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The Permian antitropical fusulinoidean genus *Monodiexodina*: Distribution, taxonomy, paleobiogeography and paleoecology

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Abstract

All the documented occurrences with illustration of specimens of the Permian fusulinoidean genus *Monodiexodina* from a total of 33 areas in 11 regions are reviewed and their taxonomic positions are reexamined in this paper. Among 17 species (including two subspecies) of *Monodiexodina* in the current taxonomy, the following 10 species are recognized as valid: *M. kattaensis*, *M. wanneri*, *M. caracorumensis*, *M. sutchanica*, *M. shiptoni*, *M. kumensis*, *M. wanganensis*, *M. neimongolensis*, *M. delicata*, and *M. rhaphidoformis*. In addition, species once referred to *Monodiexodina* but now should be excluded from the genus are also investigated in terms of their generic positions.

In reconstructed mid-Permian paleomap, *Monodiexodina*-bearing areas can be restored to either northern or southern middle latitudes between high latitudinal cool/cold-water climatic realm and paleo-tropical warm-water realm. These two middle latitudinal areas, each corresponding to the Northern and Southern Transitional Zones, respectively, can be best interpreted climatologically as mesothermal, warm temperate belts in both hemispheres, thus suggesting the genus to be a paleobiogeographically typical antitropical fusulinoidean taxon. Moreover, the genus is generally found in a monotypic, crowded manner in sandy sediments with their shells being often aligned uni-directionally. This mode of occurrence of *Monodiexodina* strongly suggests that it was adapted to shallow-marine, high-energy environments, which would probably be essentially maintained by the acquisition of highly elongated fusiform/subcylindrical shells with well-developed polar torsion. This morphological feature is adapted to increase septal pores per unit area in polar regions, thus increasing possibility to develop more pseudopodia on both sides of test. It probably has a functional significance for not only locomotion but also anchoring their tests on the surface of bottom sediments in agitated water conditions. The genus itself is considered to be a rather long-ranging taxon from the late Yakhtashian (=Artinskian) to the early Midian (=Capitanian). It is, therefore, concluded that *Monodiexodina* had an opportunistic character, occurring repeatedly only when favorable, high-energy conditions, such as sand shoal, appeared in warm temperate climatic belts in both hemispheres.

Monodiexodina originated in the Southern Transitional Zone from an elongated *Eoparafusulina* stock at late Early Permian (around late Artinskian) time. It flourished in southern middle latitudinal areas in latest Early and early Middle Permian time. The genus then migrated to the northern hemisphere (Northern Transitional Zone) by some dispersion mechanism at around the early Middle Permian, and prevailed there during the remaining period of the Middle Permian.

Keywords: Antitropical; *Monodiexodina*; Paleobiogeography; Paleoecology; Permian; Taxonomy

1. Introduction

The genus *Monodiexodina*, which generally has remarkably elongated fusiform or subcylindrical shells with strongly and regularly fluted septa (Figs. 1 and 2), was established by Sosnina (in Kiparisova et al., 1956) with *Schwagerina wanneri* var. *sutchanica* Dutkevich (in Likharev, 1939) as the type species. In addition to this outstanding shell morphology that gives distinguishable diagnosis on *Monodiexodina* from other fusulinoidean foraminifers, the genus has been known as occurring peculiarly in high-energy, arenaceous sediments such as sandy limestone. Although *Monodiexodina* has been

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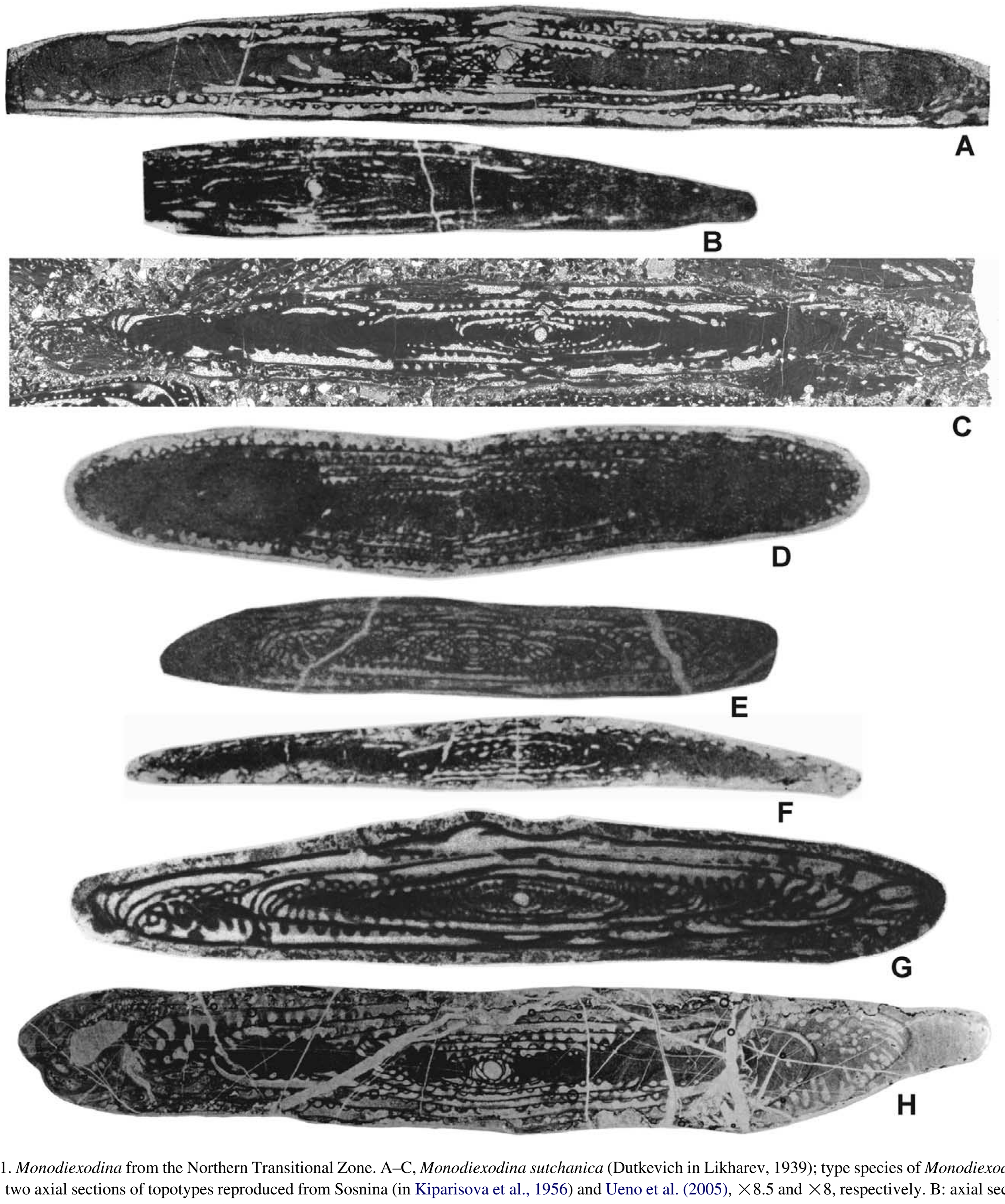

Fig. 1. *Monodiexodina* from the Northern Transitional Zone. A–C, *Monodiexodina sutchanica* (Dutkevich in Likharev, 1939); type species of *Monodiexodina*. A,C: two axial sections of topotypes reproduced from Sosnina (in Kiparisova et al., 1956) and Ueno et al. (2005), ×8.5 and ×8, respectively. B: axial section of lectotype reproduced from Dutkevich (in Likharev, 1939), ×10. D: *Monodiexodina neimongolensis* Han, 1976; axial section of holotype reproduced from Han (1976), ×8. E: *Monodiexodina delicata* Han, 1980b; axial section of holotype reproduced from Han (1980b), ×10. F: *Monodiexodina rhaphidoformis* Han, 1980b; axial section of holotype reproduced from Han (1980b), ×8. G: *Monodiexodina wanganensis* Sosnina, 1965; axial section of holotype reproduced from Sosnina (1965), ×10. H: *Monodiexodina kumensis* Kanmera, 1963; axial section of holotype reproduced from Kanmera (1963), ×10.

documented rather scarcely among Permian schwagerinid fusulinoideans, its paleobiogeographic significance as a 'cool-water' or 'bipolar' taxon has been often emphasized in many works (e.g. Fujimoto, 1955; Ishii et al., 1985; Ozawa, 1987; Metcalfe, 1988). In some recent papers (e.g. Shi et al., 1995; Shi and Grunt, 2000; Ueno and Tazawa, 2003), the paleobiogeographic antitropicality of the genus becomes more clearly demonstrated than in those previous works.

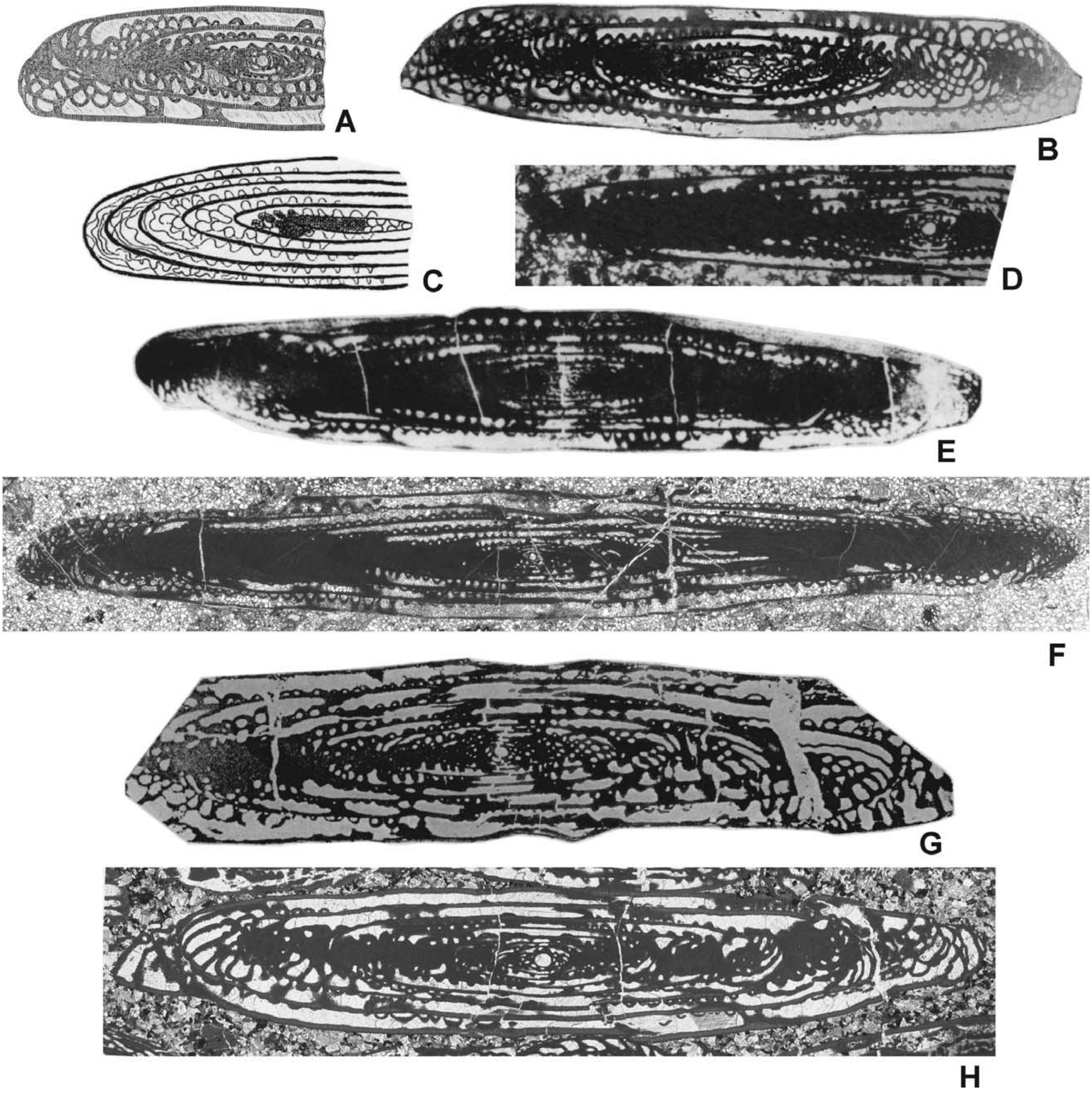

Fig. 2. *Monodiexodina* from the Southern Transitional Zone. A,B, *Monodiexodina kattaensis* (Schwager, 1887). A: incomplete axial section (line drawing) of lectotype reproduced from Schwager (1887), ×10. Note that Douglass (1970, p. G7) stated in designating types of this species that specimen illustrated by line drawing in Fig. 3 of plate CXXVI of Schwager (1887) is selected as lectotype and is photomicrographically re-illustrated on his plate 4 as Fig. 78. However, what was shown in this microphotographic figure is specimen illustrated in Fig. 8 on plate CXXVI of Schwager (1887), which should be one of paralectotypes. B: axial section of topotype reproduced from Dunbar (1933), ×8. C: *Monodiexodina caracorumensis* (Merla, 1934); incomplete subaxial section (line drawing) of lectotype designated herein, reproduced from Merla (1934), ×10. D–F, *Monodiexodina shiptoni* (Dunbar, 1940). D: incomplete axial section reported as '*Parafusulina erucaria* (Schwager) var. *caracorumensis* (Merla)' by Reichel (1940), ×8. E: axial section of lectotype designated herein, reproduced from Dunbar (1940), ×8. F: axial section from Bukit Wang Pisang in Perlis, northwestern Peninsular Malaysia, ×7. G,H, *Monodiexodina wanneri* (Schubert, 1915). G: axial section of lectotype reproduced from Thompson (1949), ×10. H: axial section from Oinlasi in Timor Island, Indonesia, ×10.

This is particularly due to advances in reconstructing Permian paleomap and understanding regional tectonic evolution of relevant areas, such as Northeast and Southwest Asia. In view of these recent increases of basic information on *Monodiexodina*, it would be timely and useful to make a comprehensive review of the essential taxonomic and paleobiogeographic aspects of the genus.

In this paper, I review the geographic distribution, stratigraphic occurrence, and taxonomy of the genus *Monodiexodina*. I further make some considerations on the paleobiogeographic, phylogenetic and paleoecologic characteristics of the genus.

2. Distribution of *Monodiexodina*

Since Schwager (1887) described *Fusulina kattaensis*, the oldest species potentially referable to the genus, from the Salt Range of Northeast Pakistan, *Monodiexodina* has been reported from various areas in the northern and southern marginal Tethys. These *Monodiexodina*-bearing localities are summarized in Fig. 3. In this section, I make comprehensive review of the geographic distribution and stratigraphic occurrences of *Monodiexodina*.

Regarding the chronostratigraphic terminology of the Permian in the following discussion, I essentially use the conventional Tethyan scale (stage names) largely progressed by Leven (1967, 1976, 1980a,b, 1982, 1993a, 1996, 2004) because *Monodiexodina* occurs in areas where the Tethyan stages have been widely adopted as regional chronostratigraphic frameworks. Also I put the presumably corresponding international series/stage names after the Tethyan standard names at each first mention. For the translation of the Tethyan stages into the International Permian chronostratigraphic scales in this paper, I provisionally follow Jin et al. (1997) and wardlaw et al. (2004), although, there rise discrepancies recently with respect to especially correlation between the Tethyan Middle Permian stages (Kubergandian, Murgabian, Midian) and the Guadalupian ones (Roadian, Wordian, Capitanian) (e.g. Henderson et al., 1999; Leven, 2001, 2004).

2.1. South Primorye

South Primorye in Far East Russia has the type locality of the type species of *Monodiexodina*. Dutkevich (in Likharev, 1939) described *Schwagerina wanneri* (Schubert) var. *sutchanica* from Senkina Shapka (Location 1 in Fig. 3) of the Partizanskaya (=Suchan) river basin in the Sergeevka Belt (Khanchuk et al., 1996). Later, Sosnina (in Kiparisova

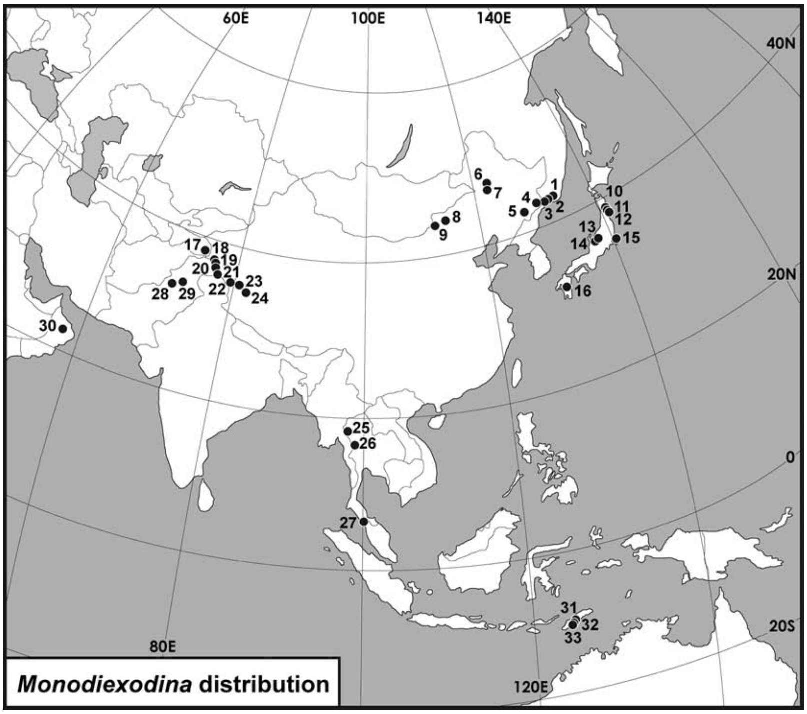

Fig. 3. Geographic distribution of *Monodiexodina*. 1: Senkina Shapka in Partizanskaya River Basin, South Primorye, Far East Russia. 2: Vangan and Golubinaya Mountains in Shkotovo, South Primorye, Far East Russia. 3: Barabashvka and Narva river valley areas, South Primorye, Far East Russia. 4: Hunchun in Jilin Province, Northeast China. 5: Huadian in Jilin Province, Northeast China. 6: Longjiang in Heilongjiang Province, Northeast China. 7: Jalaidqi in Neimongol Autonomous Region, Northeast China. 8: Zhengxiangbaiqi in Neimongol Autonomous Region, Northeast China. 9: Zhesi in Neimongol Autonomous Region, Northeast China. 10: Setamai-Yahagi area in South Kitakami Mountains, Northeast Japan. 11: Kamiyasse-Imo area in South Kitakami Mountains, Northeast Japan. 12: Iwaizaki in South Kitakami Mountains, Northeast Japan. 13: Moribu in Hida Mountains, Central Japan. 14: Ise in Hida Mountains, Central Japan. 15: Takagami in Choshi, Central Japan. 16: Kozaki in Kuma Mountains, Southwest Japan. 17: Shindy valley and Kyzyl-Beles, Southeast Pamir, Tadjikistan. 18: Durbin Jangal in Shaksgam Valley, Xinjiang Uygur Autonomous Region, Northwest China. 19: Confluence of Shaksgam Valley and Zug Shaksgam Valley, Xinjiang Uygur Autonomous Region, Northwest China. 20: Mouth of Rimu Glacier in headwater of Yarkand Valley, Xinjiang Uygur Autonomous Region, Northwest China. 21: Murgo in Aghil Range, North India. 22: Kongkashankou in westernmost part of Xinjiang-Xizang boundary, Southwest China. 23: Doumar in Rutog, Xizang Autonomous Region, Southwest China. 24: Gegyai, Xizang Autonomous Region, Southwest China. 25: Dan Tha Ta Fang in Mae Sariang, Changwat Mae Hong Son, West Thailand. 26: Huai Um Yom in Lan Sang and Mae Ka Sa Fall in Mae Ramat, Changwat Tak, West Thailand. 27: Bukit Wang Pisang, Perlis, Peninsular Malaysia. 28: Kishor Range, Northeast Pakistan. 29: Salt Range, Northeast Pakistan. 30: Jebel Akhdar, Oman. 31: Upstream of Benain River in West Timor, Indonesia. 32: Oinlasi in West Timor, Indonesia. 33: Noil Tuke in West Timor, Indonesia.

et al., 1956) established the genus *Monodiexodina* with the Dutkevich's (in Likharev, 1939) species as type species. According to Taschi et al. (1992), the Senkina Shapka section is referable stratigraphically to the Chandalaz Formation, which is biostratigraphically subdivided into the following three fusulinoidean zones; in ascending order the *Metadoliolina dutkevitchi-Monodiexodina sutchanica* Zone, the *Parafusulina stricta* Zone, and the *Metadoliolina lepida-Lepidolina kumaensis* Zone. Among them, *Monodiexodina* species is restricted in the *Metadoliolina dutkevitchi-Monodiexodina sutchanica* Zone. Very recently, Ueno et al. (2005) substantiated an early Midian (=Capitanian) age for this biozone.

Monodiexodina wanganensis Sosnina is another species of the genus reported in South Primorye, which has less developed axial fillings and a smaller form ratio than *M. sutchanica*. This species was originally established by Sosnina (1965) based on specimens from the Vangan and Golubinaya mountains near Shkotovo in the Artemovka river valley area (Location 2 in Fig. 3) of the Voznesenka Belt (or the composite Khanka Belt: Khanchuk et al., 1996). As Sosnina's (1965) work was carried out in typical monographic manner, the stratigraphic information of this species was not documented sufficiently, and is merely noted that it came from the *Monodiexodina* Zone. Nikitina (1974), in the compilation of faunal elements of foraminiferal zones established in Primorye, later showed that *M. wanganensis* is one of fusulinoidean elements in the *Metadoliolina dutkevitchi-Monodiexodina sutchanica* Zone.

Very recently, Kotlyar et al. (2003) summarized the *Monodiexodina*-bearing beds of South Primorye. Besides, the Chandalaz Formation of the Partizanskaya river valley area and the Barabash Formation of the Artemovka river valley area, they also reported the genus from the Barabash Formation of the Barabashvka and Narva river valley areas (Location 3 in Fig. 3) in the further western Laoelin-Grodekov Belt (Khanchuk et al., 1996). Kotlyar et al. (2003) listed *M. sutchanica*, *M. wanganensis*, *M. wanneri* (Schubert), *M. kattaensis* (Schwager), and *M. shiptoni* (Dunbar) from these areas and illustrated three of them: *M. sutchanica*, *M. wanneri*, and *M. kattaensis*. Kotlyar et al.'s (2003) *M. wanneri* and *M. kattaensis*, however, seem to fit well within the morphological variations of *M. sutchanica*, thus would be referable to this species (Ueno et al., 2005). In summary, two species of *Monodiexodina*, *M. sutchanica* and *M. wanganensis*, occur in South Primorye. They are restricted to the lower part of the Chandalaz Formation and its equivalents, and thus referable to the early Midian.

2.2. Northeast China

In Northeast China, Han (1976; 1980a; 1980b), Ding et al. (1985), and Ueno and Tazawa (2003) have reported *Monodiexodina* so far with illustration of specimens. The first report of the genus in this region was carried out by Han (1976) from Neimongol Autonomous Region (Inner Mongolia). He described a new species, *M. neimongolensis*, from the Sanmiangjiang Formation at Zhengxiangbaiqi (Location 8 in Fig. 3). Later, Han (1980b) described *M. shiptoni* (Dunbar) and *M. kattaensis* (Schwager) from the Sijiashan Formation in the Jalaidqi area (Location 7 in Fig. 3), eastern Inner Mongolia. Based on their gross morphologies, however, these two species can be better identified as *M. sutchanica* (Dutkevich) and *M. delicata* Han, respectively.

The Hugete (or Baotege) Formation distributed in the Zhesi area (Location 9 in Fig. 3) of central Inner Mongolia bears several *Monodiexodina* species. Xia (in Ding et al., 1985) reported *M. caracorumensis* (Merla) and *M. shiptoni* along with establishing two new taxa, *M. sutchanica baotegensis* and *M. yongwangcunensis*. Of these four species, *M. shiptoni* and *M. sutchanica baotegensis* are morphologically similar to and thus identified as *M. delicata* Han. The other two species, *M. caracorumensis* and *M. yongwangcunensis*, are better referable to *M. sutchanica* as noted already by Ueno et al. (2005).

In Heilongjiang Province, Han (1980b) reported *Monodiexodina* from the Sijiashan (and/or Gaojiawopeng) Formation of Longjiang (Location 6 in Fig. 3). Included are *M. wanneri* (Schubert), *M. caracorumensis*, *M. sutchanica*, and the following four new taxa: *M. ordinata*, *M. longa*, *M. delicata*, and *M. matsubaishi compacta*. Han (1980b) also reported the genus from two areas in Jilin Province. The Kedao Formation (Midian) of the Hunchun area (Location 4 in Fig. 3) and the Daheshen Formation of the Huadian area (Location 5 in Fig. 3) bear *M. sutchanica* and two new species, *M. rhaphidoformis* and *M. ordinata*, respectively. Among these *Monodiexodina* species reported by Han (1980b), *M. caracorumensis*, *M. shiptoni*, *M. longa*, and *M. matsubaishi compacta* are morphologically closely allied, and thus referable to *M. sutchanica* (Ueno et al., 2005). *Monodiexodina kattaensis* and probably *M. wanneri* are considered to be conspecific with *M. delicata*. On the other hand, *M. ordinata* would be referable to *M. wanganensis* Sosnina.

Very recently, Ueno and Tazawa (2003) described *Monodiexodina rhaphidoformis* and *M.* sp. from the Daheshen Formation at Daheshen in Huadian, Jilin. They also reported *Parafusulina*? *daheshenica* Han, which has been shown by Han (1980b) to coexist with *M. rhaphidoformis* in Jilin. Ueno and Tazawa (2003) admitted the close morphological similarity of *daheshenica* with some *Monodiexodina* species, and thus questionably assigned this species to *Parafusulina*.

With respect to the age of these *Monodiexodina*-bearing fusulinoidean faunas in Northeast China, Han (1981) correlated them (the Daheshen, Sijiashan, and Hugete formations) to the late Chihsian, except the Kedao Formation of Hunchun, Jilin, which he put in the late Maokouan. Moreover, Han (1981) established the *Monodiexodina* *sutchanica-Pseudodoliolina lettensis* Zone in the Sijiashan Formation of the southern Daxinganling Range of eastern Inner Mongolia and its correlatives in Jilin.

The Chihsian in China is now formally subdivided into the lower Luodianian and the upper Xiangboan stages; the latter of which corresponds to the *Cancellina elliptica* Zone to the *Neoschwagerina simplex-Presumatrina neoschwagerinoides* Zone in the standard fusulinoidean zonation of China (Editorial Committee of Stratigraphic Lexicon of China, 2000). The Xiangboan is, therefore, correlated in the Permian standard chronostratigraphic subdivision of the Tethys (e.g. Leven, 1976, 1980a, 1993a, 2004) to the Kubergandian (=Roadian) to early Murgabian (=Wordian). Li (in Editorial Committee of Stratigraphic Lexicon of China, 2000, p. 48 and p. 97) noted that shallow-marine fossils including fusulinoideans do occur in the upper part of the Sijiashan and Daheshen formations. These data let Ueno and Tazawa (2003) conclude that major *Monodiexodina*-bearing levels in Northeast China, excluding the one in the Midian Kedao Formation by Han (1980b), can probably be referable to the early Murgabian.

2.3. Japanese Islands

The basement rocks of the Japanese Islands fundamentally comprise two geotectonic domains with highly contrasted geologic features. One is composed of accretionary complexes and the other essentially exhibits coherent stratigraphy formed on a continental basement. The latter domain includes the South Kitakami Belt, Hida Gaien Belt, and Kurosegawa Belt. Recent studies (e.g. Tazawa, 1991, 2001; Yamakita and Otoh, 1998; Kojima et al., 2000) have insisted a close geotectonic and paleobiogeographic linkage before the Miocene of these three belts with Northeast China and South Primorye in various degrees. Very recently, Tazawa (2004) collectively called the three belts the South Kitakami Terrane from the viewpoint of the basic geotectonic subdivisions of the Japanese Islands. In Japan, *Monodiexodina* is found exclusively in this terrane. Up to the present, two *Monodiexodina* species, *M. matsubaishi* (Fujimoto) and *M. kumensis* Kanmera, have been reported from the Japanese Islands, but Ueno et al. (2005) pointed out that the former species should be referable to *M. sutchanica* (Dutkevich).

The South Kitakami Belt located in Northeast Japan widely underlies Permian shallow-marine strata. The Permian here is subdivided essentially into three stratigraphic units: in ascending order the Sakamotozawa, Kanokura, and Toyoma formations (or series) (Tazawa, 1988), which almost correspond to the Early (=Cisuralian), Middle (=Guadalupian), and Late Permian (=Lopingian), respectively. *Monodiexodina* has been reported from the lower part of the Kanokura Formation (and its equivalent strata) in three areas of the belt.

Fujimoto (1956) established *Parafusulina matsubaishi* based on specimens from Omotematsukawa in the Kamiyasse-Imo area (Location 11 in Fig. 3). This is the first species potentially referable to *Monodiexodina* described in Japan. Choi (1973) also reported this species from the Kanokura Formation distributed in the Setamai-Yahagi area (Location 10 in Fig. 3). These studies contributed to establish the *Monodiexodina matsubaishi* Zone in the lower half of the Kanokura Formation in the South Kitakami Belt. This zone directly underlies the Midian *Lepidolina multiseptata* and *Colania kotsuboensis* zones (Choi, 1973), thus can be referable to the Murgabian. Very recently, Ehiro and Misaki (2004), based on data from the Kamiyasse-Imo area, clarified that *M. matsubaishi* ranges up into the lower Midian *Lepidolina multiseptata* Zone.

The Iwaizaki Limestone (Location 12 in Fig. 3), interpreted as isolated shallow carbonate bank deposits embedded within the sandstone/shale-dominated Kanokura Formation (Kawamura and Machiyama, 1995), has been also known as a locality of *Monodiexodina matsubaishi*. Morikawa et al. (1958) and Morikawa (1960) established *Parafusulina matsubaishi* Zone in calcareous sandstone in the lower part of the Iwaizaki Limestone. However, this species has been neither described nor illustrated in these papers. My recent study in the Iwaizaki Limestone confirmed the presence of *Monodiexodina* species in unit 4 (lower part of the limestone) of Kawamura and Machiyama (1995) although, detailed taxonomic examination has not been carried out yet.

In summary, a single species of *Monodiexodina*, *M. sutchanica*, has been so far found in the South Kitakami Belt. Earlier studies all have referred this species to *M. matsubaishi*. Its chronostratigraphic range in the South Kitakami Belt is from the Murgabian to the lower Midian.

In the Hida Gaien Belt of Central Japan, *Monodiexodina* has been known in two areas. In the Middle Permian Moribu Formation distributed in the Moribu area (Locality 13 in Fig. 3), Tazawa et al. (1993) first reported *Monodiexodina* from sandstone in the middle part of the formation. Because the specimens are completely weathered and exhibited as external molds (which has been often expressed as the ‘Matsubaishi-type’ mode of occurrence in Japanese literature: see Ueno and Tazawa, 2004), they identified them as *M.* cf. *matsubaishi*. Very recently, Niwa et al. (2004) illustrated better specimens of *M. matsubaishi*, which occur in calcareous sandstone and remain internal shell features, from two localities in the Moribu Formation. These specimens are conspecific with those from the South Kitakami Belt, and thus should be referable to *M. sutchanica*.

Monodiexodina species was reported recently by Ueno and Tazawa (2004) from the lower part of the Middle Permian Oguradani Formation of the Ise area (Location 14 in Fig. 3) in the western part of the Hida Gaien Belt. The *Monodiexodina* specimens were found in calcareous sandstone and are more or less abraded and fragmented. Due to poor preservation, Ueno and Tazawa (2004) identified them as *Monodiexodina* sp., with suggesting some possibilities that the species could be referable to *M. matsubaishi*, thus to *M. sutchanica* in the present taxonomy.

In the Kurosegawa Belt, *Monodiexodina* has been reported from two areas. One of the two is the Choshi area (Location 15 in Fig. 3) east of Tokyo, where *M. matsubaishi* (=*M. sutchanica*) was reported by Maeda and Mitsuoka (1961) from a limestone pebble in the Takagami Conglomerate. The geologic unit bearing the Takagami Conglomerate distributed isolatedly in the Choshi Peninsula is recently regarded as a member of the Kurosegawa Belt (Tazawa, 2000). The conglomerate is unknown in age, but contains rich *Lepidolina* species in other limestone pebbles (Chisaka, 1960).

The Kozaki Formation in the Kuma Mountains (Location 16 in Fig. 3), central Kyushu, belongs to the Kurosegawa Belt (Tazawa, 2000). According to Kanmera (1963), the formation is composed mainly of shale, sandstone, and conglomerate with subordinate lenticular and conglomeratic limestone. Fusulinoideans are generally found in the lower member, especially in its lower part (units b–d), in which *Misellina claudiae* (Deprat) and *Skinnerella gruperaensis* (Thompson and Miller) are characteristic. In the upper part (units d–f), *Parafusulina kaerimizensis* (Ozawa), *Armenina sphaera* (Ozawa), and *Neoschwagerina simplex* Ozawa are dominant. *Monodiexodina kumensis* was described from the lowermost part (unit b) of the formation. Because *M. kumensis* occurs in strata just below those yielding early Murgabian *N. simplex*, the *kumensis*-bearing level would be correlated to a part of the Kubergandian.

2.4. SE Pamir

Leven (1967) described and illustrated *Monodiexodina shiptoni* (Dunbar) from the topmost part of the Bazardarinskaya (or Kochusuyskaya) Suite of the Shindy valley and Kyzyl-Beles in the Southeast Pamir, Tadjikistan (Location 17 in Fig. 3). He illustrated two specimens (axial sections) of this species, which are quite similar to the types by Dunbar (1940).

The *Monodiexodina*-bearing level in the Southeast Pamir was not easy in estimating its exact geologic age because of the absence of coexisting age-diagnostic fossils. Leven (1967) originally noted that the *M. shiptoni* from the Southeast Pamir is assignable to the Artinskian, namely the Yakhtashian in the Permian standard chronostratigraphic subdivision of the Tethys. According to Leven (1967), in the stratigraphic succession that contains *Monodiexodina* in the Shindy valley, the Bazardarinskaya Suite (>400 m thick) is overlain by the Shindyyskaya Suite composed mainly of diabase (100–120 m thick), and then overlain by Kubergandian (early Middle Permian) sandy limestone yielding *Maklaya cutalensis* (Leven), *M. pamirica* (Leven), *Armenina salgirica* Miklukho-Maklay, and others. As these primitive neoschwagerinid and verbeekinid fusulinoideans can be considered to represent rather younger Kubergandian (e.g. Leven, 1980a; Ueno, 1996), the *Monodiexodina*-bearing level, just below the thick diabase of the Shindyyskaya Suite that may only represent a short time interval, would not be very much older than the early Kubergandian. It must be pertinent to consider as the Bolorian (=Kungurian) at the oldest. Recent data from conodonts and ammonoids also agree with this age assessment for the upper part of the Bazardarinskaya Suite and the overlying Shindyyskaya Suite (Leonova and Dmitriev, 1989; Leven et al., 1992; Reimers, 1999).

2.5. Karakorum

The Karakorum Range of the India–Pakistan–China border involves some of the classic *Monodiexodina* localities. Silvestri (1934, 1935), Merla (1934), Reichel (1940), and Dunbar (1940), all as parts of the paleontologic results of several scientific expeditions organized by Italy, the Netherlands, and India in the early half of the last century, reported the occurrences of fusulinoideans from this alpine area. Of these fusulinoideans, three species, *Fusulina wanneri* Schubert, *Schellwienia erucaria* var. *caracorumensis* Merla, and *Parafusulina shiptoni* Dunbar, are potentially subsumed in the genus *Monodiexodina*.

Silvestri (1934, 1935) illustrated *Fusulina wanneri* in a rock sample collected from the middle of the Shaksgam Valley area (Location 19 in Fig. 3) in the southwesternmost part of Xinjiang Uygur Autonomous Region, Northwest China. This is the first report of species potentially referable to the genus *Monodiexodina* from the Karakorum. The locality by Silvestri (1934, 1935) is at the confluence of the Shaksgam Valley and Zug Shaksgam Valley (see the inserted map in Duke of Spoleto, 1930, for location) and very close to that of Dunbar's (1940) *Parafusulina shiptoni*. The specimens of Silvestri (1934, 1935) have elongated fusiform shells with strongly and regularly fluted septa and remarkable axial fillings. By its general shell outline, they are less similar to the types of *F. wanneri* reported by Schubert (1915) from Timor Island, Indonesia, and better identified as *M. shiptoni*.

In the same year, Merla (1934) established *Schellwienia erucaria* var. *caracorumensis* based on specimens from the headwater of the Yarkand Valley (Location 20 in Fig. 3) located in the southwesternmost part of Xinjiang, Northwest China. After the introduction of the genus *Monodiexodina* by Sosnina (in Kiparisova et al., 1956), this form has been generally subsumed in many papers in the relevant genus (e.g. Kahler and Kahler, 1966, 1967). Because the types of *caracorumensis* came from moraine of the Rimu Glacier, the stratigraphic position of this form is unknown. Moreover, the specimens that Merla (1934) reported were illustrated in line drawing only, thus the detailed morphologic features and taxonomic validity of *caracorumensis* are less clear.

Later, Dunbar (1940) described *Parafusulina shiptoni* from the south of Durbin Jangal (coordinate: N36°20′, E76°40′) in the Shaksgam Valley (Location 18 in Fig. 3), southwesternmost part of Xinjiang, Northwest China. In the same year, Reichel (1940) also reported *Parafusulina erucaria* var. *caracorumensis* (Merla) from Murgo of the Aghil Range (Location 21 in Fig. 3), northernmost part of India. These two species by Dunbar (1940) and Reichel (1940) are now referable to the genus *Monodiexodina*, and are highly probably conspecific judging from their illustrations. Then, one taxonomic question arose; whether or not *M. shiptoni* is a junior synonym of *M. caracorumensis*. If *M. caracorumensis* reported by Reichel (1940) is really conspecific with the types by Merla (1934), then *M. shiptoni* should be regarded as a junior synonym of the former. With respect to this issue, Reichel (1940) noted that his Murgo specimens, Silvestri's (1934, 1935) *Fusulina wanneri*, and Merla's (1934) *Schellwienia erucaria* var. *caracorumensis* occur in the same strata in the Karakorum and are conspecific, therefore all referable to *Parafusulina erucaria* var. *caracorumensis*. This statement, however, would not readily warrant taxonomic identity between the Merla's (1934) types of *caracorumensis* and Reichel's (1940) Murgo specimens, and thus, further, the junior synonymy of *M. shiptoni* with *M. caracorumensis* because Merla's (1934) description and illustration of *Schellwienia erucaria* var. *caracorumensis* are too poor to judge its taxonomic peculiarity. Due mainly to this poor status of documentation for the types of *M. caracorumensis* and, in contrast, the clearer taxonomic status of *M. shiptoni*, I provisionally regard these two as taxonomically independent in this study.

The *Monodiexodina*-bearing localities in the Karakorum are all located just east of the Karakorum Fault, running with an almost NW–SE direction along the Shaksgam and Nubra valleys in the eastern Karakorum (Searle and Asif Khan, 1996). From the geotectonic point of view, therefore, they are highly probably included in the western extension of the Qiangtang Block of one of the two Tibetan Cimmerian blocks.

2.6. Tibet

In the 1980's and 90's several papers reported *Monodiexodina* from the westernmost part of Xizang Autonomous Region and the southernmost part of Xinjiang Uygur Autonomous Region, both in Tibet in China. In these studies, four species, *M. sutchanica* (Dutkevich), *M. kattaensis* (Schwager), *M. wanneri* (Schubert), and *M.*? *domarensis* Wang, Sheng and Zhang, have been referred to the genus. As noted below, however, these *Monodiexodina* specimens from Tibet, except for the types of *M.*? *domarensis,* can be taxonomically summarized as constituting a single species, *M. shiptoni* (Dunbar).

Wang et al. (1981) reported *Monodiexodina sutchanica*, *M. wanneri*, and *M. kattaensis* from the Tunlonggongba Formation of the Doumar area of Rutog county (Location 23 in Fig. 3), western Tibet. *Monodiexodina*? *domarensis* from Lungmuco in Rutog was also proposed as a new species in the same article, but this species would be removed from the genus (see discussion in the next section). The Tunlonggongba Formation is a stratigraphic unit mainly distributed in around Rutog county of western Tibet and is referable to the Chihsian in the Permian chronostratigraphic nomenclature of China, thus correlated to the Bolorian to the early Murgabian (Editorial Committee of Stratigraphic Lexicon of China, 2000). Among, the three species of *Monodiexodina* from Doumar reported by Wang et al. (1981), *M. sutchanica* and *M. wanneri* both have very elongated fusiform shells with clearly developed tunnel and regular septal fluting. There are some differences in these two species in the development of axial fillings, shape of polar ends, and form ratio. However, because these differences are rather transitional in the two forms and, moreover, because they occur together, these two species can be regarded as conspecific, and are better identified as *M. shiptoni* rather than *M. sutchanica* judging from the gradual increase of their spiral volutions. On the other hand, *M. kattaensis* by Wang et al. (1981) has a less elongated fusiform shell compared with other two coexisting *Monodiexodina*, and its axial fillings are restricted in inner volutions, resulted in forming juvenile volutions. This species is better identified as *Pseudofusulina* sp., or in a lesser case *Monodiexodina*? sp.

In Doumar et al. (1983) also reported *Monodiexodina kattaensis* from the Tunlonggongba Formation. Their specimens are less similar to the types and topotypes of *M. kattaensis* reported by Schwager (1887), Dunbar (1933), and Douglass (1970), and seem to be better identified as *Monodiexodina* sp. Yang et al. (1990) also reported two *Monodiexodina*, *M. domarensis* and *M. kattaensis*, from the middle-upper parts of the Tunlonggongba Formation of Doumar. Judging from the illustration by Yang et al. (1990), however, these two species are very similar to each other in gross shell morphology, although the latter has a slightly larger form ratio than the former. *Monodiexodina domarensis* and *M. kattaensis* reported by Yang et al. (1990) are better referable to *M. shiptoni* by their elongated fusiform shells.

From one isolated locality belonging stratigraphically to the Mushirebuka (=Huoerbacuo: Bureau of Geology and Mineral Resources of Xizang Autonomous Region, 1997) Group distributed in the Gegyai area (Location 24 in Fig. 3) in western Tibet, Zhang (1991) described *Monodiexodina sutchanica*. The illustrated specimens are very closely allied to *M. shiptoni* because of their gradually expanded coiling of volutions, thus potentially identical to this species rather than *M. sutchanica*. The Mushirebuka Group is a loosely defined stratigraphic unit distributed in the Mushirebuka area of Gegyai country and almost corresponds to the late

Carboniferous to the early Permian (Editorial Committee of Stratigraphic Lexicon of China, 2000). Stratigraphically, the *Monodiexodina*-bearing level in Gegyai should be better regarded within the Tunlonggongba Formation, like as those in the Doumar area.

Sun and Zhang (1988) reported *Monodiexodina sutchanica*, *M. kattaensis*, and *M. wanneri* from the Jiawendaban Formation (Yakhtashian to early Murgabian: Editorial Committee of Stratigraphic Lexicon of China, 2000) of the Kongkashankou area (Location 22 in Fig. 3) close to the westernmost part of the Xinjiang-Xizang boundary. Like as the *Monodiexodina* species reported by Wang et al. (1981), the *M. sutchanica* and *M. wanneri* from Kongkashankou are better referable to *M. shiptoni*, and the *M. kattaensis* to be better identified as *Pseudofusulina* sp. or *Monodiexodina*? sp.

In Yinligou in Rutog county of westernmost Xizang, just south of the Kongkashankou area (Location 22 in Fig. 3), Zhang (1998) illustrated *Monodiexodina wanneri*, *M. kattaensis*, *M.*? *domarensis*, and *M.* sp. These four species occur in one locality of the Tunlonggongba Formation. The specimens illustrated exhibit rather continuous variability in axial fillings, form ratio, and shell outline. These differences would be best interpreted as intra-populational variation rather than diagnoses splitting species because of the sympatric occurrences of the four. Moreover, the four species can be referable to *M. shiptoni* by their basic shell morphology including elongated fusiform shells and gradually expanding volutions.

In summary, only one species of *Monodiexodina*, *M. shiptoni* can be recognized from Tibet, although, there are some forms with open nomenclature that are potentially referable to the genus. The stratigraphic range of *M. shiptoni* in Tibet is not easily estimated in the standard time-scale of the Permian. Existing data, however, suggest that this species occurs in Tibet in the Tunlonggongba Formation of a broadly Chihsian (Bolorian to early Murgabian) age. Moreover, all the *Monodiexodina* localities in Tibet belong geotectonically in the Qiangtang Block of the eastern Cimmerian continent (Ueno, 2003).

2.7. West Thailand

In West Thailand, which belongs geotectonically to the Sibumasu Block of the eastern Cimmerian continent (Ueno, 2003), Ingavat and Douglass (1981) described *Monodiexodina sutchanica* (Dutkevich) from Dan Tha Ta Fang west of Mae Sariang in Changwat Mae Hong Son (Location 25 in Fig. 3) and *M. shiptoni* (Dunbar) from Huai Um Yom in Lan Sang and Mae Ka Sa Fall in Mae Ramat, both in Changwat Tak (Location 26 in Fig. 3). These three *Monodiexodina*-bearing localities in West Thailand are all isolated both geographically and stratigraphically, so that it is difficult to locate their exact chronostratigraphic positions in the context of local geology. Based on recent general stratigraphic understandings of the Sibumasu Block in West Thailand, however, Ueno (2003) argued the *Monodiexodina*-bearing level to lie in the very basal part of the Ratburi Limestone or the transitional beds between the underlying siliciclastic-dominant Kaeng Krachan Group and the Ratburi Limestone. He correlated this level to the Bolorian or very early Kubergandian. A likely Bolorian age for the Kaeng Krachan/Ratburi boundary interval is also very recently justified by ammonoids from the topmost part of the Kaeng Krachan Group in southern peninsular Thailand (Fujikawa et al., 2005).

Of the two *Monodiexodina* species reported by Ingavat and Douglass (1981), the specimens of *M. sutchanica* are slightly deformed by compaction but have a very elongated shell and well-developed axial fillings, and exhibit gradually expanding volutions through growth. These shell characters suggest that this form is better identical with *M. shiptoni* than *M. sutchanica*. Thus, only *M. shiptoni* is recognized in West Thailand until now.

2.8. Western Peninsular Malaysia

As in West Thailand, two species of *Monodiexodina*, *M. sutchanica* (Dutkevich) and *M. shiptoni* (Dunbar), have been described and illustrated by Basir Jasin and Koay (1990) from near a small limestone hill, Bukit Wang Pisang (Location 27 in Fig. 3), in Perlis of western Peninsular Malaysia. They occur in the topmost part of the Kubang Pasu Formation or the transitional beds between the Kubang Pasu Formation and the overlying Chuping Limestone. The *Monodiexodina*-bearing locality in Peninsular Malaysia also geotectonically belongs to the Sibumasu Block of the eastern Cimmerian continent. Because the Kubang Pasu Formation and the Chuping Limestone broadly correspond lithostratigraphically to the Kaeng Krachan Group and the Ratburi Limestone in peninsular and West Thailand respectively, the *Monodiexodina*-bearing level in Bukit Wang Pisang is also considered to be rightly equivalent chronostratigraphically to that in West Thailand (Ueno, 2003). Although, Basir Jasin and Koay (1990) noted some minor morphological differences between the two *Monodiexodina* species from Bukit Wang Pisang, the differences must be less significant in species level. In addition, they both have gradually expanded coiling of volutions, so that they should be best identified as *M. shiptoni*.

2.9. NE Pakistan

The ‘Lower Productus Limestone’ of the Salt Range (Location 29 in Fig. 3) in Northeast Pakistan bears the first-described species that has been subsumed in the genus *Monodiexodina* in later studies; that is *Fusulina kattaensis* Schwager. Besides this species, Schwager (1887) described two other species associated with the former; *F. pailensis* Schwager and *F. longissima* von Möller, and suggested the possible existence of another species; *F. erucaria*. Among the four, the last one is the mother species of the variety proposed by Merla (1934); *Schellwienia erucaria* var.

caracorumensis. A later work by Dunbar (1933) noted that *M. kattaensis* occurs very abundantly in several localities belonging to the 'Lower Productus Limestone'.

Douglass (1970) studied an extensive collection of fusulinoidean specimens from several localities belonging to the Amb Formation (almost equal to the 'Lower Productus Limestone') of the Zaluch Group in the Salt Range and the Kishor Range (Location 28 in Fig. 3), Northeast Pakistan. He clarified the morphologic variations of *Monodiexodina kattaensis*, after synonymizing *Fusulina pailensis* and *F. longissima* reported by Schwager (1887) into *M. kattaensis*. Furthermore, this study reported *Codonofusiella laxa* Douglass associated with *M. kattaensis*.

The age of the Amb Formation has been subject to controversy for long time. The Pakistan-Japanese Research Group (1985) considered that at least the fusulinoidean-bearing middle part of the Amb Formation is referable to the Late Baigenzinian (of Waterhouse, 1976) or 'Late Artinskian' (almost equal to the Bolorian or Kungurian in the current chronostratigraphic nomenclature) of the latest Early Permian mainly by the co-occurrence of *Codonofusiella laxa*. Jin et al. (1997) suggested, in a correlation chart of selected Permian successions, the Amb Formation to be equivalent to the Roadian and Wordian of the early–middle Middle Permian (=Guadalupian). Most recent studies by Mertmann (2000, 2003) assigned the formation to the Murgabian (=Wordian) of the middle Middle Permian based on updated conodont determination (Wardlaw and Mei, 1999).

2.10. Oman

In the Jebel Akhdar area of the Oman Mountains in the eastern part of the Arabian Peninsula, Middle-Late Permian rocks are widely distributed (Montenat et al., 1976). Charles A. Ross (personal communication, 2005) informed that *Monodiexodina* that is similar or identical to *M. kattaensis* (Schwager) from Northeast Pakistan occurs in folded Permian strata tectonically emplaced on a Cretaceous thrust sheet of the Jebel Akhdar area (Location 30 in Fig. 3). Unfortunately, further stratigraphic and taxonomic details on this *Monodiexodina* occurrence have not been published yet.

2.11. Timor Island

Timor Island of the Lesser Sunda Islands, Indonesia, exhibits one of the classic localities of *Monodiexodina*. From the island, Schubert (1915) first described *Schwagerina wanneri* from several localities (both outcrops and loose blocks) upstream of the Benain River (Location 31 in Fig. 3) in West Timor. Thompson (1949) later illustrated better specimens of *M. wanneri* and gave its more detailed description, resulted in supplementing insufficiency of the original description and illustration of this old species. This study made clear the taxonomic and morphologic features of *M. wanneri*.

Recently, Charlton et al. (2002) noted that *Monodiexodina*-crowded loose blocks are also scattered in Noil (=River) Tuke (Location 33 in Fig. 3), south of Soe in West Timor. Although, they did not show specimens from Noil Tuke, I confirmed the occurrence of *M. wanneri* from Noil Tuke in the course of my field investigation in West Timor in 1994, which also made another discovery of a new *Monodiexodina*-bearing locality south of Oinlasi (Location 32 in Fig. 3). In this locality between Oinlasi and Tesi Ayofanu, *M. wanneri* are swarmed in reddish arenaceous limestone, aligning their tests almost parallel to the bedding surface.

According to Charlton et al. (2002), *Monodiexodina* occurs in Timor Island in the middle part of the Maubisse Formation, which, as a whole, has been assigned to the Lower to Upper Permian. The *Monodiexodina*-bearing levels are considered to be Artinskian–Kungurian in age (Charlton et al., 2002, p. 749), but this may be nothing but merely suggest the possible maximum age range of *M. wanneri* in Timor. Because these *Monodiexodina* localities, together with many of other well-known shallow-marine fossil localities in Timor Island (Charlton et al., 2002), have not yet been controlled and understood very in detail in the context of the Tethyan standard chronostratigraphic subdivision. Moreover, the Permian chronostratigraphic nomenclature used in Charlton et al. (2002, p. 742) is slightly different from what we are familiar to (cf. Jin et al., 1997). Under such circumstances, I provisionally regard the *Monodiexodina*-bearing levels in Timor Island to be close to the Artinskian/Bolorian boundary.

3. Taxonomy of *Monodiexodina*

3.1. Descriptive notes on the genus Monodiexodina

Superfamily FUSULINOIDEA von Möller, 1878

Family SCHWAGERINIDAE Dunbar and Henbest, 1930

Subfamily MONODIEXODININAE Kanmera, Ishii and Toriyama, 1976

Genus *Monodiexodina* Sosnina in Kiparisova, Markovsky and Radchenko, 1956

Type species: *Schwagerina wanneri* var. *sutchanica* Dutkevich *in* Likharev, 1939 from Senkina Shapka in the Partizanskaya river basin, South Primorye, Far East Russia. See Ueno et al. (2005) for the correct taxonomic (specific) name of the type species.

Diagnosis: Shell large in schwagerinids and very elongated fusiform or subcylindrical. Essentially planispiral volutions, up to 6–8, rarely 9–10 volutions, become elongated rapidly in axial direction through growth. Form ratio variable from 4.5–6.0 in subcylindrical forms to over 10.0 in elongated fusiform ones, but generally larger than 7.0 in typical species. Axis of coiling straight or slightly curved in some forms. Proloculus relatively large for shell size. Dimorphism recognized in some species; early volutions skew-coiled with minute proloculus in microspheric form but outer volutions similar to those of megalospheric form. Spirotheca less differentiated in early volutions, but coarsely alveolar as typical schwagerinid-type wall in middle and outer ones. Septa intensely and regularly fluted except for central part of shell. Septal pores well developed especially in polar regions. Cuniculi and polar torsion may be recognized. Chomata poorly developed but tunnel clearly observed. Axial fillings variable from almost free to dense.

Discussion: *Monodiexodina* differs from almost coeval *Parafusulina* Dunbar and Skinner, 1931 by generally having a more elongated shell. The genus is somewhat similar to *Ferganites* Miklukho-Maklay, 1959 and *Ruzhenzevites* Davydov (in Chuvashov et al., 1986), especially in having cigar-like subcylindrical shells and in prevailing in more or less sandy calcareous sediments representing shallow, high-energy conditions. As discussed in Davydov (1988a,b, 1990), however, these three genera have different phylogenetic origins with different stratigraphic ranges. *Ferganites* is a latest Carboniferous (Kasimovian-Gzhelian) genus, derived from *Triticites*, and has definitely less strongly fluted septa and more stably developed chomata in almost all volutions than *Monodiexodina*. *Ruzhenzevites* is a latest Carboniferous-early Early Permian (Gzhelian to Sakmarian) genus and belongs to the rugosofusulinine lineage. It can be distinguished from *Monodiexodina* by having slightly loosely coiled volutions and axial deposits restricted in inner volutions.

Some elongated subcylindrical forms of *Eoparafusulina* Coogan, 1960 (including its synonymy *Alaskanella* Skinner and Wilde, 1966; see Ross, 1967a,b for the taxonomic treatment of *Alaskanella*) with definite axial fillings found in mainly the western hemisphere lower Lower Permian (mostly later part of the Wolfcampian, thus almost corresponding to the Sakmarian-early? Artinskian in the Tethyan chronologic scale), such as *E. linearis* (Dunbar and Skinner) and *E. prolongada* (Berry), more or less closely resemble species of *Monodiexodina*. They also have been documented to occur generally in sandy calcareous sediments (e.g. Ross, 1967b; Ross and Ross, 2003a), which are essentially similar to *Monodiexodina* in the mode of occurrence. The relevant *Eoparafusulina* species may have slightly smaller shells and form ratios (generally smaller than 6.0 in *Eoparafusulina*) than true *Monodiexodina*, but other morphological characters resemble each other between *Monodiexodina* and the *Eoparafusulina*. Thus, it is not very easy to distinguish especially elongated subcylindrical *Eoparafusulina* species with definite axial fillings (such as *E. linearis* and *E. prolongada*) from *Monodiexodina* species with relatively smaller form ratios (such as *M. kattaensis*) by only morphological aspects. However, they are substantially separated in view of phylogeny, ages, and paleobiogeography although, the latter two of the three aspects are not pure taxonomic arguments. *Monodiexodina* is essentially a post-early Artinskian (mainly post-Artinskian), Eurasian genus with particularly elongated shells and distributed only in bitemperate paleoclimatic areas. In contrast, *Eoparafusulina* is a cosmopolitan genus and occurs in the late Asselian to early Artinskian in mainly paleo-equatorial areas, although, it is also found in higher paleolatitudinal areas. Morphologically, typical *Monodiexodina* has a shell with a form ratio attaining to 7.0 or larger, which is never accomplished by *Eoparafusulina*.

In summary, the following four genera, *Ferganites*, *Ruzhenzevites*, some *Eoparafusulina* (especially, elongated subcylindrical forms found in western hemisphere), and *Monodiexodina*, share similar gross shell morphology, and are prevailed in sandy calcareous sediments. They can be interpreted as homeomorphic genera, representing independent, specialized phylogenetic stocks in schwagerinid fusulinoidean foraminifers and adapted to high-energy, sandy environments. They appear to have peculiar phylogenetic origins and chronostratigraphic and paleobiogeographic distributions, respectively.

More than 20 species have been so far proposed to, or once subsumed in, the genus *Monodiexodina*. Among them, the following ten species are recognized as valid in the genus at the moment. Species once referred to *Monodiexodina* but now removed from the genus are discussed in the next section.

Monodiexodina kattaensis (Schwager, 1887)
Fig. 2A and B

Types: *Fusulina kattaensis* Schwager, 1887, p. 985–987, pl. 76, Figs. 1–11, pl. 78, Fig. 4.

Synonymy: *Fusulina pailensis* Schwager, 1887, p. 987–988, pl. 77, Figs. 1–6.

Remarks: Douglass (1970) clarified intra-specific variability of this species, which was originally described by Schwager (1887) from the Salt Range, Northeast Pakistan. According to Douglass (1970), there exist considerable morphological variations in this species in shell size, prolocular size, form ratio, and axial fillings. *Monodiexodina kattaensis* has a typical cigar-like elongated subcylindrical shell with regularly fluted septa. Moreover, this is one of the two species in *Monodiexodina* in which a microspheric form has been so far known (Douglass, 1970, pl. 7, Figs. 8–10).

As noted by Douglass (1970), *Fusulina pailensis*, which was described by Schwager (1887) together with *F. kattaensis*, is concluded as a junior synonym of *Monodiexodina kattaensis*.

Distribution: Salt Range and Kishor Range, NE Pakistan, and probably Oman; Southern Transitional Zone.

Age: Murgabian (middle Middle Permian/middle Guadalupian).

Monodiexodina wanneri (Schubert, 1915)
Fig. 2G and H

Types: *Fusulina wanneri* Schubert, 1915, p. 54–55, pl. 39, Fig. 2, pl. 40, Fig. 1, pl. 41, Figs. 1 and 7.

Remarks: *Monodiexodina wanneri* is somewhat similar to *M. kattaensis* in their cigar-like, subcylindrical shell shape. However, the former can be distinguished from the latter by the difference of shell expansion; *M. kattaensis* is more uniformly expanded whereas *M. wanneri* has gradually expanded volutions. Moreover, *M. wanneri* has less fluted septa, clearer polar torsion, and axial fillings restricted only in axial regions.

Distribution: Timor Island, Indonesia; Southern Transitional Zone.

Age: Late Yakhtashian-Bolorian (late Early Permian/late Cisuralian).

Monodiexodina caracorumensis (Merla, 1934)
Fig. 2C

Types: *Schellwienia erucaria* var. *caracorumensis* Merla, 1934, p. 308–309, Fig. 23a–f. A specimen illustrated on Fig. 23f in Merla (1934) is here selected as the lectotype of this species.

Remarks: Due to the poor status of original description and illustration by Merla (1934), the morphologic and taxonomic identity of *Monodiexodina caracorumensis* is rather ambiguous. As noted elsewhere in this paper, this species may potentially be a senior synonym of *M. shiptoni* although, I provisionally retain them as separate taxonomic entities at the moment.

Distribution: Karakorum; Southern Transitional Zone.

Age: Uncertain, but probably Bolorian (latest Early Permian/latest Cisuralian) or Kubergandian (early Middle Permian/early Guadalupian).

Monodiexodina sutchanica (Dutkevich in Likharev, 1939)
Fig. 1A–C

Types: *Schwagerina wanneri* var. *sutchanica* Dutkevich *in* Likharev, 1939, p. 39, pl. 3, Figs. 4–5.

Synonymies: *Parafusulina matsubaishi* Fujimoto, 1956, p. 158–160, pl. 25, Figs. 1–10; *Monodiexodina longa* Han, 1980b, p. 67, pl. 19, Figs. 1–4; *Monodiexodina matsubaishi compacta* Han, 1980b, p. 69, pl. 23, Figs. 1–3; *Monodiexodina yongwangcunensis* Xia *in* Ding et al., 1985, p. 58, pl. 1, Figs. 1–3, 9.

Remarks: Among the four taxa mentioned in synonymies, *Parafusulina matsubaishi*, *Monodiexodina matsubaishi compacta*, and *M. yongwangcunensis* have not been compared with *M. sutchanica*, which has nomenclatural seniority over the three, when they were established. The three forms all have elongated fusiform shells and well-developed axial fillings, and are judged as identical to *M. sutchanica*. For *Monodiexodina longa*, Han (1980b) noted that the species can be distinguished from *M. sutchanica* by a more slender shell, thinner spirotheca, wider tunnel, and more restricted septal fluting only to the lateral slopes and polar regions. The illustrated types of *M. longa*, however, seem to have no essential morphological difference from *M. sutchanica*.

Monodiexodina sutchanica was originally described from South Primorye of Far East Russia, and is widely distributed, apart from South Primorye, in Northeast China and Japan. This species is characterized by a slenderly elongated fusiform shell with bluntly pointed polar ends and uniformly expanded volutions, broadly arched to almost straight central part of shell, intensely fluted septa with regularly arranged semi-circular septal loops, well-developed tunnel, and heavy axial fillings almost limited to around the axis of coiling. This species is restricted in distribution to the Northern Transitional Zone. As in the discussion in the precedent section, all the specimens illustrated under the name of *M. sutchanica* from the Southern Transitional Zone should be assigned to *M. shiptoni*, which shows a close morphologic linkage with the former.

Distribution: South Primorye, Northeast China, Japan; Northern Transitional Zone.

Age: Murgabian-early Midian (middle-late Middle Permian/middle-late Guadalupian).

Monodiexodina shiptoni (Dunbar, 1940)
Fig. 2D–F

Types: *Parafusulina shiptoni* Dunbar, 1940, p. 1–4, pl. 1, Figs. 1–7. A specimen illustrated on Fig. 1 of Plate 1 in Dunbar (1940) is here designated as the lectotype of this species.

Remarks: *Monodiexodina shiptoni* is similar to *M. sutchanica* in having a very elongated fusiform shell with conspicuous axial fillings, but can be distinguished from the latter by the more gradually expanding volutions. This species can be easily differentiated from *M. kattaensis* and *M. wanneri* in the Southern Transitional Zone by having a more elongated fusiform shell.

As stated in the previous section, there exist some possibilities that *Monodiexodina shiptoni* is regarded as a junior synonym of *M. caracorumensis*. The types of *Parafusulina shiptoni* by Dunbar (1940) from the Shaksgam Valley and the specimens of *P. erucaria* var. *caracorumensis* described by Reichel (1940) from Murgo in the Aghil Range, both in the Karakorum, are highly probably conspecific. So if the Reichel's (1940) specimens are really identical to the Merla's (1934) types of *caracorumensis*, *M. shiptoni* should be synonymized with *M. caracorumensis*. In this taxonomy, however, because of the poor status of the original description and illustration of *caracorumensis* by

Merla (1934), I provisionally regard *shiptoni* and *caracorumensis* as independent.

Distribution: SE Pamir, Karakorum, Tibet, West Thailand, Peninsular Malaysia; all constitute parts of the Cimmerian continent; Southern Transitional Zone.

Age: Bolorian (latest Early Permian/latest Cisuralian) and Kubergandian (early Middle Permian/early Guadalupian).

Monodiexodina kumensis Kanmera, 1963
Fig. 1H

Types: *Monodiexodina kumensis* Kanmera, 1963, p. 103-104, pl. 19, Figs. 1–7.

Remarks: In the original description, Kanmera (1963) noted that *M. kumensis* most closely resembles *M. matsubaishi* (namely *M. sutchanica* in this taxonomy), but differs from the latter by more irregular and higher septal fluting, more broadly rounded polar ends, and larger proloculus. The basic morphological similarities between *M. kumensis* and *M. sutchanica*, together with the fact that the former appeared slightly earlier than the latter in the Northern Transitional Zone, seemingly suggest that *M. kumensis* is the potential ancestor of *M. sutchanica*.

Distribution: Japan; Northern Transitional Zone.

Age: Kubergandian (early Middle Permian/early Guadalupian).

Monodiexodina wanganensis Sosnina, 1965
Fig. 1G

Types: *Monodiexodina wanganensis* Sosnina, 1965, p. 149–150, pl. 1, Fig. 9, pl. 3, Figs. 1–3.

Synonymy: *Monodiexodina ordinata* Han, 1980b, p. 66, pl. 18, Figs. 5–7, 13.

Remarks: *Monodiexodina wanganensis*, originally described by Sosnina (1965) from the Vangan and Golubinaya mountains near Shkotovo in South Primorye, Far East Russia, has a cigar-like, laterally extended shell with relatively fewer number of volutions, weaker septal fluting in the central part of shell but more intensely fluted in axial ends, and slightly less tightly coiled volutions. As Sosnina (1965) noted, these diagnostic characters can be sufficient for separating *wanganensis* from *sutchanica*.

Monodiexodina ordinata described by Han (1980b) from Jilin and Heilongjiang, Northeast China, has an elongated cigar-like shell with relatively less fluted septa in the central part of shell. This species is judged a junior synonym of *M. wanganensis* by these shell characters.

Distribution: South Primorye, Northeast China; Northern Transitional Zone.

Age: Murgabian-early Midian (middle-late Middle Permian/middle-late Guadalupian).

Monodiexodina neimongolensis Han, 1976
Fig. 1D

Types: *Monodiexodina neimongolensis* Han, 1976, p. 59-60, pl. 22, Figs. 1–7.

Remarks: This species, composed of up to 9–10 volutions, has a more tightly coiled volutions, smaller form ratio, and more developed axial fillings than *M. sutchanica*. Although, a microspheric form is known in this species (Han, 1976, pl. 22, Figs. 4 and 5), its morphological details are less clear except for having a slightly larger shell than the megalospheric form.

Distribution: Northeast China; Northern Transitional Zone.

Age: Murgabian (middle Middle Permian/middle Guadalupian).

*Monodiexodina delicata*Han, 1980b
Fig. 1E

Types: *Monodiexodina delicata* Han, 1980b, p. 68–69, pl. 22, Figs. 6–10.

Synonymy: *Monodiexodina sutschanica* [sic] *baotegensis* Xia *in* Ding et al., 1985, p. 57, pl. 1, Figs. 5 and 6.

Remarks: *Monodiexodina delicata* differs from *M. sutchanica* by a smaller shell and more tightly coiled volution. It is also differentiated from *M. neimongolensis* by having a smaller shell and less developed axial fillings. *Monodiexodina delicata* is somewhat similar to *M. wanganensis* in their cigar-like shells, but can be distinguished from the latter by more fluted septa in the central part of shell.

Monodiexodina sutschanica [sic] *baotegensis* Xia (in Ding et al., 1985) has a moderately large, elongated cylindrical shell with regularly fluted septa and well-developed axial fillings. Judging from the illustration of the types, it can be regarded as taxonomically same as *M. delicata*.

Distribution: Northeast China; Northern Transitional Zone.

Age: Murgabian (middle Middle Permian/middle Guadalupian).

Monodiexodina rhaphidoformis Han, 1980b
Fig. 1F

Types: *Monodiexodina rhaphidoformis* Han, 1980b, p. 67-68, pl. 19, Figs. 5–9.

Remarks: As noted by Ueno and Tazawa (2003), this species can be differentiated from other *Monodiexodina* species by having a needle-like slender shell, tightly coiled inner volutions, and thinner spirotheca.

Distribution: Northeast China; Northern Transitional Zone.

Age: Murgabian (middle Middle Permian/middle Guadalupian).

3.2. Species once referred to Monodiexodina *but should be excluded from the genus*

In the course of scrutinizing literature on Early–Middle Permian fusulinoideans, it emerged that there exist several species that have been assigned originally to, or once transferred by later students to, *Monodiexodina*, but should be excluded from the genus in the light of the present-day criteria of fusulinoidean taxonomy, especially in view of the evolutionary origin and phylogeny of *Monodiexodina*. Moreover paleobiogeographic and chronostratigraphic information helps discrimination of the genus. In this section, I estimate the generic positions of these potentially removed species.

3.2.1. Western Hemisphere forms

In the Americas, several Early Permian schwagerinid species have been so far suggested to be referable to the genus *Monodiexodina*. The first species was reported by Coogan (1960) as *Parafusulina* (*Monodiexodina*?) sp. from the Dekkas Formation of the Shasta Lake area, northern California, USA. This species has an extremely elongated shell with a form ratio of about 10.0, although the illustrated specimen is not completely preserved. Later Skinner and Wilde (1965) established *Parafusulina juncea* based on specimens from the upper part of the Nosoni Formation distributed in the Shasta Lake area, and included the Coogan's (1960) specimen in the synonym of this species. I essentially agree with this taxonomic treatment by Skinner and Wilde (1965) and regard *Parafusulina* (*Monodiexodina*?) sp. by Coogan (1960) to be identical with *P. juncea*.

Ross (1962, 1963) described *Monodiexodina linearis* (Dunbar and Skinner) from the Lenox Hills Formation and the lower–middle part of the Leonard Formation (late Wolfcampian-earliest Leonardian) of the Glass Mountains in Texas, USA, of which the Leonardian specimens were later found to be within boulders reworked from older, Lenox Hill strata (Ross, 1986, p. 548). It is now made clear that the relevant species is restricted in the Glass Mountains in the Lenox Hill Formation (Lenoxian, Late Wolfcampian) (Ross and Ross, 2003a,b), which is correlated broadly with the Artinskian (possibly early Artinskian) by conodonts and fusulinoideans (Davydov, 1996; Wardlaw and Davydov, 2000; Ross and Ross, 2003a). This species was first described by Dunbar and Skinner (1937) from the uppermost part of the Wolfcamp Formation (Wolfcampian) of the Glass Mountains and Hueco Mountains in Texas and attributed originally to *Schwagerina*. As Ross and Ross (2003a,b) recently admitted, however, *Schwagerina linearis* can be assignable to the genus *Eoparafusulina*.

Williams (1963) established *Monodiexodina bispatulata* based on specimens from the Hueco Canyon Formation of the Hueco Mountains in Texas, USA, which is correlated with the upper part of the Nealian of Early Wolfcampian (Wahlman, 2000), thus permitting correlation with approximately the Sakmarian (Wardlaw and Davydov, 2000). This species has an elongated subcylindrical shell and dense axial fillings. Nealian *Monodiexodina bispatulata* is morphologically closely related with Lenoxian *Eoparafusulina linearis* (Dunbar and Skinner), and thus would be subsumed in *Eoparafusulina*, although dense axial fillings in *M. bispatulata* could be rather disparate in this genus. In lesser possibility, the species may be referable to *Pseudofusulina*.

Besides *Monodiexodina bispatulata*, Williams (1963) considered that *Schwagerina steinmanni* originally described by Dunbar and Newell (1946b) from the Copacabana Group in Bolivia and *Schwagerina paralinearis* established by Thorsteinsson (in Harker and Thorsteinsson, 1960) from the Belcher Channel Formation of the Grinnell Peninsula, Canadian Arctic, are also referable to the genus *Monodiexodina*. Both species have elongated cylindrical to subcylindrical shells and regularly fluted septa. Their gross shell morphologies as well as their potential late Wolfcampian ages suggest, however, that these two forms can be included in the genus *Eoparafusulina*. At least from chronologic and paleobiogeoghraphic points of view, there is no good evidence that shows direct phylogenetic relation between the two forms under discussion and Eurasian true *Monodiexodina*.

Fusulina prolongada originally reported by Berry (1933) from Bolivia is one of the Andean species that has once been assigned to the genus *Monodiexodina* by Choi (1973). Although, Berry (1933) originally illustrated only few specimens, Dunbar and Newell (1946b) later gave better description and illustration of this old species based on specimens from the Wolfcampian-equivalent part of the Copacabana Group (Dunbar and Newell, 1946a). Similar to the case of *Schwagerina steinmanni* Dunbar and Skinner, *F. prolongada* can also be included in the genus *Eoparafusulina* although it has a more elongated shell than typical *Eoparafusulina* species. Wood et al. (2002) also conceded this generic reassignment.

In the generic comparison of *Eoparafusulina* with *Monodiexodina*, Ross (1967b) noted that *Parafusulina peruana* reported by Roberts (1949) from the top of the Copacabana Group of Peru is also included in *Monodiexodina* in addition to other western hemisphere species such as *M. linearis* (Dunbar and Skinner), *M. prolongada* (Berry), and *M. bispatulata* Williams, all of which, as mentioned above, I assigned to *Eoparafusulina* in the present taxonomy. This Andean species under discussion has a subcylindrical shell with a form ratio up to about 5.0, well-defined tunnel, and regularly fluted septa. Morphologically, *P. peruana* is definitely more closely related with two other Andean *Eoparafusulina* species, *Fusulina prolongada* and *Schwagerina steinmanni*, and thus should be subsumed in the genus *Eoparafusulina*. Recent study of Copacabana fusulinoideans by Wood et al. (2002) also approved this generic reassignment.

Ross and Dunbar (1962) reported *Monodiexodina* cf. *paralinearis* (Thorsteinsson) from the lower part of the Upper Marine Group in Northeast Greenland, which has been broadly correlated with the *Pseudoschwagerina* Zone of the early Early Permian Wolfcampian (Dunbar et al., 1962). The illustrated specimen has a subcylindrical, symmetrical shell with a form ratio of about 4.0 and more or less regularly fluted septa except for the central part of shell. Just as the types of this species from the Canadian Arctic, the Greenland specimen should also be included in the genus *Eoparafusulina*.

3.2.2. Eastern Hemisphere forms

In Japan, Kanmera and Mikami (1965) reported *Monodiexodina* (*Ferganites*) *langsonensis* (Saurin) from the lower subformation of the Sakamotozawa Formation (Sakmarian-Artinskian) of the South Kitakami Belt. This species, originally described by Saurin (1950) from the Ky-Lua Limestone of Langson, Viet Nam, is potentially included in neither *Ferganites* nor *Monodiexodina*. *Ferganites* is an essentially Kasimovian–Gzhelian (Pennsylvanian/Late Carboniferous) genus (Villa and Ueno, 2002), which also prevailed, like *Monodiexodina*, in relatively high-energy, sandy (or siliciclastic) calcareous environments (Villa and Bahamonde, 2001). The Sakamotozawa species of a probable Sakmarian age has a less elongated shell than typical *Monodiexodina*, and is better referable to the genus *Eoparafusulina*.

In Southeast Asia, Toriyama (1975) reported *Monodiexodina* sp. from the late Kubergandian *Maklaya pamirica* Zone of the Saraburi Limestone exposed in the Khao Phlong Phrab area, Changwat Sara Buri, Central Thailand. This area is located in the western part of the Cathaysian Indochina Block. The Khao Phlong Phrab form has a less elongated shell and less regularly fluted septa, and is closer to the genus *Pseudofusulina* rather than *Monodiexodina*.

Ingavat and Jumnongthai (1988) illustrated *Monodiexodina* sp. from a small section along Nam Mae Heo near Wang Nua, Changwat Lampang, North Thailand. The fusulinoideans were found from argillaceous limestone interbedded with siltstone and shale just above a fossiliferous gray limestone bed yielding late Asselian–Sakmarian, large and spherical *Sphaeroschwagerina* (which Ingavat and Jumnongthai, 1988 identified as *S. glomerosa*). The illustrated specimens of *Monodiexodina* sp. show characteristically stable tunnels and regularly fluted septa, but their shells with form ratios of about 4.0 are definitely less elongated compared with typical *Monodiexodina* species such as *M. shiptoni* (Dunbar). These morphological features suggest that the specimens from Wang Nua should be better included in the genus *Eoparafusulina*.

Two species of *Monodiexodina*, *M. shiptoni* (Dunbar) and *M. kattaensis* (Schwager) were described by Igo et al. (1979) from the Sumalayang Limestone Member of the Dohol Formation exposed in the Sungei Sedili area, Johore, Peninsular Malaysia. The locality belongs geotectonically to the East Malaya Block, which, at Permian time, would be close paleogeographically to the Cathaysian Indochina Block (Metcalfe, 1988, 2002). These Malaysian forms have elongated fusiform/subcylindrical shells and regularly fluted septa, which may be suggestive these two being potentially referable to *Monodiexodina*. They, however, are better subsumed in the genus *Pseudofusulina* judging from their gross morphology. The apparent, elongated fusiform/subcylindrical shell shape of these two forms would be due to slight deformation.

Kahler (1974) reported *Monodiexodina kattaensis* (Schwager) and *M. ferganica* (Miklukho-Maklay) from two localities near Keping (Kelpin) in the northwestern margin of the Tarim Basin, Northwest China. They have moderately elongated subcylindrical shells with more or less regularly fluted septa and clear tunnel. These shell features may actually be somewhat suggestive of these two forms to be potentially referable to the genus *Monodiexodina*, but their shells are definitely smaller and less elongated than those of typical *Monodiexodina* species. Moreover, Chang (1963a,b) and Zhu and Zhang (1987) reported a good number of Late Carboniferous-Early Permian fusulinoideans from the Keping area, which enable us to have a better overview on Early Permian fusulinoidean assemblages in this area. These papers described many *Eoparafusulina* species, some of which, such as *Triticites subashiensis* Chang in Chang (1963a), *Schwagerina pailensis* (Schwager) in Chang (1963b), and *E. thompsoni* Skinner and Wilde in Zhu and Zhang (1987), have almost symmetrical, elongated subcylindrical shells somewhat similar to Kahler's (1974) species. These lines of evidence lead to a conclusion that the specimens described by Kahler (1974) can be included in the genus *Eoparafusulina*.

In Middle Asia, Bensh (1972) once assigned *Parafusulina ferganica* established by Miklukho-Maklay (1949) from the Sakmarian of South Fergana to the genus *Monodiexodina*. Later Davydov (1988a,b) put this species into the genus *Ruzhenzevites*. However, this Middle Asian form has a smaller proloculus and more tightly coiled (thus less uniformly expanded) inner volutions than typical *Ruzhenzevites* species. These morphological features are more common in *Eoparafusulina* rather than *Ruzhenzevites*. Moreover, it somewhat resembles *Alaskanella linearis* (Dunbar and Skinner) reported by Han (1980b) from the Amushan Formation (Asselian-Sakmarian) of Xiwuzhumuxinqi in Inner Mongolia, Northeast China, and is considered to be probably conspecific. In the present taxonomy, this Inner Mongolian form is subsumed in *Eoparafusulina* (see discussion below in this section), and thus *Parafusulina ferganica* can also be included in this genus.

Monodiexodina? *domarensis* originally described by Wang et al. (1981) from the Chihsian Tunlonggongba Formation (Bolorian-early Murgabian) at Lungmuco of the Lutog area, western Tibet, Southeast China, has a large and elongated cylindrical shell with regular tunnel. But this species has weaker and less regular septal fluting than typical *Monodiexodina*. *Monodiexodina*? *domarensis* is highly probably referable to the genus *Pseudofusulina*, or in lesser possibility, to *Eoparafusulina*. As noted earlier, specimens of *M. domarensis* reported by Yang et al. (1990) from Doumar of Lutog and *M.*? *domarensis* illustrated by Zhang (1998) from the south of Kongkashankou of Lutog are not conspecific with the types. They both can be identified to be *M. shiptoni* (Dunbar).

Solov'eva (1991) reported three species of elongated subcylindrical schwagerinids from the Lower Permian of Bayrim-Obo, about 30 km southwest of Dzamyn-Ude railway station, southern Mongolia. They consist of *Monodiexodina linearis* (Dunbar and Skinner) and two new species; *M.*? *monstruosa* and *M. oksanae*. Solov'eva (1991) originally referred these forms to the Sakmarian–Artinskian, probably because of the conventional view of chronostratigraphic distribution for *Monodiexodina*. According to the stratigraphic description by Suetenko et al. (1991) in the same volume that Solov'eva (1991) involved, these three forms occur right above the beds yielding middle Asselian fusulinoideans such as *Pseudoschwagerina* ex gr. *beedei* Dunbar and Skinner, *P. extensa* Kahler and Kahler, *P. uddeni* (Dunbar and Kniker), and others. At the same time, however, the *Monodiexodina*-bearing beds are overlain by strata containing *Pseudoschwagerina* species such as *P.* ex gr. *robusta* (Meek) and *P. uddeni*. This biostratigraphic information strongly suggests that the *Monodiexodina*-bearing beds in Bayrim-Obo are referable to the late Asselian (or may possibly be to the early Sakmarian) rather than the Sakmarian–Artinskian.

Among the three species described by Solov'eva (1991), at least *Monodiexodina linearis* is considered to be conspecific with *Alaskanella linearis* (Dunbar and Skinner) and *A. magna* Han (MS) reported by Han (1980a,b) from the Amushan Formation of Xiwuzhumuxinqi in Inner Mongolia, Northeast China, and further probably with aforementioned *Parafusulina ferganica* by Miklukho-Maklay (1949) from South Fergana in Middle Asia. These Eurasian forms and the original *Eoparafusulina linearis* from West Texas share many similar morphological features, and thus seem to form a unique morphological group in the genus *Eoparafusulina*, although it is slightly less clear whether or not these *linearis*-like, elongated subcylindrical forms from Eurasia are really conspecific with the types originally proposed by Dunbar and Skinner (1937).

The Amushan Formation is now correlated to the Asselian to the Sakmarian (Editorial Committee of Stratigraphic Lexicon of China, 2000). As the two Inner Mongolian forms reported by Han (1980a,b) occur in beds with *Pseudoschwagerina* species, they can be more probably referable to the middle-late Asselian (or may possibly be to the early Sakmarian). Regardless of their specific identities with true *linearis* from West Texas, these Eurasian forms discussed herein, together with two other species newly proposed by Solov'eva (1991), are clearly older than true *Monodiexodina*. They are better subsumed in the genus *Eoparafusulina* rather than *Monodiexodina* from the phylogenetic point of view, together with the gross morphological features that they have slightly more irregular nature of septal fluting, less strongly fluted septa in the central part of shell, and smaller shells than typical *Monodiexodina* species.

4. Paleobiogeography of *Monodiexodina*

The genus *Monodiexodina* has been paid special attention in the context of Permian fusulinoidean paleobiogeography (e.g. Han, 1980a; Ishii et al., 1985; Ozawa, 1987; Igo, 1989; Ishii, 1990). However, largely because of the unavailability at the time of these earlier works of reliable Permian paleomap and the relatively poor status of geotectonic understandings for the relevant areas that accommodate *Monodiexodina*, it has been only in the last decade or so since the antitropicality or bitemperate paleobiogeographic nature of this genus became understood and discussed (Tazawa et al., 1993; Shi et al., 1995; Shi and Grunt, 2000; Ueno, 2003; Ueno and Tazawa, 2003).

Fig. 4 shows the paleogeographic distribution of *Monodiexodina* on a paleomap at around mid-Permian time. The base map is taken from Ziegler et al. (1998) and modified based on recent paleogeographic, paleobiogeographic, and geotectonic data by Tazawa (2000) and Heubeck (2001) for northwestern and northeastern parts of the Chinese continent and Japanese Islands, and by Charlton (2001), Metcalfe (2002), and Ueno (2003) for Southeast Asian small continental blocks and the northern part of Sahulland (Australia and its northen shelf area). As has been already discussed by Ueno (2003) and Ueno and Tazawa (2003), the *Monodiexodina*-bearing localities summarized in the precedent section can be reconstructed in this paleomap in either northern (around the North China and Mongol-Breya blocks) or southern (in the Cimmerian continent and northern marginal Gondwanaland) middle latitudes. These two middle latitudinal areas in different hemispheres during Permian time almost correspond to the Northern and Southern Transitional Zones of Shi et al. (1995), respectively.

The *Monodiexodina*-bearing localities in the Northern Transitional Zone include those in South Primorye, Northeast China, and the South Kitakami Terrane (defined by Tazawa, 2004) of the Japanese Islands. These areas further correspond to the Inner Mongolian–Japanese Transitional Zone of Tazawa (1991) and/or the Sino-Mongolian–Japanese Province of Shi et al. (2002) recognized by brachiopod faunas, where broadly mixed, Boreal (cold water) and Tethyan/Cathaysian (warm water) faunas had prevailed during Permian time. This zone would be located within a temperate paleoclimatic belt just between the northern arctic-subarctic Boreal realm and the southern tropical-subtropical Tethyan realm, and is estimated to be within 25–40° N paleolatitude in analogy to modern latitude-dependent biogerographic zonation pattern (Shi et al., 2002).

In the Southern Transitional Zone, *Monodiexodina* is mainly distributed in the eastern part of the Cimmerian continent (SE Pamir, Qiangtang Block in the easternmost Karakorum and Tibet, and Sibumasu Block), which, according to Ueno et al. (2002), separated from mainland Gondwanaland at around Artinskian time. Among these

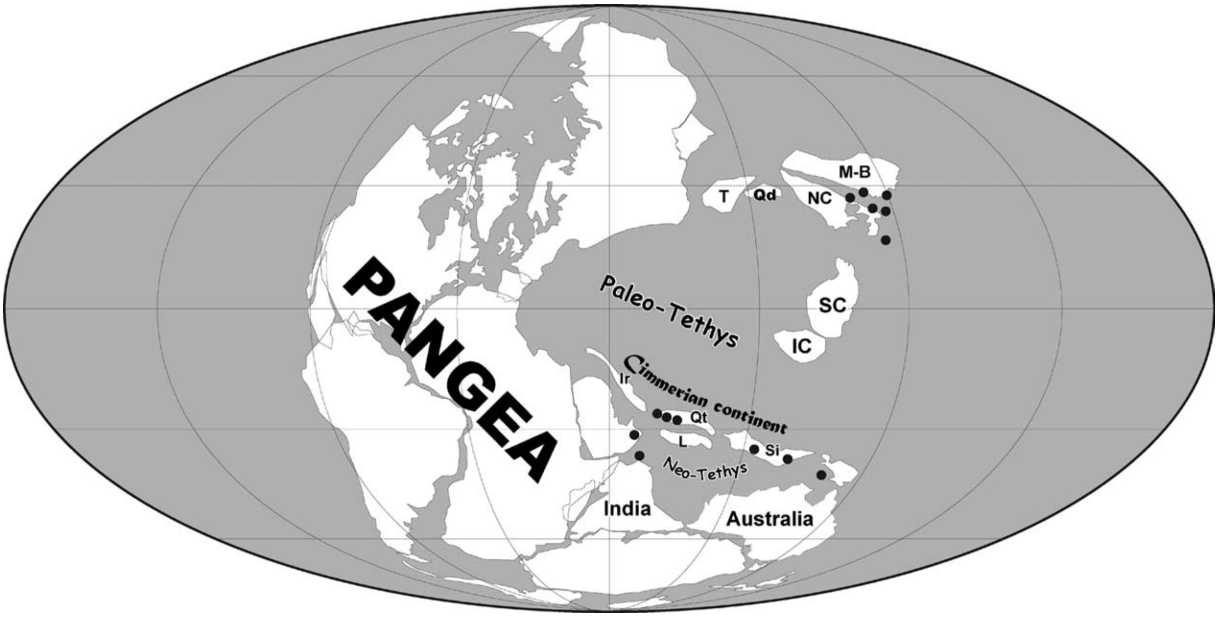

Fig. 4. Paleobiogeographic distribution of *Monodiexodina* (black circle). Paleomap at around mid-Permian time based on Ziegler et al. (1998), with modifications based on data from Tazawa (2000) and Heubeck (2001) for northwestern and northeastern parts of Chinese continent and Japanese Islands, and from Charlton (2001), Metcalfe (2002), and Ueno (2003) for Southeast Asian small continental blocks and Australia. T: Tarim, Qd: Qaidam, M-B: Mongol-Breya, NC: North China, SC: South China, IC: Indochina, Ir: Iran (including Transcaucasus and South Afghanistan), Qt: Qiangtang (including South east Pamir and Karakorum), L: Lhasa, Si: Sibumasu (including Baoshan and Tengchong in West Yunnan, Southwest China).

eastern Cimmerian areas, it is known that Gondwana glaciation had widely prevailed in the Qiangtang and Sibumasu blocks during early Early Permian (pre-Artinskian) time, forming characteristic glaciogene diamictites (e.g. Stauffer and Lee, 1986; Yin, 1997). This suggests a slightly higher southern latitudinal position of the eastern Cimmerian blocks than the remaining western ones (Ueno, 2003), implying a late Early or early Middle Permian approximate paleoposition of the former areas to be within southern middle latitudes. This time interval almost corresponds to when *Monodiexodina* flourished in the Southern Transitional Zone.

The remaining three *Monodiexodina* localities in the Southern Transitional Zone are documented in marginal Gondwanan (or marginal Neo-Tethyan) areas in a broad sense. The first is Timor, which was located in mid-Permian time at the deep eastern part of the newly created Neo-Tethys Ocean. This area was situated in late Early to early Middle Permian time in southern middle latitudes on the northern margin of the Australian Craton (See Charlton et al., 2002, for the Permian paleoposition of Timor). The second is the Salt and Kishor Ranges in NE Pakistan, which have been reconstructed to locate on the northwestern margin of the Indian Craton. The third is Oman at the southeastern margin of the Arabian Plate. In most paleogeographic reconstructions in around mid-Permian time (Golonka et al., 1994; Scotese and Langford, 1995; Ziegler et al., 1998; Stampfli, 2000) locate these marginal Gondwanan areas in southern middle latitudes of approximately 30–40° S.

In brachiopod and some other fossil groups, the Southern Transitional Zone is broadly characterized by the mixture of cool/cold Gondwanan elements and warm Tethyan/Cathaysian ones (Shi et al., 1995). These lines of evidence mentioned above are strongly suggestive that all these *Monodiexodina*-bearing localities in the Southern Transitional Zone can be interpreted to be located in a southern hemispheric temperate climatic belt in around mid-Permian time, forming a coherent single paleobiogeographic domain between high latitudinal Gondwanan (cool/cold water) realm and paleo-equatorial Tethyan/Cathaysian (warm water) realm.

In conclusion, it is clearly demonstrated that *Monodiexodina* had a distribution within mesothermal climatic belts between high latitudinal cool/cold-water climatic realms and paleo-tropical warm-water realm in two hemispheres during Permian time. In some previous studies, *Monodiexodina* was interpreted as a 'cool-water' fusulinoidean genus (Metcalfe, 1988) or a warm-water one (Basir Jasin, 1991). Neither would be correct, however, judging from the distribution pattern of the genus. It is best characterized paleobiogeographically to be an antitropical, bitemperate taxon.

5. Phylogeny of *Monodiexodina*

As reviewed and discussed in the earlier sections, which is summarized in Fig. 5, *Monodiexodina* has slightly different chronostratigraphic ranges in the Northern and

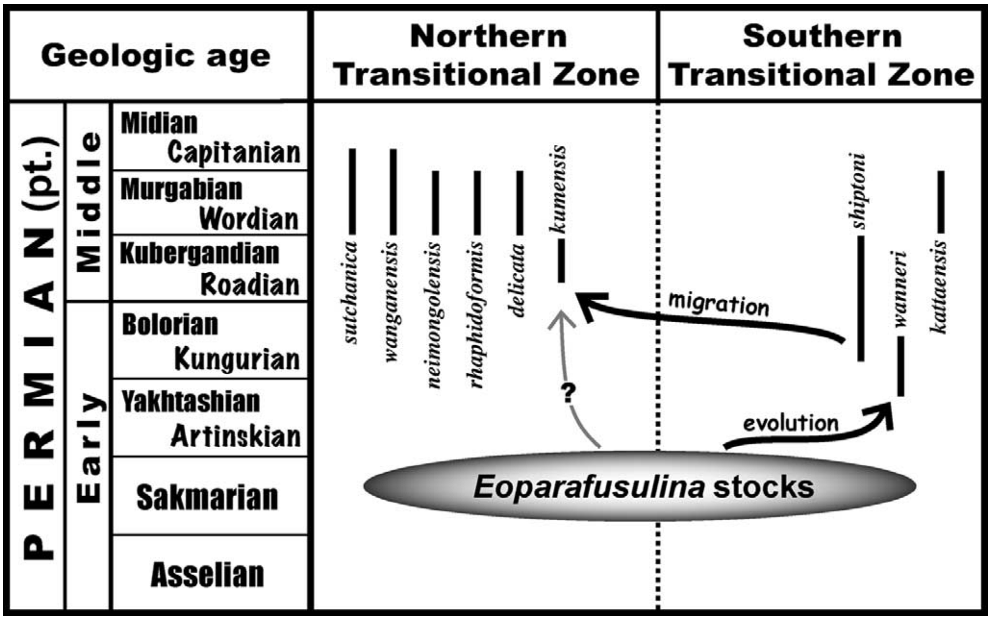

Fig. 5. Chronostratigraphic ranges of *Monodiexodina* species in Northern and Southern Transitional Zones, and schematic reconstruction of phylogeny and evolution of *Monodiexodina*. Permian chronostratigraphic terminology and correlation based on Jin et al. (1997) and Wardlaw et al. (2004).

Southern Transitional Zones, respectively. *Monodiexodina wanneri* (Schubert), the earliest species of the genus, occurred in around Artinskian/Bolorian boundary time and the genus mainly flourished in the Bolorian and Kubergandian in the Southern Transitional Zone, although one species, *M. kattaensis* (Schwager), is reported from the Murgabian. In contrast, the genus is known in the Northern Transitional Zone in slightly but definitely younger stratigraphic levels, ranging from the upper Kubergandian to the lower Midian.

This diachronic occurrence clearly indicates that the genus *Monodiexodina* originated in the Southern Transitional Zone in the late Early Permian and probably migrated later into the Northern Transitional Zone at around Early/Middle Permian boundary time (Fig. 5). The concrete migration mechanism is, however, still highly equivocal. For coeval brachiopod faunas, Shi and Grunt (2000) proposed four promising scenarios for the explanation of antitropically distributed genera. For the case of *Monodiexodina* distribution, two of the four scenarios, the stepping-stone migration through the eastern Paleo-Tethys and the shelf migration along the western coast of the Paleo-Tethys, would be applicable to some extent, although this genus has been reported from neither eastern Pangean shelves nor Cathaysian shelves.

With respect to the infra-generic taxonomy of *Monodiexodina*, Choi (1973) recognized two morphologically distinct species groups in the genus; the *M. sutchanica* group and the *M. kattaensis* group. The former includes *M. matsubaishi* (Fujimoto) and *M. shiptoni* (Dunbar) in addition to *M. sutchanica* (Dutkevich). The latter consists, apart from the nominal species, of *M. wanneri* (Schubert), *M. wanganensis* Sosnina, and several other American species that are excluded from the genus in this study, such as '*M.*' *bispatulata* Williams, '*M.*' *prolongada* (Berry), and '*M.*' *steinmanni* (Dunbar and Skinner). He further concluded that the *M. kattaensis* group is intermediate between typical *Monodiexodina* (represented by *M. sutchanica* group) and *Parafusulina*, implying a mutual ancestor-descendant relation of these two genera.

Han (1980a) essentially followed Choi's (1973) idea on the infra-generic distinction of *Monodiexodina*. He considered that the *M. kattaensis* group was derived from the '*Alaskanella*' *yukonensis* group, and the *M. sutchanica* group from the '*A.*' *linearis* group, and further concluded that the *M. kattaensis* group appeared slightly earlier than the *M. sutchanica* group (see Table 2 of Han, 1980a).

However, these conclusions in both Choi (1973) and Han (1980a) are not readily corroborated by existing data. As summarized in the precedent sections and in Fig. 5, the Northern and Southern Transitional Zones, respectively, are considered to have essentially different species compositions in *Monodiexodina*. This strongly suggests that the two species groups that Choi (1973) and Han (1980a) assumed are not existent from taxonomic viewpoint because they would not reflect the infra-generic phylogeny of *Monodiexodina*. Moreover, detailed taxonomic scrutiny have made clear that the first two *Monodiexodina* species are found in the upper Lower Permian of the Southern Transitional Zone; that is *M. wanneri* and *M. shiptoni*, which are, according to Choi (1973) and Han (1980a), the representatives of two different species groups in *Monodiexodina*. But any '*Alaskanella*' species that is regarded as the ancestor of *Monodiexodina* in Han's (1980a) phylogenetic scenario has not been reported from the Early Permian of the Southern Transitional Zone.

The direct ancestor of *Monodiexodina* is still not very clearly understood, but it must exist in the early Early Permian in around the Southern Transitional Zone judging from the probable southern hemispheric (marginal Gondwanan or Neotethyan) origin of the genus. In the Sakmarian or early Artinskian of the Southern Transitional Zone, there are several *Eoparafusulina* species that have elongated subcylindrical shells with more or less regularly arranged septal loops, which, as a whole, remind us of some morphologic and thus phylogenetic relationships with *Monodiexodina*. The candidate forms are, for example, *E. tibetica* reported by Nie and Song (1983) from Tibet and *E. pamirensis* Leven, *E.* aff. *mendenhalli* Petocz, and *E. laudoni* (Skinner and Wilde) reported by Leven (1993b) from the Central Pamir. They however, do not have strong axial fillings like *E. linearis* (Dunbar and Skinner).

Although, morphologically more similar and chronologically somewhat appropriate they may be, such forms as *Eoparafusulina linearis* (Dunbar and Skinner), *E. prolongada* (Berry), *E. yukonensis* (Skinner and Wilde), and *E. paralinearis* (Thorsteinsson) in the western hemisphere and *E. ferganica* (Miklukho-Maklay) and the elongated subcyrindrical *Eoparafusulina* reported by Han (1980a,b) and Solov'eva (1991) from the Northern Transitional Zone would not be suitable for the potential ancestor of *Monodiexodina* because of different paleobiogeographic distribution. These *Eoparafusulina* species have been mostly referable to the Sakmarian and early Artinskian, and also often documented to have unique occurrences in sandy calcareous sediments. They have been reported from the Midcontinent-Andean realm, exotic blocks in western North American terranes (which have intra-Panthalassan origin), and several localities in the Northern Transitional Zone. Moreover, *Pseudofusulina*? *perplexa* and *P. tschernyschewi* forma *oblonga* reported by Grozdilova and Lebedeva (1961) from the Tastubian (early Sakmarian) of North Timan, Russia, also may probably be involved in this kind. They, however, never dispersed into the Southern Transitional Zone in Sakmarian–Artinskian time, in which the potential ancestor of *Monodiexodina* should exist. Because the genus *Eoparafusulina* itself is not always found only in sandy facies in a crowded, monotypic manner but also in normal limestone together with other fusulinoideans, and because the relevant Eoparafusulinas, even granting them to have very elongated shells indubitably, did not accomplish form ratios of 7.0–10.0 that are commonly found in *Monodiexodina*, these especially elongated forms in *Eoparafusulina* found in western hemisphere and the Northern Transitional Zone are interpreted to constitute merely one of specialized phylogenetic branches within the genus. These Eoparafusulinas, just like *Monodiexodina*, were adapted particularly to the sandy, high-energy condition but can be considered to have had no direct phylogenetic relationship with early *Monodiexodina* species in the Southern Transitional Zone. *Monodiexodina* and the especially elongated *Eoparafusulina* with definite axial fillings typically represented by *E. linearis* can be best interpreted as homeomorphs adapted to special sandy facies in schwagerinids.

The first *Monodiexodina* in the Northern Transitional Zone is found in the upper Kubergandian. Thus, with respect to the origin of Northern Transitional Zone *Monodiexodina*, it is less likely that it was derived directly from early Early Permian, highly elongated eoparafusulinids (such as '*Alaskanella*' *linearis* reported by Han, 1980b) because there is no intermediate or transient form in the upper Lower and lowermost Middle Permian (Artinskian to Kubergandian) of the Northern Transitional Zone. Uncertain migration mechanism notwithstanding, the most plausible scenario for the origin of the *Monodiexodina* species in the Northern Transitional Zone is of migration from the Southern Transitional Zone (Fig. 5).

In summary on the phylogeny and evolution of *Monodiexodina* (Fig. 5), the genus originated in the Southern Transitional Zone from a highly elongated *Eoparafusulina* stock at around late Early Permian time. It flourished in southern middle latitudinal areas in latest Early and early–middle Middle Permian time. The genus then migrated to the northern hemisphere (Northern Transitional Zone) by unknown dispersion mechanism at around the early Middle Permian, and prevailed there during middle-late Middle Permian time.

6. Paleoecology of *Monodiexodina*

It has long been recognized that *Monodiexodina* has a unique mode of occurrence among fusulinoidean genera. Most fusulinoideans are found in normal, less terrigenous, rather pure limestone. In contrast, *Monodiexodina* almost exclusively occurs in highly arenaceous sediments, both in quartz-rich calcareous sandstone (and/or sandy limestone) and highly packed, coarse grainstone/rudstone. In addition, *Monodiexodina* tends to form a monospecific assemblage in particular beds with its tests being densely crowded (Fig. 6, and see also Douglass, 1970; Ingavat and Douglass, 1981; Tazawa et al., 1993; Ueno and Tazawa, 2003, 2004; Ueno et al., 2005, for the typical mode of occurrence of *Monodiexodina* species). Although, of course, this cannot be attributed to represent an autochthonous mode of occurrence of *Monodiexodina*, it is highly probable that this genus was adapted to particularly high-energy, shallow-marine conditions with steady current and/or wave actions (Igo, 1989), such as like sand shoal and sand beach. *Monodiexodina*-bearing beds commonly represent current-laid and/or wave-generated parallel and/or cross-beddings (e.g. Kawamura and Machiyama, 1995), showing uni-directional alignment of their tests (Fig. 6A). These lines of sedimentological evidence are consistent with the mentioned paleoecologic interpretation.

In schwagerinid fusulinoideans, there have been known several, elongated cylindrical (cigar-like) to fusiform genera with strong polar torsion, namely *Ferganites*

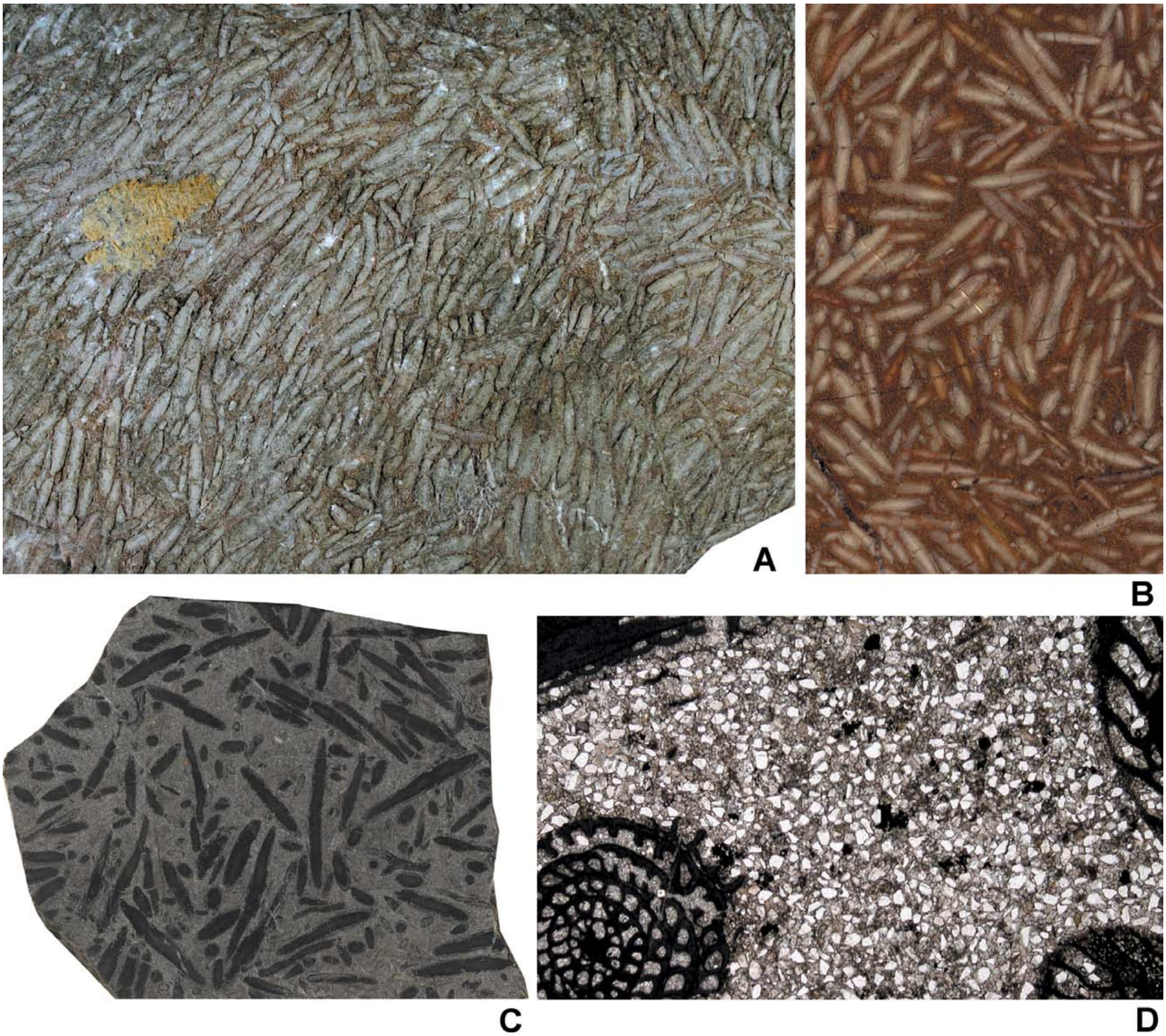

Fig. 6. Two examples showing typical mode of occurrence of *Monodiexodina*. A, B, Crowded occurrence of *Monodiexodina* from Oinlasi in Timor Island, Indonesia. A: Weathered rock surface almost parallel to bedding plane, showing uni-directional alignment of *Monodiexodina* (*M. wanneri*) tests, ×1. B: Polished slab; intra-fusulinoidean space is filled by well-sorted, sand-sized calcareous grains (mostly crinoid ossicles and bryozoan fragments) and small particles of iron oxides (which gives this limestone its distinctive red color) cemented by well-developed sparry calcite (mostly burial cement), ×1. C, D, *Monodiexodina* swarming in calcareous sandstone from Bukit Wang Pisang in Perlis, northwestern Peninsular Malaysia. C: Polished slab; darker-colored grains are mostly *Monodiexodina* (*M. shiptoni*) tests and some bryozoan and brachiopod fragments, ×1. D: Photomicrograph showing enlarged view of intra-fusulinoidean space, which is essentially filled by abundant sub-angular detrital quartz grains cemented by calcareous material, ×18.

Miklukho-Maklay, 1959; *Ruzhenzevites* Davydov (in Chuvashov et al., 1986); and *Monodiexodina* under consideration herein. Moreover, some elongated subcylindrical Eoparafusulinas, such as *E. linearis* (Dunbar and Skinner) and *E. allisonensis* Ross,) can also be involved in this morphologic category. *Ferganites* and *Ruzhenzevites*, and the relevant *Eoparafusulina* also usually exhibit the similar diagnostic feature described above to *Monodiexodina* in their mode of occurrence. That is, they particularly occur in terrigenous material-rich, high-energy sandy sediments (Ross, 1967b; Davydov, 1988a; Villa and Bahamonde, 2001; Ross and Ross, 2003a).

According to Leppig (1992), polar torsion is very effective for elongated subcylindrical to fusiform schwagerinids to increase antethecal spaces in polar regions, which generally have a smaller distance between two septal pores than other parts of a test. In these schwagerinids represented typically by *Monodiexodina*, this morphological feature would result in producing particularly abundant septal pores in the polar regions, thus increasing potential to develop more pseudopodia on both sides of test. It must have a functional significance for not only locomotion but also anchoring their tests tightly on the surface of bottom sediments in agitated water conditions.

The mode of occurrence of *Monodiexodina* strongly suggests that it was adapted to shallow-marine, high-energy environments. This ecological feature would be essentially maintained by the acquisition of the above-mentioned shell morphology. The genus itself is considered to be a rather long-ranging taxon, spanning from the late Artinskian to the early Midian. Thus, it is concluded that this genus had an opportunistic character, occurring repeatedly only when favorable, high-energy conditions, such as sand shoal, appeared in warm temperate climatic belts in both hemispheres.

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