

Trilobites of Thailand's Cambrian–Ordovician Tarutao Group and their geological setting

by SHELLY J. WERNETTE^{1,2,*} , NIGEL C. HUGHES¹ , PAUL M. MYROW³ 
and APSORN SARDSUD⁴ 

¹Department of Earth & Planetary Sciences, University of California, Riverside, California 92521, USA, swernette@txstate.edu, nigel.hughes@ucr.edu

²Department of Geography & Environmental Studies, Texas State University, San Marcos, Texas 78666, USA

³Department of Geology, Colorado College, Colorado Springs, Colorado 80903, USA

⁴Division of Mineral Resources Analysis & Identification, Department of Mineral Resources, Ministry of Natural Resources & Environment, 75/10 Rama VI Road, Ratchathewi, Bangkok 10400, Thailand

*Corresponding author

Typescript received 24 May 2021; accepted in revised form 26 April 2023

Abstract: Tuff-bearing upper Cambrian to lowermost Ordovician strata on Ko Tarutao island, Satun province, southernmost peninsular Thailand, contain a rich trilobite fauna relevant to global biostratigraphy, peri-Gondwanan palaeogeography and shifting evolutionary mode. This area of Sibumasu, a lower Palaeozoic marginal Gondwanan terrane, is shown to have been closely associated with Australia, North China (Sino-Korea) and other continental fragments from the supercontinent's northern equatorial sector, including South China at that time. Shared faunas also suggest a Kazakhstani and Laurentian association. Collections from eight sections yielded 10 newly discovered species and one new genus from ancient shoreface and inner shelf siliciclastic deposits. With the new taxa and revision of taxa known previously, we refine the age of the upper two formations of the Tarutao Group to the middle of Cambrian Stage 10, and lower–middle Tremadocian. Two biozones are erected for

Sibumasu: the *Eosaukia buravasi* Zone, encompassing all Cambrian sections from Ko Tarutao, and the *Asaphellus charoenmiti* Zone, encompassing the Tremadocian fauna discussed herein. The new genus is *Tarutaoia* and new species are *Tsinania sirindhornae*, *Pseudokoldinioidia maneekuti*, *Pagodia? uhleini*, *Asaphellus charoenmiti*, *Tarutaoia techawani*, *Jiia talowaois*, *Caznaia imsamuti*, *Anderssonella undulata*, *Lophosaukia nuchanongi* and *Corbinia perforata*. Other taxa reported for the first time from Tarutao are *Mansuyia? sp.*, *Parakoldinioidia callosa* Qian, *Pseudagnostus sp.*, *Homagnostus sp.*, *Haniwa mucronata* Shergold, *Haniwa sosanensis? Kobayashi*, *Lichengia simplex* Shergold, *Pacootasaukia sp.*, *Wuhuia? sp.*, *Plethopeltella sp.*, *Apatokephalus sp.*, *Akoldinioidia sp.* 1 and *Koldinioidia sp.*

Key words: Thailand, Trilobita, Cambrian, Ordovician, Sibumasu, Gondwana.

CAMBRIAN–ORDOVICIAN rocks of the Sibumasu terrane (Fig. 1) comprise fossiliferous siliciclastic strata with interbedded rhyolitic tuffs. These rocks provide faunal, geochemical and geochronological data for reconstruction of the early Palaeozoic marginal-Gondwanan palaeogeography, revision of the geochronological time scale, and document regional biodiversity at that time. The stratigraphic succession on Ko Tarutao (Tarutao Island) has particular significance for the interpretation of events leading up to the initiation of Ordovician biodiversification. The latest Cambrian–earliest Ordovician interval witnessed the final episodes of repeated trilobite diversification and rapid extinction (Palmer 1965; Zhou & Zhen 2008) before the sustained evolutionary radiation of the Palaeozoic fauna (Sepkoski 1978; Adrain *et al.* 1998). Iterative late Cambrian extinctions coincided with peak activity in the belt of Phanerozoic felsic magmatism (McKenzie *et al.* 2014,

2016) that rimmed equatorial Gondwana. To date, poor Furongian geochronological resolution masks any association between peaks of magmatism and extinction. Palaeontological data collected from detailed measured sections with numerous tuffs in Ko Tarutao will enable more precise chronostratigraphic correlation within Cambrian Stage 10 and the lower–middle Tremadocian across Gondwana. Trilobite systematic palaeontology is key to regional correlation and temporal calibration, and to an understanding of the transition from the ‘boom and bust’ radiations of the Cambrian into the prolonged Ordovician biodiversification. A detailed faunal inventory also facilitates palaeobiogeographic assessment of marginal Gondwanan terranes and beyond. Systematic palaeontology is fundamental to addressing all of these issues.

Recent Cambrian–Ordovician palaeogeographic reconstructions most commonly place Sibumasu as an



FIG. 1. The modern extent of the Sibumasu terrane. Modified from Wernette *et al.* (2020a).

‘outboard’ continental fragment located off northwestern Australia (e.g. Cocks & Torsvik 2013; Domeier 2018), but its exact position is not firmly constrained; Wernette *et al.* (2021) discussed the host of alternative reconstructions. The broad span of detrital zircon grain ages in Tarutao’s Furongian rocks suggest a connection to core Gondwana (e.g. McKenzie *et al.* 2014), but Sibumasu has not been specifically located using this approach. No reliable palaeomagnetic data exist, and the majority of fauna hitherto studied from Sibumasu has remained in open species-level nomenclature until this work. Hence, an aim of this study has been to provide a more comprehensive account of the Cambrian trilobite fauna so as to improve the comparative database.

Of Sibumasu’s regions, peninsular Thailand has the best studied Cambrian–Ordovician faunal record. The first systematic study of Cambrian fossils from Myanmar was done only recently (Wernette *et al.* 2021), and no notable fossils have been discovered in the tectonically altered Cambrian rocks of northern Thailand (Wongwanich *et al.* 2002). The Cambrian fauna of the Baoshan Block, debatably part of Sibumasu (Wernette *et al.* 2021), was described by Sun & Xiang (1979) with some additional documentation (e.g. Luo 1982, 1983, 1984, 1985a, 1985b). Baoshan’s fossils are generally notably deformed. Those Cambrian fossils that we have collected from Langkawi Island, Malaysia, immediately adjacent to both Ko Tarutao and peninsular Thailand, are fragmentary and have not been formally described (also see Cocks *et al.* 2005).

Kobayashi (1957) described a Furongian fauna on six slabs sent to him from a single bed on the western side of Ko Tarutao (Fig. 2). Shergold *et al.* (1988) expanded upon Kobayashi’s (1957) work using additional collections from several new locations (Fig. 2). Stait *et al.* (1984) described an Early Ordovician fauna from Ao Phante Malacca (Fig. 2). Non-trilobite fauna noted in these studies and our collections include brachiopods, cephalopods and crinoids, as well as various trace fossils. Outcrops of the Tarutao Group on the mainland are commonly tectonically deformed and have not yielded any identifiable fossils (Wongwanich *et al.*, 2002).

Prior to this work, 18 trilobite taxa had been recognized from the Tarutao Group, with eight resolved to species level (Kobayashi 1957; Stait *et al.* 1984; Shergold *et al.* 1988). Herein, 42 varieties of trilobites are reported from the Tarutao Group, of which 24 are assigned to named species. Of these 24 species, only 5 have been recorded outside Thailand (Table 1). Three of the endemic species are from monospecific endemic genera: *Tarutaoia*, *Thailandium* and *Satunarcus* (see also Wernette *et al.* 2020a, 2020b). New material of every trilobite species or form illustrated in previous studies was recovered in our work, possibly excluding one indeterminate lelostegiid (Shergold *et al.* 1988).

GEOLOGICAL SETTING & REGIONAL STRATIGRAPHY

Western and peninsular Thailand, along with Myanmar’s Shan Plateau, are part of Sibumasu (Metcalfe 1984), inclusive of the Shan–Thai Block (Bunopas & Vella, 1978).

FIG. 2. Map of Ko Tarutao. AML, Ao Mo Lae; APM, Ao Phante Malacca; ATD, Ao Talo Udang; ATT, Ao Talo Topo; ATTW, Ao Talo Topo west; ATW, Ao Talo Wao, type section of the Talo Wao Formation; LHN, Laem Hin Ngam; S1–S3, ATD Sections 1–3. Modified from Burrett & Chaodumrong (2017).

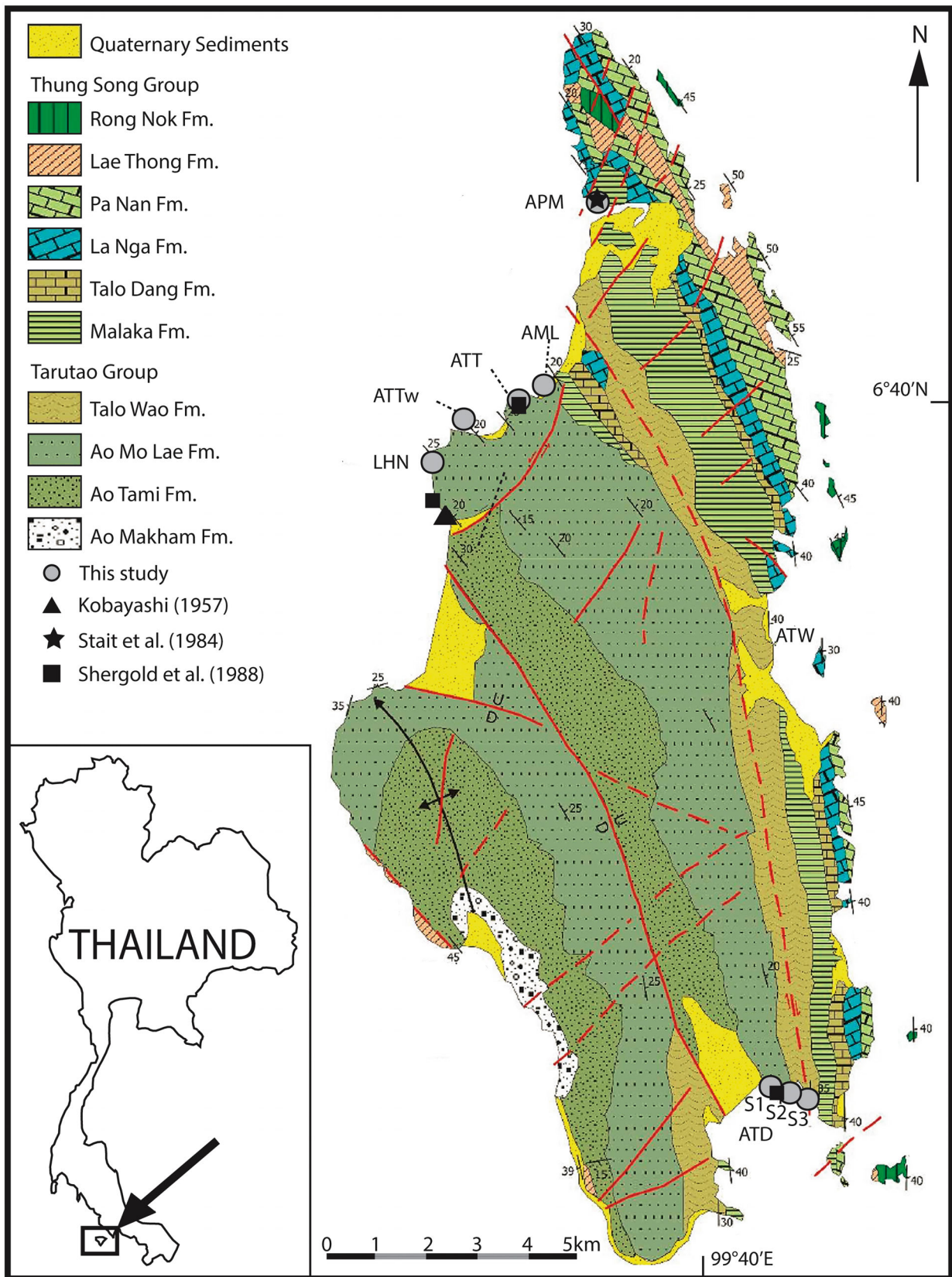


TABLE 1. Trilobites of the Tarutao Group, listed in the order of occurrence in the text.

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

‘This study’ is inclusive of recent publications that are part of this same project (i.e. Wernette *et al.* 2020a, 2020b); ‘sp. nov.’ is used if the species is/was new in the publication under which it is listed.

This terrane ultimately became the microcontinent of Sibumasu with the Late Triassic opening of the Meso-Tethys Ocean (Metcalf 2017, fig. 17); during the earliest Palaeozoic it was part of the 'outboard' margin that bordered northern equatorial Gondwana. The earlier history of this outboard material is debated, but it may have accreted to core Gondwana with the closure of a branch of the Proto-Tethys during the early Palaeozoic (Wernette *et al.* 2021). A long subduction zone located along Gondwana's northern margin facilitated this accretion, evidenced by widely distributed and high-volume felsic intrusions (LeFort *et al.* 1986; Zhu *et al.* 2012; Xu *et al.* 2014; Domeier 2018) (Fig. 3). Sibumasu was part of this shelfal volcanic belt. Rhyolite in the Bawdwin Mine area of Myanmar's northern Shan State (Brinckmann & Hinze 1981; Bender 1983) and tuffs in the southern Shan State and Thailand provide further evidence of Cambrian–Ordovician volcanism (Stait *et al.* 1984; Shergold *et al.* 1988; Imsamut & Yathakam 2011). These volcanic horizons are part of correlative uppermost Cambrian to lowest Ordovician siliciclastic units: the Molohein Group in the southern Shan State of Myanmar, the Panguyun Formation in the northern Shan State of

Myanmar and the Tarutao Group in Thailand (Thein 1973; Shergold *et al.* 1988; Aung & Cocks 2017). In Myanmar the Panguyun Formation and Molohein Group sit unconformably on top of the Precambrian or lowest Cambrian Chaung Magyi Formation (Wolfart *et al.* 1984; Wernette *et al.* 2021). In Thailand, Precambrian basement is known from the mainland where it is separated from the Tarutao Group by an unconformity; in areas where both basement and cover units are exposed, they record high- and low-grade regional metamorphism, respectively (Wongwanich *et al.* 2002). On Ko Tarutao, the Tarutao Group is the oldest lithological unit exposed and is unmetamorphosed (Shergold *et al.* 1988).

The siliciclastic and tuffaceous Tarutao Group is the lower of the two major lithostratigraphic units on Ko Tarutao, the other being the entirely calcareous Ordovician Thung Song Group. While recognized at the group level when first named (Javanaphet 1969), most 20th century literature refers to the Tarutao unit as a formation, as did Bunopas *et al.* (1983), who sought to combine it with the Thung Song Formation (presently the Thung Song Group) into the Langu Group. The Tarutao Group is now formally subdivided into four formations

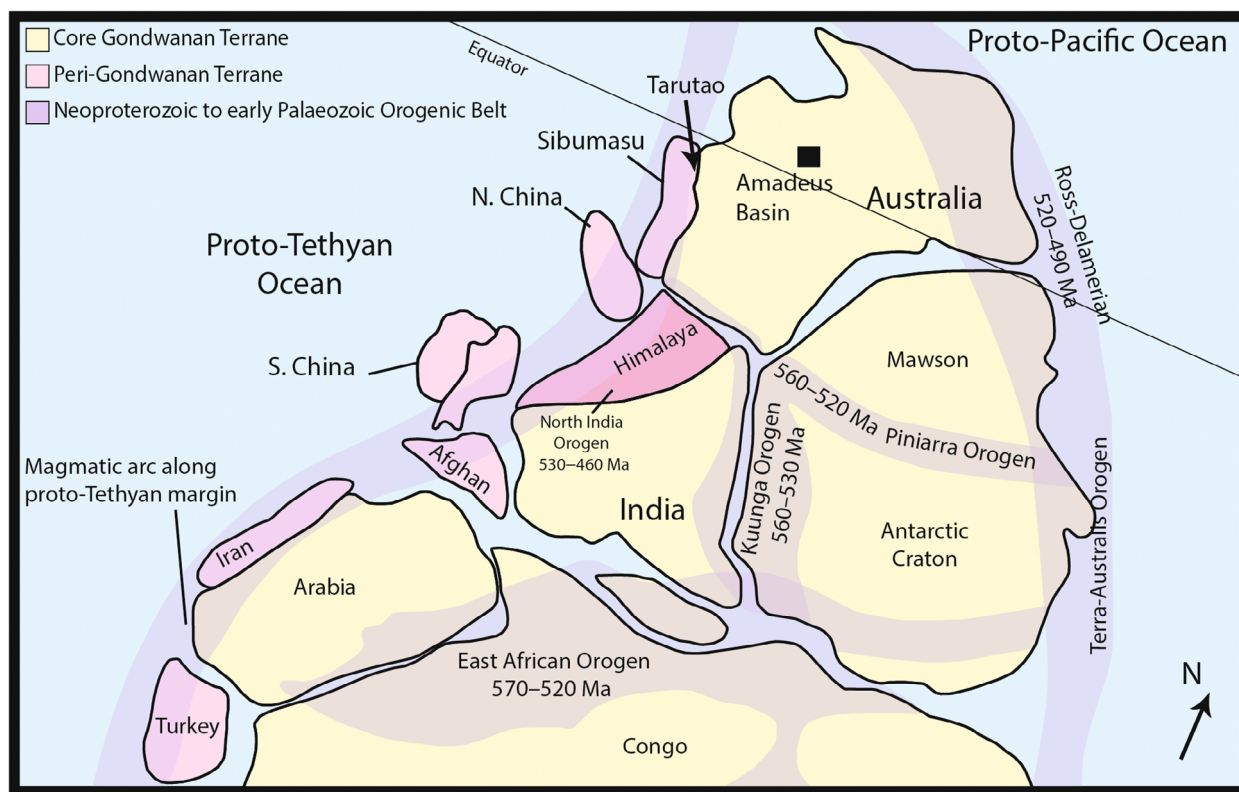


FIG. 3. One of the plausible Cambrian–Ordovician palaeogeographic reconstructions of northern Gondwana. Locations of the Amadeus Basin and Tarutao are approximations to indicate their relative proximity. Modified from Hughes (2016); orogenies from Cawood *et al.* 2007; equator from Burrett *et al.* 2014.

(Imsamut & Yathakam 2011; Fig. 2). The four formations now recognized, in ascending stratigraphic order, are the Ao Makham, Ao Tami, Ao Mo Lae and Talo Wao formations. The lower and upper formations consistently correspond with the upper and lower units described in previous literature, regardless of whether authors considered there to be three (e.g. Lee 1983; Bunopas *et al.* 1983) or four (e.g. Teraoka *et al.* 1982) formations within the group.

Due to the dense forest and discontinuous exposure along the shoreline, coupled with the prevalence of both faults and folds, estimates of the thickness of the Tarutao Group are approximate. Lee (1983) thought the group to be more than 3000 m thick (a 450+ m lower unit, 1950+ m middle unit and a 575 m upper unit), but more recent estimates are little more than 1000–1500 m thick (e.g. Burrett & Chaodumrong 2017). The oldest unit, the Ao Makham Formation, is at least 100 m of thick-bedded brown to grey-brown siltstone and sandstone with minor pebbly conglomerate; the only fossils reported are rare brachiopods preserved in thin shale units, and these were not reported to provide a significant biostratigraphical age constraint (Teraoka *et al.* 1982; Akerman 1986; Imsamut & Yathakam 2011). The next oldest unit, the Ao Tami Formation, is reported to be c. 450 m thick and consists of thick to very thick beds of cross-bedded, brown quartz arenite with interbedded grey-green shale (Wongwanich & Burrett 1983). Two trilobite species are found in this unit, *Hoytaspis thanisi* Shergold *et al.*, 1988 and *Prosaugia* sp. 2 (= *Prosaugia*? cf. *nema sensu* Shergold *et al.*, 1988), both of which are also found in the conformably overlying Ao Mo Lae Formation (Imsamut & Yathakam 2011). All Cambrian fauna described herein were collected from the Ao Mo Lae Formation. This formation is estimated to be c. 600 m thick and comprises purplish red and grey fine to medium-grained quartz arenite with small amounts of interbedded shale. Imsamut & Yathakam (2011) suggested that rhyolitic tuffs are most common in the upper part of this formation but provided no documentation of this suggestion. The youngest unit of the Tarutao Group is the Talo Wao Formation, which is c. 250 m thick and mostly consists of thin to medium beds of reddish brown to greyish brown fine-grained sandstone interbedded with micaceous siltstone and shale (Wongwanich & Burrett 1983; Stait *et al.* 1984; Imsamut & Yathakam 2011). The Tremadocian fossils described herein are from this unit.

MATERIAL AND METHOD

Field work

Fossil specimens were collected from eight sections across five localities, and one locality with only a single bed: Ao Mo Lae (AML), Ao Talo Topo (ATT), Ao Talo Topo

west (ATTw), Laem Hin Ngam (LHN), Ao Talo Udang (ATD) and Ao Phante Malacca (APM). Ao Mo Lae and Ao Talo Udang are accessible by land via roads, and the rest are accessible only by boat.

All fossils from Ko Tarutao are disarticulated, and many are fragmented. Deformation is typically negligible, except for material in the Ao Talo Udang Section 1, horizon 7.00 m. All fossils preserved in sandstone on Ko Tarutao are internal and external moulds. Some moulds, especially in Ordovician collections, are partially, but weakly, infilled with an orange oxide, presumed to be limonite; in such cases the matrix is typically brown or reddish brown. Other moulds, especially in deeply purple sandstone, have very thin coatings of silica, making the fossils stand out white against the purple matrix.

Sample preparation and analysis

The specimens were prepared manually using Dremel vibro and rotary tools. They were blackened with India ink, whitened with ammonium chloride sublimate, and photographed with a Leica stereoscopic camera model MZ16 or M205C using the z-stacking method. Broken or fragile samples were glued or impregnated using Butvar dissolved in acetone. Replicas of each of Kobayashi's (1957) figured specimens, (UMUT PB02294–PA02299), were made using vinyl polysiloxane. External moulds are figured in positive relief using image colour inversion in Adobe Photoshop, except where use of a latex cast is specified.

Landmark-based morphometric analysis used the following components of H. David Sheets' Integrated Morphometrics Package: CoordGen8, BigFix8, Regress8 and PCAGen8 (Webster & Sheets 2010; http://www.filenetica.org/cursos/Morfometria/IMP_installers/index.php).

PALAEOENVIRONMENTAL CONTEXT

The Tarutao Group is a shallow-water siliciclastic-dominated succession that is primarily composed of hummocky cross-stratified and parallel-laminated very fine sandstone without notable penetrative bioturbation. There are also thin to medium beds of siltstone and shale, and variably spaced (cm to m scale) coquina beds that are generally less than 1 cm thick. The strata also have interbeds of rhyolitic volcanic ash and a few breccia and carbonate beds. Fossils were primarily collected from the coquina beds, which are porous and friable due to dissolution of the original shells. The fossils, preserved as internal and external moulds, were recovered by breaking the coquina layers parallel to bedding.

Deposits of the Ao Mo Lae Formation are broadly similar between localities, although they vary slightly in their

sandstone/shale ratios. The common parallel lamination and hummocky cross-stratification indicate deposition under high-velocity flows. Hummocky cross-stratification is characteristic of tempestites deposited under complex waves and/or combined waves and currents (Dott & Bourgeois 1982; Arnott & Southard 1990; Myrow & Southard 1996). These Ao Mo Lae Formation strata are typical storm-dominated shoreline deposits (Walker 1984). Shoreface (above fair-weather wave base) deposits are represented by amalgamated hummocky cross-stratification beds (e.g. ATD S1 and lower ATD S2), and inner shelf deposits are represented by interbedded tempestite sandstone and shale (e.g. upper ATD S2). The Talo Wao Formation at APM (Fig. 11) and ATD S3 (Fig. 10) has thin to medium bedded sandstone and shale, with few amalgamated sandstone beds (1–2 m thick). The sandstone beds include prominent centimetre–decimetre-thick beds with ball-and-pillow structures and convolute lamination. The shale content is higher and a few carbonate beds are present near the top of the formation as it transitions into overlying middle Tremadocian carbonate strata. The higher shale content of the Talo Wao Formation indicates deposition largely below fair-weather wave base, and at the transition from lower shoreface to inner shelf. The Cambrian Ao Mo Lae Formation (i.e. AML, ATT, ATT_w and ATD S1 and S2) thus comprises more proximal facies than the Ordovician Talo Wao Formation (i.e. APM and ATD S3).

All sections contain shell-rich coquina beds, and we also interpret these beds as tempestites that formed from winnowing and hydraulic sorting under storm waves (Kidwell 1991). Such beds are also present in Cambrian strata with similar facies in Bhutan (Hughes *et al.* 2011). In nearshore shelf environments out-of-habitat sclerite transport is rare compared to within-habitat transport (Patskowsky & Holland 2012), and thus, although sclerites were disarticulated and transported, it is likely that the fauna lived in the vicinity. Coquina beds are not as well-developed in the APM section, probably because the strata were deposited in somewhat deeper water conditions, which may reflect lower abundances of trilobites and/or less frequent re-working, winnowing and concentration of fossil material.

Several horizons in a tuffaceous interval at *c.* 1.0 m at ATD S1 show trace fossils on the soles of sandstone beds. These include the narrow burrow *Cruziana problematica* (Schindewolf 1921), larger *Rusophycus* burrows and *Diplichnites* trails. Narrow U-shaped (*c.* 5-mm-wide) *Diplocraterion* burrows occur on a bedding surface of interference ripples 0.6 m above the top of the tuffaceous interval. Trace fossils including *C. problematica* and *Diplichnites* are on the bases of several beds *c.* 12 m in the APM section, and there are *Paleodictyon* of a few millimetres in diameter on the top of one bedding surface in the same interval.

Lee (1983) noted that fine-grained carbonate in the upper Talo Wao Formation transitions into the carbonate platform deposits of the Thung Song Group. In epicontinental deposits, Cambrian siliciclastic-dominated strata are commonly overlain by Ordovician carbonate-dominated strata (Myrow *et al.* 2003, 2012), in part due to global sealevel rise and associated flooding of continental source rocks. A similar facies transition may be recorded in rocks from the lower Nambeet Formation of the Canning Basin in Western Australia (Normore *et al.* 2018).

LOCALITIES

Ao Mo Lae (AML)

A 6-m-thick outcrop of the Cambrian Ao Mo Lae Formation (Fig. 4) at Ao Mo Lae is the most accessible of the Tarutao localities (06°40'13"N, 099°38'02"E). At the south end of Ao Mo Lae, dark purple sandstone crops out of the beach sand with a strike and dip of *c.* 325°/25°NE.

The fossil-bearing coquina beds (Fig. 5C) have silica films that line some moulds, causing them to appear white against the purple matrix, but silicification is insufficiently advanced to produce a durable natural cast or replacement.

There are five collections from AML (AML h1–h5) that have limited stratigraphic provenance within the section and must therefore be omitted from the log in Figure 4 (see Table 2 for their faunal contents and also Wernette *et al.* 2020a, 2020b).

Ao Talo Topo (ATT)

The shoreline of Ao Talo Topo (06°40'08"N, 099°37'46"E) contains an outcrop (Fig. 6) of the Ao Mo Lae Formation, corresponding to Shergold *et al.*'s (1988) locality 6. The ATT section is highly fossiliferous and contains several tuffs. Strike and dip at the base of the measured section is 164°/20°NE. The locality is separated from AML by a small inlet with at least one exposed fault between them, that strikes at *c.* 115° and projects into the inlet. The dip of the section is consistent with that at AML, but the strike differs and the stratigraphic relationship between these adjacent outcrops is unknown.

ATT's sandstone is similar in facies to AML. However, the lower and upper parts of ATT are notably different because the lower part has convoluted beds, and the upper has more abundant siltstone and shale. The middle of the section, where tuffs are thickest, lacks identifiable fossils. Despite these sedimentological differences, the

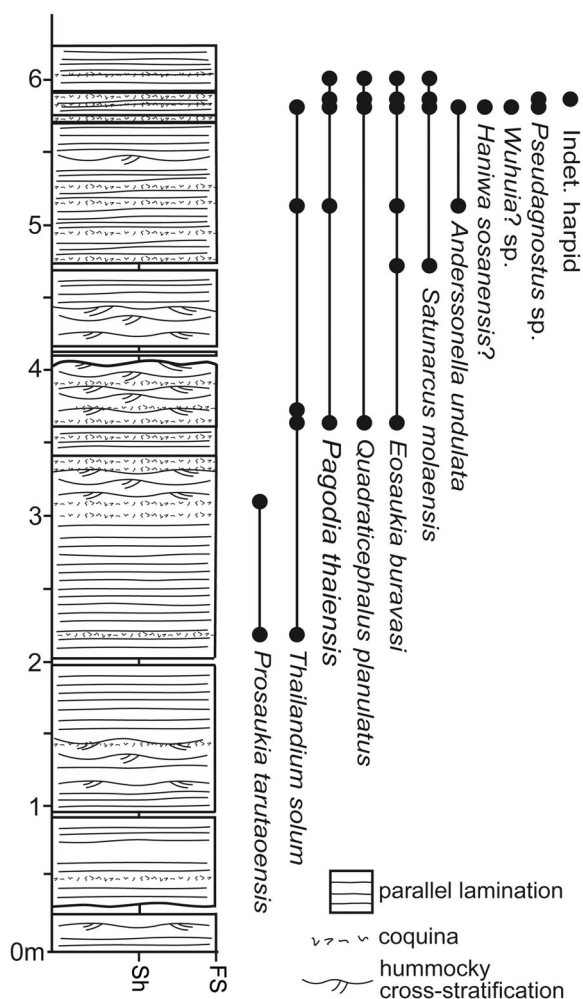


FIG. 4. AML section. Fossiliferous horizons are 2.20 m, 3.10 m, 3.62 m, 3.82 m, 4.71 m, 5.17 m, 5.81 m, 5.84 m and 6.01 m above the base. Grain size: FS, fine-grained sand; Sh, shale. Modified from Wernette *et al.* (2020a).

faunal content varies little through the section. ATT terminates at a fault ($06^{\circ}40'09''\text{N}$, $099^{\circ}37'49''\text{E}$) as noted in Shergold *et al.* (1988). About 1.5 m above this fault we collected two fossiliferous horizons (ATT h1 and ATT h2) but did not measure any additional section at this locality.

Ao Talo Topo west (ATTw)

A single fossiliferous sandstone was collected from the Ao Mo Lae Formation at Ao Talo Topo west ($06^{\circ}39'40''\text{N}$, $099^{\circ}37'04''\text{E}$), and yielded a diverse faunal assemblage. The lithology and faunal assemblage are most similar to those of AML and ATT. It is likely that this site, or one very nearby, was the location of Kobayashi's (1957) collection.

Laem Hin Ngam (LHN)

The Ao Mo Lae Formation also crops out at Laem Hin Ngam ($06^{\circ}39'19''\text{N}$, $099^{\circ}36'54''\text{E}$; Fig. 7) just south of ATTw, with a strike and dip of c. $170^{\circ}/5^{\circ}\text{E}$. The fossiliferous horizons at 1.54 m and 2.85 m contain comparatively small specimens.

Ao Talo Udang (ATD)

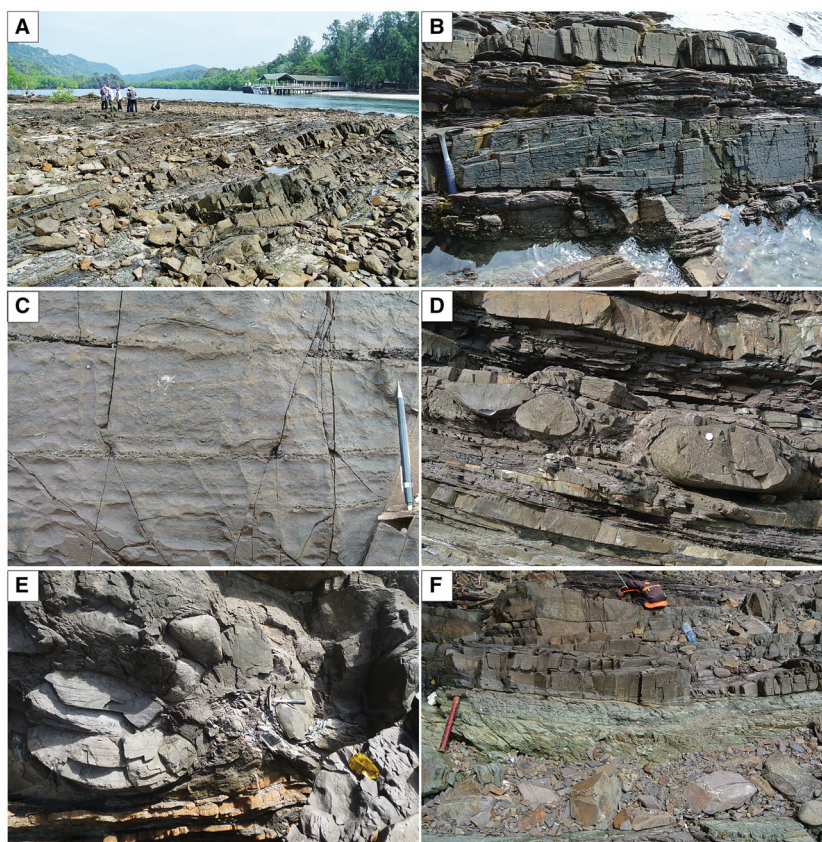
At the southeastern end of Ko Tarutao, the shoreline of ATD exposes the Ao Mo Lae and Talo Wao formations. Faults and covered intervals split this locality into three discontinuous sections (S1–S3 from west to east). S1 and S2 expose the Cambrian Ao Mo Lae Formation; S3 exposes the Tremadocian portion of the Talo Wao Formation.

ATD S1. ATD S1 ($06^{\circ}32'09''\text{N}$, $099^{\circ}40'47''\text{E}$; Fig. 8) is separated from ATD S2 by a fault of unknown throw. The base of ATD S1 is at the top of a thick (>5 m), nearly homogeneous outcrop of thinly bedded, very fine- to fine-grained purple sandstone. The fossils in the bed at 6.65 m are less densely concentrated than in other Ao Mo Lae coquinas. A 40-cm-thick bed at 7.00 m is a poorly indurated unit with irregular patches of fine sand, mud, and silt. It is unique relative to other fossiliferous beds from the Ao Mo Lae Formation because the fossils are not on a bedding surface but instead are abundant throughout and at various angles to bedding. This is the only horizon from the Ao Mo Lae Formation with abundant, although mildly distorted, fossils. At least part of the distortion was due to compression; fossils at the highest angle to bedding are the most deformed. These fossils also have a more finely preserved surface texture than that typical of the coquina horizons.

ATD S2. ATD S2 ($06^{\circ}32'07''\text{N}$, $099^{\circ}40'51''\text{E}$; Figs 5B, 9) comprises sandstone varying from light grey-purple to dark purple, making it lithologically more similar to AML and ATT than to ATD S1. Strike and dip is $009^{\circ}/52^{\circ}\text{E}$.

ATD S3. ATD S3 ($06^{\circ}32'06''\text{N}$, $099^{\circ}41'08''\text{E}$; Fig. 10) is separated from ATD S2 by a boulder-strewn coastal inlet with no rock exposure. The outcrop is part of the Talo Wao Formation but the exposure and fossil yield is poorer than at APM. Fossils have orange iron oxide infilling in a buff-coloured matrix and are very fragile casts that crumble on touch. *In situ* fossils are limited to brachiopods and a single type of librigena, but float material near this section yields a much richer faunal assemblage of both Cambrian and Ordovician fossils (Table 2, ATD S3f).

FIG. 5. A, APM section at low tide. B, hummocky cross-stratified sandstone bed at ATD; hammer is 18.5 cm long. C, hummocky cross-stratified and coquina beds at the 3.4–3.7 m zone at AML; pencil is 14 cm long. D, ball-and-pillow structures at 4.6 m above the base in the APM section; coin is 18 mm in diameter. E, ball-and-pillow structures above two thin carbonate layers at APM 12.5 m; hammer is 18.5 cm long. F, tuff (38 cm thick) at APM 22.5 m; hammer is 35 cm long.



Ao Phante Malacca (APM)

Ao Phante Malacca (06°42'14"N, 099°38'42"E; Figs 5A, D–F, 11) is the longest, best exposed, and most accessible section of the Tarutao Group given that it is directly north of the inlet harbouring the island's main pier. Strike and dip is 126°/32°N. Faults cross-cut the APM section, but offsets of marker beds show their throws to be minor. There are body fossils in both sandstone and carbonate lenses, but both dissolution and manual preparation were unsuccessful in recovering fossils from the carbonate, which primarily occurs as a dense hash. Sandstone at APM has calcite cement, which is undocumented elsewhere in the Tarutao Group. Fossil preservation is similar to that from ATD S3. In addition to trilobites and brachiopods, the top 30 m of this section contain abundant disarticulated, thin-walled crinoid columnals and thecal plates.

BIOSTRATIGRAPHICAL CORRELATION

Two distinct faunal assemblages occur in the Tarutao Group: one in the Ao Mo Lae Formation and one in the Talo Wao Formation, both of which contain a reasonably

diverse trilobite fauna and interbedded tuffs. Discontinuous sections on Ko Tarutao, taxonomic similarities between sections, and limited or absent faunal turnover within sections limit biostratigraphic resolution within each formation. Limited within-section turnover may suggest that within individual sections the rocks representing each formation were deposited quite rapidly. Apparent diversity increases (Ao Phante Malacca (APM), Ao Talo Topo (ATT), Ao Mo Lae (AML)) or decreases (Ao Talo Udang (ATD) S2) occur upwards within a section, but the overall lack of faunal turnover suggests that such fluctuation is probably an artefact of preservation and sampling (Signor & Lipps 1982). Even fauna above and below the unfossiliferous middle interval within the 29-m-thick ATT section show no differences in taxa represented. The Ao Mo Lae Formation is interpreted as the result of shore-face progradation, during which a substantial body of rock accumulated over a relatively short interval of time.

Cambrian

Of the outcrops of the Ao Mo Lae Formation studied herein, ATD S1 is likely to be the oldest, given that it yielded *Hoytaspis thanisi* and *Pagodia? uhleini*, which are

TABLE 2. Trilobite occurrences in horizons with poor stratigraphic provenance, listed in the order of occurrence in the text.

	AML					ATTw	ATT		ATD			
	h1	h2	h3	h4	h5	-----	h1	h2	S2h1	S2h2	S2h3	S3f
<i>Pseudagnostus</i> sp.						x						
<i>Tsinania sirindhornae</i>									x			
<i>Satunarcus molaensis</i>		x				x						
<i>Pseudokoldinioidia manekuti</i>						x	x					x
<i>Pagodia thaiensis</i>			x			x		x				
<i>Parapilekia bunopasi</i>												x
<i>Asaphellus charoenmiti</i>												x
<i>Yosimuraspis</i> sp.												x
<i>Pseudokainella malakaensis</i>												x
<i>Haniwa mucronata</i>						x						
<i>Anderssonella undulata</i>						x	x					
<i>Eosaukia buravasi</i>	x	x	x	x	x	x	x	x	x			
<i>Prosaukia tarutaoensis</i>			x			x						
<i>Prosaukia oculata</i>							x					
<i>Prosaukia</i> sp. 1										x		
<i>Prosaukia</i> sp. 3			x									
<i>Sinosaukia</i> sp.											x	
<i>Thailandium solum</i>		x	x	x	x	x						
<i>Pacootasaukia</i> sp.					x	x				x		
<i>Wuhuia?</i> sp.	x											
<i>Corbinia perforata</i>												x
<i>Quadraticephalus planulatus</i>		x	x	x		x	x			x		
<i>Koldinioidia</i> sp.							x					

not found in other sections, except at the base of ATD S2. *Hoytaspis thanisi* is present in the underlying Ao Tami Formation (Imsamut & Yathakam 2011). However, of the other trilobite species reported in the Ao Tami Formation, *Prosaukia* sp. 2 is present in the Ao Mo Lae Formation at LHN and ATT but not in ATD S1, therefore the occurrence of *H. thanisi* is not, by itself, a strong argument for an age greater than that of the other Ao Mo Lae Formation sections. Correlation with Laurentia, where *Hoytaspis* is known from lower Sunwaptan strata (Ludvigsen & Westrop 1983; = Jiangshanian), provides additional support for an older age, as does correlation with North China where *Mansuyia* is known from the *Kaolishania* Zone (Park *et al.* 2014; = Jiangshanian, Fig. 12). However, if ATD S1 is older than other outcrops of the Ao Mo Lae Formation, it is not likely to be Jiangshanian in age because it also contains species found in the other Ao Mo Lae sections (including *Eosaukia buravasi*, *Parakoldinioidia callosa* and *Pseudokoldinioidia manekuti*) that suggest a younger age, around the middle of Cambrian Stage 10 (see below). Occurrence of *Pagodia? uhleini* at the base of ATD S2 suggests that this section may stratigraphically succeed ATD S1, but it is otherwise faunally similar to LHN, AML and ATT, and may be age equivalent.

In each of AML, ATT, ATTW and LHN the faunal assemblage contains a mix of taxa that might reasonably

be assigned to zones spanning the late Jiangshanian through to the middle of Cambrian Stage 10 (Fig. 12). Some taxa are shared with both the *Quadraticephalus* and *Eosaukia* zones of South Korea, but the assemblage is more likely to correlate with the latter zone for reasons explained below. *Haniwa sosanensis?* (pervasive through most of ATT and the top of AML, although with some doubt regarding species-level affinity) is known only from the *Quadraticephalus* Zone (Park & Choi 2011), which in Korea is defined by the first occurrence of *Lophosaukia orientalis*, a different species of *Lophosaukia* than is found throughout the sections at both ATT and LHN. The Korean *Quadraticephalus* Zone also includes species of *Quadraticephalus*, *Koldinioidia* and *Tsinania*, which are all found in the Ao Mo Lae Formation.

Eosaukia buravasi, however, is pervasive in all Ao Mo Lae Formation localities, including co-occurrence with *Haniwa sosanensis?*. In Korea, *Eosaukia* is known only from the *Eosaukia* Zone (Choi *et al.* 2016). In North and South China *Eosaukia* extends to higher stratigraphic levels than in Korea but is unknown from the lower part of Stage 10 (Zhou & Zhen 2008). Korea's *Eosaukia* Zone is also rich in other dike-locephalid trilobites, *Quadraticephalus* and *Pagodia*, and these are the dominant taxa of the Ao Mo Lae Formation. *Lichengia simplex*, which occurs at the top of the Ao Talo

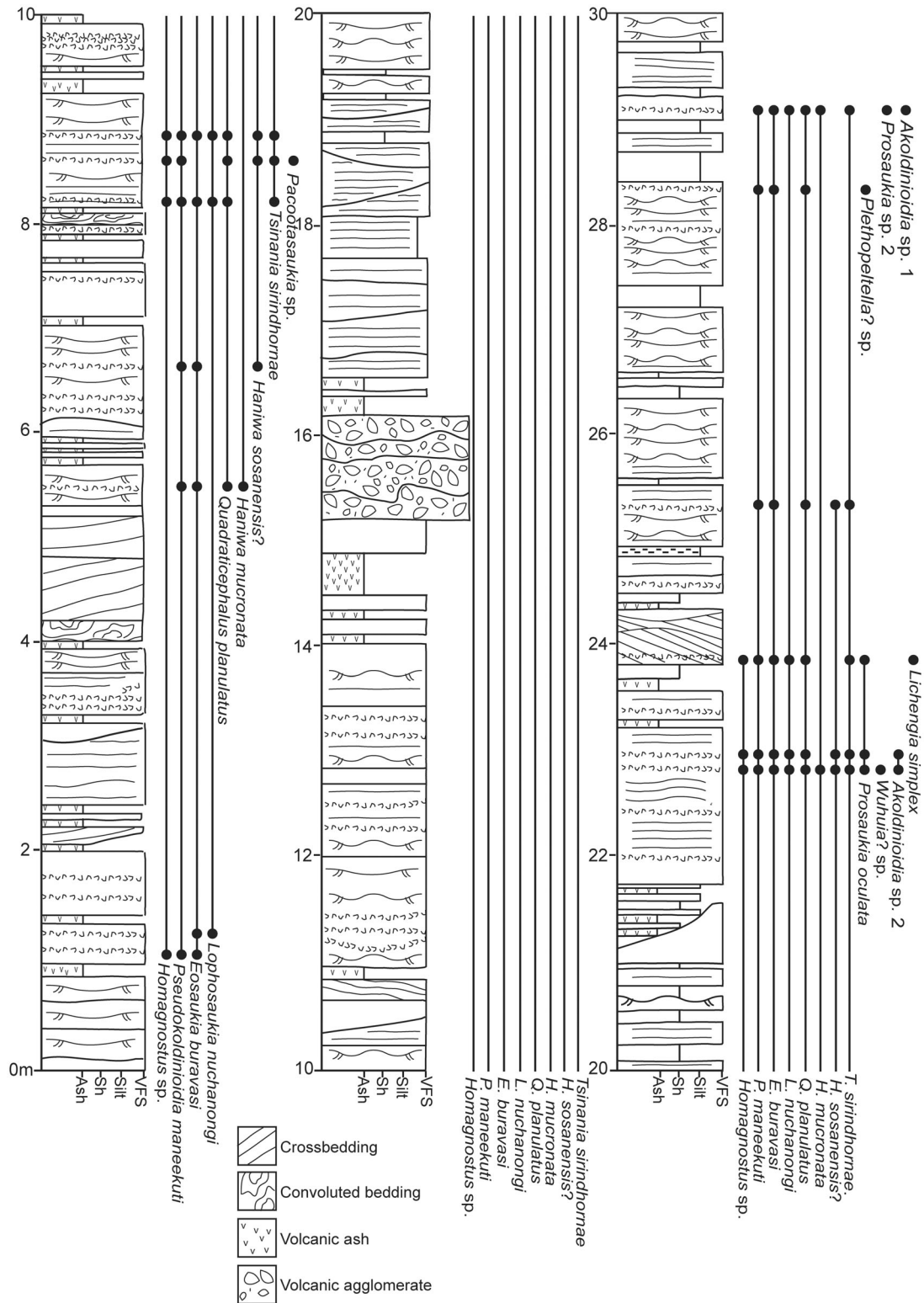


FIG. 6. ATT section. Fossiliferous horizons are 0.95 m, 1.10 m, 5.50 m, 6.65 m, 8.20 m, 8.60 m, 8.85 m, 22.78 m, 22.88 m, 23.33 m, 23.89 m, 25.34 m, 27.97 m, 28.37 m and 29.17 m above the base. Grain size: FVS, very fine-grained sand; Sh, shale. (See Fig. 4 for additional legend.) Modified from Wernette *et al.* (2020b).

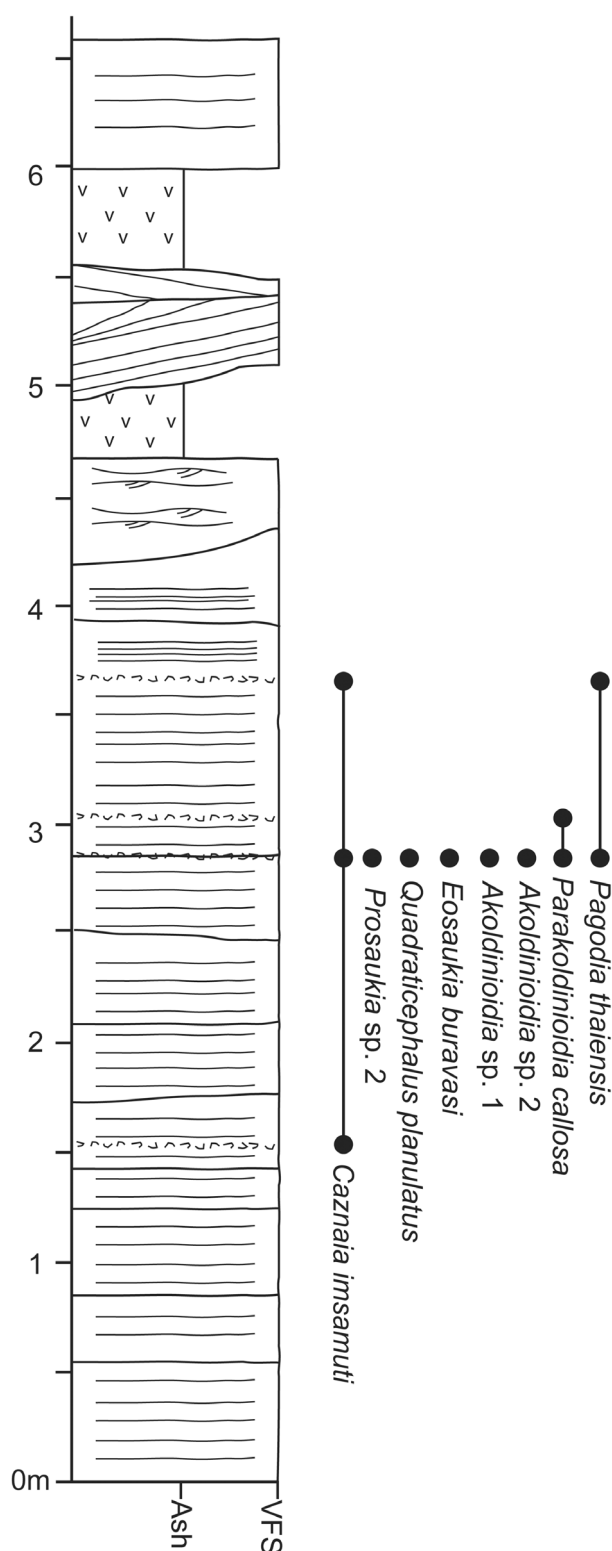


FIG. 7. LHN section. Fossiliferous horizons are 1.54 m, 2.85 m, 3.05 m and 3.69 m above the base. Grain size: FVS, very fine-grained sand. (See Figs 4 and 6 for legend.)

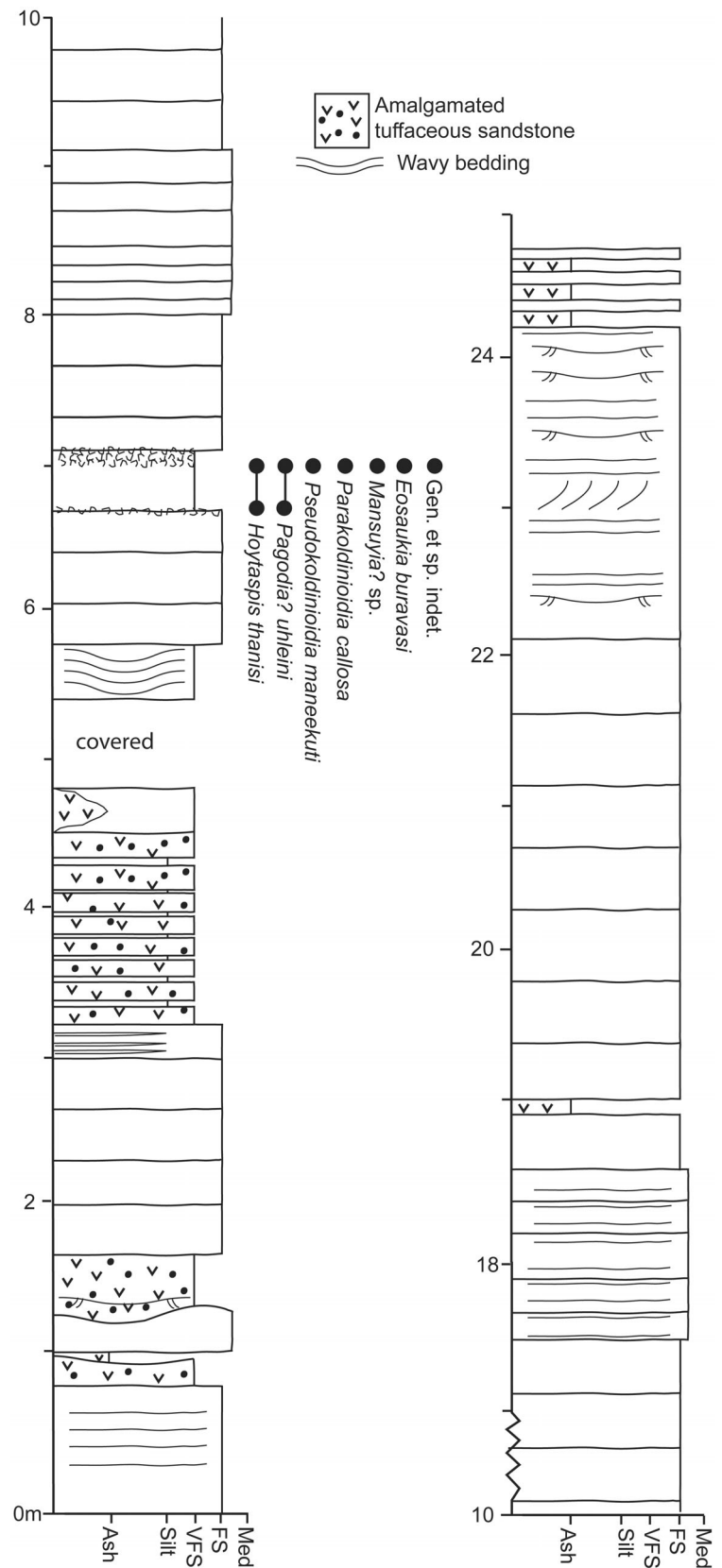
Topo section, permits species-level correlation with the late Payntonian *Neoagnostus quasibilobus* – *Shergoldia nomas* Zone of Australia (Shergold 1975, 1991), which is correlative with Korea's *Eosaukia* Zone. The recovery of *Haniwa mucronata* throughout Ao Talo Topo provides another species-level correlation with the fauna of Australia's *Shergoldia nomas* Zone (Shergold 1975). South China's *Parakoldinioidia callosa* Qian, 1985, found at Ao Talo Udang S1 and Laem Hin Ngam, is also from the middle–upper Stage 10 interval and correlative with the *Shergoldia nomas* Zone. Given the strong association with this middle Stage 10 interval (i.e. the *Mictosaukia* zones of North and South China, the *Shergoldia nomas* Zone of Australia and the *Eosaukia* Zone of South Korea), we suggest this to be the most likely age for each of the fossiliferous sections of the Ao Mo Lae Formation, with ATD S1 possibly being as old as Korea's *Quadraticephalus* Zone. The biostratigraphic correlation of Ao Mo Lae, Ao Talo Topo, Ao Talo Topo west, Ao Talo Udang S2 and Laem Hin Ngam results in probable extensions to the global ranges of *Haniwa sosanensis*? and *Caznaia*, which are currently known only from the latest Jiangshanian (Shergold 1975; Sohn & Choi 2007; Park & Kihm 2015a). These Gondwanan zones correlate with the later portions of Laurentia's *Saukia* Zone (Geyer & Shergold 2000).

The fauna at AML, ATT, ATD S1 and S2 and LHN has a known correlative faunal unit from the southern Shan State, Myanmar (Wernette *et al.* 2021), given that *Eosaukia buravasi* is common in both these areas. It is thus the best suited species for establishing a formal biostratigraphic subdivision for the Sibumasu terrane. The *E. buravasi* Zone (Fig. 12) is here defined as the interval defined by the first appearance of *E. buravasi*. Given that no other candidate Cambrian trilobite defines the base of a subsequent stage, the top of this zone cannot yet be formally determined, but other common taxa in this zone are *Hoytaspsis thanisi*, *Pagodia thaiensis*, *Thailandium solum*, *Quadraticephalus planulatus* and *Pseudokoldinioidia maneekeuti*.

Ordovician

The trilobite species from ATD S3 and APM are exclusively endemic, as is the one new genus. The lowest recorded genera at APM (*Asaphellus*, *Pseudokainella* and *Parapilekia*) could be either latest Cambrian or Ordovician (Zhou & Zhen 2008). Only the genera in the upper part of the section (*Jiia* and *Apatokephalus*) are exclusively Tremadocian (Zhou & Zhen 2008). Teraoka *et al.* (1982) interpreted the Talo Wao beds containing conodonts *Peltodus deltifer* (Lindström) and *Scolopodus rex* Lindström as upper Tremadocian. However, more recent work on Tremadocian

FIG. 8. ATD S1. The break in the scale from 10 m to 17 m abbreviates an interval of massive medium-thick-bedded sandstones, indistinguishable on this log from the units before or after; no fossils or tuff were found in this interval. Fossiliferous horizons are 6.65 m and 7.00 m above the base. *Grain size*: FS, fine sand; Med, medium-grained sand; VFS, very fine sand. (See Figs 4 and 6 for legend.)



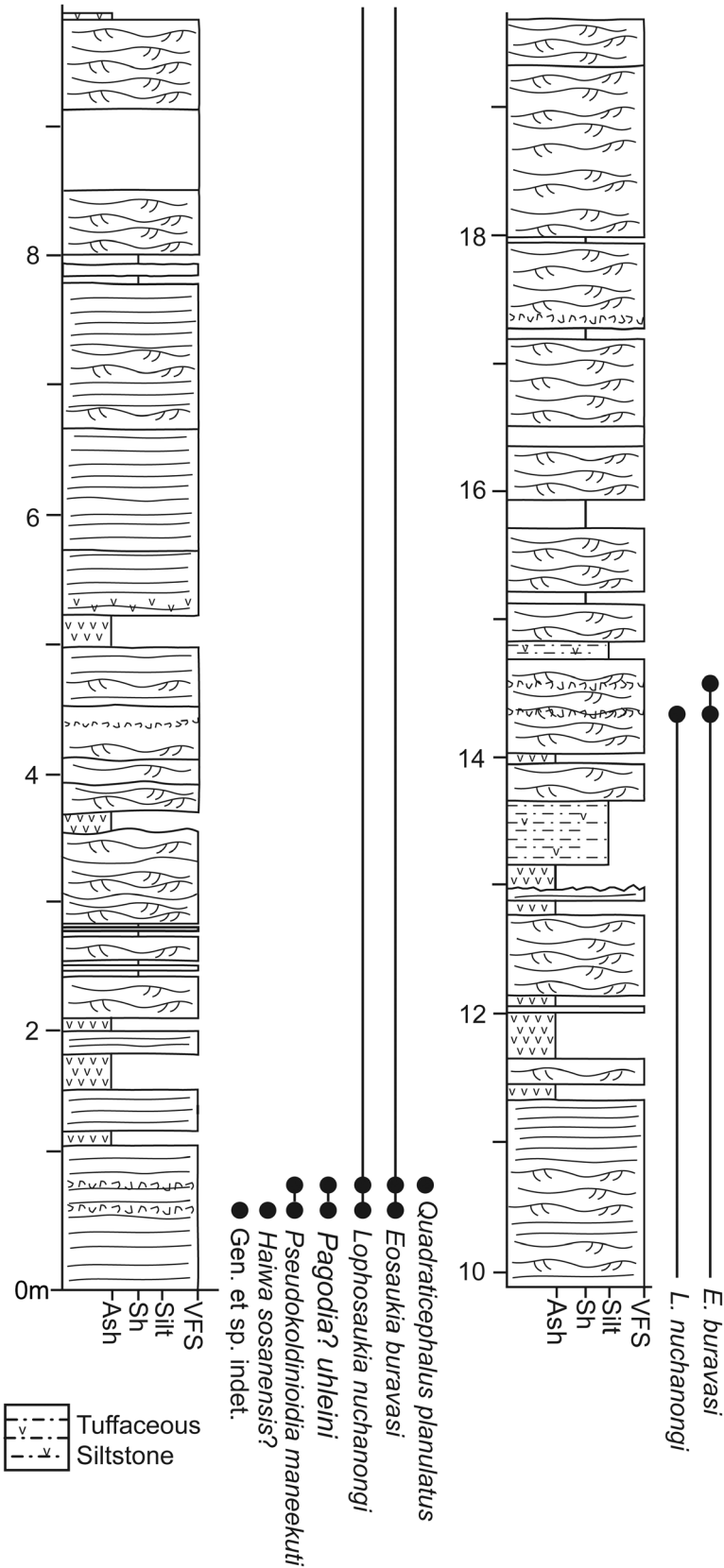


FIG. 9. ATD S2. Fossiliferous horizons are 0.52 m, 0.69 m, 14.29 m and 14.5 m above the base. Grain size: Sh, shale; VFS, very fine-grained sand. (See Figs 4, 6 and 8 for legend.)

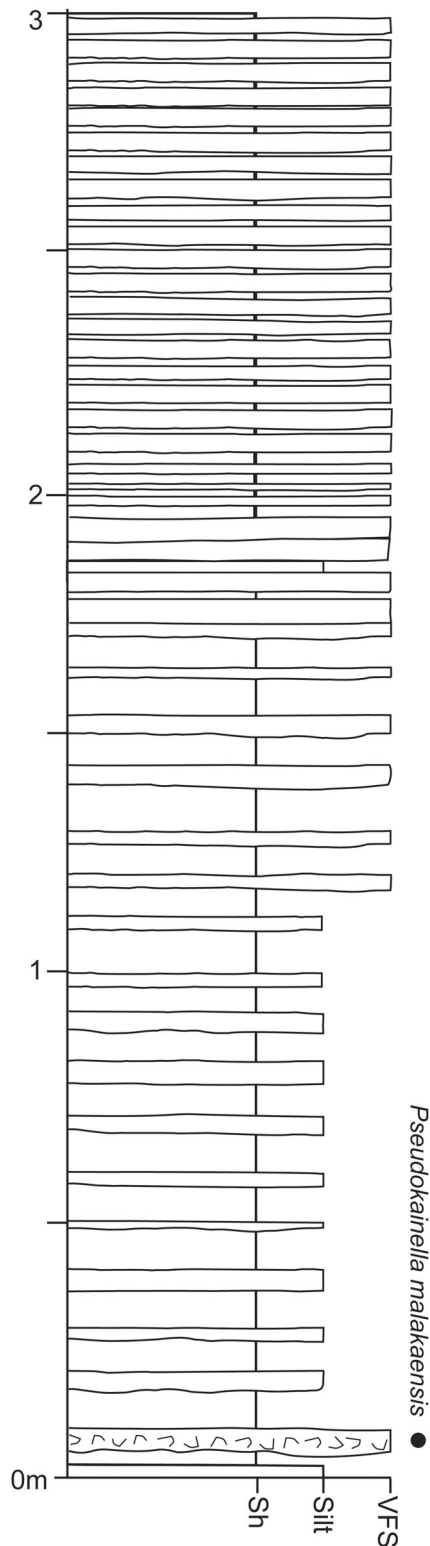


FIG. 10. ATD S3. The fossiliferous horizon is 0.03 m above the base. Grain size: Sh, shale; VFS, very fine-grained sand. (See Fig. 4 for legend.)

conodonts from the overlying Thung Song Group (Agematsu *et al.* 2008) suggests that a middle Tremadocian age is more reasonable for the uppermost Tarutao Group. The Thung Song conodonts fall into three discrete biozones: *Rossodus manitouensis*, *Utahconus tarutaoensis* and *Filodontus tenuis* (Agematsu *et al.* 2008). The lowest, *R. manitouensis*, is correlative with the middle Tremadocian Laurentian biozone of the same name. If the lowest Thung Song fauna is middle Tremadocian, the Talo Wao Formation must be at least that old.

Just as the Ao Mo Lae Formation's faunal assemblage is directly correlative with Australia's *Shergoldia nomas* Zone, particularly as expressed in the lithologically similar Pacoota Sandstone of the Amadeus Basin (Shergold 1991), the Talo Wao Formation's Ordovician trilobite assemblage is correlative with the Pacoota Sandstone's *Asaphellus*- and *Apatokephalus*-rich Tremadocian assemblage. Shergold (1991) considered the Ordovician strata of the Pacoota Sandstone to be end-Tremadocian. However, the part of the Tremadocian Pacoota fauna constrained to species level contains only distinctly endemic taxa (Shergold 1991). Given that many of the Tremadocian genera (e.g. *Asaphellus* and *Apatokephalus*) were long-lived, the Australian and Thai fauna may both be lower-middle Tremadocian, a view supported by Haines & Wingate's (2005) conodont-based correlations between the Amadeus and Canning basins.

The fauna from APM is similar to presently unpublished Ordovician material that the authors have collected from the southern Shan State, Myanmar. Notably, *Asaphellus* is shared between the regions. A lower Ordovician biozone is here established for the Sibumasu terrane, the *Asaphellus charoenmiti* Zone. Although this zone is probably equivalent to the *Asaphellus* zones of South Korea and North China (Fig. 12), the *Asaphellus charoenmiti* Zone is currently local to Sibumasu and its top has yet to be defined by the incoming of a subsequent trilobite species. The *A. charoenmiti* Zone thus currently encompasses the duration of *Asaphellus charoenmiti*, which spans the full APM section. Other prominent taxa in the *A. charoenmiti* Zone are *Parapilekia bunopasi*, *Geragnostus* and various Tremadocian remopleurids, especially *Tarutaoia techawani*.

PALAEOGEOGRAPHICAL ASSOCIATIONS

Wernette *et al.* (2021) reviewed the current understanding of palaeogeographical relationships among the equatorial peri-Gondwanan terranes that today comprise south and southeast Asia, and here we comment only on new evidence provided by the Tarutao Group's fauna.

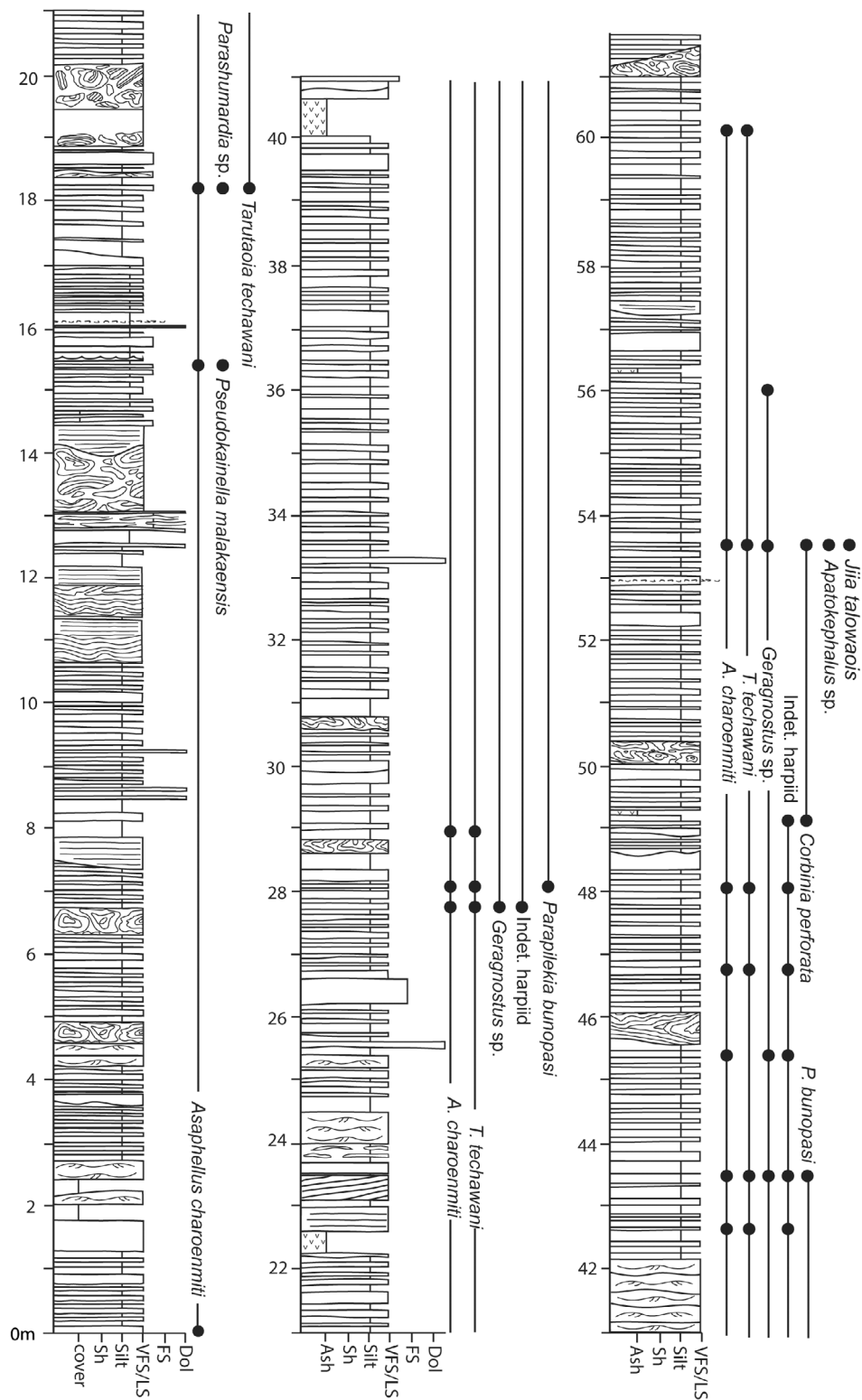


FIG. 11. APM. Fossiliferous horizons are 0.05 m, 15.10 m, 18.00 m, 27.35 m, 27.80 m, 28.70 m, 42.75 m, 43.40 m, 46.05 m, 47.30 m, 48.65 m, 49.90 m, 53.65 m, 56.00 m and 60.20 m above the base. Grain size: Dol, dolostone; FS, fine sand; Sh, shale; VFS/LS, fine-grained sand/limestone. (See Figs 4–10 for legend.)

		N. China	S. China	Australia	S. Korea	Sibumasu
L. Ordovician	Tremadocian		<i>Iliaenus</i> – <i>Guiz.</i>			
		<i>Asaphopsoides</i>	<i>Conophrys</i> – <i>Asaph.</i>		<i>Protopliomerops</i>	
		<i>Asaphellus</i>			<i>Asaphellus</i>	
			<i>Apatokephalus</i> – <i>Tao.</i>			<i>Asaphellus charoenmiti</i>
		<i>Wangliangtingia</i>	<i>Dac.</i> – <i>Asaphellus</i>			
			<i>Wangliangtingia</i>			
	Stage 10	<i>Yosimuraspis</i>	<i>Hysterolenus</i>		<i>Richardsonella</i>	
		<i>Pseudokoldinioidia</i>	<i>L. constrictum</i> – <i>S. brevis</i>		<i>Pseudokoldinioidia</i>	
		<i>Mictosaukia</i>	<i>M. striata</i> – <i>Fatocephalus</i>	<i>Mictosaukia perplexa</i>	<i>Eosaukia</i>	
		<i>Wanwanaspis</i> – <i>Plethopeltella</i>	<i>Archaeuloma taoyuanensis</i>	<i>N. quasibilobus</i> – <i>Shergoldia nomas</i>		<i>Eosaukia buravasi</i>
		<i>Changia</i>	<i>Lotagnostus americanus</i>	<i>Sinosaukia impages</i>	<i>Quadraticcephalus</i>	
Furongian	Jiangshanian	<i>Tsinania</i> – <i>Ptychaspis</i>	<i>Probinacunaspis nasalis</i> <i>Peishianshanian hunanensis</i>	<i>R. clarki</i> – <i>R. papillo</i> <i>R. bifax</i> – <i>N. denticulatus</i>	<i>Asioptychaspis</i>	
		<i>Kaolishania</i>	<i>Kaolishaniella</i>	<i>Cazania sectatrix</i> <i>C. squamosa</i> – <i>H. lilyensis</i> <i>Peichianshanian tertia</i>	<i>Kaolishania</i>	

FIG. 12. Trilobite zones from upper Furongian northern Gondwanan terranes. The South Korean biozones are for the Taebaek Group. The Sibumasu biozones are encompassed by dashed lines to indicate that their full duration is unknown based on Ko Tarutao's sections. Zone correlations are compiled from Choi *et al.* 2016 and Ogg *et al.* 2016. Abbreviations: *Asaph.*, *Asaphopsoides*; *C.*, *Cazania*; *Dac.*, *Dactylocephalus*; *Guiz.*, *Guizhouhystricus*; *H.*, *Hapsidocare*; *L.*, *Leistegium*; *M.*, *Mictosaukia*; *N.*, *Neognostus*; *R.*, *Rhaptagnostus*; *S.*, *Shenjiania*; *Tao.*, *Taoyuania*.

Sibumasu has a notably stronger Laurentian association (Table 3) than is typical for other Gondwanan terranes, with the possible exception of Australia. *Hoytasps* Ludvigsen & Westrop, 1983, *Corbinia* Walcott, 1924 and *Parapilekia* Kobayashi, 1934 all occur in Laurentia but have not been recorded in other peri-Gondwanan terranes. *Hoytasps* and *Corbinia* are exclusive to Sibumasu and Laurentia only. The abundance and diversity of dikelocephalid trilobites (inclusive of 'saukiids') in Laurentia and equatorial Gondwana is also much higher than in western Gondwana, Siberia or Baltica. Furthermore, Laurentia and the equatorial Gondwanan terranes also share several other genera of dikelocephalid trilobites (e.g. *Prosaukia* and *Mictosaukia*). A major unanswered question for studies of late Cambrian trilobites is how these dikelocephalids dispersed so effectively, apparently multiple times, between Laurentia and Gondwana. The similarities between the Thai and Laurentian fauna invite further studies of palaeocurrents and the width of the Palaeo-Pacific Ocean separating eastern Gondwana from Laurentia (Torsvik & Cocks 2017, fig. 5.1c; Li *et al.* 2018, fig. 20c).

Revision of the Thai fauna also suggests a stronger association with part of modern Kazakhstan than previously recognized, particularly for the Cambrian assemblage. Occurrences of *Lophosaukia* (Ergaliev 1980) in the

Malyi Karatau region, part of the southern group of Kazakhstani terranes, along with similarities in brachiopod faunas with South China (Popov *et al.* 2009), have encouraged other authors to consider the association of this region with equatorial peri-Gondwana (Torsvik & Cocks 2017, p. 98; Domeier 2018, fig. 19). In addition to *Lophosaukia*, occurrences of characteristic Gondwanan genera such as *Haniwa*, *Mansuyia* (?), *Pagodia* and *Koldinioidia* further support this association (Table 3), making the relative proximity of the Karatau-Naryn region to equatorial peri-Gondwana still more likely. This is further supported by the distribution of the widespread Floian trilobite *Tanhungshania* in this region and in South China (Popov & Cocks, 2017, p. 352). Tarutao genera that are shared with Kazakhstan are also common to North and South China, and generally different to those shared with Laurentia. The few taxa that are shared with Siberia are cosmopolitan forms. Equatorial currents are likely to have aided in the dispersion of those taxa shared among continents separated by oceanic basins (Hughes 2000).

Zhao *et al.* (2021) recently revived the idea that, during the Cambrian, North China was an isolated palaeocontinent situated in the Palaeo-Pacific ocean, between Gondwana and Laurentia (Li & Powell 2001, fig. 8). That study used

TABLE 3. Geographical distributions of species (S) and genera (G) with taxa listed in the order in which they occur in the text.

	Australia	North China	South China	Karatau- Kazakh.	Iran	South America	Avalonia	Laurentia	Siberia	Baltica	Armorica
Ao Mo Lae Fm.											
<i>Homagnostus</i> sp.	G ¹	S ⁶	G ⁷	S ¹³		G ²⁰		S ²⁷	G ³⁴	S ³⁶	
<i>Pseudagnostus</i> sp.		G ⁷	G ⁷	G ¹³		G ²⁰		G ²⁸	G ³⁴		G ³⁸
<i>Tsinania</i> <i>sirindhornae</i> sp. nov.	G ²	G ⁷	G ⁷		G ¹⁷						
<i>Mansuyia</i> ? sp.	G ²	G ⁸	G ⁷	G ¹⁴							
<i>Satunarcus</i> <i>molaensis</i>											
<i>Parakoldinioidia</i> <i>callosa</i>		G ⁷	S ¹²					G ²⁹			
<i>Pseudokoldinioidia</i> <i>maneekei</i> sp. nov.		G ⁷	G ⁷								
<i>Pagodia thaiensis</i>	G ²	G ⁷	G ⁷	G ¹⁵	G ¹⁸						
<i>Pagodia</i> ? <i>uhleini</i> sp. nov.	G ²	G ⁷	G ⁷	G ¹⁵	G ¹⁸						
<i>Haniwa mucronata</i>	S ²	G ⁷	G ⁷	G ¹⁴							
<i>Haniwa</i> <i>sosanensis</i> ?	G ²	S ⁹	G ⁷	G ¹⁴							
<i>Caznaia imsamuti</i> sp. nov.	G ²										
<i>Anderssonella</i> <i>undulata</i> sp. nov.	G ²										
<i>Eosaukia buravasi</i>	G ³	G ⁷	G ⁷								
<i>Hoytaspsis thanisi</i>								G ³⁰			
<i>Lichengia simplex</i>	S ³	G ⁷									
<i>Lophosaukia</i> <i>nuchanongi</i> sp. nov.	G ²	G ⁷	G ⁷	G ¹⁵							
<i>Prosaukia</i> <i>tarutaoensis</i>	G ²	G ⁷	G ⁷	G ¹⁴				G ³⁰			
<i>Prosaukia oculata</i> sp. nov.	G ²	G ⁷	G ⁷	G ¹⁴				G ³⁰			
<i>Sinosaukia</i> sp.		G ⁷									
<i>Thailandium</i> <i>solum</i>											
<i>Pacootasaukia</i> sp.	G ^{3,4}										
<i>Wuhuia</i> ? sp.	G ²	G ⁷	G ⁷	G ¹⁵							
<i>Plethopeltella</i> sp.		G ⁷									
<i>Quadricephalus</i> <i>planulatus</i>	G ²	G ⁹	G ²¹								
<i>Akoldinioidia</i> sp. 1		S ¹⁰	G ⁷			G ²¹					
<i>Akoldinioidia</i> sp. 2		G ¹⁰	G ⁷			G ²¹					
<i>Koldinioidia</i> sp.	G ³	S ¹⁰	G ⁷	G ¹⁵							
Talo Wao Fm.											
<i>Geragnostus</i> sp.	G ²	G ⁷	G ⁷	G ¹⁵	G ¹⁹	G ²²	G ²⁴	G ³¹	G ³⁵	G ³⁷	G ³⁹
<i>Parapilekia</i> <i>bunopasi</i>					G ¹⁹	G ²³		G ³²		G ³⁷	G ⁴⁰
<i>Asaphellus</i> <i>charoenmiti</i> sp. nov.	G ³	G ⁷	G ⁷	G ¹⁶	G ¹⁹	G ²⁰	G ²⁵	G ³¹		G ³⁷	G ⁴⁰
<i>Apatokephalus</i> sp.	G ³	G ¹¹	G ⁷	G ¹⁶	G ¹⁹	G ²³	G ²⁵	G ³¹	G ³⁵	G ³⁷	G ⁴⁰
<i>Yosimuraspis</i> sp.		G ⁷	G ⁷								

(continued)

TABLE 3. (Continued)

	Australia	North China	South China	Karatau- Kazakh.	Iran	South America	Avalonia	Laurentia	Siberia	Baltica	Armorica
<i>Tarutaoia</i>											
<i>techawani</i>											
gen. et sp. nov.											
<i>Jiia talowaois</i>		G ⁷	G ⁷								
sp. nov.											
<i>Pseudokainella</i>	G ⁵	G ⁷	G ⁷			G ²³	G ²⁶	G ³²			
<i>malakaensis</i>											
<i>Corbinia perforata</i>								G ³³			
sp. nov.											
<i>Parashumardia</i> sp.											

For simplicity, only a single reference is given per taxon per terrane. Selected references are given purely as proof of occurrence and do not reflect seniority of discovery or thoroughness of coverage. North China references the full Sino-Korean Block. ¹Shergold *et al.* 1990; ²Shergold 1975; ³Shergold 1991; ⁴Sohn & Choi 2005; ⁵Jell 1985; ⁶Choi *et al.* 2004; ⁷Zhou & Zhen 2008; ⁸Sun 1924; ⁹Sohn & Choi 2007; ¹⁰Park & Kihm 2015a; ¹¹Park & Kihm 2015b; ¹²Qian 1985; ¹³Ergaliev *et al.* 2008; ¹⁴Ergaliev & Ergaliev 2008; ¹⁵Ergaliev 1980; ¹⁶Apollonov 1975; ¹⁷Fortey & Rushton 1976; ¹⁸Hamdi *et al.* 1995; ¹⁹Ghobadi Pour 2006; ²⁰Bordonaro 2003; ²¹Tortello & Esteban 2003; ²²Tortello & Bordonaro 1997; ²³Harrington & Leanza 1957; ²⁴Whittington & Kindle 1963; ²⁵Stubblefield & Bulman 1927; ²⁶Fortey & Owens 1991; ²⁷Pratt 1992; ²⁸Chatterton & Ludvigsen 1998; ²⁹Landing *et al.* 2011; ³⁰Ludvigsen & Westrop 1983; ³¹Ross 1970; ³²Hintze 1951; ³³Westrop *et al.* 2005; ³⁴Rozova 1968; ³⁵Sennikov *et al.* 2019; ³⁶Terfelt 2003; ³⁷Tjernvik 1956; ³⁸Shergold & Szdzy 1991; ³⁹Wolf 1980; ⁴⁰Martin *et al.* 2016. Kazakh., Kazakhstan.

palaeomagnetic data for latitudinal constraint and to suggest physical separation from Gondwana. Soft-bodied taxa shared between North China and Laurentia were invoked to suggest that North China lay east of the Australian sector of core Gondwana, longitudinally more proximal to Laurentia, rather than west or north of Australia (Fig. 3). Being exceptionally rare, the significance of shared soft-bodied taxon occurrence is hard to evaluate, but there is little evidence based on shared shelly fauna to suggest particular similarity between Laurentia and North China during the Cambrian. With respect to our study, as noted in the discussion of Kazakhstan, numerous genera (e.g. *Haniwa*, *Koldinioidia*, *Mansuyia* and *Lophosaukia*) support North China being on the west side of equatorial Gondwana rather than the east side. Furthermore, there are no trilobite genera shared between Tarutao, Laurentia and North China that are not also shared with South China, Kazakhstan and/or Australia. Several recent studies have supported direct Cambrian links between North China and Gondwana based on biotic and detrital zircon data (see Wernette *et al.* 2021). Furthermore, given that the association between North China and Siberia was established from early in the Ordovician (Torsvik & Cocks 2017, fig. 6.1), the idea of North China's rapid migration across a quarter of the Earth's circumference while navigating around eastern Gondwana is problematical.

While there is considerable faunal evidence (Table 3) to suggest a close association between the North China, South China and Sibumasu terranes, the question of which of the Chinese blocks is more strongly affiliated with Sibumasu has been a source of contention. South

China has a strong Ordovician link to the Thai portion of Sibumasu (Fortey 1997), but Burrett *et al.* (2016) emphasized a stronger North China – Sibumasu Furongian affinity, based partly on trilobites described by Shergold *et al.* (1988). The taxonomy presented herein supports a South China affinity as much as, or more than, a North China affinity, given that South China hosts the same genera shared between Thailand and North China except *Lichengia* and *Plethopeltella*, but uniquely shares with Thailand the species *Parakoldinioidia callosa*. Other metrics of affinity, especially U–Pb detrital zircon analysis, return variable results for a Sibumasu – South China affinity based on which parts of South China are under consideration, with the Yangtze Platform being the least similar (Burrett *et al.* 2014; Wernette *et al.* 2021).

IMPLICATIONS FOR CAMBRIAN–ORDOVICIAN BIODIVERSIFICATION

The interval between the Cambrian explosion and Great Ordovician biodiversification event is dominated by a cyclical succession of repeated diversifications and extinctions known as 'biomeres' (Palmer 1965). Originally invoked based on trilobite biodiversity patterns, the biomere concept also applies to diversity patterns in other fauna including brachiopods (e.g. Freeman *et al.* 2018). While biomeres are well-documented in Laurentia, their existence in Gondwana is plausible but less well-studied

(Zhou & Zhen 2008; Babcock *et al.* 2017). The Tarutao Group spans the intervals of an important Laurentian biomere boundary, the Ptychaspis–Symphysuriniid boundary, marked in Laurentia by the end-Sunwaptan extinction. In equatorial Gondwana this correlates with the top of the *Mictosaukia* (North China, South China and Australia) and *Eosaukia* (South Korea) zones of Cambrian Stage 10 (Fig. 12) (Landing *et al.* 2011; Peng *et al.* 2020). The Ao Mo Lae Formation's rich trilobite record from near the end of the Ptychaspis biomere, coupled with tuff-based evidence of extensive felsic volcanism (McKenzie *et al.* 2011, 2014), may provide an opportunity to consider the extent to which this boundary extinction was global, and what its cause might be.

Interpretation of the complete faunal turnover between the Ao Mo Lae Formation and the Talo Wao Formation is difficult because no known Tarutao section spans this transition (Imsamut & Yathakam 2011). However, the long interval with nearly monospecific fossil content in the lower 18 m of APM could suggest low diversity early in the Talo Wao Formation. A pattern of quite diverse latest Cambrian and early Ordovician faunas separated by a depauperate interval is seen in other Gondwanan shelfal sequences. For example, the Amadeus Basin of Australia (Shergold 1991) has a similar turnover between the Pacoota Sandstone's Cambrian and Ordovician trilobite assemblages. North and South China both have relatively continuous faunal records across the Cambrian–Ordovician boundary, but latest Cambrian fauna has low genus-level richness, and there is a noticeable turnover in the early Tremadocian, after which biodiversity rapidly expanded (Zhou & Zhen 2008). The South Chinese slope environments maintained a higher diversity relative to the platform facies that dominate the North Chinese succession (Zhou & Zhen 2008).

Given that the Ao Moe Lae Formation sections on Ko Tarutao show little faunal succession, the rates of sediment deposition during their accumulation appear relatively high (see above). In Laurentia, similar nearshore deposits record rapid shoreface progradation during the *Saukia* Zone in shoreward areas following maximum flooding (Runkel *et al.* 2007). Ao Moe Lae Formation deposition may have been synchronous and responded to the same eustatic signal promoting rapid sedimentation. This *Saukia* Zone age interpretation bridges occurrences of the relatively old Laurentian genera *Hoytaspsis* and *Prosaukia* in the Ao Moe Lae Formation (approximately equivalent to the *Prosaukia*–*Ptychaspis* Zone; Ludvigsen & Westrop 1983), with reportedly younger Gondwanan forms such as *Pseudokoldinioidia* (correlative with the *Eurekia apopsis* Zone; Choi *et al.* 2016). While the *Saukia* Zone experiences relatively high rates of deposition, proximal locations from the low-stand *Eurekia apopsis* Zone are stratigraphically condensed or absent in Laurentia (Runkel *et al.* 2007; Miller

et al. 2015). The more cosmopolitan nature of the Tremadocian trilobite fauna in the Talo Wao Formation (Table 3) is reminiscent of those forms that first spread across the shelf at the base of each biomere (Palmer 1965; Westrop & Ludvigsen 1987; Westrop 1989) and may represent the initial stages of transgression before the establishment of a carbonate platform.

SYSTEMATIC PALAEOLOGY

by Shelly J. Wernette and Nigel C. Hughes

Morphological terminology follows Whittington & Kelly (1997). References to glabella length exclude the occipital ring. Dorsal views of specimens were photographed with the palpebral lobes in the horizontal plane as feasible given the surrounding matrix and condition of the fossil (Whittington 1997).

In agreement with Thailand's Department of Mineral Resources, all figured material is deposited at DGSC while unfigured material, excluding those specimens occurring on slabs with figured material, is deposited at CMC. The vinyl polysiloxane casts of Kobayashi's (1957) material is deposited in the plastotype collection at CMC. All specimens referred to in this paper are internal moulds unless otherwise stated.

Institutional abbreviations. CMC, Cincinnati Museum Center, Ohio, USA; DGSC, Department of Mineral Resources Geological Referenced Sample Collection, Bangkok, Thailand; UMUT, University of Tokyo University Museum, Tokyo, Japan.

Order AGNOSTIDA Salter, 1864

Family AGNOSTIDAE M'Coy, 1849

Remarks. We follow the spelling of M'Coy advocated by Rushton (1979).

Subfamily AGNOSTINAE M'Coy, 1849

Genus HOMAGNOSTUS Howell, 1935

Type species. *Agnostus pisiformis obesus* Belt, 1867; from the Lower Lingula Flags, Wales, UK; Stage 10, Furongian, by original designation.

Remarks. *Homagnostus*, *Oncagnostus* Whitehouse, 1936, *Micragnostus* Howell, 1935 and *Geragnostus* Howell, 1935 share similar overall morphologies. They have regularly been confused, and variably considered subgenera of each other or of *Agnostus* Brongniart, 1822 (Shergold *et al.* 1990; Pratt 1992; Choi *et al.* 2004). The *Treatise on Invertebrate Paleontology* (Shergold & Laurie 1997), however, provides the following differences in their diagnoses. *Micragnostus* is the only of these genera with a parallel-sided glabella and has a pygidial axis short enough that the pygidial acrolobe has little to no posterior tapering. *Homagnostus* is the only one of the three with a preglabellar median

furrow, although this may be significantly reduced as in *Homagnostus obesus* (Belt 1867; Choi *et al.* 2004). The anterior glabellar furrow (F3) of *Geragnostus* is distinctly curved, leaving a subovate anterior lobe. *Oncagnostus* has no preglabellar median furrow, unlike *Homagnostus*, and a pygidial axis that terminates against or near the posterior border furrow.

Homagnostus sp.
Figure 13

- ? 1957 agnostid gen. et sp. indet; Kobayashi, p. 380, pl. 4, fig. 8.
1988 *Micragnostus* sp; Shergold *et al.*, p. 305, fig. 3a–d.

Material. 14 cephalia from ATT 0.95 m (DGSC F0799), 8.85 m (DGSC F0837), 22.78 m (DGSC F0463, F0514, F0526, F0858), 22.88 m (DGSC F0540, F0542, F0898, F0906, F0919, F0922, F0926) and 23.89 m (DGSC F0944). 7 pygidia from ATT 8.20 m (DGSC F0818 internal and external mould), 8.60 m (DGSC F0836), 22.78 m (DGSC F0466, F0492, F0875) and 22.88 m (DGSC F0539, F0935).

Remarks. The agnostids from ATT 0.95–23.89 m are morphologically indistinguishable from those Shergold *et al.* (1988) described from locality 6 (= ATT) and assigned to *Micragnostus* Howell, 1935. Their assignment to *Micragnostus* includes a caveat that these specimens belong to a subgroup of *Micragnostus* that has a posteriorly curving anterior glabellar furrow (F3), which is contrary to the description of *Micragnostus* given in Shergold & Laurie (1997), who state that *Micragnostus* has a straight F3. Even more problematically for a *Micragnostus* designation, the Tarutao specimens have a distinctly anteriorly tapering glabella while the *Micragnostus* glabella is parallel-sided (Shergold & Laurie 1997). Most notably, the pygidial axis of the material from ATT reaches nearly to the posterior border furrow whereas *Micragnostus* is restricted to forms possessing a short axis (Shergold & Laurie 1997; Naimark & Pegel 2017).

This material most closely resembles *Homagnostus obesus* (Belt, 1867), especially as known from the Machari Formation in South Korea (Choi *et al.* 2004). Pratt's (1992) concept of *H. obesus* encompasses a wide array of intraspecific variation with the diagnostic character being that the pygidial F1 is medially discontinuous. The state of preservation of the Thai material makes this character difficult to determine. Notably, *H. obesus* exhibits variable expression of the preglabellar median furrow; although visible in some individuals, it may be greatly reduced or absent in others, as in specimens from the Machari Formation (Choi *et al.* 2004, figs 8.1–3 vs 8.4–6). Specimens from the Tarutao Group have an exceptionally reduced median preglabellar furrow visible only faintly in Figure 13E–F.

The indeterminate agnostid figured by Kobayashi (1957, pl. 4, fig. 8) is too poorly preserved to confidently assign a species or genus, but, given its co-occurring taxa and overall similarity in shape and proportions, it is most likely to be conspecific.

Occurrence. ATT 0.95–23.89 m; Ao Mo Lae Formation; Furongian, Cambrian Stage 10.

Family DIPLAGNOSTIDAE Whitehouse, 1936
Genus PSEUDAGNOSTUS Jaekel, 1909

Type species. *Aagnostus cyclopyge* Tullberg, 1880; from the *Parabolina* Zone of Andrarum, Sweden; Stage 10, Furongian; by original designation.

Remarks. The *Pseudagnostus* diagnosis followed herein comes from the *Treatise* and includes a spectaculate glabellar node, with wide cephalic borders, a simple and terminally angulate posterior lobe, prominent, triangular basal lobes, poorly developed lateral lobes, and a deutero lobate pygidium (Shergold & Laurie 1997).

Pseudagnostus sp.
Figure 14E–H, I?

Material. 3 cephalia from AML 5.81 m (DGSC F0346) and 5.84 m (DGSC F1189, CMC IP83148); 1? from ATTw (DGSC F0378). 2 pygidia from AML 5.81 m (DGSC F1114) and 5.84 m (DGSC F1191).

Remarks. The pygidium has a short axial lobe with a prominent chevron-shaped furrow and medial node, characteristic of *Pseudagnostus*. Of the known species of *Pseudagnostus*, these specimens most resemble *P. josepha* (Hall 1863). The specimens from Tarutao fit Peng & Robison's (2000) revised diagnosis of *Pseudagnostus josepha* in terms of the posteriorly angular glabella, straight or posteriorly bowed F3, pygidial axial furrows shallowing posterior to F2, axial constriction at M2, tubercle posteriorly indenting F2, strongly expanded posteroaxis, and small pair of posterolateral border spines. Features that disqualify these Tarutao specimens from *Pseudagnostus josepha* include the very short to effaced post-F2 axial furrows and particularly small median tubercle. Furthermore, *P. josepha* is a much older species, dating to the *Glyptagnostus stolidus* Zone (Peng & Robison 2000; Choi *et al.* 2016). These differences indicate a separate species from *P. josepha*, but the small sample size and preservation exclusively of internal moulds makes the establishment of a new species inadvisable at this time. Thus, we leave the specimens in open nomenclature.

Occurrence. AML 5.81–5.84 m, ?ATTw; Ao Mo Lae Formation; Furongian, Stage 10.

Family METAGNOSTIDAE Jaekel, 1909
Genus GERAGNOSTUS Howell, 1935

Type species. *Aagnostus sidenbladhi* Linnarson, 1869; from the Ceratopyge Limestone of Sweden; by original designation; Tremadocian.

Remarks. The diagnostic criteria for *Geragnostus* used herein follows The *Treatise*, including a semioval anterior glabellar lobe, a glabellar node immediately posterior to F3, a moderately long (sag.) pygidial axis that is constricted across M2, a nearly

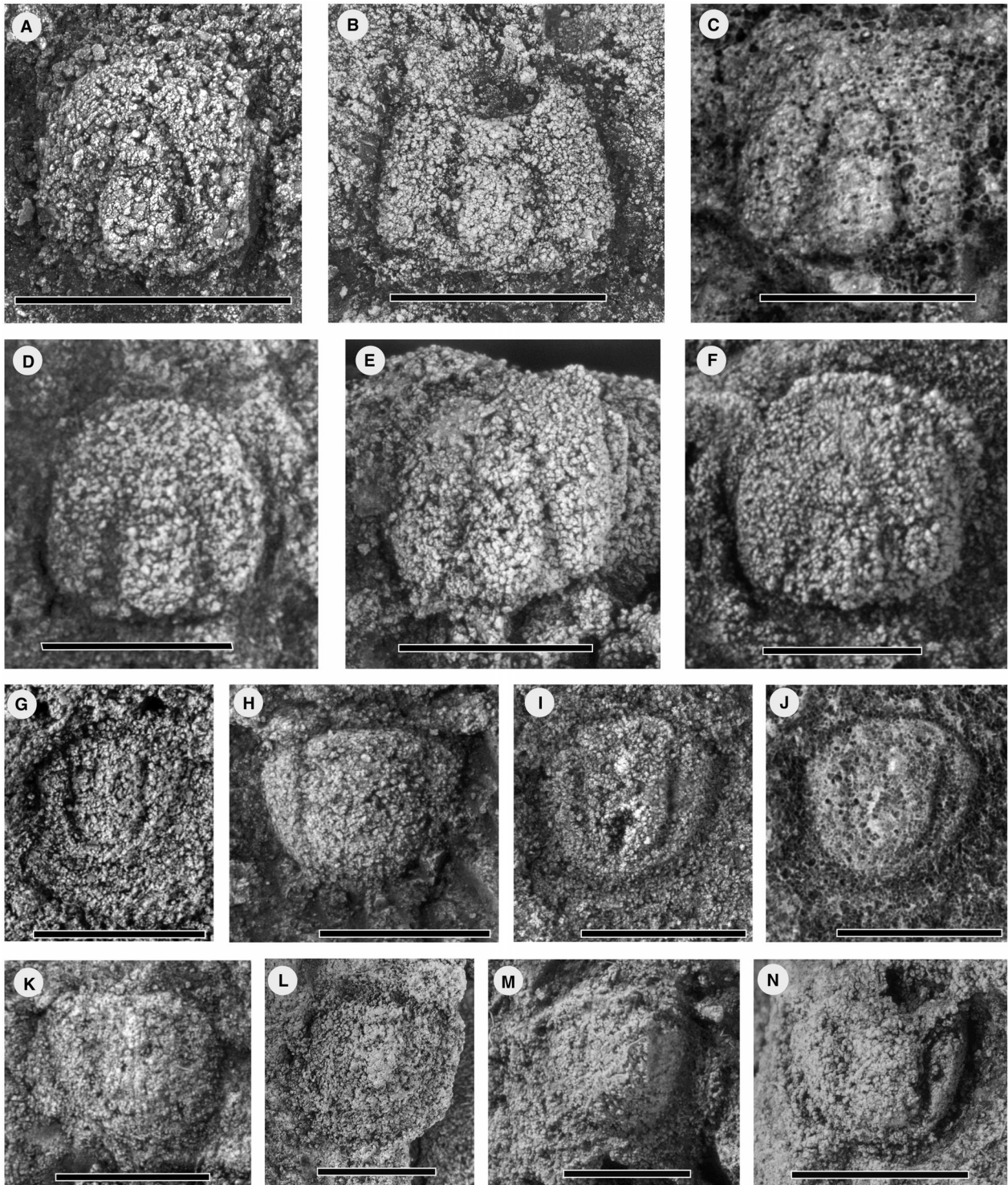


FIG. 13. *Homagnostus* sp. A, DGSC F0858, cephalon. B, DGSC F0944, cephalon. C, DGSC F0922, cephalon. D, DGSC F0837, cephalon. E, DGSC F0799, cephalon. F, DGSC F0526, cephalon. G, DGSC F0466, pygidium. H, DGSC F0836, pygidium. I–J, DGSC F0818, pygidium: I, internal; J, external mould. K, DGSC F0935, pygidium. L, DGSC F0875, pygidium. M, DGSC F0539, pygidium. N, DGSC F0492, pygidium. Scale bars represent 2 mm.

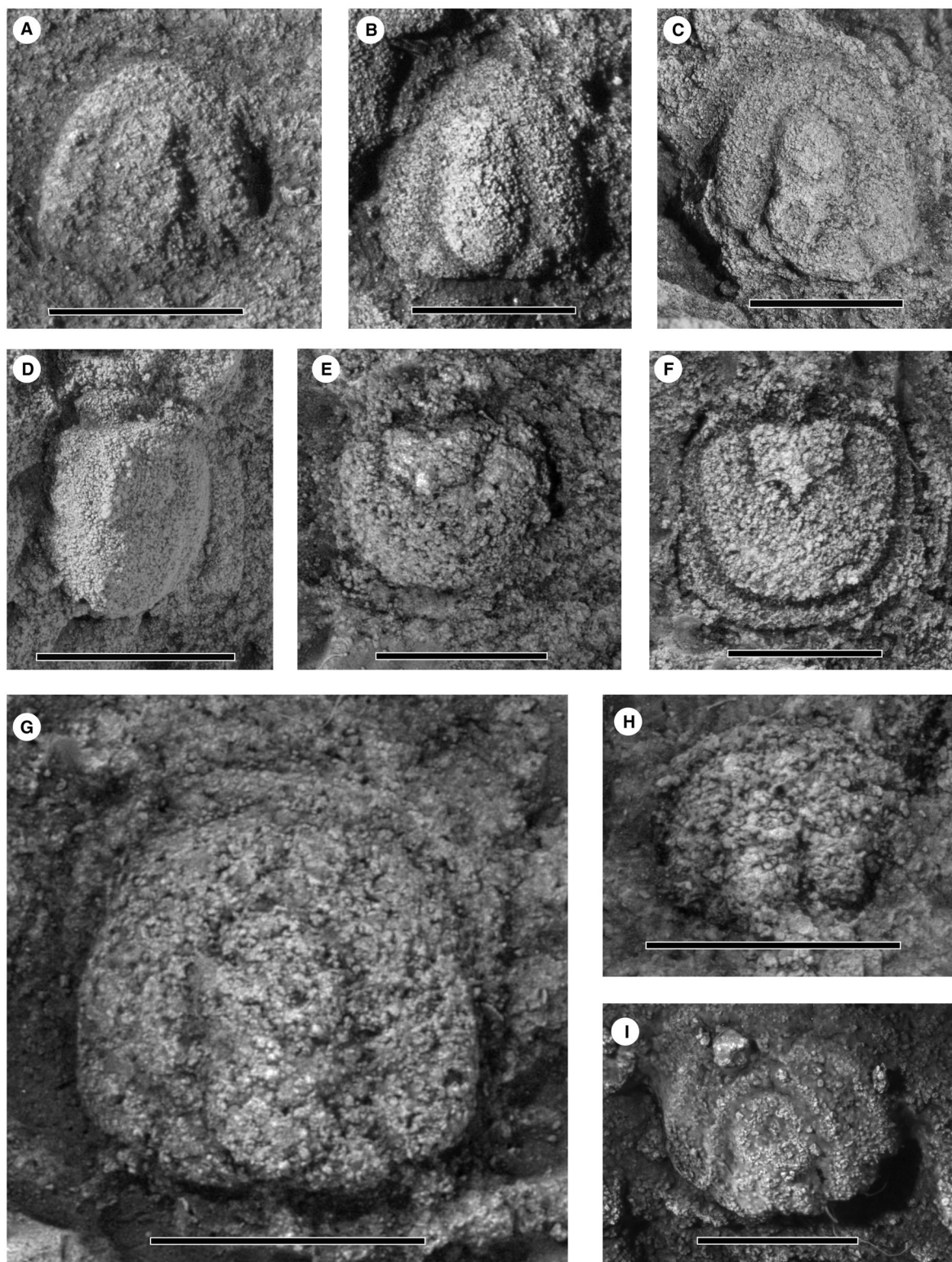


FIG. 14. A–D, *Geragnostus* sp.: A, DGSC F1409, cephalon; B, DGSC F1476, cephalon; C, DGSC F1467, cephalon; D, DGSC F1458, pygidium. E–H, *Pseudagnostus* sp.: E, DGSC F1191, pygidium; F, DGSC F1114, pygidium; G, DGSC F1189, cephalon; H, DGSC F0346, cephalon; I, DGSC F0378, cephalon. Scale bars represent 2 mm.

equidimensional and semiovalate or subrectangular posterior lobe, and a weak terminal node (Shergold & Laurie 1997).

Geragnostus sp.
Figure 14A–D

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

Material. 11 cephalon from 27.35 m (CMC IP89036), 43.60 m (CMC IP89078, IP89079, IP89201, IP89203, DGSC F1380 external mould, F1382 external mould, F1391), 46.05 m (DGSC F1409 internal and external mould), 53.65 m (DGSC F1467) and 56.00 m (DGSC F1476). 5 pygidia from 43.60 m (CMC IP89075, IP89191 external mould, IP89196 external mould, DGSC F1350) and 53.65 m (DGSC F1458). All from APM.

Remarks. The cephalon of *Geragnostus* sp. is similar to that of *Homagnostus* sp., also found in the Tarutao Group. An important distinguishing feature is that *Geragnostus* sp. has a strongly curved, subtriangular anterior margin. Stait *et al.* (1984) published a single agnostid cephalon with no description or remarks other than calling it *Geragnostus* sp. That specimen is not so strongly anteriorly curved as the specimens of *Geragnostus* sp. presented herein, but it is from the same section at APM and it is likely to be the same species. Both cephalon and pygidium are similar to those of *Geragnostus intermedius* Palmer, 1968, alternatively assigned to *Micragnostus* (e.g. as in Pratt 1988), but *Geragnostus* sp. has wider (tr.) pygidial spine bases and a more strongly curved cranial margin. The cranial margin is narrower than in *G. tilcuyensis* (Kayser 1876; *sensu* Harrington & Kay 1951). With the limited sample size available in this collection, there is insufficient information to determine whether intraspecific variation could account for *Geragnostus* sp. being conspecific with one of these similar species or whether it represents a new species.

Occurrence. APM 27.35–56.00 m; Talo Wao Formation; middle–upper Tremadocian.

Order CORYNEXOCHIDA Kobayashi, 1935
Suborder ILLAENINA Jaanusson, 1959
Family TSINANIIDAE Kobayashi, 1935

Genus *Tsinania* Walcott, 1914

Type species. *Illaeonurus canens* Walcott, 1905 from the Chaumitien Limestone, Shantung, China; by original designation; Stage 10, Furongian.

Remarks. *Tsinania* and *Shergoldia* Zhang & Jell, 1987 are sufficiently similar that it is doubtful whether they are both valid genera. Two separate cladistic analyses using different sets of taxa and characters by Zhu *et al.* (2013) and Wernette *et al.* (2020a) suggest that *Tsinania* as currently conceived is polyphyletic, belonging to a clade that also includes all species assigned to *Dictyella* Kobayashi, 1933a, *Shergoldia* and possibly *Lonchopygella* Sun & Xiang, 1979. *Shergoldia* was either polyphyletic

(Zhu *et al.* 2013) or a monophyletic descendant of *Tsinania* (Wernette *et al.* 2020a). In their work on the ontogeny of *Tsinania shanxiensis* (Zhang & Wang 1985), Lei & Liu (2014) published an emended *Tsinania* that is exclusive of morphologies traditionally assigned to *Shergoldia*; such characters include an advanced degree of cranial and pygidial effacement, especially on external surfaces, and a lack of a developed plectrum.

Tsinania sirindhorneae sp. nov.
Figures 15, 16

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

LSID. <https://zoobank.org/NomenclaturalActs/A3B75618-B75F-4976-98DF-FC8F15E0220B>

Derivation of name. Named in honour of Her Royal Highness Princess Maha Chakri Sirindhorn of Thailand for her support of science and technology, and particularly for her interest in palaeontology.

Material. Holotype: DGSC F0843 (Fig. 16C–D), cranidium, ATT 8.85 m; Ao Mo Lae Formation, Tarutao Group; Furongian, Stage 10.

Paratypes: 4 cranidia from ATT 8.60 m (DGSC F0835), 22.78 m (DGSC F0468), 22.88 m (DGSC F0894), 23.89 m (DGSC F0947); 1 librigena from ATT 23.89 m (DGSC F0938); 7 pygidia from ATT 22.78 m (DGSC F0854), 22.88 m (DGSC F0895, F0932), 23.89 m (DGSC F0480, F0951) and 29.17 m (DGSC F1023, F1038).

Other material: 3 cranidia from ATT 8.20 m (DGSC F0826) and 25.34 m (DGSC F0960, F0963 external mould); 12

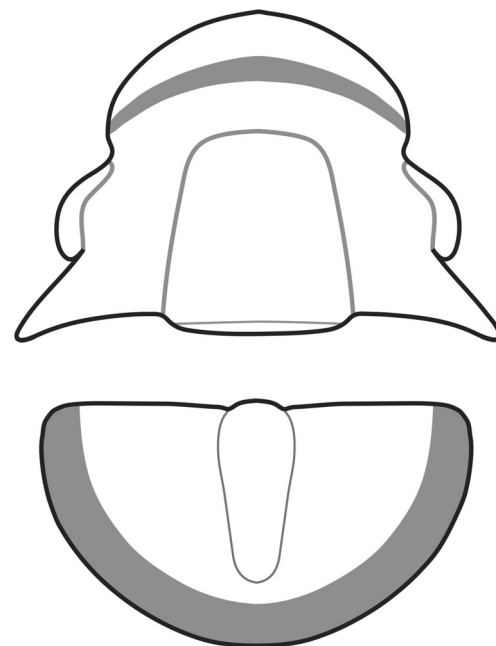


FIG. 15. *Tsinania sirindhorneae* sp. nov. line drawing. The furrows, indicated by grey, are nearly effaced. The grey border on the pygidium indicates the extent of the doublure.

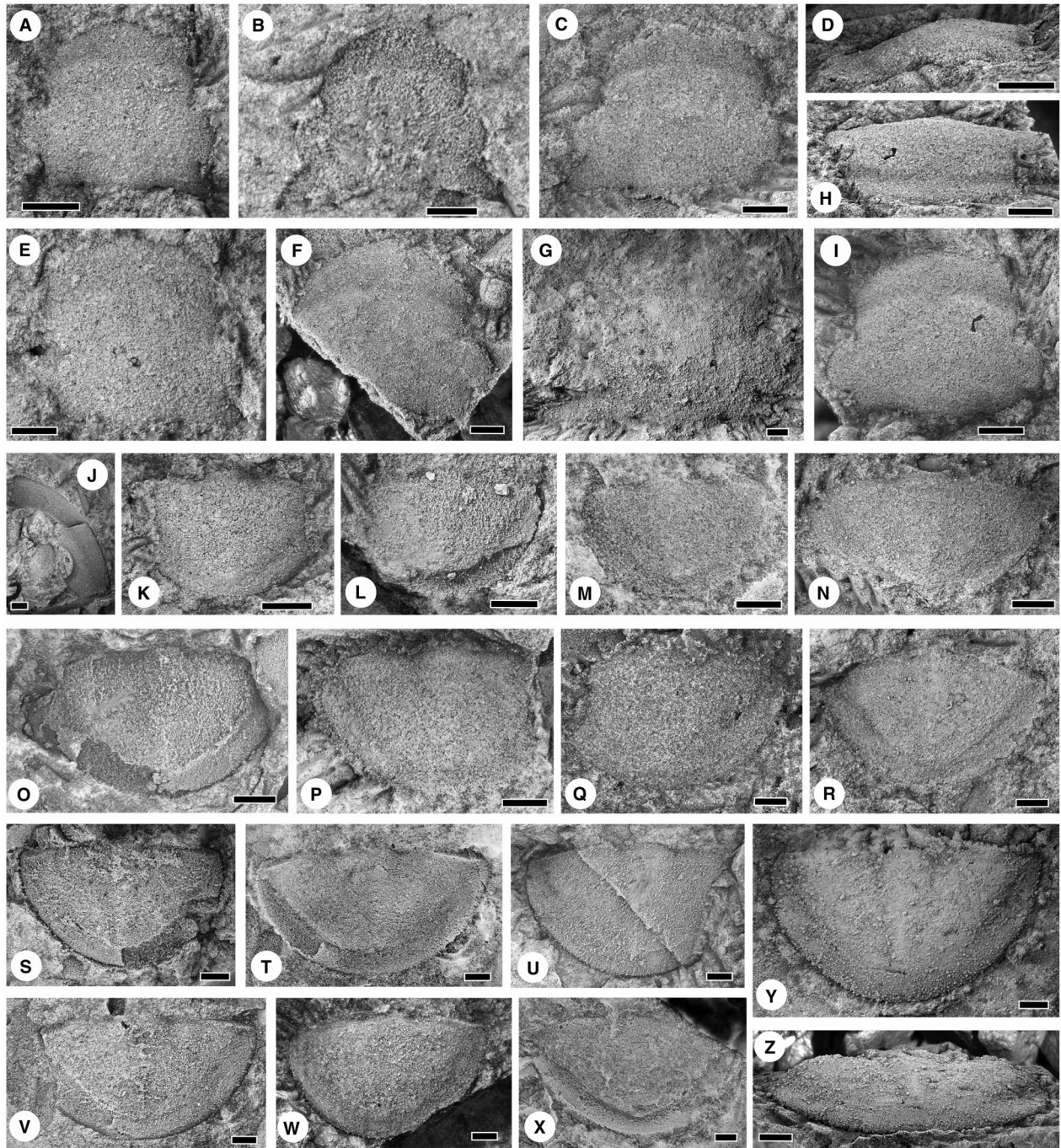


FIG. 16. *Tsinania sirindhornae* sp. nov. A, DGSC F0960, cranidium. B, DGSC F0468, cranidium. C–D, DGSC F0843, holotype, cranidium in: C, dorsal; D, lateral view. E, DGSC F0894, cranidium. F, DGSC F0835, cranidium. G, DGSC F0826, cranidium. H–I, DGSC F0947, cranidium, anterior and dorsal views, respectively. J, DGSC F0938, librigena. K, DGSC F0951, pygidium. L, DGSC F1010, pygidium. M, DGSC F0462, external mould, pygidium. N, DGSC F0844, pygidium. O, DGSC F1020, pygidium. P, DGSC F0854, pygidium. Q, DGSC F0876, pygidium. R, DGSC F0895, pygidium. S, DGSC F0480, pygidium. T, DGSC F1024, pygidium, external mould. U, DGSC F1023, pygidium. V, DGSC F1038, pygidium. W, DGSC F0932, pygidium. X, DGSC F0831, pygidium, external mould. Y–Z, DGSC F1735, pygidium in: Y, dorsal; Z, posterior view. Scale bars represent 2 mm.

pygidia from ATD S2 h1 (DGSC F1735, F1736) and ATT 8.60 m (DGSC F0831 external mould), 8.85 m (DGSC F0844), 22.78 m (DGSC F0462 external mould, F0507

external mould, F0531 external mould, F0876), 23.89 m (CMC IP88929) and 29.17 m (DGSC F1010, F1020, F1024 external mould).

Diagnosis. Cranidium with slightly angular anterior margin, long (sag., exsag.) anterior border, long (sag., exsag.) and medially shallowing anterior border furrow, axial and glabellar furrows effaced on both external and internal moulds; pygidium wide (tr.) with long and broad (sag., exsag., tr.) border, low convexity, subtriangular pleural field, relatively long post-axial area (sag.), and internally effaced axial rings, and pleural furrows.

Description. Cranidium subtriangular; width (tr.) across postero-lateral projections c. 1.5-fold cranial length (sag.), widening proportionally with growth; width (tr.) across palpebral lobes 80–90% width (tr.) across posterolateral projections; width (tr.) across anterior border 65–70% width (tr.) across posterolateral projections; anterior margin gently angular; low convexity. Glabellar length (sag., including the occipital ring (LO)) c. 65% cranial length; cranial width (tr.) across palpebral lobes c. 2.2-fold glabellar width (tr.) on same line; both externally and internally preglabellar and axial furrows nearly completely effaced; glabellar furrows and LO completely effaced; slight post-occipital transverse ridge or flange. Fixigena continuous with preglabellar field; anterior border furrow broad (sag.), medially shallowing, strongly curved, and well-defined posteriorly but anteriorly sloping gently into anterior border; anterior border long (sag.), weakly inflated. Palpebral lobe length (exsag.) 25–30% of cranial length (sag.); midpoint of lobe opposite posterior third of cranidium (sag.); palpebral lobes strongly curved with greatest curvature in posterior half; anterior facial suture branches moderately abaxially deflected then strongly adaxially curving to meet medially at anterior margin; posterior facial suture branches extend nearly straight posterolaterally at angle 45–70° from exsag.; posterior border furrows effaced.

Librigena narrow, lateral border occupying c. half width (tr.); border furrow noted only by change in slope; broad (tr., sag., exsag.) doublure lengthens (exsag., sag.) adaxially; median ventral suture.

Pygidium semicircular; pygidial width (tr.) across anterior margin 1.6–1.9-fold pygidial length (sag.); low convexity. Axis narrow (tr.), c. 25% pygidial width (tr.) across anterior margin; axial furrows nearly effaced; ring furrows, pleural furrows and interpleural furrows completely effaced. Border furrow weakly defined by change in slope at inner margin of doublure; posterior border long (sag., exsag., tr.); doublure same length (sag., exsag., tr.) as border, moderately convex.

Remarks. Shergold *et al.* (1988) initially assigned tsinaniid material from the Tarutao fauna to *Tsinania* cf. *nomas*, citing the difference in the degree of effacement between the Tarutao specimens and the type material as the reason for uncertainty. The *Tsinania nomas* holotype and one of the pygidia (CPC 11948 and 11952, Shergold 1975 pl. 47, figs 1, 5) are exfoliated, facilitating direct comparison between the internal moulds from Tarutao with those of the type material. Like Shergold *et al.*'s (1988) material, the new material herein consistently shows effaced internal moulds that are similar to the external moulds in most features. Internal surfaces of *T. nomas*, however, are less effaced than the exteriors, showing prominent pygidial furrows, eye ridges and a plectrum. The different degree of effacement among internal features warrants the establishment of a separate species, *Tsinania sirindhornae*. Other differences between *T. sirindhornae* and *T. nomas* include the former's longer (sag.) anterior border, less

strongly incised anterior border furrow and less developed plectrum, although this structure is not well-developed in either species. The pygidium of *T. sirindhornae* has a noticeably wider (tr.) border and more effaced axial and pleural furrows. The slight postoccipital transverse ridge or flange that is discernible on some specimens of *T. sirindhornae* (e.g. Fig. 16C–D) is better developed on *T. nomas* (e.g. Shergold, 1975, pl. 47, fig. 1).

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

Occurrence. ATT 8.20–25.34 m and ATD S2 h1; Ao Mo Lae Formation; Furongian, Stage 10.

Suborder LEIOSTEGIINA Bradley, 1925
Superfamily LEIOSTEGIOIDEA Bradley, 1925
Family KAOLISHANIIDAE Kobayashi, 1935
Subfamily MANSUYIINAE Hupé, 1955

Remarks. Mansuyiinae was restricted by Shergold (1972) to contain 'Mansuyia-like' genera: *Mansuyia* (Grabau) Sun, 1924, *Paramansuyella* Endo in Endo & Resser, 1937, *Kaolishaniella* Sun, 1935 and *Mansuyites* Shergold, 1972. However, cladistic consideration of relationships between tsinaniids and kaolishaniids suggests that Mansuyiinae is polyphyletic (Wernette *et al.* 2020a). Thus, the use of Mansuyiinae herein refers exclusively to *Mansuyia*; *Mansuyites* and *Mansuyites*-like taxa belong to Ceronocarinae.

Genus MANSUYIA Sun, 1924

Type species. *Mansuyia orientalis* (Grabau) Sun, 1924; from the Fengshan Stage in the Yehli Limestone, China; Stage 10, Furongian.

Remarks. Phylogenetic analysis of *Mansuyia* and *Tsinania* Walcott, 1914 suggested that *Mansuyia* is part of a stem lineage leading to *Tsinania* (Park *et al.* 2014), a relationship refuted by a taxonomically broader study that found *Mansuyia* to be a sister clade to tsinaniids (Wernette *et al.* 2020a). Despite having different phylogenetic results, the second phylogenetic study did not dispute Park *et al.*'s (2014) emended diagnosis of *Mansuyia*, which is also followed herein.

Mansuyia? sp.
Figure 17

Material. 13 cranidia (DGSC F1496, F1546, F1563, F1575, F1594, F1662, F1690, F1702, F1708, F1717, F1726, CMC

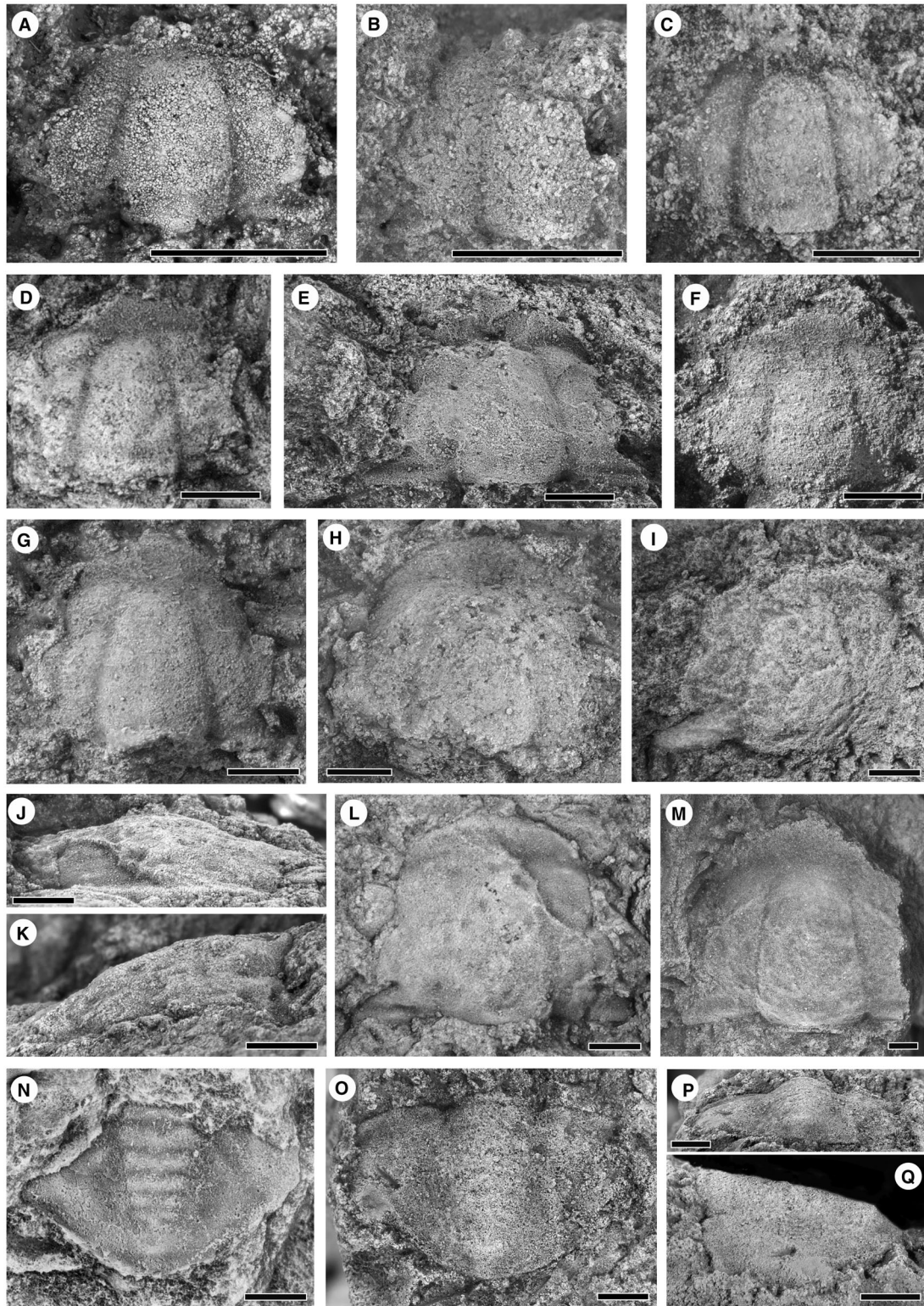


FIG. 17. *Mansuyia?* sp. A, DGSC F1690, cranidium. B, DGSC F1708, cranidium. C, DGSC F1662, cranidium. D, DGSC F1563, cranidium. E, DGSC F1717, cranidium. F, DGSC F1726, cranidium. G, DGSC F1575, cranidium. H, DGSC F1594, cranidium. I, DGSC F1546, cranidium. J–L, DGSC F1496, cranidium in: J, anterior; K, left lateral; L, dorsal view. M, DGSC F1702, cranidium. N, DGSC F1507, external mould, pygidium. O–Q, DGSC F1668, pygidium in: O, dorsal; P, posterior; Q, left lateral view. Scale bars represent 2 mm.

IP89260, IP89275) and 2 pygidia (DGSC F1507, F1668) from ATD S1 7.00 m.

Remarks. The tentative assignment (?) of new Thai material to *Mansuyia* relates to poor preservation of the pygidia in the Tarutao collections and because to date the genus has been recorded only in rocks older than the time range suggested by other, co-occurrent taxa on Ko Tarutao (see above). The genus *Mansuyites* Shergold, 1972 is younger, somewhat similar in form, and geographically related, being known from Australia. Diagnostic differences between *Mansuyites* and *Mansuyia* relate to the pygidial spines that are not well preserved in the Tarutao material. However, there are sufficient cranial similarities to suggest that this material is more likely to belong to *Mansuyia* than to *Mansuyites*. The traits shared with *Mansuyia* include the more anterior placement of the eyes, longer (exsag.) posterolateral projections, rim-like anterior border longer than preglabellar field, and eye ridges. Although the cranial evidence in favour of assignment to *Mansuyia* is reasonably strong, uncertainty regarding the pygidial morphology, and the fact that this significantly extends the overall stratigraphic range of *Mansuyia* warrant the uncertainty noted in this taxonomic assignment.

Occurrence. ATD S1 7.00 m, Ao Mo Lae Formation; Furongian, Stage 10.

Subfamily CERONOCARINAE Wernette & Hughes in

Wernette *et al.*, 2020a

Genus SATUNARCUS Wernette & Hughes in Wernette *et al.*, 2020a

Type species. *Satunarcus molaensis* Wernette & Hughes in Wernette *et al.*, 2020a, pp. 876–878 from the Ao Mo Lae Formation; Stage 10, Furongian.

Satunarcus molaensis Wernette & Hughes in Wernette

et al., 2020a

Figure 18A–C

2020a *Satunarcus molaensis* Wernette & Hughes in Wernette *et al.* pp. 876–878, figs 8–10.

Holotype. DGSC F0343, cranidium, Wernette *et al.* 2020a, p. 10, figs 9.1–3 from AML 5.81 m, the Ao Mo Lae Formation, Furongian.

Material. See Wernette *et al.* 2020a. Additionally: 10 cranidia from AML 5.81 m (DGSC F0586, F0632, F1125, F1161, CMC IP88953), AML 6.01 m (CMC IP88984), AML h2 (DGSC F1232) and ATTw (DGSC F0423, F0776, F0781); 2 librigenae from AML 5.81 m (CMC IP88950) and ATTw (DGSC F0411); 15 pygidia from AML 5.81 m (DGSC F0585, F0587–F0589, F0599 external mould, F0613, F1089, F1102, F1131, F1139, F1187, CMC IP88970), AML 6.01 m (CMC IP88987 external mould) and ATTw (DGSC F0436).

Remarks. Wernette *et al.* (2020a) described *S. molaensis* without librigenae; two are here identified from the same sampling

horizon (AML 5.81 m, Fig. 18C and CMC IP88950). The exceptionally long preglabellar field and short, poorly defined anterior border match and confirm the assignment. Unfortunately, neither has a completely preserved anterior facial suture, therefore the ventral structure remains unknown.

Occurrence. ATTw and AML 4.71–6.01 m and AML h2; Ao Mo Lae Formation; Furongian, Cambrian Stage 10.

Family MISSISQUOIDAE Hupé, 1955

Genus PARAKOLDINIOIDIA Endo in Endo & Resser, 1937

Type species. *Parakoldinioidia typicalis* Endo in Endo & Resser, 1937 from Liaoning Province, North China; Stage 10, Furongian.

Parakoldinioidia callosa Qian, 1985

Figure 18D–K

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

1988 *Parakoldinioidia thaiensis* Kobayashi; Shergold *et al.*, p. 316, fig. 3S–T only (non figs 3Q, R, U–X = *Pseudokoldinioidia manekuti*).

Holotype. NIGP 79327, cranidium (Qian 1985, p. 151, pl. 1 figs 12, 13) from the Tangcun Formation, late Cambrian.

Additional material. 6 cranidia from ATD S1 7.00 m (DGSC F1640 external mould, F1652, F1703) and LHN 2.85 m (DGSC F0746 external mould, F0754) and 3.05 m (DGSC F0758). 1 pygidium from ATD S1 7.00 m (DGSC F1733).

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

Specimens from ATD S1 tend to have less rounded anterior glabellar corners and a narrower glabella while the smaller specimens from LHN have a shorter, more robust glabella, a possibly ontogenetic difference.

Compared with the types from southern Anhui (Qian 1985), the Thai material has a less strongly rounded anterior glabellar margin. One specimen from ATD S1 (Fig. 18F) has prominent eye ridges; the eye ridges are either effaced or only very faint in all other known specimens. The granulation on the material figured by Qian (1985) occurs inconsistently on the Tarutao specimens, possibly resulting from preservational variation.

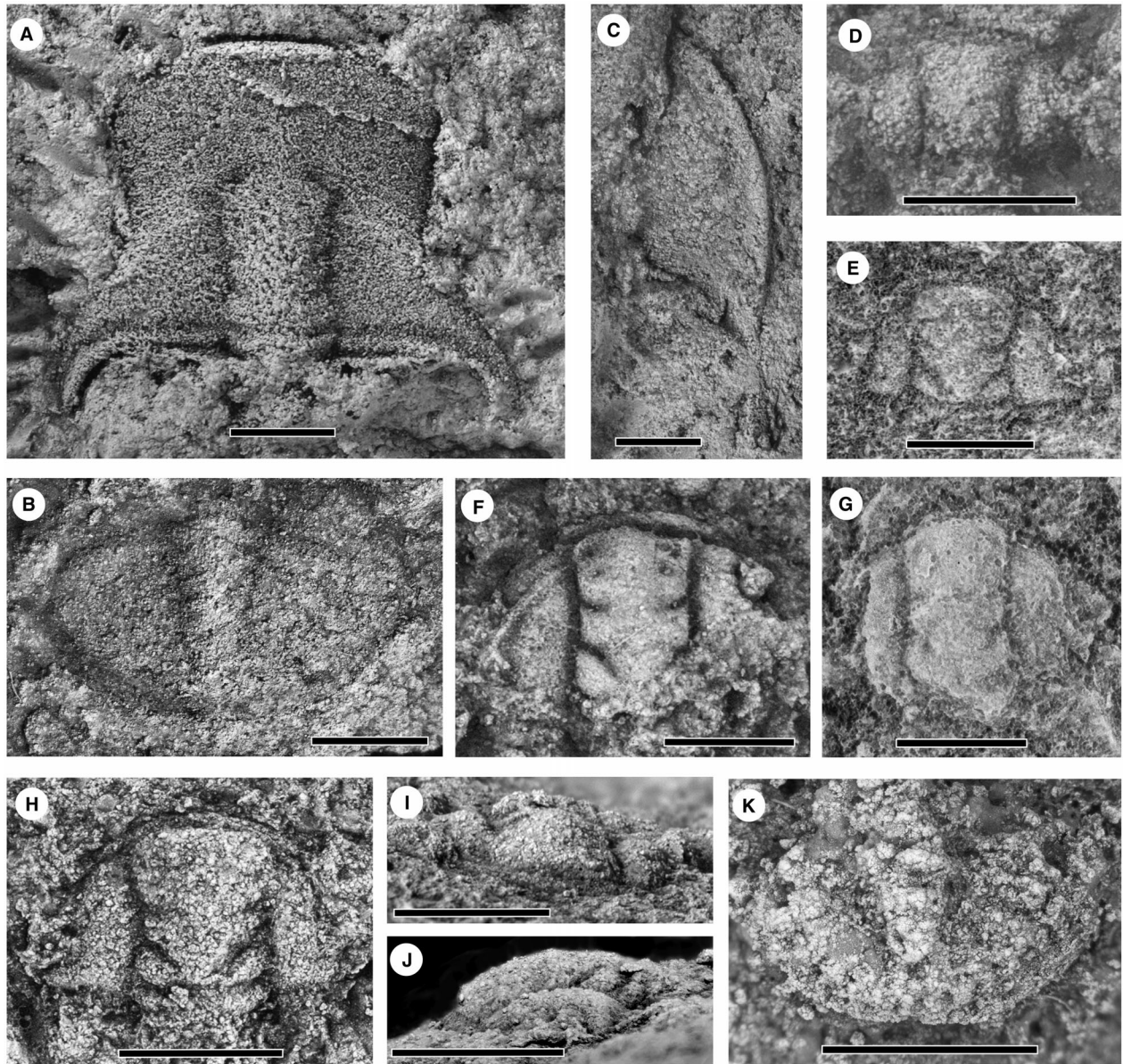


FIG. 18. A–C, *Satunarcus molaensis* Wernette & Hughes in Wernette *et al.*, 2020a: A, DGSC F0343, holotype, cranidium (Wernette *et al.* 2020a, fig. 9.1); B, DGSC F0381, pygidium (Wernette *et al.* 2020a, fig. 10.1); C, DGSC F0411, librigena. D–K, *Parakoldinioidia callosa* Qian, 1985: D, DGSC F0758, cranidium; E, DGSC F0746, cranidium, external mould; F, DGSC F1652, cranidium; G, DGSC F1640, cranidium; H–J, DGSC F0754, cranidium in: H, dorsal; I, anterior; J, left lateral view; K, DGSC F1733, pygidium. Scale bars represent: 2 mm (A–J); 1 mm (K).

Occurrence. ATD S1, 7.00 m; LHN 2.85–3.05 m; Ao Mo Lae Formation; Furongian, Cambrian Stage 10.

Genus PSEUDOKOLDINIOIDIA Endo, 1944

Type species. *Pseudokoldinioidia granulosa* Endo, 1944; from the *Tsinania canens* Zone of Liaoning Province, North China; Stage 10, Furongian.

Remarks. Lee *et al.* (2008) performed a phylogenetic analysis of several missisquoiid genera and, in doing so, provided phylogenetically backed emended diagnoses for these taxa, including *Parakoldinioidia* Endo in Endo & Resser, 1937 and *Pseudokoldinioidia*. Their emended diagnosis for *Pseudokoldinioidia* is followed herein, with especially notable features being the inverted trapezoidal glabella, the broadly rounded anterior cranidial margin, the semi-elliptical pygidium, and clearly incised pygidial interpleural furrows.

Pseudokoldinioidia maneeuti sp. nov.

Figures 19–21

1988 *Parakoldinioidia thaiensis*; Shergold *et al.*, figs 3Q, R, U–X only (non fig. 3S–T = *Parakoldinioidia callosa*).

LSID. <https://zoobank.org/NomenclaturalActs/8C9383BE-AA90-4B06-9E3F-7A9C9BA8C317>

Derivation of name. Named for Mr Niwat Maneeut, Deputy-Director General of the Thai Department of Mineral Resources.

Material. Holotype: DGSC F0522 (Fig. 20AA), cranidium from ATT 22.78 m; Ao Mo Lae Formation, Tarutao Group, Ko Tarutao, Furongian.

Paratypes: 48 cranidia from ATT 0.98 m (DGSC F0800, F0802, F0805 internal and external mould), 5.50 m (CMC IP88918), 6.65 m (F0814), 8.20 m (DGSC F0820), 8.60 m (DGSC F0833), 8.85 m (DGSC F0847), 22.78 m (DGSC F0465, F0473, F0474, F0484, F0486, F0515, F0517, F0521, F0860, F0863, F0866, F0870), 22.88 m (DGSC F0880, F0882, F0885, F0886, F0888, F0891, F0896, F0899, F0903, F0905, F0908, F0909, F0911, F0913, F0914, F0916–F0918, F0920, F0927, F0928, F0936), 23.89 m (DGSC F0943, F0948), 25.34 m (DGSC F0966), 28.37 m (DGSC F0978), 29.17 m (DGSC F1018) and ATT h1 (CMC IP88914).

Other material: 4 cranidia from ATDS1 7.00 m (DGSC F1709), S2 0.52 m (CMC IP89313) and 0.69 m (DGSC F1763), and S3 float (CMC IP89357). 40 pygidia from ATT 0.95 m (DGSC

F0803), 6.65 m (CMC IP88921), 8.20 m (DGSC F0821, F0827), 8.85 m (DGSC F0838), 22.78 m (DGSC F0478, F0519, F0856, F0861, F0872), 22.88 m (DGSC F0537, F0879, F0881, F0883, F887, F0890, F0892, F0897, F0901, F0907, F0910, F0912, F0915, F0921, F0923, F0924, F0929), 23.89 m (DGSC F0945, F0946 external mould), 29.17 m (DGSC F0994, F0998, F1011, F1021, F1027, F1033, CMC IP88939) and ATT h1 (DGSC F0793); from ATTw (DGSC F0403, F0404); from ATD S3 float (CMC IP89367).

Diagnosis. Cranidium with glabella expanding anteriorly to 1.35–1.40-fold L1 width; lateral glabellar furrows anterior to S1 poorly defined to effaced; palpebral lobes short (exsag.) and positioned anteriorly with midpoint opposite L3; posterolateral projections long (exsag.) with a posterior border that is medially nearly transverse but curving strongly posteriorly at distal tips. Pygidium long (sag.) and semi-elliptical with long axis reaching nearly to posterior margin; four axial rings and poorly defined terminal piece; axial furrows slightly posteromedially curved; pleura lengthen (exsag.) distally and shorten (exsag.) posteriorly with straight, moderately well-defined pleural furrows and effaced interpleural furrows.

Description. Cranidium subtrapezoidal to semicircular; cranial width (tr.) across midpoints of palpebral lobes c. 1.1–1.4-fold cranial length (sag.); anterior margin strongly curved lacking anterior border, and glabella occupying full cranial length; anterior glabellar margin variably confluent with pre-ocular curvature of anterior suture branches or sutures dogleg at anterolateral glabellar corners to outline anteriorly protruding (sag., exsag.) glabella; glabella anteriorly widening (tr.) with anterior glabella 1.35–1.4-fold width of L1; LO equal width or slightly broader than L1; axial furrows weakly to moderately incised and smoothly curved; S1 variably expressed from well-incised to faint and with transverse to gently posteriorly oblique orientation; S2 short and poorly defined to effaced; S3 and S4 nearly always effaced; occipital furrow (SO) straight (tr.) and moderately incised. Palpebral lobes short (exsag.), strongly oblique, and anteriorly positioned with midpoint opposite S2 to S3. Posterolateral projections long (exsag., tr.); posterior margin medially transverse to slightly posterolaterally deflected; curves strongly posteriorly near distal end; posterior border lengthens at distal end into fixigenal spine; posterior border furrow moderately to strongly incised.

Pygidium semi-elliptical with width (tr.) across anterior pleural band, the widest point, 1.35–1.55-fold pygidial length (sag.); anterior margin gently anteriorly bowed; posterior margin strongly curved. Axial length 85–90% cranial length (sag.); axial width across anterior-most ring c. 35% cranial width (tr.) at widest point; axial furrows moderately to strongly incised with slight posteromedial curve; lateral axial ring furrows

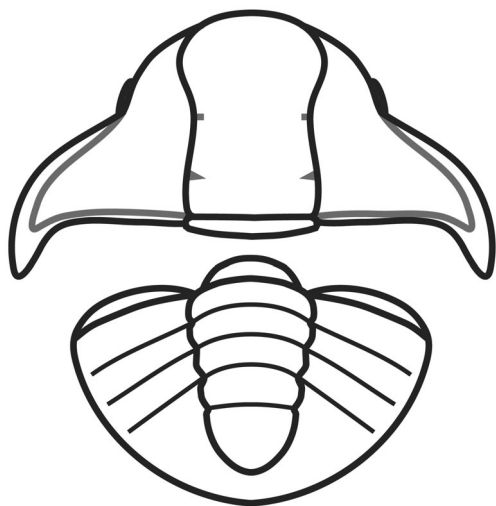
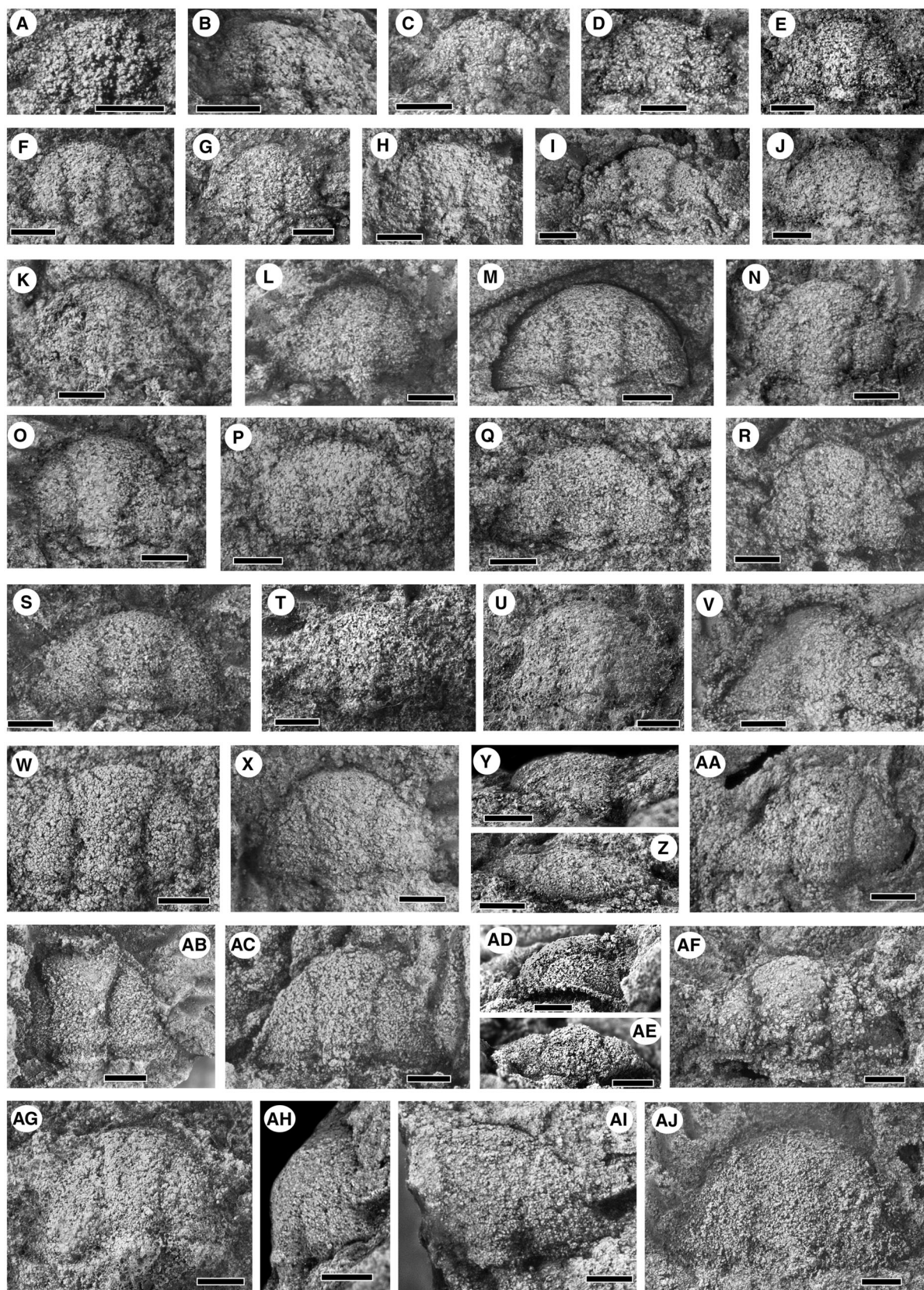


FIG. 19. *Pseudokoldinioidia maneeuti* sp. nov. line drawing.

FIG. 20. *Pseudokoldinioidia maneeuti* sp. nov. cranidia. A, DGSC F0885. B, DGSC F0948. C, DGSC F0888. D, DGSC F0521. E, DGSC F0515. F, DGSC F0914. G, DGSC F0899. H, DGSC F0902. I, DGSC F0800. J, DGSC F0916. K, DGSC F0917. L, DGSC F0882. M, DGSC F0926. N, DGSC F0936. O, DGSC F0943. P, DGSC F0908. Q, DGSC F0820. R, DGSC F0847. S, DGSC F0833. T, DGSC F0909. U, DGSC F0920. V, DGSC F0474. W, DGSC F0805. X–Z, DGSC F0905 in: X, dorsal; Y, left lateral; Z, anterior view. AA, DGSC F0522, holotype. AB, DGSC F0966. AC–AE, DGSC F0814 in: AC, dorsal; AD, left lateral; AE, anterior view. AF, DGSC F1763. AG, DGSC F0928. AH–AI, DGSC F0891 in: AH, right lateral; AI, dorsal view. AJ, DGSC F0465. Scale bars represent 1 mm.



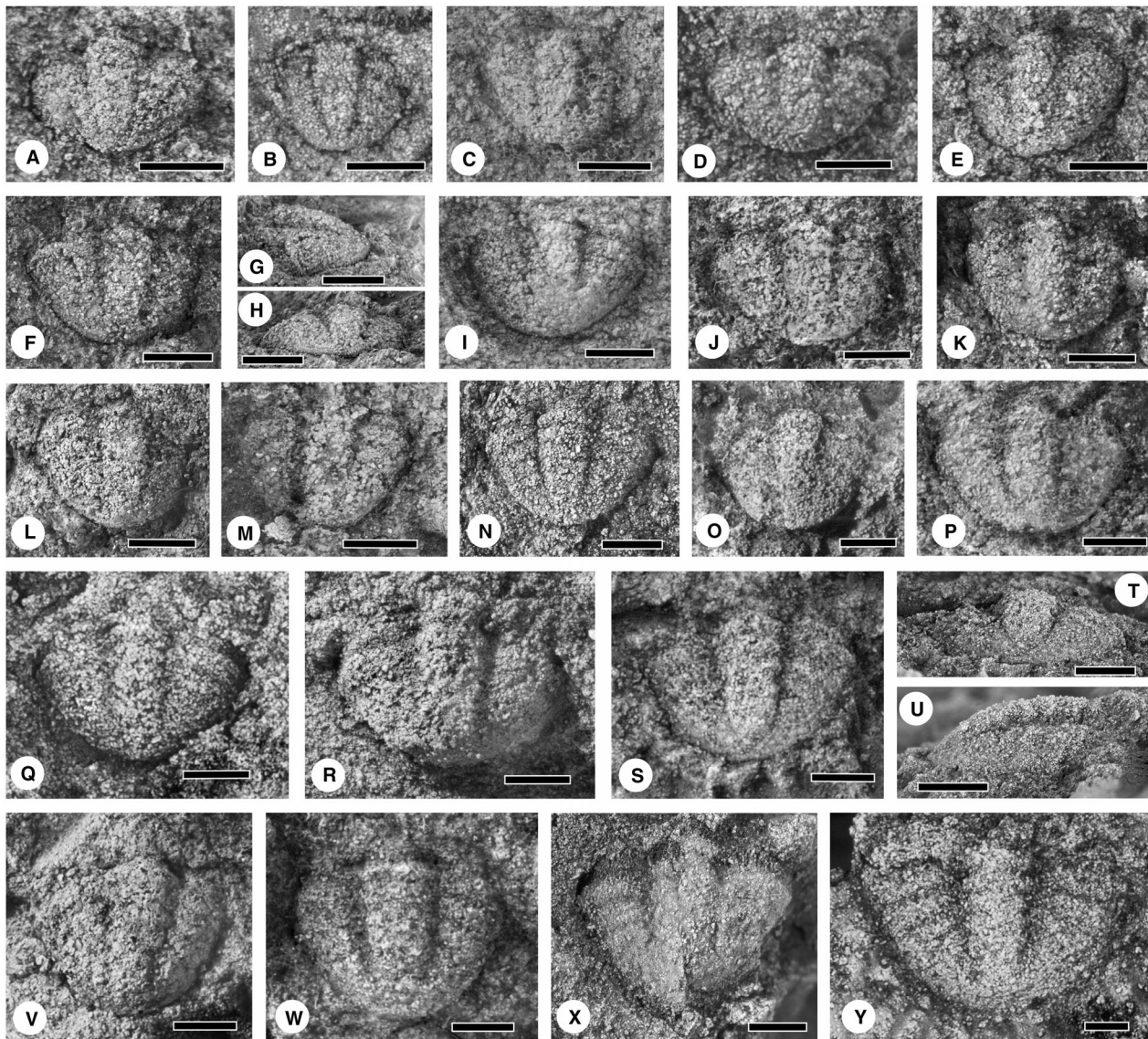


FIG. 21. *Pseudokoldinioidia maneekuti* sp. nov. pygidia. A, DGSC F1033. B, DGSC F0994. C, DGSC F0901. D, DGSC F0537. E, DGSC F0821. F–H, DGSSC F0883 in: F, dorsal; G, left lateral; H, posterior view. I, DGSC F1021. J, DGSC F0911. K, DGSC F0881. L, DGSC F0897. M, DGSC F0945. N, DGSC F0892. O, DGSC F0879. P, DGSC F0912. Q, DGSC F0838. R, DGSC F1011. S–U, DGSC F0872 in: S, dorsal; T, posterior; U, right lateral view. V, DGSC F0907. W, DGSC F0923. X, DGSC F0998. Y, DGSC F0793. Scale bars represent 1 mm.

laterally well-defined but shallow medially, often becoming effaced; 4 axial rings and terminal piece with poorly defined posterior tip. Pleural bands not clearly aligned with axial rings; interpleural furrows effaced; pleural furrows straight and moderately incised to effaced; pleurae slightly laterally lengthening (tr.); pleural furrows terminate at lateral margin.

Remarks. The posterolateral projections of *P. maneekuti* are posteriorly curved, as is typical for *Pseudokoldinioidia*. However, the proximal portions of the posterolateral projection, including the posterior border, are sufficiently transverse in orientation that only those specimens with the distal part preserved show a clear posterior bend. This trait is somewhat variable, with some

specimens (e.g. Fig. 20G) having a stronger curve and others (e.g. Fig. 20AA) being more medially transverse with only a curve in the most distal part. *Pseudokoldinioidia granulosa* Endo, 1944, *Pseudokoldinioidia perpetis* (Zhou & Zhang, 1984) and *Pseudokoldinioidia* sp. cf. *granulosa* (Park & Kihm 2015a) exhibit stronger posterior curvature than the most strongly curved specimens from Ko Tarutao. The palpebral lobes of *P. maneekuti* are smaller than those of these other species, accommodating longer (exsag.) posterolateral projections.

The cranidial outline is variable, with the eyes close to the glabella in some specimens (e.g. Fig. 20G) such that there is a noticeable concavity to the cranidial outline, but more distally set in others (e.g. Fig. 20M), such that the palpebral lobes are

almost confluent with the anterior margin and the transition between anterior and posterior facial sutures. This trait is not size dependent, given that the most distally set eyes occur in one of the medium-sized specimens and both the largest and smallest specimens have relatively narrowly set eyes. Likewise, the variation is not locality specific, given that both extremes occur in the collection from ATT. It may be partially stratigraphically controlled, given that the specimen with the widest set eyes occurs in the uppermost horizon; but if there was a strong stratigraphic trend, then the long gap in fossiliferous horizons at ATT from 8.85 to 22.78 m might be expected to expose that difference in the collections from above and below the gap, and no such clear difference is apparent.

Occurrence. ATT 0.95 m–30.30 m and ATT h1; ATD S1 7.00 m, S2 0.52 m and 0.69 m, and S3 as float; Ao Mo Lae Formation; Furongian, Stage 10.

Family LEIOSTEGIIDAE Bradley, 1925
Subfamily PAGODIINAE Kobayashi, 1935

Remarks. The relegation of Pagodiinae to a subfamily within Leiostegiidae follows Zhou & Zhen (2008) and Adrain (2011).

Genus PAGODIA Walcott, 1905

Type species. *Pagodia lotos* Walcott, 1905; from the *Tsinania* Zone of Shandong, North China; designated by Kobayashi 1935; Stage 10, Furongian.

Remarks. Lu (1975) provided the genus-level diagnosis of *Pagodia* used herein. Diagnostic characters include anteriorly convergent facial sutures, coarse granulation, and broad fixigena.

***Pagodia thaiensis* Kobayashi, 1957**
Figures 22, 23

- 1957 *Pagodia thaiensis* Kobayashi, p. 372, pl. 4 figs 5–7.
? 1988 Leiostegiid gen. et sp. indet.; Shergold *et al.*, p. 314, fig. 3E.

Holotype. UMUT PA02296 a-1, cranidium, Kobayashi, 1957, p. 372, pl. 4 fig. 6 (CMC 88015; Fig. 22X) from the Ao Mo Lae Formation, Furongian.

Material. 31 cranidia from LHN 2.85 m (DGSC F0737), ATTw (DGSC F0380, F0407, F0439 external mould, F0444), AML 3.62 m (DGSC F1041), 5.17 m (DGSC F1063, F1065, F1066, F1082 external mould), 5.81 m (DGSC F0350, F0577 external mould, F0581, F0597, F0617, F1090, F1094, F1095, F1110, F1112, F1116, F1120, F1159, F1163 external mould, F1170, F1171, F1184 external mould, CMC IP88963), 5.84 m (DGSC F0370), 6.01 m (DGSC F1198), and h3 (DGSC F0522). 10 pygidia from LHN 3.69 m (CMC IP88911), ATT h2 (DGSC F0798),

AML 5.17 m (DGSC F1075, F1084) and 5.81 m (DGSC F0355, F0580, F0603, F1132, F1140, F1166).

Remarks. Shergold *et al.* (1988) reassigned Kobayashi's 1957 *Pagodia thaiensis* to *Parakoldinioidia* Endo in Endo & Resser, 1937, based on material that he assigned to that species but which is here shown to be two separate species. Abundant material in our collections confirms the existence of three distinct species from three separate genera: *Parakoldinioidia*, *Pseudokoldinioidia* Endo, 1944 and *Pagodia*.

As initially published, the single *Pagodia thaiensis* type pygidium (UMUT PB02294b-2, Kobayashi, 1957, pl. 4, fig. 7; Fig. 23J) looks similar to that of the narrower *P. maneeekuti*. However, shadow concealed much of the pleural field area in the original photograph, and the *P. thaiensis* pygidium is broader with a relatively narrower axis, consistent with new material of *Pagodia thaiensis*.

The cranidium, leiostegiid gen. et sp. indet. (Shergold *et al.* 1988, fig. 3E), more closely resembles *P. thaiensis* than any other Ko Tarutao taxon. It has a convex glabellar outline rather than the slightly concave lateral margin of *P. thaiensis* and narrow fixigenae. *Pagodia thaiensis* varies in glabellar shape, with some specimens (e.g. Fig. 22A, K) approaching a similarly shaped glabellar outline. It also varies in the width of the fixigena. Therefore, the unidentified leiostegiid documented by Shergold *et al.* (1988) is herein tentatively assigned to *P. thaiensis*.

Occurrence. LHN 2.85–3.69 m, ATTw, ATT h2 and AML 3.62–6.01 m; Ao Mo Lae Formation; Furongian, Cambrian Stage 10.

***Pagodia? uhleini* sp. nov.**
Figures 24–26

- 1988 *Szechuanella?* cf. *damujingensis* (sensu Luo, 1974);
Shergold *et al.*, pp. 313–314, fig. 3F–N.

LSID. <https://zoobank.org/NomenclaturalActs/6D648BD9-38D0-46D6-94EB-4D6EA7BD325F>

Derivation of name. Named for Dr Gabriel Uhlein in gratitude for his finding of the bed in which this species was first recognized.

Material. Holotype: DGSC F1494 (Fig. 25W–Y), cranidium from ATD S1 7.00 m; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Cambrian Stage 10.

Paratypes: 52 cranidia from ATD S1 6.65 m (DGSC F1482, F1483), ATD S1 7.00 m (DGSC F0878, F0930, F1100, F1495, F1503, F1524, F1527, F1535, F1537, F1545, F1549, F1551, F1553, F1558 external mould, F1560 external mould, F1568, F1574, F1577, F1580, F1583, F1585 external mould, F1587, F1602, F1605, F1613, F1615, F1620 external mould, F1623, F1627, F1628, F1635, F1645, F1660, F1679, F1683, F1696, F1711, F1712, F1714, F1720, F1725, CMC IP89258, IP89261, IP89267, IP89269, IP89279), ATD S2 0.52 m (CMC IP89307, IP89317) and 0.69 m (DGSC F1767, CMC IP89327); 24 pygidia from ATD S1 6.65 m (DGSC F1485, F1486, F1488, F1489) and 7.00 m (DGSC F1506, F1518, F1519,

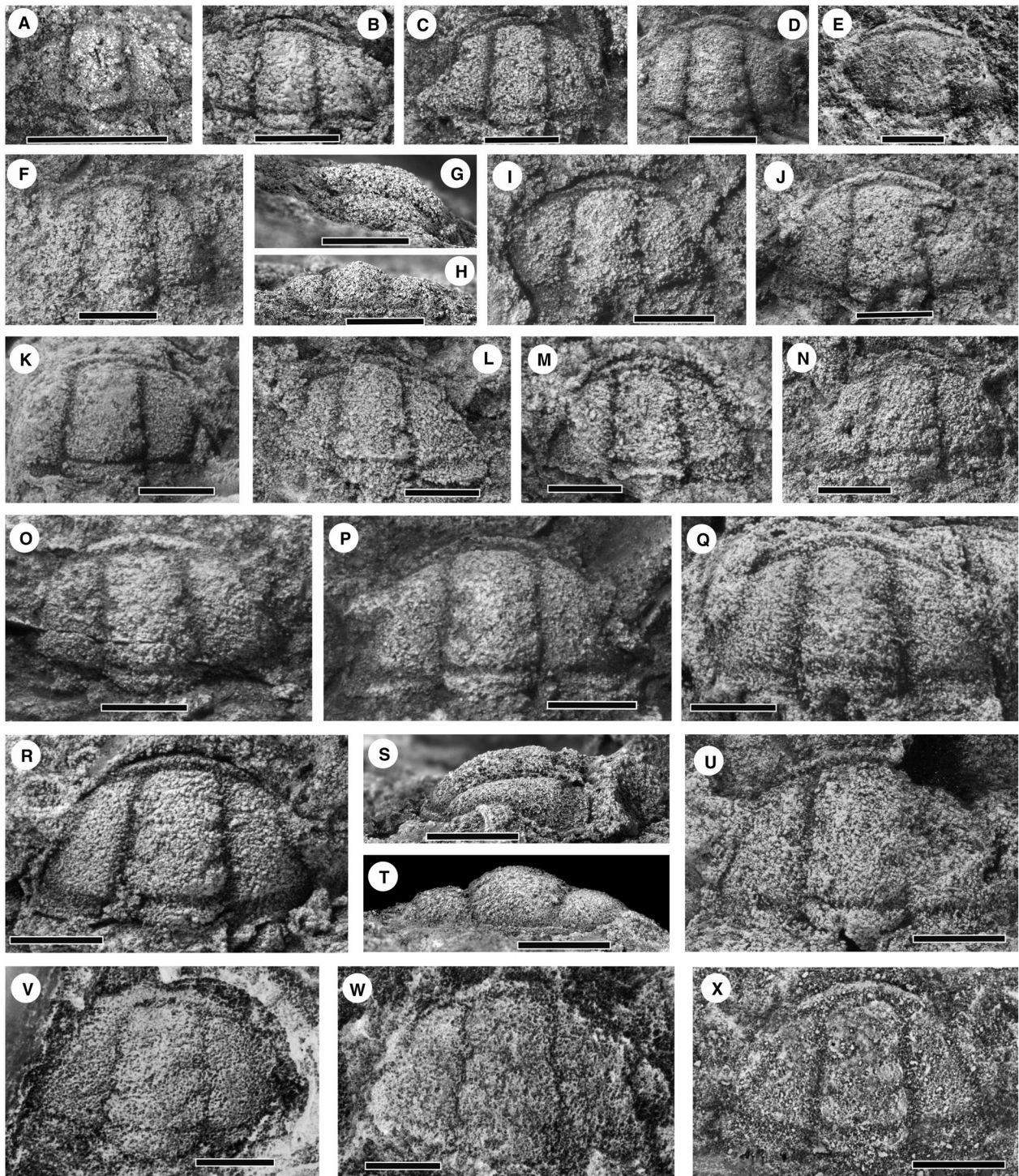


FIG. 22. *Pagodia thaiensis* Kobayashi, 1957, cranidia. A, DGSC F0737. B, DGSC F1110. C, DGSC F1063. D, DGSC F1095. E, DGSC F0577, external mould. F–H, DGSC F0617 in: F, dorsal; G, right lateral; H, anterior view. I, DGSC F1198. J, DGSC F1159. K, DGSC F0350. L, DGSC F1170. M, DGSC F1112. N, DGSC F1065. O, DGSC F0552. P, DGSC F0581. Q, DGSC F1171. R–T, DGSC F1116 in: R, dorsal; S, left lateral; T, anterior view. U, DGSC F1120. V, DGSC F1184, external mould. W, DGSC F1082, external mould. X, CMC IP88003, vinyl polysiloxane cast of UMUT PB 02294b-1, holotype (Kobayashi 1957, pl. 4 fig. 5). Scale bars represent: 1 mm (A); 2 mm (B–X).

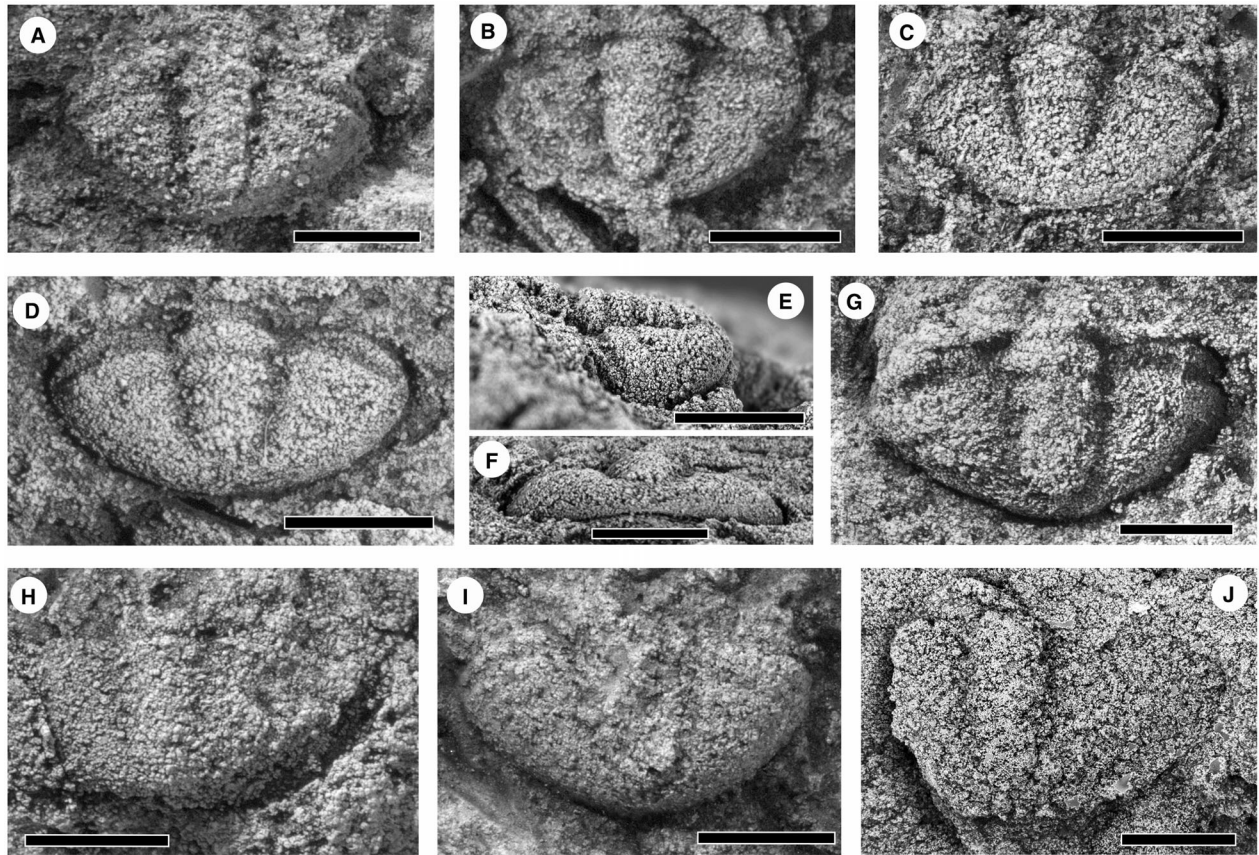


FIG. 23. *Pagodia thaiensis* Kobayashi, 1957, pygidia. A, DGSC F0603. B, DGSC F1075. C, DGSC F1140. D–F, DGSC F1132 in: D, dorsal; E, left lateral; F, posterior view. G, DGSC F1084. H, DGSC F0355. I, DGSC F1166. J, CMC IP88003, vinyl polysiloxane cast of UMUT PB 02294b-2 (Kobayashi 1957, pl. 4 fig. 7). Scale bars represent 2 mm.

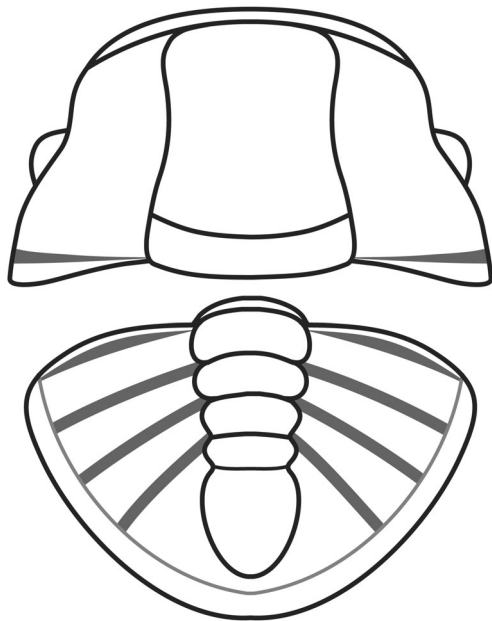


FIG. 24. *Pagodia? uhlei* sp. nov. line drawing.

F1544 external mould, F1570, F1586, F1593, F1595 external mould, F1648, F1653, F1654, F1687, F1697, F1698, F1710, F1722, F1734 external mould, CMC IP83146, IP87621, IP89265).

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

Description. Cranium subtrapezoidal to subtriangular, width (tr.) across the palpebral lobes 1.15–1.45-fold cranial length (sag.); anterior margin strongly curved to subangular. Glabella long (sag.), protruding beyond anterior margin of fixigenae; preglabellar furrow deeply incised; anterior glabellar margin moderately to strongly convex, variably with medial cleft; axial furrows deeply incised; glabella gently anteriorly tapering (tr.) with anterior glabella 85–95% of L1; LO equal width or slightly

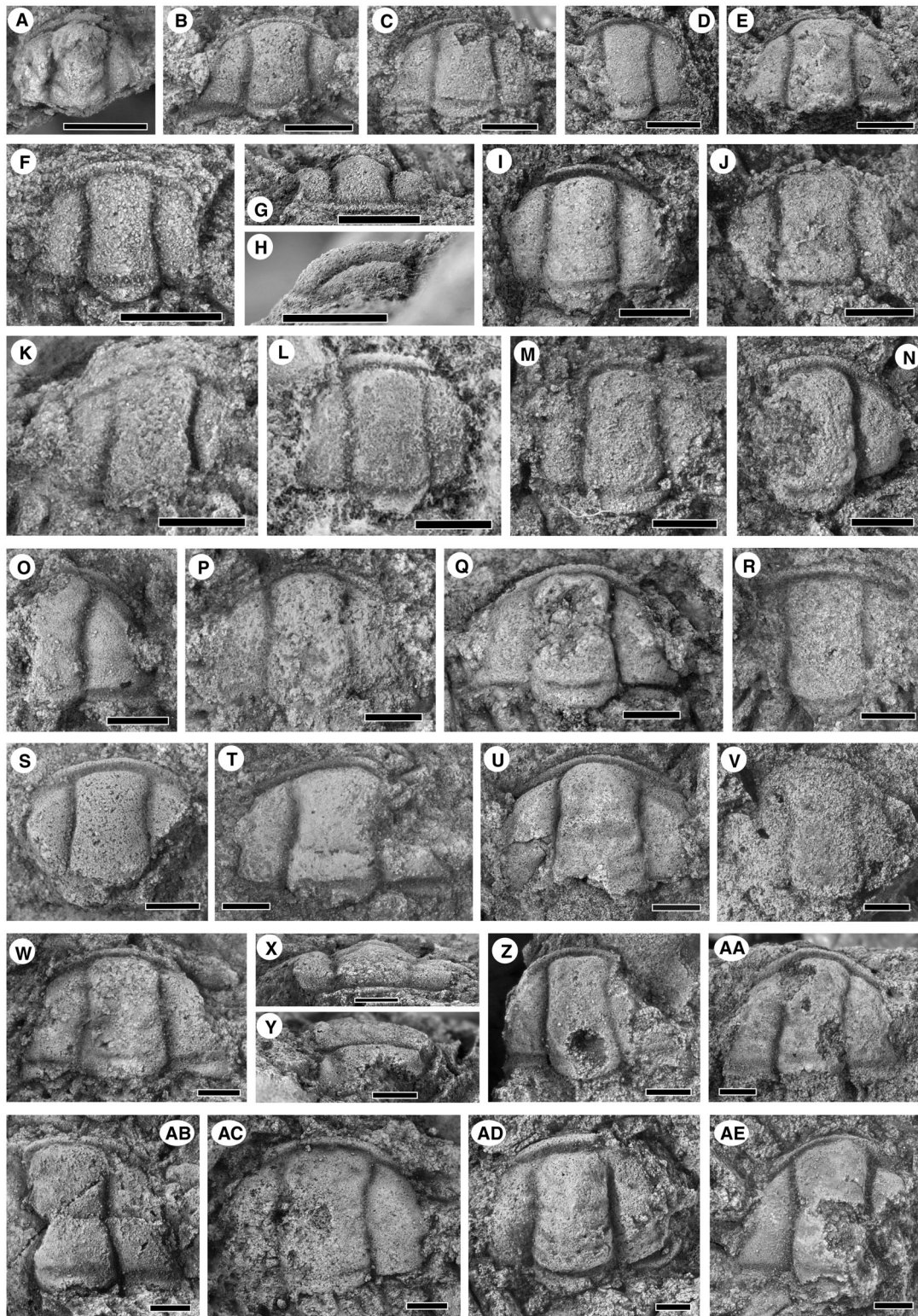


FIG. 25. *Pagodia? uhleini* sp. nov. cranidia. A, DGSC F1587. B, DGSC F1482. C, DGSC F0930. D, DGSC F1551. E, DGSC F1545. F–H, DGSC F1635 in: F, dorsal; G, anterior; H, left lateral view. I, DGSC F1574. J, DGSC F1100. K, DGSC F1615. L, DGSC F1711, external mould. M, DGSC F1714. N, DGSC F1715. O, DGSC F1725. P, DGSC F1712. Q, DGSC F1495. R, DGSC F1660. S, DGSC F1683. T, DGSC F1613. U, DGSC F1483. V, DGSC F1767. W–Y, DGSC F1494, holotype in: W, dorsal; X, anterior; Y, right lateral view. Z, DGSC F0878. AA, DGSC F1580. AB, DGSC F1720. AC, DGSC F1549. AD, DGSC F1577. AE, DGSC F1645. Scale bars represent 2 mm.

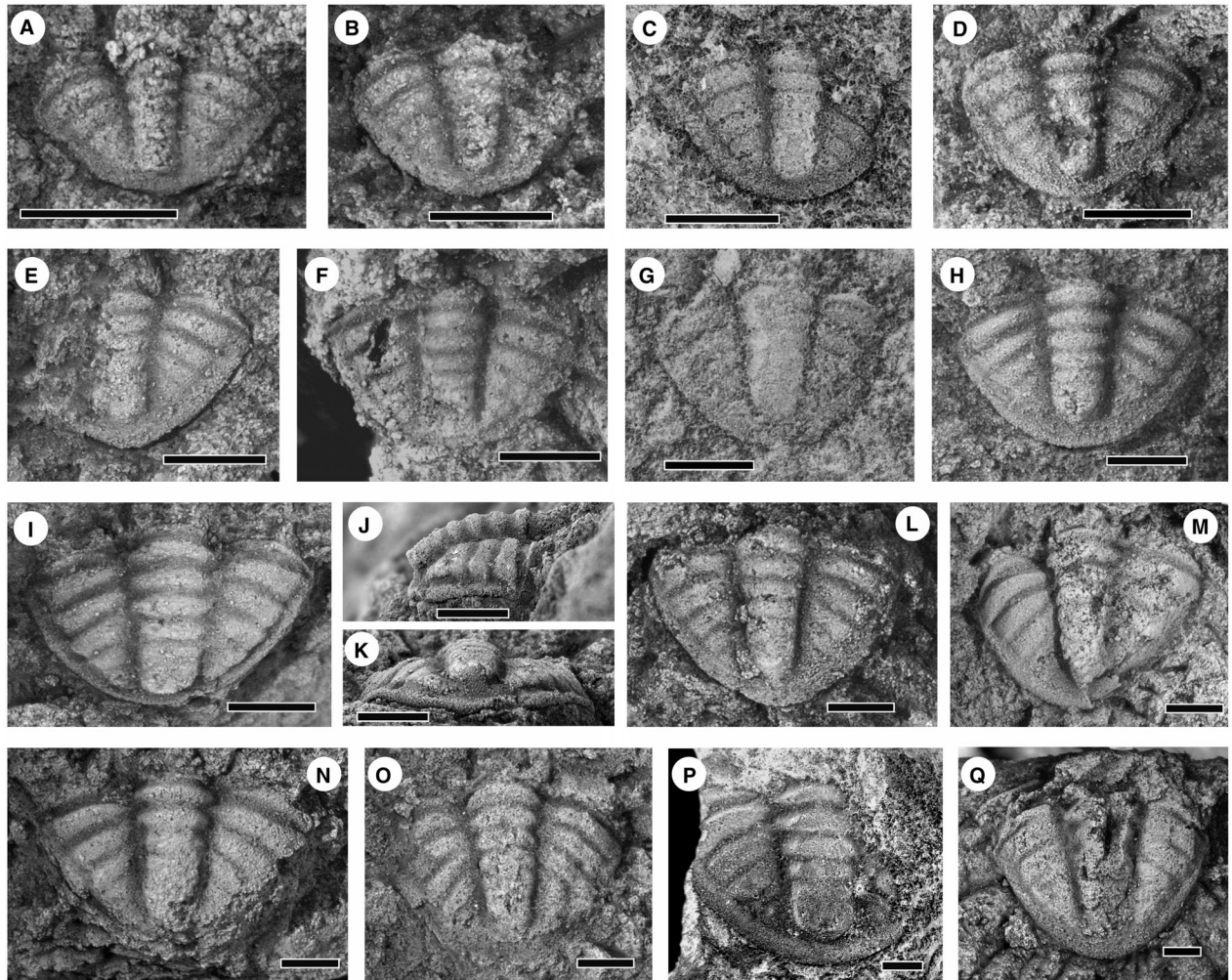


FIG. 26. *Pagodia? uhleini* sp. nov. pygidia. A, DGSC F1488. B, DGSC F1653. C, DGSC F1595, external mould. D, DGSC F1722. E, DGSC F1489. F, DGSC F1687. G, DGSC F1734, external mould. H, DGSC F1486. I–K, DGSC F1654 in: I, dorsal; J, right lateral; K, posterior view. L, DGSC F1570. M, DGSC F1506. N, DGSC F1698. O, DGSC F1485. P, DGSC F1593, external mould. Q, DGSC F1710. Scale bars represent 2 mm.

broader (tr.) than L1; glabellar margin concave, weakly to strongly constricted at S2; lateral glabellar furrows nearly effaced with S1 and S2 faintly defined in some specimens; S1 short and curved posteriorly; S2 short and straight, slightly posteromedially oblique; SO posteriorly bowed and firmly incised; occipital ring lengthens (sag.) becoming dorsally elevated medially with small occipital node. Palpebral lobes short (exsag.), strongly and evenly curved, and positioned with midpoint opposite L2; faint eye ridge present. Anterior suture branches anteriorly convergent to subparallel or slightly divergent. Anterior border short (sag., exsag.); anterior border furrow strongly incised and confluent with preglabellar furrow; anterior border curved. Posterolateral projections long (exsag.) and triangular; posterior margin medially transverse; posterior border furrow strongly incised; posterior border short and slightly lengthening laterally (exsag.).

Pygidium semi-elliptical, width (tr.) across anterior pleural band, the widest point, 1.4–1.6-fold pygidial length (sag.); anterior margin gently anteriorly bowed; posterior margin strongly

curved. Axial length 85–90% cranial length (sag.); axial width across anterior-most ring c. 25% cranial width (tr.) at widest point; axial furrows moderately to strongly incised, gently curved yielding concave axial outline; axial ring furrows straight (tr.); 4 axial rings defined by firmly incised furrows, one axial ring poorly defined, and strongly posteriorly rounded terminal piece with a well-defined posterior axial furrow. Pleural bands of sub-equal length (exsag.), interpleural furrows effaced; pleural furrows straight and strongly incised, terminating at lateral margin. Pygidial border narrow but well-defined by sharp termination of pleural bands and gently incised border furrow; lateral and posterior border of constant thickness (tr., exsag., sag.).

Remarks. The specimens herein assigned to *Pagodia? uhleini* are synonymous with the material assigned by Shergold *et al.* (1988) to *Szechuanella? cf. damujingensis* (Luo, 1974). Both collections are from ATD. When Shergold *et al.* (1988) assigned their material to *Szechuanella* Zhang & Fan, 1960, they left it in open

nomenclature, commenting that it could also be plausibly assigned to *Leioestegium* Raymond, 1913 but that *Szechuanella* was preferred because of pygidial similarities between *Szechuanella szechuanensis* and the Thai material. The pygidial border furrow and well-defined pleural furrows of the Thai material are inconsistent with *Leioestegium*.

We consider *Pagodia* a better genus-level assignment for this material. Several authors have remarked on the similarities between *Szechuanella* and *Pagodia* (e.g. Lu 1975; Shergold *et al.* 1988). Lu (1975, p. 296) enumerated the differences between *Pagodia* and *Szechuanella* with the conclusion that *Pagodia*, exclusively described from the upper Cambrian, may be ancestral to *Szechuanella*, exclusively described from the Tremadocian (with the exceptions of Shergold *et al.* 1988; Zhou & Zhou *in* Zhou & Zhen 2008). Differences between *Pagodia* and *Szechuanella* (*sensu* Lu 1975) include the width of the fixigena, coarseness of granulation, acuteness of the edge of the frontal border, and orientation of the anterior facial branches. The most diagnostic character among these is that *Pagodia* has anteriorly convergent facial sutures while *Szechuanella* has anteriorly divergent sutures. The material presented herein has fine or no granulation and relatively narrow fixigena like *Szechuanella*, but the angularity of the anterior margin is variable and the anterior facial suture branches may be convergent or divergent. The lateral glabellar furrows of *Szechuanella* tend to be more effaced than in *Pagodia*, but the effacement of *Pagodia* is variable both between species (Kobayashi 1933a, pl. 11 figs 4–11) and within each species (e.g. *Pagodia thaiensis* Kobayashi, 1957, fig. 10). The pygidium of *Szechuanella* cannot be reliably differentiated from that of *Pagodia* given that both have long axes, well-defined pleural furrows but effaced interpleural furrows, and a defined pygidial border and border furrow. Based on the anterior suture branches being anteriorly convergent more often than divergent and the clear expression of lateral glabellar furrows on numerous specimens at varying sizes, we herein tentatively assign the Thai material to *Pagodia* as *P.?* *uhleini*. *Pagodia?* *uhleini* encompasses specimens larger than those found in other species of *Pagodia*, with the largest specimen reaching a cranial length of 8.7 mm compared with a maximum length of 5.3 mm for *Pagodia thaiensis*.

Rather than defining a species using the material then available, Shergold *et al.* (1988) made a comparative assignment to *Szechuanella* cf. *damujiangensis*. The type material for *S. damujiangensis* is a single mildly deformed cranidium and probably also deformed pygidium, although whether the pygidium is naturally short or has been artificially shortened by deformation is unclear (Luo 1974). Despite this difficulty, it is clear that the palpebral lobes of *S. damujiangensis* are too far posterior and the anterior border is too wide (tr.) to be the same species as the Thai material. Furthermore, the pleural furrows extend to the margin of the pygidium of *S. damujiangensis* rather than leaving a distinct, unfurrowed pygidial border. As such, a new species is erected herein.

Occurrence. ATD S1 6.65–7.00 m and S2 0.52–0.69 m; Ao Mo Lae Formation; Furongian, Stage 10.

Order PHACOPIDA Salter, 1864
Suborder CHEIRURUINA Harrington & Leanza, 1957
Family PLIOMERIDAE Raymond, 1913

Genus PARAPILEKIA Kobayashi, 1934

Type species. *Calymene? speciosa* Dalman, 1827; Tremadocian.

Parapilekia bunopasi Stait *et al.*, 1984
Figure 27

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

Holotype. TF1538, cranidium (Stait *et al.* 1984, p. 60, fig. 5.5) from the Talo Wao Formation, Tremadocian.

Additional material. 2 cranidia from APM 27.80 m (DGSC F1294) and ATD S3 float (DGSC F1773); 1 pygidium from APM 43.60 m (DGSC F1390).

Remarks. When Stait *et al.* (1984) tentatively assigned this species to *Rossaspis* Harrington, 1957 they said that it is likely to belong to a similar genus such as *Parapilekia* or *Kanoshia* Harrington, 1957. They chose to assign the species to *Rossaspis* on the grounds of the lack of preglabellar field, the size of the anterior border, the size and position of the eye ridges, and the position of the spines on the pygidium, but considered the genus assignment questionable due to the deeply incised interpleural furrows and the presence of a spine on the posterolateral projection. *Parapilekia* includes forms with the same traits that led Stait *et al.* (1984) to assign this species to *Rossaspis*, as well as the short (exsag.) but well-defined anterior pleural bands, deeply incised interpleural furrows, and spines on the posterolateral projections (e.g. *Parapilekia olesnaensis* Ruzicka, 1935 and *Parapilekia ferrigena* Mergl, 1994).

Occurrence. APM 27.80 m and 43.60 m and ATD S3 float; Talo Wao Formation; Tremadocian.

Order ASAPHIDA Salter, 1864
Superfamily ASAPHOIDEA Burmeister, 1843
Family ASAPHIDAE Burmeister, 1843

Genus ASAPHELLUS Callaway, 1877

Type species. *Asaphus (Isotelus?) homfrayi* Salter, 1866; North Wales; Tremadocian.

Remarks. When establishing three new species of *Asaphellus* from Mexico, Robison & Pantoja-Alor (1968) provided a diagnosis of that genus that remains functional across this relatively cosmopolitan genus. Diagnostic traits include: a broad, concave cephalic border; a long (sag.) frontal area; isoteliform facial sutures; a large (sag. and tr.), roughly parallel-sided glabella with

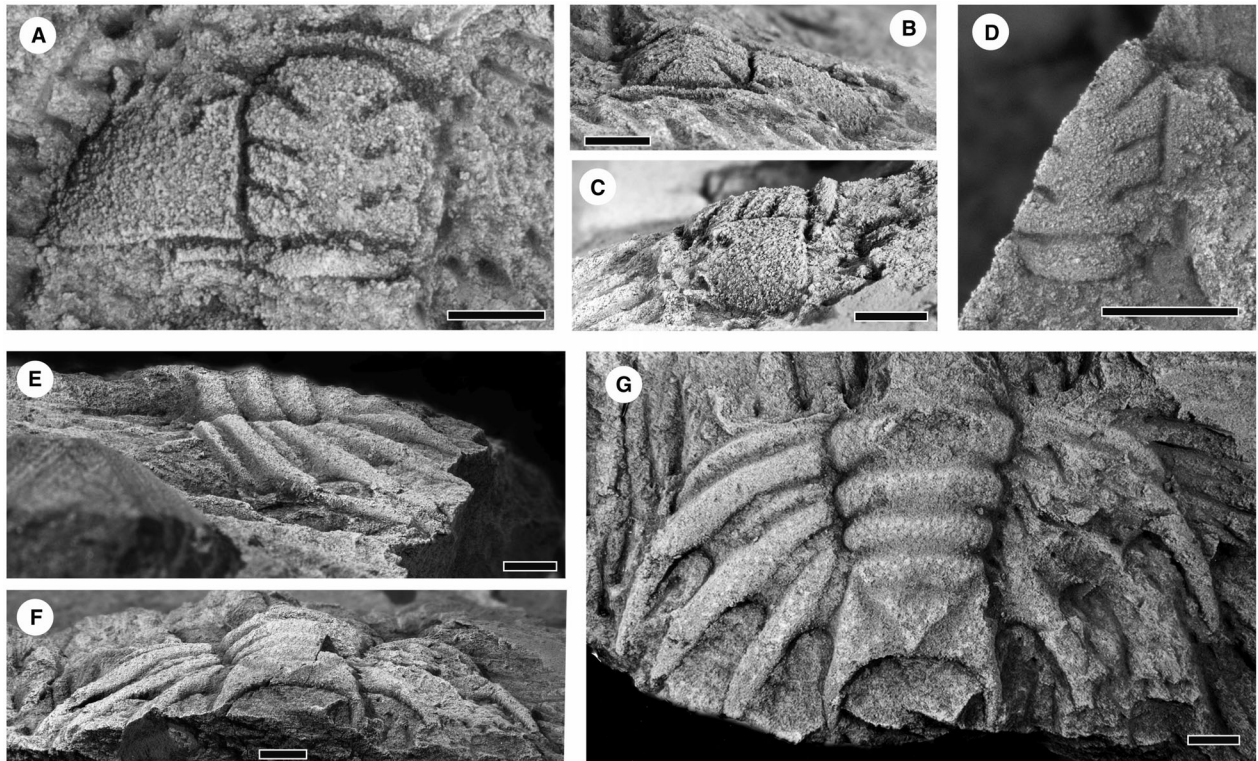


FIG. 27. *Parapilekia bunopasi* Stait *et al.*, 1984. A–C, DGSC F1773 cranidium in: A, dorsal; B, anterior; C, left lateral view. D, DGSC F1294, cranidium. E–G, DGSC F1390, pygidium in: E, left lateral; F, posterior; G, dorsal view. Scale bars represent 2 mm.

low relief and effaced lateral and occipital furrows; faint axial furrows; eyes adjacent to axial furrows; and a semicircular pygidium with a narrow, long and tapered axis surrounded by nearly unfurrowed pleural regions and a broadly concave border; pygidial articulating facets are well defined.

Asaphellus charoenmiti sp. nov.

Figures 28–30

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

LSID. <https://zoobank.org/NomenclaturalActs/F7715962-E3E5-4DFE-92A8-5885D7BA2D70>

Derivation of name. Named for Mr Jirasak Charoenmit of the Thai Department of Mineral Resources in recognition for his extensive help with fieldwork on Ko Tarutao.

Material. Holotype: DGSC F1400 (Fig. 29E–G), cranidium from Ao Phante Malacca 43.60 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; uppermost Furongian–Tremadocian.

Paratypes: 26 cranidia from APM 18.00 m (CMC IP89024), 27.35 m (CMC IP89038), 27.80 m (DGSC F1293, CMC IP89042), 42.75 m (DGSC F1314, F1317, F1318), 43.60 m

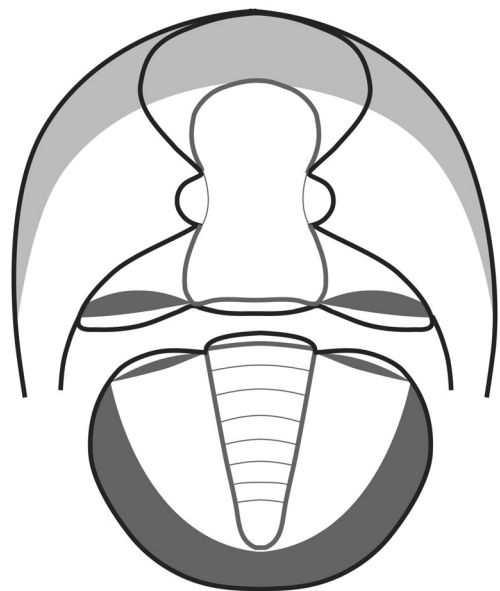


FIG. 28. *Asaphellus charoenmiti* sp. nov. line drawing.

(DGSC F1347, F1355 external mould, F1365, F1376, F1393, F1404, F1405, CMC IP89081 external mould, IP89197, IP89202), 46.05 m (CMC IP89210), 47.30 m (DGSC F1413, CMC

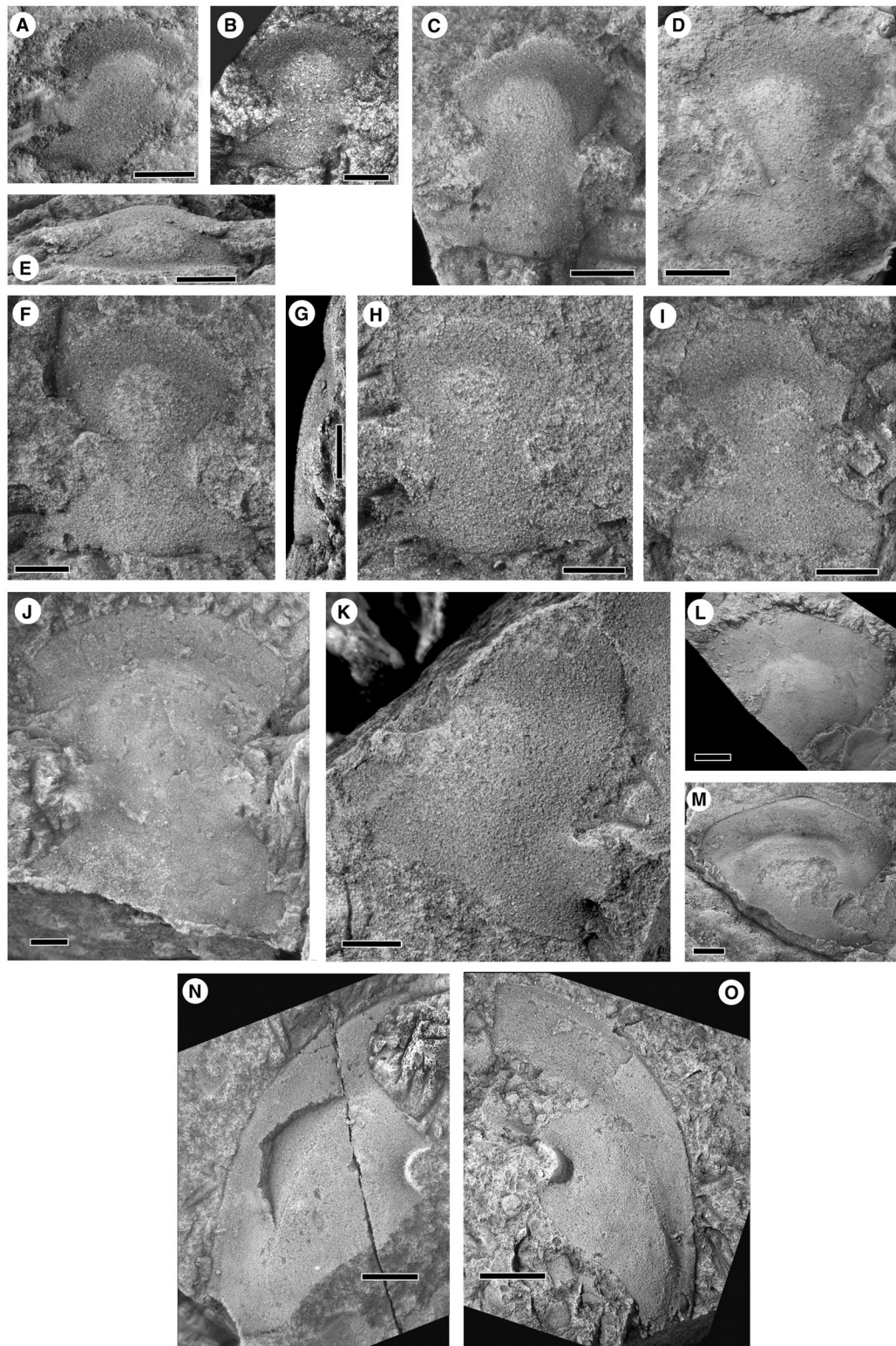


FIG. 29. *Asaphellus charoenmiti* sp. nov. A, DGSC F1442, cranidium, external mould. B, DGSC F1365, cranidium. C, DGSC F1293, cranidium. D, DGSC F1355, cranidium, latex cast. E–G, DGSC F1400, holotype, cranidium, in: E, anterior; F, dorsal; G, right lateral view. H, DGSC F1404, cranidium. I, DGSC F1393, cranidium. J, DGSC F1425, cranidium. K, DGSC F1405, cranidium. L, DGSC F1318, cranidium. M, DGSC F1480, cranidium. N, DGSSC F1280, librigena. O, DGSC F1459, librigena. Scale bars represent: 2 mm (A–K); 4 mm (L–O).

IP89211), 48.65 m (CMC IP89228), 53.65 m (DGSC F1425, F1428, F1434, F1442 external mould) and 60.20 m (DGSC F1480). 14 librigenae from APM 15.10 m (DGSC F1280), 18.00 m (DGSC F1286), 27.80 m (DGSC F1300), 28.70 m (DGSC F1304), 42.75 m (DGSC F1316 external mould, F1321 external mould, F1327, CMC IP89068 external mould), 43.60 m (DGSC F1379), 47.30 m (CMC IP89219 external mould), 48.65 m (CMC IP89227, DGSC F1419), and 53.65 m (DGSC F1427, F1459). 72 pygidia from APM 0.05 m (DGSC F1273, F1274, CMC IP89001, IP89004, IP89005 external mould, IP89007 external mould), 15.10 m (DGSC F1278, CMC IP89008, IP89010, IP89011), 18.00 m (CMC IP89016, IP89025 external mould), 27.35 m (CMC IP89037, IP89039, DGSC F1287, F1288), 27.80 m (DGSC F1290 internal and external mould, F1291, F1292, CMC IP89043, F1296, F1297, F1299, F1301, F1302), 28.70 m (CMC IP89046 internal and external mould, IP89047), 42.75 m (DGSC F1306 external mould, F1307–F1309, F1310 external mould, F1311, F1312 external mould, F1313, F1315, F1322 external mould, F1325, F1326, F1329, CMC IP89059, IP89063 external mould, IP89065, IP89066, IP89072 external mould, IP89073), 43.60 m (DGSC F1330, F1335 external mould, F1356–1359, F1373, F1377, F1388, F1389, F1403, F1406–1408), 48.65 m (CMC IP89226, IP89233, DGSC F1417), 53.65 m (DGSC F1435, F1457, F1466 external mould, F1473) and 60.20 m (DGSC F1478, CMC IP89245, IP89249, IP89252, DGSC F1479 external mould).

Other material: 9 pygidia from ATD S3 float (CMC IP89352, IP89354, IP89358, IP89359, IP89364 external mould, IP89368 external mould, DGSC F1106, F1774, F1783).

Diagnosis. Long (sag.), waisted cranidium with medially constricted, strongly anteriorly rounded glabella; palpebral lobes short (exsag.) and strongly curved. Pygidium subelliptical with broad, depressed border, effaced pleural and interpleural furrows, 7 or more axial rings, well-defined axial and post-axial furrows and inflated, broad (exsag.) articulating facets.

Description. Cranidium of low convexity; cranial length (sag.) 1.8–2.25-fold cranial width (tr.) at anterior corner of palpebral lobe; width (tr.) across posterolateral projections nearly equal to cranial length; width (tr.) across frontal area 1.5–1.75-fold width (tr.) across anterior corner of palpebral lobes; anterior branches of facial sutures diverge at 35–45°, reach widest point at lateral corners of anterior border and then converge to meet medially; curvature of anterior facial suture branches and anterior margin variable with angular anterior margin more common in larger specimens; posterior suture branches gently sigmoidal. Glabella 75–80% cranial length, strongly anteriorly rounded; nearly straight, parallel to slightly anteriorly convergent axial furrows; axial furrows and preglabellar furrow faint; lateral glabellar furrows completely effaced; SO faint; LO short (sag., exsag.), lenticular, especially at larger sizes. Anterior border gently inflated; separated from glabella by broad preglabellar field; anterior border furrow effaced. Palpebral areas narrow; palpebral lobes short, c. 20% glabellar length including LO, adjacent to glabella, located at glabellar mid-length, and strongly curved. Posterolateral projections triangular with nearly blunt termination at facial sutures;

posterior border furrow broad and distinct, outlining gently inflated posterior border.

Librigena gently curved with broad border and doublure, narrowing posteriorly; lateral and posterior border furrow absent. Ocular surface sharply upturned, short (exsag.) and strongly rounded. Genal spine broad at base and weakly tapering. Doublure broad with faint, irregular ridges; ventral median suture.

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

Remarks. The cranidium of *Asaphellus charoenmiti* is similar to *Asaphellus acutulus* Zhou & Zhang, 1978 except for the anterior border of the latter being slightly more strongly curved. The two species, however, are readily differentiated by the broader pygidium of *A. acutulus*. Compared with *Asaphellus homfrayi* (Zhang, 1989) and *Asaphellus trinodus* Zhang, 1949, *A. charoenmiti* has a broader (tr.) frontal area between more strongly diverging anterior suture branches. *Asaphellus tomkoleensis* Kobayashi, 1934 has a concave point to its anterior margin that distinguishes it from *A. charoenmiti* and other species of *Asaphellus*. *Asaphellus coreanicus* Kobayashi, 1934 is different from *A. charoenmiti* in the anterolateral sweep of the preocular anterior facial sutures and palpebral lobes that stick out further than in other species of *Asaphellus*.

The occipital ring described herein is considerably longer (sag.) than that described by Stait *et al.* (1984). Stait *et al.* (1984) were able to distinguish only a short (sag.) band on the posterior edge of the occipital ring, which we refer to as an occipital posterior band. This feature is lenticular and evident in more specimens than the occipital ring due to effacement of SO. The full occipital ring is equal in length (exsag.) to the cranidium's posterior border and c. 15% the glabellar length (e.g. Fig. 29C).

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

Occurrence. APM 0.05–60.20 m and ATD S3 float; Talo Wao Formation; Tremadocian.

Family REMOPLEURIDIDAE Hawle & Corda, 1847

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

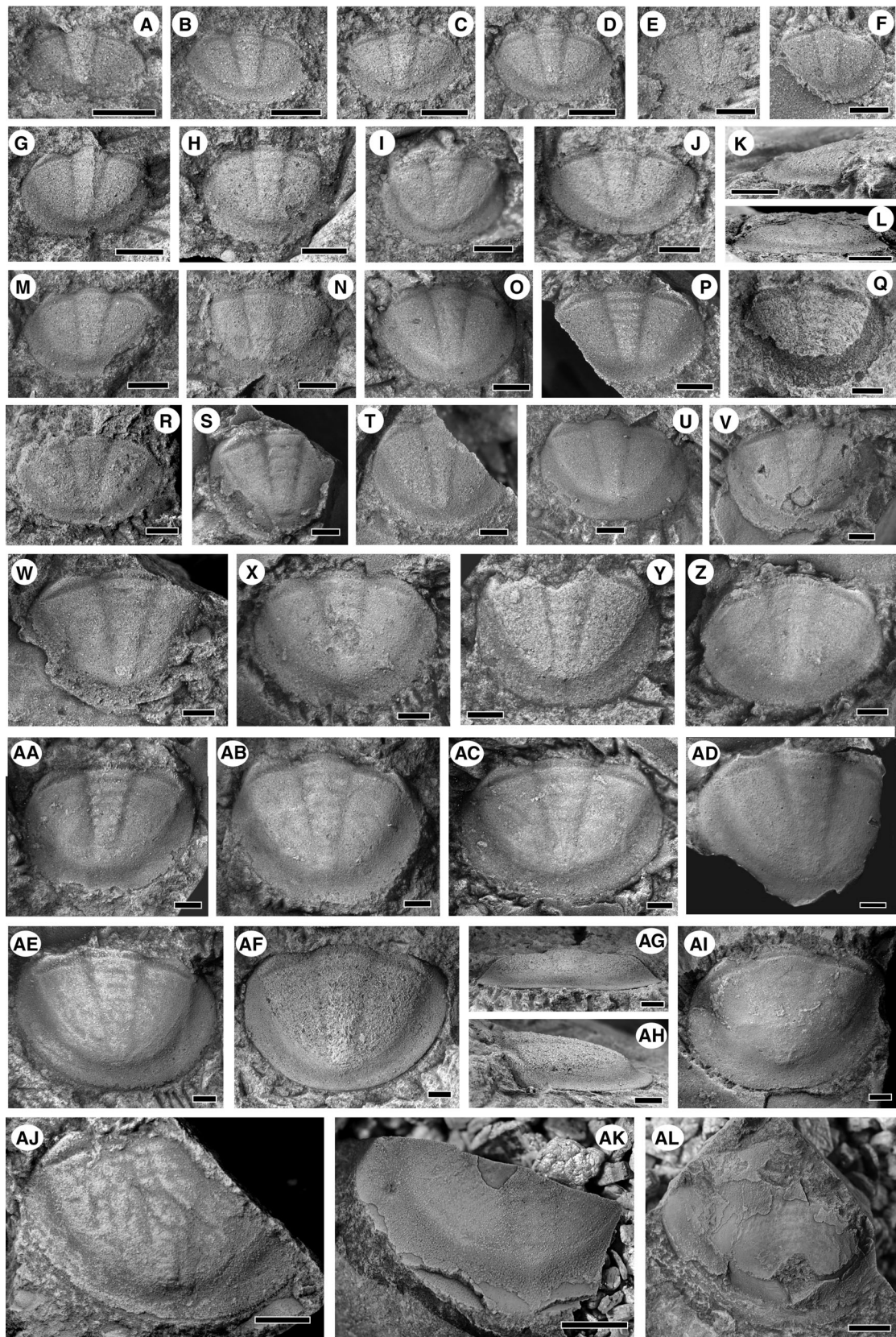


FIG. 30. *Asaphellus charoenmiti* sp. nov. pygidia. A, DGSC F1417. B, DGSC F1290. C, DGSC F1288. D, DGSC F1299. E, DGSC F1403. F, DGSC F1478. G, DGSC F1292. H, DGSC F1287. I, DGSC F1356. J–L, DGSC F1377 in: J, dorsal; K, right lateral; L, posterior view. M, DGSC F1302. N, DGSC F1435. O, DGSC F1296. P, DGSC F1291. Q, DGSC F1106. R, DGSC F1457. S, DGSC F1315. T, DGSC F1389. U, DGSC F1301. V, DGSC F1408. W, DGSC F1406. X, DGSC F1326. Y, DGSC F1330. Z, DGSC F1313. AA, DGSC F1358. AB, DGSC F1357. AC, DGSC F1308. AD, DGSC F1322, latex cast. AE, DGSC F1311. AF–AH, DGSC F1783 in: AF, dorsal; AG, posterior; AH, left lateral view. AI, DGSC F1325. AJ, DGSC F1307. AK, DGSC F1273. AL, DGSC F1274. Scale bars represent: 2 mm (A–AI); 4 mm (AJ); 8 mm (AK, AL).

Genus APATOKEPHALUS Brögger, 1896

Type species. *Trilobites serratus* Boeck, 1838; subsequently designated by Bassler (1915); Tremadocian.

Remarks. *Apatokephalus* is distinguished by the combination of an urceolate glabella closely flanked by long (exsag.) arcuate palpebral lobes and a distinct preglabellar field (Brögger 1896; Shergold 1991; Ebbestad, 1999). Although Ebbestad's diagnosis (1999) encompasses only those species in which the interpalpebral areas are fully occupied by the laterally expanded glabella, Park & Kihm (2015b) demonstrated that this characteristic lateral expansion does not occur until the final developmental stage of the cranidium. Some species (e.g. *Apatokephalus hyotan* Kobayashi, 1953) have been assigned to *Apatokephalus* despite the lack of a preglabellar field, giving this genus considerable morphological overlap with *Fatocephalus* Duan & An in Kuo et al., 1982. Morphological distinctions between *Apatokephalus* and *Fatocephalus* are inconsistent with the comment by Shergold (1991) that they can be delineated only using difference in stratigraphic age (with *Fatocephalus* being the older genus, although *Apatokephalus* has also been reported from Cambrian Stage 10; Zhou & Zhen 2008). Age is not a criterion we consider valid in assessing systematic placement, but a thorough analysis of remopleuridids and the potential synonyms of its genera is outside the scope of this paper.

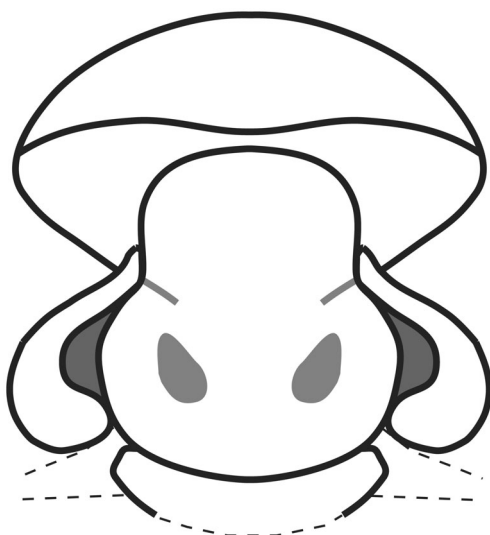


FIG. 31. *Apatokephalus* sp. line drawing. Dashed lines indicate unknown features.

Apatokephalus sp.

Figures 31, 32A–C

Material. One cranidium from APM 53.65 m (DGSC F1469 internal mould).

Description. Glabella urceolate, expanded (tr.) around firmly incised, posteromedially oriented S1 pit that is disconnected from axial furrow; glabellar width (tr.) at S2 equal to posterior-most and anterior-most glabellar width; S2 firmly incised and posteromedially angled; anterior glabellar margin moderately curved. Palpebral lobes arcuate adjacent to glabella with no interpalpebral fixigena except depressed, crescent-shaped, palpebral area fully encompassed by axial furrow and palpebral lobe; palpebral lobe inflated and broad (tr.), extending from posterior L1 to S2; palpebral lobe asymmetrically curved with posterior end more strongly curved. Axial furrow weakly incised, preglabellar furrow strongly incised. Anterior suture branches slightly undercut anterior palpebral lobe, diverging moderately outward for broad preocular fixigena that are continuous with the depressed, broad (tr.) preglabellar field. Undulating anterior border furrow with distinct posteromedial bend that separates frontal area into medially long anterior border and short preglabellar field, but exsagittally long preglabellar field and short anterior border.

Remarks. Although it is known from only a single specimen, *Apatokephalus* sp. is distinct from all other species of *Apatokephalus* and is probably a new species; the paucity of material prevents it from being named as such here. The frontal area is long and has a distinctly undulated or bowed anterior border furrow. A single specimen of *Apatokephalus latilimbatus* Peng, 1990, also has a slight undulation to its anterior border (Park & Kihm 2015b, fig. 5R), not so striking as that of *Apatokephalus* sp., but sufficiently distinct to demonstrate that this character occurs in *Apatokephalus* and that a new genus is unnecessary. *Apatokephalus* sp. varies from *A. latilimbatus* in having a more strongly bowed anterior border furrow, a longer frontal area, and palpebral lobes that more closely mimic the curvature of the glabella.

Occurrence. Ao Phante Malacca 53.65 m; Talo Wao Formation; Tremadocian.

Genus YOSIMURASPIIS Kobayashi, 1960

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

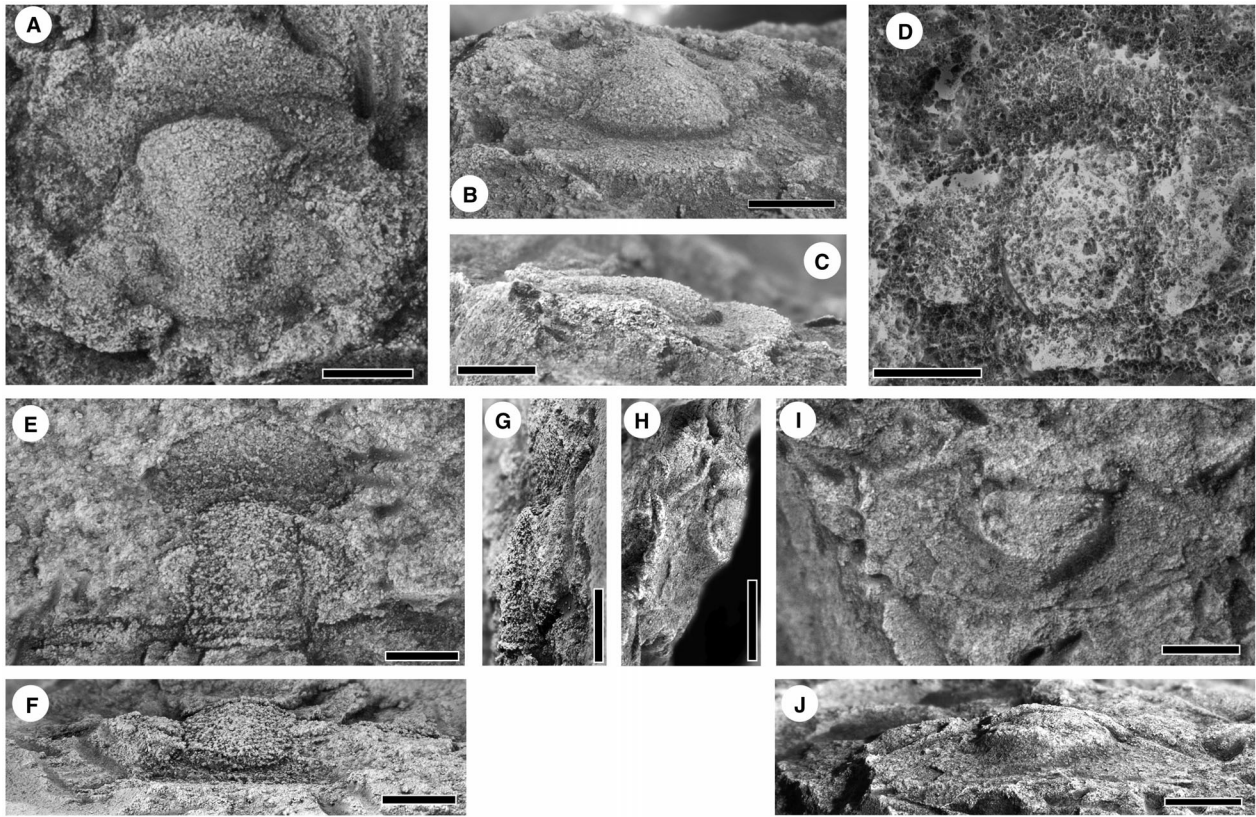


FIG. 32. A–C, *Apatokephalus* sp., cranidium, DGSC F1469 in: A, dorsal; B, anterior; C, right lateral view. D?, E–J *Yosimuraspis* sp.: D, cranidium, DGSC F1772, external mould; E–G, DGSC F1775, cranidium in: E, dorsal; F, anterior; G, right lateral view; H–J, DGSC F1374, pygidium in: H, left lateral; I, dorsal; J, posterior view. Scale bars represent: 1 mm (A–D); 2 mm (E–J).

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

Yosimuraspis sp.

Figure 32D?, E–J

Material. 1 cranidium from ATD S3 float (DGSC F1775 internal mould); 1 tentatively assigned cranidium from ATD S3 float (DGSC F1772 external mould).

Description. Glabella subrectangular to gently urceolate, expanded (tr.) around weakly pitted, posteromedially oriented S1 that is disconnected from axial furrow; glabellar width (tr.) at S2 slightly narrower than posterior-most and anterior-most glabellar widths; S2 nearly effaced, faintly visible proximal axial furrow; LO short and wider than glabella at S1; SO straight (tr.); glabellar anterior moderately rounded. Palpebral lobes longitudinally symmetrically arcuate and adjacent to glabella with no fixigena except

semicircular palpebral area fully encompassed by axial furrow and palpebral lobe; palpebral lobe extending from nearly opposite SO to anterior of S2. Axial and preglabellar furrows strongly incised. Anterior branches of facial sutures strongly anteriorly divergent; convex preglabellar field longer exsagittally than sagittally; anterior border furrow less strongly curved than preglabellar furrow and gently incised; anterior border subpentagonal and long, more than fourfold length (sag.) of preglabellar field; anterior margin angular. Posterolateral projections short (exsag.) and broad (tr.) with straight (tr.) posterior border furrow; posterior border occupies nearly entire length (exsag.) of posterolateral projections.

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

Remarks. *Yosimuraspis* sp. differs from *Yosimuraspis vulgaris* primarily in the length and angularity of the anterior border and in the more strongly arched palpebral lobes. The length of the anterior border most resembles that of *Yosimuraspis luna* Kuo & Duan in Kuo *et al.*, 1982, but *Y. luna* has a longer glabella and a less angular anterior margin.

The smaller cranidium (Fig. 32D) is only tentatively assigned to *Yosimuraspis* sp. Although it is similar to the larger *Yosimuraspis* sp. cranidium in glabellar shape and anterior border length,

Park & Kihm (2015b) showed that urceolate glabellar shape is subject to early holaspid ontogenetic change in remopleuridids, and *Apatokephalus arcuatus* has a similarly divided anterior border and preglabellar field, and hence this specimen might belong to that taxon.

The cranidium of *Yosimuraspis* sp. is known only from float at ATD section 3, but a *Yosimuraspis*-type pygidium occurs at APM (Fig. 32H–J). The pleural field is effaced, unlike for *Apatokephalus*, and the axis is short and pauci-segmented, unlike for *Pseudokainella* and *Jiia* (Harrington & Leanza 1957; Zhou & Zhang 1978; Kim & Choi 2000; Park & Kihm 2015b). The only other potential match for this remopleurid pygidium is *Tarutaoia* gen. nov. However, a second lens-shaped pygidium (Fig. 33R–T), morphologically distinct from Figure 32H–J, from known pygidia of *Yosimuraspis*, and from the other previously described remopleurid genera found on Ko Tarutao, was also found at APM. Thus, by process of elimination, the pygidium that is not consistent with known remopleurid genera (DGSC F1303) is assigned to *Tarutaoia techawani*, and DGSC F1374 is assigned to *Yosimuraspis* sp.

Occurrence. ATD S3 float; Talo Wao Formation; Tremadocian.

Genus TARUTAOIA nov.

LSID. <https://zoobank.org/NomenclaturalActs/8EEDCB41-CB61-4C48-AEF0-EAD768EBBE87>

Derivation of name. Named for the Tarutao Group and Ko Tarutao.

Type species. *Tarutaoia techawani* sp. nov.; by monotypy.

Diagnosis. As for the type and only species.

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

(e.g. Fig. 33O), or it may be oblique to the medial portion of the anterior border furrow (e.g. Fig. 33M).

Occurrence. APM 18.00–60.20 m; Talo Wao Formation; Tremadocian.

Tarutaoia techawani sp. nov.

Figures 33, 34

? 1984 *Pseudokainella malakaensis* Stait et al., pp. 56–59, figs 3.3,7 only [figs 3.1,2,4–6 = *Pseudokainella malakaensis*].

LSID. <https://zoobank.org/NomenclaturalActs/D20D9387-6163-437C-81F6-BC427C0E29CA>

Derivation of name. Named for Dr Sommai Techawan, Director-General of Thai Department of Mineral Resources.

Material. Holotype: DGSC F1364 (Fig. 33L), cranidium from APM 53.65 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian.

Paratypes: 37 cranidia from APM 27.80 m (DGSC F1295, F1298), 28.70 m (CMC IP89051), 43.60 m (DGSC F1332–F1334, F1336, F1338, F1341, F1343, F1344, F1346, F1349, F1352, F1353, F1361, F1368, F1383 external mould, F1392, F1394, F1398, F1399, F1401, CMC IP89204, IP89082), 47.30 m (DGSC F1412, F1415) and 53.65 m (DGSC F1429, F1431, F1432, F1438–F1440, F1446, F1449, F1453, F1463).

Other material: 61 cranidia from APM 18.00 m (CMC IP89021), 27.35 m (CMC IP89035), 28.70 m (DGSC F1305), 42.75 m (CMC IP89074), 43.60 m (DGSC F1331 external mould, F1337, F1339, F1340, F1342, F1345, F1348, F1354, F1360, F1362, F1366, F1369, F1370, F1372, F1375, F1381, F1384, F1386, F1387, F1403, CMC IP89076, IP89077, IP89080, IP89083, IP89084–7, IP89192–5, IP89198, IP89199), 47.30 m (CMC IP89212, IP89215, IP89216), 48.65 m (DGSC F1416, F1418 external mould, F1420, CMC IP89220 external mould, IP89221, IP89224 external mould, IP89230 external mould, IP89232), 53.65 m (DGSC F1430, F1441, F1448, F1451, F1462–F1465, F1471, F1472, CMCIP781234) and 60.20 m (CMC IP89248). 1 pygidium from APM 28.70 m (DGSC F1303).

Diagnosis. Cranidium with strongly urceolate glabella, preglabellar field absent, and narrow (tr.) border; S1 firmly incised and disconnected from axial furrows; S2 firmly incised and curved; strongly curved palpebral lobes touching axial furrows; preocular fixigena narrow and separated from anterior border by subtransverse or anterolaterally oblique furrow. Pygidium lenticular with broad, strongly tapering axis, two axial rings, short terminal piece, effaced pleural area except first pleural furrow, and smooth posterior margin.

Description. Glabella urceolate, expanded (tr.) around firmly incised, posteromedially oriented S1 pit that is disconnected from axial furrow; glabellar width (tr.) at S2 equal to posterior-most

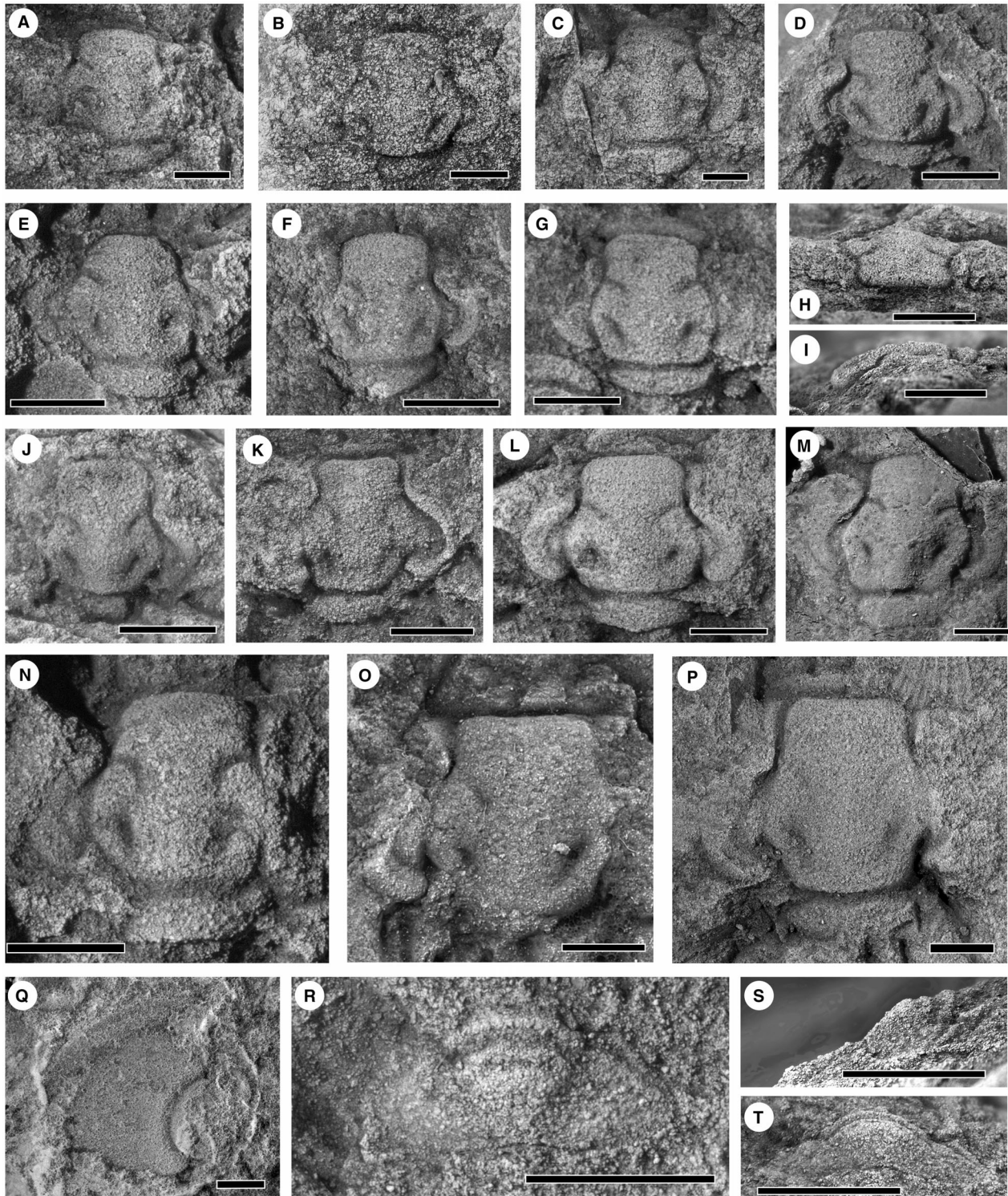


FIG. 33. *Tarutaioia techawani* gen. et sp. nov. A, DGSC F1429, cranidium. B, DGSC F1349, cranidium. C, DGSC F1392. D, DGSC F1415, cranidium. E, DGSC F1412, cranidium. F, DGSC F1431, cranidium. G–I, DGSC F1398, cranidium in: G, dorsal; H, anterior; I, left lateral view. J, DGSC F1453, cranidium. K, DGSC F1401, cranidium. L, DGSC F1472, holotype, cranidium. M, DGSC F1383, cranidium, latex cast. N, DGSC F1438, cranidium. O, DGSC F1361, cranidium. P, DGSC F1394, cranidium. Q, DGSC F1447, indeterminate librigena, external mould. R–T, DGSC F1303, pygidium in: R, dorsal; S, right lateral; T, posterior view. Scale bars represent: 1 mm (A–C); 2 mm (D–T).

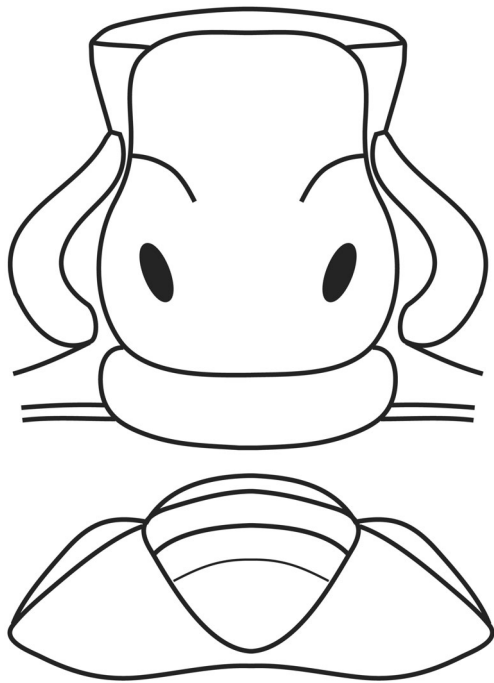


FIG. 34. *Tarutaoia techawani* gen. et sp. nov. line drawing.

and anterior-most glabellar widths; S2 firmly incised and postero-medially arched; LO subequal in width (tr.) to posterior glabella, and variably has broad node in some specimens; anterior glabellar margin variable including straight (tr.), gently convex, or gently concave. Palpebral lobes arcuate adjacent to glabella with no fixigena excepting narrow, inflated preocular strap and narrow, depressed crescent-shaped palpebral area fully encompassed by axial furrow and palpebral lobe; palpebral lobe inflated, broad (tr.), and long (exsag.) extending from posterior L1 to S2; palpebral lobe asymmetrically curved with anterior end slightly recurved into preocular areas and posterior end more strongly curved. Axial and preglabellar furrows firmly incised. Preglabellar field absent; anterior border furrow fully confluent with preglabellar furrow; firmly incised furrow with oblique or subtransverse orientation separating inflated fixigena and anterior border. Anterior facial sutures gently divergent.

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

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

Remarks. *Tarutaoia techawani* is most easily distinguished from other remopleurids by its unique frontal area. However, even without a preserved frontal area it can be differentiated from the other remopleurids in the Talo Wao Formation by its deeply incised, lateral glabellar furrows, particularly the strongly curved S2, which are straight and shallow or nearly effaced in *Yosimuraspis* sp., *Apatokephalus* sp. and *Jiia talowaois*. On more effaced

specimens of *T. techawani*, a distinction can also be made from *Yosimuraspis* sp. and *J. talowaois* based on the strongly urceolate glabellar outline.

A remopleurid-type pygidium is assigned to *Tarutaoia* based on its association with the cranidia at Ao Phante Malacca and its incompatibility with any of the other remopleurids in the Talo Wao Formation. It is too short for *Pseudokainella* or *Jiia*, too effaced for *Apatokephalus*, and has a more strongly tapering, v-shaped axis than *Yosimuraspis* (Harrington & Leanza 1957; Zhou & Zhang 1978; Jell 1985; Kim & Choi 2000; Park & Kihm 2015b). Stait *et al.* (1984, figs 3.3, 3.7) found pygidia of this form and assigned it to their new species *Pseudokainella malakaensis*, the only remopleurid known from the Tarutao Group at that time. They remarked on the pauci-segmented form being more similar to *Elkanaspis* or another remopleurid than to other species of *Pseudokainella*.

Occurrence. APM 18.00–60.20 m; Talo Wao Formation; Tremadocian.

Genus *Jiia* Zhou & Zhang, 1978

Type species. *Jiia ampuliformis* Zhou & Zhang, 1978, from the Yehli Formation, Hebei, China; by original designation; Tremadocian.

Remarks. Zhou & Zhang (1978) diagnosed *Jiia* mainly using differential characters to distinguish it from *Apatokephalops* Zhou & Zhang, 1978. These characters include a broad, anteriorly tapering glabella, short preocular area and anterior facial sutures, a narrow and strongly depressed preglabellar field, convex palpebral lobes with deep palpebral furrows, and a test with fine granules.

Jiia talowaois sp. nov.

Figures 35, 36A–G, ?H–J

LSID. <https://zoobank.org/NomenclaturalActs/3CD25116-8433-4041-9CD7-B3A1ABFA8814>



FIG. 35. *Jiia talowaois* sp. nov. line drawing.

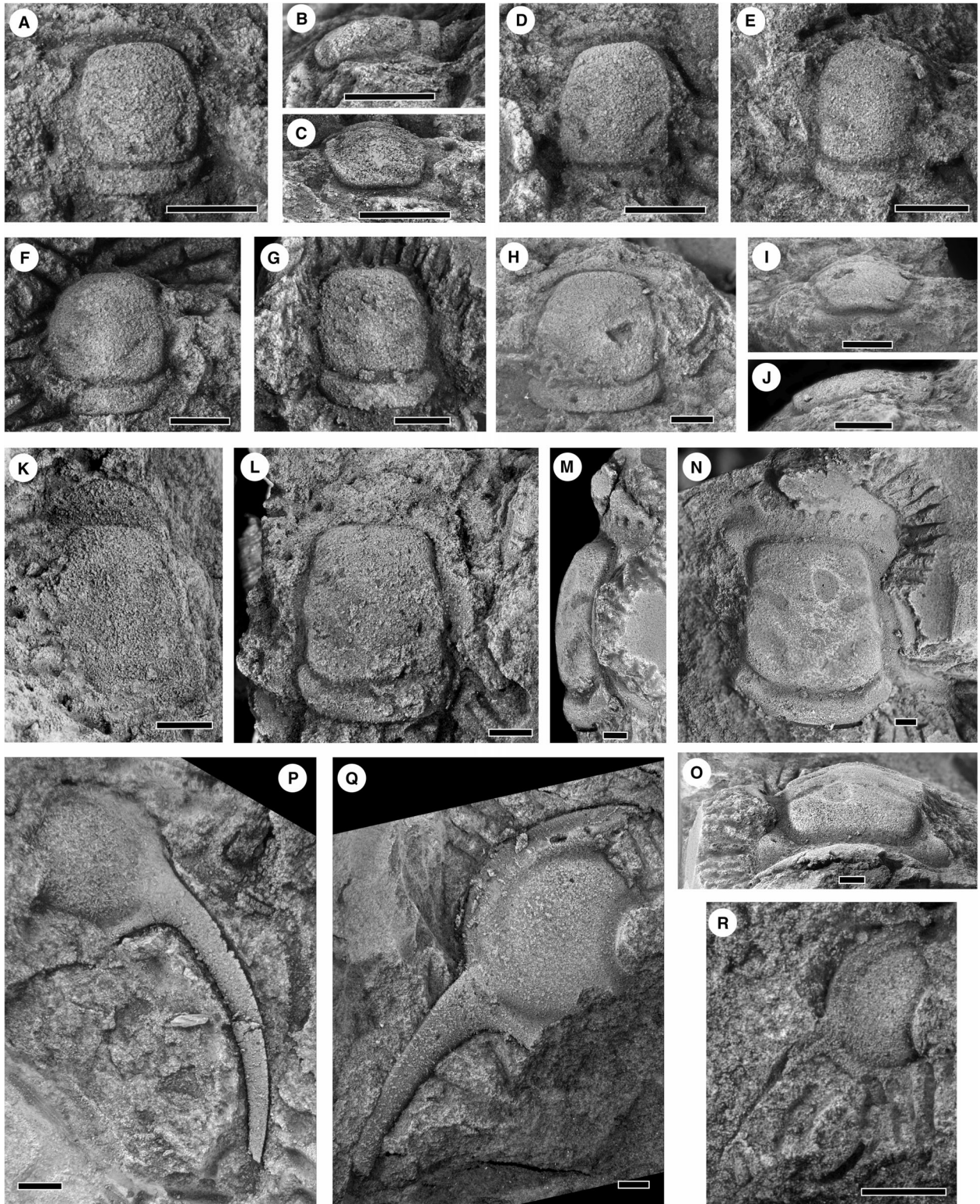


FIG. 36. A–G, *Jiia talowaois* sp. nov. cranidia: A–C, DGSC F1443 in: A, dorsal; B, left lateral; C, anterior view; D, DGSC F1454; E, DGSC F1470; F, DGSC F1455; G, DGSC F1445; H–J, DGSC F1474, *Jiia talowaois*? external mould in: H, dorsal; I, anterior; J, left lateral view. K, DGSC F1724, *Pseudokainella malakaensis*?, cranidium. L–R, *Pseudokainella malakaensis* Stait *et al.*, 1984; L, DGSC F1279, cranidium; M–O, DGSC F1277, cranidium in: M, right lateral; N, dorsal; O, anterior view; P, DGSC F1779, librigena; Q, DGSC F1281, librigena; R, DGSC F1284, librigena. Scale bars represent 2 mm.

Derivation of name. Named for the Talo Wao Formation.

Material. Holotype: DGSC F1443, (Fig. 36A–C), cranidium from APM 53.65 m; Talo Wao Formation, Tarutao Group, Tremadocian.

Paratypes: 7 cranidia from APM 53.65 m (DGSC F1445, F1450, F1454–F1456, F1468, F1470).

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

Description. Cranidium subrectangular and short; width (tr.) across palpebral lobes subequal (95–110%) to cranial length (sag.). Glabella gently anteriorly tapering; glabellar length (sag., including LO) 85–90% cranial length; glabellar width (tr.) at S1 subequal (90–105%) to preoccipital glabellar length (sag.); anterior glabellar margin gently convex or straight (tr.); axial furrows broad and deeply incised, gently curved; S1 posteromedially oblique, variably straight to strongly curved and effaced to deeply incised; S2 short, posteromedially oblique, weakly incised; SO firmly incised with posteromedial bow; LO wider (tr.) than L1 and long (sag.), c. 20% total glabellar length, with constant length sag. and exsag. Narrow (tr.), moderately arcuate palpebral lobes adjacent to broad axial furrows; palpebral lobes moderately long (exsag.), extending from posterior L1 to S2; anterior palpebral tip gently recurved; depressed but centrally gently inflated palpebral area fully encompassed by palpebral lobe and axial furrow. Anterior facial sutures diverge gently and then curve toward convergence at lateral corners of anterior border. Anterior border furrow medially confluent with but less strongly curved than preglabellar furrow; depressed preocular fixigena continuous with lateral preglabellar field; anterior border short (sag., exsag.). Long (exsag.), strap-like posterolateral projections with deep and broad (exsag.) posterior border furrow and inflated posterior border. Entire cranidium finely granulated.

Remarks. This species adheres to Zhou & Zhang's (1978) diagnosis of *Jiia* as having an anteriorly tapering glabella, short anterior branches of the facial sutures, a short and depressed preglabellar field, and a finely granulated surface. It differs from the type species, *J. ampuliformis*, in having a less strongly tapering glabella. S1 and S2 are also not so firmly incised.

The identity of the largest specimen of *J. talowaois*, (DGSC F1474; Fig. 36H–J) is questionable. Its anterior border is angular, and the preglabellar and anterior border furrows are confluent along the entire anterior glabellar margin. Other than this, its morphology is consistent with other specimens of *J. talowaois*. Because the only other two specimens with preserved frontal areas are the two smallest (Fig. 36A–D), it is unclear whether the difference in anterior border is ontogenetic with intermediate stages that have not been preserved or whether DGSC F1474 belongs to a different taxon. The ontogeny of other species of *Jiia* is unknown. Preservation type is unlikely to be the source

of variation. DGSC F1474 is the only external mould in the collection, and the others are internal moulds. Although differences in external and internal contouring can result in some artificial divisions in trilobites (e.g. see Zhu & Peng 2006 on synonymy of *Koldinioidia* and *Eoshumardia*), the lateral corners of the anterior border in the *J. talowaois* type material are too anteriorly placed to have been contained within the more angular border of DGSC F1474.

Occurrence. APM 53.65 m; Talo Wao Formation; Tremadocian.

Genus PSEUDOKAINELLA Harrington, 1938

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

Pseudokainella malakaensis Stait et al., 1984

Figure 36 ?K, L–R

1984 *Pseudokainella malakaensis* Stait et al., pp. 56–59, fig. 3.1, 2, 4–6, 8 (non 3.3, 7 = *Tarutaoia techawani*).

Additional material. 3 cranidia from APM 15.10 m (DGSC F1277, F1279) and ATD S3 0.03 m (F1724). 18 librigenae from APM 0.05 m (DGSC F1275, F1276, CMC IP89002, IP89003, IP89006), 15.10 m (DGSC F1281), 18.00 m (DGSC F1284) and 53.65 m (DGSC F1437) and ATD S3 0.03 m (CMC IP89383, IP89387, IP89396) and float (DGSC F1769, F1771, F1778–F1780, F1785, CMC IP89355).

Remarks. Stait et al. (1984) expressed uncertainty regarding the genus assignment to *Pseudokainella* due to questionable distinction between *Pseudokainella* and *Elkanaspis* Ludvigsen, 1982. *Pseudokainella* and *Elkanaspis* are now considered synonymous (Jell 1985; Jell & Adrain 2002), and the lack of preglabellar field that Harrington (1938) included in the diagnosis of *Pseudokainella* is no longer considered a diagnostic trait under this concept.

The cranidium from Ao Talo Udang ATD S3 0.03 m (Fig. 36K) is much narrower (tr.) than the two cranidia from Ao Phante Malacca figured herein. It is also considerably smaller than the other two specimens; possible ontogenetic differences cannot be recognized based on the limited material presently available. This difference could also be tectonic but there is no clear evidence of such distortion. Alternatively, the specimen from Ao Talo Udang may represent a different species from that known at Ao Phante Malacca. Given this possibility, DGSC F1724 (Fig. 36K) is only tentatively ascribed to *P. malakaensis*.

The *Pseudokainella* pygidial form, known from fully articulated specimens, has four or more segments and is spiny (Harrington & Leanza 1957). The pygidium originally assigned to *Pseudokainella malakaensis* (Stait et al. 1984) is pauci-segmented with a smooth posterior margin. It is herein reassigned to *Tarutaoia techawani*.

Occurrence. APM 15.10 m (questionably 0.05 m)–53.65 m; ATD S3 0.03 m and float; Talo Wao Formation; Tremadocian.

Genus HANIWA Kobayashi, 1933a

Type species. *Haniwa sasanensis* Kobayashi, 1933a; from the Tsinania Zone of the Chosan (= Sosan) area, Korea; Stage 10, Furongian.

Haniwa mucronata Shergold, 1975

Figure 37A–E, ?AA

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

Additional material. 6 cranidia from ATT 5.50 m (DGSC F0810), 22.78 m (DGSC F0467, F0869), 29.17 m (DGSC F1013) and ATTW (DGSC F0401, F0422).

Remarks. When first describing *H. mucronata* from the Chatsworth Limestone, Shergold (1975) gave it a differential diagnosis to distinguish it from other species of *Haniwa* known at the time. The main differential character of *H. mucronata* is its possession of pygidial spines (Shergold 1975). Of the *Haniwa*-type pygidia recovered from the Ao Mo Lae Formation, only DGSC F0902 (Fig. 37AA) is a potential match, and its posterior margin is insufficiently preserved to determine whether it bore spines. However, comparisons of cranidial features led to the reasonably confident assignment of Thai material to *H. mucronata*. Such features include the acutely anteriorly rounded glabella, palpebral lobes extending from SO to the anterolateral glabellar corners, gently anteriorly divergent facial sutures, faint glabellar furrows, and a preglabellar field separating the preglabellar and anterior border furrows. The length (sag.) of the preglabellar field is longer relative to the anterior border than in most other members of *Haniwa* although the range of this ratio is highly susceptible to dorso-ventral flattening and the angle of viewing of the specimen. Additionally, the posterolateral projections are longer (exsag.) and less strap-like than in other species of *Haniwa*. While the relative length of the glabella is similar to that of *Haniwa elongata* Qian in Qian et al., 1985, *H. elongata* lacks a genal spine and well-defined anterior border furrow.

The other species of *Haniwa* found in the Ao Mo Lae Formation, *H. sasanensis*? Kobayashi, 1933a, has a proximally nearly transverse anterior pygidial margin at all stages of development (Park & Choi 2011). The pygidium of *H. mucronata* has a more strongly curved anterior margin. The specimens shown in Figure 37X–Z are representative of the former condition and assigned to *H. sasanensis*?, while that in Figure 37AA has a more strongly curved margin and is tentatively assigned to *H. mucronata*.

Occurrence. ATT 5.50–29.17 m and ATTW; Ao Mo Lae Formation; Furongian, Stage 10.

Haniwa sasanensis? Kobayashi, 1933a

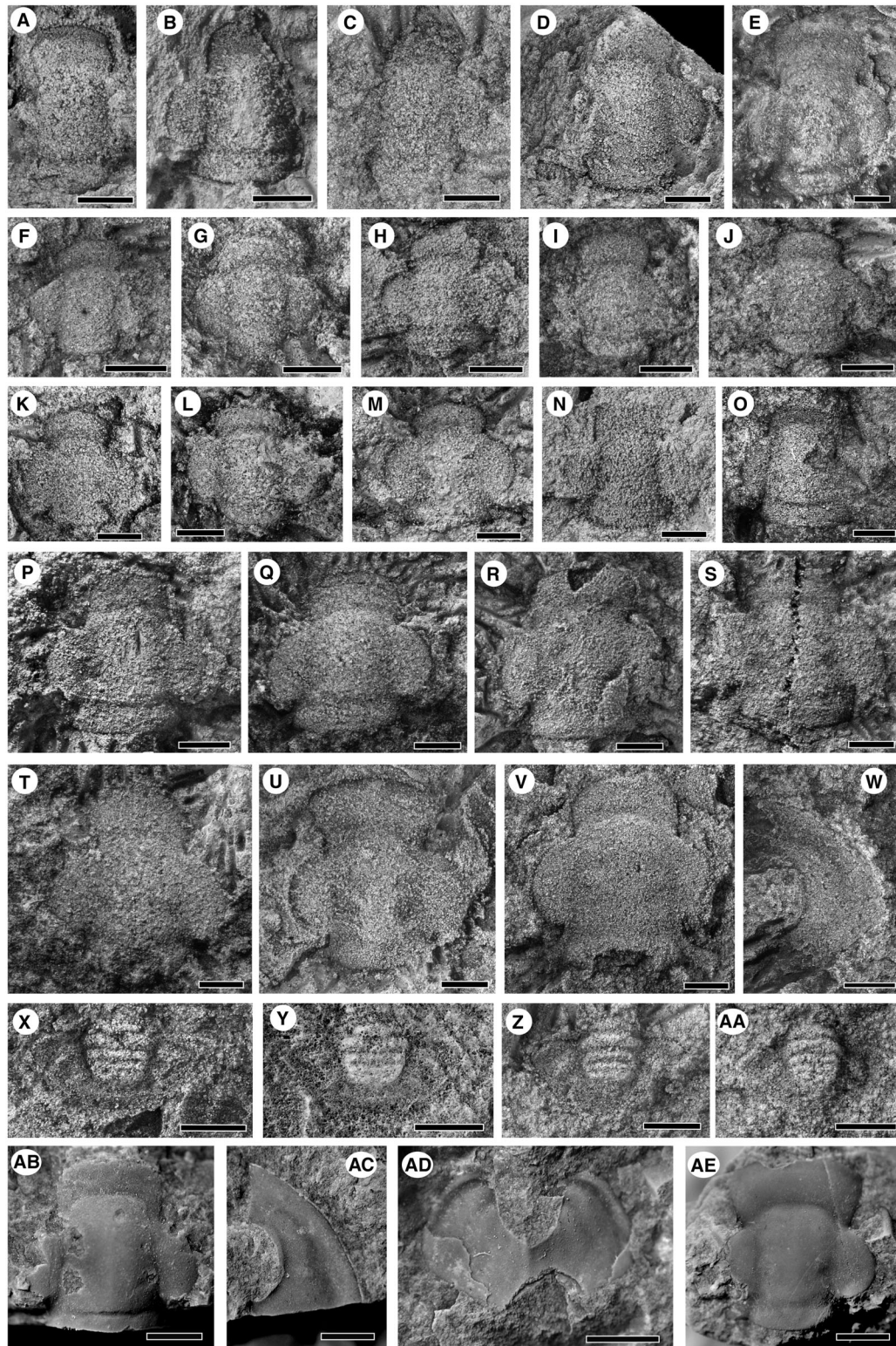
Figure 37F–Z

- ? 1933a *Haniwa sasanensis* Kobayashi, pp. 148–149, pl. 15, figs 1–4 (non fig. 5).
- ? 2007 *Haniwa sasanensis* Kobayashi; Sohn & Choi, p. 310, fig. 6p–s.
- ? 2011 *Haniwa quadrata* Kobayashi; Park & Choi, figs 6, 10, 11.
- ? 2015a *Haniwa quadrata* Kobayashi; Park & Kihm, p. 191, fig. 9.

Material. 34 cranidia from Ao Mo Lae AML 5.81 m (DGSC F0354, F1146, F1176, F1181), ATT 6.65 m (DGSC 0815), 8.60 m (DGSC F0829 external mould), 8.85 m (DGSC F0841, F0845), 22.78 m (DGSC F0464, F0475, F0487, F0493, F0494, F0496, F0499, F0502, F0504 external mould, F0518, F0520, F0525, F0527, F0528, F0857, F0859, F0862, F0873 external mould, F0874 external mould), 22.88 m (DGSC F0900, F0904, F0933, F0934) and 25.34 m (DGSC F0954, F0964) and ATD S2 0.69 m (CMC IP89342). 2 librigenae from AML 5.81 m (DGSC F0614, F1180). 4 pygidia from ATT 22.78 m (DGSC F0469, F0481) and 22.88 m (DGSC F0884, F0893 external mould).

Remarks. When Kobayashi (1933a) first established *Haniwa*, two new species were assigned to the genus: *H. sasanensis* and *H. quadrata*. Based on the lectotypes (Figure 37AB, AE), these two species are readily distinguishable by the anteriorly tapered glabella and parallel anterior facial sutures of the former and the parallel-sided glabella with anteriorly divergent facial sutures of the latter. When Sohn & Choi (2007) described specimens of *Haniwa* from the Taebaeksan Basin, they directly contrasted

FIG. 37. A–E, *Haniwa mucronata* Shergold, 1975, cranidia: A, DGSC F0810; B, DGSC F1013; C, DGSC F1023; D, DGSC F0422; E, DGSC F0401. F–Z, *Haniwa sasanensis*? Kobayashi, 1933a: F, DGSC F0845, cranidium; G, DGSC F0502, cranidium; H, DGSC F0525, cranidium; I, DGSC F0518, cranidium; J, DGSC F0857, cranidium; K, DGSC F0499, cranidium; L, DGSC F0862, cranidium; M, DGSC F0934, cranidium; N, DGSC F0496, cranidium; O, DGSC F0954, cranidium; P, DGSC F1176, cranidium; Q, DGSC F1146, cranidium; R, DGSC F0964, cranidium; S, DGSC F0354, cranidium; T, DGSC F1181, cranidium; U, DGSC F0815, cranidium; V, DGSC F0493, cranidium; W, DGSC F0614, librigena; X, DGSC F0884, pygidium; Y, DGSC F0893, pygidium, external mould; Z, DGSC F0469, pygidium. AA, *Haniwa mucronata*?, DGSC F0902, pygidium. AB–AD, *Haniwa sasanensis*: AB, lectotype, UMUT PA041, cranidium, original of Kobayashi (1933a pl. 15, fig. 2). AC, UMUT PA0422, librigena, original of Kobayashi (1933a pl. 15, fig. 7); AD, UMUT PA0423, pygidium, original of Kobayashi (1933a, pl. 15, fig. 5). AE, *Haniwa quadrata*, lectotype, UMUT PA0424, cranidium, original of Kobayashi (1933a, pl. 15, fig. 7). Scale bars represent 2 mm.



H. sosanensis with other species of *Haniwa* but not with *H. quadrata*. They assigned the specimens in their paper to *H. sosanensis* due to the undifferentiated frontal area, obsolete

palpebral furrows, and nearly effaced glabella. The cranidia (Sohn & Choi 2007, fig. 6p-r) have anteriorly tapering glabellae, but only their figure 6p has parallel or nearly parallel anterior

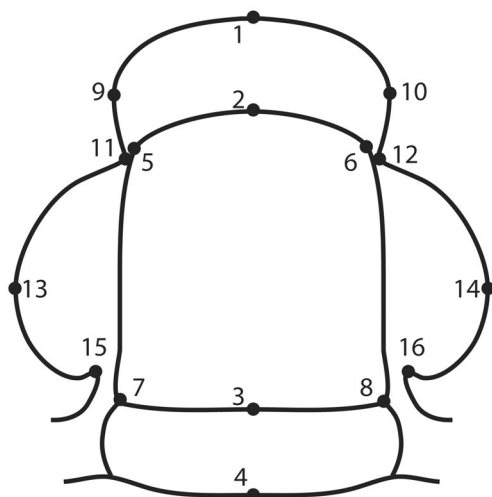


FIG. 38. *Haniwa* landmark scheme.

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

At a minimum, the collection of *Haniwa* from the Ao Mo Lae Formation contains two distinct species: *H. sosanensis*? and *H. mucronata* Shergold, 1975. *Haniwa mucronata* has a clearly differentiated, relatively narrow (tr.) frontal area and a long, strongly tapering and anteriorly curved glabella that readily distinguishes it from *H. sosanensis* and *H. quadrata*. Analysis of the collections herein assigned to *H. sosanensis*? highlights morphological variation that casts doubt on a distinction between *H. sosanensis* and *H. quadrata*. A landmark-based morphometric analysis using 16 landmarks (Fig. 38; data in Wernette *et al.* 2023) and 23 specimens (16 specimens of *H. sosanensis* from Tarutao, the *H. sosanensis* and *H. quadrata* lectotypes from Kobayashi 1933a and five cranidia of *H. quadrata* from Park & Choi 2011), results in a relatively even distribution and undifferentiated grouping of all specimens of *H. sosanensis*? from Tarutao (Fig. 39). Within this group some specimens have strongly divergent anterior sutures (e.g. Fig. 37L, R, U) while others have parallel-sided or even anteriorly convergent facial sutures (e.g. Fig. 37N, P, V), character states considered diagnostic of *H. sosanensis* and *H. quadrata* respectively. Of those that

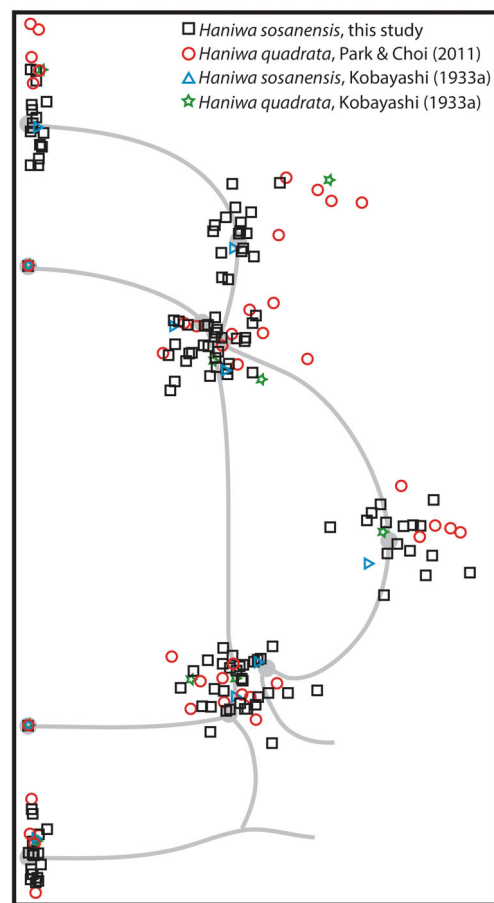


FIG. 39. *Haniwa* landmark distribution using Bookstein coordinates (BC) with landmarks 2 and 3 as base points.

have anteriorly divergent sutures, some have parallel-sided glabellae (e.g. Fig. 37U), thus adhering to Kobayashi's (1933a) diagnosis of *H. quadrata*, while others have anteriorly convergent glabellae (e.g. Fig. 37L), thus representing a mix of characters used to differentiate *H. quadrata* and *H. sosanensis*. Scores for the Thai specimens are plotted against the lectotypes of *H. quadrata* and *H. sosanensis* (Fig. 40) for the first two relative warps, and scores for the lectotype of *H. sosanensis* fall to one side but are very close to the cloud of points representing Thai specimens, while scores for the lectotype of *H. quadrata* fall on the other side but also close to this cloud. The *H. quadrata* and *H. sosanensis* lectotypes, as well as the Thai specimens, are differentiated only on relative warp 1, which accounts for 30.5% of the variance. Relative warp 1 primarily encapsulates variation (Fig. 41) in the relative length of the frontal area and the lateral position of the cranidium's anterolateral corner. The holotype of *H. quadrata* has a relatively short glabella and long frontal area compared with the material from Thailand.

Specimens assigned to *H. quadrata* from the Taebaeksan Basin further blur the differentiation between *H. quadrata* and *H. sosanensis*. Five of the largest cranidia from Park & Choi's (2011) ontogenetic analysis of *H. quadrata* in the

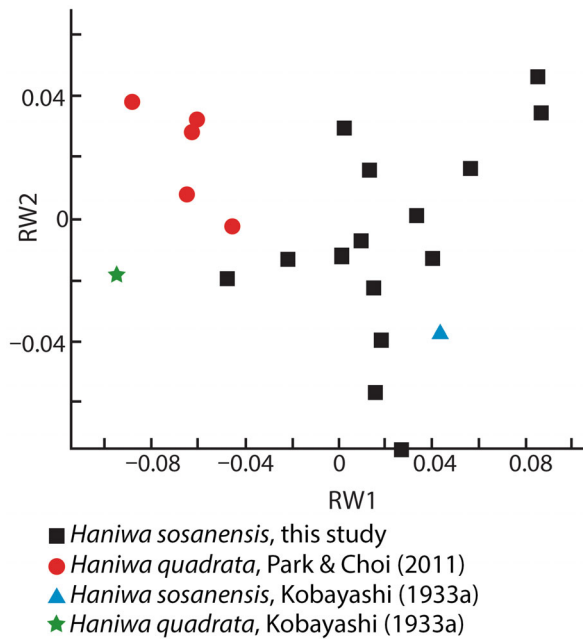


FIG. 40. Relative warps (RW) 1 and 2 for principal component analysis of the landmark distribution in Figure 39. Relative warps 1 and 2 account for 30.49% and 15.48% of the variance, respectively.

Taebaeksan Basin were included in the landmark-based morphometric analysis via the digitization of their published images. These specimens, on average, fall closer to the *H. quadrata* holotype than the Thai material on relative warp 1 (Figs 39, 41). Their intermediate morphology applies to the anterolateral placement of the anterior border corners, and relative lengths of the glabella and frontal area. Elsewhere there is little differentiation between these and the Thai specimens.

The morphometric analysis thus indicates that the extent of anterior divergence of the facial sutures is one of the most useful characteristics by which to differentiate *H. sosanensis* from *H. quadrata*, as used by Park & Choi (2011) and Park & Kihm (2015a), but that divergence is not, by itself, especially useful. The length (sag.) of the frontal area relative to the length of the glabella is more useful. The anterior tapering of the glabella was considered important in the original diagnoses (Kobayashi 1933a) but this trait is subject to considerable intra-species variation, which makes it an unreliable character for systematic differentiation. This analysis supports Park & Choi's (2011) assignment of specimens from the Taebaeksan Basin to *H. quadrata* rather than to *H. sosanensis*, but also shows that the Taebaek material spans a morphological spectrum between type specimens of these two species. These results suggest, but are not sufficiently strong to confirm, that *H. sosanensis* and *H. quadrata* are synonymous, with morphotype occurrence showing some component of geographic or stratigraphic variation. One additional source of variation within this population that is not captured by the landmark-based analysis is that the facial sutures may vary in the position of their intersection with the anterior border. Typically, the sutures

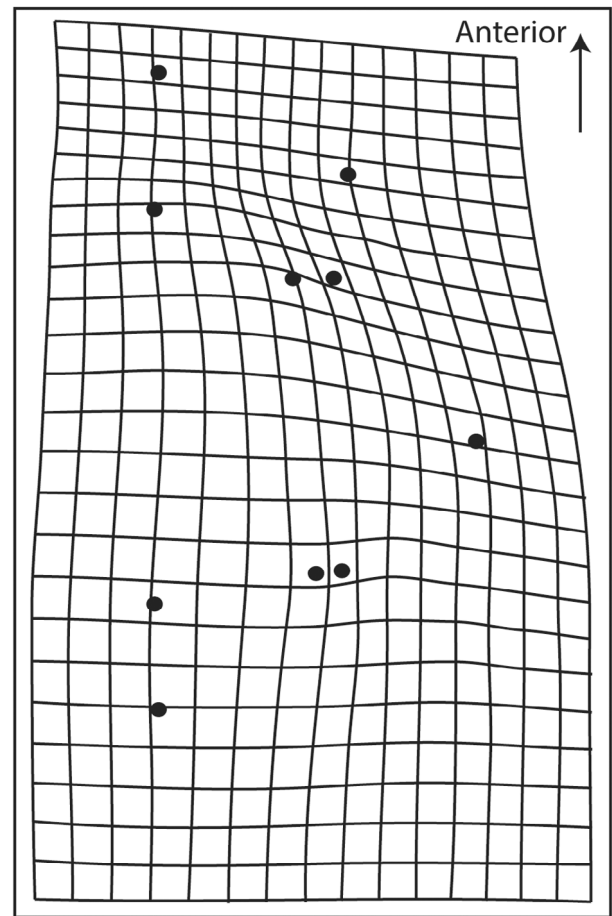


FIG. 41. Warp grid for morphological variance described by relative warp (W) 1 (Fig. 40).

connect dorsomedially posteriorly to the anterior border, thus leaving the entire border intact on the yoked librigena. Rarely (e.g. Fig. 37Q) the sutures may connect medially in such a way that a small portion of the anterior border is included on the cranidium. This variation in the 'retraction' of the facial suture is similar to that documented in the description of *Dikelocephalus minnestoensis* Owen, 1852 (see Hughes 1994).

If the pygidium initially assigned to *H. sosanensis*? is correctly associated, then the pygidium may offer reliable characters for differentiating *H. quadrata* and *H. sosanensis*, given that it differs in curvature, incision and distribution of pleural furrows from that which Park & Choi (2011) attributed to *H. quadrata*. In outline, axial length and furrow expression, pygidia from Tarutao (Fig. 37X–Z) resemble those of *H. quadrata* more than *H. sosanensis*. Allometric repatterning may account for differences between the Thai material and the collection of *H. quadrata* from the Taebaeksan Basin. Thai specimen DGSC F0469 (Fig. 37Z) is 2.56 mm in pygidial length (sag.) and yet it bears closer resemblance in outline and furrow expression to Park & Choi's (2011, fig. 11j) small specimen, which measures c. 0.5 mm in pygidial length, than to their fig. 11r, which is more similar in size. The largest Thai pygidium (DGSC F0902; Fig. 37AA) is 3.5 mm long (sag.). This pygidium is c. 75% larger

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

In summary, although the Thai material more closely resembles *H. sosanensis* than *H. quadrata*, the assignment to *H. sosanensis* is tentative due to the possible continuity of variation between the two species, including between the Thai and Taebaek material, as well as the differences between the available pygidium and previously known *H. sosanensis* pygidia. Furthermore, assigning this material to *H. sosanensis* suggests some stratigraphic discrepancy because that species is known from the Jiangshanian while other Ao Mo Lae taxa (e.g. *Eosaukia*) suggest Cambrian Stage 10 for the Thai form.

Occurrence. AML 5.81 m, ATT 6.65–25.34 m and ATD S2 0.69 m; Ao Mo Lae Formation; Furongian, Stage 10.

Superfamily DIKELOCEPHALOIDEA Miller, 1889

Family DIKELOCEPHALIDAE Miller, 1889

Remarks. The dikelocephalid trilobites discussed herein are those historically assigned to Saukiidae Ulrich & Resser, 1930, and still commonly referred to as ‘saukiid’ trilobites. The taxonomic ranking or validity of the saukiid grouping has long been controversial. Saukiinae was initially established as a subfamily within Dikelocephalidae (Ulrich & Resser 1930). Raasch (1951) elevated Saukiinae to family level, arguing for a closer link to Ptychaspidae Raymond, 1924 than to other dikelocephalids. This view quickly became widely accepted (e.g. Hupé 1953; Lochman 1956). Many new genera have since been added to Saukiidae, with the family encompassing more than 30 genera by the end of the 20th century (Jell & Adrain 2002). However, its taxonomic position has not been stable, with Kobayashi (1960), Longacre (1970), Stitt (1971, 1977) and Taylor & Halley (1974) relegating it to a subfamily of Ptychaspidae, and Ludvigsen & Westrop (1983) retaining the family designation but reassigning it to Dikelocephaloidea. Ludvigsen *et al.* (1989), due to the inability to establish synapomorphic characters for Saukiidae, later abandoned the use of this grouping, suggesting that it is a paraphyletic junior synonym of Dikelocephalidae. This scheme has been widely accepted by Laurentian and Gondwanan trilobite workers (e.g. Adrain 2011; Lee & Choi 2011), although some authors continue to use Saukiidae as a family-level designation within Dikelocephaloidea (e.g. Park & Kihm 2015a; Shergold *et al.* 2007). Herein we follow the scheme assigning the saukiid trilobites to Dikelocephalidae but without strong opinion or new evidence as to the existence of ‘Saukiidae’ even as a paraphyletic group. It contains trilobites with a broadly rectangular or trapezoidal glabella with SO and S1 entire and a slight bulge in L1 just posterior to where S1 meets the axial furrow, S1 being distinctive in its abaxial posteromedial course becoming transverse axially, and with crescentic

palpebral lobes located close to the glabella and defined by a firmly and evenly incised palpebral furrow. Saukiids share these characteristics with other dikelocephalids, but are distinguished from them by having a narrow cephalic doublure, rather than the extended doublure of dikelocephalids such as in *Briscoia*, *Elkia*, *Osceolia*, *Walcottaspis* and *Dikelocephalus*. If the extended doublure is a derived feature, saukiids may be a paraphyletic sister group to a derived clade of dikelocephalids defined by this character state (Westrop 1986). Investigation of dikelocephalid phylogenetics is currently in progress (e.g. Srivastava & Hughes 2023), but is beyond the scope of this study.

Genus CAZNAIA Shergold, 1975

Type species. *Caznaia squamosa* Shergold, 1975; from the pre-Payntonian B interval at Black Mountain (by original designation); Stage 10, Furongian.

Remarks. Shergold (1975) provided many distinguishing cranial characters when first diagnosing *Caznaia*. The glabella is anteriorly tapering with curved or ‘sinuous’ axial furrows; this sinuosity manifests as a slight lateral expansion at S1. The palpebral lobes are centred between S1 and S2. The posterolateral projections are long and triangular. The frontal area is short, but this is in comparison with ‘saukiids’ such as *Anderssonella* Kobayashi, 1936, to which Shergold (1975) suggested *Caznaia* is most related. This frontal area is convex and differentiated into a preglabellar field and anterior border abaxially, but medially they are differentiable only on testaceous specimens. Additionally, Shergold (1975) described the genus as having anteriorly divergent facial sutures and small eyes. The value of anteriorly divergent facial sutures as a diagnostic character is questionable given that both *C. squamosa* Shergold, 1975, and *C. sectarix* Shergold, 1975, the two species on which the genus was established, possess nearly parallel to convergent anterior suture branches. The line drawings for both species (Shergold 1975, p. 129, figs 48, 49) show a reconstruction with convergent sutures, and the description for the type species, *C. squamosa*, states that the ‘facial sutures strike directly forwards ... but curve slightly abaxially before reaching the anterior margin.’ This description suggests that the divergent orientation of the facial sutures is very slight or inconsistent, and that the character should not be strongly considered in the diagnosis of *Caznaia*. Small eye size is also a character of doubtful taxonomic significance: both the Thai collections herein and the Australian collections on which the genus was first described (Shergold 1975) show variability in eye size, from only weakly protruding from the fixigena to strongly curved. More reliable characters on which to base *Caznaia* are the shape of the glabella, the position of the palpebral lobes, the convex preglabellar field, and the peculiar adaxial lack of differentiation of the anterior border and preglabellar field. The latter two characters are comparable to the features differentiating *Hoytasps* Ludvigsen & Westrop, 1983 and *Prosaikia* Ulrich & Resser, 1933. *Caznaia* and *Hoytasps* are otherwise dissimilar beyond the characters common to most ‘saukiids’, which suggests that an inflated preglabellar field may have arisen independently in multiple

'saukiid' lineages. The medial effacement of the anterior border seems to be the direct result of this inflation.

Caznaia imsamuti sp. nov.

Figures 42, 43A–O

LSID. <https://zoobank.org/NomenclaturalActs/3ACD4B83-71D8-437B-AC1F-06AC20CA94A4>

Derivation of name. Named for Mr Suvapak Imsamut, Thai Department of Mineral Resources, in honour of his work on the stratigraphy of the Tarutao Group.

Material. Holotype: DGSC F0748 (Fig. 43D–F), cranidium from LHN horizon 2.85 m; Ao Mo Lae Formation; Furongian, Stage 10.

Paratypes: 4 cranidia from LHN 2.85 m (DGSC F0594, F0743 external mould, F0756 and F0757).

Other material: 14 cranidia from LHN 1.54 m (DGSC F0733), 2.85 m (DGSC F0735, F0738, F0739 external mould, F0740, F0742, F0744, F0755, CMC IP83131, IP83133, IP83134 external mould, IP83167, IP83168) and 3.69 m (DGSC F0760).

Diagnosis. Trapezoidal cranidium with long, anteriorly tapering glabella, moderately long frontal area nearly entirely occupied by convex preglabellar field, strongly incised S1 that is medially disconnected or strongly shallowed, divergent anterior facial sutures, effaced anterior border furrow, and short, medially situated palpebral lobes.

Description. Trapezoidal cranidium with width (tr.) across palpebral lobes 85–100% of cranidial length (sag.); frontal area occupies 10–15% of cranidial length (sag.) and LO occupies c. 15% of cranidial length (sag.). Glabella convex and anteriorly tapering with curved axial furrows forming convex outline; anterior glabellar margin straight (tr.) to gently curved; glabellar width (tr.) at L1 60–65% of cranidial width across palpebral lobes; S1 firmly incised, gently posteriorly bowed, medially discontinuous or shallow and nearly discontinuous; S2 weakly incised and straight, posteromedially oblique. SO posteriorly bowed, subconcentric with S1; LO medially lengthening (sag.) and subequal in width (tr.) to L1. Fixigena narrow. Palpebral lobes weakly curved, longitudinally

asymmetric with greatest curvature in posterior portion; palpebral lobes moderately long (exsag.), 45–50% of glabellar length (sag.) and midpoint positioned opposite S2. Anterior facial sutures gently divergent and curved around frontal area; frontal area unequally divided with convex preglabellar field occupying most preglabellar length (sag.) with only narrow, brim-like anterior border; anterior border furrow faint. Posterior suture branches straight and diverge c. 45° (from exsag. axis), encompassing triangular posterolateral projection; posterior border furrow gently incised but distinct; posterior border short; posterior margin straight (tr.).

Remarks. *Caznaia imsamuti* has narrower fixigenae than either *C. squamosa* Shergold, 1975, or *C. sectarix* Shergold, 1975; the fixigenae are more comparable with those of *Caznaia coreaensis* Park & Kihm, 2015a. The anterior border is reduced to only a thin brim as in mature specimens of *C. coreaensis* (Park & Kihm 2015a). As in all species of *Caznaia*, the anterior border is differentiated from the preglabellar field only abaxially. The short, posteriorly set palpebral lobes are similar to those of *C. squamosa* and *C. coreaensis*. Of the known species of *Caznaia*, *C. imsamuti* is most similar to *C. coreaensis*. Unlike *C. coreaensis*, no occipital spine is known at any holaspis stage, the occipital ring is medially inflated but there is no evidence for a node or the base of a broken spine. *Caznaia coreaensis* has a relatively wider glabella than *C. imsamuti*, although this trait exhibits intraspecific variation in both species. The relatively small holotype of *C. imsamuti* has a morphology that is intermediate in the total variation found in the species. The greatest variation in glabellar width occurs in the middle size range, and largest specimens appear to consistently possess a narrower glabella. The glabella of *C. coreaensis* becomes relatively broader, particularly across the anterior lobe, in later holaspis stages. In all known ontogenetic stages, *C. coreaensis* has a relatively short S1 that is distinctly medially disconnected; this furrow deepens in later ontogenetic stages but does not become medially connected. *Caznaia imsamuti* has a long, broad and deep S1 that is medially connected in some specimens but disconnected or significantly shallowing in most. All other species of *Caznaia* vary in the extent to which this furrow is expressed medially. No associated pygidium is known, but cranidial differences are sufficiently pronounced to merit a new species.

Occurrence. LHN 1.54–3.69 m; Ao Mo Lae Formation; Furongian, Stage 10.



FIG. 42. *Caznaia imsamuti* sp. nov. line drawing.

Genus ANDERSSONELLA Kobayashi, 1936

Type species. *Ptychaspis (Anderssonia) jengtienensis* Sun, 1924; from the Shakuntal Limestone of Fengtien, northern China; Stage 10, Furongian.

Remarks. Following Kobayashi (1936), *Anderssonella* was made a separate genus from *Ptychaspis* and comprises those species with convex frontal areas and palpebral lobes that are exceptionally large (tr. and exsag.) for 'saukiid' and non-saukiid dikelecephalids alike. The large palpebral lobes are an important trait that

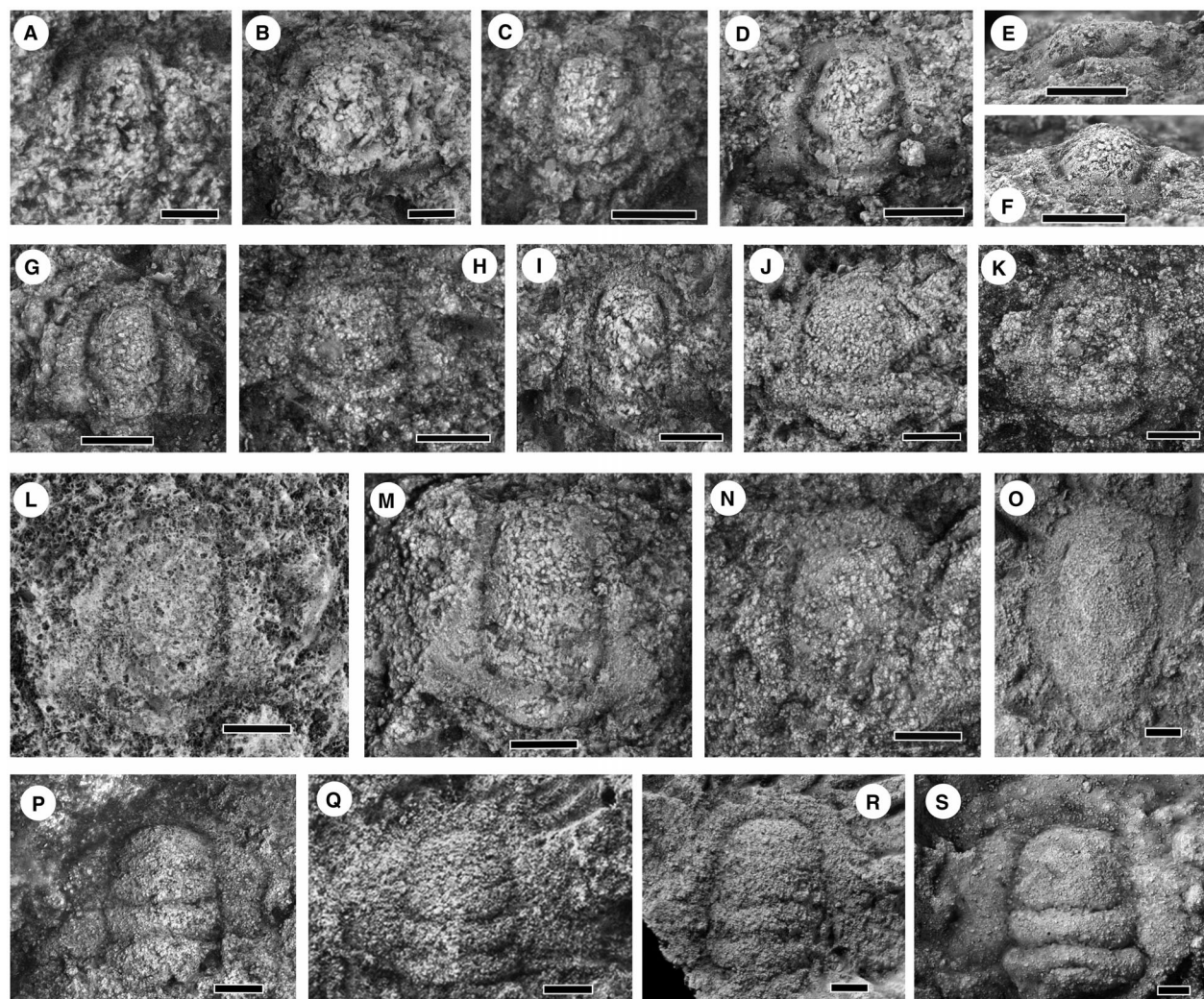


FIG. 43. A–O, *Caznaia imsamuti* sp. nov. cranidia: A, DGSC F0756; B, DGSC F0594; C, DGSC F0757; D–F, DGSC F0748, holotype in: D, dorsal; E, left lateral; F, anterior view; G, DGSC F0755; H, DGSC F0742; I, DGSC F0735; J, DGSC F0738; K, DGSC F0733; L, DGSC F0743, external mould; M, DGSC F0744; N, DGSC F0740; O, DGSC F0760. P–S, *Anderssonella undulata* sp. nov. cranidia: P, DGSC F0392; Q, DGSC F1103; R, DGSC F1133; S, DGSC F0377, holotype. Scale bars represent 1 mm.

initially caused species later assigned to *Anderssonella* to be grouped with *Ptychaspis*. Shergold (1975) extended the diagnosis to include features differentiating *Anderssonella* from similar genera such as *Prosaugia*, including the anteriorly tapered glabella and adaxial curvature of the anterior suture branches. As suggested by Shergold (1975), *Anderssonella* is here grouped with ‘saukiid’ trilobites.

Anderssonella undulata sp. nov.

Figures 43P–S, 44

LSID. <https://zoobank.org/NomenclaturalActs/58D8A64E-0505-49A2-BAC3-BD256D8B6C48>

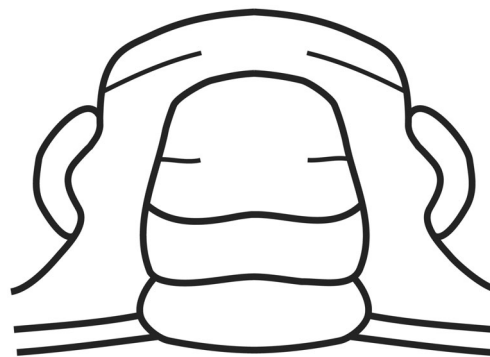


FIG. 44. *Anderssonella undulata* sp. nov. line drawing.

Derivation of name. Latin for wavy, in reference to the wavy or undulating occipital furrow.

Material. Holotype: DGSC F0377, (Fig. 43S), cranidium from ATTW; Ao Mo Lae Formation, Tarutao Group; Ko Tarutao, Thailand; Furongian, Stage 10.

Paratypes: 3 cranidia from ATTW (DGSC F0392) and AML 5.81 m (DGSC F1103, F1133).

Other material: 3 cranidia from ATT h1 (DGSC F0458), AML 5.17 m (DGSC F1070) and 5.81 m (DGSC F0340).

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

Description. Trapezoidal cranidium with width (tr.) across palpebral lobes *c.* 1.5-fold cranial length (sag.). Glabella gently anteriorly tapering with widest point at S1; anterior glabellar margin gently curved; glabellar width (tr.) at S1 *c.* 50% of cranial width across palpebral lobes; S1 firmly incised and undulated or recurved in shape with lateral portion oriented posteromedially and medial portion continuous, bending anteriorly; S2 weakly incised and straight, gently posteromedially oblique. SO subparallel or more strongly undulating than S1; LO medially lengthened (sag.) and wider than S1. Fixigena broad with interpalpebral width 1.8–2-fold glabellar width across L2 (tr.). Palpebral lobes moderately long (exsag.), 25–30% cranial length (sag.) and midpoint positioned opposite L2. Anterior facial sutures moderately convergent. Frontal area unequally divided with convex preglabellar field occupying most of frontal area (sag.).

Remarks. This species is known only from cranidia. A key feature of the *Anderssonella* cranidium is that the frontal area is clearly divided into an inflated preglabellar field and an even more inflated anterior border. In the type species, *A. jengtienensis*, the preglabellar field is longer (sag.) than the anterior border, while the division is more equal in *A. tani* (Sun, 1924) and *A. beauchampi* Shergold, 1975. The frontal area of *A. undulata* is poorly preserved with the anterior border being visible only in the holotype (Fig. 43S). A faint trace of it may be seen in Figure 43P, although differentiation of the mould and matrix makes this unclear. Based on the available material, it seems that the division of the frontal area is variable, with the type specimen having a longer (sag.) anterior border and shorter preglabellar field relative to other specimens, which have longer preglabellar fields. Kobayashi (1936) described *Anderssonella* as having large (tr. and exsag.) palpebral lobes. It should be noted that the palpebral areas are not especially long on *A. undulata* or any other species of *Anderssonella*, but rather the lobes themselves are markedly wide. *Anderssonella undulata* is readily distinguishable from other species in this genus by the undulating or recurved shapes of both S1 and SO, from which is derived its name. This curvature is best developed in larger specimens.

Occurrence. ATTW, ATT h1 and AML 5.17 m, 5.81 m. Ao Mo Lae Formation; Furongian, Stage 10.

Genus EOSAUKIA Lu, 1954

Type species. *Eosaukia latilimbata* Lu, 1954; from the Sandu Formation, Guizhou, China; Stage 10, Furongian.

Remarks. Since *Eosaukia buravasi* Kobayashi, 1957, was described from Ko Tarutao, several additional species of *Eosaukia* have been reported. The genus now includes *E. latilimbata*, *E. angustilimbata* (Qian, 1986), *E. acuta* (Kuo & Duan in Kuo et al., 1982), *E. bella* (Walcott, 1906), *E. rectangulata* Lu & Zhou, 1990, *E. walcotti* (Mansuy, 1915) and *E. micropora* (Qian in Qian et al., 1985). Some of these species have alternatively been assigned to *Calvinella* Walcott, 1914 (e.g. *E. micropora* by Qian et al. 1985), to *Mictosaukia* Shergold, 1975 (e.g. *E. walcotti* by Zhou & Zhang 1984), or to another 'saukiid' genus lacking a preglabellar field. As more species of *Eosaukia* have been discovered and the cranidia associated with librigenae and pygidia, it has become increasingly clear that it is a well-constrained genus with diagnosable cranidial, librigenal and pygidial characters. Lee & Choi (2011) offered a thorough emended genus diagnosis. Among other characters they cited the strongly convex cephalon, abaxially well-defined and anterolaterally oriented anterior border furrow, three pairs of well-defined glabellar furrows with S3 anteromedially deflected, and moderately short palpebral lobes well-separated from the axial furrows. The absence of a preglabellar field and the anterolateral orientation of the abaxial portion of the anterior border furrow are especially important in recognizing *Eosaukia*. The librigena has a vincular structure of ridges and furrows on the doublure (Kobayashi 1957; Lee & Choi 2011). This character may be only weakly expressed in some *Eosaukia* (e.g. *E. micropora*) but, when present, it is considered diagnostic of this genus (Lee & Choi 2011). The pauci-segmented, micropygous pygidium with a rim-like border is also considered a defining character of *Eosaukia*.

Eosaukia buravasi Kobayashi, 1957

Figures 45–50

- 1957 '*Eosaukia*' *buravasi* Kobayashi, p. 376, pl. 5 figs 1–6, 10, 14–20, ?7–9, ?13.
- 1988 '*Eosaukia*' *buravasi* Kobayashi; Shergold et al., p. 310, figs 40–X.
- ? 2007 *Ptychaspis?* sp. aff. *P. cacus* (Walcott, 1905); Shergold et al., p. 65, fig. 38.
- 2021 *Eosaukia buravasi* Kobayashi; Wernette et al., p. 16, figs 11–12.
- 2022 *Eosaukia buravasi* Kobayashi; Hughes et al., p. 64, fig 10a–l.

Additional material. 230 cranidia from AML 3.62 m (CMC IP88941), 4.71 m (DGSC F0334–F0336, F1045, F1047), 5.17 m (F0575 external mould, F1048, F1053, F1055–F1058, F1061, F1067, F1068, F1071, F1074, F1076, F1078, F1080, F1081, F1083, F1085, CMC IP88946, IP88947), 5.81 m (DGSC F0345, F0349, F0605 external mould, F0608, F0634, F0635, F1091, F1096, F1097, F1098, F1099 external mould, F1104, F1105, F1107, F1122, F1124, F1126, F1127, F1128, F1135, F1138, F1142, F1143, F1148 external

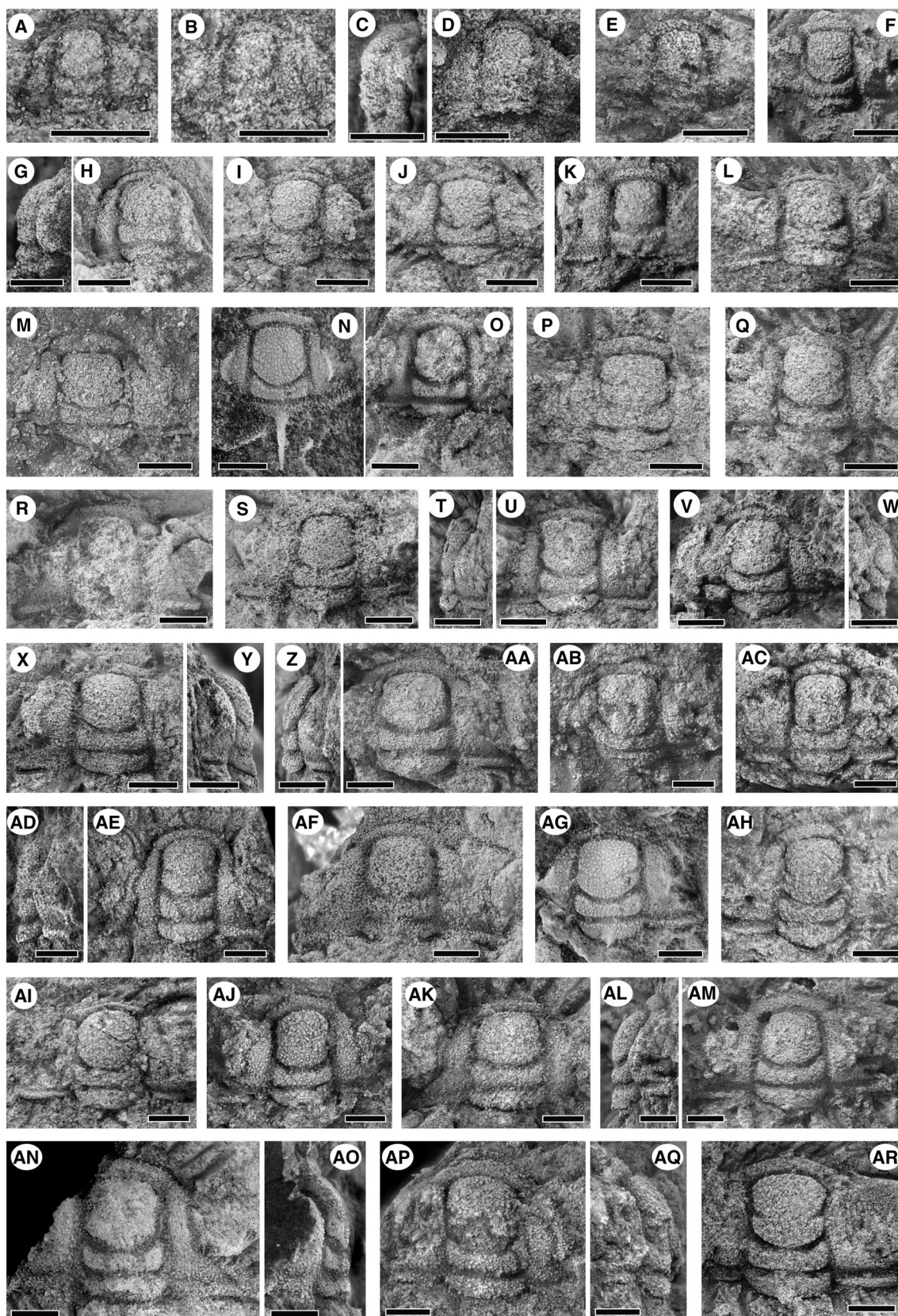


FIG. 45. *Eosaukia buravasi* Kobayashi, 1957. First of four figures of *E. buravasi* cranidia arranged in increasing size order. A, DGSC F0751. B, DGSC F0747. C–D, DGSC F0969 in: C, right lateral; D, dorsal view. E, DGSC F1174. F, DGSC F1206. G–H, DGSC F0977 in: G, right lateral; H, dorsal view. I, DGSC F1173. J, DGSC F1105. K, DGSC F0765. L, DGSC F1104. M, DGSC F0446. N–O, DGSC F0983: N, external; O, internal mould. P, DGSC F1149. Q, DGSC F1127. R, DGSC F0967. S, DGSC F0877. T–U, DGSC F0959 in: T, right lateral; U, dorsal view. V–W, DGSC F1055 in: V, dorsal; W, left lateral view. X–Y, DGSC F1047 in: X, dorsal; Y, left lateral view. Z–AA, DGSC F1009 in: Z, right lateral; AA, dorsal view. AB, DGSC F0450. AC, DGSC F0399. AD–AE, DGSC F1755 in: AD, right lateral; AE, dorsal view. AF, DGSC F0855. AG, DGSC F1014, external mould. AH, DGSC F0410. AI, DGSC F1182. AJ, DGSC F1738. AK, DGSC F1022. AL–AM, DGSC F1254 in: AL, dorsal; AM, right lateral view. AN–AO, DGSC F1037 in: AN, dorsal; AO, left lateral view. AP–AQ, DGSC F1765 in: AP, dorsal; AQ, left lateral view. AR, DGSC F1142. Scale bars represent 2 mm.

mould, F1149–F1152, F1156–F1158, F1168 external mould, F1173–F1175, F1177–F1179, F1182, F1185, F1186, CMC IP83140, IP88957–IP88959, IP88961, IP88962, IP88972), 5.84 m (DGSC F0366, F0369, F1196, CMC IP88977), 6.01 m (CMC IP83155, IP88985, DGSC F1206), AML h1 (DGSC F1208, CMC IP88988, IP88990), AML h2 (DGSC F0623–0625, CMC IP83166 external mould, IP83167, IP83169, IP87608, IP87609, F1210, F1216, F1217, F1219–F1221, F1224, F1228, F1229, F1231 external mould, F1238–F1242), AML h3 (DGSC F0556, F0557), AML h4 (DGSC F1247, F1248 external mould, F1250–F1257, F1265–F1267, F1269, F1270, CMC IP88996, IP88997), AML h5 (DGSC F1272), ATD S1 7.00 m (DGSC F1540, CMC IP89273), S2 0.52 m (DGSC F1751, F1755, F1756, F1757, CMC IP89314, IP89319), S2 0.69 m (CMC IP89326 external mould, DGSC F1765, F0787), S2 14.29 (CMC IP89347), S2 14.50 m (CMC IP89349, IP89350 external mould), ATD S2 h1 (DGSC F0801, F1738), ATT 0.95 m (DGSC F0804), 1.10 m (DGSC F0806), 5.50 m (DGSC F0811, F0812, CMC IP88919), 8.85 m (DGSC F0850), 22.78 m (DGSC F0476, F0477, F0479 external mould, F0491, F0495, F0501, F0505, F0533, F0524, F0855, F0877), 22.88 m (DGSC F0535, F0536, F0541), 23.89 m (DGSC F0939), 25.34 m (DGSC F0955, F0956, F0959, F0961, F0967), 28.37 m (DGSC F0969, F0970, F0972, F0974, F0977, CMC IP88930–IP88932), 29.17 m (CMC IP88935, F0983 internal and external moulds, DGSC F0984, F0987, F1006, F1009, F1014 external mould, F1017, F1022, F1208, F1029, F1031, F1037), ATT h1 (CMC IP88915), ATT h2 (CMC IP88916), ATTw (DGSC F0376, F0379 external mould, F0390, F0393, F0394, F0399, F0405, F0410, F0412, F0414, F0416, F0424, F0425, F0427–F0430, F0438, F0443, F0445, F0446, F0450–F0452, F0454, F0456, F0457, F0761, F0763–F0768, F0769 external mould, F0771 external mould, F0772–F0775, F0778, F0780, F0784, F0786, F0789) and LHN 2.85 m (DGSC F0747, F0751, CMC IP83169). 41 Librigena from AML 3.62 m (DGSC F1042), 3.72 m (DGSC F0573), 5.17 m (DGSC F1049, F1051, F1054, F1064 external mould), 5.81 m (DGSC F0600, F1087 external mould, F1088 external mould, F1093, F1118, F1134, F1154, F1155 external mould, F1169, F1183 external mould, F1188), 5.84 m (DGSC F0364 external mould, F1190, F1193, F1195 external mould, CMC IP88974, IP88979 external mould), 6.01 m (CMC IP83157, IP83158 external mould), AML h2 (DGSC F0627, F0628, F1223, F1225, F1226, F1237 external mould, CMC IP88994 external mould), AML h4 (DGSC F1264), AML h5 (CMC IP89000) and ATTw (DGSC F0396, F0397, F0409, F0455, F782, F0785 external mould, F0791 external mould). 47 pygidia from AML 5.17 m (DGSC F1050, F1059, F1060, F1062, F1069, F1073, F1077, F1079 external mould, CMC IP88943, IP88948, IP88949 external mould), 5.81 m (DGSC F0347, F0357, F0432, F0578 external mould, F1109, F1141, F1145, F1164, CMC IP88964, IP88971), 5.84 m (DGSC F0367, F1197,

CMC IP88981 external mould), 6.01 m (DGSC F1202 external mould, F1203), AML h1 (CMC IP88992), AML h2 (DGSC F1211, F1214), AML h4 (CMC IP88999), ATT 6.65 m (CMC IP88922), 8.20 (DGSC F0822), 22.78 m (DGSC F0508 external mould, DGSC F0867, F0868, F0870 external mould), 25.34 m (DGSC F0957), 29.17 m (DGSC F0985, F0993 external mould, F1012, F1032, F1034 external mould, F1039), ATT h2 (DGSC F0797), ATTw (DGSC F0432) and ATD S2 0.52 m (DGSC F1758, F1759).

Remarks. *Eosaukia buravasi* is the most abundant and widely distributed species in the Tarutao Group. It is also the only species currently known to occur elsewhere on Sibumasu, having also been found in the Molohein Group of Myanmar (Wernette *et al.* 2021). Wernette *et al.* (2021) presented a landmark-based geometric morphometric analysis of *E. buravasi* using 120 of the Thai specimens included herein as well as two specimens from the southern part of Shan State. The undifferentiated distribution of scores, particularly on the first two relative warps (Wernette *et al.* 2021, fig. 14), indicated that all of the specimens herein assigned to *E. buravasi*, as well as those from Myanmar, constitute a single species.

It is a species with much variation across numerous characters, such that a small sample might appear to consist of two or three separate species. While Wernette *et al.* (2021) determined the conspecificity of *E. buravasi*, the sources and examples of this variation are explored more fully here. The palpebral lobe varies in its obliquity relative to the exsagittal plane; the specimens with high obliquity (e.g. Figs 45I, 47S, 48V) appear to have a trapezoidal outline while those with more exsagittally oriented palpebral lobes (e.g. Figs 45N–O, 46U, 47F, 48K) have more rectangular outlines. The glabella is anteriorly tapering in some specimens (e.g. Figs 45AL–AM, 46Q, 47K–L, 48V) and parallel-sided in others (e.g. Figs 45AD–AE, 46AB–AC, 47X, 48K). The length (sag.) of the anterior border is also variable with shorter, more brim-like borders in some specimens (e.g. Figs 45L, 46A, 47E, 48W–X) and long, inflated borders in others (e.g. Figs 45M, 46AH–AI, 47T–U, 48O–P). The anterior glabellar margin may be strongly and smoothly curved (e.g. Figs 46Q, 47P–Q, 48N) or nearly straight with distinct anterior glabellar corners (e.g. Figs 45F, 46AH–AI, 47A–C, 48T–U). The cranium may be relatively dorsoventrally flat (e.g. Figs 45Z–AA, 46AH–AI, 47N–O, 48T–U) or strongly convex (e.g. Figs 45C–D, 46Z–AA, 47K–L, 48W–X). The anterior cranial margin can vary from straight (e.g. Figs 45R, 47Y, 48V) to strongly curved (e.g. Figs 45AD–AE, 46AJ–AK, 47Z–AA, 48N) and even angular (e.g. Figs 46R, 47A–C, 48N). Kobayashi (1957) and Shergold *et al.* (1988) suggested that some of the variation, particularly the convexity of the cranium, is size related but in the extensive collection presented herein it is clear that each of these noted variations are

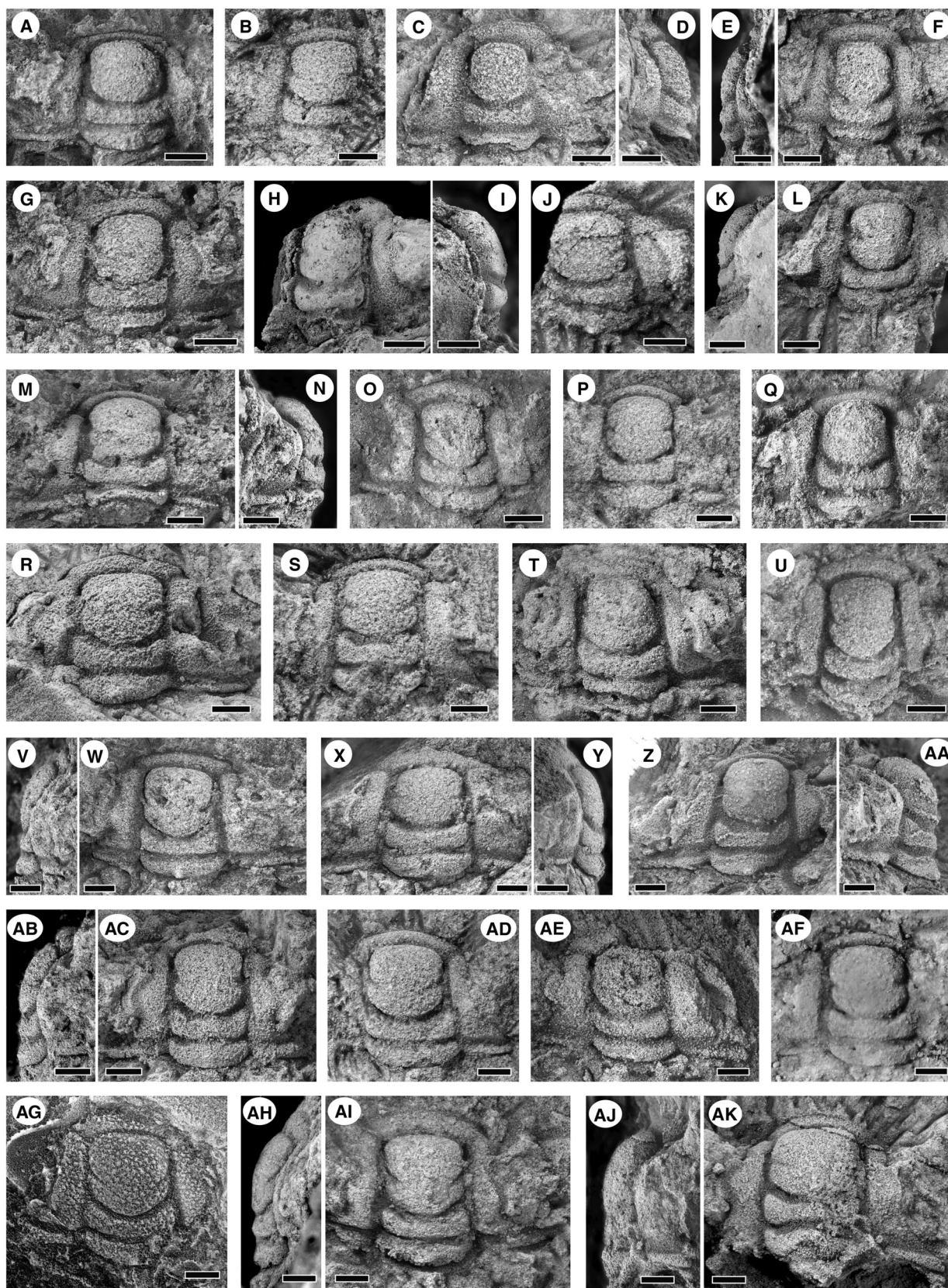


FIG. 46. *Eosaukia buravasi* Kobayashi, 1957. Second of four figures of *E. buravasi* cranidia arranged in increasing size order. A, DGSC F0784. B, DGSC F1135. C–D, DGSC F0812 in: C, dorsal; D, left lateral view. E–F, DGSC F1028 in: E, right lateral; F, dorsal view. G, DGSC F1138. H–I, DGSC F0939 in: H, dorsal; I, left lateral view. J, DGSC F1091. K–L, DGSC F1045 in: K, right lateral; L, dorsal view. M–N, DGSC F1067 in: M, dorsal; N, left lateral view. O, DGSC F0443. P, DGSC F0635. Q, DGSC F0773. R, DGSC F1128. S, DGSC F1126. T, DGSC F0789. U, DGSC F0390. V–W, DGSC F1185 in: V, right lateral; W, dorsal view. X–Y, DGSC F1247 in: X, dorsal; Y, left lateral view. Z–AA, DGSC F1081 in: Z, dorsal; AA, left lateral view. AB–AC, DGSC F0336 in: AB, right lateral; AC, dorsal view. AD, DGSC F1177. AE, DGSC F0787. AF, DGSC F0412. AG DGSC F0575, external mould. AH–AI, DGSC F1255 in: AH, right lateral; AI, dorsal view. AJ–AK, DGSC F1272 in: AJ, right lateral; AK, dorsal view. Scale bars represent 2 mm.

independent of size; each of Figures 45–48 contains a different size range of cranidia, with Figure 48 showing the largest.

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

Shergold *et al.* (1988) reassigned most of the librigenae assigned to this species by Kobayashi (1957, pl. 5, figs 7, 13–15) to *Lophosaukia* cf. *jiangnanensis*. Only two of Kobayashi's librigenae (1957, pl. 5, figs 8, 9) were retained as *E. buravasi* by Shergold *et al.* (1988); these have a vincular pattern of ridges and furrows crossing the doublure, now known to be characteristic of *Eosaukia*. In our new collections, no librigenae have been found bearing this pattern, but a few have been found with the ventral lateral border exposed. The librigenae assigned here to *E. buravasi* based on their shape and the size of the eye, show variation in the shape of the anterior suture branch and projection of the genal spine. This variation complements the variation in the palpebral orientation and frontal areas displayed by the cranidia. Such librigenae are abundant and regularly co-occur with cranidia of *E. buravasi*, supporting their association with it. *Lophosaukia* cf. *jiangnanensis* is an unlikely association for these librigenae, because this species has relatively long (exsag.) eyes compared with the shorter eyes of *E. buravasi*, matching the ocular part of these librigenae. Furthermore, the librigenae of *Lophosaukia* have a distinct pattern of pustules.

The pygidium of *E. buravasi* exhibits less variation than the cranidium. It is lenticular with a wide (tr.) axis that occupies the full length of the pygidium and consists of two well-defined axial rings, a narrow (tr.) articulating half ring, and a weakly double-ridged terminal piece that is quite distinct from the part bearing axial rings. There are two notable variations: the curvature of the lateral corners, with a few specimens (e.g. Fig. 50U) exhibiting rounded rather than the typical angular corners, and the retention of interpleural and pleural furrows in the usually effaced pleural field (e.g. Fig. 50S, X). The pygidia that have pleural furrows have subequally divided pleural bands with the anterior band slightly longer than the posterior. *Eosaukia micropora* (Qian in Qian *et al.*, 1985) (Lee & Choi 2011) and *E. bella* also have furrowed pleural fields, but the longitudinal ridges on their terminal pieces are more prominent than the weakly defined ridges in *E. buravasi*. The boundary between the axial rings and the terminal piece may mark the front of the telson (Hughes 2003).

Occurrence. AML 3.62–6.01 m, h1–h5, ATD S1 7.00 m, ATD S2 0.52–14.5 m and ATD S2 h1; ATT 0.95–29.17 m and ATT h2; ATTw; LHN 2.85 m; Ao Mo Lae Formation; Furongian, Stage 10.

Genus HOYTASPIIS Ludvigsen & Westrop, 1983

Type species. *Ptychaspis speciosus* Walcott, 1879 (p. 131; 1913, pp. 272–273, pl. 43, figs 16–19); designated by Ludvigsen & Westrop (1983, p. 34); Hoyt Limestone, New York State, USA; Stage 10, Furongian.

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

Hoytaspis thanisi Shergold *et al.*, 1988

Figures 51–53

1988 *Hoytaspis? thanisi* Shergold *et al.*, p. 308, pl. 5, figs A–I.

Material. 93 cranidia from ATD S1 6.65 m (DGSC F1484, F1492) and 7.00 m (DGSC F1493, F1498, F1500, F1504, F1505, F1508, F1514, F1516, F1517, F1520, F1525, F1526, F1529, F1531, F1532, F1533, F1536, F1538, F1541, F1543, F1550, F1552, F1554, F1555, F1559, F1564, F1565, F1569, F1571, F1573, F1576, F1581, F1588 external mould, F1589, F1590, F1591 internal and external mould, F1597, F1600, F1606, F1609, F1611, F1618, F1619, F1621, F1624, F1626, F1634, F1641, F1644, F1650, F1651, F1655, F1656, F1658, F1659, F1664, F1665, F1667, F1669, F1670, F1671, F1673, F1674, F1675, F1677, F1678, F1682, F1684, F1685, F1689, F1692, F16944, F1695, F1700, F1701, F1707, F1713, F1719, F1721, F1730, F1731, CMC IP89254, IP89256, IP89257, IP89262, IP89268, IP89270, IP89272, IP89274, IP89277, IP89278). 31 librigenae from ATD S1 7.00 m (DGSC F1515, F1534, F1548 external mould, F1556, F1557, F1562, F1578, F1584, F1599, F1603 external mould, F1608, F1622, F1629 internal and external moulds, F1630 internal and external moulds, F1631, F1632 external mould, F1643, F1646, F1647, F1649, F1661, F1663, F1681, F1686, F1691, F1705, F1706, F1716, F1727 external mould, F1729 external mould, CMC IP89264). 32 pygidia from

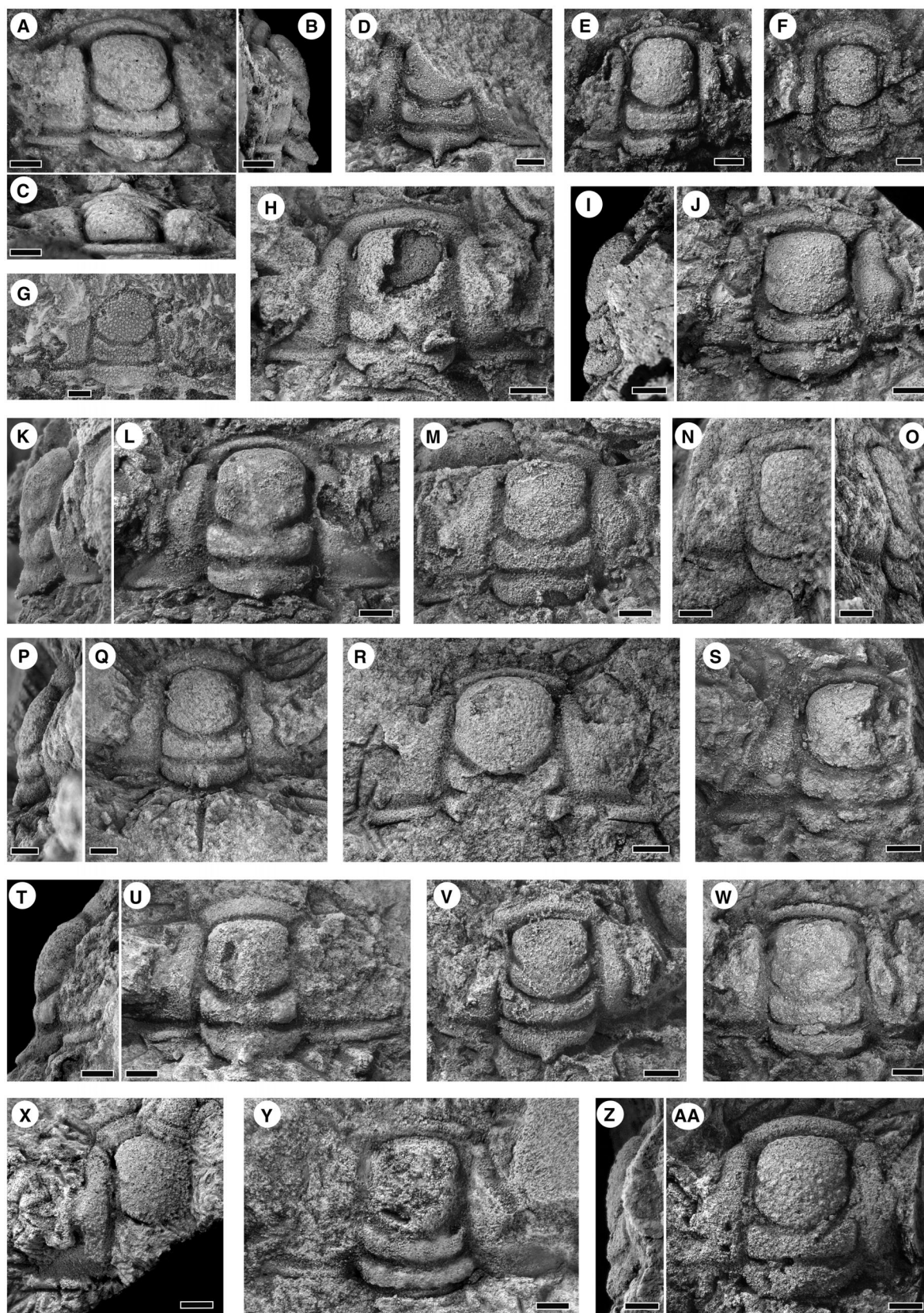


FIG. 47. *Eosaukia buravasi* Kobayashi, 1957. Third of four figures of *E. buravasi* cranidia arranged in increasing size order. A–C, DGSC F0763 in: A, dorsal; B, left lateral; C, anterior view. D, DGSC F0961. E, DGSC F0376. F, DGSC F0801. G, DGSC F1076, external mould. H, DGSC F1074. I–J, DGSC F0335 in: I, right lateral; J, dorsal view. K–L, DGSC F1058 in: K, dorsal; L, right lateral view. M, DGSC F1071. N–O, DGSC F1057 in: N, dorsal; O, left lateral view. P–Q, DGSC F1250 in: P, right lateral; Q, dorsal view. R, DGSC F1156. S, DGSC F1215. T–U, DGSC F1252 in: T, right lateral; U, dorsal view. V, DGSC F1056. W, DGSC F1220. X, DGSC F1178. Y, DGSC F1239. Z–AA, DGSC F1186 in: Z, right lateral; AA, dorsal view. Scale bars represent 2 mm.

6.65 m (DGSC F1481) and 7.00 m (DGSC F1499 external mould, F1501, F1502 external mould, F1513, F1522, F1523, F1528, F1539, F1542 external mould, F1561, F1572, F1579, F1582 external mould, F1592 external mould, F1596, F1598, F1601 external mould, F1607, F1610 external mould, F164, F1617, F1625, F1657, F1676, F1680, F1699, F1728, F1732, CMC IP89259, IP89263, IP89266 external mould).

Remarks. While the majority of the specimens included herein have inflated preglabellar fields as in *Hoytaspis*, some have depressed preglabellar areas as in *Prosaugia* Ulrich & Reser, 1933. The depressed field is most common in larger cranidia. Shergold *et al.* (1988) remarked on the same trend within specimens from their collections, citing the variability of this character as the reason for indicating doubt in the genus assignment. The individuals with depressed preglabellar fields occur in the same horizon and otherwise appear to fall within the morphological variation exhibited by specimens with inflated preglabellar fields. Determining the full range of that morphological variation is difficult due to moderate deformation of specimens.

The pygidium has a narrow border similar to, although less clearly defined than, that of the Laurentian species, *Hoytaspis speciosa* (Walcott, 1879). On most internal moulds the broad (tr., exsag.) doublure has prevented preservation of the distal pleural field and border although the well-developed post-axial ridge is consistently preserved due to the doublure's pronounced medial shortening (sag.). The axis of *H. thanisi* is longer than that of *H. speciosa* and contains more axial segments. In both species the expression of segments is somewhat variable, possibly indicating that segments continued to be added to holaspis instars and that trunk growth is thus protarthrous (Hughes *et al.* 2006). *Hoytaspis speciosa* is described as having four axial segments excluding the terminal piece, although the fourth segment is sometimes poorly developed (e.g. Ludvigsen & Westrop 1983, pl. 15, fig. 10) and other times well developed with a fifth poorly developed segment (e.g. Ludvigsen & Westrop 1983, pl. 15, figs 8, 12). *Hoytaspis thanisi* typically has five well-developed axial segments, and a sixth segment may occur in larger specimens (e.g. Fig. 53T).

Occurrence. ATD S1 6.65–7.00 m; Ao Mo Lae Formation; Furongian, Stage 10.

Genus LICHENGIA Kobayashi, 1942

Type species. *Lichengia onigawara* Kobayashi, 1942 [= *Prosaugia brizo* Sun, 1935]: Licheng Formation, Shangyaochen, Shanxi, China; Stage 10, Furongian.

Lichengia simplex Shergold, 1991

Figure 54A–B

- | | | |
|-----|------|---|
| non | 1957 | <i>Saukiella tarutaoensis</i> Kobayashi, p. 378, pl. 5, fig. 12 (= <i>Prosaugia tarutaoensis</i>). |
| non | 1957 | <i>Coreanocephalus planulatus</i> Kobayashi, p. 379, pl. 4, figs 16–17 (= <i>Thailandium solum</i>). |
| | 1988 | <i>Lichengia? tarutaoensis</i> (Kobayashi); Shergold <i>et al.</i> , pp. 309–310, fig. 5S–V, ?W. |
| | 1991 | <i>Lichengia simplex</i> Shergold, pp. 27–28, pl. 4, figs 1–7. |

Material. 2 cranidia from ATT 23.89 m (DGSC F0989, F0953), both internal moulds.

Remarks. Shergold *et al.* (1988) reassigned *Saukiella tarutaoensis* Kobayashi, 1957 to *Lichengia*, establishing *Lichengia? tarutaoensis*. However, the new material figured in Shergold *et al.* (1988) is not synonymous with the cranidium assigned by Kobayashi to *Saukiella*, which has been revised to *Prosaugia tarutaoensis* (Kobayashi, 1957) based on additional material (Wernette *et al.* 2020b).

When Shergold (1991) described *Lichengia simplex* from the Pacoota Sandstone of Australia, he remarked on the high degree of similarity between *L. simplex* and *Lichengia? tarutaoensis*, suggesting a deeper, wider (sag.) preglabellar field and anterior border furrow on the latter as the only distinguishing cranidial differences. The divisions and furrows of the frontal area vary between specimens, with overlap between the Thai and Australian material even in the few specimens known from each location. As such, based on the cranidium, these collections should be considered the same species. Pygidial differences were also cited, notably that the outline of *L. simplex* is more ovoid than the outline of *Lichengia? tarutaoensis*. However, this comparison included the mistaken assignment of the large, shovel-like pygidia of *Thailandium solum* to *Lichengia? tarutaoensis* (Shergold *et al.* 1988; Kobayashi 1957, fig. 4.16, 17). The one pygidium figured in Shergold *et al.* (1988, fig. 5W) in association with the cranidia of *Lichengia? tarutaoensis* is similar to both the pygidia of *P. oculata* Wernette *et al.*, 2020b and *L. simplex* and is here associated with *L.? tarutaoensis* only tentatively. Despite being published later, *Lichengia simplex* has nomenclatorial priority over *Lichengia? tarutaoensis* because Shergold *et al.* (1988) used the species designation 'tarutaoensis' only out of mistaken association with *Prosaugia tarutaoensis* (Kobayashi, 1957) (formerly *Saukiella tarutaoensis*; Wernette *et al.* 2020b).

Occurrence. ATT 23.89 m; Ao Mo Lae Formation; Furongian, Stage 10.

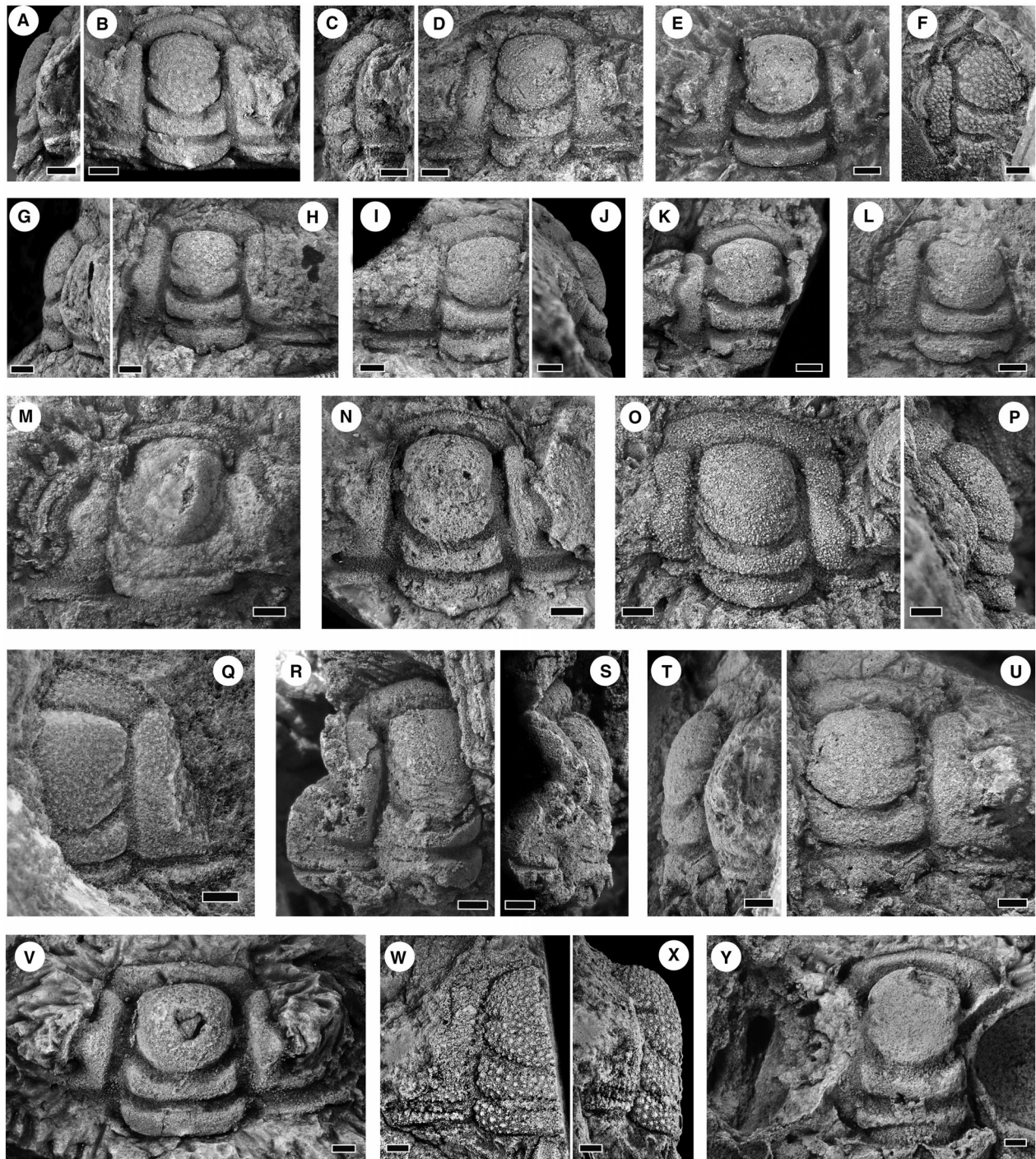


FIG. 48. *Eosaukia buravasi* Kobayashi, 1957. Fourth of four figures of *E. buravasi* cranidia arranged in increasing size order. A–B, DGSC F0761 in: A, right lateral; B, dorsal view. C–D, DGSC F1751 in: C, right lateral; D, dorsal view. E, DGSC F1216. F, DGSC F1168, external mould. G–H, DGSC F1253 in: G, right lateral; H, dorsal view. I–J, DGSC F1266 in: I, dorsal; J, left lateral view. K, DGSC F0334. L, DGSC F0625. M, DGSC F0624. N, DGSC F0778. O–P, DGSC F1756 in: O, left lateral; P, dorsal view. Q, DGSC F1248, external mould. R–S, DGSC F1068 in: R, dorsal; S, left lateral view. T–U, DGSC F1265 in: T, right lateral; U, dorsal view. V, DGSC F1219. W–X, DGSC F1757 in: W, dorsal; X, left lateral view. Y, DGSC F1228. Scale bars represent 2 mm.

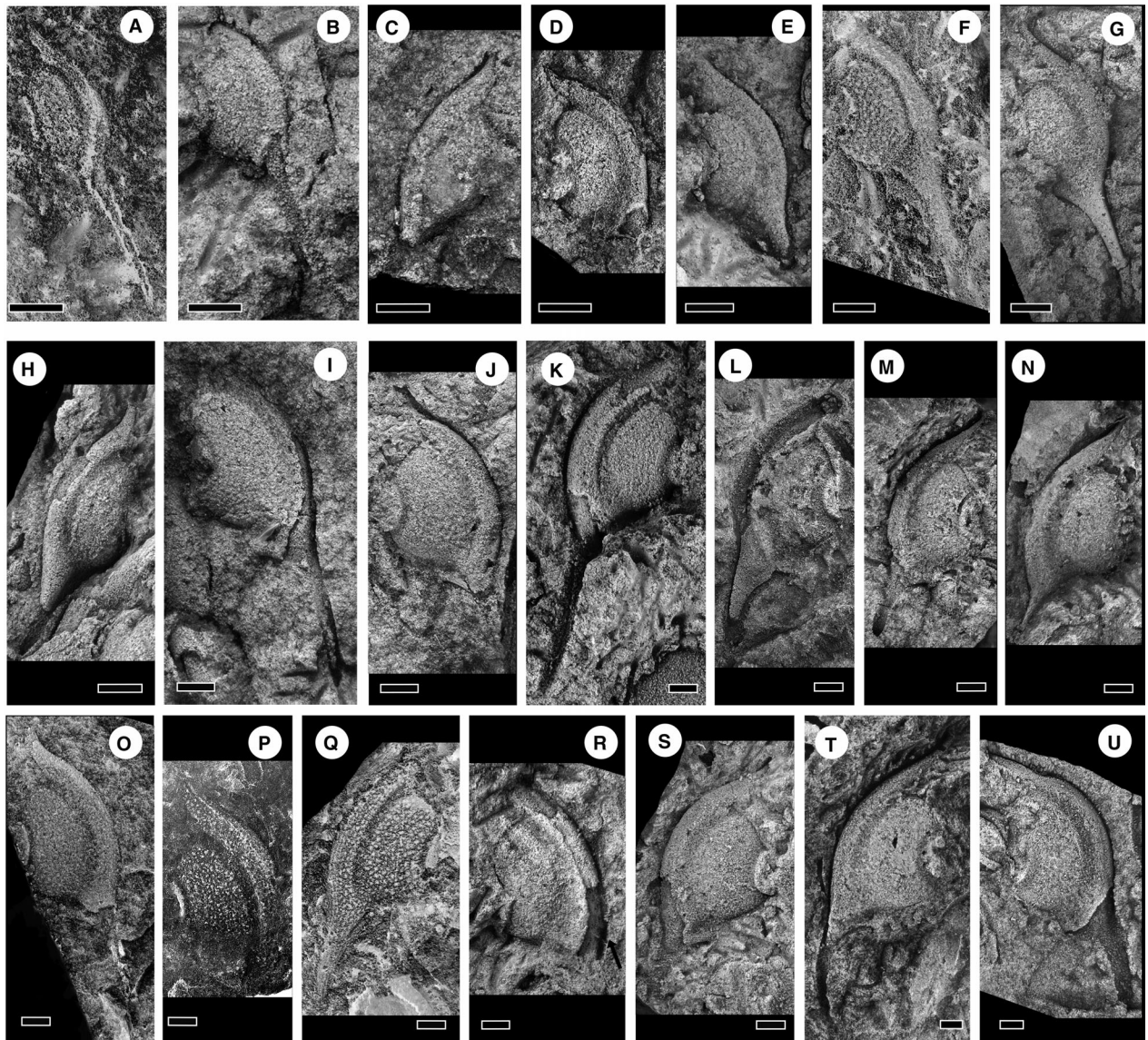


FIG. 49. *Eosaukia buravasi* Kobayashi, 1957, librigenae. A, DGSC F0782, external mould. B, DGSC F1190. C, DGSC F0627. D, DGSC F0396. E, DGSC F1193. F, DGSC F0791, external mould. G, DGSC F0573. H, DGSC F1051. I, DGSC F1134. J, DGSC F1154. K, DGSC F1264. L, DGSC F1226. M, DGSC F0600. N, DGSC F1042. O, DGSC F1087, external mould. P, DGSC F1195, external mould. Q, DGSC F1064, external mould. R, DGSC F1223. S, DGSC F1169. T, DGSC F1188. U, DGSC F1225. Scale bars represent 2 mm.

Genus LOPHOSAUKIA Shergold, 1972

Type species. *Lophosaukia torquata* Shergold, 1972; by original designation; Gola beds, Mobedah Creek, western Queensland, Australia; *Rhaptagnostus clarki maximum* – *Rhaptagnostus papilio* Zone, Stage 10, Furongian.

Remarks. Shergold's (1972) diagnosis of *Lophosaukia* is based on the frontal area, referring only to the exsagittally shortened, triangular anterior cranial border and deep prelabellar furrow that partly extends underneath the frontal lobe. Apart from the frontal area, *Lophosaukia*'s features are considered typical of 'saukiids' and difficult to distinguish from taxa such as *Eosaukia* and *Prosaukia*.

Lophosaukia nuchanongi sp. nov.

Figures 55, 56

- ? 1957 *Eosaukia buravasi* Kobayashi, p. 376, pl. 5, figs 7, 13 only.
1988 *Lophosaukia* cf. *jiangnanensis* Lu & Lin; Shergold et al., pp. 310–312, fig. 5J–P.

LSID. <https://zoobank.org/NomenclaturalActs/DFEFEEAA5-3FBD-48D2-B0E3-71D5CE48EB54>

Derivation of name. Named for Dr Tawsaporn Nuchanong, former Director General of Thailand's Department of Mineral Resources.

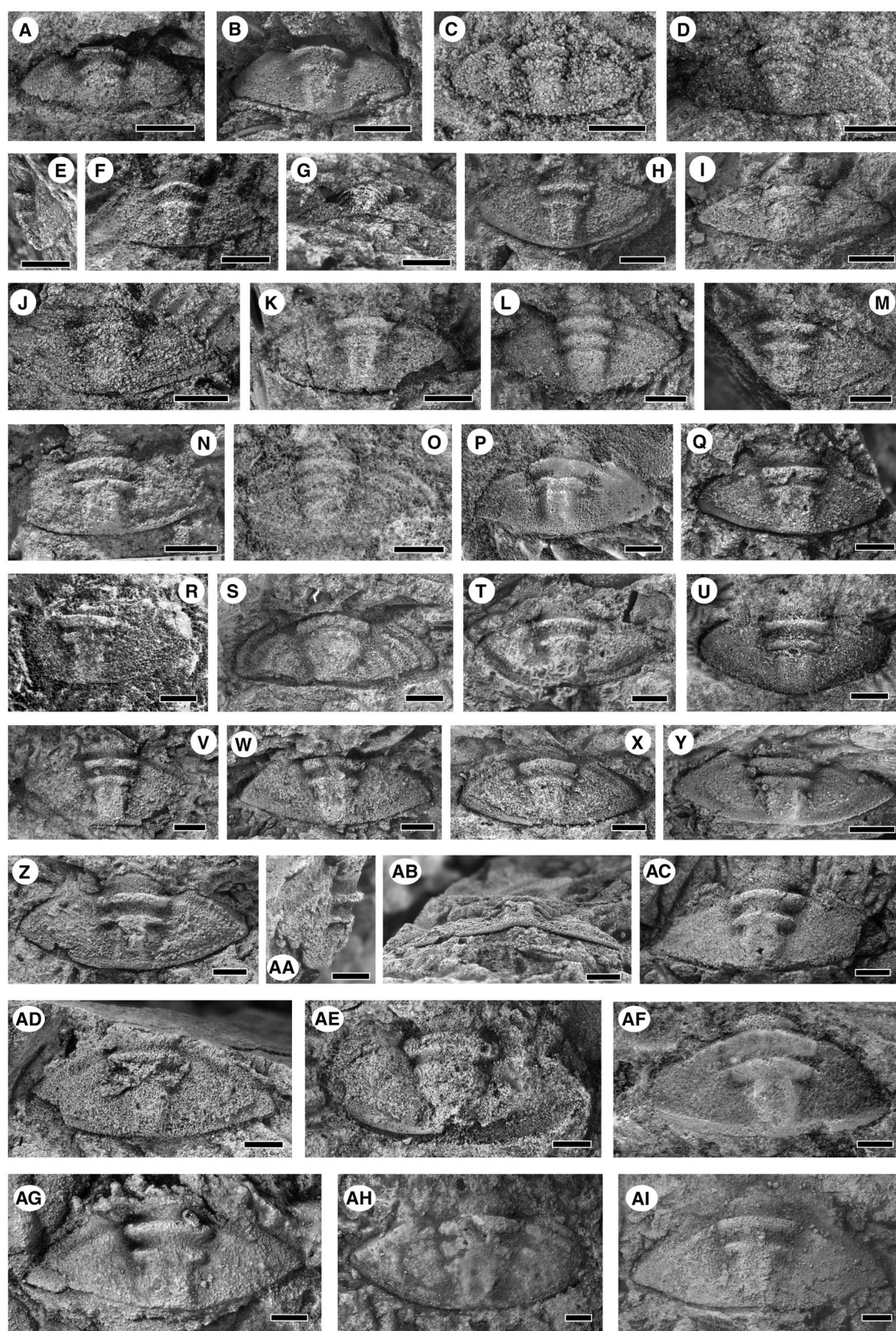


FIG. 50. *Eosaukia buravasi* Kobayashi, 1957, pygidia. A, DGSC F0985. B, DGSC F1032. C, DGSC F1759. D, DGSC F0868. E–G, DGSC F0367 in: E, right lateral; F, dorsal; G, anterior view. H, DGSC F1060. I, DGSC F1012. J, DGSC F0867. K, DGSC F1197. L, DGSC F0797. M, DGSC F1211. N, DGSC F1145. O, DGSC F0508, external mould. P, DGSC F1034, external mould. Q, DGSC F1050. R, DGSC F1202, external mould. S, DGSC F1039. T, DGSC F1073. U, DGSC F0957. V, DGSC F123. W, DGSC F1059. X, DGSC F0347. Y, DGSC F1069. Z–AB, DGSC F1109 in: Z, dorsal; AA, left lateral; AB, posterior view. AC, DGSC F1164. AD, DGSC F1141. AE, DGSC F0822. AF, DGSC F0578, external mould. AG, DGSC C0432. AH, DGSC F1214. AI, DGSC F1077. Scale bars represent 2 mm.

Material. Holotype: DGSC F0529 (Fig. 56C, D), cranidium from ATT 22.78 m; Ao Mo Lae Formation.

Paratypes: 2 cranidia from ATT 22.78 m (DGSC F0472), 23.89 m (CMC IP88924).

Other material: 4 cranidia from ATT 23.89 m (DGSC F0950, F0952 external mould), 25.34 m (DGSC F0965), ATD S2 14.29 m (DGSC F0777). 6 librigena from ATT 1.10 m (DGSC F0808 external mould), 8.20 m (DGSC F0819), 8.85 m (DGSC F0849 external mould, F0852 external mould), 23.89 m (CMC IP88928 external mould) and ATD S2 0.52 m (DGSC F1760 external mould). 4 pygidia from ATT 22.88 m (DGSC F0925) and 29.17 m (DGSC F0991 external mould, F1005 external mould, CMC IP88934).

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

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

posterolateral projections short (exsag.), mostly comprising posterior border and broad posterior border furrow. Entire cranidium, excluding palpebral lobes, strongly pustulated; pustules on anterior limb of posterior border furrow arranged in single row.

Librigena strongly convex with moderately broad genal field and wide lateral and posterior borders; lateral and posterior border furrows broad and deeply incised; lateral border furrow shallow and broadens near junction with posterior border furrow, becoming effaced in some individuals. Genal spine broad-based and posteriorly curved, beak-like with fine, sub-parallel to anastomosing ridges oriented along length. Excluding genal spine, surface covered in pustules of intermixed size; pustules on medial genal field of mixed size and less ordered; pustules nearest lateral furrow coarsest and arranged in rows; pustules on lateral border coarsest near furrow, and those proximal to furrow may be elongated into radiating pattern orthogonal to furrow.

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

Remarks. Shergold *et al.* (1988) reassigned several cranidia and librigenae previously identified as *Eosaukia buravasi* Kobayashi (1957, pl. 5, figs 6–7, 13–15, 19–20) to *Lophosaukia cf. jiangnanensis*. The anteriorly tapering glabellae of certain specimens (Kobayashi 1957, pl. 5, figs 6, 19, 20) make their reassignment dubious, especially in the absence of well-preserved palpebral or frontal areas; Kobayashi's specimens (1957, pl. 5, figs 19, 20) have a preserved frontal area that is distinctly *Eosaukia*-like in the furrows. Both *Lophosaukia* and *Eosaukia* show extensive cephalic intraspecific variation (Kobayashi 1957; Shergold 1975; Shergold *et al.* 1988; Wernette *et al.* 2021) with extensive overlap between these genera in all but the frontal area. *Lophosaukia*, however, consistently bears coarser pustulation. Without such pustulation or the anterior margin preserved, unambiguous identification of specimens, particularly librigenae, as *Lophosaukia* is challenging.

Shergold *et al.* (1988) argued that their specimens, here assigned to *L. nuchanongi*, most closely resemble *L. jiangnanensis* Lu & Lin, 1984 but noted that the latter has a longer preglabellar protrusion and a more sharply furrowed pygidium. Additionally, *L. nuchanongi* has a distinctly narrower, shorter and less anteriorly rounded glabella. *Lophosaukia cf. jiangnanensis* (*sensu* Peng 1992) has a longer frontal area, broader glabella and less arcuate palpebral lobes. Compared with *L. torquata* or *L. acuta*, *L. nuchanongi* is not as convex and has finer granulation. The

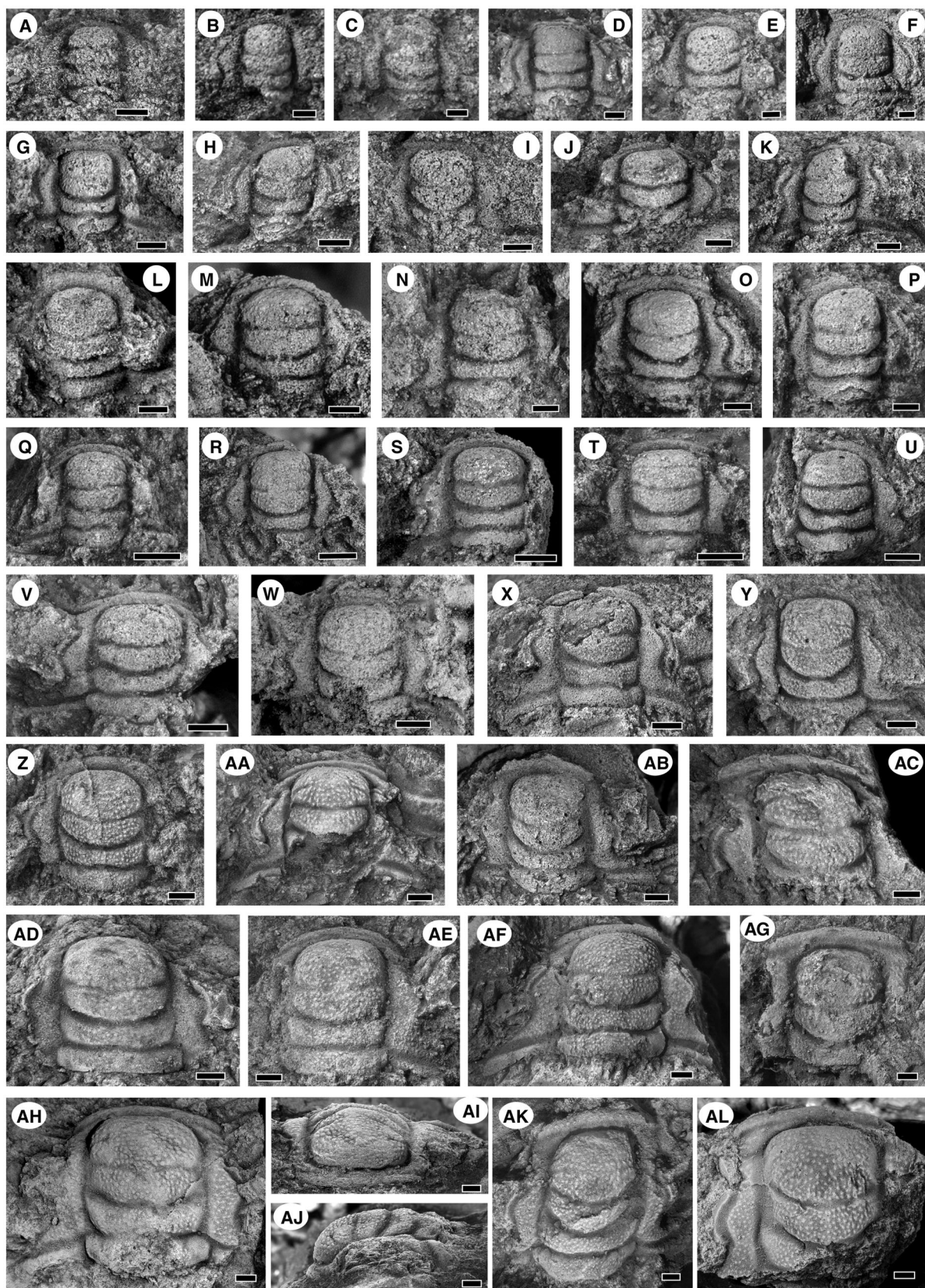


FIG. 51. *Hoytaspsis thanisi* Shergold *et al.*, 1988, cranidia. A, DGSC F1634. B, DGSSC F1500. C, DGSC F1569. D, DGSC F1658. E, DGSC F1550. F, DGSC F1491. G, DGSC F1624. H, DGSC F1656. I, DGSC F1664. J, DGSC F1678. K, DGSC F1665. L, DGSC F1694. M, DGSC F1536. N, DGSC F1674. O, DGSC F1514. P, DGSC F1555. Q, DGSC F1581. R, DGSC F1538. S, DGSC F1730. T, DGSC F1517. U, DGSC F1731. V, DGSC F1673. W, DGSC F1508. X, DGSC F1707. Y, DGSC F1695. Z, DGSC F1692. AA, DGSC F1591. AB, DGSC F1701. AC, DGSC F1650. AD, DGSC F1493. AE, DGSC F1554. AF, DGSC F1721. AG, DGSC F1531. AH–AJ, DGSC F1618 in: AH, dorsal; AI, anterior; AJ, left lateral view. AK, DGSC F1529. AL, DGSC F1651. Scale bars represent: 0.5 mm (A–F); 1 mm (G–P); 2 mm (Q–AL).

angularity of the anterior margin is consistent with what Shergold (1975) referred to as *Lophosaukia* sp. C, although fixigena of *L. nuchanongi* are wider. *Lophosaukia rectangulata* Ergaliev, 1980 has a straighter anterior glabellar margin.

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

Occurrence. ATT 1.10–29.17 m and ATD S2 0.52–14.29 m; Ao Mo Lae Formation; Furongian, Stage 10.

Genus PROSAUKIA Ulrich & Resser, 1933

Type species. *Dikelocephalus misa* Hall, 1863 (pp. 144–145, pl. 8 fig. 15, pl. 10 figs 4, 5, 6?, 7); designated by Ulrich & Resser (1933, pp. 141–144); Tunnel City Group, Wisconsin, USA; Sunwaptan Stage, Furongian.

Remarks. *Prosaugia* is a diverse and widespread genus, best known from Laurentia, but also represented on many continental blocks associated with Gondwana. The cranidium is characterized by an anteriorly narrowing subrectangular glabella, depressed preglabellar field, medially shallowing anterior border furrow and divergent anterior suture branches. The librigenae have disconnected lateral and posterior border furrows with the posterior border furrow extending into the genal spine base, and the pygidium is transversely subelliptical with relatively equally divided pleurae (Ludvigsen & Westrop 1983; Wernette *et al.* 2020b).

Where *Prosaugia* occurs in abundance, it is commonly remarkably diverse both in the number of species present and for the intraspecific variation in each of those species. Ulrich & Resser (1933) assigned 29 species when establishing the genus based on material from the Upper Mississippi Valley. Raasch (1951)

recognized only 13 of those species as valid. Marked intraspecific variation resulting in over-differentiation of species is consistent with trends in other dikelocephalids (Hughes 1994; Wernette *et al.* 2021). Three distinct new forms of *Prosaugia* appear to exist in the Ao Mo Lae Formation in addition to *Prosaugia tarutaoensis* (Kobayashi, 1957) and *Prosaugia oculata* Wernette *et al.*, 2020b. Each of these species is based only on a few cranidia, and librigenae and pygidia have not been assigned for all of them. They occur in different horizons and locations, and each is consistently diagnosable. However, given the small sample size of each form, and in consideration of the dikelocephalid trend of high intraspecific variation, none of the new forms is formally named herein lest further sampling shows them to be variants of only one or two new species rather than three distinct species.

Prosaugia tarutaoensis (Kobayashi, 1957)

Figure 57A–C

- 1957 *Saukiella tarutaoensis* Kobayashi, p. 378, pl. 5, fig. 12.
non 1988 *Lichengia? Tarutaoensis* (Kobayashi); Shergold *et al.*, p. 309, fig. 5S–W.
2020b *Prosaugia tarutaoensis* (Kobayashi); Wernette *et al.*, p. 77, fig. 12.

Material. 5 cranidia from AML 2.20 m (DGSC F0566), 3.10 m (DGSC F0567), AML h3 (DGSC F0545, F0546), ATTW (DGSC F0413). 1 pygidium from ATTW (DGSC F0453) and 1 possible pygidium from AML 5.81 m (CMC IP88952).

Remarks. Wernette *et al.* (2020b) have recently figured and discussed all known specimens of *Prosaugia tarutaoensis* from the Tarutao Group.

Occurrence. AML 2.20–3.10 (?5.81) m, AML h3 and ATTW; Ao Mo Lae Formation; Furongian, Stage 10.

Prosaugia oculata Wernette *et al.*, 2020b

Figure 57D–F

- ? 1988 *Lichengia? tarutaoensis* (Kobayashi); Shergold *et al.*, pp. 309–310, fig. 5W only (non fig. 5S–V = *Prosaugia tarutaoensis*).
2020b *Prosaugia oculata* Wernette *et al.*, p. 79, fig. 13.

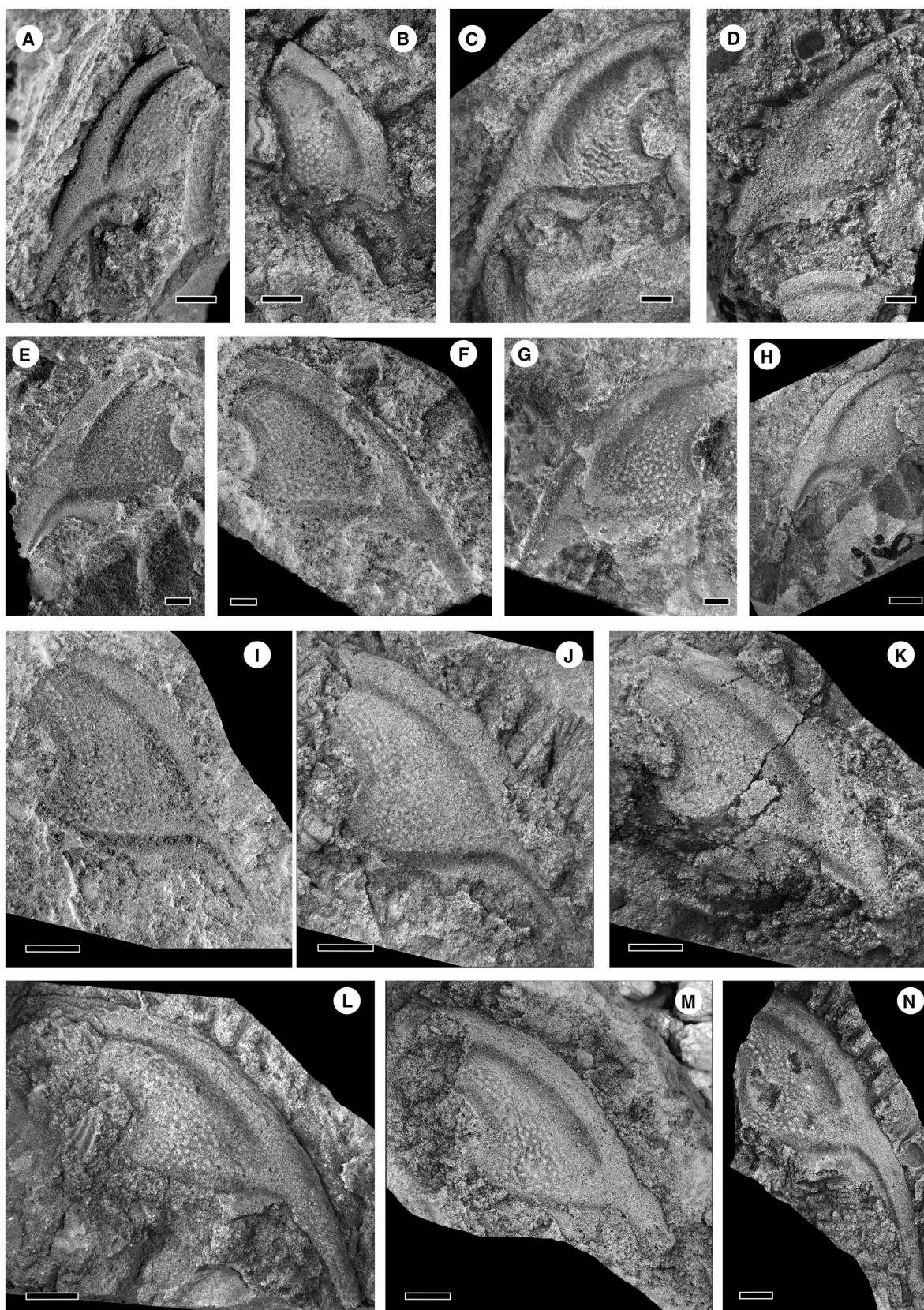


FIG. 52. *Hoytaspsis thanisi* Shergold et al., 1988, librigenae. A, DGSC F1562. B, DGSC F1515. C, DGSC F1647. D, DGSC F1557. E, DGSC F1727, external mould. F, DGSC F1729, external mould. G, DGSC F1534, external mould. H, DGSC F1649. I–J, DGSC F1629: I, external; J, internal mould. K, DGSC F1578. L, DGSC F1630. M, DGSC F1706. N, DGSC F1705. Scale bars represent: 2 mm (A–F); 4 mm (G–N).

Material. 10 cranidia from ATT 22.78 m (DGSC F0461, F0489, F0498, F0512, F0511, F0532, DGSC F0503 external mould), 22.88 m (DGSC F0534), 23.89 (CMC IP88927) and ATT h1 (DGSC F0459). 2 librigenae from ATT 22.78 m (DGSC F0488, F0513). 4 pygidia from ATT 22.78 m (DGSC F0510 internal and external mould, F0430 external mould, F0470 external mould, F0467). This list is inclusive of material published in Wernette et al. (2020b).

Remarks. Wernette et al. (2020b) discussed *Prosaugia tarutaoensis* from the Tarutao Group.

Occurrence. ATT 22.78–23.89 m and h1, Ao Mo Lae Formation; Furongian, Stage 10.

Prosaugia sp. 1 Figures 58, 59

Material. 2 cranidia (DGSC F1746 internal and external mould, F1744), 3 librigenae (DGSC F1741, F1747, F1748) and 4 pygidia (DGSC F1740, F1745, CMC IP8928, IP8922 external mould) from ATD S2 h2.

Description. Cranidium subrectangular; width across palpebral areas subequal to cranial length (sag.). Glabellar width (tr.) across S1 c. 60% width across palpebral areas; frontal area 15–20% cranial length (sag.); glabella nearly parallel sided to gently anteriorly tapering; axial furrows straight; anterior glabellar margin moderately to strongly curved; S1 posteriorly bowed and medially shallowing; S2 short, narrow, posteromedially deflected and shallow; S3 effaced; SO straight; LO subequal width or slightly wider than L1. Palpebral lobe strongly curved, recurved on both ends, symmetric about the midpoint, centred (exsag.) slightly anterior S1 and extending from SO to S2; width (tr.) across anterior palpebral tips equal or slightly less than width across posterior tips. Fixigena narrow (tr.); anterior suture branches divergent. Frontal area subequally divided into preglabellar field and anterior border (sag.) with preglabellar field relatively longer and anterior border relatively shorter abaxially; anterior border furrow laterally deep and medially shallow, less strongly curved than preglabellar furrow or anterior cranial margin; anterior border inflated above gently inflated preglabellar field. Posterior suture branches curve laterally; posterolateral projections short (exsag.) and wide (tr.), mostly comprising posterior border and broad, deep posterior border furrow. Entire cranidium, excluding palpebral lobes, covered with large granules.

Librigena narrow, anteriorly subequally divided into genal field lateral border; posteriorly genal field widens relative to

border. Lateral and posterior border furrows broad and well-incised; lateral border furrow shallows near junction with posterior border furrow; posterior border furrow extends into genal spine base.

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

Remarks. *Prosaugia* sp. 1 has a particularly long, evenly divided and strongly curved frontal area. In this way it is unlike any other species of *Prosaugia* known from the Tarutao Group. The Laurentian species *Saukiella subconica* Ulrich & Resser, 1933 also has a strongly curved frontal area, but its anterior border furrow is more strongly curved and the axial furrows smoothly curved anteromedially into the preglabellar furrow.

Prosaugia sp. 1 has a somewhat inflated preglabellar field and a medially shallowing anterior border furrow, traits common in *Hoytaspsis* Ludvigsen & Westrop, 1983. Furthermore, the posterior border furrow of the librigena extends slightly into the genal spine base and the pygidium has a narrow border and short postaxial area, as occurs in *Hoytaspsis*. These characters cast some doubt on the genus-level affinity of *Prosaugia* sp. 1. However, although slightly inflated, the preglabellar field is not inflated above the anterior border. Additionally, the S1 furrow is only weakly bowed, the S2 furrows are short and shallow and the granulation, while coarse in diameter, has little relief; these traits are more common in *Prosaugia*.

The posterolateral projection of *Prosaugia* sp. 1 is long (tr.) and, in the best preserved specimen (Fig. 59B), the suture cuts subtangentially to the broad border furrow such that the anterior band of the posterolateral projection is relatively short (tr.) and the posterior border furrow is discernible on the anterior edge of the posterolateral projection for much of its length (tr.).

Occurrence. ATD S2 h2; Ao Mo Lae Formation; Furongian, Stage 10.

Prosaugia sp. 2 Figures 54C–G, 60

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

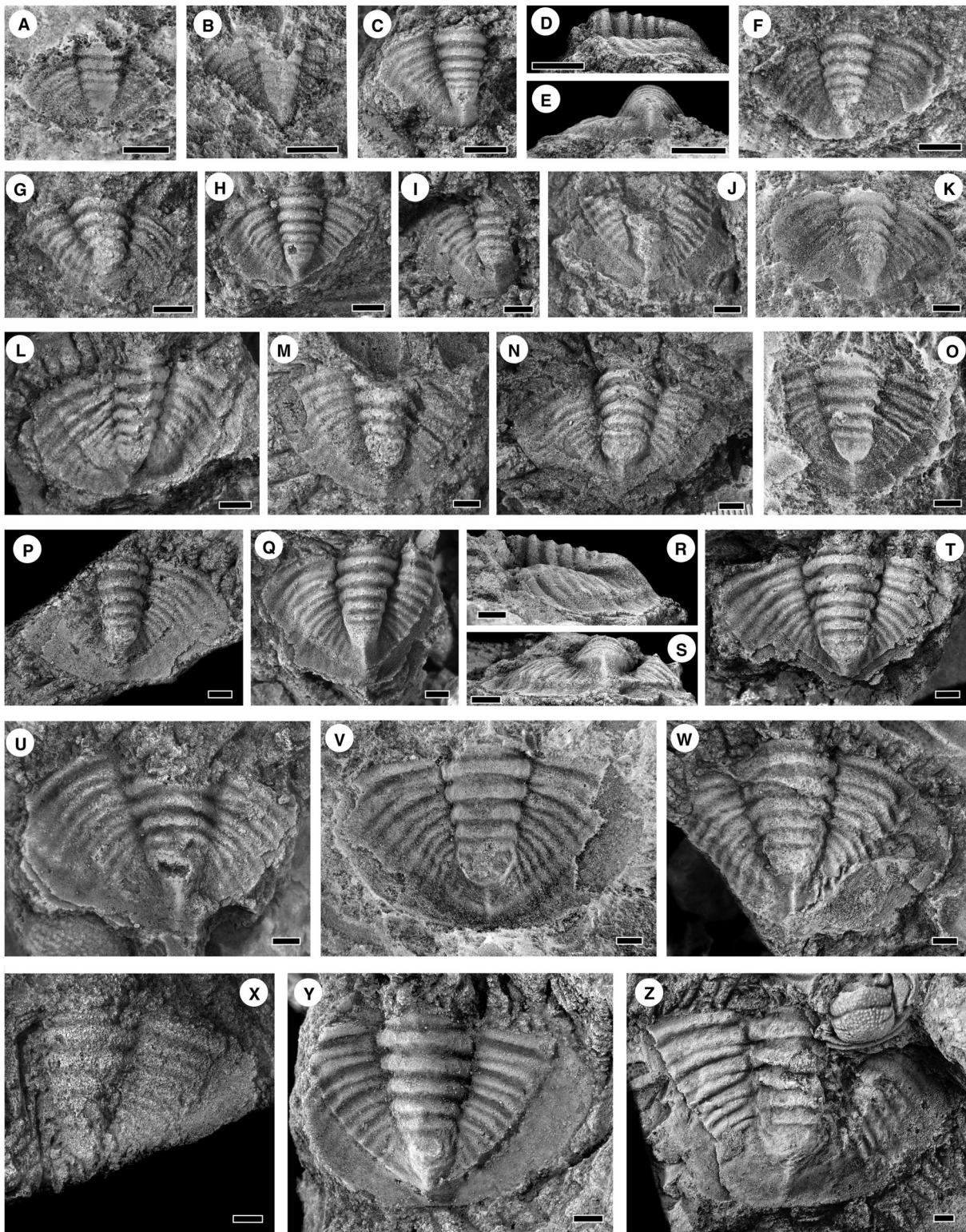


FIG. 53. *Hoytaspis thanisi* Shergold *et al.*, 1988, pygidia. A, DGSC F1499, external mould. B, DGSC F1601. C–E, DGSC F1523 in: C, dorsal; D, left lateral; E, posterior view. F, DGSC F1542. G, DGSC F1699, external mould. H, DGSC F1657. I, DGSC F1501. J, DGSC F1539. K, DGSC F1610. L, DGSC F1513. M, DGSC F1614. N, DGSC F1617. O, DGSC F1592, external mould. P, DGSC F1579. Q–S, DGSC F1676 in: Q, dorsal; R, left lateral; S, posterior view. T, DGSC F1522. U, DGSC F1680. V, DGSC F1582, external mould. W, DGSC F1596. X, DGSC F1572. Y, DGSC F1728. Z, DGSC F1598. Scale bars represent: 1 mm (A); 2 mm (B–Z).

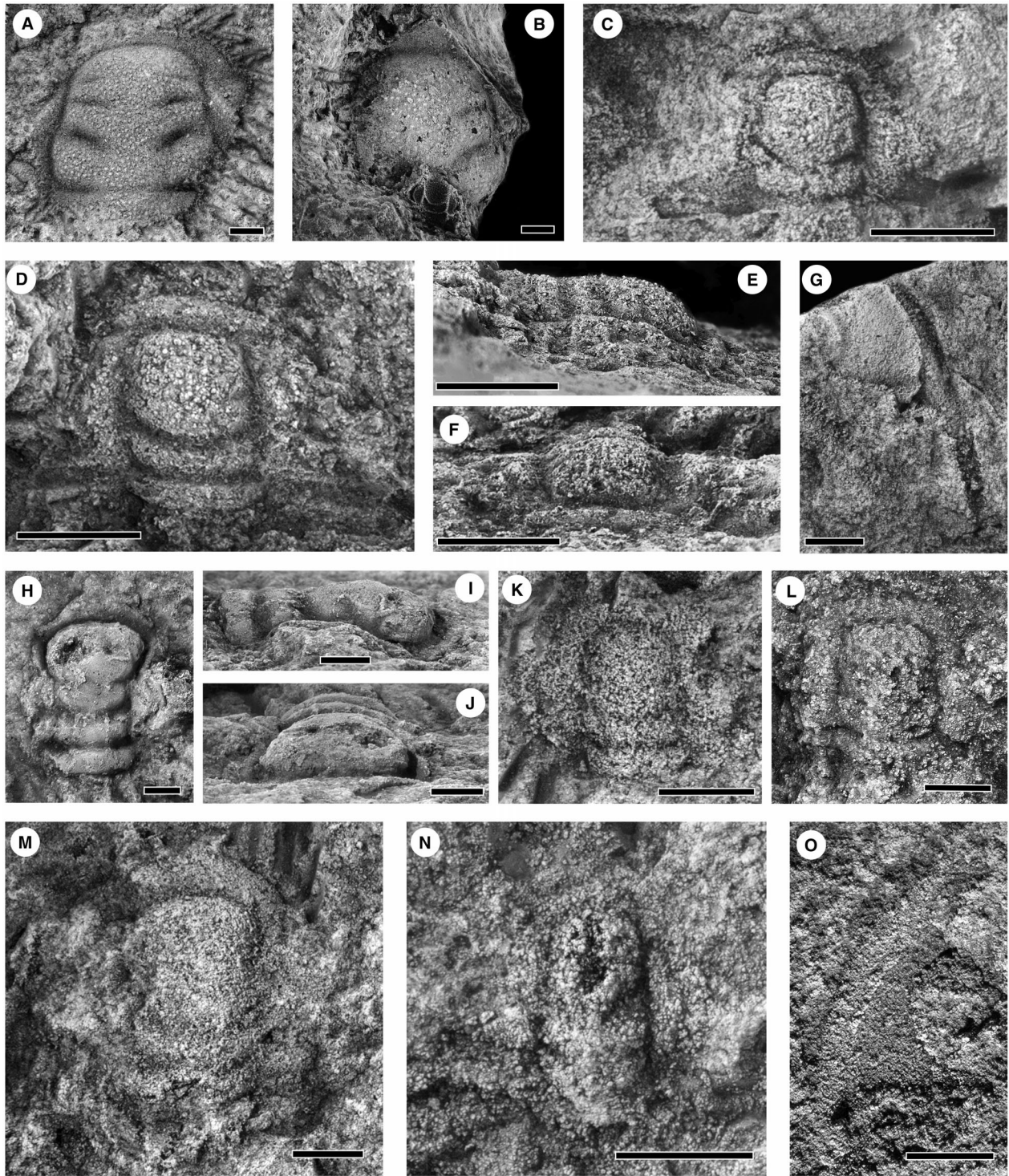


FIG. 54. A–B, *Lichengia simplex* Shergold, 1991, cranidia: A, DGSC F0949; B, DGSC F0953. C–G, *Prosaukia* sp. 2: C, DGSC F0979, cranidium; D–F, DGSC F0750, holotype, cranidium in: D, dorsal; E, right lateral; F, anterior view; G, DGSC F0980, librigena. H–J, DGSC F0792, *Sinosaukia* sp., cranidium in: H, dorsal; I, right lateral; J, anterior view. K–M, *Pacootasaukia* sp., cranidia: K, DGSC F0619; L, DGSC F1742; M, DGSC F0828. N–O, *Wuhuia?* sp.: N, DGSC F0482, cranidium; O, DGSC F1209, librigena. Scale bars represent: 2 mm (A, C–O); 4 mm (B).

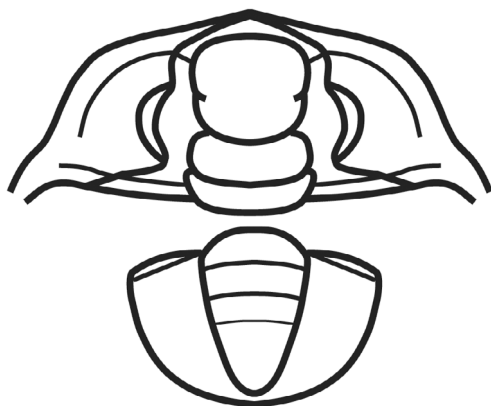


FIG. 55. *Lophosaukia nuchanongi* sp. nov. line drawing.

Additional material. 3 cranidia from LHN 2.85 m (DGSC F0750), ATT 22.78 m (F0471) and ATT 29.17 m (DGSC F0979). 1 librigena from ATT 29.17 m (DGSC F0980).

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

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

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

The cranidium of *Prosaugia?* aff. *nema* figured by Shergold *et al.* (1988, fig. 5Q) has a wider, somewhat more rounded

glabella, but the similarity of the long palpebral lobes, broad frontal area with a short (sag.) preglabellar, and long, narrow (exsag.) S2 suggest that this cranidium belongs to *Prosaugia* sp. 2, and it is also from the same locality as the best preserved cranidium, Laem Hin Ngam. Shergold *et al.* (1988) suggested that the lateral glabellar furrows, wide LO and short anterior border were all reminiscent of *Prosaugia? nema* Shergold, 1975, but *P.? nema* has a more dome-shaped glabella and shorter (sag.) anterior border. Because *P.? nema* is known from only a single, incomplete cranidium and a second cranidial fragment, the full extent of other similarities or differences is unknown. The reason *P.? nema* was noted as having a dubious genus-level assignment is due to its similarity to a range of genera including *Saukiella* Ulrich & Resser, 1933, *Liquania* Zhou in Zhou *et al.*, 1982 and *Wedekindia* Sun, 1935. The type species of *Wedekindia* does not have a medially connected S1, and the posterior curvature of those furrows indicates that the lack of medial continuity is not merely due to shallowing of the furrow (Sun 1935, pl. 4, fig. 26, text fig. 8). *Liquania*, although recognized as a valid genus by Jell & Adrain (2002), is a problematical genus. It is based on a single fragmented cranidium, and although Zhou *et al.* (1982) assigned *Prosaugia? nema* Shergold to this genus, Shergold *et al.* (1988, 2007) challenged this assignment. The incomplete preservation of the frontal area and palpebral lobes on the only known specimen of the genus type of *Liquania* makes assignment to this genus dubious for even very similar material. *Prosaugia* sp. 2 is distinguished by its undulating occipital furrow. *Prosaugia* and *Saukiella* cranidia are notably difficult to differentiate although most authors accept the genera to be separate (e.g. Jell & Adrain 2002). The differentiating characters are variable within each genus, with considerable overlap (e.g. presence of a preglabellar field, confluence of lateral and posterior border furrows, occipital spines and granular ornamentation; Lochman 1970), although their librigenae and pygidia can be distinctly different. The defining cranidial character for *Prosaugia* is a depressed preglabellar field, but in some *Saukiella* species the confluent preglabellar and anterior border furrows are sufficiently long that they are indistinguishable from a short and depressed preglabellar field. Although very short, there is a distinct preglabellar field separating the preglabellar and anterior border furrows on *Prosaugia* sp. 2, supporting this genus assignment.

Occurrence. LHN 2.85 m and Ao Talo Topo 22.78–29.17 m; Ao Mo Lae Formation; Furongian, Stage 10.

Prosaugia sp. 3

Figures 61, 62

Material. 3 cranidia from AML h3 (DGSC F0547, DGSC F0551 internal and external mould, F0553).

Description. Cranidium subrectangular; width across palpebral areas c. 90% of cranidial length. Glabellar width across S1 c. 65% of width across palpebral areas; frontal area c. 15–20% of cranidial length. Glabella very gently anteriorly tapering with slight lateral

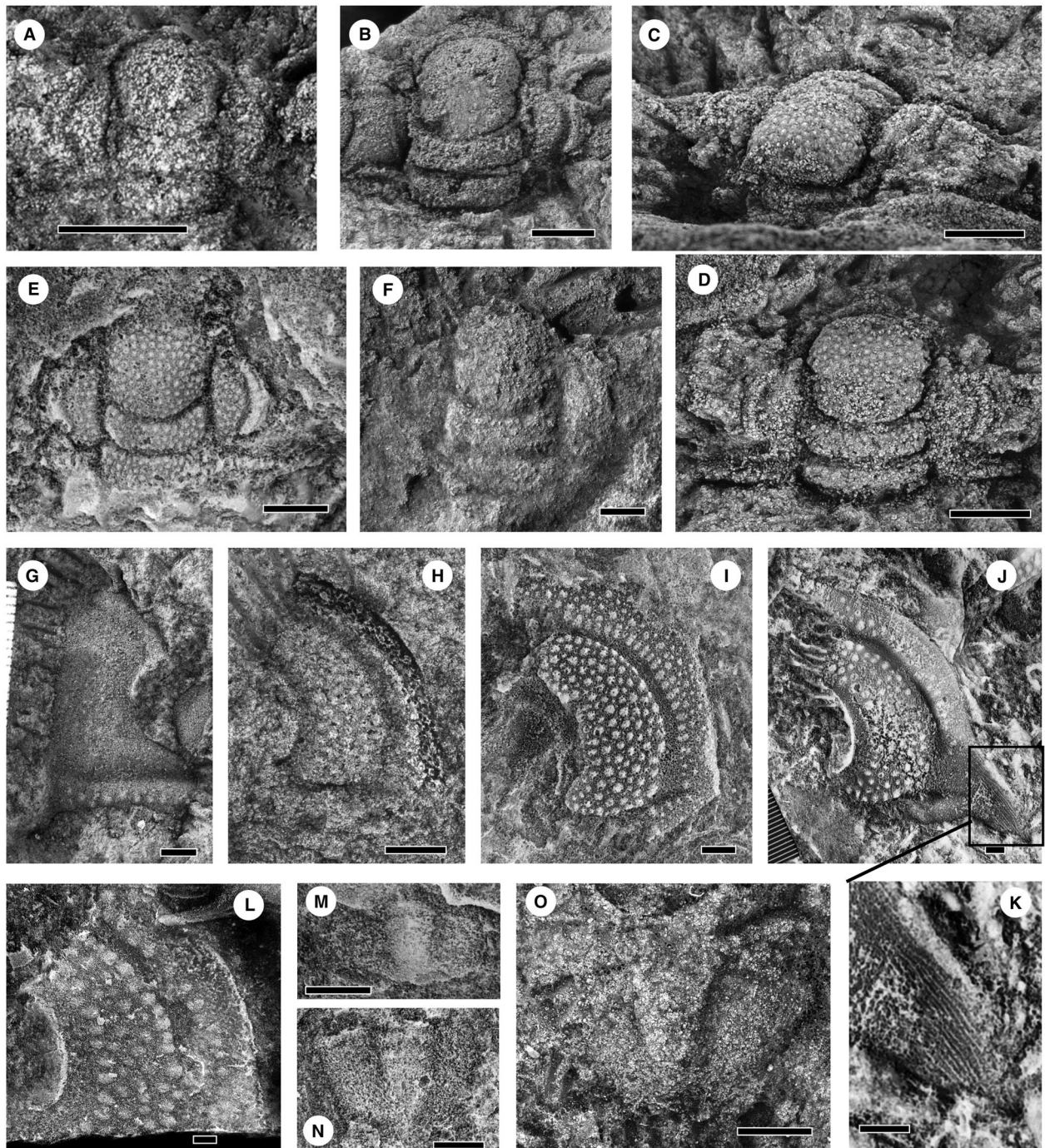


FIG. 56. *Lophosaukia nuchanongi* sp. nov. A, DGSC F0472, cranidium. B, DGSC F0965, cranidium. C–D, DGSC F0529, cranidium in: C, left oblique; D, dorsal view. E, DGSC F0952, cranidium, external mould. F, DGSC F0777, cranidium. G, DGSC F0950, cranidium. H, DGSC F0819, librigena. I, DGSC F1760, librigena, external mould. J–K, DGSSC F0808, librigena: J, external mould; K, magnification of structure on genal spine. L, DGSC F0852, librigenal external mould. M, DGSC F0991, pygidium, external mould. N, DGSC F1005, pygidium. O, DGSC F0925, pygidium. Scale bars represent 2 mm.

expansion at S1 and constriction at S2 in weakly developed urceolate form; anterior glabellar margin medially embayed; LO narrower than L1; SO gently posteromedially bowed; S1 strongly posteromedially bowed but less strongly curved, nearly transverse,

or slightly undulating medially; S2 short (tr.) and well-defined, nearly as posteromedially angled as S1; S3 transverse and narrow (exsag.), poorly defined to effaced. Palpebral lobe arcuate and centred opposite S1; posterior palpebral tip opposite posterior L1

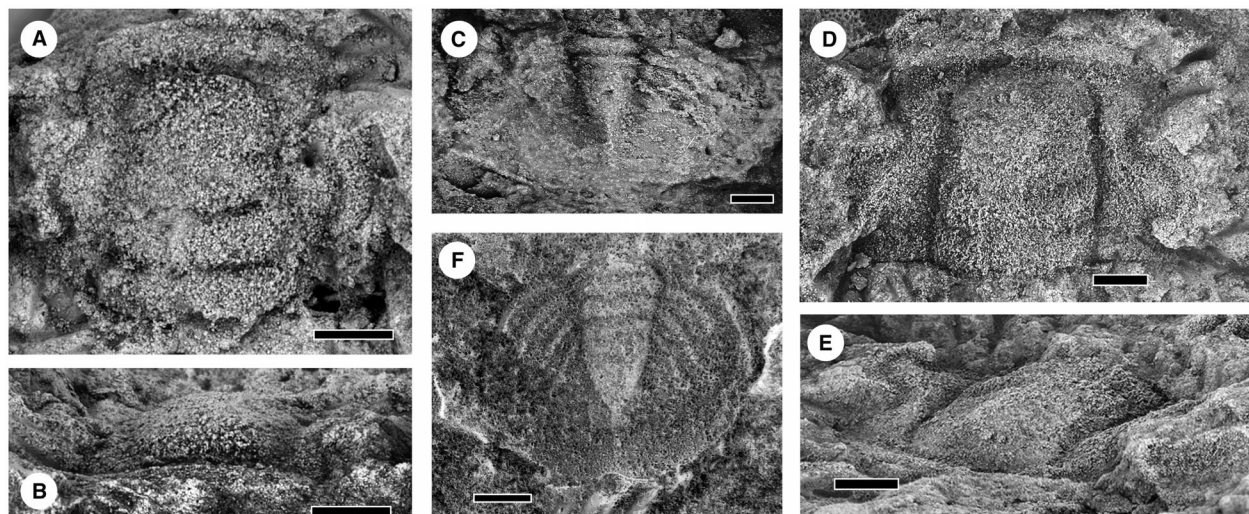


FIG. 57. A–C, *Prosaukia tarutaoensis* (Kobayashi, 1957): A–B, DGSC F0566, cranium in: A, dorsal; B, anterior view; C, DGSC F0453, pygidium. D–F, *Prosaukia oculata* Wernette *et al.*, 2020b: D–E DGSC F0512, holotype, cranium in: D, dorsal; E, left oblique view. F, DGSC F0510, pygidium, external mould. Refigured from Wernette *et al.*, 2020b. Scale bars represent 2 mm.

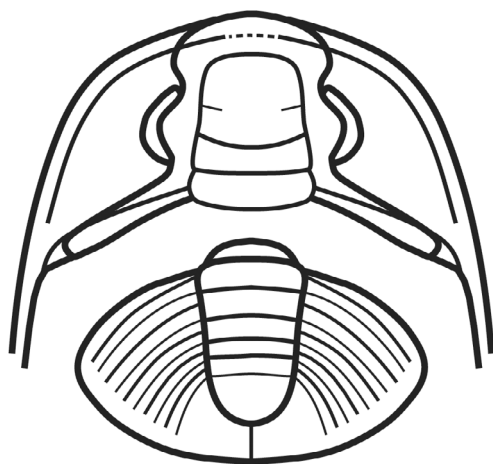


FIG. 58. *Prosaukia* sp. 1 line drawing.

and anterior tip opposite S2; anterior tip slightly more medial than posterior tip; palpebral furrow strongly incised. Fixigena narrow (tr.) with moderately wide preocular areas; anterior suture branches anteriorly divergent from anterior palpebral corners, curving gently adaxially for rounded lateral margins of frontal area; frontal area widest (tr.) point on anterior border furrow. Preglabellar field short, depressed; anterior border furrow straight or very gently curved; anterior border strongly inflated and much longer than prelabellar field.

Remarks. With regards to division and relief of the frontal area, *Prosaukia* sp. 3 is similar to *Prosaukia tarutaoensis* (Kobayashi, 1933a), which also occurs in Ao Mo Lae horizon 3. These species are distinguishable by *Prosaukia* sp. 3's less strongly tapering glabella, narrow LO, and medial embayment in the anterior

glabellar margin. The anterior glabellar tapering of *P. tarutaoensis* varies with size (Wernette *et al.* 2020b), but it is consistently more than the tapering exhibited by *Prosaukia* sp. 3.

Occurrence. Ao Mo Lae h3; Ao Mo Lae Formation; Furongian, Stage 10.

Genus SINOSAUKIA Sun, 1935

Type species. *Sinosaukia pustulosa* Sun, 1935 (pl. 5 figs 1–11, pl. 6 fig. 2). Stage 10, Furongian.

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

Sinosaukia sp.

Figure 54H–J

Material. 1 cranium from ATD S2 h3 (DGSC F0792, internal mould).

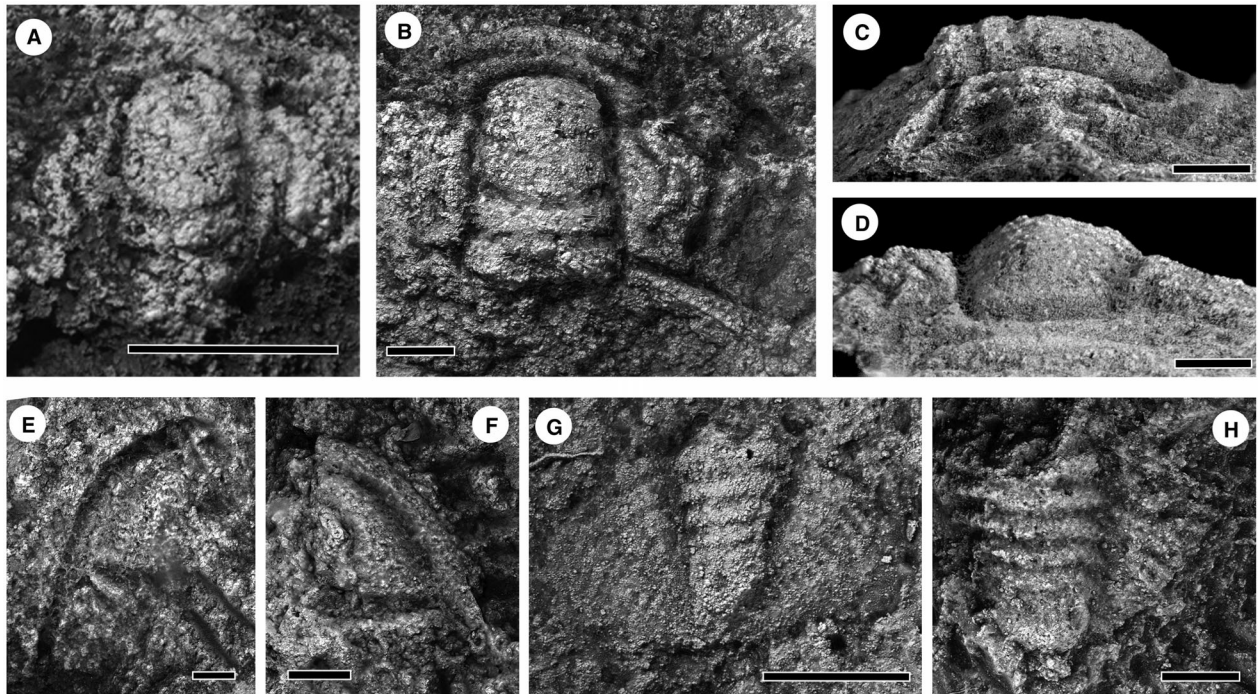


FIG. 59. *Prosaukia* sp. 1. A, DGSC F1744, cranidium. B–D, DGSC F1746, cranidium in: B, dorsal; C, right lateral; D, anterior view. E, DGSC F1748, librigena. F, DGSC F1747, librigena. G, DGSC F1745, pygidium. H, DGSC F1740, pygidium. Scale bars represent 2 mm.



FIG. 60. *Prosaukia* sp. 2 line drawing.

Description. Cranidium subrectangular; width across palpebral areas c. 75% of cranial length excluding anterior border. Glabellar width across S1 c. 65% of width across palpebral areas; frontal area more than 15% of cranial length. Axial furrows subparallel to anteriorly converging from LO to S2 and then sharply anteriorly diverging, resulting in anterior lobe width (tr.) more than 1.2-fold LO width; anterior glabellar margin smoothly curved; LO slightly wider than L1; SO gently posteromedially bowed, laterally deep and medially shallowing; S1 posteromedially bowed and medially shallowing; S2 short (tr.), transversely oriented, and well-defined. Palpebral lobe short and strongly curved, centred opposite S1; posterior palpebral tip opposite anterior L1 and anterior tip opposite S2; anterior tip slightly

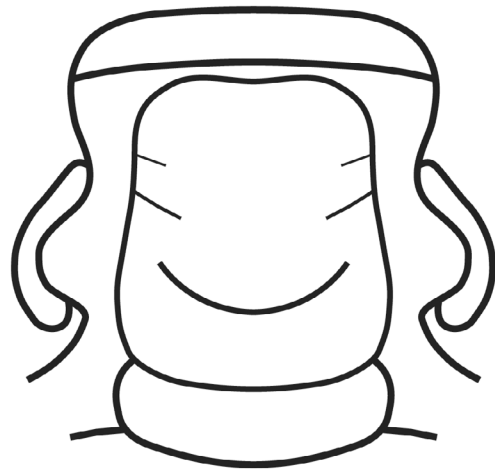


FIG. 61. *Prosaukia* sp. 3 line drawing.

more medial or longitudinally aligned with posterior tip; palpebral furrow weakly incised. Fixigena narrow (tr.) with strap-like preocular areas; anterior suture strongly divergent from anterior palpebral corners, subparallel axial furrows, curving adaxially subconcentrically with anterolateral glabellar corners. Axial furrows and preglabellar furrow deeply incised; anterior border strongly inflated above preglabellar furrow and preocular areas, medially strongly elongated and laterally short.

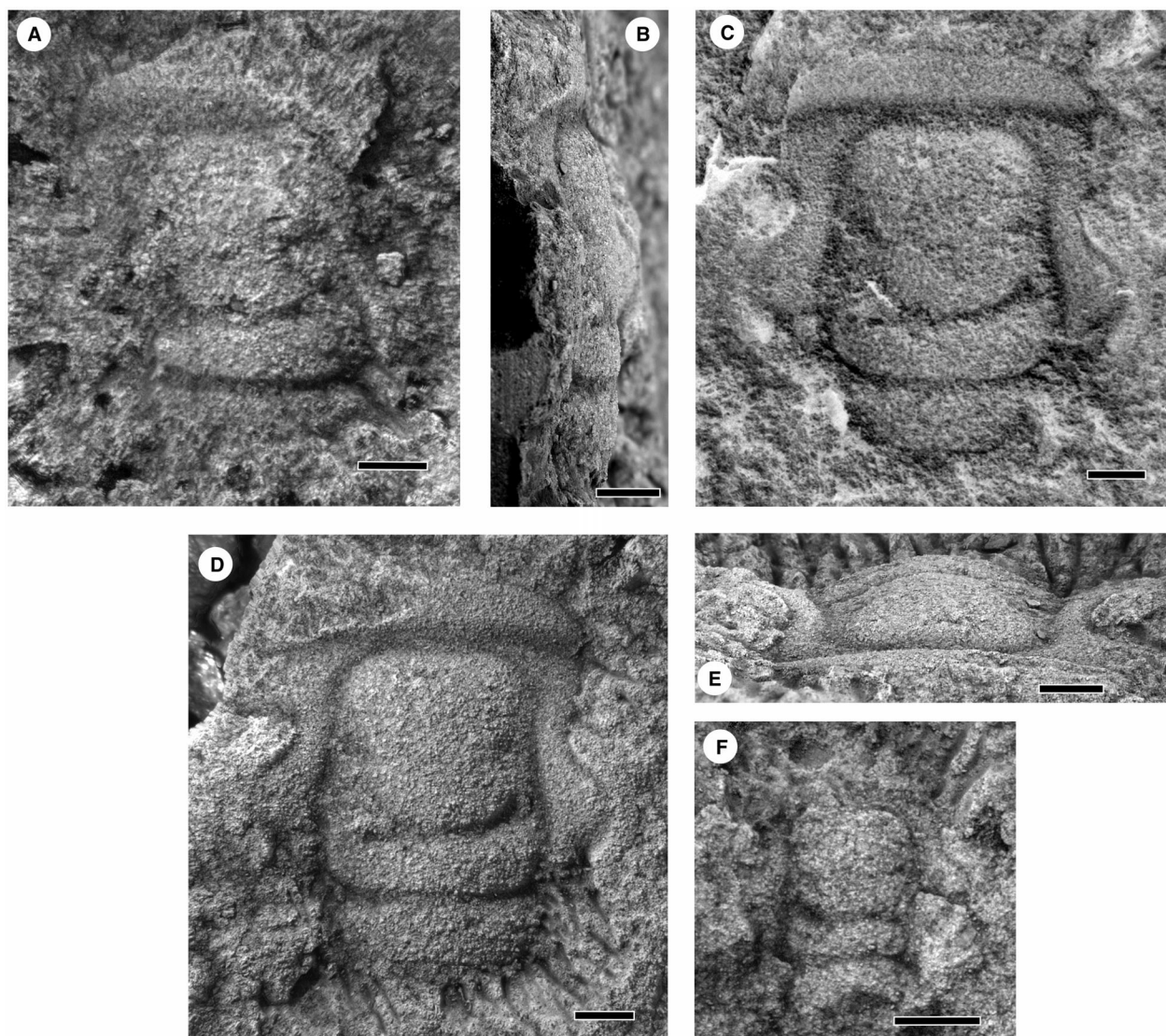


FIG. 62. *Prosaukia* sp. 3, cranidia. A, DGSC F0547. B–E, DGSC F0551: B, left lateral internal mould; C, dorsal internal mould; D, dorsal external mould; E, anterior dorsal mould. F, DGSC F0553. Scale bars represent 2 mm.

Remarks. This single cranidium is assigned to *Sinosaukia* on the basis of having a glabella strongly constricted at L2 and an undifferentiated frontal area, bounded by a broad, deeply incised preglabellar furrow, with a tongue-shaped, anteriorly protruding margin. It differs from *Sinosaukia impages* Shergold, 1975, by having a more strongly protruding frontal area, shorter (exsag.) palpebral lobes, a more strongly constricted glabella, and a longer (sag.), more medially anteriorly protruding anterior margin. With its poorly developed anterior protrusion, relatively long palpebral lobes, and ridges on the librigenal margin, *Sinosaukia impages* should probably be reassigned to *Lophosaukia*. *Sinosaukia* sp. most closely resembles *Sinosaukia pustulosa* Sun, 1935, in its strong dorsal deflection of the anterior border, very short (exsag.) palpebral lobes, and exceptionally deep axial and preglabellar furrows. However, *S. pustulosa* has notable granulation, which is absent in *Sinosaukia* sp.

Occurrence. ATD S2 h3; Ao Mo Lae Formation; Stage 10, Furongian.

Genus THAILANDIUM Kobayashi, 1957

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

Remarks. Wernette *et al.* (2020b) recently re-evaluated *Thailandium* using landmark-based geometric morphometric analysis. They determined that the anterior convergence of the anterior suture branches is a key feature differentiating *Thailandium* and *Prosaukia* Ulrich & Resser, 1933. A relatively flat morphology lacking fixigenal and palpebral inflation or deep incision of

furrows is also distinctive for *Thailandium*. Wernette *et al.* (2020b) found that the only material assigned to *Thailandium* from outside of Thailand (Zhou *et al.* 1977; Shergold 1991) is not congeneric, and therefore *Thailandium* is currently a monospecific genus known exclusively from Thailand.

Thailandium solum Kobayashi, 1957

Figure 63

- 1957 *Thailandium solum* Kobayashi, p. 373, pl. 4, fig. 9 (non figs 10, 11, 12 = *Quadraticephalus planulatus*).
 1957 *Coreanocephalus planulatus* Kobayashi, pl. 4, figs 16–17 only (non figs 13–15 = *Quadraticephalus planulatus*).
 2020b *Thailandium solum* Kobayashi; Wernette *et al.*, p. 74, figs 9, 10.

Additional material. 32 cranidia from AML 3.62 m (DGSC F0568, F0569), 3.72 m (DGSC F0570, F0571), 5.17 m (DGSC F0574), 5.81 m (DGSC F0576, F0583, F0595, F0596, F0598, F0601, F0602, F0606, F0607, F0609, F1162 external mould, CMC IP87611, IP87617, IP87618, IP88969), AML h3 (DGSC F0543, F0544), AML h4 (CMC IP88998), AML h5 (DGSC F0591 external mould, F0618 external mould), and ATTW (DGSC F0388, F0398, F0419, F0421 external mould, F0434, F0435, F0783). 15 librigenae from AML 5.81 m (DGSC F0616, F0612, F0631, F1165, CMC IP87612, IP87622, IP87623),

AML h2 (DGSC F0621, F1227, CMC IP87607), AML h3 (DGSC F0554, F1246), AML h4 (DGSC F1263), ATT 29.17 m (DGSC F0982), and ATTW (DGSC F0418). 10 pygidia from AML 2.20 m (DGSC F0565), 5.81 m (CMC IP87610, DGSC F0509 external mould, F0584 external mould, F0604 external mould, F0610, F0611), AML h4 (DGSC F0560), and ATTW (DGSC F0395, F0420). This list is inclusive of material published in Wernette *et al.* 2020b.

Remarks. Wernette *et al.* (2020b) have recently discussed all known specimens of *Thailandium solum* from the Tarutao Group.

Occurrence. AML 2.20–5.81 m, AML h2–h5, ATTW and ?ATT 29.17 m; Ao Mo Lae Formation; Furongian, Stage 10.

Genus PACOOTASAUKIA Sohn & Choi, 2005

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

Remarks. *Pacootasaukia* accommodates those ‘saukiid’ trilobites with a broad, gently convex preglabellar area that is not differentiated into a border and preglabellar field. Other distinguishing characters include a broad, rectangular glabella, palpebral lobes

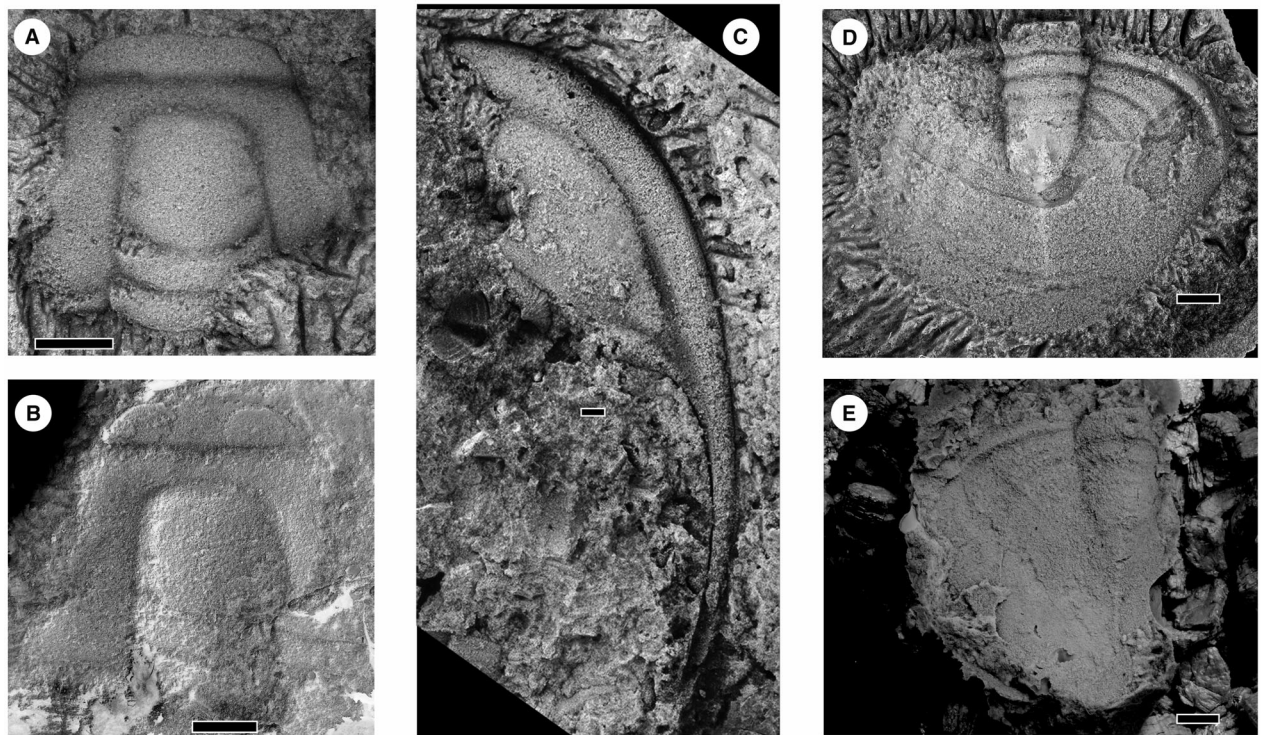


FIG. 63. *Thailandium solum* Kobayashi, 1957. A, DGSC F0609, cranidium. B, CMC IP88037, cranidium, cast of UMUT PA02299b-1, holotype (Kobayashi 1957, pl. 4 fig. 9). C, DGSC F0612, librigena. D, DGSC F0565, pygidium. E, CMC IP88046, pygidium, cast of UMUT PA02299d-1, (Kobayashi 1957, pl. 4 fig. 10). All refigured from Wernette *et al.* 2020b. Scale bars represent 2 mm.

laterally separated from the axial furrows, and a subcircular to fusiform pygidium with well-defined pleural and faint interpleural furrows (Sohn & Choi 2005).

Pacootasaukia sp.

Figure 54K–M

Material. 4 cranidia from AML h5 (DGSC F0619), ATT 8.60 m (DGSC F0828), ATTw (DGSC F0415) and ATD S2 h2 (DGSC F1742).

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

Occurrence. AML h5, ATT 8.60 m, ATD S2 h2 and ATTw; Ao Mo Lae Formation; Furongian, Stage 10.

Order OLENIDA Adrain, 2011

Family DOKIMOCEPHALIDAE Kobayashi, 1935

Genus WUHUIA Kobayashi, 1933a

Type species. *Solenopleura belus* Walcott, 1905; from the Fengshan Formation, Shandong, North China; Stage 10, Furongian.

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

Wuhuia? sp.

Figure 54N–O

Material. 3 cranidia from ATT 22.78 m (DGSC F0482, F0483) and AML 5.81 m (DGSC F1130). 1 librigena from AML h1 (DGSC F1209).

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

Three poorly preserved cranidia from the Ao Mo Lae Formation are similar to *W. belus* (*sensu* Park & Kihm 2015a) in the nearly obsolete fixigena, long palpebral lobes, depressed frontal area, long glabella and long occipital ring. Whether these specimens are synonymous with the material from the Hwajeol Formation cannot be determined due to the poor preservation of the frontal area. The only observable difference is that the specimens from the Ao Mo Lae Formation have narrower (tr.) occipital rings. Thus, while Thai material here assigned to *Wuhuia*? sp. is only questionably conspecific with material from the Hwajeol formation assigned to *W. belus* (*sensu* Park & Kihm 2015a), the Thai and Korean material are almost certainly congeneric. Whether this genus is definitely *Wuhuia* is questionable due to the poorly established genus concept.

Occurrence. ATT 22.78 m and AML 5.81 m and h1; Ao Mo Lae Formation; Furongian, Stage 10.

Order UNCERTAIN

Family EUREKIIDAE Hupé, 1953

Genus CORBINIA Walcott, 1924

Type species. *Corbinia horatio* Walcott, 1924.

Remarks. Westrop & Ludvigsen (1986) re-examined the type species of *Corbinia*, *C. horatio* Walcott, 1924 and restricted the genus to only that type species based a new, more detailed diagnosis. Several species have been added to the genus since then (e.g. Westrop *et al.* 2005) using this diagnosis, which is followed herein. The defining cranidial characters for *Corbinia*-type eurekaids include short (exsag.) palpebral lobes opposite L2 and long (exsag.) and triangular anterolateral projections.

Corbinia perforata sp. nov.

Figures 64A–E, 65

LSID. <https://zoobank.org/NomenclaturalActs/AF9F17F6-FC2C-4151-B322-10B573959C8A>

Derivation of name. Latin for pierced or bored, referring to the pitted anterior border.

Material. Holotype: DGSC F1460 (Fig. 64B–D), cranidium from APM 53.65 m; Talo Wao Formation, Tarutao Group; Ko Tarutao, Thailand; Tremadocian.

Paratypes: 3 cranidia from APM 49.90 (DGSC F1424) and ATD S3 float (DGSC F1776, F1781).

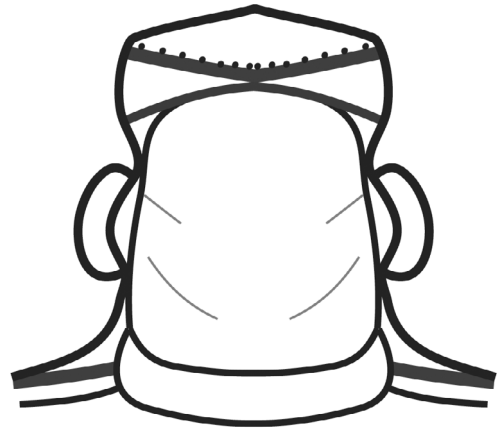


FIG. 65. *Corbinia perforata* sp. nov. line drawing.

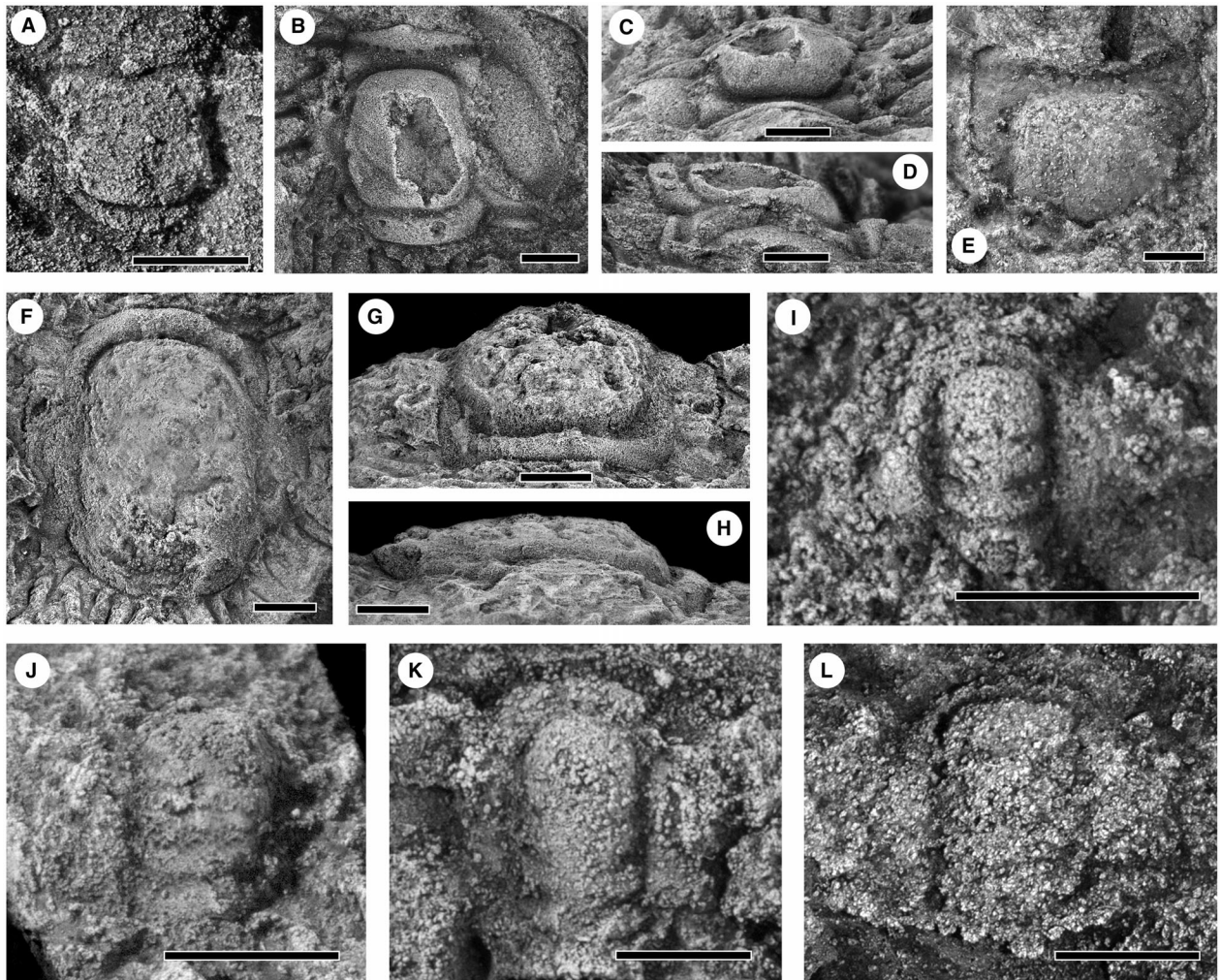


FIG. 64. A–E, *Corbinia perforata* sp. nov.: A, DGSC F1424, cranidium; B–D, DGSC F1460, cranidium in: B, dorsal; C, anterior; D, right lateral view; E, DGSC F1781, cranidium. F–H, *Plethopeltella* sp., DGSC F0975, cranidium in: F, dorsal; G, anterior; H, right lateral view. I–K, *Asiptychaspis* sp.: I, DGSC F1787, cranidium; J, DGSC F1567, cranidium; K, DGSC F1753. L, indeterminate cranidium, DGSC F0629. Scale bars represent: 2 mm (A–E, I–L); 4 mm (F–H).

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

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

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

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

Occurrence. APM 49.90–53.65 m and ATD S3 float; Talo Wao Formation; Tremadocian.

Family PLETHOPELTIDAE Raymond, 1925

Remarks. In Laurentia, the Plethopeltidae are considered an outer-shelf or slope facies until the middle to late Sunwaptan (late Jiangshanian to early Stage 10) and may indicate biogeographical shifts associated with the recovery of biodiversity following the extinction separating the 'Ptychaspid' and 'Symphisurinid' biomes in the latest Furongian (Westrop & Ludvigsen 1987). No studies have yet considered whether the fossil record of Gondwana contains a similar biofacies shift.

Genus PLETOPELTELLA Kobayashi, 1943

Type species. *Plethopeltis resseri* Kobayashi (1933b, p. 280, pl. 6, fig. 6a, b), Fengshan Formation, Wanwankou, Liaoning, China; Stage 10, Furongian.

Remarks. The genus and the diagnosis for *Plethopeltella* have not been notably altered since it was established by Kobayashi (1943). Key attributes include a broad, unfurrowed glabella and narrow fixigenae.

Plethopeltella sp.

Figure 64F–H

Material. One cranium from ATT 28.37 m (DGSC F0975).

Remarks. *Plethopeltella* sp. is similar to *Plethopeltella resseri* (Kobayashi, 1933b), *Plethopeltella shantungensis* (Lu, 1957) and *Plethopeltella* cf. *shantungensis* (*sensu* Shergold *et al.* 2007) in the broad, unfurrowed glabella, facial sutures concentric with the axial and preglabellar furrows, and narrow fixigenae. It differs from these species in having longer (exsag.) palpebral lobes and a pronounced preglabellar furrow. A shallow remnant of the anterior border furrow is also visible distally.

Occurrence. ATT 28.37 m; Ao Mo Lae Formation; Furongian, Stage 10.

Family PTYCHASPIDIDAE Raymond, 1924

Remarks. Descriptions of the order Asaphida (Fortey & Chatterton 1988; Fortey 1990) have caused some researchers to dispute the order's monophyly on the grounds of independent evolution of the ventral median suture in several groups (e.g. Adrain *et al.* 2009; Park & Choi 2009). Park & Choi (2010) demonstrated that Ptychaspidae is one such group that independently developed the ventral median suture and suggested its removal from Asaphida, a position supported by others working on the resolution of higher-level trilobite taxonomy (e.g. Adrain 2011). We follow this conservative taxonomic approach of refraining from assigning Ptychaspidae to an order until further phylogenetic analysis suggests a more reliable grouping.

Genus QUADRATICEPHALUS Sun, 1924

Type species. *Quadratricephalus walcotti* Sun, 1924; from the Kaolishan Limestone, Taian, Shandong, China (by original designation); Stage 10, Furongian.

Remarks. Since their inception, *Quadratricephalus* Sun, 1924, *Changia* Sun, 1924, and *Coreanocephalus* Kobayashi, 1935, have been variably considered valid or synonymized. Resser (1942, p. 48) synonymized *Quadratricephalus* and *Changia*, designating *Quadratricephalus* as the senior synonym given that they were

first described in the same publication and the name *Changia* is easily confused with *Chuangia* Sun, 1924. Zhang & Jell (1987) later added *Coreanocephalus* as a junior synonym of *Changia* (Zhou & Zhang 1984) and therefore also of *Quadraticephalus*. Shergold (1975), however, considered *Changia* and *Quadraticephalus* to be distinct based on the size and position of the palpebral lobes and the shape of the posterolateral projections; the palpebral lobes are smaller and more anteriorly placed and the posterolateral projections are more triangular in *Quadraticephalus*. The palpebral lobes of *Changia* extend posteriorly past S1. Additionally, Shergold (1975) suggested that the anterior border on *Changia* may not be anteroventrally angled, as it is in *Quadraticephalus*. Herein we find that the length and placement of palpebral lobes are subject to ontogenetic and other forms of intraspecific variation with larger specimens especially having palpebral lobes located fully anterior to S1. Given the historical difficulty in differentiating these genera and the morphometric findings described below, this study treats *Changia*, *Quadraticephalus* and *Coreanocephalus* as synonymous and, as per Resser (1942), uses the name *Quadraticephalus* to describe the genus. There may be palaeogeographic, palaeoecological or biostratigraphic merit to continuing to use *Changia* as a subgenus to describe forms with particularly posteriorly extended palpebral lobes, but this is not applied herein.

Quadraticephalus planulatus (Kobayashi, 1957)

Figures 66–68

- 1957 *Coreanocephalus planulatus* Kobayashi, p. 379, pl. 4, figs 13–15 only (non figs 16, 17 = *Thailandium solum*).
 1957 *Thailandium solum* Kobayashi, pl. 4, figs 10–12 only (non fig. 9).
 1986 *Changia planulatus* (Kobayashi); Qian, pl. 74, figs 2, 5, 6, 8–10; pl. 75, fig. 1.
 1988 *Quadraticephalus planulatus* (Kobayashi); Shergold *et al.*, pl. 4, figs H–M (non? fig. N).

Additional material. 69 cranidia from AML 3.62 m (DGSC F1040, CMC IP88940), 5.81 m (DGSC F0338, F0339, F0579, F0633, F1086 external mould, F1092 external mould, F1101, F1117, F1119, F1123, F1136, F1147, CMC IP87615 external mould, IP88951, IP88960 external mould), 5.84 m (CMC IP88973, IP88980 external mould), 6.01 m (CMC IP88966, DGSC F1204), AML h2 (DGSC F0622, F0626, F1234, F1235), AML h4 (DGSC F1260), ATT 5.50 m (DGSC F0809), 8.20 m (DGSC F0824), 8.60 m (DGSC F0834), 8.85 m (DGSC F0846, F0851), 22.78 m (DGSC F0490, F0500, F0516, F0523, F0530, F0865), 22.88 m (DGSC F0889), 23.89 m (DGSC F0940 external mould, F0941), 25.34 m (DGSC F0958, F0968 external mould), 28.37 m (DGSC F0971, F0973, F0976), 29.17 m (DGSC F0988, F0990, F0992, F0996 external mould, F0997, F1001–F1004, F0986, F1007, F1008, F1025, F1026, F1030, F1035, CMC IP88938), ATTw (DGSC F0402, F0406, F0408, F0442, F0762), ATD S2 0.69 m (DGSC F1764) and S2 h2 (DGSC F1739). 8 librigenae from AML 5.81 m (DGSC F0582, CMC IP88956), 5.84 m (DGSC F0365, CMC IP83149), AML h3 (DGSC F0559), AML h4 (DGSC F0561), ATT 29.17 m (DGSC F1019) and

ATTw (DGSC F0400). 20 pygidia from AML 3.62 m (DGSC F1044), 5.81 m (DGSC F1111, F1121, F1129 external mould, F1172), AML h2 (DGSC F1233, F1236), AML h3 (DGSC F0555), AML h4 (DGSC F0563, F1262), ATT 8.85 m (DGSC F0848), 23.89 m (DGSC F0937), 25.34 m (DGSC F0962), 29.17 m (DGSC F0999), ATT h1 (DGSC F0796), ATTw (DGSC F0431, F0437, F0779) and LHN 2.85 m (DGSC F0417).

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

The synonymy of specimens from Kobayashi (1957), Qian (1986) and Shergold *et al.* (1988) has resulted in a species with significant variation in the length of the frontal area, the angularity of the anterior border corners, and the length and exsagittal position of the palpebral lobes. This variation is reflected in the more recent collections presented herein. The two most extreme end members have either short frontal areas with angular corners and short, anteriorly placed palpebral lobes (e.g. Fig. 67AG) or long frontal areas with rounded corners and long palpebral lobes (e.g. Fig. 67H). Without a sample size sufficient to assess whether variation in form is continuous, the end members might be classified as two separate species or even genera.

A landmark-based morphometric analysis was used to determine whether morphological distinctions could be made within the collections from 2008 to 2018. The analysis used 22 landmarks (Fig. 69) and 31 individuals (data available in Wernette *et al.* 2023). The Procrustes superimposition of landmarks, grouped by sampling horizon (Fig. 70), does not show distinct groupings other than suggesting that specimens from ATT's 22.78 m horizon are generally wider in the frontal area and palpebral (= interocular) area but narrower at S1 than most other specimens. Principal component analysis of a thin-plate spline decomposition of the landmark distribution was used to determine whether plausible divisions exist that were not clear from the Procrustes distribution. No clear groupings emerged by which to explain the distribution of scores along relative warps

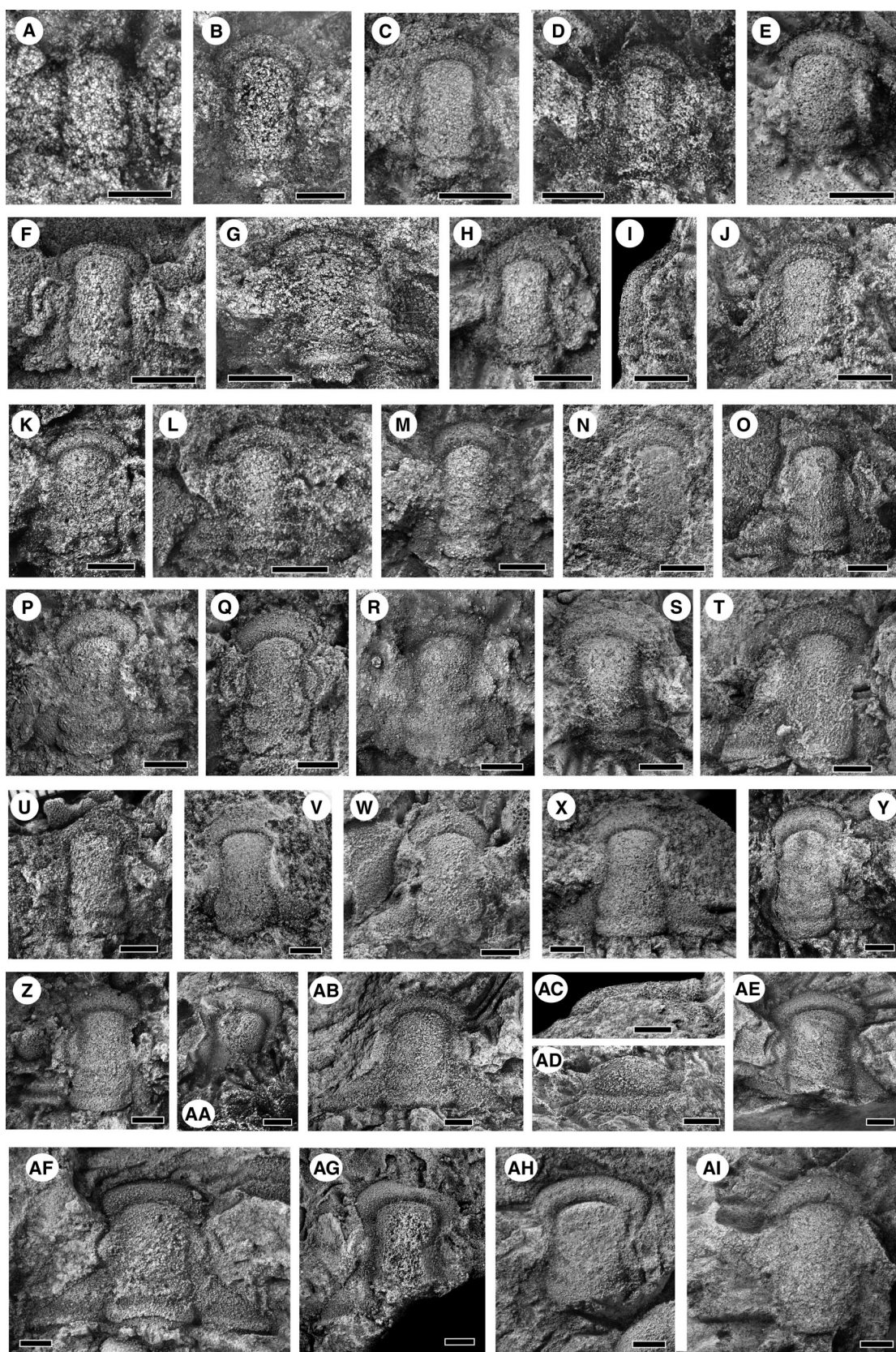


FIG. 66. *Quadraticephalus planulatus* Kobayashi, 1957, cranidia. A, DGSC F1003. B, DGSC F0889. C, DGSC F1002. D, DGSC F1136. E, DGSC F0941. F, DGSC F0976. G, DGSC F0523. H, DGSC F0988. I–J, DGSC F0490 in: I, right lateral; J, dorsal view. K, DGSC F0402. L, DGSC F0516. M, DGSC F0579. N, DGSC F1092, external mould. O, DGSC F0622. P, DGSC F0406. Q, DGSC F1101. R, DGSC F0442. S, DGSC F0992. T, DGSC F1117. U, DGSC F0973. V, DGSC F1086, external mould. W, DGSC F1119. X, DGSC F0339. Y, DGSC F0408. Z, DGSC F1040. AA, DGSC F1007. AB–AD, DGSC F0865 in: AB, dorsal; AC, left lateral; AD, anterior view. AE, DGSC F1004. AF, DGSC F0530. AG, DGSC F0971. AH, DGSC F1030. AI, DGSC F1147. Scale bars represent 1 mm (A, B); 2 mm (C–AI).

(RW) 1 and 2 (Fig. 71; 26.4% and 16.76% of the variance, respectively). There is a general trend for specimens in collections from AML and ATTw to have lower RW1 and RW2 scores than specimens from ATT. AML and ATTw are generally considered to have the most fauna in common, being also the only localities with *Thailandium* and *Satunarcus*. As such, they are likely to be the same depositional age. If these hypotheses about ages are true, then the transition from low RW1 and RW2 in AML and ATTw to more variation and higher scores of each in the ATT section may represent stratigraphical change, although the stratigraphic position of ATT with respect to the other two is not constrained. AML 5.81 m, one of the highest beds at Ao Mo Lae, certainly shows a wider range of scores than in the few specimens known from ATTw and other AML horizons.

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

The variation in eye size has an ontogenetic aspect. A regression analysis using mean Procrustes distance versus the log of the centroid size performed on the same dataset shows that exsagittal position of the posterior palpebral point is size controlled (Fig. 72; $p = 0.0119$ for 1600 bootstraps using the three smallest specimens as the reference). The specimens with high RW2 scores, despite some overlap, are generally smaller than those with lower RW2 scores, supporting that the group differences may reflect ontogeny more than other styles of variation. Such size-related reduction in the relative length of the eye is well known in other trilobite groups, such as the dikelecephalids (e.g. Hughes 1993). The shape of the frontal area is less strongly size related, although there seems to be a general trend for a relatively longer frontal area in larger specimens.

As with the cranidia, there is notable morphological variation among pygidia. The more angular pygidial form that contributed to Qian's (1986) assignment of this taxon to *Changia* and the more rounded pygidial form that contributed to Shergold *et al.* (1988) assigning it to *Quadraticephalus* are end members

linked by variation in the width of the axis, expression of the pygidial border, and expression of interpleural furrows. Both pygidial forms and the bridging spectrum are found in the collections herein (Fig. 68).

Tarutao occurrence. AML 3.62–6.01 m, AML h2, AML h3, AML h4, ATT 5.50–29.17 m, ATT h1, ATTw, LHN 2.85 m, ATD S2 0.69 m and ATD S2 h2; Ao Mo Lae Formation; Furongian, Stage 10.

Gen. et sp. indet.

Figure 64I–K

Material. 4 cranidia from ATD S1 7.00 m (DGSC F1567, F1612, F1787) and S2 0.52 m (DGSC F1753).

Remarks. The glabellar shape, long (exsag.) posterolateral projections and lack of lateral fixigenal expansion in the palpebral areas suggest that this material is most closely related to *Asioptychaspis*. However, the medially continuous S1 and S2 furrow of *Asioptychaspis* are not readily apparent in this poorly preserved material. The relatively short, wide and slightly anteriorly expanding glabella is characteristic of *Asioptychaspis asiatica* Endo & Resser, 1937, but the palpebral lobe is too short and the fixigena too narrow for *A. asiatica*. In the fixigena, these specimens resemble *Asioptychaspis cacus* (Walcott, 1905), but that species is granulated, and no granulation is evident on the specimens from the Tarutao Group, although this is probably due to their coarse preservation, relative to the small mean specimen size, in sandstone. The cranidia from the Tarutao Group are considerably smaller than most known material for *Asioptychaspis*. In consideration of this, doubts about the ontogenetic stages they represent, and poor preservation, we leave these specimens in open nomenclature.

Occurrence. ATD S1 7.00 m and S2 0.52 m; Ao Mo Lae Formation; Furongian, Stage 10.

Family SHUMARDIIDAE Lake, 1907

Genus PARASHUMARDIA Sun & Xiang, 1979

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

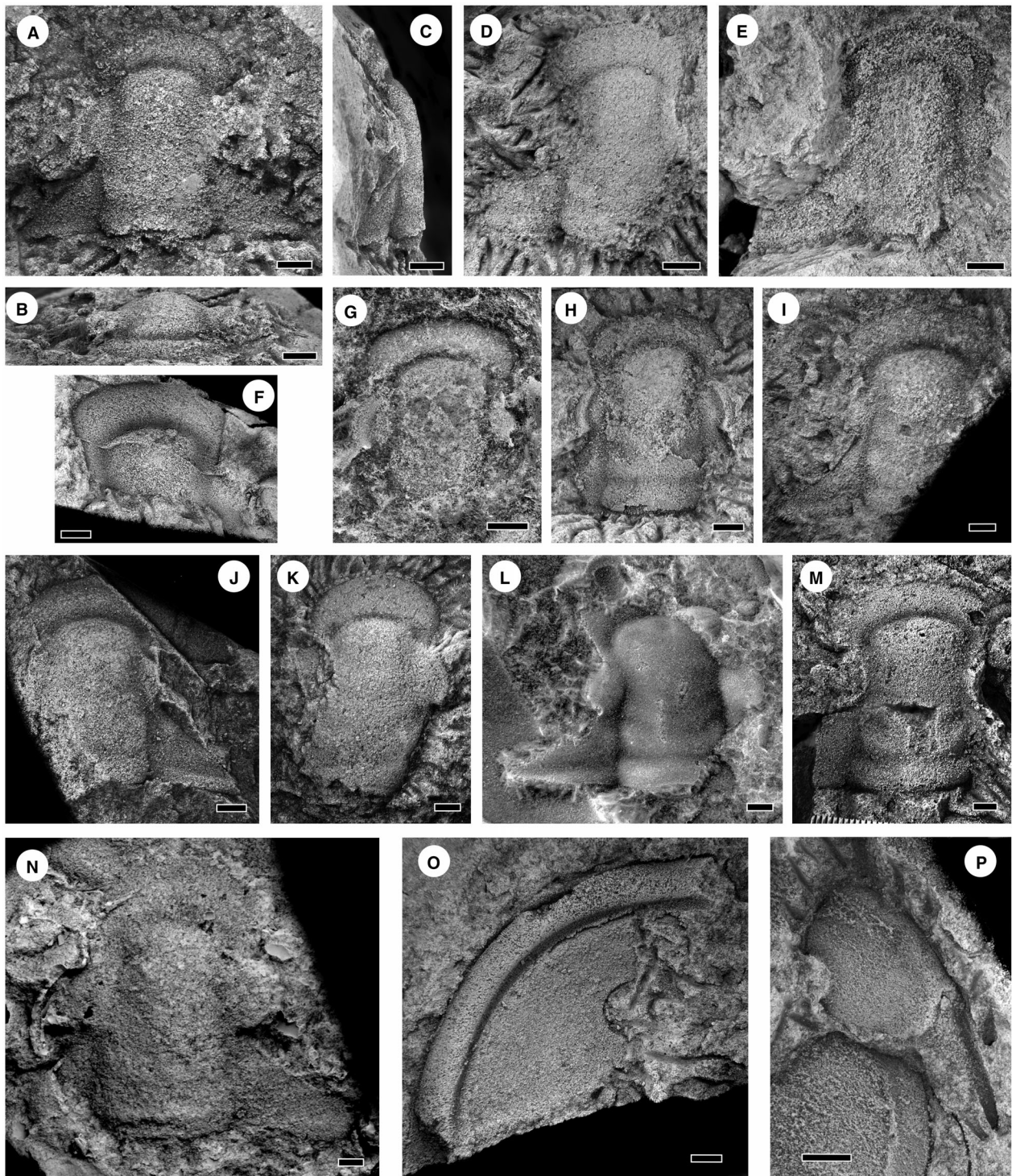


FIG. 67. *Quadraticephalus planulatus* Kobayashi, 1957. A–C, DGSC F1260, cranidium in: A, dorsal; B, anterior; C, left lateral view. D, DGSC F0633, cranidium. E, DGSC F0824, cranidium. F, DGSC F0997, cranidium. G, DGSC F0996, cranidium, external mould. H, DGSC F0809, cranidium. I, DGSSC F1234, cranidium. J, DGSC F1123, cranidium. K, DGSC F1204. L, DGSC F0940, cranidium, external mould. M, DGSC F0851, cranidium. N, CMC IP88048, holotype, cranidium, vinyl polysiloxane cast of UMUT PA02299 (Kobayashi 1957, pl. 4, fig. 13). O, DGSC F0561, librigena. P, DGSC F1019, librigena. Scale bars represent 2 mm.

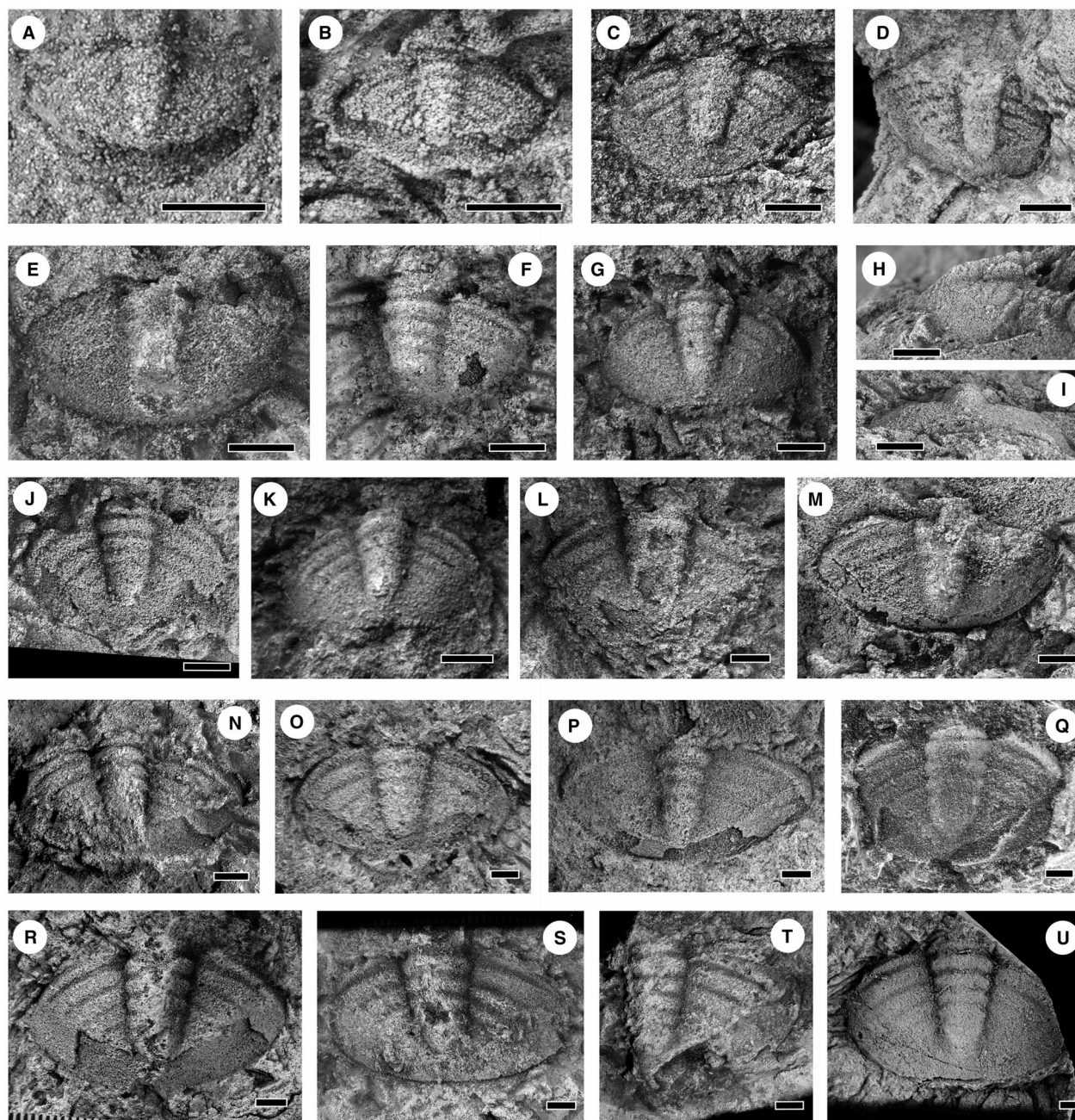


FIG. 68. *Quadraticephalus planulatus* Kobayashi, 1957, pygidia. A, DGSC F0796. B, DGSC F1111. C, DGSC F0417. D, DGSC F1121. E, DGSC F0999. F, DGSC F0937. G–I, DGSC F1044: G, dorsal; H, right lateral; I, posterior view. J, DGSC F0437. K, DGSC F0555. L, DGSC F0563. M, DGSC F0962. N, DGSC F1233. O, DGSC F1244. P, DGSC F0848. Q, DGSC F1129, external mould. R, DGSC F1172. S, DGSC F0779. T, DGSC F1236. U, DGSC F1262. Scale bars represent 2 mm.

Remarks. The concept of *Parashumardia* as a genus is based on the type species, *P. sinensis* Sun & Xiang, 1979 by monotypy when the genus was established. Characters applicable at the genus level include a semicircular cranidium, an anteriorly expanding glabella and a wide pygidium with spines.

Parashumardia sp.

Figure 73K–L

Material. 1 cranidium (DGSC F1285, internal mould) and 1 pygidium (DGSC F1282, external mould) from APM 18.00 m.

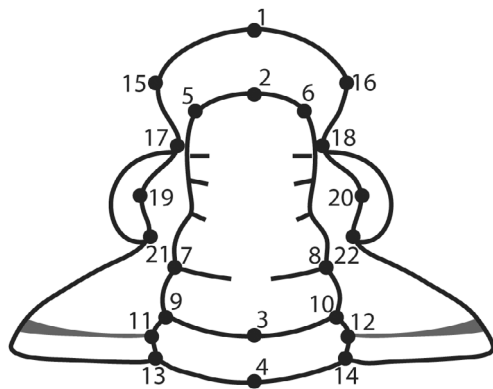


FIG. 69. *Quadraticcephalus* landmark scheme.

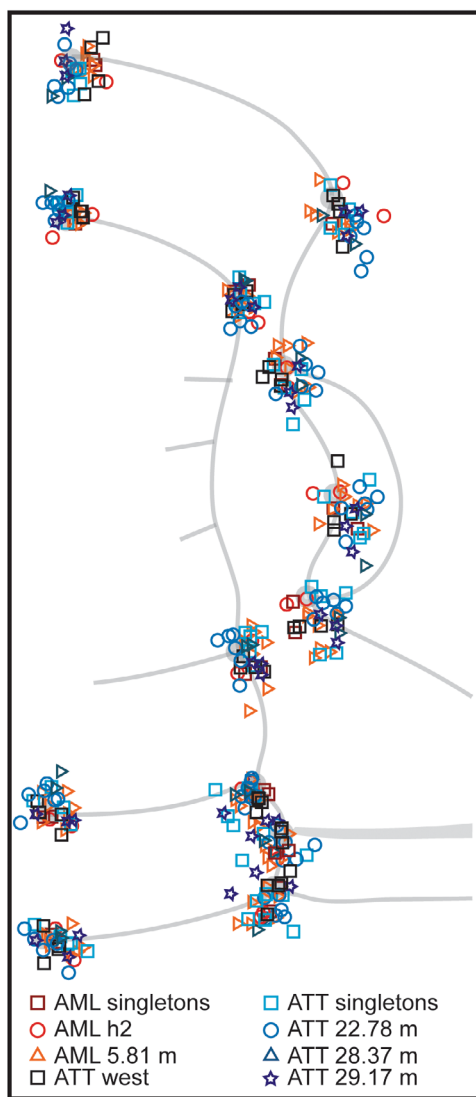


FIG. 70. Distribution of landmarks using Procrustes superimposition. See Figure 69 for landmark scheme. Singletons are those individuals that are the only specimens from their sampling horizons used in the analysis.

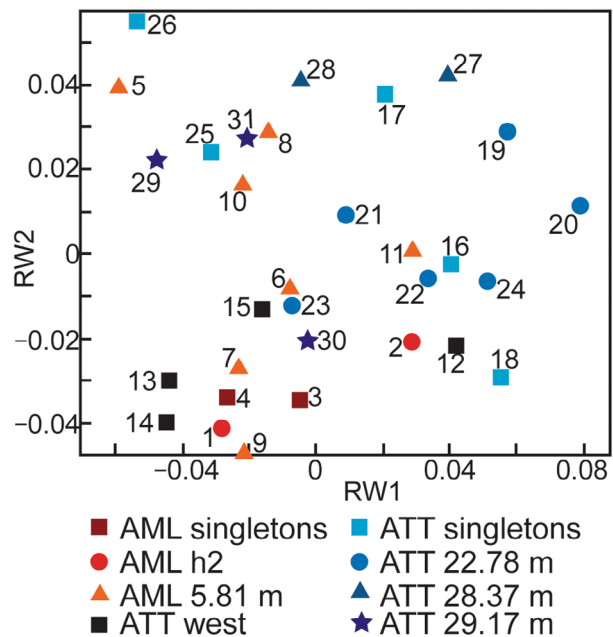


FIG. 71. Relative warps (RW) 1 and 2 from principal component analysis of the Procrustes distribution in Figure 70. RW 1 and 2 account for 26.4% and 16.76% of the variance, respectively. Specimens in analysis: 1, DGSC F0622; 2, DGSC F1234; 3, DGSC F1260; 4, DGSC F1040; 5, DGSC F0579; 6, DGSC F1101; 7, DGSC F1117; 8, DGSC F1136; 9, DGSC F0633; 10, DGSC F1147; 11, DGSC F0339; 12, DGSC F0402; 13, DGSC F0408; 14, DGSC F0406; 15, DGSC F0378; 16, DGSC F0809; 17, DGSC F0824; 18, DGSC F0851; 19, DGSC F0490; 20, DGSC F0865; 21, DGSC F0500; 22, DGSC F0519; 23, DGSC F0523; 24, DGSC F0530; 25, DGSC F0889; 26, DGSC F0968; 27, DGSC F0976; 28, DGSC F0973; 29, DGSC F0988; 30, DGSC F0992; 31, DGSC F1002. Singletons are those individuals that are the only specimens from their respective sampling horizons used in the analysis.

Remarks. *Parashumardia* sp. from the Tarutao group has a broad anterior glabellar lobe that is undifferentiated by furrows from the rest of the glabella. The anterior expansion differentiates it from other shumardiids such as *Akoldinioidia* Zhou in Zhou & Zhang, 1984 and *Koldinioidia* Kobayashi, 1931, and the lack of lateral glabellar furrows differentiates it from *Shumardia* Billings, 1862. The *Parashumardia* type species, *Parashumardia sinensis* Sun & Xiang, 1979, from Baoshan has a similarly shaped and undivided glabella, but the genal field is broader, suggesting that they are not the same species. *Parashumardia* sp. also resembles *Shumardia* sp. (*sensu* Shergold 1991) from the Pacoota Sandstone of the Amadeus Basin, Australia and *Shumardia erquensis* Kobayashi, 1937 (*sensu* Jell 1985) from Digger Island, Victoria, Australia. These three species differ primarily in the posterolateral cranial margin. *Shumardia* sp. (*sensu* Shergold 1991) has a subrounded shape in which the arc formed by the cranial margin exceeds 180°, that is, the posterolateral margin is starting to curve medially. In *S. erquensis* (*sensu* Jell 1985) the posterolateral cranial margin is oriented

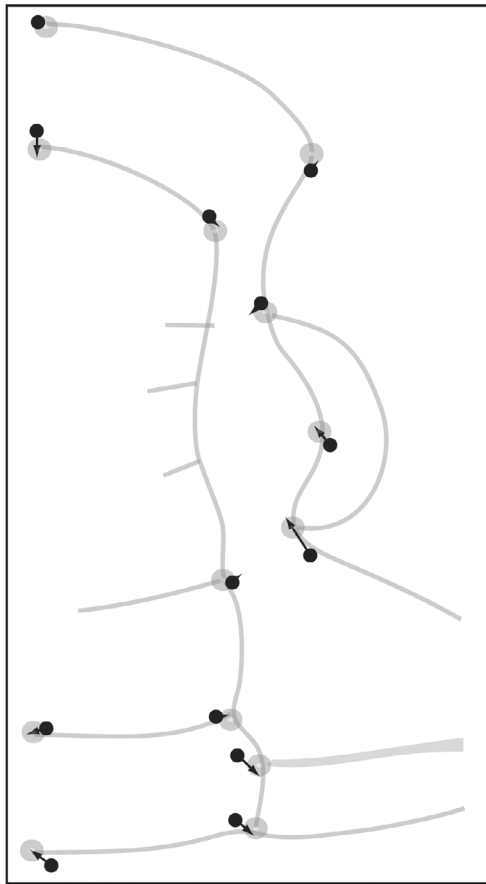


FIG. 72. Deformation pattern produced from regression of Procrustes distance vs log of centroid size using the three smallest specimens as reference ($p = 0.0119$ for 1600 bootstraps).

longitudinally. In *Parashumardia* sp. from the Tarutao Group, the posterolateral margin is strongly posterolaterally oriented. In this respect it resembles *Shumardia alata* Robison & Pantoja-Alor, 1968, but the latter has a considerably broader genal area.

Occurrence. APM 18.00 m; Talo Wao Formation; Tremadocian.

Genus AKOLDINIOIDIA Zhou in Zhou & Zhang, 1984

Type species. *Akoldinioidia pustulosa* Zhou & Zhang, 1984, upper Cambrian of Lulong, Hebei, China (by original designation); Stage 10, Furongian.

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

Akoldinioidia sp. 1

Figure 73A–F

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

Material. 9 cranidia from ATT 29.17 m (CMC IP88937) and LHN 2.85 m (CMC IP83166, IP87619, IP87620, DGSC F0734, F0736 external mould, F0745, F0749, F0753); 1 pygidium from LHN 2.85 m (DGSC F0752).

Remarks. The cranidia of *Akoldinioidia* sp. 1 from the Tarutao Group most closely resembles the silicified cranidia of the Tae-baek Group's *Akoldinioidia lata* Park & Kihm, 2015a (originally *A. latus*, which does not follow genus–species gender agreement) in terms of cranidial dimensions and glabellar furrowing. The single shumardiid pygidium found in the Ao Mo Lae Formation, however, has one fewer axial segment and less inflation of the posterior pleural bands.

Occurrence. ATT 29.17 m, LHN 2.85 m; Ao Mo Lae Formation; Furongian, Stage 10.

Akoldinioidia sp. 2

Figure 73G–J

Material. 4 cranidia from LHN 2.85 m (DGSC F0593), and ATT 22.78 m (DGSC F0506) and 22.88 m (DGSC F0538, F0931).

Remarks. *Akoldinioidia* sp. 2 is similar to *Akoldinioidia* sp. 1 in the broad-based glabella and shape of the cephalic margin. The two species differ in the relative width and outline of the glabella. *Akoldinioidia* sp. 2 has a tapering glabella with a weakly to moderately expanded (tr.) anterior glabellar lobe and weakly to moderately concave glabellar outline. *Akoldinioidia convexalimbata* Qian, 1986, *Akoldinioidia pustulosa* Zhou & Zhang, 1984 and *Akoldinioidia expansa* Qian, 1986 also have a slightly expanded (tr.) anterior glabellar lobe, but in all three of these species the entirety of the glabella is straight or anteriorly expanding whereas the anterior lobe of *Akoldinioidia* sp. is distinctly narrower than LO and L1.

Occurrence. ATT 22.78–22.88 m and LHN 2.85 m; Ao Mo Lae Formation; Furongian, Stage 10.

Genus KOLDINIOIDIA Kobayashi, 1931

Type species. *Koldinioidia typicalis* Kobayashi, 1931 (p. 187).

Remarks. The genus concept of *Koldinioidia* followed herein is the emended diagnosis by Park & Kihm (2015a), which includes a shallow to effaced preglabellar furrow and absent or poorly defined anterolateral lobes.

Koldinioidia sp.

Figure 73M

Material. One cranidium from ATT h1 (DGSC F0794).

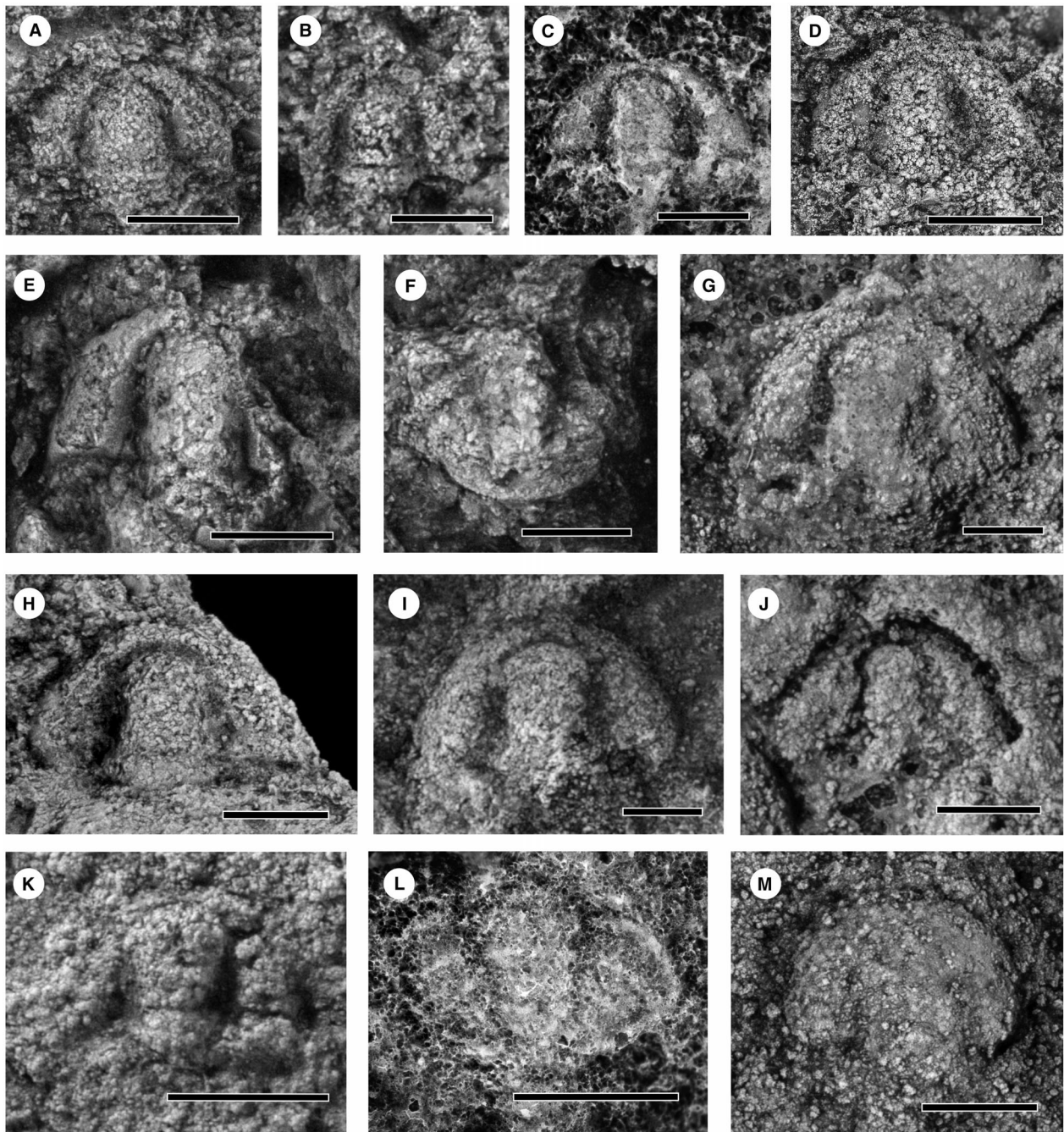


FIG. 73. A–F, *Akoldinioidia* sp. 1: A, DGSC F0753, cranidium; B, DGSC F0745, cranidium; C, DGSC F0736, cranidium, external mould; D, DGSC F0734, cranidium; E, DGSC F0749, cranidium; F, DGSC F0752, pygidium. G–J, *Akoldinioidia* sp. 2, cranidia: G, DGSC F0538; H, DGSC F0593; I, DGSC F0506; J, DGSC F0931; K–L, *Parashumardia* sp.: K, DGSC F1285, cranidium; L, DGSC F1282, pygidium, external mould. M, *Koldinioidia* sp., DGSC F0794, cranidium. Scale bars represent 1 mm.

Remarks. The effacement characteristic of *Koldinioidia* means that there are few characters on which to determine the species assignment. The only specimen recovered from Tarutao further lacks defined posterolateral projections, the curvature of which can be useful in considering species affinity. One of the

few discernible characters is the especially wide glabellar base that accounts for *c.* 50% of cranial width. This is the diagnostic character of *Koldinioidia choii* Park & Kihm, 2015a, which the Tarutao cranidium most closely resembles. However, *K. choii*, known only from silicified cranidia, has a

prominent preglabellar ridge on the ventral surface of the cranidium and would be expected to have a noticeable preglabellar furrow on internal moulds that would not be visible on external moulds. The Tarutao specimen is an internal mould that does not have a preglabellar furrow, instead resembling the dorsal surface of *K. choii*. These are not, therefore, likely to be the same species.

Occurrence. ATT h1; Ao Mo Lae Formation; Furongian, Stage 10.

Indet. harpid
Figure 74

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

Occurrence. AML 5.84 m, Ao Mo Lae Formation; APM 27.80–49.90 m, Talo Wao Formation; Furongian–Tremadocian.

Indet. cranidium
Figure 55L

- ? 1988 Leiostegiid gen. et sp. indet.; Shergold *et al.*, p. 314, fig. 3E.
? 2015a *Saukia? aojii* Kobayashi; Park & Kihm, pp. 190–191, fig. 7.

Material. 1 cranidium from AML h2 (DGSC F0629).

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

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

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

CONCLUSIONS

1. The trilobite fauna of the Tarutao Group is significantly more diverse than previously known, with this work introducing 11 new species and 1 new genus, making for 42 discrete taxa, 25 of which have species-level resolution.
2. The Ao Mo Lae Formation dates to the middle of Cambrian Stage 10, correlative with the *Eosaukia*, *Mictosaukia perplexa* and *Mictosaukia striata* zones of South Korea, Australia and South China, respectively.
3. The Talo Wao Formation is middle Tremadocian where its fauna is most diverse, and may extend down into the lower Tremadocian.
4. Sibumasu's first two formal biozones are erected, the *Eosaukia buravasi* Zone, encompassing all known

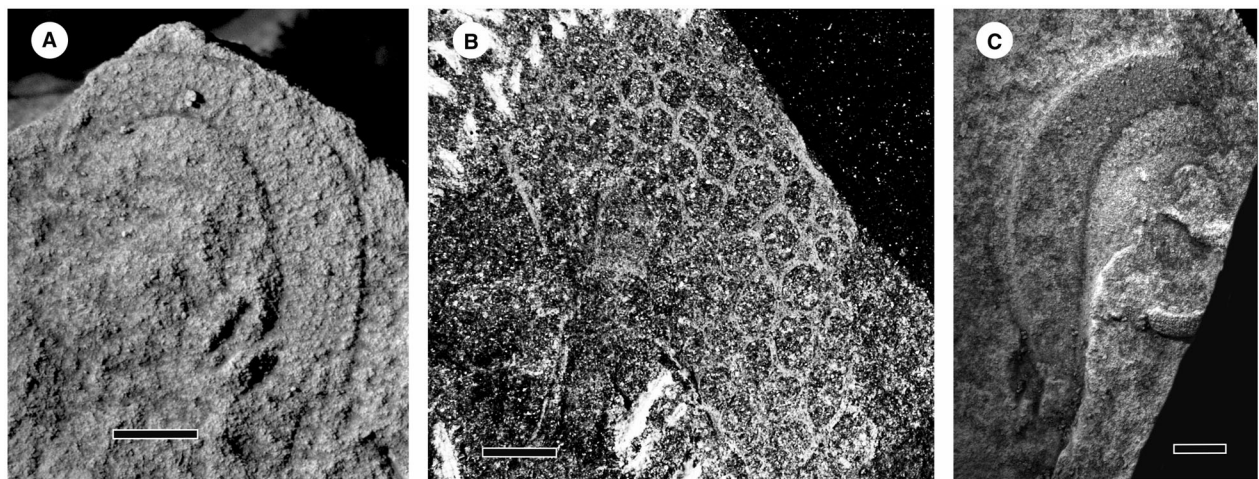


FIG. 74. Indeterminate harpid border. A, DGSC F1421. B, DGSC F1396. C, DGSC F1371. Scale bars represent 2 mm.

sections of the Ao Mo Lae Formation, and the *Asaphellus charoenmiti* Zone, encompassing all known sections of the Talo Wao Formation. Their correlations are as noted in Conclusions 2 and 3 and Figure 12.

5. Shared trilobite species and genera from these formations suggest that during the latest Furongian and early Tremadocian Sibumasu was palaeogeographically associated with South China, North China and Australia, with a less strong, but still notable, association with Kazakhstan. Sibumasu shared more taxa with Laurentia than did most other parts of Gondwana.

Acknowledgements. Our thanks to Thailand's Department of Mineral Resources, particularly Director-General Sommai Techanwan and former Director-General Dr Tawaporn Nuchanong for their support of our field program. We also thank Drs Thanis Wongwanich, Suwapak Imsamut and Jirasak Charoenmit, along with many others from that institution for all their help in the field, and the officers of the Satun Global Geopark for permission to conduct this research. Drs C. P. Lee, Shanchi Peng, Xuejian Zhu, Cody Collops and the participants of IGCP 668's inaugural meeting and excursion also collected enthusiastically in the field. Likewise, thanks to Dr Gabriela Mangano and others for identifying and discussing trace fossils on the IPC6/IGCP668 excursion in 2022. We thank Dr Seung-bae Lee for photographs of some of Kobayashi's type material. Thank you to Dr Takenori Sasaki at the University of Tokyo University Museum for helping us access and make casts of the Kobayashi (1957) type material, and to Dr Yutaro Susuki and Ms Setsu Makino for their help with arrangements there. Thank you also to Dr Rhiannon LaVine for consulting on agnostids. Drs Peter Jell and Tae-Yoon Park are much appreciated for their thoughtful reviews and the many improvements those brought to this work. This study was funded partly by student grants from the Geological Society of America, the American Museum of Natural History (Lerner-Gray Memorial Fund), the Evolving Earth Foundation, the American Association of Petroleum Geologists (David Worthington Named Grant) and the Paleontological Society (Allison R. 'Pete' Palmer Grant). Additional funds are from the National Science Foundation grants EAR-1849963, EAR-1124303 and EAR-053868 to NCH and EAR-1849968 and EAR-1124518 to PMM. NCH acknowledges receipt of Fulbright Academic and Professional Excellence Award 2019 APE-R/107 and thanks the Geological Studies Unit, Indian Statistical Institute, Kolkata for kindly hosting him. This study is a contribution towards IGCP 668: Equatorial Gondwanan History and Early Palaeozoic Evolutionary Dynamics.

Author contributions. **Conceptualization** NC Hughes (NCH), PM Myrow (PMM), SJ Wernette (SJW); **Data Curation** NCH, SJW; **Formal Analysis** SJW; **Funding Acquisition** NCH, PMM, SJW; **Investigation** SJW, A Sardsub, NCH, PMM; **Methodology** NCH, PMM, SJW; **Project Administration** NCH, SJW; **Resources** NCH, SJW; **Software** SJW; **Supervision** NCH; **Validation** NCH, PMM, SJW; **Writing – Original Draft**

Preparation SJW, NCH, PMM; **Writing – Review & Editing** SJW, NCH, PMM.

DATA ARCHIVING STATEMENT

This published work, and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/0B69BE5E-D947-4DD9-AC84-F73AEA6376A7>

Data for this study, including the point coordinates for each specimen used in the morphometric studies, are available in the Dryad Digital Repository: <https://doi.org/10.6086/D1697P>

Editor. Javier Álvaro

REFERENCES

- ADRAIN, J. M. 2011. Class Trilobita Walch, 1771. In ZHANG, Z.-Q. (ed.) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. *Zootaxa*, **3148**, 104–109.
- ADRAIN, J. M. and WESTROP, S. R. 2004. A Late Cambrian (Sunwaptan) silicified trilobite fauna from Nevada. *Bulletins of American Paleontology*, **365**, 1–262.
- ADRAIN, J. M., FORTEY, R. A. and WESTROP, S. R. 1998. Post-Cambrian trilobite diversity and evolutionary faunas. *Science*, **280**, 1922–1925.
- ADRAIN, J. M., PETERS, S. E. and WESTROP, S. R. 2009. The Marjuman trilobite *Cedarina* Lochman: thoracic morphology, systematics, and new species from western Utah and eastern Nevada, USA. *Zootaxa*, **2218**, 35–58.
- AGEMATSU, S., SASHIDA, K., SALYPONGSE, S. and SARDSUD, A. 2008. Early Ordovician conodonts from Tarutao Island, southern peninsular Thailand. *Palaeontology*, **51**, 1435–1453.
- AKERMAN, T. 1986. The Geology of the Lower Palaeozoic Tarutao Formation, Tarutao Island, Southern Thailand. Unpublished Honours thesis, University of Tasmania, 84 pp.
- APOLLONOV, M. K. 1975. Ordovician trilobite assemblages of Kazakhstan. *Fossils & Strata*, **4**, 375–380.
- ARNOTT, R. W. and SOUTHARD, J. B. 1990. Exploratory flow-duct experiments on combined-flow bed configurations, and some implications for interpreting storm-event stratification. *Journal of Sedimentary Petrology*, **60**, 211–219.
- AUNG, A. K. and COCKS, L. R. M. 2017. Chapter 14. Cambrian–Devonian stratigraphy of the Shan Plateau, Myanmar (Burma). *Memoirs of the Geological Society of London*, **48**, 317–342.
- BABCOCK, L. E., PENG, S.-C. and AHLBERG, P. 2017. Cambrian trilobite biostratigraphy and its role in developing an integrated history of the Earth system. *Lethaia*, **50**, 381–399.
- BASSLER, R. S. 1915. Bibliographic index of American Ordovician and Silurian fossils. Volume 1. *Bulletin of the United States National Museum*, **97**, 1–718.

- BELT, T. 1867. On some new trilobites from the Upper Cambrian rocks of North Wales. *Geological Magazine*, **4**, 294–295.
- BENDER, F. 1983. *Geology of Burma*. Gebrüder Borntraeger, Berlin, 293 pp.
- BILLINGS, E. 1862. *Palaeozoic fossils. Vol. I (2)*. Geological Survey of Canada. Dawson Brothers, Montreal. <https://doi.org/10.5962/bhl.title.69671>
- BOECK, C. P. B. 1838. Uebersicht der bisher in Norwegen gefundenen Formen der Trilobiten-Familie. *Gaea Norvegica*, **1**, 138–145.
- BORDONARO, O. 2003. Review of the Cambrian stratigraphy of the Argentine Precordillera. *Geologica Acta*, **1**, 11–21.
- BRADLEY, J. H. 1925. Trilobites of the Beekmantown in the Phillipsburg region of Quebec. *Canadian Field Naturalist*, **39**, 5–9.
- BRINCKMANN, J. and HINZE, C. 1981. On the geology of the Bawdwin lead-zinc mine, northern Shan State, Burma. *Geologisches Jahrbuch*, **D43**, 7–45.
- BRÖGGER, W. G. 1896. Ueber die Verbreitung der *Euloma-Niobe* Fauna (der Ceratopygen-kalkfauna) in Europa. *Nyt Magazin for Naturvidenskaberne*, **35**, 16–24.
- BRONGNIART, A. 1822. Les Trilobites. 1–65, pls 1–2. In BRONGNIART, A. and DESMAREST, A.-G. (eds) *Histoire naturelle des crustacés fossiles, sous les rapports zoologiques et géologiques*. Levrault, Paris, 154 pp.
- BUNOPAS, S. and VELLA, P. 1978. Late Palaeozoic and Mesozoic structural evolution of Thailand. 133–140. In NUTALAYA, P. (ed.) *Proceedings of the 3rd regional conference on geology and mineral resources of Southeast Asia*. Asian Institute of Technology, Bangkok.
- BUNOPAS, S., MUENLEK, S. and TANSUWAN, V. 1983. Geology of Tarutao Island. *Journal of the Geological Society of Thailand*, **6**, 121–138.
- BURMEISTER, H. 1843. *Die Organisation der Trilobiten aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Uebersicht aller zeither beschriebenen Arten*. Reimer, Berlin, 147 pp. [in German]
- BURRETT, C. and CHAODUMRONG, P. 2017. *Summary of the geology and palaeontology of the proposed Satun Geopark peninsular Thailand*. Royal Thai Department of Mineral Resources, Bangkok, 100 pp.
- BURRETT, C., KHIN, Z., MEFFRE, S., LAI, C. K., KHOSITANOT, S., CHAODUMRONG, P., UDCHACHON, M., EKINS, S. and HALPIN, J. 2014. The configuration of Greater Gondwana: evidence from LA ICPMS, U–Pb geochronology of detrital zircons from the Palaeozoic and Mesozoic of Southeast Asia and China. *Gondwana Research*, **26**, 31–51.
- BURRETT, C., UDCHACHON, M. and THASSANAPAK, H. 2016. Palaeozoic correlations and the palaeogeography of the Sibumasu (Shan-Thai) Terrane: a brief review. *Research & Knowledge*, **2**, 1–17.
- CALLAWAY, C. 1877. On a new area of Upper Cambrian rocks in South Shropshire, with a description of a new fauna. *Quarterly Journal of the Geological Society of London*, **33**, 652–672.
- CAWOOD, P. A., JOHNSON, M. R. W. and NEMCHIN, A. A. 2007. Early Palaeozoic orogenesis along the Indian margin of Gondwana: tectonic response to Gondwana assembly. *Earth & Planetary Science Letters*, **255**, 70–84.
- CHATTERTON, B. D. E. and LUDVIGSEN, R. 1998. Upper Steptoean (Upper Cambrian) trilobites from the McKay Group of southeastern British Columbia, Canada. *Journal of Paleontology*, **72**, 1–43.
- CHOI, D.-K., LEE, J.-G. and SHEEN, B. C. 2004. Upper Cambrian agnostoid trilobites from the Machari Formation, Yongwol, Korea. *Geobios*, **37**, 159–189.
- CHOI, D.-K., LEE, J.-G., LEE, S.-B., PARK, T.-Y. and HONG, P. S. 2016. Trilobite biostratigraphy of the lower Palaeozoic (Cambrian-Ordovician) Joseon Supergroup, Taebaeksan Basin, Korea. *Acta Geologica Sinica*, **90**, 1976–1999.
- COCKS, L. R. M. and TORSVIK, T. H. 2013. The dynamic evolution of the Palaeozoic geography of eastern Asia. *Earth-Science Reviews*, **117**, 40–79.
- COCKS, L. R. M., FORTEY, R. A. and LEE, C.-P. 2005. A review of lower and middle Palaeozoic biostratigraphy in west peninsular Malaysia and southern Thailand in its context within the Sibumasu Terrane. *Journal of Asian Earth Sciences*, **24**, 703–717.
- DALMAN, J. W. 1827. Om Palaeaderna eller de så kallade Trilobiterna. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **1826**, 113–162, 226–294.
- DOMIER, M. 2018. Early Paleozoic tectonics of Asia: towards a full-plate model. *Geoscience Frontiers*, **9**, 789–862.
- DOTT, R. H. Jr and BOURGEOIS, J. 1982. Hummocky stratification: significance of its variable bedding sequences. *Geological Society of America Bulletin*, **93**, 663–680.
- EBBESTAD, J. O. R. 1999. Trilobites of the Tremadoc Bjørkåsholmen formation in the Oslo Region, Norway. *Fossils & Strata*, **47**, pp. 118.
- ENDO, R. 1944. Restudies on the Cambrian formations and fossils in southern Manchoukuo. *Bulletin of the Central National Museum of Manchoukuo*, **7**, 1–100.
- ENDO, R. and RESSER, C. E. 1937. The Sinian and Cambrian formations and fossils of southern Manchoukuo. *Manchurian Science Museum Bulletin*, **1**, 23–365.
- ERGALIEV, G. K. 1980. *Middle and Upper Cambrian trilobites from Maly Karatau*. Akademiya Nauk Kazakhskoi SSR, Alma-Ata, 211 pp. [in Russian]
- ERGALIEV, G. K. and ERGALIEV, F. G. 2008. *Agnostidy srednego i verkhnego Kembriya Aksayskogo Gosudarstvennogo Geologicheskogo Zakaznika v yushnom Kazakhstane (Kyrshabakty, Maly Karatau)* [Middle and Upper Cambrian Agnostida from the Aksai National Geological Reserve in southern Kazakhstan (Kyrshabakty River, Maly Karatau Range)]. Palaeontological Institute, Almaty, Gylm, 359 pp.
- ERGALIEV, G. K., ZHEMCHUZHNIKOV, V. A., ERGALIEV, F. G., POPOV, L. E., GHOBADI POUR, M. and BASSETT, M. G. 2008. Trilobite biostratigraphy and biodiversity patterns through the Middle-Upper Cambrian transition in the Kyrshabakty section, Malyi Karatau, southern Kazakhstan. *Advances in Trilobite Research*, **9**, 91–98.
- FORTEY, R. A. 1990. Ontogeny, hypostome attachment, and trilobite classification. *Palaeontology*, **33**, 529–576.

- FORTEY, R. A. 1997. Late Ordovician trilobites from southern Thailand. *Palaeontology*, **40**, 397–469.
- FORTEY, R. A. and CHATTERTON, B. D. E. 1988. Classification of the trilobite Suborder Asaphina. *Palaeontology*, **31**, 165–222.
- FORTEY, R. A. and OWENS, R. M. 1991. A trilobite fauna from the highest Shinton Shales in Shropshire, and the correlation of the latest Tremadoc. *Geological Magazine*, **128**, 437–464.
- FORTEY, R. A. and RUSHTON, A. W. A. 1976. *Chelidonecephalus* trilobite fauna from the Cambrian of Iran. *Bulletin of the British Museum of Natural History, Geology*, **27**, 321–340.
- FREEMAN, R. L., MILLER, J. F. and DATTILO, B. F. 2018. Linguliform brachiopods across a Cambrian–Ordovician (Furongian, Early Ordovician) biomere boundary: the Sunwaptan–Skullrockian North American Stage boundary in the Wilberns and Tanyard formations of central Texas. *Journal of Paleontology*, **92**, 751–767.
- GEYER, G. and SHERGOLD, J. H. 2000. The quest for internationally recognized divisions of Cambrian time. *Episodes*, **23**, 188–195.
- GHOBADI POUR, M. 2006. Early Ordovician (Tremadocian) trilobites from Simeh-Kuh, Eastern Alborz, Iran. 93–118. In BASSETT, M. G. and DEISLER, V. K. (eds) *Studies in Palaeozoic palaeontology*. National Museum of Wales Geological Series, **25**.
- HAINES, P. W. and WINGATE, M. T. D. 2005. Contrasting depositional histories, detrital zircon provenance and hydrocarbon systems: did the Larapintine Seaway link the Canning and Amadeus basins during the Ordovician. 16–18. In MUNSON, T. J. and AMBROSE, G. J. (eds) *Proceedings of the Central Australian Basins Symposium (CABS), Alice Springs Northern Territory, 16–18 August 2005*. Northern Territory Geological Survey, NTGS Special Publication, **2**.
- HALL, J. 1863. Preliminary notice of the fauna of the Potsdam sandstone, with remarks upon the previously known species of fossils, and description of some new ones from the sandstones of the Upper Mississippi Valley. *Report of the New York State Cabinet of Natural History*, **16**, 119–222.
- HAMDI, B., ROZANOV, A. Y. and ZHURAVLEV, A. Y. 1995. Latest Middle Cambrian metazoan reef from northern Iran. *Geological Magazine*, **132**, 367–373.
- HARRINGTON, H. J. 1938. Sobre las faunas del Ordoviciano Inferior del Norte Argentino. *Revista del Museo de La Plata, Sección Paleontología, New Series*, **1**, 109–289.
- HARRINGTON, H. J. 1957. Notes on new genera of Plimeridae (Trilobita). *Journal of Paleontology*, **31**, 811–812.
- HARRINGTON, H. J. and KAY, M. 1951. Cambrian and Ordovician faunas of Eastern Colombia. *Journal of Paleontology*, **25**, 655–668.
- HARRINGTON, H. J. and LEANZA, A. F. 1957. Ordovician trilobites of Argentina. *Special Publications, Department of Geology, University of Kansas*, **1**, 1–276.
- HAWLE, I. and CORDA, A. J. C. 1847. Prodrum einer Monographie der böhmischen Trilobiten. *Abhandlungen Kongl. Böhmerischen Gesellschaft der Wissenschaften*, **5** (5), 1–176.
- HINTZE, L. F. 1951. Lower Ordovician detailed stratigraphic sections for western Utah. *Utah Geological & Mineralogical Survey. Bulletin*, **39**, 99.
- HOWELL, B. F. 1935. Some New Brunswick Cambrian agnostians. *Bulletin of the Wagner Free Institute of Science (Philadelphia)*, **10**, 13–16.
- HUGHES, N. C. 1993. Distribution, taphonomy, and functional morphology of the Upper Cambrian trilobite *Dikelocephalus*. *Milwaukee Public Museum Contributions in Biology & Geology*, **84**, 1–49.
- HUGHES, N. C. 1994. Ontogeny, intraspecific variation, and systematics of the Late Cambrian trilobite *Dikelocephalus*. *Smithsonian Contributions to Paleobiology*, **79**, 1–89.
- HUGHES, N. C. 2000. Ecologic evolution of Cambrian trilobites. 370–403. In ZHURAVLEV, A. Y. and RIDING, R. (eds) *The ecology of the Cambrian radiation*. Columbia University Press.
- HUGHES, N. C. 2003. Trilobite tagmosis and body patterning from morphological and developmental perspectives. *Integrative & Comparative Biology*, **41**, 185–206.
- HUGHES, N. C. 2016. The Cambrian palaeontological record of the Indian subcontinent. *Earth-Science Reviews*, **159**, 428–461.
- HUGHES, N. C., MINELLI, A. and FUSCO, G. 2006. The ontogeny of trilobite segmentation: a comparative approach. *Paleobiology*, **32**, 602–627.
- HUGHES, N. C., MYROW, P. M., MCKENZIE, N. R., HARPER, D. A. T., BHARGAVA, O. N., TANGRI, S. K., GHALLEY, K. S. and FANNING, C. M. 2011. Cambrian rocks and faunas of the Wachi La, Black Mountains, Bhutan. *Geological Magazine*, **148**, 351–379.
- HUGHES, N. C., PENG, S.-C., HARPER, D. A. T., MYROW, P. M., PHAM, N. K., WERNETTE, S. J. and ZHU, X.-J. 2022. Cambrian and earliest Ordovician fauna and geology of the Sông Đà and adjacent terranes in Việt Nam (Vietnam). *Geological Magazine*, **159**, 55–80.
- HUPÉ, P. 1953. Classification des trilobites [Part I]. *Annales de Paleontologie*, **39**, 61–168.
- HUPÉ, P. 1955. Classification des trilobites [Part II]. *Annales de Paleontologie*, **41**, 91–325.
- IMSAMUT, S. and YATHAKAM, W. 2011. *Stratigraphic correlation of the Tarutao-Langkawi, area, (Thai side)*. Report of the Bureau of Geological Survey, DMR, Bangkok, Thailand, 64 pp.
- JAANUSSON, V. 1959. Suborder Asaphina Salter, 1864. 334–365. In MOORE, R. C. (ed.) *Treatise on invertebrate paleontology. Part O. Arthropoda 1*. Geological Society of America & University of Kansas Press.
- JAEEKEL, O. 1909. Über die Agnostiden. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **61**, 380–400. [in German]
- JAVANAPHET, J. C. 1969. Geological Map of Thailand, scale 1:1,000,000. Department of Mineral Resources, Bangkok, Thailand.
- JELL, P. A. 1985. Tremadoc trilobites of the Digger Island Formation, Waratah Bay, Victoria. *Memoirs of the Museum of Victoria*, **46**, 53–88.
- JELL, P. A. and ADRAIN, J. M. 2002. Available generic names for trilobites. *Memoirs of the Queensland Museum*, **48**, 331–552.
- KAYSER, E. 1876. Über primordiale und untersilurische Fossilien aus der Argentinischen Republik. In STELZNER, A. W.

- (ed.) *Beiträge zur Geologie und Palaeontologie der Argentinischen Republik*, Vol. 2. T. Fischer, Kassel *Palaeontographica* 1900, Suppl. 3, pp. 1–33. [in German]
- KIDWELL, S. M. 1991. The stratigraphy of shell concentrations. 211–290. In ALLISON, P. A. and BRIGGS, E. G. (eds) *Taphonomy: Releasing the data locked in the fossil record*. Topics in Geobiology, 9. Plenum Press.
- KIHM, J.-H., PARK, T.-Y. and CHOI, D. K. 2013. Ontogeny of the ptychaspidid trilobite *Quadricephalus elongatus* Kobayashi, 1935 from the Furongian (late Cambrian) Hwajaeol Formation, Korea. *Journal of Paleontology*, **87**, 379–390.
- KIM, D. H. and CHOI, D. K. 2000. *Jujuyaspis* and associated trilobites from the Mungok Formation (Lower Ordovician), Yongwol, Korea. *Journal of Paleontology*, **74**, 1031–1042.
- KOBAYASHI, T. 1931. Studies on the stratigraphy and palaeontology of the Cambro-Ordovician formation of Hualienchai and Niuhsintai, south Manchuria. *Japanese Journal of Geology & Geography*, **8**, 131–189.
- KOBAYASHI, T. 1933a. Upper Cambrian of the Wuhutsui Basin, Liaotung, with special reference to the limit of the Chaumtien (or Upper Cambrian) of eastern Asia, and its subdivision. *Japanese Journal of Geology & Geography*, **11**, 55–155.
- KOBAYASHI, T. 1933b. Faunal study of the Wanwanian (basal Ordovician) Series with special notes on the Ribeiridae and the ellesmereoceroids. *Journal of the Faculty of Science, Imperial University of Tokyo, Section 2: Geology*, **3** (7), 249–328.
- KOBAYASHI, T. 1934. The Cambro-Ordovician Formations and Faunas of South Chosen. Palaeontology. Part 2: Lower Ordovician Faunas. *Journal of the Faculty of Science of the Imperial University of Tokyo, Section 2: Geology*, **3**, 521–585.
- KOBAYASHI, T. 1935. The Cambro-Ordovician Formations and Faunas of South Chosen. Palaeontology. Part 3. Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. *Journal of the Faculty of Science, Imperial University of Tokyo, Section 2: Geology*, **4** (2), 49–344.
- KOBAYASHI, T. 1936. Notes on nomenclature of some Cambro-Ordovician genera. *Journal of the Geological Society of Japan*, **43** (519), 922.
- KOBAYASHI, T. 1937. The Cambro-Ordovician shelly faunas of South America. *Journal of the Faculty of Science, Imperial University of Tokyo, Section 2: Geology*, **4** (2), 369–522.
- KOBAYASHI, T. 1942. The Rakuroan complex of the Shansi Basin and its surroundings, miscellaneous notes on the Cambro Ordovician geology and palaeontology. *Japanese Journal of Geology & Geography*, **28**, 283–306.
- KOBAYASHI, T. 1943. Cambrian faunas of Siberia. *Journal of the Faculty of Science of the Imperial University of Tokyo, section 2: Geology*, **6**, 271–334.
- KOBAYASHI, T. 1953. On the Kainellidae. *Japanese Journal of Geology & Geography*, **23**, 37–61.
- KOBAYASHI, T. 1957. Upper Cambrian fossils from peninsular Thailand. *Journal of the Faculty of Sciences of the University of Tokyo, Section 2: Geology*, **10** (3), 367–382.
- KOBAYASHI, T. 1960. Cambro-Ordovician formations and faunas of South Korea, Pt. 7, Paleontology 6. *Journal of the Faculty of Science of the University of Tokyo, Section 2: Geology*, **12**, 329–420.
- KUO, H.-J., DUAN, J.-Y. and AN, S.-L. 1982. Cambrian–Ordovician boundary in the north China Platform with descriptions of trilobites. 1–31. In *Papers for the Fourth International Symposium on the Ordovician System*, 1982. Changchun College of Geology, Changchun.
- LAKE, P. 1907. A monograph of the British Cambrian trilobites. *Monographs of the Palaeontographical Society*, **61** (296), 29–48.
- LANDING, E., WESTROP, S. R., KRÖGER, B. and ENGLISH, A. M. 2011. Left behind: delayed extinction and a relict trilobite fauna in the Cambrian–Ordovician boundary succession (east Laurentian platform, New York). *Geological Magazine*, **148**, 529–557.
- LEE, C.-P. 1983. Stratigraphy of the Tarutao and Machinchang Formations. 20–38. *Proceedings of the workshop on Stratigraphic correlation of Thailand and Malaysia, Volume 1*. Haad Yai, Thailand.
- LEE, S.-B. and CHOI, D.-K. 2011. Dikelocephalid trilobites from the *Eosaukia* fauna (Upper Furongian) of the Taebaek Group, Korea. *Journal of Paleontology*, **85**, 279–297.
- LEE, S.-B., LEE, D.-C. and CHOI, D. K. 2008. Cambrian–Ordovician trilobite family Mississquoiidae Hupé, 1955: systematic revision and palaeogeographical considerations based on cladistic analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **260**, 315–341.
- LEFORT, P., DEBON, F., PÊCHER, A., SONET, J. and VIDAL, P. 1986. The 500 Ma magmatic event in Alpine southern Asia, a thermal episode at Gondwana scale. *Sciences de la Terre*, **47**, 191–209.
- LEI, Q.-P. and LIU, Q. 2014. Late ontogeny of the trilobite *Tsinania shanxiensis* (Zhang and Wang, 1985) from the Cambrian (Furongian) of Anhui, China and its systematic implications. *Palaeoworld*, **23**, 229–239.
- LI, Z. X. and POWELL, C. M. 2001. An outline of the palaeogeographic evolution of the Australasian region since the beginning of the Neoproterozoic. *Earth-Science Reviews*, **53**, 237–277.
- LI, S.-Z., ZHAO, S.-J., LIU, X., CAO, H.-H., YU, S.-Y., LI, X.-Y., SOMERVILLE, I., YU, S.-Y. and SUO, Y.-H. 2018. Closure of the Proto-Tethys Ocean and early Paleozoic amalgamation of microcontinental blocks in East Asia. *Earth-Science Reviews*, **186**, 37–75.
- LINNARSSON, J. G. O. 1869. Om Vestergötlands Cambriska och Siluriska aflagringar. *Kongliga Svenska Vetenskapsakademiens Handlingar*, **8**, 1–89.
- LOCHMAN, C. 1956. The evolution of some Upper Cambrian and Lower Ordovician trilobite families. *Journal of Paleontology*, **30**, 445–462.
- LOCHMAN, C. 1970. Upper Cambrian faunal patterns on the craton. *Bulletin of the Geological Society of America*, **81**, 3197–3224.
- LONGACRE, S. A. 1970. Trilobites of the Upper Cambrian Ptychaspid Biome Wilberns Formation, central Texas. *Paleontological Society Memoir*, **4**, 1–70.
- LU, Y.-H. 1954. Upper Cambrian trilobites from Santu, south-eastern Kueichou. *Acta Palaeontologica Sinica*, **2**, 117–152.

- LU, Y.-H. 1957. Trilobites. 249–294. In *Fossils of China, part 3*. Institute of Palaeontology, Academia Sinica & Geological Publishing House, Beijing. [in Chinese]
- LU, Y.-H. 1975. Ordovician trilobite faunas of central and southwestern China. *Palaeontologica Sinica, New Series B*, **11**, 1–463.
- LU, Y.-H. and LIN, H.-L. 1984. Late Cambrian and earliest Ordovician trilobites of Jiangshan-Changshan area, Zhejiang. 5–143. In *Stratigraphy and palaeontology of systemic boundaries in China, Cambrian–Ordovician boundary, volume 2*. Anhui Science and Technology Publishing House, Hefei.
- LU, Y.-H. and ZHOU, T. 1990. Trilobites across the Cambrian–Ordovician boundary of the transitional region of Sandu, Southeastern Guizhou. *Palaeontologia Cathayana*, **5**, 1–84.
- LUDVIGSEN, R. 1982. Upper Cambrian and Lower Ordovician trilobite biostratigraphy of the Rabbitkettle Formation, western District of Mackenzie. *Life Sciences Contributions Royal Ontario Museum*, **134**, 1–188.
- LUDVIGSEN, R. and WESTROP, S. R. 1983. Franconian Trilobites of New York State. *New York State Museum Memoir*, **23**, 1–45.
- LUDVIGSEN, R., WESTROP, S. R. and KINDLE, C. H. 1989. Sunwaptan (Upper Cambrian) trilobites of the Cow Head Group, western Newfoundland, Canada. *Palaeontographica Canadiana*, **6**, 1–175.
- LUO, H.-L. 1974. Cambrian trilobites. 597–694. In *Palaeontological Atlas of Yunnan Province*. People's Press of Yunnan Province, Kunming. [in Chinese]
- LUO, H.-L. 1982. On the occurrence of Late Cambrian Gushan trilobite fauna in western Yunnan. *Contribution to the Geology of the Qinghai-Xizhang (Tibet) Plateau*, **10**, 1–12.
- LUO, H.-L. 1983. New finds of trilobites from Late Cambrian in western Yunnan. *Contribution to the Geology of the Qinghai-Xizhang (Tibet) Plateau*, **11**, 1–30.
- LUO, H.-L. 1984. The discovery of the Late Cambrian Gushan-aged strata in western Yunnan and their significance. *Geological Review*, **30**, 425–429.
- LUO, H.-L. 1985a. Subdivision and correlation of the Cambrian system in western Yunnan. *Yunnan Geology*, **4**, 69–83. [in Chinese]
- LUO, H.-L. 1985b. Cambrian subdivision and faunal characters in western Yunnan. *Journal of Stratigraphy*, **9**, 72–75.
- MANSUY, H. 1915. Faunes Cambriennes du Haut-Tonkin. *Memoires du Service Geologique de l'Indo-Chine*, **4**, 1–35. [in French]
- MARTIN, E. L. O., VIDAL, M., VIZCAÏNO, D., VAUCHER, R., SANSJOFRE, P., LEFEBVRE, B. and DESTOMBES, J. 2016. Biostratigraphic and palaeoenvironmental controls on the trilobite associations from the Lower Ordovician Fezouata Shale of the central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 142–154.
- McKENZIE, N. R., HUGHES, N. C., MYROW, P. M., CHOI, D.-K. and PARK, T.-Y. 2011. Trilobites and zircons link north China with the eastern Himalaya during the Cambrian. *Geology*, **39**, 591–594.
- McKENZIE, N. R., HUGHES, N. C., GILL, B. C. and MYROW, P. M. 2014. Plate tectonic influences on Neoproterozoic–early Paleozoic climate and animal evolution. *Geology*, **42**, 127–130.
- McKENZIE, N. R., HORTON, B. K., LOOMIS, S. E., SOTCKLI, D. F., PLANAVSKY, N. J. and LEE, C.-T. A. 2016. Continental arc volcanism as the principal driver of icehouse–greenhouse variability. *Science*, **352**, 444–447.
- M'COY, F. 1849. On the classification of some British fossil Crustacea, with notices of some new forms in the University collection at Cambridge. *Annals & Magazine of Natural History (London), Series 3*, **4**, 161–179, 330–335, 392–419.
- MERGL, M. 1994. Trilobite fauna from the Trenice Formation (Tremadoc) in Central Bohemia. *Geologica*, **39**, 1–31.
- METCALFE, I. 1984. Stratigraphy, palaeontology and palaeogeography of the Carboniferous of Southeast Asia. *Memoirs of the Geological Society of France*, **147**, 107–118.
- METCALFE, I. 2017. Tectonic evolution of Sundaland. *Bulletin of the Geological Society of Malaysia*, **63**, 27–60.
- MILLER, S. A. 1889. *North American geology and palaeontology for the use of amateurs, students, and scientists*. The Western Methodist Book Concern, Cincinnati, OH, 664 pp.
- MILLER, J. F., RIPPERDAN, R. L., LOCH, J. D., FREEMAN, R. L., EVANS, K. R., TAYLOR, J. F. and TOLBART, Z. C. 2015. Proposed GSSP for the base of Cambrian Stage 10 at the lowest occurrence of *Eoconodontus notchpeakensis* in the House Range, Utah, USA. *Annales de Paleontologie*, **101**, 199–211.
- MYROW, P. M. and SOUTHARD, J. B. 1996. Tempestite deposition. *Journal of Sedimentary Research*, **66**, 875–887.
- MYROW, P. M., TAYLOR, J., MILLER, J. F., ETHINGTON, R., RIPPERDAN, R. L. and ALLEN, J. 2003. Fallen arches: dispelling myths concerning Cambrian and Ordovician paleogeography of the Rocky Mountain region. *Geological Society of America Bulletin*, **115**, 695–713.
- MYROW, P. M., TAYLOR, J., RUNKEL, A. C. and RIPPERDAN, R. L. 2012. Mixed siliciclastic–carbonate upward-deepening cycles of the Upper Cambrian inner detrital belt of Laurentia. *Journal of Sedimentary Research*, **82**, 216–231.
- NAIMARK, E. B. and PEGEL, T. V. 2017. Revision of the Cambrian Agnostina (Trilobita?) from Russia. *Palaeontological Journal*, **51**, 1167–1248.
- NORMORE, L. S., ZHEN, Y.-Y., DENT, L. M., CROWLEY, J. L., PERCIVAL, I. G. and WINGATE, M. T. D. 2018. Early Ordovician CA-IDTIMS U–Pb zircon dating and conodont biostratigraphy, Canning Basin, Western Australia. *Australian Journal of Earth Sciences*, **65**, 61–73.
- OGG, J. G., OGG, G. M. and GRADSTEIN, F. M. 2016. *A concise geologic time scale*. Elsevier, 242 pp.
- OWEN, D. D. 1852. *Report of a geological survey of Wisconsin, Iowa and Minnesota, and a portion of the Nebraska Territory*. Lippincott, Grambo & Co., Philadelphia, 638 pp.
- PALMER, A. R. 1965. Biome: a new kind of biostratigraphic unit. *Journal of Paleontology*, **39**, 149–153.
- PALMER, A. R. 1968. Cambrian trilobites of east-central Alaska. *United States Geological Survey Professional Paper*, **559** (B), 1–115.
- PARK, T.-Y. and CHOI, D.-K. 2009. Post-embryonic development of the Furongian (late Cambrian) trilobite *Tsinania*

- canens*: implications for life mode and phylogeny. *Evolution & Development*, **11**, 441–455.
- PARK, T.-Y. and CHOI, D.-K. 2010. Ontogeny and ventral median suture of the ptychaspid trilobite *Asioptychaspis subglobosa* (Sun, 1924) from the Furongian (Upper Cambrian) Hwajeol Formation, Korea. *Journal of Paleontology*, **84**, 309–320.
- PARK, T.-Y. and CHOI, D.-K. 2011. Ontogeny of the Furongian (late Cambrian) remopleuridioid trilobite *Haniwa quadrata* Kobayashi, 1933 from Korea: implications for trilobite taxonomy. *Geological Magazine*, **148**, 288–303.
- PARK, T.-Y. and KIHM, J.-H. 2015a. Furongian (late Cambrian) trilobites from the *Asioptychaspis subglobosa* Zone of the Hwajeol Formation, Korea. *Alcheringa*, **39**, 181–199.
- PARK, T.-Y. and KIHM, J.-H. 2015b. Post-embryonic development of the Early Ordovician (ca. 480 Ma) trilobite *Apatokephalus latilimbatus* Peng, 1990 and the evolution of metamorphosis. *Evolution & Development*, **17**, 289–301.
- PARK, T.-Y., KIM, J.-E., LEE, S.-B. and CHOI, D.-K. 2014. *Mansuyia* Sun, and *Tsinania* Walcott, from the Furongian of North China and the evolution of the trilobite family Tsinaniidae. *Palaentology*, **57**, 269–282.
- PATZKOWSKY, M. E. and HOLLAND, S. M. 2012. *Stratigraphic paleobiology*. University of Chicago Press, 256 pp.
- PENG, S.-C. 1990. Tremadoc stratigraphy and trilobite fauna of northwestern Hunan. *Beringeria*, **2**, 55–271.
- PENG, S.-C. 1992. Upper Cambrian biostratigraphy and trilobite faunas of the Cili-Taoyuan area, northwestern Hunan, China. *Memoir of the Association of Australasian Palaeontologists, Brisbane*, **13**, 1–119.
- PENG, S.-C. and ROBISON, R. A. 2000. Agnostoid biostratigraphy across the middle–upper Cambrian boundary in Hunan, China. *Memoir of the Paleontological Society*, **53**, 1–104.
- PENG, S.-C., BABCOCK, L. E. and AHLBERG, P. 2020. The Cambrian Period. 565–629. In GRADSTEIN, F. M., OGG, J. G., SCHMITZ, M. D. and OGG, M. G. (eds) *Geologic time scale 2020*. Elsevier.
- POPOV, L. E. and COCKS, L. R. M. 2017. Late Ordovician palaeogeography and the positions of the Kazakh terranes through analysis of their brachiopod faunas. *Acta Geologica Polonica*, **67**, 323–380.
- POPOV, L. E., BASSETT, M. G., ZHEMCHUZHNIKOV, V. G., HOLMER, L. E. and KLISHEVICH, I. A. 2009. Gondwanan faunal signatures from early Palaeozoic terranes of Kazakhstan and Central Asia: evidence and tectonic implications. *Geological Society, London, Special Publications*, **325**, 23–64.
- PRATT, B. R. 1988. An Ibexian (Early Ordovician) trilobite faunule from the type section of the Rabbitkettle Formation (southern Mackenzie Mountains, Northwest Territories). *Canadian Journal of Earth Sciences*, **25**, 1595–1607.
- PRATT, B. R. 1992. Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. *Palaentographica Canadiana*, **9**, 1–179.
- QIAN, Y.-Y. 1985. Late Cambrian trilobites from the Tangcun Formation of Jiangxian, southern Anhui. *Palaentologia Cathayana*, **2**, 137–167.
- QIAN, Y.-Y. 1986. Trilobites. 255–313. In CHEN, J.-Y. (ed.) *Aspects of Cambrian–Ordovician boundary in Dayangcha, China*. China Prospect Publishing House, Beijing, 410 pp.
- QIAN, Y.-Y., LIN, Y., ZHANG, J., WANG, Z., YIN, L. and ERDTMANN, B. D. 1985. *Study on Cambrian–Ordovician boundary strata and its biota in Dayangcha, Hunjiang, Jilin, China*. China Prospect Publishing House, Beijing, 138 pp.
- RAASCH, G. O. 1951. Revision of the Croxian dikelocephalids. *Transactions of the Illinois State Academy of Science*, **44**, 137–151.
- RAYMOND, P. E. 1913. A revision of the species which have been referred to the genus *Bathyurus*. *Bulletin of the Victoria Memorial Museum*, **1**, 51–69.
- RAYMOND, P. E. 1924. New Upper Cambrian and Lower Ordovician trilobites from Vermont. *Proceedings of the Boston Society of Natural History*, **37**, 389–466.
- RAYMOND, P. E. 1925. Some trilobites of the lower Middle Ordovician of eastern North America. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **67**, 1–180.
- RESSER, C. E. 1942. Fifth contribution to nomenclature of Cambrian fossils. *Smithsonian Miscellaneous Collections*, **101** (15), 1–58.
- ROBISON, R. A. and PANTOJA-ALOR, J. 1968. Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico. *Journal of Paleontology*, **42**, 767–800.
- ROSS, R. J. Jr 1970. Ordovician brachiopods, trilobites, and stratigraphy in Eastern and Central Nevada. *United States Geological Survey Professional Paper*, **639**, 1–99.
- ROZOVA, A. V. 1968. Biostratigrafiya i trilobity verkhnego Kembriya i nizhnego Ordovika severo-zapada Sibirskoy Platformy [Biostratigraphy and trilobites of the Upper Cambrian and Lower Ordovician of the northwestern Siberian platform]. *Trudy Instituta Geologii i Geofiziki, Sibirskoye Otdeleniye*, **36**, 1–195.
- RUNKEL, A. C., MILLER, J. F., MCKAY, R. M., PALMER, A. R. and TAYLOR, J. T. 2007. High-resolution sequence stratigraphy of lower Paleozoic sheet sandstones in central North America: The role of special conditions of cratonic interiors in development of stratal architecture. *Geological Society of America Bulletin*, **119**, 860–881.
- RUSHTON, A. W. A. 1979. The real M'Coy. *Lethaia*, **12**, 226.
- RUZICKA, R. 1935. Příspěvek k poznání trilobitu Barrandienu: Rozpravy České akademie věd a umění, Trída II (Contribution to the recognition of the Barrandian trilobites). *Matematickopřírodovědecká*, **46** (37), 1–8. [in Czech]
- SALTER, J. W. 1864. A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations. *Monographs of the Palaeontographical Society of London*, **16**(67), 1–83.
- SALTER, J. W. 1866. A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations. *Monographs of the Palaeontographical Society of London*, **18**(77), 129–176.
- SCHINDEWOLF, O. H. 1921. Studien aus dem Marburger Buntsandstein, I–II. *Senckenbergiana*, **3**, 33–49.
- SENNIKOV, N. V., OBUT, O. T., LYKOVA, E. V., TIMOKHIN, A. V., GONTA, T. V., Khabibulina,

- R. A., SHCHERBANENKO, T. A. and KIPRIYANOVA, T. P. 2019. *Ordovician sedimentary basin and paleobiotas of the Gorny Altai*. Siberian Branch of the Russian Academy of Sciences (SB RAS), Novosibirsk, 183 pp. [in Russian]
- SEPKOSKI, J. J. Jr 1978. A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. *Paleobiology*, **4**, 223–251.
- SHERGOLD, J. H. 1972. Late Upper Cambrian Trilobites from the Gola Beds, Western Queensland. *Bulletin of the Bureau of Mineral Resources, Geology & Geophysics*, **112**, 1–126.
- SHERGOLD, J. H. 1975. Late Cambrian and Early Ordovician trilobites from the Burke River Structural Belt, Western Queensland, Australia. *Bulletin of the Bureau of Mineral Resources, Geology & Geophysics*, **153**, 1–251.
- SHERGOLD, J. H. 1991. The Pacoota sandstone, Amadeus Basin, Northern Territory: stratigraphy and palaeontology. *Bulletin of the Bureau of Mineral Resources, Geology & Geophysics*, **237**, 1–93.
- SHERGOLD, J. H. and LAURIE, J. R. 1997. Introduction to the Suborder Agnostina. 331–383. In KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part O. Trilobita (revised)*. Geological Society of America & University of Kansas Press.
- SHERGOLD, J. H. and SDZUY, K. 1991. Late Cambrian trilobites from the Iberian Mountains, Zaragoza Province, Spain. *Beringeria-Würzburger Geowissenschaftliche Mitteilungen*, **4**, 193–235.
- SHERGOLD, J. H., BURRETT, C., AKERMAN, T. and STAIT, B. 1988. Late Cambrian trilobites from Tarutao Island, Thailand. *New Mexico Bureau of Mines & Mineral Resources Memoir*, **44**, 303–320.
- SHERGOLD, J. H., LAURIE, J. R. and SUN, X. 1990. Classification and review of the trilobite order, Agnostida Salter, 1864: an Australian perspective. *Report of the Bureau of Mineral Resources, Geology & Geophysics*, **296**, 1–92.
- SHERGOLD, J. H., LAURIE, J. R. and SHERGOLD, J. E. 2007. Cambrian and Early Ordovician trilobite taxonomy and biostratigraphy, Bonaparte Basin, Western Australia. *Memoirs of the Association of Australasian Palaeontologists*, **34**, 17–86.
- SIGNOR, P. W. III and LIPPS, J. H. 1982. Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. 291–296. In SILVER, L. T. and SCHULTZ, P. H. (eds) *Geological implications of impacts of large asteroids and comets on the Earth*. Geological Society of America Special Publication, **190**.
- SOHN, J.-W. and CHOI, D.-K. 2005. The Late Cambrian trilobite *Hamashania* from Korea. *Alcheringa*, **29**, 195–203.
- SOHN, J.-W. and CHOI, D.-K. 2007. Furongian trilobites from the *Asioptychaspis* and *Quadricephalus* zones of the Hwajeol Formation, Taebaeksan Basin, Korea. *Geosciences Journal*, **11**, 297–314.
- SRIVASTAVA, S. and HUGHES, N. 2023. Morphology, variation, and systematics of the late Cambrian Laurentian dikelocephalid trilobite *Walcottaspis vanhornei* (Walcott, 1914). *Journal of Paleontology*. <https://doi.org/10.1017/jpa.2023.29>
- STAIT, B. A., BURRETT, C. F. and WONGWANICH, T. 1984. Ordovician trilobites from the Tarutao Formation, southern Thailand. *Neues Jahrbuch für Geologie und Paläontologie (Monatsheft)*, **1**, 53–64.
- STITT, J. H. 1971. Late Cambrian and earliest Ordovician trilobites, Timbered Hills and lower Arbuckle Groups, western Arbuckle Mountains, Murray County, Oklahoma. *Oklahoma Geological Survey Bulletin*, **110**, 1–83.
- STITT, J. H. 1977. Late Cambrian and earliest Ordovician trilobites, Wichita Mountains area, Oklahoma. *Oklahoma Geological Survey Bulletin*, **124**, 1–79.
- STUBBLEFIELD, C. J. and BULMAN, O. M. B. 1927. The Shineton Shales of the Wrekin District: with notes on their development in other parts of Shropshire and Herefordshire. *Quarterly Journal of the Geological Society*, **83**, 96–146.
- SUN, Y.-C. 1924. Contributions to the Cambrian faunas of north China. *Palaeontologica Sinica: Series B*, **1**, 1–109.
- SUN, Y.-C. 1935. The Upper Cambrian trilobite faunas of north China. *Palaeontologica Sinica: Series B*, **7**, 1–69.
- SUN, Y.-C. and XIANG, L. 1979. Late upper Cambrian trilobite fauna from western Yunnan. *Bulletin of the Chinese Academy of Geological Science*, **1**, 1–17.
- TAYLOR, M. E. and HALLEY, R. B. 1974. Systematics, environment, and biogeography of some Late Cambrian and Early Ordovician trilobites from eastern New York State. *US Geological Survey Professional Paper*, **834** 38 pp.
- TERAOKA, Y., SAWATA, H., YOSHIDA, T. and PUNGRASSAMI, T. 1982. Lower Paleozoic formations of the Tarutao Islands, Southern Thailand. *Prince of Songkhla University, Geological Research Project Publication*, **6**, 1–54.
- TERFELT, F. 2003. Upper Cambrian trilobite biostratigraphy and taphonomy at Kakeled on Kinnekulle, Västergötland, Sweden. *Acta Palaeontologica Polonica*, **48**, 409–416.
- THEIN, M. L. 1973. The lower Paleozoic stratigraphy of western part of the Southern Shan State, Burma. *Geological Society of Malaysia Bulletin*, **6**, 143–163.
- TJERNVIK, E. 1956. On the Early Ordovician of Sweden: stratigraphy and fauna. *Bulletin of the Geological Institutions of the University of Uppsala*, **36**, 109–284.
- TORSVIK, T. H. and COCKS, L. R. M. 2017. *Earth history and palaeogeography*. Cambridge University Press, 317 pp.
- TORTELO, M. F. and BORDONARO, O. L. 1997. Cambrian agnostoid trilobites from Mendoza, Argentina: a systematic revision and biostratigraphic implications. *Journal of Paleontology*, **71**, 74–86.
- TORTELO, M. F. and ESTEBAN, S. B. 2003. Trilobites del Cámbrico Tardío de la Formación Lampazar (sierra de Cajas, Jujuy, Argentina). Implicancias bioestratigráficas y paleoambientales. *Ameghiniana*, **40**, 323–344.
- TULLBERG, S. A. 1880. Om *Agnostus*-arterna i de kambriska aflägringarna vid Andrarum. *Sveriges Geologiska Undersökning, Avhandlingar och uppsatser, Series C*, **42**, 1–38.
- ULRICH, E. O. and RESSER, C. 1930. The Cambrian of the upper Mississippi valley, Part 1, Trilobita, Dikelocephalinae and Osceolinae. *Bulletin of the Public Museum of the City of Milwaukee*, **12**, 1–222.
- ULRICH, E. O. and RESSER, C. E. 1933. The Cambrian of the Upper Mississippi Valley, Part 2, Trilobita; Saukiinae. *Bulletin of the Milwaukee Public Museum*, **12**, 123–306.

- WALCOTT, C. D. 1879. Description of new species of fossils from the Calciferous formation. 32nd Report of the New York State Cabinet of Natural History [pamphlet published in advance of the Report].
- WALCOTT, C. D. 1905. Cambrian faunas of China. *Proceedings of the United States National Museum*, **29**, 1–106. <https://doi.org/10.5479/si.00963801.1415>
- WALCOTT, C. D. 1906. Cambrian faunas of China. *Proceedings of the United States National Museum*, **30**, 563–595. <https://doi.org/10.5479/si.00963801.1458.563>
- WALCOTT, C. D. 1913. The Cambrian faunas of China. *Research in China*, Vol. 3, *Carnegie Institution Publication*, **54**, 3–27. <https://doi.org/10.5962/bhl.title.31910>
- WALCOTT, C. D. 1914. Cambrian geology and paleontology, No. 1. The Cambrian faunas of eastern Asia. *Smithsonian Miscellaneous Collections*, **64**, 1–75.
- WALCOTT, C. D. 1924. Cambrian and Lower Ozarkian trilobites. *Smithsonian Miscellaneous Collections*, **75**, 53–60.
- WALKER, R. G. 1984. Shelf and shallow marine sands. 141–170. In WALKER, R. G. (ed.) *Facies models*, Second edition. Geoscience Canada, Reprint Series 1.
- WEBSTER, M. and SHEETS, H. D. 2010. A practical introduction to landmark-based geometric morphometrics. *The Palaeontological Society Papers*, **16**, 163–188.
- WERNETTE, S. J., HUGHES, N. C., MYROW, P. M. and SARSDUD, A. 2020a. *Satunarcus*, a new late Cambrian trilobite genus from southernmost Thailand and a reevaluation of the subfamily Mansuyiinae Hupé, 1955. *Journal of Paleontology*, **94**, 867–880.
- WERNETTE, S. J., HUGHES, N. C., MYROW, P. M. and SARSDUD, A. 2020b. The Furongian (late Cambrian) trilobite *Thailandium*'s endemism reassessed along with a new species of *Prosaugia* from Ko Tarutao, Thailand. *Thai Geoscience Journal*, **1**, 63–82.
- WERNETTE, S. J., HUGHES, N. C., MYROW, P. M. and AUNG, A. K. 2021. The first systematic description of Cambrian fossils from Myanmar: Late Furongian trilobites from the southern part of the Shan State and the early Palaeozoic palaeogeographical affinities of Sibumasu. *Journal of Asian Earth Sciences*, **214**, 104775.
- WERNETTE, S. J., HUGHES, N. C., MYROW, P. M. and SARSDUD, A. 2023. Data from: Trilobites of Thailand's Cambrian–Ordovician Tarutao Group. Dryad Digital Repository. <https://doi.org/10.6086/D1697P>
- WESTROP, S. R. 1986. Trilobites of the Upper Cambrian Sunwaptan Stage, southern Canadian Rocky Mountains, Alberta. *Palaeontographica Canadiana*, **3**, 1–179.
- WESTROP, S. R. 1989. Macroevolutionary implications of mass extinction: evidence from an Upper Cambrian stage boundary. *Paleobiology*, **15**, 46–52.
- WESTROP, S. R. and LUDVIGSEN, R. 1986. Type species of the basal Ibexian trilobite *Corbinia* Walcott, 1924. *Journal of Paleontology*, **60**, 68–75.
- WESTROP, S. R. and LUDVIGSEN, R. 1987. Biogeographic control of trilobite mass extinction at an Upper Cambrian “biomere” boundary. *Paleobiology*, **13**, 84–99.
- WESTROP, S. R., PALMER, A. R. and RUNKEL, A. 2005. A new Sunwaptan (Late Cambrian) trilobite fauna from the upper Mississippi Valley. *Journal of Paleontology*, **79**, 72–88.
- WHITEHOUSE, F. W. 1936. The Cambrian faunas of north-eastern Australia. Parts 1 and 2. *Memoirs of the Queensland Museum*, **11**, 59–112.
- WHITTINGTON, H. B. 1997. Morphology of the exoskeleton. 1–85. In KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part O. Trilobita (revised)*. Geological Society of America & University of Kansas Press.
- WHITTINGTON, H. B. and KELLY, S. R. A. 1997. Morphological terms applied to Trilobita. 313–329. In KAESLER, R. L. (ed.) *Treatise on invertebrate paleontology. Part O. Trilobita (revised)*. Geological Society of America & University of Kansas Press.
- WHITTINGTON, H. B. and KINDLE, C. H. 1963. Middle Ordovician Table Head Formation, Western Newfoundland. *Bulletin of the Geological Society of America*, **74**, 745–758.
- WINSTON, D. and NICHOLLS, H. 1967. Late Cambrian and Early Ordovician faunas from the Wilberns Formation of Central Texas. *Journal of Paleontology*, **41**, 66–95.
- WOLF, R. 1980. The lower and upper boundary of the Ordovician System of some selected regions (Celtiberia, eastern Sierra Morena) in Spain; Part I, The Lower Ordovician sequence of Celtiberia. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **160**, 118–137.
- WOLFART, R., MYO WIN, U., BOITEAU, S., MYO WAI, U., UK CUNG, P. and THIY LWIN, U. 1984. Stratigraphy of the western Shan Massif, Burma. *Geologisches Jahrbuch Reihe B*, **57**, 3–92.
- WONGWANICH, T. and BURRETT, C. 1983. The lower Palaeozoic of Thailand. *Journal of the Geological Society of Thailand*, **6** (2), 21–29.
- WONGWANICH, T., TANSATHIEN, W., LEEVONGCHAROEN, S., PAENGKAEW, W., THIAMWONG, P., CHAEROENMIT, J. and SAENGSRICHAN, W. 2002. The Lower Paleozoic Rocks of Thailand. *The Symposium on Geology of Thailand, 26–31 August 2002, Bangkok, Thailand*, Thai Department of Mineral Resources, Bangkok.
- XU, Y., CAWOOD, P. A., DU, Y., HUANG, H. and WANG, X. 2014. Early Paleozoic orogenesis along Gondwana's northern margin constrained by provenance data from South China. *Tectonophysics*, **636**, 40–51.
- ZHANG, W. T. 1949. Ordovician trilobites from the Kaiping Basin, Hopei. *Bulletin of the Geological Society of China*, **29**, 111–125.
- ZHANG, W.-T. 1989. *World Cambrian biogeography*. 209–220. *Developments in Geoscience*. Science Press, Beijing.
- ZHANG, W.-T. and FAN, J.-S. 1960. Ordovician and Silurian trilobites of the Chilian Mountains. 83–148. *Geological Gazetteer of the Chilian Mountains*, **4**. [in Chinese]
- ZHANG, W.-T. and JELL, P. A. 1987. *Cambrian trilobites of North China: Chinese Cambrian trilobites housed in the Smithsonian Institution*. Science Press, Beijing, 459 pp.
- ZHANG, W.-T. and WANG, S.-X. 1985. Trilobites. 27–488. In TIANJIN INSTITUTE OF GEOLOGY AND

- MINERAL RESOURCES (ed.) *Palaeontological atlas of North China, Vol. 1. Palaeozoic*. Geological Publishing House, Beijing. [in Chinese]
- ZHAO, H.-Q., ZHANG, S.-H., ZHU, M.-Y., DING, J.-K., LI, H.-Y., YANG, T.-S. and WU, H.-C. 2021. Paleomagnetic insights into the Cambrian biogeographic conundrum: did the North China Craton link Laurentia and East Gondwana? *Geology*, **49**, 372–376.
- ZHOU, Z.-Y. and ZHANG, J.-L. 1978. Cambrian–Ordovician boundary of the Tangshan area with descriptions of the related trilobite fauna. *Acta Palaeontologica Sinica*, **17**, 1–28. [in Chinese]
- ZHOU, Z.-Y. and ZHANG, J.-L. 1984. Uppermost Cambrian and lowest Ordovician trilobites of north and north-east China. 63–194. In *Stratigraphy and palaeontology of systemic boundaries in China, Cambrian-Ordovician boundary 2*. Anhui Science and Technology Publishing House, Hefei, 412 pp. [in Chinese]
- ZHOU, Z.-Y. and ZHEN, Y.-Y. 2008. *Trilobite record of China*. Science Press, Beijing, 401 pp.
- ZHOU, T.-M., LUI, Y.-R., MENG, X.-S. and SUN, Z.-H. 1977. Trilobita. 104–226. In HUBEI INSTITUTE OF GEOLOGY AND SCIENCE (ed.) *Palaeontological Atlas of Central and Southern China, 1*. Geological Publishing House, Beijing.
- ZHOU, Z.-Y., LI, J.-S. and QU, X.-G. 1982. Trilobita. 215–294. In *Palaeontological atlas of northwest China, Shanxi-Gansu-Ningxia Volume. Part 1: Pre-Cambrian and Early Paleozoic*. Geological Publishing House, Beijing. [in Chinese]
- ZHU, X.-J. and PENG, S.-C. 2006. *Eosumardia* (Trilobita, Cambrian), a junior synonym of *Koldinioidia*. *Alcheringa*, **30**, 183–189.
- ZHU, D.-C., ZHAO, Z.-D., NIU, Y., DILEK, Y., WANG, Q., JI, W.-H., DONG, G.-C., SUI, Q.-L., LIU, Y.-S., YUAN, H.-L. and MO, X.-X. 2012. Cambrian bimodal volcanism in the Lhasa Terrane, southern Tibet: record of an early Paleozoic Andean-type magmatic arc in the Australian proto-Tethyan margin. *Chemical Geology*, **328**, 290–308.
- ZHU, X.-J., HUGHES, N. C. and PENG, S.-C. 2013. Onset of maturity and ontogenetic tagmatization of the pygidium in the development of *Lonchopygella megaspina* (Trilobita, later Furongian, Cambrian). *Journal of Paleontology*, **87**, 472–483.