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Permian brachiopods from new localities in northeast Thailand: Implications for paleobiogeographic analysis

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Abstract

A small Permian brachiopod fauna is described from new localities in northeastern Thailand. Brachiopods were collected from early Permian (Asselian) limestones of the Nam Maholan Formation and middle Permian (Murgabian) sandstones of the Nam Duk Formation and limestones of the Khao Khwang Formation. Analyses of taxa confirm preliminary hypotheses of Cathaysian affinities for brachiopods and fusulinids found in this part of Thailand. Fossils found in sandstones of the Nam Duk molasse facies, however, also show possible Gondwanan relationships with brachiopod taxa described in Australia. This has to be further tested with ongoing research in a better understanding of the paleobiogeography of this part of Southeast Asia.

Keywords: Permian; brachiopods; Thailand; paleobiogeography.

1. Introduction

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Southeast Asia paleogeography is quite complex because it comprises an agglomeration of allochthonous terranes, mostly derived from Gondwana (e.g. Metcalfe, 1991, 1996). The complexity increases during the Late Paleozoic since this was a time of rifting and amalgamation of continental blocks and openings of oceanic gateways (e.g. Metcalfe, 1996; Shi and Archbold, 1998). Fossil faunas have proven to be very useful to test and constrain the tectonic models and paleogeography, particularly during the Permian (Shi and Archbold, 1998). Thus, ammonoids (e.g. Fujikawa et al., 2005) and brachiopods (e.g. Shi et al., 2001; Shi et al., 2002) have been used to reveal the paleobiogeography of Peninsular Thailand, which belonged to the Shan-Thai terrane (Shi and Archbold, 1998).

Less is known, however, about the Late Paleozoic paleobiogeography of northeastern Thailand, which is included in the Indochina terrane (Shi and Archbold, 1998; Shi et al., 2002). Yanagida (1964, 1966) conducted extensive work on Carboniferous-Permian brachiopod faunas to clarify paleobiogeography resulting in a preliminary report of results (Yanagida, 1976) and subsequent publications (Yanagida, 1988; Yanagida and Nakornsri, 1999). Despite these studies, findings of brachiopods, which are mostly poorly preserved, are quite rare in this part of Thailand making any paleobiogeographic analysis difficult.

This paper provides a systematic and taxonomic study of Permian brachiopods from new localities of northeastern Thailand (Table 1). Additionally, it includes a preliminary discussion of faunal affinities for testing the previous paleobiogeographic hypothesis (e. g. Yanagida, 1976) and determining the existence of migratory routes in response to tectonic displacement of allochthonous terranes.

2. Geographical and Geological Settings

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Permian sediments, consisting predominantly of thick carbonates and siliciclastics, are distributed extensively in the study area covering north-central and northeastern Thailand (Fig. 1). Paleogeographically from west to east, these deposists can be divided into the Khao Khwang Platform, the Nam Duk Basin, and the Pha Nok Khao Platform sequences respectively (Wielchowsky and Young, 1985). Brachiopod faunas collected from these three different sequences are described and discussed herein.

Fossiliferous samples from the first locality (SUTP; 100 55' 35"E / 15 50' 03"N) are from limestones of the Khao Khwang Platform that outcrop along Highway No. 225 about 9 km west of Bung Sam Phan and 70 km southwest of Phetchabun (see Fig. 1). The Khao Khwang limestones are biomicrite and fossiliferous wackestones, more than 70 m in thickness, are intercalated with shales, and overlyacidic to intermediate volcanics of possible Late Carboniferous age (Fig. 2). These limestones can be correlated lithostratigraphically to the nearby limestones assigned to the Middle Permian (Murgabian) (Chonglakmani and Fontaine, 1990).

The second locality (SUTS; 101 31' 22"E / 16 45' 38"N) is exposed on Highway No.12 about 40 km east of Lom Sak (Fig. 1). Samples were collected from sandstones belonging to the molasse facies of the Nam Duk Formation (Chonglakmani and Helmcke, 2001) (Fig. 2). The molasse facies is composed of sandstones and shales with some limestones in the upper part and it overlies flysch facies consisting of graywackes and shales. Limestones of the molasse facies contain a rich fusulinid fauna characterized by *Verbeekina verbeeki* Geinitz, *Pseudodoliolina* sp., *Chusenella* sp., and *Khalerina* sp. (Altermann, 1989) of Middle Permian (Murgabian) age.

The third locality (SUTL; 101 51' 30"E / 17 26' 45" N) is about 15 km southeast of Loei (Fig. 1) and brachiopod samples (SUTL01-12) were collected from limestones belonging to the Nam Maholan Formation (Fig. 2). These limestones have been dated as

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Asselian-early Sakmarian based on fusulinids of the *Triticites ozawai-Paraschwagerina yanagidai* zone (Igo, 1972). These limestones overlie conformably the Wang Saphung Formation of Carboniferous age (Charoenprawat et al., 1976).

All Permian sequences outlined above are covered by conglomerate beds of the Huai Hin Lat Formation (Norian) (Chonglakmani and Sattayarak, 1978), suggesting that the main orogenic movement in this region occurred before the Late Triassic (Norian) (Chonglakmani and Helmcke, 2001).

3. Terminology and Classification

Terminology used here follows Williams and Brunton (1997) and Williams et al. (1997). The supraordinal classification follows Williams et al. (1996) and the supraspecific classifications for taxa within the class Strophomenata of the order Productida follow Brunton et al. (2000). Supraspecific classifications for taxa within the class Rhynchonellata of orders Athyridida, Spiriferida, and Terebratulida follow Alvarez and Rong (2002), Carter et al. (1994), and Stehli (1965) respectively.

4. Systematic paleontology

Repository: Studied material is housed at the School of Geotechnology of the Suranaree University of Technology (Thailand) with specimen numbers prefixed herein SUTS, SUTP, and SUTL.

Phylum BRACHIOPODA Duméril, 1805

Subphylum RHYNCHONELLIFORMEA Williams et al., 1996

Class STROPHOMENATA Williams et al., 1996

Order PRODUCTIDA Sarytcheva and Sokolskaya, 1959

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Suborder CHONETIDINA Muir-Wood, 1955

Superfamily CHONETOIDEA Bronn, 1862

Family RUGOSOCHONETIDAE Muir-Wood, 1962

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Genus *Neochonetes* Muir-Wood, 1962

?*Neochonetes* sp.

Fig.3: 1-3

Material examined: Eight internal molds of ventral valves and two poorly preserved external molds of ventral valves. Registered material: Three internal molds of ventral valves (SUTS01-3).

Description: Small-sized shells up to 10 mm in length and 20 mm in width. Shell outline subrectangular, moderately transverse, greatest width anterior of hinge. Lateral commissure subrounded; nearly rectimarginate anterior commissure. Ventral valve moderately convex; surface with fine costellae and weakly developed concentric lines; sulcus weakly developed anteriorly; possibly three orthomorph oblique tubular spines. Ventral interior with traces of nearly parallel mantle canals; pitted surface.

Remarks: Only few poorly preserved internal and external molds of ventral valves are available, preventing clear generic and specific assignments. Specimens, however, present several diagnostic characters of *Neochonetes* Muir-Wood 1962 (Racheboeuf, 2000, p. 407). There are six susbgenera recognized as belonging to *Neochonetes*: *N*. (*Neochonetes*) Muir-Wood 1962, *N*. (*Sommeriella*) Archbold 1982, *N*. (*Nongtaia*) Archbold 1999, *N*. (*Zechiella*) Archbold 1999, *N*. (*Zhongyingia*) Shen and Archbold 2002 and *N*. (*Huangichonetes*) Shen and Archbold 2002. Studied specimens are closer to *N*. (*Sommeriella*) because of greater convexity of ventral valve, sulcus, and maximum

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width anterior of hinge (see Archbold, 1981, 1982; Racheboeuf, 2000; Shen and Archbold, 2002).

Occurrence: Sandstones in the molasse facies of the Nam Duk Formation, Middle Permian (Murgabian).

Suborder PRODUCTIDINA Waagen, 1883

Superfamily PRODUCTOIDEA Gray, 1840

Family PRODUCTELLIDAE Schuchert, 1929

Subfamily MARGINIFERINAE Stehli, 1954

Tribe MARGINIFERINI Stehli, 1954

Genus *Probolionia* Cooper, 1957

?*Probolionia* sp.

Fig. 4: 1 and 2

Material examined: Four poorly preserved external molds of ventral valves. Registered material: Two external molds (SUTL01-2).

Description: Small-sized shells up to 20 mm in length and 15 mm in width. Ventral valve subquadrate in outline; moderately convex in lateral profile; ears short, when present forming the widest part of shell (if not present, maximum width at mid-length); geniculation present; strong reticulation, only on posterior region; fairly narrow median sulcus; shell surface costate; hollow thick spines based, preferentially on the crest of the costae.

Remarks: Just a few poorly preserved external molds of ventral valves are available for study. This situation creates systematic difficulties and taxonomic problems in terms of specific and generic classification. However, some external characters of the ventral valve in these specimens place them within the genus *Probolionia* Cooper 1957. These

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characters are the presence of small geniculate shells, weakly convex in lateral profile, narrow well developed sulcus, and thick spines bases preferentially located on the crest of costae. Furthermore, specimens are very similar to those of *Probolionia* aff. *P. posteroreticulatia* described by Yanagida (1966) in a locality nearby. However, species of the genus *Probolionia* can be confused to those assigned to the genera *Retimarginifera* Waterhouse 1970, *Transennatia* Waterhouse 1975 and *Uraloproductus* Ustritskiy 1971 (for comparison among these genera see Shi and Waterhouse, 1996; Brunton et al., 2000; Shi et al., 2003).

Occurrence: Limestones of the Nam Maholan Formation, Lower Permian (Asselian)

Tribe PAUCISPINIFERINI Muir-Wood and Cooper, 1960

Genus *Lamnimargus* Waterhouse, 1975

?*Lamnimargus* sp.

Fig. 3: 4 and 5

Material examined: Three internal molds and two external molds of ventral valves. Registered material: One internal and external molds of ventral valves (SUTS04).

Description: Small-sized shells up to 15 mm. in length and 10 mm. in width. Shell outline subcircular to subquadrate, transverse; large, triangular, acute ears, when present forming the widest part of shell. Lateral commissure rounded; nearly rectimarginate anterior commissure. Ventral valve convex; surface with fine costellae; sulcus weakly developed anteriorly. Dorsal valve moderately convex; costellate surface. Ventral interior with traces of striated adductor scars; pitted surface.

Remarks: Scarce, poorly preserved specimens are available preventing clear generic and specific assignments. Specimens, however, present several diagnostic characters of

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Lamnimargus Waterhouse1975 (Brunton et al., 2000; p. 407), particularly the morphology of ears, type of ribbing, and the sulcus.

Occurrence: Sandstones in the molasse facies of the Nam Duk Formation, Middle Permian (Murgabian).

Genus *Retimarginifera* Waterhouse, 1970

Retimarginifera alata Waterhouse et al., 1981

Fig. 4: 3 and 4

Material examined: Four external molds of ventral valves. Registered material: One mold of a ventral valve (SUTL03).

Description: Small-sized shells up to 15 mm in length and 20 mm in width. Shell outline subtriangular, transverse; alate ears, when present forming the widest part of shell. Ventral valve strongly concave; umbo prolonged beyond hinge; deep, U-shaped, moderately narrow sulcus; not well-developed reticulation on disk; coarse costae; faint rugae.

Remarks: Although only a few specimens were collected, they clearly resemble those of *Retimarginifera alata* (Waterhouse et al., 1981, p. 81), because of distinctive ventral valves. Only one other species, *Retimarginifera celeteria* Grant 1976, has been previously described in Thailand, but it is less transverse and has finer ribbing than *R. alata*. See comparison with other species and similar taxa in Waterhouse et al. (1981).

Occurrence: Limestone of the Nam Maholan Formation, Lower Permian (Asselian)

Family PRODUCTIDAE Gray, 1840

Subfamily PRODUCTINAE Gray, 1840

Tribe RETARIINI Muir-Wood and Cooper, 1960

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Genus *Kutorginella* Ivanova, 1951

Kutorginella fraterculus Waterhouse et al., 1981

Fig. 4: 5 and 6

Material examined: Three external molds of ventral valves and two external molds of dorsal valves. Registered material: One mold of a ventral valve and one mold of a dorsal valve (SUTL04, SUTL05).

Description: Small-sized shells up to 12 mm in length and 20 mm in width. Shell outline subtriangular to suboval, transverse, maximum width anterior to the mid-length; short, triangular ears. Shell surface costate to costellate. Ventral valve convex; umbo slightly prolonged beyond hinge; moderately deep, fairly narrow sulcus, developing mostly anteriorly; faint reticulation on posterior region of disk; few scattered spine bases. Dorsal valve gently concave; well-developed brachial ridge; trilobed cardinal process; well-developed reticulation; sparse spine bases.

Remarks: Specimens could be confused with those of *Retimarginifera alata* Waterhouse et al. 1981, co-occurring in the same rock samples. However, molds of ventral valves display a finer ribbing, narrower and shallower sulcus, and maximum width in front of mid-length. Also, the dorsal discs show sparse spine bases that are absent in *Retimarginifera*. Characters shown in these specimens place them within *Kutorginella* Ivanova 1951 (see Brunton et al., 2000, p. 472; Waterhouse et al., 1981, p. 77).

These specimens resemble those of *Kurtoginella fraterculus* Waterhouse et al. 1981. *K. fraterculus* can be distinguished from *Kurtoginella paucispinosa* Waterhouse et al. 1981 by being smaller and having a deeper sulcus and numerous spines on dorsal valve. Waterhouse et al. (1981) argued some similarity of this species to *Retaria* sp. of Termier et al. (1974), although some key features are not well-known. For comparison

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to other similar taxa under discussion for *K. paucispinosa* see Watehouse et al. (1981, p. 77).

Occurrence: Limestone of the Nam Maholan Formation, Lower Permian (Asselian)

Subfamily DICTYOCLOSTINAE Stehli, 1954

Genus *Reticulatia* Muir-Wood and Cooper, 1960

Reticulatia aff. *R. uralica* (Chernyschev, 1902)

Fig. 4: 10

Material examined: Four partially complete calcareous Ventral valves. Registered material: One calcareous valve (SUTL09).

Description: Medium to large-sized shells up to 45 mm in length and 60 mm in width. Shell outline subquadrate; greatest width along hinge, when specimen is complete; lateral profile with largest convexity in posterior region. Ventral valve strongly convex, geniculate, steep flanks; umbo slightly incurved over hinge; median sulcus, mostly developed anteriorly; strong costae and rugae, developing well-marked reticulation; scattered spines bases over disc, particularly concentrated near hinge line and depression between ears and flanks.

Remarks: Although only partially preserved ventral valves are available, specimens clearly belong to *Reticulatia* Muir-Wood and Cooper 1960. Despite the diagnostic characters for the genus (see Brunton et al., 2000, p. 496), the pattern of reticulation on ventral disc is characteristic and it can be used to distinguish *Reticulatia* from other taxa in the subfamily.

Specimens are very similar to those of *Reticulatia uralica* (see complete synonym list in Shi and Waterhouse, 1996, p. 85) described by Yanagida (1966) from the same formation in a locality nearby, which is similar to *Reticulatia moelleri* (Stuckenberg,

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1898) (see Yanagida, 1966). Since the available material is scarce and poorly preserved, the comparison of recorded specimens to the type species of *R. uralica* (Chernyschev, 1902) and other conspecific material (e.g. *R. uralica* from Canada, described and illustrated by Shi and Waterhouse,1996) is problematic. However, this Thai material seems to be represented by smaller and less convex ventral disks with a weak development of transverse ears.

Occurrence: Limestones of the Nam Maholan Formation, Lower Permian (Asselian)

Superfamily LINOPRODUCTOIDEA Stehli, 1954

Family LINOPRODUCTIDAE Stehli, 1954

Subfamily LINOPRODUCTINAE Stehli, 1954

Genus *Linoproductus* Chao, 1927

Remarks: Among specimens collected, there are incomplete external molds of ventral valves that clearly belong to two different species of *Linoproductus*. Since the material is scarce and poorly preserved, these taxa are classified using open nomenclature preventing further detailed taxonomy. Future collection of brachiopods may contribute to clarify this preliminary classification.

Linoproductus sp. A

Fig. 4: 7 and 8

Material examined: Three incomplete and partially decorticated external molds of ventral valves. Registered material: One external mold of a ventral valve (SUTL06-07).

Description: Large-sized shells up to 60 mm in length and 65 mm in width. Transversely subpentagonal in outline, maximum width anterior to mid-length of shell. Ventral valve highly convex; flanks steep, slightly convex or spreading; umbo slightly

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incurved beyond hinge; costellate surface with rugae, well-marked on flanks and posterior region; few, scattered spine bases on venter.

Remarks: Yanagida (1966) described some slightly similar specimens as *Linoproductus* sp. and compare them to *Linoproductus cora* (d'Orbigny, 1842), type-species of the genus. However, the preservation of the present material prevents any comparison to Yanagida´s specimens or other species of *Linoproductus*.

Occurrence: Limestones of the Nam Maholan Formation, Lower Permian (Asselian)

Linoproductus sp. B

Fig. 4: 9

Material examined: One partially complete specimen and fragmentary material of external molds of ventral valves. Registered material: One external mold of a ventral valve (SUTL08).

Description: Medium to large-sized shells up to 45 mm in length and 55 mm in width. Transversely subpentagonal in outline, maximum width at hinge line. Ventral valve moderately convex; flanks gentle to slightly steep, spreading; umbo moderately incurved beyond hinge; faint sulcus, developing anteriorly; costellate surface with rugae, well-marked on flanks and posterior region; few, scattered spine bases on venter.

Remarks: *Linoproductus* sp. B can be distinguished from *Linoproductus* sp. A because of its smaller size, maximum width at hinge, less steep flanks, and faint sulcus developing anteriorly. However, the preservation prevents any further comparison to other species of *Linoproductus*.

Occurrence: Limestones of the Nam Maholan Formation, Lower Permian (Asselian)

Class RHYNCHONELLATA Williams et al., 1996

Order ATHYRIDIDA Boucot, Johnson and Staton, 1964

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Suborder ATHYRIDIDINA Boucot, Johnson and Staton, 1964

Superfamily ATHYRIDOIDEA Davidson, 1881

Family ATHYRIDIDAE Davidson, 1881

Subfamily SPIRIGERELLINAE Grunt, 1965

Genus *Composita* Brown, 1845

Remarks: Several specimens correspond to taxa within the Order Athyridida because of external morphology and fragmentary and poorly preserved internal molds showing traces of a spiralium. There are two species assigned to the genus *Composita* (see diagnosis in Alvarez and Rong, 2002). Specimens, however, are internally recrystallized preventing serial sectioning to determine a clear specific, and even generic, identification. Many calcareous specimens are available, but most of them are poorly preserved. External features are not sufficient to determine species since the genus displays great external morphological variability (see Grinnell and Andrews, 1964). These taxa, therefore, are classified using open nomenclature preventing further detailed taxonomy. Future collection of brachiopods may contribute to clarify this preliminary classification.

?*Composita* sp. A

Fig. 5: 1-4

Material examined: Fifty calcareous specimens, mostly poorly preserved, and a few fragmentary internal molds. Registered material: Two nearly complete calcareous specimens (SUTP01-4).

Description: Small-sized shells up to 20 mm in length, 20 mm in width, and 15 mm in thickness. Shell outline subpentagonal to subcircular, greatest width at mid-length; equally biconvex. Posterolateral margins rounded, converging gradually to a narrow

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beak; anterolateral margins slightly folding ventrally; slightly uniplicate anterior commissure. Shell surface covered with regularly spaced growth lines. Ventral valve with a well-developed, narrow, moderately deep sulcus, occupying less than one-third of the anterior commissure length, developed anteriorly and disappearing posteriorly; low and narrow umbo; usually a short beak, slightly incurved beyond hinge. Dorsal valve with anterior region nearly flat or developing a faint sulcus in some specimens.

Remarks: Specimens are assigned with doubt to *Composita* because of external morphology (e.g. shell outline and absence of dorsal fold). Although the genus displays great external morphological variability, there are no Thai species previously described resembling these specimens. However, the external features are closer to those of *Cleiothyridina* Buckman 1906, but there are no interiors available for study and evidence of typical flat spines or fimbriae projecting on the margin of growth lamellae (see Alvarez and Rong, 2002).

Occurrence: Limestones of the Khao Khwang Formation, Middle Permian (Murgabian)

?*Composita* sp. B

Fig. 5: 5-8

Material examined: Thirty-five calcareous specimens, mostly poorly preserved, and few fragmentary internal molds. Registered material: Two nearly complete calcareous specimens (SUTP03-4).

Description: Small-sized, elongate shells up to 20 mm in length, 18 mm in width, and 15 mm in thickness. Shell outline suboval, greatest width at valve mid-length; subequally biconvex, with dorsal valve slightly more convex, particularly in the umbonal region. Posterolateral margins rounded, converging gradually to a narrow

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beak; anterolateral margins narrowing and folding ventrally; strongly unisulcate anterior commissure. Shell surface covered with regularly spaced growth lines. Ventral valve with a moderately narrow, shallow sulcus, developed anteriorly very close to the commissure and disappearing posteriorly; high and narrow umbo, projecting a strongly incurved beak. Dorsal valve with a narrow and a moderately high fold.

Remarks: As stated previously, it is not possible to determine the species. However, this species differs from ?*Composita* sp. A by having a suboval shell outline, strongly unisulcate anterior commissure, a ventral valve with a shallow sulcus, and a dorsal valve with a narrow and high fold. In addition, these specimens resemble some described as *Composita* sp. from central Thailand (Yanagida, 1988).

Occurrence: Limestones of the Khao Khwang Formation, Middle Permian (Murgabian)

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily SPIRIFEROIDEA King, 1846

Family CHORISTITIDAE Waterhouse, 1968

Subfamily CHORISTITINAE Waterhouse, 1968

Genus *Choristites* Fischer de Waldheim, 1825

?*Choristites loeyensis* Yanagida, 1966

Fig. 6: 1 and 2

Material examined: Two nearly complete calcareous specimens. Registered material: One calcareous specimen (SUTL010).

Description: Medium to large-sized shells up to 40 mm in length, 55 mm in width, and 25 mm in thickness. Shell outline suboval to subtriangular, transverse, maximum

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width at hinge line, cardinal extremities subrectangular to slightly mucronate; equally biconvex. Moderately uniplicate anterior commissure. Shell surface costellate with narrow, well-rounded, bifurcating (sometimes trifucarting) costellae on both valves, with about 25-30 on each flank; covered with irregularly spaced, faintly developed, growth lamellae. Ventral valve with umbo elevated; subtriangular, wide cardinal area, nearly flat transversely and gently convex longitudinally, apsacline to anacline; extended interarea, occupying the whole hinge length and narrowing laterally; large triangular delthyrium; shallow, broad ventral sulcus, with about 10 costellae. Dorsal valve with low, broad median fold, with about 9-10 rounded costellae.

Remarks: Specimens are assigned with doubts to the genus *Choristites* because they have some diagnostic external morphological features of this taxon. However, internal characters are not observed preventing a clear assignment at generic level. In addition, the presence of bundles of costellae (trifurcating) is more characteristic of the genus *Neospirifer* than *Choristites*. On the other hand, specimens have the diagnostic characters of *Choristites loeyensis* as originally described by Yanagida (1966). This species is externally very similar to *Choristites taiyuanensis* (Chao, 1925), but internally differing in the disposition of dental lamellae (Yanagida, 1966). Although interiors were not observed, these two species are also slightly dissimilar in the number, shape, and pattern of costellae. Yanagida (1966) argued that there is also similarity to *Choristites pavlovi* (Stuckenberg, 1905), but, however, *C. loeyensis* has more costellae, and with different shape, on each lateral slope.

Occurrence: Limestones of the Nam Maholan Formation, Lower Permian (Asselian)

Family TRIGONOTRETIDAE Schuchert, 1893

Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Genus *Neospirifer* Fredericks, 1919

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Neospirifer koewbaidhoni Yanagida, 1966

Fig. 6: 3 and 4

Material examined: Two poorly preserved calcareous specimens. Registered material: One calcareous specimen (SUTL011).

Description: Medium to large-sized shells up to 40 mm in length and 60 mm in width. Shell outline triangular, transverse to alate, with maximum width slightly anterior of hinge line, cardinal extremities acute and triangular. Gently convex longitudinally; cardinal area low, transversely extended; parasulcate anterior commissure. Shell surface costellate with bifurcating, subrounded costellae on both valves. Ventral valve ventral umbo pointed, slightly incurved; well-developed, nearly flat intearea, with wide subtriangular delthyrium; narrow, angular sulcus; 13-15 costellae in sulcus and about 25 on each flank; fine, longitudinal striae, intersected by finer growth lines. Dorsal valve with elevated, triangular median fold, originating at the umbo and gradually elevating anteriorly; 10 costellae on fold and about 25 on each flank, often fasciculate.

Remarks: Specimens show diagnostic characters of *Neospirifer koewbaidhoni* Yanagida, 1966, but having more costellate surface rather than costate and acute, triangular cardinal extremities. This species is similar to *Spirifer wynni* Waagen 1883, but *S. wynni* has non-fasciculate costae and a slightly concave interarea (Yanagida, 1966).

Occurrence: Limestones of the Nam Maholan Formation, Lower Permian (Asselian)

Genus *Gypospirifer* Cooper and Grant, 1976

Gypospirifer sp.

Fig. 6: 5 and 6

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Material examined: One poorly preserved calcareous specimen (SUTL012) and fragmentary material of another specimen.

Description: Large-sized shells up to 40 mm in length and 70 mm in width. Shell outline subrombic to diamond-shaped, alate, with maximum width at hinge line, cardinal extremities acute and subtiangular to subrounded. Gently convex longitudinally, transversely extended; strongly parasulcate anterior commissure. Shell surface costate with fine, bifurcating, only in posterior region and thereafter remaining simple, rounded costae on both valves. Ventral valve convex, with low umbo, slightly incurved; short, hooked beak; well-developed, short intearea, transversely straight; shallow, triangular sulcus, widening anteriorly; 12-15 costellae in sulcus and about 22-25 on each flank; well-developed growth lamellae, slightly raised above valve surface in the intersection with costellae. Dorsal valve with highly rised, triangular median fold, originating at the umbo and gradually elevating anteriorly forming a single costa; 12-13 costellae on fold and about 25 on each flank.

Remarks: Although there is only one nearly complete specimen, it clearly corresponds to *Gypospirifer* as described by Cooper and Grant (1976, p. 2209), but further taxonomic classification at species level is not possible. This taxon has been previously described in South America and Texas (USA) with four species. Of all these species, the available material resembles *Gypospirifer nelsoni* Cooper and Grant 1976, because of the morphology of sulcus and fold and the pattern of bifurcation of costellae (see Cooper and Grant, 1976, p. 2214). However, *G. nelsoni* is more alate and has wider fold and sulcus. Cooper and Grant (1976) compared *G. nelsoni* to *Gypospirifer condor* (d'Orbigny, 1842), but *G. nelsoni*, as well as *Gypospirifer* sp., has lower fold, shallower sulcus, and costellae bifurcating only on posterior region.

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Occurrence: Limestones of the Nam Maholan Formation, Lower Permian (Asselian)

Order TEREBRATULIDA Waagen, 1883

Suborder TEREBRATULIDINA Waagen, 1883

Superfamily DIELASMATOIDEA Schuchert, 1913

Family DIELASMATIDAE Schuchert, 1913

Subfamily DIELASMATINAE Schuchert, 1913

Genus *Fletcherithyris* Campbell, 1965

?*Fletcherithyris* sp.

Fig. 5: 9

Material: Ten fragmented and mostly compressed calcareous specimens. Registered material: One nearly complete calcareous specimen (SUTP05).

Description: Small to medium-sized shells up to 30 mm in length, 20 mm in width, and 10 mm in thickness. Shell outline elliptical, with greatest width at mid-length; lenticular, equally biconvex in lateral profile; posterolateral margins short; uniplicate anterior commissure; well-developed growth lines on shell surface. Ventral valve convex to nearly flat, maximum convexity at mid-length; short interarea; prominent beak, incurved dorsally, erect with submesothyrid to mesothyrid pedicle opening; narrow sulcus, only developing anteriorly, flanked by two low folds. Dorsal valve slightly lobate; shallow sulcus, with faint median fold, flanked by two low folds.

Remarks: It is difficult to determine an accurate generic assignation for Paleozoic terebratuloids unless internal characters are observed (e.g. Pérez-Huerta, 2004). External morphology, however, can provide some approximation for such determination. Thus, specimens have diagnostic external features of *Fletcherithyris*

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Campbell 1965. *Fletcherithyris* can be confused with *Dielasma* King 1859, but usually it has dorsal fold and ventral sulcus, and *Whitspakia* Stehli 1965, which has sulciplicate anterior commissure. Similar specimens (e.g. Yanagida, 1988) to those described herein have been previously assigned to *Notothyris* Waagen 1882, but this taxon has rectimarginate to faintly sulcate anterior commissure and numerous plications toward the anterior margin (Stehli, 1965).

Occurrence: Limestones of the Khao Khwang Formation, Middle Permian (Murgabian)

5. Discussion

Yanagida (1976) conducted a preliminary paleobiogeographic study of Late Paleozoic brachiopods from northeastern Thailand. Analyses of Early Permian faunas were based on brachiopods collected from massive grainstones near the locality of Thum Nam Maholan (see Yanagida, 1976). These deposits were dated as early Asselian-early Sakmarian because of fusulinids of the *Triticites ozawai-Paraschwagerina yanagidai* zone (Igo, 1972). Yanagida concluded that the "Thum Nam Maholan Fauna" shows strong similarities with faunas from the Early Permian of Eurasia (e.g. Carnic Alps and Urals) and the Indochinese Peninsula. Strong relationships with Late Carboniferous faunas from southwestern Europe (e.g., Spain) and western North America tend to disappear in the Early Permian due to the post-Moscovian closure of the oceanic gateway connecting Thailand with these regions (Yanagida, 1976). Also, faunal links with Australia are weak in the Late Carboniferous, due to the closure of migration route in the Moscovian (e.g. Campbell and McKellar, 1969), and the Early Permian because of the Sakmarian glaciation over the whole of Australia (e.g. Dickins and Thomas, 1959; Thomas, 1969).

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Yanagida's conclusions were based on a few specimens collected from a single facies and, therefore, his paleobiogeographic analyses could be challenged by the absence of sufficient data. Taxa described in this work contribute to expand the database of brachiopod faunas of Early to Middle Permian age in different facies from new localities of northeastern Thailand. Brachiopods collected at locality 1 (SUTP), southwest of Phetchabun, are of Middle Permian age and were collected from relatively deep water limestones. Faunas from locality 2 (SUTS), east of Lom Sak, are also of Middle Permian age and were found as molds preserved in sandstones reflecting a relatively higher energy shelf depositional environment. Finally, faunas from Loei (SUTL) are of similar age (Early Permian) and facies to the "Thum Nam Maholan Fauna" (Yanagida, 1976). The present study is also established on relatively few and mostly poorly preserved specimens, which complicates taxonomic classification, but still contributes to clarification of some paleobiogeographic aspects.

Faunas from locality 2 (SUTS) contain a brachiopod association with ?*Neochonetes* sp. and ?*Lamnimargus* sp. that is possibly of Gondwanan affinity, since the taxa have been previously described in Lower Permian rocks of Australia. This is in contradiction to the fusulinid fauna, which clearly has affinities to the warm Cathaysian faunas, found in the intercalated limestones (Toriyama et al., 1978; Ingavat et al., 1980; Altermann, 1989). If brachiopod taxonomy holds up, this would demonstrate the mixed Gondwanan and Cathaysian faunas in this region at least in Middle Permian. Such a conclusion is supported because of findings of ?*Fletcherithyris* sp. in this study and the mixed Cathaysian and Gondwanan floras in localities southwest of Phetchabun (Konno, 1963). In addition, Permian faunas of a mixed biogeographic affinity in this part of Thailand is not unlikely considering some Early to early Middle Permian brachiopod faunas of South China that also appear to show mixed affinities (e.g. Shi and Grunt, 2000; Shi, 2001).

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Also, analyses of brachiopods from Loei also tend to confirm Yanagida´s affirmation of weak faunal affinities between this part of Thailand and western North America and the absence of correlation with regions of western Europe. Only two brachiopod species, ?*Probolionia* sp. and *Gypospirifer* sp., are similar to some taxa described in North America. On the other hand, strong faunal relationships are present with taxa from other regions of Thailand (*Retimarginifera alata* and *Kutorginella fraterculus*) and the Indo-Chinese Peninsula (*Reticulatia* aff. *R. uralica*, *Choristites loeyensis*, and *Neospirifer koewbaidhoni*) (see Yanagida, 1966, 1976).

Paleobiogeography of northeastern Thailand is quite complex, often inconclusive and somewhat speculative, because of rare findings of abundant and well-preserved fossils. Ongoing and future research on Carboniferous and Permian brachiopod faunas will contribute to clarify the affinity of faunas from this region. In addition, further studies will help determining the existence of migratory routes following the opening and closure of oceanic gateways related to the formation of the Late Paleozoic Pangea.

Acknowledgements

Authors would like to acknowledge thorough and helpful reviews by Drs. G.R. Shi, M. Campi and A.J. Boucot and the editor, Dr. J. Lytwyn, which have improved considerably the quality of this manuscript. APH would like to acknowledge help and support from the Palaeontological Research Centre (Mahasarakham University) and the School of Geotechnology (Suranaree University of Technology) and to Drs. G.R. Shi, N.W. Archbold, G. Cisterna and M.L. Martínez-Chacón for helping with references. CC and AC are grateful to the Biodiversity Research and Training Program (BRT) and the Thailand Research Fund (TRF) who provided the financial support for this project.

ACCEPTED MANUSCRIPT

References

Altermann, W., 1989. Facies development in the Permian of Phetchabun basin in central Thailand. VWB-Verlag fur Wissenschaft und Bildung, Berlin, pp. 1–275.

Alvarez, F., Rong Jia-yu, 2002. Order Athyridida. 1475–1601. In: Kaesler, R. (Ed.), Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised) 4. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 753 pp.

Archbold, N.W., 1981. Studies on Western Australian Permian brachiopods. 2. The family Rugosochonetidae Muir-Wood, 1962. Proceedings of the Royal Society of Victoria 93, 109–128.

———, 1982. Classification and evolution of the brachiopod family Rugosochonetidae Muir-Wood, 1962. Proceedings of the Royal Society of Victoria 94, 1–10.

———, 1999. Additional records of Permian brachiopods from near Rat Buri, Thailand. Proceedings of the Royal Society of Victoria 111, 71–86.

Boucot, A.J., Johnson, J.G., Staton, R.D., 1964. On some atrypoid, retzioid, and athyridoid Brachiopoda. Journal of Paleontology 38, 805–822.

Bronn, H.G., 1862. Die Klassen und Ordnungen der Weichthiere (Malacozoa), vol. 3 (1). C. F. Winter'sche Verlagshandlung, Leipzig & Heidelberg, 518 pp., 44 pls.

Brown, T., 1845. Illustrations of the fossil conchology of Great Britain and Ireland, with descriptions and localities of all species, parts 24–28. Maclachlan and Stuwart, Smith, Elder, Edinburgh & London, pp. 117–136.

ACCEPTED MANUSCRIPT

Brunton, C.H.C., Lazarev, S.S., Grant, R.E., Yugan Jin, 2000. Order Productida. 350–643. In: Kaesler, R. (Ed.): Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised) 2 and 3. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 919 p.

Buckman, S.S., 1906. Brachiopod nomenclature: *Epithyris*, *Hypothyris*, *Cleiothyris* Phillips, 1841. Annual Magazine of Natural History (series 7) 18, 321–327.

Campbell, K.S.W., 1965. Australian Permian terebratuloids. Bulletin of the Bureau of the Mineral Resources of Australia, Geology and Geophysics 68, 1–147.

Campbell, K.S.W., McKeller, R.G., 1969. Eastern Australian Carboniferous invertebrates: Sequence and affinities. In: Campbell, K.S.W. (Ed.), Stratigraphy and Palaeontology. Australian National University Press, pp. 77–119.

Carter, J.L., Johnson, J.G., Gourvennec, R., Hou Hong-fei, 1994. A revised classification of the spiriferid brachiopods. Annals of the Carnegie Museum 63, 327–374.

Chao, Y.T., 1925. On the age of the Taiyuan Series of North China. Bulletin of the Geological Society of China 4, 221–249.

———, 1927. Productidae of China, part 1: Productida. Palaeontologica Sinica (series B) 5, 1–192.

Chernyschev, T.N., 1902. Die obercarboniferischen Brachiopoden des Ural und des Timan. Trudy Geologicheskogo Komiteta [Mémoires de la Comité Géologique] 16, pp. 1–749, pls. 63.

Charoenprawat, A., Wongwanich, T., Tantiwanich, W., Kitipariwat, K., 1976. Geological map of Thailand on 1:250,000 scale: Sheet Changwat Loei (NE47-12). Geological Survey Division, Department of Mineral Resources, Bangkok.

ACCEPTED MANUSCRIPT

Chonglakmani, C., Sattayalak, N., 1978. Stratigraphy of the Huai Hin Lat Formation (Upper Triassic) in northeastern Thailand. In: Nutalaya, P. (Ed.), Proceedings of the Third GEOSEA (Bangkok), pp. 739–774.

Chonglakmani, C., Fontaine, H., 1990. The Lam Narai-Phetchabun region: A platform of Early Carboniferous to Late Permian age. In: Charusiri, P., Pisutha-Arnond, V., Jarupongsakul, S. (Eds.), Proceedings of the development geology of Thailand into the year 2000**,** Chulalongkorn University (Bangkok), pp. 39–98.

Chonglakmani, C., Helmcke, D., 2001. Geodynamic evolution of Loei and Phetchabun regions-does the discovery of detrital Chromian Spinels from the Nam Duk Formation (Permian, North-Central Thailand) provide new constraint? Gondwana Research 4, 437–442.

Cooper, G.A., 1957. Permian brachiopods from central Oregon. Smithsonian Miscellaneous Collection 134, 1–79.

Cooper, G.A., Grant, R.E., 1976. Permian Brachiopods of West Texas, IV. Smithsonian Contributions to Paleobiology 21, 1923–2607.

Davidson, T., 1881. On genera and species of spiral-bearing Brachiopoda from specimens developed by Rev. Norman Glass: with notes on the results obtained by Mr. George Maw from extensive washing of the Wenlock and Ludlow shales of Shropshire. Geological Magazine (new series, Decade II) 8, 1–13.

Dickins, J.M., Thomas, G.A., 1959. The Marine Fauna of the Lyons Group and Carrandibby Formation of Carnarvon Basin, western Australia. Bureau of Mineral Resources of Australia Report 38, 65–95.

d'Orbigny, A., 1842. Voyage dans l'Amérique Méridionale. Géologie, Paléontologie; Foraminifères, vol. 3. Pitois- Levrault, Paris, 50–56.

Duméril, A.M.C., 1805. Zoologie analytique, ou méthode naturelle de classification des animaux. Allais, Paris, xxiv + 344 pp.

ACCEPTED MANUSCRIPT

Fischer de Waldheim, G., 1825. Notice sur la Choristite. – Programme d'invitation à la Société Impériale des Naturalistes de Moscou, 12 pp., 1 pl.

Fredericks, G., 1919 [1926]. Tablitsa dlya opredeleniia rodov semeistva Spiriferidae King [Table for determination of the genera of the family Spiriferidae King]. Akademiia Nauk SSSR, Izvestiia (series 6) 20, 393– 422.

Fujikawa, M., Ueno, K., Sardsud, A., Saengsrichan, W., Kamata, Y., Hisada, K., 2005. Early Permian ammonoids from the Kaeng Krachan Group of the Phatthalung-Hat Yai area, southern peninsular Thailand. Journal of Asian Earth Sciences 24, 739–752.

Grant, R.E., 1976. Permian brachiopods from southern Thailand. Journal of Paleontology Memoir 9, 269 pp., 71 pls.

Gray, J.E., 1840. Synopsis of the contents of the British Museum, 42nd edition. British Museum, London, 370 pp.

Grinnell, R.S., Andrews, G.W., 1964. Morphological studies of the brachiopod genus *Composita*. Journal of Paleontology 38, 227–248.

Grunt, T.A., 1965. Nadsemeistvo Athyridasea [Superfamily Athyridacea]. In: Ruzhencev, V.E., Sarytcheva, T.G. (Eds.), Razvitie i smena morskikh organizmov na rubezhe paleozoia i mesozoia [Evolution and change of marine organisms at the Paleozoic-Mesozoic boundary]. Akademiia Nauk SSSR, Trudy Paleontologicheskogo Instituta 108, pp. 237–253.

Igo, H., 1972. Fusulinacean fossils from north Thailand. Geology and Palaeontology of Southeast Asia 10, 63–116.

Ingavat, R., Toriyama, R., Pitakpaivan, K., 1980. Fusuline zonation and faunal characteristics of the Ratburi Limestone in Thailand and its equivalent in Malaysia. Geology and Palaeontology of Southeast Asia 21, 43–62.

Ivanova, E.A., 1951. New data on Productid systematics genus *Kutorginella*. Doklai Akademyia Nauk SSSR 77, 329–331.

ACCEPTED MANUSCRIPT

King, W., 1846 [Aug.]. Remarks on certain genera belonging to the class Palliobranchiata. Annals of the Magazine of Natural History (series 1) 18 (117), art. 11, 26– 42, 83–94.

———, 1859. On *Gwynia*, *Dielasma*, and *Macandrevia*, three new genera. Proceedings of the Dublin Univiversity Zoological and Botanical Association 1, 256–262.

Konno, E., 1963. Some Permian plants from Thailand. Japan Journal of Geology and Geography 34, 139–159 [reprinted in GPSEA 1, 89–109].

Metcalfe, I., 1991. Late Palaeozic and Mesozoic palaeogeography of Southeast Asia. Palaeogeography, Palaeoclimatology, Palaeoecology 87, 211–221.

———, 1996. Gondwanaland dispersion, Asian accretion and evolution of eastern Tethys. Australian Journal of Earth Sciences 43, 605–623.

Muir-Wood, H.M., 1955. A History of the Classification of the References Phylum Brachiopoda. British Museum of Natural History Monograph, London, v + 124 pp., 12 figs.

———, 1962. On the Morphology and Classification of the Brachiopod Suborder Chonetoidea. British Museum of Natural History Monograph, London, viii + 132 pp., 24 figs., 16 pls.

Muir-Wood, H.M., Cooper, G.A., 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). Geological Society of America Memoir 81, Boulder (Colorado), 447 pp., 8 figs., 135 pls.

Pérez-Huerta, A., 2004. New Carboniferous brachiopods from the eastern Great Basin, Nevada (U. S. A.): Implications for loop ontogeny and evolution in Late Paleozoic terebratuloids. Palaeontology 47, 1519–1537.

Racheboeuf, P.R., 2000. Suborder Chonetidina. 362– 423. In: Kaesler, R. (Ed.), Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised) 2. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 424 pp.

ACCEPTED MANUSCRIPT

Sarytcheva, T.G., Sokolskaya, A.N., 1959. O klassifikatsin lozhnoporistykh brakhiopod [On the classification of pseudopunctate brachiopods]. Akademiia Nauk SSSR, Doklady (Moscow) 125, 181–184.

Schuchert, C., 1893. Classification of the Brachiopoda. American Geologists 11, 141–167, 5 pls.

———, 1913. Class 2. Brachiopoda. In: von Zittel, K.A. (Ed.), Text-book of Palaeontology, vol. 1, part 1, 2nd ed., translated and edited by C. R. Eastman. MacMillan & Co., Ltd. (London), pp. 355– 420, figs. 526–636.

———, 1929. Classification of Brachiopod Genera, fossil and recent. [In: Charles Schuchert, C., LeVene, C.M. (Eds.): Animalia pars 42.] In: Pompeckj, J.F. (Ed.), Fossilium Catalogus, vol. 1. Junk. (Berlin), pp. 10–25.

Shen, S., Archbold, N.W., 2002. Chonetoidea (Brachiopoda) from the Lonpingian (Late Permian) of South China. Alcheringa 25, 327–349.

Shi, G.R., 2001. Possible influence of Gondwanan glaciation on low-latitude carbonate sedimentation and trans-equatorial faunal migration: the Lower Permian of South China. Geosciences Journal 5, 57-63.

Shi, G.R., Waterhouse, J.B., 1996. Lower Permian brachiopods and mollusks from the Upper Jungle Creek Formation, northern Yukon Territory, Canada. Bulletin of the Geological Survey of Canada 224, 1–241.

Shi, G.R., Archbold, N.W., 1998. Permian marine biogeography of SE Asia. In: Hall, R., Holloway, J.D. (Eds.), Biogeography and Geological Evolution of SE Asia, Backhuys Publishers, Leiden, pp. 57–72.

Shi, G.R., Grunt, T.A., 2000. Permian Gondwana-Boreal antitropicality with special reference to brachiopod faunas. Palaeogeography, Palaeoclimatology, Palaeoecology 155, 239–263.

ACCEPTED MANUSCRIPT

Shi, G.R., Shen, S., Campbell, H.J., Raksaskulwong, L., 2001. A *Meekella*-dominated Early Permian brachiopod assemblage from central Peninsular Thailand. In: Weiss, R.H. (Ed.), Contributions to Geology and Palaeontology of Gondwana, In Honour of Helmut Wopfner, Cologne, pp. 441–451.

Shi, G.R., Raksaskulwong, L., Campbell, H.J., 2002. Early Permian brachiopods from central and northern Peninsular Thailand. In: Hills, L.V., Henderson, C.M., Bamber, E.W. (Eds.), Carboniferous and Permian of the World: XIV ICCP Proceedings, Canadian Society of Petroleum Geologists Memoir 19, pp. 596–608.

Shi, G.R., Shen, S., Zhan, L., 2003. A Guadalupian-Lopingian (Middle to Late Permian) brachiopod fauna from the Juripu Formation in the Yarlung-Zangbo suture zone, southern Tibet, China. Journal of Paleontology 77, 1053–1068.

Stehli, F.G., 1954. Lower Leonardian Brachiopoda of the Sierra Diablo. American Museum of Natural History Bulletin 105, 257–358, 1–55 figs., 17–27 pls.

———, 1965. Paleozoic Terebratulida. 730–762. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Volume 2. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 404 pp.

Stuckenberg, A.A., 1898. Allgemeine geologische Karte von Russland (Blatt 127). Trudy Geologicheskogo Komiteta [Mémoires de la Comité Géologique] 16, pp. 1–362.

———, 1905. Fauna verkhne-kamennougol'noi Tolshchi Samarskoi Luki [Die Fauna der obercarbonischen Suite des Wolgadurchbruches]. Trudy Geologicheskogo Komiteta [Mémoires de la Comité Géologique] 23, pp. 1–144, pls. 13.

Termier, G., Termier, H., Lapparent, A.F., Martin, P., 1974. Monographie du Permo-Carbonifére de Wardak (Afghanistan Central). Documents des Laboratoires de la Faculté des Sciences de Lyon, Hors Série 2, 1–168.

Thomas, G.A., 1969. The Permian brachiopod faunas of western Australia. 217–234 Gondwana Stratigraphy. IUGS Symposium, UNESCO, Paris, 983 pp.

ACCEPTED MANUSCRIPT

Toriyama, R., Pitakpaivan, K., Ingavat, R., 1978. The paleogeographic characteristics of Fusuline faunas of the Ratburi Group in Thailand and its equivalent in Malaysia. In: Nutalaya, P. (Ed.), Proceedings of the Third GEOSEA (Bangkok), pp. 107–111.

Ustritskiy, V.I., 1971. Biostratigraphy of the Upper Paleozoic in the Arctic. Nauchno-Issledovatel'skii Institut Geologii Arktiki (NIIGA), Trudy 164, 279 pp.

Waagen, W., 1882. Salt Range fossils, vol. I, part 4. Productus Limestone fossils, Brachiopoda. Memoirs of the Geological Survey of India, Palaeontologica Indica (series 13), fasc. 1, 329–390.

———, 1883. Salt Range fossils, vol. I, part 4. Productus Limestone fossils, Brachiopoda. Memoirs of the Geological Survey of India, Palaeontologica Indica (series 13), fasc. 2, 391–546, 29– 49 pls.

Waterhouse, J.B., 1968. The classification and descriptions of Permian Spiriferida (Brachiopoda) from New Zealand. Palaeontographica (Abt. A) 129, 94 pp., 18 pls.

———, 1970. Permian brachiopod *Retimarginifera perforata* n. gen. n. sp. from the Byro Group of Carnarvon Basin, western Australia. Journal of the Royal Society of Western Australia 53, 120–128.

———, 1975. New Permian and Triassic brachiopod taxa. Papers of the Department of Geology, University of Quesland, 7, 1–23.

Waterhouse, J.B., Pitakpaivan, K., Mantajit, N., 1981. The Permian stratigraphy and paleontology of southern Thailand. Thailand Geological Survey Memoir 4, 1–213.

Wielchowsky, C., Young, J., 1985. Regional facies variation in Permian of the Phetchabun fold and thrust belt, Thailand. In: Thanvarachon, P., Hokjaroen, S., Yanungme, W. (Eds), Proceedings of the Conference on Geology and Mineral Resources Development of Northeastern Thailand, Department of Geotechnology, (Khon Kaen Univesity), Khon Kaen, pp. 41–45.

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

Williams, A., Brunton, C.H.C., MacKinnon, D.I., 1997. Morphology. 321– 422. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), 1. Geological Society of America and The University of Kansas. Boulder and Lawrence, 539 pp.

Williams, A., Brunton, C.H.C., 1997. Morphological and anatomical terms applied to brachiopods. 423–440. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), 1. Geological Society of America and The University of Kansas. Boulder and Lawrence, 539 pp.

Williams, A., Carlson, S J., Brunton, C.H.C., Holmer, L.E., Popov, L.E., 1996. A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society of London B 351, 1171–1193.

Yanagida, J., 1964. Permian brachiopods from central Thailand. Geology and Palaeontology of Southeast Asia 1, 143–175.

———, 1966. Early Permian brachiopods from north-central Thailand. Geology and Palaeontology of Southeast Asia 3, 46–97.

———, 1976. Palaeobiogeographical considerations on the Late Carboniferous and Early Permian brachiopods of central north Thailand. Geology and Palaeontology of Southeast Asia 17, 173–189.

———, 1988. Biostratigraphic study of Paleozoic and Mesozoic groups in central and northern Thailand: An interim Report. Geological Survey Division of the Department of Mineral Resources, Bangkok, 47 pp., 33 pls.

Yanagida, J., Nakornsri, N., 1999. Permian brachiopods from the Khao Hin Kling Area near Petchabun, North-central Thailand. Bulletin of the Kitakyushu Museum of Natural History 18, 105–136.

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Explanation of Figures

Fig. 1. Index map showing location of brachiopod localities (SUTL, SUTS, and SUTP) within the tecto-stratigraphic sequences (Khao Khwang Platform, Nam Duk Basin, and Pha Nok Khao Platform) in northeastern Thailand.

Fig. 2. Schematic stratigraphic columns for each locality showing beds of brachiopod collection in the Khao Khwang limestones, Nam Duk Fm., and the Nam Maholan Fm.

Fig. 3. 1-3. ?*Neochonetes* (*Sommeriella*) sp.: internal molds of Ventral valves of three poorly preserved specimens, SUTS01-03, x 2. 4, 5. ?*Lamnimargus* sp., 4: internal (left) and external (right) molds of a Ventral valve, SUTS04, x 2, 5. enlargement of the internal mold, x 3.

Fig. 4. 1, 2. ?*Probolionia* sp., 1: posterior view of an internal mold of a Ventral valve, SUTL01, x 2, 2: posterior view of a incomplete calcareous specimen showing reticulation, SUTL02, x 2. 3, 4. *Retimarginifera alata* Watehouse et al. 1981: postero-ventral views of a calcareous specimen, SUTL03, x 2. 5, 6. *Kutorginella fraterculus* Waterhouse et al. 1981, 5: postero-ventral view of a calcareous external mold, SUTL04, x 2, 6: dorsal exterior of a calcareous external mold, SUTL05, x 2. 7, 8. *Linoproductus* sp. A: ventral views of calcareous external molds of two specimens, SUTL06-07, x 1. 9. *Linoproductus* sp. B: postero-ventral view of a calcareous external molds, SUTL08, x 1. 10. *Reticulatia* aff. *R. uralica* (Chernyschev, 1902): ventral view of a calcareous external mold, SUTL09, x 1.

Fig. 5. 1-4. ?*Composita* sp. A, 1, 2: dorsal and ventral views of a incomplete calcareous specimen, SUTP01, x 2, 3, 4: dorsal and ventral views of a incomplete calcareous juvenile specimen, SUTP02, x 3. 5-8. *Composita* sp. B, 5, 6: dorsal and ventral views of a incomplete calcareous, partially silicified, specimen, SUTP03, x 2, 7, 8: dorsal and ventral views of a calcareous, partially silicified, juvenile specimen,

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SUTP04, x 4. 9. ?*Fletcherithyris* sp.: dorsal view of a calcareous specimen, SUTP05, x 1.

Fig. 6. 1, 2. *Choristites loeyensis* Yanagida 1966: dorsal and ventral views of a calcareous specimen, SUTL10. 3, 4, *Neospirifer koewbaidhoni* Yanagida 1966: dorsal and ventral views of calcareous specimen, SUTL11. 5, 6: *Gypospirifer* sp.: dorsal and ventral views of broken calcareous specimen, SUTL12.

Taxa	Locality 1- SUTP Khao Khwang Platform	Locality 2 - SUTS Nam Duk Basin	Locality 3 - SUTL Pha Nok Khao Platform
? *Neochonetes* sp.		X	
? *Probolionia* sp.			X
? *Lamnimargus* sp.		X	
Retimarginifera alata			X
Kutorginella fraterculus			X
Reticulatia aff. *R. uralica*			X
Linoproductus sp. A			X
Linoproductus sp. B			X
? *Composita* sp. A	X		
? *Composita* sp. B	X		
Choristites loeyensis			X
Neospirifer koewbaidhoni			X
Gyposspirifer sp.			X
? *Fletcherithyris* sp.	X		

Table 1. Brachiopod taxa found at each locality.

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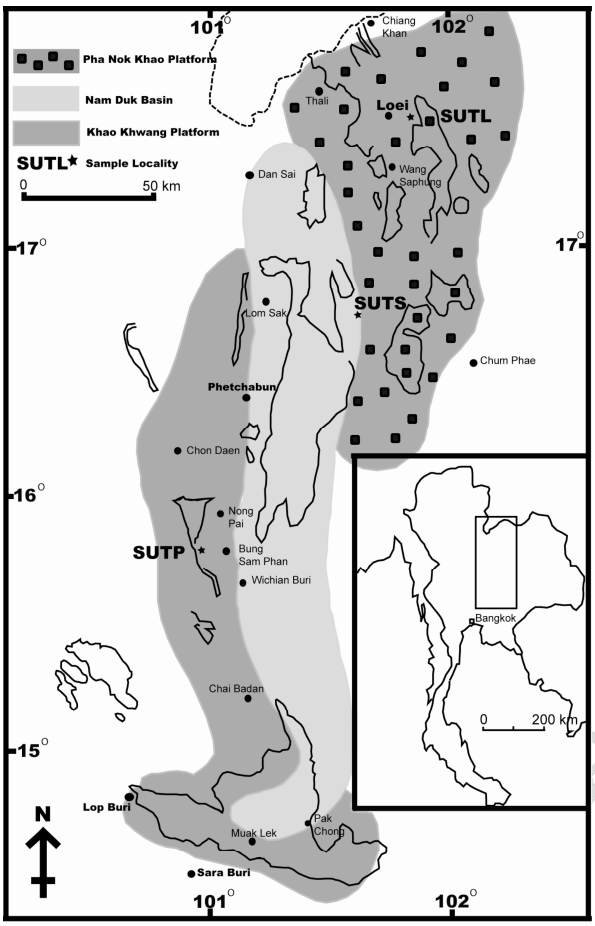

Pérez-Huerta et al. - Figure 1

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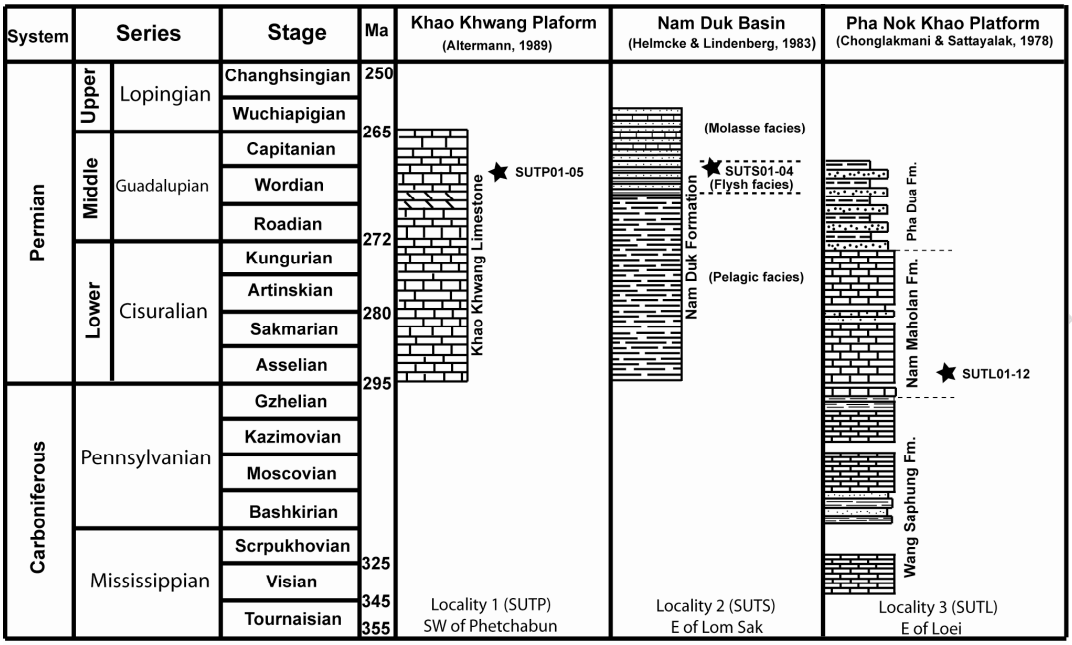

Pérez-Huerta et al. - Figure 2

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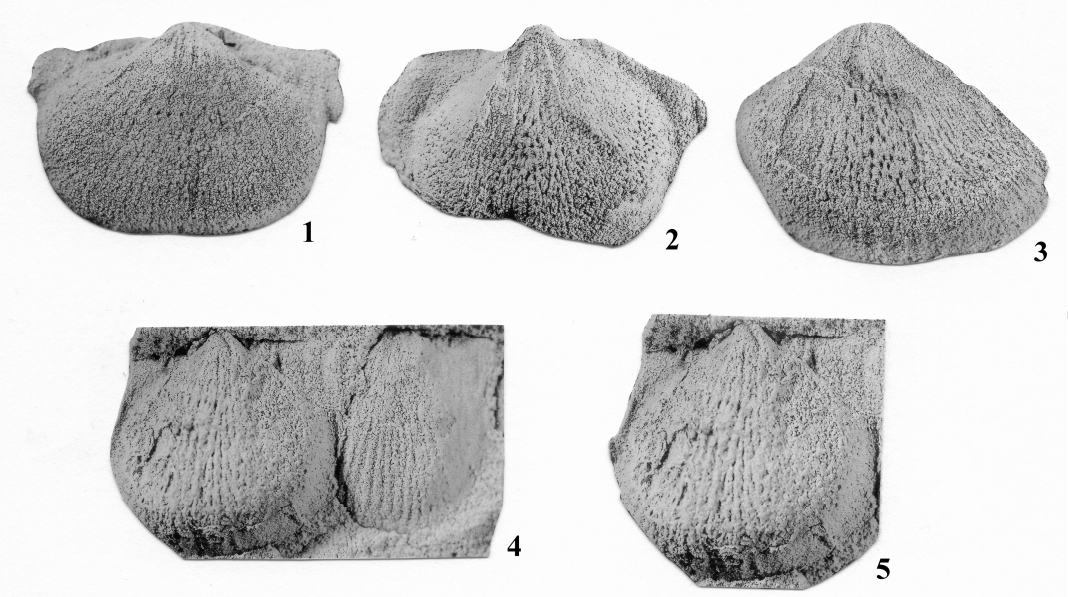

Pérez-Huerta et al. - Figure 3

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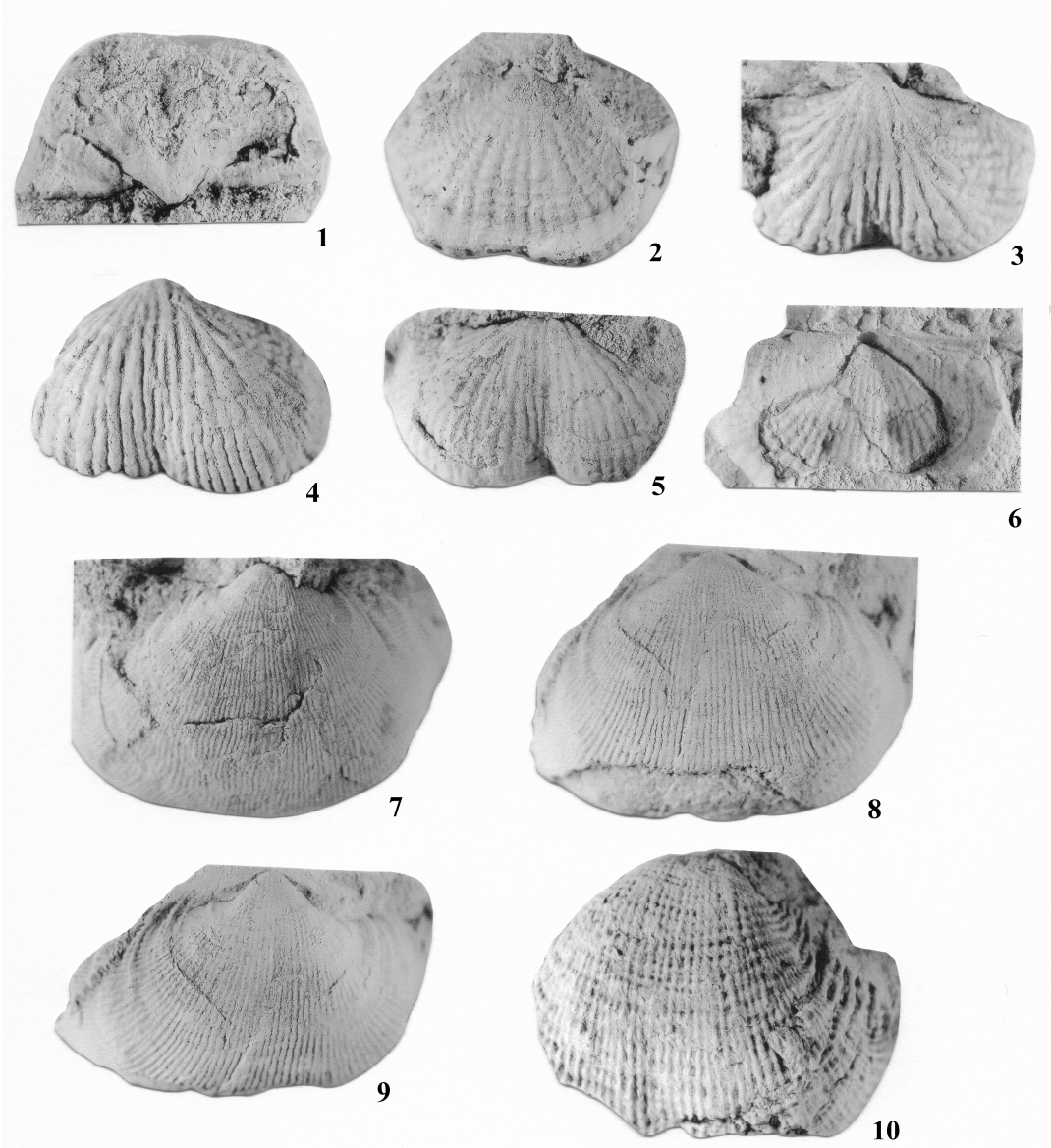

Pérez-Huerta et al. - Figure 4

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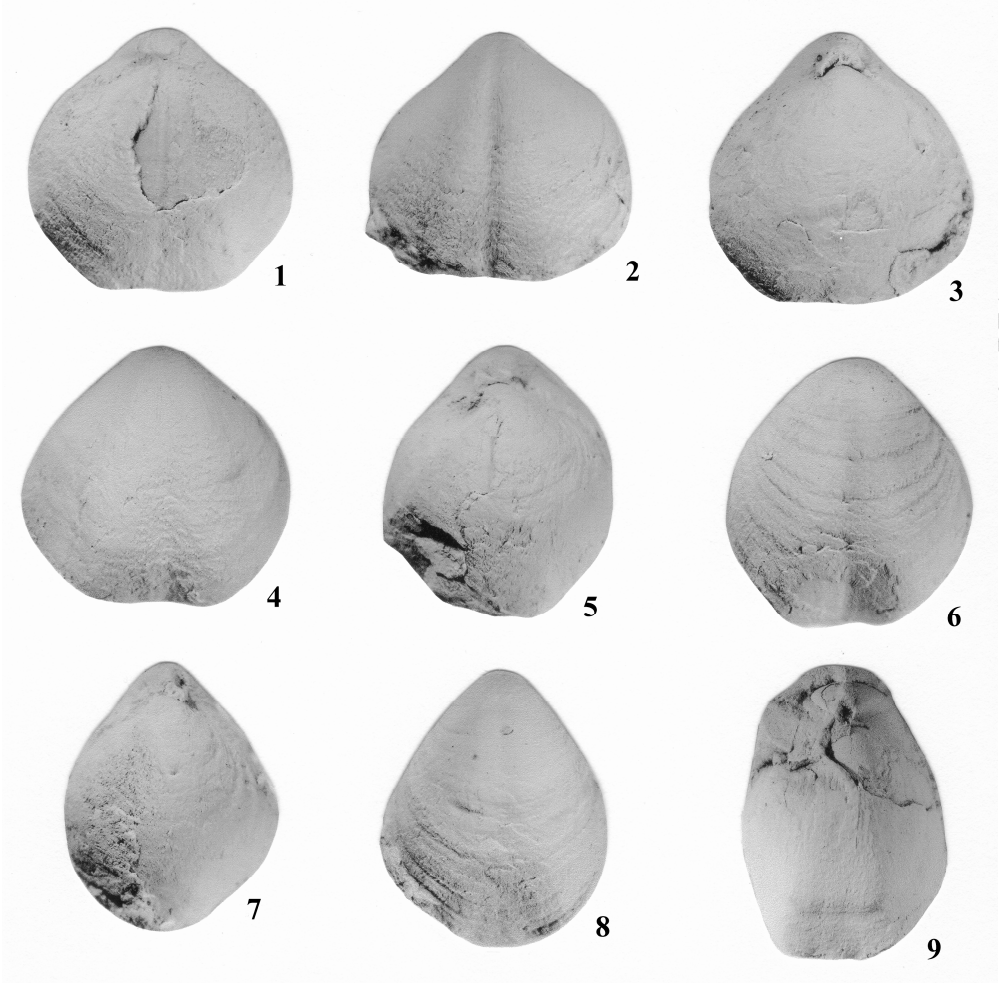
ACCEPTED MANUSCRIPT



Pérez-Huerta et al. - Figure 5

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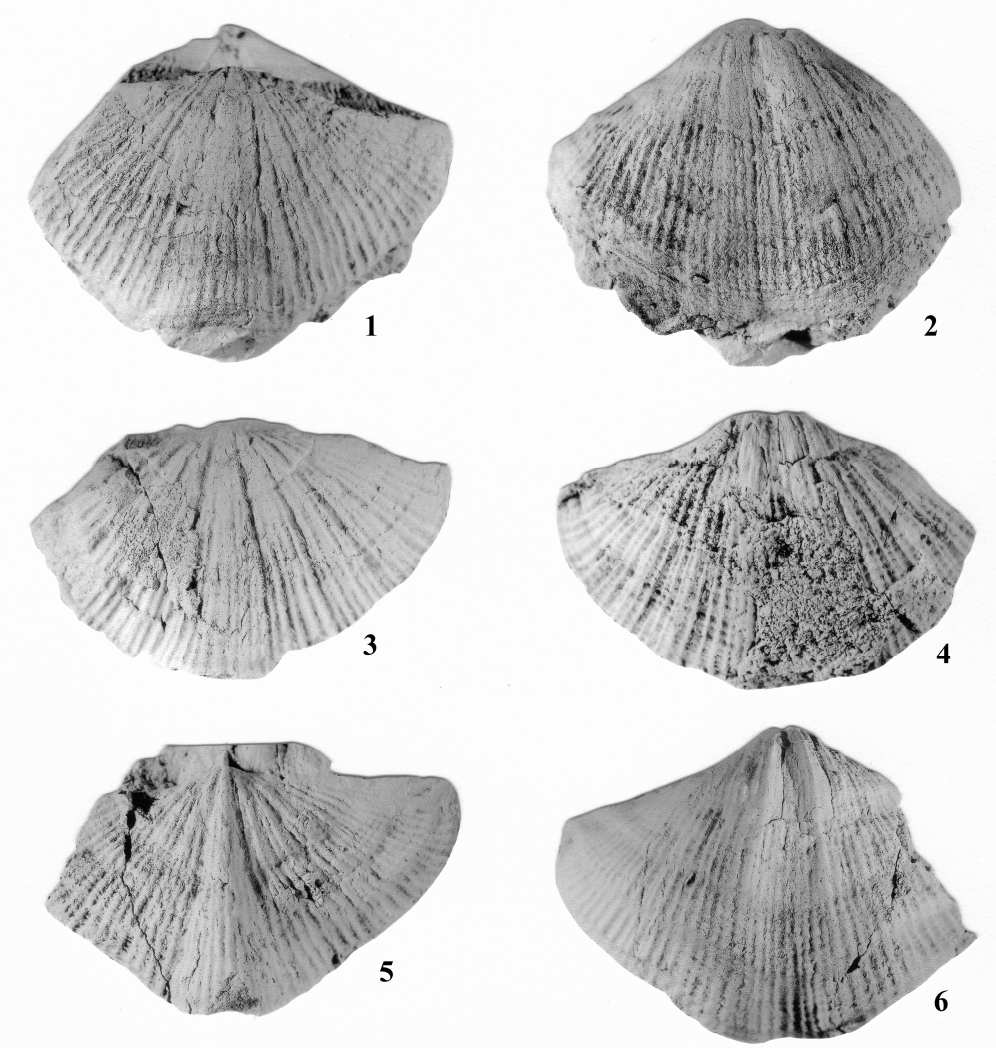
ACCEPTED MANUSCRIPT



Pérez-Huerta et al. - Figure 6

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