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

Shelly J. Wernette[1], Nigel C. Hughes[1, 2], Paul M. Myrow[3], Apsorn Sardsud[4]
[1] Department of Earth and Planetary Sciences, University of California, Riverside, CA 92521, USA.
[2] Geological Studies Unit, Indian Statistical Institute, 208 B.T. Road, Kolkata, 700018, India
[3]Department of Geology, Colorado College, Colorado Springs, CO 80903, USA
[4] Division of Mineral Resources Analysis and Identification, Department of Mineral Resources, 75/10 Rama VI Road, Ratchatewi, Bangkok 10400, Thailand
**Corresponding author: swern001@ucr.edu*

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Abstract

The trilobite *Thailandium solum*, the type species of *Thailandium*, is a large "saukiid" species known only from the Ao Mo Lae Formation of the Tarutao Group, Thailand. In addition to the type species occurrence in Thailand, *Thailandium* is also reported from northern Henan, China as *Thailandium truncatum* Zhou and from Australia's Pacoota Sandstone as an undeterminate species. Type material of *Prosaukia misa*, the type species of *Prosaukia*, as well as recent collections of *Thailandium solum*, *Prosaukia tarutaoensis* (Kobayashi, 1957), and a new species of *Prosaukia*, *P. oculata*, from Ko Tarutao, Thailand are used to reevaluate the generic identity of the Australian and north Chinese material using landmark-based morphometric analysis. The new material of *Prosaukia* and *Thailandium*, all from the Ao Mo Lae Formation, reveal that the Australian material is better characterized as *Prosaukia*. The cranidium of north China's *Thailandium truncatum* is geometrically comparable to *Thailandium solum*, but differs notably in overall relief and in the anterior border structure and proportions. Here we assign it tentatively to another "saukiid" genus. These morphometric and qualitative comparisons facilitate a refined generic diagnosis for *Thailandium*, resulting in its restriction to a monospecific genus.

Keywords: *Thailandium*, *Prosaukia*, Tarutao, "saukiid", landmark morphometric

Introduction:

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

The taxonomic challenges associated with "saukiids" limit their current application to broader geologic questions. The characters differentiating many of the "saukiid" genera are not the discrete presence or absence of particular traits but rather the exaggeration or reduction of traits common to many or all "saukiids". Some are differentiated by the presence, length, or inflation of the preglabellar field (Ulrich and Resser, 1933; Ludvigsen and Westrop, 1983). Shergold (1991) recognized three morphological groupings of "saukiid" cranidia, the first of which comprises *Prosaukia*-like genera, including *Thailandium*, *Caznaia*, *Lichengia*, and *Saukiella*, which have a distinct preglabellar field fully distinguishable from the anterior border.

Within this group of "saukiids" with a distinct preglabellar field, *Thailandium* Kobayashi, 1957 has an exceptionally long preglabellar field and a strongly differentiated anterior border. This genus has been reported from three regions: Thailand's Ko Tarutao (also called Tarutao Island) in Satun Global Geopark (Kobayashi, 1957), northern Henan, China (Zhou et al., 1977), and Australia's Amadeus Basin (Shergold, 1991). The type species, *Thailandium solum* Kobayashi, 1957, was described from the Ao Mo Lae Formation of the Tarutao Group, then known as the Tarutao Formation, in the initial description of the fauna of Ko Tarutao. Zhou et al. (1977) erected a second species, *Thailandium truncatum*, on a single specimen and reassigned the genus to Elviniidae Kobayashi, 1935 with no reasons given for this change in family assignment. This species was characterized as coming from the North China block by Zhu (2008). In their more extensive description of the Tarutao Group's trilobite fauna, Shergold et al. (1988) did not illustrate or discuss *Thailandium* with the exception of reassigning certain librigena and pygidia form Kobayashi's (1957) figured material to other species such as *Quadraticephalus planulatus* (Kobayashi, 1957) and *Lichengia tarutaoensis* (Kobayashi, 1957; *sensu* Shergold et al., 1988). Shergold (1991) assigned specimens from the Pacoota Sandstone of the Amadeus Basin (Fig. 1) to an

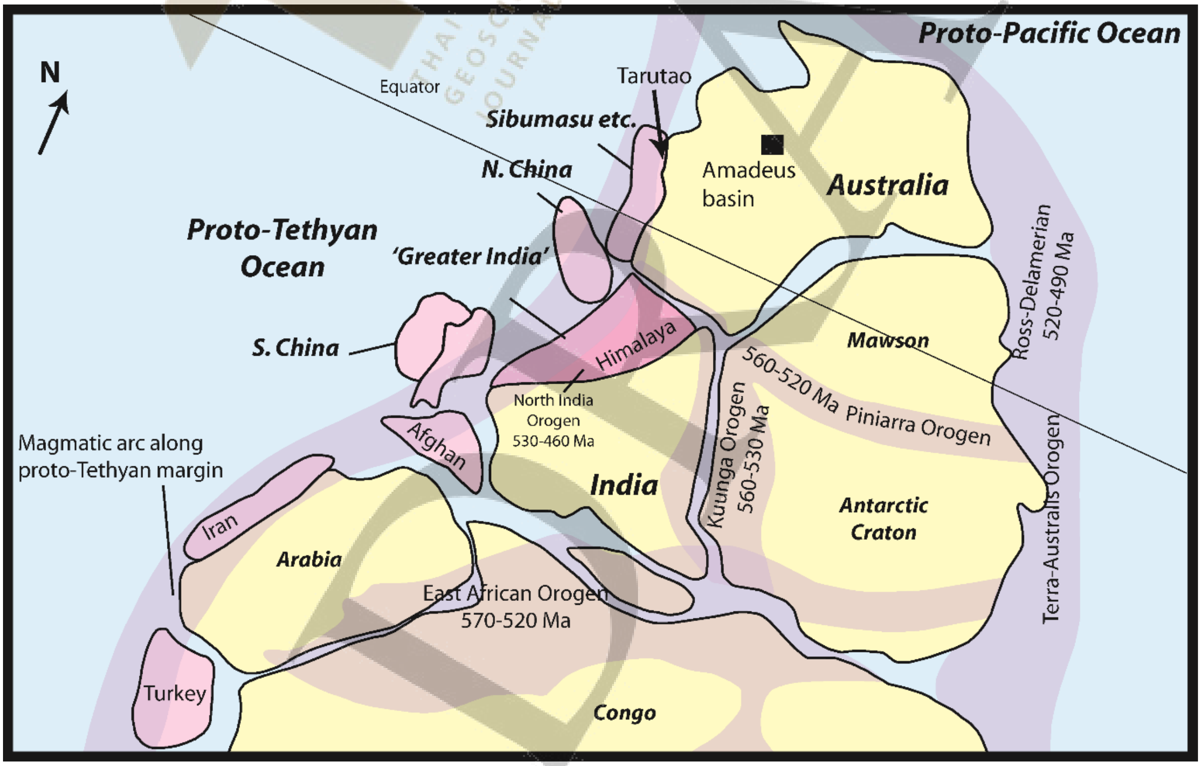

Figure 1—Cambro-Ordovician paleogeographic reconstruction of northern Gondwana. Locations of the Amadeus Basin and Tarutao are only approximations to indicate their relative locations and proximity. Modified from Hughes, 2016; orogenies from Cawood et al., 2007; equator from Cocks and Torsvik, 2013.

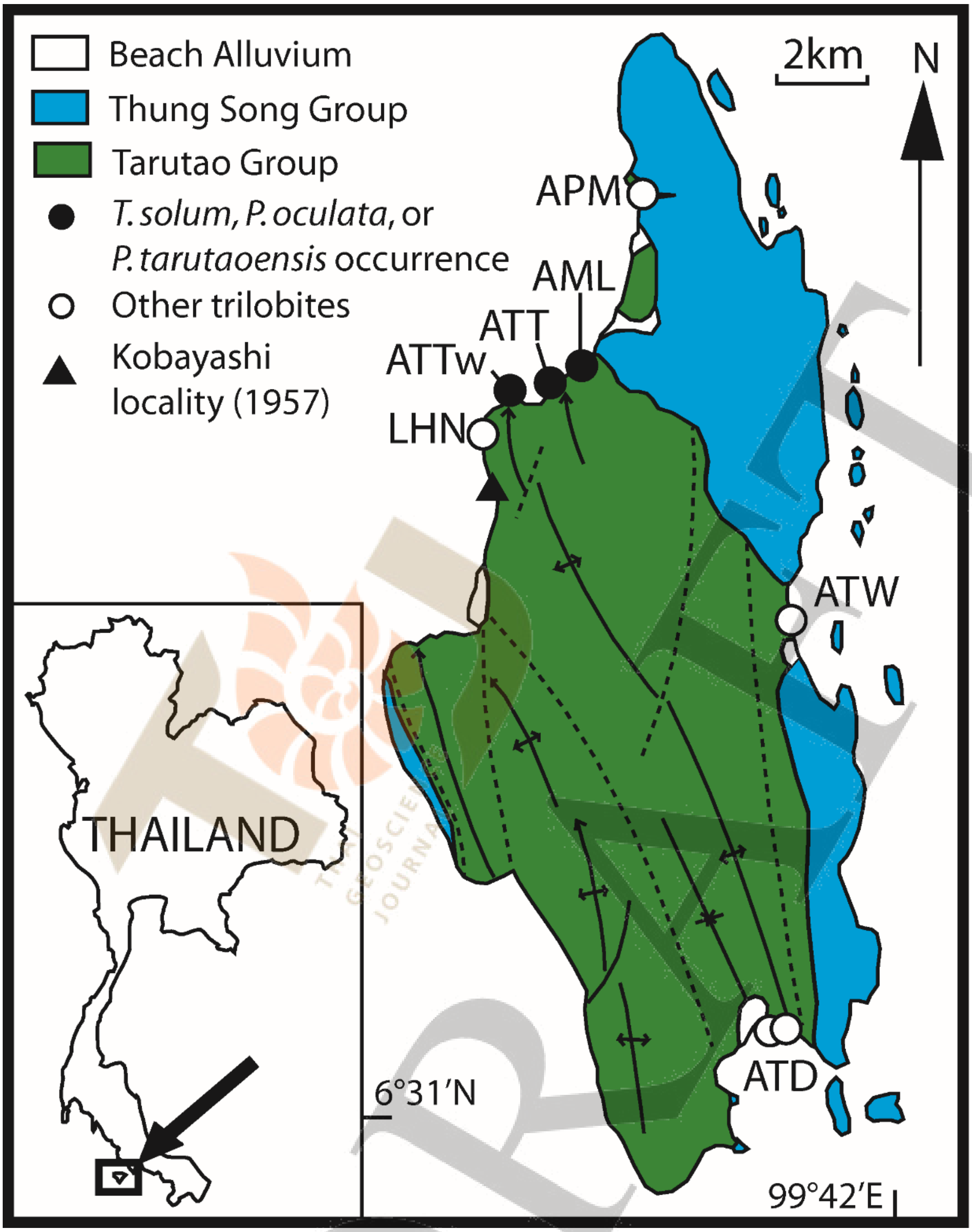

Figure 2—Trilobite Occurrences on Ko Tarutao: AML = Ao Mo Lae; ATT = Ao Talo Topo; ATTw = Ao Talo Topo west; LHN = Laem Hin Ngam; ATD = Ao Talo Udang; APM = Ao Phante Malacca; ATW = Ao Talo Wao. Modified from Bunopas et al., 1983 and Wernette et al., 2020.

undetermined species of *Thailandium* based on a similarly long frontal area and defined anterior border as *Thailandium solum* with the caveat that they likely belong to *Prosaukia.* Shergold (1991) suggested that the status of his Australian material could be meaningfully evaluated only after reevaluation of the *T. solum* type material with greater consideration of possible morphologic variation within it and did not comment on *T. truncatum*. A series of excursions from 2008 to 2018 have greatly expanded trilobite collections from Ko Tarutao (Fig. 2). This new material permits reevaluation of the cranidial morphology of *T. solum*, prompting reassessment of Shergold's (1991) question of whether the specimens from the Pacoota

Sandstone are truly *Thailandium* and reconsideration of the relationship of *Thailandium truncatum* from North China. Species of *Prosaukia* found during the same excursions, *Prosaukia tarutaoensis* (Kobayashi, 1957; *non Lichengia tarutaoensis* in Shergold et al., 1988) and *P. oculata* n. sp. facilitate comparison of species assigned to *Thailandium* with those of the related genus, *Prosaukia*.

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

Tarutao Localities:

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

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

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

The similarity of faunal content indicates that the Ao Mo Lae Formation is from

Cambrian Stage 10, and the ATTw and AML fauna appear to be of nearly the same depositional age (see Fig. 3 and following paragraph for faunal content); ATT (Fig. 4) may have a slightly different age than the other two. Based on the shallow northeastward dip evident at both ATT and AML, the latter may be slightly younger if these sections are in stratigraphic continuity, but they are separated by a small, sandy inlet which may conceal one of Ko Tarutao's many faults. The lithology of all three localities is similar except that ATT and ATTw contain several prominent horizons of rhyolitic tuffs. ATT has a slightly different faunal assemblage than the other two localities (Figs 3 and 4) with much of their shared fauna occurring only in material from ATT or AML that was not located to a specific horizon.

Collections of fossils made from single beds at specified localities, but whose particular horizon was not located within a measured section are included here, because these collections are informative regarding the diversity of the Ao Mo Lae Formation and regarding taxon cooccurrences. The single horizon at ATTw contains *Thailandium solum* Kobayashi (1957), *Prosaukia tarutaoensis* (Kobayashi, 1957), *Haniwa* sp. 1, *Pagodia thaiensis* Kobayashi (1957), *Quadraticephalus planulatus* (Kobayashi, 1957), *Satunarcus molaensis* (Wernette et al., *2020*), and *Eosaukia buravasi* Kobayashi (1957). One poorly localized horizon at Ao Talo Topo, henceforth referred to as ATT h1 contains *Koldinioidia* sp. and *Prosaukia oculata*. Five not-localized-within-section collections were assembled from AML, henceforth referred to as Ao Mo Lae horizons 1–5 (AML h1–AML h5). AML h1 and AML h2 correspond to horizons 1 and 2 from Wernette et al. (2020). AML h2 contains *Thailandium solum*, *Quadraticephalus planulatus*, *Satunarcus molaensis*, and *Eosaukia buravasi*; AML h3 contains *T. solum*, *P. tarutaoensis*, *P. thaiensis*, and *E. buravasi*; AML h4 contains *T. solum*, *Q. planulatus*, and *E. buravasi*; AML h5 contains *T. solum*, *E. buravasi*, and *Pacootasaukia*? sp. The fauna listed herein, excluding *P. tarutaoensis* and *P. oculata*, uses the names originally given by Kobayashi (1957), Shergold et al. (1988), or Wernette et al. (2020); previously undescribed species collected on the recent excursions (excluding those described herein) are listed by genus only. This paper is part of ongoing work revising the Kobayashi (1957) and Shergold et al. (1988) material as well as describing newly collected material (e.g. Wernette et al. 2020).

Materials and Methods:

The morphometric analysis that follows is based on 22 discrete landmarks (Fig. 5) and 30 cranidia. Only specimens with sufficient preservation to distinguish all axial landmarks and at least one of each paired landmark were eligible for use in the analysis. 15 cranidia are of *Thailandium solum*, all from Ko Tarutao (DGSC F0419, F0435, F0543, F0544, F0568, F06569, F0570, F0574, F0583, F0595, F0601, F0606, F0607, F0609, and CMC IP87617). The holotype of *Thailandium*, though figured from a vinyl polysiloxane cast herein, was excluded from the analysis as the original figure (Kobayashi, 1957, pl. 4, fig. 9) lacks a clear posterior occipital margin Four cranidia assigned to *Thailandium* sp. undet. from the Pacoota Sandstone in the Amadeus Basin of Australia are considered (Shergold, 1991 pl. 4, figs 16–18, 21; CPC26805A, CPC26806, CPC26807, CPC26825). One cranidium assigned to *Thailandium truncatum* from northern Henan, China is included (Zhou et al., 1977 pl. 55, fig. 23; Hubei Institute of Geoscience IV70109). Two syntype cranidia are included of *Prosaukia misa* (Hall, 1863), the type species of *Prosaukia* Ulrich and Resser, 1933 (pl. 24 figs 3 and 7; USNM 84538, MPM 5968). Four cranidia belong to *Prosaukia oculata* n. sp. (DGSC F0461, F0503, F0511, and F0512), and four cranidia are of *Prosaukia tarutaoensis* (Kobayashi, 1957, pl. 5 fig. 12, and three recently collected specimens; UMUT PA02298c, DGSC F0566, F0546, and F0545 respectively). The published figures of *P. misa* (in Ulrich and Resser, 1933), *Prosaukia tarutaoensis* (Kobayashi, 1957), *Thailandium truncatum* Zhou, 1977, and *Thailandium* undet. (Shergold, 1991) are of

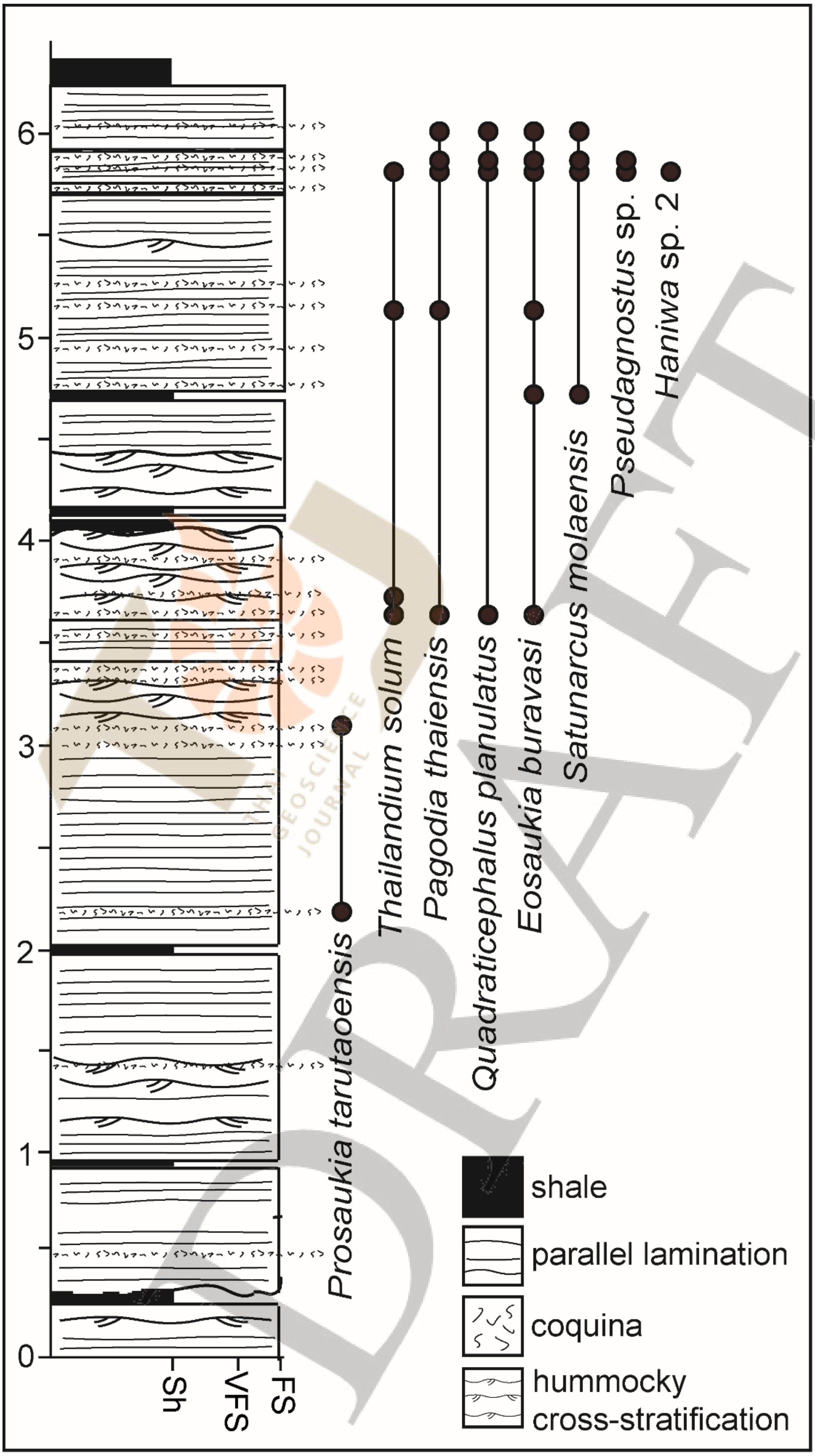

Figure 3—Measured lithostratigraphic section and faunal ranges for Ao Mo Lae (AML). Sh = shale; vfs = very fine sand; fs = fine sand; coq = coquina. Measurements are in meters.

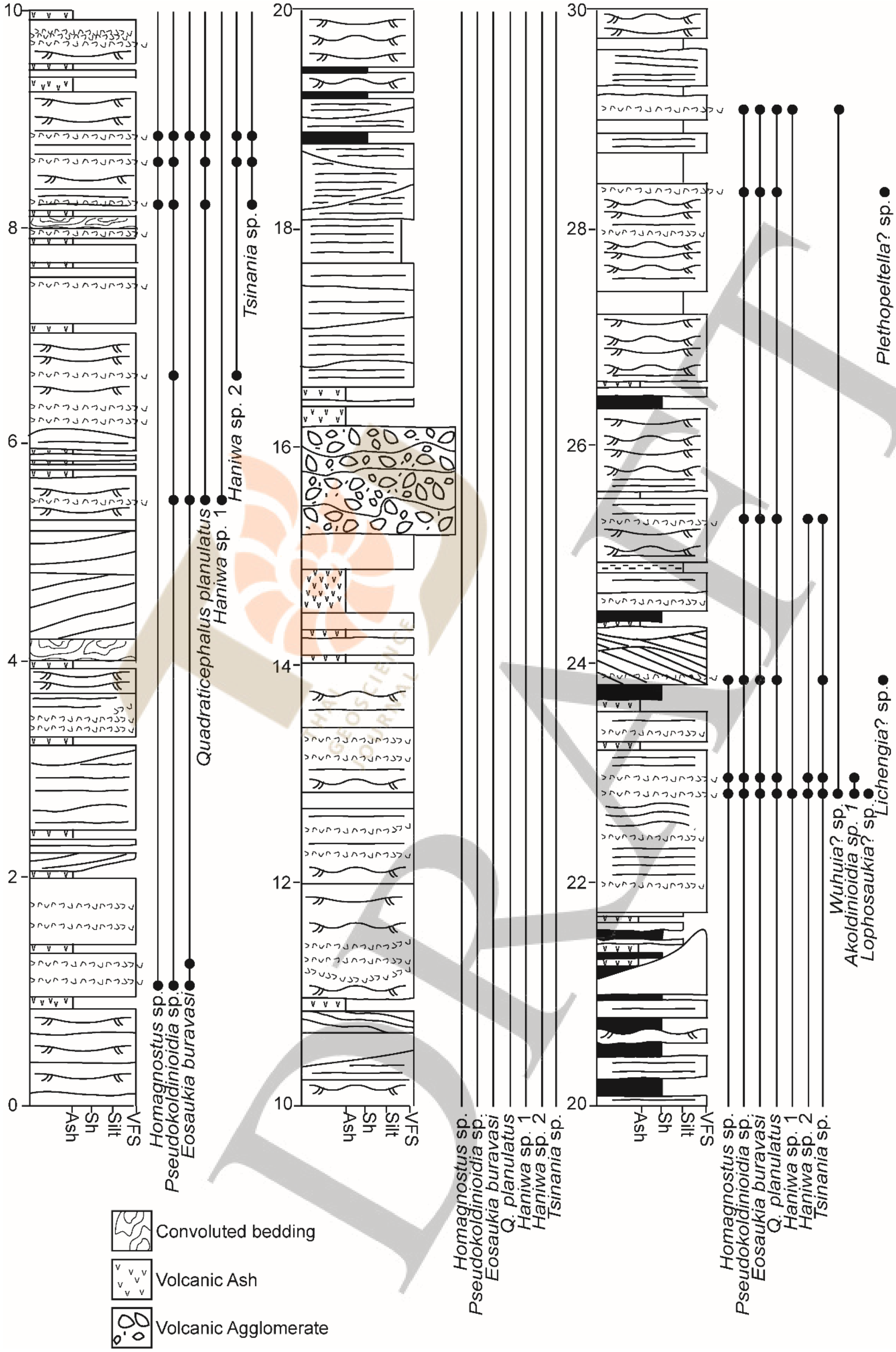

Figure 4—Measured lithostratigraphic section and faunal ranges for Ao Talo Topo (ATT). Measurements are in meters. See Fig. 3 for abbreviations and additional legend symbols.

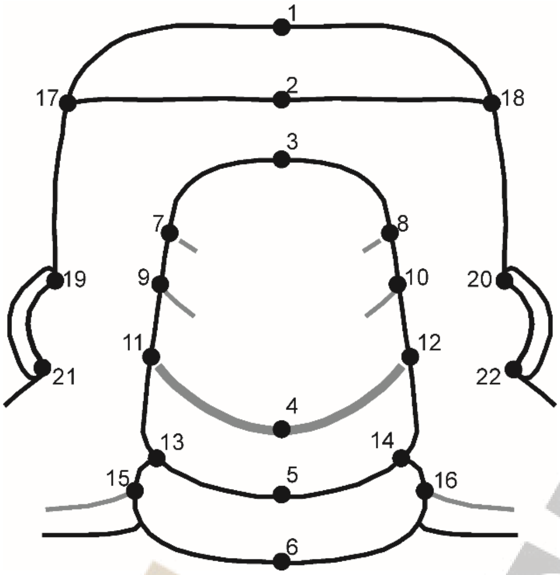

Figure 5—Landmark scheme showing the 22 landmarks used in the morphometric analysis of *Prosaukia* and *Thailandium*.

sufficient quality that landmarks could be mapped directly onto digitized copies of the original published illustrations. The size range for each taxon, measured by the length of the preoccipital glabella, is as follows: 2.47–16.53 mm for *Thailandium solum*, 4.57–8.37 mm for *Thailandium* sp. undet., 11.03–15.96 mm for *P. misa*, 2.31–6.34 mm for *P. oculata*, and 2.50–7.71 mm for *P. tarutaoensis*.

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

Geometric morphometric analysis was conducted using the free software ImageJ and the Integrated Morphometrics Package (CoordGen8, BigFix8, Regress8, and PCAGen8), a set of compiled software tools for displaying and analyzing 2-D landmark-based geometric morphometric data (Webster and Sheets, 2010; http://www.filogenetica.org/cursos/Morfometria/IMP_installers/index.php). Landmarks were reflected and averaged across the sagittal axis.

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

Results and Discussion:

Sliding baseline registration (SBR) best displays the variation within the dataset and so is used consistently throughout the following discussion of morphometrics except where Procrustes superimposition is required for statistical calculations of group mean differences (Webster and Sheets, 2010). The SBR distribution of landmarks (Fig. 6) indicates that *Thailandium solum* and *Thailandium* sp. undet. (*sensu* Shergold, 1991) have similarly long frontal areas relative to glabellar length and similar division of the frontal area into preglabellar field and anterior border. The relative length of the frontal area of *Thailandium truncatum* is, however, somewhat shorter than that of *Prosaukia misa*. With regard to the palpebral lobe position (Fig. 5, landmarks 19–22), *T. solum*'s positions align more with *Prosaukia oculata*; the eyes for these species are more abaxially placed than in the other species; the palpebral lobes of *P. oculata* are, however, longer with the posterior end extending further backwards. *Prosaukia misa*, *Prosaukia tarutaoensis*, and *Thailandium* sp. undet. have similarly long palpebral lobes that are more posteriorly centered than in *T. solum*. The palpebral lobes of *T. truncatum* are relatively short and anteriorly placed, as in *T. solum*. All six species have a similar longitudinal placement of the anterior end of the palpebral lobe, so it is the position of the posterior end that reveals differences in overall palpebral length. The lateral corner of the anterior border (Fig. 5, landmarks 17, 18) is similarly placed in *P. misa*, *P. tarutaoensis*, *T. solum*, *T. truncatum*, and *Thailandium* sp. undet., but in *P. oculata* it is more posterolaterally positioned, attributable to the very short preglabellar field and wide-set fixigena in that form. If isolated clusters of landmarks were to be required for generic distinction, no evident differences separate *Thailandium* from *Prosaukia*. However, the collective alignment of the six lateral most landmarks (Fig. 5, landmarks 17–22) is different in *T. solum* and *T. truncatum* than in the other four species. In *T. solum* the landmarks aligned along an anteromedial trendline. In the other four species the anterior palpebral landmarks (Fig. 5, landmarks 19, 20) are more medial than the posterior palpebral landmarks or lateral corners of the anterior border (Fig. 5, landmarks 21, 22, 17, 18). In this way *T. solum* and *T. truncatum* form a distinctly separate group, and *Thailandium* sp. undet. follows the same trend as the species of *Prosaukia*.

The first two relative warps of a thin plate spline decomposition (Bookstein 1991) of the shape variation in the sample (RW1 and RW2; Fig. 7) account for 42.90% and 20.19% of the variance respectively; other relative warps account for less than 10% of variance each. The distribution of specimens along the first two relative warps, particularly RW1, further support the differentiation of *Thailandium solum* and *Thailandium truncatum* from the other four species discussed with a distinct group of the former two and overlap among *P. misa*, *P. tarutaoensis*, *P. oculata*, and *Thailandium* sp. undet. This view is supported by the significant shape difference between *Thailandium* sp. undet. and *T. solum* (using a Procrustes superimposition to compare shape differences Goodalls's F, $p > 0.00001$; F test $p = 0.0004$ with 2500 bootstraps). Between *Thailandium* sp. undet. and the pooled *Prosaukia* sample the difference is not significant (using a Procrustes superimposition to compare shape differences Goodalls's F, $p = 0.28578$; resampling F test with 2500 bootstraps $p = 0.3188$). Thus the similarity of specimens of *Thailandium* sp. undet. to those of the three species of *Prosaukia* (Fig. 7) and its evident separation from the specimens of *T. solum* and *T. truncatum* indicate that *Thailandium* sp. undet. should be reclassified as a species of *Prosaukia*.

Relative warp 1 largely captures differences in the lateral placement of the anterior border's lateral corner, the length of the frontal area, and the longitudinal placement of the palpebral lobe's posterior point (Fig. 8). Relative warp 2 primarily captures the width of the fixigena and lateral position of the palpebral lobes. The differentiation of *Prosaukia* and *Thailandium* along RW1 (Fig. 7) is consistent with the SBR landmark distribution (Fig. 6) in differentiating *Thailandium solum* and *Thailandium truncatum* from *Prosaukia*, including *Thailandium* sp. undet., by the anterior

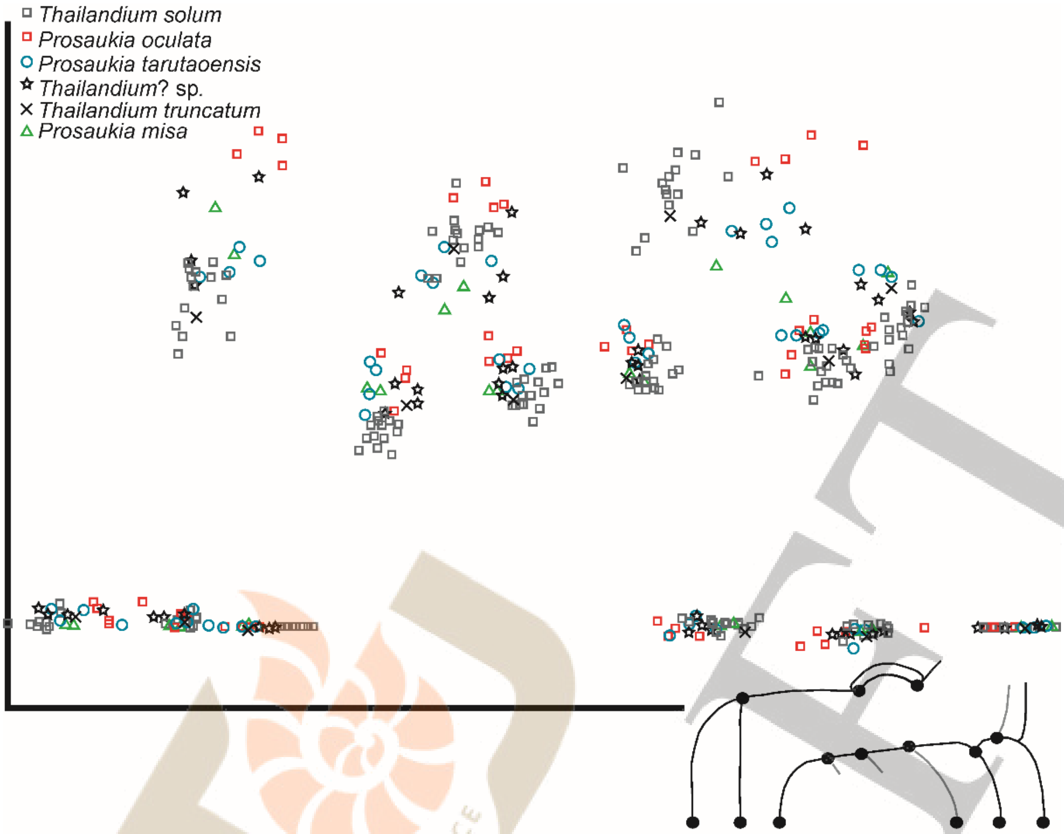

Figure 6—Sliding baseline registration of 22 landmarks across 30 cranidia of “saukiid” dikelocephalids. The *x*-axis anchored baseline landmarks are landmarks 3 and 6. See Fig. 5 for landmark scheme. *Thailandium*? sp. is the taxon from Australia (Shergold, 1991) herein reassigned to *Prosaukia* sp.

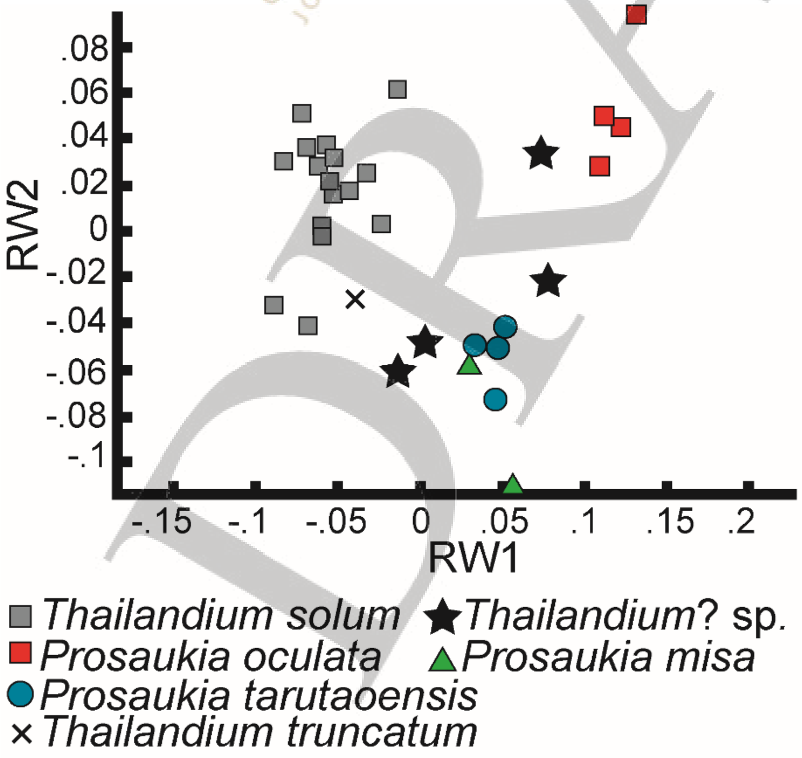

Figure 7—First two relative warps (RW1 and RW2), accounting for 42.90% and 20.19% of the variance respectively. *Thailandium*? sp. is the taxon from Australia (Shergold, 1991) herein reassigned to *Prosaukia* sp.

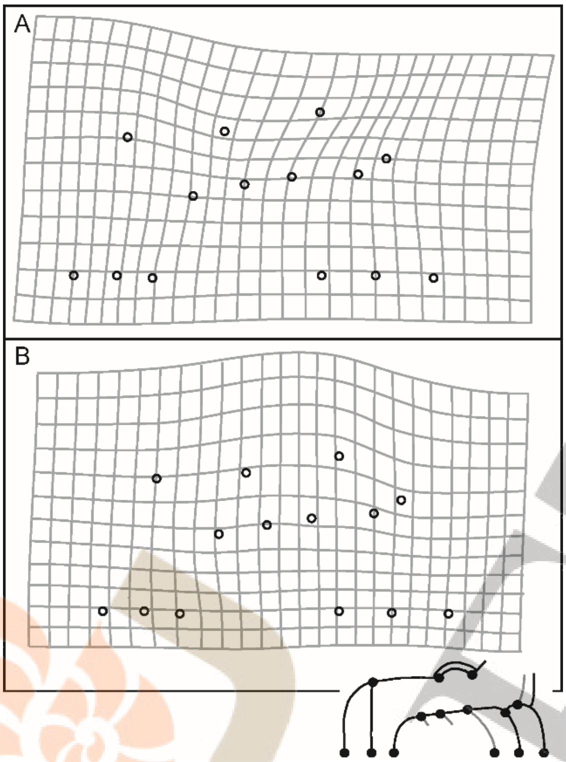

Figure 8—Relative warp grids using SBR superimposition for RW1 and RW2 for the 22 cranidial landmarks of all specimens of *Thailandium solum*, *Prosaukia misa*, *Prosaukia oculata*, *Prosaukia tarutaoensis*, and *Thailandium* sp. undet. (1) shape variation related to Relative Warp (RW) 1, 42.90% of total variance; (2) shape variation related to RW2, 20.19% of total variance.

convergence of the anterior facial suture branches, shorter palpebral lobes, and a particularly long frontal area. *Thailandium solum* also has wider fixigena than is typical for *Prosaukia* as indicated by distribution along RW2, but this is not a reliably diagnostic character since *P. oculata* has fixigena of comparable width to *T. solum*. A reliable diagnosis for the difference in length and longitudinal position of the palpebral lobe of *Thailandium* versus *Prosaukia* is that the posterior end of the palpebral lobe is opposite S1 in *T. solum* but in all other species included herein it is opposite L1.

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

Based on the landmark morphometric analysis alone, *T. solum* and *T. truncatum* differ only in the length of the frontal area and width of the occipital lobe. However, they are readily distinguished by characters not captured in our geometric analysis, including overall convexity and the manner of incision of the anterior border furrow, to the extent that *T. truncatum* is unlikely to be a species of *Thailandium*. For additional comments regarding the affinity of *T. truncatum* see the generic remarks for *Thailandium.*

Systematic Paleontology:

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

Superfamily DIKELOCEPHALOIDEA Miller, 1889
Family DIKELOCEPHALIDAE Miller, 1889

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

Genus *Thailandium* Kobayashi, 1957

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

Emended diagnosis.—As for *Thailandium solum.*

Remarks: The results of the above landmark morphometric analysis indicate that *Thailandium* possesses anteriorly convergent facial sutures and that *Thailandium* sp. undet. (*sensu* Shergold, 1991) is a species of *Prosaukia* rather than of *Thailandium.* The shorter frontal area of *T. truncatum* is evident from the morphometrics, but other notable differences between *T. solum* and *T. truncatum* are not. In *Thailandium truncatum* Zhou et al., 1977 the anterior border furrow shallows notably medially, while other furrows are deeply incised, and the fixigena and preglabellar field are inflated, strongly convex rather than relatively flat as in *T. solum*. Furthermore the occipital lobe is much broader than L1.

The single cranidium known for *T. truncatum* does not fit with the concept of *Thailandium* as a flat, broad taxon with a long frontal area. The inflated preglabellar field with a medially shallowing anterior border furrow is well-developed in two “saukiid” genera, *Hoytaspis* Ludvigsen and Westrop, 1983 and *Caznaia* Shergold, 1975. The short (tr.) S2 and S3, nearly straight (tr.) anterior border furrow, strongly anteriorly tapering glabella, and lack of coarse granulation preclude assignment to *Hoytaspis* (Ludvigsen and Westrop, 1983; Shergold, 1975). *Caznaia* Shergold, 1975 is a better match. Though the generic diagnosis for *Caznaia* includes anteriorly divergent facial sutures, *Caznaia sectarix* Shergold, 1975, one of the two species originally included in the genus, has anteriorly convergent sutures. The medially deep S1 of *T. truncatum* and relatively straight-sided preoccipital glabella are more problematic for assignment to *Caznaia*, but variation among *C. sectarix* and *Caznaia squamosa* is sufficient to suggest that these character states may not preclude assignment. The pygidia and librigena of *Thailandium* and *Caznaia* are sufficiently distinct that recovery of these would help significantly in determining to which, if either, of these genera *T. truncatum* belongs, but until such material is recovered, we reassign

T. truncatum to *Caznaia*? *truncata*. While its genus is uncertain, *Caznaia*? *truncata* more likely belongs to Dikelocephalidae than to Elviniidae Kobayashi, 1935 as it lacks the notable eye ridges evident in species that have been assigned to Elviniidae (e.g. Palmer 1965, pl. 3, figs. 9, 11, 12, 14, 16).

With the exclusion of *Caznaia*? *truncata* and *Thailandium* sp. undet. *Thailandium* is left as a monospecific genus known only from Ko Tarutao, Thailand.

Thailandium solum Kobayashi, 1957

Figs 9, 10

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

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

Diagnosis.—Trapezoidal cranidium with long frontal area long (sag.) equally to subequally divided into the anterior border and preglabellar field, anteriorly convergent facial suture branches, low convexity, shallow furrows, strongly bowed, medially continuous S1; palpebral lobes short (exsag.) with posterior point opposite S1. Pygidium subcircular to subtriangular, axis short with four axial rings and long post-axial ridge occupying about half the pygidial length (sag.), pleural field broad, effaced.

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

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

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

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

Materials.—The new collections of *Thailandium solum* include 27 cranidia: 21 from Ao Mo Lae (AML) 3.62 m (DGSC F0568, F0569), 3.72 m (DGSC F0571, F0570), 5.17 m (DGSC F0574), 5.81 m (DGSC F0576, F0583, F0595, F0596, F0598, F0601, F0602, F0606, F0607, F0609, and CMC IP87617, IP87618), AML h3 (DGSC F0543, F0544), and AML h5 (DGSC F0591, F0618); six from Ao Talo Topo west (ATTw) (DGSC F0398, F0388, F0421, F0419, F0434, F0435). Nine librigenae: eight from AML 5.81 m (DGSC F0612, F0616, F0631 and CMC IP87612, IP87622, IP87623), AML h1 (DGSC F0554), and AML h4 (CMC IP87607); one from ATTw (DGSC F0418). 10 pygidia: eight from AML 2.2 m (DGSC F0565), 5.81 m (DGSC F0509, F0584, F0604, F0610, F0611 and CMC IP87610), and AML h4 (DGSC F0560); 2 from ATTw (DGSC F0395, F0420).

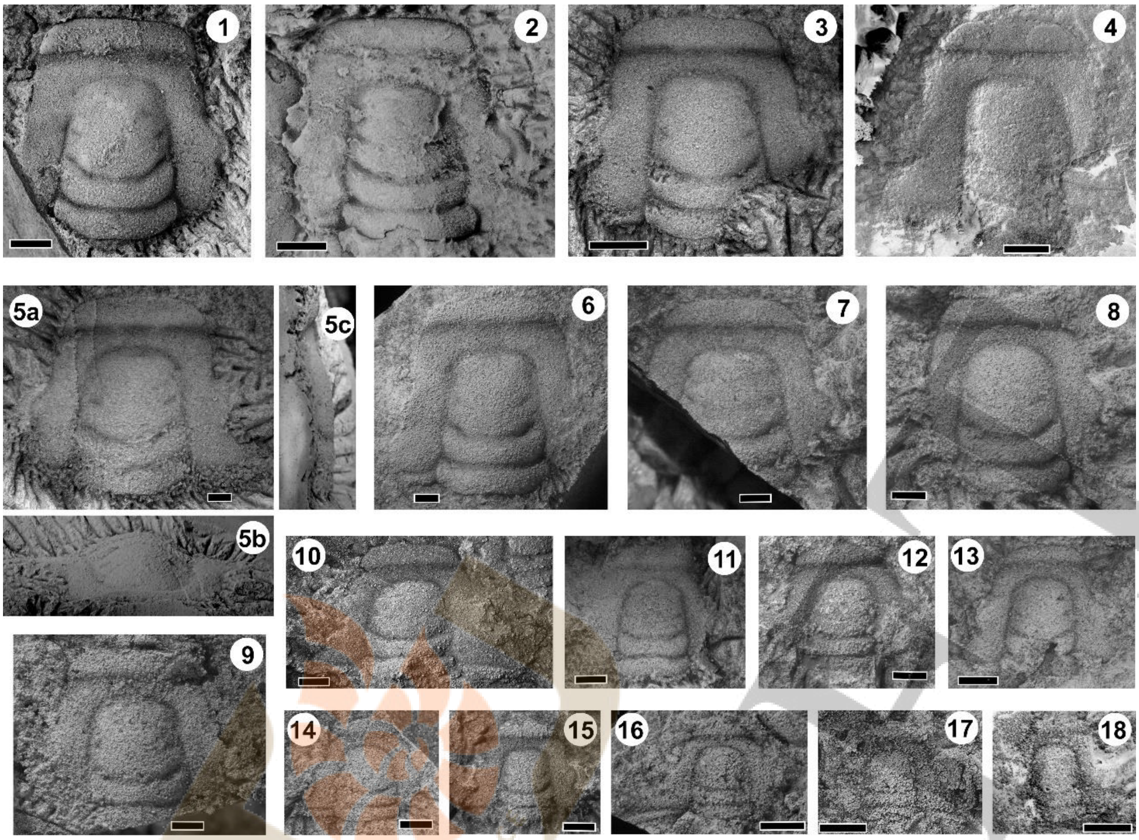

Figure 9—*Thailandium solum* Kobayashi, 1957 cranidia from Ko Tarutao. (1) DGSC F0570, Ao Mo Lae (AML) 3.72 m; (2) DGSC F0419, Ao Talo Topo west (ATTw); (3) DGSC F0609, AML 581 m; (4) CMC IP87037, vinyl polysiloxane cast, original of UMUT PA02299b-1, Kobayashi (1957) pl. 4 fig. 9, holotype; (5a–c) dorsal,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

Remarks.—The larger sample size available in this study allows for new understanding of the ontogeny of *Thailandium solum*. The regression of partial Procrustes distances compared to the mean of the smallest specimens determines the extent to which shape change is related to size (Webster and Sheets, 2010). The same landmark configurations of 15 specimens of *T. solum* used in the shape analysis were regressed against the mean shape of the smallest 3 specimens in the sample (e.g. DGSC F0544, Fig. 9.15) and the partial Procrustes distance from the mean calculated. While there is considerable scatter of this partial Procrustes distance plotted against log of the centroid size, ontogenetic change accounts for 16.63% of morphological variance (Fig. 11; p = 0.0075 bootstrapped by 1600 repetitions)

The most prominent ontogenetic change is the widening (tr.) of the frontal area. Additionally, the palpebral lobe shortens (exsag.) by both anterior and posterior migration of the posterior and anterior ends respectively. Another change with increasing size is that the relative glabellar length anterior to S1 increases, and the S1 furrow becomes more strongly posteriorly bowed. In terms of partial Procrustes distance from the mean form, shape variance for all 15 specimens of *T. solum* was 0.0048 (bootstrapped by 1600 repetitions with a 95% confidence interval of 0.0031–0.0060). For comparison, a single specimen (Fig. 9.3, DGSC F0609) was remounted, photographed, and marked for landmarks ten times; the variance for these ten images of a single specimen was 0.0008 over 1600 bootstraps.

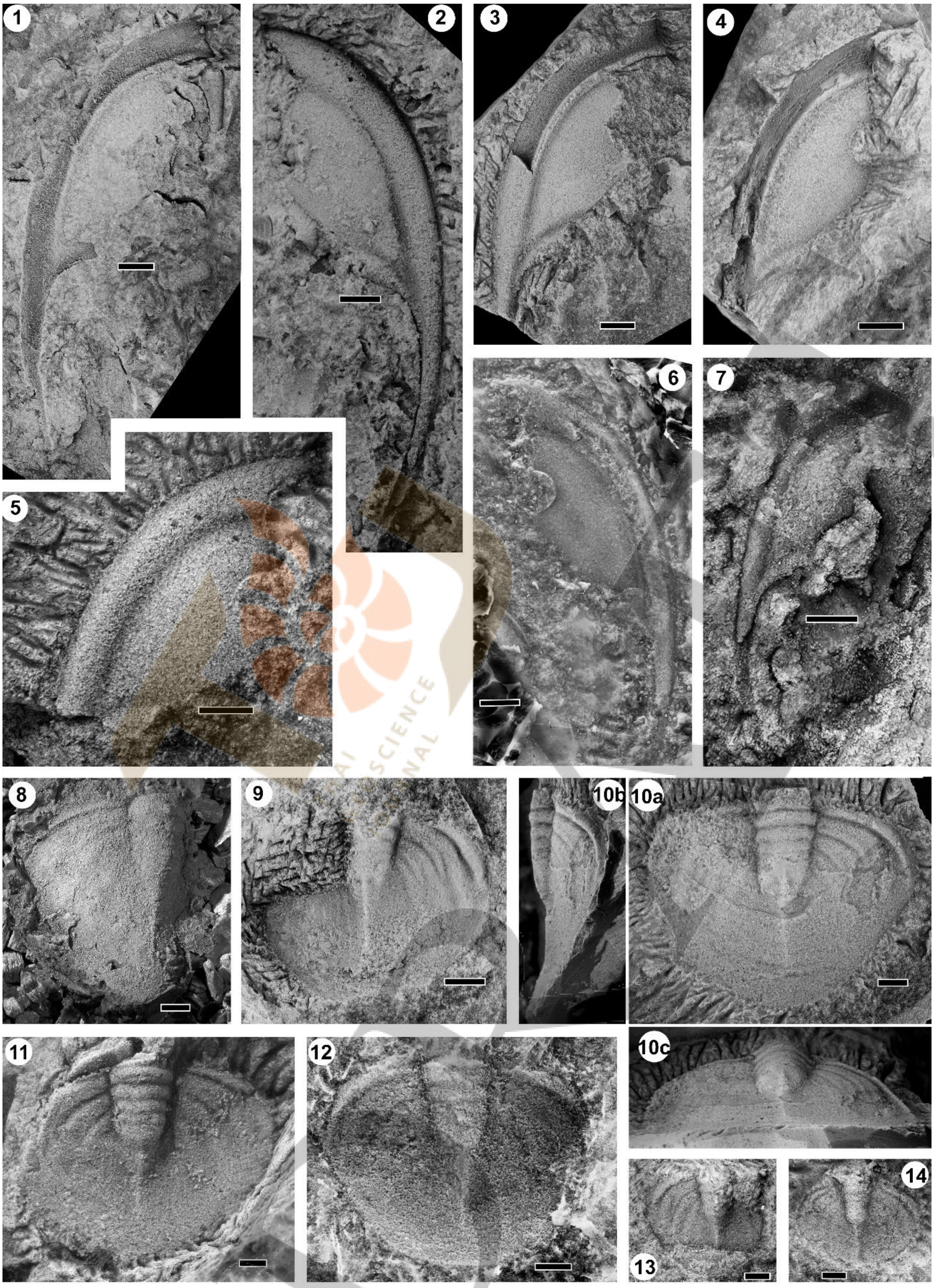

Figure 10—Thailandium solum Kobayashi, 1957 librigena (1–7) and pygidia (8–14) from Ko Tarutao. (1) DGSC F0621 Ao Mo Lae (AML) h2; (2) DGSC F0554, AML h3; (3) DGSC F0612, AML 5.81 m; (4) DGSC F0616, AML 5.81 m; (5) DGSC F0631, AML 5.81 m; (6) CMC IP87039, vinyl polysiloxane cast, original of UMUT PA02299b-2, Kobayashi, 1957 pl. 4, fig. 10; (7) DGSC F0418, Ao Talo Topo west (ATTw); (8) CMC IP87046, vinyl polysiloxane cast, original of UMUT PA02299d-1, Kobayashi (1957) pl. 4, fig. 16; (9) DGSC F0610, AML 5.81 m; (10a–c) dorsal, right lateral, and posterior views respectively, DGSC F0611, AML 5.81 m; (11) DGSC F0565 AML 2.2 m; (12) DGSC F0509, AML 5.81 m, external mold; (13) DGSC F0604, AML 5.81 m; (14) DGSC F0560, AML h4. All internal molds except 5. Scale bars = 5mm for 1–3, 8–13 and 2mm for 4–7, 14.

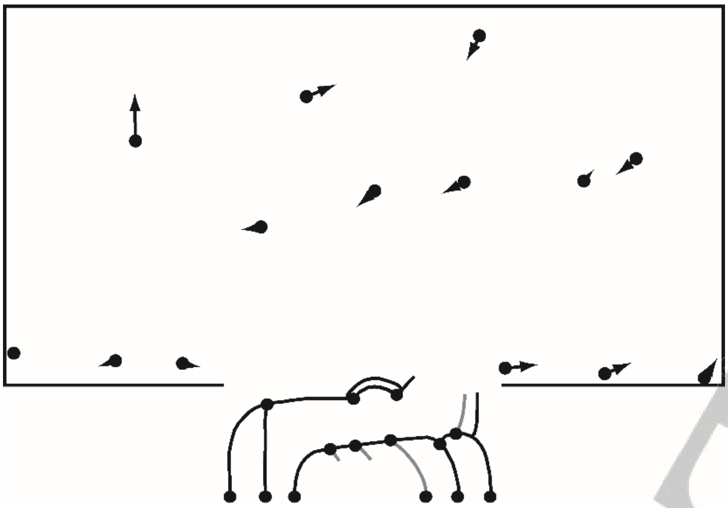

Figure 11—Shape change with growth for *Thailandium solum* Kobayashi, 1957, produced from the regression of Procrustes distance vs. log of centroid size (LCS) using the three smallest specimens as reference. P=0.007 for 1600 bootstraps.

Accordingly, morphological variation among cranidia of *T. solum* greatly exceeds measurement error. The shape variance value for the sample is broadly comparable to that seen among cranidial meraspid instars in the Silurian aulacopleurid *Aulacopleura koninckii* (see Hong et al., 2014, supplemental data 4), although the set of cranidial landmarks assessed in the two studies were different in both landmark number and location. At present studies of comparative morphological variance among trilobite taxa in landmark selection are too few to allow assessment of the effects of landmark scheme selection and taphonomic factors such as flattening in shales on variance, but the consistent distinction between sample variance and measurement error seen in these studies does suggest that future comparative studies of this kind may be worthwhile.

When defining *Thailandium solum* Kobayashi (1957) tentatively assigned a relatively short and broad pygidium to the species. That pygidium instead belongs to *Quadraticephalus planulatus* (Kobayashi, 1957). Shergold et al. (1988) reassigned this pygidium to *Lichengia*? *tarutaoensis* (Kobayashi, 1957), recognizing it as "saukiid" in form and with a somewhat similar shape to the *Lichengia*? *tarutaoensis* pygidium (Shergold et al., 1988, fig. 5W).

However, the pygidium herein assigned to *T. solum* has a notably broader pleural and postaxial region and is not easily confused with that of *L.*? *tarutaoensis*. Shergold et al.'s (1988) assumption that their collections came from the same stratigraphic horizons as those of Kobayashi (1957) was the basis for some of their taxonomic decisions (e.g. *Pagodia thaiensis* as *Parakoldinioidia thaiensis* and *Saukiella tarutaoensis* as *Lichengia*? *tarutaoensis*; *S. tarutaoensis* instead is herein recognized as a species of *Prosaukia*). It is now clear that Kobayashi's (1957) collection represents an interval distinct from Shergold et al.'s (1988) and the only cooccurring taxa are those that are relatively long-lived in the Ao Mo Lae Formation, including *Eosaukia buravasi* Kobayashi (1957) and *Quadraticephalus planulatus* (Kobayashi, 1957). The pygidium initially assigned to *C. planulatus* Kobayashi (1957) and incorrectly assigned to *Lichengia? tarutaoensis* by Shergold et al. (1988), belongs to in fact to *Thailandium*, which itself was absent from all the collections that Shergold et al. (1988) observed. The large pygidium is inconsistent with even the largest cranidia of any other species in either Kobayashi's (1957) collection or the collection presented herein excepting perhaps *Quadraticephalus planulatus* and *Eosaukia buravasi*; the shape and pleural divisions are notably "saukiid"-like, ruling out assignation to *Quadraticephalus*, and the broad pleural field is inconsistent with the lenticular shape of an *Eosaukia* pygidium which is otherwise well-documented in the Tarutao collections.

The cranidium of *Thailandium* is similar to that of *Prosaukia* Ulrich and Resser (1933) save for the angle of the anterior suture branches and length of the palpebral lobe (Fig. 9). Likewise, the pygidium of *Thailandium* differs from that of *Prosaukia*, at least the type species, mainly by degree of axial length, post-axial length, and effacement of the pleural field (Fig. 10). *Thailandium's* cranidium also approaches the condition seem in some dikelocephalinids, such as *Osceolia* and some *Briscoia* in form of the preglabellar field (Ulrich and Resser, 1930), but the form of the glabella, anterior position of the eyes, and the convergent anterior sutures are distinctive in *Thailandium.*

The librigena of *Thailandium solum* is distinct from the librigena of similar genera, including *Prosaukia* and *Tellerina* Ulrich and Resser (1933), in that the posterior and lateral border furrows are firmly-incised and truly confluent (e.g. DGSC F0418, Fig. 10.7). In both *Tellerina* and *Prosaukia* the joining of the furrows is marked by a continuous curve for the posterior border furrow and a bend, often sharply dog-legged, in the lateral border furrow. In *Prosaukia* the lateral furrow may become effaced with an inflated extension of the pleural field separating it from the posterior border furrow; this state is particularly well-developed on *Prosaukia misa* (Hall, 1863) and to a lesser extent on *Prosaukia oculata* n. sp.

Though cephalically distinct, particularly in the frontal area, *Thailandium* has a similar overall pygidial structure to that of *Tellerina* Ulrich and Resser (1933) and *Calvinella* Walcott, 1914. Similarities include a short axis, long postaxis, broad and poorly-defined flat to concave border without a border furrow. Some species of *Calvinella* (e.g. the type species, *C. spiniger*) have well-defined postaxial ridges; these are rare in *Tellerina*. In *C. spiniger* the pygidium is more circular or subellipsoidal than in *Thailandium*, but *Tellerina*, at least for the type species *Tellerina crassimargniata* (Whitfield, 1882), has a subtriangular to spatulate pygidium, like that of *Thailandium*. Of the three genera, *Thailandium* has the most effaced interpleural furrows and shortest (tr.) pleural furrows (Fig. 10). All three genera grow to sizes larger than is typical for "saukiids" though not as large as some species of *Dikelocephalus* (e.g. *Dikelocephalus minnesotensis* Owen, 1852; see Hughes, 1994). *Dikelocephalus minnesotensis* has a similarly broad, poorly defined and flat border with a long postaxial area. The broad, flat, effaced border may reflect a convergence of all dikelocephalid trilobites that grow to be more than a few centimeters in total length.

Genus *Prosaukia* Ulrich and Resser, 1933

Type species.—*Dikelocephalus misa* Hall (1863)

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

Prosaukia tarutaoensis (Kobayashi, 1957)

Fig. 12

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

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

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

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

Emended description.—Cranidium subtrapezoidal; width across palpebral areas 90% of cranidial length in smallest holaspids to 105% of cranidial length in largest holaspids. Occipital glabellar length (sag.) up to 1.1cm; glabellar width across L1 60%

width across palpebral areas in smaller holaspids and 70% in larger; length of glabella and LO 82–85% of cranidial length; glabella trunco-conical with low dorso-ventral relief; axial furrows straight or slightly pinched at S2, weakly incised; anterior glabellar margin transverse to gently curved; LO 15–20% wider than L1; SO gently posteromedially bowed, shallowing medially; S1 moderately to strongly posteromedially bowed, shallowing medially; S2 short (tr.) and well-defined, less posteromedially angled than S1; anteromedially angled S3 poorly-defined to effaced. Palpebral lobe moderately arched with greatest curvature in posterior part; widest palpebral point slightly anterior to S1 in smaller holaspids and slightly posterior in larger; palpebral lobe length (exsag.) 30% cranidial length (sag.) in smaller holaspids to 40% in larger; width (tr.) across anterior palpebral corners 80–90% width across posterior corners. Fixigena narrow (tr.) with moderately wide preocular areas; anterior suture branches anteriorly divergent from anterior palpebral corners, curving gently adaxially for rounded lateral margins of frontal area; frontal area widest (tr.) point slightly posterior to anterior border. Preglabellar field short, depressed; anterior border furrow gently anteromedially bowed; anterior border 15% cranidial length, weakly inflated, horizontally oriented. All surfaces densely granulated.

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

Material.—Five cranidia from Ao Mo Lae (AML) 2.20 m (DGSC F0566), AML 3.1 m (DGSC F0567), AML h3 (DGSC F0545, F0546), and Ao Talo Topo west (ATTw) (DGSC F0413); one pygidium from ATTw (DGSC F0453); all internal molds.

Remarks.—*Prosaukia tarutaoensis* represents a typical species of *Prosaukia* in many ways; in the dimensions and shape of the glabella, length of the palpebral lobes, width of the fixigena, length of the anterior border, surface texture, and expression of furrows it clearly resembles the type species, *Prosaukia misa* (Hall, 1863). *Prosaukia tarutaoensis* differs cranidially from many other known species of *Prosaukia* primarily in the notably short (sag.) preglabellar field and wide (tr.) occipital lobe (e.g. DGSC F0566, Fig. 12.1a). In *Prosaukia misa* (Hall, 1863) and most other species of *Prosaukia* the occipital lobe is either slightly narrower than L1 as in *Prosaukia oculata* n. sp. or else the axial furrows flank the occipital lobe along the same path as the preoccipital glabella. In *P. tarutaoensis* the axial furrows curve sharply around the occipital lobe (Fig. 12). The pygidium of *P. tarutaoensis* is distinct as it is the only known species of *Prosaukia* with a lenticular pygidium.

Shergold et al. (1988) considered the single specimen of *Prosaukia tarutaoensis* known at that time (Kobayashi, 1957; pl. 5 fig. 12; Fig. 12.5) to be synonymous with new material that they called *Lichengia*? *tarutaoensis* on account of the frontal area and palpebral lengths and positions. It is clear from the strong anteriorly narrowing glabella and medial discontinuity of the lateral glabellar furrows in the latter material that these specimens are not synonymous with *Prosaukia tarutaoensis*. Therefore *Lichengia*? *tarutaoensis* is excluded from Kobayshi's (1957) concept of the species. Additional specimens of *Lichengia tarutaoensis* (*sensu* Shergold et al., 1988) have been recovered from the Ao Mo Lae Formation, and revision of this species will appear in future work.

Prosaukia oculata n. sp.

Fig. 13

?1988 *Lichengia*? *tarutaoensis* (Kobayashi) Shergold et al., p. 309–310, fig. 5W only, *not* figs 5S–V = *Lichengia simplex* Shergold, 1991)

Type material.—Holotype, DGSC F0512 (Fig. 13.1a–b) from Ao Talo Topo 22.78 m; paratypes DGSC F0461, F0489, F0498, F0503, F0511, F0532, F0534; Ao Mo Lae

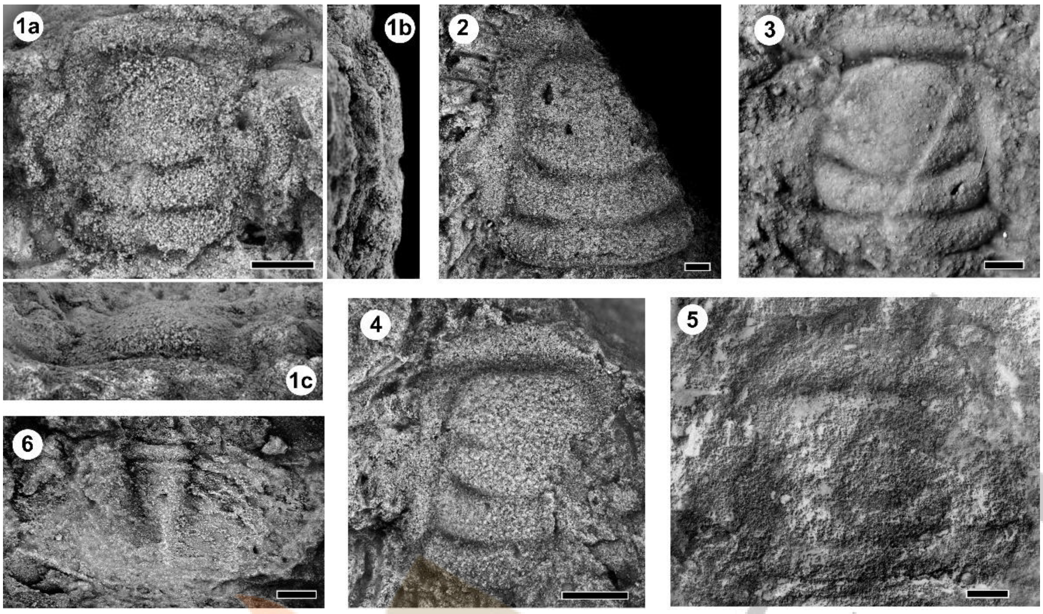

Figure 12—Prosaukia tarutaoensis n. sp. cranidia (1–5) and pygidium (6). (1a–c) dorsal, left lateral, and anterior views respectively, DGSC F0566, AML 2.2 m; (2) DGSC F0567, Ao Mo Lae (AML) 3.1 m; (3) DGSC F0413, Ao Talo Topo west (ATTw); (4) DGSC F0546, AML h3; (5) CMC IP87029, vinyl polysiloxane cast, holotype, original of UMUT PA02298c, Kobayashi, 1957, pl. 5, fig. 12; (6) DGSC F0453, ATTw. All internal molds. Scale bars = 2mm.

Formation, Tarutao Group, Ko Tarutao, Thailand; Furongian.

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

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

Description.—Cranidium subrectangular; width across palpebral areas 120%–135% cranidial length (sag.). Occipital glabellar length (sag.) up to 0.9cm; glabellar width (tr.) across L1 50% width across palpebral areas; length of glabella and LO 85% cranidial length (sag.); glabella bullet-shaped with moderate dorso-ventral relief; axial furrows smoothly curved around glabella or slightly bowed at L1, well-defined; anterior glabellar margin transverse to gently curved; L1 slightly wider than LO; SO transverse or gently posteromedially bowed, shallowing medially; S1 slightly more stronglyposteromedially bowed than SO, shallowing medially; S2 medially discontinuous and weakly to moderately well defined, less posteromedially angled than S1; S3 poorly-defined to effaced, oriented slightly postermedially to transverse. Palpebral lobe strongly curved, nearly symmetric about the midpoint; palpebral midpoint opposite S1; palpebral lobe length (exsag.) 35%–40% cranidial length (sag.); width (tr.) across anterior palpebral corners equal or slightly less than width across posterior corners. Fixigena broad (tr.) with wide preocular areas only slightly narrower than palpebral areas; anterior suture branches anteriorly divergent 3540° from sagittal, curving strongly adaxially at anterior border furrow. Preglabellar field very short to furrow-like, depressed; anterior border furrow gently anteromedially bowed; anterior border 15% cranidial length, strongly inflated, horizontally oriented. Weakly granulated surface sometimes effaced.

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

Pygidium subcircular with slight posterior marginal embayment; length (sag.) 80%

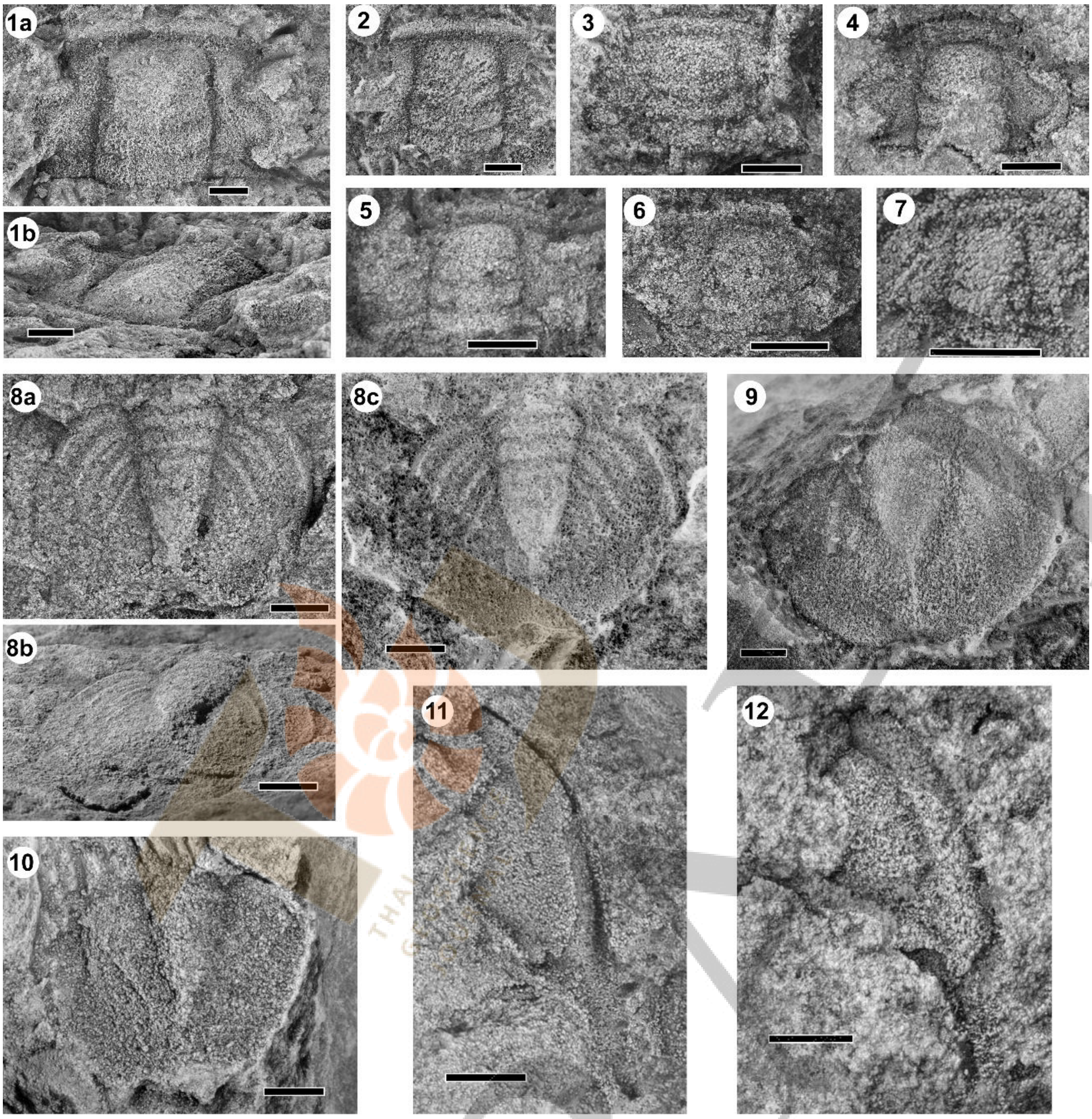

Figure 13—*Prosaukia oculata* n. sp. cranidia (1–7), pygidia (8–10), and librigena (11,12). (1a–b) dorsal and left anterolateral views respectively, DGSC F0512; (2) DGSC F0503; (3) DGSC F0498; (4) DGSC F0532; (5) DGSC F0511; (6) DGSC F0461; (7) DGSC F0534, Ao Talo Topo (ATT) 22.88 m; (8a–c) internal dorsal, internal right posterolateral oblique, and external dorsal views respectively, DGSC F0510; (9) DGSC F0470, external mold; (10) DGSC F0497; (11) DGSC F0488; (12) DGSC F0513. All from ATT 22.78 m except 7; all internal molds unless otherwise indicated. Scale bars = 2mm.

width (exsag.); widest (tr.) point of pygidium near pygidial mid-length (exsag.); axial width (tr.) at anterior-most ring 30%–35% pygidial width at widest point; axial length (sag.) 60%–70% pygidial length (sag.); 4 axial rings, only first 2 clearly defined; axial furrows converging at 10°–15° from sagittal axis; terminal piece posteriorly angular; postaxial ridge distinct and extending to pygidial margin. Pleural furrows and interpleural furrows well-defined; anterior pleural bands narrow; posterior pleural bands strongly inflated; pleural furrows broader than interpleural furrows; all pleurae well-aligned with axial rings; all pleurae maintain width to edge of pleural field and become effaced where pleural field slopes into border; border flat without defined furrow; doublure short, not reaching terminal axial piece.

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

Material.—Seven cranidia (DGSC F0461, F0489, F0498, F0512, F0511, F0532 –

internal molds, DGSC F0503 – external mold), 2 librigena (DGSC F0488, F0513 – internal molds), and 4 pygidia (DGSC F0510 – internal and external mold, F0430 – external mold, F0470 – external mold, F0497 – internal mold) all from Ao Talo Topo 22.78 m, one cranidium internal mold from Ao Talo Topo 24.1 m (DGSC F0534), and one cranidium from ATT h1 (DGSC F0459).

Remarks.—Prosaukia oculata, as its name suggests, has more widely set apart palpebral lobes than is typical for the genus (e.g. DGSC F0532, Fig. 13.4). The greater distance between the eyes results from broader fixigena rather than a wider glabella. *Prosaukia delcostata* Ulrich and Resser (1933) also has relatively broad fixigena, but it differs from *P. oculata* by the former's longer preglabellar field, broader lateral cephalic border, more rectangular anterior glabellar margin, and less circular pygidium.

The preglabellar field of *P. oculata* is very short, nearly absent compared with most *Prosaukia*, but it is still clearly recognizable on some specimens (e.g. DGS F0532, Fig. 13.4), and this intraspecific variation proves the presence of the preglabellar field within the taxon.

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