Carboniferous Rugosa in the Hina Limestone, Akiyoshi Terrane, Southwest Japan: fauna endemic to the Panthalassan Ocean

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Abstract: Rugose corals of the Akiyoshi Terrane in the Inner Zone of Southwest Japan are notable for two reasons, their role in reef construction and their highly endemic nature. Until now, little has been known about the faunal characteristics of the Rugosa-rich Hina Limestone (early Visean to late Bashkirian) in the Akiyoshi Terrane. The early Visean non-dissepimented solitary corals are replaced in the middle to late Visean by large, dissepimented solitary corals. These solitary faunas are followed by dominantly pseudopavonid corals of variable form. During the late Visean warm-water transgression, the Akiyoshi fauna contrasted markedly with Tethyan faunas (e.g. the *Kueichouphyllum* fauna), forming a characteristic Akiyoshian faunal type.

Ozakiphyllum, *Pseudopavona*, and *Omiphyllum* exhibit their close phylogenetic continuity through intergradational morphology. Abundant new species of these genera are recognized in the Hina Limestone, and will help clarify genus-level phylogenetic relationships. Although *Hiroshimaphyllum* may be ancestral to this clade, its solitary representatives are not yet well known.

Of special interest is the presence of the Australian "*Orionastraea*", which perhaps is separable from European *Orionastraea*. Phylogenetically close genera ("sister-groups") have been noted in Eastern Australia and the Akiyoshi Terrane. However, no pseudopavonid genera have yet been interpreted as exhibiting true "sister-group" relationships with any genera outside of the Japanese Islands. If true "sister-group" relationships are recognized within pseudopavonids and non-pseudopavonids, phylogenetic problems would arise as to the monophyly of the family Pseudopavonidae. More importantly, invaluable clues about the origins of the Akiyoshi fauna can be obtained by combining palaeogeographic and phylogenetic analyses.

Key words: Akiyoshi Terrane, Carboniferous, Palaeobiogeography, Panthalassan Ocean, Rugosa, Visean

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Contents

1. INTRODUCTION

Exotic limestone masses of seamount origin are sporadically present within the Akiyoshi Terrane, a Permian accretionary complex present in the Inner Zone of Southwest Japan. Those limestones were formed on basaltic seamounts in an open-ocean setting in Panthalassa. The limestones are free of terrigenous sediment and are excellent counterparts of coeval continental-shelf deposits. In particular, the Early Carboniferous fauna is represented by a "survival and recovery biota" following the Late Devonian extinction event. That fauna provides us with important insights into not only the provinciality of the recovery phase but also into the phylogenetic relationships between Devonian and Carboniferous biotas.

Rugose coral faunas of the Akiyoshi Terrane have been remarked upon from two points of view. The first point concerns their role in reef construction. The reconstruction of an organic reef complex by Ota (1968) is particularly well known. Wave-resistant, atoll-type buildups are known to have been produced by constructors such as chaetetids, and rugose and tabulate corals, as well as by encrusting bryozoans and calcareous algae, from the *Millerella yowarensis* Zone to the *Profusulinella beppensis* Zone: from lower Serpukhovian to upper Bashkirian (e.g. Ota, 1968; Nagai, 1985; Sugiyama & Nagai, 1994). The Carboniferous construction of an organic reef complex took place earlier than in other regions after the Late Devonian extinctions, and their palaeoecological and palaeobiogeographic backgrounds are remarkable.

A second notable point is related to the highly endemic nature of these rugose corals. The publication of a monograph on the Pseudopavonidae by Kato & Minato (1975) emphasized the family's palaeobiogeographic peculiarity. The Pseudopavonidae was endemic to certain terranes of the Japanese Islands (Akiyoshi, Kurosegawa, Mino-Tamba-Ashio, and Chichibu terranes), with the single exception of its occurrence in Sichuan Province of South China (Wu & Zhang, 1979). The family is therefore also important when discussing subdivisions of terranes and the geological development of the Japanese Islands (Kato, 1990). Problems associated with this palaeobiogeographic peculiarity have given rise to additional questions about palaeobiogeographic variability within specific terranes, and the origin and phylogenetic relationships of the family.

Rugose-faunal analyses of the Akiyoshi Terrane have been conducted separately at individual localities (e.g. Yamagiwa, 1962; Haikawa & Ota, 1978; Yoshida et al., 1987; Haikawa, 1995). Chronologically successive faunas have been summarized for the Aki-

yoshi Limestone Group at the generic level by SUGIYAMA & HAIKAWA (1993). However, from the Hina Limestone of the same terrane, there has been only one description of *Lithostrotion* (*Siphonodendron*) *hinense* (YAMAGIWA et al., 2000), although several tabulate corals have been described by NIKO (1999, 2002). As a result, little has been known about the faunal characteristics of the Rugosa-rich limestone. The Hina Limestone of Okayama Prefecture is present in the middle part of both the Akiyoshi Limestone Group of Yamaguchi Prefecture and the Omi Limestone Group of Niigata Prefecture (Fig. 1) and has attracted significant attention because of its faunal features.

Abundant coral specimens were qualitatively and quantitatively obtained from the Hina Limestone of Carboniferous (early Visean to late Bashkirian) age. The present study focuses on rugose faunal features as a basis for comparisons with contemporaneous faunas elsewhere; it also focuses on the phylogenetic and palaeogeographic problems of Carboniferous Rugosa with regard to their origins and provinciality.

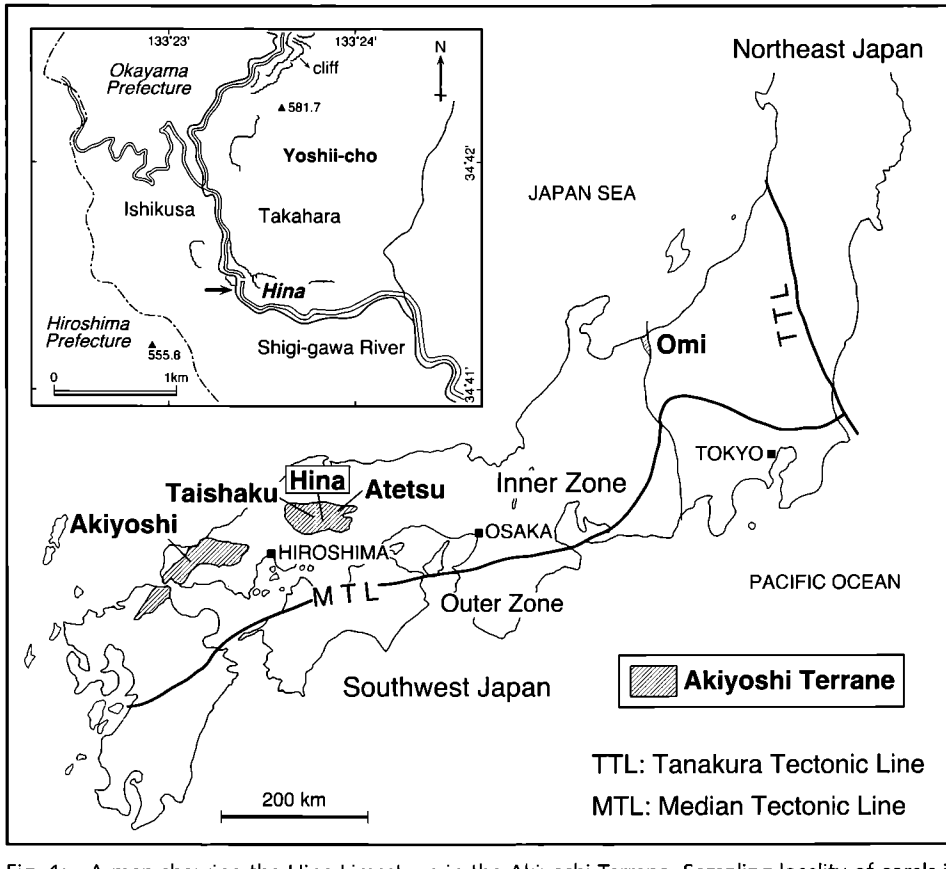

Fig. 1: A map showing the Hina Limestone in the Akiyoshi Terrane. Sampling locality of corals is indicated by an arrow (inset). Tectonic map of the Japanese Islands is simplified from ICHIKAWA (1990).

2. GEOLOGIC SETTING

The Akiyoshi Terrane is a Permian accretionary complex in the Inner Zone of southwest Japan (Fig. 1) and contains various sizes of limestone masses. The Hina Limestone is one of those masses and measures about 2 km in an east-west direction and about 0.8 km in a north-south direction. This limestone body is in fault contact with the Yoshii Group of Permian in the north and with the Triassic Nariwa Group to the south, and is unconformably overlain by the Takada Rhyolitic Rocks of Middle Cretaceous age in the west (e.g. NAKANO, 1952; SADA et al., 1979). Several major and minor faults have destroyed the original stratigraphic relationships, but the original relations can be approximated by the study of individual coherent bodies. The basal part of the strata is underlain by basaltic pyroclastic rocks that include limestone pebbles with bioclasts of crinoids, bryozoans and solitary corals in their upper part. The middle and upper parts are made up of limestones up to 300 m thick.

Based on a detailed biostratigraphic study of brachiopods by HASE & YOKOYAMA (1975) and conodonts by MIZUNO (1997), the Hina Limestone ranges in age from early Visean to late Bashkirian (MIZUNO, 1997), and correlates with smaller-foraminiferal zones (from the *Endothyra* Zone to the *Profusulinella beppensis* Zone of MATSUSUE, 1986).

3. MATERIALS AND METHODS

Most materials treated in this study were collected as float pebbles and cobbles along the Shigi-gawa River, which traverses the Hina Limestone masses in a north-south direction. The sampling took place in the Kamishigi region of Shitsuki-gun, Yoshii-cho, Okayama Prefecture (Fig. 1). All float specimens came from the Hina Limestone, although several specimens were collected directly from outcrops that belong to the *Endothyra* Zone through the *Mediocris mediocris* Zone of MATSUSUE (1986). Transverse and longitudinal thin sections (52 x 76 mm in maximum size) were prepared for detailed morphological observations of the corals with a binocular microscope, and age determinations were done using smaller foraminifers. Polished slabs were made (when needed) for detailed observations of modes of occurrence and growth by the naked eye. The authors follow the smaller-foraminiferal studies of OKIMURA (1963, 1966) and MATSUSUE (1986). The higher taxonomic categories of Rugosa are based mainly on KATO (1975), KATO & MINATO (1975), and HILL (1981). Specimens are housed in the Department of Geosciences, Graduate School of Science, Osaka City University (OCU 6581–6588).

4. FAUNAL ANALYSIS

Seventeen rugose genera belonging to eight families are known from the Hina Limestone. Most characteristic and predominant families include pseudopavonids, amygdalophyllids, lithostrotionids and aulophyllids, followed by less-common cyathaxonids, zaphrentoids, axophyllids and geyerophyllids (Pls. 1, 2). A variety of growth forms predominate among the pseudopavonid corals. The thamnasterioid *Pseudopavona* and cerioid *Ozakiphyllum* are most abundant and comprise several species, including new

ones (Pl. 2, Figs. A, C). Massive, tabular, and laminar growth forms are present. Other pseudopavonid corals comprise fasciculate *Hiroshimaphyllum* (Pl. 1, Fig. E), aphroid *Omiphyllum*, and large cerioid *Ibukiphyllum* with tertiary septa. Absent are solitary *Amygdalophyllidium* and large, fasciculate *Taisyakuphyllum* with tertiary septa. The lithostrotionids include *Siphonodendron hinense* (Pl. 1, Fig. D), *Lithostrotion* sp., "*Orionastraea*" cf. "*O.*" *columellaris* (Pl. 1, Fig. C), and *Akiyosiphyllum*? sp. "*Orionastraea*" has not yet been found from the Akiyoshi Terrane. Non-dissepimented corals include *Cyathaxonia* sp. (Pl. 1, Fig. A) and *Zaphrentoides* sp. Solitary aulophyllid *Echigophyllum* (*E. atetsuense*; Pl. 1, Fig. B), and its fasciculate forms ("*Corwenia*" *omiensis*), and *Hiroshimaphyllum* (*H. toriyamai*; Pl. 1, Fig. E) are often associated with solitary geyerophyllid *Amygdalophylloides* (*A. gracilis*).

Of special interest is the presence of "*Orionastraea*" cf. "*O.*" *columellaris* in the Hina Limestone. "*Orionastraea*" *columellaris* was first described from the middle Visean Back Creek Limestone of the Merlewood Formation in New South Wales, Australia (Pickett, 1966). Webb (1990) emphasized that Australian "*Orionastraea*" differs from European representatives in their age (being older than European examples) and their skeletal construction (wall structure, axial structure, and skeletal thickness). He also suggested that another genus name should be used for the Australian "*Orionastraea*." The same is true for Australian "*Siphonodendron*," based on the structures of their tabellae and dissepiments as well as microstructure (Webb, 1990, p. 92). Webb (1990, p. 93) noted that *Siphonodendron nakazawai*, which was described by Minato & Kato (1957) from the originally Carboniferous clasts of the Maizuru Terrane, might be congeneric with Australian "*Siphonodendron*." However, *Siphonodendron hinense* from the Hina Limestone exhibits a wall structure characteristic of the European type of *Siphonodendron* (i.e. the septa not being deeply embayed into the wall) rather than the Australian type that has a peripheral stereozone and wedge-shaped septa (Webb, 1990, p. 93, Fig. 51).

The Akiyoshian assemblage has fewer features in common with coeval corals of the Hida-Gaien Belt and the South Kitakami Terrane, where geyerophyllids and *Petalaxis* commonly occur (Kato, 1990, p. 310). The Boreal influence on the Akiyoshian faunas was shown by *Petalaxis taishakuensis* from the middle to late Viséan of the Taishakugawa Group (Yokoyama, 1957) and *Arachnastraea* sp. from the *Beedeina akiyoshiensis* Zone of the Akiyoshi Limestone Group during the Moscovian (Nagai et al., 1999, p. 54, Pl. 9, Fig. 2). However, *Petalaxis*-like *Ozakiphyllum* with undeveloped axial columns and trabecular type septal structure was very common in the Hina Limestone and the Akiyoshi Limestone Group during the Serpukhovian. It is probable that Yokoyama's *Petalaxis* is assigned to *Ozakiphyllum* with thin walls and acolumellate structure, although a final decision should be left for a future study of the fine skeletal structure in the type specimen.

The fact that most, if not all, specimens treated here came from float cobbles and pebbles along the Shigi-gawa River prevents us from describing detailed stratigraphic successions for the coral faunas. However, the overall trend of rugosan succession is as follows: *Cyathaxonia* is characteristically abundant in the early Visean, occasionally along with volcaniclastic rocks. These non-dissepimented solitary corals are replaced in the middle to late Visean by large dissepimented solitary corals such as *Amygdalophyllum*, *Dibunophyllum*, *Nagatophyllum*, and *Echigophyllum*. These solitary faunas are followed

by dominantly pseudopavonid corals of variable form, including the fasciculate *Hiroshimaphyllum*, cerioid *Ozakiphyllum*, and thamnasterioid *Pseudopavona*.

5. DISCUSSION

The faunal characteristics of the Hina Limestone are typically Akiyoshian in that they include a number of endemic elements, represented by a variety of pseudopavonids and large solitary amygdalophyllids. Those faunal successions exhibit the features that were summarized by KATO (1990), as follows: The early to middle Visean fauna is similar to those from the South Kitakami Terrane, northeastern Japan, and from Eastern Australia. However, during the late Viséan warm-water transgression, the Akiyoshi fauna includes abundant *Hiroshimaphyllum* and contrasts markedly with Tethyan faunas (e.g. the *Kueichouphyllum* fauna), thereby forming a distinctive Akiyoshian type. From the Serpukhovian onward, the Akiyoshian fauna became more distinctive, with the dominance of *Pseudopavona*, *Ozakiphyllum*, and *Amygdalophylloides* in the tropics of Panthalassa. *Taisyakuphyllum* and *Ibukiphyllum* became common in the Moscovian (KATO, 1990).

The intergradational morphology of *Ozakiphyllum*, *Pseudopavona*, and *Omiphyllum* suggests close phylogenetic continuity, as observed by KATO & MINATO (1975). The supposed evolutionary polarity in corallite interrelationships may be provisionally considered as cerioid (*Ozakiphyllum*), via thamnasterioid (*Pseudopavona*) to aphroid (*Omiphyllum*). However, these three genera, especially *Pseudopavona* and *Omiphyllum*, exhibit irregularly laminar growth forms (sometimes acting as an important sediment stabilizer), and highly variable morphologies in transverse section, even within a single colony. Taking also into consideration the morphological plasticity in overall growth forms of those corals, phylogenetic relationships should be decipherable based on their stratigraphic ranges. Only four species of *Ozakiphyllum*, three of *Pseudopavona*, and one of *Omiphyllum* were previously known elsewhere in specific terranes of the Japanese Islands (KATO & MINATO, 1975). The abundant new species of these genera in the Hina Limestone will clarify their phylogenetic relationships.

Hiroshimaphyllum may be ancestral to this clade, because *Ozakiphyllum* is a cerioid representative of fasciculate *Hiroshimaphyllum* (KATO & MINATO, 1975, p. 100). However, a solitary representative of this clade may not be solely *Amygdalophyllidium*, although this is the only solitary genus established previously within the Pseudopavonidae (KATO & MINATO, 1975, p. 98). Phylogenetically close relationships may be found, at least from an apparent morphological point of view, in *Axophyllum* in the Axophyllidae (=? *Carcinophyllum* in the Carcinophyllidae).

KATO (1990, p. 309) noted the affinity of early to middle Visean Akiyoshi corals with those of the Kitakami Terrane and Eastern Australia, based on the common occurrence of *Amygdalophyllum*, *Nagatophyllum* (often compared with *Symplectophyllum*), and *Akiyosiphyllum* (similar to *Siphonodendron stanvellense*). In addition, WEBB (1999, 2000) noted close phylogenetic ("sister-group") relationships between Lower Carboniferous genera in Eastern Australia and the Akiyoshi Terrane, including *"Siphonodendron"* vs. *Akiyosiphyllum*, *Symplectophyllum* vs. *Nagatophyllum*, and *Dinostrophinx* vs. *Echigophyllum*, respectively. The latter genera are highly endemic to the Akiyoshi

Terrane. He therefore presented ideas on a common source of both faunas in the Panthalassa Ocean during the Late Devonian or early Tournaisian, but with very limited or absent genetic interchange subsequently. It is clear that recognizing true one-to-one "sister-group" relationships between presently separated terranes is quite useful for elucidating the palaeogeographic migration history of terranes (including seamounts), the origin of the Akiyoshi fauna in the present instance, and the vicariance and dispersal patterns of coral faunas in western Panthalassa. Wu & Zhang (1979) studied pseudopavonids from the Lower Carboniferous Xuchika Formation of Batang and Yidun, western Szechuan (= Sichuan), and some of them might be assignable to the Pseudopavonidae. However, *Ramiphyllum* that was established therein is not a pseudopavonid. The same is also true for *Parapavona* that was established by Wu et al. (1985) from northwestern British Columbia, western Canada. It is therefore notable that no pseudopavonid genera have yet been interpreted as having true "sister-group" relationships with genera from regions other than the Japanese Islands.

Additionally, the typical pseudopavonids *Ozakiphyllum* and *Hiroshimaphyllum* resemble *Actinocyathus* and *Lonsdaleia*, respectively. However, the two former genera exhibit a trabecular type of fine septal structure, whereas the latter genera are fibronormal or diffuso-trabecular (Kato & Minato, 1975, p. 100, 101). Those similar morphologies are more apparent than real due to parallelism, and each taxon forms "analogous-group" relationships. One particular species of *Ozakiphyllum* [*O.* sp. nov. (Pl. 2, Fig. A)] is characterized by a poorly developed axial structure and looks like *Petalaxis*. However, this apparent similarity was brought about only by convergence resulting from the lack of development of an axial structure within *Ozakiphyllum*. Similarly, *Ivanovia*, which was also one of the typical Boreal elements, has been reported from the Akiyoshi Limestone Group (Nagai & Sugiyama, 1995). However, it is probable that these so-called "*Ivanovia*" belong to *Omiphyllum*, which is distinctive in having a trabecular type of fine septal structure.

If true "sister-group" rather than "analogous-group" relationships are recognized within pseudopavonids and non-pseudopavonids, phylogenetic problems may arise as to the monophyly of the family Pseudopavonidae. In such a case, Pseudopavonidae might require redefinition as a higher taxonomic category. More importantly, invaluable clues about the origins of the Akiyoshi fauna can be obtained from a combination of palaeogeographic and phylogenetic analyses.

6. FURTHER PROBLEMS

The Carboniferous Akiyoshian rugose faunas have the potential to elucidate phylogenetic relationships between Devonian and Carboniferous corals following the Late Devonian extinction. Such Akiyoshian corals may solve the intriguing question of why they recovered and constructed organic reefs earlier than did corals elsewhere in the world. Further research is needed, especially on the species-level identification of corals, taking into full consideration their ontogenetic growth changes, intra- and interspecific morphological variability, and fine skeletal structures of the septa. It will not be until we conduct such studies that we will realize the real phylogenetic importance of Akiyoshian rugose corals, and more accurately reconstruct the palaeogeography and palaeoenvironments of the Carboniferous.

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Plate 1

Rugose corals characteristic of the Hina Limestone.

A: *Cyathaxonia* sp., early Visean, the *Endothyra* Zone, OCU 6581, Scale = 1 mm.

B: *Echigophyllum atetsuense* (MINATO & NAKAZAWA, 1957), possibly late Visean (including *Tetrataxis conica*, *T.* sp., *Mediocris breviscula*, *Endothyra* sp., and *Endostaffella* sp.), OCU 6582, Scale = 5 mm.

C: "*Orionastraea*" cf. "*O.*" *columellaris* PICKETT, 1966, possibly middle Visean (including *Endostaffella* sp.), OCU 6583, Scale = 2 mm.

D: *Siphonodendron hinense* YAMAGIWA, SUZUKI & OKIMURA, 2000, possibly middle to late Visean (including *Tetrataxis conica* and *T.* sp.), OCU 6584, Scale = 2.5 mm.

E: *Hiroshimaphyllum toriyamai* (MINATO, 1955), possibly late Visean (including *Tetrataxis elongata*, *T. angusta*, *T.* sp., *Endothyra* sp., and *Endostaffella* sp.), OCU 6585, Solitary geyerophyllid *Amygdalophylloides* is found together, Scale = 5 mm.

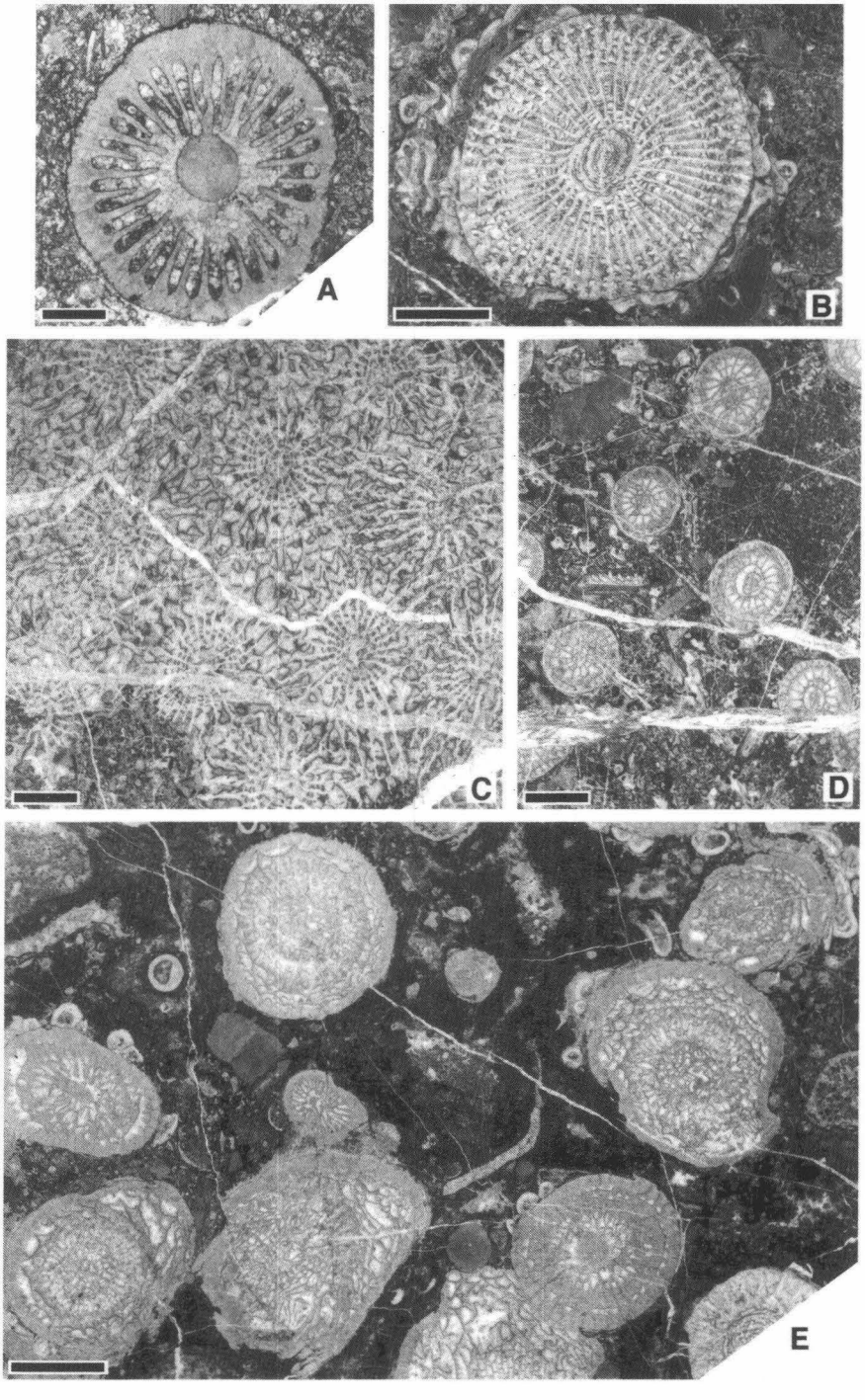

A
B
C
D
E

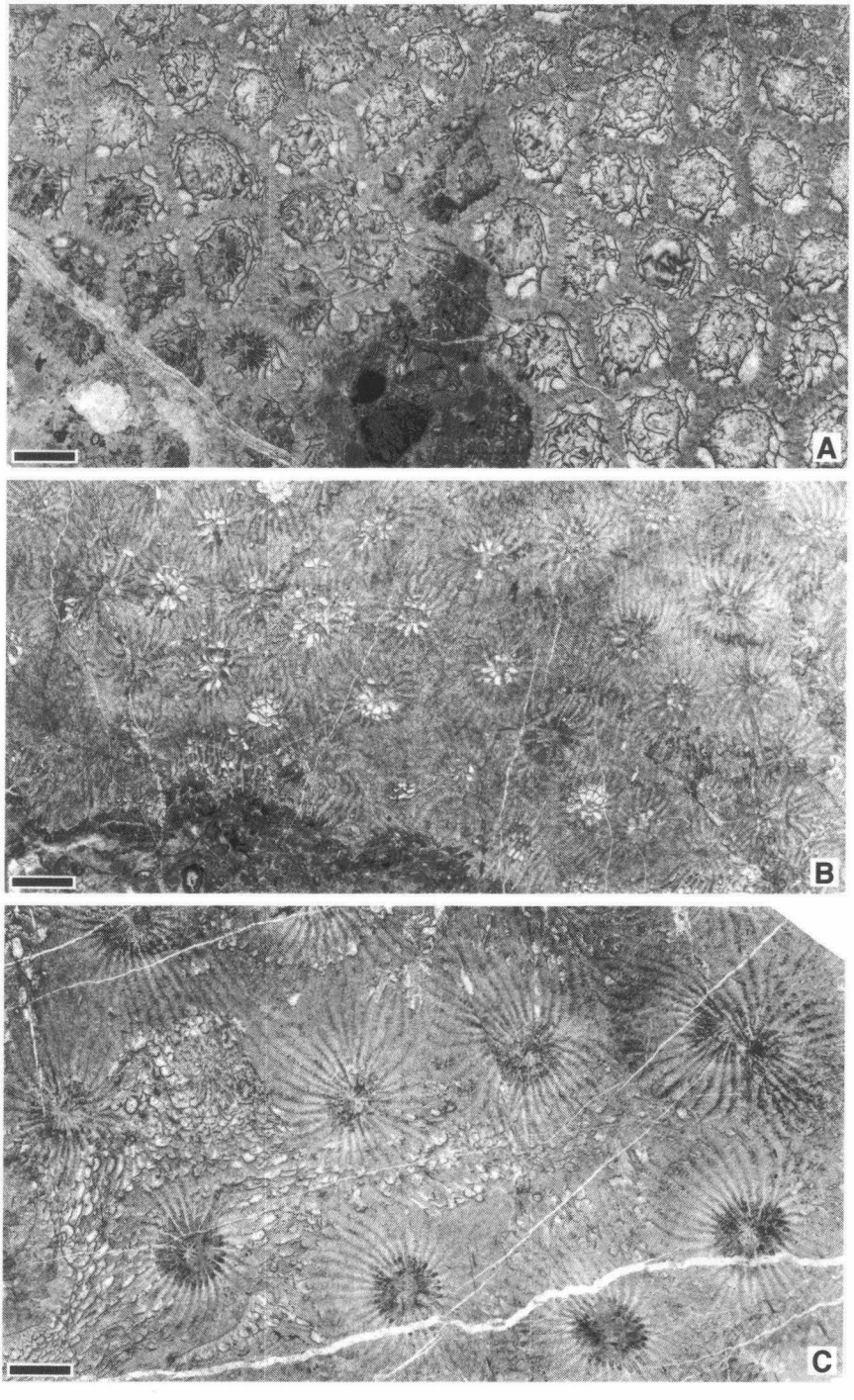
Plate 2

Rugose corals characteristic of the Hina Limestone.
Scale = 2.5 mm.

A: *Ozakiphyllum* sp. nov., OCU 6586.

B: *Pseudopavona taisyakuana* Yabe, Sugiyama & Eguchi, 1943, OCU 6587.

C: *Pseudopavona* sp. nov., OCU 6588.


A
B
C