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Late Cambrian and Early Ordovician Trilobites From the Southern Shan State of Myanmar

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

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by

Horus Balogh-Zanin

June 2024

Thesis Committee:
Dr. Nigel Hughes, Chairperson
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ABSTRACT OF THE THESIS

Late Cambrian and Early Ordovician Trilobites From the Southern Shan State of Myanmar

by

Horus Balogh-Zanin

Master of Science, Graduate Program in Earth and Planetary Sciences
University of California, Riverside, June 2024
Dr. Nigel Hughes, Chairperson

The Shan State of Eastern Myanmar forms the western portion of the Sibumasu Terrane, an originally *peri*-Gondwanan microcontinental fragment that also includes northwest and peninsular Thailand, peninsular Malaysia, and the Baoshan block of western Yunnan. Various lines of evidence, including shared trilobite fauna, support the close association of the Sibumasu Terrane with western Australia, North China, and South China, as well as with more distant terranes such as Laurentia and Kazakhstan. Although the presence of Cambrian trilobites in Sibumasu has been documented from Baoshan and the Tarutao Group of Thailand since the mid-1900s, and Cambrian trilobites have been known from Myanmar's upper Molohein Group (Furongian-Tremadocian) since the 1970s, formal descriptions of Myanmar's Cambrian trilobite fauna remained unpublished until 2021. A comprehensive systematic description of these trilobites is thus necessary for a more complete understanding of the biostratigraphy, paleogeography and evolution of *peri*-Gondwanan terranes, as well as of the geochronology and biostratigraphy of the latest Cambrian.

In 2016 and 2020, field expeditions to the southern Shan State yielded abundant trilobite material from 12 localities representing the Myet-Ye formation of the upper Molohein Group, only three taxa of which have been described in a prior publication (Wernette *et al.,* 2021). Here I present an integrated, complete systematic description of the Cambrian trilobite fauna of Myanmar collected to date.

I describe 20 different trilobite taxa from the Myet-Ye material. 17 of these taxa have been identified to the genus level, and 11 have been further resolved to a species level. 2 new species of saukiid, *Prosaukia kyaingseini* and *Diemanosaukia* sp. 1, are described, as well as a potentially new species of tsinaniid, *Tsinania?* sp., though existing material is not sufficient for further specific diagnosis. The trilobite fauna of the Shan State largely corresponds to the *Eosaukia buravasi* and *Asaphellus charoenmiti* biozones of Thailand, representing the latest Cambrian and Early Ordovician respectively. The similarities between trilobite genera of the Shan State and those of Ko Tarutao, Baoshan, and western Australia are significant; however, other genera common to these areas, such as *Quadraticephalus*, have yet to be recovered in the Shan State.

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INTRODUCTION

Although Burmese Ordovician and younger trilobites have been known since early in the 20th century (Reed, 1906, 1915, 1936; Fortey et al., 2022), Cambrian trilobites of Myanmar are not as well-documented, with initial discovery reported in the 1970s (Tint, 1972; Myint Lwin Thein, 1973), preliminary and unpublished systematic description in the 1980's (Soe, 1983), and the first formal descriptions in 2021 (Wernette et al., 2021). All reports of Burmese Cambrian trilobites originate from the Shan State of Myanmar, which, with Thailand, peninsular Malaysia, and the Baoshan Block of western Yunnan, comprises the Sibumasu terrane (Metcalfe, 1984), a long, thin continental fragment which rifted off the eastern margin of Gondwana following the opening of the Meso-Tethys in the late Carboniferous-early Permian (Metcalfe, 1996a, 1996b). Of the areas in the Sibumasu terrane, Cambrian fossils have been recovered from the Baoshan Formation (Sun, 1945; Sun & Situ, 1947; Sun & Xiang, 1979; Luo, 1984a, 1984b) and the Tarutao Group of southern Thailand (Kobayashi, 1957; Shergold et al., 1988; Wernette et al., 2020a, 2020b; Wernette et al., 2023), as well as in the Machinchang Formation of northwestern Malaysia (Cocks et al., 2005; Lee, 2006), although no comprehensive systematic description of the Machinchang Cambrian material has been performed to date due to the fragmentary nature of the material (Cocks et al., 2005). Such investigations are receiving renewed attention because of the role of paleontological data and inter-terrane faunal associations in evaluating the location, scope and internal structure along the *peri*-Gondwanan margin of what later became the Sibumasu terrane, which remains a matter of ongoing debate (reviewed in Wernette et al. (2021)). Furthermore, not only are these Cambrian fossils relevant to the history of the breakup of Gondwana and the assembly of eastern Asia, they are also informative about the final stages of Gondwana assembly via closure of a putative "proto-Tethyan" ocean (Stampfli & Borel, 2002; Wang et al., 2008; Hu et al., 2013; Li et al., 2018). With detrital zircon provenance data showing only modest regional differentiation and paleomagnetic data sparse or unreliable for the regional Palaeozoic (Burrett et al., 2014), fossils may provide important constraints on paleogeographic reconstruction. The frequent intercalation of fossil-bearing beds in Sibumasu with rhyolitic tuffs (Shergold, 1988; Wernette et al., 2021; Wernette et al., 2023) may also prove useful for resolving the geochronology of the latest Cambrian with respect to existing biostratigraphical constraints.

Wernette et al.'s (2021) systematic description of the trilobites of the late Cambrian Myet-Ye Formation of Myanmar described material belonging to three species, *Asioptychaspis asiatica* Endo and Resser (1937)*, A. lata* Wernette and Hughes in Wernette et al. (2021), and *Eosaukia buruvasi* Kobayashi (1957). Other material collected in 2016 remained undescribed, and a second fossil-gathering trip was conducted to the same area in 2020, yielding additional trilobite material. Altogether, upwards of five hundred trilobite specimens were collected from localities in the Myet-Ye Formation, representing rocks of both Furongian and Tremadocian age. Fossil representatives of various other phyla, including brachiopods, molluscs, and echinoderms, were also collected and will be described in future publications; trilobite material previously undescribed from these collections are described herein.

The best-known late Cambrian-early Ordovician trilobite faunal assemblages from the Sibumasu terrane are those of the Tarutao Group of Southern Thailand, from which Wernette et al. (2023) identified 42 trilobite taxa, 24 of which are resolved to species level. Baoshan trilobite material representing the late Cambrian was first described in 1939 from a yellow shale near Pupiao, and included 8 trilobite taxa, as well as brachiopods and hyoliths (Sun, 1945; Luo, 1985). Later study of the Baoshan late Cambrian fossil fauna from the 1940s through the 1980s described an abundant trilobite fauna later divided into two formations and 7 fossil zones, with one earlier formation and zone, the *Protospongia* assemblage zone of the Upper Gongyanghe Subgroup, belonging to the lower Cambrian (Luo, 1985). The Cambrian sections in Baoshan are significantly thicker than those of the Tarutao Group, Malaysia, and the Shan State (Luo, 1985; Wernette et al., 2021); the Baoshan material extends earlier into the Cambrian, with *Protospongia* spicules representing the likely lower to middle Cambrian Gondyanghe Subgroup (Luo, 1985), and upper Cambrian strata extending into the latest Cambrian Baoshan Formation. The Baoshan trilobite fauna has been documented to contain from 22 taxa representing 16 distinct genera (Sun & Xiang, 1979) to 50 taxa representing 20 genera (Luo, 1983). However, much of the systematic work on the Baoshan trilobite fauna requires revision. Additionally, Baoshan trilobites often exhibit significant tectonic deformation (e.g. Sun & Xiang, 1979, pl. 3 fig 12); identification is thus rendered difficult. Even so, genera such as *Prosaukia* Ulrich and Resser (1933), *Quadraticephalus*

Sun (1924), and *Calvinella* Walcott (1914) are routinely reported, and many identified trilobite taxa correspond to those found in the Tarutao Group (Shergold et al., 1988; Wernette et al., 2023).

Geological setting and history

Sibumasu

The Sibumasu Terrane comprises the western portion of the Sundaland block, a geographic region that forms the southeast promontory of the Eurasian plate and which represents the majority of Southeast Asia (Metcalfe, 1984, 2013, 2017; Wernette et al., 2021). The formation of Sundaland, which is described by Metcalfe (2017) as a heterogenous collage of crustal continental blocks, volcanic arcs, and suture zones, occurred gradually over the course of the Paleozoic and Mesozoic, as the opening and closure of the Paleo-Tethys (Devonian to Triassic), Meso-Tethys (latest Carboniferous/earliest Permian to Cretaceous), and Ceno-Tethys (Jurassic to Cretaceous) oceans caused material to rift off the eastern margin of Gondwana and to accrete in the north gradually building eastern Asia (Metcalfe, 1996a; Hall, 2002; Metcalfe, 2006, 2011a; Cawood et al., 2013; Metcalfe, 2013; Cai et al., 2017). Core Sundaland is composed of the Sibumasu Terrane to the west, the Indochina block to the east, and the Sukhothai arc in-between. Sibumasu itself is comprised of the bulk of peninsular Thailand, the Shan states of Myanmar, the western belt of the Malay Peninsula and parts of Sumatra (Metcalfe, 2011b, 2013, 2017; Wernette et al., 2021). It is often regarded as

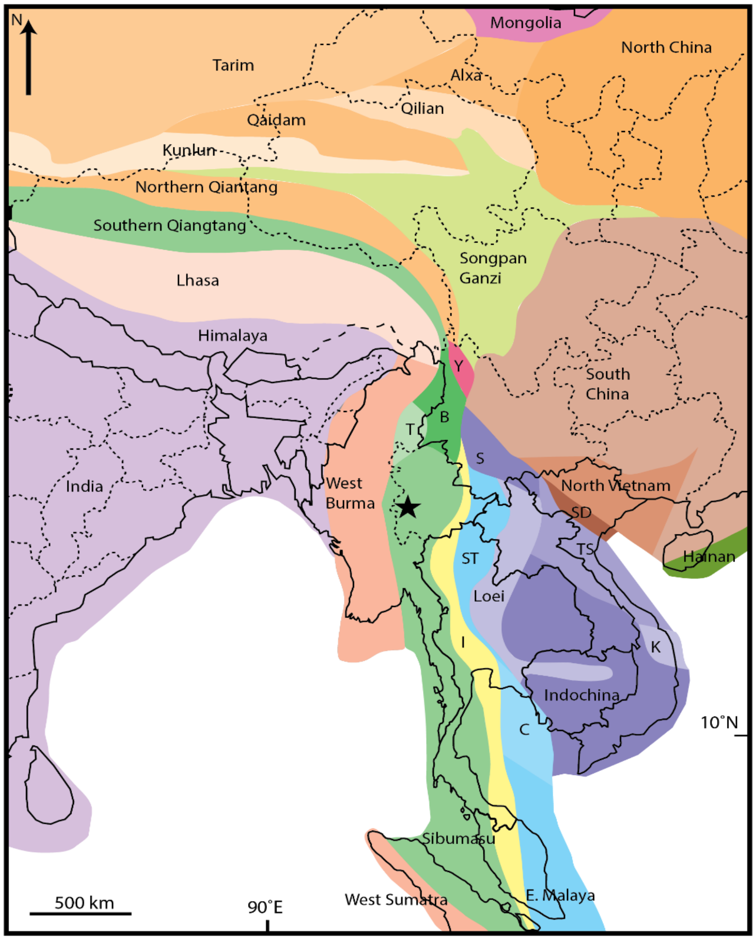

Figure 1. Map of Asian equatorial Gondwanan terranes in their modern configuration, modified from Wernette et al. (2023). Terrane abbreviations: B = Baoshan; C = Chanthaburi Terrane; I = Inthanon; K = Kontum; L = Loei; S = Simao; SD = Song Da; ST = Sukhothai; T = Tenchong;

Figure 1

extending northwards into the Baoshan block of Yunnan, and potentially as far as the South Qiangtang block of Tibet (Ridd, 2015; Metcalfe, 2017; Wernette et al., 2021). By this definition, Sibumasu is similar to the Shan-Thai block defined by Bunopas (1981), but with the inclusion of Baoshan and Sumatra (Burrett et al., 2016).

The history of Sibumasu as a *peri-*Gondwana terrane and its provenance prior to its accretion onto the Gondwanan rim is not well known. Assembly of the Gondwanan supercontinent is thought to have continued through the Early Paleozoic (Meert, 2003; Cawood & Buchan, 2007; Cawood et al., 2007; Hu et al., 2015); granitic intrusions, tuff beds, and other evidence of volcanic activity in terranes thought to represent the Gondwanan rim suggest the presence of a subduction zone in the Early Paleozoic leading to the closure of the Proto-Tethys and the accretion of various Asian and Southeast Asian terranes onto the Gondwanan rim (Cawood & Buchan, 2007; Cawood et al., 2007; Zhu et al., 2012). The presence of these intercalated tuff beds representing late Cambrian-early Ordovician formations throughout Sibumasu, including in the Molohein Group, the Tarutao Group, and the Pangyun Formation, presents a possible advantage for resolving the geochronology of the latest Cambrian, as tuff beds can be radioisotopically dated, then compared to the biostratigraphy of adjacent strata in order to better constrain the ranges of genera and species representing the late Furongian through early Tremadocian.

U-Pb detrital zircon geochronology of sedimentary layers lower than the Triassic-Jurassic in the Shan State show peaks at 567-470 Ma and 982-917 Ma, consistent with a Gondwanan origin. Beginning in Triassic strata, peaks of 350-200 Ma, 500-400 Ma, and 2000-1700 Ma have been identified in Myanmar, indicating a shift in position north towards the Sukhothai Arc (Cai et al., 2017). This reflects the most commonly accepted series of events, in which Sibumasu rifted from the eastern margin of Gondwana in the late Carboniferous or early Permian with the opening of the Meso-Tethys (Metcalfe, 2011b, 2011a; Ridd, 2015; Metcalfe, 2017; Wernette et al., 2021). As the Meso-Tethys widened and the Paleo-Tethys began to close, the continental fragment that now forms the Sibumasu Terrane drifted northwards over the latter part of the Paleozoic and early Mesozoic, with the eastern flank eventually colliding with the Indochina and South China blocks in the Triassic (Richter et al., 1999; Sone & Metcalfe, 2008; Barber & Crow, 2009; Aung Aye Ko & Cocks, 2017; Metcalfe, 2017). Evidence of this collision can now be seen in the suture zones found east of Sibumasu, which are known as the Paleo-

Tethyan sutures; from north to south, the closure of the Paleo-Tethys is represented by the Changning-Menglian suture zone (SW China), the Chiang Mai-Chiang Rai and Chanthaburi suture zones (Thailand), and the Bentong-Raub suture zone (Malay Peninsula) (Metcalfe, 2011b, 2011a, 2017). These suture zones represent the eastern and northeastern boundaries of the Sibumasu Terrane. In-between the eastern margin of Sibumasu and the western margin of Indochina lies the Sukhothai Arc, which formed in the Late Carboniferous-Early Permian along the Indochina-Simao margin and subsequently rifted from the Gondwanan margin in the Permian, moving northwards (Cai et al., 2017). To the west of Sibumasu lies the Sagaing strike-slip fault and West Burma, with the Mogok Metamorphic Belt between the two terranes; the Andaman Sea; and West Sumatra (Barber & Crow, 2009; Metcalfe, 2017).

Prior to the formation of the Meso-Tethys and above-mentioned rifting event in the late Paleozoic, the opening of the Paleo-Tethys had caused the rifting of much of what is now Asia and Southeast Asia away from Gondwana, which placed Sibumasu at the leading edge of Gondwana from the Devonian to its separation in the early Permian. The history of rifting may indicate that Sibumasu was located farther inland than other blocks, such as North and South China, in the Early Paleozoic (Wernette et al., 2021). In keeping with Wernette et al. (2021), we use the term equatorial *peri*-Gondwana to indicate those terranes located in and around the Gondwanan rim in the Paleozoic, including Sibumasu, the West Burma block, North and South China, Indochina, Simao, etc. The timeline of Sibumasu's accretion onto the Gondwanan rim in the early Paleozoic is not well-known, but it may have been the result of subduction under Gondwana's northern rim from the Neoproterozoic to the early Paleozoic, which is consistent with volcanic intrusions and U-Pb detrital zircon analysis (Cawood & Buchan, 2007; Xu et al., 2014; Domeier, 2018).

Four lines of evidence are primarily used in determining Sibumasu's placement on the Gondwanan rim in the early Paleozoic: paleomagnetic data, stratigraphic data, detrital zircon geochronology, and paleobiology (Wernette et al., 2021). It is widely accepted that Sibumasu was adjacent to NW Australia for much of the Paleozoic prior to the opening of the Meso-Tethys, and recent reconstructions and theories reflect this view (Ali et al., 2013; Metcalfe, 2013; Hu et al., 2015; Cai et al., 2017; Domeier, 2018). Paleomagnetic data from Baoshan and Devonian and post-Devonian rocks from Sibumasu, as well as apparent polar wander paths, place Sibumasu at or near the *peri*-Gondwanan margin outboard NW Australia in the middle Cambrian, with several placing the Baoshan Block directly adjacent to the Lhasa and Qiangtang blocks or near the location of North China at the time (Huang et al., 1999; Li et al., 2004; Ali et al., 2013; Domeier, 2018; Wernette et al., 2021). As such, when Sibumasu rifted from Gondwana in the late Paleozoic-early Mesozoic, it may have done so in conjunction with the Qiangtang block (Wernette et al., 2021).

Detrital zircon data is consistent across Sibumasu, which suggests that Sibumasu is not a composite terrane (Dew et al., 2019; Dew et al., 2021). When comparing the U-Pb isotope data of detrital zircons from Thailand and Malaysia to other areas in SE Asia and China, as well as to previously published data from other areas of Australia and Asia, Burrett et al. (2014) found strong similarities between Late Cambrian sandstones from

Ko Tarutao (S Thailand) and the Ordovician Tumblagooda Sandstone (W Australia) using the Kolmogorov-Smirnov statistical test (p=0.895), further supporting the Sibumasu-W Australia association. However, other W Australian samples yield lower p-scores when compared to Tarutao samples (Burrett et al., 2014; Wernette et al., 2021). Coupled U-Pb and Lu-HF zircon analysis on Cambrian-Ordovician rocks from the Sibumasu Terrane in NW Thailand (Dew et al., 2021) suggest potential zircon sources in NW Australia, the North and South China Cratons, and the Tethyan Himalaya, as well as similarities with other areas of Sibumasu such as the Chaung Magyi Group of Myanmar (Dew et al., 2019). In addition, U-Pb-based detrital zircon age profiles show similarities between Sibumasu, North China, South China, and the Himalaya, though these associations are poorly supported by the Kolmogorov-Smirnov test (McKenzie et al., 2014). The association of Sibumasu with South China may be less strongly supported, as it shows a Neoproterozoic peak not shared by North China or Sibumasu; however, including northeast Vietnam in South China strengthens the association (Burrett et al., 2014; Wernette et al., 2021). It is well-established that there was widespread sediment transport and mixing in the Cambrian-Ordovician of Gondwana, especially in relation to the Tethyan Himalaya, with paleocurrent data suggesting a flow roughly from the south/southwest to the north/northeast (Myrow et al., 2010). However, detrital zircon age spectra do not significantly clarify the position of Sibumasu relative to other areas within equatorial *peri*-Gondwana (Wernette et al., 2021).

Faunal associations suggest that the West Burma block and West Sumatra block were in fact once continuous prior to the formation of the Andaman Sea (Barber & Crow, 2009). Views on the rifting of the West Burma block vary, with some hypotheses (e.g. (Barber et al., 2005; Barber & Crow, 2009; Hall, 2012) suggesting that the West Burma block was already a part of SE Asia by the early Mesozoic, and others (e.g. Sengör et al. (1988); Metcalfe (1990); Audley Charles (1991); Metcalfe (1996a); Gardiner et al. (2015) suggesting that the West Burma block did not rift off from NW Australia until the Jurassic and collided with Sibumasu in the Late Jurassic or Early Cretaceous with the closing of the Meso-Tethys. Regardless, West Burma is generally accepted to have been close to NW Australia and likely Sibumasu until the Mid-Devonian at least; detrital zircon data supports this (Sevastjanova et al., 2016). A decreasing abundance of Archaean zircons moving from NW Australia, through West Burma, and finally into Sibumasu may indicate that Sibumasu was located further outward from Australia than West Burma (Sevastjanova et al., 2016), but associations of West Burma are still currently being debated, and it may in fact be an Indochina-South China derived terrane (Barber & Crow, 2008; Metcalfe, 2009; Metcalfe & Aung, 2014; Metcalfe, 2017).

Sun (1945) posited first the existence of a Sino-Burmese geosyncline stretching from western Yunnan into Sibumasu, which he considered the southern extension of the Himalayan geosyncline. This view was later considered by Shergold et al. (1988) to suggest an “inner detrital belt”, comparable to that of Laurentia at the same time, running from the Gansu and Qinghai Provinces of China into central Australia). As later studies suggest that the northern Chinese portion of this region was a series of island arcs and accretionary complexes during the Paleozoic, this view has since fallen out of favor (Wernette et al., 2021). Lower Paleozoic rocks are well-known throughout Sibumasu, extending from the southernmost portions of the terrane in Malaysia northwards into Baoshan; however, the age of the oldest rocks is mostly upper Cambrian (Udchachon et al., 2018). The exceptions to this rule are in Myanmar, where the Cambrian Molohein Group unconformably overlies the possibly Neoproterozoic Chaung Magyi Group, and in Baoshan, which contains earlier Cambrian rocks (Luo, 1985; Aung Aye Ko & Cocks, 2017; Wernette et al., 2021). Sedimentological comparisons to other areas reveal similarities to several formations in Australia, including the Bonaparte Basin's Clark and Pander sandstone units, though the Pander Sandstone features glauconite not present in Sibumasu (Wernette et al., 2021); the Amadeus Basin's Pacoota sandstone; and an unnamed sandstone/siltstone formation in Misery Hill, Tasmania (Jago & Corbett, 1990). The lower Nambeet Formation of the Canning Basin features a succession particularly similar to stratigraphic sections on Ko Tarutao (Thailand), with ash beds comparable to the Lower Ordovician sections of peninsular Thailand deposited about 469.7 Ma (Normore et al., 2018; Wernette et al., 2021; Li et al., 2023), an age obtained through calcite and zircon U-Pb dating. Stratigraphic correlations ultimately agree with reconstructions placing Sibumasu adjacent to W. Australia in the Cambrian and Ordovician.

Paleobiological data from the Cambrian of Sibumasu has until recently been largely limited to areas in southern Thailand (including Ko Tarutao) and Baoshan. While Furongian-Tremadocian rocks are known from peninsular Malaysia, particularly from the Langkawi Islands, metamorphism by the Late Triassic Kuah Granite has led to fossils being relatively scarce (Burrett et al., 2016) and available fossils are fragmented and difficult to identify. Sibumasu's trilobite fauna shows broad eastern Gondwanan affinities (Zhou & Dean, 1989; Zhu, 2008), and evidence suggests faunal similarities throughout Australian core Gondwana and equatorial *peri*-Gondwana in the Paleozoic, in what Metcalfe (2013b) termed the "Sino-Australian faunal province". Available Cambrian-early Ordovician data strongly suggests an association between western Australia and Sibumasu; both areas share such genera as *Tsinania* Walcott (1914), *Mansuyia* Sun (1924), *Parakoldinioidia* Endo in Endo and Resser (1937), *Koldinioidia* Kobayashi (1931), *Quadraticephalus, Asaphellus* Callaway (1877), *Haniwa* Kobayashi (1933), and *Pagodia* Walcott (1905), as well as a variety of saukiids, including *Prosaukia, Eosaukia* Lu (1954), *Lophosaukia* Shergold (1972), *Anderssonella* Kobayashi (1936), and *Lichengia* Kobayashi (1942) (Shergold, 1972, 1980; Shergold et al., 1988; Shergold, 1991; Shergold et al., 2007; Wernette et al., 2021; Wernette et al., 2023). Some early surveys of late Cambrian trilobites from Baoshan also report *Saukia* Walcott (1914), which is shared with Misery Hill, Tasmania (Sun, 1945; Sun & Xiang, 1979; Jago & Corbett, 1990); however, this is debatable, as older identifications of trilobite materials do not take into account generic re-assignments and the re-defining of generic traits. These genera are broadly shared with North and South China, with the exception of *Quadraticephalus,* a genus not found in South China (Zhou & Zhen, 2008; Wernette et al., 2021). Several genera are also shared between Yunnan and the Qinghai-Xizang terrane of Tibet, including *Tsinania, Quadraticephalus, Chuangia* Sun (1924), and *Eosaukia* (Sun, 1945; Sun & Xiang, 1979; Luo, 1983). There are broad similarities between the trilobite fauna of the Baoshan block and those of the South and North China plates (Zhou & Zhen, 2008). In general, the Cambrian trilobite fauna of Sibumasu is more similar to that of North China, before an increase in water depth in the Ordovician caused a shift to more South China-like affinities (Zhou & Zhen, 2008; Burrett et al., 2016; Zhou et al., 2016). Conodont faunas from the same time intervals also show a shift to deep-water forms (Agematsu et al., 2007; Wernette et al., 2021).

All lines of biotic data point towards a link between Sibumasu and western Australia within core Gondwana, with strong links to North and South China through the Sino-Australian faunal province. Affinities with the Qiangtang and Lhasa blocks of Tibet, West Burma, and the Tethyan Himalaya are also supported. While Sibumasu's position is difficult to constrain precisely, it may have been closest to either the Canning or Bonaparte Basins of West Australia.

Stratigraphy

U-Pb and Hf-isotope data from detrital zircon studies suggest that the basement of the Sibumasu terrane is Proterozoic in age, primarily Palaeoproterozoic (1.9-2 Ga) (Sevastjanova et al., 2011; Hall & Sevastjanova, 2012; Metcalfe, 2017) with minor Neoarchean inclusions. The Shan Plateau is an elevated region of Myanmar stretching from the northern Shan States into the Tenasserim Range of peninsular Myanmar, bounded to the west by the Tertiary Shan Boundary Fault (Chhibber, 1934; Aung Aye Ko & Cocks, 2017). While Upper Paleozoic (Carboniferous-Permian) rocks are represented in the Phuket-Slate belt of Southern Myanmar, the Shan Plateau is the only part of

Myanmar where rocks from the Lower Paleozoic and earlier are found (Aung Aye Ko & Cocks, 2017). In Myanmar, Precambrian sedimentary rocks are represented by the Chaung Magyi Group, an unfossiliferous metasedimentary formation that crops out extensively in the Northern and Southern Shan State of Myanmar, as well as in the Baoshan block of western Yunnan (Aung Aye Ko & Cocks, 2017). The upper Chaung Magyi is composed largely of schists, phyllites, and slates, and the lower Chaung Magyi is composed of garnet-mica schists (Myint Lwin Thein, 1973; Aung Aye Ko & Cocks, 2017; Dew et al., 2019). There has been some debate on the exact age of the Chaung Magyi, but detrital zircon age spectra currently suggest a depositional age in the Neoproterozoic, with metamorphism and purported horizontal burrows in the uppermost formation perhaps extending the range into the early to mid-Cambrian (Aung Aye Ko & Cocks, 2017; Dew et al., 2019; Wernette et al., 2021). However, reported horizontal burrows from the Tawngma Siltstone of the uppermost Chaung Magyi were never formally figured or described (Mitchell et al., 1977). The Chaung Magyi Group has an angular unconformity the overlying Furongian-Tremadocian Molohein Group, and which is considered equivalent to the late Cambrian-early Ordovician sediments represented by the Pangyun Formation in the northern Shan Plateau, as well as the Machinchang Formation in Malaysia, the Tarutao Group in Thailand, and the Baoshan Formation in the Baoshan block (Wernette et al., 2021). The Molohein Group is composed of the Pandung Formation (lower) and the Myet-Ye Formation (higher). Of the two, to date only the Myet-Ye has yielded fossils.

The Molohein Group in the southern Shan Plateau is comprised largely of siliciclastics, primarily pink, purple, and red-brown fine-grained micaceous sandstones and white, pink-white, or purple-white quartzites, with occasional thin beds of siltstone or mudstone (Myint Lwin Thein, 1973; Aung Aye Ko & Cocks, 2017; Wernette et al., 2021). It is thought to be equivalent in age to the Pangyun Formation of the Northern Shan State (Aung Aye Ko & Cocks, 2017). Some early reports posit slight regional metamorphosis, but the Molohein Group is generally considered to be unmetamorphosed (Myint Lwin Thein, 1973; Aung Aye Ko & Cocks, 2017; Dew et al., 2019; Wernette et al., 2021). It is gradationally overlain by the Lokepyin Formation (part of the Pindaya Group), representing later Ordovician sediments, and a basal conglomerate of quartzite pebbles overlies its contact with the lower Chaung Magyi (Myint Lwin Thein, 1973; Aung Aye Ko & Cocks, 2017). The Tremadocian of the Southern Shan State was initially thought to be represented in the Pindaya Group, but the collection of Tremadocian trilobite fossils from the upper Molohein Group during the 2016 and 2020 trips indicate that the Furongian-Tremadocian boundary in fact lies within the Myet-Ye Formation. Estimates for the Molohein Group’s thickness vary considerably; a 1973 paper by Myint Lwin Thein indicates a thickness of 1066 m, but later estimates range from 784 m to 2400 m (Garson et al., 1976). The exact thickness is difficult to determine; the Molohein Group crops out in various isolated locations, and its thickness is made more difficult to determine by heavy forestation and other cover, as well as by faulting and the angular unconformity at the base where the Pandung and Chaung Magyi Formations meet (Wernette et al., 2021).

The Pandung Formation, the lowest unit of the Molohein Group, was originally defined in 1977 by Myint Lwin Thein. The type section of the Pandung Formation, as seen in Yengan township (Southern Shan State), is 392 m thick (Aung Aye Ko & Cocks, 2017). It is composed of thin- or medium-bedded, quartz-rich, pinkish-white or purplish-white micaceous sandstones (Myint Lwin Thein, 1973; Aung Aye Ko & Cocks, 2017). Minor amounts of white tuffaceous sandstone are also reported (Aung Aye Ko & Cocks, 2017). With respect to other stratigraphic units in Myanmar and Sibumasu, it is correlated with the Sibaing Orthoquartzite (Mandalay region, west), and the lower part of the Pangyun (Northern Shan State). Although no Cambrian fossils have yet been found from the Pandung Formation, it is thought to represent a shallow-marine barrier beach environment (Aung Aye Ko & Cocks, 2017; Wernette et al., 2021).

Of the two formations of the Molohein Group, the overlying Myet-Ye Formation (Myint Lwin Thein, 1973) is the sole fossiliferous formation, yielding a variety of latest Cambrian and Early Ordovician fossils, including various trilobites, brachiopods, molluscs and echinoderms. It has been most recently estimated to have a thickness of 392 m (Aung Aye Ko & Cocks, 2017), and is composed largely of thin- or medium-bedded pink, purple, buff-colored, or reddish-brown sandstones, also micaceous in nature (Aung Aye Ko & Cocks, 2017; Wernette et al., 2021). The Myet-Ye represents a shallow marine, nearshore or beach environment, well-suited to saukiids and other shallow water trilobites, and is correlated with the Tangyun Sandstone (Pyin Oo Lwin township), the upper Pangyun Formation of the northern part of Shan State, the Machinchang Formation of Malaysia, and the Tarutao Group of Thailand (Aung Aye Ko & Cocks, 2017; Wernette et al., 2021). The Myet-Ye Formation conformably overlies the Pandung Formation and underlies the later Ordovician Lokepyin Formation with gradational contact. The Myet-Ye Formation and the Lokepyin Formation can be distinguished by the progressively finer grain size, as well as by a transition from the pink-purple sandstones of the Myet-Ye Formation to the grey and buff-colored sandstones of the Lokepyin Formation (Aung Aye Ko & Cocks, 2017; Wernette et al., 2021).

MATERIAL AND METHODS

Localities

The localities sampled during the 2016 and 2020 trips to the Shan State were chosen based on the thesis of Soe (1983) (see Wernette et al. (2021)), which represents the first attempt at systematic description of the Shan State trilobites. Of the 2016 sites, four are locations along the road to Padongaing village, one site is located slightly north, near the Kyaukgnet monastery, and one is farther north-east, near Ko Hsu. Several of these localities were revisited during the 2020 trip. In 2020, new localities sampled consisted of three sites along the road to Padongaing, one near the Kyaukgnet monastery, and two near Ko Hsu and the road to Yechanbyin. Ordovician fossils were found in 2020 at the

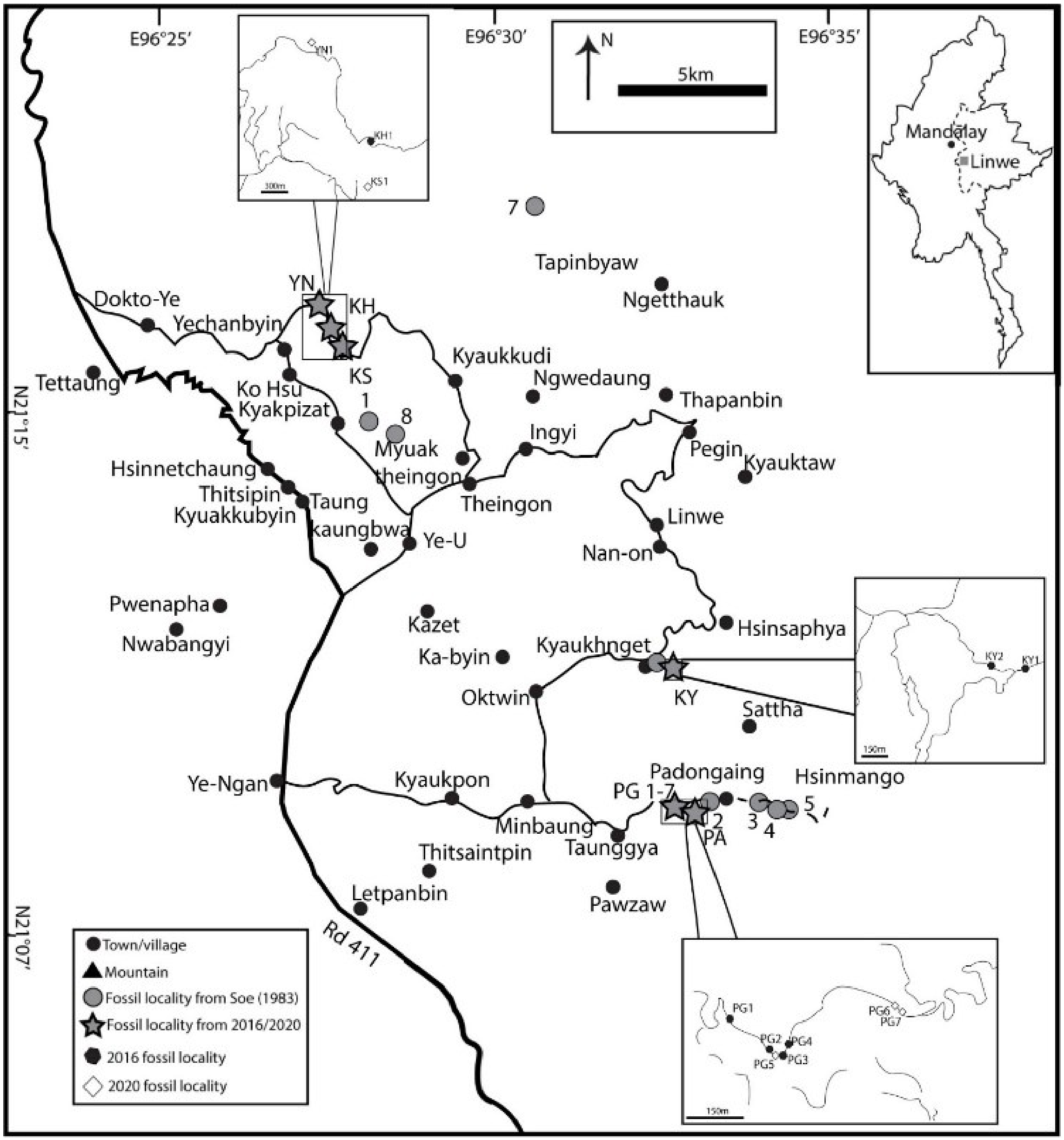

Fig. 2. Map of the Linwe area with marked 2016 and 2020 fossil localities and comparisons to fossil localities from Soe (1983). Modified from Wernette *et al.* (2021).

Figure 2

PG6&7 localities, farther east along the road to Padongaing. Detrital zircon and tuff bed samples were collected from each locality where possible.

In total, Cambrian and Ordovician fossils were found at 12 localities during the 2016 and 2020 trips to Myanmar. Fossils were collected on a bed-by-bed basis and recorded in stratigraphic logs.

PG1 (Fig. 3)

All PG sections were found on the unpaved road to Padongaing village. PG1 (21°8'56.82"N, 96°32'57.42"E) was located adjacent to a stream crossing, and consisted of a 6-meter-thick outcrop of the Myet-Ye Formation. The section is composed of 13-23 cm thick fine to very fine ferruginous and micaceous sandstone beds, with thin, shaley bed contacts. The sandstone also features magnetite grains measuring about 2 mm in diameter. Higher in the section the sandstone becomes coarser-grained and redder. Beds of the section are laminated, and hummocky cross-stratification is present about 2-2.5 m from the base. Several distinct tuff layers are also present, ranging from 3-16 cm thick, with a thicker layer of sandy ash near the base. Fossils are found in coquinas in storm-dominated beds, and specimens in PG1 are preferentially oriented convex-up. Of the 2016 sections, PG1 is the only one with more than one fossiliferous bed, and was revisited in 2020. Fossils in the sampling localities are preserved as internal or external molds.

PG2

PG2 (21°8’54.06”N, 96°33’3.00”E) is located about 200 m east of PG1, up the road. Lithologically it is similar, with micaceous, fine to very fine reddish sandstone, 15-30 cm thick beds, and tuff layers, though PG2 is heavily weathered. Fossils from this section are rare and fragmented, not found in more than one bed.

PG3

PG3 (21°8’53.58”N, 96°33’4.26”E), similarly to PG2, is an outcrop of sparse, heavily weathered sandstone (Wernette et al., 2021). Fossils from PG3 originate from float embedded in the roadside mud rather than from the outcrop itself; the fossils themselves are fragmented, with random orientations. Rocks in the sampled areas are generally friable, with transport dependent on conditions. In general, float that originates from a particular section is unlikely to have been widely transported.

PG4

PG4 (21°8’53.94”N, 96°33’5.16”E) is the next outcrop, about 20 m up the road from PG3. It is rockier, but poorly exposed (Wernette *et al.,* 2021). Material from PG4 may also be float.

PG5 (Fig. 4)

PG5 (21°8’53.28”N, 96°33’3.78”E) is the first of the 2020 sections not previously investigated in 2016. It is a 24-m-thick section located between PG2 and PG3, located around a sharp bend in the road to Padongaing. Stratigraphically, the PG5 section is later than PG1-PG4. Multiple trilobite-bearing fossil horizons were found within the section, which lithologically resembled lower PG sections as a fine to very fine grained sandstone with some instances of siltstone. Lamination and hummocky cross-stratification are present. Fossil coquinas containing disarticulated trilobites in PG5 were found interbedded with green-white ash beds.

PG6 & 7 (Fig. 7)

PG6 and PG7 (21°8’59.76” N, 96°33’18” E) are 2020 sections in approximately the same location 300 m uproad from PG5, and so have been grouped here. The strike and dip of PG6 are unmeasured, but PG8 has a S/D of 019˚/21˚SE. In contrast to the late Cambrian fauna of lower sections, PG8 and PG9 fossil fauna represent the early Tremadocian, including *Parapilekia* Kobayashi (1934) and pygidia and free cheeks perhaps representing *Asaphellus.* Non-trilobite material from the PG6 and PG7 localities includes brachiopods and crinoids. Cephalic fringes representing the orders Odontopleurida and Harpetida were also found at these localities.

KY1

The first of the Kyaukgnet monastery samples, KY1 (21°11’6.6” N, 96°33’3.12” E) was sampled in both 2016 and 2020. This locality represents an area south of the monastery at a point where a bamboo bridge crosses the river (Wernette et al., 2021), where float material was collected. All 2016 fossil material was found in two rounded fossiliferous cobbles in float, and the cobbles themselves were composed of a medium to coarse grained sandstone. In 2020, four additoinal fossiliferous cobbles were found at KY1 (20-KY-02 a-d), and each cobble was treated as if it were its own collection. Trilobite fossils from this area largely consist of *Asioptychaspis asiatica*; however, some examples of *Pagodia thaiensis?* Kobayashi (1957) exist in the form of various pygidia.

KY2

In contrast to KY1, the KY2 locality (21°11’16.02” N, 96°32’46.5” E) is an outcrop of silty white shale. Fossils were collected in the upper portion of the last third of the outcrop; however, no measured section or detailed stratigraphy records are available. Some material was also collected from float nearby. Trilobite material from this outcrop consists of unidentified librigenae.

KH1 (Fig. 5)

First sampled in 2016, KH1 (21°15’53.64” N, 96°27’36.48” E) is the first of four localities near Ko Hsu. The lowest part of the section is primarily tuff beds, transitioning to a largely thin-bedded siltstone and very fine grained sandstone composition upsection; the contacts between siltstone or sandstone layers and tuffaceous beds are wavy. Some cross-bedding is present in the sandstone layers. This section yielded only fragmented trilobite material from the late Cambrian in 2016, but when the same outcrop was revisited in 2020 it was found to contain fossil beds at multiple horizons. Trilobite material collected in 2020 includes cranidia, librigenae, hypostomes, and pygidia; non-trilobite material includes ostracods and brachiopods. Brachiopods were also found in nearby float. The preservation of material from the KH1 section is similar to that of the Padongaing sections, consisting of internal and external molds in very fine grained sandstone.

KS1 (Fig. 6)

KS1 (21°15’37.52” N, 96°27’35.28” E) is a 2020 sample locality located about 250m up the road from KH1, consisting of alternating conglomerate-sandstone beds, with some crossbedding present downsection. The strike and dip of the section is 050˚/34˚SE. The presence of conglomerates separates KS1 from the other sampled localities, which largely consist of fine to very fine grained sandstones, siltstones, shales, and tuff beds. Trilobite fossils are found in a medium bed of fine grained, poorly sorted quartzarenite, 14.28m above the base of the section. The fossils themselves are orange in color. The trilobites, in addition to the pebbles of the layer, are apparently infilled with limonite, perhaps due to replacement of carbonates in this locality. This locality is the only one of the Shan State localities in which *Pacootasaukia jokliki* Shergold (1991) is found, and it is here present in abundance. It is also the only locality in which trilobite eye surfaces are preserved. Non-trilobite fossils include bradoriids and linguilid brachiopods.

YN1

YN1 (21˚16’ 28.4” N, 096˚ 27’ 14.4” E) is a 2020 sample locality a short distance from the KH and KS localities on the road to Yechanbyin, with a S/D of 242˚/25˚S. Its lithology is generally Molohein in appearance, consisting largely of sandstones (sampled for detrital zircons) and phyllitic rocks, with tuffaceous interbeds. Trilobite material is fairly scarce, but includes some small holaspid members of *Prosaukia kyaingseini,* as well as various librigenae and disarticulated thoracic segments.

Fossil preparation and analysis

Following manual prep with a Dremel tool, fossils were blackened with India ink, whitened with ammonium chloride sublimate, and photographed with a Leica stereoscopic camera model MZ16 or M205C. Figures and plates were created using Adobe Photoshop v. 24.7 and Adobe Illustrator v. 27.8.1.

Morphometric analysis was performed using the geomorph package (v. 4.0.5, Adams *et al.*), in Rstudio v. 2023.03.2. Geomorph is available for download free of charge at https://cran.r-project.org/web/packages/geomorph/index.html.

BIOSTRATIGRAPHY AND ASSOCIATIONS

In total, 20 trilobite taxa have been resolved from the Shan State. Seventeen of these taxa have been identified to a genus-level, and 12 have further been resolved to existing or new species. These taxa represent 7 different trilobite families in 5 orders spanning the time period from the late Furongian to early Tremadocian.

The Shan State trilobite material can be divided into two distinct groups: upper Cambrian trilobite taxa, as seen in collections PG1-5, KY1 & 2, KH1 & 2, KS1, and YN1, and Lower Ordovician trilobite taxa, as seen in PG6-7. Although some taxa are present throughout most or all of the upper Cambrian sections (e.g. *Prosaukia kyaingseini, Lichengia simplex* Shergold (1991)), other upper Cambrian trilobite taxa are only found in a single locality; for example, the saukiid *Pacootasaukia jokliki* is the only well-represented trilobite taxon at the KS1 locality, where it is present in abundance despite not being found at any other locality. The Southern Shan State, particularly at the Padongaing sections, apparently lacks the repeated faulting of the Tarutao Group (Wernette *et al.,* 2023) with the section showing quite consistent strike and dip, suggesting continuity although exposure is somewhat sporadic. The localities along the road to Padongaing are interpreted to range from the westernmost and stratigraphically lowest section (PG1), representing a slightly older interval in the upper Cambrian, to the easternmost and stratigraphically highest sections (PG6 & PG7), representing the lower Ordovician. However, conclusively reconstructing the biostratigraphic succession is rendered difficult due to the extensive cover, that could obscure minor faults between sections, or significant surfaces of erosion or non-deposition.

Similarly to the Tarutao Group's lack of in-section faunal turnover (Wernette et al., 2023), faunal turnover is not apparent within several of the latest Cambrian sections in the Southern Shan State. Although faunal diversity may change over a section, the appearance and disappearance of certain genera do not necessarily represent temporally successive faunas, and section trilobite composition appears generally static. The most abundant and characteristic species, such as *L. simplex* and *E. buravasi*, have apparently extensive local stratigraphic ranges, although this does not necessarily indicate particular species longevity but is more likely indicative of relatively rapid sedimentary accumulation.

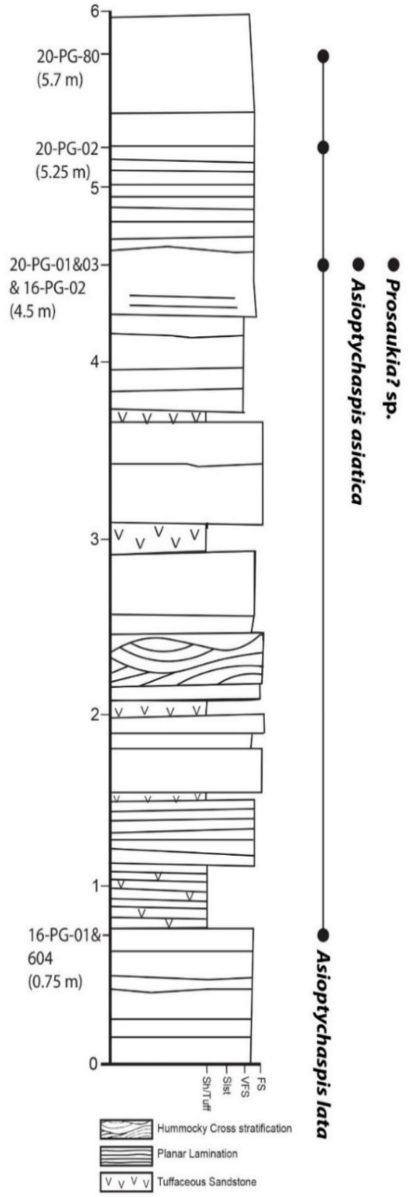

Figure 3. PG1 section. Fossiliferous horizons are 0.75 m, 4.5 m, 5.25 m, and 5.7 m above base. Sh/Tuff=shale with ash tuffs, Slst=siltstone, VFS=very fine sandstone, FS=fine sandstone

Figure 3

Cambrian

Of the Shan State material, PG1, a 6 m-thick section also referred to as the “river section”, is the westernmost section along the road to Padongaing. PG1 is near entirely dominated by two species of *Asioptychaspis Kobayashi (1933)*, *A. asiatica*, and *A. lata*. Of the two species, *A. lata* is endemic to the Shan State, while *A. asiatica* is also present in Australia and North China (Shergold, 1975; Shergold et al., 2007; Zhang & Jell, 1987). Only one other genus is represented within the section, a single instance of *Prosaukia kyaingseini* sp. nov. approximately 4.5 m from the base of the section.

Asioptychaspis lata is by far the most abundant genus within the section and is present throughout, from about 0.75 m to 5.7 m from the base of the section.

In contrast, *A. asiatica* co-occurs with *P. kyaingseini* in the 4.5 m horizon and does not appear elsewhere in the section, though it is more abundant than *P. kyaingseini.* Prior to 2020 the presence of *A. asiatica* in the Shan State material was known solely from two cobbles of float from KY1, but its presence in-section at PG1 has constrained its stratigraphic placement. In one cobble found in float from KY1 in 2020, a pygidium representing *A. asiatica* co-exists with pygidia of *Pagodia thaiensis?*; despite this co-occurrence, no evidence of *P. thaiensis?* has been found *in situ* at PG1.

Asioptychaspis was initially reported as co-occurring with *Eosaukia buravasi* in PG1 (Wernette et al., 2021). However, the specimens previously assigned to *E. buravasi* were later reassigned to *A. lata*. While co-occurrence between *Asioptychaspis* and *Eosaukia* was not evident at PG1, *A. lata* re-appears upsection at PG5 alongside taxa such as *E. buravasi*, *Lichengia simplex,* and *Tsinania?* sp., indicating that it may have a longer geochronological range than *A. asiatica,* a species generally considered to occur slightly earlier in the Furongian (Shergold et al., 2007). Due to the presence of *A. asiatica,* a species first appearing in the late Jiangshanian, and its location along the road to Padongaing, PG1 is tentatively considered to be the stratigraphically lowest section, representing a slightly earlier interval within the Furongian; however, this evidence is not presently a sufficiently strong argument for the erection of an *A. asiatica* biozone in the Shan State.

Farther up-section on the road to Padongaing, the PG5 locality represents 24 m of continuously exposed trilobite-bearing section. The lowest portion of the section (0.59 m-5.8 m) is largely saukiid dominated, yielding *Prosaukia kyaingseini,* a new species of *Prosaukia* also found in the Tarutao Group of Thailand and described by Wernette et al. (2023) as *Prosaukia* sp. 1. The lower two horizons of PG5 (0.59 m and 0.89 m) also yield *Lophosaukia?* sp. Shergold et al. (2007), *Pseudokoldinioidia maneekuti* Wernette et al. (2023)*, Lichengia simplex, Pagodia thaiensis?,* and *Eosaukia buravasi,* along with several indeterminate missisquoiid pygidia. Of these species, *L. simplex, Pagodia thaiensis?,* and *E. buravasi* continue to the top of the section, and *L. simplex* and *E. buravasi* are particularly abundant. *Tsinania?* sp. and *Diemanosaukia* sp. 1 (a genus also found in Tasmania but not previously found on Ko Tarutao) arise 5.8 m from the base of the section, followed by the appearance of *Parakoldinioidia callosa* Qian (1985) at 7.24 m from the base. While *Parakoldinioidia* is characteristic of the middle portion of the section, terminating at about 13.11 m from the base, *Tsinania?* and *Diemanosaukia* Jago and Corbett (1990) continue to the top of the PG5 section. Additionally, one instance of *Prosaukia oculata* Wernette et al. (2020a) is present in-section at 13.11 m. The uppermost fossil-bearing horizon, at 23.87 m, yields *Tsinania?* sp., *E. buravasi*, *L. simplex, Pagodia thaiensis?, Diemanosaukia* sp. 1*,* two occurrences of *A. lata,* and one pygidium which may belong to *Lonchopygella* Sun and Xiang (1979).

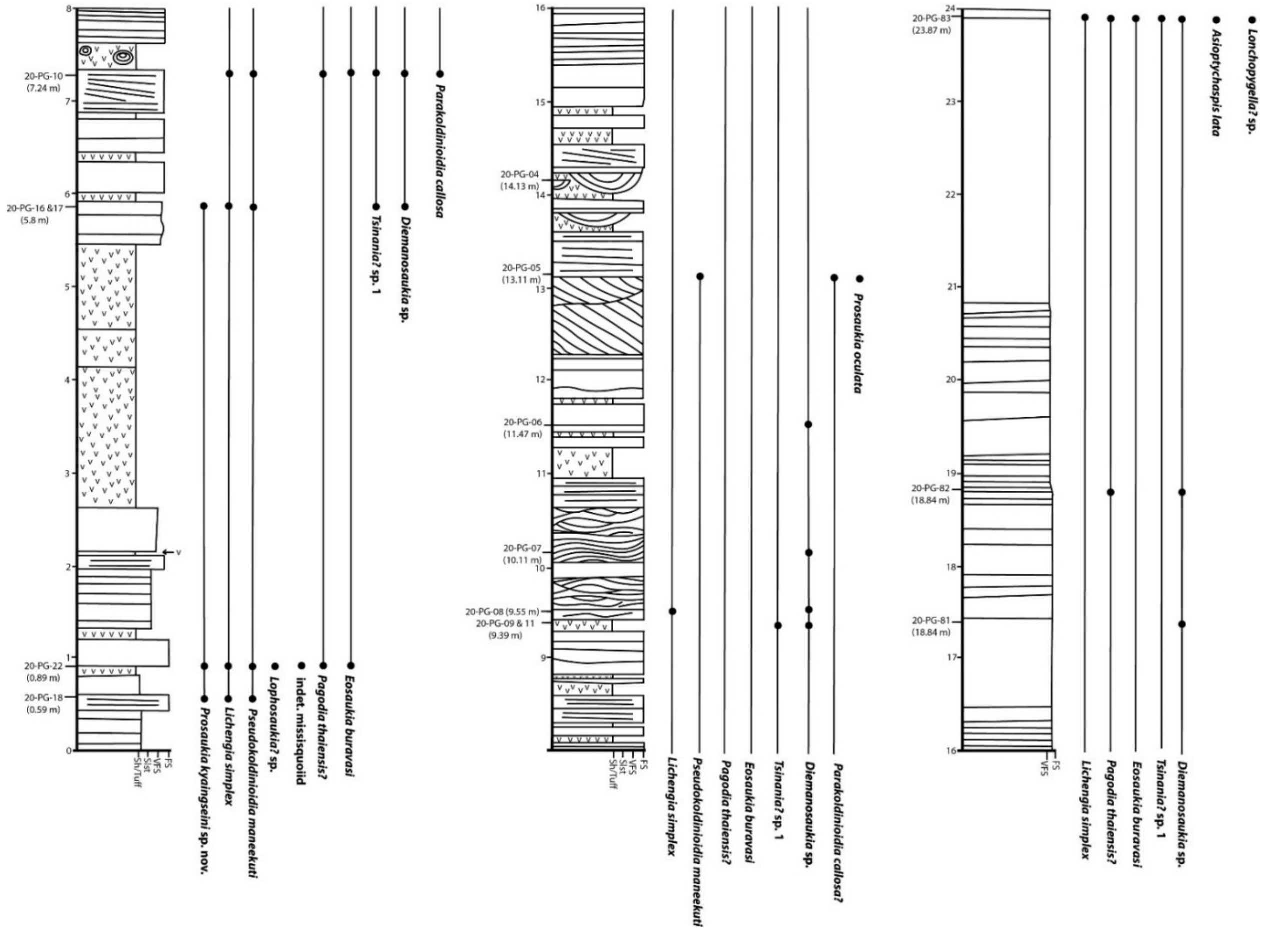

Figure 4. PG5 section. Fossiliferous horizons are 0.59 m, 0.89 m, 5.8 m, 7.24 m, 9.39 m, 10.11 m, 11.47 m, 13.11 m, 14.13 m, 17.5 m, 18.84 m, 23.87 m above base. Sh/Tuff=shale with ash tuffs, Slst=siltstone, VFS=very fine sandstone, FS=fine sandstone. Modified from the logs of Paul Myrow.

Figure 4

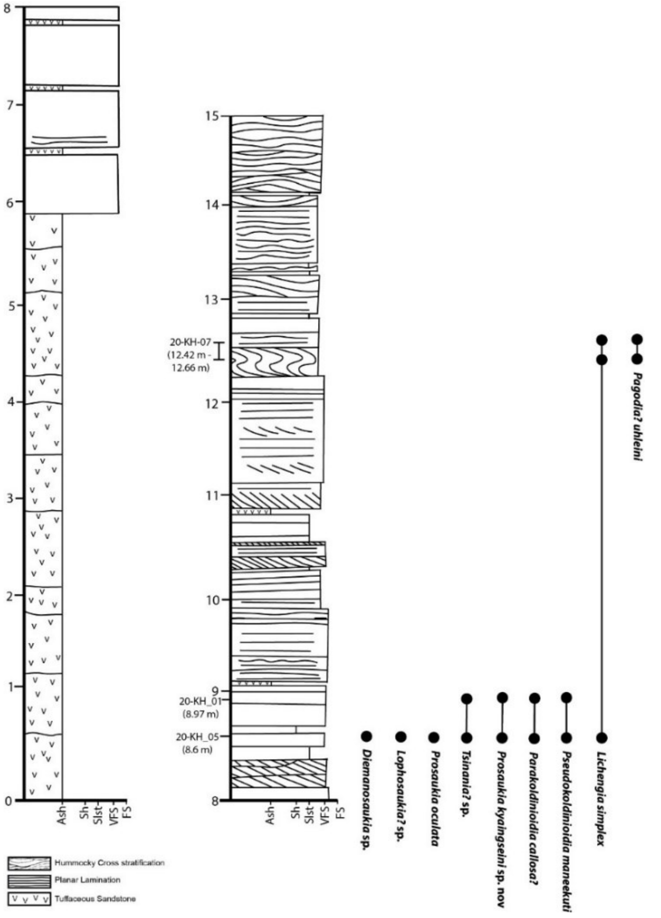

Figure 5. KH1 section. Fossiliferous horizons are 8.6 m, 8.97 m, and 12.42-12.66 m above base. Sh=shale, Slst=siltstone, VFS=very fine sandstone, FS=fine sandstone. Modified from the logs of Paul Myrow.

Figure 5

Northwards at the KH1 outcrop near the village of Kho Hsu, a 15 m section contains several different fossil-bearing horizons. *Diemanosaukia* sp. 1, *Lophosaukia?* sp., *Prosaukia oculata, Tsinania?* sp., *Prosaukia kyaingseini*, *Pseudokoldinioidia maneekuti, Parakoldinioidia callosa*, and *Lichengia simplex* are present in the first fossil-bearing horizon 8.6 m from the base of the section. Of these taxa, *Tsinania?* sp., *P. kyaingseini, P. maneekuti,* and *P. callosa* continue upwards to the fossil-bearing horizon 8.97 m from the section base, but only *L. simplex* continues to the uppermost fossil-bearing bed between 12.43-12.66 m. *Pagodia? uhleini* Wernette et al. (2023) is present in the upper 12.43-12.66 m horizon assemblage. *Pagodia? uhleini* has been noted to occur alongside *Hoytaspis thanisi* Shergold et al. (1988) in the Ao Talo Udang (ATD) section of the Tarutao Group. *Hoytaspis thanisi* has also been noted in the underlying Ao Tami Formation of the Tarutao Group as well as in the lower Sunwaptan strata of Laurentia

(Ludvigsen & Westrop, 1983; Wernette et al., 2023). However, evidence for *H. thanisi* being an indicator of an older Furongian or even Jiangshanian age in Sibumasu is scant, given its association with *P.? uhleini* which is a later form and co-occurs with *E. buravasi, Parakoldinioidia callosa,* and *Pseudokoldinioidia maneekuti* in the Tarutao Group, placing it within the *E. buravasi* biozone of Ko Tarutao. The mix of taxa within KH1 and the lack of *A. asiatica* thus suggest a correlation with the lower middle of the PG5 section, that represents Stage 10 of the Cambrian, rather than with the slightly older PG1 section that could be late Jiangshanian. Although *E. buravasi* is not present within KH1, the other fauna is consistent with the proposed *E. buravasi* biozone of the Shan State, as all these taxa co-occur with *E. buravasi* in PG5.

Only one fossil-bearing bed exists in the KS1 locality, and it is dominated by *Pacootasaukia jokliki,* a saukiid initially described by Shergold (1991) as *Platysaukia jokliki*. *Pacootasaukia jokliki* is known to be contemporary with *Tsinania* cf. *T. canens* Walcott (1905), *Eosaukia* cf. *E. walcotti* Mansuy (1915), *Lichengia simplex* and *Prosaukia? pentacosti* Shergold et al. (2007) in western Australian strata (Shergold, 1991; Shergold et al., 2007), all of which are known from the Shan State material. This is largely consistent with material from the Tarutao group, which documents one instance of *Pacootasaukia* at 8.6 m from the base of the Ao Talo Topo (ATT) section, co-occurring with *Tsinania sirindhornae* Wernette et al. (2023), *Lophosaukia nuchanongi* Wernette et al. (2023), and *Eosaukia buravasi,* as well as with *Pseudokoldinioidia, Quadraticephalus,* and *Haniwa* (Wernette et al. (2023), fig. 6).

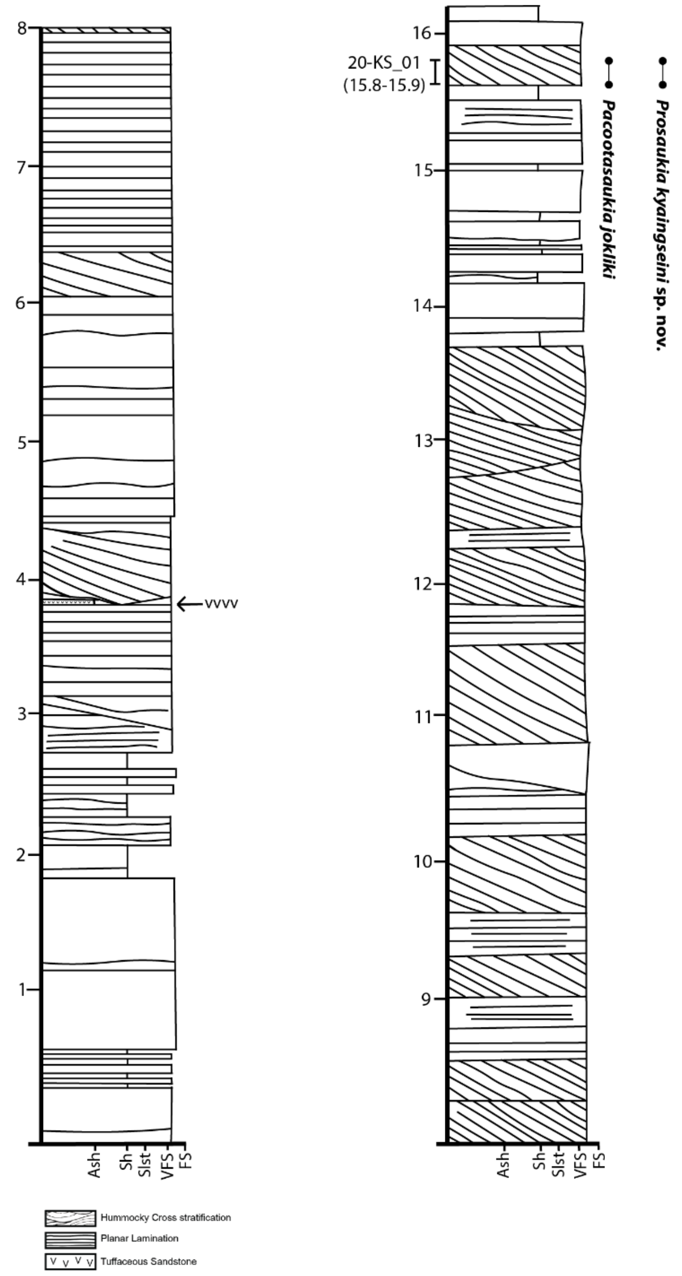

Figure 6. KS1 section. Fossiliferous horizons are 15.8-15.9 m above the base. Sh=shale, Slst=siltstone, VFS=very fine sandstone, FS=fine sandstone. Modified from the logs of Paul Myrow.

Figure 6

Although *Quadraticephalus* and *Haniwa* are not represented in the Shan State material, *Lichengia, Eosaukia, Tsinania, Prosaukia*, and *Pseudokoldinioidia* are all genera with long biostratigraphic ranges both within the Shan State (figs. 4, 5) and elsewhere among *peri*-Gondwanan terranes (Wernette et al., 2023), and do not particularly constrain the time period to which KS1 belongs; however, the presence of small holaspid cranidia representing *Prosaukia kyaingseini* in KS1 indicates that it likely corresponds to a similar time period as the PG5 section.

Several collections were made from spot localities where no stratigraphic section could be constructed, or occurred solely as float. These include locality YN1 near Yechanbyin village, locality KY1 near the Kyaukgnet monastery, and localities PG3 and PG4 along the road to Padongaing. However, some biostratigraphic information can still be gleaned from material.

Material from KY1 was gathered entirely from float in 2016 and 2020 and consists of a total of 6 fossiliferous cobbles. These cobbles show examples of *Asioptychaspis asiatica* and *Pagodia thaiensis?* pygidia. This is of some interest, as *A. asiatica* and *P. thaiensis?* are not known to co-exist in-section at PG1, the only locality in which *A. asiatica* is found *in situ*. Identifiable material from the YN1 collection consists primarily of small holaspid specimens of *Prosaukia kyaingseini* and pygidia representing *Pagodia thaiensis?* The presence of these genera suggest an association with the lower PG5 section.

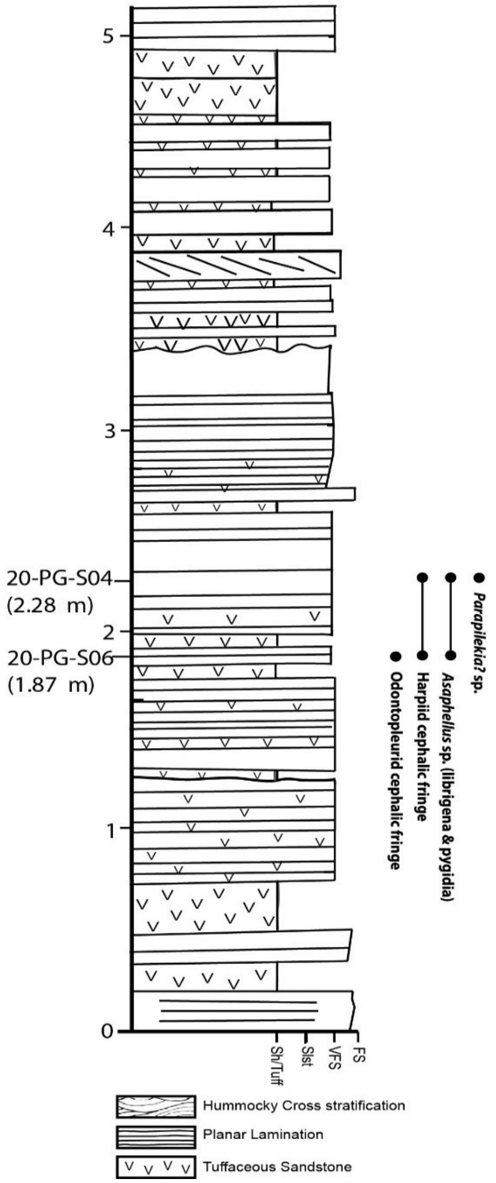

Figure 7. PG6-7 section. Fossiliferous horizons are 1.87-2.28 m above the base. Sh/Tuff=shale with ash tuffs, Slst=siltstone, VFS=very fine sandstone, FS=fine sandstone. Modified from the logs of Paul Myrow.

Figure 7

Ordovician

Farther up the road to Padongaing village, PG6-7 show characteristically Ordovician fossils: undetermined harpiid and odontopleurid cephalic fringes, *Parapilekia?*, and pygidia and librigenae that may represent *Asaphellus.*

Paleogeographic associations with Gondwanan and Laurentian terranes

The trilobite material representing the late Cambrian and Early Ordovician of the Shan State shows broad similarities with other *peri*-Gondwanan terranes, as well as associations with other Gondwanan terranes such as Kazakhstan and with Laurentia. Many genera represented in the Shan State material were spatially and temporally widespread in the late Cambrian; however, some genera with less wide distribution and many species-level similarities suggest association between the Shan State material, recently described Thai material, and material from western and central Australia.

The abundant presence of *E. buravasi* within PG5 presents a strong association of the upper Cambrian material of the Shan State with the recently described *E. buravasi* biozone of the Tarutao Group (Wernette et al., 2023), a conclusion supported by a number of shared genera and species, including *L. simplex, P. maneekuti, P. callosa, P.? uhleini, P. thaiensis*, and *P. kyaingseini* within PG5 and the corresponding KH1 section. KS1, a section defined by an abundance of *Pacootasaukia jokliki*, is also herein assigned to the *E. buravasi* biozone. Although the Shan State material in which *Pacootasaukia* is represented otherwise only contains *Prosaukia kyaingseini*, *Pacootasaukia* occurs within the ATT section of the recently-documented Ko Tarutao material where the ATT section is placed within the *E. buravasi* biozone (Wernette et al., 2023). The *E. buravasi* biozone is therefore proposed to be indicative of the late Cambrian of Sibumasu, as *E. buravasi* is endemic to Sibumasu.

Lichengia simplex, a taxon present in the upper ATT section of the Tarutao Group, is widespread within the PG5 and KH1 sections of the Shan State and presents a species-level association with the upper *Neoagnostus quasibilobus-Shergoldia nomas* zone of Australia (Shergold, 1975, 1991; Wernette et al., 2023), representing the mid- to late Paytonian (middle Stage 10) of the upper Cambrian. The *Shergoldia nomas* zone corresponds to the lower *Eosaukia* zone of South Korea (Lee & Choi, 2011; Wernette et al., 2023).

Although the Tarutao material is documented to have genera also or solely found in the lower *Quadraticephalus* biozone of South Korea, e.g. *Haniwa sosanensis?* (see Wernette et al. (2023))*,* the Shan State material lacks all taxa corresponding to the *Quadraticephalus* zone save *Tsinania,* a genus also present within the upper *Eosaukia* biozone and therefore not diagnostic of the earlier zone. The *E. buravasi* zone of Sibumasu equates better with the *Eosaukia* biozone of South Korea than with the *Quadraticephalus* zone. The upper *Eosaukia* zone of South Korea also corresponds with the upper Stage 10 *'Mictosaukia' perplexa* zone of Australia, the *'Mictosaukia'* zone of N China, and the '*Mictosaukia' striata-Fatocephalus* zone of S China, all of which also define the putative upper regions of the *E. buravasi* zone of the Tarutao Group (Wernette et al., 2023), though the true upper boundary cannot be determined due to gaps in Sibumasu's geochronological record.

PG1 is proposed to be a slightly older section within the Shan State material based on the presence of *Asioptychaspis asiatica* in the section, which constitutes a species-level association with the informally proposed Faunal Unit X (*Ptychaspis/Prosaukia*) of the Bonaparte Basin of W Australia (Öpik, 1967; Shergold et al., 2007), where *Ptychaspis* and *Asioptychaspis* have been considered synonymous. Faunal Unit X has previously been divided into Xa and Xb (Kaulback & Veevers, 1969); these subunits are poorly defined, though *Ptychaspis* is understood by Shergold et al. (2007) to be present earlier than *Prosaukia* in the sequence. The combined Faunal Unit X is proposed to correspond with the lower *Sinosaukia impages* and upper *N. quasibilobus-S. nomas* zones of W Australia (Shergold et al., 2007). The presence of *Asioptychaspis* forms a genus-level association with the *A. subglobosa* zone of South Korea, a biozone existing below the *Quadraticephalus* zone in the lower Hwajeol Fomation and corresponding with the *Asioptychaspis-Tsinania* zone of N China (Sohn & Choi, 2007; Park & Choi, 2008; Lee & Choi, 2011; T.-Y. S. Park & J.-H. Kihm, 2015), as well as the *Probilacunaspis nasalis-Peichiashania hunanensis* and lower *Lotagnostus punctatus-Hedinaspis regalis* zones of S China and the Iverian *Rhaptagnostus clarki patulus-Caznaia squamosa Hapsidocare lilyensis* and *Rhaptagnostus clarki prolatus-Caznaia sectatrix* zones, placing it well below the *E. buravasi* zone of Sibumasu (Lee & Choi, 2011). However, it is unlikely that the PG1 collection correlates with these lower biozones, and more likely that *Asioptychaspis* extends later in the Cambrian in Sibumasu and W Australia than in N and

S China. Additionally, though the Shan State material lacks other corresponding genera (e.g. *Haniwa, Caznaia* Shergold (1975)) present in the *A. globosa* zone and its contemporary zones in N and S China, these genera are present within the *E. buravasi* zone of the Tarutao Group (Wernette et al., 2023). PG1 ultimately cannot be used to definitively erect an older biozone within the Shan State material, as the most abundant and defining taxon of the section, *Asioptychaspis lata,* co-occurs with *E. buravasi* in the upper PG5 section, as does *P. kyaingseini,* a single specimen of which co-occurs with *A. asiatica*. PG1 is therefore also assigned to the *E. buravasi* biozone of Sibumasu. With regards to the lower Ordovician strata of the Shan State at PG6 & 7, the presence of material representing *Asaphellus* suggests a correspondence between these sections and the *Asaphellus charoenmiti* zone proposed in Wernette et al. (2023). Although the boundaries of this zone are poorly defined, it is tentatively associated with the middle-upper Tremadocian *Asaphellus* zones of N China and South Korea and the *Apatokephalus-Taoyuania* and *Conophrys-Asaphopsoides* zones of S China (Wernette et al., 2023).

Further genus-level associations can be made between the Shan State material and other *peri*–Gondwanan and Laurentian terranes. *Lichengia, Tsinania, Pseudokoldinioidia, Parakoldinioidia, Eosaukia, Prosaukia, Lophosaukia,* and *Pagodia* are all associated with upper Cambrian strata from W Australia and N and S China (Shergold, 1975; Zhang & Jell, 1987; Shergold, 1991; Shergold et al., 2007; Lee & Choi, 2011; Wernette et al., 2023). Additionally, *Prosaukia, Parakoldinioidia,* and the Ordovician genera *Parapilekia* and *Asaphellus* are represented in Laurentian (Holliday, 1942; Ross, 1970). These associations suggest that the Shan State material lacks *Hoytaspis*, a Cambrian genus tying the Tarutao Group trilobite fauna to Laurentia, as well as several widespread Ordovician genera such as *Apatokephalus* Brøgger (1896) and *Pseudokainella* Harrington (1938). Ultimately, the Burmese and Thai trilobite faunas are most strongly associated with that of Australia. Associations between the Shan State material and equatorial Gondwanan terranes include shared genera (e.g. *Prosaukia, Pagodia)* with modern Kazakhstan and Iran, though this association is less well-established in the Shan State than in Thailand due to the apparent absence of *Haniwa, Koldinioidia,* and *Mansuyia*.

An interesting feature of the Shan State material is the lack of certain genera. Two genera previously thought to be endemic to Thailand, *Satunarcus* Wernette et al. (2020b) and *Thailandium* Kobayashi (1957)*,* have yet to be recovered in the Shan State, which may support their endemicity; however, genera widespread among other *peri*-Gondwanan terranes are also missing in the Shan State material, including *Quadraticephalus, Haniwa,* and *Sinosaukia* Sun (1935) (fig. 9). Several taxa missing within the Shan State are present in W Australia, Thailand, and/or N China, while being absent in S China; these include *Andersonella, Corbinia* Walcott (1924)*, Mansuyia,* and *Haniwa*. While this may initially seem to indicate a stronger association between Sibumasu and S China, it is important to note that this apparent gap may only exist because less trilobite material has been collected and described representing the late Cambrian of Myanmar to date.

	Thailand	Australia	N China (Sino-Korean)	S China	Kazakhstan	Iran	South America	Avalonia	Laurentia	Baltica	Armorica
Diemanosaukia sp. 1		G[1]									
Eosaukia buravasi	S[2]	G[3]	G[4]	G[4]							
Lichengia simplex	S[2,5]	S[3]	G[6]								
Lophosaukia? sp.	G?[2]	S[7]*	G?[6]	G?[6]	G?[8]						
Pacootasaukia jokliki	G[2]	S[3]									
Prosaukia kyaingseini	S[2]	G[9]	G[6]	G[6]	G[10]				G[11]		
Prosaukia oculata	S[12]	G[9]	G[6]	G[6]	G[10]				G[11]		
Asioptychaspis lata	G?[2]	G[7]*	G[13]*								
Asioptychaspis asiatica	G?[2]	S[7]*	S[14]*								
Asaphellus sp.	G?[2]	G?[3]	G?[6]	G?[6]	G?[15]	G?[16]	G?[17]	G?[18]	G?[19]	G?[20]	G?[21]

Pseudokoldinioidia maneekuti	S[2]		G[6]	G[6]							
Parakoldinioidia callosa	S[2]		G[6]	S[22]					G[23]		
Pagodia thaiensis?	S?[2]	G[7]	G?[6]	G?[6]	G[24]	G[25]					G[26]
Pagodia? uhleini	S?[2]	G?[7]	G?[6]	G?[6]	G?[24]	G?[25]					G?[26]
Tsinania? sp.	G[2]	G[9]	G[6]	G[6]							
Lonchopygella? sp.				G?[27]							
Parapilekia? sp.	G?[2]	G?[7]		G?[28]		G?[16]	G?[29]		G?[30]	G?[31]	G?[21]

Figure 8

Figure 8. Generic and species associations of the Shan State late Cambrian-early Ordovician trilobite fauna with other terranes, modified from (Wernette et al., 2023). As in that paper, only a single reference is given per taxon per terrane, and selected references are given purely as proof of occurrence and do not reflect seniority of discovery or thoroughness of coverage. [1] Jago and Corbett (1990); [2] Wernette et al. (2023); [3] Shergold et al. (1991); [4] Lee and Choi (2011); [5] Shergold et al. (1988); [6] Zhou and Zhen (2008); [7] Shergold et al. (2007); [8] Ergaliev et al. (2008); [9] Shergold (1975); [10] Ergaliev and Ergaliev (2008); [11] Ludvigsen and Westrop (1983); [12] Wernette et al. (2020a); [13] Sohn and Choi (2007); [14] Zhang and Jell (1987); [15] Apollonov (1975); [16] Pour (2006); [17] Bordonaro (2003); [18] Stubblefield and Bulman (1927); [19] Ross (1970); [20] Bergström et al. (2013); [21] Martin et al. (2016); [22] Qian (1985); [23] Landing et al. (2011); [24] Ergaliev (1980); [25] Hamdi et al. (1995); [26] Shergold and Sdzuy (1991); [27] Sun and Xiang (1979); [28] Peng (1990); [29] Harrington and Leanza (1957); [30] Holliday (1942); [31] Ebbestad (1996)

	Thailand	Australia	N China (Sino-Korean)	S China	Kazakhstan	Laurentia
Satunarcus	X[1]					
Thailandium	X[1]					
Caznaia	X[1]	X[2]	X[3]			
Mictosaukia		X[2]	X[4]	X[4]		
Sinosaukia	X[1]		X[5]			
Hoytaspis	X[1]					X[6]
Mansuyia	X?[1]	X[7]	X[8]	X[5]	X[9]	
Haniwa	X[1]	X[2]	X[5]	X[5]	X[9]	
Wuhuia	X?[1]	X[2]	X[5]	X[10]	X[11]	
Quadraticephalus	X[1]	X[7]	X[12]			
Akoldinioidia	X[1]		X[3]	X[5]		
Koldinioidia	X[1]	X[7]	X[3]	X[5]	X[11]	
Corbinia	X[1]					X[13]
Yosimuraspis	X[1]		X[5]	X[5]		
Jiia	X[1]		X[5]	X[5]		
Apatokephalus	X[1]	X[7]	X[14]	X[5]	X[15]	X[16]
Pseudokainella	X[1]	X[17]	X[5]	X[5]		X[18]

Figure 9. Genera present in the Tarutao Group and other terranes, but not present in the Shan State. See fig. 8 for conditions of citation. [1] Wernette et al. (2023);[2] Shergold (1975);[3] T.-Y. S. Park and J.-H. Kihm (2015); [4] Lee and Choi (2011); [5] Zhou and Zhen (2008); [6] Ludvigsen and Westrop (1983); [7] Shergold et al. (1991); [8] Sun (1924); [9] Ergaliev and Ergaliev (2008); [10] Qian (1994); [11] Ergaliev (1980); [12] Sohn and Choi (2007); [13] Westrop et al. (2005); [14] T. Y. S. Park and J. H. Kihm (2015); [15] Apollonov (1975); [16] Ross (1970); [17] Jell and Stait (1985); [18] Hintze

Figure 9

SYSTEMATICS

Note: As there is presently no secure specimen repository available in Myanmar with the written endorsement of the Myanmar Geosciences Society specimens illustrated in work will be reposited in the invertebrate paleontology collections of the Cincinnati Museum Center. Formal CMC-IP specimen numbers will be assigned once the monograph resulting from this work is accepted for publication.

Order Asaphida Salter (1864)

Superfamily Dikelocephaloidea Miller (1889)

Family Dikelocephalidae Miller (1889)

Diemanosaukia Jago and Corbett (1990)

Type species. *Diemanosaukia miserabilis* Jago and Corbett (1990)

Emended Diagnosis. Subrectangular, coarsely granulated cranidium. Undifferentiated frontal area consisting of anterior border; preglabellar furrow deeply incised. Anterolateral furrows extending transversely to mildly posteriorly directed from glabellar anterior corners. Glabella widest at LO, parallel-sided from L1 forward. S1 furrow deeply incised and continuous, shallowing across midline, and posteriorly bowed. S2 and S3 furrows shallow and discontinuous, with posteriorly-directed S2 and anteriorly-directed S3. Palpebral lobes strongly arched, extending from opposite or posterior S1 to anterior S2. Fixigenae wide. Posterolateral projections narrow and long, posteriorly directed, with degree of posterior angling increasing abaxially. Librigenae wide; genal spines not advanced. Lateral and posterior furrows disconnected, posterior furrow continuing short distance into genal spine base. Thorax 12-13 segments, pleural spines posteriorly directed. Pygidium subtriangular to semicircular in outline, with 7-9 axial rings. Pleurae evenly divided and transverse to slightly posteriorly angular, flat pygidial border narrowing posteriorly.

Discussion. *Diemanosaukia* was first established as a genus by Jago and Corbett (1990), who erected it based on isolated tagmata (cranidia, librigenae, pygidia, and hypostomes), as well as a partially articulated cranidium and several pygidia with attached thoracic segments. The most striking feature of *Diemanosaukia* is the pygidium; while most saukiid pygidia have 3-5 axial rings or less, the pygidium of *Diemanosaukia* displays between 7 and 9 axial rings. Jago and Corbett (1990) noted that the only comparable saukiid pygidia are *Danzhaisaukia* Lee & Chien (1978) and *Metacalvinella* Lee & Yin (1973); however, *Danzhaisaukia* is considerably smaller in maximum size than the material attributed to *Diemanosaukia*, and both *Metacalvinella* and *Danzhaisaukia* possess fewer axial rings in the pygidium than *Diemanosaukia*—*Metacalvinella* displays 6, *Danzhaisaukia* has 6-7 (Lu and Qian (1983) pl. 9, fig. 10 & 12).

Diemanosaukia and *Danzhaisaukia* are comparable: both display a parallel-sided glabella, librigenae with non-advanced genal spines and disconnected posterior and lateral border furrows, the latter of which continues into the base of the genal spine, and a multi-segmented semicircular to subtriangular pygidium, with equally divided pleurae and a wide border. Several significant differences separate the two genera. In addition to the differences in pygidium noted above, the cranidium of *Diemanosaukia* is considerably more rectangular in shape than the subtrapezoidal cranidium of *Danzhaisaukia* and possesses much wider fixigenae, as well as significantly smaller palpebral lobes. Although both show a parallel-sided glabella, the *Diemanosaukia* glabella is considerably wider (tr.) at LO, while the occipital lobe of *Danzhaisaukia* is approximately equivalent in width to L1. Additionally, the anterolateral furrows of *Danzhaisaukia* are anteriorly-directed, in contrast to the transverse or posterorly directed anterolateral furrows of *Diemanosaukia*. The *Diemanosaukia* librigenae possess a much stouter and shorter (exsag.) genal spine than those of *Danzhaisaukia*.

Jago and Corbett (1990) noted that *Danzhaisaukia* is considerably smaller in maximum size than *Diemanosaukia.* While complete specimens of *Diemanosaukia* depicted in Jago & Corbett are between 60-70 mm in length, the complete holotype specimen of *Danzhaisaukia* figured in Lu & Chien (1978) measures only about 8 mm in length. This, along with the considerably longer eyes of *Danzhaisaukia* and fewer thoracic segments (11, compared to the 12-13 of *Diemanosaukia*) suggests that *Danzhaisaukia* is likely a juvenile form. However, it is unlikely to represent a juvenile form of *Diemanosaukia.* Although the relatively longer palpebral lobes and perhaps fewer thoracic segments of *Danzhaisaukia* suggests an earlier ontogenetic stage, other distinguishing features of *Danzhaisaukia*, such as the anteriorly-directed anterolateral furrows, narrow fixigenae, short LO, and subtrapezoidal cranidium, are not known in saukiids to show marked allometry. Notably, some of the Shan State material here assigned to *Diemanosaukia* is smaller than the material figured in Jago and Corbett (1990), yet retains the characteristic subrectangular cranidium and transverse to posteriorly-directed anterolateral furrows. Although the palpebral lobes of the Shan State material are proportionally longer than those of the Misery Hill material (36% of occipital-glabellar length on average compared to 29%), they remain considerably shorter than those of *Danzhaisaukia,* which represent approximately 70% of the occipital-glabellar length. This is true even for Shan State specimens assigned to *Diemanosaukia* that are of a comparable size to *Danzhaisaukia*. Therefore it is unlikely that *Danzhaisaukia* represents the juvenile form of *Diemanosaukia.*

Diemanosaukia's cranidium displays similarities to several other *Saukia*-like saukiid genera lacking differentiation in the frontal area, including *Saukia* itself. This is notable as Jago and Corbett (1990) document *Diemanosaukia* co-occuring with *Saukia? blissetti* Jago & Corbett, 1990 in the Misery Conglomerate at Misery Hill, Tasmania. Both display a parallel-sided glabella extending to the anterior border, an undifferentiated frontal area, and palpebral lobes extending from slightly posterior to opposite S1 to anterior S2. However, *Diemanosaukia* displays a more rectangular cranidium with generally wider fixigenae, as well as more strongly arcuate palpebral lobes, transversely-directed anterolateral furrows, and sagittally short posterolateral projections which extend farther outwards. The librigenae of *Diemanosaukia* also differ significantly from those of *Saukia? blissetti;* while the latter has broad, semicircular librigenae with a narrow genal spine advanced at a near right angle to the posterior border, as well as confluent lateral and posterior border furrows, the former displays a more gently curved, teardrop-shaped librigenal form, with a wide, non-advanced genal spine and disconnected lateral and posterior border furrows. Although the pygidia of *Saukia? blissetti* are subtriangular to semicircular in shape and display evenly-divided pleurae, traits shared with *Diemanosaukia*, the *Saukia? blissetti* pygidium displays only 4 axial rings, and lacks the wide, posteriorly-narrowing border of *Diemanosaukia*. Additionally, the interpleural furrows of *Saukia? blissetti* appear fainter than those in *Diemanosaukia;* however, this may be an artifact of preservation. While the presence of *Diemanosaukia* in shale horizons preserves aspects of original relief and of furrowing and ornamentation (though not without distortion), *Saukia? blissetti* is only found in fine- to medium-grained sandstone horizons of the Misery Conglomerate, which may obscure some features of the prosopon and furrows.

Another genus sharing several cranidial traits with *Diemanosaukia* is *Mictosaukia* Shergold, 1975. *Mictosaukia,* like *Diemanosaukia*, has a long (sag.) undifferentiated frontal area and wide anterior border, transverse or slightly posteriorly-directed anterolateral furrows, and long and narrow posterolateral limbs. Additionally, while the palpebral lobes of *Mictosaukia* are slightly less arcuate than those of *Diemanosaukia*, species of both genera display palpebral lobe midlengths located posterior to the glabellar midline, with posterior margins opposite or slightly posterior to S1 and anterior margins slightly anterior to S2 (Shergold, 1975; Lee & Choi, 2011). The largest differences between the cranidia of *Mictosaukia* and *Diemanosaukia* species are in the fixigenae, which are slightly wider in *Diemanosaukia,* and the condition of the glabella, which in *Diemanosaukia* is also slightly wider and does not display the midlength constriction found in some specimens of *Mictosaukia*. Despite these differences, species of *Diemanosaukia* are demonstrably similar to those of *Mictosaukia* in cranidial form. The librigena of *Diemanosaukia* and *Mictosaukia* display some significant differences; for example, *Mictosaukia* possesses a somewhat advanced genal spine, as well as confluent lateral and posterior furrows that do not continue into the genal spine base. The pygidia again display the most significant difference between the two. *Mictosaukia*, despite also possessing subtriangular pygidia in some cases, only has 4 axial rings, a stark contrast from the 7-9 axial rings of *Diemanosaukia* (Shergold, 1975; Jago & Corbett, 1990; Lee & Choi, 2011). The wide and flat pygidial border of *Diemanosaukia* is also not present in *Mictosaukia*. While the cranidial similarities suggest that *Mictosaukia* and *Diemanosaukia* are closely-related, the two are clearly distinct, and though *Mictosaukia* is a widespread genus throughout terranes from the Gondwanan rim and beyond, including in Mexico and Afghanistan (Robison & Pantoja-alor, 1968; Wolfart, 1970; Peng, 1984; Lee et al., 2008; Lee & Choi, 2011), *Diemanosaukia* has only been documented from Tasmania and the Shan State, which may indicate particular faunal affinity between these areas. Fragments of cranidia and librigenae similar to that of *Diemanosaukia* have been described from Antarctica (see Wright et al. (1984) fig. 2A); however, the lack of the distinctive *Diemanosaukia* pygidium makes any determination unqualified.

***Diemanosaukia* sp. 1**

Figs. 10-12

Material. 10 cranidia from PG5 5.8 m (20-PG-17_14), 7.24 m (20-PG-10_47, 20-PG-10_92), 9.39 m (20-PG-09_1), 9.55 m (20-PG-08_8), 11.47 m (20-PG-06_4), 17.4 m (20-

PG-81_1), 23.87 m (20-PG-83_16, 20-PG-83_18, 20-PG-83_35), 1 cranidium from KH1 8.6 m (20-KH-05_26). 1 pygidium from PG3 float (16-PG-602_7), 19 pygidia from PG5 7.24 m (20-PG-10_2, 20-PG-10_16, 20-PG-10_22, 20-PG-10_44, 20-PG-10_49, 20-PG-10_56 external mold and latex cast, 20-PG-10_59, 20-PG-10_61, 20-PG-10_62, 20-PG-10_67, 20-PG-10_76, 20-PG-10_84, 20-PG-10_88), 9.39 m (20-PG-08_10), 9.55 m (20-PG-08_10 and external mold), 10.11 m (20-PG-07_2, 20-PG-07_4, 20-PG-07_09), 11.47 m (20-PG-06_1 and external mold), 18.84 m (20-PG-82_5), 1 pygidium from 8.6 m (20-KH-05_43).

Diagnosis. Species of *Diemanosaukia* possessing subrectangular to subtrapezoidal cranidium with parallel-sided to slightly anteriorly narrowing glabella. Widest point of glabella at L1, with LO approx. 11% wider. Anterior border long (sag.) and gently downsloping, undifferentiated. Comparatively narrow fixigena with long palpebral lobes. Posterolateral limbs long and narrow, transverse. Subtriangular pygidium with between 7 and 9 axial rings. Pleurae equally divided, interpleural furrows shallower than pleural furrows. Pygidium with high length:width ratio. Wide pygidial border, with limited medial narrowing.

Description. The Shan material of *Diemanosaukia* possesses the distinctive undifferentiated frontal area, transverse to slightly posteriorly directed anterolateral furrows, and subrectangular cranidium of the genus; however, it differs from the *Diemanosaukia miserabilis* type material in several distinctive ways. First, the Shan material is considerably smaller than the Misery Hill material. The longest measured occipital-glabellar length of the Shan material is 8.84 mm, and the shortest is 1.55 mm. In contrast, the Misery Hill material ranges between 7 and 15 mm in length. The Shan material also shows a higher degree of anterior narrowing; while the anterior glabellar lobe of the Misery Hill material represents approximately 89% of the L1 width, the anterior glabellar lobe of the Shan State material only represents on average about 80% of the L1 length. When comparing the same measurement from largest Shan State cranidium, which is of comparable occipital-glabellar length to the smallest Misery Hill cranidia (8.84 mm compared to 7.33 and 8 mm), the Shan State cranidia displays an anterior glabellar lobe width approximately 82% of the L1 width,

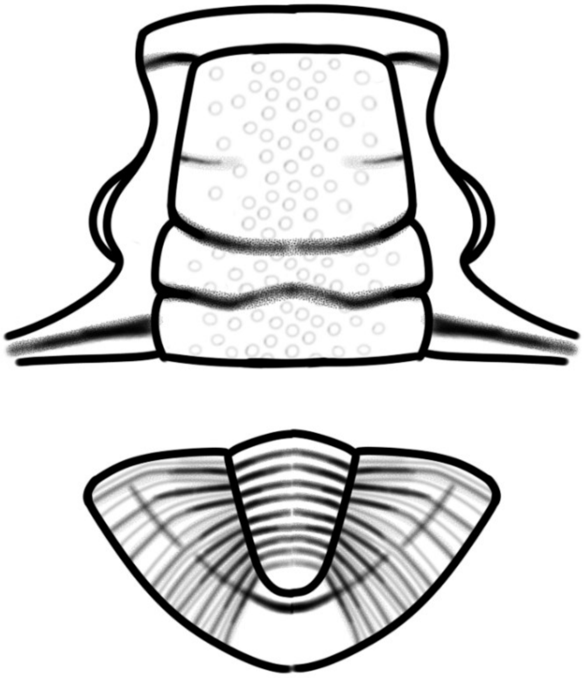

Figure 10. *Diemanosaukia* sp. 1 reconstruction. Posterolateral projections not figured, as Shan State material lacks complete representations.

Figure 10

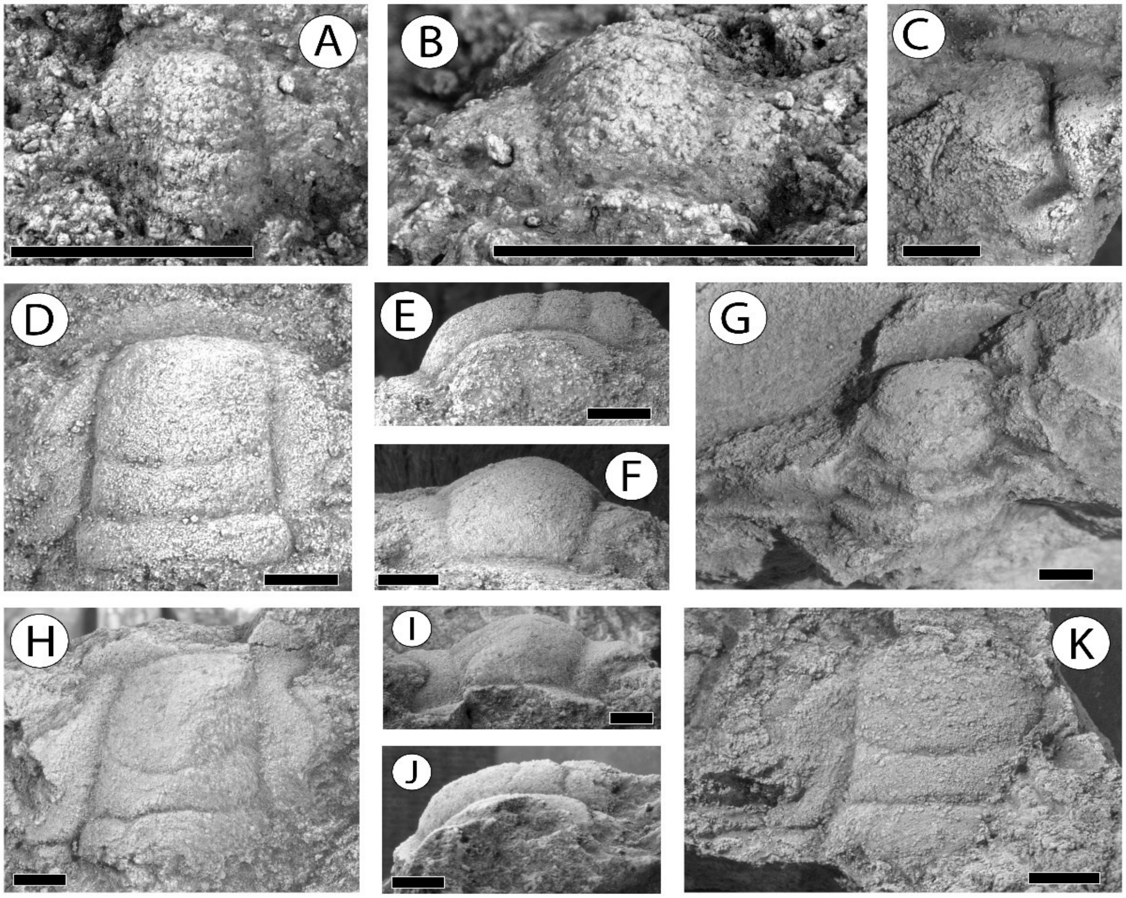

Figure 11. *Diemanosaukia* sp. 1 cranidia. A-B, 20-PG-10_47, in: B, anterior. C, 20-PG-83_35. D-F, 20-PG-81_1, in: E, lateral; F, anterior. G, 20-PG-83_18. H-J, 20-PG-08_8, in: I, anterior; J, lateral. K, 20-KH-05_26. Scale bars represent 2 mm.

Figure 11

while the two Misery Hill cranidia anterior glabellar lobes are 100% and 95% of the L1 width respectively. This is a significant discrepancy and suggests that the increased anterior tapering of the Shan State material is not a result of differing ontogenetic change alone. Much of the anterior tapering of the Shan State material occurs anterior to S2; L1 width is approximately 89% of occipital lobe width, negligably different from the 91% of *D. miserabilis.*

Pygidia of the Shan State are similarly multi-segmented when compared to Misery Hill material, though on average the Shan material possesses up to 9 axial rings, where the Misery Hill material only represents 7-8 axial rings.

Librigenae representing *Diemanosaukia* have not been definitively identified from the Myet-Ye Formation and thus cannot be compared to those from the Misery Hill material.

Discussion. The material of *Diemanosaukia* found in the Shan State displays several differences from the Misery Hill type species. The Shan material has longer palpebral lobes; as noted above, however, this may be explained by the fact that this small material represents earlier stages of development. The comparatively narrow fixed cheeks of the Shan State material enhance its *Mictosaukia*-like in appearance; however, the pygidia differ considerably from those of *Mictosaukia*, which possess 4 axial rings, and those of *Diemanosaukia miserabilis,* which possess 8 or fewer axial rings, compared to the Shan State's 7 to 9 axial rings. Additionally, the Shan pygidia are more subtriangular than semicircular in shape. Despite these differences, the pygidia are otherwise similar to the Misery Hill material, as they are multisegmented with wide

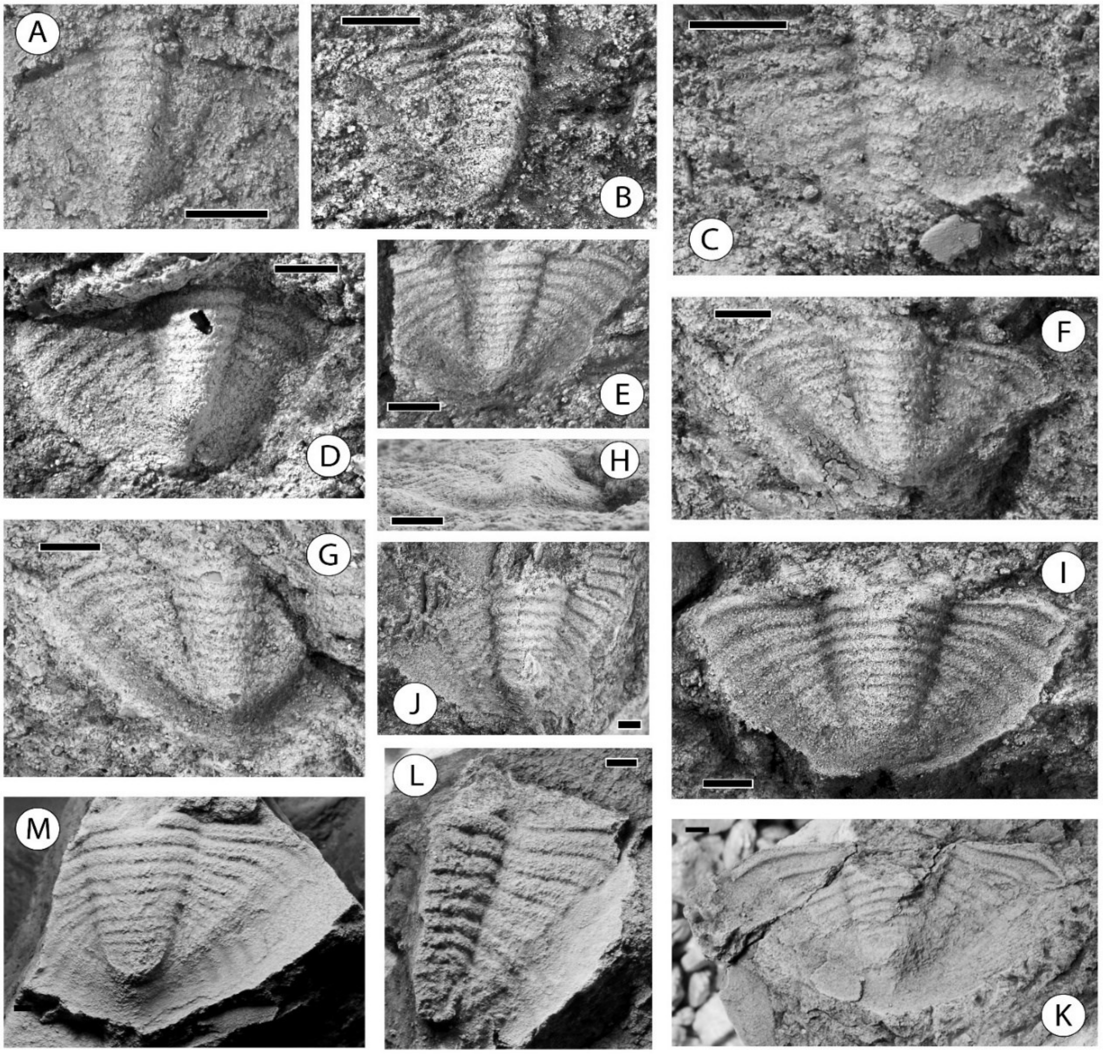

Figure 12. *Diemanosaukia* sp. 1 pygidia. A, 20-KH-05_43. B, 20-PG-10_59. C, 20-PG-10_22. D, 20-PG-10_88. E, 20-PG-10_62. F, 20-PG-10_67. G-H, 20-PG-10_44, in: H, posterior view. I, 20-PG-10_84. J, 20-PG-07_2. K, 20-PG-07_4. L, 20-PG-08_10. M, 20-PG-07_09. Scale represents 2 mm.

Figure 12

borders and equally-divided pleurae. Additionally, the differences in cranidia are not considered significant enough to assign the Shan State material to another genus.

The presence of *Diemanosaukia* in the Shan State indicates a faunal association between Tasmania and Sibumasu. Although an association has been previously established between the Sibumasu terrane and mainland W/NW Australia, no previous work on Sibumasu terrane trilobites has revealed an association specific to Tasmania.

Eosaukia **Lu (1954)**

Type species. *Eosaukia latilimbata* Lu (1954)

Diagnosis. A recent emended diagnosis was published in Lee and Choi (2011).

Discussion. Of the diagnostic features of *Eosaukia*, the most significant are the presence of strongly-incised anterolateral furrows directed abaxially outwards at a strong diagonal from the anterior corners of the glabella, the lack of a preglabellar field, and the pauci-segmented, micropygous pygidium. Other diagnostic features include strong convexity of the cranidium and a steeply sloping anterior border, short palpebral lobes, and wide fixigena.

Although other saukiid genera, including Laurentian forms such as *Tellerina* Ulrich and Resser (1933), *Calvinella*, and *Saukia* also possess an undifferentiated frontal area lacking a preglabellar field and anterolateral furrows, which may indicate homology, the anterolateral furrows of these forms tend to be more shallowly incised and range from slightly anteriorly divergent to slightly convergent (Lee & Choi, 2011). These Laurentian forms also have longer and more posteriorly-positioned palpebral lobes than *Eosaukia;* where *Tellerina/Calvinella* have palpebral lobes with posterior corners level with or slightly anterior to SO, those of *Eosaukia* are level with or slightly posterior to S1 (Westrop (1986), pl. 3 figs 8-9, 12, pl. 5 figs. 1-4; Westrop (1995) pl. 8 figs 3, 5). Additionally, the pygidium condition of *Eosaukia* is not seen in *Tellerina/Calvinella,* which have larger pygidia and wider pygidial borders (Westrop (1986), pl. 3 fig. 10). Several Gondwanan forms of *Calvinella* such as *Calvinella acuta* Kuo and Duan *in* Kuo et al. (1982) and *Calvinella micropora* Qian *in* Chen (1985) have been re-assigned to *Eosaukia*, as has the species *Tellerina coreanica* Kobayashi (1935) (Lee & Choi, 2008; Lee & Choi, 2011)

When considering genera similar to *Eosaukia,* special attention may be afforded to the Asian genus *Mictosaukia* Shergold, 1975. Many Gondwanan species of *Tellerina, Calvinella, Saukia* and *Ptychaspis* Hall, 1863 have been reassigned to *Mictosaukia* over time (Lee & Choi, 2008), resulting in a genus containing 23 different species. Lee and Choi (2011) noted a group possessing the diagnostic features of *Eosaukia*—strong convexity, anterolateral furrows divergent anteriorly, short palpebral lobes, wide fixigena and reduced pygidia with 4 or fewer axial rings—within those species assigned to *Mictosaukia*. These species, which included *M. perplexa* Shergold (1975)*, M. angustlimbata* Qian *in* Chen (1986)*,* and *M. maculata* Qian (1985) have been reassigned to *Eosaukia* (Lee & Choi, 2011). Despite this reassignment, the fact remains that, similarly to *Calvinella/Tellerina, Mictosaukia* possesses an undifferentiated frontal area, as well as a cranidium that overwhelmingly resembles the *Eosaukia* cranidium in shape. *Mictosaukia* also possesses strongly incised anterolateral furrows, similarly to *Eosaukia* and distinct from the fainter furrows of Laurentian saukiid forms. While *Mictosaukia* can ultimately be distinguished from *Eosaukia* due to the transverse condition of its anterolateral furrows, as well as possessing a larger pygidium with a wider posterior border, a more gently sloping anterior border, longer palpebral lobes, and narrower fixigena, *Mictosaukia* and *Eosaukia* appear to be closely related. Closer examination of the two genera may provide valuable information for understanding the position of those taxa with undifferentiated frontal areas within the saukiids.

Taebaeksaukia Lee and Choi (2011) resembles *Eosaukia* in the position and orientation of its anterolateral furrows, as well as in the pauci-segmented pygidium. However, the anterolateral furrows of *Taebaeksaukia* are shallow, and the large, posteriorly-located palpebral lobes with narrow fixigenae differs from the wide fixigenae and short eye of *Eosaukia*. Additionally, the genal spines of *Eosaukia* are much shorter than those of *Taebaeksaukia,* and the *Taebaeksaukia* pygidium bears a distinctive pair of spines at the anterolateral corners of the pygidium (Lee & Choi, 2011).

Lee and Choi (2011) synonymize *Scolosaukia* Sun (1990) with *Eosaukia*. *Scolosaukia* was initially established based on *"Calvinella" micropora* Qian (1985)*,* itself later redefined as *Eosaukia micropora* Lee and Choi (2011) due to its oblique anterolateral furrows, strongly convex cephalon, occipital node, wide fixigenae, and short, pauci-segmented pygidium (Lee et al., 2008; Lee & Choi, 2011).

Eosaukia buravasi Kobayashi (1957)

Fig. 13-14

1957 *“Eosaukia” buravasi* Kobayashi, p. 376-378, pl. 5, figs 1-10, 13-20, ?7-9, ?13

1988 *“Eosaukia” buravasi* Shergold *et al.,* p. 310, fig. 4O-4X

2007 *Ptychaspis?* sp. aff. *P. caucus* Walcott, 1905; Shergold *et al.,* p. 65, fig. 38

2008 *Calvinella walcotti* Mansuy, p. 194, pl. 10, fig. 1

2021 *Eosaukia buravasi* Wernette *et al.,* p. 15-16, figs. 11-12

2022 *Eosaukia buravasi* Hughes *et al.,* p. 64, fig. 10a-l

2023 *Eosaukia buravasi* Wernette *et al.,* p. 57-61, figs. 45-50.

Material. 8 cranidia from PG3 float (16-PG-602_1, 16-PG-602_2, 16-PG-602_3, 16-PG-602_5, 16-PG-602_9, 16-602_10, 16-PG-602_13, 16-PG-603_2), 14 cranidia from PG5 7.24 m (20-PG-10_10), 23.87 m (20-PG-83_28, 20-PG-83_41, 20-PG-83_46, 20-PG-83_47, 20-PG-83_48, 20-PG-83_51, 20-PG-83_54, 20-PG-83_57, 20-PG-83_58, 20-PG-83_59, 20-PG-83_69, 20-PG-83_73, 20-PG-83_75). 1 librigena from PG3 float (16-PG-602_12), 7 librigenae from PG5 0.89 m (20-PG-22_16, 20-PG-22_18, 20-PG-22_26, 20-PG-22_57), 7.24 m (20-PG-10_55, 20-PG-10_60), 23.87 m (20-PG-83_53). 1 pygidium from PG3 float (16-PG-602_4), 1 pygidium from PG5 23.87 m (20-PG-83_36).

Diagnosis. Glabella sub-rectangular to anteriorly narrowing with widest point at occipital lobe, with rounded to transverse anterior. Undifferentiated anterior border varying between 7% and 21% of occipital-glabellar length, with deeply incised anterolateral furrows. Cranidial outline variable with obliqueness of palpebral lobes. Fixigenae wide compared to other species of *Eosaukia.* Deeply incised, long, posteriorly bowed SO & S1 furrows; faint to discontinuous S2 and S3. Short occipital node present but not as prominent in Burmese specimens as in some Thai specimens (e.g. Wernette et al. (2023) figs. 45N, 47D, 47Q). Broad fixigenae with palpebral lobes between 30-60% of occipital-glabellar length, averaging 45% of occipital-glabellar length. Cranidium exhibits tuberculate ornamentation. Librigenae strongly curved to near-semicircular, with variable projection of advanced genal spine, confluent posterior and lateral borders. Wide lateral border. Pygidium short (sag.) and lenticular in shape, with only two axial segments. Pleural and interpleural furrows effaced. Terminal axial segment weakly double-ridged (exsag.). Pygidial border narrow.

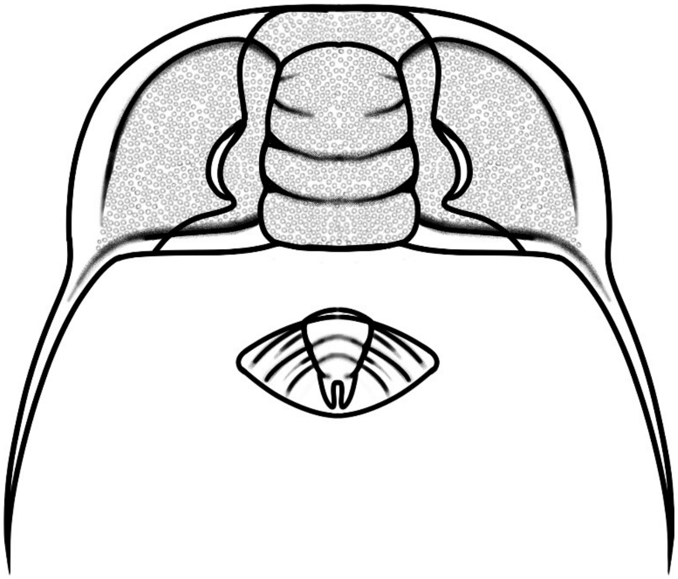

Figure 13. *Eosaukia buravasi* reconstruction. Though this reconstruction displays the average of *E. buravasi* measurements, individual specimens may appear significantly different due to the large degree of intraspecific variation.
Figure 13

Discussion. While species of *Eosaukia* are present in other Gondwanan localities (e.g. the Taebaek Group of South Korea), *E. buravasi* is the only species of the genus found in Sibumasu, where it is extremely abundant. Wernette et al. (2023) documented 230 cranidia in total, as well as 41 librigenae and 47 pygidia, from the Tarutao Group of Thailand. In the Shan State *E. buravasi* is less well known, with only 22 cranidia, 8 librigenae, and 2 pygidia documented, but as less trilobite material has been collected from the Shan State overall, this still indicates that *E. buravasi* is relatively abundant. Its prominence in both the Ko Tarutao and Shan State trilobite assemblages has supported its use in biozone definition in the latest Cambrian, though the base and top of the *E. buravasi* biozone are not yet precisely defined within continuous sections in either Thailand or Burma. Much of the material collected by Shergold et al. (1988) initially assigned to *Lophosaukia* cf. *jiangnanensis* Lu and Lin (1984) has since been reverted to *E. buravasi* (Wernette et al., 2023), and the morphological differences prompting the reassignment have been recognized as the result of intraspecific variation. However, the figured librigenae of *Lophosaukia* cf. *jiangnanensis* remain uncertain.

Eosaukia buravasi exhibits a high degree of intraspecific variation in the cranidium apparently unrelated to taphonomic or ontogenetic factors (Wernette et al., 2021; Wernette et al., 2023). Specimens vary in a wide range of characters, including length of the anterior border, width of the cranidium, width and length of glabella, and angles of anterolateral border furrows (Wernette et al., 2021; Wernette et al., 2023). Accordingly, there is some difficulty establishing diagnostic characteristics for the species, as well as confusion about whether certain Sibumasu specimens belong within *E. buravasi* and uncertainty about the relationship between *E. buravasi* and other species of *Eosaukia.* A morphometric analysis of 18 landmarks on 120 Thai cranidia and 2 Burmese cranidia indicated that the Burmese material falls within a continuous range of variation seen in the Thai material in a Procrustes superposition, and no independent groupings were found within the first two relative warps in a thin-plate spline analysis (Wernette et al., 2021); this would support the conclusion that *E. buravasi* is in fact one species with significant variation, rather than multiple species. Further analysis of cranidial variation in *E. buravasi* indicates that it is not size-controlled. The intraspecific variation of *Eosaukia buravasi* has been documented extensively in Wernette et al. (2023).

As a result of the range of intraspecific variation within the *E. buravasi* cranidium, the most widely shared characteristics among all specimens are more generally shared among all *Eosaukia* cranidia: deeply incised anterolateral furrows angled abaxially anterior to the glabella, lack of preglabellar field, deep, posteriorly-bowed S1, broad fixigenae, and short palpebral lobes (Wernette et al., 2023). The occipital node/spine is also consistently present, but varies in apparent prominence. While most specimens appear to maintain a moderately visible node, some specimens (e.g. Wernette et al. (2023) figs. 45N, 47Q) display a much longer and more prominent occipital spine, similar to that of *Eosaukia micropora,* if shorter. The presence of a significant occipital node/spine separates *E. buravasi* from species of *Eosaukia* lacking occipital nodes or spines or possessing only very small ones, such as *E. bella* Walcott

(1906) and *E. rectangula* Lu and Zhou (1990); however, as the *E. buravasi* occipital node varies in prominence and occipital nodes and spines are often poorly-preserved, the prominence of the occipital node/spine cannot be definitively used as a means of distinguishing *E. buravasi* from other species of *Eosaukia*.

Apart from the condition of the occipital node/spine, the *E. buravasi* cranidium requires close comparison with other species of *Eosaukia* to identify distinguishing characteristics. The frontal area of *E. buravasi* varies significantly in length, with a mean of about 13% of the occipital-glabellar length. The frontal area margin and glabellar anterior can be near-transverse (Wernette et al. (2023) figs. 46A, 48D, L, U), or anteriorly curved to various degrees. Several specimens representing *E. buravasi* show a more strongly tapering and angular margin of the frontal area (Wernette et al. (2023) figs. 46R, 47A-C, 48N); however, these cases are rare among *E. buravasi,* and this condition is not apparent among the Shan State material representing *E. buravasi.* The rarely angular condition of the frontal area immediately distinguishes *E. buravasi* from *E. acuta,* which possesses a strongly and consistently angular frontal area much longer than that of *E. buravasi,* with a mean of about 24% of occipital-glabellar length. Examination of the frontal area length also establishes the frontal area of *E. buravasi* as being slightly proportionally longer on average than that of *E. bella*, which has a mean of 7% of occipital-glabellar length. However, the range of measurements for *E. bella* shows significant overlap with *E. buravasi,* with most measured specimens of *E. bella* showing a frontal area between 8-10% of occipital-glabellar length, indicating that this

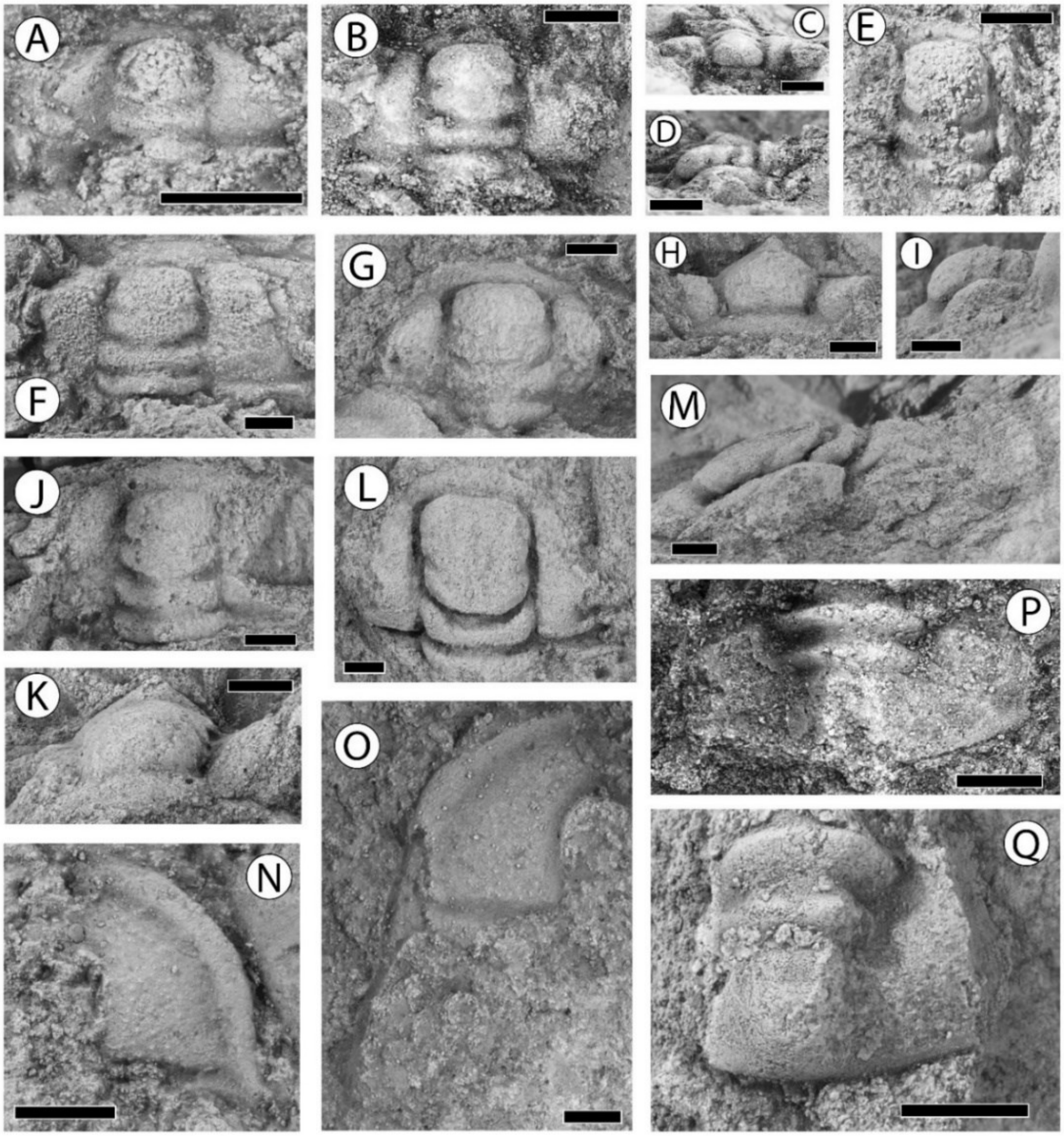

Figure 14. *Eosaukia buravasi.* A, 20-PG-83_57, cranidium. B-D, 16-PG-602_5, cranidium in: C, anterior; D, lateral. E, 20-PG-83_41, cranidium. F, 20-PG-83_41, cranidium. G-I, 20-PG-83_28, cranidium in: H, anterior; I, lateral. J-K, 20-PG-83_46, cranidium in: K, anterior. L-M, 20-PG-83_47, cranidium in: M, lateral. N, 20-PG-22_57, librigena. O, 20-PG-22_26, librigena. P, 16-PG-602_4, pygidium. Q, 20-PG-83_36, pygidium. Scale bars represent 2 mm.

Figure 14

measurement may not be the reliable means of differentiating between *E. bella* and *E. buravasi*. The *E. buravasi* glabella varies from nearly parallel-sided to strongly anteriorly narrowing, with a widest point at LO (a mean of approximately 70% of the occipital-glabellar length and a range of 55-88%), and an L1 length (a mean of approximately 66% of the occipital-glabellar length and a range of 55-75%). The palpebral lobes of *E. buravasi* vary widely in length but are proportionally short, ranging from 22-45% of occipital-glabellar length, with a mean of 27% and a median of 26%. Although the palpebral lobe lengths of most *Eosaukia* also fall within this range, several are significantly longer on average than those of *E. buravasi;* the palpebral lobes of *E. acuta* and *E. solitaria* Shergold (1975) are a mean of ~32-33% of the occipital-glabellar length, those of *E. micropora* and *E. bella* have a mean of 34-35%, and those of *E. elongata* Xiang *in* Sun and Xiang (1979) have a mean of approximately 39% of the occipital-glabellar length. However, it is difficult to say if these differences alone are sufficient to be distinguishing factors between *E. buravasi* and other species of *Eosaukia,* especially considering the limited number of available specimens figured for *E. solitaria* and *E. elongata.*

Although the *E. buravasi* cranidium cannot be distinguished from that of *E. bella* or *E. micropora* solely on the basis of the condition of the occipital node/spine or the length of the palpebral lobes, the combination of these cranidial differences presents a stronger argument that *E. buravasi* is not synonymous with these species.

Lee and Choi (2011) note that some species of *Eosaukia* display a characteristic and unique vincular structure on the librigenae in which the thoracic pleural tips fit into appropriate sockets in the cephalic doublure. This librigenal structure is not documented in other dikelocephalids, and can be seen in *E. buravasi* (Kobayashi (1957), pl. 5, figs. 8-9, re-figured in Wernette et al. (2021), fig. 12E), *E. perplexa* (Shergold (1975), pl. 24 fig. 3), and *E. angustlimbata* (Qian et al. (1986), pl. 71, fig. 11, pl. 72, fig. 2). This is a distinctive characteristic of the librigenae among dikelocephalids, but does not occur in all species of *Eosaukia*, and therefore cannot be used as a diagnostic feature for the genus. Although the type material of *E. buravasi* in Kobayashi (1957) appears to show this vincular structure, other *E. buravasi* material does not document this trait; of the 21 librigenae of *E. buravasi* figured in Wernette et al. (2023), none can confidently be stated to show the structure in question. Nevertheless, Wernette et al. (2023) note that this trait remains characteristic of *Eosaukia,* if not specifically of *E. buravasi*.

Kobayashi (1957) initially considered the *E. buravasi* pygidium too short to represent the genus and therefore represented uncertainty in generic assignment with the use of quotation marks; this was maintained in Shergold et al. (1988), who described "*E". buravasi* from the Tarutao Group and re-assigned several specimens and librigenae from the Kobayashi (1957) original study to *Lophosaukia* cf. *jiangnanensis.* However, the *E. buravasi* pygidium is characteristic of *Eosaukia* with its lenticular shape and narrow border. Additionally, other species of *Eosaukia* have since been found with a similar micropygous condition (e.g. *Eosaukia perplexa*), indicating that *E. buravasi* is not unique in this regard and the pygidium therefore represents a known morphological variant of the genus. The micropygous pygidial condition of *E. buravasi*, in combination with the two faint longitudinal ridges present on the post-axial portion of the pygidium, distinguishes it from several other *Eosaukia* species. *Eosaukia angustlimbata, E. acuta, E. latilimbata* Lu (1954)*, E. rectangula,* and *E. perplexa* possess 3-4 axial rings, in comparison to the 2 of *E. buravasi*, as well as lacking the post-axial ridges of *E. buravasi*. Several other species (*E. micropora, E. bella*) possess the 2 axial rings and post-axial ridges of *E. buravasi*; however, the *E. buravasi* post-axial ridges are less pronounced (Wernette et al., 2023). This would appear to indicate an association between a shorter pygidia with 2 axial rings and the presence of post-axial ridges.

Some species of *Eosaukia* are difficult or impossible to properly assess with regards to their relationship to *E. buravasi*. This may be because too few specimens exist, material is incomplete and difficult to conclusively examine, or only cranidia of the species have been figured. These genera include *E. coreanica* Kobayashi (1935), *E. combinata* Peng (1992), *E. diversa* Endo and Resser (1937), *E. lineata* Sun (1990), *E. maculata* Qian (1985), *E. transita* Lu and Zhou (1990), and *E. solitaria* Shergold (1975). In the case of *E. mansuyi* Hsiang, 1965, a species of *Eosaukia* re-assigned from *Prosaukia? mansuyi,* which Hsiang in Lu et al. (1965) erected based on *Ptychaspis? angulata* in Mansuy (1916), the original figured material (Mansuy (1916), vol. 4 pl. III figs. 2t-u; vol. 5 pl. V figs. 12a-b, pl. VI figs. 1a-d) lacks the diagnostic features of *Eosaukia*, including the biconvex/lenticular pygidium, anteriorly-directed anterolateral furrows, and wide fixed cheeks, casting doubt on its generic assignation to *Eosaukia*. The paratype and sole figured pygidium of *Tellerina coreanica*, later reassigned to *Eosaukia* *coreanica* (Kobayashi (1935), pl. 4 fig. 5) is significantly more triangular than those of other species of *Eosaukia* and possesses a much wider posterior border. These characters are otherwise unknown in *Eosaukia*, and suggest that this specimen does not represent an *Eosaukia* pygidium. In contrast, the figured cranidia in Kobayashi (1935) (pl. 4 figs. 12-13) are comparable to those of *Eosaukia*; most significantly, the anteriorly-directed anterolateral furrows are strongly incised in the cranidium figured in pl. 4 fig. 12. Thus, we suggest both that *E. coreanica* is a valid species of *Eosaukia,* though it cannot be definitely differentiated from *E. buravasi* due to the lack of material*,* and that the paratype pygidium is misattributed.

***Lichengia* Kobayashi, 1942**

Type species. *Lichengia onigawara* Kobayashi, 1942, Licheng Formation, Shengyaochen, Licheng, Shanxi, China. [=*Prosaukia brizo* (Walcott) *sensu* Sun, 1935]

Diagnosis. Cranidium rectangular to sub-trapezoidal in shape with rounded anterior. Poorly differentiated to undifferentiated frontal area with poorly-defined preglabellar field. Anterior border furrow partially to completely obscured by expanded anterior border, shallowing significantly near midline. Glabella narrowing anteriorly from expanded L1, anterior corners rounded. LO equal or subequal in width to maximum glabellar width. Palpebral lobes situated posteriorly with midpoint opposite S1. Discontinuous, slit-like S2 and S3 glabellar furrows, S1 discontinuous to weakly connected across midline. Pygidium trapezoidal to sub-trapezoidal, pleural furrows swept strongly posteriorly towards narrow, indistinct border. Pleural and interpleural furrows relatively few and strongly incised.

Discussion. Lu et al. (1965) re-assigned specimens previously assigned to *Prosaukia brizo* Sun (1935) to *Lichengia onigawara* Kobayashi (1942) under the generic and species name of the latter (see Shergold et al. (1988)), on the basis of the expanded anterior border obscuring the differentiation of the frontal area. Originally considered monotypic, Shergold et al. (1988) assigned several pieces of Thai material, including a cranidium previously assigned to *Saukiella tarutaoensis* Kobayashi (1957) (Kobayashi (1957) pl. 5 fig. 12)*,* to *Lichengia? tarutaoensis,* as well as suggesting that northern Australian material previously assigned to *Prosaukia? absona* Shergold (1975) and various previously unnamed fragments from northern Victoria Land, Antarctica (Wright et al., 1984) also belonged to *Lichengia*. Subsequently, *Lichengia simplex* was established based on material from the Pacoota Sandstone of Australia. Wernette et al. (2023) re-assigned the cranidium assigned by Kobayashi to *Saukiella* to *Prosaukia tarutaoensis* Wernette et al. (2020a), and synonymized *Lichengia? tarutaoensis* and *L. simplex* (Wernette et al., 2023) (see below).

The type species of *Lichengia, L. onigawara,* features a dramatic swelling of L1, forming an almost pear-shaped glabella. Although other species of *Lichengia* also exhibit comparable lateral expansion of the glabella, it is rarely so dramatic. Additionally, *L. onigawara* displays a slight constriction of the glabellar anterior between S2 and S3 (e.g. Lu et al. (1965) pl. 89 fig. 1), a feature not seen in other *Lichengia* material. Material is therefore usually assigned to *Lichengia* on the basis of characteristics of the glabellar furrows, frontal area, and palpebral area.

A key trait of *Lichengia* is the presence of an effaced anterior border furrow further obscured adaxially by an inflated anterior border; this trait separates it from any *Prosaukia,* despite the otherwise generally prosaukoid form of the cranidium and pygidium, as well as from and *Saukiella*, which also possesses a distinct, untruncated anterior border furrow. The degree to which the anterior border furrow is effaced varies significantly within a species; it is therefore difficult to assess the average relative lengths of the preglabellar field and anterior border.

Lichengia simplex **Shergold, 1991**

Fig. 15-16

non 1957. *Saukiella tarutaoensis* Kobayashi, p. 378, pl. 5, fig. 12 (= *Prosaukia tarutaoensis* Kobayashi, 1957).

non 1957. *Coreanocephalus planulatus* Kobayashi, p. 379, pl. 4, figs 16–17 (= *Thailandium solum* Kobayashi, 1957).

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

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

2007 *Lichengia* sp. undet. Shergold; pg. 59-60, fig. 33.

2023 *Lichengia simplex* Wernette *et al.*, pg. 73, fig. 54A-B.

Material. 29 cranidia from PG5 0.59 m (20-PG-18_1 interrnal and external mold), 0.89 m (20-PG-22_12), 5.8 m (20-PG-16_8, 20-PG-17_2, 20-PG-17_3, 20-PG-17_8, 20-PG-17_16, 20-PG-17_20, 20-PG-17_24, 20-PG-17_25, 20-PG-17_26, 20-PG-17_29, 20-PG-17_46, 20-PG-17_49, 20-PG-17_50), 7.24 m (20-PG-10_5, 20-PG-10_9, 20-PG-10_35), 9.55 m (20-PG-08_1, 20-PG-08_4 internal and external mold), 23.87 m (20-PG-83_11, 20-PG-83_13, 20-PG-83_14, 20-PG-83_26, 20-PG-83_29, 20-PG-83_31, 20-PG-83_50, 20-PG-83_65, 20-PG-83_67, 20-PG-83_71). 5 cranidia from KH1 8.6 m (20-KH-05_15, 20-KH-05_23, 20-KH-05_27, 20-KH-05_40), 12.42-12.66 m (20-KH-07_4). 6 librigena from PG5 0.59 m (20-PG-18_10, 20-PG-18_11), 0.89 m (20-PG-22_11), 7.24 m (20-PG-10_68, 20-PG-10_69), 23.87 m (20-PG-83_64). 9 pygidia from PG5 0.59 m (20-PG-18_4, 20-PG-18_9), 5.8 m (20-PG-17_9, 20-PG-17_23), 7.24 m (20-PG-10_30 external mold, 20-PG-10_51, 20-PG-10_58, 20-PG-10_65), 9.55 m (20-PG-08_9), 23.87 m (20-PG-83_45). 1 pygidium from KH1 8.6 m (20-KH-05_20 internal and external mold).

Diagnosis. Cranidium subrectangular to subtrapezoidal, with subtrapezoidal anteriorly-narrowing glabella. Up to three pairs of glabellar furrows discontinuous across midline, S2 and S3 not confluent with axial furrows. S1 and S2 posteriorly-directed, S3 transverse to anteriorly-directed. Elongate anterior border partially obscuring medially shallowing anterior border furrow; differentiation of frontal area difficult to determine. Small, densely packed tubercules ornamenting glabella, palpebral lobes, and frontal area. Short, strongly arcuate palpebral lobes parallel to slightly abaxially slanted posteriorly, with midpoint opposite to slightly posterior S1. Narrow librigenae with wide lateral border and confluent posterior and lateral border furrows continuing a short distance into genal spine. Pygidium subovoid to sub-trapezoidal, with 3-4 axial rings and long post-axial area. Post-axial ridge follows terminal axial segment. Pleural and interpleural furrows deeply incised, strongly swept towards narrow posterior border. Anterior propleurae reduced between segments 2-4.

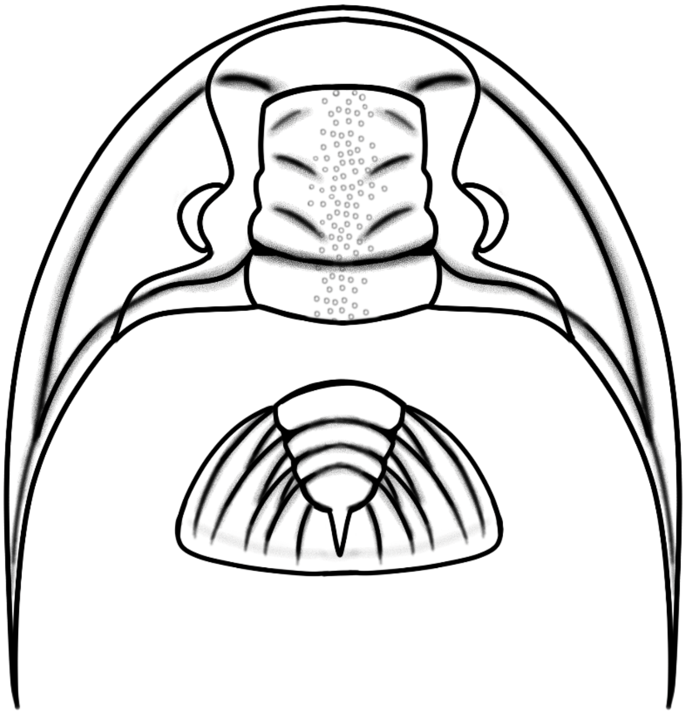

Figure 15. *Lichengia simplex* reconstruction.

Figure 15

Discussion. Shergold et al. (1991) differentiated *Lichengia simplex* from *Lichengia? tarutaoensis* based on the supposed deeper, wider anterior border furrow and more ovoid pygidium of *tarutaoensis* (Shergold et al., 1988). However, the Thai material representing *Lichengia? tarutaoensis* and the Australian material of *L. simplex* show overlapping instraspecific variation in frontal area form and anterior border furrow completion, and pygidial differences between the two are explained by the misattribution of the pygidium of *Thailandium solum* Kobayashi (1957) to *Lichengia? tarutaoensis* (see Wernette et al. (2020a)). Based on these features and the corrected association, Wernette et al. (2023) synonymized the two species. The Shan State material representing *L. simplex* has a number of individuals with less complete anterior border furrows than those figured in Shergold et al. (1991) (compare fig. 16I, N, O to Shergold et al. (1991) pl. 4 figs. 1-2) but this trait is not sufficiently distinct to warrant a new species name considering the significant intraspecific variation and the fact that some Shan State material (e.g. fig. A) shows a comparable condition of the anterior border furrow. Therefore, the Shan State material is here assigned to *L. simplex.*

Specimens of *Lichengia simplex* with a more complete anterior border furrow (e.g. fig. 16A, E, F, J, K) appear similar in many respects to *Prosaukia tarutaoensis,* a species of *Prosaukia* found in the Tarutao Group of Thailand defined by its short preglabellar field and long anterior border. However, *L. simplex* is differentiated from *P. tarutaoensis* by its discontinuous or only weakly continuous S1, as well as by the presence of a sub-trapezoidal pygidium with strongly posteriorly-directed and clearly incised pleural and interpleural furrows, which presents a strong contrast to the elliptical, effaced *P. tarutaoensis* pygidium.

Three cranidial and three pygidial fragments from the Clark Sandstone of the Bonaparte Basin, Australia (Shergold et al. (2007) figs. 33A-E) were assigned to *Lichengia* sp. undet on the basis of the incomplete, medially obscured anterior border furrow. Affinity with *L. onigawara* was suggested by the subtrapezoidal pygidium with a truncated second propleura, deeply incised and sagitally disconnected glabellar furrows, and expanded anterior border obscuring the preglabellar furrow; however, the suggested similarities are generally diagnostic of *Lichengia* rather than specifically suggestive of *L. onigawara.* Additionally, the Bonaparte material possesses the transverse to slightly anteriorly-directed

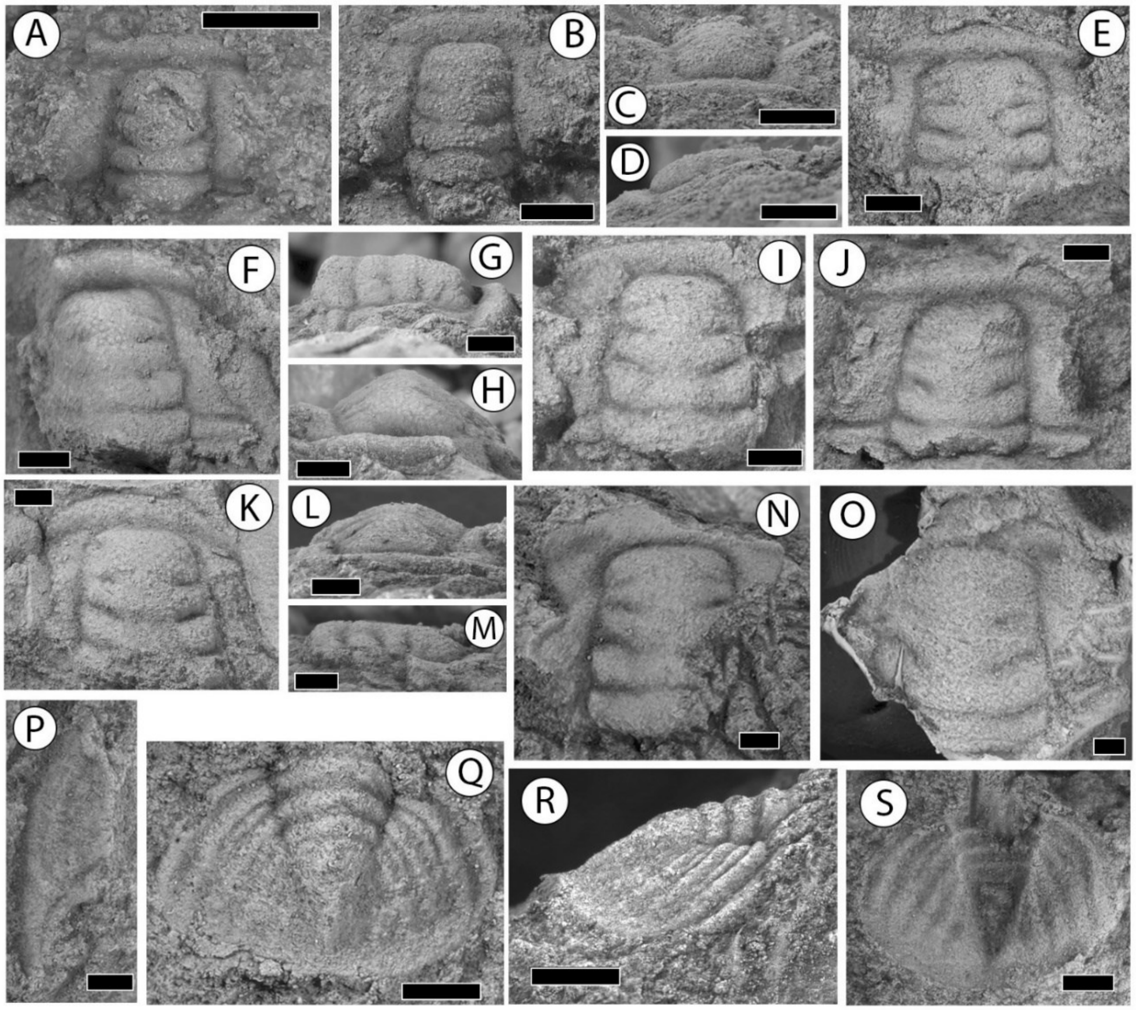

Figure 16. *Lichengia simplex.* A, 20-KH-05_40, cranidium. B-D, 20-KH-05_27, cranidium in: C, anterior; D, lateral. E, 20-PG-83_29, cranidium. F-H, 20-PG-83_13, cranidium in: G, lateral; H, anterior. I, L-M 20-PG-08_1, cranidium in: L, anterior; M, lateral. J, 20-PG-83_50, cranidium. K, 20-PG-83_14, cranidium. N, 20-PG-16_8, cranidium. O, 20-PG-17_3, cranidium. P, 20-PG-18_10, librigena. Q-R, 20-KH-05_20cp, pygidium in: Q, counterpart; R, lateral. S, 20-PG-83_45, pygidium.

Figure 16

S3 of *L. simplex,* as well as being significantly less expanded at L1 than in *L. onigawara,* which exhibits an L2:L1 width ratio of about 83% (see Lu et al. (1965) pl. 89 fig. 1) in comparison to the 92% of the Bonaparte material, a ratio much more comparable to the 89-96% L2:L1 width range of *L. simplex*. Though Shergold et al. (2007) suggests that the pygidia of *Lichengia* sp. undet. are unbordered, it is difficult to confidently accept this assessment due to the incomplete nature of the pygidia. On this basis we tentatively assign *Lichengia* sp. undet. to *L. simplex.*

***Lophosaukia* Shergold (1972)**

Type species. *Lophosaukia torquata* Shergold, 1972 Gola Beds, Western Queensland, Australia

Discussion. *Lophosaukia* is in many respects similar to other saukiid taxa, possessing a long, subparallel-sided to anteriorly-expanding glabella, with narrow fixigenae, large and posteriorly-positioned palpebral lobes located close to the axial furrows, an undifferentiated frontal area, and a deep, clearly-incised preglabellar furrow undercutting the glabellar anterior (Shergold, 1972; Sohn & Choi, 2007; Wernette et al., 2023). The defining feature of the genus is the angular, downsloping projection of its frontal area, which differentiates it from other saukiid genera with undifferentiated frontal areas, such as *Eosaukia.* This angular projection is similar to that of *Linguisaukia* Peng (1984) and *Sinosaukia* Sun (1935). *Lophosaukia* can be differentiated from *Linguisaukia* by its long palpebral lobes, narrow fixigenae, anteriorly-expanding glabella, and the lack of a prominent occipital spine. The anterior angular tongue of *Linguisaukia* is often longer than that of *Lophosaukia;* however, this is not the most influential differentiating characteristic, as the anterior projection of *Lophosaukia jiangnanensis* is comparatively long proportional to the glabella. The convex anterior border, shallow preglabellar furrow, and slightly wider fixigenae of *Sinosaukia* serve to distinguish the genus from *Lophosaukia.*

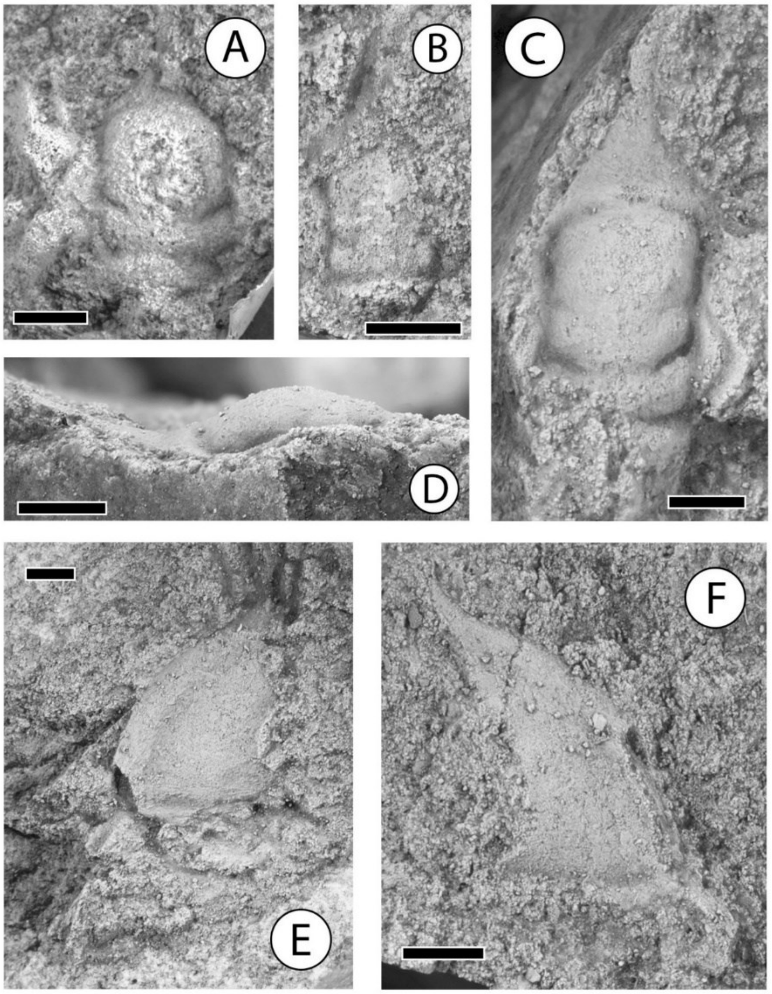

Figure 17. *Lophosaukia?* sp. undet. A, 20-PG-22_49, cranidium. B, 20-KH-05_3, cranidium. C-D, 20-PG-22_1, cranidium in: D, lateral. E, 20-PG-22_31, librigena. F, 20-PG-22_30, librigena. Scale bars represent 2 mm.

Figure 17

Lophosaukia librigena are characterized by the confluent lateral and posterior border furrows, the semicircular shape, the curved genal spine, and the presence of ridged or striated structures on the lateral border and/or genal spine. The *Lophosaukia* pygidium is short, ovate to near-biconvex in shape, and pauci-segmented, with 2-4 axial segments; it is thus similar to the *E. buravasi* pygidium.

***Lophosaukia?* sp. undet. Öpik *in* Kaulback and Veevers (1969)**

1969 "saukiid… distinguished by a long frontal spike", Öpik in Kaulback & Veevers
2007 Shergold *et al.,* fig. 36 pg. 62

Material. 2 cranidia from PG5 0.89 m (20-PG-22_1, 20-PG-22_49 external mold). 1 cranidium from KH1 8.6 m (20-KH-05_3). 2 librigena from PG5 0.89 m (20-PG-22_30, 20-PG-22_31).

Description. A saukiid species defined primarily by a frontal area extending into a long and tapering "spike" approximately 67% of occipital-glabellar length, which slopes upwards anteriorly of the glabellar margin. The spike is proportionally longer in smaller specimens, up to 1.35x of the occipital-glabellar length. The cranidium is subrectangular, and the glabella is parallel-sided to slightly anteriorly narrowing, with an anterior width between 85-95% of its L1 width. Glabellar width at L1 varies between 60-75% of occipital-glabellar length, and the occipital lobe is approx. 1-1.11x the widest glabellar point. The fixigena are narrow, and the palpebral lobes are short and posteriorly-located, approximately 32% of occipital-glabellar length. The palpebral lobes are nearly confluent with the axial furrows, with a midpoint approximately level with S1. Oblique, anteriorly-directed anterolateral furrows can be seen extending from the glabellar anterior. The preglabellar furrow is shallow and does not appear to undercut the glabellar anterior. Ornamentation is unclear on cranidium and associated librigena, save for striation visible on the lateral border of the teardrop-shaped librigena, which are characterized by long, narrow genal spine and confluent lateral and posterior furrows. No associated pygidia are known.

Discussion. *Lophosaukia?* sp. undet. was first described in detail in Shergold et al. (2007), where two incomplete cranidia and three librigenae were described from the Bonaparte Basin of Australia. It is primarily characterized by the extension of its anterior border into an extended “spike”, which tapers anteriorly to an angular point. This spike is exceptionally long; in specimens where it is complete or near-complete, its length is near-equal to the occipital-glabellar length. Despite this unusual feature, it is unquestionably saukiid in form particularly in the glabella, which appears similar to those of other saukiid genera such as *Prosaukia, Lophosaukia,* and *Eosaukia* (e.g. *E. acuta* and some *E. buravasi*). The presence of an S1 furrow continuous across the midline also supports its position within the saukiids.

The assignment of this saukiid species to *Lophosaukia* is questionable, as it possesses features present in *Lophosaukia, Linguisaukia,* and *Sinosaukia* (Shergold et al., 2007). Although its short, posteriorly-positioned palpebral lobes and shallow preglabellar furrow are *Linguisaukia*-like, the anterior expansion of the glabella, narrow fixigenae, and lack of an occipital spine are more similar to *Lophosaukia* and *Sinosaukia.* However, the degree of angularity of the anterior margin is also more pronounced than is characteristic of *Sinosaukia,* as is the relatively mild degree of anterior expansion. Additionally, one cranidium figured in Shergold et al. (2007) (fig. 36B) appears to possess an oblique anterolateral furrow extending from the anterior corner of the glabella, a characteristic also seen in some *Lophosaukia*, e.g. *L. nuchangoni* Wernette et al. (2023) figs. 56B, 56D. The associated librigenae present a striated lateral border, similar to that observed in other species of *Lophosaukia* (see (Peng, 1992) fig. 24C). The long frontal spike, however, is unlike the anterior projection assigned to either genus, and distinguishes it significantly from both; it is therefore likely that *Lophosaukia?* sp. undet. represents a new species or potentially a new genus. However, no pygidia have been assigned to this species, preventing a full diagnosis of the novel species or potentially novel genus it represents. Here it is assigned to *Lophosaukia?* sp. undet., in keeping with Shergold et al. (2007).

Pacootasaukia **Sohn and Choi (2005)**

Type species. *Platysaukia jokliki* Shergold, 1991, Pacoota Sandstone, Amadeus Basin, Northern Territory, Australia.

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Diagnosis. Cranidium subtrapezoidal. Broad, rectangular to subrectangular glabella, anterior transverse. Long, gently convex undifferentiated frontal area continuous with fixigenae. SO & S1 furrows continuous and clearly incised, S2 furrow discontinuous across midline. All furrows gently bowed posteriorly. Palpebral lobes strongly arcuate, laterally separated from axial furrows. Midpoint of palpebral lobes S1. Posterolateral projections posteriorly directed abaxially. Librigenae with wide lateral and posterior borders, lateral border furrow shallow, confluent with deeply incised posterior border furrow and continuing a short way into base of genal spine. Ridged structure on doublure. Pygidium subtriangular to semicircular in outline, with 4-7 axial rings. Pleural furrows well-defined, interpleural furrows fainter. Furrows swept strongly posteriorly. Pleurae unevenly divided. Propleurae of second and subsequent segments reduced, opisthopleura prominent, extending to broad pygidial border.

Discussion. *Platysaukia* Kobayashi (1960) was originally erected based on a single, poorly-preserved cranidium lacking a frontal area from the Hwaejol Formation of South Korea assigned to *P. euryrachis* Kobayashi (1960). Sohn and Choi (2005) considered *Platysaukia euryrachis* to be a junior synonym of *Hamashania pulcheri* Kobayashi (1942) due to its weakly bulging glabella and large palpebral lobes, rendering the genus invalid. However, two other species of *Platysaukia* described from the Pacoota Sandstone of Western Australia, *Platysaukia jokliki* Shergold (1991) and *Platysaukia tomichi* Shergold (1991), were considered to be distinct from both *Hamashania* and from existing saukiid genera. The genus *Pacootasaukia* was erected based on this material, with type species *Platysaukia jokliki* (Sohn & Choi, 2005). Features distinguishing *P. jokliki* and *P. tomichi* from *Hamashania* include a continuous, firmly incised S1 furrow, a gently convex and undifferentiated frontal area, and palpebral furrows that do not merge with the axial furrow (as is the condition in *Hamashania*), but rather are separated by the fixigenae. Therefore, the genus *Pacootasaukia* Sohn & Choi (2005) was erected to contain both species, with type species being *P. jokliki*.

While Shergold et al. (1991) assert that species now assigned to *Pacootasaukia* possesses faint differentiation between the preglabellar field and anterior border, visual examination of the illustrations of *P. jokliki* and *P. tomichi* specimens depicted in Shergold et al. (1991) does not reveal any such division. Here we describe *Pacootasaukia* as possessing an undifferentiated frontal area, a trait which distinguishes it from *Prosaukia*, which it is otherwise visually similar to, and aligns it with other saukiids possessing an undifferentiated frontal area, such as *Calvinella* and *Mictosaukia*. The length of the frontal area and the lack of anterolateral furrows distinguishes *Pacootasaukia* from other saukiids with undifferentiated frontal areas, such as *Eosaukia, Mictosaukia,* and *Diemanosaukia*, as well as from *Tellerina* and *Calvinella.* This lack of anterolateral furrows can be distinctly seen in fig. 18J.

Two pygidia from the Clark Sandstone of the Bonaparte Basin, Australia were assigned to *Pacootasaukia* sp. undet. by Shergold et al. (2007), based on the markedly reduced propleurae of the second and subsequent pygidial segments that are both notably short (exsag) and narrow (tr.). However, both pygidia are considerably narrower and longer than previously documented from *P. jokliki* and *P. tomichi*, and in fact resemble the highly distinctive ovoid/fusiform pygidia of *Hamashania pulchera* and *Hamashania* cf. *H. busiris* Walcott (1905) (Sohn and Choi (2005), fig. 3D & F-J). Close examination of the illustrations of the *Hamashania* pygidia depicted in Sohn and Choi (2005) (fig. 3D & H-J) reveals a similar reduction in the propleurae, as in *Pacootasaukia*. This trait links *Hamashania* with saukiids such as *P. jokliki*, despite the striking similarity of its cranidial characters and proportions to the dikelocephalid *Osceolia osceola* Hall (1863). Both parsimony-based and Bayesian phylogenies of dikelocephalids in Srivastava and Hughes (2023) placed *Hamashania pulchera* near the base of the dikelocephalid phylogeny, indicating that it is not closely related to *Osceolia*; the shared trait of reduced propleurae suggests that it is instead located close to forms such as *Pacootosaukia* within the "Saukiidae" a group that, as currently defined, is paraphyletic at best. Cranidial similarity of *Osceolia* and *Hamashania,* especially in the narrow fixigena and elongated glabella and frontal area with an upturned anterior lip, may indicate convergent evolution of the cranidium in both Laurentian dikelocephalids and certain Gondwanan saukiids, although their pygidia are notably dissimilar.

***Pacootasaukia jokliki* Shergold (1991)**

Fig. 18

1991 *Platysaukia jokliki* Shergold; p. 25-26, pl. 3 figs. 1-22.

Material. 16 cranidia from 15.8-15.9 m (20-KS-01_4, 20-KS-01_5, 20-KS-01_7, 20-KS-01_9, 20-KS-01_33, 20-KS-01_34, 20-KS-01_37, 20-KS-01_38, 20-KS-01_41, 20-KS-01_42, 20-KS-01_43, 20-KS_01_45, 20-KS-01_46, 20-KS-01_48, 20-KS-01_51, 20-KS-01_60). 11 librigena from 15.8-15.9 (20-KS-01_2, 20-KS-01_13, 20-KS-01_14, 20-KS-01_16, 20-KS-01_20, 20-KS-01_24, 20-KS-01_27, 20-KS-01_47, 20-KS-01_52, 20-KS-01_53, 20-KS-01_58). 8 pygidia from 15.8-15.9 m (20-KS-01_10, 20-KS-01_15, 20-KS-

01_17, 20-KS-01_26, 20-KS-01_28 external mold, 20-KS-01_40, 20-KS-01_50, 20-KS-01_59 external mold).

Diagnosis. Slightly anteriorly narrow glabella widest at L1. Wide frontal area and occipital ring. Semicircular to subelliptical pygidia with 4-7 axial segments and narrow border.

Description. These remarks supplement the description given by Shergold et al. (1991). The Shan State cranidia range from 2.3 mm to 7.6 mm in length (posterior of SO to anterior border), though the largest specimen may have been >9 mm in length when intact; this is comparable in size to the material illustrated by Shergold et al. (1991). The glabella is subrectangular, with a transversely flat anterior border and anterior corners more rounded in smaller holaspids. Shergold et al. (1991) noted pronounced anterior glabella narrowing in small specimens, but the Shan State material displays a glabella anterior about 80-85% of L1 length at all sizes, suggesting that apparent size-related variation in the glabella is an artifact of the more rounded anterior glabellar corners in small holaspids rather than the glabella becoming more uniformly rectangular with growth. Palpebral lobes are approximately 50% of glabellar length in all specimens. Occipital lobe ranges from 5-17% wider than L1 with a mean of 11%. Shergold et al. (1991) suggested the presence of an occipital node in younger holaspids; however, this feature is not evident in the Shan State cranidia despite the similar size range. The long, undifferentiated frontal area is continuous with the fixigenae, which are relatively wide compared to those of other saukiids.

Pygidia are semicircular to subelliptical in shape, with 4-7 axial rings; those from the Shan State material most often have 4-5 axial rings. Well-incised pleural furrows and fainter interpleural furrows both sweep backwards towards a wide pygidial border, with interpleural furrows truncating the propleuron of the following segment. Opisthopleurae extend across much of the pleural field.

Discussion. Previous *Pacootasaukia* material found in Sibumasu consists of three cranidia from the Ao Mo Lae Formation of Ko Tarutao (Wernette et al., 2023). These were not assigned to *P. jokliki* due to the presence of wider fixigenae and a more rounded anterior glabella margin. Comparing the Thai material to the material described herein, the fixigenae are narrower in the Burmese material, consistent with *P. jokliki.* While we acknowledge the rounding of the anterior glabellar corners in many of the smaller Shan State cranidia, the anterior border appears flat and transverse, consistent with the condition in *P. jokliki*, to which we assign it.

While the cranidia of the Shan State material are comparable in size to the material depicted in Shergold et al. (1991) from the Pacoota Sandstone, the Shan State pygidia are small, with length ranging from 3 to 7 mm and width ranging from 5 to 9 mm. The largest pygidium (fig. 18N-O) may have been 13-14 mm wide when whole. In contrast, the Australian pygidia are larger; while the smallest is 5 mm wide and 2.63 mm long, the others range from 13-43 mm wide

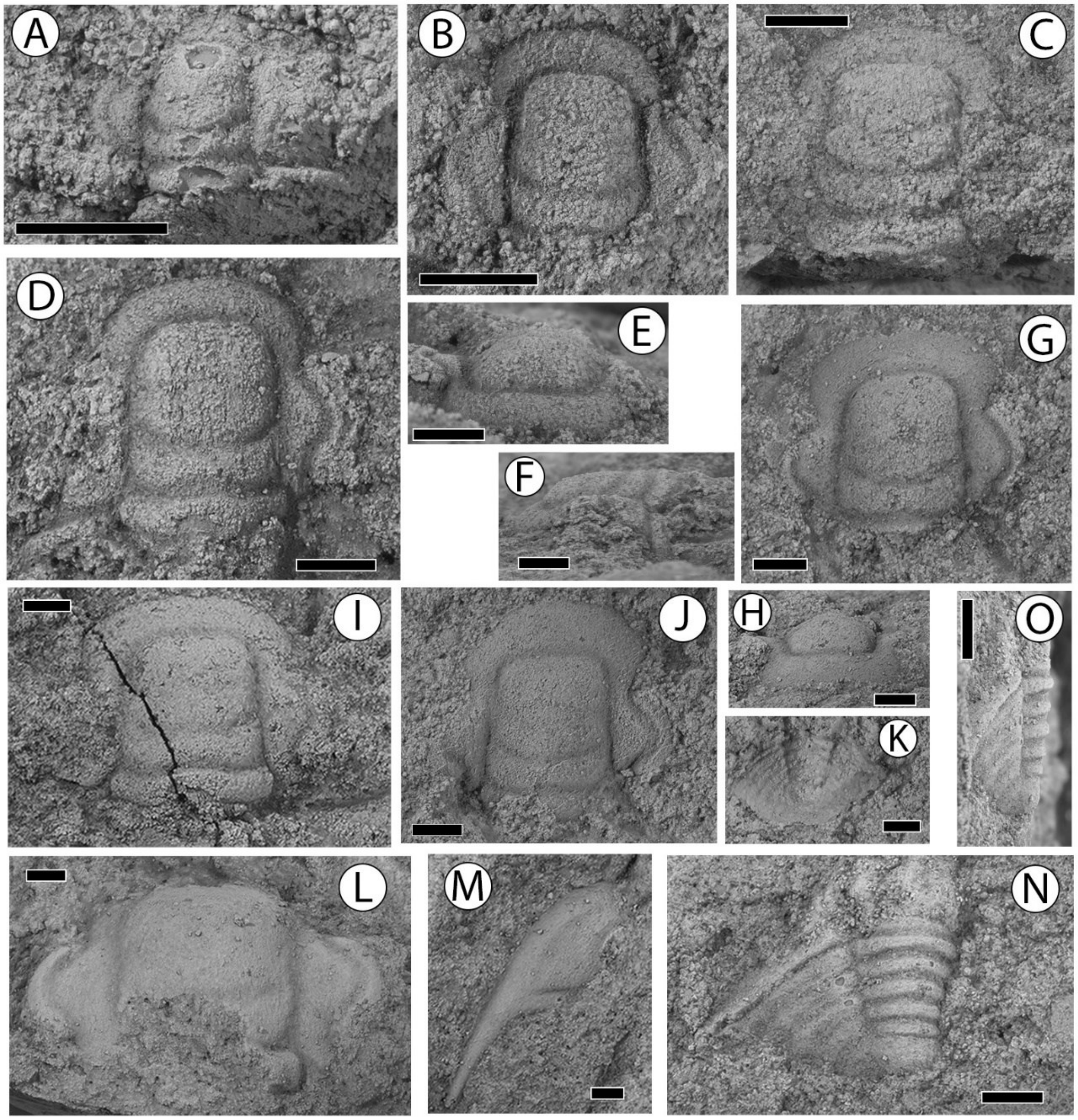

Figure 18. *Pacootasaukia jokliki.* A, 20-KS-01_60, cranidium. B, 20-KS-01_41, cranidium. C, 20-KS-01_45, cranidium. D-F, 20-KS-01_37, cranidium in: E, anterior; F, lateral. G-H, 20-KS-01_33, cranidium in: H, anterior. I, 20-KS-01_5, cranidium. J, 20-KS-01_43, cranidium. K, 20-KS-01_26, pygidium. L, 20-KS-01_7, cranidium. M, 20-KS-01_20, librigena. N-O, 20-KS-01_59, pygidium in: O, lateral. Scale bars represent 2 mm.

Figure 18

and 7-25 mm long. The two largest pygidia depicted from the W Australian material, (Shergold et al. (1991), pl. 3 figs. 12 & 13) both have 7 axial rings, while other, smaller pygidia in both the Australian and Shan State material only possess 4-5. This increase in axial rings among larger pygidia suggests that *Pacootasaukia* may have undergone protarthrous development, in which the addition of segments in the pygidia continued after the onset of the holaspid phase (Hughes et al., 2006).

Prosaukia **Ulrich and Resser (1933)**

Type species. *Dikelocephalus misa* Hall, 1863, Tunnel City Group, Wisconsin, U.S.A.

Discussion. *Prosaukia* is a widespread genus found in abundance in both Laurentian and Gondwanan late Cambrian strata, and diverse both intra- and inter-specifically (Wernette et al., 2023). Although it was initially established by Ulrich and Resser (1933), the original generic diagnosis is vague and nonspecific; initially established diagnostic traits of the genus, including a subrectangular glabella tapering slightly anteriorly, shallowing anterior border furrows, lack of confluence in lateral and posterior border furrows, and glabellar furrows varying in depth and number (Ulrich & Resser, 1933; Taylor & Halley, 1974) could apply more generally to many saukiid genera. While these traits are present in *Prosaukia*, the most prominent diagnostic feature of the genus is the division of the frontal area into a depressed preglabellar field and convex anterior border (Ludvigsen & Westrop, 1983), with an additional subsequently established diagnostic trait in the form of anteriorly divergent facial sutures, established by Wernette et al. (2020a). The librigenae of *Prosaukia* possess an unadvanced genal spine, and the pygidium is subelliptical, with evenly-divided pleurae and a broad border (Ludvigsen & Westrop, 1983; Wernette et al., 2020a; Wernette et al., 2023). The division of the frontal area into preglabellar field and anterior border distinguishes *Prosaukia* from *Saukia* and *Tellerina,* but it is more difficult to separate from *Saukiella* on the basis of cranidial characteristics, as *Saukiella* also possesses a preglabellar field, though it may be narrower than that of *Prosaukia* (Ludvigsen & Westrop, 1983; Wernette et al., 2023). Among saukiids, *Prosaukia* can be compared to other genera possessing a preglabellar field, such as *Andersonella, Caznaia, Thailandium,* and *Sinosaukia*.

Prosaukia and *Hoytaspis* Ludvigsen and Westrop (1983) are similar in many respects, but differ most notably in that the preglabellar field among *Prosaukia* species is depressed and lies below the level of the anterior border, whereas the preglabellar field in *Hoytaspis* is inflated to or above the level of the anterior border (Ludvigsen & Westrop, 1983; Wernette et al., 2023). In the *Hoytaspis* librigenae, as in *Prosaukia*, the lateral and posterior border furrows are non-confluent; however, the posterior furrow of *Hoytaspis* most often extends into the genal spine (Shergold et al., 1988). Pygidia of *Hoytaspis* also have a narrower border and more pronounced post-axial ridge than those of *Prosaukia*.

Ulrich and Resser (1933) initially established 29 species of *Prosaukia* from the Upper Mississippi Valley; however, this number was artificially inflated due to the disregard for intraspecific variation, establishment of species based on insufficient material and type specimens, and the exaggerated importance of minor differences.

Raasch (1951) condensed these assignments to 13 valid species (Raasch, 1951; Ludvigsen & Westrop, 1983). Intraspecific variation is further complicated by ontogenetic variation, which may affect various diagnostic traits, e.g. depth and width of anterior border furrow, width of pygidial border, and ornamentation (Ludvigsen & Westrop, 1983). Additionally, otherwise morphologically identical species of *Prosaukia* have historically been given different assignments based on their respective paleogeographical continent, further splitting the genus. A detailed geometric morphometric analysis of the genus *Prosaukia* is required to fully resolve the validity of species within the genus.

In the Tarutao Group of Thailand, five different species of *Prosaukia* have been documented: *P. tarutaoensis, P. oculata,* and three unnamed species known from sparse tagma found in the Ao Mo Lae formation (Wernette et al., 2020a; Wernette et al., 2023).

Prosaukia oculata **Wernette et al. (2020a)**

Fig. 19

1988 *Lichengia? tarutaoensis* (Kobayashi); Shergold *et al.*, p. 309–310, fig. 5W only (*non* figs. 5S-V = *Lichengia simplex*)

2020 *Prosaukia oculata* Wernette *et al.,* p. 79, fig. 13.

2023 *Prosaukia oculata* Wernette *et al.,*

Material. 2 cranidia from PG5 8.6 mj (20-PG-05_6, 20-PG-05_7). 1 pygidium from PG5 13.11 m (20-PG-05_1). 1 pygidium from KH1 8.6 m (20-KH-05_35).

Diagnosis. Rectangular cranidium with wide (tr.) fixed cheeks and palpebral lobes. Short preglabellar field. Palpebral lobes strongly arcuate, midpoint at or posterior to S1. Pygidium subcircular in shape with wide border, propleurae reduced, opisthopleurae inflated (exsag., tr.). 3-4 axial rings. Post-axial ridge continues to pygidial edge.

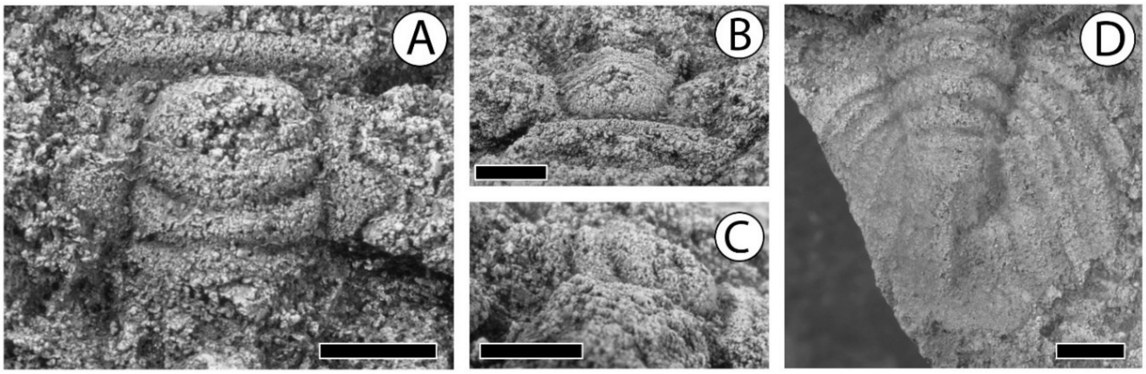

Figure 19. *Prosaukia oculata.* A-C, 20-PG-05_6, cranidium in: B, anterior; C, lateral. D, 20-KH-05_35, pygidium. Scale bars represent 2 mm.

Figure 19

Description. Comprehensive recent description in Wernette et al. (2020a).

Remarks. The pygidium of *Prosaukia oculata* is in some ways similar to the pygidium of *Lichengia simplex,* with 3-4 axial rings, pleural and interpleural furrows strongly posterior-sweeping, reduced propleurae, and expanded opisthopleurae. The two can be distinguished primarily by shape; the *P. oculata* pygidium is subcircular in shape and has a much wider border, whereas the *L. simplex* pygidium flattens towards the back, creating a subovoid to subtrapezoidal shape. Further remarks on *P. oculata* can be found in Wernette et al. (2020a).

***Prosaukia kyaingseini* sp. nov.**

Fig. 20-23

Material. 34 cranidia from PG5 0.59 m (20-PG-18_12), 0.89 m (20-PG-22_2, 20-PG-22_3, 20-PG-22_8, 20-PG-22_19, 20-PG-22_20, 20-PG-22_22, 20-PG-22_25, 20-PG-22_29, 20-PG-22_34, 20-PG-22_44, 20-PG-22_45, 20-PG-22_48, 20-PG-22_54), 5.8 m (20-PG-16_3, 20-PG-16_6, 20-PG-16_7, 20-PG-16_9, 20-PG-17_1, 20-PG-17_5, 20-PG-17_7, 20-PG-17_17, 20-PG-17_21 internal and external mold, 20-PG-17_22 external mold, 20-PG-17_27, 20-PG-17_28, 20-PG-17_30, 20-PG-17_33, 20-PG-17_35, 20-PG-17_36, 20-PG-17_40, 20-PG-17_43, 20-PG-17_47, 20-PG-17_53). 2 cranidia from KH1 8.6 m (20-KH-05_9), 8.97 m (20-KH-01_3). 1 cranidium from PG1 4.5 m (16-PG-02_16). KS1 15.8-15.9 (20-KS-01_31). 4 librigenae from PG5 0.89 m (20-PG-22_43 external mold, 20-PG-22_55), 5.8 m (20-PG-17_51, 20-PG-17_52). 1 librigena from KH1 8.97 m (20-KH-01_8). 2 pygidia from PG5 0.59 m (20-PG-18_2), 5.8 m (20-PG-17_34).

Diagnosis. Glabella subrectangular with slight tapering and gently curved anterior. Maximum glabellar width at L1 with LO of equal width or slightly wider. Long frontal area divided subequally by medially-shallowing anterior border furrow into longer preglabellar field and shorter anterior border. Anterior border furrow slightly arced to near transverse. Preglabellar field slightly inflated to level of anterior border. S1 and S2 furrows continuous across midline, S1 strongly incised and gently posteriorly bowed, S2 shallow and more transverse across midline, both medially shallowing. S3 effaced. Glabellar furrows confluent with axial furrows. Strongly arcuate palpebral lobes. Narrow fixigenae, anterior facial sutures divergent. Prominent tubercules covering entire cranidium with exception of palpebral lobes and anterior border; rows of large tubercles present on preglabellar field correspond with pits in anterior border furrow. Maximum occipital-glabellar length ~10 mm. Posterolateral projections long, posterior facial sutures angled with respect to posterior border furrow.

Narrow librigenae with lateral and posterior border furrows non-confluent, posterior border furrow extends some distance into base of genal spine. Notably broad lateral border, narrower posterior border, both lateral and posterior border furrows well-incised.

Pygidium broad and ovoid in shape, 5 clearly-incised axial rings plus more effaced sixth ring. Narrow, concave pygidial border. Protruding node present on either side (exsag.) of terminal axial segment. Interpleural furrows fainter than pleural furrows and occasionally difficult to distinguish. Maximum pygidium width ~4.79 mm.

Description. The cranidium is subrectangular, with a slightly anteriorly-tapering glabella widest at L1, ranging between 61-73% of occipital-glabellar length, and a maximum anterior glabellar width (measured across inflection point) on average 88% of the maximum L1 width. The occipital lobe is on average 10% wider than the maximum L1 width. The S1 and S2 furrows are continuous across the midline with slight medial shallowing, though the S2 furrow is shallower and more transverse adaxially than the posteriorly bowed S1. The S3 furrow is discontinuous and effaced. The fixigena are approx. 25% of occipital-glabellar length when measured from the midpoint of the palpebral furrow, and the palpebral lobes are 35-40% of occipital-glabellar length and symmetrically curved, with the midpoint opposite to slightly anterior abaxial S1 and the endpoints opposite S2 and SO. The palpebral lobes are approximately parallel to glabellar sides, with slight abaxial tilting towards the posterior. The frontal area is notably long (approx. 25-30% occipital-glabellar length) and convex, with an inflated preglabellar field representing approx. 60% of frontal area length. The anterior border furrow shallows slightly medially. The maximum frontal area width is equal to or slightly less than the width across the palpebral lobe midpoints. A tuberculate prosopon covers the entire cranidial surface, except the anterior border and palpebral lobes; rows of tubercles on the preglabellar field correspond with pits within the anterior border furrow, forming a striation-like appearance in some individuals (see fig. 22L). Thai material assigned to *P. kyaingseini* records long, posteriorly-directed posterolateral projections, though this trait is less clear in the Shan State material due to preservation bias.

The librigena are narrow, with broad, non-confluent lateral and posterior border furrows and short genal spines. The lateral border furrow shallows approaching the genal spine, though the posterior border furrow continues some distance along genal spine.

The pygidium is broad and ovoid to subovoid in shape, with a width approximately 1.65-1.7x pygidium length. It possesses 6 axial rings, as well as two protruding nodes on either side (exsag.) of terminal axial segment. The pleural furrows are deeply incised, though the interpleural furrows are shallower. One pygidium (fig. 21G, I) appears to have reduced propleuraem, while the opisthopleurae continue to the narrow, concave border, angling sharply towards posterior; this trait is not clear in the other pygidium assigned to *P. kyaingseini* (fig. 20H). The post-axial length and presence of a post-axial ridge are difficult to determine in the Shan State material; in the Thai material the axis represents approximately 88% of pygidial length, with the post-axial length very short.

Discussion. *Prosaukia* has been described from the Tarutao Group of Thailand since 2020, when Wernette et al. (2020a) re-assigned *Saukiella tarutaoensis* Kobayashi, 1957 and *Lichengia? tarutaoensis* (Kobayashi) Shergold, 1988 to *Prosaukia tarutaoensis* Kobayashi, 1957 and *Prosaukia oculata* Wernette, 2020 respectively, as well as figuring new material of both species. Since then, five putative species of *Prosaukia* have been described from Sibumasu: *P. tarutaoensis, P. oculata,* and three unnamed species from Tarutao, *Prosaukia* sp. 1, *Prosaukia* sp. 2, and *Prosaukia* sp. 3.

Prosaukia kyaingseini can be easily distinguished from figured *Prosaukia* material from Thailand representing *P. tarutaoensis* and *P. oculata. Prosaukia tarutaoensis* is a species of *Prosaukia* that has only been documented from Thailand's Tarutao Group and lacks representatives from the Myet-Ye Formation of Myanmar. It

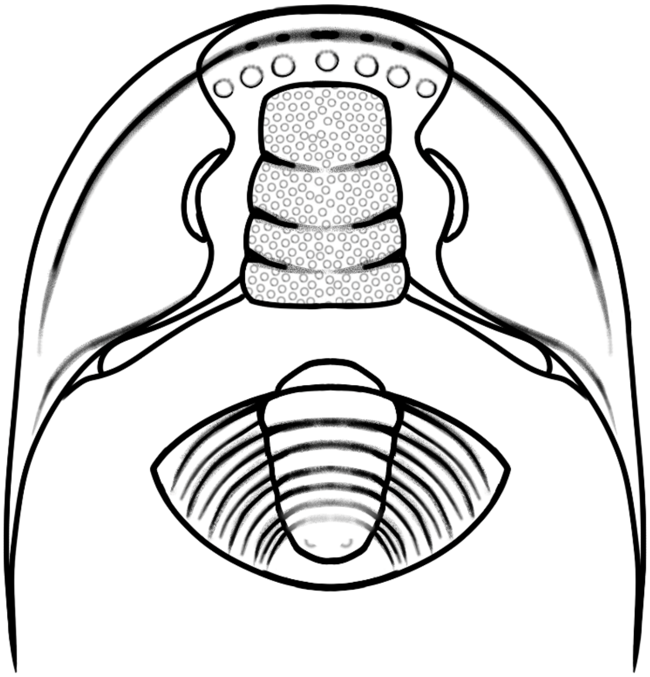

Figure 20. *Prosaukia kyaingseini* reconstruction.

Figure 20

possesses a subequally divided frontal area, with a short, concave preglabellar field and long anterior border, in comparison to the long and gently inflated preglabellar field of *P. kyaingseini.* The anterior tapering of the *P. kyaingseini* glabella is significantly less pronounced than in *P. tarutaoensis*; while the *P. kyaingseini* glabella is near parallel-sided, with an anterior glabellar lobe on average only 12% narrower than L1, the *P. tarutaoensis* anterior glabellar lobe on average is 23% than its L1. In contrast to the symmetrically-arched palpebral lobes of *P. kyaingseini,* the *P. tarutaoensis* palpebral lobes show greatest curvature posterior to the midpoint. Additionally, the pygidium of *P. tarutaoensis* is short and lenticular, a condition unusual in *Prosaukia* (Wernette et al., 2020a) and directly contrasting with the ovoid pygidium of *P. kyaingseini. Prosaukia oculata,* in contrast to *P. tarutaoensis,* has been described from the Shan State material (above); however, the short, concave preglabellar field, notably wide fixigenae, short, strongly arched palpebral lobes, and subcircular pygidium with consistently reduced propleurae of *P. oculata* (Wernette et al., 2020a) render it distinct from both *P. tarutaoensis* and *P. kyaingseini.*

Specimens of *Prosaukia kyaingseini* from the Shan State have not previously been compared to the unnamed species of *Prosaukia* described from the Tarutao Group. We here provide the first comprehensive comparison of the described *Prosaukia* material. *Prosaukia kyaingseini* differs significantly from both *Prosaukia* sp. 2 and *Prosaukia* sp. 3 of the Tarutao Group.

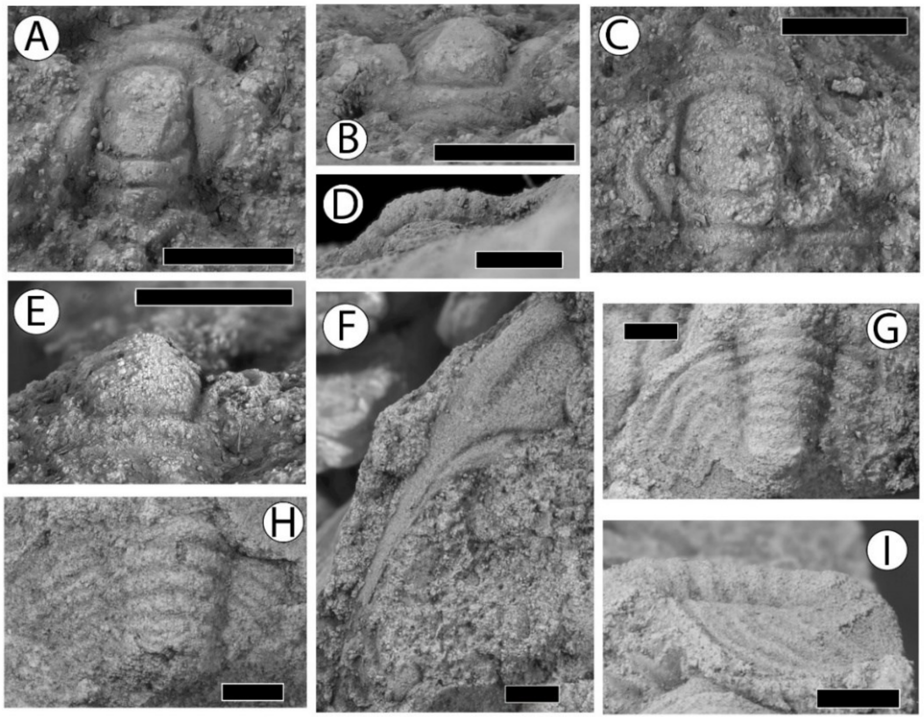

Figure 21. *Prosaukia kyaingseini.* A-B, 20-PG-22_54, cranidium in: B, anterior. C-E, 20-PG-22_29, cranidium in: D, lateral; E, anterior. F, 20-PG-22_55, librigena. G, I, 20-PG-17_34, pygidium in: I, lateral. H, 20-PG-18_2, pygidium. Scale bars represent 2 mm.

Figure 21

Prosaukia sp. 2 possesses a cranidium with abnormally long palpebral lobes, a barrel-shaped glabella with widest point at L2 and an occipital lobe narrower than L1, though

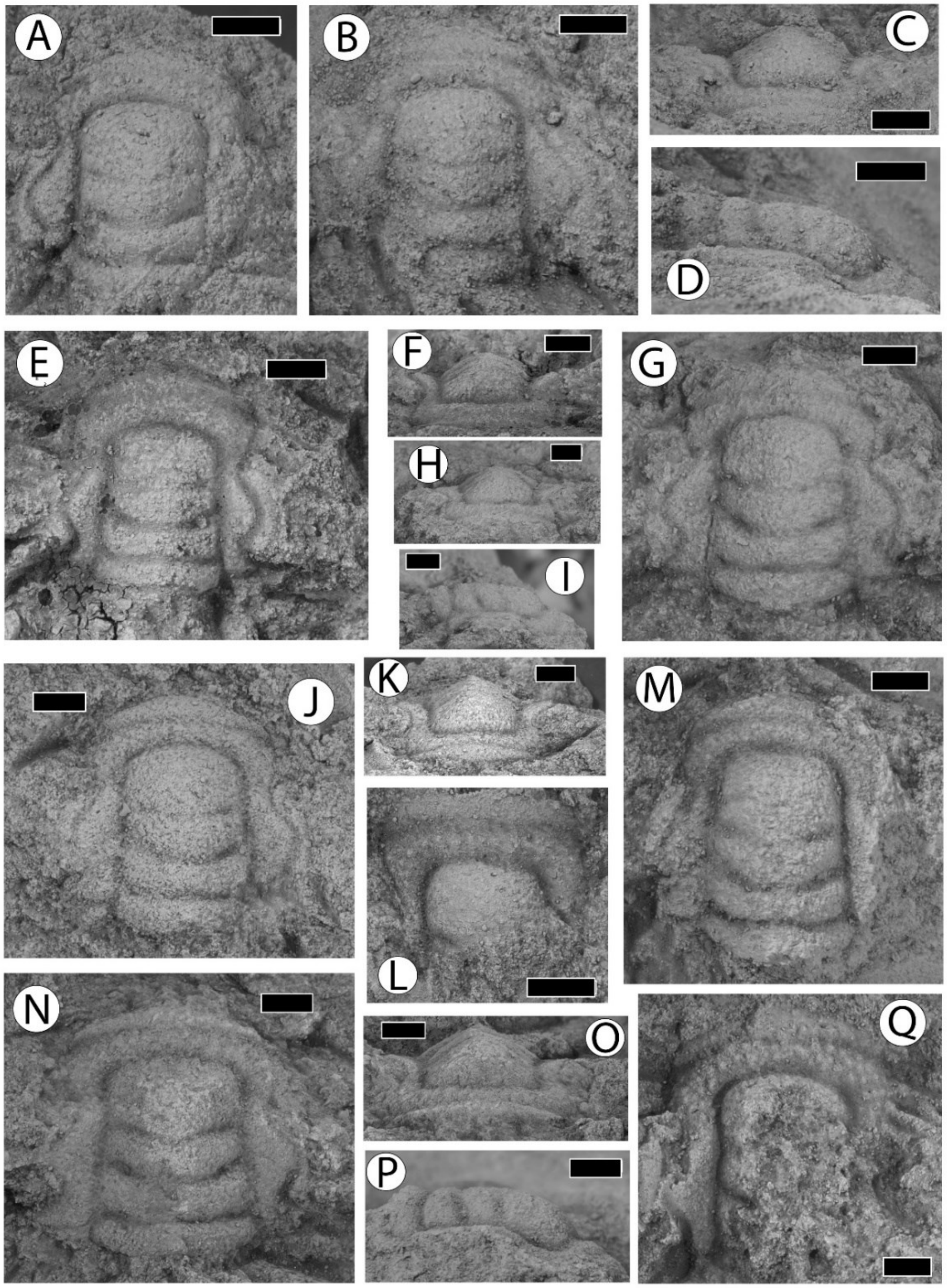

Figure 22. *Prosaukia kyaingseini.* A, 20-PG-17_28, cranidium. B-D, 20-PG-17_30, cranidium in: C, anterior; D, lateral. E-F, 20-PG-16_9, cranidium in: F, anterior. G-I, 20-PG-17_40, cranidium in: H, anterior; I, lateral. J-K, 20-PG-17_27, cranidium in: K, anterior. L, 20-PG-22_2, cranidium. M, 20-PG-17_5, cranidium. N-P, 20-PG-17_47, cranidium in: O, anterior; P, lateral. Q, 20-PG-22_22, cranidium. Scale bars represent 2 mm.

Figure 22

wider than preoccipital glabella. These present a significant difference from the slightly anteriorly tapering glabella and wide occipital lobe of *P. kyaingseini*. *Prosaukia* sp. 3, in contrast, is similar to *P. tarutaoensis,* but with a less strongly tapering glabella and narrow LO (Wernette et al., 2023), and thus shows many of the same differences with *P. kyaingseini.*

Both *Prosaukia* sp. 2 and *Prosaukia* sp. 3 possess a short preglabellar field depressed below the level of the anterior border.

In contrast to the other species of *Prosaukia* described from the Tarutao Group, the two Thai cranidia assigned to *Prosaukia* sp. 1 are morphologically extremely similar to those of *Prosaukia kyaingseini*. In particular, all possess a convex preglabellar field inflated to the level of the anterior border, a trait unusual in *Prosaukia.* A landmark-based morphometric analysis using 31 landmarks (fig. 23) on 8 specimens (7 cranidia representing *P. kyaingseini* from

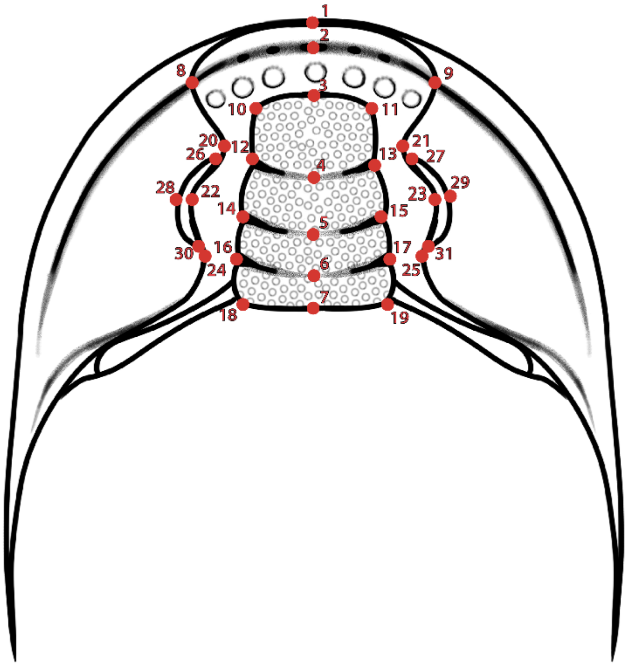

Figure 23. Landmark scheme used in geometric morphometric analysis of *Prosaukia kyaingseini* overlaid on *P. kyaingseini* reconstruction.

Figure 23

the Shan State, 1 cranidium representing *Prosaukia* sp. 1 from Tarutao) was performed, with non-axial landmarks reflected across the axis to maximize available sample size. A Procrustes superposition (fig. 24) shows that the Thai *Prosaukia* sp. 1 cranidium lies within the range of cranidial variation of the Shan State material depicting *Prosaukia kyaingseini.* This result is supported by the Principal Components Analysis (fig. 24), which shows the Thai specimen of *Prosaukia* sp. 1 as within the range of variation charted by *P. kyaingseini*. Ontogeny-related shape change manifests primarily in the shortening of the palpebral lobes and lengthening of the frontal area. These results support the synonymy of *P. kyaingseini* and *Prosaukia* sp. 1.

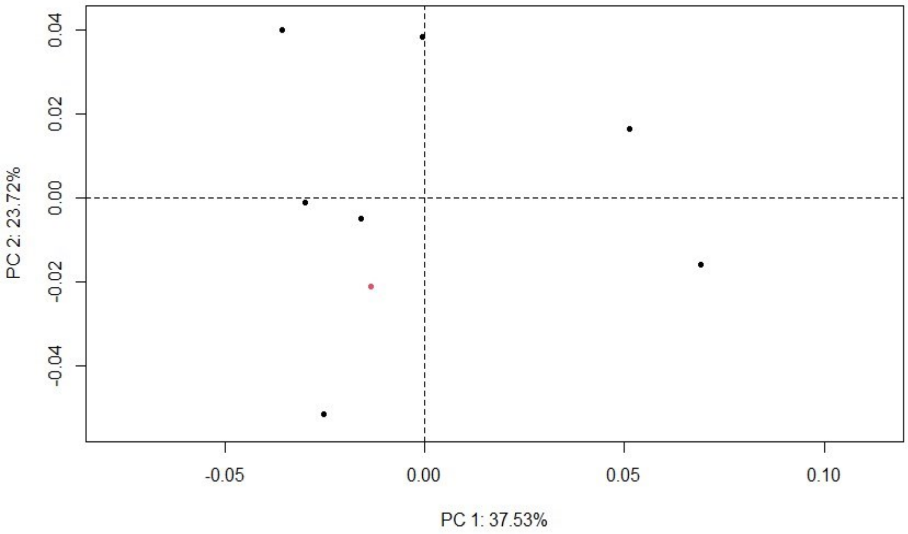

Figure 24. Principal Components Analysis for the analyzed specimens of *P. kyaingseini* from the Myet-Ye Formation and *Prosaukia* sp. 1 from the Tarutao Group. PC1 accounts for 37.53% of variance, and PC2 accounts for 23.72% of variance. The Thai cranidium representing *Prosaukia* sp. 1, figured in red, is within the cluster defined by the Shan State material, indicating that the degree by which it varies is not sufficient to differentiate

Figure 24

Several traits of *Prosaukia* sp. 1 are difficult to assess in *P. kyaingseini.* Particularly notable are the long, narrow, posteriorly-directed posterolateral limbs of *Prosaukia* sp. 1, which were identified as a diagnostic feature of the species (Wernette et al., 2023). As the posterolateral limbs of Shan State cranidia representing *P. kyaingseini* are not preserved in the majority of specimens and only partially preserved in others, it is impossible to fully assess whether this feature is present in the Shan material; this is similarly true for the ornamentation found in the Shan State cranidia, which is not clearly preserved in the *Prosaukia* sp. 1 cranidia from the Tarutao Group. Additionally, although the pygidia are similar in overall shape and in the condition of the axial segments and interpleural/pleural furrows, one of the Shan State pygidia (fig. 21G, I) appears to possess reduced propleurae, a feature not found in the Thai material. As this condition is not found in the second Shan State pygidium, however, it is not considered a significant distinction between the Thai and Shan State

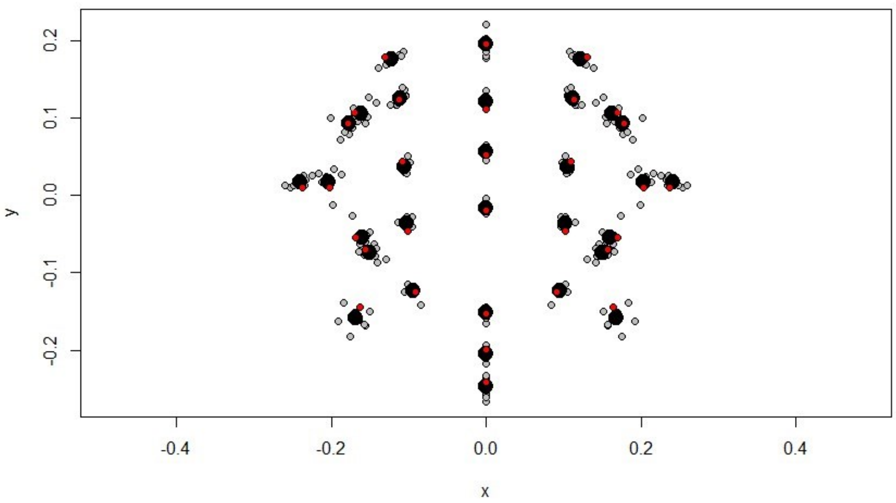

Figure 24. Landmark distribution plot using Procrustes superposition for 9 specimens of *Prosaukia kyaingseini* from the Shan State (grey) and 1 Thai cranidium representing *Prosaukia* sp. 1 Wernette et al (2023) (red). Consensus shape figured in large black dots. See figure 23 for the landmark scheme. The plotted landmarks are oriented anterior-down.

material. As the material representing *P. kyaingseini* in the Shan State and *Prosaukia* sp. 1 in the Tarutao Group are otherwise morphologically identical, we here propose that *Prosaukia* sp. 1 be reassigned to *P. kyaingseini* and that long, narrow posterolateral limbs and pygidia with evenly-divided pleurae be considered diagnostic of the species.

Prosaukia kyaingseini possesses a number of *Hoytaspis*-like traits (inflated preglabellar field, medially shallowing anterior border furrow, posterior border furrow extending into base of genal spine, narrow pygidial border) (Wernette et al., 2023). However, the shape and condition of the *P. kyaingseini* cranidium are significantly more prosaukiid, and the material also possesses distinctly *Prosaukia*-like traits such as short, shallow S2 furrows discontinuous across the midline, low-relief granulation, and anteriorly divergent facial sutures. As the preglabellar field is not inflated above the level of the anterior border, we here consider *P. kyaingseini* to in fact be representative of *Prosaukia.*

Family Ptychaspididae Raymond (1924)

Asioptychaspis Kobayashi (1933)

Type species. *Ptychaspis ceto* Walcott (1905), Chaumitien Formation, Shandong Province, China.

Diagnosis. See Sohn and Choi (2007).

Discussion. Following its erection in 1933 to contain certain Asian species formerly assigned to *Ptychaspis,* the relationship between *Asioptychaspis* and *Ptychaspis* has been much-debated, with *Asioptychaspis* variably considered a distinct genus (Kobayashi, 1933, 1960; Westrop, 1986; Sohn & Choi, 2007; Wernette et al., 2021), a subgenus of *Ptychaspis* (Shergold, 1975)*,* or synonymous with *Ptychaspis* (Lu in Lu (1957); Xiang in Lu et al. (1965); (Zhang & Jell, 1987; Shergold et al., 2007). Differences in the pygidia, noted by Westrop (1986), were dismissed by Zhang and Jell (1987) as insufficient to distinguish the two. In 2007, Sohn & Choi presented a number of new differences separating *Asioptychaspis* and *Ptychaspis* based on silicified specimens of *Asioptychaspis* from the Hwajeol Formation, including a short preglabellar area, a long parallel-sided to anteriorly-expanding glabella, and anteriorly-placed palpebral lobes. Upon comparison of the North China species of *Ptychaspis* described by Zhang and Jell (1987), many of which (e.g. *P. ceto, P. calyce, P. subglobosa,* and *P. asiatica*) had previously been assigned to *Asioptychaspis* either at a genus or subgenus level, Sohn and Choi (2007) note that the Gondwanan species assigned to *Ptychaspis* share a number of characteristics with *Asioptychaspis* that are not common to the Laurentian species of *Ptychaspis.* In contrast to the Gondwanan examples of both *Ptychaspis* and *Asioptychaspis,* Laurentian species assigned to *Ptychaspis* have a shorter, less convex, anteriorly-narrowing glabella, with palpebral lobes situated at the glabellar midpoint rather than anteriorly advanced.

Here, *Asioptychaspis* and Laurentian species of *Ptychaspis* are considered distinct genera in keeping with Sohn and Choi (2007).

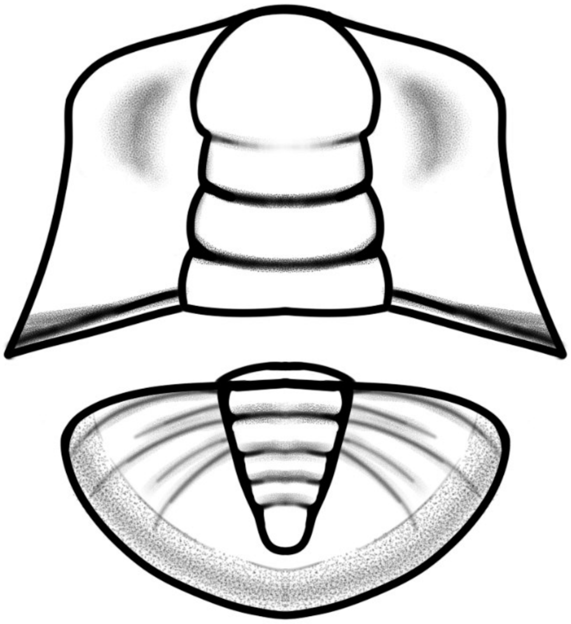

Figure 25. *Asioptychaspis lata* reconstruction.

Figure 25

Asioptychaspis lata **Wernette & Hughes *in* Wernette et al. (2021)**

Fig. 25-26

2021 *Asioptychaspis lata* Wernette & Hughes *in* Wernette *et al.,* p. 12-13, figs. 7-8.

Material. 64 cranidia from PG1 0.75 m (16-PG-604_2), 4.5 m (16-PG-02_2 to 16-PG-02_4 , 16-PG-02_6, 16-PG-02_9, 16-PG-02_10 external mold, 16-PG-02_11 to 16-PG-02_14, 16-PG-02_15 external mold, 16-PG-02_19 to 16-PG-02_22, 16-PG-02_24, 16-PG-02_26, 16-PG-02_29 external mold, 16-PG-02_30 to 16-PG-02_32, 16-PG-02_33 external mold, 16-PG-02_34, 16-PG-02_40, 16-PG-02_41, 16-PG-02_43 to 16-PG-02_45, 16-PG-02_47 external mold, 16-PG-02_48 external mold, 16-PG-02_49, 16-PG-02_51 to 16-PG-02_60, 16-PG-02_62, 20-PG-01_3, 20-PG-01_9 to 20-PG-01_12, 20-PG-01_14, 20-PG-01_23 to 20-PG-01_25, 20-PG-01_28, 20-PG-01_31 external mold, 20-PG-01_32 external mold, 20-PG-01_33 external mold, 20-PG-01_34, 20-PG-03_2, 20-PG-03_4, 20-PG-03_8, 20-PG-03_10, 20-PG-03_17), 5.7 m (20-PG-80_2, 20-PG-80_5). 2 cranidia from PG5 23.87 m (20-PG-83_5, 20-PG-83_9). 14 pygidia from PG1 0.75 m (16-PG-604_1), 4.5 m (16-PG-02_1, 16-PG-02_5, 16-PG-02_7 internal and external molds, 16-PG-02_17 external mold, 16-PG-02_25, 16-PG-02_27 internal and external molds, 16-PG-02_35 external mold, 16-PG-02_38 external mold, 16-PG-02_29, 16-PG-02_61), 5.25 m (20-PG-02_1 internal and external molds), 5.7 m (20-PG-03_14, 20-PG-03_16).

Diagnosis. Comprehensive recent diagnosis and description of *Asioptychaspis lata* in Wernette et al. (2021).

Discussion. *Asioptychaspis lata* is by far the most abundant species in all horizons within the PG1 section and was initially reported as co-occurring there with *Eosaukia buravasi*. While the PG1 specimen initially assigned to *Eosaukia* has since been reassigned to *A. lata*, 3 *A. lata* cranidia and 1 pygidium collected in 2020 and present in stratigraphically higher sections at PG5 do co-occurr with *E. buravasi,* as well as *Tsinania?* sp. and *Lichengia simplex*. As *Asioptychaspis* is generally considered to occur earlier in the Furongian than these co-occurrent genera in the Shan State, the presence of *A. lata* in the Burmese uppermost Cambrian implies that this species was an enduring representative of the genus, as *Asioptychaspis asiatica,* the other species of *Asioptychaspis* found in the Shan State, is only found in situ in two horizons within PG1, indicating that its temporal range is far more limited than that of *A. lata.* More broadly, although the global ptychaspid acme was in the late Jiangshanian, endurance of the group into Stage 10 is by no means uncommon, with species beloning into ptychaspid genera such as *Euptychaspis* and *Idiomisus* well know in the late Sunwaptan of Laurentia for example (Raasch, 1939; Westrop, 1986).

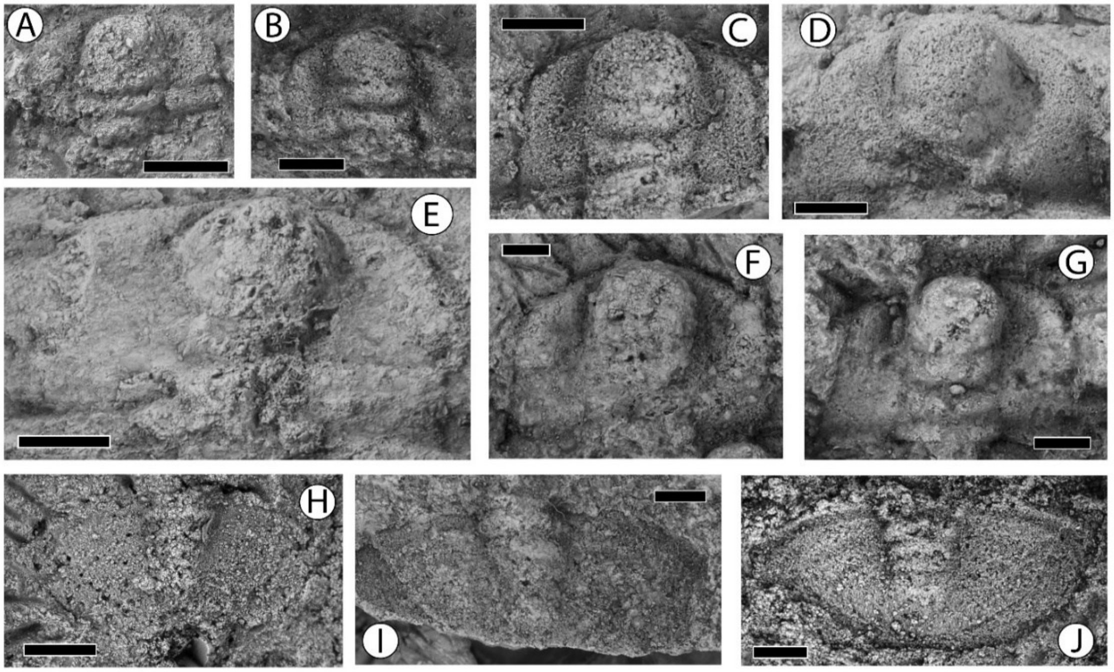

Figure 26. *Asioptychaspis lata.* A, 20-PG-03_4, cranidium. B, 16-PG-02_43, cranidium. C, 16-PG-02_45, cranidium. D, 20-PG-01_23, cranidium. E, 20-PG-01_9, cranidium. F, 16-PG-02_13, cranidium. G, 16-PG-02_14, cranidium. H, 16-PG-02-61, pygidium. I, 16-PG-02_7, pygidium. J, 16-PG-02_1, pygidium. Scale bars represent 2 mm.

Figure 26

Asioptychaspis asiatica Endo & Resser, 1937

Fig. 27

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

1987 *Ptychaspis asiatica* Zhang & Jell, p. 228, pl. 112, figs. 12, 13; pl. 113 figs. 1-4.

2021 *Asioptychaspis asiatica* Wernette *et al.*, p. 14, fig. 10A-L.

Material. 5 cranidia from KY1 float (16-KY-03_1 to 16-KY-03_3, 16-KY-03_5, 16-PG-03_6), 4 cranidia from KY2 float (20-KY-02c_2, 20-KY-02c_3, 20-KY-02d_1, 20-KY-02d_2). 4 cranidia from PG1 4.5 m (20-PG-01_13, 20-PG-01_18, 20-PG-03_5, 20-PG-03_18 internal and external molds). 1 pygidium from KY1 float (16-KY-03_4). 1 pygidium from KY2 float (20-KY-02a-7).

Emended Diagnosis. Subtrapezoidal and strongly convex cranidium with glabella expanding forward of L1. LO slightly wider than L1, glabella widest at anterior lobe. Frontal area short and strongly downsloping. Palpebral lobes slightly oblique and outwardly-directed towards posterior, with midpoint approximately level with L2/S2. Posterolateral limbs short and thick, with wide, firmly-incised posterior border furrow. SO and S1 furrows deeply incised and continuous though shallowing across midline, S2 furrows shallowing or discontinuous across midline, all posteriorly-bowed. S3 furrows faint, discontinuous across midline, anteriorly-directed. Glabellar anterior rounded and inflated dorsally above glabellar level; occipital lobe similarly inflated. Cranidium pustulated. Librigenae notably narrow, with long genal spine. Posterior and lateral border furrows confluent, genal spine advanced. Pygidium biconvex to lenticular in shape, with 4 axial rings and terminal piece. Pleural and interpleural furrows clearly incised at anterior, effaced posteriorly.

Discussion. *Asioptychaspis asiatica* was first described from North China (Endo & Resser, 1937; Wernette et al., 2021) as *Ptychaspis asiatica*. Specimens of *A. asiatica* from the Shan State were first described in Wernette et al. (2021) based on float from the

KY1 locality; however, an in-depth look at the 2020 material representing *A. asiatica* confirms its presence in-section in the PG1 section. Its occurrence within this section,

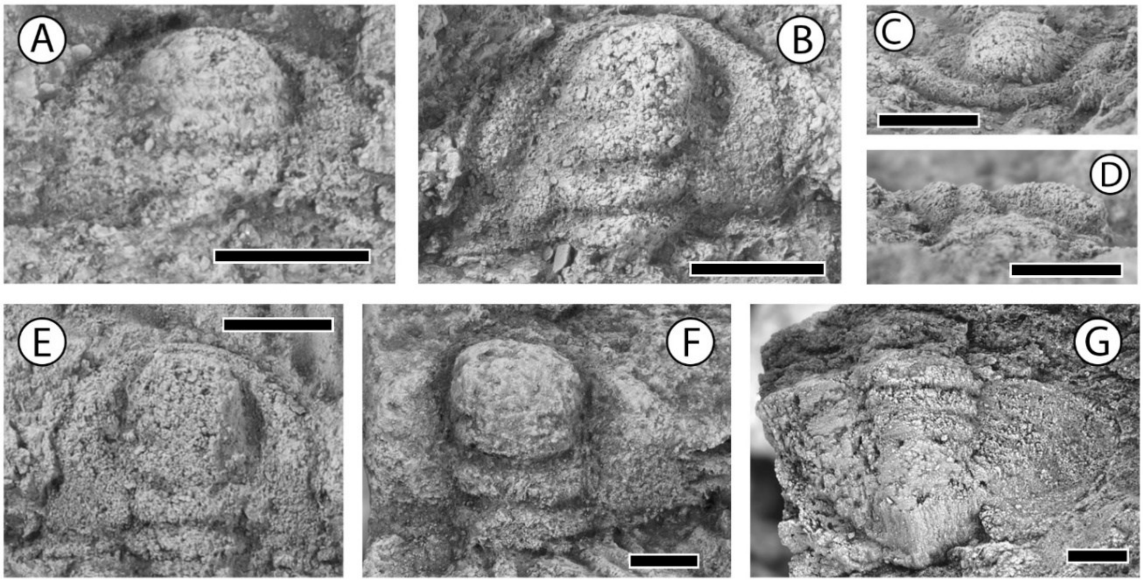

Figure 27. *Asioptychaspis asiatica.* A, 20-PG-01_13, cranidium. B-D, 20-PG-03_18, cranidium in: C, anterior; D, lateral. E, 20-PG-03_5, cranidium. F, 20-KY-02c_3, cranidium. G, 16-KY-03_4, pygidium. Scale bars represent 2 mm.

Figure 27

which occurs downsection from other PG localities and is considered to be the stratigraphically oldest section of those examined from the Shan State, coincides with the presence of *A. lata*.

The fixigenae of *A. asiatica* are markedly narrower than the extremely wide fixigenae of *A. lata,* rendering the two species easy to distinguish in the Shan State material. However, Wernette et al. (2021) noted that *Ptychaspis* sp. cf. *P. asiatica* Resser and Endo (1937) (refigured in Shergold et al. (2007), fig. 37) from W Australia possesses much wider fixigenae than specimens assigned to this species found in the Shan State and in N China, and is more comparable to *A. lata*, as well as apparently lacking the significant pustulation of *A. asiatica* from other Gondwanan terranes (e.g. Shergold et al. (2007), fig. 37D). *Ptychaspis* sp. cf. *P. asiatica* does, however, display the dorsal inflation of the anterior glabellar and occipital lobes characteristic of *A. asiatica.* Due to the conflicting traits of *Ptychaspis* cf. *P. asiatica,* we maintain its current unresolved status, and therefore it remains a tentative additional ptychaspid species-level association between the Bonaparte Basin, N China, and Sibumasu.

Superfamily Asaphoidea Burmeister (1843)

Family Asaphidae Burmeister (1843)

Asaphellus Callaway (1877)

Type species. *Asaphus (Isotelus?) homfrayi* Salter (1866), Tremadocian of N Wales

Diagnosis. See Robison and Pantoja-alor (1968).

Discussion. *Asaphellus,* an exceptionally cosmopolitan genus characteristic of the lower Ordovician, was characterized by Robison and Pantoja-alor (1968) as possessing a flattened cephalon with a broad border and a broad and elongate parallel-sided glabella with a rounded to pointed anterior, as well as the presence of a posterior median node and the lack of glabellar furrows, with only faint axial furrows visible; the pygidium was characterized by its semicircular shape, posteriorly narrowing axis, and externally effaced pleural regions. In some cases the *Asaphellus* pygidium appears almost completely effaced (e.g. Wernette et al. (2023), fig. 30AI); however, in most cases the axial furrows and axial segments are at least partially visible.

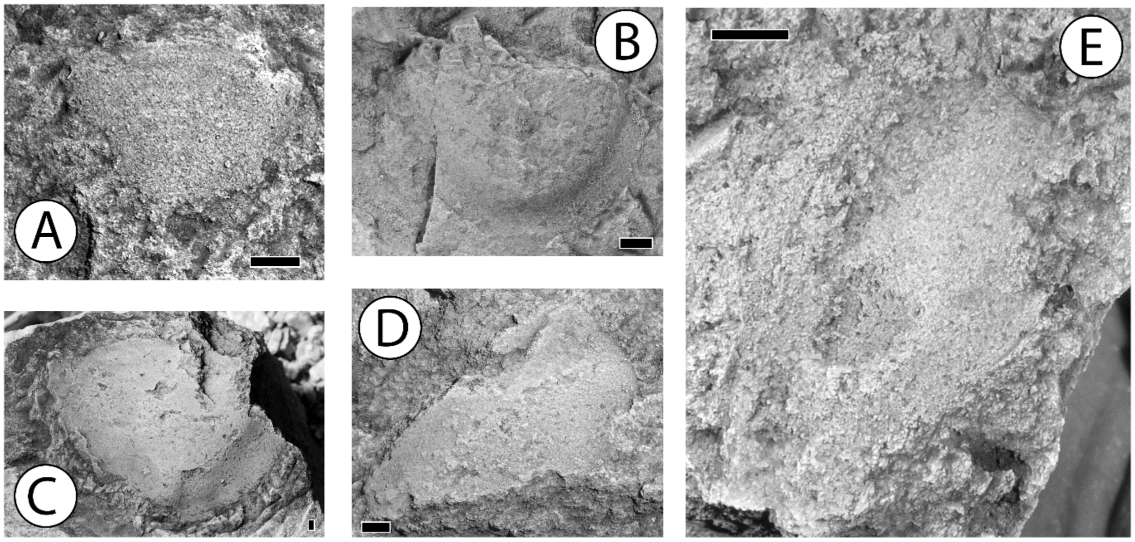

Figure 28. *Asaphellus* sp. A, 20-PG-S04_2, pygidium. B, 20-PG-S06_4, pygidium. C, 20-PG-S04_11, pygidium. D, 20-PG-S04_4, librigena. E, 20-PG-S04_14, librigena. Scale bars represent 2 mm.

Figure 28

***Asaphellus* sp.**

Fig. 28

Material. 2 librigena from PG6&7 2.28 m (20-PG-S04_4, 20-PG-S04_14). 5 pygidia from PG6&7 1.87 m (20-PG-S06_4), 2.28 m (20-PG-S04_2, 20-PG-S04_11, 20-PG-S04_12, 20-PG-S04_15).

Discussion. *Asaphellus* is represented in the Shan State material entirely by associated pygidia and librigenae from the PG6 & 7 sections. All tagmata representing

Asaphellus are of poor quality; the pygidia are either partially (fig. 28A, B) or totally effaced (fig. 28C), and the two librigenae potentially representing the genus are partial. Nevertheless, the material shows signs characteristic of the genus, including small eyes (as represented by the librigenae) and a wide lateral border on the librigenae and a semi-circular pygidium with a wide border, effaced pleural furrows, and a narrow, posteriorly-tapering axis. Though the Thai material representing *Asaphellus* contains well-preserved cranidia, pygidia, and librigenae and could be assigned to the new species *Asaphellus charoenmiti* Wernette, 2023, the Shan State material is not of sufficient quantity or quality to confidently assign to any species of *Asaphellus* and is here denoted as *Asaphellus* sp.

Order Corynexochida Kobayashi (1935)

Suborder Leiostegiina Bradley (1925)

Superfamily Leiostegioidea Bradley (1925)

Family Missisquoiidae Hupé (1955)

***Pseudokoldinioidia* Endo (1944)**

Type species. *Pseudokoldinioidia granulosa* Endo (1944) Yenchou Formation, Liaoning, China.

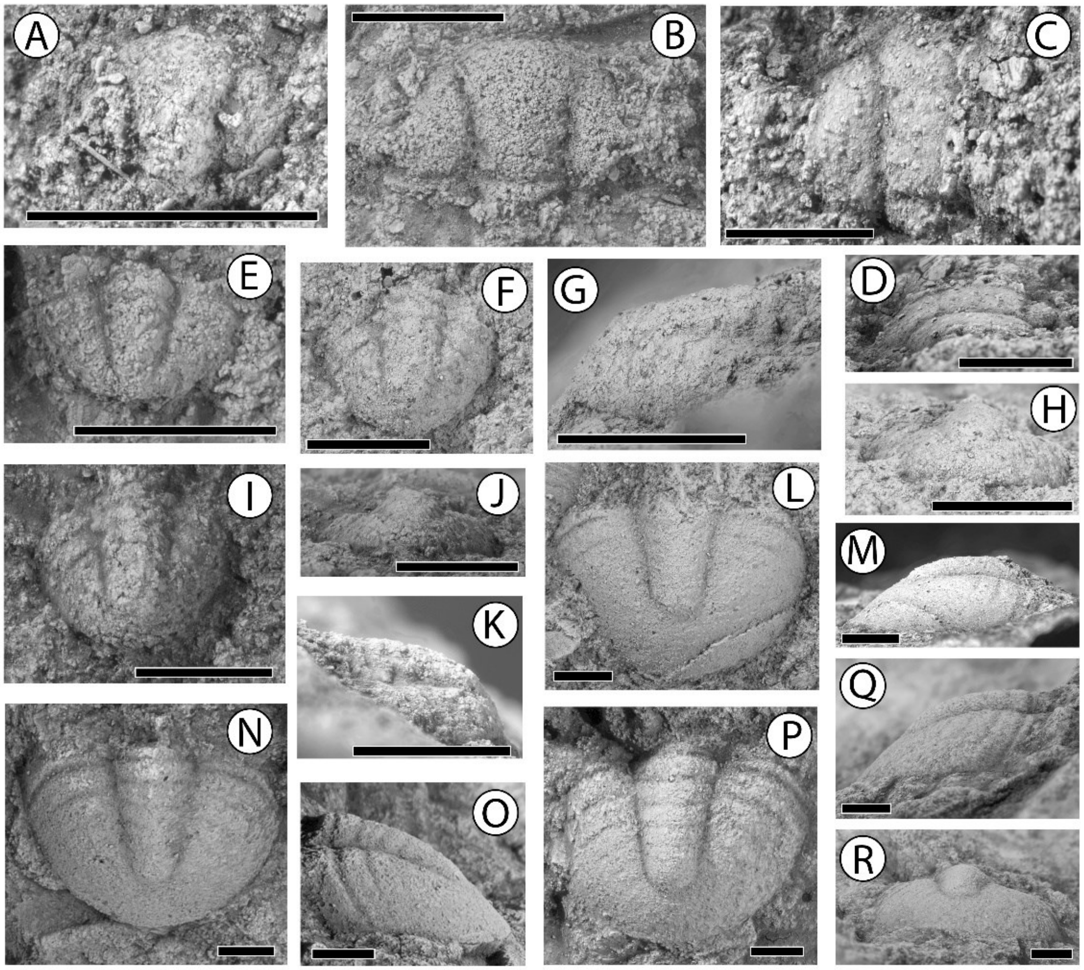

Figure 29. *Pseudokoldinioidia maneekuti.* A, 20-PG-17_10, cranidium. B, 20-KH-01_7, cranidium. C-D, 20-PG-05_2, cranidium in: D, lateral. E, 20-KH-05_4, pygidium. F-H, 20-KH-05_22, pygidium in: G, lateral; H, posterior. I-K, 20-KH-16, pygidium in: J, posterior; K, lateral. L-M, 20-PG-22_52, pygidium in: M, lateral. N-O, 20-PG-16_1, pygidium in: O, lateral. P-R, 20-PG-17_13, pygidium in: Q, lateral; R, posterior. Scale bars represent 2 mm.

Figure 29

Emended Diagnosis. Cranidium convex, semicircular. Inverted trapezoidal glabella expanding anteriorly from S2, widest point of glabella at anterior lobe. Anterior border short (sag.), strongly downsloping. Short (tr.) S1, S2, and S3 glabellar furrows deeply incised and merging with axial furrows, discontinuous across midline. S2 and S3 furrows anteriorly directed, S1 posteriorly directed. Fixigena wide. Gently arcuate moderate to long palpebral lobes situated posterior glabellar midpoint. Posterolateral limbs abaxially strongly posteriorly directed. Pygidium generally convex, semicircular to semielliptical in shape, axial segments inflated above level of postaxial region. 4-7 axial rings and terminal piece, pleural and interpleural furrows distinctly incised, equal pleural division.

Discussion. *Pseudokoldinioidia* was initially established based on a single cranidium from the Yenchou Formation of Liaoning Province, in N China. Due to both poor specimen and illustration quality, as well as difficulty accessing the type material, *Pseudokoldinioidia* was initially poorly resolved within the Missisquoiidae; the genus was later re-evaluated in Duan et al. (1986) and Lu and Zhou (1990) and differentiated morphologically from other missisquoiid genera (e.g. *Missiquoia*) based on its anteriorly expanding glabella (Lee et al., 2008). A phylogenetic analysis of the Missisquoiidae (Lee et al., 2008) further resolved the genus *Parakoldinioidia* to include the species *Missisquoia perpetis* Zhou and Zhang (1985) and *M. cyclochila* Hu (1971). Lee et al. (2008) document the pygidial condition of *Pseudokoldinioidia* as including spinose anterior pleurae; this is dubious as a diagnostic feature, however, as it is lacking in several species, including the Thai form *P. maneekuti.*

Pseudokoldinioidia is primarily distinguished from *Pagodia* and *Parakoldinioidia* based on the condition of the glabella (Wernette et al., 2023). The *Pagodia* glabella narrows anteriorly, while the *Pseudokoldinioidia* glabella expands anteriorly and the *Parakoldinioidia* glabella is subrectangular with moderate constriction about the midpoint (Lee et al., 2008; Wernette et al., 2023). The anteriorly-expanding glabella is therefore the most significant diagnostic feature *Pseudokoldinioidia.*

***Pseudokoldinioidia maneekuti* Wernette and Hughes, *in* Wernette et al. (2023)**

Figs. 29-30

1988. *Parakoldinioidia thaiensis* Shergold, figs 3Q-R, U-X (non fig. 3S-T = *Parakoldinioidia callosa*)

Material. 4 cranidia from PG5 5.8 m (20-PG-17_10), 7.24 m (10-PG-10_77, 20-PG-10_83), 13.11 m (20-PG-05_2). 4 cranidia from KH1 8.6 m (20-KH-05_3, 20-KH-05_12), 8.97 m (20-KH-01_7, 20-KH-01_9). 1 pygidium from PG1 float (16-PG-603_1). 7 pygidia PG5 0.59 m (20-PG-18_14), 0.89 m (20-PG-22_39, 20-PG-22_52, 20-PG-22_56), 5.8 m (20-PG-16_1, 20-PG-17_13), 7.24 m (20-PG-10_94). 7 pygidia from KH1 8.6 m (20-KH-05_4, 20-KH-05_16, 20-KH-05_22, 20-KH-05_25, 20-KH-05_34, 20-KH-05_36, 20-KH-05_37).

Diagnosis. See Wernette *et al.,* 2023.

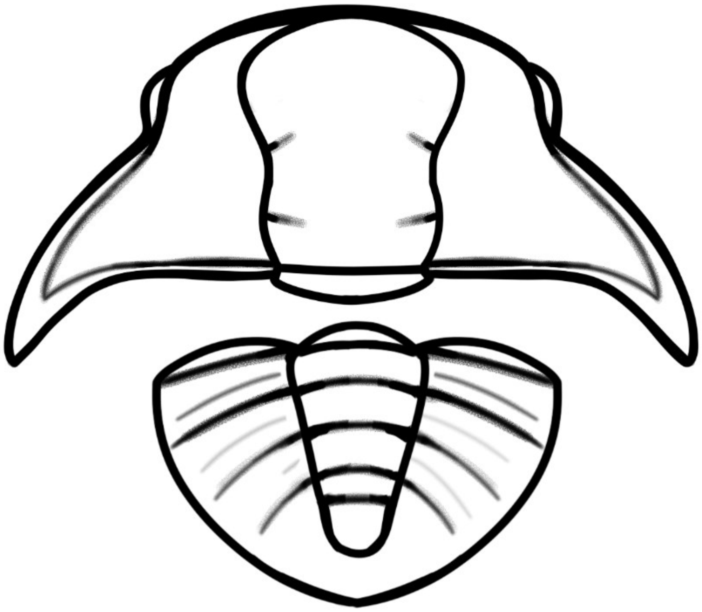

Figure 30. *Pseudokoldinioidia maneekuti* reconstruction.

Figure 30

Discussion. The characters of *P. maneekuti* are extensively discussed in Wernette et al. (2023), which outlined diagnostic criteria, including a glabellar anterior width of approximately 1.3-1.4x L1 width. The Shan State material of *P. maneekuti* is less well preserved than the Thai material; of particular note is the fact that the posterolateral limbs, which represent a significant diagnostic trait in that they are adaxially transverse with a strong distal posterior curve, are not preserved in their entirety in the Shan State material. Although the adaxial portions of the posterolateral limbs appear to be transverse in nature, the distal tips are missing and cannot be evaluated. However, the Shan State material does display the characteristically small and anteriorly placed palpebral lobes of *P. maneekuti*, as well as the long, non-spinose pygidia with 4 axial rings, straight and posteriorly directed pleural furrows, and effaced interpleural furrows. On this basis we suggest that the Shan State material also represents *P. maneekuti.*

Parakoldinioidia **Endo *in* Endo and Resser (1937)**

Type species. *Parakoldinioidia typicalis* Endo *in* Endo and Resser (1937) Liaoning Province, North China.

Diagnosis. See Lee et al. (2008).

Parakoldinioidia callosa **Qian, 1985**

Fig. 31

1985. *Parakoldinioidia callosa* Qian, pl. 1 figs. 12-13.

1988. *Parakoldinioidia thaiensis* Kobayashi, Shergold *et al.,* figs. 3S-T (non fig. 3Q-R, 3U-X = *Pseudokoldinioidia maneekuti*)

Material. 3 cranidia from PG5 7.24 m (20-PG-10_11), 13.11 m (20-PG-05_3, 20-PG-05_4, 20-PG-05_5). 2 cranidia from KH1 8.6 m (20-KH-05_3), 8.97 m (20-KH-01_6).

Emended Diagnosis. Subpentagonal cranidium with subrectangular glabella varying in length, medial constriction approximately level with L2. Three pairs of glabellar furrows. S1 continuous and deeply incised abaxially, shallowing at midline, S2 clearly incised but discontinuous across the midline, both posteriorly-directed. S3 faint and anteriorly-directed. Palpebral lobes of moderate length with midpoint situated approximately midway between S1 and S2.

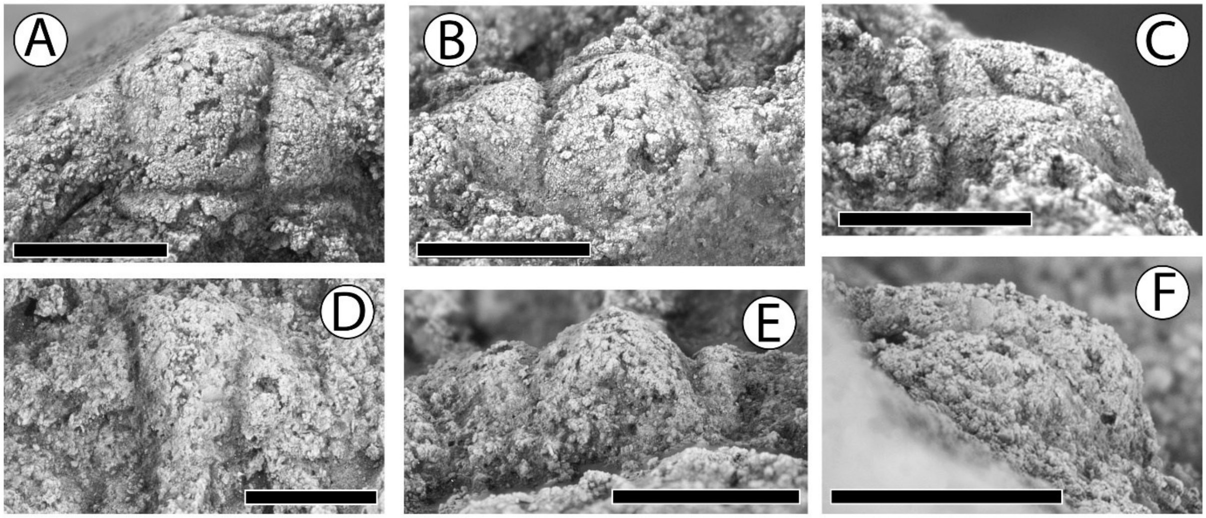

Figure 31. *Parakoldinioidia callosa.* A-C, 20-PG-05_5, cranidium in: B, anterior; C, lateral. D-F, 20-PG-10_11, cranidium in: E, anterior; F, lateral. Scale bars represent 2 mm.

Figure 31

Discussion. The *P. callosa* diagnosis as described in Qian (1985) and re-evaluated in Wernette *et al.* (2023) is herein accepted as describing the distinguishing features of the species; these include a subrectangular glabella with slight medial constriction (as seen in Qian (1985), pl. 1 fig. 12; Shergold et al. (1988) figs. 3S-T; Wernette et al. (2023) fig. 18D-18H). Other diagnostic features include a subpentagonal cranidium, palpebral lobes positioned posteriorly, and three pairs of glabellar furrows: a strongly-incised and posteriorly-directed S1 and S2, and a fainter, anteriorly-directed S3. Shergold et al. (1988) synonymized *P. callosa* with *Pagodia thaiensis;* however, the two genera are clearly distinguished by glabellar condition (see *Pseudokoldinioidia* discussion above).

Prior to Wernette et al. (2023), pygidia of *P. callosa* had not been figured. The single pygidium figured in Wernette et al. (2023) fig. 18K remains the sole known figured pygidium, and is difficult to properly assess due to poor preservation quality. However, some characteristics can be determined from the specimen. The *P. callosa* pygidium is subelliptical in shape with a width approximately 2 times its length. It is convex with a narrow, concave posterior border. The Thai specimen appears to possess 3 axial segments, the posteriormost of which is less clearly distinguished from the terminal segment. The anteriormost pleural and interpleural furrows of the figured specimen can be seen; they are strongly incised and continue to the narrow border, with a slight posterior angle. Though other pleural and interpleural furrows are difficult to discern from the Thai pygidium, evidence of regularly-spaced "notches" near the pygidial border indicate that the lack of posterior pleural and interpleural furrows in the figured specimen is likely the result of poor preservation. The Shan State material contains no pygidia matching that of *P. callosa.*

No librigenae have yet been figured or described for *P. callosa.*

Gen. et sp. indet.

Fig. 32

Material. 1 pygidium from PG5 0.59 m (20-PG-22_33).

Discussion. This material represents a single pygidium from near the base of the PG5 section, which is assigned to the Missisquoiidae on the basis of its narrow, inflated axis, 4 axial rings separated by shallow furrows, and effaced posterior pleural furrows. The near-circular shape and wide border of this pygidium distinguish it from those of *Parakoldinioidia callosa?* and *Pseudokoldinioidia maneekuti,* both of which co-occur in the horizon; however, there appear to be no cranidia that can be associated with the pygidium, preventing assignation to a specific genus or species.

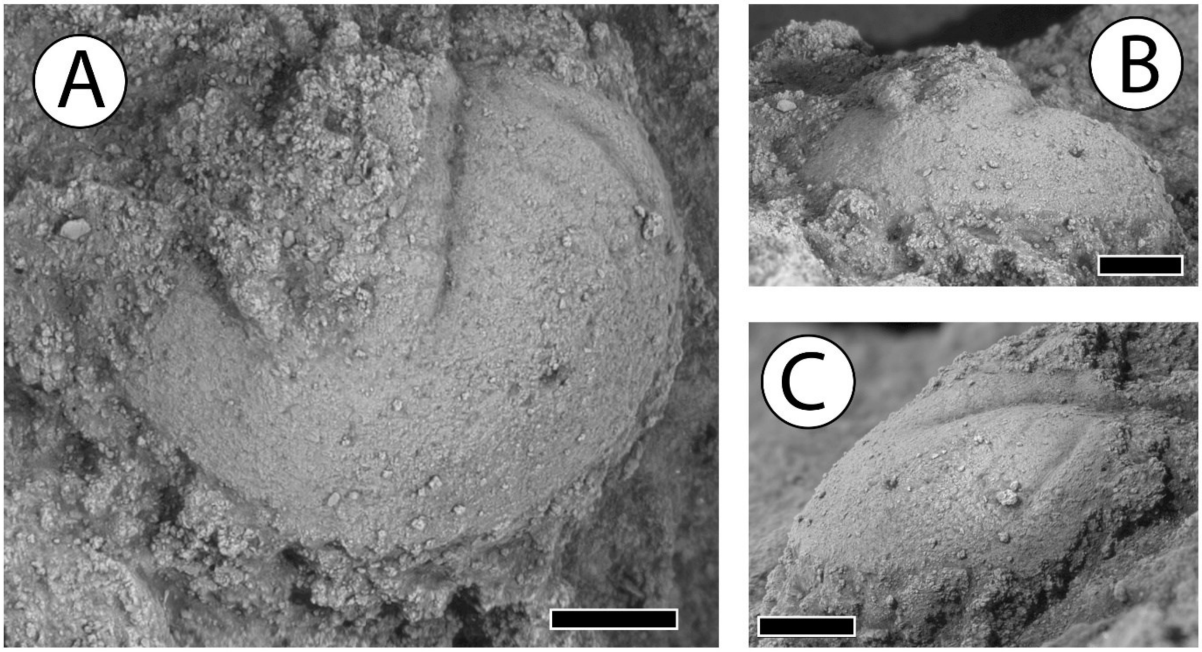

Figure 32. Missisquoiid gen. et sp. undet. A-C, 20-PG-22_33, pygidium in: B, posterior; C, lateral. Scale bars represent 2 mm.

Figure 32

Family Leiostegiidae Bradley (1925)

Subfamily Pagodiinae Kobayashi (1935)

Discussion. Pagodiidae was initially established by Kobayashi (1935) as a family on the basis of what were considered to be significant differences between the group members of Pagodiidae and Leiostegiidae in both cranidial and pygidial conditions, Later, Pagodiidae were relegated to the subfamily rank within the Leiostegiidae as the subfamily Pagodiinae, a reassignment accepted by later publications (Shergold, 1975; Zhou & Zhen, 2008; Adrain, 2011; Wernette et al., 2023). We here accept Pagodiinae as a subfamily of Leiostegiidae.

Pagodia Walcott (1905)

Type species. *Pagodia lotos* Walcott (1905) Shandong Province, N China

Diagnosis. An extensive emended diagnosis of *Pagodia* was recently published in Lei et al. (2023). We accept this diagnosis, with the exception of anteriorly divergent facial sutures as a diagnostic criteria (see below).

Discussion. The nature of *Pagodia* as a genus has been extensively discussed (Öpik, 1967; Lu, 1975; Shergold, 1975; Zhang & Jell, 1987; Peng, 1992; Shergold et al., 2007; Lei et al., 2023). It has been varyingly described as possessing anteriorly divergent facial sutures (e.g. Lei et al. (2023)) and anteriorly convergent facial sutures (e.g. Lu (1975); Wernette et al. (2023)). We here accept the condition of the facial suture as variable within the genus and thus not diagnostic. Multiple subgenera have been described within *Pagodia,* including *Pagodia (Lotosoides)* Shergold (1975), *Pagodia (Oreadella)* Shergold (1975), and *Pagodia (Idamea)* Öpik (1967); however, many of the intrageneric differences cited may be the product of intraspecific variation or differences in preservation mode (see Lei et al. (2023)).

Pagodia has been noted to possess similar characteristics to *Chuangia* (e.g. Zhang and Jell (1987)) and to *Szechuanella* (e.g. Shergold et al. (1988)). *Chuangia* and *Pagodia* are especially difficult to distinguish, being in some cases only separated by the pygidium, which in *Chuangia* possesses fewer and less well-defined axial segments (Zhang & Jell, 1987). *Pagodia* differs more markedly from *Szechuanella,* as it has broader fixigena, a less well-defined border to the frontal area, and coarse granulated ornamentation on both the pygidium and cranidium (Lu, 1975); additionally, *Szechuanella* is a solely Ordovician genus. Due to the number of similarities between *Szechuanella* and various other members of the subfamily Leiostegiinae, *Szechuanella* may be related to or descended from the late Cambrian leiostegiids.

Pagodia thaiensis? Kobayashi (1957)

Figs. 33-34

1957 *Pagodia thaiensis* Kobayashi, pl. 4 figs. 5-7

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

2023 *Pagodia thaiensis* Wernette and Hughes, figs. 22-23

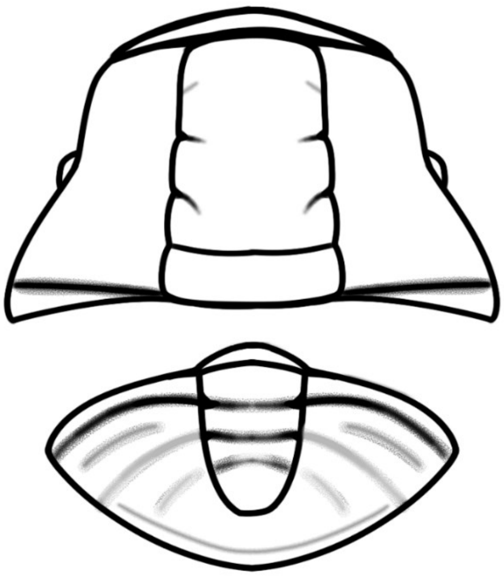

Figure 33. *Pagodia thaiensis?* reconstruction.

Figure 33

Material. 2 cranidia from PG5 7.24 m (20-PG-10_33, 20-PG-10_70). 16 pygidia from PG5 0.59 m (20-PG-22_6, 20-PG-22_27, 20-PG-22_46, 20-PG-22_51), 7.24 m (20-PG-10_26, 20-PG-10_32, 20-PG-10_42, 20-PG-10_54, 20-PG-10_72, 20-PG-10_73, 20-PG-10_74, 20-PG-10_75, 20-PG-10_81 external mold), 18.84 m (20-PG-82_4), 23.87 m (20-PG-83_19, 20-PG-83_52). 1 pygidium from KY1 float (20-K-02a_1). 1 pygidium from YN1 (20-YN-04_10 internal and external molds).

Diagnosis. Medially constricted glabella narrowing significantly towards the anterior. Short glabellar furrows extending only partially into the glabella. Fixigena wide, eye located approximately opposite S1. Short, subtriangular to semicircular pygidium with 3-4 poorly-defined axial segments. Anteriormost two pleural furrows clearly incised, with faint interpleural furrows; all furrows effaced moving posteriorly to narrow border.

Discussion. Cranidial material representing *P. thaiensis* from the Shan State is limited to two poorly-preserved specimens 7.24 m from the base of PG5. Both these pagodiid cranidia are assigned to *P. thaiensis* on the basis of the characteristic medially constricted, significantly anteriorly narrowing glabella. Pygidial material is more strongly represented throughout all levels of the PG5 locality, as well as in cobbles found at KY1, where it is found alongside a single *Asioptychaspis asiatica* pygidium. The *P. thaiensis?* pygidia appear similar to those figured in Wernette et al. (2023) (fig. 23) due to the broad, subtriangular to semicircular or elliptical shape, short, 3-4 segment axis, poorly-defined segmentation, and narrow border. Additionally, the anteriormost 1-2 pleural and interpleural furrows are strongly incised and posteriorly effaced, consistent with those of *P. thaiensis* (Wernette et al. (2023), fig. 23).

One significant difference between the Thai and Shan State pygidia is that of their size ranges. The Shan State pygidia range from 1.79-11.05 mm in length and 3.55-24.19 mm in width, in general much larger than the Thai pygidia, which range from 2.09-3.66 mm in length and 4.10-5.22 mm in width. Twelve of the 17 Shan State pygidia are between 6-24 mm in width, and 8 are wider than 9 mm. The significant size disparity between the pygidia is further compounded by the small size of the *P. thaiensis* cranidia represented in the Shan State; the largest *P. thaiensis* cranidium of the two Shan State specimens (fig. 34B) has an occipital-glabellar length of 2.15 mm and a width across

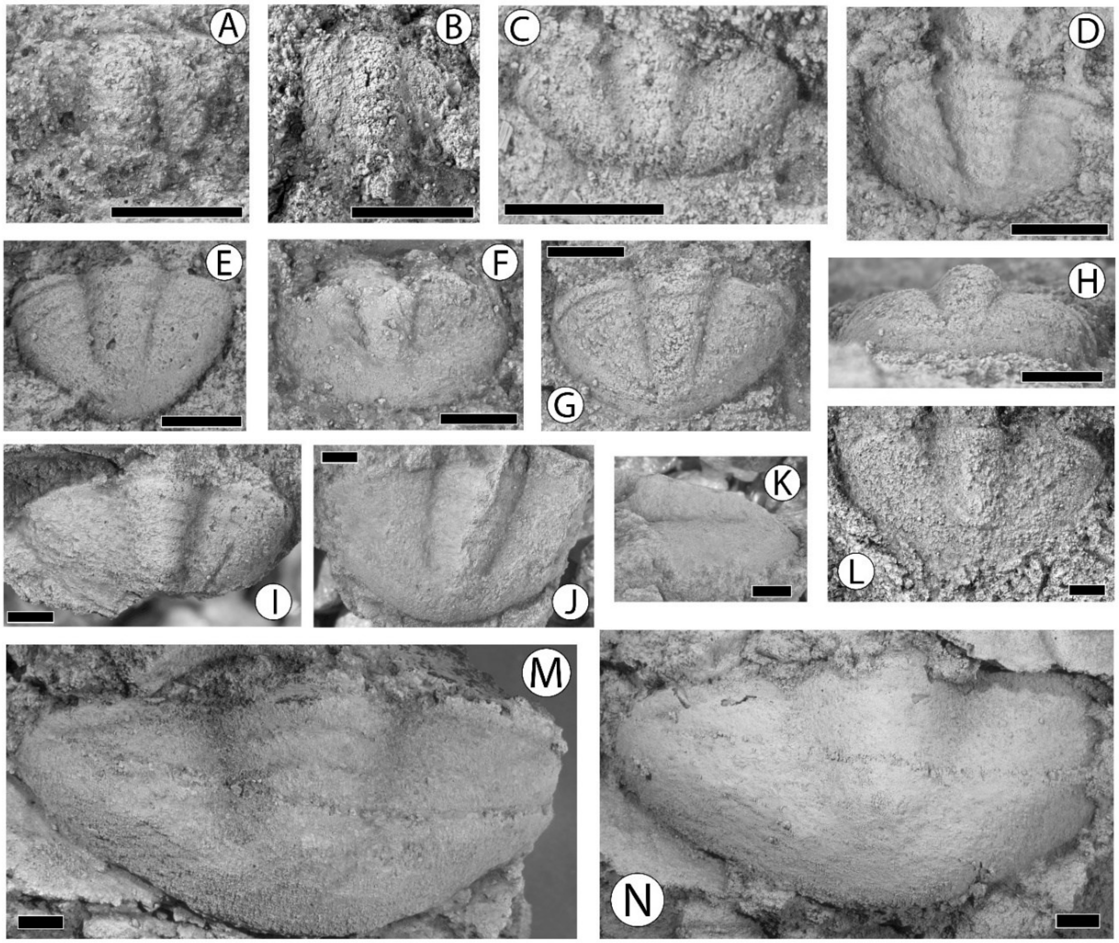

Figure 34. *Pagodia thaiensis?* A, 20-PG-10_33, cranidium. B, 20-PG-10_70, cranidium. C, 20-PG-82_4, pygidium. D, 20-PG-22_46, pygidium. E, 20-PG-22_51, pygidium. F, 20-PG-22_27, pygidium. G-H, 20-PG-22_6, pygidium in: H, posterior. I, 20-PG-83_52, pygidium. J-K, 20-PG-83_19, pygidium in: K, posterior. L, 20-PG-10_72, pygidium. M-N, 20-YN-04_10, pygidium in: N, counterpart. Scale bars represent 2 mm.

Figure 34

the palpebral lobes of 2.31 mm, significantly smaller than the largest pygidium. Due to this disparity, the assignment of these Shan State pygidia to *P. thaiensis* is treated as tentative.

The lack of strongly incised pleural, interpleural, and axial furrows in the *P. thaiensis* pygidia differentiate it from other species of *Pagodia.* In this respect, the *P. thaiensis* material more strongly resembles pygidia assigned to *Chuangia,* e.g. *Chuangia tolli* (see Zhang and Jell (1987), pl. 93, figs. 9-10; pl. 94, figs. 1-2).

Pagodia? uhleini **Wernette and Hughes *in* Wernette et al. (2023)**

Fig. 35

1988 *Szechuanella?* cf. *damujingensis* (*sensu* Luo, 1974) Shergold *et al.,* fig. 3F-N

2023 *Pagodia? uhelini* Wernette and Hughes, figs. 24-26

Material. 1 cranidium from PG5 7.24 m (20-PG-10_66). 1 pygidium from KH1 12.42-12.66 m (20-KH-07_ 5).

Description. See Wernette et al. (2023) for a comprehensive diagnosis and description of *P.? uhleini.*

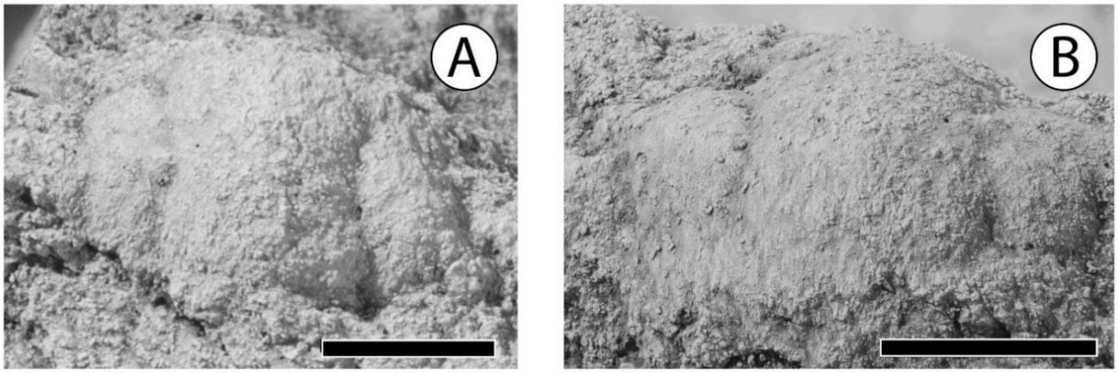

Figure 35. *Pagodia? uhleini.* A-B, 20-KH-07_5, cranidium in: B, anterior. Scale bars represent 2 mm.

Figure 35

Discussion. Though the material attributable to *P.? uhleini* in the Shan State is limited to a single cranidium from the KH1 locality and one cranidium from the PG5 locality, the specimen in question exhibits a medially constricted glabella with effaced furrows that protrudes anteriorly of the fixigenae, a key feature of the *P.? uhleini* cranidium (Wernette et al., 2023). Except for this anteriormost glabellar expansion, overall anterior narrowing of the glabella is present but not pronounced, distinguishing it from the Shan State cranidia representing *P. thaiensis,* which exhibit much more significant anterior narrowing. Therefore, this specimen is tentatively assigned to *P.? uhleini.*

Suborder Illaenina Jaanusson (1959)

Family Tsinaniidae Kobayashi (1935)

***Tsinania* Walcott (1914)**

Type species. *Illaenurus canens* Walcott (1905) Chaumitien Limestone, Shantung, China

Diagnosis. See emended diagnosis of Lei and Liu (2014).

Discussion. Phylogenetic relationships within the Tsinaniidae have been the subject of extensive debate. Recent phylogenetic analyses of the tsinaniids suggest a polyphyletic *Tsinania* belonging to a clade containing *Shergoldia* Zhang & Jell, 1987, *Lonchopygella* Sun & Xiang, 1979 and *Dictyella* Kobayashi, 1933a (Zhu et al., 2013; Wernette et al., 2020b). *Shergoldia*, a tsinaniid exhibiting significant morphological similarities to *Tsinania,* has been variously suggested to be a similarly polyphyletic group (Zhu et al., 2013), or as monophyletic and nested within a paraphyletic *Tsinania* (Wernette et al., 2020b; Wernette et al., 2023). *Shergoldia* is often considered to be less strongly effaced in both the cranidium and pygidium than *Tsinania* (Zhang & Jell, 1987; Zhu et al., 2007), as well as possessing a visible plectrum, which is not present in members of *Tsinania*. However, degree of effacement can vary intraspecifically as well as through preservation, as internal molds of both *Shergoldia* and *Tsinania* often appear significantly less effaced than external molds. Additionally, prominence of the plectrum varies between species of *Shergoldia* (Lei & Liu, 2021). We here consider *Shergoldia* to be a junior synonym of *Tsinania*, in agreement with Lei and Liu (2021).

The emended diagnosis of *Tsinania* published in Lei and Liu (2014) highlighted the subquadrate to subtriangular cranidium, palpebral lobes of moderate size, and short posterolateral limbs. Pygidia are subtriangular to semicircular, with anterior pleural spines present in meraspid and early holaspid stages but lost in later holaspid stages. Where holaspid pygidial axial segments can be seen, they number 9 or more.

***Tsinania?* sp.**

Figs. 36-37

Material. 5 cranidia from PG5 5.8 m (20-PG-16_4), 7.24 m (20-PG-10_52, 20-PG-10_78), 23.87 (20-PG-83_23, 20-PG-83_42). 1 cranidium from KH1 8.97 m (20-KH-01_10). 8 pygidia from PG5 7.24 m (20-PG-10_6 external mold, 20-PG-10_21, 20-PG-10_28, 20-PG-10_29 external mold, 20-PG-10_50, 20-PG-10_56 external mold, 20-PG-10_85 external mold), 9.39 m (20-PG-11_1 internal and external molds), 23.87 m (20-PG-83_44). 5 cranidia from KH1 8.6 m (20-KH-05_19, 20-KH-05_21), 8.97 m (20-KH-01_1, 20-KH-01_2).

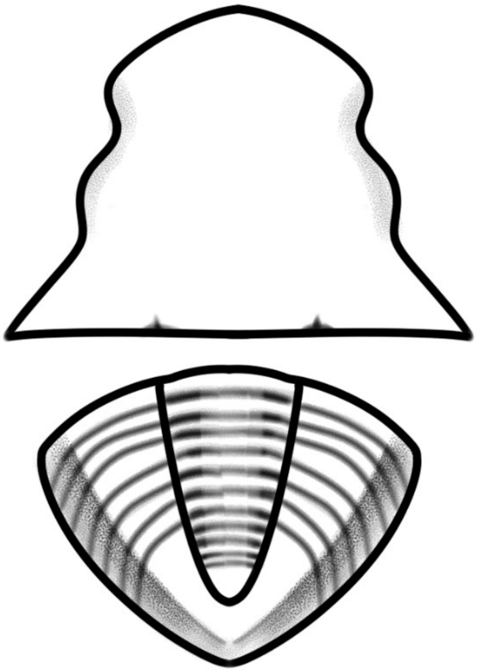

Figure 35. *Tsinania?* sp. reconstruction.

Figure 36

Diagnosis. Cranidium subtriangular, with strongly curved anterior margin. Axial, glabellar, and anterior border furrows effaced. Palpebral lobes moderately sized, posterolateral limbs short (tr.) and mildly posteriorly directed. Pygidium long and subtriangular, with relatively strongly incised axial, anterior pleural, and anterior interpleural furrows, long and broad border, low convexity, and long post-axial area.

Description. The cranidium is subtriangular, with low convexity and a strongly curved to gently angular anterior margin. The width across posterolateral projections is 1.2 to 1.4x fold the cranidial length, and the width across the palpebral lobes is on average 71% the width across posterolateral projections. Width across the cranidial anterior measured from the anterior inflection points is on average 65% the width across posterolateral projections. The fixigena and frontal area are continuous. The palpebral lobes are short, approximately 22-29% cranidial length, and strongly curved, with a midpoint located approximately opposite or slightly anterior the cranidial midpoint. The posterior facial sutures extend from initially straight to slightly posterolaterally directed at a 34-47 degree angle from exsag. The posterolateral projections are thick (exsag.) and extend nearly transversely.

The pygidium is subtriangular with low convexity, similar to the cranidium. Pygidial width is approximately 1.2-1.4-fold pygidial length. The axial furrows and anterior pleural and interpleural furrows are clearly incised, though the posterior pleural and interpleural furrows are more strongly effaced. The axial rings number from 9-12. The border furrow is defined by change in slope to wide border, and measures approx. 14% of pygidial width at the anterior. The postaxial region is long, approx. 23% pygidial length and 31% axial length. When compared to the border at the pygidial anterior, the

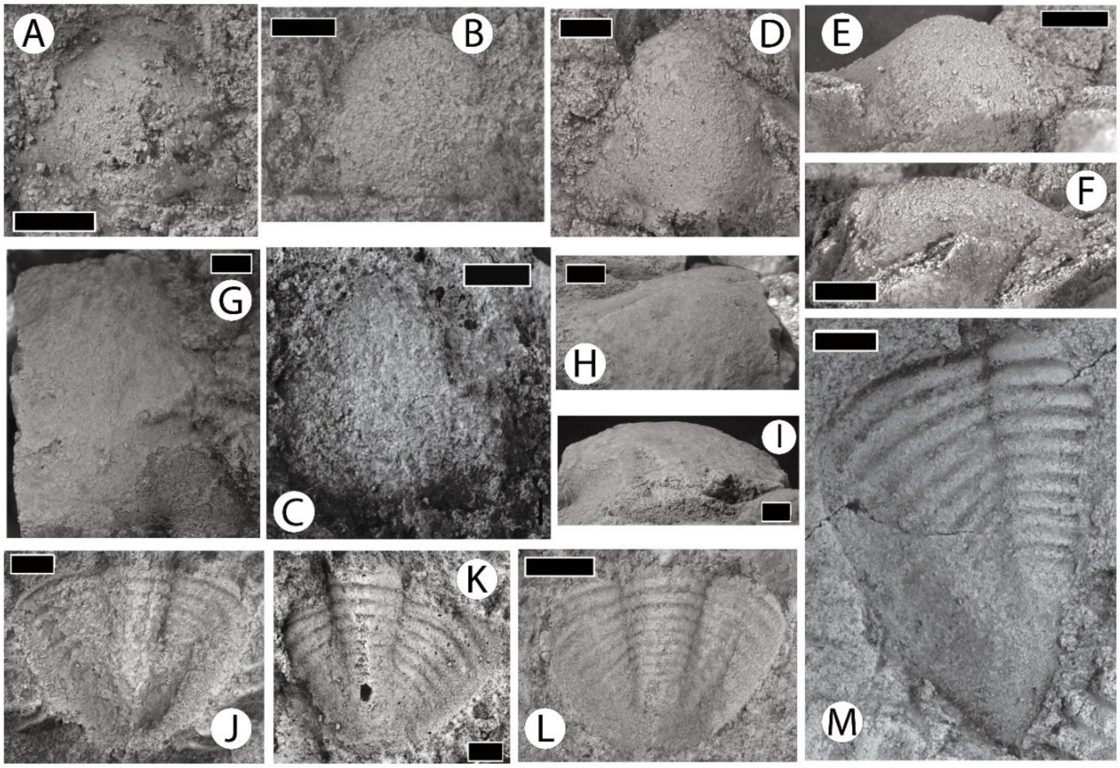

Figure 37. *Tsinania?* sp. 1. A, 20-PG-83_42, cranidium. B, 20-KH-01_10, cranidium. C, 20-PG-10_78, cranidium. D-F, 20-PG-83_23, cranidium in: E, anterior; F, lateral. G-I, 20-PG-16_4, cranidium in: H, anterior; I, lateral. J, 20-PG-11_1cp, pygidium, external mold. K, 20-PG-10_56, pygidium. L, 20-KH-05_21, pygidium. M, 20-PG-83_44, pygidium. Scale bars represent 2 mm.

Figure 37

postaxial region is approximately 1.24x longer. The pleural regions appear divided equally at the anterior.

Discussion. The cranidium of *Tsinania?* sp. is very similar to those of various other species of *Tsinania,* such as *Tsinania canens* Walcott, 1905 Walcott (1905); it is highly effaced, possessing little in the way of furrows or other distinguishing marks. A single specimen (fig. 37A) shows an apparent anterior border furrow; however, this feature appears to be an artifact of preservation.

The defining feature of *Tsinania?* sp. is its pygidium, which is less effaced than those of other *Tsinania* species such as *Tsinania canens* and *Tsinania sirindhornae*, the latter of which represents all tsinaniid material known from the Tarutao Group. The lack of such extensive effacement is similar to several pygidia assigned to species of *Shergoldia,* such as *Shergoldia australis* Peng (1992) and *Shergoldia? manchuria* Kobayashi (1933)*,* as well as some pygidia documented from *T. canens,* in which the axial rings and pleural and interpleural furrows can be clearly seen; however, these pygidia are significantly exfoliated, and no testaceous representatives of the pygidium assigned to *Tsinania?* sp. are present within the Shan State material. As these differences in the pygidium are potentially significant, the assignment of this material to *Tsinania* is tentative and uncertain.

The unusual state of the pygidium, as well as the difference between the heavily effaced cranidium and clearly segmented pygidial axis, initially cast doubt on the association of the two; as such, the *Tsinania?* sp. pygidia were first assigned to *Diemanosaukia* sp. 1*,* as both pygidia contain large numbers of axial segments and are found in a similar stratigraphic range. Upon the organization of all pygidia assigned to *Diemanosaukia* sp. 1 by size, it was determined that there in fact exist two separate pygidial morphologies, rather than an ontogenetic series. While both pygidial morphologies possess a multi-segmented axis and wide border, the *Diemanosaukia* sp. 1 pygidia are significantly wider than those of *Tsinania?* sp., with a width between 1.5-2x the pygidial length on average, and possess a semicircular outline, in contrast to the subtriangular outline of the *Tsinania?* sp. pygidium. Additionally, the axial segments of *Tsinania?* sp. can number up to 12, while *D.* axial segments number 9 or fewer. The pygidial anterior of the *Dienamosaukia* sp. pygidium is largely transverse, in contrast to the posteriorly rounding anterior of the *Tsinania?* sp. pygidium; this holds as well for the anteriormost pleural furrows. Finally, the *Tsinania?* sp. pygidium possesses a wider axis than the *Diemanosaukia* sp. 1 axis, which is approximately 32% of the width of the pygidium. On this basis, the *Tsinania?* sp. pygidia were distinguished from that of *Diemanosaukia* sp. 1. These pygidia were allied with their corresponding cranidia in part on the basis of stratigraphy: *Tsinania?* sp. pygidia are found throughout the 5.8-24.87 m interval of the PG5 section, as well as the horizon of KH1 8.97 m from the section base, which corresponds to the interval in which *Tsinania?* sp. cranidia are found in both localities. Of the other taxa present in these stratigraphic ranges, none possess pygidia similar to those of *Tsinania?* sp.. Additionally, the *Tsinania?* sp. cranidia found in the Shan State material are of a similar size range to the associated pygidia, with the largest cranidium (fig. 36G-I) being 12 mm in length, and the largest pygidium (fig. 36M) being

13 mm in length. As a result, we here consider the figured pygidia to be those of *Tsinania?* sp..

Lonchopygella Sun and Xiang (1979)

Type species. *Lonchopygella megaspina* Zhou *in* Zhou et al. (1977)

Lonchopygella sp.

Fig. 38

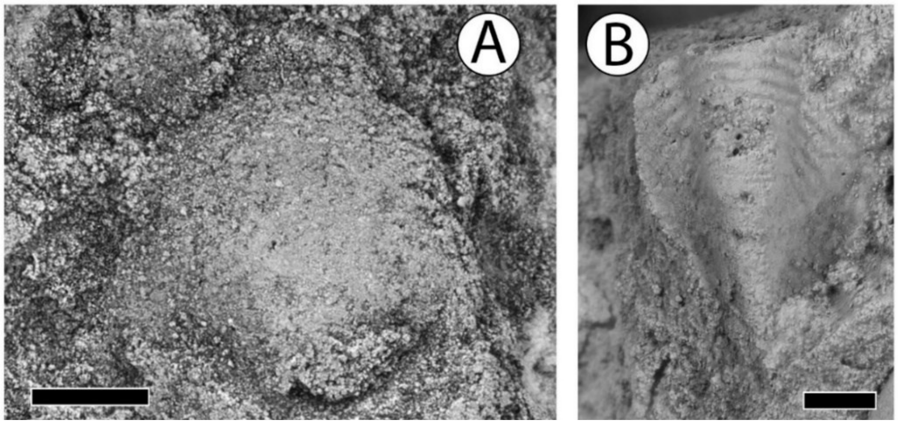

Figure 38. *Lonchopygella?* A, 16-PG-602_6, cranidium. B, 20-PG-83_34, pygidium. Scale bars represent 2 mm.

Figure 38

Material. 1 cranidium from PG3 float (16-PG-602_6). 1 pygidium from 23.87 m (20-PG-83_34).

Discussion. Material that can be definitively assigned to *Lonchopygella* sp, from the Shan State is limited to a single pygidium from the uppermost fossil-bearing horizon of the PG5 section, which displays the characteristic long axial spine, transverse axial furrows lacking bowing, and straight, posteriorly-angled pleural and interpleural furrows of *Lonchopygella megaspina* Zhou et al. (1977). A near-complete ontogeny of the *L. megaspina* head and tail was published in Zhu et al. (2013); through this ontogeny, we are able to determine that the Shan State pygidium representing *Lochopygella* is likely of a later holaspid stage, as it lacks the lateral spines characteristic of meraspid and early holaspid phases of development.

A single cranidium that may be assignable to *Lonchopygella* was found in float along the road to Padongaing village. This cranidium is broad and features a short, blunt anterior, both of which serve to differentiate it from *Tsinania?* sp.; however, it is otherwise generally tsinaniid in appearance, with the characteristic effaced axial and glabellar furrows. The poor preservation of the cranidium further prevents securing its generic affinity. Here we tentatively assign this cranidium to *Lonchopygella* sp..

Order Phacopida Salter (1864)

Suborder Cheiruruina Harrington and Leanza (1957)

Family Pliomeridae Raymond (1913)

***Parapilekia* Kobayashi (1934)**

Type species. *Calymene? speciosa* Dalman (1827) Tremadoc series, Öland, Sweden.

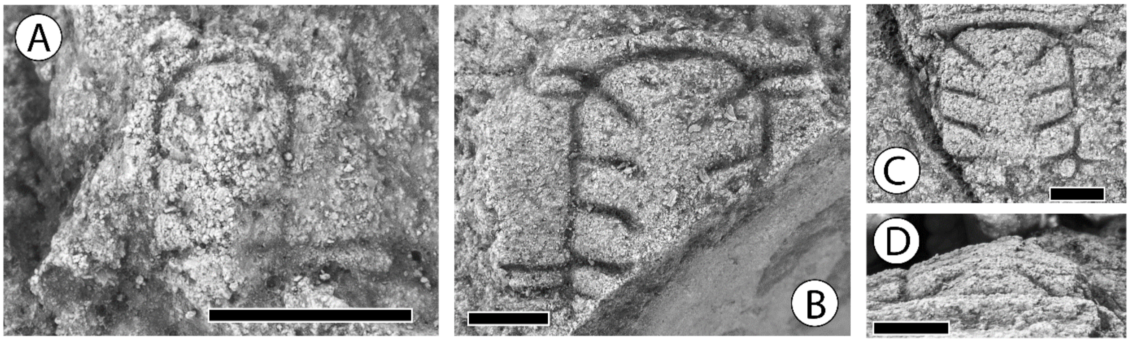

Figure 39. *Parapilekia?* sp. A, 20-PG-S04_7, cranidium. B, 20-PG-S04_5, cranidium. C-D, 20-PG-S04_9, cranidium in: D, anterior. Scale bars represent 2 mm.

Figure 39

Discussion. *Parapilekia* is a somewhat widespread species, found in Tremadocian strata from several Gondwanan terranes, including *peri*-Gondwanan Thailand (Wernette et al., 2023), Australia (Shergold et al., 2007) and S. China (Peng, 1991), as well as Iran (Pour, 2006), Laurentia (Holliday, 1942), Baltica (Ebbestad, 1996), and Armorica (Martin et al., 2016).

The *Parapilekia* cranidium can be defined by possessing an elongated, parallel-sided to slightly anteriorly narrowing glabella, as well as 3 pairs of deeply-incised glabellar furrows that extend only partway across the glabellar width. The S3 furrows originate from the anterior corners of the glabella and are strongly posteriorly directed, while the S1 and S2 furrows are more transverse in nature, with innermost tips directed slightly posteriorly (Holliday, 1942). The pygidium of *Parapilekia* is subelliptical and marginally spinose, with 4 pairs of spines confluent with pygidial inter-furrow segments and a wide axis with 5 axial segments, as can be seen in Ebbestad (1999) fig. 79D. The pleural and interpleural furrows are both deeply incised and impressed on the first two ribs (Lee & Chatterton, 1997).

Peng (1990) provided a detailed and emended description of *Parapilekia* which distinguished it from the similar genera *Pilekia* Barton, 1915 and *Anacheirurus* Reed (1896). The *Parapilekia* cranidium can be distinguished from *Pilekia* by the inflated L1 and strong anterior tapering of the glabella in the latter, in contrast to the parallel-sided glabellar condition of *Parapilekia*. The pygidia of both genera are marginally spinose with 4 pairs of spines, but can be distinguished primarily by the number of axial segments, as *Pilekia* has 4 and *Parapilekia* has 5. *Anacheirurus* has been posed to be more difficult to distinguish from *Parapilekia* on the basis of its cranidium, as both possess a parallel-sided to slightly anteriorly narrowing glabella (Peng, 1990; Sdzuy et al., 2001). Thus, the pygidia were thought to be the distinguishing factor, as *Anacheirurus* only possesses a maximum of 3 pairs of pygidial spines (Sdzuy et al., 2001). However, in a later analysis of *Anacheirurus,* various species were shown to have only two pairs of spines (Perez-Peris et al., 2021), including the type species, *A. frederici* Salter (1864), and some have as few as one pair of pygidial spines, such as *A. adserai* Vela *in* Vela and Corbacho (2007). This indicates a high degree of variability in number of marginal spines, rendering them less useful for identification than was initially believed. Thus, *Anacheirurus* and *Parapilekia* are difficult to distinguish; however, in keeping with Perez-Peris et al. (2021), we here consider the two genera to be distinct.

Parapilekia can be distinguished from another similar cheirurid, *Rossaspis,* by several characteristics of the cranidium and pygidium; the eye ridges of *Rossaspis* are positioned more anteriorly than those of *Parapilekia,* with no fixigenal area between the ridges and anterior border, and *Rossaspis* lacks the anterior plural furrows characteristic of *Parapilekia* (Lee & Chatterton, 1997). The only species of *Parapilekia* documented from Thailand, *Parapilekia bunopasi* Stait et al. (1984), was initially assigned to *Rossaspis?* on the basis of a lack of preglabellar field, a short anterior border, and significantly anteriorly-positioned eye ridges; however, these features are also present in some forms of *Parapilekia,* and *P. bunopasi* possesses an anterior fixigenal area as well as deeply incised interpleural furrows and spines on the posterolateral projections, none of which are characteristic of *Rossaspis.*

***Parapilekia?* sp.**

Fig. 39

Material. 3 cranidia from PG6&7 2.28 m (20-PG-S04_5, 20-PG-S04_7, 20-PG-S09 internal and external mold).

Discussion. The Shan State material consists of 3 incomplete cranidia, which possess a parallel-sided to slightly anteriorly narrowing glabella and glabellar furrows very similar to those of *Parapilekia bunopasi* Stait *et al.,* 1984. However, lacking pygidia and complete cranidia it is difficult to conclusively assign the Shan State material to *Parapilekia.* It is therefore referred to as *Parapilekia?* sp.

Order Odontopleurida

Indet. odontopleurid

Fig. 40

Material. 1 cephalic fringe from PG6&7 1.87 m (20-PG-S06_3).

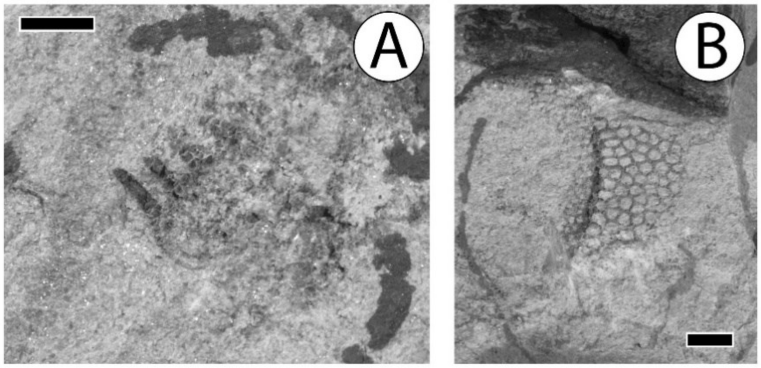

Figure 40. Indet. odontopleurid. A, 20-PG-S06_3, cephalic fringe. Indet. harpiid. B, 20-PG-S06_2, cephalic fringe. Scale bars represent 2 mm.

Figure 40

Discussion. Similarly to above, this odontopleurid is represented solely by a single cephalic fringe found from the lowest fossil horizon in the PG6 & 7 sections, approx. 1.87 m from the section base. Though the cephalic fringe is incomplete, the characteristic enfringing spines identify it as an odontopleurid (Whittington, 1956; Ramsköld, 1991).

Order Harpetida

Indet. harpiid

Fig. 40

Material. 2 cephalic fringes from PG6&7 1.87 m (20-PG-S06_2), 2.28 m (20-PG-S04_16).

Discussion. The presence of this harpid is represented by two cephalic fringes from the Tremadocian PG6 & 7 section. These fringes are assigned to the order Harpetida on the basis of small, hexagonal perforations in the exoskeleton, though other features cannot be concretely identified, as both specimens are incomplete.

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