H. sosanensis* and *H. quadrata*. A landmark-based morphometric analysis using 16 landmarks (Fig. 3:38) and 23 specimens (16 specimens of *H. sosanensis* from Tarutao, the *H. sosanensis* and *H. quadrata lectotypes* from Kobayashi 1933, and five cranidia of *H. quadrata* from Park and Kihm, 2015a), results in a relatively even distribution and undifferentiated grouping of all specimens of *H. sosanensis* from Tarutao (Fig. 3:39). Within this group some specimens have strongly divergent anterior sutures (e.g. ATT24.00_37, ATT26.50_8, and ATT6.65_3; figs 3:37.12, 3:37.18, and 33:7.21 respectively) while others have parallel-sided or even anteriorly convergent facial sutures (e.g. ATT24.00_47, AML5.81_162, and ATT24.00_43; Figs 3:37.14, 3:37.16, and 3:37.22, respectively): character states considered diagnostic of *H. sosanensis* and *H quadrata* respectively. Of those that have anteriorly divergent sutures, some have parallel-sided glabellae (e.g. AML5.81_175, Fig. 3:37.21), thus adhering to Kobayashi's (1933) diagnosis of *H. quadrata*, while others

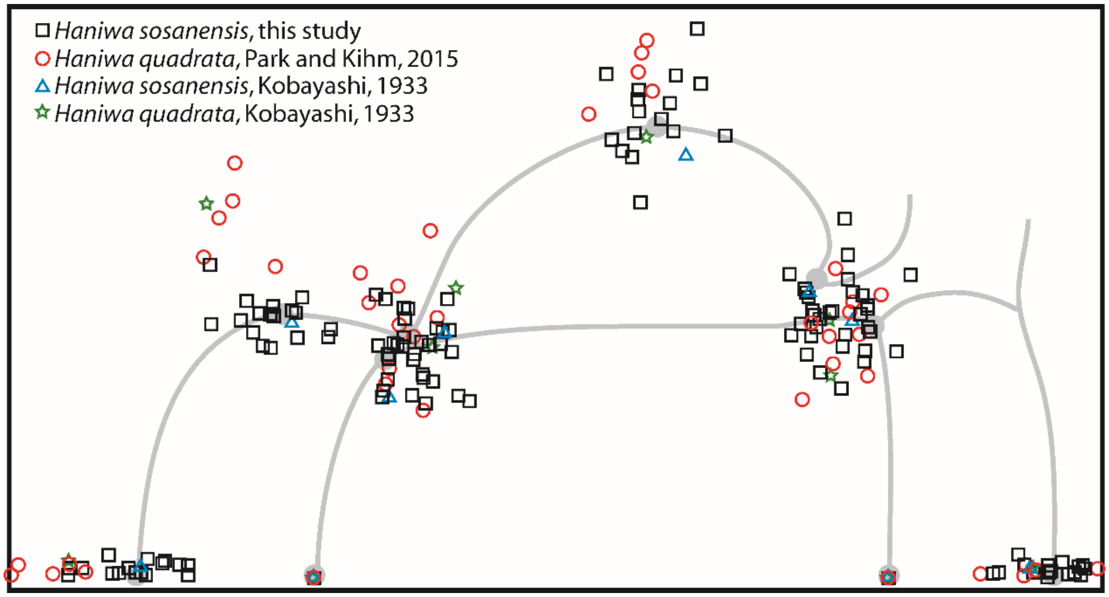


Figure 3:39 Haniwa landmark distribution using Bookstein coordinates (BC) with landmarks 2 and 3 as basepoints

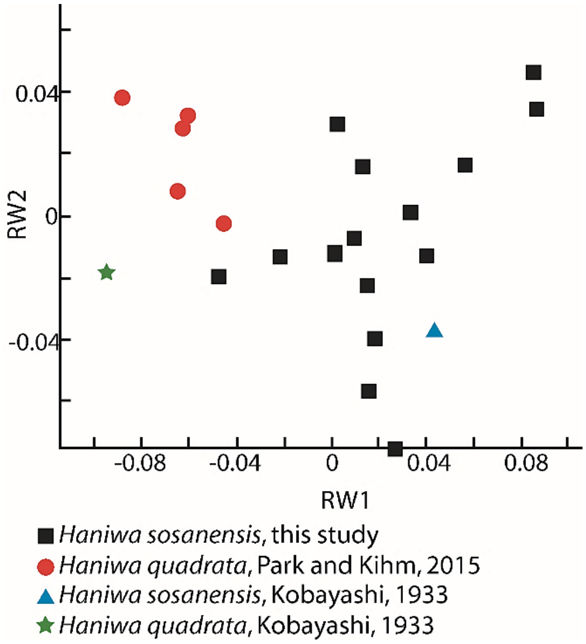


Figure 3:40 Relative warps (RW) 1 and 2 for principal component analysis of the landmark distribution in Fig. 39. Relative warps account for 30.49% and 15.48% of the variance respectively.

have anteriorly convergent glabellae (e.g. ATT24.00_37, Fig. 3:37.12), thus representing a mix of characters used to differentiate *H. quadrata* and *H. sosanensis*. With scores for the Thai specimens plotted against the lectotypes of *H. quadrata* and *H. sosanensis* (Fig. 3:40) for the first two relative warps, scores for the lectotype of *H. sosanensis* fall to one side but nearly within the cloud of points representing Thai specimens, while scores for the lectotype of *H. quadrata* fall on the other side but also close to this cloud. *Haniwa quadrata* and *H. sosanensis*, inclusive of the Thai specimens, are differentiated only on relative warp 1, which accounts for 35% of variance. The pattern of shape change that relative warp 1 represents (Fig. 3:41) suggests that this variance is controlled most strongly by the relative length of the frontal area and the lateral position of cranidium's anterolateral corner. However, the relative length of the glabella also has a marked influence. The holotype of *H. quadrata* has a relatively short glabella and long frontal area compared to the material from Thailand.

The specimens assigned to *H. quadrata* from the Taebaek Basin further blur the differentiation between *H. quadrata* and *H. sosanensis*. Five of the largest cranidia from Park and Choi's (2011) ontogenetic analysis of *H. quadrata* in the Taebaek Basin were included in the landmark-based morphometric analysis. These specimens, which are morphologically consistent relative to those from Thailand, fall closer to the *H. quadrata* holotype than the Thai material on relative warp 1 (Figs 3:39, 3:40). Their intermediate morphology applies to the anterolateral placement of the anterior border corners, and relative lengths of the glabella and frontal area. Elsewhere there is no differentiation between these and the Thai specimens.

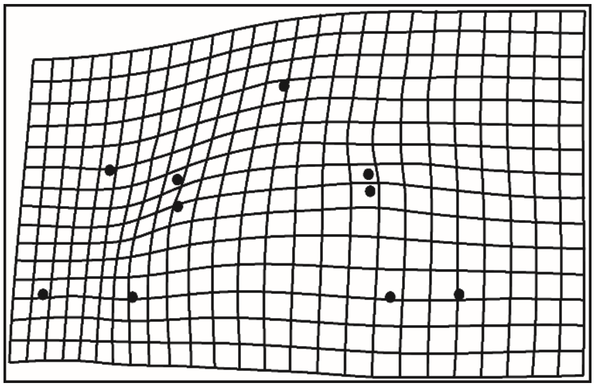


Figure 3:41 Warp grid for morphological variance described by RW1 (Fig. 40).

The morphometric analysis thus indicates that the anterior divergence of the facial sutures is not a sufficient character on which to differentiate of *H. sosanensis* from *H. quadrata*. If these are separate species, then the relative lengths of the glabella and the frontal area are also important characters. The shape of the glabella should also be considered, as in the original diagnoses (Kobayashi, 1933), but this trait is subject to intercollectional variation as demonstrated by the Thai material. This analysis also reveals that the specimens analyzed by Park and Choi (2011) from the Taebaeksan Basin fall morphologically in between the type specimens of *H. sosanensis* and *H. quadrata*, and that their assignment to *H. quadrata* is not securely based. These results suggest, but are not sufficiently strong to confirm, that these species are synonymous, with morphometric frequency variation showing some geographic or stratigraphic structure, such as the rather consistent morphology within the Taebaeksan Basin, compared to the variation seen in our collections.

One additional source of variation within this population that is not captured by the landmark-based analysis is that the facial sutures may vary in the position of their intersection of the anterior border. Typically, the sutures connect dorsomedially posteriorly to the anterior border, thus leaving the entire border intact on the yoked librigena. Rarely (e.g. AML5.81_118, Fig. 3:37.17) the sutures may connect medially in such a way that a small portion of the anterior border is included on the cranidium. This variation in the "retraction" of the facial suture is similar to that documented in the *Dikelocephalus minnesotensis* Owen, 1852 (Hughes, 1994).

If the pygidium initially assigned to *H. sosanensis* is correctly associated, then the pygidium may offer reliable characters for differentiating *H. quadrata* and *H. sosanensis,* since it differs in curvature and incision and distribution of pleural furrows from that which Park and Choi (2011) attributed to *H. quadrata*. In outline, axial length, and furrow expression, pygidia from Tarutao (ATT24.10_6, DGSC F0469, and ATT24.00_10; Figs 3:37.24–26) resemble those of *H. quadata* more than *H. sosanensis*. However, there may have been allometric repatterning between the Thai material and the collection of *H. quadrata* from the Taebaeksan Basin. Thai specimen DGSC F0469 (Fig. 3:37.26) is 2.56 mm in pygidial length (sag.) and yet it bears closer resemblance in outline and furrow expression to Park and Choi's (2011) fig. 11.j which measures ~0.5 mm in pygidial length than to their fig. 11.r, which is more similar in size. The largest Thai pygidium (ATT24.10_24; Fig. 3:37.27) is 3.5 mm (sag.). This pygidium is ~75%

larger than Park and Choi's (2011) fig. 11.r; while it has acquired the shape of the mature pygidia from the Taebaeksan Basin, it maintains a remnant of the pleural furrows that better characterize the much smaller pygidia from the ontogenetic study by Park and Choi (2011, fig.10). This largest pygidium has tentatively been assigned to *Haniwa mucronata*; that it may represent a later ontogenetic stage than the other three pygidia is one reason that assignment is tentative.

Superfamily DIKELOCEPHALOIDEA Miller, 1889

Family DIKELOCEPHALIDAE Miller, 1989

Remarks.—The dikelocephalid trilobites discussed herein are those historically assigned to Saukiidae Ulrich and Resser, 1930 and still commonly referred to as "saukiid" trilobites. The taxonomic ranking or validity of the saukiid grouping has long been controversial. Saukiinae was initially established as a subfamily within Dikelocephalidae (Ulrich and Resser, 1930). Raasch (1951) elevated Saukiinae to the level of family, arguing for a closer link to Ptychaspidiidae Raymond, 1924 than to other dikelocephalids. This view quickly became widely accepted (e.g. Hupé, 1953; Lochman, 1956). Many new genera have since been added to Saukiidae with the family encompassing more than 30 genera by the end of the twentieth century (Jell and Adrain, 2002). However its taxonomic position has not been stable with Kobayashi (1960), Longacre (1970), Stitt (1971, 1977), and Taylor and Halley (1974) relegating it to a subfamily of Ptychaspididae and Westrop and Ludvigsen (1983) retaining the family designation but reassigning it to Dikelocephaloidea. Ludvigsen et al. (1989), due to the inability to establish synapomorphic characters for all of Saukiidae, later abandoned the use of this grouping, suggesting that it is a paraphyletic junior synonym of Dikelocephalidae. This scheme has been widely accepted by Laurentian and Gondwanan trilobite workers (e.g. Adrain, 2011 and Lee and Choi, 2011), although some authors continue to use Saukiidae as a family-level designation within Dikelocephaloidea (e.g. Park and Kihm, 2015a; Shergold et al., 2007). Herein we follow the scheme assigning the saukiid trilobites to Dikelocephalidae but without strong opinion or new evidence as to the existence of "Saukiidae" even as a paraphyletic gorup.

Genus *Caznaia* Shergold, 1975

Type species.—Caznaia squamosa Shergold, 1975 from the pre-Payntonian B interval at Black Mountain (by original designation).

*Remarks.—*Shergold (1975) provided many distinguishing cranidial characters when first diagnosing *Caznaia.* The glabella is anteriorly tapering with curved or "sinuous" axial furrows; this "sinuosity" manifests as a slight lateral expansion at S1. The palpebral lobes are centered between S1 and S2. The posterolateral projections are long and triangular. The frontal area is short, but this is in comparison with "saukiids" such as *Anderssonella* Kobayashi, 1936 to which Shergold (1975) suggested *Caznaia* is most related. This frontal area is convex and differentiated into a preglabellar field and anterior border abaxially, but medially they are only differentiable on testaceous specimens. Additionally, Shergold (1975) describes the genus having anteriorly divergent facial sutures and small eyes. The anteriorly divergent facial sutures are a dubious character as both *C. squamosa* Shergold, 1975 and *C. sectarix* Shergold, 1975, the two species on which the genus was established, possess nearly parallel to convergent anterior suture branches. The line drawings for both species (Shergold, 1975 figs 48, 49) show a reconstruction with convergent sutures, and the description for the type species, *C. squamosa*, states that the "facial sutures strike directly forwards…but curve slightly abaxially before reaching the anterior margin." This description suggests that the divergent orientation of the facial sutures is very slight or inconsistent, and that character should not be strongly considered in the diagnosis of *Caznaia*. Small eye size is also a dubious character; both the Thai collections herein and the Australian collections on which the genus was first described (Shergold, 1975) display variability in eye size from only weakly protruding from the fixigena to strongly curved. The most significant characters on which to base *Caznaia* are the shape of the glabella, position of the palpebral lobes, convex preglabellar field, and peculiar adaxial lack of differentiation of the anterior border and preglabellar field. The latter two characters are comparable to the features differentiating *Hoytaspis* Ludvigsen and Westrop, 1983, and *Prosaukia* Ulrich and Resser, 1933. *Caznaia* and *Hoytaspis* are otherwise dissimilar relative to their similarities to other "saukiids", which suggests that an inflated preglabellar field may have arisen independently in multiple "saukiid" lineages. The medial effacement of the anterior border seems to be the direct result of this inflation.

Caznaia imsamuti n. sp.

Figs 3:42,43.1–13

Type material.—Holotype: LHN2.85_27 (Fig. 3:43.4), Laem Hin Ngam horizon 2.85 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10. Paratypes: LHN2.85_6, 16, 38, 41, and LHN1.54_1.

Diagnosis.—Trapezoidal cranidium with long, anteriorly tapering glabella, moderately long frontal area nearly entirely occupied by convex preglabellar field, strongly incised S1, divergent anterior sutures, effaced anterior border furrow, and short, medially placed palpebral lobes.

Occurrence.—Laem Hin Ngam 1.54–3.69 m; Ao Mo Lae Formation, Tarutao Group, Tarutao, Furongian.

Description.—Trapezoidal cranidium with width (tr.) across palpebral lobes 85%–100% of cranidial length (sag.); frontal area occupies 10%–15% of cranidial length (sag.) and LO occupies ~15% of cranidial length (sag.). Glabella convex and anteriorly tapering with curved axial furrows forming convex outline; anterior glabellar margin straight (tr.) to gently curved; glabellar width (tr.) at L1 60%–65% of cranidial

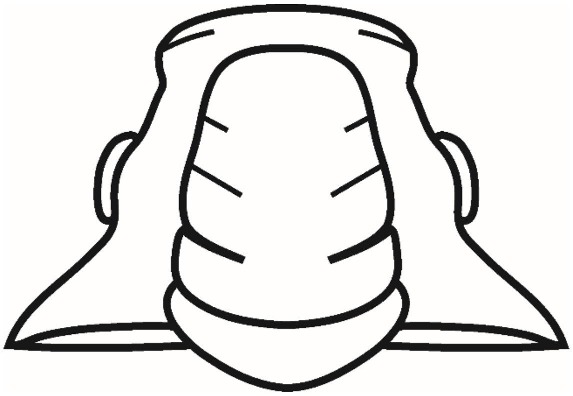


Figure 3:42 Caznaia imsamuti n. sp. line drawing

width across palpebral lobes; S1 firmly incised, gently posteriorly bowed, medially discontinuous or shallow and nearly discontinuous; S2 weakly incised and straight, posteromedially oblique. SO posteriorly bowed, subconcentric with S1; LO medially lengthening (sag.) and subequal in width (tr.) to L1. Fixigena narrow. Palpebral lobes weakly curved, longitudinally a symmetric with greatest curvature in posterior portion; palpebral lobes moderately long (exsag.), 25%–30% of cranidial length (sag.) and midpoint positioned opposite S2. Anterior facial sutures gently divergent and curved around frontal area; frontal area unequally divided with convex preglabellar field occupying most preglabellar length (sag.) with only very narrow, brim like anterior border; anterior border furrow faint. Posterior suture branches straight and diverge ~45° (from sag.), encompassing triangular posterolateral projection; posterior border furrow gently incised but distinct; posterior border short; posterior margin straight (tr.).

Etymology.—Named in honor of Mr. Suvapak Imsamut, Thai Department of Mineral Resources.

Material.—19 cranidia from Laem Hin Ngam 1.54 m (_1), 2.85 m (_6, 8, 11, 12 – external mold, 13, 15, 16 – external mold, 17, 18, 20, 21 – external mold, 25, 27, 33, 37, 38, 41, and 3.69_5. All internal molds unless otherwise indicated.

Remarks.—Caznaia imsamuti n. sp. has narrower fixigenae than either *C. squamosa* Shergold, 1975 or *C. sectarix* Shergold, 1975; the fixigenae are more comparable with those of *Caznaia coreaensis* Park and Kihm, 2015. The anterior border is reduced to only a thin brim as in mature specimens of *C. coreanensis* (Park and Kihm, 2015a); as in all species of *Caznaia*, the anterior border is only differentiated from the preglabellar field abaxially. The short, posteriorly set palpebral lobes are similar to those of *C. squamosa* and *C. coreaensis*. Of the known species of *Caznaia*, *C. imsamuti* is most similar to *C. coraensis*. While overall similar to *C. coreaensis*, a few characters distinguish it. Unlike

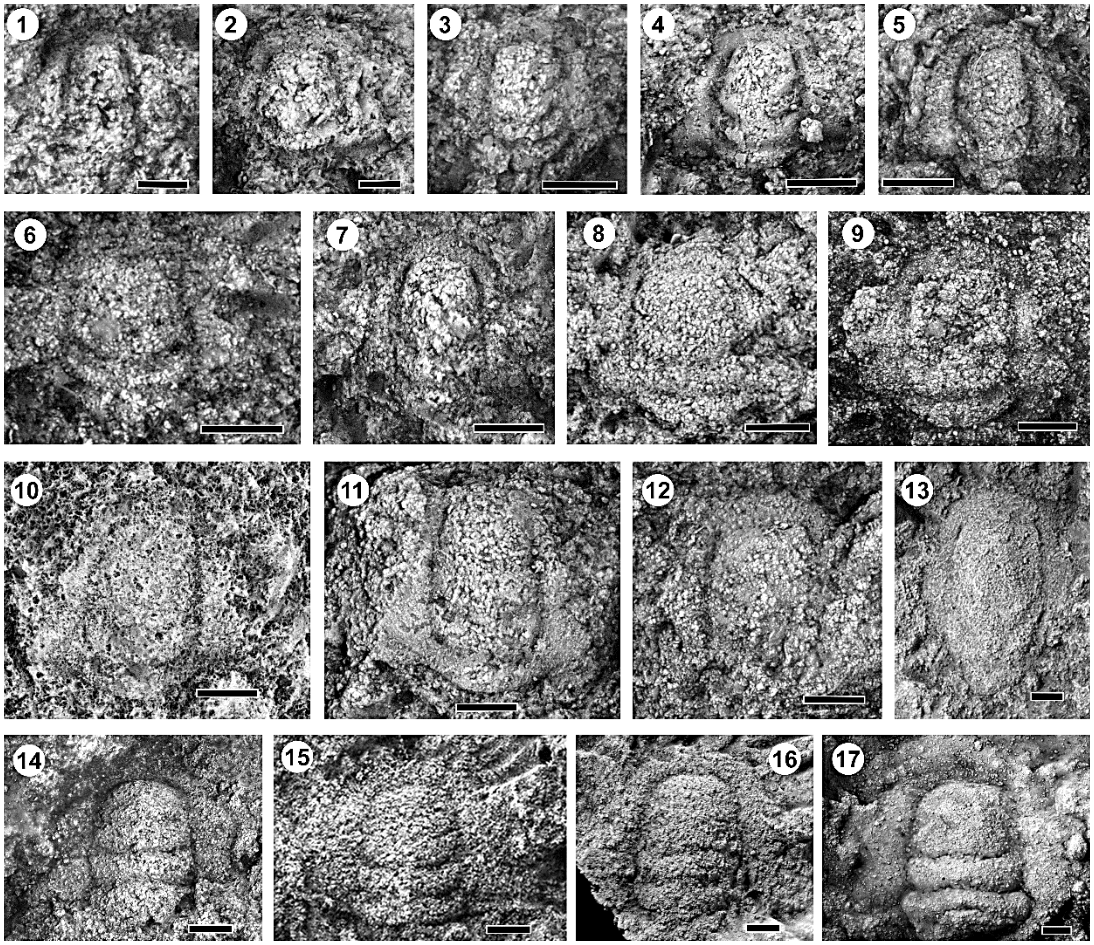


Figure 3:43 Caznaia imsamuti n. sp. and *Caznaia*? *undualata* n. sp., all cranidia. *Caznaia imsamuti* (1–13) **(1)** _38, LHN 2.85 m; **(2)** _6, LHN 2.85 m; **(3)** _41, LHN 2.85 m; **(4)** _27, holotype, LHN 2.85 m; **(5)** _37, LHN 2.85 m; **(6)** _15, LHN 2.85 m; **(7)** _8, LHN 2.85 m; **(8)** _11, LHN 2.85 m; **(9)** _1, LHN 1.54 m; **(10)** _16, external mold, LHN 2.85 m; **(11)** _17, LHN 2.85 m; **(12)** _13, LHN 2.85 m; **(13)** _5, LHN 3.69 m. *Caznaia*? *undulata* (14–17) **(14)** _47, ATTw **(15)** _53, AML 5.81 m; **(16)** _83, AML 5.81 m; **(17)** _17, holotype, ATTw. All internal molds unless otherwise indicated. ATTw = Ao Talo Topo west; AML = Ao Mo Lae; LHN = Laem Hin Ngam. Scale bars = 1mm.

C. coreaensis, there does not appear to be an occipital spine at any ontogenetic stage; across all holaspid stages, the occipital lobe is medially inflated, and it is possible that such spines have broken off. *C. coreaensis* has a relatively wider glabella, though this trait exhibits intraspecific variation within both species. The relatively small holotype of *C. imsamuti* is intermediate in morphology; the greatest variation in glabellar width occurs in the middle size range, and largest specimens appear to consistently possess a narrower glabella. The glabella of *C. coreaensis* becomes relatively broader, particularly across the anterior lobe, at in later ontogenetically stages. In all ontogetnetic stages, *C. coreaensis* has a relatively short S1 that is distinctly medially disconnected; this furrow deepens only in later ontogenetic stages. *Caznaia imsamuti* has a long, broad and deep S1 that is medially connected in some specimens. This furrow shallows with ontogeny; even in this longest specimen it is still long and is strongly posteromedially oriented.

Caznaia? undulata n. sp.

Figs 3:43.14–17, 44

Type material.—Holotype: ATT1_17 (Fig. 3:43.17), Ao Talo Topo west; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10. Paratypes: ATT1_47, AML5.81_53, 83.

Diagnosis. — Trapezoidal cranidium with strongly anteriorly tapering glabella, moderately long frontal area mostly comprising convex preglabellar field, medially continuous S1 with recurve shape medially bowing anteriorly, LO with stronger recurve shape, anteriorly convergent facial sutures.

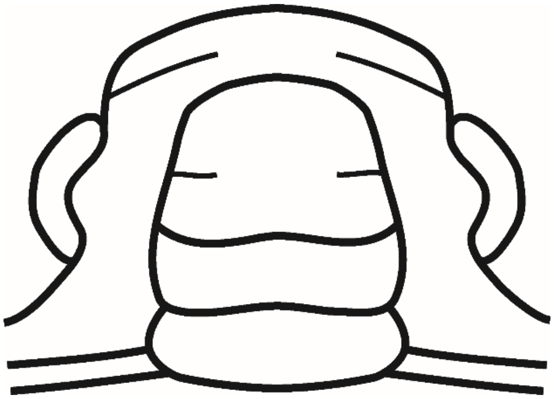


Figure 3:44 Caznaia undulata n. sp. line drawing

Occurrence.—Ao Talo Topo west, Ao Talo Topo h1, and Ao Mo Lae 5.81 m. Ao Mo Lae Formation, Tarutao Group, Tarutao, Furongian.

Description.—Trapezoidal cranidium with width (tr.) across palpebral lobes ~1.5 times cranidial length (sag.). Glabella anteriorly tapering with widest point at S1; anterior glabellar margin gently curved; glabellar width (tr.) at S1 ~50% of cranidial width across palpebral lobes; S1 firmly incised and undulated or recurved in shape with lateral portion oriented posteromedially and medial portion with anterior bend, medially continuous; S2 weakly incised and straight, gently posteromedially oblique. SO subparallel or more strongly undulated than S1; LO medially lengthening (sag.) and wider than S1. Fixigena broad. Palpebral lobes moderately long (exsag.), 25%–30% cranidial length (sag.) and midpoint positioned opposite L2. Anterior facial sutures moderately convergent. Frontal area unequally divided with convex preglabellar field occupying most preglabellar length (sag.).

Etymology.—Latin for wavy in reference to the wavy or undulating occipital furrow.

Material.—Six cranidia: two from Ao Talo Topo (ATT) west (_17,47), one from ATT h1 (_7); three from Ao Mo Lae 5.81 m (_53,83,140). All internal molds.

Remarks.—The cranidia of *C. udulata* are all larger than those of *C. imsamuti* n. sp. They are readily distinguishable by their broad cranidial outline and glabella, curvature of SO and S1, the anterior convergence of the facial sutures, and by the stronger, more even anterior tapering of the glabella. These differences seem independent of size in both sets of material, which is why they have herein been assigned to two separate species rather than considering the larger specimens from Ao Talo Topo to be conspecific with the smaller specimens from Laem Hin Ngam. The anteriorly convergent anterior suture branches are comparable to those of *C. sectarix* Shergold, 1975, but the curvature of the anterior glabellar margin, bigger eyes, and wavy SO distinguish them. *Caznaia squamosa* Shergold, 1975 may have a gently undulatig SO, but not so pronounced as in *C. undulata*, and the anterior facial sutures of the former are convergent. *Caznaia. coreania* Park and Kihm, 2015 has a medially discontinuous S1 and a more parallel-sided glabella.

Genus *Eosaukia* Lu, 1954

Type species.—*Eosaukia latilimbata* Lu, 1954.

Remarks.—Since *Eosaukia buravasi* Kobayashi, 1957 was described and assigned to *Eosaukia*, monotypic prior to that assignment (Kobayashi, 1957), several new species of

Eosaukia have been discovered. The genus now includes *E. latilimbata, E. angustilimbata* (Qian, 1986), *E. acuta* (Kuo and Duan in Kuo et al., 1982), *E. bella* (Walcott, 1906), *E. rectangulata* Lu and Zhou, 1990, *E. walcotti* (Mansuy, 1915) and *E. micorpora* (Qian in Qian et al., 1985). Some of these species have alternatively been assigned to *Calvinella* Walcott, 1914 (e.g. *E. micropora*), *Mictosaukia* Shergold, 1975 (e.g. *E. walcotti*), or another "saukiid" genus lacking a preglabellar field. As more species of *Eosaukia* have been discovered and the cranidia associated with librigena and pygidia, it has become increasingly clear that it is a well-constrained genus with diagnosable characters on the cranidium, librigena, and pygidium. Lee and Choi (2011) offered a thorough emended genus diagnosis. Among other characters they cite the strongly convex cephalon, abaxially well-defined and anterolaterally oriented anterior border furrow, three pairs of well-defined glabellar furrows with S3 anteromedially deflected, and moderately short palpebral lobes well-separated from the axial furrows. The complete lack of any semblance of a preglabellar field along perfectly confluent preglabellar and anterior border furrows and the anterolateral orientation of the abaxial portion of the anterior border furrow are especially important in recognizing *Eosaukia*. The librigena has a vincular structure of ridges and furrows on the doublure (Kobayashi, 1957; Lee and Choi, 2011). This character may be only weakly expressed in some *Eosaukia*, *e.g. micropora*, but, when present, it is considered diagnostic of this genus (Lee and Choi, 2011). The paucisegmented, micropygous pygidium with a rim-like border is also considered a uniquely defining character for *Eosaukia.*

Eosaukia buravasi Kobayashi, 1957

Figs 3:45–50

1957 . *"Eosaukia" buravasi* Kobayashi, p. 376, pl. 5 figs 1–6, 10, 14–20, ?7–9, ?13.

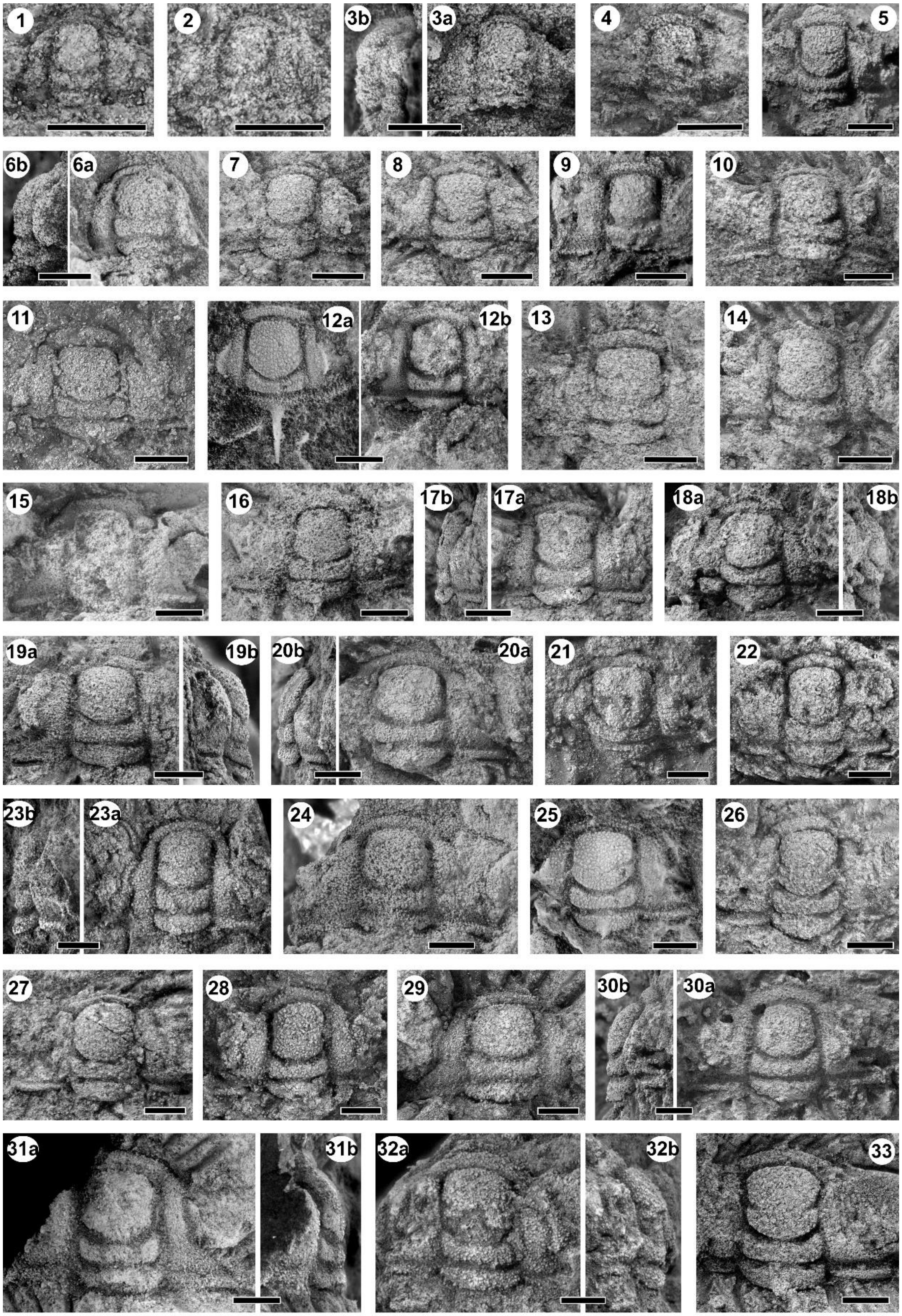
1988. *"Eosaukia" buravasi* Kobayashi, Shergold et al., p. 310, figs 4.0–X.

?2007. *Ptychaspis*? sp. aff. *P. cacus* (Walcott, 1905) Shergold et al., p. 65, fig. 38.

Occurrence.—Ao Mo Lae 3.62–6.01 m, h1–h5; Ao Talo Udang (ATD) S1 7.00 m, S2 0.52–14.5 m, and ATD S2 h1; Ao Talo Topo (ATT) 0.95–29.17 m and ATT h2; ATT west; Laem Hin Ngam 2.85 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Material.—231 cranidia: 127 from Ao Mo Lae (AML) 3.62 m (_9), 4.71 m (_1, 4, 5, 6, 7), 5.17 m (_1, 6, 7, 8, 11, 17, 22, 23, 26, 27, 29, 32, 35, 37 – external mold, 39, 41, 43, 44, 46, 48), 5.81 m (_25, 30, 31, 32, 33 – external mold, 54, 56, 57, 71, 74, 76, 77, 78, 89, 96, 97, 99, 108, 113, 115, 116, 120 – external mold, 121, 122, 123, 124, 132, 133, 134,

Figure 3:45 (*Next page*) *Eosaukia buravasi* Kobayashi, 1957. First of four figures of *E. buravasi* cranidia arranged in increasing size order. **(1)** _30, LHN2.85 m; **(2)** _26, LHN2.85 m; **(3)** _3, *a* dorsal view, *b* right lateral view, ATT28.37 m **(4)** _159, AML 5.81 m; **(5)** _21, AML 6.01 m; **(6)** _12, *a* dorsal view, *b* right lateral view, ATT 28.37 m; **(7)** _158, AML 5.81 m; **(8)** _56, AML 5.81 m; **(9)** _8, ATTw; **(10)** _54, AML 5.81 m; **(11)** _110, ATTw **(12)** _4, *a* external mold, *b* internal mold, ATT 29.17 m; **(13)** _121, AMl 5.81 m; **(14)** _77, AML 5.81 m; **(15)** _14, ATT 25.34 m; **(16)** _99, ATT 22.78 m; **(17)** _5, *a* dorsal view, *b* right lateral view, ATT 25.34 m; **(18)** _6, *a* dorsal view, *b* left lateral view, AML 5.17 m; **(19)** _7, *a* dorsal view, *b* left lateral view, AML 4.71 m; **(20)** _35, *a* dorsal view, *b* right lateral view, ATT 29.17 m; **(21)** _114, ATTw; **(22)** _32, ATTw; **(23)** _20, *a* dorsal view, *b* right lateral view, ATD S2 0.52 m; **(24)** _12, ATT 22.78 m; **(25)** _44, external mold, ATT 29.17 m; **(26)** _37, ATTw; **(27)** _176, AML 5.81 m; **(28)** _19, ATD S2 h1; **(29)** _52, ATT 29.17; **(30)** _3, *a* dorsal view, *b* right lateral view, AML h4; **(31)** _67, *a* dorsal view, *b* left lateral view, ATT 29.17 m; **(32)** _18, *a* dorsal view**,** ***b*** left lateral view, ATD S2 0.69 m; **(33)** _108, AML 5.81 m. All internal molds unless otherwise indicated. ATT(w) = Ao Talo Topo (west); AML = Ao Mo Lae; ATD S2 = Ao Talo Udang section 2; LHN = Laem Hin Ngam. Scale bars = 2mm.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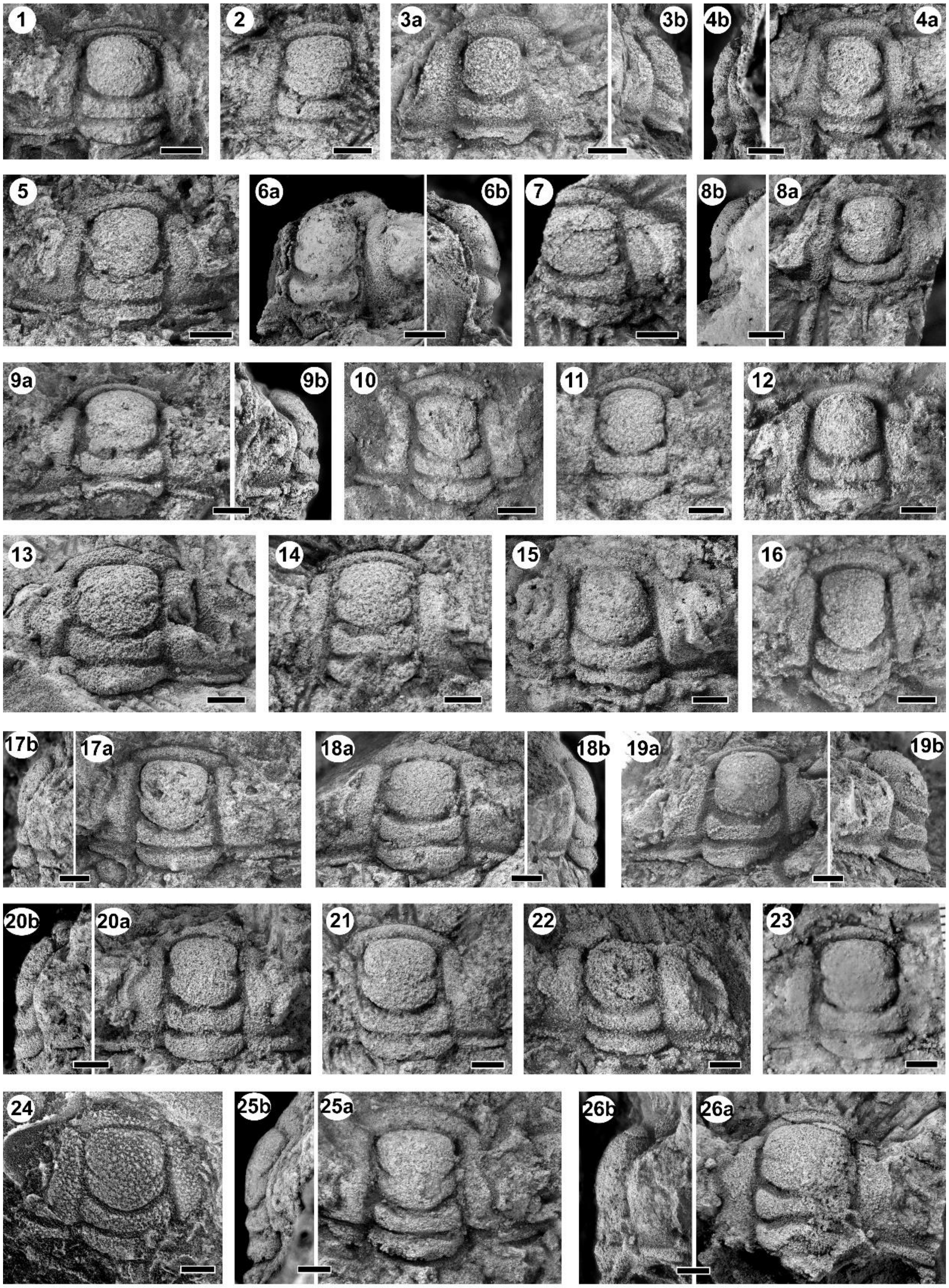
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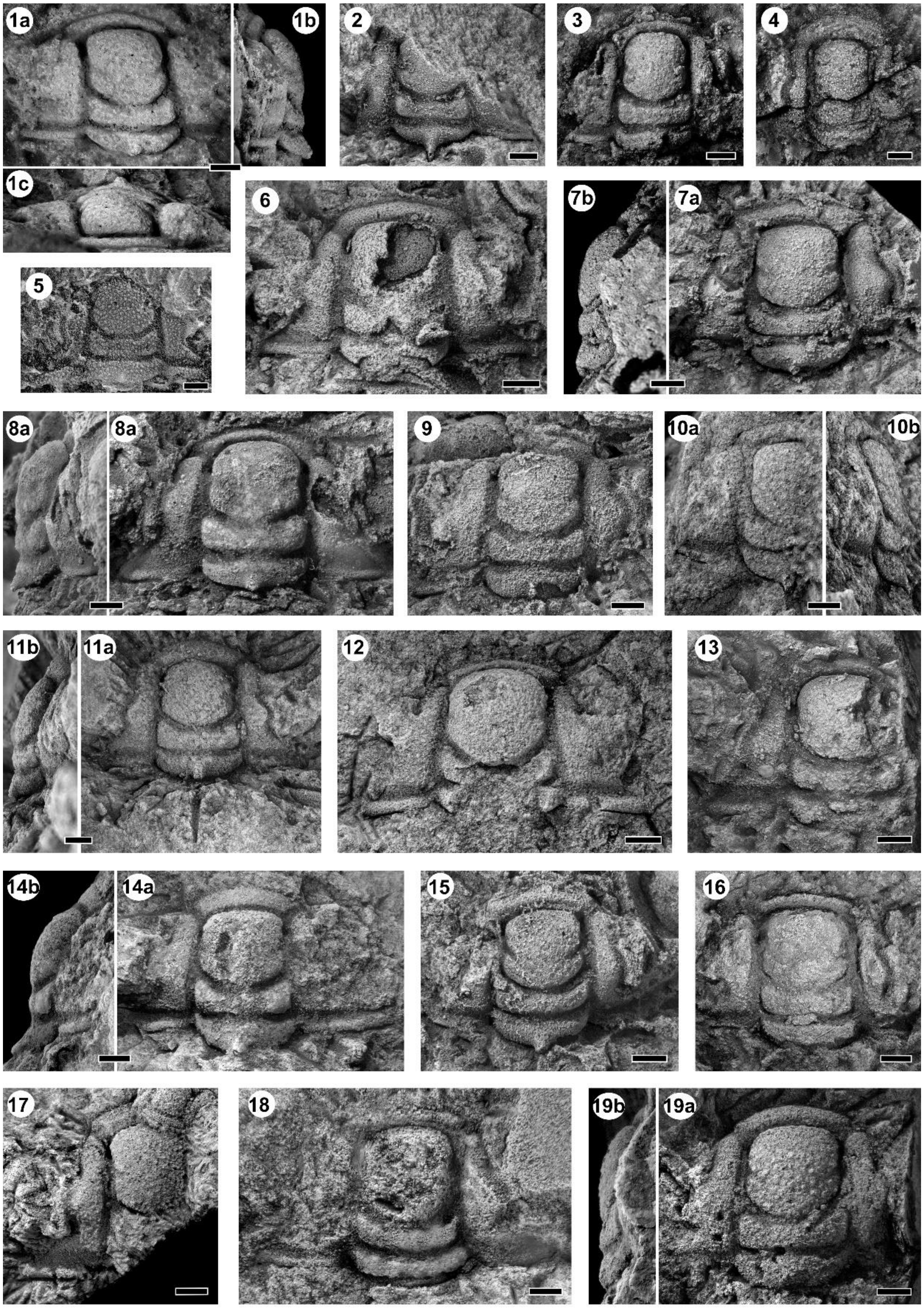
Figure 3:46 (*Previous page*) *Eosaukia buravasi* Kobayashi, 1957. Second of four figures of *E. buravasi* cranidia arranged in increasing size order. **(1)** _92, ATTw; **(2)** _89, AML 5.81 m; **(3)** _6, *a* dorsal view, *b* left lateral view, ATT 5.50 m; **(4)** _58, *a* dorsal view, *b* right lateral view, ATT 29.17 m; **(5)** _99, AML 5.81 m; **(6)** _5, *a* dorsal view, *b* left lateral view, ATT 23.89 m; **(7)** _25, AML 5.81 m; **(8)** _1, *a* dorsal view, *b* right lateral view, AML 4.71 m; **(9)** _22, *a* dorsal view, *b* left lateral view, AML 5.17 m; **(10)** _106, ATTw; **(11)** _97, AML 5.81 m; **(12)** _65, ATTw; **(13)** _78, AML 5.81 m; **(14)** _76, AML 5.81 m; **(15)** _97, ATTw; **(16)** _29, ATTw; **(17)** _204, *a* dorsal view, *b* right lateral view, AML 5.81 m; **(18)** _1, a dorsal view, *b* left lateral view, AML h4; **(19)** _44, *a* dorsal view, *b* left lateral view, AML 5.17 m; **(20)** _6, *a* dorsal view *b* right lateral view, AML 4.71 m; **(21)** _171, AML 5.81 m; **(22)** _19, ATD S2 0.69 m; **(23)** _59, ATTw; **(24)** _37, external mold, AML 5.17 m; **(25)** _14, *a* dorsal view, *b* right lateral view, AML h4; **(26)** _8, *a* dorsal view, *b* right lateral view, AML h5. All internal molds unless otherwise indicated. ATD S2= Ao Talo Udang Section 2; ATT(w) = Ao Talo Topo (west); AML = Ao Mo Lae. Scale bars = 2mm.

135, 142, 152 – external mold, 158, 159, 163, 165, 166, 171, 172, 173, 176, 186, 192, 198, 203, 204, 205, 208), 5.84 m (_7, 28, 32, 36), 6.01 m (_3, 12, 21), AML h1 (AML 1_1, 3, 5), AML h2 (AML 2_1, 4, 5, 7, 10, 11, 13, 14, 15, 18, 23, 24, 25, 33, 34, 35, 36, 39, 46, 47, 48, 49, 50), AML h3 (AML P_21, 22), AML h4 (AML X_1, 2 – external mold, 3, 8, 9, 14, 15, 16, 18, 19, 20, 21, 23, 24, 25, 27, 28), and AML h5 (AML Z_8); 15 from Ao Talo Udang (ATD) S1 7.00 m (_48, 265), 0.52 m (_14, 20, 21, 24, 28, 35), S2 0.69 m (_7 – external mold, 18, 19), S2 14.29 , (_2), S2 14.50 m (_1,2 – external mold), and ATD S2 h1 (_19, 23); 96 from Ao Talo Topo (ATT) 0.95 m (_6), 1.10 m (_1), 5.50 m (_4, 5, 6), 8.85 m (_15) 22.78 m (_12, 14, 20, 21, 23 – external mold, 41, 46, 59, 63, 68, 84, 99), 22.88 m (_54, 55, 60), 23.89 m (_4, 5), 25.34 m (_2, 3, 5, 13, 14), 28.37m (_1, 2, 3, 4, 5, 7, 9, 12), 29.17 m (_25, 27, 29 – internal and external molds, 31, 32, 35, 44

Figure 3:47 (*Next page*) *Eosaukia buravasi* Kobayashi, 1957. Third of four figures of *E. buravasi* cranidia arranged in increasing size order. **(1)** _4, *a* dorsal view, *b* left lateral view, *c* anterior view, ATTw; **(2)** _13, ATT 25.34 m; **(3)** _18, ATTw; **(4)** _23, ATD S2 h1; **(5)** _39, external mold, AML 5.17 m; **(6)** _35, AML 5.17 m; **(7)** _5, *a* dorsal view, *b* right lateral view, AMl 4.71 m; **(8)** _8, *a* dorsal view, *b* right lateral view, AML 5.17 m; **(9)** _27, AML 5.17 m; **(10)** _17, *a* dorsal view, *b* left lateral view, AML 5.17 m; **(11)** _18, *a* dorsal view, *b* right lateral view, AML h4; **(12)** _132, AML 5.81 m; **(13)** _7, AML h2; **(14)** _20, *a* dorsal view, *b* right lateral view, AML h4; **(15)** _7, AMlL 5.17 m; **(16)** _14, AML h2; **(17)** _172, AML 5.81 m; **(18)** _47, AML h2; **(19)** _208, *a* dorsal view, *b* right lateral view, AML 5.81. All internal molds unless otherwise indicated. ATD S2 = Ao Talo Udang Section 2; ATTw = Ao Talo Topo west; AML = Ao Mo Lae. Scale bars = 2 mm.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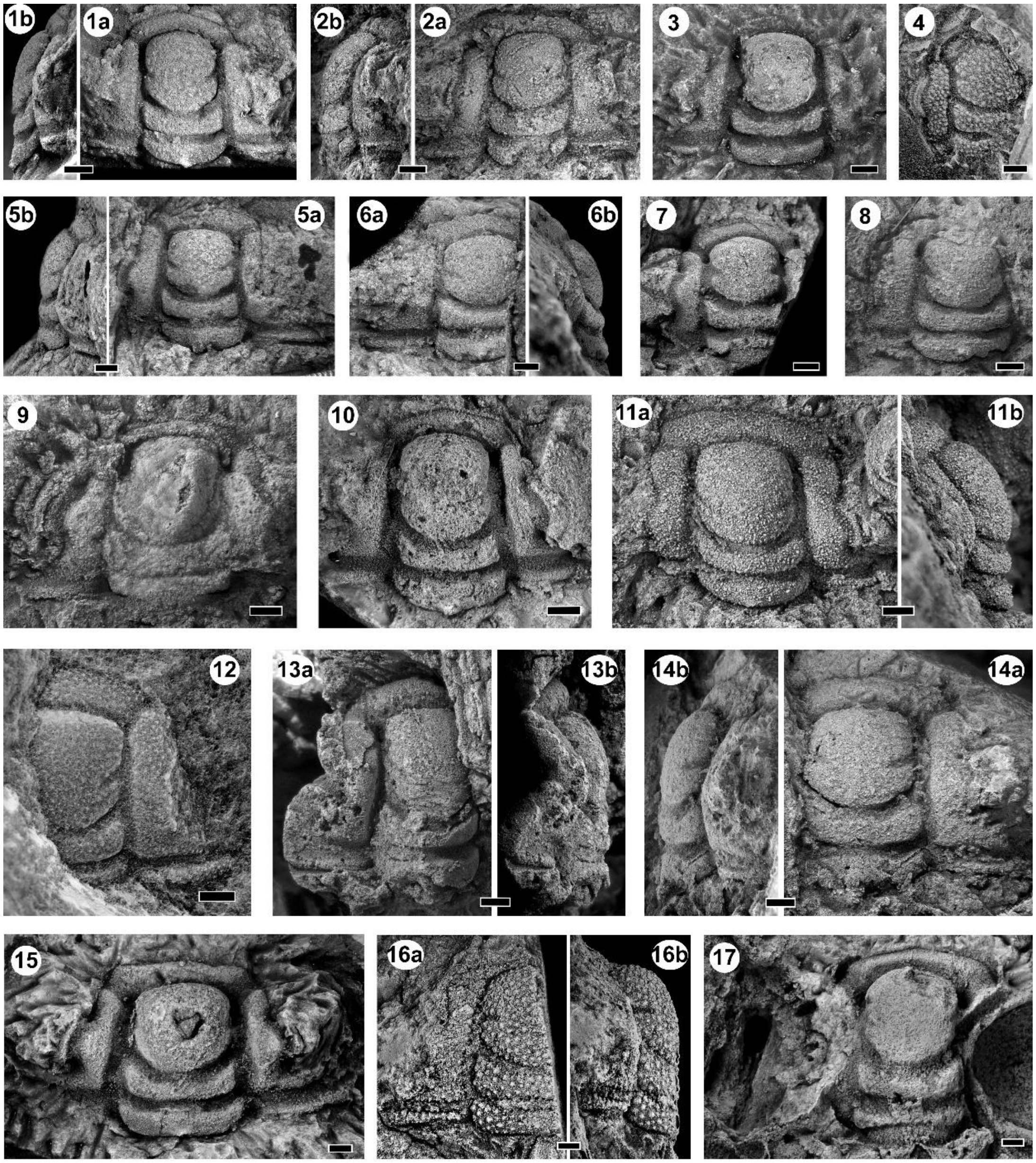


Figure 3:48 Eosaukia buravasi Kobayashi, 1957. Fourth of four figures of *E. buravasi* cranidia arranged in increasing size order. **(1)** _1, *a* dorsal view, *b* right lateral view, ATTw; **(2)** _14, *a* dorsal view, *b* right lateral view, ATD S2 0.52 m; **(3)** _,10, AML h2; **(4)** _152, external mold, AML 5.81 m; **(5)** _21, *a* dorsal view, *b* right lateral view, AML h4; **(6)** _24, *a* dorsal view, *b* left lateral view, AML h4; **(7)** _4, AML 4.71 m; **(8)** _25, AML h2; **(9)** _24, AML h2; **(10)** _70, ATTw; **(11)** _21, *a* dorsal view, *b* left lateral view, ATD 0.52 m; **(12)** _2, external mold, AML h4; **(13)** _23, *a* dorsal view, *b* left lateral view, AML 5.17 m; **(14)** _23, *a* dorsal view, *b* right lateral view, AML h4; **(15)** _13, AMLh2; **(16)** _24, *a* dorsal view, *b* left lateral view, ATD S2 0.52 m; **(17)** _35, AML h2. All internal molds unless otherwise indicated. ATTw = Ao Talo Topo west; AML = Ao Mo Lae; ATD S2 = Ao Talo Udsang Section 2. Scale bars = 2 mm.

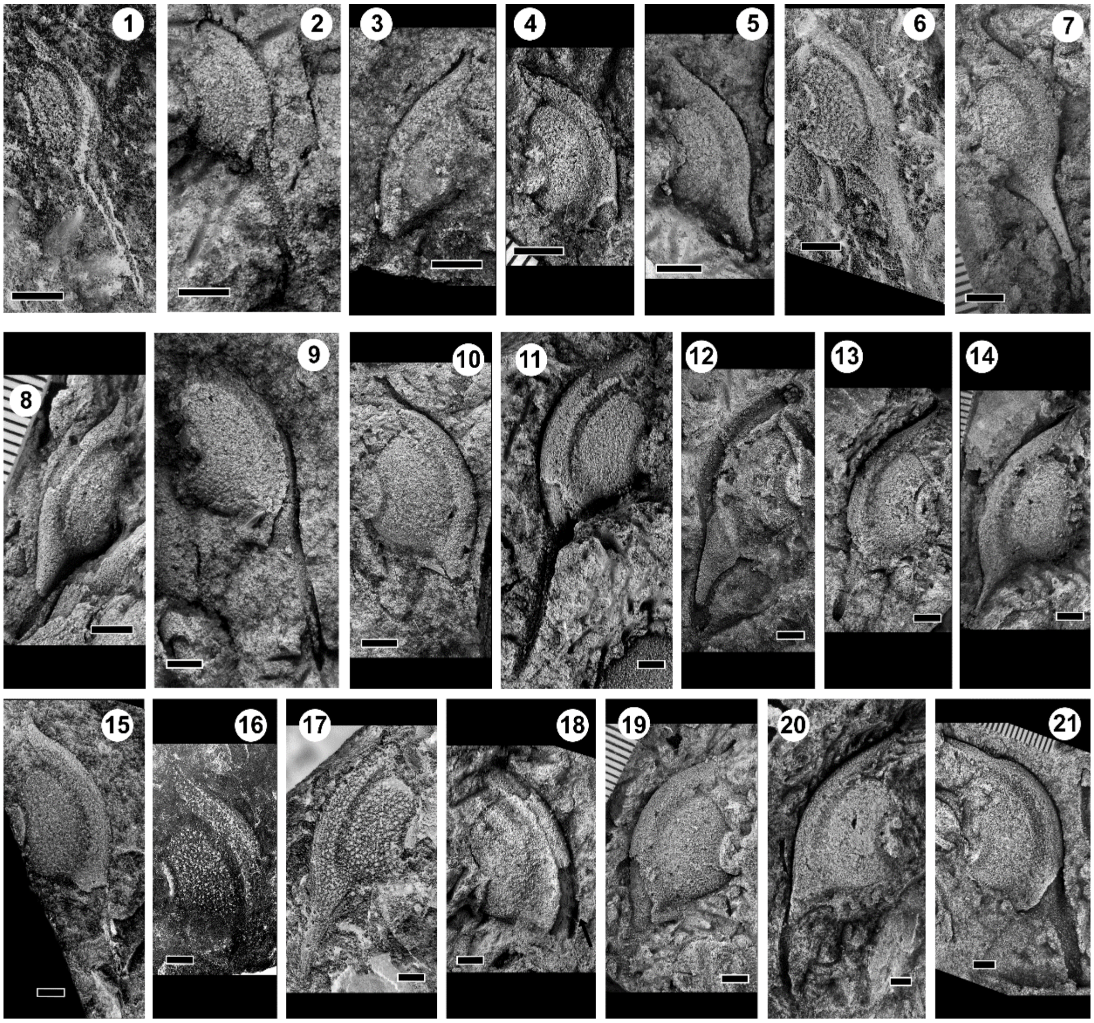
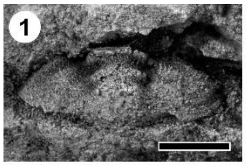


Figure 3:49 Eosaukia buravasi Kobayashi, 1957, all librigena. **(1)** _74, external mold, ATTw; **(2)** _17, AML5.84 m; **(3)** _27, AML h2; **(4)** 48_, ATTw; **(5)** _25, AML 5.84 m; **(6)** _118, external mold, ATTw; **(7)** _3, AML3.72 m; **(8)** _4, AML 5.17 m; **(9)** _88, AML 5.81 m; **(10)** _129, AML 5.81 m; **(11)** _22, AML h4; **(12)** _20, AML h2; **(13)** _126, AML 5.81 m; **(14)** _4, AML 3.62 m; **(15)** _14, external mold, AML 5.81 m; **(16)** _27, external mold, AML 5.84 m; **(17)** _18, external mold, AML 5.17 m; **(18)** _17, AML h2; **(19)** _153, AML 5.81 m; **(20)** _210, AML 5.81 m; **(21)** _19, AML h2. All internal molds unless otherwise indicates. ATTw = Ao Talo Topo west; AML = Ao Mo Lae. Scale bars = 2 mm.

Figure 3:50 (*Next page*) *Eosaukia buravasi* Kobayashi, 1957, all pygidia. **(1)** _28, ATT 29.17 m; **(2)** _62, ATT 29.17 m; **(3)** _12, ATD S2 0.52 m; **(4)** _202, AML 5.81 m; **(5)** _52, ATT 22.78 m; **(6)** _33, AML 5.84 m; **(7)** _10, AML 5.17 m; **(8)** _42, ATT 29.17m; **(9)** _51, ATT 22.78 m; **(10)** _29, AML 5.84 m; **(11)** _1, ATT h2; **(12)** _2, AML h2; **(13)** _11, external mold, AML 5.84 m; **(14)** _117, AML 5.81 m; **(15)** _66, external mold, ATT 22.78 m; **(16)** _64, external mold, ATT 29.17 m; **(17)** _3, AML 5.17 m; **(18)** _17, external mold, AML 6.01 m; **(19)** _69, ATT 29.17 m; **(20)** _31, AML 5.17 m; **(21)** _4, ATT 25.34 m; **(22)** _18, AML 6.01 m; **(23)** _9, AML 5.17 m; **(24)** _196, AML 5.81 m; **(25)** _24, AML 5.17 m; **(26)** _59, AML 5.81 m; **(27)** _150, AML 5.81 m; **(28)** _130, AML 5.81 m; **(29)** _3, ATT 8.20 m; **(30)** _17, external mold, AML 5.81 m; **(31)** _8, ATTw; **(32)** _6, AML h2; **(33)** _40, AML 5.17 m. All internal molds unless otherwise indicated. ATT(w) = Ao Talo Topo (west); AML = Ao Mo Lae; ATD S2 = Ao Talo Udang Section 2. Scale bars = 2mm.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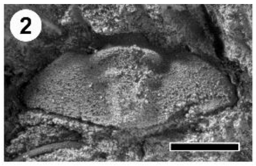
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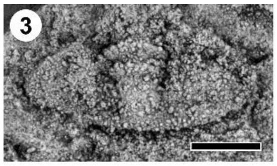
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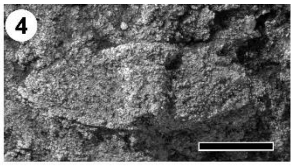
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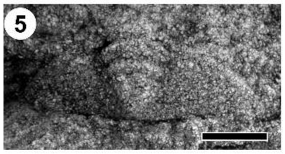
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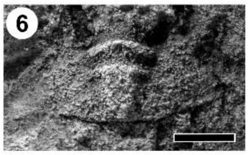
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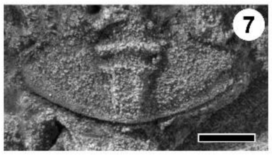
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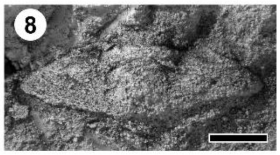
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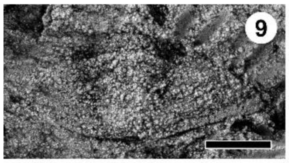
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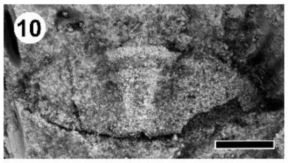
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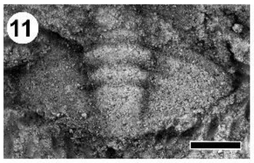
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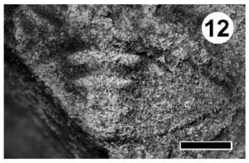
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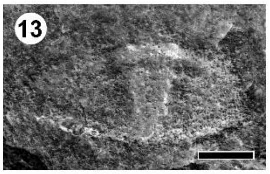
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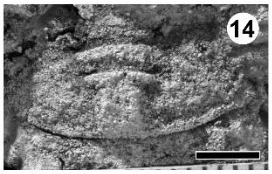
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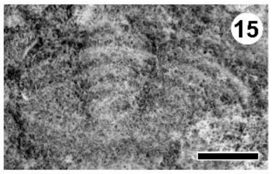
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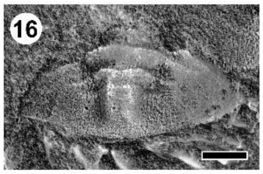
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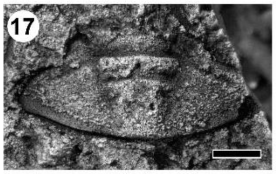
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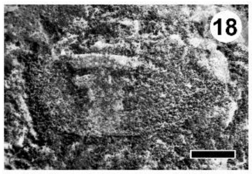
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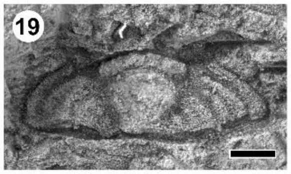
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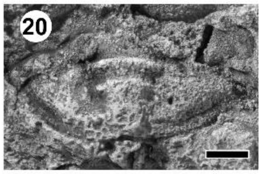
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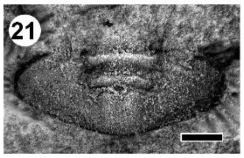
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– external mold, 47, 52, 58, 59, 61, 67), ATT h1 (_4), ATT h2 (_3), and Ao Talo Topo west (ATTw) (_1, 4, 7, 8, 9, 10, 11, 16 – external mold, 18, 29, 32, 37,44, 45, 46, 55 – external mold, 57 – external mold, 58, 59, 61, 63, 65, 66, 67, 70, 72, 77, 78, 80, 81, 82, 83, 92, 94, 97, 101, 106, 109, 110, 115, 114, 116, 120, 122, 124); three from Laem Hin Ngam (LHN) 2.85 m (_26, 30, 35). 40 Librigena: 32 from AML 3.62 m (_4), 3.72 m (_3), 5.17 m (_2, 4, 18 – external mold, 30), 5.81 m (_14 – external mold, 15 – external mold, 27, 68, 88, 126, 129, 131 – external mold, 153, 194 – external mold, 210), 5.84 m (_3, 9 – external mold, 17, 25, 27 – external mold), 6.01 m (_6, 7 – external mold), AML h2 (_3 – external mold, 17, 19, 20, 27, 28, 45 – external mold), AML h4 (X_22), and AML h5 (_2); seven from ATTw (ATT1_48, 49, 52, 74, 93 – external mold, 118 – external mold, 121). 46 pygidia: 29 from AML 5.17 m (_3, 9, 10, 12, 15, 24, 31, 33, 34 – external mold, 40, 42 – external mold), 5.81 m (_17 – external mold, 59, 103, 117, 136, 150, 177, 196, 202), 5.84 m (_11 – external mold, 29, 33), 6.01 m (_17 – external mold, 18), AML h1 (1_7), AML h2 (2_2, 6), and AML h4 (_13); 14 from Ao Talo Topo 6.65 m (_6), 8.20 (_3), 22.78 m (_51, 52, 55 – external mold, 66 – external mold), 25.34 m (_4), 29.17 m (_11 – external mold, 28, 42, 62, 64 – external mold, 69), and ATT h1 (_1); one from ATTw (_85); two from ATD S2 0.52 m (_22, 12). All internal molds unless otherwise indicated.

Remarks.—Eosaukia buravasi is the most abundant and widely distributed species in the Tarutao Group. It is also the only species known to occur elsewhere on Sibumasu having also been found in the Molohein Group of Myanmar (Wernette et al., *in prep*). Wernette et al. (*in prep*) presented a landmark-based geometric morphometric analysis of *E. buravasi* using 120 of the Thai specimens included herein as well as two specimens from the southern Shan State. The undifferentiated distribution of scores, particularly on the first two relative warps (Wernette et al., *in prep* fig. 14), indicated that all the specimens herein assigned to *E. buravasi* as well as those from Myanmar are a single species.

It is a species with much variation across numerous characters, such that a small sample could haphazardly appear to consist of two or three separate species. There is variation in obliquity relative to the longitudinal plane of the fixigena and palpebral lobes; the specimens with high obliquity (e.g. ATT1_37, AML2_7, and AML2_13; Figs 3:45.26, 47.13, and 48.15) appear to have a trapezoidal outline while those with more exsagitally oriented palpebral lobes (e.g. ATT30.30_29, ATT1_29, ATD1_3, and AML4.71_4; Figs 3:45.12, 46.16, 47.4, and 48.7) have more rectangular outlines. The glabella is anteriorly tapering in some specimens (e.g. AMLX_3, ATT1_65, AML5.17_8, and AML2_13; Figs 3:45.30, 46.12, 47.8, and 48.15) and parallel-sided in others (e.g. ATDA_20, AML4.71_6, AML5.81_172, and AML4.71_4; Figs 3:45.23, 46.20, 47.17, and 48.7). The length (sag.) of the anterior border is also variable with shorter, more brim-like borders in some specimens (e.g. AML5.81_54, ATT1_92, ATT1_18, and ATDA_24; Figs 3:45.10, 46.1, 47.3, and 48.16) and quite long, inflated borders in others (e.g. ATT1_110, AMLX_14, AMLX_20, and ATDA_21; Figs 3:45.11, 46.25, 47.14, and 48.11). The anterior glabellar margin may be strongly and smoothly curved (e.g. ATT1_65, AMLX_18, and ATT1_70; Figs 3:46.12, 47.11, and 48.10) or nearly straight with distinct anterior glabellar corners (e.g. AMLL6.01_21, AMLX_14, ATT1_4, and

AMLX_23; Figs 3:45.5, 46.25, 47.1, and 48.14). The cranidium may be relatively dorsoventrally flat (e.g. ATT30.30_35, AMLX_14, AML5.17_17, and AMLX_23; Figs 3:45.20, 46.25, 47.10, and 48.14) or strongly convex (e.g. ATT29.50_3, AML5.17_44, AML5.17_8, and ATDA_24; Figs 3:45.3, 46.19, 47.8, and 48.16). The anterior cranidial margin can vary from straight (e.g. ATT26.50_14, AML2_47, and AML2_13; Figs 3:45.15, 47.18, and 48.15) to strongly curved (e.g. ATDA_20, AMLZ_8, AML5.81_208, and ATT1_70; Figs 3:45.23, 46.26, 47.19, and 48.10) and even angular (e.g. AML5.81_78, ATT1_4, and ATT1_70; Figs 3:46.13, 47.1, and 48.10). Kobayashi (1957) and Shergold et al. (1988) suggested that some of the variation, particularly the convexity of the cranidium is size-related, but in the extensive collection presented herein, it is clear that each of these noted variations are independent of size with each of Figs 3:45–48 containing a different size range of cranidia, Fig. 3:48 displaying the largest.

The most consistent cranidial characters for *E. buravasi* are the anterolaterally oblique preocular furrows, lack of preglabellar field, deeply incised and strongly curved S1, relatively broad fixigena, and short palpebral lobes.

Shergold et al. (1988) reassigned most of the librigenae assigned to this species by Kobayashi (1957; pl. 5, figs 7,13,14,15) to *Lophosaukia* cf. *jiangnanensis* instead. The only two of Kobayashi's (1957) librigenae retained as *E. buravasi* by Shergold et al. (1988) were pl. 5, figs 8 and 9 (Kobayashi, 1957) which have a vincular pattern of ridges furrows crossing the doublure, now known to be characteristic of *Eosaukia*. In the new collections presented herein, no librigenae have been found with this pattern, but very few librigenae have been found with the ventral librigena exposed. The librigenae that are here assigned to *E. buravasi* on the basis of their shape and the size of the eye, show variation in the shape of the anterior suture branch and projection of the genal spine. This variation is expected as a complement to the variation in the palpebral orientation and frontal areas displayed by the cranidia. These librigenae are abundant and regularly co-occur with cranidia of *E. buravasi*, providing support that the librigena without furrows crossing the lateral border are correctly associated with *E. buravasi*. *Lophosaukia* cf. *jiangnanensis* is an unlikely association for the librigena, because this species has relatively long (exsag.) eyes compared with the shorter eyes of *E. buravasi*. Furthermore, the librigenae of *Lophosaukia* have a distinct pattern of pustulation.

The pygidium of *E. buravasi* exhibits less variation than the cranidium. It is lenticular with a wide (tr.) axis that occupies the full length of the glabella and consists of two well-defined axial rings, a narrow (tr.) articulating half ring, and a weakly double-ridged terminal piece. There are two notable variations: the curvature of the lateral corners, with a few specimens (e.g. ATT26.20_4, Fig. 3:50.22) exhibiting rounded rather than the typical angular corners, and the retention of interpleural and pleural furrows in the usually effaced pleural field (e.g. ATT30.30_69 and AML5.81_196; Figs 3:50.20,25). The pygidia that display pleural furrows reflect the subequal pleural and interpleural furrow distribution common in other saukiids. *Eosaukia micropora* (Qian, 1985a; Lee and Choi, 2011) and *E. bella* also have furrowed pleural fields, but the longitudinal ridges on their terminal pieces are more prominent than the weakly defined ridges in *E. buravasi.*

Genus *Hoytaspis* Ludvigsen and Westrop, 1983

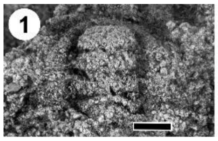
Type species.—*Ptychaspis specious* Walcott, 1879: 131; 1913:272–273, pl. 43, figs. 16–19; designated by Ludvigsen and Westrop 1983: 34; Hoyt Limestone, New York State, U.S.A.; Late Cambrian, Franconian.

Remarks: The cranidium of *Hoytaspis* is similar in all respects to that of *Prosaukia* Ulrich and Resser, 1933 with the exception of the elevation of the preglabellar field. It is elevated above the anterior border in *Hoytaspis* and depressed below the anterior border in *Prosaukia* (Ludvigsen and Westrop, 1983). The librigenae are also similar; the most notable feature on each is the separation of the lateral and posterior border furrows with the posterior furrow extending into the genal spine (Ludvigsen and Westrop, 1983; Shergold et al., 1988). The pygidia are most distinguishable by *Hoytaspis*' narrower border. The sagittal keel (post-axial ridge) tends to be more pronounced in *Hoytaspis* (Ludvigsen and Westrop, 1983) though this feature is also seen in some species of *Prosaukia* such as *P. hartii* (Walcott, 1879).

Hoytaspis thanisi Shergold et al., 1988

Figs 51–53

1988. *Hoytaspis*? *thanisi* Shergold et al. p. 308 pl. 5, figs A-I.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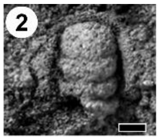
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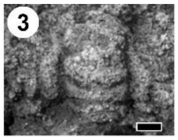
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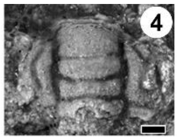
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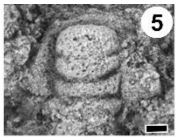
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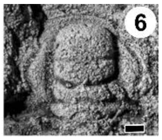
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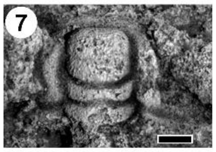
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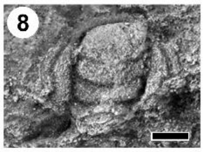
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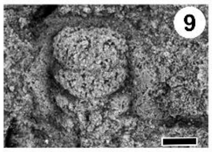
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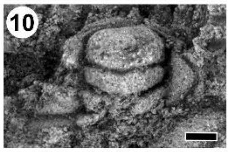
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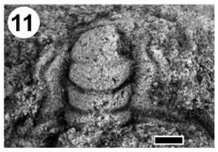
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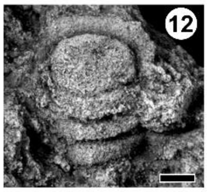
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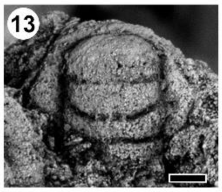
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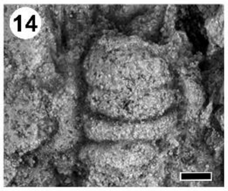
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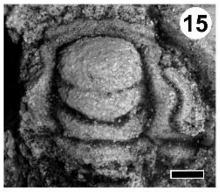
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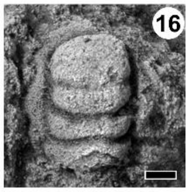
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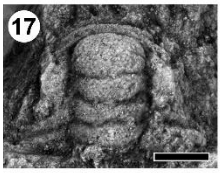
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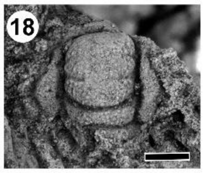
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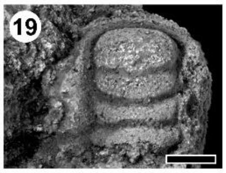
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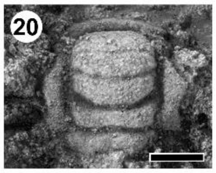
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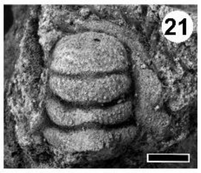
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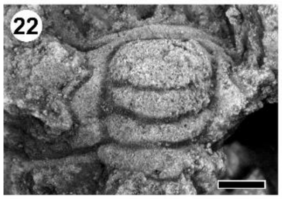
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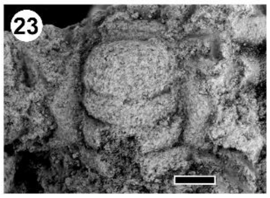
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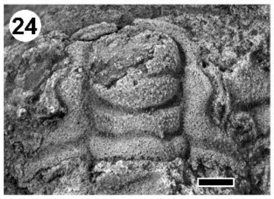
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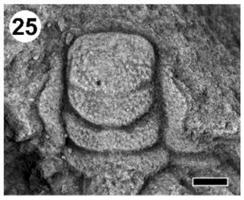
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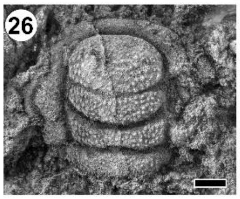
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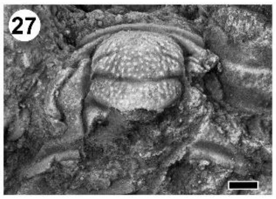
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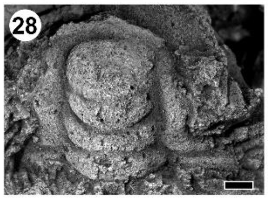
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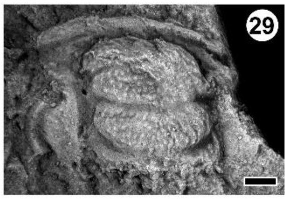
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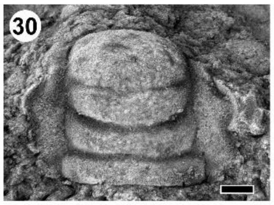
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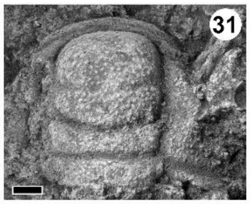
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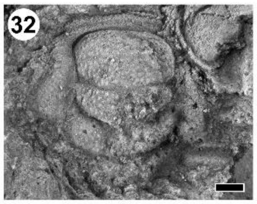
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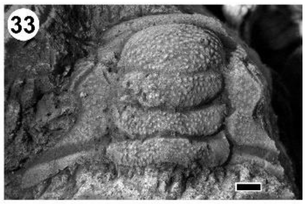
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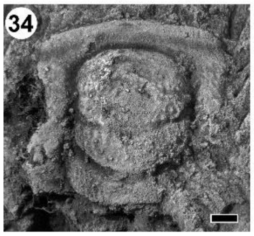
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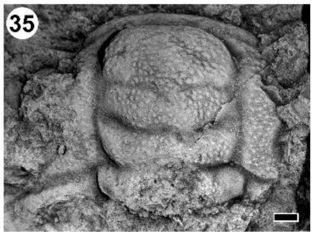
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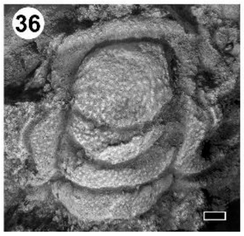
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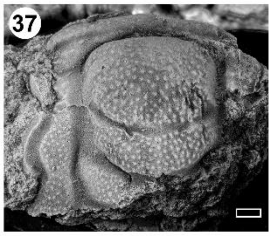
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Figure 3:51 (*Previous Page*) *Hoytaspis thanisi* Shergold et al., 1988, all cranidia. **(1)** _149; **(2)** _8; **(3)** _80; **(4)** _177; **(5)** _61; **(6)** _12, ATD S1 6.65 m; **(7)** _; **(8)** _173; **(9)** _183; **(10)** _203; **(11)** _184; **(12)** _221; **(13)** _44; **(14)** _195; **(15)** _22; **(16)** _66; **(17)** _93; **(18)** _46; **(19)** _262; **(20)** _25; **(21)** _264; **(22)** _194; **(23)** _16; **(24)** _234; **(25)** _222; **(26)** _219; **(27)** _109; **(28)** _228; **(29)** _167; **(30)** _1; **(31)** _65; **(32)** _246; **(33)** _250; **(34)** _39; **(35)** _131; **(36)** _37; **(37)** _168. All internal molds. All from Ao Talo Udang (ATD) Section 1 (S1) 7.00 m unless otherwise indicated. Scale bars = 0.5 mm for 1–6; = 1 mm for 7–16; = 2 mm for 17–37.

Occurrence.—Ao Talo Udang S1 6.65–7.00 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Material.—94 cranidia from Ao Talo Udang (ATD) S1 6.65 m (_4,12) and 7.00 m (_1, 6, 8, 12, 13, 16, 22, 24, 25, 28, 33, 34, 37, 39, 40, 41, 44, 46, 49, 51, 54, 61, 63, 65, 66, 70, 75, 76, 80, 82, 84, 87, 92, 93, 100 – external mold, 101, 102, 103 – external mold, 109, 110, 113, 119, 122, 124, 131, 132, 134, 137, 139, 141, 149, 156, 159, 167, 168, 172, 173, 175, 177, 178, 183, 184, 186, 188, 189, 190, 194. 195, 198, 200, 203, 207, 210, 211, 212, 216, 219, 221, 222, 227, 228, 234, 240, 246, 249, 250, 256, 262, 264, 266, 269, 270). 33 librigenae from ATD S1 7.00 m (_180, 182, 132, 133, 67, 23, 42, 59 – external mold, 68, 73, 89, 96, 112, 116 – external mold, 121, 135, 144 – internal and external molds, 145 – internal and external molds, 146, 147 – external mold, 158, 161, 162, 166, 193, 206, 213, 218, 243, 258 – external mold, 260 – external mold). 32 pygidia from 6.65 m (_1) and 7.00 m (_7 – external mold, 9, 10 – external mold, 21, 30, 31, 36, 47, 53 – external mold, 72, 83, 90, 94 – external mold, 104 – external mold, 108, 111, 114 – external mold, 120,

Figure 3:52 Hoytaspis thanisi Shergold et al., 1988, all librigena. **(1)** _73; **(2)** _23; **(3)** _162; **(4)** _68; **(5)** _258, external mold; **(6)** _260, external mold; **(7)** _42, external mold; **(8)** _166; **(9)** _144, *a* external mold, *b* internal mold; **(10)** _89; **(11)** _145; **(12)** _233; **(13)** _232. All internal molds unless otherwise indicated. All from Ao Talo Udang Section 1 7.00 m. Scale bars = 2 mm for 1–7; 4 mm for 8–13.


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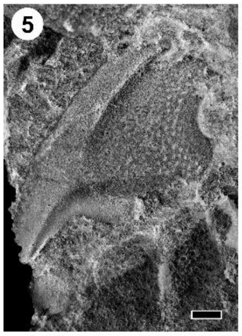
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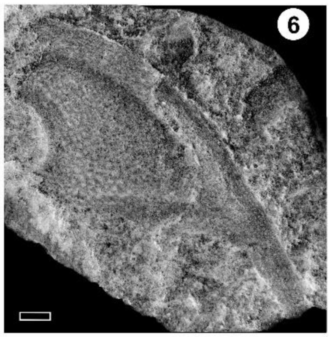
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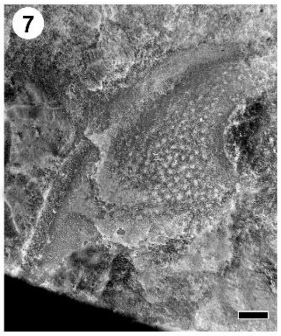
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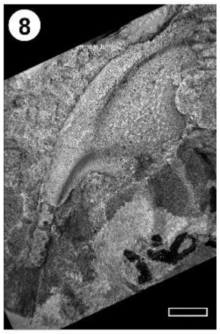
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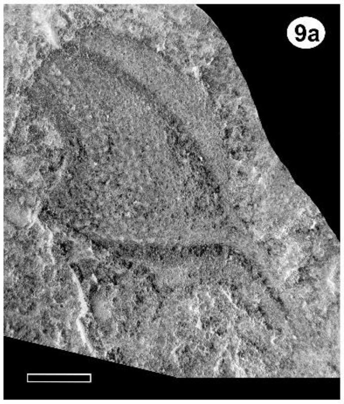
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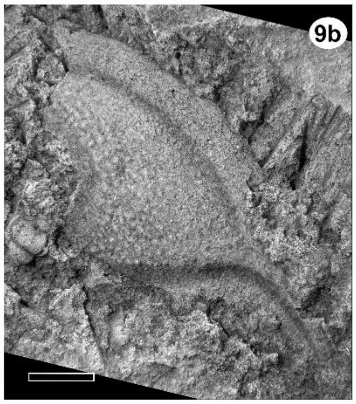
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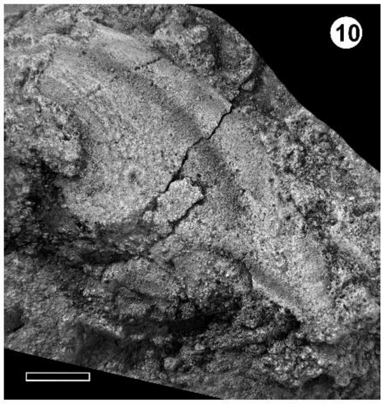
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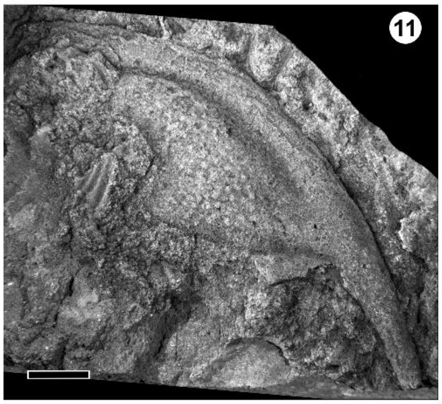
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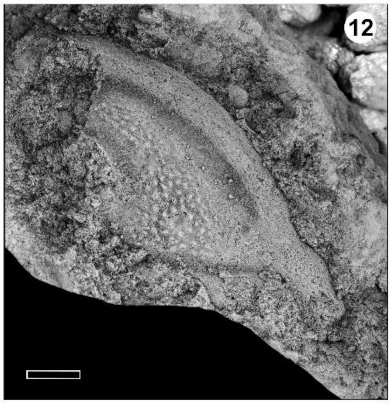
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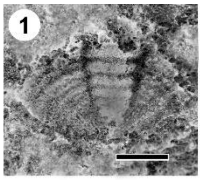

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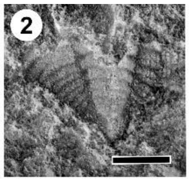

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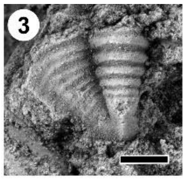

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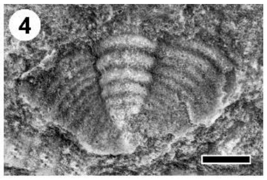

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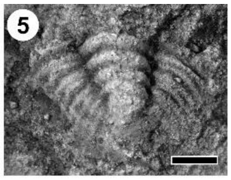

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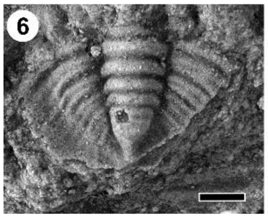

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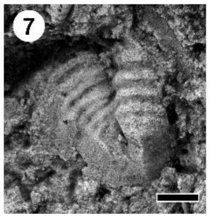

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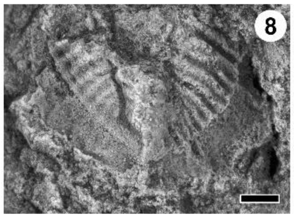

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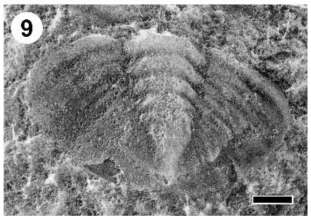

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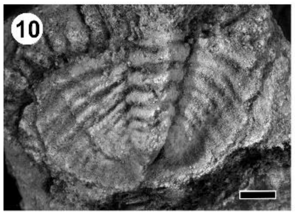

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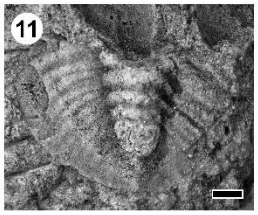

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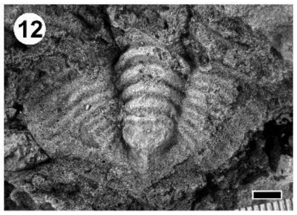

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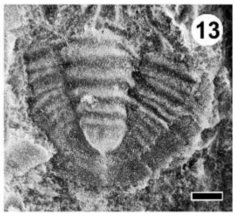

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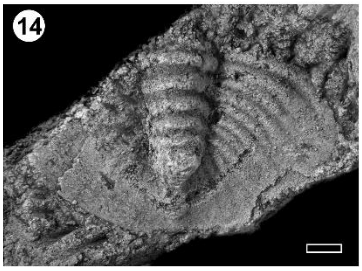

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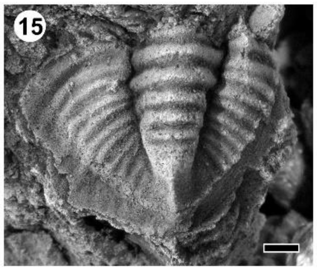

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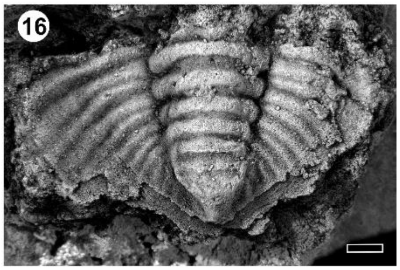

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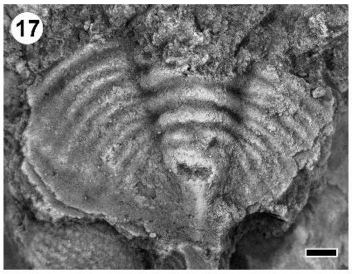

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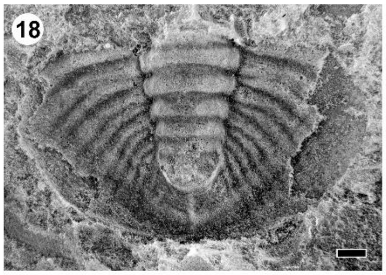

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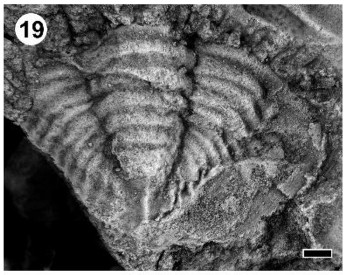

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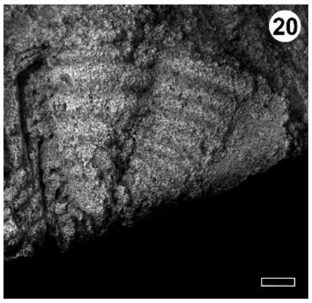

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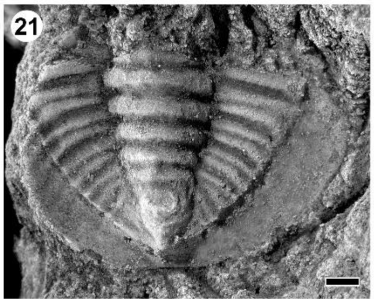

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Figure 3:53 (*Previous page*) *Hoytaspis thanisi* Shergold et al., 1988, all pygidia. **(1)** _7, external mold; **(2)** _114; **(3)** _31; **(4)** _53; **(5)** _226, external mold; **(6)** _176; **(7)** _9; **(8)** _47; **(9)** _123; **(10)** _21; **(11)** _127; **(12)** _130; **(13)** _104, external mold; **(14)** _90; **(15)** _199; **(16)** _30; **(17)** _205; **(18)** _94, external mold; **(19)** _108; **(20)** _83; **(21)** _259; **(22)** 111. All internal molds unless otherwise indicated. All from Ao Talo Udang Section 1 7.00 m. Scale bars = 1 mm for 1; = 2 mm for 2–22.

123 – external mold, 127, 130, 138, 164, 176, 192, 199, 202 – external mold, 205, 226, 259, 271). All internal molds unless otherwise indicated

Remarks.—While the majority of the specimens included herein have inflated preglabellar fields as in the genus *Hoytaspis*, some have seemingly depressed preglabellar areas as in *Prosaukia* Ulrich and Resser, 1933. The depressed field is most common in larger cranidia. Shergold et al. (1988) remarked on the same trend within specimens from their collections, citing the variability of this character as the reason for indicating doubt in the generic assignment. The individuals with depressed preglabellar fields occur in the same horizon and otherwise appear to fall within the morphological variation exhibited by specimens with inflated preglabellar fields. Determining the full range of that morphological variation is difficult due to tectonic and burial deformation of specimens. The 7.0 m horizon in Ao Talo Udang section 1 lies close to a fold axis and is the least cemented of all fossiliferous horizons known from Ko Tarutao. Furthermore, the specimens within this bed are randomly oriented within the bed rather than positioned relatively flat on the bedding planes. As a result, these specimens have experienced abnormal levels of distortion for the Tarutao Group. Even strong distortion for the Tarutao Group is relatively weak compared to distortion in more tectonically active regions. It is possible that dorso-ventral compaction and dorsal deflection of the anterior borders caused seemingly more depressed preglabellar fields. If the depressed border is an original character rather than result of distortion, the consistency of the inflated preglabellar field in smaller holaspids suggests a late onset ontogenetic shift but overall affinity with *Hoytaspis*.

The pygidium has a narrow border similar to, though less clearly defined than, that of the Laurentian species, *Hoytaspis speciosa* (Walcott, 1879). On most internal molds the broad (tr., exsag.) doublure has prevented preservation of the distal pleural field and border though the well-developed post-axial ridge is consistently preserved due to the doublure's pronounced medial shortening (sag.). The axis of *H. thanisi* is longer than that of *H. speciosa*, and contains more axial segments. In both species the expression of segments is somewhat variable, possibly indicating that segments are continuing to be added into late holaspid stages. *H. speciosa* is described as having four axial segments excluding the terminal piece, though the fourth segment is sometimes poorly developed (e.g. Ludvigsen and Westrop, 1983, pl. 15, fig. 10) and other times well developed with a fifth poorly developed segment (e.g. Ludvigsen and Westrop, 1983, pl. 15, figs 8, 12). *Hoytaspis thanisi* typically has five well-developed axial segments though the fifth segment may be poorly developed in smaller specimens (e.g. Figs 53.6, 7); alternatively a sixth poorly-developed segment may occur in larger specimens (e.g. Figs 53.16, 21).

Genus *Lichengia* Kobayashi, 1942

Type species.—Lichengia onigawara Kobayashi, 1942: 297–298, fig. 1 [= *Prosaukia brizo* Sun (*non* Walcott), 1935: 43–44, pl. 4 figs. 22–33]: Licheng Formation, Shangyaochen, Licheng, Shanxi, China; Late Cambrian, Fengshanian.

Lichengia simplex Shergold, 1991

Figs 3:54.1,2

not 1957. *Saukiella tarutaoensis* Kobayashi, p 378, pl. 5, fig. 12 (= *Prosaukia tarutaoensis*).

not 1957. *Coreanocephalus planulatus* Kobayashi, p. 379, pl. 4, figs. 16–17 (= *Thailandium solum*).

1988. *Lichengia*? *tarutaoensis* (Kobayashi); Shergold et al., 1988 p. 309–310, figs 5.S–V,?W.

1991. *Lichengia simplex* Shergold p. 27–28, pl. 4, figs. 1–7.

Occurrence.—Ao Talo Topo 23.89 m; Ao Mo Lae Formation, Tarutao Group, Tarutao, Furongian.

Material.—Two cranidia from Ao Talo Topo 23.89 m (_22, 18), both internal molds.

Remarks.—Shergold et al. (1988) reassigned *Saukiella tarutaoensis* Kobayashi, 1957 to *Lichengia*, establishing *Lichengia*? *tarutaoensis*. However, the new material figured in

Shergold et al. (1988) is not synonymous with the cranidium assigned by Kobayashi to *Saukiella* which has been revised to *Prosaukia tarutaoensis* (Kobayashi, 1957) based on additional material from the collections described herein (Wernette et al., in review).

When Shergold (1991) described *Lichengia simplex* from the Pacoota Sandstone of Australia, he remarked on the high degree of similarity between *L. simplex* and *Lichengia*? *tarutaoensis*, suggesting a deeper, wider (sag.) preglabellar field and anterior border furrow on the latter as the only distinguishing cranidial differences. The divisions and furrows of the frontal area vary between specimens with overlap between the Thai and Australian material even in the few specimens known from each location. As such, based on the cranidium, these populations should be considered the same species. Pygidial differences were also cited, notably that the outline of *L. simplex* is more ovoid than the outline of *Lichengia*? *tarutaoensis*. However, this comparison included the mistaken assignment of the large, shovel-like pygidia of *Thailandium solum* to *Lichengia*? *tarutaoensis* (Shergold et al., 1988). The one pygidium figured in Shergold et al. (1988) with the cranidia of *Lichengia*? *tarutaoensis* is similar to both the pygidia of *P. oculata* Wernette et al. (in review) and *L. simplex*. Other *Prosaukia* and *Lichengia* have similar pygidial morphology so the assignment to *P. oculata* rather than to *Lichengia*? *tarutaoensis* is largely based on abundance and co-occurrence of sclerites. While the *Lichengia* cranidia are quite rare in Ao Talo Topo horizon 24.70 m and unknown elsewhere, the pygidia and cranidia assigned to *P. oculata* occur in roughly similar numbers in Ao Talo Topo horizon 24.00 m. Regardless of whether the pygidium figured

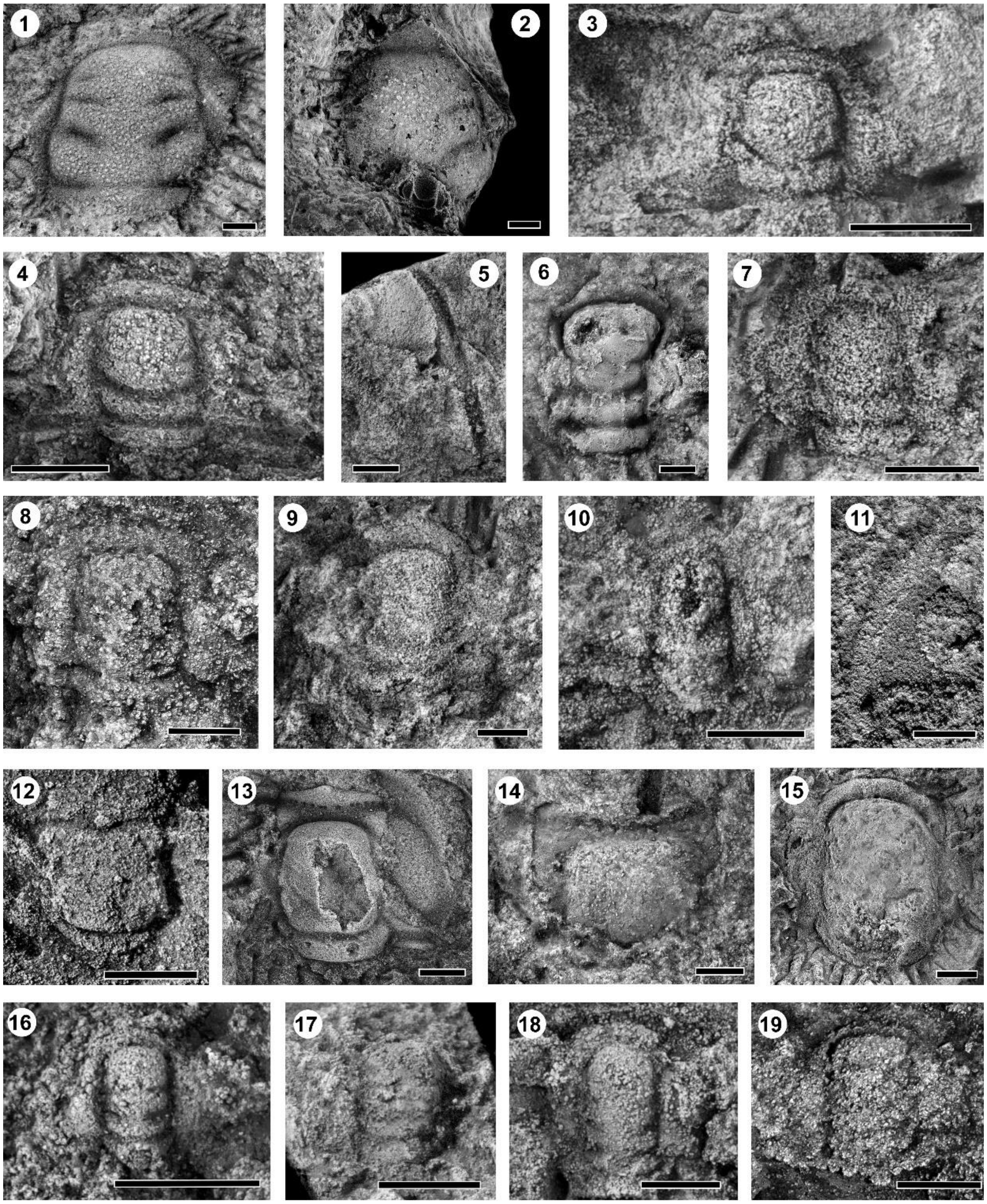
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Figure 3:54 (*Previous page*) *Lichengia simplex* Shergold, 1991, *Prosaukia* sp. 2, *Sinosaukia* sp., *Pacootasaukia* sp., *Wuhuia*? sp., *Corbinia perforata* n. sp., *Plethopeltella* sp., and *Asioptychaspis* sp. *Lichengia simplex* (1, 2) **(1)** _18, cranidium, ATT 23.89 m; **(2)** _22, cranidium, ATT 23.89 m. *Prosaukia* sp. 2 (3–5) **(3)** _1, cranidium, ATT 29.17 m; **(4)** _29, holotype, cranidium, LHN 2.85 m; **(5)** _2, librigena, ATT 29.17 m. **(6)** _22, *Sinosaukia* sp., cranidium, ATD S2 h1. *Pacootasaukia* sp. (7–9) **(7)** _3, cranidium, AML h5; **(8)** _6, cranidium, ATD h2; **(9)** _1, cranidium, ATT 8.60 m. *Wuhuia*? sp. (10–11) **(10)** 26, cranidium, ATT 22.78 m; **(11)** _2, librigena, AML h1. *Corbinia perforata* (12–14) **(12)** _4, cranidium, APM 49.90 m; **(13)** _37, cranidium, APM 53.65 m; **(14)** _36, cranidium, ATD S3 float. **(15)** _10, *Plethopeltella* sp., cranidium, ATT 28.37 m. *Asioptychaspis* sp. (16–18) **(16)** _253, cranidium, ATD S1 7.00 m; **(17)** _78, cranidium, ATD S1 7.00 m; **(18)** _18, indeterminate cranidium, ATD S2 0.52 m. **(19)** _29, indeterminate cranidium, AML h2. All internal molds. ATD S1–S3 = Ao Talo Udang sections 1–3; AML = Ao Mo Lae; ATT = Ao Talo Topo. Scale bars = 2 mm for 1, 3–14, 16–19; = 4 mm for 2, 15.

in Shergold et al. (1988) fig. 5W is more properly associated with *Lichengia* or *P. oculata*, it is morphologically similar enough to the paratype pygidia for *L. simplex* as to plausibly fall within the variation encompassed by this species. As such, no diagnosable characters separate the *Lichengia* material from the Tarutao Group and the Pacoota Sandstone, and they should be considered synonymous with the name *L. simplex* having priority due to Kobayashi’s (1957) *S. tarutaoensis* being a separate species entirely.

Genus *Lophosaukia* Shergold, 1972

Type species.—Lophosaukia torquata Shergold, 1972, p. 62–64, pl. 18, figs 1–6; by original designation; Gola beds, Mobedah Creek, western Queensland, Australia; Furongian, *Rhaptagnostus clarki maximum/Rhaptagnostus papilio* Zone.

Lophosaukia nuchanongi n. sp.

Figs. 3:55,56

?1957. *Eosaukia buravasi* Kobayashi, p. 376, pl. 5, figs 7,13 only.

1988 . *Lophosaukia* cf. *jiangnanensis* Lu and Lin, Shergold et al., p. 310–312, figs 5J–P.

Type material.—Holotype: ATT 24.00_89 (Fig. 3:56.3), Ao Talo Topo 22.78 m; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian. Paratypes: ATT 24.00_15, ATT 24.70_19, 21, and ATT26.50_9.

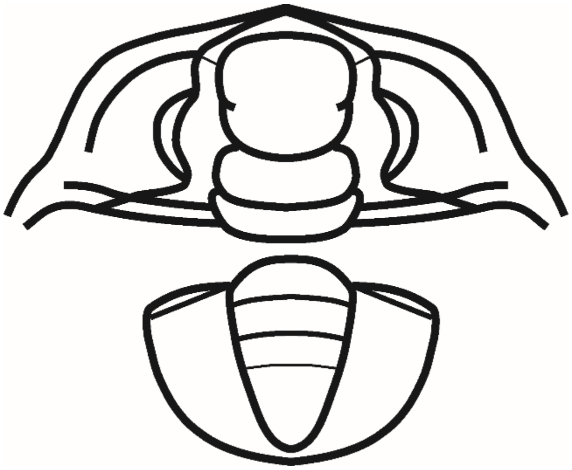

Figure 3:55 Lophosaukia nuchanongi n. sp. line drawing.

Diagnosis.—Cranidium of subequal length and width with short and obtusely angular anterior border, parallel-sided to gently anteriorly expanding glabella weakly constricted at S1, arcuate palpebral lobes extending from SO to anterior to S2, narrow fixigenae, and moderate to coarse granulation across entire cranidium and forming single row of pustules on posterior border. Librigena with deep border furrow broad border, and short, broad based, curved genal spine covered in fine, subparallel ridges; all other surfaces covered by intermixed coarse and fine pustulation with pustules forming rows parallel to cranidial margin and an elongated radiating pattern extending along limb immediately anterior to border furrow. Pygidium stubtriangular to subovoid and weakly furrowed with axis reaching nearly the full length bearing four axial rings.

Occurrence.—Ao Talo Topo 1.10–29.17 m and Ao Talo Udang S2 0.52–14.29 m; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

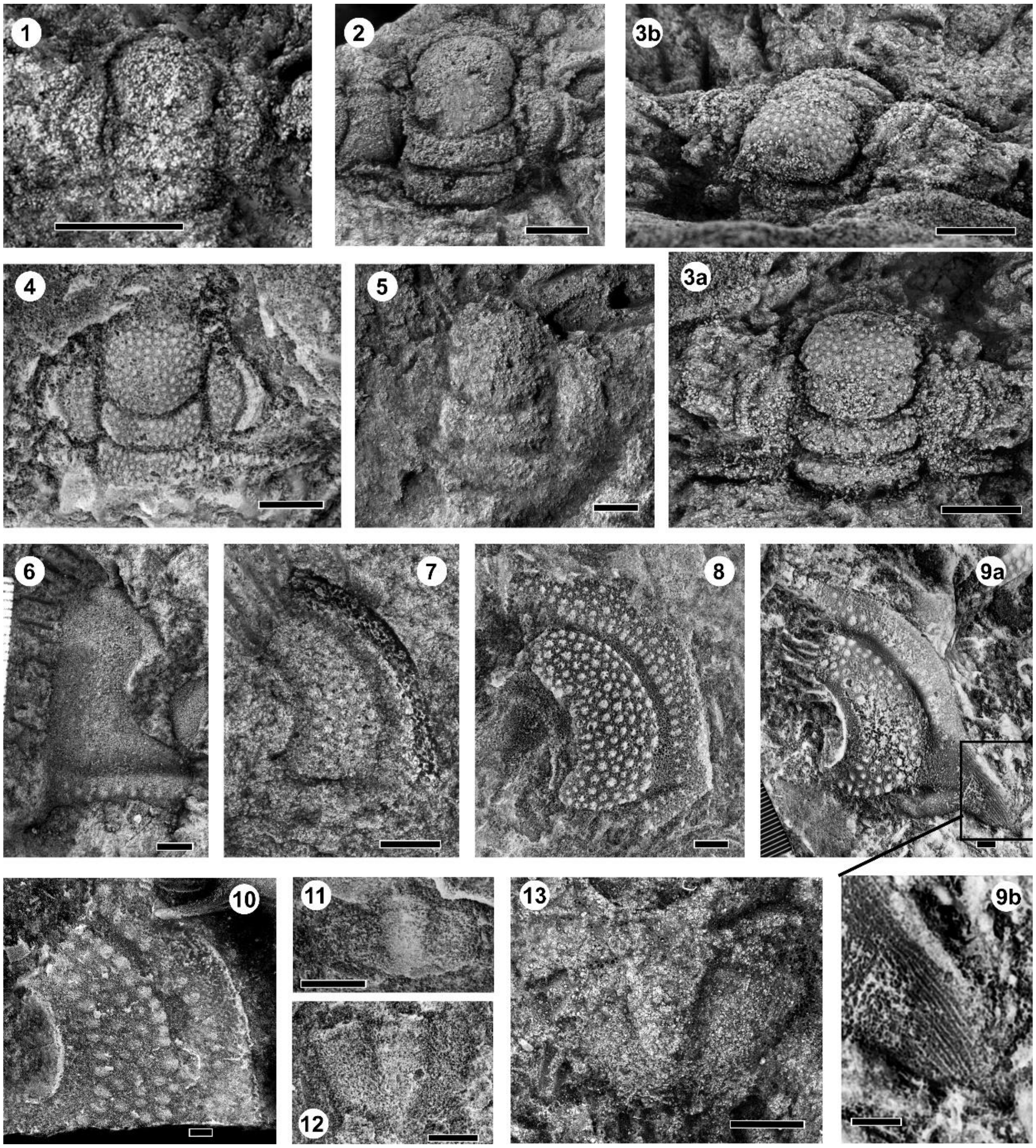

Figure 3:56 Lophosaukia nuchanongi n. sp. **(1)** _15, cranidium, ATT 22.78 m; **(2)** _, 9, cranidium, ATT 25.34 m; **(3)** _89, cranidium, *a* dorsal view, *b* left lateral oblique view, ATT 22.78 m; **(4)** _21, cranidium, external mold, ATT 23.89 m; **(5)** _1, cranidium, ATD S2 14.29 m; **(6)** _19, cranidium, ATT 23.89 m; **(7)** _9, librigena, ATT 8.20 m; **(8)** _30, librigena, external mold, ATD S2 0.52 m, ATT m; **(9)** _3, librigena, external mold, *b* magnification of structure on genal spine; ATT 1.1 m; **(10)** _17, librigenal external mold, ATT 8.85 m; **(11)** _9, pygidium, external mold, ATT 29.17 m; **(12)** _26, pygidium, ATT m; **(13)** _47, pygidium, ATT 22.88 m. All internal molds unless otherwise indicated. ATT = Ao Talo Topo; ATD S2 = Ao Talo Udang section 2. Scale bars = 2mm.

*Description.—*Cranidium subtrapezoidal; width across palpebral areas ~110% cranidial length (sag.). Glabellar width (tr.) across S1 ~55% width across palpebral areas; anterior border ~10% cranidial length (sag.); glabella nearly parallel sided and weakly laterally pinched at S1*;* anterior glabellar margin moderately to strongly curved; S1 posteriorly bowed and deeply incised across glabella; S2 short, posteromedially deflected, and firmly incised; S3 effaced; SO less strongly bowed than S1; LO subequal width to L1. Palpebral lobe arcuate, nearly symmetric about the midpoint; palpebral midpoint opposite S1; palpebral lobe length (exsag.) 35%–40% cranidial length (sag.); width (tr.) across anterior palpebral corners equal or slightly less than width across posterior corners; palpebral furrows firmly incised. Fixigena narrow (tr.); anterior suture branches subparallel. Frontal area narrow (tr.) comprising only anterior border with no preglabellar field; lateral anterior border furrow narrow and shallow, anterolaterally oriented joining preglabellar furrow at sharp angle; anterior border strongly ventrally sloping, exsag. short and sag. elongated into broad, obtuse angle. Posterior suture branches nearly transverse; posterolateral projections short (exsag.), mostly comprising posterior border and broad posterior border furrow. Entire cranidium, excluding palpebral lobes, strongly pustulated; pustules on anterior limb of posterior border furrow arranged in single row.

Librigena strongly convex with moderately broad genal field and wide lateral and posterior borders*;* lateral and posterior border furrows broad and deeply incised; lateral border furrow shallows and broadens near junction with posterior border furrow, becoming effaced in some individuals. Genal spine broad-based and posteriorly curved, beak-like with fine, sub-parallel to anastomizing ridges oriented along length of spine.

Excluding genal spine, entire surface covered in pustules of intermixed sizes; pustules on medial genal field of mixed sizes and less ordered; pustules nearest lateral furrow coarsest and arranged in rows; pustules on lateral border coarsest near furrow, and those proximal to furrow may be elongated into radiating pattern orthogonal to furrow.

Pygidium subtriangular to subovoid. Axis posteriorly tapering, nearly full pygidial length with short postaxial section; four axial rings, only first two clearly defined. Pleural furrows and interpleural furrows nearly effaced with pleural furrows deeper than interpleural furrows. Very narrow pygidial border.

Etymology.—Named in honor of Dr. Tossaporn Nuchanong, former Director General of Thailand's Department of Mineral Resources.

Material.—Six cranidia: four from Ao Talo Topo (ATT) 22.78 m (_15, 19), 23.89 m (_19, 21 – external mold), and 25.34 m (_9); one from Ao Talo Udang (ATD) S2 14.29 m (_1). Five librigena: four from ATT 1.10 m (_3 – external mold), 8.20 m (_9), and 8.85 m (_14 – external mold, 17 – external mold); one from ATD S2 0.52 m (_30 – external mold). Four pygidia from ATT 22.88 m (_47) and 29.17 m (_9, 24, 26 – external mold). All internal molds unless otherwise indicated.

Remarks.—In addition to describing newly recovered material, Shergold et al. (1988) reassigned several cranidia and librigena previously identified as *Eosaukia buravasi* Kobayashi (1957, pl. 5, figs 6–7,13–15,19–20) to *Lophosaukia* as *Lophosaukia* cf.

jiangnanensis, herein reassigned to *Lophosaukia nuchanongi*. The anteriorly tapering glabellae of pl. 5, figs 6, 19, and 20 (Kobayashi, 1957) questions their reassignment, especially in the absence of well-preserved palpebral or frontal areas; pl. 5, figs 19 and 20 (Kobayashi, 1957) have a preserved frontal area that is distinctly *Eosaukia*-like in the furrows. Both *Lophosaukia* and *Eosaukia* show extensive intraspecific cephalic variability (Kobayashi, 1957; Shergold, 1975; Shergold et al., 1988; Wernette et al in prep) with extensive overlap between these genera in all but the frontal area. *Lophosaukia*, however, consistently bears coarser pustulation. Without such pustulation or the anterior margin preserved, confident assignment to of sclerites, particularly librigenae, to *Lophosaukia*, is challenging.

Shergold et al. (1988) argued that the specimens from the Tarutao Group most closely resemble *L. jiangnanensis* Lu and Lin, 1983 but noted that the latter has a longer preglabellar protrusion and a more sharply furrowed pygidium. Additionally, *Lophosaukia nuchanongi*. has a distinctly narrower, shorter, and less anteriorly rounded glabella. *Lophosaukia* cf. *jiangnanensis* (*sensu* Peng, 1992) has a longer frontal area, broader glabella, and less arcuate palpebral lobes. *Compared* with *Lophosaukia torquata* or *Lophosaukia acuta*, *Lophosaukia nuchanongi*. is not as convex and has finer granulation. The angularity of the anterior margin is consistent with what Shergold (1975) referred to as *Lophosaukia* sp. C, though fixigena of *L. nuchanongi* are wider. *Lophosaukia rectangulata* Ergaliev, 1980 has a straighter anterior glabellar margin.

The librigenae of *L. nuchanongi* have coarse granulation of mixed sizes distributed in a somewhat orderly pattern, especially on the cephalic border. Along the border furrow, the granules are elongated in a radiating pattern orthogonal to the furrow. This differs from Australian *Lophosaukia* librigenae (e.g. *L. torquata* Shergold 1972, and *Lophosaukia* sps A and B *sensu* Shergold, 1975) as well as *Lophosaukia orientalis* (Kobayashi, 1933) which have irregular ridges running parallel to the cephalic margin. In *L. nuchanongi* these ridges are restricted to the genal spine. This may partly reflect preservational state, as most librigenae known from the Tarutao Group are external molds whereas those featured in Shergold, 1975 pls 18–19 are internal molds, but it is also consistent with the patterning on *L. jiangnanensis* and *Lophosaukia* cf. *jiangnanensis* (*sensu* Peng, 1992). The latter lacks the radiating granules close to the lateral border furrow and has a ridged external surface with a pustulated internal surface.

Genus *Prosaukia* Ulrich and Resser, 1933

Type species.—Dikelocephalus misa Hall, 1863: 144–145, pl. 8 fig. 15, pl. 10 figs 4,5,6?,7,7; designated by Ulrich and Resser (1933: 141–144); Ranconia Formation, Wisconsin, U.S.A.; Late Cambrian, Franconian.

Remarks.—Prosaukia is a diverse and widespread genus, best known from Laurentia, but also existing on most other continental blocks. The cranidium is characterized by an anteriorly narrowing subrectangular glabella, depressed preglabellar field, medially shallowing anterior border furrow, and divergent anterior suture branches. The librigena have disconnected lateral and posterior border furrows with the posterior border furrow extending into the genal spine base, and the pygidium is transversely subelliptical with relatively equally divided pleurae (Ludvigsen and Westrop, 1983; Wernette et al., *in review*).

Where *Prosaukia* occurs in abundance, it may be remarkably diverse both in the number of species present and in the intraspecific variation of each of those species. Ulrich and Resser (1933) assigned 29 species when establishing the genus based on material from the Upper Mississippi Valley. Raasch (1951) recognized only 13 of those species as valid. High rates of intraspecific variation resulting in over differentiation of species is consistent with trends in other dikelocephalids (Hughes, 1994; Wernette et al., *in prep*). Three distinct forms new forms of *Prosaukia* appear to exist in the Ao Mo Lae Formation in addition to *Prosaukia tarutaoensis* (Kobayashi, 1957) and *Prosaukia oculata* (Wernette et al., *in review*). Each of these species is based only on a few cranidia, and librigena and pygidia have not been assigned for all of them. They occur in different horizons and locations, and each is consistently diagnosable. However, given the small sample size of each form, and in consideration of the dikelocephalid trend of deceptively strong intraspecific variation, none of the new forms are formally named lest further sampling reveal them to be variations on only one or two species.

Prosaukia tarutaoensis (Kobayashi, 1957)

Figs 3:57.1,2

1957. *Saukiella tarutaoensis* Kobayashi, p. 378, pl. 5, fig. 12, UMUT PA2298c.

not 1988. *Lichengia? tarutaoensis* (Kobayashi) Shergold et al., p. 309, figs. 5S–W.

in review. Prosaukia tarutaoensis (Kobayashi) Wernette et al., fig. 11.

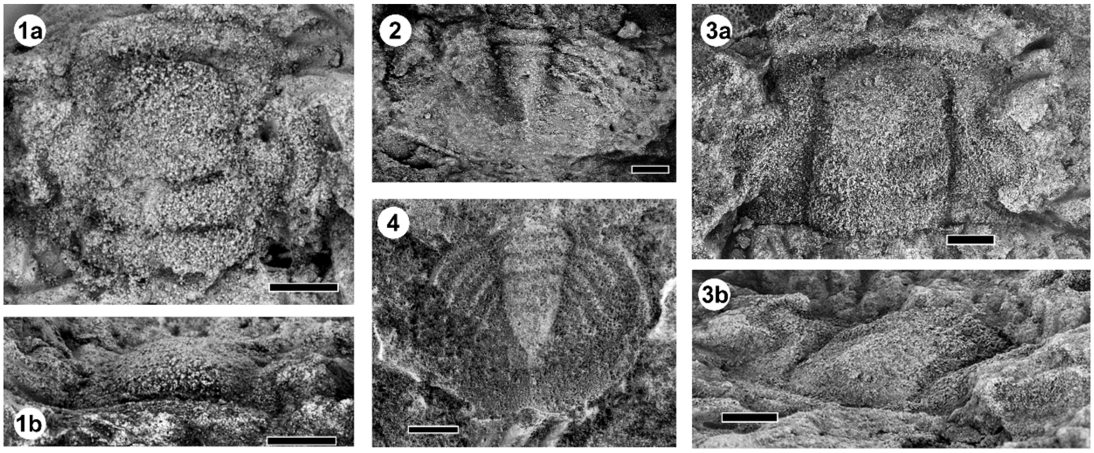

*Figure 3:57 Prosaukia tarutaoensis (*Kobayshi, 1957) and *Prosaukia oculata* Wernette et al., *in review*. *Prosaukia tarutaoensis* (1,2) **(1)** DGSC F0566, cranidium, *a* dorsal view, *b* anterior view, Ao Mo Lae 2.2 m; **(2)** DGSC F0453, pygidium, ATT west. *Prosaukia oculata* (3,4) **(3)** DGSC F0512, holotype, cranidium, *a* dorsal view, *b* left lateral oblique view, ATT 22.78 m; **(4)** DGSCF0510, pygidium, external mold, ATT 22.78 m. All internal molds unless otherwise indicated. ATT = Ao Talo Topo. Scale bars = 2 mm. Refigured from Wernette et al., *in review*.

Occurrence.—Ao Mo Lae (AML) 2.20 –3.10 m, AML h3, and Ao Talo Topo west; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Cambrian Stage 10.

Material.—Five cranidia: four from Ao Mo Lae 2.20 m (DGSC F0566), 3.10 m (DGSC F0567), and AML h3 (DGSC F0545, F0546); one from Ao Talo Topo west (ATTw) (DGSC F0414). One pygidium from ATTw (DGSC F0453); all internal molds.

Remarks.—Wernette et al. (in review) have recently figured and discussed all known specimens of *Prosaukia tarutaoensis* from the Tarutao Group.

Prosaukia oculata Wernette et al. (in review)

Figs 3:57.3,4

?1988. *Lichengia*? *tarutaoensis* (Kobayashi) Shergold et al., p. 309–310, fig. 5W only, not figs 5S–V = (*Prosaukia tarutaoensis*).
In review. *Prosaukia oculata* Wernette et al.

Occurrence.—Ao Talo Topo 22.78–22.88 m and h1, Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—Nine cranidia from Ao Talo Topo (ATT) 22.78 m (DGSC F0461, F0489, F0498, F0512, F0511, F0532, DGSC F0503 – external mold), 24.1 m (DGSC F0534), and ATT h1 (DGSC F0459). Two librigenae from ATT 22.78 m (DGSC F0488, F0513). Four pygidia from ATT 22.78 m (DGSC F0510 – internal and external mold, F0430 – external mold, F0470 – external mold, F0467). All internal molds unless otherwise indicated.

Remarks.—Wernette et al. (in review) have recently discussed all known specimens of *Prosaukia tarutaoensis* from the Tarutao Group. It is included here to assist in describing the trilobite assemblage.

Prosaukia sp. 1

Figs 3:58,59

Occurrence.—Ao Talo Udang S2 h2; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Description.—Cranidium subrectangular; width across palpebral areas subequal to cranidial length (sag.). Glabellar width (tr.) across S1 ~60% width across palpebral areas; frontal area 15–20% cranidial length (sag.); glabella nearly parallel sided to gently anteriorly tapering; axial furrows straight; anterior glabellar margin moderately to strongly curved; S1 posteriorly bowed and medially shallowing; S2 short, narrow, posteromedially deflected, and shallow; S3 effaced; SO straight; LO subequal width or slightly wider than L1. Palpebral lobe strongly curved, recurved on both ends, symmetric about the midpoint, centered (exsag.) slightly anterior S1, and extending from SO to S2; width (tr.) across anterior palpebral tips equal or slightly less than width across posterior tips. Fixigena narrow (tr.); anterior suture branches divergent. Frontal area subequally divided into preglabellar field and anterior border (sag.) with preglabellar field relatively longer and

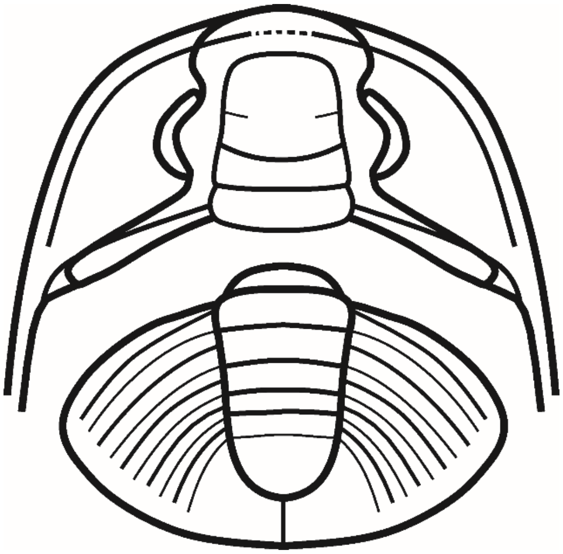

Figure 3:58 Prosaukia sp. 1 line drawing.

anterior border relatively shorter abaxially; anterior border furrow laterally deep and medially shallow, less strongly curved than preglabellar furrow or anterior cranidial margin; anterior border inflated above gently inflated preglabellar field. Posterior suture branches curve laterally; posterolateral projections short (exsag.) and wide (tr.), mostly comprising posterior border and broad, deep posterior border furrow. Entire cranidium, excluding palpebral lobes, covered with large granules.

Librigena narrow, anteriorly subequally divided into genal field lateral border; posteriorly genal field widens relative to border. Lateral and posterior border furrows broad and well-incised; lateral border furrow shallows near junction with posterior border furrow; posterior border furrow extends into genal spine base.

Pygidium broad and subovoid with maximum width (tr.) ~1.65 times length (sag.). Axis posteriorly tapering, nearly full pygidial length with short postaxial section; axial width (tr.) at anterior-most ring ~35% maximum pygidial width (tr.) five axial rings with the fifth more clearly defined in larger specimens; transverse axial furrows straight (tr.). Anterior and posterior pleural bands evenly divided and of constant width from proximal to distal pleural field; interpleural furrows shallower than pleural furrows but both consistently incised. Pygidial border notably narrow.

Material.—Two cranidia (_9, 13), three librigenae (_7, 10, 11), and four pygidia (_3, 5, 8 – external mold, 14). All from Ao Talo Udang S2 h2; all internal molds unless otherwise indicated.

Remarks.—Prosaukia sp. 1 has a particularly long, evenly divided, and strongly curved frontal area including the preglabellar furrow, the cranidial anterior margin, and the anterior border furrow. In this way it is unlike any other species of *Prosaukia* known from the Tarutao Group. The Laurentian species *Saukiella subconica* Ulrich and Resser, 1933 also has a strongly curved frontal area, but its anterior border furrow is more strongly curved and the axial furrows are more curved into a dome-like shape.

Prosaukia sp. 1 has a somewhat inflated preglabellar field and a medially shallowing anterior border, traits common in *Hoytaspis* Ludvigsen and Westrop, 1983. Furthermore the posterior border furrow of the librigena extends slightly into the genal spine base and the pygidium has a narrow border and short postaxial area as occurs in *Hoytaspis*. These characters cast some doubt on the generic affinity of *Prosaukia* sp. 1.

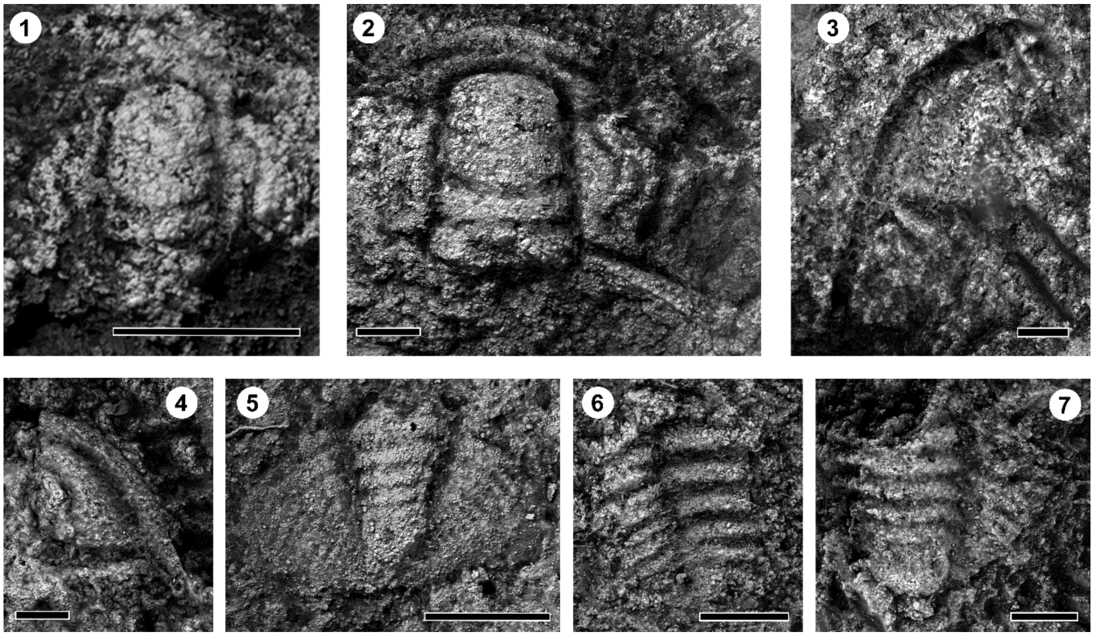

Figure 3:59 Prosaukia sp 1. **(1)** _13, cranidium; **(2)** _9, holotype, cranidium; **(3)** _11, librigena; **(4)** _10, librigena; **(5)** _14, pygidium; **(6)** _5, pygidium; **(7)** _3, pygidium. All internal molds from Ao Talo Udang S2 horizon 2. Scale bars = 2mm.

However, while slightly inflated the preglabellar field is not inflated above the anterior border. Additionally the S1 furrow is only weakly bowed, the S2 furrows are short and shallow, and the granulation, while coarse in diameter, has little relief; these traits are more common in *Prosaukia*.

The posterolateral projection of *P.* sp. 1 is long (tr.), and, in the holotype, the suture cuts subtangentially to the border furrow such that the furrow is retained on the cranidium for much of the length. While the posterolateral projections are missing from the smaller cranidium collected from Ao Talo Udang S2 h2 (ATD2_13, Fig. 3:59.1) the small librigenae recovered possess a long segment of the posterior border, suggesting that the facial sutures cut the posterolateral projection more adaxially and posteriorly in smaller individuals. A larger sample size is needed to test whether this suggested anterior and abaxial progression of the posterior suture branch is a real ontogenetic trend or size-independent intraspecific variation amongst the few specimens in the collection.

Prosaukia sp. 2.

Figs 3:54.3–5, 60

1988. *Prosaukia*? cf. *nema* Shergold; Shergold et al., p. 308, figs 3O, 5Q–R.

Occurrence.—Laem Hin Ngam 2.85 m and Ao Talo Topo 22.78–29.17 m; Ao Mo Lae Formation of the Tarutao Group, Ko Tarutao, Furongian.

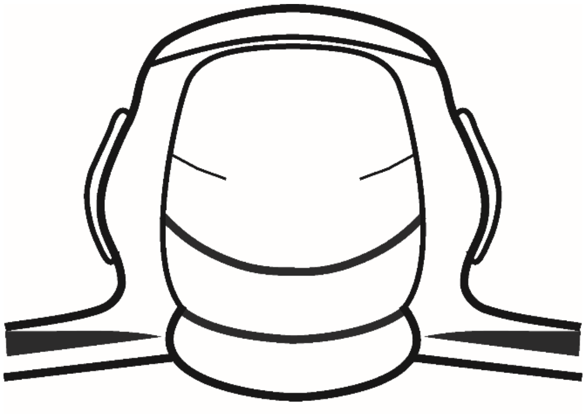

Figure 3:60 Prosaukia sp. 2, line drawing.

Description.—Cranidium subtrapezoidal to semicircular; width across palpebral areas subequal cranidial length (sag.). Glabellar width (tr.) across S1 50–60% width across palpebral areas; frontal area 15% cranidial length (sag.); anterior and posterior glabella nearly constant width but axial furrows bowed laterally with maximum width at L2*;* anterior glabellar margin moderately to strongly curved; S1 posteriorly strongly bowed, deep, and broad (sag., exsag.); S2 long (tr.) but narrow (exsag.), posteromedially deflected, and shallow; S3 effaced; SO slightly curved; LO wider than preoccipital glabella. Palpebral lobe strongly curved, slightly symmetric about the midpoint, straightening towards anterior end, centered (exsag.) slightly anterior S1, and extending from mid L1 to anterior S2; width (tr.) across anterior palpebral tips slightly less than width across posterior tips. Fixigena narrow (tr.); anterior suture branches gently divergent. Frontal area unequally divided into short, depressed preglabellar field and longer (sag.), strongly inflated anterior border; anterior border shortens laterally. Posterior suture branches nearly transverse; posterolateral projections short (exsag.), mostly comprising short posterior border and broad (exsag.), deep posterior border furrow; furrow broadens abaxially.

Librigena moderately broad with relatively narrow genal field and broad lateral border. Lateral border furrow shallow; genal spine straight.

Material.—One cranidium from Ao Laem Hin Ngam 2.85 m (_29); one cranidium (_14 from Ao Talo Topo dd.78 m; one cranidium (_1) and one librigena (_2) from Ao Talo Topo 29.17 m. All internal molds.

Remarks.—*Prosaukia* sp. 2 has abnormally long palpebral lobes that extend from near LO to anterior S2, even anterior S3. In this way it is similar to the Laurentian species *Prosaukia oldyelleri* Adrain and Westrop, 2004. These species differ in important ways. *P*. *oldyelleri* has a more angular to crescent-shaped anterior margin, and though both species have narrow fixigena, they distinctly separate the palpebral lobes from the axial furrows in *P*. sp. 2 whereas the palpebral lobes abut the axial furrows in *P. oldyelleri*.

The cranidium of *Prosaukia*? aff. *nema* figured by Shergold et al. (1988, fig. 5.Q) has a wider, somewhat more rounded glabella, but the similarity of the long palpebral lobes, broad frontal area with a short (sag.) preglabellar, and long, narrow (exsag.) S2 suggest that this cranidium belongs to *Prosaukia* sp. 2, and it is also from the same locality as the holotype, Laem Hin Ngam. Shergold et al. (1988) suggested that the lateral glabellar furrows, wide LO, and short anterior border were all reminiscent of *Prosaukia*? *nema* Shergold, 1975, but *P*.? *nema* has a more dome-shaped glabella and shorter (sag.) anterior border. Because it is known from only a single, fragmented cranidium, the full extent of other similarities or differences is unknown. The reason *Prosaukia*? *nema* was noted as having a dubious generic assignment is due to its similarity to a range of genera including *Saukiella* Ulrich and Resser, 1933, *Liquania* Zhou (in Zhou et al.), 1982, and

Wedekindia Sun, 1935. The type species of *Wedekindia* does not have a medially connected S1, and the posterior curvature of those furrows indicates that the lack of medial continuity is not merely due to shallowing of the furrow (Sun, 1935 pl. IV, fig. 26, text fig. 8). *Liquania*, though recognized as a valid genus by Jell and Adrain (2002), is a problematic genus. It is based on a single fragmented cranidium, and though Zhou et al. (1982) assigned *Prosaukia*? *nema* Shergold to this genus, Shergold et al. (1988, 2007) challenged this assignment. The incomplete preservation of the frontal area and palpebral lobes on the only known specimen of the type genus makes assignment to this genus dubious for even material very similar to the type species, which *Prosaukia* sp. 2 is not since it does not possess an undulated occipital furrow. *Prosaukia* and *Saukiella* are remarkably difficult to differentiate though most authors accept them as separate genera (e.g. Jell and Adrain, 2002). The differentiating criteria are variable in both groups with considerable overlap (e.g. presence of a preglabellar field, confluence of lateral and posterior border furrows, occipital spines, and granular ornamentation; Lochman, 1970). The defining character for *Prosaukia* is a preglabellar field, but a wideset confluence of the preglabellar and anterior border furrows may be indistinguishable from a short and depressed preglabellar field. Though very short, there is a distinct preglabellar field separating the preglabellar and anterior border furrows on *Prosaukia* sp. 2, suggesting that this generic assignment is correct.

Prosaukia sp. 3

Figs 3:61, 62

*Occurrence.—*Ao Mo Lae h3; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Description.— Cranidium subrectangular; width across palpebral areas ~90% of cranidial length. Glabellar width across S1 ~65% of width across palpebral areas; frontal area ~15–20% of cranidial length. Glabella very gently anteriorly tapering with slight lateral expansion at S1 and constriction at S2 in weakly developed urceolate form; anterior glabellar margin medially embayed; LO narrower than L1; SO gently posteromedially bowed; S1 strongly posteromedially bowed but less strongly curved, nearly transverse, or slightly undulating medially; S2 short (tr.) and well-defined, nearly as posteromedially angled as S1; S3 transverse and narrow (exsag.), poorly-defined to effaced. Palpebral lobe arcuate and centered opposite S1; posterior palpebral tip opposite posterior L1 and anterior tip opposite S2; anterior tip slightly more medial than posterior tip; palpebral furrow strongly incised. Fixigena narrow (tr.) with moderately wide preocular

Figure 3:61 Prosaukia sp. 3 line drawing

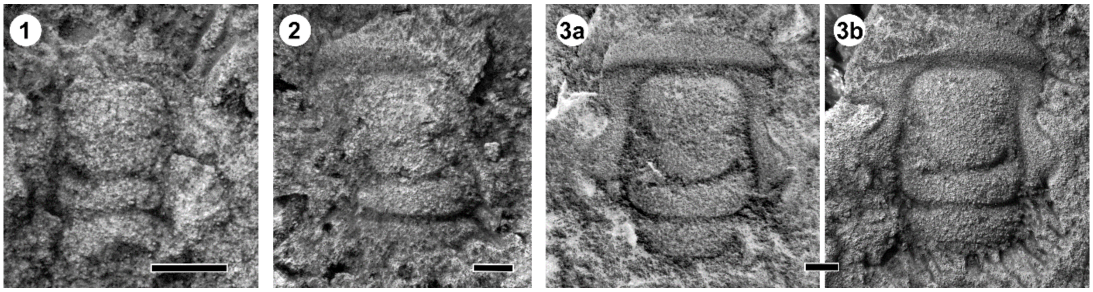

Figure 3:62 Prosaukia sp. 3, all cranidia. **(1)** _15; **(2)** _8; **(3)** _6, holotype. All internal molds except 6a, external mold. All from Ao Mo Lae h3. Scale bars = 2 mm.

areas; anterior suture branches anteriorly divergent from anterior palpebral corners, curving gently adaxially for rounded lateral margins of frontal area; frontal area widest (tr.) point on anterior border furrow. Preglabellar field short, depressed; anterior border furrow straight or very gently curved; anterior border strongly inflated and much longer than preglabellar field.

Material.—Three cranidia from Ao Mo Lae h3 (_6, 8, 15). All internal molds plus external counterpart to AML P_6.

Remarks.—In regard to divisions and relief of the frontal area, *Prosaukia* sp. 3 is similar to *Prosaukia tarutaoensis* (Kobayashi, 1933) which also occurs in Ao Mo Lae horizon 3. These species are distinguishable by *Prosaukia* sp. 3's less strongly tapering glabella, narrow LO, and medial embayment in the anterior glabellar margin. The anterior glabellar tapering of *P. tarutaoensis* varies with size (Wernette et al., in review), but it is consistently more than the tapering exhibited by *Prosaukia* sp. 3.

Genus *Sinosaukia* Sun, 1935

Type species.—Sinosaukia pustulosa Sun, 1935 pl. 5 figs. 1–11, pl. 6 fig. 2.

*Remarks.—*According to Shergold et al. (1988), *Sinosaukia* differs from *Lophosaukia* Shergold, 1975 in its more laterally constricted glabella, longer (exsag.) palpebral lobes, and less pronouncedly angulate anterior margin, although reconsideration of the available figured material of *Sinosaukia pustulosa* indicates that *Lophosaukia* typically has the longer palpebral lobes. Shergold et al. (1988) suggested that *Sinosaukia* should be restricted to the type material due to the poor quality of Sun's (1935) figures precluding comparisons with new material. However, the pinched and anteriorly expanding glabella is a sufficiently diagnostic trait compared with other "saukiids" that *Sinosaukia* can continue to be utilized. Assignment of species to *Sinosaukia* is based on the constricted and anteriorly expanding glabella in addition to the forward protrusion of the medial portion of the anterior border.

Sinosaukia sp.

Fig. 3:54.6

*Occurrence.—*Ao Talo Udang S2 h1; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

*Description.—*Cranidium subrectangular; width across palpebral areas ~75% of cranidial length excluding anterior border. Glabellar width across S1 ~65% of width across palpebral areas; frontal area more than 15% of cranidial length. Axial furrows subparallel to anteriorly converging from LO to S2 and then sharply anteriorly diverging resulting in anterior lobe width(tr.) more than 1.2 times LO width; anterior glabellar margin smoothly curved; LO slightly wider than L1; SO gently posteromedially bowed, laterally deep and medially shallowing; S1 posteromedially bowed and medially shallowing; S2 short (tr.), transversely oriented, and well-defined. Palpebral lobe short and strongly curved, centered opposite S1; posterior palpebral tip opposite anterior L1 and anterior tip opposite S2; anterior tip slightly more medial or longitudinally aligned with posterior tip; palpebral furrow weakly incised. Fixigena narrow (tr.) with strap-like preocular areas; anterior suture strongly divergent from anterior palpebral corners, subparallel axial furrows, curving adaxially subconcentrically with anterolateral glabellar corners. Axial furrows and preglabellar furrow deeply incised; anterior strongly inflated above preglabellar furrow and preocular areas, medially strongly elongated and laterally short.

Material.—One cranidium from Ao Talo Udang S2 h1 (_22), internal mold.

Remarks.—This single cranidium is assigned to *Sinosaukia* on the basis of having a glabella strongly constricted at L2 and an undifferentiated frontal area, bounded by a broad, deeply incised preglabellar furrow, with a tongue-shaped, anteriorly protruding margin. It differs from *Sinosaukia impages* Shergold, 1975 by having a more strongly protruding frontal area, shorter (exsag.) palpebral lobes, a more strongly constricted glabella, and a longer, more medially anteriorly protruding anterior margin. With its poorly developed anterior protrusion, relatively long palpebral lobes, and ridges on the librigenal margin, *Sinosaukia impages* likely should be reassigned to *Lophosaukia*.

While Shergold et al. (1988) suggested full synonymy of *Sinosaukia* with *Lophosaukia*, *Sinosaukia* sp. differs sufficiently from known species of *Lophosaukia* to justify maintenance of *Sinoaukia*. Such differences include the lack of granulation found on the cranidium, strong dorsal deflection of the anterior border, very short (exsag.) palpebral lobes, and exceptionally deep axial and preglabellar furrows. Apart from the lack of granulation, these traits are consistent with what can be determined from the available illustrations of *Sinosaukia pustulosa* Sun (1935).

Genus *Thailandium* Kobayashi, 1957

Type species.—Thailandium solum Kobayashi, 1957 from the Tarutao Group, Ko Tarutao, Thailand; Cambrian Stage 10.

Remarks.—Wernette et al. (in review) recently reevaluated *Thailandium* using landmark-based geometric morphometric analysis. They determined that the anteriorward convergence of the anterior suture branches is a key feature differentiating *Thailandium* and *Prosaukia* Ulrich and Resser, 1933. Furthermore, by indicating that the only material assigned to *Thailandium* from outside of Thailand (Shergold, 1991) is more accurately assigned to *Prosaukia*, the morphometric analysis determined that *Thailandium* is currently a monospecific genus known exclusively from Thailand.

Thailandium solum Kobayashi, 1957

Fig. 3:63

1957. *Thailandium solum* Kobayashi p. 373, pl. 4 fig. 9, not figs 10,11,12 (*Quadraticephalus planulatus*).

1957. *Coreanocephalus planulatus* Kobayashi pl. 4 figs 16–17 only, not figs 13–15 (*Quadraticephalus planulatus*).

In review. *Thailandium solum* Kobayashi; Wernette et al.

Occurrence.—Ao Mo Lae (AML) 2.20–5.81 m, AML h2–h5, Ao Talo Topo west, and ?Ao Talo Topo 29.17 m; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

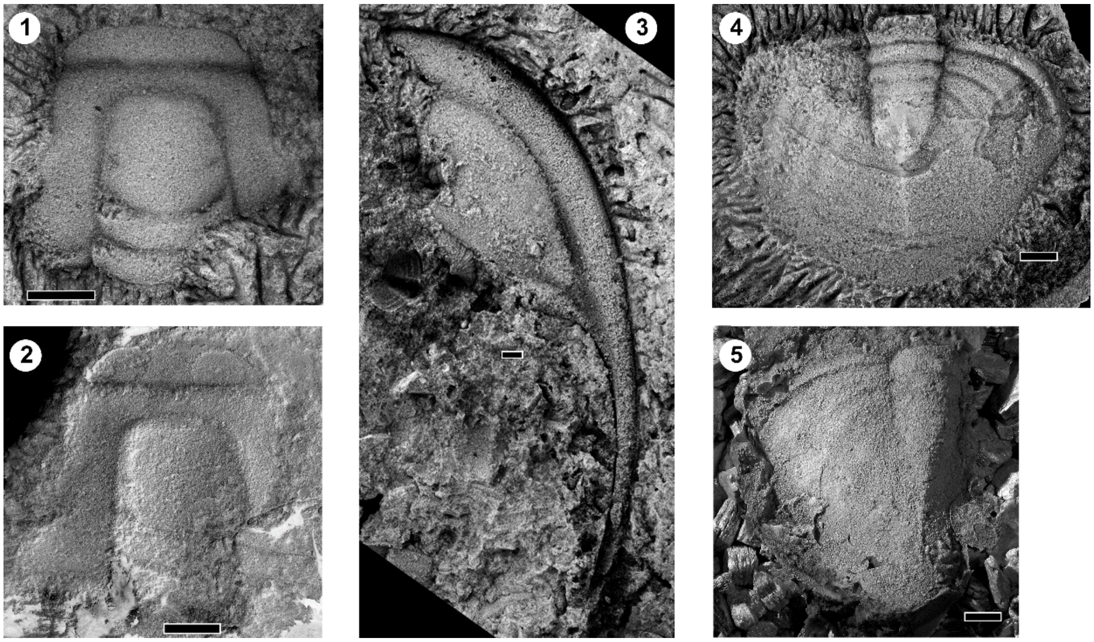

Figure 3:63 Thailandium solum Kobayashi, 1957. **(1)** DGSC F0609, cranidium, AML 5.81 m; **(2)** CMC IP87037, cranidium, cast of UMUT PA02299b-1, holotype, Kobayashi (1957) pl. 4 fig. 9; **(3)** DGSC F0612, librigena, AML 5.81 m; **(4)** DGSC F0565, pygidium, AML 5.81 m; **(5)** CMC IP87046, pygidium, cast of UMUT PA02299d-1, Kobayashi (1957) pl. 4 fig. 10. All internal molds. AML = Ao Mo Lae. All refigured from Wernette et a., *in review.* Scale bars = 2 mm.

Material.—33 cranidia: 26 from Ao Mo Lae (AML) 3.62 m (_1, 8), 3.72 m (_1, 4), 5.17 m (_36), 5.81 m (_21, 40, 42, 102, 105, 206, 109, 125, 130, 146 – external mold,154, 160,169, 200, 206, 207), AML h3 (_1, 3), AML h4 (_10), and AML h5 (_5 – external mold, 9 – external old); seven from Ao Talo Topo west (ATTw) (_33, 40, 88 – external mold, 89, 91, 100, 108). 15 librigena: 13 from AML 5.81 m (_39, 98, 148, 213,2 14, 215, 220), AML h2 (_21, 30, 32), AML h3 (_19, 25), and AML h4 (_12); one from ATT 29.17 m (_5); one from ATTw (_86). 10 pygidia: eight from AML 2.20 m (_4), 5.81 m (_41, 43 – external mold, 48 – external mold, 164, 211, 212), and AML h4 (_31); two from ATT w (_42, 87). All internal molds unless otherwise indicated.

Remarks.— Wernette et al. (*in review*) have recently discussed all known specimens of *Prosaukia tarutaoensis* from the Tarutao Group. It is included here only for completeness in describing the trilobite assemblage.

Genus *Pacootasaukia* Sohn and Choi, 2005

Type species.—*Platysaukia jokliki* Shergold (1991) from the Pacoota Sandstone of Australia, Furongian; designated by Sohn and Choi (2005).

Pacootasaukia sp.

Figs 3:54.7–9

Occurrence.—Ao Mo Lae h5, Ao Talo Topo 8.60 m, Ao Talo Udang S2 h2; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Material.—Three cranidia from Ao Mo Lae h5 (_3), Ao Talo Topo 8.60 m (_1), and Ao Talo Udang S2 h2 (_6), all internal molds.

Remarks.—The three cranidia included together herein are insufficiently preserved, particularly in the palpebral areas to warant a new species, but they differ from *Pacootasaukia jokliki* (Shergold, 1991) in the width of the fixigena and rounding of the anterior glabellar margin. The Thai material is otherwise very similar to *P. jokliki*, particularly in the broad, undifferentiated frontal area that is continuous with the fixigenae. Shergold (1991) originally assigned *P. jokliki* to *Platysaukia* Kobayashi, 1960 based on the similarly broad frontal area and overall low relief. However, *Platysaukia* has large, arcuate palpebral lobes that abut the glabella while *P. jokliki* has shorter palpebral lobes and narrow but distinct fixigenae. The other known species of *Pacootasaukia*, *P. tomichi* (Shergold, 1991) was also initially assigned to *Platysaukia*, but it is known only from the pygidium. Sohn and Choi (2005) erected the genus *Pacootasaukia* to encompass species with the *Platysaukia*-like frontal area but shorter palpebral lobes and a medially continuous S1.

Order OLENIDA Adrain, 2011

Family DOKIMOCEPHALIDAE Kobayashi, 1935

Genus *Wuhuia* Kobayashi, 1933

Type Species.—Solenopleura belus Walcott, 1905 from the Fengshan Formation, Shandong, North China.

Remarks.—In establishing *Wuhuia* Kobayashi, 1933, Kobayashi did not give a through list of diagnostic characters. Rather he gave an indirect differential diagnosis, stating that the genus was erected to encompass *Conocephalina* (=*Solenopleura*) *belus* and *Conocephalina dryope.* These species have narrow fixed cheeks and strong glabellar furrows relative to other *Conocephalina.* They are distinct from *Conocepalina ornata* in having two rather than three pairs of glabellar furrows, and from *Iddingsia* in their narrower fixed cheeks and absence of an eye ridge. A more rigorous diagnosis for *Wuhuia* has not since been established. Kobayashi's concept of *Wuhuia belus,* the type species, is dubious, because Kobayashi's figured specimen from this species (1933, fig. 15.1) differs from Walcott's concept (1913, pl. 13, fig. 12,12a) in its nearly obsolete rather than simply narrow fixigena and longer palpebral lobes.

Wuhuia? sp.

Figs 3:54.10,11

Occurrence.— Ao Talo Topo 22.78 m and Ao Mo Lae 5.81 m and AML h1; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—Three cranidia, internal molds from Ao Talo Topo 22.78 m (_26,27) and Ao Mo Lae 5.81 m (_80). One librigena from Ao Mo Lae h1 (_2).

Remarks.— Since *Conocephalina belus* was first illustrated (Walcott, 1913), each subsequent assignment of material to this species has included increasingly divergent forms. *Wuhuia belus* sensu Kobayashi, 1933 has much longer, more curved, more posteriorly placed palpebral lobes and narrower, nearly obsolete fixigena relative to *C. belus*. The cranidia from the Hwajeol Formation assigned to *W. belus* by Park and Kihm (2015a) have even longer palpebral lobes that span nearly the full length of the glabella rather than palpebral lobes that are little more than one third of the glabellar length, as initially described by Walcott (1905). Furthermore the occipital ring is notably long and broad (tr., sag.) and the posterior border is long (exsag.) in the material from the Hwajeol Formation. Despite similarities in the shape and incision of the transverse glabellar furrows, there is little reason to consider the material from the Hwajeol Formation the same species, and possibly not the same genus, as *Wuhuia belus.*

Three poorly preserved cranidia from the Ao Mo Lae Formation are similar to *W. belus* (*sensu* Park and Choi, 2015) in the nearly obsolete fixigena, long palpebral lobes, depressed frontal area, long glabella, and long occipital ring. Whether these specimens are synonymous with the material from the Hwajeol Formation cannot be determined due to the poor preservation of the frontal area. Likely they are not, because the specimens from the Ao Mo Lae Formation have narrower (tr.) occipital rings.

Order Uncertain

Family EUREKIIDAE Hupé, 1953

Genus *Corbinia* Walcott (1924)

Type species.—Corbinia horatio Walcott (1924).

Corbinia perforata n. sp.

Figs 3:54.12–14; 64

Type material.—Holotype: APMB1_37 (Fig. 3:54.13) from Ao Phante Malacca 53.65 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian. Paratypes: APM49.90_4, ATDGf_36, and ATDGf_17.

Diagnosis.—Cranidium with short (sag.) and narrow (tr.) kite-shaped anterior border, pitted anterior border furrow, short preglabellar field, subparallel anterior suture branches and very narrow fixigena, strongly inflated palpebral lobes encompassing depressed palpebral areas, and nearly effaced lateral glabellar furrows.

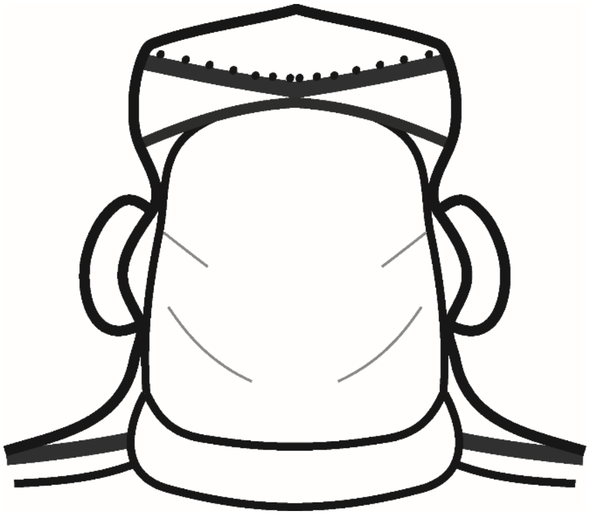

Figure 3:64 Corbinia perforata n. sp. line drawing.

Occurrence.—Ao Phante Malacca 49.90–53.65 m and Ao Talo Udang S3 float; Talo Wao Formation, Tarutao Group, Ko Tarutao, Tremadocian.

Description.— Cranidium subtrapezoidal with narrow, angular anterior margin; width across palpebral areas ~75% of cranidial length. Glabellar width across S1 ~80% width across palpebral areas; frontal area ~20% of cranidial length. Axial furrows smoothly curved reaching widest point at S1 and narrowing anteriorly; width (tr.) of anterior glabellar lobe ~90% of width at SO; anterior glabellar margin smoothly curved with strongly incised preglabellar furrow; LO wider than L1 and inflated; SO gently posteromedially bowed, and medially transverse; S1 strongly posteromedially oriented and shallow, disconnected from axial furrow; S2 shallow and strongly posteromedially oriented. Palpebral lobe strongly inflated and abutting glabella, centered opposite L2. Fixigena narrow (tr.) with strap-like preocular areas; anterior suture branches subparallel. Preglabellar field laterally long (exsag.) ad medially short; anterior border strongly inflated above preglabellar field and kite or diamond-shaped; anterior border furrow marked by row of pits. Posterior suture branches curve laterally; short (exsag.) posterolateral projections; posterior border furrow deep and broad, even breadth (exsag.) along full length (tr.) of projection; posterior border inflated, gently lengthening (exsag.) laterally.

Etymology.—Latin for pierced or bored, referring to the pitted anterior border.

Materials.—Four cranidia from Ao Phante Malacca 49.90 m (_4) and 53.65 m (_37) and Ao Talo Udang S3 float (_36, 17), all internal molds.

Remarks.—Corbinia sp. is similar to *Pseduokainella malakaensis* Stait et al., 1984 in the large (tr. and sag.) glabella, defined but sort preglabellar field, well-defined and inflated anterior border, and very narrow fixigena. However it differs in the strongly curved palpebral lobes, the posteromedial bend in the anterior border furrow, and the nearly parallel rather than strongly divergent anterior suture branches.

Pitting in the anterior border furrow helps differentiate *Corbinia* sp. from *Corbinia implumis* Winston and Nicholls, 1967 (*sensu* Adrain and Westrop, 2004) and *Corbinia burkhalteri* Westrop and Palmer (in Westrop et al.), 2005.

Family PLETHOPELTIDAE Raymond, 1925

Remarks.—In Laurentia, the Plethopeltidae were considered an outer-shelf or slope facies until the mid to late Sunwaptan (late Jiangshanian to early Stage 10) and may indicate biogeographic shifts associated with the recovery of biodiversity following the extinction separating the "Ptychaspid" and "Symphisurinid" biomeres in the latest Furongian (Westrop and Ludvigsen, 1987). No studies have yet considered whether the fossil record of Gondwana contains a similar biofacies shift. The Ao Mo Lae Formation is a near-shore clastic succession.

Genus *Plethopeltella* Kobayashi, 1943

Type Species.— *Plethopeltis resseri* Kobayashi (1933a, p. 280, pl. 6, figs 6a, 6b), Fengshan Formation, Wanwankou, Liaoning, China.

Plethopeltella sp.

Fig. 3:54.15

Occurrence.—Ao Talo Topo 28.37 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Material.—One cranidium, internal mold, from Ao Talo Topo 28.37 m (_10).

Remarks.—Plethopeltella sp. is similar to *Plethopeltella resseri* (Kobayashi, 933), *Plethopeltella shantungensis* (Lu, 1957), and *Plethopeltella* cf. *shantungensis* (*sensu* Shergold et al., 2007) in the broad, unfurrowed glabella, facial sutures concentric with the axial and preglabellar furrows, and narrow fixigena. It differs from these species in having longer (exsag.) palpebral lobes and a pronounced preglabellar furrow. A shallow remnant of the anterior border furrow is also distally visible.

Family PTYCHASPIDIDAE Raymond, 1924

Genus Quadraticephalus Sun, 1924

Type species.—Quadraticephalus walcotti Sun, 1924, Kaolishan Limestone, Taian, Shandong, China (by original designation).

Remarks.— *Quadraticephalus* Sun, 1924, *Changia* Sun, 1924, and *Coreanocephalus* Kobayashi, 1935 have variably been considered separate genera or synonymous since their inception. Resser (1942, p. 48) synonymized *Quadraticephalus* and *Changia*, designating *Quadraticephalus* as the senior synonym since they were first described in the same publication and the name *Changia* is easily confused with *Chuangia* Sun, 1924. Zhang and Jell (1987) later added *Coreanocephalus* as a junior synonym of *Changia* (Zhou and Zhang, 1984) and therefore also of *Quadraticephalus*. Shergold (1975), however, considered *Changia* and *Quadraticephalus* to be distinct based on the size and position of the palpebral lobes and the shape of the posterolateral projections; the palpebral lobes are smaller and more anteriorly placed and the posterolateral projections are more triangular in *Quadraticephalus*. The palpebral lobes of *Changia* extend posteriorly past S1. Additionally, Shergold (1975) suggested that the anterior border on *Changia* may not be anteroventrally angled, as it is on *Quadraticephalus*.

Quadraticephalus planulatus (Kobayashi, 1957)

Figs 3:65–67

1957. *Coreanocephalus planulatus* Kobayashi p. 379, pl. 4 figs 13–15 only, not figs 16,17 (*Thailandium solum*).

1957. *Thailandium solum* Kobayashi pl. 4 figs10–12 only, not fig. 9.

1986. *Changia planulatus* (Kobayashi), Qian, pl. 74 figs 2,5,6,8–10; pl. 75 fig. 1.

1988. *Quadraticephalus planulatus* (Kobayashi) Shergold et al. pl. 4 figs H–M, non? fig N.

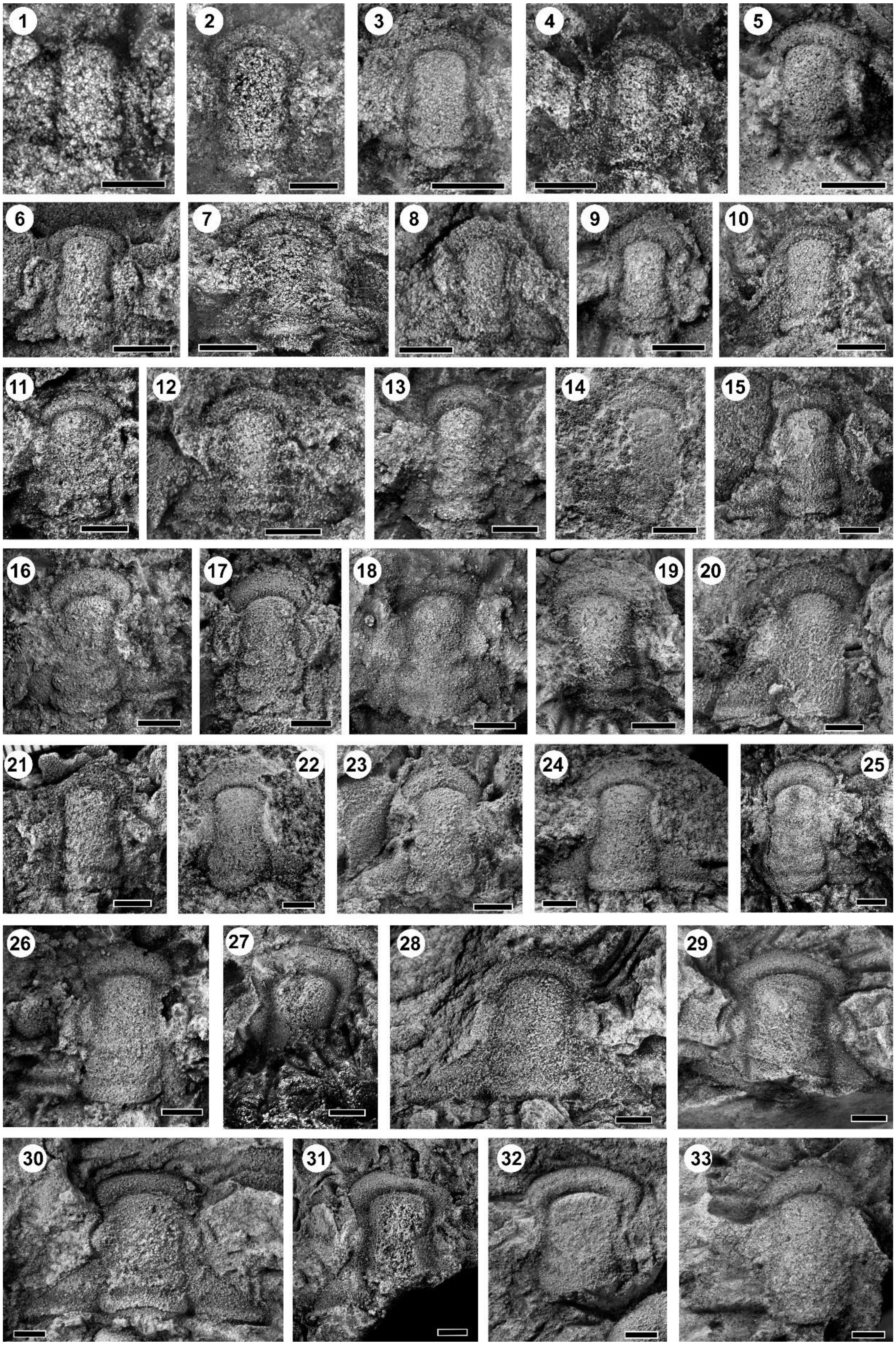
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Figure 3:65 Quadraticephalus planulatus Kobayashi, 1957, all cranidia. **(1)** _21, ATT 29.17 m; **(2)** _11, ATT 22.88 m; **(3)** _20, ATT 29.17 m; **(4)** _92, AML 5.81 m; **(5)** _7, ATT 23.89 m; **(6)** _11, ATT 28.37 m; **(7)** _82, ATT 22.78 m; **(8)** _58, ATT 22.78 m; **(9)** _6, ATT 29.17 m; **(10)** _39, ATT 22.78 m; **(11)** _34, ATTw; **(12)** _75, ATT 22.78 m; **(13)** _18, AML 5.81 m; **(14)** _34, external mold, AML 5.81 m; **(15)** _22, AML h2; **(16)** _43, ATTw; **(17)** _51, ML 5.81 m; **(18)** _105, ATTw; **(19)** _10, ATT 29.17 m; **(20)** _67, AML 5.81 m; **(21)** _8, ATT 28.37 m; **(22)** _13, external mold, AML 5.81 m; **(23)** _69, AML 5.81 m; **(24)** _139, AML 5.81 m; **(25)** _35, ATTw; **(26)** _2, ATT 3.62 m; **(27)** _33, ATT 29.17 m; **(28)** _48, ATT 22.78 m; **(29)** _22, ATT 29.17 m; **(30)** _90, ATT 22.78 m; **(31)** _6, ATT 28.37 m; **(32)** _60, ATT 29.17 m; **(33)** _119, AML 5.81 m. All internal molds unless otherwise indicated. ATT(w) = Ao Talo Topo (west); AML = Ao Mo Lae. Scale bars = 1mm for 1, 2; = 2 mm for 3–33.

Occurrence.—Ao Mo Lae (AML) 3.62–6.01 m, AML h2, AML h3, AML h4, Ao Talo Topo (ATT) 5.50–29.17 m , ATT h1, ATTw, Laem Hin Ngam 2.85 m, Ao Talo Udang (ATD) S2 0.69 m, and ATD S2 h2; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—69 cranidia: 26 from Ao Mo Lae (AML) 3.62 m (_2, 7), 5.81 m (_13 – external mold, 18, 34 – external mold, 37 – external mold, 51, 67, 69, 70, 85, 92, 94, 119, 138, 139, 141 – external mold), 5.84 m (_2, 10 – external mold), 6.01 m (_13, 19), AML h2 (_22, 26, 42, 43), and AML h4 (_6); 36 from Ao Talo Topo (ATT) 5.50 m (_1), 8.20 (_5), 8.60 m (_7), 8.85 m (_11, 16), 22.78 m (_39, 48, 58, 75, 82, 90), 24.10 m (_11), 23.89 (_6 – external mold, 7), 25.34 m (_11, 15 – external mold), 28.37 (_6, 8, 11), and 29.17 m (_6, 8, 10, 14 – external mold, 15, 19, 20, 21, 22, 30, 33, 34, 38, 55, 56, 60, 65); five from ATTw (_3, 34, 35, 43, 105); two from Ao Talo Udang S2 0.69 m (_17) and S2h2 (_4). Eight librigena: six from AML 5.81 m (_22, 111), 5.84 m (_20, 31), AML h3 (_24), and AML h4 (_29); one from ATT 29.17 m (_49); one from ATTw (_31). 19 pygidia: 11 from AML 3.62 m (_6), 5.81 m (_61, 73, 79 – external mold, 157), AML h2 (_41, 44), AML h2 (_17, 20), and AML h4 (_11, 32); five from ATT 8.85 m (_13), 24.70

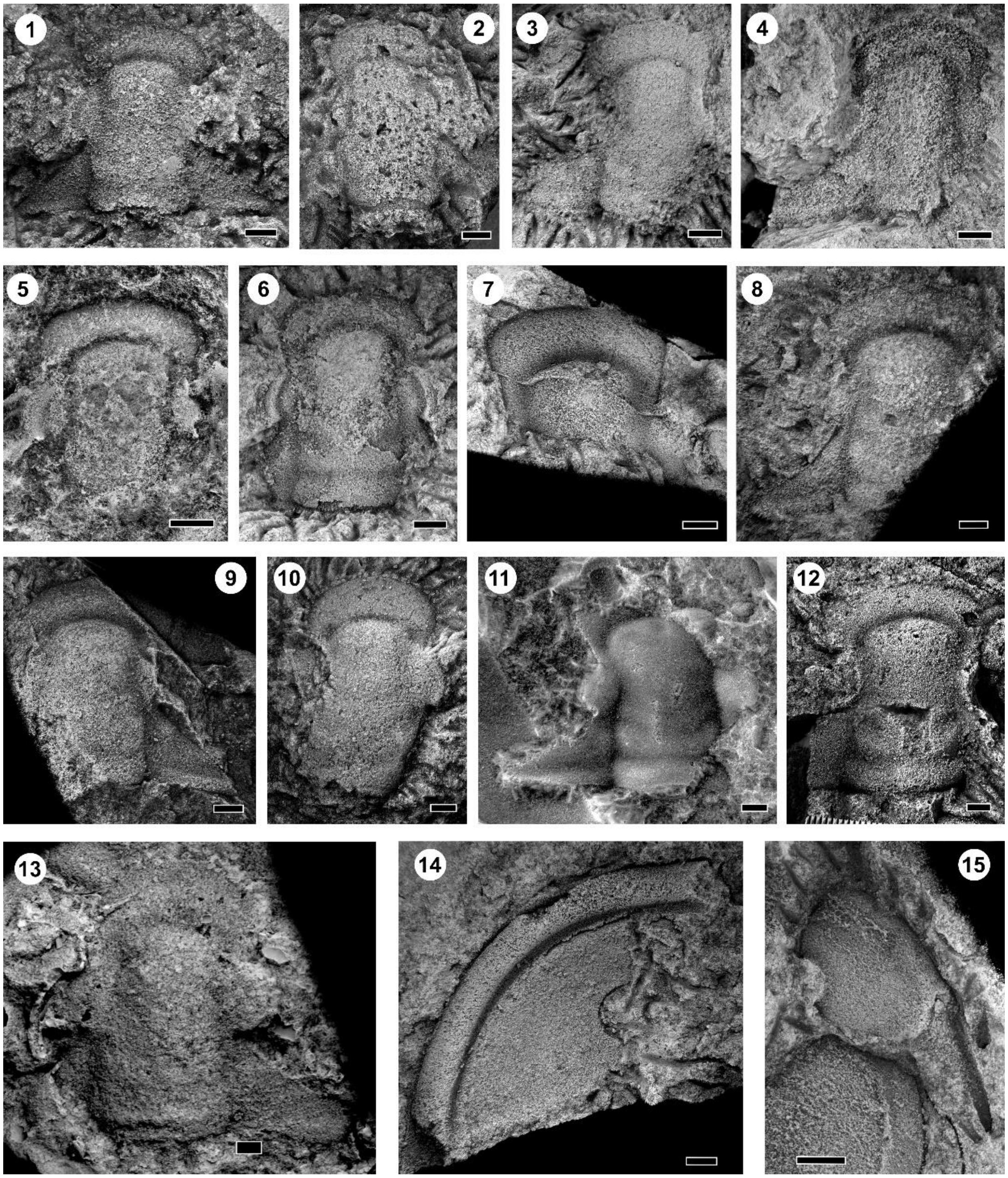


Figure 3:66 Quadraticephalus planulatus Kobayashi, 1957. **(1)** _6, cranidium, AML h4; **(2)** _3, cranidium, ATTw; **(3)** _94, cranidium, AML 5.81 m; **(4)** _5, cranidium, ATT 8.20 m; **(5)** _14, cranidium, external mold, ATT 29.17 m; **(6)** _1, cranidium, ATT 5.50 m; **(7)** _15, cranidium, ATT 29.17 m; **(8)** _42, cranidium, AML h2; **(9)** _70, cranidium, AML 5.81 m; **(10)** _19, AML 6.01 m; **(11)** _6, cranidium, external mold, ATT 23.89 m; **(12)** _16, cranidium, ATT 8.85 m; **(13)** CMC IP87048, holotype, cranidium, vinyl polysiloxane cast of UMUT PA02299, Kobayashi (1957) pl. 4, fig. 13; **(14)** _29, librigena, AML h4; **(15)** _49, librigena, ATT 29.17 m. All internal molds unless otherwise indicated. AML = Ao Mo Lae; ATT(w) = Ao Talo Topo (west). All scale bars = 2mm.

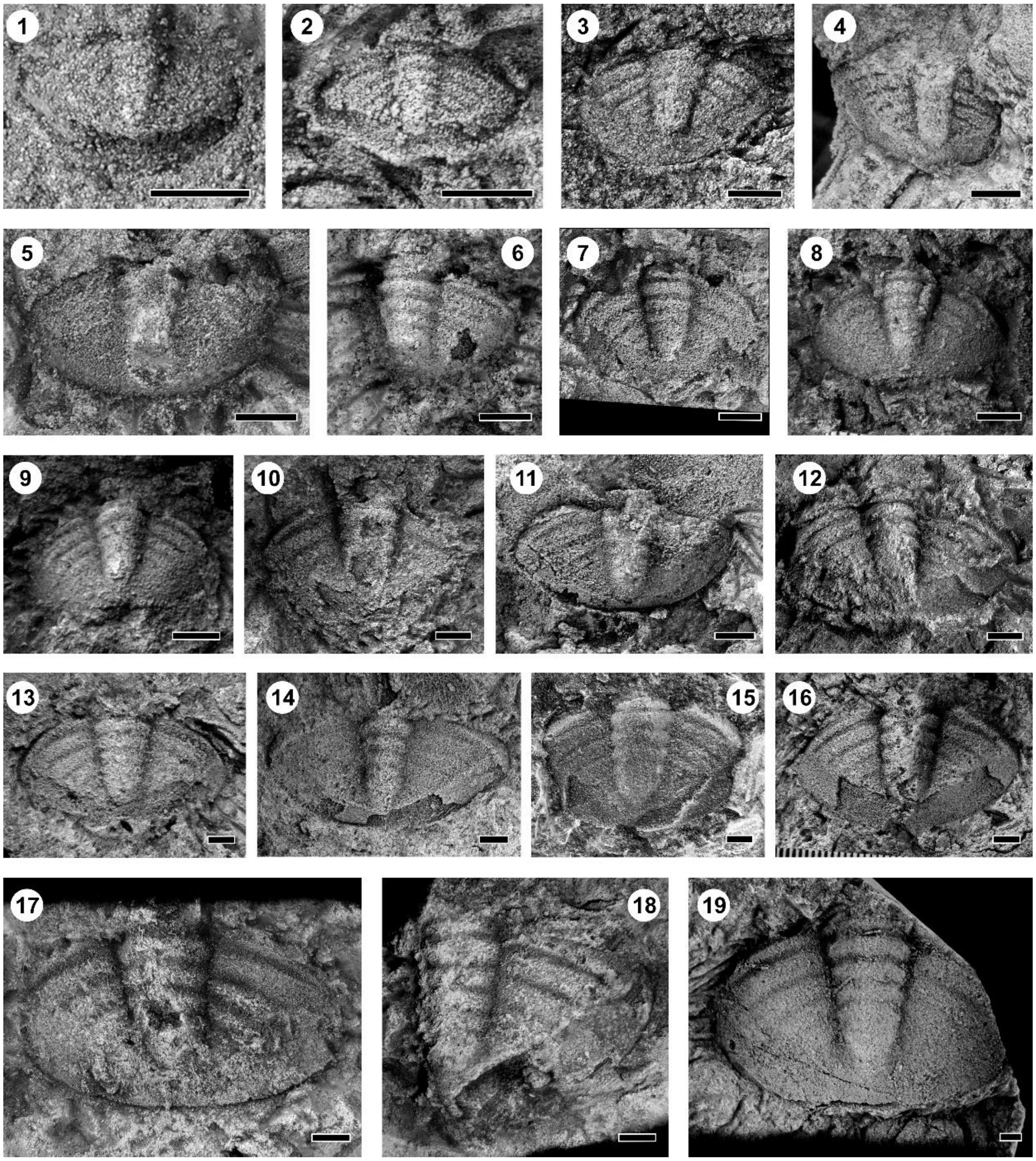


Figure 3:67 Quadraticephalus planulatus Kobayashi, 1957, all pygidia. **(1)** _6, ATT h1; **(2)** _61, AML 5.81 m; **(3)** _3, LHN 2.85 m; **(4)** _73, AML 5.81 m; **(5)** _17, ATT 29.17 m; **(6)** _2, ATT 23.89 m; **(7)** _98, ATTw; **(8)** _6, AML 3.62 m; **(9)** _20, AML h3; **(10)** _32, AML h4; **(11)** _6, ATT 25.34 m; **(12)** _41, AML h2; **(13)** _17, AML h3; **(14)** _13, ATT 8.85 m; **(15)** _79, external mold, AML 5.81 m; **(16)** _157, AML 5.81 m; **(17)** _71, ATTw; **(18)** _44, AML h2; **(19)** _11, AML h4. All internal molds unless otherwise indicated. ATT(w) = Ao Talo Topo (west); AML = Ao Mo Lae; LHN = Laem Hin Ngam. Scale bars = 2 mm.

m (_2), 25.34 m (_6), 29.17 m (_17), and ATT h1 (_6); two from ATTw (_71, 98); one from Laem Hin Ngam 2.85 m (_3). All internal molds unless otherwise indicated.

Remarks.— Shergold et al. (1988) assigned additional specimens to C*oreanocephalus planulatus* Kobayashi, 1957 and reassigned it to *Quadraticephalus* Sun, 1924 based on the previously established synonymy of *Quadraticephalus* and *Coreanocephalus* (Kobayashi, 1960). Prior to Shergold et al.'s (1988) revisions of the Tarutao fauna, Qian (1986) illustrated *Q. planulatus* material from the Dayangcha section and assigned the species it to *Changia*. Both Shergold et al. (1988) and Qian (1986) noted that the pygidium assigned to *Q. planulatus* by Kobayashi (1957) belonged to a "saukiid" and assigned a new pygidium to *Q. planulatus*, but each assigned a different form. Both pygidial morphologies occur with *Q. planulatus* cranidia on Tarutao. The pygidium assigned by Qian is more consistent with other pygidia assigned to species of *Quadraticephalus*, such as *Q. elongatus* (Kobayashi, 1935; Kihm et al., 2013) and *Q.* cf. *coreanicus* (Kobayashi, 1960; Shergold, 1991) in that the doublure is well developed, there are weak interpleural furrows dividing subequal pleural bands, the axis is less than 33% pygidial width with moderate to strong posterior tapering, and the lateral anterior corners are subangular. The pygidium assigned by Shergold et al. (1988) is more consistent with that generally assigned to species of *Changia* (e.g. Sohn and Choi, 2007) but has also been used for species of *Quadraticephalus* (e.g. Shergold, 1975).

The synonymy of specimens from Kobayashi (1957), Qian (1986), and Shergold et al. (1988) has resulted in a species with significant variation in the length of the frontal area, the angularity of the anterior border corners, and the length and exsagittal position of the palpebral lobes. This variation is reflected in the more recent collections presented herein. The two most extreme end-members have either short frontal areas with angular corners and short, anteriorly placed palpebral lobes (e.g. ATT29.50_6, Fig. 3:65.31) or long frontal areas with rounded corners and long palpebral lobes (e.g. ATT5.50_1, Fig. 3:66.6). Without a sample size sufficient to assess whether variation inform is continuous, the end members might be classified as two separate species or even genera.

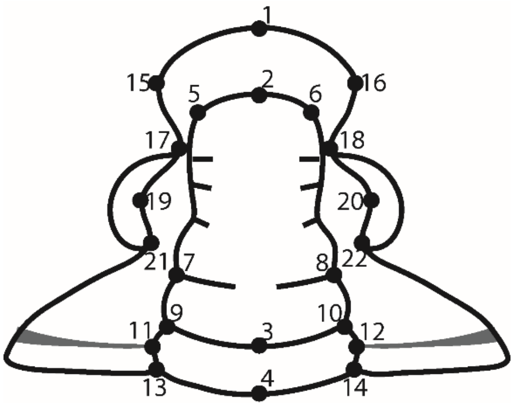


Figure 3:68 Quadraticephalus landmark scheme.

A landmark-based morphometric analysis was used to determine whether morphological distinctions could be made within the collections from 2008–2018. The analysis used 22 landmarks (Fig. 3:68) and 31 individuals. The Procrustes superimposition of landmarks, grouped by sampling horizon (Fig. 3:69), does not obiously reveal any distinct groupings other than that specimens from Ao Talo Topo’s 22.78 m horizon are generally wider in the frontal area and palpebral (=interocular) area but narrower at S1 than most other specimens. Principal component analysis (PCA) of a thin plate spline decomposition of the landmark distribution was used to determine plausible divisions not clear from the Procrustes distribution. There are no clear groupings by which to explain the distribution of scores along relative warps (RW) 1 and 2 (Fig. 3:70, 26.4% and 16.76% of variance respectively). There is a general trend for

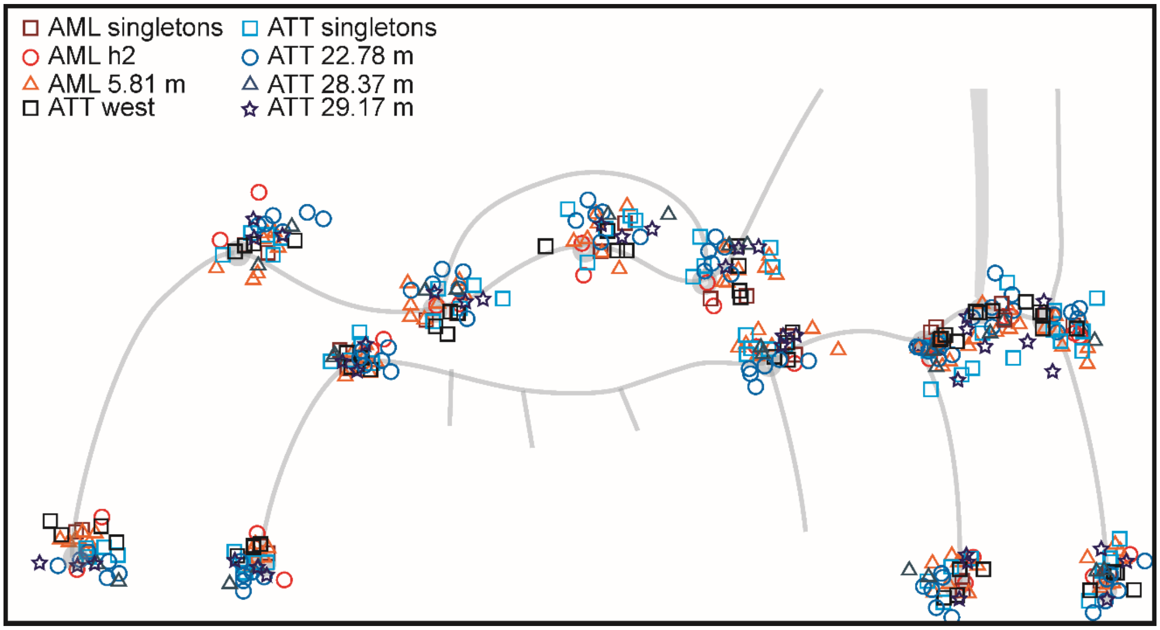


Figure 3:69 Distribution of landmarks using Procrustes superimposition. See Fig. 68 for landmark scheme. Singletons are those individuals which are the only from their sampling horizon used in the analysis. ATT(w) = Ao Talo Topo (west); AML = Ao Mo Lae.

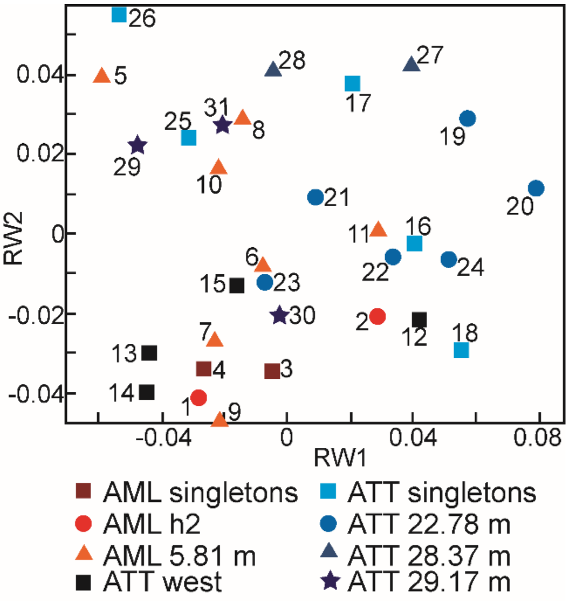


Figure 3:70 Relative warps (RW) 1 and 2 from principal component analysis performed on the Procrustes distribution in Fig. 69. RW 1 and 2 account for 26.4% and 16.76% of variance respectively. Specimens in analysis: 1) _22, AML h2; 2) _42, AML h2; 3) _6, AML h4; 4) _2, AML 3.62 m; 5) _18, AML 5.81 m; 6) _51, AML 5.81 m; 7) _67, AML 5.81 m; 8) _92, AML 5.81 m; 9) _94, AML 5.81 m; 10) _119, AML 5.81 m; 11) _139, AML 5.81 m; 12) _34, ATTw; 13) _35, ATTw; 14) _43, ATTw; 15) _105, ATTw; 16) _1, ATT 5.50 m; 17) _5, ATT 8.20 m; 18) _16, ATT 8.85 m; 19) _39, ATT 22.78 m; 20) _48, ATT 22.78 m; 21) _58, ATT 22.78 m; 22) _78, ATT 22.78 m; 23) _82, ATT 22.78 m; 24) _90, 22.78 m; 25) _11, ATT 22.88 m; 26) _15, ATT 25.34 m; 27) _11, ATT 28.39 m; 28) _8, ATT 28.39 m; 29) _6, ATT 29.17 m; 30) _10, ATT 29.17 m; 31) _20, ATT 29.17 m. Singletons are those individuals which are the only from their sampling horizon used in the analysis. ATT(w) = Ao Talo Topo (west); AML = Ao Mo Lae.

specimens in collections from Ao Mo Lae (AML) and Ao Talo Topo west (ATTw) to have lower RW1 and RW2 scores than specimens from the measured Ao Talo Topo section (ATT). AML and ATTw are generally considered to have the most fauna in

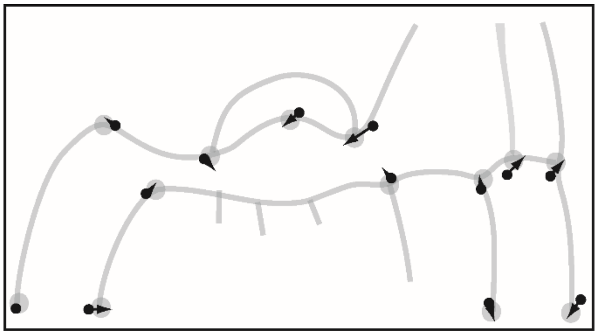


Figure 3:71 Deformation pattern produced from regression of Procrustes distance vs log of centroid size (LCS) using the three smallest specimens as reference. P=0.0119 for 1600 bootstraps.

common being the only localities with *Thailandium* and *Satunarcus.* As such, they are likely the same age. ATT is likely to be younger than these other two localities, given its down-dip location, though faults between localities may make this assumption false. If these hypotheses about ages are true, then the grade from low RW1 and RW2 in AML and ATT to more variation and higher scores of each in the ATT section may represent stratigraphic change. AML 5.81 m, one of the highest beds at Ao Mo Lae, certainly shows a wider range of scores than in the few specimens known from ATTw and other AML horizons.

The RW2 score most reflects the position of the posterior point of the palpebral lobe. In specimens with high RW2 scores, the posterior palpebral lobe is opposite S; in specimens with a low RW2 score, it is anterior to S1. The RW1 score is controlled partly by palpebral lobe length but also by the relative length of the frontal area. A longer frontal area corresponds to a lower RW1 score. While there is a diagnosable difference in specimens whose posterior palpebral area extends to opposite to S1 and those with a palpebral area entirely anterior to S1, that character does not reliably differentiate species in this sample. A range of frontal area morphologies may accompany long palpebral lobes.

The variation in eye size has an ontogenetic factor. A regression analysis using mean Procrustes distance versus the log of the centroid size (LCS) performed on the same dataset reveals that exsagittal position of the posterior palpebral point is size controlled (Fig. 3:71; P=0.0119 for 1600 bootstraps using the three smallest specimens as the reference). The specimens with high RW2 scores, despite some overlap, are generally smaller than those with lower RW2 scores, supporting that the group differences reflect ontogeny more than taxonomy or even stratigraphy. Such size-related reduction in the relative length of the eye is well known among the dikelocephalid trilobites (e.g. Hughes, 1993). The shape of the frontal area is less strongly size-related, though there seems to be a general trend for a relatively longer frontal area in larger specimens.

As with the cranidia, there is morphological variation among pygidia. The pygidium assigned by Qian (1986) and that assigneded by Shergold et al. (1988) are end members linked by variation in the width of the axis, expression of the pygidial border, and expression of interpleural furrows.

Genus *Asioptychaspis* Kobayashi, 1933

Type species.—Ptychaspis ceto Walcott, 1905 from the Chaumitien Formation of Shandong Province, China.

Asioptychaspis sp.

Figs 3:54.16–18

Occurrence.—Ao Talo Udang S1 7.00 m; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—Three cranidia from Ao Talo Udang S1 7.00 m (_78, 125, 253).

Remarks.—The glabellar shape, lateral glabellar furrows, long (exsag.) posterolateral projections, and lack of lateral fixigenal expansion in the palpebral areas are all consistent with *Asioptychaspis*. The relatively short, wide, slightly anteriorly expanding glabella is characteristic of *Asioptychaspis asiatica* Endo and Resser, 1937, but the palpebral lobe is too short and the fixigena too narrow for *A. asiatica*. In the fixigena, these specimens resemble *Asioptychaspis cacus* (Walcott, 1905), but that species is granulated, and no granulation is evident on the specimens from Ko Tarutao, though ths is likely due to their coarse preservation, relative to specimen size, in sandstone. The cranidia from the Tarutao Group are considerably smaller than most known material for *Asioptychaspis.* Due to their small size and thus the possibility that they belong to the earlier stage of a species known elsewhere, along with the poor preservation, we leave these specimens in open nomenclature.

Family SHUMARDIIDAE Lake, 1907

Genus *Parashumardia* Sun and Xian, 1979

Type species.—*Parashumardia sinensis* Sun and Xiang, 1979, Baoshan, western Yunnan, late Furongian.

Parashumardia sp.

Fig. 3:72.11,12

Occurrence.—Ao Phante Malacca 18.00 m; Talo Wao Formation, Tarutao Group, Ko Tarutao, Tremadocian

Material.—One cranidium (_12, internal mold) and one pygidium (_1, external mold) from Ao Phante Malacca 18.00 m.

Remarks.—Parashumardia sp. from the Tarutao group has a broad anterior glabellar lobe that is undifferentiated by furrows from the rest of the glabella. The anterior expansion differentiates it from other shumardiids such as *Akoldinioidia* Zhou (in Zhou and Zhang), 1984 and *Koldinioidia* Kobayashi, 1931, and the lack of lateral glabellar furrows differentiates it from *Shumardia* Billings, 1862. The *Parashumardia* type species, *Parashumardia sinensis* Sun and Xiang, 1979, from Baoshan has a similarly shaped and undivided glabella, but the genal field is broader, suggesting they are not the same species. *Parashumardia* sp. also resembles *Shumardia* sp. (*sensu* Shergold 1991) from the Pacoota Sandstone of the Amadaeus Basin, Australia and *Shumardia erquensis* Kobayashi, 1937; *sensu* Jell, 1985) from Digger Island, Victoria, Australia. These three species differ primarily in the lateral cranidial margin. *Shumardia* sp. (*sensu* Shergold,

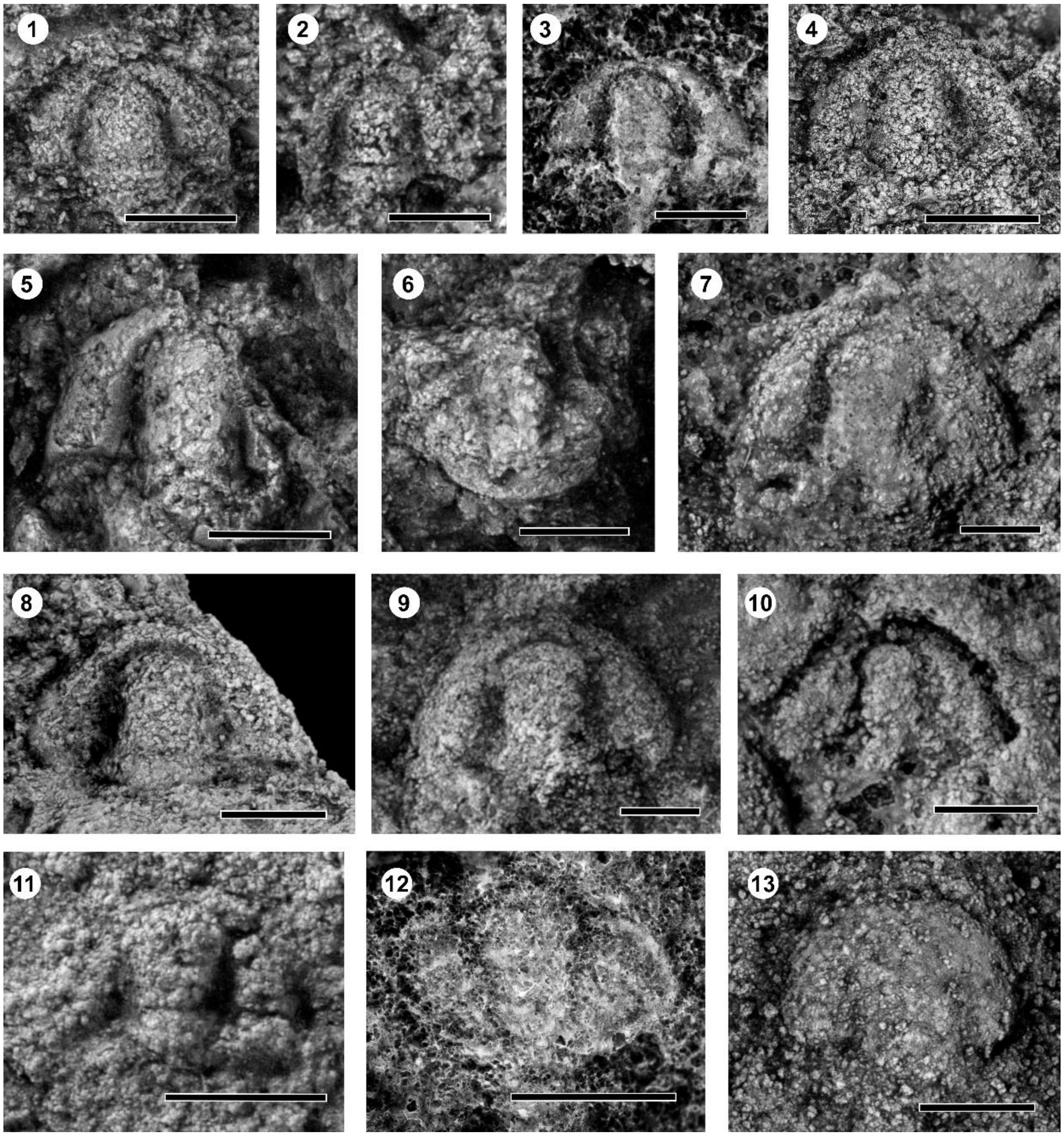


Figure 3:72 Akoldinioidia lata Park and Kihm, 2015, *Akoldinioidia* sp., *Parashumardia* sp., and *Koldinioidia choii* Park and Kihm, 2015. *Akoldinioidia lata* (1–6) **(1)** _32, cranidium, LHN 2.85 m; **(2)** _19, cranidium, LHN 2.85 m; **(3)** _9, cranidium, external mold, LHN 2.85 m; **(4)** _7, cranidium, LHN 2.85 m; **(5)** _28, cranidium, LHN 2.85 m; **(6)** _31, pygidium, LHN 2.85 m. *Akoldinioidia* sp. (7–10) **(7)** _57, cranidium, ATT 22.88 m; **(8)** _4, cranidium, LHN 2.85 m; **(9)** _64, cranidium, ATT 22.78 m; **(10)** _57b, cranidium, ATT 22.88 m. *Parashumardia* sp. (11,12) **(11)** _12, cranidium, APM 18.00 m; **(12)** _1, pygidium, external mold, APM 18.00 m. **(13)** _3, *Koldinioidia choii*, cranidium, ATT h2. All internal molds unless otherwise indicated. ATT = Ao Talo Topo; LHN = Laem Hin Ngam; APM = Ao Phante Malacca. Scale bars = 1 mm.

1991) has a subrounded shape in which the arc formed by the cranidial margin exceeds 180°, that is the posterolateral margin is starting to curve medially. In *S. erquensis* (*sensu* Jell, 1985) the posterolateral cranidial margin is oriented longitudinally. In *Parashumardia* sp. from the Tarutao Group, the posterolateral margin is strongly posterolaterally oriented. In this respect it resembles *Shumardia alata* Robison and Pantoja-Alor, 1968, but the latter has a considerably broader genal area.

Genus *Akoldinioidia* Zhou in Zhou and Zhang, 1984

Type species.—Akoldinoidia pustulosa Zhou and Zhang, 1984, upper Cambrian of Lulong, Hebei, China (by original designation).

Remarks.— In the emended diagnosis provided by Park and Kihm (2015a), *Akoldinioidia* differs from *Koldinioidia* Kobayashi, 1931 in possessing a well-defined rather than effaced preglabellar furrow. This distinction is followed herein.

Akoldinoidia lata Park and Kihm, 2015

Fig. 3:72.1–6

1988. Shumardiid gen. et sp. indet. Shergold et al., p. 317, fig. 3.P.

2015a. *Akoldinioidia latus* Park and Kihm, p. 196, figs 11U–LL.

Occurrence.—Ao Talo Topo 29.17 m, Laem Hin Ngam 2.85 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Material.—Nine cranidia from Ao Talo Topo 29.17 m (_37) and Laem Hin Ngam (LHN) 2.85 m (_7, 9 – external mold, 19, 22, 28, 32, 39, 40); one pygidium from LHN 2.85 m (_31) . All internal molds unless otherwise indicated.

Remarks.—The cranidia of *Akoldinioidia lata* from the Tarutao Group exhibit the same cranidial dimensions and glabellar furrowing as the silicified cranidia of *A. lata* from the Taebaek Group in Korea. The single shumardiid pygidium found in the Ao Mo Lae Formation also exhibits the same gross morphology as the pygidia from Korea, but it is too poorly preserved to evaluate whether the expression of furrows and numbers of axial rings are the same. It may have one fewer axial segments and less inflation of the posterior pleural bands. Park and Kihm (2015a) refer to this species as *A. latus*. In order for this adjectival species name to agree with the genus in gender and case, as required by the international code for zoological nomenclature, *latus* should be *lata*, and the species name is herein revised to *Akoldinioidia lata*.

Akoldinioidia sp.

Fig. 3:72.7–10

Occurrence.—Ao Talo Topo 22.78–22.88 m and Laem Hin Ngam 2.85 m; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—Four cranidia from Laem Hin Ngam 2.85 m (_4) and Ao Talo Topo 22.78 m (_64) and 22.88 m (_57, 57b), all internal molds.

Remarks.—Akoldinioidia sp. is similar to *Akoldinioidia lata* Park and Kihm, 2015a in the broad-based glabella and shape of the cephalic margin. The two species differ in the width and outline of the glabella. *Akoldinoidia* sp. has a rapidly tapering glabella with an expanded (tr.) anterior glabellar lobe such that the glabellar outline is concave. *Akoldinioidia convexalimbata* Qian, 1986, *Akoldinoidia pustulosa* Zhou and Zhang, 1984, and *Akoldinioidia expansa* Qian, 1986 also have a slightly expanded (tr.) anterior glabellar lobe, but in all three of these species the entirety of the glabella is straight or anteriorly expanding whereas the anterior lobe of *Akoldinioidia* sp. is distinctly narrower than LO and L1.

Genus *Koldinioidia* Kobayashi, 1931

Type species.—Koldinioidia typicalis Kobayashi, 1931, p. 187.

Koldinioidia choii Park and Kihm, 2015

Fig. 3:72.13

2015a. *Koldinioidia choii* Park and Kihm, p. 195, fig. 11a–t.

Occurrence.—Ao Talo Topo h1; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—One cranidium from Ao Talo Topo h1 (_3), internal mold.

*Remarks.—*The effacement characteristic of *Koldinioidia* means there are few characters on which to determine specific assignment. The only specimen recovered from Tarutao further lacks defined postero-lateral projections, the curvature of which can be useful in considering specific affinity. One of the few discernible characters is the especially wide glabellar base that accounts for ~50% of cranidial width. This is the diagnostic character of *Koldinioidia choii* and the cranidium has therefore been assigned to this species. In the Taebaeksan Basin of South Korea, *K. choii* regularly co-occurs with *Akoldinoidia lata* Park and Kihm, 2015a (Park, 2018). While the single cranidium of *K. choii* from Ko Tarutao was found in a different horizon than *A. lata* (ATT h1 versus ATT 29.17 m/Laem Hin Ngam 2.85 m), the two collections share other fauna such as *Quadraticephalus planulatus* (Kobayashi, 1957) and *Eosaukia buravasi* Kobayashi, 1957 suggesting that these horizons are of similar ages and that the relative rarity of each of these species may explain why they have yet to be found together. It is surprising that the species co-occur in both the Taebaeksan Basin and the Tarutao Group, as the Tarutao Group otherwise has a relatively endemic fauna at the species level. This co-occurrence could be interpreted as supporting evidence for Park’s (2018) supposition that the two species may be one species with sexual dimorphism. Further stratigraphy-based tests, as suggested by Park (2018), are needed to evaluate this hypothesis.

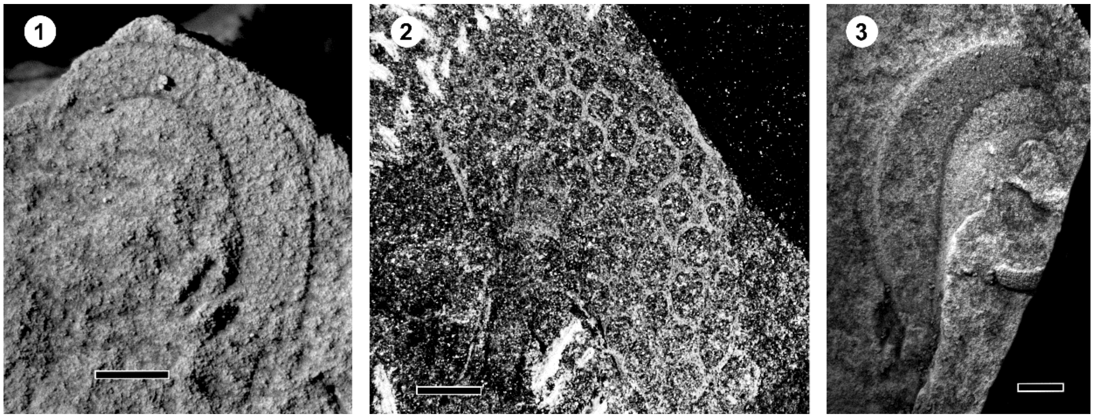


Figure 3:73 Indeterminate harpid border. **(1)** _3, APM 49.90 m; **(2)** _100, APM 43.60 m; **(3)** _56, APM 43.60m. All internal molds. APM = Ao Phante Malacca. Scale bars = 2 mm.

Indeterminate harpid

Fig. 3:73

Occurrence.—Ao Mo Lae 5.84 m, Ao Mo Lae Formation; Ao Phante Malacca 27.80–49.90 m, Talo Wao Formation; Tarutao Group, Ko Tarutao, Furongian–Tremadocian.

Remarks.—Various fragments of genal fields occur at Ao Phante Malacca that cannot be linked to any known glabellae. These are distinct in that they consist of closely spaced round to hexagonal perforations separated by thin exoskeletal walls. The most complete sclerite has both a small, strongly rounded eye and a long posterior projection of the wide cephalic brim as is characteristic for harpids. Stait et al. (1984) also found unidentifiable fragments of harpid borders but no fragments of the glabella.

Indeterminate cranidium

Fig.3:54.19

?1988. Leiostegiid gen. et sp. indet. Shergold et al., p.314, fig. 3.E.

?2015a. *Saukia*? *aojii* Kobayashi; Park and Kihm, p. 190–191, fig. 7.

Occurrence.—Ao Mo Lae h2; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Material.—One cranidium from Ao Mo Lae h2 (_29), internal mold.

Remarks.—This specimen has a different morphology of the frontal area and axial furrows than any other trilobite known from the Ao Mo Lae Formation. Unfortunately the glabella is nearly completely effaced, likely due to preservational quality more than to original morphology, and the palpebral areas are not well preserved. Without these features, we cannot reliably assign this material. However, while the shape of the glabella and frontal area and plausible shape of the fi°xigena are consistent with *Saukia*? *aojii* (sensu Park and Kihm, 2015a) the dimensions of the frontal area and fixigena differ strongly from those of *Saukia aojii* Kobayashi, 1933.

Alternatively this cranidium could instead be synonymous with the indeterminate leiostegiid illustrated by Shergold et al. (1988). This synonymy is less likely as the latter has a less rectangular glabella and narrower anterior border.

Chapter 4. Initial description of Cambrian fossils from Myanmar: Late Furongian trilobites of the southern part of Shan State

Introduction

The Shan Plateau, the defining physiographic feature of Shan Sate in Myanmar (also known as Burma), is marked by the uplift of a large mass of Precambrian, Paleozoic, and Mesozoic rock. This plateau is part of the ancient terrane of Sibumasu, also known as the Shan-Thai Block, and separated from the West Burma Block of western Myanmar by the Shan Scarp and associated Sagaing Fault (Fig. 4:1). Lower Paleozoic faunal assemblages are a key source of evidence for determining paleogeographic relationships and tectonic history among Perigondwanan terranes which include Sibumasu and the West Burma Block as

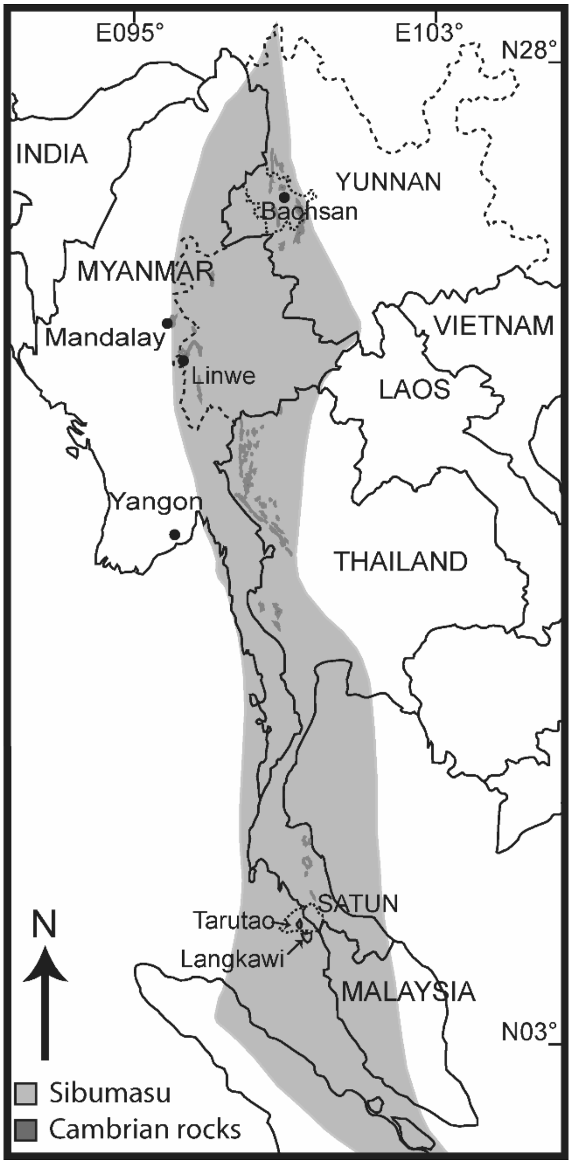


Figure 4:1 The modern extent of the Sibumasu terrane. Modified from Wernette et al., 2020.

well as North China, South China, Tarim, and others (Fortey and Cocks 2003). Furthermore, the Cambrian fauna of Sibumasu is interbedded with rhyolites and tuffs or ash beds, making it of critical potential utility for calibrating late Cambrian and earliest Ordovician geochronology which, in terms of the density of reliable absolute dates, is one of the most poorly constrained intervals of Phanerozoic time (see Gradstein *et al*., 2012).

Cowper Reed (1906, 1908, 1915, 1936) published descriptions of the Ordovician through Devonian fauna as part of the Geological Survey of India's early work on the regional geology, including the "Lower Paleozoic Faunas of the Southern Shan State" (1936), but Myanmar's Cambrian strata were unrecognized at that time, as the Ordovician Naungkangyi beds were thought to directly and unconformably overlie the Precambrian Chaung Magyi (La Touche 1913). Following an initial, informal report of Cambrian rocks from the Pangyun Formation in the northern Shan State (Tint 1972), the Molohein Group was the first Cambrian unit to be described in a formal publication (Thein 1973). Although these Cambrian deposits have been mentioned in numerous subsequent publications on Burmese geology (e.g. Bender 1983; Wolfart *et al*. 1984; Bhargava 1995; Aung and Cocks 2017), including the cursory suggestion of several trilobite species names (e.g. Tint 1972; Thein 1973), no material has ever been illustrated in a publication or formally described. Taxa historically reported to occur in the Molohein Group include *Saukiella junia* (Walcott) var. A Winston and Nicholls, 1967, *Eosaukia buravasi* Kobayashi, 1957, and *Drumaspis texana* Resser, 1942 (Tint, 1972; Thein, 1973; Aung and Cocks, 2017). The recognition of saukiids has been considered sufficient to assign an upper-most Cambrian age to the Molohein Group (e.g. Bender

1983; Wolfart *et al*. 1984; Aung and Cocks 2017) but given that *Saukiella* and *Drumaspis* are both characteristically Laurentian taxa, these generic assignments are surprising and, without published illustrations and descriptions, remain unconfirmed.

The only figured and described record of Myanmar's Cambrian trilobites is a comprehensive Master's thesis on the lower Paleozoic fauna and stratigraphy of the Ye-Ngan township (Soe 1983). In his faunal analysis for this area, Soe (1983) noted the following taxa: *Saukiella junia* (Walcott) var. B Winston and Nicholls, *Saukiella* cf. *S. junia* (Walcott) var. A Winston and Nicholls, *Saukiella* cf. *S. fallax* (Walcott), *Saukiella* sp., *Calvinella* cf. *C. prethoparis* (Longacre), *Calvinella* cf. *C. ozarkensis* (Walcott), *Calvinella* sp., *Eosaukia buravasi* Kobayashi, *Ptychaspis* cf. *P.* (*Asioptychaspis*) *delta* (Shergold), *Solenopleura* sp., *Prosaukia* cf. *P.*? *absoma* Shergold, and *Ptychaspis* sp. No new taxa were proposed. While this thesis provided valuable new information about the fauna of Myanmar, the work was never published and the specimens have been subsequently lost. Furthermore, all of the specimens were found in float. This and our subsequent work will discuss Soe's (1983) determinations, and we here informally re-illustrate one specimen of *Solenopleura* sp. which Soe recovered and illustrated but that we have yet to duplicate in our collections (Fig. 4:2).

Figure 4:2 Solenopleura sp., cranidium, refigured from Soe, 1983, pl. 2, fig. 20. No scale bars are available, because the refigured image is from a scan with unknown dimensions.

Based on specimens collected during an expedition to the Linwe area in November–December 2016 we describe the Cambrian trilobite fauna in the southern Shan State to include *Eosaukia buravasi*, *Asioptychaspis lata* n. sp., and *Asioptychaspis asiatica* Endo and Resser. This article is the first of several reports on the fauna, environments, and geochronology of Burmese sections through the later part of the Furongian and into the early Ordovician.

Geologic setting

Tectonic history

Sibumasu consists of Myanmar's Shan State and part of Kayin State, southwest Yunnan, western Thailand, and northern Malaysia (Mitchell *et al.* 2012; Udchachon *et al*. 2018)(Fig. 4:1). In the lower Paleozoic Sibumasu is thought to have been one of a number of "outboard" continental fragments that were peripheral to "core" Gondwana, consisting of South America, Africa, India, Antarctica and Australia. Most reconstructions (e.g. Meert 2002; Boger and Miller 2004; Cocks and Torsvik 2013) suggest that core Gondwana had amalgamated by the middle Cambrian although this view is not universally accepted (e.g. Schmitt *et al*. 2004). Regardless of which interpretation of core Gondwana is correct, outboard terranes evidently continued to accrete around the margins of core Gondwana into the early Paleozoic. This accretion was associated with widespread felsic intrusion in the equatorial Gondwana region (e.g LeFort *et al*. 1986; Zhu *et al*. 2012; Xu *et al*. 2014; Domeier 2018). The Gondwanan margin hosted various subduction zones that accommodated the accretion of island arcs and microcontinents which included parts of Turkey, Iran, North and South China, Tarim, and Indochina, and the Sibumasu block (Metcalfe 1998; Cocks and Torsvik 2013; Burrett *et al*. 2014; Hughes 2016; Torsvik and Cocks 2017), but the palaeogeographical relationships among these remain debated. Faunal similarities associate the southern portion of Sibumasu with Australia and North China during the late Cambrian and early Ordovician (Fortey and Cocks 1998, 2003), and Sibumasu reportedly retained such similarity to Australia until the mid to late Paleozoic (Metcalfe 1998; Burrett *et al.* 2016). Despite the existence of widespread intrusion, almost no extrusive volcanic strata have been preserved in the equatorial Gondwanan region except in Sibumasu (Brinckmann and Hinze 1981; Stait *et al*. 1984; Shergold *et al*. 1988; Bhargava 1995; Hughes 2016: Gardiner *et al*. 2017). In Myanmar, the only part of Sibumasu with exposed Precambrian basement, there is evidence of pre-Furongian uplift and modest metamorphism of Neoproterozoic strata that has traditionally been linked to the Assynian or Charnian orogenies (Garson *et al*. 1976; Wolfart *et al*. 1984).

The Kurgiakh (also known as Bhimphedian) orogeny took place along the Himalayan margin and perhaps more widely across equatorial Gondwana during the late Cambrian and early Ordovician (Srikantia *et al*. 1980; Cawood *et al*. 2007; Myrow *et al*. 2016; Myrow *et al*. 2019). This event may relate to the pre-Furongian, sub-Molohein Group unconformity in Myanmar. If the unconformity on Sibumasu is related to the Kurgiakh orogeny, then the event occurred earlier in Sibumasu because there is a continuous succession across the Cambrian–Ordovician boundary interval (e.g. Stait *et al*. 1984) that is absent in northwestern India (Hughes, 2016). Relationships with the northeastern Himalaya, particularly sections in Bhutan, remain intriguing because the later Cambrian Himalayan facies and fauna closely resemble those of Sibumasu (Hughes *et al*. 2011; McKenzie *et al.* 2011; Myrow *et al*. 2016), including reports of volcanic rocks (Tangri and Pande 1994, 1995. Whether or not Sibumasu and Bhutan were closely related at the time, Sibumasu was clearly experiencing intensive magmatic activity during the late Cambrian evinced by the numerous tuffaceous horizons and by the volcanic suite at Bawdwin (Brinckmann and Hinze 1981) in the northern part of the Shan State.

Uplift and subsequent exposure of Sibumasu's Paleozoic strata is the result of two Mesozoic convergence events. Sibumasu and Indochina reportedly sutured across a subduction zone during the Triassic (Cocks *et al.* 2005; Metcalfe 2006; Ridd 2016; Aung and Cocks 2017), forming the Sukhotai-Lao fold belt and the Nan-Uttaradit suture zone that define Sibumasu's eastern boundary (Searle *et al.* 2007). It then sutured with the West Burma Block along the Shan Scarp during the closure of the Neotethys Ocean in the late Mesozoic and early Cenozoic (Searle *et al*. 2007, 2011; Mitchell *et al*. 2012; Gardiner *et al*. 2015).

Stratigraphy

The lowest sedimentary unit (Fig. 4:3) of the Shan Plateau is the mildly metamorphosed Chaung Magyi Group (La Touche 1907) which is interpreted as Precambrian in age (La Touche 1913; Thein 1973; Mitchell *et al*. 1977). The Chaung Magyi is characterized by greywacke, whitish-gray siltstones, red or gray quartzite, and slates, with a minor carbonate component (Wolfart *et al*. 1984; Aung and Cocks 2017).

Flute casts and soft-sediment deformation have been recorded (Wolfart *et al*. 1984). Its uppermost member, the Tawngma Siltstone (Mitchell *et al*. 1977), is purported to contain horizontal burrows, although figures or descriptions of these have not been published to date; this member of the Chaung Magyi is limited to the northern Shan State. The presence of metamorphism and horizontal burrows led Garson *et al*. (1976) and Mitchell *et al*. (1977) to interpret the Chaung Magyi as latest Precambrian to Cambrian in age. The Furongian Molohein Group and Pangyun Formation, which overlie the Chaung Magyi with an angular unconformity (Thein 1973), are not metamorphosed. Near Bawdwin, the Tawng Peng granite intrudes the Chaung Magyi but not the Pangyun Formation. The

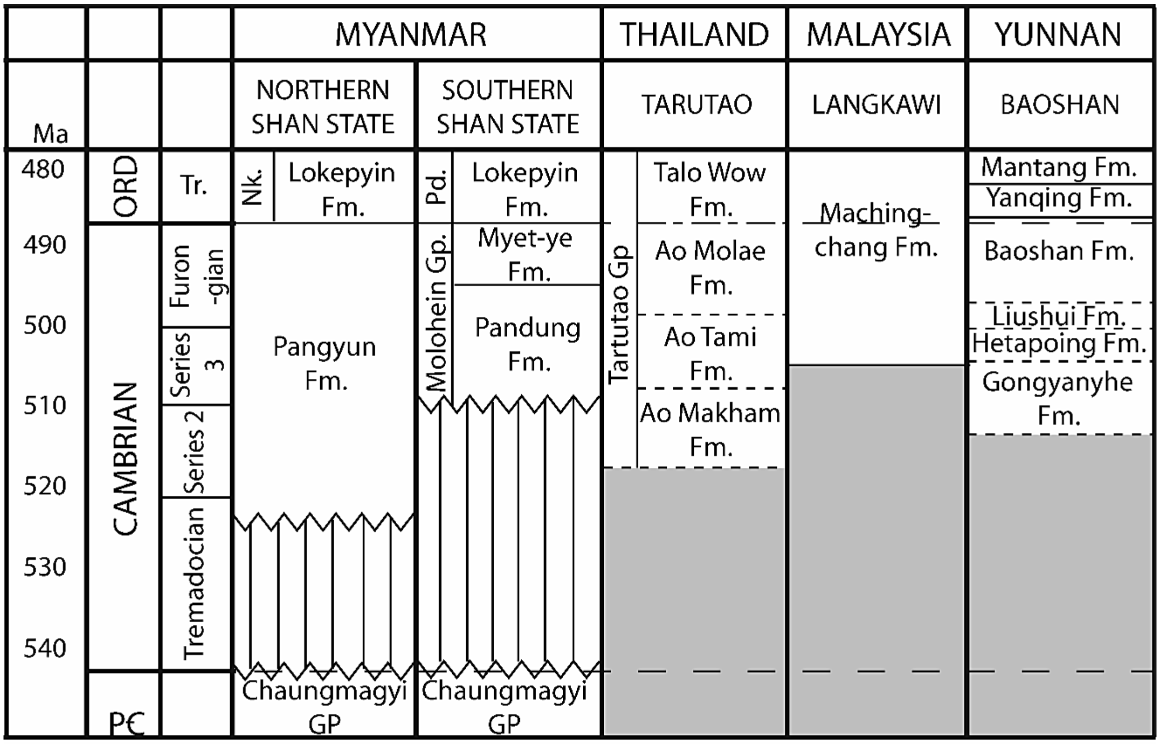


Figure 4:3 Precambrian-lower Ordovician stratigraphic successions for each area of Sibumasu including Myanmar's northern and southern Shan State, western Thailand, southwestern Yunnan, and northern Malaysia. Abbreviations are as follows: Tr. = Tremadocian; Nk. = Naungkangyi Group; Pd. = Pindaya Group. Vertical stripes indicate unconformity; gray indicates unknown strata with no outcrops. Modified from Aung and Cocks, 2017 using Imsamut and Yathakam, 2011 and Luo, 1985.

intrusion, angular unconformity, and metamorphism suggest a substantial time interval between the deposition of the Chaung Magyi and the overlying, definitively Cambrian strata (Krishnan 1968).

In the southern part of Shan State the lowest definitively Paleozoic unit is the Molohein Group, which we show here to be Furongian in age, at least in part. Although good exposure is sparse, a thin basal conglomerate of quartzite pebbles and an angular unconformity reportedly marks the boundary of the Chaung Magyi and Molohein Group (Wolfart *et al*. 1984). The Molohein Group is a clastic succession of red, gray, white, or purple sandstones with thin interbedded siltstones and mudstones. Sandstones may be rippled, trough cross-bedded, or show hummocky cross stratification. Carbonate lenses are reported in some places (Wolfart *et al*. 1984; Aung and Cocks 2017). The Pandung and Myet-Ye formations together comprise the Molohein Group (Thein 1973), though most authors refer to the group as a whole. The Pandung Formation is more quartz-rich with a pinkish-white color whereas the overlying Myet-Ye Formation is generally darker pink or purplish; both are micaceous though the Myet-Ye Formation is reportedly more so (Wolfart *et al*. 1984). To date fossils have been reported only from the Myet-Ye Formation (Aung and Cocks 2017). The collective thickness of the Molohein Group is poorly understood with various estimates being 300m (Thein 1973), 1200m (Wolfart *et al*. 1984), or even 2400m (Garson *et al*. 1976). Soe (1983) estimated a thickness of 540m for the Pandung Formation and 230m for the Myet-Ye Formation in the Ye-Ngan area, but this was a rough estimate compiled from many isolated outcrops (Maung Kyi Soe pers. comm. 2020). The Shan State's heavy forestation, sharp topographic relief, and numerous faults hinder establishing a continuous section. Furthermore, given that the base of the Pandung Formation is an angular unconformity, it is likely the thickness of this unit varies laterally.

The Molohein Group includes both siliciclastic deposits and volcanic tuffs. This unit's counterpart in the northern portion of the Shan State, the Pangyun Formation, refers only to the sedimentary rocks that interfinger with the Bawdwin Volcanic Series (Aung and Cocks 2017). The Molohein Group's volcanic deposits are not as thick as those to the north, where a remnant volcanic center is preserved, and thus the lithostratigraphic nomenclature is undifferentiated for sedimentary and volcanogenic components. The Molohein Group's volcanic component is rhyolitic tuff that is often welded into a flinty texture with a dull to bright green tinge. These tuffs may be up to a meter or more thick.

The upper boundary of the Molohein Group is marked by a gradual reduction of clast grainsize into the siltstones of the Ordovician Lokepyin Formation, the lowest unit of the Pindaya Group that is the equivalent of the northern Shan State's Naungkangyi Group (Reed 1936; Thein 1973; Aung and Cocks 2017). In addition to the reduction of grain size, the Lokepyin Formation is marked by a distinct buff or tan color to its siltstones, rather than the purple, pink, red, or white of the Molohein sandstones.

Materials and methods

Sampling localities for the 2016 excursion (Fig. 4:4) were chosen based on Soe's (1983) thesis, though most, if not all, of that material was found in float. At each locality detrital zircon samples, fossils, and tuff beds were collected where possible. Fossils were collected on a bed-by-bed basis, each marked as a separate collection. Four localities with Cambrian fossils (PG1–PG4) were found on the unpaved road to Padongaing village, and one locality was found near Kyaukngget Monastery (KY). PG1 (21° 8'56.82"N, 96°32'57.42"E) is adjacent to where the road crosses a stream; this is the only location at which identifiable fossils were found in multiple beds (Fig. 4:5). PG2 (21°8'54.06"N, 96°33'3.00"E) is a roadcut about 200m east along the road from PG1. PG3

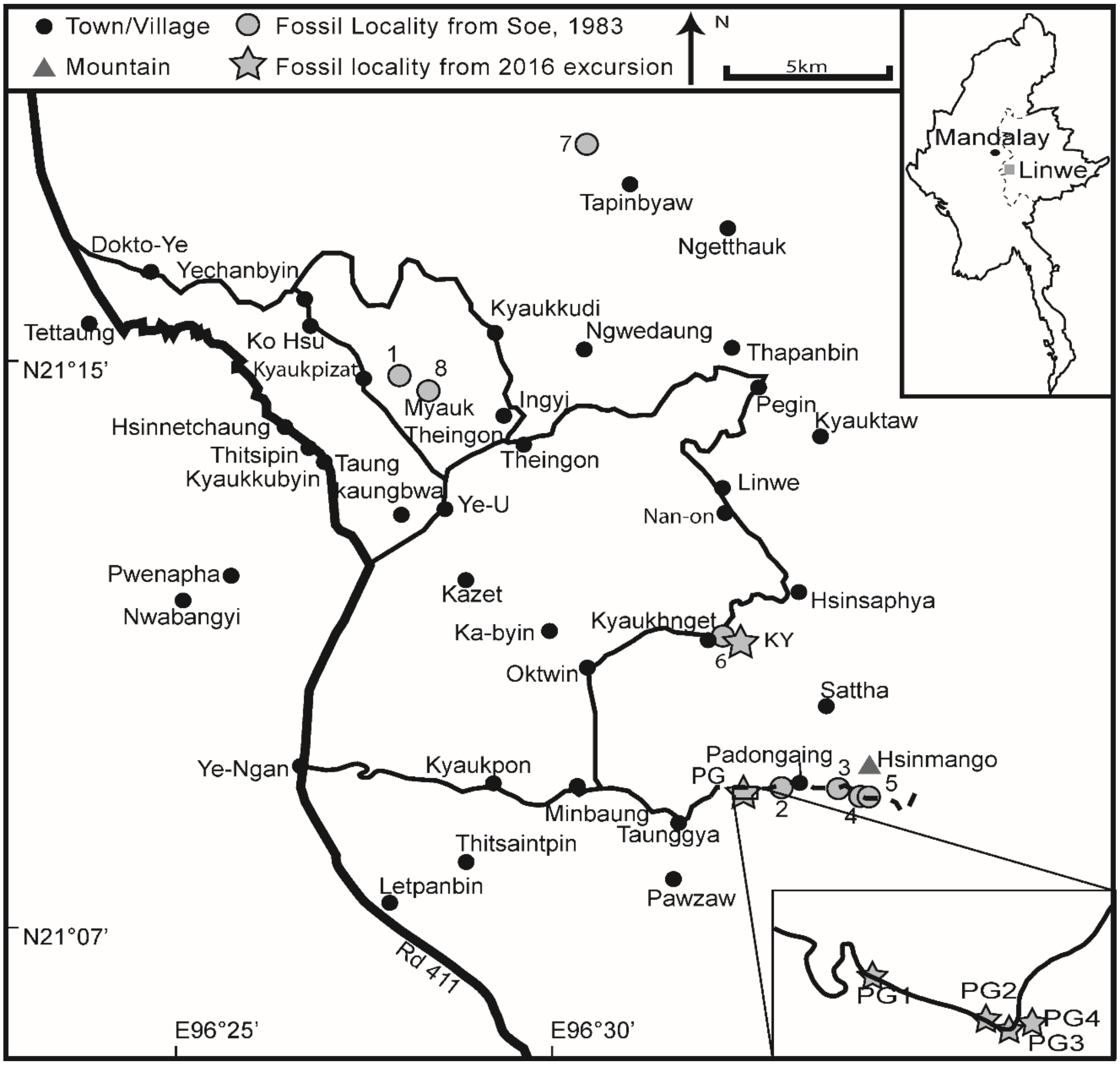


Figure 4:4 Map of the Linwe area with localities of fossil collections.

(21°8'53.58"N, 96°33'4.26"E) comprises sparse, intensely weathered blocks of sandstone jutting out from an outcrop otherwise surrounded by mud on the inside of the bend in the road. PG4 (21° 8'53.97"N, 96°33'5.06"E) also consists of material from the next rocky but poorly exposed outcrop further up the track from PG3. The KY (21°11'6.60"N, 96°33'3.12"E) sample is from the stream bed down the trail south of Kyaukngет Monastery. Fossils at KY occur in loose cobbles with no stratigraphic provenance that have been washed downstream from the Cambrian core of the Pindaya Range.

Within the Molohein Group trilobites are preserved as undeformed or only mildly deformed internal and external molds in very fine to fine-grained quartzarenite with varying quantities of mica; the mica may become concentrated on the surface of the fossil, imparting a smooth, almost glittery appearance. Other specimens show a slight infilling of limonite that leaves an orange film on the mold.

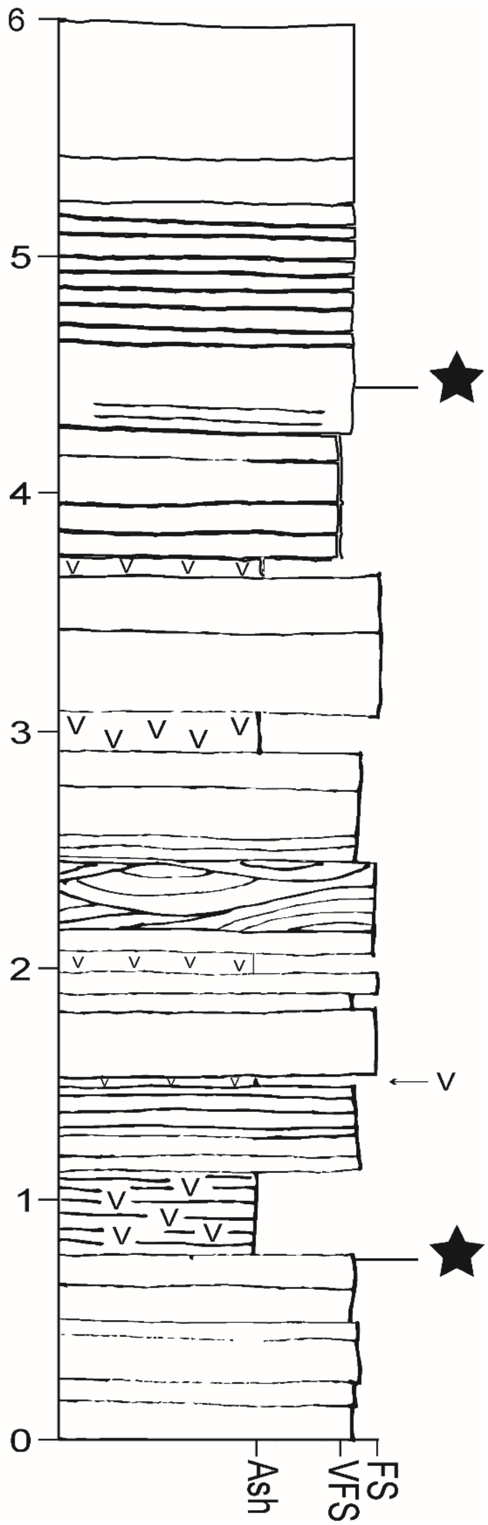


Figure 4:5 Measured section from Locality PG1. Black stars indicate trilobite fossils.

Diagenetic pyrite cubes occur within the sandstone; the pyrite is in the matrix, and is not associated with fossil preservation.

The specimens were prepared manually using a Dremel tool, then blackened with India ink, whitened with ammonium chloride, and photographed with a Leica stereoscopic camera model MZ16 or M205C. All figures and plates were created using Adobe Photoshop CC2017 and Adobe Illustrator CS2.

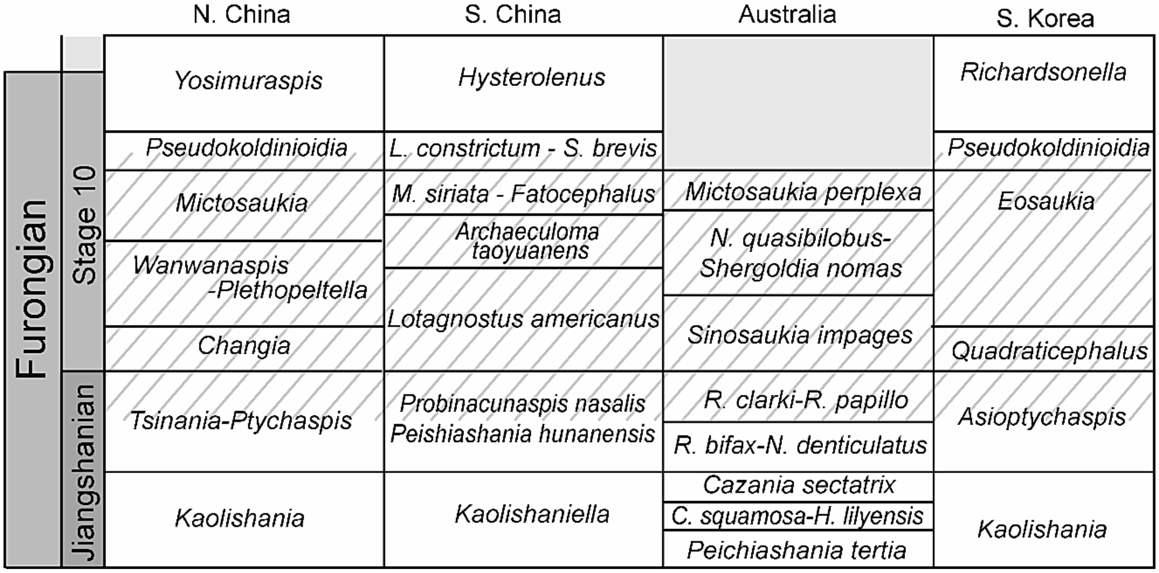
Morphometric analysis used the following software created by H. David Sheets as part of the Integrated Morphometrics Package: CoordGen8, BigFix8, Regress8, and PCAGen8 (Webster and Sheets, 2010; available free of charge at http://www.filogenetica.org/cursos/Morfometria/IMP_installers/index.php). Statistical tests for allometry were performed using PAST4.01 (Hammer *et al*. 2001).

In consultation with senior scientists in Myanmar, specimens are reposited at the Cincinnati Museum Center as CMC IP88051 - IP88137.

Paleogeographic distribution and biostratigraphic correlation

The known fossils by which to spatio-temporally constrain the Cambrian units of Shan State are currently limited. Of the southern Shan State Cambrian fauna that is presently identifiable to the species level, only *Eosaukia buravasi* Kobayashi (1957), which is common in the Thailand's Tarutao Group (Kobayashi 1957; Shergold et al. 1988), is known to occur elsewhere in Sibumasu. This species also likely occurs in the Bonaparte Basin of western Australia (Shergold et al. 2007). *Asioptychaspis asiatica* Endo and Resser (1937) occurs in the Liaoning Province of the North China Block (Endo and Resser 1937). The occurrences of these two species are consistent with Furongian palaeogeographic reconstructions placing Sibumasu adjacent to Northwest Australia with the North China Block nearby (e.g. Metcalfe 2013; Burrett *et al*. 2014).

Of the southern Shan State species known elsewhere, *A. asiatica* is the oldest. It belongs to the *Tsinania–Ptychaspis* zone of North China (Zhou and Zhen 2008); alternatively known as the *Asioptychaspis–Tsinania* Zone or *Asioptychaspis* Zone (Park and Kihm 2015a; Choi *et al*. 2016), which is the latest part of the Jiangshanian (Peng et al. 2012)(Fig. 4:6). All Chinese species of *Ptychaspis* or *Asioptychaspis* date to this interval (Zhou and Zhen 2008; Park and Kihm 2015a), but *Asioptychaspis delta* Shergold (1975) occurs in Cambrian Stage 10 of Australia. As *Asioptychaspis lata* n. sp. co-occurs with *E. buravasi*, distinctive of Cambrian Stage 10 (Zhu and Zhen 2008; Choi et al.



		N. China	S. China	Australia	S. Korea
Furongian	Stage 10	*Yosimuraspis*	*Hysterolenus*		*Richardsonella*
		Pseudokoldinioidia	*L. constrictum - S. brevis*		*Pseudokoldinioidia*
		Mictosaukia	*M. siriata - Fatocephalus*	*Mictosaukia perplexa*	*Eosaukia*
		Wanwanaspis -Plethopeltella	*Archaeculoma taoyuanens*	*N. quasibilobus-Shergoldia nomas*	
			Lotagnostus americanus	*Sinosaukia impages*	
		Changia			*Quadraticephalus*
	Jiangshanian	*Tsinania-Ptychaspis*	*Probinacunaspis nasalis* *Peishiashania hunanensis*	*R. clarki-R. papillo*	*Asioptychaspis*
				R. bifax-N. denticulatus	
		Kaolishania	*Kaolishaniella*	*Cazania sectatrix*	*Kaolishania*
				C. squamosa-H. lilyensis	
				Peichiashania tertia	

Figure 4:6 Upper Jiangshanian and Cambrian Stage 10 trilobite zones for northern Gondwanan terranes. Hatching indicates the likely range of the fauna described herein. Some genera have been abbreviated in the chart for readability; the full names are: *Caznaia squamosa, Hapsidocare lilyiensis, Leiostegium constrictum, Mictosaukia striata, Neoagnostus denticulatus, Neoagnostus quasibilobus, Rhaptagnostus clarki, Rhaptagnostus papillo, Rhaptagnostus bifax,* and *Shenjiania brevis,*. The South Korean biozones are for the Taebaek Group. Zone correlations are compiled from Choi et al., 2016 and Ogg et al., 2016; where unreconcilable differences exist between these references, preference is given to Ogg et al., 2016.

2016), *A. lata* must also be a later species of *Asioptychaspis*. In the Tarutao Group *E. buravasi* co-occurs with other stage 10 taxa such as *Quadraticephalus* and *Pagodia* (Kobayashi 1957; Shergold et al. 1988).

Systematic paleontology

Family PTYCHASPIDIDAE Raymond, 1924

Genus *Asioptychaspis* Kobayashi, 1933

Type species.—Ptychaspis ceto Walcott, 1905 from the Chaumitien Formation of Shandong Province, China

Remarks.—The possibly synonymy of *Asioptychaspis* and *Ptychaspis* Hall, 1863 has been repeatedly debated. Kobayashi (1933) designated *Asioptychaspis* as containing only Asian taxa while Shergold (1975) recognized differences between the genera but did not consider these to be sufficient to warrant generic distinction, preferring *Asioptychaspis* to be a subgenus within *Ptychaspis*. Westrop (1986) disagreed, returning *Asioptychaspis* to generic level based on the flat, poorly defined pygidial border found in *Asioptychaspis* but not in *Ptychaspis.* Zhang and Jell (1987) thought these differences insufficient for even subgeneric distinction. Sohn and Choi (2007) expanded the list of characters differentiating *Asioptychaspis* from *Ptychaspis* including a strongly convex, long, parallel-sided or forward expanding glabella and large palpebral lobes situated anteriorly to glabellar midlength. We follow Sohn and Choi's (2007) differential diagnosis herein.

Asioptychaspis lata n. sp.

Figs 4:7.1–8, 4:8

Type material.—Holotype, CMC IP88,078, Fig. 4:7.3a–c; Molohein Group, Myet-Ye Formation; Furongian, lower to middle of Cambrian Stage 10; Padongaing 1 bed 4.50m. Paratypes: CMC IP88051–87057, IP88060–87066, IP88068–87072, IP88074, IP88076–87078, IP88080–87084, IP88087, IP88090–87094, IP88096–87098, and IP88100–87111.

Diagnosis.—Species of *Asioptychaspis* with particularly wide fixigena, width (tr.) at anterior corners of palpebral lobes ~1.5 times preoccipital glabellar length (sag.); midpoint of palpebral lobes anterior to S2. Glabella inflated and anteriorly extended above and beyond strong ventrally curved anterior border. Pygidia effaced, pleural and interpleural furrows weakly incised; axis strongly tapering with four rings; entire pleural field with fine granular texture including broad, flat border which overlies doublure as long (sag., exsag.) postaxis.

Occurrence.—Linwe Area of the southern Shan State, Myanmar at Padongaing (PG) 1, beds 0.75m and 4.50m, and as float at Soe (1983) locality 6; Myet-Ye Formation, Molohein Group; Furongian, lower to middle of Cambrian Stage 10.

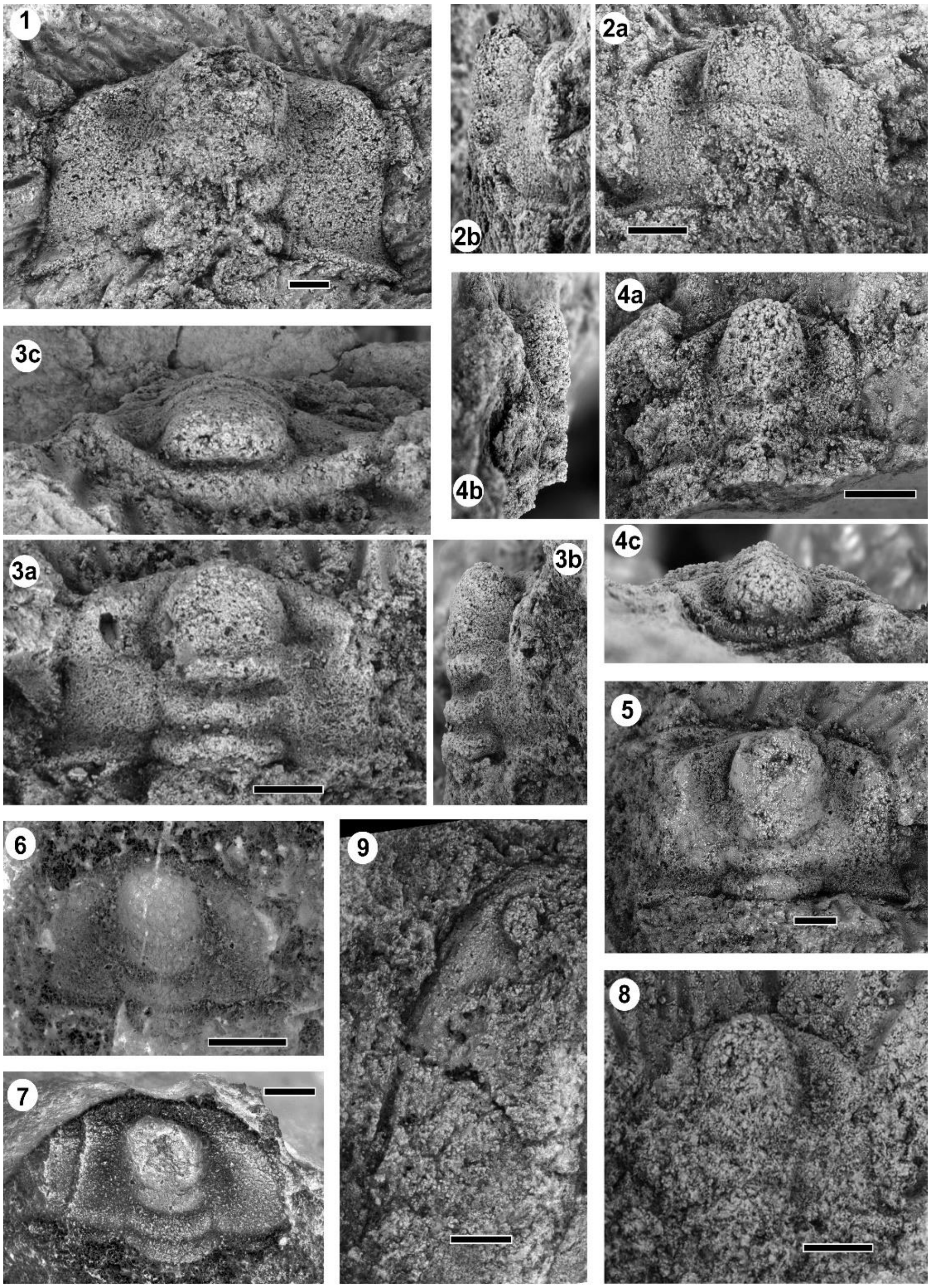


Figure 4:7 Asioptychaspis lata n. sp. **(1)** CMC IP87061, cranidium, internal mold, dorsal view; **(2)** CMC IP87084, cranidium, internal mold, *a* dorsal view, *b* right lateral view; **(3)** CMC IP87078, cranidium, internal mold, *a* dorsal view, *b* right lateral view, *c* anterior view; **(4)** CMC IP87056, cranidium, internal mold, *a* dorsal view, *b* left lateral view, *c* anterior view; **(5)** CMC IP87052, cranidium, internal mold, dorsal view; **(6)** CMC IP87065, cranidium, external mold with inverted colors, dorsal view; **(7)** CMC IP87060, cranidium, latex peel of external mold, dorsal view; **(8)** CMC IP87128, cranidium, internal mold, dorsal view; **(9)** CMC IP87079, indeterminate librigena, internal mold, dorsal view. All scale bars 2 mm.

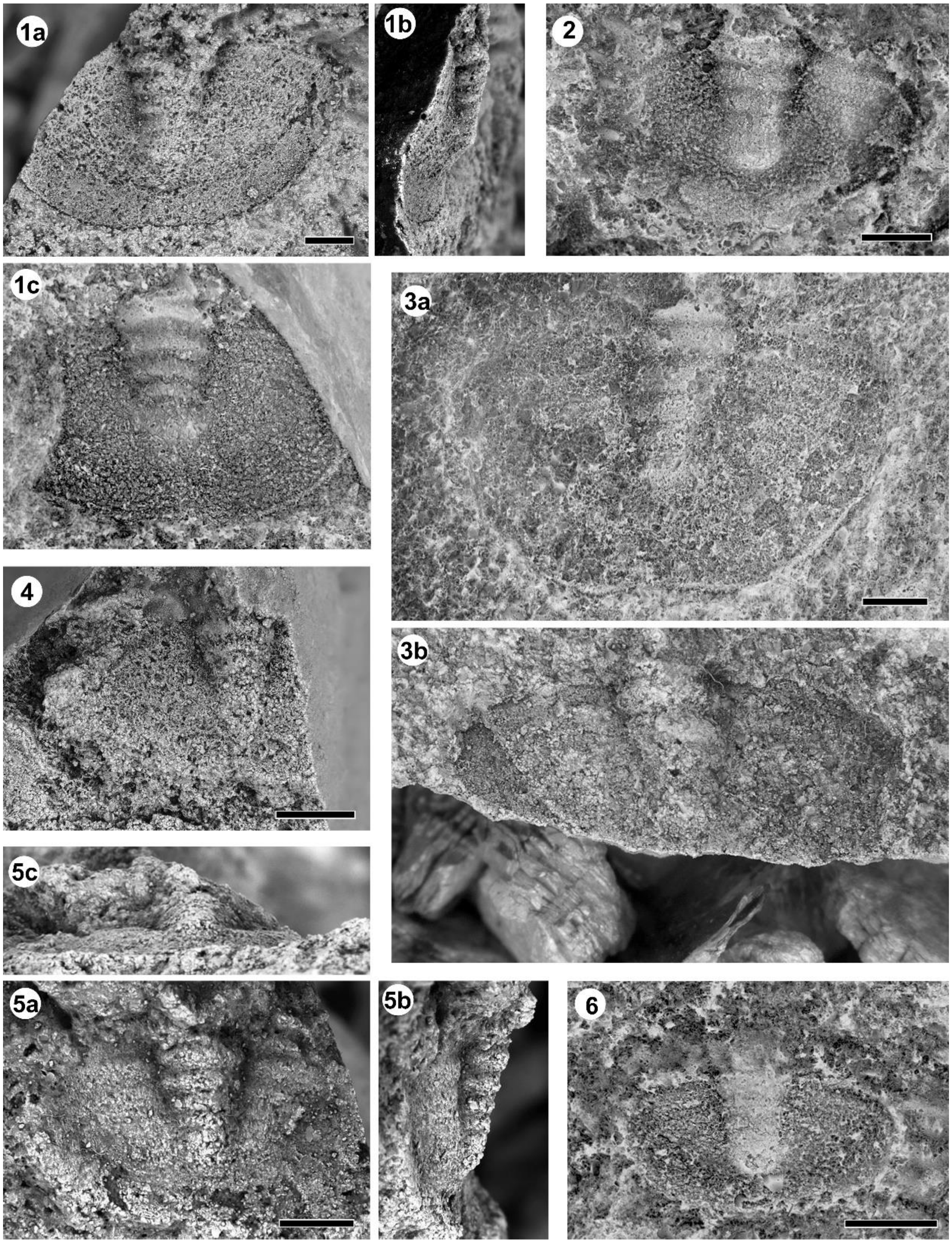


Figure 4:8 Asioptychaspis lata n. sp., all pygidia. **(1)** CMC IP87051, *a* internal mold dorsal view, *b* internal mold left lateral view, *c* external mold dorsal view; **(2)** CMC IP87083, internal mold dorsal view; **(3)** CMC IP87057, internal mold dorsal view, *b* external mold dorsal view; **(4)** CMC IP87055, internal mold, dorsal view; **(5)** CMC IP87075, internal mold, *a* dorsal view, *b* left lateral view, *c* posterior view; **(6)** CMC IP87088, external mold, dorsal view. All scale bars 2 mm.

Description.—Cranidium subtrapezoidal; glabella occupies entire cranidial length (sag.) with inflated anterior lobe protruding over anterior cranidial margin; cranidial width (tr.) at posterior end of palpebral lobe 1.5–2.1 times preoccipital glabellar length (sag.) and 2.0–2.3 times glabellar width across anterior lobe; frontal area slopes ventrally with gently inflated anterior border separated from glabella by firmly-incised furrow; anterior border uninterrupted continuation of preocular areas; anterior margin laterally straight from preglabellar area to anterior corner of palpebral lobe, oriented ~15° from transverse, and medially gently curved. Glabella parallel-sided or gently narrowing at L2; S1 firmly incised and medially continuous, bowed posteriorly; S2 posteriorly oblique to transverse and variably medially continuous or effaced, deeply impressed laterally and shallowing medially; anterior lobe equal width or broader (tr.) than rest of glabella with strong anterior expansion but dorsally not inflated above height of L2. SO firmly incised evenly across glabella and transverse to slightly posteriorly bowed; LO broader (tr.) than L1 and subequal in length (sag.) and dorsal inflation, occipital spine absent. Cranidial posterior border short (exsag.) and defined by broad, deep furrow; posterolateral projections broad (exsag.) and short (tr.) with the maximum cranidial width (tr.) at the posterolateral projection 1.1–1.15 times cranidial width (tr.) at posterior corner of palpebral lobe; posterior facial suture branch curves gently posterolaterally. Palpebral lobe weakly curved and anteriorly positioned with palpebral midpoint opposite or anterior S2; palpebral lobe, 40–50% preoccipital glabellar length; fixigena expanded (tr.) little or not at all across palpebral area.

Pygidium wide (tr.), width at anterior corners ~1.6 times pygidial length; anterior margin gently curved; posterior margin strongly curved, median portion of margin transverse or slightly embayed. Axis ~75% pygidial length, conical with 4 axial rings and terminal piece; first three transverse axial furrows strongly incised and last axial furrow faint. Pleural field nearly effaced with only faint pleural furrows; furrows nearly straight and parallel to anterior pleural furrow; furrows become completely effaced near margin; pleural field covered in fine granules. Doublure occupies entire postaxial length and narrows only slightly from postaxial position to anterior corners.

Etymology.—lata, Latin for wide, referring to the wideset eyes that differentiate this species from other *Asioptychaspis*.

Material.—Cranidia: from Padongaing (PG) 1 bed 4.50m five figured internal molds (CMC IP88052, IP88056, IP88061, IP88078, and IP88084), 29 unfigured internal molds (CMC IP88053, IP88054, IP88057, IP88062–87064, IP88069–87072, IP88076, IP88081, IP88082, IP88087, IP88090, IP88091, IP880912–87094, IP88098, IP88100–87109, and IP88111), two figured external molds (CMC IP88060 and IP88065), and four unfigured external molds (CMC IP88080, IP88083, IP88096 and IP88097); from PG1 bed 0.75m one figured internal mold (CMC IP88128). Pygidia: from PG1 bed 4.50m four figured internal molds (CMC IP88055, IP88057, IP88075, and IP88077), two unfigured internal molds (CMC IP88051 and IP88110), four figured external molds (CMC IP88057, IP88077, IP88088, and IP88089), and two unfigured external molds (CMC IP88066 and IP88085); from PG1 bed 0.75 mm one unfigured internal mold (CMC IP88127).

Remarks.—In the horizons in which it occurs near Padongaing village, *Asioptychaspis lata* is the dominant taxon: 41 cranidia of *A. lata* in the 4.50 m horizon at PG1 and only 5 other cranidia are present in the collection; the 0.75 m bed contains only *A. lata*, but only two specimens were found therein. *Asioptychaspis lata* is readily distinguishable from all other species of the genus by its exceptionally wide (tr.) fixigena. In a set of 25 individuals, with preoccipital glabellar lengths ranging from 1.7 mm to 8.25 mm, there is a subtle trend of the cranidial width to increase relative to the preoccipital glabellar length. The smallest specimens have an average cranidial width versus preoccipital glabellar length ratio of ~1.5 and the largest a ratio of ~1.65. However, when the logarithms of glabellar length and cranidial width are plotted against each other using ordinary least squares regression (OLS; Fig. 4:9), the slope is 1.0293, with a 95% confidence bracket of 0.91548–1.1322. A slope of 1, indicating isometry, is well within this confidence interval suggesting no significantly detectable allometry.

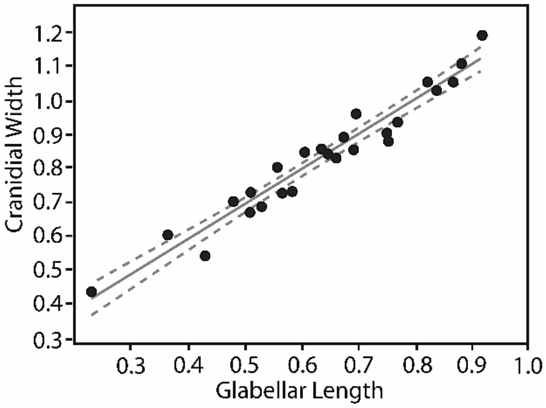


Figure 4:9 Log of preoccipital glabellar length (sag.) versus log of cranidial width (tr.) for *Asioptychaspis lata* n. sp. using ordinary least squares regression. Preoccipital glabellar length is used as a standardization of size; cranidial width was measured across the anterior corners of the palpebral lobes. The slope is 1.0293 with 95% confidence intrvals (N=1999) of 0.91548–1.1322). All units are in mm.

The cranidial width (tr.) of *A. lata* at all sizes considerably exceeds that of other species of *Asioptychaspis*. For comparison, the largest known specimen of the *Asioptychaspis* type species, *A. ceto* (Wacott 1905), has a glabellar length of 14 mm, including LO, but a width to length ratio of less 1.42, less than the average of the smallest specimens of *A. lata*, 1.5. There are nine heretofore recognized species of *Asioptychaspis* (Sohn and Choi 2007): *A. ceto* (Walcott 1905), *A. calyce* (Walcott 1905), *A. cacus* (Walcott 1905), *A. calchas* (Walcott 1905), *A. asiatica* (Endo and Resser 1937), *A. subglobosa* (Sun 1924), *A. brevicus* (Sun 1935), *A. fengshanensis* (Sun 1935), and *A. shansiensis* (Sun 1935), all of which have narrower fixigenae than *A. lata*. The wideset, anteriorly positioned eyes of *A. lata* contribute to a more box-like, rectangular shape with longer (exsag.) posterolateral projections and a more gently curved margin than in other *Asioptychaspis*. The exceptionally broad (tr.) and deep axial furrows occupy much of the palpebral areas as opposed to the more inflated palpebral areas common in other *Asioptychaspsis*. However, because all these characters are attributable to the outward and anterior movement of the eyes, they do not prevent the assignment of this new species to *Asioptychaspis*, such that a new, monspecific genus is uncalled for. *Asioptychaspis lata* was identified and figured by Soe (1983; p. 151–154, pl. 3, fig. 27) as *Ptychaspis* sp. from cobbles found at his locality 6 (Fig. 4:4).

Ptychaspis sp. cf. *P. asiaticus* Resser and Endo (*sensu* Shergold *et al*. 2007) has nearly similarly broad fixigenae, but its occipital ring is strongly dorsally expanded. Its anterior border is also strongly sloped, and almost completely dorso-ventral in orientation. The most dorsal point of the occipital ring of *A. lata* is on the same plane as the most dorsal points of the other glabellar lobes, and the frontal area is more gently sloped.

Asioptychaspis lata co-occurs with *Eosaukia buravasi*, which occurs in Cambrian Stage 10 in the Tarutao Group on the southern end of Sibumasu. However, most known species of *Asioptychaspis* date to the *Ptychaspis–Tsinania* Zone of the latest Jiangshanian (Zhou and Zhen 2008; Peng 2009; Peng *et al*. 2012). The wideset eyes of *A. lata* may be a derived feature of this later-occurring ptychaspid.

The only associated librigena (Fig. 4:7.9) is a potential but uncertain match. It has a narrow genal field and a broad and deep posterior border furrow comparable with *A. lata*. The eye is large and strongly rounded, and where palpebral lobes are preserved on the cranidium, they widen (tr.) at their midpoint, possibly being able to fill this space. The overall morphology of the librigena is similar to that of *A. subglobosa* (Sun, 1924). However, in the one specimen available the preservation is incomplete and it appears that there is not sufficient postpalpebral length (exsag.) to allow this librigena to be paired with the cranidium of *A. lata*. Without additional and better preserved librigenae, the assignment of this sclerite is tentative.

Asioptychaspis asiatica (Endo and Resser 1937)

Fig. 4:10

1937. *Ptychaspis asiatica* Endo and Resser, p. 272–273, pl. 56, figs 4–9

1987. *Ptychaspis asiatica* Zhang and Jell, p. 228, pl. 112, figs 12,13, pl. 113 figs 1–4

Lectotype.— "*Ptychaspis*" *asiatica* Endo and Resser, 1937 pl. 56, fig.4 USNM 86895a designated in Zhang and Jell, 1987.

Occurrence.—Linwe area of the southern Shan State, Myanmar at Kyauknget (KY) and as float at Soe (1983) locality 1, Myet-Ye Formation, Molohein Group; Furongian, upper Jiangshanian.

Material.— Cranidia: Five figured internal molds (CMC IP88130, IP88133, IP88431, IP88136, and IP88137). Thoracic segments: one figured internal mold (CMC IP88131). All from float at KY.

Remarks.— The cranidium of *A. asiatica*, first known from Liaoning (formerly southern Manchouko) in north China, is recognizable by its anteriorly expanding glabella, pustulation, medially shallowing lateral glabellar furrows, and subtriangular pygidium, all of which are visible in the material from Kyauknget. The anteriorly expanding glabella differentiates it from *A. calchas* (Walcott 1905) which can also have granulation. *Asioptychaspis brevicus* (Sun 1935) lacks both granulation and the medial shallowing of the lateral glabellar furrows.

Ptychaspis sp. cf. *P. asiaticus* Resser and Endo (*sensu* Shergold et al. 2007 from Bonaparte Basin, western Australia) has broader fixigenae compared with *A. asiatica* as well as a more strongly ventrally curved frontal area. An unusual trait shared by both species is the expanded LO that is strongly elevated along the posterior margin.

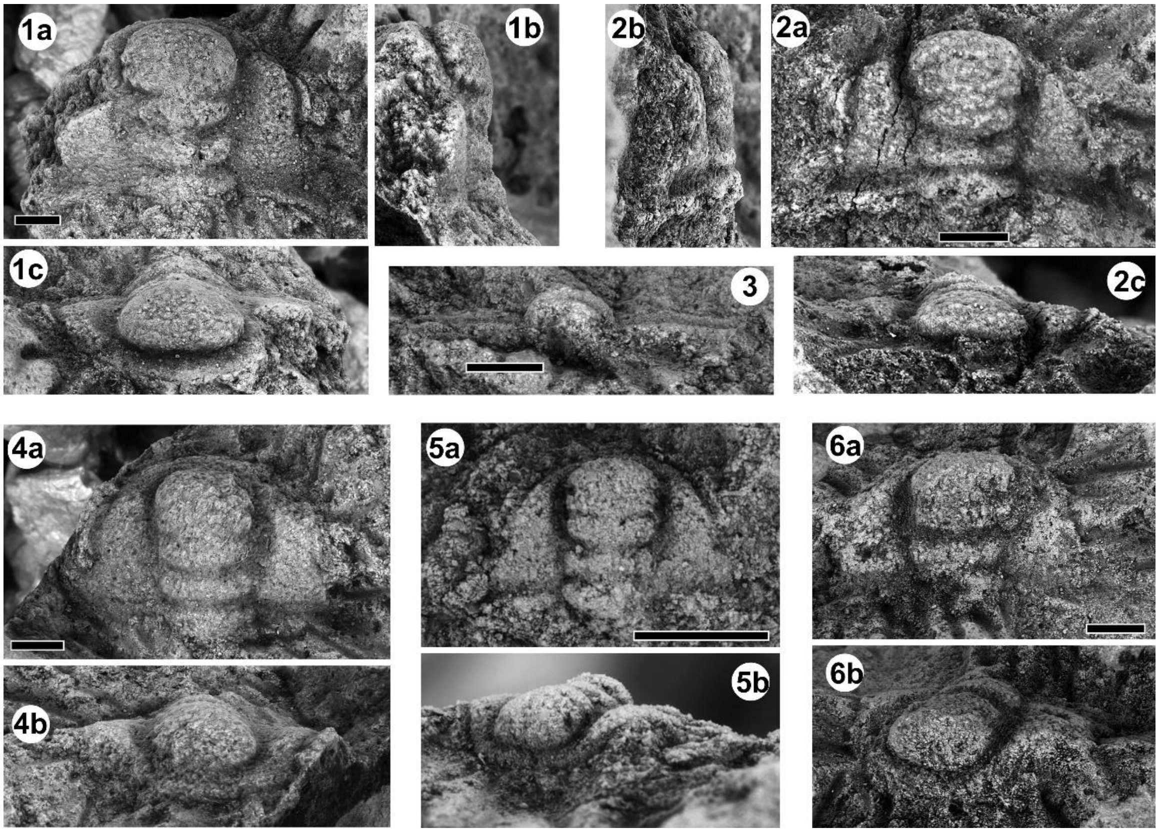


Figure 4:10 Asioptychaspis asiatica (Endo and Resser, 1937) 1,2,4–6. **(1)** CMC IP87130, cranidium, *a* dorsal view, *b* left lateral view, *c* anterior view; **(2)** CMC IP87133, cranidium, *a* dorsal view, *b* left lateral view, *c* anterior view; **(3)** CMC IP87131, indet. thoracic segment; **(4)** CMC IP87134, cranidium, *a* dorsal view, *b*, anterior view; **(5)** CMC IP87137, cranidium, *a* dorsal view, *b* oblique view; **(6)** CMC IP87136, cranidium, *a* dorsal view, *b* oblique view. All internal molds; all scale bars 2 mm.

Family SAUKIIDAE Ulrich and Resser, 1930

Genus *Eosaukia* Lu, 1954

Type species.—Eosaukia latilimbata Lu, 1954

Remarks.— Species of *Eosaukia* have often been erroneously assigned to other genera, particularly to *Mictosaukia* Shergold, 1975. However, following the work of Lee and Choi (2011) it is clear that *Eosaukia* is distinguished from other saukiids by the lack of a preglabellar field, the strongly incised, anterolaterally oblique furrows separating the fixigena from the anterior border, and the short (sag.), lenticular pygidial axis with four or fewer axial rings (Kobayashi 1957; Lee and Choi 2011). The cranidium of *Eosaukia* is distinguished from that of *Mictosaukia* particularly by the lateral segments of the anterior border furrow being anterolaterally oblique in the former and posterolaterally oblique in the latter (Lee and Choi 2011). *Saukia* also has anterolaterally oblique furrows in many species, but, compared with *Eosaukia*, *Saukia* has narrower fixigena, longer palpebral lobes, and no occipital spine or node. Both *Mictosaukia* and *Saukia* possess a more typically rounded saukiid pygidium rather than the lenticular pygidium of *Eosaukia*.

Eosaukia buravasi Kobayashi, 1957

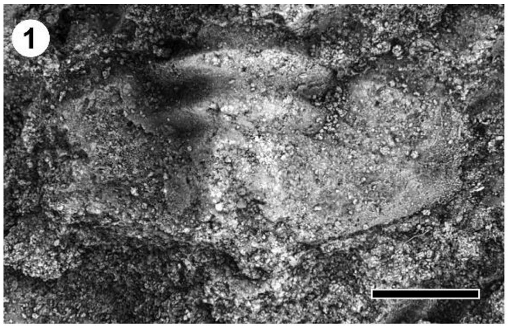
Fig. 4:11,12

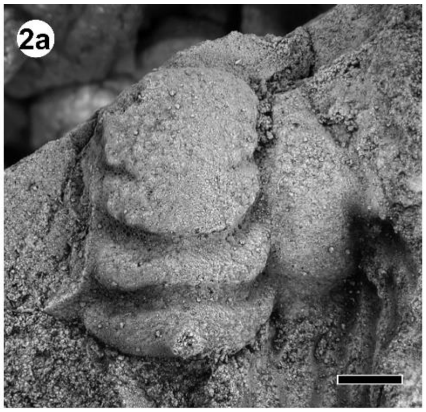
1957. "*Eosaukia*" *buravasi* Kobayashi, p. 376–368, pl. 5, figs 1–10, 13–20

1988. *“Eosaukia” buravasi* Kobayashi, Shergold *et al*., p. 310, figs 4.O–X

2007? *Ptychaspis*? sp. aff. *P. cacus* (Walcott 1905) Shergold et al., p. 65, fig. 38

Material.—Cranidia: One unfigured internal mold from Padongaing (PG) 1 (CMC IP84059), six figured internal molds (CMC IP88112, IP88113, IP88116, IP88120 and IP88121) and two unfigured internal molds (CMC IP88114 and IP88124) from PG3, and one unfigured internal mold from PG4 (CMC IP88128). Pygidia: one figured internal mold (CMC IP88115) from PG3.


1


2a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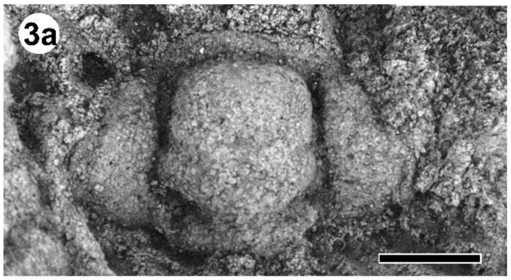
3a


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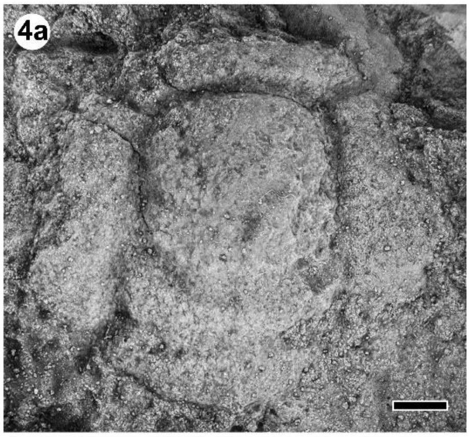
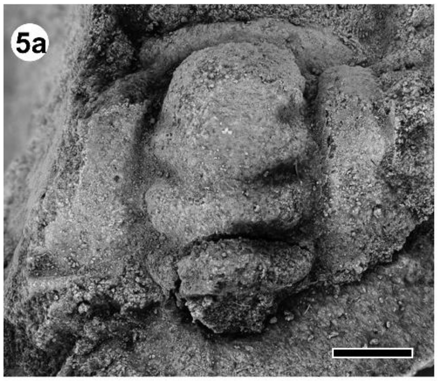
4b


4a


5a


5c


4c


6b


5b


6c

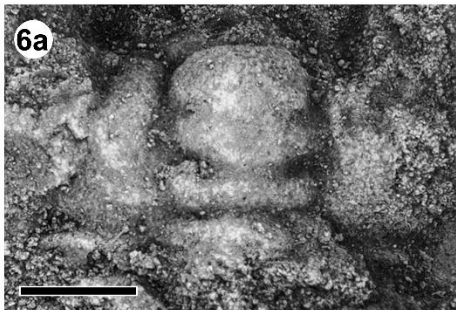

6a

Figure 4:11 (Previous Page) *Eosaukia buravasi* Kobayashi 1957. **(1)** CMC IP88115, pygidium, dorsal view; **(2)** CMC IP88120, cranidium, *a* dorsal view, *b* right lateral view; 6; **(3)** CMC IP88121, cranidium, *a* dorsal view, *b* oblique view; **(4)** CMC IP88113, cranidium, *a* dorsal view, *b* left lateral view, *c* anterior view; **(5)** CMC IP88112, cranidium, *a* dorsal view, *b* anterior view, *c* left lateral view; **(6)** CMC IP88117, cranidium, *a* dorsal view, *b* anterior view, *c* left lateral view. All internal molds; all scale bars 2 mm.

Occurrence.— Linwe area of the southern Shan State, Myanmar at Padongaing PG1 and PG3, and Soe (1983) localities L-1, L-2, and L-7, Myet-Ye Formation, Molohein Group; Furongian, lower to middle of Cambrian Stage 10.

Remarks.— Kobayashi (1957) expressed uncertainty regarding the nomenclatorial validity and family-level association of *Eosaukia* by using quotation marks to dub this species “*Eosaukia” buravasi.* Though its cranidium resembled that of *E. latilimbata*, the only *Eosaukia* species then known, Kobayashi (1957) thought the *E. buravasi* pygidium, the first *Eosaukia* pygidium discovered, too short and with too few segments to be saukiid. Rather he thought it resembled *Asioptychaspis* or *Quadraticephalus*.

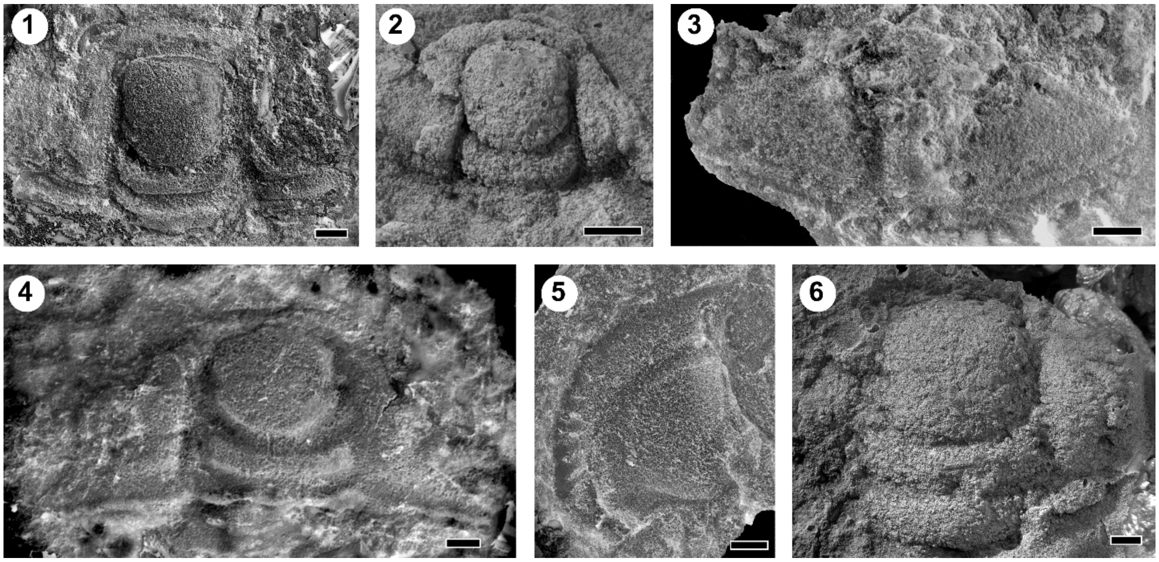


Figure 4:12 Eosaukia buravasi Kobayshi 1957. Originals of type material produced from vinyl polysiloxane casts. **(1)** CMC IP87025, holotype, cranidium, from UMUT PA02298b-1, Kobayashi, 1957, pl. 5, fig. 5; **(2)** CMC IP87043, cranidium, from UMUT PA02299, previously unfigured; **(3)** CMC IP87022, pygidium, from UMUT PB02297b-2, Kobayashi, 1957, pl. 5, fig. 5; **(4)** CMC IP87035, cranidium, from UMUT PB02299, previously unfigured; **(5)** CMC IP87042, cranidium, from UMUT PA02299c-3, Kobayashi, 1957, pl. 5, fig. 6; **(6)** CMC IP87027, librigena, from UMUT 02298b-3, Kobayashi, 1957, pl. 5, fig. 8. All scale bars 2mm.

Figure 4:13 Landmark scheme showing the 18 landmarks used in the morphometric analysis of *Eosaukia buravasi.Figure 4:14 Eosaukia buravasi* Kobayshi 1957. Originals of type material produced from vinyl polysiloxane casts. **(1)** CMC IP87025, holotype, cranidium, from UMUT PA02298b-1, Kobayashi, 1957, pl. 5, fig. 5; **(2)** CMC IP87043, cranidium, from UMUT PA02299, previously unfigured; **(3)** CMC IP87022, pygidium, from UMUT PB02297b-2, Kobayashi, 1957, pl. 5, fig. 5; **(4)** CMC IP87035, cranidium, from UMUT PB02299, previously unfigured; **(5)** CMC IP87042, cranidium, from UMUT PA02299c-3, Kobayashi, 1957, pl. 5, fig. 6; **(6)** CMC IP87027, librigena, from UMUT 02298b-3, Kobayashi, 1957, pl. 5, fig. 8. All scale bars 2mm.

Shergold (1975) moved *E. buravasi* to *Mictosaukia* when first describing the latter genus. However, Shergold *et al*. (1988) later returned it to "*Eosaukia" * on account of its relatively short palpebral lobes, wide fixigena, and small, lenticular pygidium compared to species of *Mictosaukia*. Shergold *et al.* (1988) retained the quotation marks around "*Eosaukia*" though without comment regarding Kobayashi's (1957) original use of the quotations marks or the choice to retain them. The later study excluded some of Kobayashi's specimens attributed to the species, referring these to *Lophosaukia* cf. *jiangnanensis* Lu and Lin, 1983, an assignment herein rejected in recognition of substantial intraspecific variation within *E. buravasi* and the lack of the distinctly angular cranidial anterior margin that characterizes *Lophosaukia.* Considering that *Eosaukia* species subsequently discovered have a similarly short pygidium, such as *E. bella* (Walcott 1906; genus designation by Lee and Choi 2011) and *E. micropora* (Qian 1985; genus designation by Lee and Choi 2011), there is little doubt that *E. buravasi* is a typical member of this genus. For these reasons, and the distinct angle of the anterior border furrow mentioned above, the genus is now clearly defined.

There is a high level of intraspecific variation within *E. buravasi.* This variation is apparently independent of geographic or stratigraphic distribution. A morphometric analysis was conducted on 120 specimens recently collected from the Ao Mo Lae Formation, Tarutao Group, Thailand and two sufficiently complete specimens from the Myet-Ye Formation (CMC IP88113 and IP88116). The analysis used 18 landmarks (Fig.

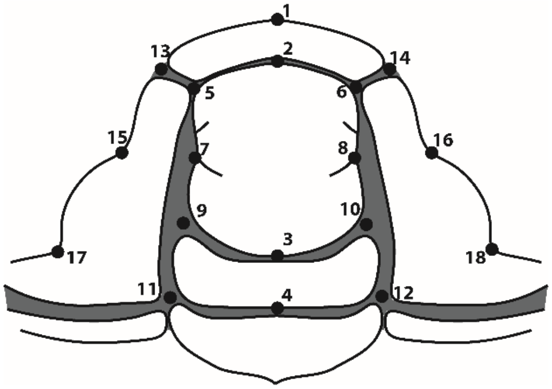


Figure 4:15 Landmark scheme showing the 18 landmarks used in the morphometric analysis of *Eosaukia buravasi.*

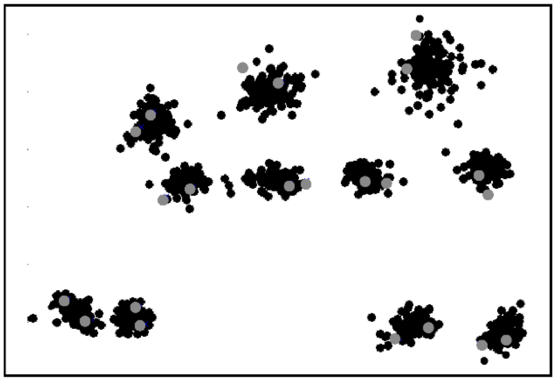


Figure 4:18 Landmark distribution plot for 120 specimens of *Eosaukia buravasi* from the Tarutao Group, Thailand (black) and 2 from the Myet-Ye Formation, Myanmar (grey). See Fig. 7 for the landmark scheme.

4:13); non-axial landmarks were reflected across the axis in order to optimize sample size. A Procrustes superimposition (Fig. 4:14) shows that both Myanmar specimens lie within the range of variation exhibited by the Thai material. The first two relative warps (RW) of a thin plate spline analysis of these cranidia shows that the Myanmar specimens do not form an independent grouping. They do have similar second relative warp (RW2) scores, but this is within the range of RW2 scores of specimens from Thailand (Fig. 4:15). RW1 and RW2 account for 27.48% and 17.38% of the variance respectively.

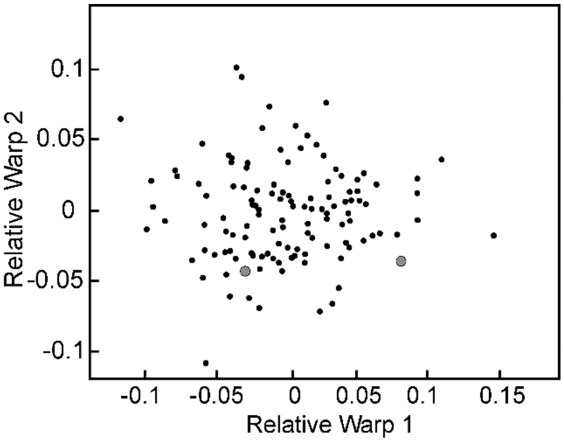


Figure 4:21 Relative Warps 1 and 2 for 122 specimens of *Eosaukia buravasi* from the Tarutao Group, Thailand (black) and the Myet-Ye Formation, Myanmar (grey. See Figs 6 and 7 for the landmark scheme and landmark distribution plot. Relative Warp (RW) 1 accounts for 27.48% of variance and RW 2 accounts for 17.38%.

Shergold *et al.* (1988) suggested that much of the variation within *E. buravasi* was likely due to ontogenetic change. Using the same set of landmarks and specimens as for the thin plate spline detailed above, we compared the regression of partial Procrustes distances with the natural log of the centroid size, a technique for determining the extent to which shape change is related to size (Webster and Sheets 2010). The mean of the three smallest specimens was used as the reference form. The result was a scatter of generalized Procrustes distance from the mean, with no significant trend associating size and shape change. Shape variance across all 122 specimens of *E. buravasi* was 0.0079 (bootstrapped by 1600 repetitions with a 95% confidence interval of 0.0068–0.0088). Although comparative studies of intraspecific variation in cranidial shape remain in infancy, what comparisons can be made (e.g. Hong *et al.* 2014) apparently suggest that *E. buravasi* displayed a high degree of variance, particularly when not associated with clear ontogenetic changes. For comparison, a single specimen was remounted, photographed, and marked for landmarks ten times; the variance for these ten images of a single specimen was 0.0005 over 1600 bootstraps.

Shergold *et al*. (1988) reassigned many of the librigena and cranidia included as "*E.*" *buravasi* by Kobayashi (1957; pl. 5 figs 6,7, 13–15, 19–20) to *Lophosaukia* cf. *jiangnanensis* Lu and Lin (1984). After reexamining Kobayashi's material (Fig. 12) we revert all specimens that Shergold *et al.* (1988) transferred to *L.* cf. *jiangnanensis* back to *E. buravasi.* Variation among this material is attributable to the intraspecific variation recognized in the geometric morphometric analysis described herein.

Eosaukia sp. (Shergold *et al*. 2007, p. 61) from the Bonaparte Basin of western Australia differs from *E. buravasi* in the pygidium possessing a third, though poorly developed axial ring, and a more robust occipital spine. While these differences are sufficient to recommend a separate species for the Australian material, cranidia with poorly preserved occipital lobes are indistinguishable from *E. buravasi*.

A different set of specimens from the Bonaparte Basin was assigned to *Ptychaspis*? sp. aff. *P. cacus* (Walcott 1905) (Shergold *et al*. 2007 p. 65, fig. 38). These specimens may belong to *Eosaukia buravasi*. Certainly, the anterolaterally oriented lateral segments of the cranidium are characteristic of *Eosaukia* rather than *Ptychaspis*, and both the Myanmar and Thai collections contain notably bulbous, anteroventrally curved cranidia (e.g. Fig. 11.5). However, apart from fig. 38.I,J of Shergold *et al.* (2007) the fixigenae of *P.*? sp. aff. *P. cacus* are generally narrower than those the *E. buravasi* from Sibumasu. *Ptychaspis*? sp. aff. *P. cacus* may be a variant of *E. buravasi* with a tendency towards narrower fixigena or it may be a separate species.

Conclusions

With the completion of the study described in the preceding chapters, the trilobite fauna of Sibumasu is revealed to be far more diverse than previously known. For the first time, Myanmar Cambrian trilobites are described and made available for analysis by the scientific community, including a new and unusual species of *Asioptychaspis*. The Cambrian and lowest Ordovician trilobites from Thailand are given rigorous consideration with the inventory of species known to occur in the Tarutao Group more than doubling in length. Biostratigraphic and paleogeographic resolution are improved for the whole of Sibumasu with the Myanmar fauna dating the Molohein Group to the Jiangshanian through middle of Cambrian Stage 10 and the Thai fauna dating the Tarutao Group to the middle of Cambrian Stage 10 through the middle to upper Tremadocian. Faunal similarities with other realms suggest that Sibumasu was most likely geographically associated with Australia and the Sino-Korean (North China) Block, particularly with the region that is now Korea in the eastern portion of that block. Despite a relatively high level of endemicity, limited influx of taxa from as far away as Laurentia also occurred. With the taxonomic resolution provided herein, the Sibumasu faunal assemblage is now available for use in geologic studies that were heretofore limited by the poor quality of available taxonomic data.

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