Age of the Early Triassic Ichthyopterygian Thaisaurus Inferred from Ammonoid Biostratigraphy

Authors: Tongtherm, Kittichai, Shigeta, Yasunari, Sardsud, Apsorn, Sashida, Katsuo, and Agematsu, Sachiko

Source: Paleontological Research, 24(4) : 276-284

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/2019PR022

Paleontological Research, vol. 24, no. 4, pp. 276–284, October 1, 2020

doi:10.2517/2019PR022

Age of the Early Triassic ichthyopterygian *Thaisaurus* inferred from ammonoid biostratigraphy

KITTICHAI TONGTHERM[1], YASUNARI SHIGETA[2], APSORN SARDSUD[3], KATSUO SASHIDA[1,4] AND SACHIKO AGEMATSU[1]

[1]*Graduate School of Life and Environmental Sciences, University of Tsukuba, 1-1-1 Ten-nodai, Tsukuba, Ibaraki 305-8572, Japan (e-mail: tongtherm@gmail.com)*
[2]*Department of Geology and Paleontology, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan*
[3]*Mineral Resources Research and Development Center, Department of Mineral Resources, 75/10 Rama VI Road, Ratchatewi, Bangkok 10400, Thailand*
[4]*Geoscience Program, School of Interdisciplinary Studies, Mahidol University, Kanchanaburi Campus, 199 Moo 9, Sai Yok, Kanchanaburi 71150, Thailand*

Received June 24, 2019; Revised manuscript accepted October 20, 2019

Abstract. The age of the primitive ichthyopterygian *Thaisaurus* is more accurately defined due to the discovery of a new species of the ammonoid genus *Marcouxia* from beds about 2.4 m below the horizon from which the holotype of *Thaisaurus chonglakmanii* was collected in the Phukhaothong Dolomite Member of the Chaiburi Formation in the Phatthalung area, southern Thailand. The shell of *Marcouxia chaiburiensis* sp. nov. is characterized by a quadrate whorl section, an arched venter with a sub-acute keel-like elevation, and spiny tubercles on the ventrolateral shoulders as well as numerous regularly spaced, radial or slightly prorsiradiate ribs. Because the range of *Marcouxia* is limited to the *Columbites parisianus* Subzone of the lower Spathian (upper Olenekian, Lower Triassic) in the western USA, the age of *Thaisaurus* is likely constrained to the early Spathian, thus suggesting it is one of the oldest known ichthyopterygians.

Key words: ammonoid, *Marcouxia*, Spathian, Thailand, *Thaisaurus*, Triassic

Introduction

The Ichthyopterygia, which was the most successful Mesozoic secondary aquatic reptile group, appeared in the Early Triassic and thrived until going extinct in the early Late Cretaceous (Bardet, 1992; McGowan and Motani, 2003). *Chaohusaurus* from the upper part of the lower Spathian (upper Olenekian) in South China is the oldest known ichthyopterygian (Ji *et al*., 2015). Fragments of ichthyopterygian skeletons have been reported from the upper part of the lower Spathian in South Primorye, Russian Far East (Nakajima *et al*., 2018), and middle Spathian-aged early ichthyopterygians have been found at many localities, including South China, Japan, British Columbia, western USA and Svalbard (Shikama *et al*., 1978; Brinkman *et al*., 1992; Maxwell and Kear, 2013; Ji *et al*., 2015; Kelley *et al*., 2016). Some undetermined remains of early ichthyopterygians were also described by Massare and Callaway (1994) and reported by Brayard *et al*. (2017) from different lower Spathian exposures in the western USA.

The early ichthyopterygian *Thaisaurus chonglakmanii* was described from the Phatthalung area in southern Thailand by Mazin *et al*. (1991), who considered it to be of Early Triassic age. This age assignment was later supported by the discovery of co-occurring Olenekian (Smithian to Spathian) conodonts (Ampornmaha, 1995, 1996), but until now, the section's ammonoid biostratigraphy with its inherent more accurate age determination potential had not been studied.

Over the past two decades, much research has been accomplished regarding the classification and biostratigraphy of the Early Triassic ammonoids around the world, thus enabling highly accurate correlation (e.g. Jenks *et al*., 2015). The recent discovery of ammonoids in close stratigraphic proximity to *Thaisaurus* likely provides an important key for the determination of its exact age.

We recently discovered many specimens referable to the ammonoid *Marcouxia* from beds about 2.4 m below the horizon from which the holotype of *Thaisaurus chonglakmanii* was collected in the Phatthalung area of southern Thailand (Figure 1). In this paper, we describe these specimens as a new species of *Marcouxia* and discuss the age of *Thaisaurus* based on the high resolution

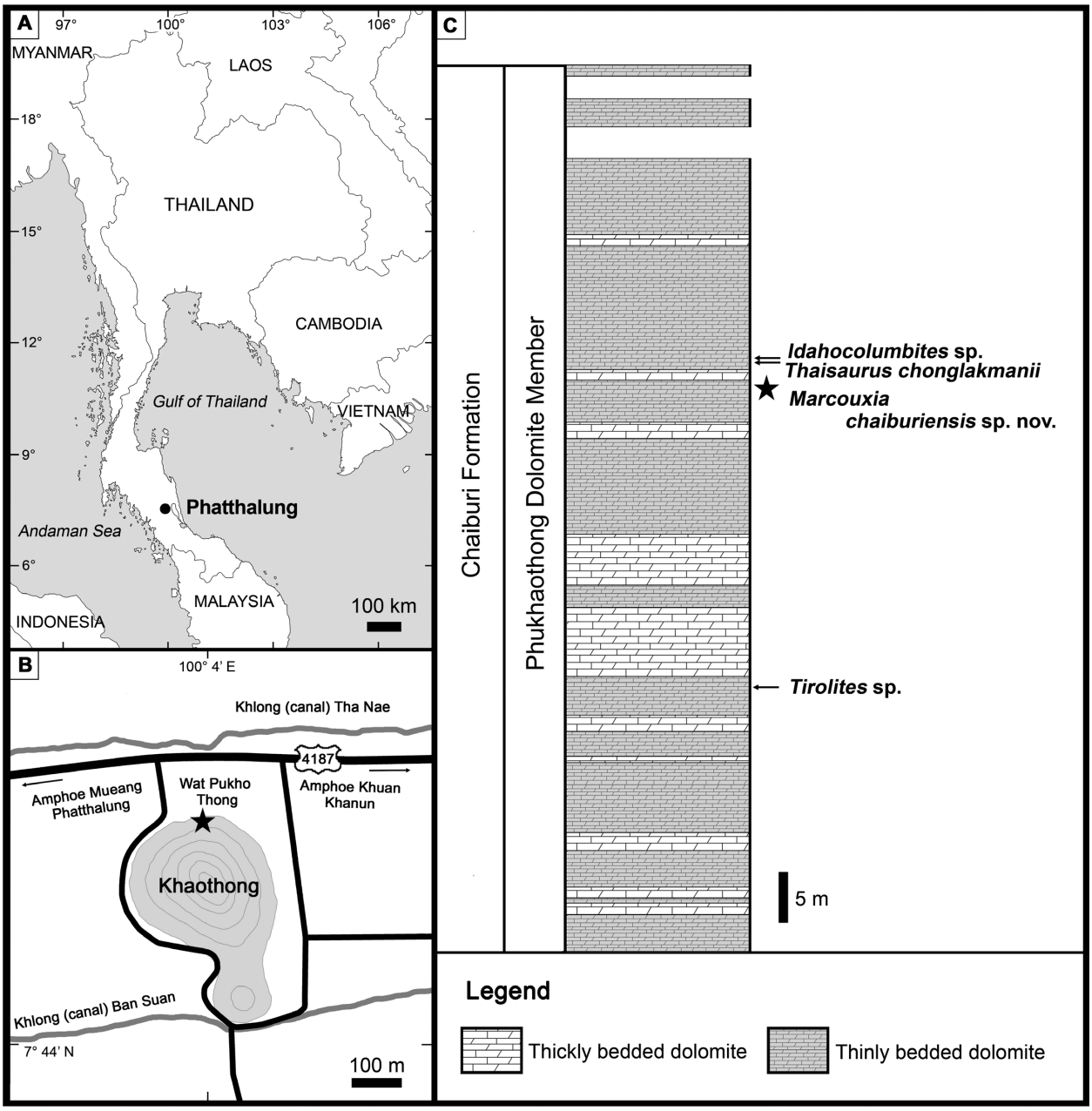

Figure 1. Locality **(A, B)** and horizons **(C)** of the *Thaisaurus chonglakmanii* and *Marcouxia chaiburiensis* sp. nov. and other ammonoid specimens.

potential for age determination provided by this new taxon.

Notes on stratigraphy

Marine Triassic carbonate rocks of the Chaiburi Formation in the Phatthalung area, which belong to the Shan-Thai Terrane, are widely distributed as isolated mountains in the plain formed by Quaternary sediments. They are divided into three members: the Phukhaothong Dolomite, Chiak Limestone and Phanomwang Limestone members in ascending order (Ampornmaha, 1995).

The Phukhaothong Dolomite Member, mainly consisting of a 80 m+ thick dolomite sequence, contains Dienerian (late Induan) to Spathian (late Olenekian) conodont assemblages as well as the ichthyopterygian *Thaisaurus chonglakmanii* (Mazin *et al*., 1991; Ampornmaha, 1995, 1996; Sardsud *et al*., 2017). The uppermost part of the

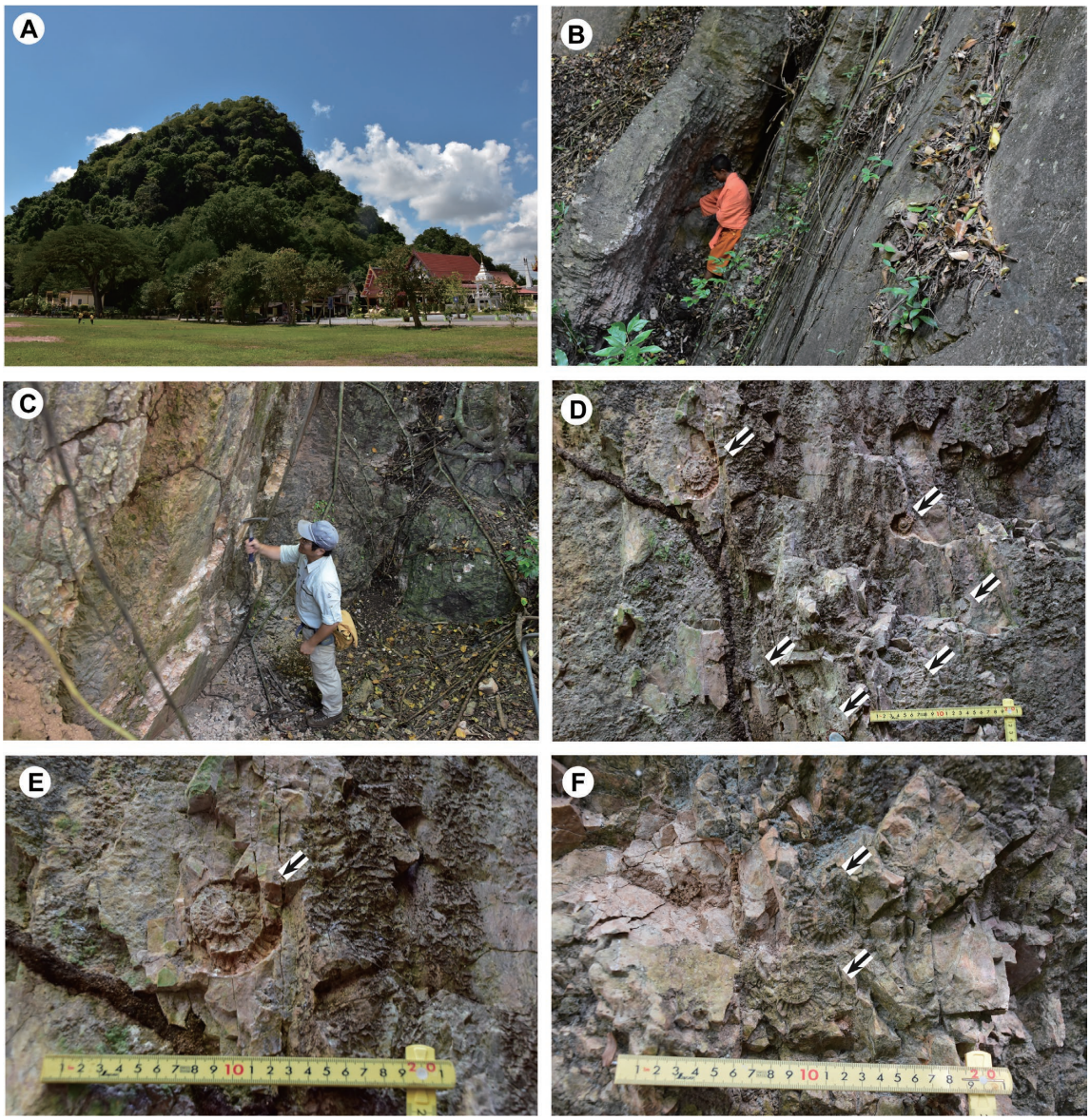

Figure 2. Selected photographs from the Khao Thong section in the Phatthalung area. **A,** distant view of the section located on the north side of the mountain, just south of the Wat Pukhao Thong temple, in which the Phukhaothong Dolomite Member of the lower part of Chaiburi Formation is well exposed. **B,** thinly bedded dolomite from which the holotype of ichthyopterygian *Thaisaurus chonglakmanii* described by Mazin *et al*. (1991) was collected, indicated by a Buddhist monk Phra Phonpon Palapon who remembers where it was excavated. **C–F,** thinly bedded dolomite containing the outer molds of many *Macouxia chaiburiensis* sp. nov. ammonoid specimens (arrows). This horizon is located about 1 m below the bed in which *T. chonglakmanii* was found.

member includes a conodont assemblage of Spathian to earliest Anisian age (Ampornmaha, 1995, 1996; Sardsud *et al*., 2017). Three specimens of *T. chonglakmanii* were found in this area: two of them consist only of much-weathered natural impressions without bone and the third specimen is a near-complete skeleton, consisting of the skull, part of the right fore-limb and left hind-limb, and part of the vertebral column (Mazin *et al.*, 1991).

The overlying 300 m thick, Chiak Limestone Member consists of limestones intercalated with nodular and thin-bedded cherts. Conodonts (Ampornmaha, 1995, 1996; Sardsud *et al*., 2017) and radiolarians (Sashida and Igo, 1992) from limestone samples indicate that the lower part is Spathian to middle Anisian, while the uppermost part is probably lower Carnian (Sardsud *et al*., 2017).

The Phanomwang Limestone Member consists of a

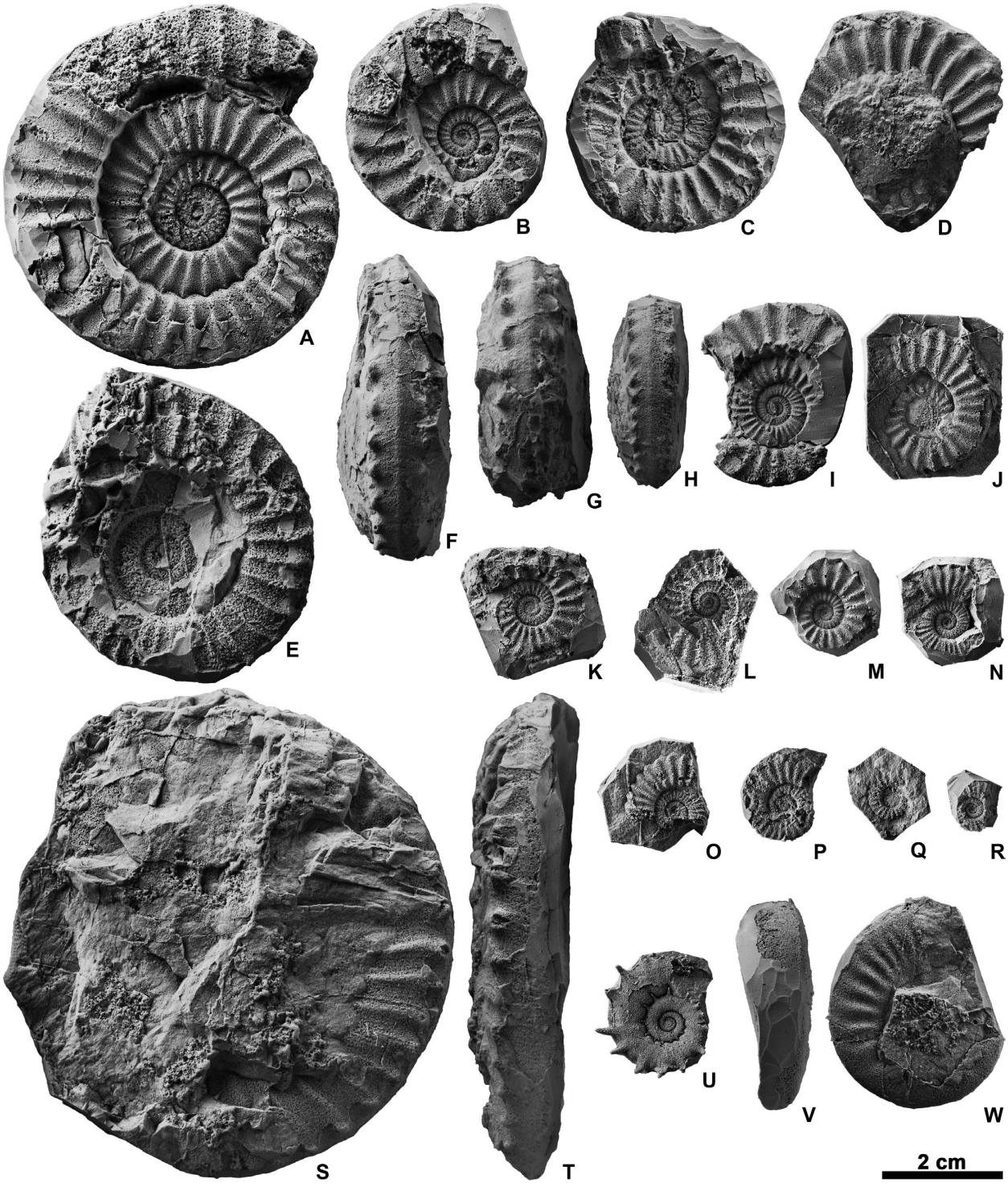

Figure 3. Ammonoids from the Phukhaothong Dolomite Member of the lower part of Chaiburi Formation at the Khao Thong section in the Phatthalung area. **A–T,** *Marcouxia chaiburiensis* sp. nov.; A, holotype, NMNS PM35431; B–T, paratypes; B, NMNS PM35432; C, NMNS PM35433; D, NMNS PM35436; E, NMNS PM35437; F, NMNS PM35434; G, NMNS PM35435; H, NMNS PM35438; I, NMNS PM35440; J, NMNS PM35441; K, NMNS PM35442; L, NMNS PM35443; M, NMNS PM35444; N, NMNS PM354345; O, NMNS PM35446; P, NMNS PM35447; Q, NMNS PM35448; R, NMNS PM35449; S, T, NMNS PM35439; **U,** *Tirolites* sp., NMNS PM35462; **V, W,** *Idahocolumbites* sp., NMNS PM35463. A–E, I–S, Z, W, lateral views; F–H, T, V, ventral views. All specimens are silicon rubber casts of outer molds.

~90 m thick massive limestone, part of which includes reef limestone composed of corals, algae, bivalves, brachiopods and foraminifers, suggesting an early to middle Norian age (Adachi *et al*., 1993; Ueno *et al*., 2003; Sardsud *et al*., 2017).

Based on microfacies analysis, Ampornmaha (1995) reported that the depositional setting of the Chaiburi Formation shifted from a deep to shallow water environment, with a corresponding change from low to high energy conditions.

Ammonoid occurrences

The Khao Thong section, situated 17 km north of the center of Phatthalung, is located on the north side of an isolated mountain, just south side of the Wat Pukhao Thong, in which the 85.49 m thick Phukhaothong Dolomite Member is well exposed (Figures 1, 2). These strata strike N–S and dip 55–76° eastward; light grey, thickly bedded (10–30 cm thick/bed) and thinly bedded (1–10 cm thick/bed) dolomites are predominant.

The ammonoid specimens described herein as a new species of *Marcouxia* together with specimens illustrated as *Tirolites* sp. and *Idahocolumbites* sp. in Figure 3 were obtained from three levels within thinly bedded dolomite beds, i.e., about 2.4 m below, 31.0 m below and 0.2 m above the bed from which the holotype of *Thaisaurus chonglakmanii* was collected, respectively. Most ammonoid specimens are external molds resulting from excessive weathering.

Paleontological description

(by K. Tongtherm and Y. Shigeta)

Systematic description basically follows the classification of Triassic ammonoids established by Shevyrev (1986), Tozer (1981) and Guex *et al*. (2010). Morphological terms are those used in Arkell (1957).

Institution abbreviation.—NMNS, National Museum of Nature and Science, Tsukuba.

Order Ceratitida Hyatt, 1884
Superfamily Dinaritoidea Mojsisovics, 1882
Family Columbitidae Spath, 1934
Genus ***Marcouxia*** Guex *et al*., 2005

Type species.—*Tirolites astakhovi* Kummel, 1969.

Discussion.—*Marcouxia astakhovi* has a rounded venter, but its peculiar median part becomes more highly elevated (but not acute) with shell growth. Even though the new species described below has an arched venter with a sub-acute, keel-like elevation, its very evolute shell ornamented with spiny tubercles on the ventrolateral shoulders and numerous, radial or slightly prorsiradiate ribs enable us to assign it to the genus *Marcouxia*.

Marcouxia chaiburiensis sp. nov.

Figure 3

Type specimens.—Holotype, NMNS PM35431; paratypes, eighteen specimens, NMNS PM35432–35449. All specimens are silicon rubber casts of external molds from the Phukhaothong Dolomite Member of the lower part of Chaiburi Formation at the Khao Thong section, located about 17 km north of Phatthalung City, Khuan Khanun District, Phatthalung Province (7°44’16.4” N, 100° 03’59.8” E; Figure 1). Because the molds are fragile due to weathering, it was only possible to collect silicon casts of the molds.

Diagnosis.—*Marcouxia* characterized by quadrate whorl section, arched venter with a sub-acute, keel-like elevation, and spiny tubercles on ventrolateral shoulders as well as regularly spaced, numerous, radial or slightly prorsiradiate ribs.

Etymology.—Named after Chaiburi, which is an old city in Phatthalung.

Description.—Very evolute, fairly compressed shell with quadrate whorl section, arched venter with a sub-acute, keel-like elevation, abruptly rounded ventral shoulders, and slightly convex flanks with maximum whorl width at midflank. Umbilicus fairly wide with moderately high, vertical wall and rounded shoulders. Ornamentation consists of regularly spaced, numerous, radial or slightly prorsiradiate ribs arising on umbilical shoulder and culminating in prominent spiny tubercles high on ventrolateral shoulders.

Measurements.—See Table 1.

Comparison.—*Marcouxia chaiburiensis* sp. nov. differs from *M. astakhovi* by its quadrate whorl section, venter with a slightly acute, keel-like elevation at all growth stages and numerous, radial or slightly prorsiradiate ribs. *Marcouxia astakhovi* has a trapezoidal whorl section and rounded venter, whose peculiar median part becomes more highly elevated (but not acute) with shell growth. This feature becomes much more pronounced on the body chamber of the larger shells. The ribs of *M. astakhovi* with a highly triangular cross-section are stronger than those of *M. chaiburiensis* sp. nov. (Guex *et al*., 2010; Jenks *et al*., 2013).

Occurrence.—Described specimens were collected from the Phukhaothong Dolomite Member of the lower part of the Chaiburi Formation. This interval correlates with the lower Spathian (see discussion below).

Table 1. Measurements (in mm) of herein described *Marcouxia chaiburiensis* sp. nov. specimens from the Khao Thong section in the Phatthalung area. Abbreviations for shell dimensions: *D*, shell diameter; *U*, umbilical diameter; *H*, whorl height; *W*, whorl width.

Specimen no.	*D*	*U*	*H*	*W*	*U*/*D*	*W*/*H*
NMNS PM35431	59.70	30.30	16.40	8.20	0.51	0.50
NMNS PM35432	34.80	14.50	13.10	9.00	0.42	0.69
NMNS PM35433	36.40	17.60	11.50	6.20	0.48	0.54
NMNS PM35434	52.10	–	–	10.80	–	–
NMNS PM35435	45.30	–	–	11.60	–	–
NMNS PM35436	37.30	–	–	10.20	–	–
NMNS PM35437	38.10	18.10	9.60	–	0.48	–
NMNS PM35438	32.10	–	–	8.20	–	–
NMNS PM35439	80.60	–	–	–	–	–
NMNS PM35440	29.90	15.70	8.80	8.60	0.53	0.98
NMNS PM35441	24.10	11.30	7.10	6.20	0.47	0.87
NMNS PM35442	18.70	8.20	5.20	–	0.44	–
NMNS PM35443	12.70	5.50	5.10	3.60	0.43	0.71
NMNS PM35444	9.50	4.70	3.50	–	0.49	–
NMNS PM35445	8.90	3.60	3.20	–	0.40	–
NMNS PM35446	7.60	3.60	3.30	–	0.47	–
NMNS PM35447	14.10	5.40	4.10	–	0.38	–
NMNS PM35448	8.10	3.60	2.50	–	0.44	–
NMNS PM35449	6.80	4.10	2.20	–	0.60	–

Discussion

Guex *et al*. (2010) studied the classification and biostratigraphy of Spathian ammonoids from the western USA, and divided the Spathian into three ammonoid zones: the *Columbites* Zone of early Spathian age, *Subcolumbites* Zone of middle Spathian age and *Haugi* Zone of late Spathian age (Figure 4). The *Columbites* Zone is subdivided into four subzones: the "*Bajarunia confusionensis* beds", "*Tirolites harti* beds", *Columbites parisianus* Subzone, and *Procolumbites* Subzone in ascending order. Guex *et al*. (2010) recognized four biochronological horizons (H4–7) in the *Columbites parisianus* Subzone and stated that *Marcouxia astakhovi* occurs only in the horizon H6. Jenks *et al*. (2013) also recognized four ammonoid horizons in the *Columbites parisianus* Subzone (*Yvesgalleticeras montpeliense* bed, *Columbites parisianus* bed, *Arctomeekoceras popovi* bed and *Columbites isabellae* beds in ascending order), and reported that *M. astakhovi* occurs only in the *Columbites isabellae* beds. These studies constrain the range of *M. astakhovi* to the *Columbites parisianus* Subzone of the lower Spathian in the western USA.

The family Columbitidae, which represents very characteristic Spathian ammonoid faunas, includes strongly ornamented or tuberculate taxa, most of which have a narrow or restricted stratigraphic range and a relatively broad geographical distribution in the low to middle latitude regions. For this reason, they are regarded as ideal taxa for precising biostratigraphic correlation of the Spathian (Tozer, 1971; Jenks *et al*., 2015). Since the range of *Marcouxia* is limited to the *Columbites parisianus* Subzone of the lower Spathian in the western USA, its occurrence in the Phukhaothong Dolomite Member in the Phatthalung area demonstrates that this particular horizon is of early Spathian age and can be correlated with horizon H6 and the *Columbites isabellae* beds in the *Columbites parisianus* Subzone of the western USA.

This correlation is also supported by the occurrence of *Idahocolumbites* sp. in a bed about 2.6 m above the horizon in which *Marcouxia chaiburiensis* sp. nov occurs, because the range of *Idahocolumbites* is limited to horizons H6–7 and the *Columbites isabellae* beds in the *Columbites parisianus* Subzone in the western USA (Guex *et al*., 2010; Jenks *et al*., 2013).

Thaisaurus chonglakmanii was collected from a bed 2.4 m above the horizon in which *Marcouxia chaiburiensis* sp. nov. occurs. This 2.4 m interval contains no evidence of a large depositional gap. Based on Ampornmaha's (1995) thickness and age data for the Chaiburi Formation, its sedimentation rate is roughly estimated to be 0.1 Ma/m. This evidence suggests that the early Spathian age of *Thaisaurus chonglakmanii* is nearly identical to that of *M. chaiburiensis* sp. nov.

Chaohusaurus has been considered to be the oldest ichthyopterygian and the earliest record of its occurrence is from the *Procolumbites* Zone of Chaohu, South China (Ji *et al*., 2015), which is a correlative of the *Procolumbites* Subzone in the western USA (Jenks *et al*., 2015; Figure 4). The *Procolumbites* Subzone represents the uppermost part of the lower Spathian, and it definitely overlies the *Columbites parisianus* Subzone, which contains *Marcouxia*, thus suggesting that *Thaisaurus* is older than *Chaohusaurus*.

Fragments of ichthyopterygian skeletons have been reported from the *Neocolumbites insignis* Zone of South Primorye, Russian Far East (Nakajima *et al*., 2018), and according to Jenks *et al*. (2015), this zone correlates with the *Columbites parisianus* and *Procolumbites* subzones of the western USA (Figure 4). The upper part of the

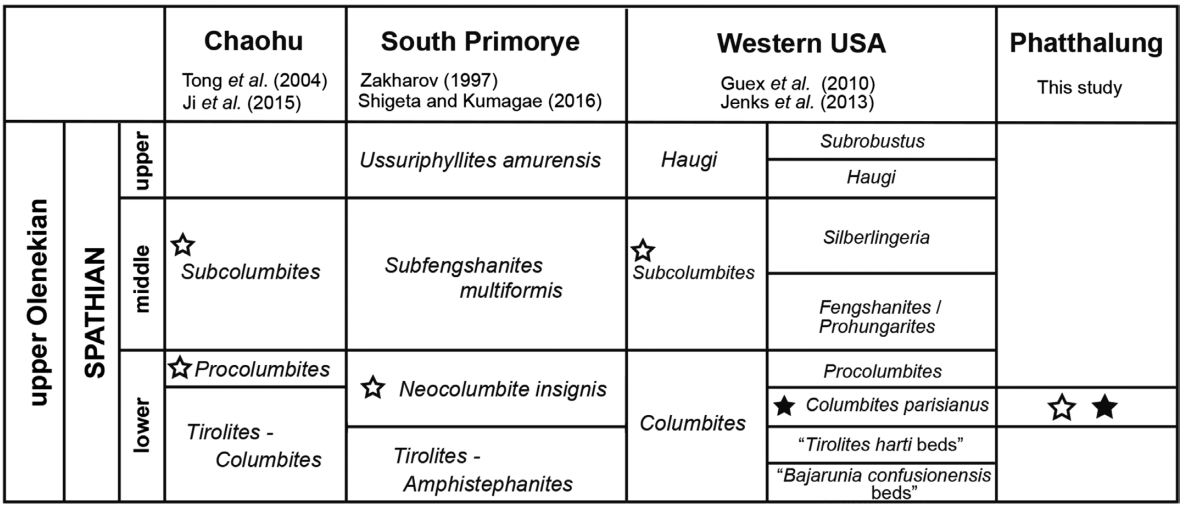

Figure 4. Spathian (upper Olenekian, Lower Triassic) ammonoid zones and their correlation with the fossil record of Ichthyopterygia (white stars) and *Marcouxia* (black stars).

Neocolumbites insignis Zone, yielding *Procolumbites subquadratus*, probably correlates with the *Procolumbites* Subzone (Zakharov *et al*., 2004). The middle part of the zone, where fragments of ichthyopterygian skeletons were found, probably correlates with the *Columbites parisianus* Subzone. Thus, *Thaisaurus chonglakmanii* and Ichthyopterygia from South Primorye are likely among the oldest known ichthyopterygians.

Utatsusaurus, from the *Subcolumbites* and *Arnautoceltites* zones of Shikama *et al*. (1978) in the Osawa Formation in the South Kitakami Belt, Northeast Japan, has also been considered to be one of the oldest ichthyopterygians (Ehiro *et al*., 2019). The *Subcolumbites* Zone is subdivided into the *Columbites parisianus* and *Subcolumbites perrinismithi* subzones in ascending order (Bando and Shimoyama, 1974). However, the specimens described as *C. parisianus* by Ehiro *et al*. (2016) should probably be assigned to *Hellenites inopinatus* or *H. tscernyschewiensis*, which were described from the *Neocolumbites insignis* Zone of South Primorye (Kiparisova, 1961; Zakharov, 1968; Zakharov *et al*., 2004). We question the co-occurrence of *Utatsusaurus* and *C. parisianus*, but it is still possible that *Utatsusaurus* is one of the oldest known ichthyopterygians.

Concluding remarks

Over the past two decades, extensive research has been conducted on the classification and biostratigraphy of Early Triassic ammonoids from many worldwide localities and consequently, it has become possible to achieve high-resolution correlation between most of these localities. However, the study of Early Triassic ammonoids from Thailand has only just begun, and the main reason for this lack of attention is most likely the type of preservation (external molds). In this study, it was possible to obtain many quality specimens by making silicon rubber casts from these outer molds. Thus, it became possible to describe the specimens and recognize their age, which ultimately constrained the age of co-occurring *Thaisaurus* as early Spathian.

Acknowledgements

We thank Masayuki Ehiro (Tohoku University, Sendai) and an anonymous reviewer for valuable comments on the first draft. We are very grateful to all personnel of the Earth Evolution Sciences, University of Tsukuba (Tsukuba) and Department of Mineral Resources (DMR), Thailand (Bangkok) for their kind help and cooperation. We are very grateful to Jun Liu (Hefei University of Technology, Hefei) and Martin Sander (University of Bonn, Bonn) for showing us ammonoid specimens from the Khao Thong section, and Rachan Leotphayakkarat and Inthat Chanpheng (DMR) and Kaito Asato (Fukui Prefectural Dinosaur Museum, Katsuyama) for their cooperation in the field. Thanks are extended to Jim Jenks (West Jordan, Utah) for helpful suggestions. K. T. is indebted to the MEXT scholarship: A Special Course on "Trans-world Professional Human Resources Development Program on Food Security and Natural Resources Management (TPHRD)" at University of Tsukuba. This work was financially supported by grants from the National Museum of Nature and Science in 2018–2019 and JSPS KAKENHI Grant Number JP19K04062 for Y. S.

References

Adachi, S., Igo, H., Ampornmaha, A., Sashida, K. and Nakornsri, N., 1993: Triassic coral buildups observed in the Chaiburi Formation, near Phattalung, Peninsular Thailand. *Annual report of the Institute of Geoscience*, *the University of Tsukuba*, no. 19, p. 27–31.

Ampornmaha, A., 1995: Triassic carbonate rocks in the Phattalung area, Peninsular Thailand. *Journal of Southeast Asian Earth Sciences*, vol. 11, p. 225–236.

Ampornmaha, A., 1996: *Triassic carbonate rocks in Peninsular Thailand*, 173 p. PhD thesis, University of Tsukuba, Tsukuba.

Arkell, W. J., 1957: Introduction to Mesozoic Ammonoidea. *In*, Arkell, W. J., Furnish, W. M., Kummel, B., Miller, A. K., Moore, R. C., Schindewolf, O. H., Sylvester-Bradley, P. C. and Wright, C. W. *eds*., *Treatise on Invertebrate Paleontology*, *Part L*, *Mollusca 4*, *Cephalopoda*, *Ammonoidea*, p. L81–129. Geological Society of America, New York and University of Kansas Press, Lawrence.

Bando, Y. and Shimoyama, S., 1974: Late Schythian ammonoids from the Kitakami Massif. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 94, p. 293–312.

Bardet, N., 1992: Stratigraphic evidence for the extinction of the ichthyosaurs. *Terra Nova*, vol. 4, p. 649–656.

Brayard, A., Krumenacker, L. J., Botting, J. P., Jenks, J. F., Bylund, K. G., Fara, E., Vennin, E., Olivier, N., Goudemand, N., Saucède, T., Charbonnier, S., Romano, C., Doguzhaeva, L., Thuy, B., Hautmann, M., Stephen, D. A., Thomazo, C. and Escarguel, G., 2017: Unexpected Early Triassic marine ecosystem and the rise of the Modern evolutionary fauna. *Science Advances*, vol. 3, doi:10.1126/sciadv.1602159.

Brinkman, D. B., Zhao, X. and Nicholls, E. L., 1992: A primitive ichthyosaur from the Lower Triassic of British Columbia, Canada. *Palaeontology*, vol. 35, p. 465–474.

Ehiro, M., Sasaki, O. and Kano, H., 2016: Ammonoid fauna of the upper Olenekian Osawa Formation in the Utatsu area, South Kitakami Belt, Northeast Japan. *Paleontological Research*, vol. 20, p. 90–104.

Ehiro, M., Sasaki, O., Kano H. and Nagase, T., 2019: Additional thylacocephalans (Arthropoda) from the Lower Triassic (upper Olenekian) Osawa Formation of the South Kitakami Belt, Northeast Japan. *Palaeoworld*, vol. 28, p. 320–333.

Guex, J., Hungerbühler, A., Jenks, J. F., O'Dogherty, L., Atudorei, V., Taylor, D. G., Bucher, H. and Bartolini, A., 2010: Spathian (Lower Triassic) ammonoids from western USA (Idaho, California, Utah and Nevada). *Mémoires de Géologie (Lausanne)*, no. 49, p. 1–82.

Guex, J., Hungerbühler, A., Jenks, J., Taylor, D. G. and Bucher, H., 2005: Dix-huit nouveaux genres d'ammonites du Spathien (Trias inférieur) de l'0uest américain (Idaho, Nevada, Utah et Californie): Note préliminaire. *Bulletin de Géologie Lausanne*, no. 362, p. 1–31.

Hyatt, A., 1883–1884: Genera of fossil cephalopods. *Proceedings of the Boston Society of Natural History*, vol. 22, p. 253–338.

Jenks, J., Guex, J., Hungerbühler, A., Taylor, D. G. and Bucher, H., 2013: Ammonoid biostratigraphy of the Early Spathian *Columbites parisianus* Zone (Early Triassic) at Bear Lake Hot Springs, Idaho. *New Mexico Museum of Natural History and Science*, *Bulletin*, 61, p. 268–283.

Jenks, J. F., Monnet, C., Balini, M., Brayard, A. and Meier, M., 2015: Biostratigraphy of Triassic ammonoids. *In*, Klug, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R. H. *eds*., *Ammonoid Paleobiology: From macroevolution to paleogeography*, p. 329–388. Topics in Geobiology, vol. 44, Springer, Dordrecht.

Ji, C., Zhang, C., Jiang, D.-Y., Bucher, H., Motani, R. and Tintori, A., 2015: Ammonoid age control of the Early Triassic marine reptiles from Chaohu (South China). *Palaeoworld*, vol. 24, p. 277–282.

Kelley, N. P., Motani, R., Embree, P. and Orchard, M. J., 2016: A new Lower Triassic ichthyopterygian assemblage from Fossil Hill, Nevada. *PeerJ*, doi: 10.7717/peerj.1626.

Kiparisova, L. D., 1961: Paleontological basis for the stratigraphy of Triassic deposits of the Primorye region. 1. Cephalopod Mollusca. *Trudy Vsesoyuznogo Geologicheskogo Nauchno-Issledovatel'skogo Instituta (VSEGEI)*, *Novaya Seriya*, vol. 48, p. 1–278. (*in Russian; original title translated*)

Kummel, B., 1969: Ammonoids of the Late Scythian (Lower Triassic). *Bulletin of the Museum of Comparative Zoology*, *Harvard University*, vol. 137, p. 311–701.

Massare, J. A. and Callaway, J. M., 1994: *Cymbospondylus* (Ichthyosauria: Shastasauridae) from the Lower Triassic Thaynes Formation of southeastern Idaho. *Journal of Vertebrate Paleontology*, vol. 14, p. 139–141.

Maxwell, E. E. and Kear, B. P., 2013: Triassic ichthyopterygian assemblages of the Svalbard archipelago: a reassessment of taxonomy and distribution. *GFF*, vol. 135, p. 85–94.

Mazin, J. M., Suteethorn, V., Buffetaut, E., Jaeger, J. J. and Helmcke-Ingavat, R., 1991: Preliminary description of *Thaisaurus chonglakmanii* n. g., n. sp., a new ichthyopterygian (Reptilia) from the Early Triassic of Thailand. *Comptes Rendus de l'Académie des Sciences de Paris*, vol. 313, p. 1207–1212.

McGowan, C. and Motani, R., 2003: *Handbook of Paleoherpetology, Part 8*, *Ichthyopterygia*, 173 p. Verlag Dr. Friedrich Pfeil, Munich.

Mojsisovics, E., 1882: Die Cephalopoden der mediterranen Triasprovinz. *Abhandlungen der Geologischen Reichsanstalt (Wien)*, Band 10, p. 1–322, pls. 1–94.

Nakajima, Y., Shigeta, Y., Houssays, A. and Sander, P. M., 2018: Morphology and osteohistology of new Early Triassic ichthyosauriform fossils from the Russian Far East. *Abstract Book*, *5th International Paleontological Congress IPC 5*, *Paris*, p. 139.

Sardsud, A., Agematsu-Watanabe, S., Wongwanich, T., Igo, H. and Sashida, K., 2017: Triassic conodont biostratigraphy of the Chaiburi Formation in peninsular Thailand; the Early to Late Triassic carbonates succession evidence in Shan-Thai Terrane. *Abstract Volume*, *The 16th Gondwana International Conference*, *Bangkok*, *Thailand*, p. 148–150.

Sashida, K. and Igo, H., 1992: Triassic radiolarians from a limestone exposed at Khao Chiak near Phatthalung, southern Thailand. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 168, p. 1296–1310.

Shevyrev, A. A., 1986: Triassic ammonoids. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR*, vol. 217, p. 1–184. (*in Russian; original title translated*)

Shigeta, Y. and Kumagae, T., 2016: Spathian (late Olenekian, Early Triassic) ammonoids from the Artyom area, South Primorye, Russian Far East and implications for the timing of the recovery of the oceanic environment. *Paleontological Research*, vol. 20, p. 48–60.

Shikama, T., Kamei, T. and Murata, M., 1978: Early Triassic ichthyosaurus, *Utatsusaurus hataii* gen. et sp. nov., from the Kitakami Massif, Northeast Japan. *Science Report of the Tohoku University*, *Second Series (Geology)*, vol. 48, p. 77–97.

Spath, L. F., 1934: *Catalogue of the fossil Cephalopoda in the British Museum (Natural History). Part 4, The Ammonoidea of the Trias*, 521 p., 18 pls. The Trustees of the British Museum, London.

Tong, J.-N., Zakharov, Y. D. and Wum S.-B., 2004: Early Triassic ammonoid succession in Chaohu, Anhui Province. *Acta Palaeontologica Sinica*, vol. 43, p. 192–204.

Tozer, E. T., 1971: Triassic time and ammonoids. *Canadian Journal of Earth Sciences*, vol. 8, p. 989–1031.

Tozer, E. T., 1981: Triassic ammonoidea: Classification, evolution and

relationship with Permian and Jurassic forms. *In*, House, M. R. and Senior, J. R. *eds*., *The Ammonoidea*. *Systematic Association Special Volume 18*, p. 65–100. Academic Press, London.

Ueno, K., Meno, S., Arita, M., Sardsud, A., Saesaengseerung, D. and Saengsrichan, W., 2003: Triassic carbonates and foraminifers in southern Peninsular Thailand. *Procceedings of the 1st International Conference on Palaeontology of Southeast Asia (27-30 October 2003)*, *Mahasarakham University Journal*, *Special Issue*, vol. 22, p. 258–259.

Zakharov, Y. D., 1968: *Lower Triassic Biostratigraphy and Ammonoids of South Primorye*, 175 p. Nauka, Moscow. (*in Russian; original title translated*)

Zakharov, Y. D., 1997: Ammonoid evolution and the problem of the stage and substage division of the Lower Triassic. *Mémoires de Géologie (Lausanne)*, vol. 30, p. 121–136.

Zakharov, Y. D., Popov, A. M. and Burij, G. I., 2004: Triassic ammonoid succession in South Primorye: 2. middle Olenekian *Tirolites-Amphistephanites* Zone. *Albertiana*, vol. 29, p. 29–37.

Author contributions

K. T. and Y. S. collected fossils and conduced taxonomic studies. A. S., K. S. and S. A. contributed to the geological aspect of the study. All authors contributed to the writing of the paper.