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Global Distribution of Permian Conulariids and Palaeobiogeographical Implications

Elizabeth A. Weldon and G.R. Shi

School of Ecology and Environment, Deakin University, Melbourne Campus, 221 Burwood Highway, Burwood, Victoria 3125, Australia, E-mail: eweldon@deakin.edu.au

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Abstract

Previously, minimal work has been carried out on conulariids due to their rare occurrences and resultant biostratigraphical limitations. The palaeobiogeographical distribution of Permian conulariids suggests that they have a marked preference for cold to cool-water regions, that they are significant indicators for migration patterns, and that they can potentially provide information on the palaeogeographical configuration and movement of terranes. Permian conulariids are found in Australia, India, New Zealand, Pakistan, Iran, Afghanistan, Kashmir, China, Japan, Russia, Germany, Canada, United States of America, and Bolivia. The diversity of Permian conulariids is markedly higher in the polar regions than in the palaeoequatorial region.

Permian conulariid genera include *Notoconularia* Thomas 1969, *Gondaconularia* Waterhouse 1986, *Cheliconularia* Waterhouse 1986, *Neoconularia* Sugiyama 1942, *Calloconularia* Sinclair 1952, *Diconularia* Sinclair 1952, *Paraconularia* Sinclair 1940, *Mesoconularia* Boucek 1939 and *Conularia* Sowerby 1821. This paper describes two new species of conulariids: *Diconularia meadepeakensis* sp. nov. from the Phosphoria Formation (Guadalupian), Idaho, USA and *Paraconularia kazanensis* sp. nov. from the Sokian Horizon (?Roadian), Volga Region, Russia.

Key words: Conulariids, Permian, palaeobiogeography, bipolar, bitemperate.

Introduction

Permian conulariids have not been widely studied and much of the older taxonomic work needs revision. Prior to 1939, all Permian conulariids were associated with the long-ranging genus *Conularia* Sowerby, 1821. In 1939, Boucek made a first attempt to subdivide the genus *Conularia*. This was followed by Sinclair's proposal of *Paraconularia* (1940) and Sugiyama's 1942 subdivision of *Conularia* into 5 subgenera, which were subsequently elevated to generic level by Sinclair (1952). In 1948, Branson continued to call all Permian conulariids *Paraconularia*, omitting Sugiyama's 1942 Permian genus *Neoconularia*. Taxonomic work in the 1960s and 1980s has led to the development of a number of new Permian genera including *Notoconularia* (Thomas, 1969), *Gondaconularia* (Waterhouse, 1986) and *Cheliconularia* (Waterhouse, 1986).

Currently, Permian conulariid genera include: *Notoconularia* Thomas, 1969; *Gondaconularia* Waterhouse, 1986; *Cheliconularia* Waterhouse, 1986; *Neoconularia* Sugiyama, 1942; *Calloconularia* Sinclair, 1952; *Paraconularia* Sinclair, 1940; *Mesoconularia* Boucek, 1939; *Diconularia* Sinclair, 1952 and *Conularia* Sowerby, 1821. Although the genus *Conularia* was widely used in older literature many of the descriptions appear to suggest that the specimens are more closely related to *Paraconularia*, except perhaps the *Conularia* species from Russia described by Zavodowsky (1960, 1968) and Zavodowsky et al. (1970). Therefore, for the purpose of this study we have placed *Conularia* specimens not revised post 1952 in *Paraconularia* until further taxonomic work is conducted.

Correspondingly, relatively little work has been published on the palaeobiogeography of Permian conulariids. Waterhouse (1979) conducted a study on the global distribution of Permian conulariids and noted that they exhibited a marked preference for cold-cool temperate waters. Murata and Golshani (1981) noted that the Iranian species strongly resembled species from Australia and Pakistan, which could be considered significant for understanding the palaeogeography of the Palaeotethys. Further taxonomic work must be conducted on both the Iranian material and specimens from the Salt Range and Himalayas to provide a more informative account of the palaeobiogeographical affinity of these conulariids and the implications this places on the palaeogeography of the Palaeotethys.

Palaeobiogeography

The Permian is well known for its marine provincialism especially in the early Permian. In general, three distinct realms are readily recognizable in view of the distribution of brachiopod faunas: the Gondwanan Realm, the Boreal Realm, and the Palaeoequatorial Realm (Waterhouse and Boham-Carter, 1975; Grunt and Shi, 1997; Shi and Grunt, 2000). In addition, zones or areas with distinctly mixed cold-water and warm-water brachiopod faunas between the Gondwanan and Palaeoequatorial Realms and between the Boreal and Palaeoequatorial Realms have also been recognized. These zones have been named transitional biogeographical regions or provinces (Tazawa, 1991; Shi et al., 1995) (Fig. 1a). In a recent study on the global distribution and migration patterns of certain Permian brachiopod taxa, Shi and Grunt (2000) suggested a number of migration pathways and dispersal mechanisms including ocean currents, 'stepping-stone' migration, shelf upwelling along the western coast of Pangea, and tectonic vicariance. It appears that during the Permian conulariids were also primarily distributed in the cool-cold water regions of the globe and displayed similar migration patterns (Table 1; Fig. 1b-d).

There are currently two hypotheses documenting different modes of life for conulariids. Both hypotheses would allow for migration to easily take place along current paths, and have an effect on distribution patterns. The first hypothesis suggests that conulariids were pseudoplanktonic organisms (Babcock and Feldmann, 1984) which clustered together as adults and may have floated on ocean currents attached to seaweed or masses of jelly-like protoplasm. In contrast, the second hypothesis suggests that conulariids had a planktonic larval stage but a free swimming adult life was apparently impossible. An aggregate of larvae settled on substrate and the adults lived a sessile life attached by a disk or stalk (Brood, 1995).

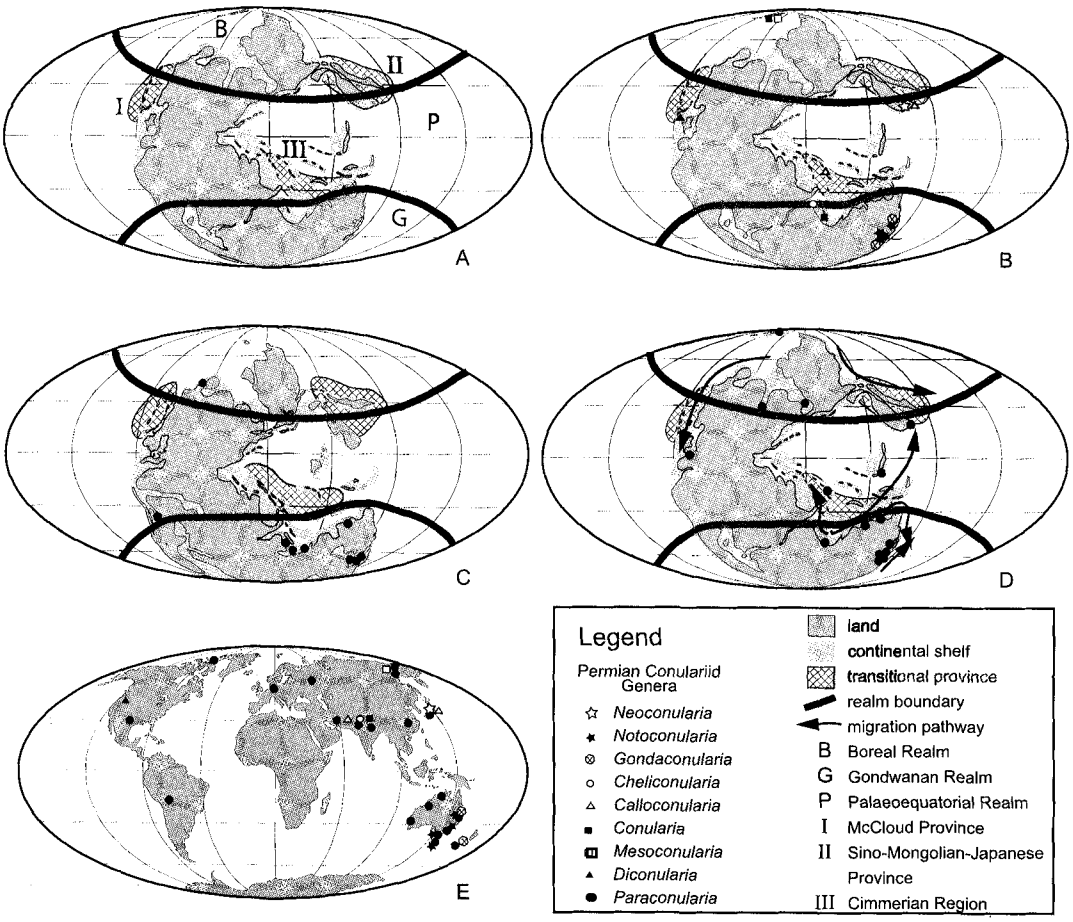


Fig. 1. Global distribution of Permian conulariids (Palaeogeographic reconstructions after Ziegler et al., 1997: Data from Table 1). A–Permian biogeographic realms and transitional provinces (Biogeographic boundaries; Shi, 1995). B–Global distribution of Permian conulariids (except *Paraconularia*) illustrating a marked preference for the Boreal and Gondwanan Realms and transitional provinces. C–Early Permian distribution of *Paraconularia* illustrating a bipolar distribution of the genus. D–Mid-late Permian distribution of *Paraconularia*, illustrating possible migration pathways of the genus from the early Permian (1C) into bitemperate (transitional) regions, during the Mid-late Permian. E–Global geographic distribution of Permian conulariids.

Table 1. Stratigraphic and geographic distribution of Permian conulariids.

Species	Stratigraphic/Geographic Distribution	Age Range (after Jin et al., 1997)	Key References
Calloconularia? kitakamiensis Murata, 1967	Kitakami Mts, Japan	Kattisawa Stage (Wordian-Capitanian)	Murata, 1967; Minato et al., 1978
Calloconularia sp. Termier et al., 1974	Wardak, Afghanistan	Asselian	Termier et al., 1974
Cheliconularia cheliensis (Reed, 1936)	Salt Range, Pakistan	Olive Series, Cisuralian (?late Sakmarian)	Reed, 1936; Waterhouse, 1986
Conularia anuiensis Zavodowsky, 1968	Parenskiy Horizon, Bolshogo Anuya River Basin, Russia	early Sakmarian	Zavodowsky, 1968; Zavodowsky et al. 1970
Conularia gijigensis Zavodowsky, 1960	Dzigdalinskiy Horizon, Gijigi River Basin, Russia	Roadian	Zavodowsky, 1960; Zavodowsky et al., 1970
Conularia kaibabensis McKee, 1935	Coral: not a conulariid		
Conularia kolymaensis Zavodowsky, 1968	Burgalinskiy Horizon, Kolymy River Basin, Russia	Asselian	Zavodowsky, 1968; Zavodowsky et al., 1970
Conularia parenensis Zavodowsky, 1960	Parenskiy Horizon, Paren River Basin, Russia	early Sakmarian	Zavodowsky, 1960; Zavodowsky et al., 1970
Conularia snjatkovi Zavodowsky, 1960	Omolonskiy Horizon, Omolon River Basin, Russia	Wordian	Zavodowsky, 1960; Zavodowsky, et al. 1970
?Conularia sp. Chang, 1976	Selong Group, South Tibet	Wuchiapingian	Chang, 1976
Conularia vassetskyi Zavodowsky et al., 1970	Dziltinskiy Horizon, Omolon River Basin, Russia	Kungurian	Zavodowsky et al., 1970
Diconularia meadpeakensis sp. nov.	Phosphoria Fm, Park City Fm, USA	Roadian	Girty, 1910; This paper
Gondaconularia elviniaria Waterhouse, 1986	Elvinia Fm, Bowen Basin, Australia	Artinskian	Waterhouse, 1986
Gondaconularia? hollandi Waterhouse, 1986	Stephens Fm, Matai Group, NZ	Capitanian	Waterhouse, 1979; 1986
Gondaconularia? magnicosta Waterhouse, 1986	Brae Fm, Bowen Basin, Australia	Artinskian? (Wordian?)	Waterhouse, 1986
Mesoconularia omolonensis Zavodowsky et al., 1970	Parenskiy Horizon, Omolon River Basin, Russia	early Sakmarian	Zavodowsky et al., 1970
Neoconularia sp. (Hayasaka, 1963)	Kitakami Mts, Japan	Kattisawa Stage (Wordian-Capitanian)	Hayasaka, 1963; Minato et al., 1978
Neoconularia rectangularis (Hayasaka, 1920)	*Leptodus* Beds, Iimô, Kitakami Mts, Japan	Wordian-Capitanian	Hayasaka, 1920; Sugiyama, 1942; Minato et al., 1978
Notoconularia inornata (Dana, 1849)	East of Maydera, Unnamed Lmst. nr. Judbury, Tas; Bacchus Marsh Fm, Vic; Murree Fm, Broughton Fm, NSW; Australia	Artinskian – Wordian	Dana, 1849; De Koninck, 1877; Fletcher, 1938; Thomas, 1969; Parfrey, 1982
Notoconularia levigata (Morris, 1845)	"Erratic Zone" below Darlington Lmst, Darlington Lmst, Malbina Fm, Siltst River Ouse south of Waddamana, Tas; Allandale Fm, Maitland District, SE Bowen Basin; Australia	Sakmarian – Wordian?	Morris, 1845; Dana, 1849; Johnston, 1887; De Koninck, 1877; Laseron, 1911; Fletcher, 1938; Thomas, 1969; Parfrey, 1982
Notoconularia tenuistriata (McCoy, 1847)	Porter Hill Beds, Tas; Muree Fm, Ravensfield, Raymond Terrace, NSW; Gympie Beds, Qld; Australia	Cisuralian-Guadalupian	McCoy, 1847; De Koninck, 1877
Paraconularia abadehnsis Murata and Golshani, 1981	lower Julfa Bed, Kuh-e Hambast Central Iran	Wuchiapingian (Lopingian?)	Murata and Golshani, 1981
Paraconularia acutilirata (Fletcher, 1938)	Branxton, NSW, Australia	Guadalupian	Fletcher, 1938; Parfrey, 1982
Paraconularia arctica Babcock, 1988b	Assistance Fm, Devon Island, Canada	Wordian	Babcock, 1988b
Paraconularia crenulata (Fletcher, 1938)	Farley, NSW, Australia	Artinskian	Fletcher, 1938
Paraconularia derwentensis (Johnston, 1887)	Berriedale Lmst, Flowerdale River, Arcadia Siding, Unnamed Lmst Judbury,Tas; Barfield Fm, South Curra Lmst, Qld; Australia: Letham Fm, New Zealand	late Artinskian-Kungurian?	Johnston, 1887; Fletcher, 1938; Waterhouse, 1979; Parfrey, 1982
Paraconularia elegans Waterhouse and Gupta, 1977	Ladakh, India	Guadalupian (Punjabian)	Waterhouse and Gupta, 1977
Paraconularia hollebeni (Geinitz, 1853)	Ilmenau, Germany	Wuchiapingian	Geinitz, 1853; Geinitz, 1861

Table 1. *Contd.*

Species	Stratigraphic/Geographic Distribution	Age Range (after Jin et al., 1997)	Key References
Paraconularia kazanensis sp. nov.	Sokian Horizon, Karkali Quarry, Volga Region, Russia	?Roadian	Burov et al., 1998; This Paper
Paraconularia laskeri (Sahni and Srivastava, 1956)	Sikkim	Sakmarian	Sahni and Srivastava, 1956
Paraconularia leonardensis (Finks, 1955)	Leonard Fm, Cherry Canyon Fm, West Texas, USA	Kungurian-Guadalupian	Finks, 1955; Van Iten, 1991
Paraconularia margaritae Babcock, 1988b	Assistance Fm, Devon Island, Canada	Wordian	Babcock, 1988b
Paraconularia ornata Waterhouse, 1979	AG4 Fm, New Zealand	Guadalupian (Punjabian)	Waterhouse, 1979; 1986
Paraconularia punjabica (Reed, 1936)	Salt Range, Pakistan; Kashmir	Cisuralian	Reed, 1936; Diener, 1899
Paraconularia salaria (Reed, 1936)	Salt Range, Pakistan	Sakmarian	Reed, 1936
Paraconularia siitai Sugiyama, 1942	Hutatumori bed, Toyoma Fm, Japan	Lopingian	Sugiyama, 1942; Murata, 1967
Paraconularia simplicosta (Grabau, 1924)	Peichien Fm, NW Hupeh, China	Lopingian	Grabau 1924
Paraconularia sorelli Parfrey, 1982	Quarry south of Sorrel, Tas, Australia	Cisuralian	Parfrey 1982
Paraconularia sp. (Garratt, 1970)	Bacchus Marsh Fm, Vic, Australia	late Asselian – early Sakmarian	Garratt 1970; Thomas 1969; Archbold 1998
Paraconularia sp. (Glauert, 1912)	Byro Station, WA, Australia	Carboniferous-Permian	Glauert 1912
Paraconularia sp. Acharyya et al., 1975	Rilu Fm, Eastern Himalaya	Sakmarian	Acharyya et al. 1975
Paraconularia sp. Acharyya and Shah 1975	Malung Shale, Ladakh, Himalaya	Sakmarian	Acharyya and Shah 1975
Paraconularia sp. Waterhouse, 2001	Glandale Fm, New Zealand	Lopingian	Waterhouse 2001
Paraconularia sp. A (Dickins and Thomas 1956)	Poole Sst, Canning Basin, WA, Australia	late Sakmarian	Dickins and Thomas 1956; Thomas 1993
Paraconularia sp. B (Dickins and Thomas 1958)	Upper part Lyons Gp, Carnarvon Basin, WA, Australia	early Sakmarian	Dickins and Thomas 1958; Dickins and Thomas 1959
Paraconularia sp. C (Teichert 1952)	Coolkilya Sst, Carnarvon Basin, WA, Australia	Roadian	Teichert 1952; Thomas 1993
Paraconularia sp. cf. *N. levigata* (Licharew 1934)	Kolyma region	Guadalupian-Lopingian	Licharew 1934, 1939
Paraconularia sp. D (Guppy et al. 1952)	Lower Liveringa Gp, Canning Basin, WA, Australia	Ufimian-Roadian	Guppy et al. 1952; Thomas 1993
Paraconularia sp. E (Clarke et al. 1951)	Upper Holmwood Shale, Perth Basin, WA, Australia	early Sakmarian	Clarke et al. 1951; Fairbridge 1952; Thomas 1993
Paraconularia sp. indet. (Reed 1936)	Salt Range, Pakistan	Cisuralian	Reed 1936
Paraconularia sp. Thomas 1993	Port Keats, Bonaparte Basin, NT, Australia	Kungurian - late Wuchiapingian	Thomas 1993
Paraconularia sp. Thomas 1993 cf. *P. warthi* (Waagen 1886)	Callytharra Fm, Coyrie Fm? Mallens Sst, Wandagee Fm, Carnarvon Basin, WA, Australia	Asselian - Kungurian	Hosking 1933; Thomas 1993
Paraconularia spatia Waterhouse 1986	SE Bowen Basin, Australia	Artinskian? – Wordian?	Waterhouse 1986
Paraconularia spp. (Condon 1967)	Cundlego Fm, Wandagee Fm, Keogh Fm, Coyrie Fm, Mallens Sst, Bulgadoo Shale, Carnarvon Basin, WA, Australia	early Sakmarian - Kungurian	Condon 1967; Thomas 1993
Paraconularia suareziglosi Babcock 1988a	Copacabana Fm, Apillapampa, Bolivia	Sakmarian - Artinskian	Babcock 1988a
Paraconularia tarazi Murata & Golshani 1981	lower Julfa Bed, Kuh-e Hambast, Central Iran	Wuchiapingian (or Lopingian)	Murata and Golshani, 1981
Paraconularia tasmanica see *P. derwentensis*			
Paraconularia torta (McCoy 1847)	Muree, NSW, Australia	Wordian	McCoy 1847
Paraconularia tuberculata (Fletcher 1938)	Myall Lakes, Clarencetown, Taree, Kempsey, NSW, Australia	Carboniferous – Cisularian	Fletcher 1938; Parfrey 1982
Paraconularia warthi (Waagen 1891)	Talchir Boulder Bed, Salt Range, Pakistan	Asselian-Sakmarian	Waagen 1891; Reed 1936
Paraconularia? sp. cf. *N. levigata* (Waagen 1886)	Salt Range, Pakistan	Cisuralian	Waagen 1886; Waagen 1891; Reed 1936
Paraconularia? sp. cf. *N. tenuistriata* (Waagen 1891)	Salt Range, India	Cisuralian	Waagen 1891

Global distribution of Permian Conulariid Genera

Cheliconularia Waterhouse, 1986

The one species of *Cheliconularia* identified to date, *Cheliconularia cheliensis* Reed, 1936, is endemic to the Salt Range, India, which formed a part of the Gondwanan Realm during the Permian (Fig. 1b). The species is found in the *Conularia* Bed at the base of the Olive Series above the Talchir Boulder Bed and is of early Permian age (possibly late Sakmarian) (Reed, 1936; Waterhouse, 1986). The base of the Olive Series has a number of pebbly layers similar to the underlying Talchir boulder bed but is much thinner. The Talchir Boulder Bed is striated and was formed during glacial conditions (Waagen, 1891).

From the *Conularia* Bed Waagen (1891) and Reed (1936) also documented several other conulariid species associated with *C. cheliensis* including *Paraconularia?* sp. (cf. *Notoconularia levigata*) (Licharew, 1934), *Paraconularia warthi* (Waagen, 1891), *P. salaria* (Reed, 1936), *P. punjabica* (Reed, 1936), *Paraconularia?* sp. (cf. *Notoconularia tenuistriata*) (Waagen, 1891), and *Paraconularia* sp. (Reed, 1936). Based on this information the *Conularia* Bed in the Salt Range has one of the most diverse range of conulariid species for a single horizon.

Gondaconularia Waterhouse, 1986

Gondaconularia is composed of four species (one of which is Triassic and not listed in Table 1 and, two of which are tentatively attributed to this genus) found in the Austrazean Province of the Gondwanan Realm (Waterhouse, 1986) (Table 1, Fig. 1b). Based on their age and location, it appears that *Gondaconularia* originated in the Bowen Basin, Queensland, Australia during the Artinskian and had migrated down through the Austrazean Province to New Zealand by the Capitanian (late Middle Permian), where it survived through to the Oretian Stage in the Triassic. Waterhouse (1986) noted that *Gondaconularia* is morphologically similar to the older *Cheliconularia*. If this is accepted, it is reasonable to suggest that the evolutionary lineage began in India, then dispersed to eastern Australia and New Zealand. Alternatively, *Gondaconularia* and *Cheliconularia* may have evolved independently from *Paraconularia*.

The *Gondaconularia* species from the Bowen Basin, Australia, are found associated with bipolar and bitemperate (terminology of Shi and Grunt, 2000) brachiopod genera such as *Echinalosia, Magniplicatina, Stenoscisma,* and brachiopod genera with strict bipolar distributions such as *Terrakea* and *Arctitreta*, as well as endemic Gondwanan genera such as *Taeniothaerus*.

Neoconularia Sugiyama, 1942

In the Permian *Neoconularia* is endemic to the southern Kitakami Mountains of Japan (Table 1, Fig. 1b). It is represented by one species, *Neoconularia rectangularis* (Hayasaka, 1920) found in the Wordian '*Lyttonia* beds' (revised as '*Leptodus*' beds). During the Middle Permian it is inferred that the southern Kitakami Mountains occupied an area on the northern or eastern margin of the Sino-Korean block (Tazawa, 2000). *Leptodus* is typically accepted as being a warm-water Tethyan genus. However, in the Kitakami Mountains it is associated with typical Boreal elements such as *Yakovlevia* and bipolar forms such as *Spiriferella*. This mixed brachiopod fauna is characteristic of the Sino-Mongolian-Japanese Province in East Asia (Shi and Tazawa, 2001).

Calloconularia Sinclair, 1952

In the Permian *Calloconularia* first occurred in the Indoralian Province of the Gondwanan Realm (Shi and Archbold, 1993) in Central Afghanistan where it is found associated with an Asselian-early Sakmarian (early Early Permian) brachiopod fauna of strong Gondwanan affinity (Termier et al., 1974). The brachiopod fauna comprises cold-water genera such as *Gilledia* and *Eurydesma,* a typical bipolar and bitemperate genus *Tomiopsis (Ambikella),* as well as some wide-ranging genera including *Spiriferellina, Punctospirifer,* and *Neospirifer. Calloconularia* has also been found in the Sino-Mongolian-Japanese Province in the upper Kattisawa Stage (of probable Wordian-Capitanian age according to Ehiro (1998)) in Japan (Murata, 1967; Minato et al., 1978) (Fig. 1b). The latter occurrence of *Calloconularia* in the Sino-Mongolian Province suggests a northward migration from the Indoralian Province during the late Cisularian or early Guadalupian.

Notoconularia Thomas, 1969

Notoconularia Thomas, 1969 is endemic to the Austrazean Province in the Gondwanan Realm (Fig. 1b). Three species of *Notoconularia* are found in southeastern Australia during the Permian; *N. levigata* (Morris, 1845), *N. inornata* (Dana, 1849), and *N. tenuistriata* (McCoy, 1847) (Table 1). Earlier literature indicated that these species occurred over a broader geographic range. *C. tenuistriata* extends further north to Kashmir (Diener, 1899) and the Salt Range (Waagen, 1891) and, *C. levigata* is also located in the Salt Range, (Waagen, 1891) and the Kolyma Region (Licharew, 1934; 1939). However, the specimens from these localities do not appear to possess the distinctive longitudinal ridge in each of the corner furrows characteristic of *Notoconularia* and have been placed in *Paraconularia* for the purposes of this study.

N. levigata is found in the fossil record from the early

to Middle Permian, whereas *N. inornata* is more abundant from the Artinskian to Middle Permian (Guadalupian) (Thomas, 1969). The localities along the southeastern coast of Australia where conulariid species can be found were typically influenced by glacial conditions. For example; at Bacchus Marsh, Victoria, *Notoconularia* is found in a marine incursion of reworked till. This genus is also found in the Broughton Formation, Shoalhaven Group of the southern Sydney Basin, New South Wales. The sandstone members of the Broughton Formation includes large, thick-shelled cool-water fauna, along with glendonites and dropstones suggestive of high-latitude cold climatic conditions, as well as permafrosted palaeosols indicative of humid and frigid climate (Retallack, 1999).

Paraconularia Sinclair, 1940

Paraconularia is a long ranging genus (Mid Silurian–Lower Carboniferous) (Moore and Harrington, 1956) capable of providing useful information on migration pathways for biotic exchange and mechanisms of migration. However, it would benefit from a thorough revision.

Based on current data *Paraconularia* is distributed throughout the Gondwanan Realm during the early Permian. It is also present in the Kolyma region of Siberia (Licharew, 1934; 1939) and Arctic Canada (Boreal Realm) (Babcock, 1988a and b), while it is entirely absent from the Palaeoequatorial Realm (Fig. 1c).

During the Middle to late Permian *Paraconularia* can be found in the Gondwanan and Boreal Realms and scattered throughout the transitional provinces (Fig. 1d). Specimens have been collected in West Texas, USA (Finks, 1955); in the Sino-Mongolian-Japanese Province in East Asia (Sugiyama, 1942; Murata 1967), and in the Iranian Province from Iran (Murata and Golshani, 1981). One specimen has also been collected from Hubei Province of South China (Grabau, 1924). In addition, *Paraconularia* has also been reported from Ilmenau, Germany (Geinitz, 1853) and the Volga Region of the Russian Platform (this paper). In the Gondwanan Realm species of *Paraconularia* have been found as far south as Tasmania and New Zealand, and also occurs in the Sydney, Bowen, Bonaparte, Canning, Carnarvon and Perth Basins of mainland Australia, as well as India (for stratigraphical information and references to these locations see Table 1).

Distribution patterns in the Permian suggest *Paraconularia* was migrating from the polar regions of the Boreal Realm in a southwesterly direction along the continental shelf into the temperate waters of the Zechstein sea, and the Russian Platform and then progressing further south on a cold water 'Californian-type' current (e.g., Skinner et al., 1999, p. 251) into West Texas. Migration also occurred in a southeasterly direction from the polar regions to the Sino-Mongolian-Japanese Province (Fig. 1d). Similar migration routes have been proposed for the Boreal Realm brachiopod *Yakovlevia* (Shi, 1995). In the southern hemisphere it is possible migration was also taking place along the continental margins of Gondwana; by island hopping and terrane movement in the Tethys; and via deep, cold water currents running in a northerly direction through the Tethys. Figures 1c and 1d illustrate the change in distribution of *Paraconularia* from the early Permian to the Mid-late Permian and, the possible patterns for migration as *Paraconularia* spreads from the Sydney Basin into the Bowen Basin through the Austrazean Province, and from the Indoralian Province (Salt Range/Himalaya) into the Cathaysian Province (Hubei) and Iranian Province (Iran). These pathways are comparable to those outlined by Shi and Grunt (2000) which allow biotic interchanges between the Gondwanan and Boreal Realms.

Diconularia Sinclair, 1952

Previously *Diconularia* was reported from the Middle Ordovician to the Upper Carboniferous in Europe and North America. This age range of *Diconularia* is extended into the Middle Permian (Roadian) with the occurrence of *Diconularia meadepeakensis* sp. nov. in the Meade Peak Member of the Phosphoria Formation, Idaho, USA (see below) (Fig. 1b). The brachiopod fauna found with the conulariid suggests that there is a strong relationship of the Phosphoria fauna with the Boreal Realm. The Boreal Realm brachiopods found include *Yakovlevia, Bathymyonia, Komiella,* and *Rhynoleichus.* Two antitropical elements, *Costatumulus* and *Megousia,* were also present. The inferred palaeogeographic setting for the Phosphoria Basin indicates that cool-water longshore currents provided a medium for migration and cool-water upwelling currents provided suitable conditions for Boreal and antitropical faunas to exist at equatorial latitudes.

Mesoconularia Boucek, 1939

A single species of *Mesoconularia* is found in the Parenskiy horizon in the Omolon River Basin, Russia during the early Sakmarian (Zavodowsky et al., 1970) (Fig. 1b). In the same horizon, typical Boreal fauna such as *Jakutoproductus, Sowerbina,* and *Paeckelmannella* is present and bipolar and bitemperate fauna such as *Rhynchopora, Spiriferella, Attenuatella* and large, thick-shelled *Neospirifer* can also be found. The Omolon River Basin was situated in the Boreal Realm during the Permian.

Conularia Sinclair, 1940

Conularia is a long ranging genus spanning the Upper Cambrian to the Permian (Moore and Harrington, 1956).

Currently, six species of *Conularia* are reported in the Kolyma-Omolon Block region of Russia (Boreal Realm) during the Asselian to Wordian (Zavodowsky, 1960; 1968; Zavodowsky et al., 1970) (Table 1, Fig. 1b). Taxonomic revision of these species may result in the transfer of these species to other genera, and a shorter biostratigraphic range for *Conularia*. Chang (1976) reported another possible occurrence of *Conularia* in the Wuchiapingian Selong Group of Tibet. During the Wuchiapingian southern Tibet formed a part of the Himalayan Province (Shen and Shi, 2000). Typical brachiopod fauna of the Selong Group include a number of temperate genera such as *Taeniothaerus, Retimarginifera* and *?Lamnimargus,* and a number of bipolar genera such as *Marginalosia, Trigonotreta, Spirelytha, Echinauris, Spiriferella,* and large *Neospirifer* (Shen et al., 2001).

In summary, during the Permian *Notoconularia* and *Gondaconularia* were endemic to the Austrazean Province; *Cheliconularia* was endemic to the Himalayan Province; *Neoconularia* was endemic to the Sino-Mongolian-Japanese Province; *Diconularia* was endemic to the McCloud Cordilleran Province; *Calloconularia* was bitemperate and could be found in both the Himalayan and the Sino-Mongolian-Japanese Province; *Paraconularia* was bipolar-bitemperate and had the widest distribution; *Mesoconularia* occurred only in the Boreal Realm; and *Conularia* had an affinity with the Boreal Realm and possibly also occurred within the temperate Himalayan Province.

Diversity

Waterhouse (1979) commented on the higher diversity of species in the polar regions as opposed to the equatorial region during the Permian. Since Waterhouse's study, a number of new species have been found and additional information from older literature is added in this study. Figures 2a and 2b illustrate these diversity patterns. The Gondwanan Realm has the highest diversity with 38 species in comparison to 11 species in the Boreal Realm, 9 species from transitional provinces and one in the Cathaysian Province (Palaeoequatorial Realm). This data supports Waterhouse's initial findings and suggests that in general Permian conulariids had a marked preference for cool-cold water environments.

Taxonomy

All material is deposited in the Museum of Victoria, Melbourne, Australia (MVP).

Phylum COELENTERATA Frey and Leuckart, 1847

Class SCYPHOZOA Götte, 1887

Subclass CONULATA Moore and Harrington, 1956

Order CONULARIIDA Miller and Gurley, 1896

Suborder CONULARIINA Miller and Gurley, 1896

Superfamily CONULAROIDEA Walcott, 1886

Family CONULARIIDAE Walcott, 1886

Subfamily CONULARIINAE Walcott, 1886

Diconularia Sinclair, 1952

Type species: *Conularia micronema* Meek, 1871.

Diagnosis: The diagnosis of the genus provided by Sinclair (1952) is accepted.

Diconularia meadepeakensis sp. nov.

Figure 3a-b

Etymology: Derived from the Meade Peak Member in which it is found.

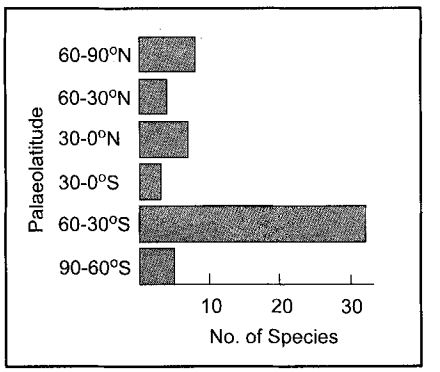
Holotype: MVP310916, Fig. 3a-b.

Conularia sp. Girty 1910, pl. 6, Fig 8.

Material: 1 test (weathered).

Diagnosis: *Diconularia* with rhomboid cross-section and 7–8 transverse ridges in 10 mm.

Description: small test; rhomboid cross section; convex, equal sided faces; 27 mm in length; 9 mm diameter at aperatural end; apical angle 18–20°; 7–8 transverse ridges in 10 mm; transverse ridges convex towards aperture with poorly preserved tubercules, rarely offset at midline; corner furrow deep; midline not distinct on outer shell,



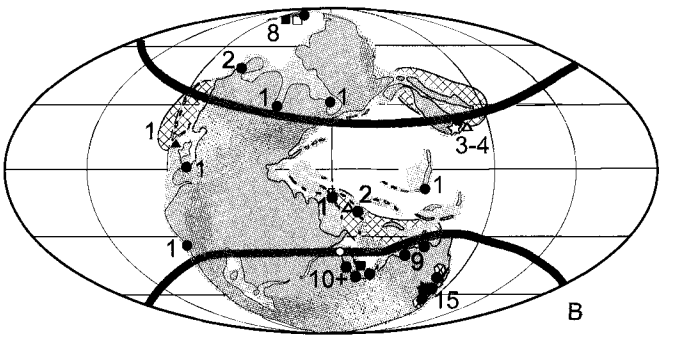


Fig. 2. Conulariid species diversity in the Permian (data from Table 1). Legend: see Fig. 1. A–Graphic illustration of the variation in species diversity at different latitudes. B–Geographic distribution of conulariid genera and number of species in provinces/regions.

but forms a very prominent septa internally; interspaces two times the size of transverse ridges.

Remarks: *Diconuluria* has previously been recorded from the Middle Ordovician to the Pennsylvanian. This occurrence of *Diconularia* extends its age range to the Middle Permian. In comparison to the Mississippian *Diconularia?* sp. Lammers and Young, 1984 (Lodgepole Formation, Manitoba), this specimen is slightly smaller and has much broader transverse ridges. In proposing *Diconularia,* Sinclair (1952) notes that it should be considered a form-genus, and studies should be carried out on the relationship of the convergent evolution of the species.

Age: Roadian.

Occurrences: 'Cap Rock', Meade Peak Member, Phosphoria Formation: Montpelier Canyon, Idaho, USA (Fig. 4).

Subfamily PARACONULARIINAE Sinclair, 1952

Paraconularia Sinclair, 1940

Type species: *Conularia inaequicostata* de Koninck, 1883.

Diagnosis: The diagnosis of the genus provided by Sinclair (1940) is accepted.

Paraconularia kazanensis sp. nov.

Figure 3c-d.

Etymology: Derived from the Kazanian Stage.

Holotype: MVP310917, Fig. 3c-d.

Material: Part of 1 flattened mould (1 face and 2 corner furrows preserved).

Diagnosis: *Paraconularia* with distinct interspaces that are broader near the midline and are steeper in angle toward the corner furrow with angle decreasing toward the midline.

Description: moderate sized test; over 70 mm in length; 16 mm diameter at widest preserved point; apical angle 17°; 13 transverse ridges in 10 mm at apical end, 10 in 10 mm closer to aperture, alternating at corner furrow, offset at midline, small tubercles prominent, convex

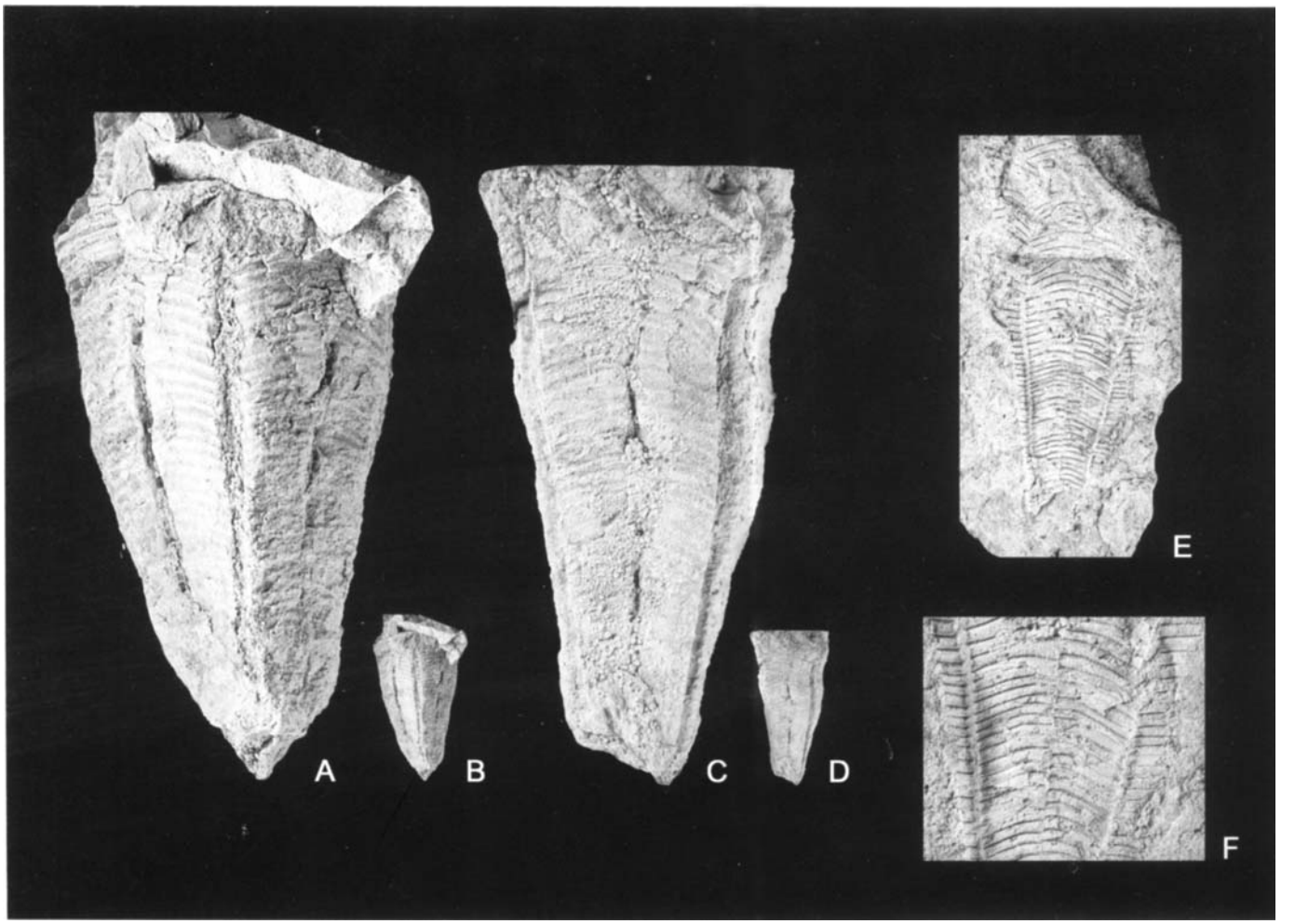


Fig. 3. A-D–*Diconularia meadepeakensis* sp.nov.(MVP310916). A–Corner furrow x3. B–Corner furrow x1. C–Midline x3. D–As above x1. E-F–*Paraconularia kazanensis* sp. nov. (MVP310917). E– Flattened specimen x1. F–Tubercles on transverse ridges x2.

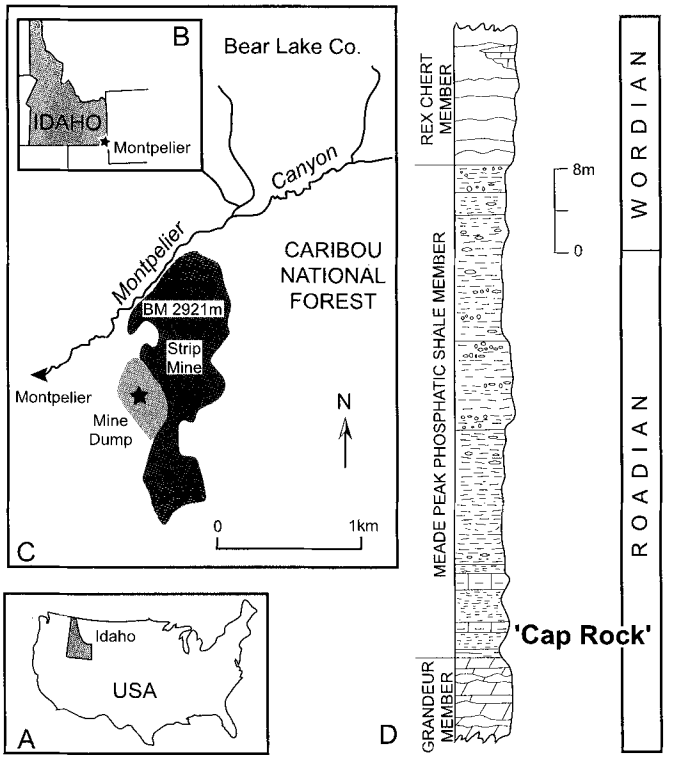


Fig. 4. Geographic and stratigraphic location of *Diconularia meadepeakensis* sp. nov. A-C–Location of Mine, Montpelier Canyon, Idaho, USA. D–Stratigraphic position of the 'Cap Rock,' Meade Peak Member, Phosphoria Formation (Behnken et al., 1986).

toward aperature, steeper in angle toward the corner furrow and slope decreases toward the midline; broad interspaces up to three times the size of the ridge, often broader near midline (rarely joining).

Remarks: *Conularia hollebeni* Geinitz, 1853 has been recorded from the same Bed (Burov et al., 1998) as *Paraconularia kazanensis*, however without illustration or description of the specimen sampled. The specimen of *Conularia hollebeni* sketched by Geinitz (1853) is similar in general appearance to *Paraconularia kazanensis* but its transverse ridges are on a shallower angle. Burov et al. (1998) record of *Conularia hollebeni* is likely to be synonymous with *Paracconularia kazanensis*. *Paraconularia kazanensis* can also be distinguished from the two Canadian Arctic species *Paraconularia arctica* (Babcock, 1988b) and *Paraconularia margaritae* (Babcock, 1988b). *Paraconularia arctica* has more closely spaced transverse ridges and *Paraconularia margaritae* has a larger exoskelton, and transverse ridges on a slightly shallower angle. In comparison to *Paraconularia leonardensis* (Finks, 1955) from West Texas, *Paraconularia kazanensis* has wider faces and a less prominent midline.

Age: Lower Kazanian (?Roadian).

Occurrences: Bed 10, Kamyshlinskie Beds, Sokian Horizon: Karkali, Volga Region, Russia (Fig. 5).

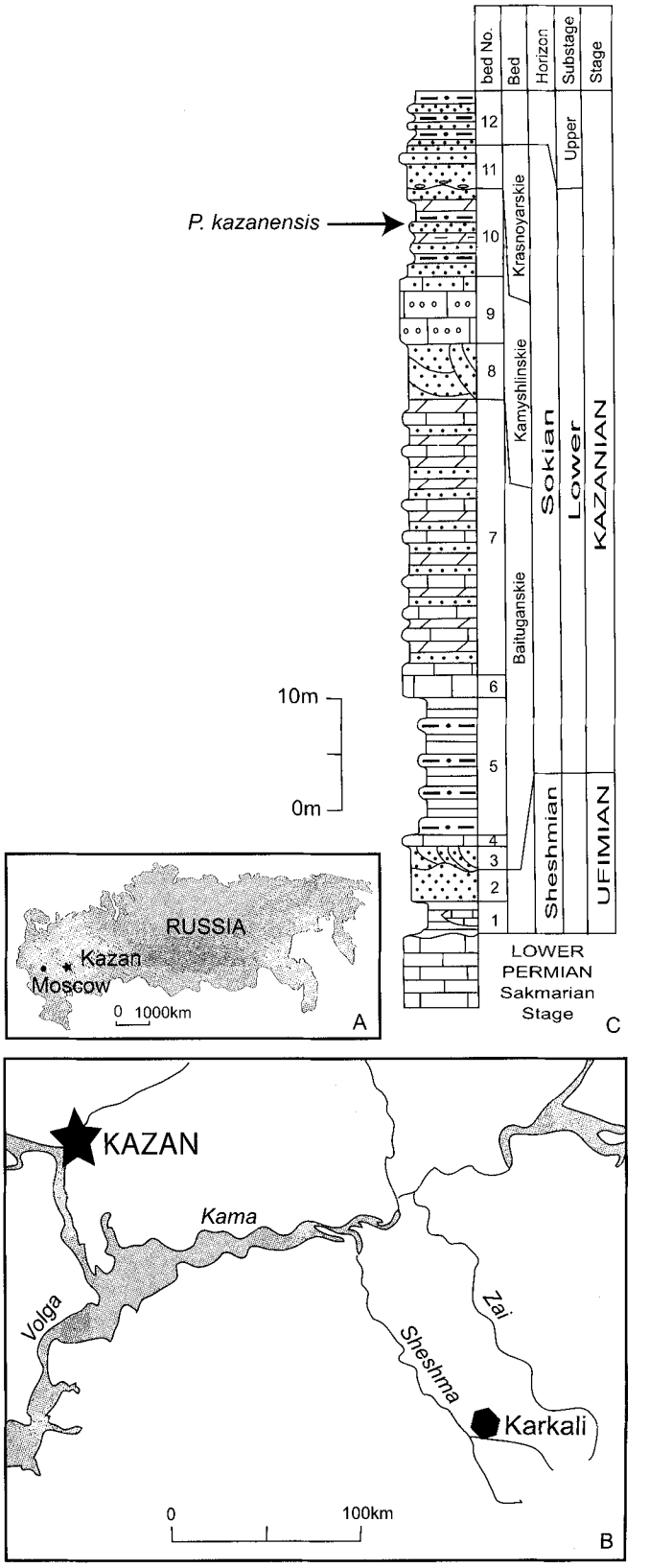


Fig. 5. Geographic and stratigraphic location of *Paraconularia kazanensis* sp.nov. A-B–Location of Karkali, near Kazan, Russia. C–Stratigraphic position of Bed 10, Kamyshlinskie Beds, Sokian Horizon, in the Karkali section (Burov et al., 1998).

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