The rugose linoproductoid *Permundaria* Nakamura, Kato, and Choi, 1970 was stated to be a "poorly understood genus" in the new Brachiopoda Treatise (Brunton et al., 2000, p. 563). It is an uncommon genus confined to the Middle–early Late Permian Tethys Sea, and reports of it have usually been based on only a small number of specimens. In this study, some 30 samples of *Permundaria* were recovered from the Bera South beds (Wordian, Middle Permian) of the Bera Formation, Pahang, Peninsular Malaysia. The material represents a new species of the genus, which is here described. Its new morphological information enables taxonomic revision of this often misunderstood genus, and helps to clarify some confusion among related, or superficially similar, linoproductoid genera.

**INTRODUCTION**

The sampling locality (Fig. 1) is the Bera South outcrop of Sone et al. (2001) and Locality BF1 of Leman et al. (2000), and is at 03°04′10″N, 102°41′13″E (by Garmin GPS 12XL). Note that this GPS measurement is now more accurately indicated with the newer GPS instrument than in Sone et al. (2001, p. 806), who previously coordinated 03°04′01″N, 102°41′06″E for the same locality.

The geological details of the Bera South outcrop were described in Leman et al. (2000) and Sone et al. (2001). Fossils are confined to beds 3 m thick, which consist of tuffaceous siltstone, and are dominated by brachiopods and, to a lesser extent, cephalopods, bivalves, trilobites, and gastropods (Fig. 2). The brachiopod *Martinia* sp. and the trilobite *Pseudophilippia*? sp. were illustrated in Leman et al. (2000).

The cephalopods were studied by Sone et al. (2001) and consist of four ammonoids: *Tauroceras aff. T. scrobiculatum* (Gemmellaro, 1887), *Agathiceras sp., Bannyaniceras orientale* Sone, Leman, and Ehiro, 2001, Pronoritidae gen. and sp. indet., and two nautiloids: *Tainoceras* sp. and *Orthocerida fam. indet.* The age of the Bera South beds is interpreted to be Wordian (Guadalupian/Middle Permian), based chiefly on ammonoid correlations (Sone et al., 2001).

**SYSTEMATIC PALEONTOLOGY**

Morphological terms in current use follow Williams and Brunton (1997). The described specimens are housed at the Geology Program, National University of Malaysia (Univesiti Kebangsaan Malaysia), Bangi (UKM-F).

Superfamily LINOPRODUCTOIDEA Stehli, 1954

?Family MONTICULIFERIDAE Muir-Wood and Cooper, 1960

Subfamily SCHRENKIELLINAE Lazarev, 1990

[= Schrenkiellinae Lazarev, 1986, nomen nudum]

**Discussion.**—In the new Brachiopoda Treatise (see Brunton et al., 2000, p. 562), the publication date of the subfamily name *Schrenkiellinae* was referred to Lazarev (1986). However, in Lazarev (1986, p. 30), the subfamily name was merely stated as new with a list of constituent genera but without any accompanying explanatory notes. This does not satisfy any of three independent requirements in Article 13.1 of the International Code of Zoological Nomenclature. Thus, the subfamily name as proposed in Lazarev (1986) is invalid, but it became formally valid in Lazarev (1990, p. 122), where sufficient taxonomic information of the Schrenkiellinae was first provided.

The Schrenkiellinae were originally classified within the Monticuliferidae by Lazarev (1990) and subsequently by Brunton et al. (1995) and Brunton et al. (2000). Although the concept of the Schrenkiellinae Lazarev is principally supported, its inclusion in the Monticuliferidae is here questioned. In the revised Treatise, the superfamily Linoproductoida was divided into two families, namely, the Linoproductidae Stehli, 1954 and the Monticuliferidae. This was based largely on the depth of the corpus cavity, with members of the Monticuliferidae having a distinctly shallower cavity. This concept seems applicable for the classification of many linoproductoids, and, in that sense, the Schrenkiellinae are classifiable in the Monticuliferidae. However, the subfamily Monticuliferinae Muir-Wood and Cooper, 1960 are defined as being typified by possessing monticules (specialized nodal spine bases) or similar tubercles, with interrupted costellae or capitellae. Moreover, they may have large flabellate diductor marks in the ventral interior, as typically seen in *Monticulifera* Muir-Wood and Cooper, 1960 (pl. 125, fig. 13) and its probable synonym *Choano-productus* Termier and Termier, 1970 (fig. 12b; also see Termier and Termier, 1966, fig. 2). These are rather atypical characteristics among the Linoproductoida, and this implies that the true Monticuliferidae may be a specialized linoproductoid group, excluding the Schrenkiellinae and some others. Waterhouse (2001, p. 28) also argued that the Monticuliferidae are unusual members of the Linoproductoida. He (p. 25) then transferred the Schrenkiellinae (as downgraded to the subtribal level) into the Linoproductidae, yet this was based on a mistaken interpretation that the possession of a row of conspicuous hinge spines, as in the Schrenkiellinae, was regarded as indicative of linoproduct affinity. Such a character, however, is rather common throughout many linoproductoids, reported also from *Monticulifera* (e.g., Muir-Wood and Cooper, 1960, p. 327). In conclusion, the Schrenkiellinae should probably be included in an independent family.

**Genus PERMUNDARIA Nakamura, Kato, and Choi, 1970, emend.**


**Emended diagnosis.**—Ornament of fine costellae to capillae and low concentric rugae over both valves. Two sets of spines confined to ventral valve: 1) a row of thick hinge spines and 2)
thin body spines that arise from single costellae, not forming distinct spine bases. Concavo-convex, some species geniculately concavo-convex. Corpus cavity commonly very shallow with flattened disks. Ventral umbo low and weakly inflated, beak only slightly beyond hinge line. No median sulcus or fold. Marginal structures such as a subperipheral rim may be present. Trail short.

**Occurrence.**—Endemic to the Tethys Sea; western Iran?, central Afghanistan, southern Tibet (in the India block), South China, northeast China, Japan (the Kitakami Mountains and the Hida Gaien Belt), western Cambodia, northeastern Thailand?, Indonesia (central Sumatra), Peninsular Malaysia (in the East Malay block); Roadian?–Wuchiapingian (Middle Permian–lower Upper Permian).

**Discussion.**—*Permundaria* is a poorly recorded and ill-defined genus. It was proposed by Nakamura et al. (1970), based on poorly preserved and limited material (three ventral valves) and on material illustrated in other literature. It was defined originally as having no spines and no demarcation of ears from the visceral disk; both structures however are confirmed in the new species below. No information of the interior was provided. Since then, the genus has been recognized widely in sediments of the Permian Tethys Sea, but each species was often represented by only one or a few specimens. Although first observed in this study, most internal structures of *Permundaria* still remain insufficiently described; in particular, the cardinal process and details of the brachial ridges remain unknown.

Lazarev (1990) and Brunton et al. (2000) included *Permundaria* in the Schrenkiellinae. Waterhouse (2002, p. 36), however,
placed the genus questionably under Auriculispininae Waterhouse, 1986. New Malaysian material confirms that the ventral valve of _Permundaria_ has fine body spines and a row of coarser hinge spines, suggesting closer affinity to the Schrenkiellinae. _Permundaria_ is characteristically rugose, but this feature is atypical among the Schrenkiellinae.

_Bandoproductus_ Jin and Sun, 1981 and _Permundaria_ share thin body spines and a row of thick hinge spines in a ventral valve. _Bandoproductus_ also is possibly a member of the Schrenkiellinae (Lazarev, personal commun., 2003). A notable generic difference can be referred to the nature of close-set concentric rugae which characterize _Permundaria_ but are not well developed in _Bandoproductus_.

_Striatospica_ Waterhouse, 1975 was proposed with the type species _Striatifera? kayseri_ Chao, 1927 (p. 115, pl. 13, figs. 8–11) from the Loping Coal Series (Wuchiapingian) of South China. _Striatospica_ is also placed in the Schrenkiellinae by Brunton et al. (2000). Yet, Tazawa (1974, p. 316) previously interpreted the same Loping species to be _Permundaria_. The Loping species, herein accepted as _Striatifera kayseri_ (Chao, 1927), has a row of sturdy spines along the ventral hinge line and a short ventral trail, resembling the Malaysian new species of _Permundaria_ described below. _Striatospica_, however, has feeble rugae and supposedly has no body spines, thus it is distinguished from _Permundaria_.

_Undaria_ Muir Wood and Cooper, 1960 and_Compressoproductus_ Sarytcheva in Sarytcheva et al. (1960) have superficially very similar rugose linoproductid ornamentation to _Permundaria_. They, however, differ from _Permundaria_ in typically having an elongate trigonal outline with a short hinge line and narrow umbo (see also discussion in Nakamura et al., 1970).

_Papillolinus_ Waterhouse and Gupta, 1977 was proposed with the type species _P. eishmakami_ Waterhouse and Gupta, 1977, which was based on the Kashmir form _Productus undatus_ De France s. Diener (1899, p. 23, pl. 1, figs. 9, 10) with additional material. This Carboniferous genus superficially resembles _Permundaria_ in showing a flatly inflated shell with fine ribs and concentric rugae (or growth lines). It, however, differs in having many erect fine dense spines over the inner ears near the hinge line, as clarified by Waterhouse in _Waterhouse and Gupta_ (1977, p. 160–163), who examined the original two Kashmir specimens of _Diener_ (1899) in the Geological Survey of India, Calcutta. On the other hand, Nakamura et al. (1970, p. 296) and Jin (in Zhang and Jin, 1976, p. 186) separately assigned the Kashmir _P. undatus_ as synonyms of their _Permundaria asiatica_ and _Permundaria magna_, respectively. These are mistaken synonyms, resulting from an age misinterpretation, as those latter authors relied on Diener’s (1899) initial report of his _P. undatus_ from the Zewan beds (known as Peru) of the Kashmir Valley. However, as pointed out by Waterhouse and Gupta (1977, p. 163), Diener (1915, p. 14) later elucidated that the material came from the so-called Fenestella Shales, whose age has now been interpreted to be Bashkirian (Garzanti et al., 1998). _Papillolinus_ has now been placed in the Auriculispininae by Brunton et al. (2000) followed by Waterhouse (2002, p. 51), who re-diagnosed the genus.

**PERMUNDARIA PERPLEXA new species**

_Figure 3–1.321_


**Description.**—Outline subovate to transversely subquadrate, wider than long, widest part at hinge line to midvalve. Ornament of concentric rugae and costellae over both valves; rugae low, irregular in strength and width, sometimes oblique; costellae fine (9–12 in 5 mm at anterior margin of disk), widening anteriorly with increase by intercalation, rounded with narrower interspaces. Ventral valve moderately convex, gently geniculate; trail short (Fig. 3.14, 3.15, 3.20); subperipheral rim around disk, demarcating ears and trail (Fig. 3.18, 3.20); umbo weakly inflated; beak short just beyond hinge line; ears well ornamented, small or moderately extended. Two sets of spines confined to ventral valve: 1) hinge spines in a row, thick and pointing medially, as many as seven in number on one side in Holotype UKM-F564 (Fig. 3.17); 2) body spines thin, scattered over disk, each spine arises from single costella, forming small spine ridge but no distinct hollow base (Fig. 3.10–3.12). Dorsal valve flat to weakly concave; short trail may be developed; no spines or dimples present; ears flat, not well ornamented. Ventral interior lightly thickened with small muscle field (Fig. 3.21); adductor muscle scars small, triangular, posteriorly placed, unknown whether dendritic or smooth, bound to both sides by smooth ridges of possible callus wash covering posterior diductor muscle scars; anterior diductor muscle scars weak, striate. Dorsal interior not well observed, median septum thin and long, muscle scars seemingly weak (Fig. 3.6).

**Etymology.**—From the Latin _perplexus_ = confused, intricate, obscure, ambiguous.

**Types.**—Holotype UKM-F564; paratypes UKM-F551–563, 565–567.

**Measurements (retrodeformed).**—The largest ventral valve UKM-F567 (Fig. 3.20, 3.21) is approximately 28 mm long and 39 mm wide. The average length/width ratio for the all measurable type specimens is 0.73.

**Occurrence.**—The Bera South beds (Wordian, Middle Permian) of the Bera Formation, Pahang, Peninsular Malaysia (see Figs. 1, 2).

**Discussion.**—All specimens illustrated in Figure 3 were originally tectonically deformed. Thus, computer-graphic retrodeformation has been attempted for most images (see Fig. 3 caption for explanation). From the restorations, there seems to be a little intraspecific variation in outline and profile in the present collection, due to ontogeny and individuality. Nevertheless, it can be said that _Permundaria perplexa_ is a rather undersized _Permundaria_ having a moderately inflated geniculate ventral valve with a short trail. The geniculate shell with a defined trail and irregular concentric rugae are uncommon in known species of _Permundaria_. Moreover, the ventral valve of _P. perplexa_ displays thick hinge spines and thin sparse body spines, which are first confirmed in the genus. These characters warrant the validity of the new species, which is compared to most other representatives of the genus (see below).

Nakamura et al. (1970) proposed _Permundaria_ with two species; _P. asiatica_ (type species) and _P. sisophonensis_. The two species differ from _P. perplexa_ in having more rounded and flattened shells with more regular, coarser rugae. _P. asiatica_ Nakamura et al. (1970, p. 296, pl. 2, figs. 1a–c, 2) was based on two relatively large ventral valves: the holotype UHR19015 from the lower Kanokura Series (Middle Permian) of the Kitakami Mountains, Japan, and the paratype UHR19016 from the lower Member C (early Capitanian/late Middle Permian) of the Sisophon limestone in western Cambodia. Additional Japanese materials of _P. asiatica_ have been reported by Tazawa (1974, 2001). _P. sisophonensis_ Nakamura et al. (1970, p. 297, pl. 2, fig. 3a, 3b) was based on the single ventral shell UHR19017 from the same Cambodian horizon as the paratype UHR19016 of _P. asiatica_. It was defined as a smaller species with finer costellae than the type species. However, the Cambodian specimens UHR19016 and UHR19017, assigned to the two separate species, are similar in outline and nature of rugae. They show no significant difference, except for the size and the density of costellation which may in fact be of
intraspescific ontogenetic variation. It is considered that the two Cambodian specimens are conspecific, as the paratype of *P. asiatica* represents a more mature form of *P. sisophonensis*.

The classic South Chinese form, *Productus undatus* Defrance s. Kayser (1883, p. 188, pl. 26, figs. 12, 13, 13a), from the Wuchipingian of Loping, was interpreted by Nakamura et al. (1970, p. 297) as a synonym of *Permundaria sisophonensis*. The Loping form, however, has a more inflated ventral shell with a proportionally shorter hinge line than *P. sisophonensis*, and thus probably represents another species of *Permundaria*. It has a narrower outline than *P. perplexa*.

The most comparable form to the present new species is based on the Afghan shells described as *Permundaria sisophonensis* by Termier et al. [1974, p. 131, pl. 27, figs. 1–3, 3(7, 8)] from the early Murghabian of Wardak. They have a moderate concavocavity with a short trail, similar to *P. perplexa*, while the true *P. sisophonensis* is more flattened in profile. The Afghan form, however, differs from the Malaysian species in being larger (more than 70 mm wide). In addition, Angiolini (2001, p. 320) interpreted the above Afghan form to be a species of *Compressoproductus*. However, the Afghan species has a transverse outline, so is more referable to *Permundaria*.

*Permundaria shizipuenensis* is known from several Maokouan (Wordian) beds of South China (see also Feng and Jiang, 1978; Wang et al., 1982; Yang, 1984: sometimes reported as (Wordian) beds of South China (see also Feng and Jiang, 1978; up to 70 mm wide) with a slightly inflated small umbo but without a strong sulcus and a reduction in the number of coarse hinge spines. The Ratburi species may be allied to *Permundaria* but a relationship cannot be clear without more material from Ko Mukt.

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