Geol. Mag. **140** (*5*), *2003, pp. 523–538. © 2003 Cambridge University Press*
DOI: 10.1017/S0016756803007854 *Printed in the United Kingdom*

Palaeobiogeographic implications of Middle Permian brachiopods from Johore (Peninsular Malaysia)

MASATOSHI SONE*†, IAN METCALFE* & MOHD SHAFEEA LEMAN*‡

*Asia Centre, University of New England, Armidale, NSW 2351, Australia
‡School of Environmental Sciences and Natural Resources, Universiti Kebangsaan Malaysia,
43600 Bangi, Selangor, Malaysia

(*Received* 13 June 2002; *accepted* 24 March 2003)

Abstract – A new Middle Permian locality in northern Johore, Peninsular Malaysia, yields a small-sized, but compositionally unique, brachiopod fauna consisting of eight species: *Pseudoleptodus* sp., *Caricula* cf. *salebrosa* Grant, *Neochonetes (Nongtaia)* aff. *arabicus* (Hudson & Sudbury), *Karavankina* sp., *Transennatia* cf. *insculpta* (Grant), *Hustedia* sp., *Orthothetina* sp., and martiniid indet. The first four genera are new records for Malaysia; in particular, the rare taxa *Pseudoleptodus* and *Caricula* characterize the fauna. The brachiopods occur together with the ammonoid *Agathiceras* sp., the nautiloid *Foordiceras*? sp., bivalves, and crinoid stems. The locality belongs to the East Malaya terrane of the Cathaysian biotic region, but some affinities to species of the Sibumasu province are recognized. The Malaysian forms of *Pseudoleptodus, Caricula* and *Transennatia* are similar to those of the Ratburi Limestone (southern Thailand). A Roadian–early Wordian age is interpreted for the Johore fauna. The similarity of brachiopods reported here with those from the Ratburi Limestone suggests that there was species interchange or one-way migration between shallow waters of East Malaya and Sibumasu across the main Palaeo-Tethys. The Tethyan seaway between the two terranes must have been narrower than previously interpreted by some authors to allow such faunal traffic during the Roadian–Wordian time period.

Keywords: Permian, Malaysia, brachiopods, palaeobiogeography.

1. Introduction

The Permian geology of Johore is poorly understood, and Permian marine fossils are known only from a few records, in particular reports of the Geological Survey of Malaysia (GSM), as compiled by Ibrahim (1987). Igo, Rajah & Kobayashi (1979) described a diverse fusulinid fauna (27 species) of probable Kungurian (late Early Permian) age from the Sumalayang limestone, southern Johore. The fauna includes two species of the so-called anti-tropical genus *Monodiexodina* Sosnina, namely *M. shiptoni* (Dunbar) and *M. kattaensis* (Schwager). This was the only systematically studied Permian marine fossil assemblage of Johore.

This paper reports and describes a small faunal assemblage of brachiopods and cephalopods from a new Middle Permian (Guadalupian) exposure in Sermin, northern Johore. This is the second record of Permian brachiopods from Johore, the first being that of Rahman (1986).

The international Permian time-scale and suggested correlation chart (Jin *et al*. 1997; Wardlaw, 1999) are utilized in this paper. The Permian fossils reported here were discovered by Sone and Leman in August, 1999, and additional samples were collected in March and October, 2000. All described specimens are deposited at the National University of Malaysia (Universiti Kebangsaan Malaysia) with a number prefixed UKM-F.

2. Regional geology

Prior to this study, the current fossil locality was included in the Middle–Late Triassic Gemas (=Semantan) Formation (see the most recent official geological map of Peninsular Malaysia, Geological Survey of Malaysia, 1985). These Triassic clastic sediments are the most common rock type in the central to southern part of the Central Belt, and are distributed extensively in the west of the present region.

Bachik (1985) first reported the occurrence of marine fossils from the present area, which he considered to be Triassic in age. Rahman (1986) subsequently listed names of brachiopods and one ammonoid *Agathiceras* from this fauna. The brachiopods were identified as *Spiriferellina* cf. *adunctata* Waterhouse & Piyasin, *Leptodus* sp., *Retimarginifera* sp., echinoconchid cf. ‘*Echinoconchus*’ *fasciatus* (Kutorga), and linoproductid gen. and sp. indet., and a general Middle Permian age was suggested for this assemblage (C. H. C. Brunton, GSM unpub. report, 1986).

Bachik’s outcrop was a road-cut on a dirt road and was near a tributary of the Sungai (River) Kapeh Kubang (R. Bachik, GSM, pers. comm. August, 2001). According to the grid reference WL416934 (see Ibrahim, 1987), it should be a few hundred metres

---

† Author for correspondence: msone2@pobox.une.edu.au

First published in *Geological Magazine*, Volume 140: Issue 5 (2003).
Published by Cambridge University Press. Copyright © 2003 Cambridge University Press.
This article online at: http://dx.doi.org/10.1017/S0016756803007854

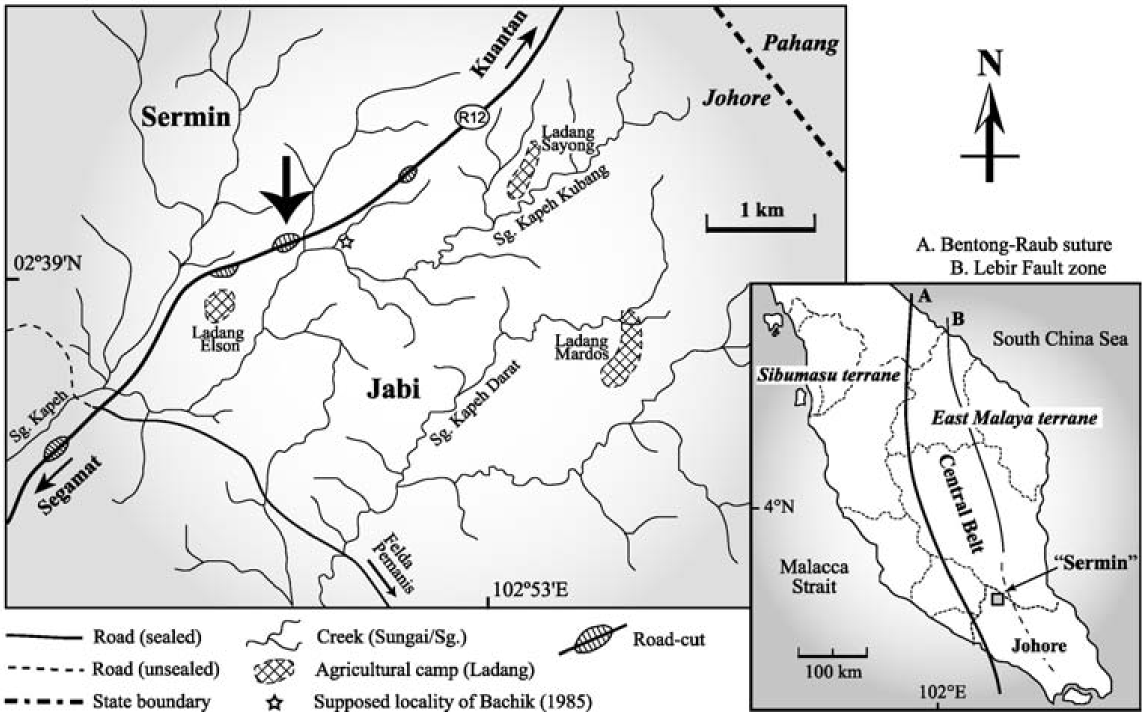

Figure 1. Map of the Middle Permian fossil locality in Sermin, northern Johore.

east of the current road-cut outcrop beyond Route 12 (Fig. 1). The present area has undergone extensive development of oil palm plantations and subsequent severe erosion over the last ten years. The present authors failed to relocate Bachik's locality in the field, and it is uncertain whether it was stratigraphically equivalent to the newly found fossil horizon. No other Permian sediment is known to be distributed around this region.

3. Fossil locality

The present fossil outcrop (02° 39′ 06″ N, 102° 51′ 51″ E, by Magellan GPS Tracker) is located in the Sermin area on the Kuantan–Segamat Highway (Route 12), and is about 2.3 km NE of the T-junction to the agricultural township Felda Pemanis (Fig. 1). It is a large road-cut on the northern side of the road, and is approximately 20 m in height and 400 m in lateral length, but is mostly covered with vegetation. The fossils were found in the middle part of the road-cut. The exposure is divided by a normal fault into two lithologically distinct sedimentary units. The sequence in which the fossils were found is in the foot wall (Fig. 2), and it dips 54° W with a strike of N 48° W. Another sequence in the hanging wall dips 70° W with a strike of N 40° W.

The fossils were recovered from a band about 8 m below the upper boundary of the foot-wall sequence (Fig. 3). The fossil band is about 2 m thick and consists of brown to purple, tuffaceous, coarse-grained sandstone and black siltstone. Small fragments of crinoid stems are abundant. Brachiopods, cephalopods (ammonoids and one nautiloid) and bivalves are rare. The fossil band is underlain by beds of black shale, sandstone and siltstone. Mud clasts in the lower part of a sandstone layer scraped off from an underlying shale bed indicate the stratigraphic younging direction (Figs 2, 3). On the other hand, another unit of the hanging wall is made up of massive to thickly bedded, coarse yellowish sandstone. No age-indicative fossil was found in this sediment; hence the stratigraphic relationship of the two fault-detached units is unknown.

4. Brachiopod systematics (M. Sone)

Class STROPHOMENATA Williams, Carlson,
Brunton, Holmer & Popov, 1996
Order PRODUCTIDA Sarytcheva &
Sokolskaya, 1959
Suborder LYTTONIIDINA Williams,
Harper & Grant, 2000
Superfamily LYTTONIOIDEA Waagen, 1883
Family LYTTONIIDAE Waagen, 1883
Subfamily POIKILOSAKINAE Williams, 1953
Genus *Pseudoleptodus* Stehli, 1956

Pseudoleptodus sp.
Figure 4a–i

1976 *Pseudoleptodus*? sp. indet. Grant, p. 160, pl. 43, figs 1–7.

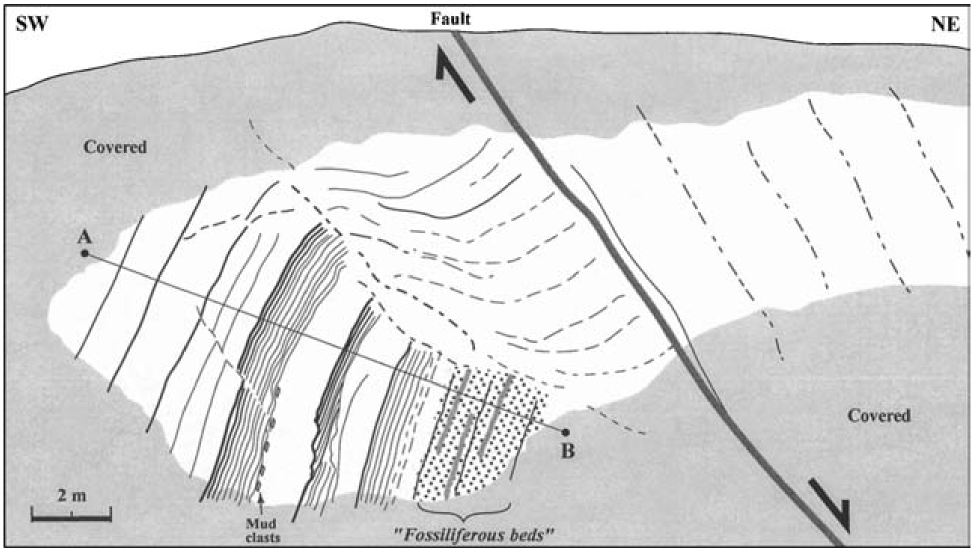

Figure 2. Sketch of the road-cut fossil outcrop studied in this paper. Line A–B corresponds to that of Figure 3.

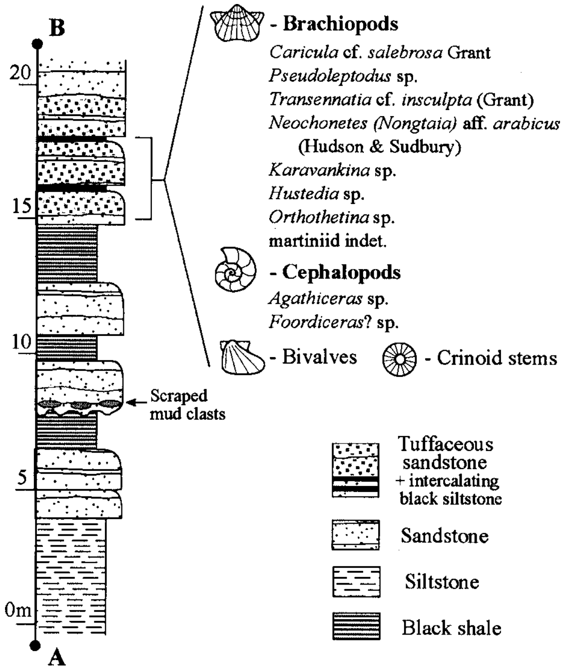

Figure 3. Stratigraphic column of the fossil sequence.

Size ranges of available specimens. Eight ventral internal moulds were available, of which seven specimens UKM-F441–447 are illustrated, ranging in size from 2.5 to 13.5 mm in half width and from 3 to at least 18 mm in length.

Description. The assemblage of small shells exhibits ontogenetic stages. In profile, juveniles are cup-shaped and mature specimens are more spatulate. The outline is ovate. Very fine tubercles are present over the ventral internal surface of both inlobes and outlobes. Internally, the lobar apparatus varies considerably in form from shell to shell. In juvenile stages, the vallum (a wall bounding outlobes and inlobes) is very weak and instead lobar channels are marked by two parallel grooves separated by a narrowly rounded median thickening (UKM-F441,442; Fig. 4a–c). In later but still immature growth stages, the vallum becomes higher with wide outlobes, as the loops of the vallum are often highly rounded, showing a latilobate condition (UKM-F443–445; Fig. 4d–g). Lobes become angustilobate in later growth stages (UKM-F446,447; Fig. 4h, i). Mature lobation is fairly regular and as many as six relatively long lateral outlobes are developed. As is common for the genus, outlobe channels are commonly wider than inlobes.

Remarks. An asymmetrical muscle apparatus is the most obvious characteristic of Poikilosakinae but is not preserved in the present material. The mature shell UKM-F447 displays extended lateral lobes, atypical for *Pseudoleptodus*. Hence, there is some possibility that the Malaysian material may be allied to the larger Lyttoniinae genus, *Eolyttonia* Frederiks or *Collemataria* Cooper & Grant, whose immature forms also have latilobate to angustilobate features similar to *Pseudoleptodus*. However, the overall appearance of the small Malaysian shells is comparable to that of *Pseudoleptodus*. The present form may represent an advanced species of the genus.

A Ratburi form of *Pseudoleptodus*? sp. indet. described by Grant (1976, p. 160, pl. 43, figs 1–7) is represented by three shells. The semi-mature ventral shell in his figures 1–3 is about 19 mm wide and has angustilobate lobes alike to the Malaysian forms. The mature larger ventral shell in his figure 7 is

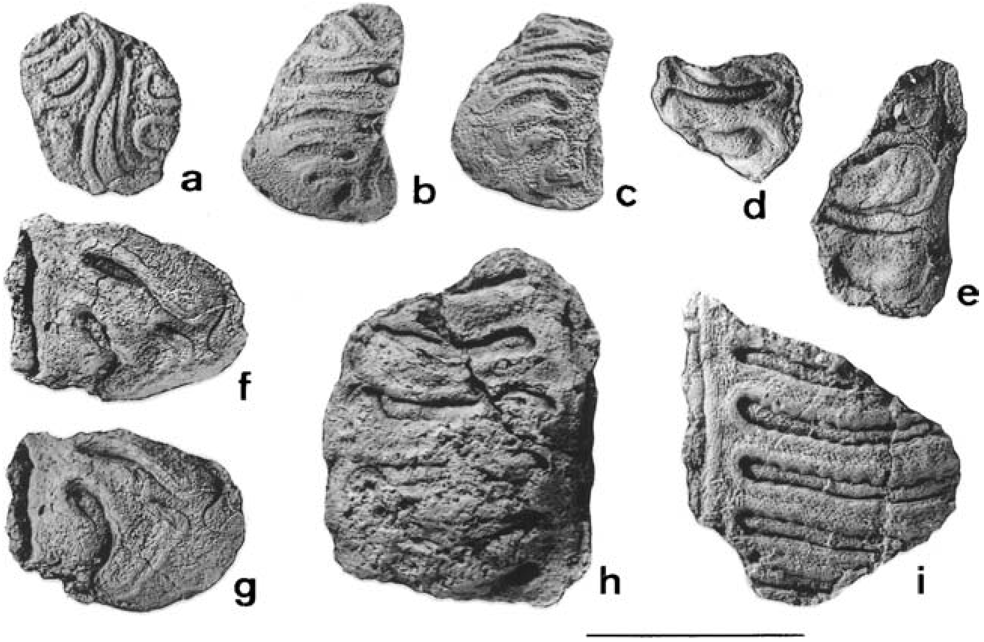

Figure 4. *Pseudoleptodus* sp., all specimens are ventral internal moulds. (a) UKM-F441, juvenile shell showing an irregular, asymmetrical lobation and open trough-like median inlobe. (b, c) UKM-F442, left half of a cup-shaped juvenile shell with a weak vallum, in ventral (b) and anterior (c) views. (d) UKM-F443, fragment of inlobate left lateral lobes. (e) UKM-F444, fragment of inlobate right lateral lobes with rounded loops. (f, g) UKM-F445, shell in ventral (f) and anterior (g) views; anterior part of a shell (right half) showing latilobate condition with highly rounded loops of an incomplete vallum. (h) UKM-F446, left half of a possible mature shell. (i) UKM-F447, right half of a possible mature shell showing angustilobate lobes, strong vallum, and part of hollow median inlobe. Scale bar = 10 mm.

20 mm in half width, and displays strongly slanting solidiseptate lobes. This feature corresponds to the observation of Cooper & Grant (1974, p. 392) that, in some species of *Pseudoleptodus*, large and mature shells tend to develop moderately to strongly oblique lateral lobes. Grant's classification of his species into *Pseudoleptodus* is supported here. The Thai species develops five or more lateral outlobes. It is most comparable to the Malaysian shells among all known species, although the Thai material shows slightly more oblique lateral lobes.

The type species of the genus, *Pseudoleptodus getawayensis* Stehli (1956, p. 312, pl. 41, figs 2, 5; pl. 42, figs 1, 3; also in Cooper & Grant, 1974, p. 395, pl. 130, figs 18–34), is known from the Getaway Limestone Member (upper Roadian–lowermost Wordian) of the lower Cherry Canyon Formation, West Texas. It has relatively regular lobation, with four to five outlobes, and although not the youngest it is the most advanced form among all Texan species, approaching the Southeast Asian representatives. However, the Malaysian and Thai forms have longer lateral lobes.

Cooper & Grant (1974, p. 393) considered some Timorese lyttoniids of Wanner (1935, p. 212, pl. 6, (figs 1, 2 as *Cardinocrania*), (fig. 8b, c as *Poikilosakos*)) to be *Pseudoleptodus*. This was noted but not incorporated into the new Treatise (see Williams, Harper & Grant, 2000, pp. 631, 637). Wanner's materials, however, clearly possess asymmetrical ventral muscle scars and relatively thick shells, so they are not either *Cardinocrania* Waagen (Lyttoniinae, muscle scars on both sides of the muscle region) or *Poikilosakos* Watson (thin shell). As for the above-mentioned Timorese shells, *Cardinocrania waageni* Wanner (1935, pl. 6, figs 1, 2) probably represents a new poikilosakinid genus, and the one ventral valve of Wanner (1935, pl. 6, fig. 8b, c) included in *Poikilosakos variabile* Wanner possibly belongs to *Pseudoleptodus* in agreement with Cooper & Grant (1974).

Waterhouse & Piyasin (1970, p. 134, pl. 24, figs 1–9) described small shells as *Leptodus* sp. from the Ratburi Limestone in Khao Phrik, Thailand. It is oval in outline, with up to six short outlobes. They superficially resemble *Pseudoleptodus*, but possess a symmetric muscle scar and develop solidiseptate ridges, suggesting no relation to Poikilosakinae.

Suborder CHONETIDINA Muir-Wood, 1955
Superfamily CHONETOIDEA Bronn, 1862
Family RUGOSOCHONETIDAE Muir-Wood, 1962
Subfamily RUGOSOCHONETINAE Muir-Wood, 1962
Genus *Neochonetes* Muir-Wood, 1962
Subgenus *Nongtaia* Archbold, 1999
Neochonetes (Nongtaia) aff. *arabicus*

(Hudson & Sudbury, 1959)
Figure 5a–l

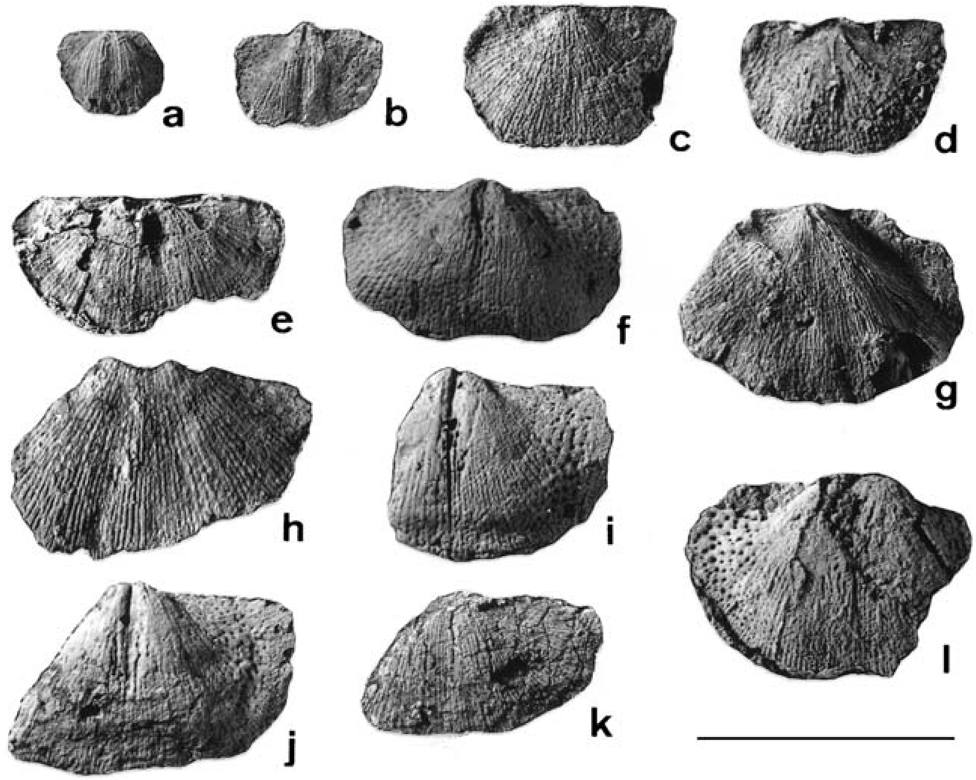

Figure 5. *Neochonetes (Nongtaia)* aff. *arabicus* (Hudson & Sudbury, 1959). (a) UKM-F449, internal mould of a juvenile ventral valve. (b) UKM-F450, internal mould of a juvenile ventral valve. (c, d) UKM-F451a,b, dorsal external mould (c), dorsal interior (d) of the same valve (rubber cast). (e) UKM-F452, dorsal external mould. (f) UKM-F453, ventral internal mould. (g) UKM-F454, dorsal external mould. (h) UKM-F455, dorsal external mould. (i) UKM-F456, ventral internal mould. (j, k) UKM-F457a,b, internal mould of a ventral valve (j), incomplete exterior (k) of the same valve (rubber cast). (l) UKM-F458, ventral internal mould. Scale bar = 10 mm.

1959 *Chonetes arabicus* Hudson & Sudbury, p. 26, pl. 3, figs 6–16; pl. 6, figs 14–18.
1990 *Neochonetes (Sommeriella) arabicus* Hudson & Sudbury; Archbold & Burrett, p. 121, fig. 1A–C.
1999 *N. (S.) arabicus* Hudson & Sudbury; Angiolini *in* Angiolini & Bucher, p. 678, fig. 12:15–21.

Size ranges of available specimens. Maximum width 4.5–14 mm in range; the maximum width of mature shells is slightly anterior of the hinge. Ventral length 3–8.5 mm in range; dorsal length up to 8 mm.

Remarks. This species is a small *Neochonetes* with relatively fine capillae. Ventral valves are relatively convex. The ventral sulcus is broad and very weakly developed, and the dorsal fold is obsolescent or almost absent.

Archbold (1999) proposed two new subgenera of *Neochonetes*, namely *Nongtaia* and *Zechiella*. The former is characterized most importantly by its small size, while the latter has weak ornament and an obsolescent sulcus as represented by those known in the Late Permian Zechstein Basin of Europe. The type species of the former subgenus, *Neochonetes (Nongtaia) taoni* Archbold (1999, p. 76, fig. 3A–O), is a small *Neochonetes* characterized by a narrow, distinct ventral sulcus and dorsal fold, and relatively coarse capillae. It is unlike the present Malaysian form.

Archbold (1999, p. 76) tentatively included *Chonetes arabicus* Hudson & Sudbury (1959) in *Nongtaia*. This is a tiny species of *Neochonetes* from Member 1 of the lower Khuff Formation (Wordian) in Oman, previously referred to another subgenus *Sommeriella* by Archbold & Burrett (1990) and by Angiolini & Bucher (1999). Unlike *N. (Nongtaia) taoni*, the Arabian species has relatively fine capillae and a weakly developed sulcus and fold, and hence is atypical of *N. (Nongtaia)*. The subsurface material of Hudson & Sudbury (1959, pl. 6, figs 14–18) and a recent collection of Angiolini & Bucher (1999, fig. 12:15–21) exhibit obsolescent folds and sulci, and are comparable to the Malaysian form. The Malaysian species is slightly larger than the recorded specimens of *N. (Nongtaia) arabicus*.

The present chonetids also share some similarities to *Chonetes variolata* var. *baroghilensis* Reed (1925, p. 40, pl. 3, figs 1–4) from Baroghil, northern Pakistan,

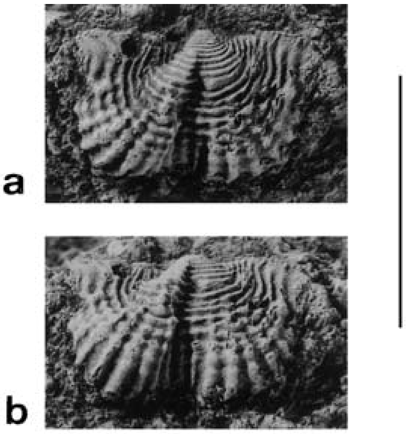

Figure 6. *Caricula* cf. *salebrosa* Grant, 1976. UKM-F459, dorsal external mould. Shell in ventral (a) and anterior (b) views. Scale bar = 10 mm.

particularly in having strong convexity and a broad sulcus. The appearance of the ventral interior is also similar. The same species *Neochonetes (Sommeriella) baroghilensis* was revised from the Bolorian–Kubergandian (Kungurian–Roadian) beds of Baroghil and Lashkargaz by Angiolini (1996, p. 10, pl. 1, figs 12–17). The Pakistani species, however, differs from the Malaysian form in having much larger shells (11.5–27.6 mm wide and 7–14.2 mm long) which suggests it belongs to *Sommeriella*. Likewise, superficial similarities between *N. (N.) arabicus* and *N. (S.) baroghilensis* have been noted by Hudson & Sudbury (1959, p. 28) and by Angiolini & Bucher (1999, p. 678), who both, however, differentiated the two species by means of their sizes. The Malaysian species is here placed provisionally under *N. (Nongtaia)* in view of its small size and notable affinities to *N. (N.) arabicus*.

Archbold (1981*a*, p. 113) pointed out that Kungurian and younger Permian representatives of *Neochonetes* are small in size. This view was reflected in his new classification of the four subgenera (see Archbold, 1999). It seems possible that the larger *N. (S.) baroghilensis* had direct evolutionary linkage to either *N. (N.) arabicus* or the present species through the Kungurian–Wordian lineage of *Neochonetes* in the southern Tethys.

Suborder PRODUCTIDINA Waagen, 1883
Superfamily PRODUCTOIDEA Gray, 1840
Family PRODUCTELLIDAE Schuchert, 1929
Subfamily MARGINIFERINAE Stehli, 1954
Tribe Paucispiniferini Muir-Wood & Cooper, 1960
Genus *Caricula* Grant, 1976

Caricula cf. *salebrosa* Grant, 1976
Figure 6a, b

1976 *Caricula salebrosa* Grant, p. 131, pl. 31, figs 1–30.

Remarks. A single mould of the dorsal exterior UKM-F459 was available, 9 mm wide and 7 mm long. This small dorsal valve is fairly concave in profile and transverse in outline, with ears slightly extended. The visceral disc is ornamented strongly by regular rugae but is very weakly reticulated by low costae. Only the trail is well costate. The fold is high anteriorly, and no dorsal spine is present. In all visible morphological characters, the present material is unequivocally assigned to the distinctive genus *Caricula*.

The type species *Caricula salebrosa* Grant (1976) from the Ratburi Limestone in Ko Muk NE is the only known species of the genus. The exterior of the Malaysian dorsal valve appears almost identical to that of *C. salebrosa*, of which six specimens for the dorsal exterior were illustrated by Grant (1976, pl. 31, figs 2, 3, 11, 15–18, 23, 24, 28, 29). The Thai and Malaysian forms are probably conspecific, but the identification is tentative due to a lack of ventral information in the present collection. Waterhouse, Pitakpaivan & Mantajit (1981, p. 80) also reported *Caricula* sp. from Ko Yao Noi, peninsular Thailand (of possible Late Artinskian (Baigendzhinian) age according to Archbold (1999, p. 74)), but the material was not illustrated.

Genus *Transennatia* Waterhouse, 1975

Transennatia cf. *insculpta* (Grant, 1976)
Figures 7a–i, 8c

1976 *Gratiosina insculpta* Grant, p. 135, pl. 32, figs 1–37; pl. 33, figs 1–16.

Size ranges of available specimens. Maximum hinge width up to 16 mm (ventral); 9–14 mm (dorsal). Length 10.5–15.5 mm (ventral); 7–9 mm (dorsal).

Description. Its small ears and distinctive reticulation are indicative of *Transennatia*. The shells are medium-sized for the genus. It is subquadrate or slightly transverse in outline and is weak to moderately geniculate in ventral profile. The visceral disc is sharply reticulated by fine costae and rugae; costae converge onto the fold. The trail is relatively short. In the dorsal interior, a median septum is short and low, and anterior adductor muscle pads are non-dendritic and slightly opened anteriorly.

Remarks. This species is most abundant in the present fauna. The present form shares some close similarities to the Ratburi species *Transennatia insculpta* (Grant, 1976) from Ko Muk; most notably in having a relatively small size, subquadrate outline, feeble ventral geniculation, very fine reticulation, and opened anterior adductor scars. The Malaysian form is distinguished from the type species *Transennatia gratiosa* (Waagen, 1884, p. 691, pl. 72, figs 3–7) from the Wargal and Chhidru formations of the Salt Range, Pakistan, by being only about half the size. *T. insculpta* is also half as large as *T. gratiosa*, as compared by Grant (1976, p. 136). Most notably, anterior adductor muscle pads of

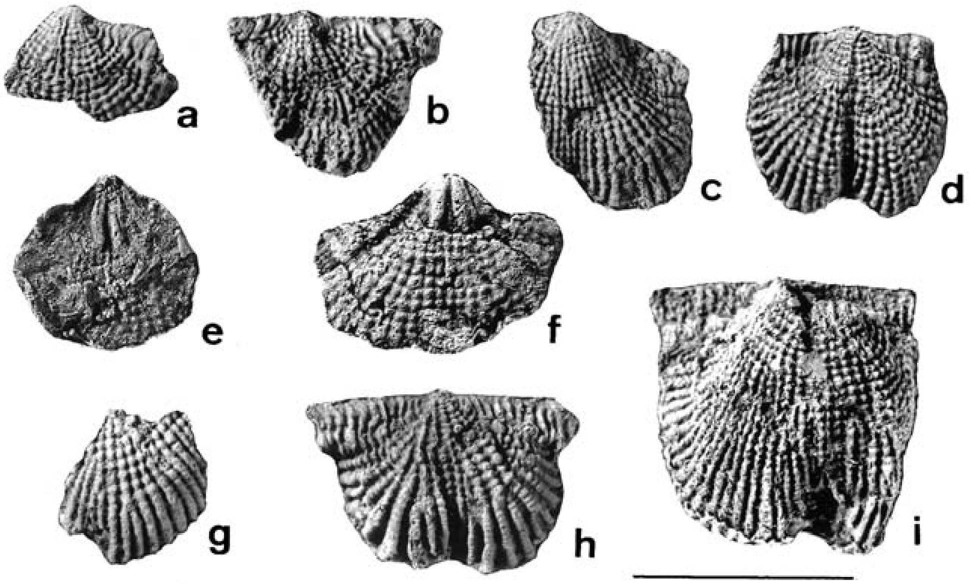

Figure 7. *Transennatia* cf. *insculpta* (Grant, 1976). (a) UKM-F460, posterior part of a ventral internal mould. (b) UKM-F461, incomplete external mould of a dorsal shell. (c) UKM-F462, incomplete internal mould of a ventral shell. (d) UKM-F463, external mould of a semi-mature dorsal shell; ears probably lost. (e) UKM-F464, dorsal interior of an immature shell (rubber cast). (f) UKM-F465, dorsal interior (rubber cast) of a semi-mature shell showing anteriorly opened muscle pads. (g) UKM-F466, fragment of a ventral? internal mould. (h) UKM-F467, external mould of a semi-mature dorsal shell having relatively coarse ornament. (i) UKM-F468, internal mould of a large mature ventral shell. Scale bar = 10 mm for all, except 12 mm for (i).

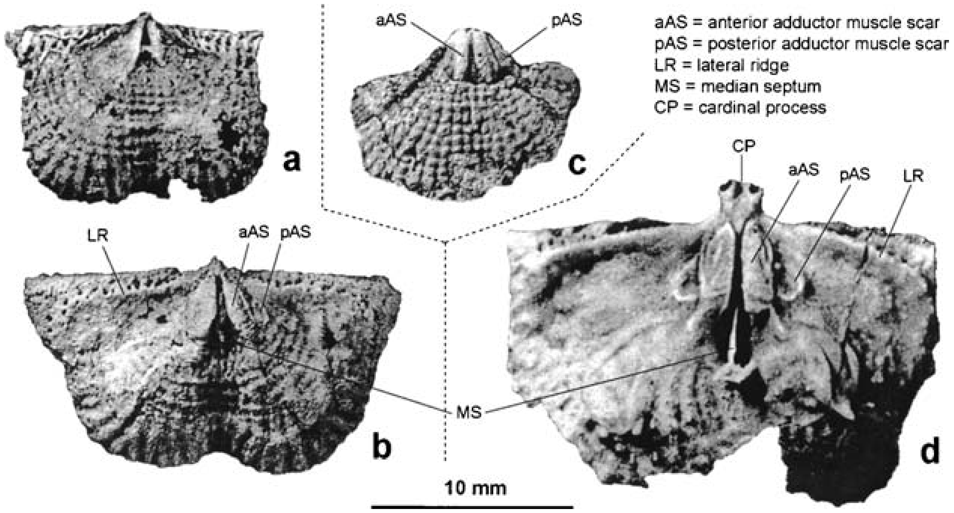

Figure 8. Comparison of internal structures of three *Transennatia* species. (a, b) *T. insculpta* (Grant) from the Ratburi Limestone of Ko Muk, southern Thailand (from Grant, 1976, pl. 33, figs 9, 14). (c) *T*. cf. *insculpta* (Grant) from Johore, UKM-F465. (d) Type species *T. gratiosa* (Waagen) from the Kalabagh Member of the Wargal Limestone in the Salt Range, Pakistan (from Grant, 1976, pl. 33, fig. 23). Figure 8a, b, d reproduced with permission of SEPM (Society for Sedimentary Geology).

both the present form and *T. insculpta* are alike, and are more open anteriorly than those of *T. gratiosa* as shown by Reed (1944, pl. 19, figs 6, 7) and Grant (1976, pl. 33) (see comparison in Fig. 8).

In addition to the Ratburi *T. insculpta*, one conjoined shell specimen from Ko Muk NW (Grant, 1976, pl. 32, figs 15–17) as noted 'small but apparently mature shell' in the caption is more strongly sulcate and more sturdily costate than those of Ko Muk NE. A similar intraspecific variation can also be recognized in the Malaysian collection as seen in Specimen UKM-F467 (Fig. 7h).

Another Malaysian species *Transennatia termierorum* Sone (in Sone, Leman & Shi, 2001, p. 12, fig. 7:1–10, 13–15) from the early Capitanian of Pahang is characterized by large extended ears and strong

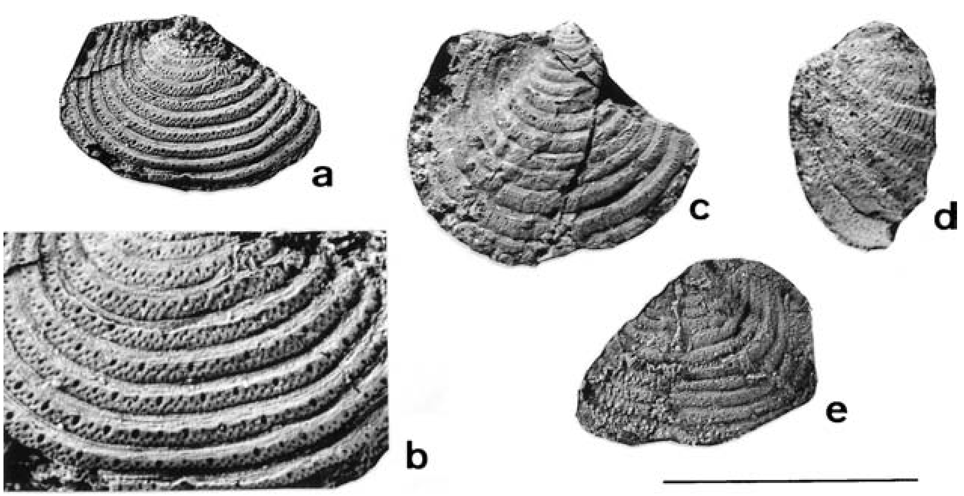

Figure 9. (a–e) *Karavankina* sp., (a, b) UKM-F471, dorsal external mould. (c) UKM-F472, dorsal external mould. (d) UKM-F473, incomplete ventral internal mould (left flank). (e) UKM-F474, incomplete dorsal interior (rubber cast). Scale bar = 10 mm, except 5 mm for (b).

geniculation, and its reticulation is coarser than that of the Johore forms. Among many other known species of the genus, Early–early Middle Permian representatives are rather rare. The Kubergandian (Roadian) species *Transennatia reedi* Angiolini (1995, p. 205, fig. 16:4; also in Angiolini, 1996, p. 14, pl. 1, figs 27, 28; pl. 2, figs 1–4) from northern Pakistan is large and is coarsely reticulated, with costae not converging into a sulcus.

Retimarginifera praelecta (Reed, 1925) *sensu* Angiolini (1996, pl. 1, figs 25, 26) from the Bolorian–Kubergandian (Kungurian–Roadian) of northern Pakistan has notably sturdy, coarse costae which converge into a deep sulcus and diverge on flanks. Its appearance and description seem to suggest a more reasonable assignment to *Transennatia* rather than *Retimarginifera*. Its ornament is much coarser than the Malaysian form.

Superfamily ECHINOCONCHOIDEA Stehli, 1954
Family ECHINOCONCHIDAE Stehli, 1954
Subfamily ECHINOCONCHINAE Stehli, 1954
Tribe Karavankinini Ramovš, 1966
Genus *Karavankina* Ramovš, 1966

Comments. The genus *Karavankina* was fully described and defined in Ramovš (1969). His 1969 publication, in which he proposed this new generic name (and the new subfamily name Karavankininae and four new species-group names), was originally intended to be published in 1966. Prior to its publication in 1969, Ramovš (1966) first published the names accompanied by fixation of the type species *Karavankina typica* (as indicated on the figure) and by comparison of the genus with other pre-existing taxa. This 1966 paper satisfies the provisions of Articles 13.1–3 of the International Code of Zoological Nomenclature, and therefore establishes priority for all the names made available in Ramovš (1966). *Karavankina* Ramovš, 1969 [=*Karavankina* Ramovš, 1966, *nomen nudum*] as stated in the new Brachiopoda Treatise (Brunton *et al*. 2000, p. 512) is incorrect. Sarytcheva (1968) accepted *Karavankina* Ramovš, 1966, yet as a subgenus of *Echinoconchus* Weller.

Karavankina sp.
Figure 9a–e

Description. The species is small-sized (10.5–16 mm wide and 7.5–10 mm long in dorsal valves) for the genus. The outline varies from transverse to subcircular. Coarse, high relief concentric bands consisting of alternating smooth and spinous regions are indicative of *Karavankina*. Numerous spines are present on both valves. Ventral external spines are oblique anteriorly. Dorsal external spines are erect and are regularly arranged as differentiated by size. Fine, weak wrinkles are observed on dorsal spine-free bands transversely. Dorsal endo-spines are present.

Remarks. Many Carbo-Permian species of *Karavankina* share considerable superficial similarities. Examination of dorsal spine patterns may help with more effective identification at the species level, although these features are not sufficiently understood in most known species. The type species *Karavankina typica* Ramovš (1966, fig. 7; also in Ramovš, 1969, p. 254, pl. 1, figs 1–4) from the Middle Permian of northeastern Slovenia is similar to the Malaysian shells in overall appearance, but is a little larger.

Another Slovenian echinoconchid has been known from the Karawanken Mountains, originally as *Productus elegans* M'Coy *sensu* Schellwien (1900*b*, p. 52, pl. 8, figs 14–17). This was later revised to

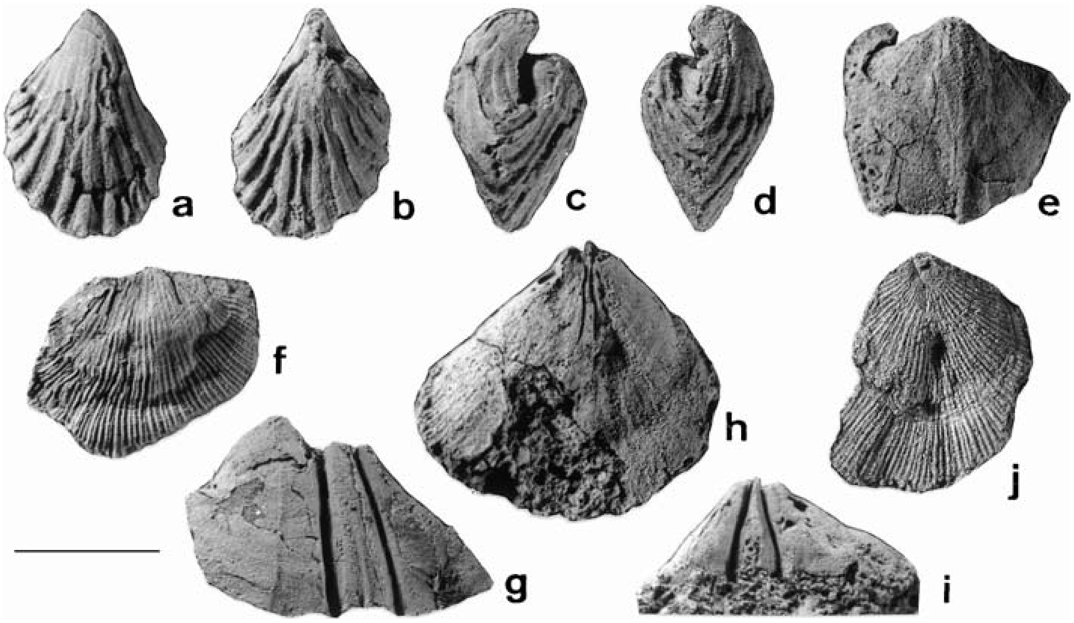

Figure 10. (a–d) *Hustedia* sp., UKM-F475, conjoined shells in ventral (a), dorsal (b), right lateral (c) and left lateral (d) views. (e) martiniid indet., UKM-F476, ventralinternal mould. (f–j) *Orthothetina* sp., (f) UKM-F477, internal mould of an immature dorsal valve. (g) UKM-F478, incomplete internal mould of a large mature shell's beak in ventral view. (h–j) UKM-F479a, internal mould of a semi-mature ventral valve in ventral view (h), interarea in dorsal view (i), (j) UKM-F479b, incomplete exterior (rubber cast) of the same ventral valve. Scale bar = 5 mm for (a–d), 10 mm for (e, g), 6.7 mm for (f), 8 mm for (h–j).

Karavankina schellwieni Ramovš (1966, fig. 6a–c; also in Ramovš, 1969, p. 264, pl. 2, figs 1–4) with additional material. It was also reported from the *Neoschwagerina craticulifera* fusulinid bed (Wordian) of the Julian Alps, northwestern Slovenia (Flügel, Kochansky-Devidé & Ramovš, 1984, pl. 39, fig. 8). *K. schellwieni* is a relatively small species with narrow dorsal concentric bands, and appears comparable to the present form, although precise identification is not possible without dorsal spinous details of the Slovenian species. The true *P. elegans* M'Coy has now been designated as the type species of the mid-Carboniferous genus *Echinoconchella* Lazarev (1985, p. 70).

Echinoconchus cristatus Reed (1931, p. 12, pl. 2, figs 7–10a), proposed as a variation of *E. fasciatus* (Kutorga), from the Bamyan limestone (Wordian) of central Afghanistan, is interpreted as a species of *Karavankina*, based on its characteristic concentric bands. It is about twice as large as the Malaysian form. *E. fasciatus* has now been placed under *Karavankina* (see Sarytcheva, 1968, p. 95).

Laotian (Kham-keut) and Vietnamese (Van-yên) echinoconchids both from the *Pseudoschwagerina princeps* fusulinid beds (Early Permian) were illustrated as *Productus elegans* by Mansuy (1913, p. 30, pl. 2, fig. 3a–d). They also unequivocally belong to *Karavankina* owing to their possession of high-relief bands. Their dorsal views are not available, preventing detailed comparison to other species.

The Malaysian form exhibits a distinctive dorsal spine pattern (Fig. 9b), and thus may represent a new species. However, more morphological information, particularly on the ventral valve, is required before a new species can be established.

Order ORTHOTETIDA Waagen, 1884
Suborder ORTHOTETIDINA Waagen, 1884
Superfamily ORTHOTETOIDEA Waagen, 1884
Family MEEKELLIDAE Stehli, 1954
Subfamily MEEKELLINAE Stehli, 1954
Genus *Orthothetina* Schellwien, 1900*a*

Orthothetina sp.
Figure 10f–j

Remarks. Generic assignment to *Orthothetina* is verified most precisely by a non-plicate orthotetidine shell with a pair of sub-parallel dental plates extending one-third of the valve length. It is medium-sized for the genus, with the greatest width at mid-valve, and is semi-ovate in outline, with a short beak. Surface is ornamented by radial capillae of uneven width.

In Pahang (Peninsular Malaysia), two other forms of *Orthothetina* have been found: *Orthothetina* sp. in the Jengka Pass shale of the late? Middle Permian (Nakazawa, 1973) and *O.* cf. *iljinae* Sokolskaya in the early Capitanian of the Bera Formation (Sone, Leman & Shi, 2001). They are not similar to the Johore species.

Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order ATHYRIDIDA Boucot, Johnson & Staton, 1964
Suborder RETZIIDINA Boucot, Johnson & Staton, 1964
Superfamily RETZIOIDEA Waagen, 1883
Family NEORETZIIDAE Dagis, 1972
Subfamily HUSTEDIINAE Grunt, 1986
Genus *Hustedia* Hall & Clarke, 1893

Hustedia sp.
Figure 10a–d

Remarks. A single specimen UKM-F475 of slightly deformed conjoined shells was available. It is 6 mm wide and 8 mm long. Two Ratburi species, namely *Hustedia ratburiensis* Waterhouse & Piyasin (1970) (=*H. nakornsrii* Yanagida, 1971 (imprint 1970)) and *H. funaria* Grant (1976), are known. The Johore form is more similar to the former than the latter which is distinctively long and narrow in outline. Further comparison is difficult due to the limited material.

Order SPIRIFERIDA Waagen, 1883
Suborder SPIRIFERIDINA Waagen, 1883
Superfamily MARTINIOIDEA Waagen, 1883
Family MARTINIIDAE Waagen, 1883

martiniid indet.
Figure 10e

Remarks. One ventral internal mould UKM-F476 reveals straight pallial markings, a muscle field bisected by a median groove, and smooth lateral slopes, suggestive of Martiniidae. Generic assignment is not possible because of the limited collection.

5. Correlation and age

Two species of cephalopods and eight species of brachiopods are recognized in the present fauna (Table 1). The ammonoid *Agathiceras* sp. (Fig. 11a) indicates a pre-Capitanian age for the fauna. The genus ranges from the Moscovian (Late Carboniferous) through to the Wordian, with greatest abundance in Roadian and Wordian rocks (Glenister *et al*. 1990; Zhou *et al*. 1999). Two other Malaysian forms, both as *Agathiceras* sp., were described from two horizons of the Bera Formation in Pahang: one from a Roadian or Wordian bed of Felda Mayam (Sone & Leman, 2000) and the other from the Wordian cephalopod fauna of Bera South (Sone, Leman & Ehiro, 2001). The Felda Mayam form has a flattened lateral flank and high umbilical angle, resembling the Johore shells. The nautiloid *Foordiceras*? sp. (Fig. 11b) is also discriminated; it has little stratigraphic value.

The key brachiopod species of Johore belongs to the extremely rare genus *Caricula*, as it is probably conspecific to *C. salebrosa* Grant of Ko Muk NE, which is the only known species of the genus. This signifies linkage to the Ratburi fauna. The occurrence of *Pseudoleptodus* sp. is also significant. This genus is rare in the Tethys, having been known only in the Ratburi Limestone of Ko Muk NE, although in West Texas it occurs from the Wolfcampian to throughout the Guadalupian (Early–Middle Permian). The Malaysian form appears to be a very advanced species. Third, the Johore form of *Transennatia* again resembles the Ratburi *T. insculpta* (Grant) of Ko Muk NE and NW. *Transennatia* is common through the Middle to Late Permian, but is extremely rare or absent in the Early Permian. Thus, the similarities of Johore forms of *Caricula, Pseudoleptodus* and *Transennatia* to the Thai species strongly suggest correlation to the Ko Muk (NE and NW) horizons of the Ratburi Limestone.

The genus *Orthothetina* is most common during the Guadalupian–Lopingian (Middle–Late Permian). The genus *Karavankina* ranges in age from the Late Carboniferous to the Wordian, except the Oman form of Yanagida & Pillevuit (1994) whose age may be slightly

Table 1. Middle Permian cephalopods and brachiopods of Sermin, northern Johore, Peninsular Malaysia; cephalopod shells undifferentiated

	Number of samples		
Species	Ventral	Dorsal	Conjoined
Cephalopods			
Agathiceras sp.			4
Foordiceras? sp.			1
Brachiopods			
Caricula cf. *salebrosa* Grant, 1976		1	
Pseudoleptodus sp.	7		
Transennatia cf. *insculpta* (Grant, 1976)	4	9	
Neochonetes (Nongtaia) aff. *arabicus* (Hudson & Sudbury, 1959)	6	4	
Karavankina sp.	1	3	
Hustedia sp.			1
Orthothetina sp.	2	1	
martiniid indet.	1		

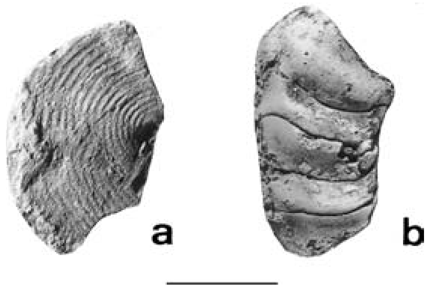

Figure 11. Two mid-Permian cephalopods from northern Johore. (a) ammonoid *Agathiceras* sp., UKM-F480. (b) nautiloid *Foordiceras*? sp., UKM-F481. Scale bar = 10 mm for (a), 7.5 mm for (b).

younger suggested by foraminifers (see Angiolini & Bucher, 1999, p. 674). The two genera are not known from the Ratburi Limestone.

The age of the Ratburi Limestone brachiopods has been of great dispute. Age assignments have differed from author to author, for instance, Kazanian (Waterhouse & Piyasin, 1970), late Artinskian (Yanagida, 1970; Grant, 1976), Kungurian (Waterhouse, 1973, 1981), late Artinskian–early Kungurian (Shi & Archbold, 1995), and Roadian–Wordian (Angiolini & Bucher, 1999). Archbold (1999) suggested an Ufimian age (roughly equivalent to the Roadian of the international standard, see Archbold, 1998), based primarily on faunal similarities with Bitauni Timor, West Irian Jaya and Western Australia. Comprehensive biostratigraphic analyses of the Ratburi Limestone were provided by Baird, Dawson & Vachard (1993) and Fontaine *et al*. (1994*a*).

The Ratburi brachiopods have been considered to be to some degree similar to those of the Amb fauna of Pakistan (Yanagida, 1970; Grant, 1976) and the Khuff fauna of Oman (Angiolini *et al*. 1998; Angiolini & Bucher, 1999). The similarities are largely in the generic level. Based on studies of Gomankov & Burov (1999), Iqbal *et al*. (1998) and Wardlaw & Pogue (1995), the age of the Amb Formation can be constrained to a range of Bolorian–Kazanian (Kungurian–Wordian). Angiolini (2001*a*, p. 312) considered the Amb brachiopod fauna to be no younger than mid-Wordian, based on brachiopod correlations. Yet, a recent conodont study shows that an even slightly younger age is possible for the upper part of the Amb Formation (see Mei & Henderson, 2001; Wardlaw & Mei, 1999). The Johore brachiopods reveal no definable linkage to the Amb fauna.

On the other hand, the Johore *Neochonetes* shares notable similarities with the Oman *N. (Nongtaia) arabicus* (Hudson & Sudbury), which suggests possible correlation with Member 1 of the lower Khuff Formation. The Khuff fauna was assigned by Angiolini *et al*. (1998, 2003) to a Wordian age, which seems most likely, considering all fossil data.

Kotlyar *et al*. (1999) reported a brachiopod assemblage from limestone blocks of the Marta River Basin, Crimea, which curiously includes several Ratburi species, although it is yet undescribed. The Crimean brachiopods are associated with many fusulinids including index fossils *Neoshwagerina simplex* Ozawa and *Presumatrina neoshwagerinoides* (Deprat) and with Wordian ammonoids such as *Tauroceras wanneri* Toumanskaya. Kotlyar *et al*. (1999) assigned this fauna to a late Kubergandian age. Leven (1998), however, assigned the *N. simplex–P. neoshwagerinoides* zone to the lower Murghabian. Jin *et al*. (1997) and Jin & Shang (2000) correlated the same biozone to the middle–upper Roadian. A late Roadian/early Wordian age for the Crimean fauna seems most probable in view of fusulinid and ammonoid biozonations.

On balance, as well as the Ufimian suggested by Archbold (1999), the early Wordian is here considered also possible for the age of the Ratburi brachiopod faunas. A Roadian–early Wordian age is favoured for the Johore fauna. This is based on correlation to the Ratburi brachiopod horizons, the presence of the advanced form of *Pseudoleptodus*, and the specific affinity of the small Wordian species *Neochonetes (Nongtaia) arabicus*.

6. Palaeobiogeographic implications

The East Malaya terrane, on which the present fauna is located, has been considered to be an extended part of the Indochina block and has been broadly referred to as a unit of the tropical Cathaysian region throughout the Permian (e.g. Metcalfe, 1998, 2002; Shi & Archbold, 1998). The present Johore brachiopods, however, show some faunal linkage to the Sibumasu province (Fang, 1991) of the Cimmerian region.

The Johore assemblage as a whole represents a warm-water Tethyan-type fauna, which, however, contains no diagnostic Cathaysian (South China) genera and species. Of seven genera identified, *Caricula* and *Pseudoleptodus* can be referred to as Sibumasu elements, as they are known, elsewhere in the Tethys, only in peninsular Thailand. The other four, *Transennatia, Karavankina, Orthothetina* and *Hustedia*, suggest a general warm-water environment, as they were distributed throughout shallow waters of the Tethys, although not restricted to the Cathaysian region; the first three are endemic to the Tethyan ocean.

The presence of a mid-Permian *Karavankina* in Johore implies another non-Cathaysian element in East Malaya/Indochina. This echinoconchid genus is quite common in Carboniferous rocks of South China. It seems, however, to have disappeared from South China since the Early Permian, while it still persisted in some other regions of the Tethys, including Indochina and the Cimmerian region, up to the Middle Permian. (Note: *Echinoconchus mapingensis* Grabau (1936) from the so-called 'Maping Limestone brachiopod fauna' of Guizhou, South China, is a species of *Karavankina* (or *Echinoconchella*), but the age is most likely early Bashkirian (mid-Carboniferous) (see Liao, 1999, p. 319)).

At the species level, the Johore forms of *Caricula*, *Pseudoleptodus* and *Transennatia* are more or less similar to those of the Ko Muk limestone, suggesting specific linkage between East Malaya and Sibumasu over the main Palaeo-Tethys ocean (Fig. 12). Another Johore form compared to *Neochonetes (Nongtaia) arabicus* of Oman may also suggest linkage to the Cimmerian biota, with particular respect to the emended Sibumasu province of Angiolini (2001*b*) which includes the Roadian–Wordian of Oman and the Salt Range.

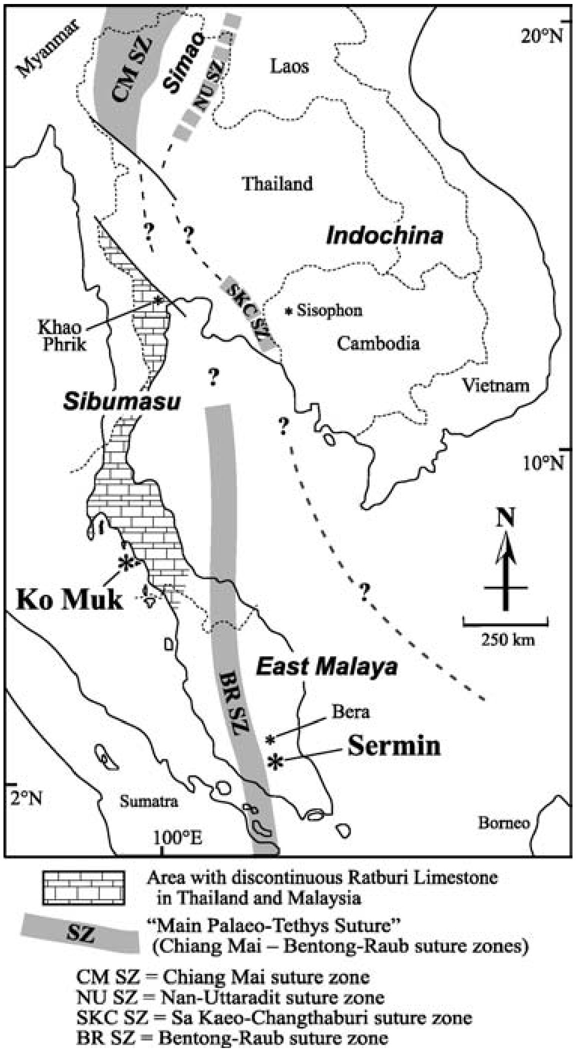

Figure 12. Southeast Asian map showing the major tectonic terranes, the main Palaeo-Tethys Suture and other suture zones, the locations of Sermin on the East Malaya terrane and Ko Muk on the Sibumasu terrane, and the area with discontinuous Permian Ratburi Limestone (after Fontaine *et al*. 1994*a*). Both the Chiang Mai suture zone and the Simao terrane modified after Metcalfe (2002).

Possible influences of Sibumasu faunas or sub-tropical climates are also tangible in Permian brachiopods of the Indochina block. Hogeboom & Archbold (1999, p. 260) noted that some Early and Late Permian forms of Laos are referable to *Stictozoster* Grant, a genus common to the Sibumasu and Westralian provinces. Termier & Termier (1970, p. 451, pl. 30, figs 3, 10) described *Megousia* sp. from the mid-Permian Sisophon Limestone of Cambodia, which (if not a species of *Anidanthus* Whitehouse) may also suggest an anti-tropical climatic influence, distinctive from South China.

Such faunal linkage between Sibumasu and East Malaya/Indochina is also recognized in distributions of two Midian foraminifers, *Hemigordiopsis* Reichel and *Sphairionia* Nguyen (the latter may be *incertae sedis*). The two genera are found in both the East Malaya/Indochina and Sibumasu terranes, and throughout the Cimmerian region, but are absent in the South China block (see Fontaine *et al*. 1994*a*,*b*; Fontaine, Suteethorn & Vachard, 1998; Pronina, 1996; Nestell & Pronina, 1997; Vachard *et al*. 2001, and references therein).

A similar and biogeographically even more restricted linkage is indicated by the distribution of late Murghabian–Midian fusulinid *Pseudofusulina padangensis* (Lange). The species is restricted to Sibumasu (the Ratburi Limestone), East Malaya (Padang in West Sumatra and Jengka Pass in Malaysia) and Indochina terranes (see Fontaine *et al*. 1994*b*; Ueno, Sugiyama & Nagai, 1996), and occurs in both sides of the main Palaeo-Tethys.

The distribution pattern of the Wordian ammonoid *Tauroceras scrobiculatum* Toumanskaya and its allies is shown to extend from the western Tethys through the Cimmerian region up to East Malaya (Sone, Leman & Ehiro, 2001). They are, however, not known from Indochina or South China of the main Cathaysian region. *Monodiexodina* in southern Johore (Igo, Rajah & Kobayashi, 1979) suggests a possible Sibumasu biotic influence on East Malaya in the late Early Permian.

Thus, the Permian marine biota of East Malaya/Indochina is not exclusively of the tropical Cathaysian type, but includes some minor Sibumasu/Cimmerian elements, likely indicating sub-tropical climatic episodes. The Bentong-Raub suture zone of Peninsular Malaysia is widely accepted as representing the main Palaeo-Tethys in Southeast Asia and the palaeobiogeographic boundary between the Gondwanan and Cathaysian floral provinces (Metcalfe, 2000). This is in good agreement with general distributions of faunal and floral groups. However, as outlined above, the Gondwana–Cathaysia divide between Sibumasu and East Malaya appears not to have precluded some faunal exchange during the mid-Permian.

It is perhaps too early to discuss the Permian palaeogeographic relationship between East Malaya and Indochina at this stage, because of the limited data available. Sone, Leman & Shi (2001) concluded that early Capitanian brachiopods of the Bera Formation in East Malaya have linkage to the correlative fauna of Indochina (western Cambodia) but have weaker affinity to those of South China, although the Malaysian fauna is broadly referable to the Cathaysian type. On the other hand, the older Johore fauna reported here shows a weaker (if any) connection to Indochina and South China than the Capitanian Bera fauna. Further work is required to reveal detailed bio-provincial characters of East Malaya and Indochina in comparison to the typical Cathaysian marine biota of South China.

Archbold (1981*b*, 1991), Archbold & Shi (1995) and Archbold *et al*. (1982) suggested that late Early Permian brachiopod faunas of Bitauni Timor and

West Irian Jaya also share close similarities to those of the Ratburi Limestone. A similar conclusion was made by Sakagami (2000) in terms of bryozoan palaeobiogeographic affinity. All those brachiopod faunas, however, contain more or less Gondwanan (Westralian) affinity taxa, which are not associated with the Johore fauna. This suggests that East Malaya was in warmer climates and/or in lower latitudes than Timor, West Irian Jaya and Sibumasu of eastern Cimmeria.

In conclusion, there was specific interchange or one-way migration of some brachiopods between the shallow waters of the East Malaya and Sibumasu terranes across the main Palaeo-Tethys during the Roadian–Wordian period. This perhaps suggests a subtropical climatic episode for East Malaya at this time. The mid-Permian Palaeo-Tethys seaway between the two terranes must have been narrower than previously interpreted to allow such faunal traffic. A vast ocean between Sibumasu and East Malaya/Indochina as reconstructed by Ricou in Baud *et al*. (1993), Ricou (1995) and Stampfli (2000) appears to be highly unlikely.

Acknowledgements. M. Sone's Ph.D. study on which this paper is based is supported by both a University of New England Research Scholarship and an International Postgraduate Research Scholarship. I. Metcalfe acknowledges ongoing support by the Australian Research Council. We also acknowledge funding from two IGCP Grants-in-Aid. Critical reviews from Professors N. W. Archbold and A. J. Barber improved this article. Our fieldwork was supported by the Malaysian Government IRPA Project (02-02-0012-EA186) and the National University of Malaysia FST Project (ST-014-2002). University of New England's Divisions of 'Earth Sciences' and 'Archaeology and Palaeoanthropology' provided Sone with laboratory and darkroom facilities respectively. Permission to reproduce photographs from the *Palaeontological Society Memoir 9* used in Figure 8a, b, d was kindly granted by SEPM (Society for Sedimentary Geology).

References

ANGIOLINI, L. 1995. Permian brachiopods from Karakorum (Pakistan) Pt. 1. *Rivista Italiana di Paleontologia e Stratigrafia* **101**, 165–214.

ANGIOLINI, L. 1996. Permian brachiopods from Karakorum (Pakistan) Pt. 2. *Rivista Italiana di Paleontologia e Stratigrafia* **102**, 3–26.

ANGIOLINI, L. 2001*a*. Permian brachiopods from Karakorum (Pakistan) Pt. 3. *Rivista Italiana di Paleontologia e Stratigrafia* **107**, 307–44.

ANGIOLINI, L. 2001*b*. Lower and Middle Permian brachiopods from Oman and Peri-Gondwanan palaeogeographical reconstructions. In *Brachiopods Past and Present* (eds C. H. C. Brunton, L. R. M. Cocks and S. L. Long), pp. 352–62. The Systematics Association Special Volume Series 63. London: Taylor & Francis.

ANGIOLINI, L., BALINI, M., GARZANTI, E., NICORA, A., TINTORI, A., CRASQUIN, S. & MUTTONI, G. 2003. Permian climatic and paleogeographic changes in Northern Gondwana: the Khuff Formation of Interior Oman. *Palaeogeography, Palaeoclimatology, Palaeoecology* **191**, 269–300.

ANGIOLINI, L. & BUCHER, H. 1999. Taxonomy and quantitative biochronology of Guadalupian brachiopods from the Khuff Formation, southeastern Oman. *Geobios* **32**, 665–99.

ANGIOLINI, L., NICORA, A., BUCHER, H., VACHARD, D., PILLEVUIT, A., PLATEL, J. P., BAUD, A., BROUTIN, J., HASMI, H. A. & MARCOUX, J. 1998. Evidence of a Guadalupian age for the Khuff Formation of southeastern Oman: preliminary report. *Rivista Italiana di Paleontologia e Stratigrafia* **104**, 329–40.

ARCHBOLD, N. W. 1981*a*. Studies on Western Australian Permian brachiopods 2. The family Rugosochonetidae Muir-Wood 1962. *Proceedings of the Royal Society of Victoria* **93**, 109–28.

ARCHBOLD, N. W. 1981*b*. Permian brachiopods from Western Irian Jaya, Indonesia. *Geological Research Development Centre, Paleontology Series* **2**, 1–25.

ARCHBOLD, N. W. 1991. Early Permian Brachiopoda from Irian Jaya. *BMR Journal of Australian Geology & Geophysics* **12**, 287–96.

ARCHBOLD, N. W. 1998. Marine biostratigraphy and correlation of the West Australian Permian Basins. In *The Sedimentary Basins of Western Australia 2* (eds P. G. Purcell and R. P. Purcell), pp. 141–51. Perth: Petroleum Exploration Society of Australia Limited.

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

ARCHBOLD, N. W. & BURRETT, C. F. 1990. Re-assessment of the Arabian Permian chonetid brachiopod *Chonetes arabicus* Hudson & Sudbury. *Proceedings of the Royal Society of Victoria* **102**, 121–2.

ARCHBOLD, N. W., PIGRAM, C. J., RATMAN, N. & HAKIM, S. 1982. Indonesian Permian brachiopod fauna and Gondwana–South-East Asia relationships. *Nature* **296**, 556–8.

ARCHBOLD, N. W. & SHI, G. R. 1995. Permian brachiopod faunas of Western Australia: Gondwanan–Asian relationships and Permian climate. *Journal of Southeast Asian Earth Sciences* **11**, 207–15.

BACHIK, R. 1985. Laporan kemajuan: pemetaan geologi, kawasan Batu Enam, syit 106, Johore, Pahang. *Geological Survey of Malaysia Annual Report* **1985**. 196–203.

BAIRD, A., DAWSON, O. & VACHARD, D. 1993. New data on biostratigraphy of the Permian Rat Buri Limestone from north peninsular Thailand. In *Proceedings of the International Symposium on Biostratigraphy of Mainland Southeast Asia: Facies & Paleontology* (ed. T. Thanasuthipitak), pp. 243–59. Chiang Mai University.

BAUD, A., MARCOUX, J., GUIRAUD, R., RICOU, L. E. & GAETANI, M. 1993. Late Murgabian Palaeoenvironments (266 to 264 Ma). In *Atlas Tethys Palaeoenvironmental Maps* (eds J. Dercourt, L. E. Ricou and B. Vrielynck), Explanatory Notes, pp. 9–20. Paris: Gauthier-Villars. Maps, Rueil-Malmaison: BEICIP-FRANLAB.

BOUCOT, A. J., JOHNSON, J. G. & STATON, R. D. 1964. On some atrypoid, retzioid, and athyridoid Brachiopoda. *Journal of Paleontology* **38**, 805–22.

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

BRUNTON, C. H. C., LAZAREV, S. S., GRANT, R. E. & JIN, Y. 2000. Productidina. In *Treatise on Invertebrate Paleontology Part H, Brachiopoda Revised Volume 3* (eds A. Williams and others), pp. 424–609. Kansas: The

Geological Society of America and the University of Kansas.

COOPER, G. A. & GRANT, R. E. 1974. Permian brachiopods of West Texas II. *Smithsonian Contributions to Paleobiology* **15**, 233–793.

DAGIS, A. S. 1972. Morfologiia i systematika mezozoikikh retsiodnykh brakhiopod (Morphology and systematics of Mesozoic retzioid brachiopods). In *Morfologicheskie i filogeneticheskie voprosy paleontologii (Morphological and Phylogenetic Questions of Palaeontology),* pp. 94–105. Trudy Akademiia Nauk SSSR Sibiroskoe Otdelenie Institut Geologii i Geofiziki 112.

FANG, Z. 1991. Sibumasu biotic province and its position in Palaeotethys. *Acta Palaeontologica Sinica* **30**, 511–32.

FLÜGEL, E., KOCHANSKY-DEVIDÉ, V. & RAMOVŠ, A. 1984. A Middle Permian calcisponge/algal/cement reef: Straža near Bled, Slovenia. *Facies* **10**, 179–256.

FONTAINE, H., CHONGLAKMANI, C., AMNAN, I. & PIYASIN, S. 1994*a*. A well-defined Permian biogeographic unit: Peninsular Thailand and northwest Peninsular Malaysia. *Journal of Southeast Asian Earth Sciences* **9**, 129–51.

FONTAINE, H., IBRAHIM, A., KHOO, H. P., NGUYEN, D. T. & VACHARD, D. 1994*b*. *Geological Papers Volume 4.* Ipoh: Geological Survey of Malaysia, 175 pp.

FONTAINE, H., SUTEETHORN, V. & VACHARD, D. 1998. Khao Yoi, a Permian limestone hill of the Rat Buri area, Peninsular Thailand. *CCOP (Coordinating Committee for Geoscience Programmes in East and Southeast Asia) Newsletter* **23/3**, 12–4.

GEOLOGICAL SURVEY OF MALAYSIA. 1985. *Geological Map of Peninsular Malaysia 8th Edition,* Scale 1:500,000, Kuala Lumpur.

GLENISTER, B. F., FURNISH, W. M., ZHOU, Z. & POLAHAN, M. 1990. Ammonoid cephalopods from the Lower Permian of Thailand. *Journal of Paleontology* **64**, 479–80.

GOMANKOV, A. V. & BUROV, B. V. 1999. Correlations between Tatarian (Permian) type section (Russia) and the Salt Range (Pakistan): palynology and palaeomagnetism. *Geodiversitas* **21**, 291–7.

GRABAU, A. W. 1936. Early Permian fossils of China Pt. II. (fauna of the Maping Limestone of Kwangsi and Kweichow). *Palaeontologia Sinica, Series B* **8**, 441 pp.

GRANT, R. E. 1976. Permian brachiopods from southern Thailand. *Paleontological Society Memoir* **9** *(Journal of Paleontology* **50***),* 269 pp.

GRAY, J. E. 1840. *Synopsis of the Contents of the British Museum,* 42nd ed. London: British Museum, 370 pp.

GRUNT, T. A. 1986. Sistema brakhiopod otriada Atiridida. (Classification of brachiopods of the order Athyridida). *Trudy Academiia Nauk SSSR Paleontogicheskii Institut* **215**, 200 pp.

HALL, J. & CLARKE, J. M. 1893. An introduction to the study of the genera of Palaeozoic Brachiopoda. *Natural History of New York, Palaeontology* **8**, 1–317.

HOGEBOOM, T. & ARCHBOLD, N. W. 1999. Additional specimens of Early Permian brachiopods from the Callytharra Formation, Carnarvon Basin, Western Australia: new morphological data. *Proceedings of the Royal Society of Victoria* **111**, 255–69.

HUDSON, R. G. S. & SUDBURY, M. 1959. Permian Brachiopoda from south-east Arabia. *Notes et Mémoires sur le Moyen-Orient* **7**, 19–55, 6 pls.

IBRAHIM, A. 1987. Progress report of fossil indexing for Johore. *Geological Survey of Malaysia Annual Report* **1987**, 147–55.

IGO, H., RAJAH, S. S. & KOBAYASHI, F. 1979. Permian fusulinaceans from the Sungei Sedili area, Johore, Malaysia. *Geology and Palaeontology of Southeast Asia* **20**, 95–118, pls 15–26.

IQBAL, N., BROUTIN, J., IZART, A., COQUEL, R., VACHARD, D. & HASAN BAQRI, S. R. 1998. Quelques données stratigraphiques sur le Permien inférieur du Salt Range (Pakistan). *Geodiversitas* **20**, 724–30.

JIN, Y. & SHANG, Q. 2000. The Permian of China and its interregional correlation. In *Permian-Triassic Evolution of Tethys and Western Circum-Pacific* (eds H. Yin, J. M. Dickins, G. R. Shi and J. Tong), pp. 71–98. Developments in Palaeontology and Stratigraphy 18. Amsterdam: Elsevier.

JIN, Y., WARDLAW, B. R., GLENISTER, B. F. & KOTLYAR, G. V. 1997. Permian chronostratigraphic subdivisions. *Episodes* **20**, 10–5.

KOTLYAR, G. V., BAUD, A., PRONINA, G. P., ZAKHAROV, Y. D., VUKS, V. D., NESTELL, M. K., BELYAEVA, G. V. & MARCOUX, J. 1999. Permian and Triassic exotic limestone blocks of the Crimea. *Geodiversitas* **21**, 299–323.

LAZAREV, S. S. 1985. Brakhiopody Echinoconchidae i Buxtoniidae (Brachiopods of the families Echinoconchidae and Buxtoniidae). *Paleontologicheskii Zhurnal* **1985**, 64–74, (English translation in 1985. *Paleontological Journal* **16**, 62–72).

LEVEN, E. JA. 1998. Permian fusulinid assemblages and stratigraphy of the Transcaucasia. *Rivista Italiana di Paleontologia e Stratigrafia* **104**, 299–328.

LIAO, Z.-T. 1999. A history of the brachiopod ages of the Maping Limestone. *Acta Palaeontologica Sinica* **38**, 313–26.

MANSUY, H. 1913. Faunes des calcaires à *Productus* de l'Indochine, Première Série. *Mémoires du Service Géologique de l'Indochine* **2** *(fascicule 4),* 133 pp, 13 pls.

MEI, S. & HENDERSON, C. M. 2001. Evolution of Permian conodont provincialism and its significance in global correlation and paleoclimate implication. *Palaeogeography, Palaeoclimatology, Palaeoecology* **170**, 237–60.

METCALFE, I. 1998. Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. In *Biogeography and Geological Evolution of SE Asia* (eds R. Hall and J. D. Holloway), pp. 25–41. Leiden: Backhuys Publishers.

METCALFE, I. 2000. The Bentong–Raub Suture Zone. *Journal of Asian Earth Sciences* **18**, 691–712.

METCALFE, I. 2002. Permian tectonic framework and palaeogeography of SE Asia. *Journal of Asian Earth Sciences* **20**, 551–66.

MUIR-WOOD, H. M. 1955. *A History of the Classification of the Phylum Brachiopoda.* London: British Museum (Natural History), 124 pp.

MUIR-WOOD, H. M. 1962. *On the Morphology and Classification of the Brachiopod Suborder Chonetoidea.* London: British Museum (Natural History), 132 pp, 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**, 447 pp, 135 pls.

NAKAZAWA, K. 1973. On the Permian fossils from Jengka Pass, Pahang, Malay Peninsula. *Tohoku University Science Report Series 2 (Geology) Special Volume* **6**, 277–96.

Nestell, M. K. & Pronina, G. P. 1997. The distribution and age of the genus *Hemigordiopsis.* In *Late Paleozoic Foraminifera; their biostratigraphy, evolution, and paleoecology; and the Mid-Carboniferous boundary* (eds C. A. Ross, J. R. P. Ross and P. L. Brenckle), pp. 105–10. Cushman Foundation for Foraminiferal Research, Special Publication no. 36.

Pronina, G. P. 1996. Genus *Sphairionia* and its stratigraphic significance. *Supplemento agli Annali dei Musei Civici di Rovereto, Sezione Archeologia, Storia e Scienze Naturali* **11**, 105–18.

Rahman, W. A. 1986. Unit batuan brusia Perm di bahagian Barat dan Baratlaut Johore. *Geological Survey of Malaysia Annual Report* **1986**. 167–71.

Ramovš, A. 1966. Revision des "*Productus elegans*" (Brachiopoda) im ostalpinen Jungpaläozoikum. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **125**, 118–24.

Ramovš, A. 1969. Karavankininae, nova poddružina produktid (Brachiopoda) iz alpskih zgornjekarbonskih in permijskih skladov. *Jeklo in Ljudje Jeseniški Zbornik* **2**, 251–68.

Reed, F. R. C. 1925. Upper Carboniferous fossils from Chitral and the Pamirs. *Palaeontologia Indica New Series* **6** *(Memoir 4)*, 1–157.

Reed, F. R. C. 1931. Upper Carboniferous fossils from Afghanistan. *Palaeontologia Indica New Series* **19**, 1–39, pls 1–9.

Reed, F. R. C. 1944. Brachiopoda and Mollusca from the Productus limestones of the Salt Range. *Palaeontologia Indica New Series* **23** *(Memoir 2)*, 1–678, 65 pls.

Ricou, L. E. 1995. The plate tectonic history of the past Tethys Ocean. In *The Ocean Basins and Margins, Volume 8: The Tethys Ocean* (eds A. E. M. Nairn, L. E. Ricou, B. Vrielynck and J. Dercourt), pp. 3–70. New York: Plenum Press.

Sakagami, S. 2000. Middle Permian Bryozoa from Irian Jaya, Indonesia. *Bulletin of the National Science Museum, Tokyo, Series C* **26**, 139–68.

Sarytcheva, T. G. 1968. Brakhiopody verkhnego paleozoiia vostochnogo Kazakhstana. (Upper Paleozoic brachiopods from eastern Kazakhstan). *Trudy Akademiia Nauk SSSR Paleontologicheskii Institut* **121**, 212 pp, 33 pls.

Sarytcheva, T. G. & Sokolskaya, A. N. 1959. O klassifikatsin lozhnoporistykh brakhiopod. (On the classification of pseudopunctate brachiopods). *Doklady Akademiia Nauk SSSR* **125**, 181–4.

Schellwien, E. 1900*a*. Beiträge zur Systematik der Strophomeniden des oberen Palaeozoicum. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* **1**, 1–15.

Schellwien, E. 1900*b*. Die Fauna der Trogkofelschichten in den Karnischen Alpen und den Karawanken. 1 Theil: Die Brachiopoden. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* **16**, 1–122, 15 pls.

Schuchert, C. 1929. Classification of brachiopod genera, fossil and recent. In Brachiopoda (generum et genotyporum index et bibliographia), by C. Schuchert and C. M. LeVene. In *Fossilium Catalogus I. Animalia Part 42* (ed. J. F. Pompeckj), pp. 10–25. Berlin: W. Junk.

Shi, G. R. & Archbold, N. W. 1995. Permian brachiopod faunal sequence of the Shan-Thai terrane: biostratigraphy, palaeobiogeographical affinities and plate tectonic/palaeoclimatic implications. *Journal of Southeast Asian Earth Sciences* **11**, 177–87.

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

Sone, M. & Leman, M. S. 2000. Some mid-Permian fossils from Felda Mayam, central Peninsular Malaysia. In *Proceedings of the Geological Society of Malaysia, Annual Geological Conference 2000* (eds G. H. Teh, J. J. Pereira and T. F. Ng), pp. 143–9. Kuala Lumpur.

Sone, M., Leman, M. S. & Ehiro, M. 2001. Middle Permian cephalopods from central Peninsular Malaysia: implications for faunal migration through the southern Tethys. *Journal of Asian Earth Sciences* **19**, 805–14.

Sone, M., Leman, M. S. & Shi, G. R. 2001. Middle Permian brachiopods from central Peninsular Malaysia – faunal affinities between Malaysia and west Cambodia. *Journal of Asian Earth Sciences* **19**, 177–94.

Stampfli, G. M. 2000. Tethyan oceans. In *Tectonics and Magmatism in Turkey and the Surrounding Area* (eds E. Bozkurt, J. A. Winchester and J. D. A. Piper), pp. 1–23. Geological Society London, Special Publication no. 173.

Stehli, F. G. 1954. Lower Leonardian Brachiopoda of the Sierra Diablo. *Bulletin of the American Museum of Natural History* **105**, 257–358.

Stehli, F. G. 1956. Notes on oldhaminid brachiopods. *Journal of Paleontology* **30**, 305–13.

Termier, H. & Termier, G. 1970. Les Productoïdés du Djoulfien (Permien supérieur) dans la Téthys orientale: essai sur l'agonie d'un phylum. *Annales de la Société Géologique du Nord* **90**, 443–61, pls 29–31.

Ueno, K., Sugiyama, T. & Nagai, K. 1996. Discovery of Permian foraminifers and corals from the Ratburi Limestone of the Phatthalung area, southern Peninsular Thailand. In *Professor Hisayoshi Igo Commemorative Volume on Geology and Paleontology of Japan and Southeast Asia* (eds H. Noda and K. Sashida), pp. 201–16. Tokyo: Gakujutsu Tosho Insatsu.

Vachard, D., Hauser, M., Martini, R., Zaninetti, L., Matter, A. & Peters, T. 2001. New algae and problematica of algal affinity from the Permian of the Aseelah Unit of the Batain Plain (East Oman). *Geobios* **34**, 375–404.

Waagen, W. 1883. Salt Range fossils volume 1, part 4, *Productus* Limestone fossils, Brachiopoda. *Palaeontologia Indica* **13** (*fascicle 2*), 391–546.

Waagen, W. 1884. Salt Range fossils volume 1, part 4, *Productus* Limestone fossils, Brachiopoda. *Palaeontologia Indica* **13** *(fascicle 3–4),* 547–728.

Wanner, J. 1935. Lyttoniidae und ihre biologische und stammesgeschichtiiche Bedeutung. In *Zur Kenntnis der permischen Brachiopoden von Timor* (eds J. Wanner and H. Sieverts), pp. 201–81. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Abt. B* **74**, 4 pls.

Wardlaw, B. R. 1999. Notes from the SPS Chair. Executive notes. *Permophiles* **35**, 1–3.

Wardlaw, B. R. & Mei, S. 1999. Refined conodont biostratigraphy of the Permian and lowest Triassic of the Salt and Khizor Ranges, Pakistan. In *Proceedings of the International Conference on Pangea and the Paleozoic–Mesozoic Transition* (eds H. Yin and J. Tong), pp. 154–6. Wuhan: China University of Geosciences Press.

WARDLAW, B. R. & POGUE, K. R. 1995. The Permian of Pakistan. In *The Permian of Northern Pangea, Volume 2: Sedimentary Basins and Economic Resources* (eds P. A. Scholle, T. M. Peryt and D. S. Ulmer-Scholle), pp. 215–24. Berlin: Springer-Verlag.

WATERHOUSE, J. B. 1973. Permian brachiopod correlations for South-East Asia. *Bulletins of the Geological Society of Malaysia* **6**, 187–210.

WATERHOUSE, J. B. 1975. New Permian and Triassic brachiopod taxa. *Papers of Department of Geology, University of Queensland* **7**, 1–23.

WATERHOUSE, J. B. 1981. Age of the Rat Buri Limestone of southern Thailand. In *The Permian Stratigraphy and Palaeontology of Southern Thailand* (eds J. B. Waterhouse, K. Pitakpaivan and N. Mantajit), pp. 2–42. Geological Survey of Thailand Memoir 4.

WATERHOUSE, J. B., PITAKPAIVAN, K. & MANTAJIT, N. 1981. Early Permian brachiopods from Ko Yao Noi and near Krabi, southern Thailand. In *The Permian Stratigraphy and Palaeontology of Southern Thailand* (eds J. B. Waterhouse, K. Pitakpaivan and N. Mantajit), pp. 45–213. Geological Survey of Thailand Memoir 4.

WATERHOUSE, J. B. & PIYASIN, S. 1970. Mid-Permian brachiopods from Khao Phrik, Thailand. *Palaeontographica Abt. A* **135**, 83–197, pls 14–32.

WILLIAMS, A. 1953. The morphology and classification of the oldhaminid brachiopods. *Journal of the Washington Academy of Sciences* **43**, 279–87.

WILLIAMS, A., CARLSON, S. J., BRUNTON, C. H. C., HOLMER, L. E. & POPOV, L. 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London Series B* **351**, 1171–93.

WILLIAMS, A., HARPER, D. A. T. & GRANT, R. E. 2000. Lyttoniidina. In *Treatise on Invertebrate Paleontology Part H, Brachiopoda Revised Volume 3* (eds A. Williams and others), pp. 619–42. Kansas: The Geological Society of America and the University of Kansas.

YANAGIDA, J. 1970. Permian brachiopods from Khao Phrik, near Rat Buri, Thailand. *Geology and Palaeontology of Southeast Asia* **8**, 69–96 (issued in 1971).

YANAGIDA, J. & PILLEVUIT, A. 1994. Permian brachiopods from Oman. *Memoirs of the Faculty of Sciences, Kyushu University, Series D Earth & Planetary Sciences* **28**, 61–99.

ZHOU, Z., GLENISTER, B. F., FURNISH, W. M. & SPINOSA, C. 1999. Multi-episodal extinction and ecological differentiation of Permian ammonoids. In *Fossil Cephalopods: Recent Advances in their Study* (eds A. Y. Rozanov and A. A. Shevyrev), pp. 195–212. Moscow: Paleontological Institute, Russian Academy of Sciences.

First published in *Geological Magazine*, Volume 140: Issue 5 (2003).
Published by Cambridge University Press. Copyright © 2003 Cambridge University Press.
This article online at: http://dx.doi.org/10.1017/S0016756803007854