Low-diversity shallow marine benthic fauna from the Smithian of northeast Japan: paleoecologic and paleobiogeographic implications

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Abstract. An unusually low-diversity shallow marine benthic community in a siliciclastic setting was identified and described from the Lower Triassic (Smithian) Hiraiso Formation (Southern Kitakami Mountains, northeast Japan). The Hiraiso fauna includes bivalve species of widespread genera, such as *Eumorphotis*, *Entolium*, *Bakevellia* (*Maizuria*), *Unionites*, *Neoschizodus*, and the oldest record of the crinoid genus *Holocrinus*. Facies analysis enabled reconstruction of an environmental gradient ranging through storm-dominated sedimentary settings of various depths, thus allowing us to estimate the probable habitats of the shelly fossil assemblage. Regional comparison of contemporaneous shallow marine fossil localities (i.e., Southern Primorye, Maizuru Terrane, and Chichibu Terrane) demonstrated particularly striking similarity among the shallow marine benthic communities of these siliciclastic settings. We thus infer no substantial ecological recovery among these tropical shallow marine benthic communities in Smithian time.

Key words: crinoid, HCS, Lower Triassic, Maizuru, mass extinction, recovery, Permian-Triassic event, Smithian, South Kitakami, South Primorye

Introduction

Among the global biotic crises of the Phanerozoic, the Permian-Triassic (P/Tr) mass extinction was the largest and eliminated more than 90% of marine genera (Erwin, 1994). Besides the magnitude of the extinction, one other striking, yet enigmatic, aspect of the P/Tr event is its aftermath. Low-diversity, depauperate marine ecosystems continued well into the Early Triassic. Unlike other major mass extinction events, substantial ecological recovery is not observed among marine communities until the end of the Early Triassic (some 10 < Ma; Erwin, 1994; Schubert and Bottjer, 1995; Twitchett, 1999; Bottjer, 2001). This apparently unusual situation has been attributed to various causes including the intensity of the extinction, prolonged environmental stresses, and preservational bias (Hallam, 1989; Erwin, 1993; Schubert and Bottjer, 1995; Erwin, 1996; Erwin and Pan, 1996; Twitchett, 1999). Twitchett (1999) studied the benthic macrofauna and the ichnofossils across the P/Tr boundary of northern Italy (Werfen Formation) and showed that the delayed recovery of the fossil community in the Lower Triassic of northern Italy is partly explained by prolonged low-oxygen conditions. To fully answer this question, however, further paleoecologic studies are required so that the temporal and geographic patterns of ecological recovery become better illustrated.

Early Triassic shallow marine benthic faunas have been reported from several localities in Japan (summarized in Hayami, 1975). It has been previously noted that these localities are grouped into two types: the first type is carbonates that are sporadically distributed in the Outer Zone of Southwest Japan; the second type is siliciclastic formations that are located in the Inner Zone of Southeast Japan (Maizuru Terrane) and Southern Kitakami Mountains (hereafter, S. Kitakami; Nakazawa, 1971; Nakazawa *et al.*, 1994).

We studied the fossil record of the Hiraiso Formation: a siliciclastic Lower Triassic unit from S. Kitakami. The benthic invertebrates were described and the sedimentology and taphonomy were assessed in order to estimate the probable habitats of the
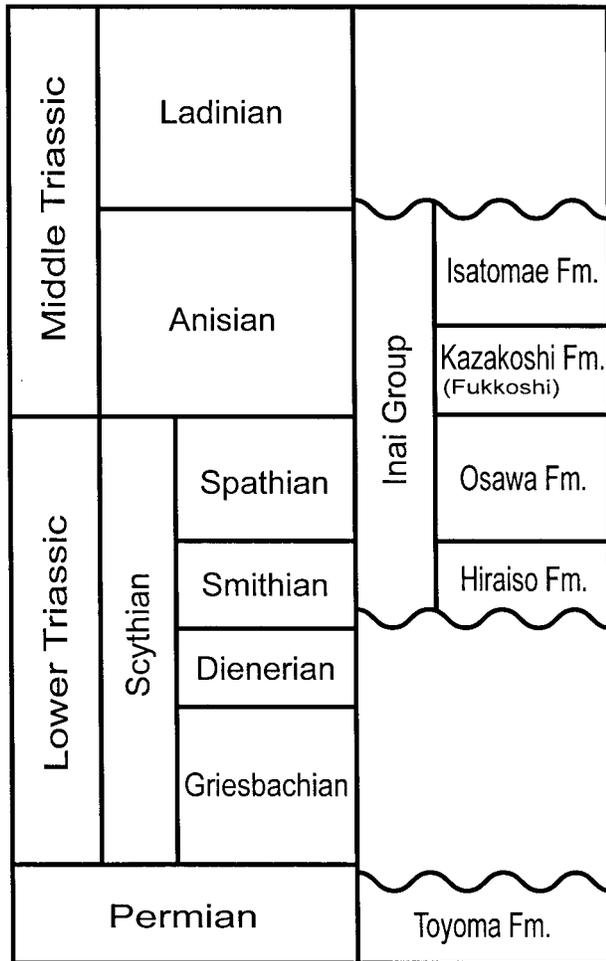
Figure 1. Stages from the Late Permian through the Middle Triassic and the stratigraphy of the South Kitakami Mountains.

assemblage. Finally, the fossil community was compared to those of other Lower Triassic units in nearby localities.

Geologic settings

In northwestern Japan, the Lower and Middle Triassic are represented by thick siliciclastic shelf deposits of the Inai Group, exposed in the southeast to southern region of S. Kitakami (Figure 2). The Inai Group unconformably overlies the Upper Permian and is itself unconformably overlain by the Upper Triassic Saragai Group or the Jurassic Shizugawa and Hashiura Groups. It consists of two major transgressive sequences; the Hiraiso Formation and the overlying Osawa Formation represent the first sequence.

The Hiraiso Formation unconformably overlies the uppermost Permian Toyoma Formation (Shiida, 1940; Kambe, 1963) with slight angular unconformity (Kamada, 1993). The base of the Hiraiso Formation consists of a conglomerate facies, which is overlain by alternating laminated sandstone and bioturbated siltstone. Finally, it grades up to a finely laminated siltstone facies of the Osawa Formation.

S. Kitakami is regarded as an allochthonous terrane (the South Kitakami Terrane; Kobayashi, 1999). Paleomagnetic and paleobiogeographic data have set the paleolatitude of S. Kitakami in Permian-Triassic time within $0°{\sim}S20°$ (Saito and Hashimoto, 1982; Ozawa, 1987; Maruyama et al., 1989; Davydov et al., 1996). Based on the micropaleontologic data, Kobayashi (1999) reconstructed S. Kitakami together with Kurosegawa Terrane as an arc-trench system and concluded that the South Kitakami-Kurosegawa Arc was located near South China during the Late Permian (Figure 3).

The sedimentary basin of the Inai group was thus probably located in an active margin (Kamada, 1989). Kamada (1989) inferred a high rate of sedimentation due to tectonic instability at the source area – large-scale strike-slip faults that were active in Permian-Triassic time.

Locality

The field survey was conducted on the Hiraiso Coast in Motoyoshi-cho, Miyagi Pref., Japan (Figure 2), the type locality of the Hiraiso Formation. The rocky coast between Maekawara and Akaushi fishing ports provides a continuous 800 m outcrop that embraces the entire Hiraiso Formation.

Previous works

Biostratigraphy. The age of the Hiraiso Formation is currently considered as Smithian along the Hiraiso Coast (Bando, 1970). Bando (1970) originally assigned the Hiraiso Formation to the Griesbachian based on a single specimen of the ammonite *Glyptophiceras* cf. *gracile*. However, later it was assigned to the Smithian by Nakazawa et al. (1994) who reidentified the ammonite as *G. aequicostatus*. This new correlation seems reasonable because the overlaying Osawa Formation ranges from the Smithian to the uppermost Spathian, assigned also by ammonite fossils (Bando, 1968; Bando and Shimoyama, 1974; Nakazawa et al., 1994).

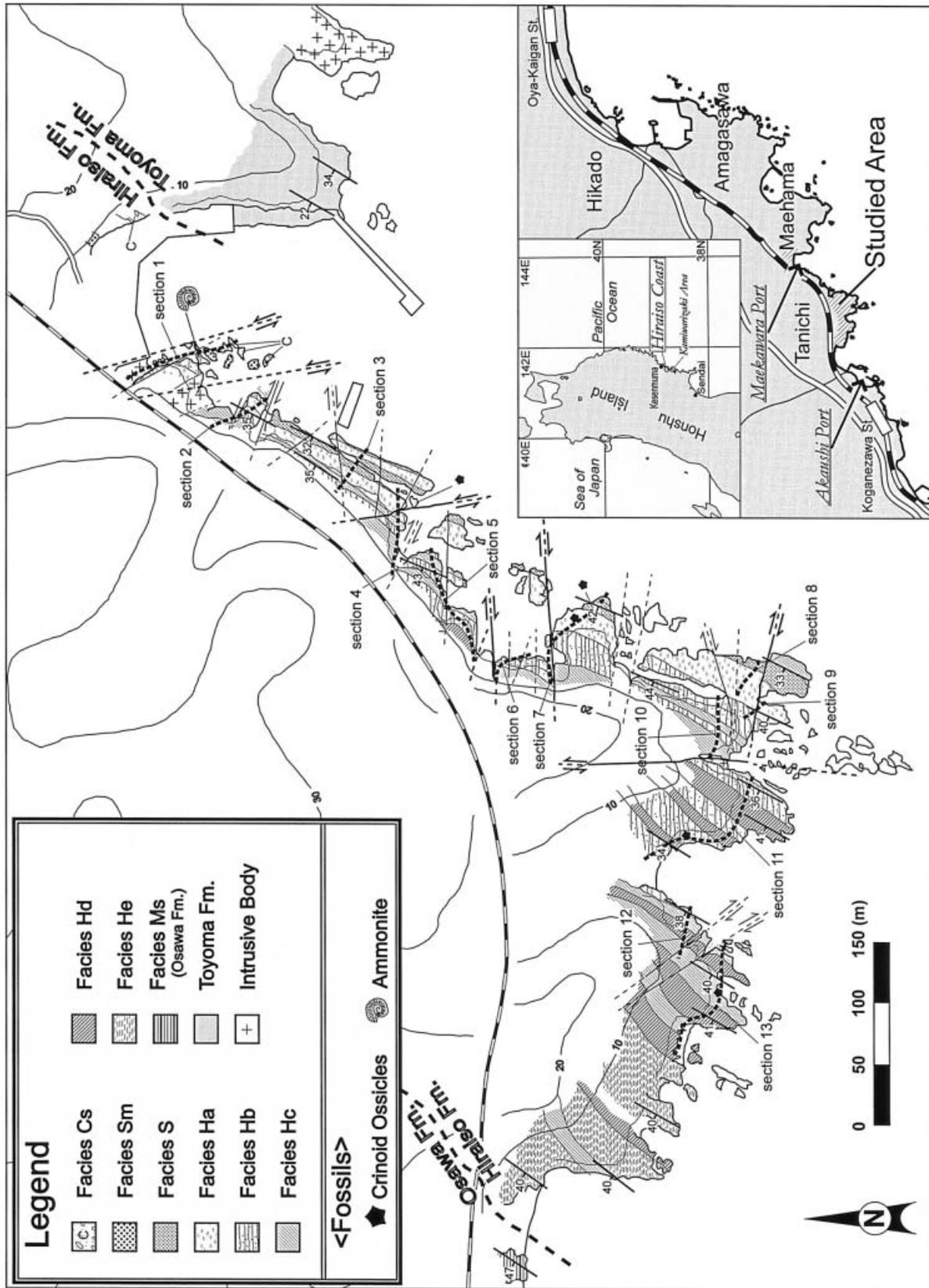*Paleontology.* Ichikawa (1951) presented the first

Figure 2. Locality map and map of the studied area showing facies distribution. "Section" with numbers indicating routes for stratigraphic sections appearing in Figure 4.
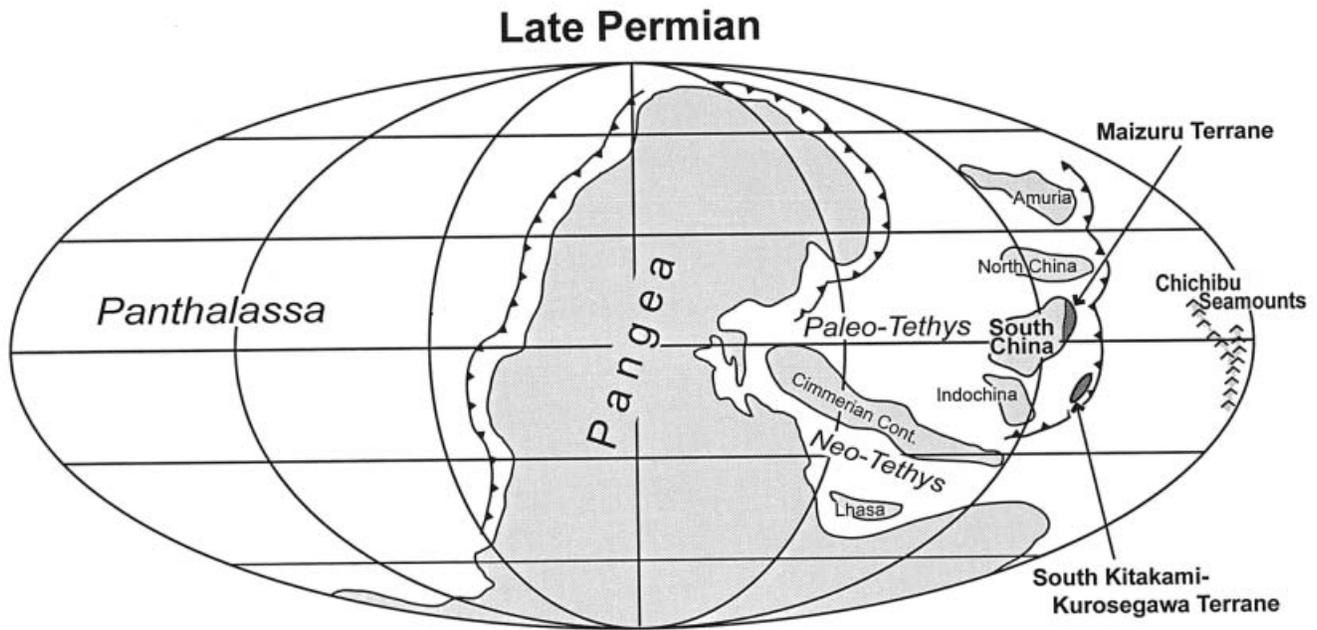
Figure 3. Late Permian paleogeography after Kobayashi (1999). Reconstructed locations of S. Kitakami and Maizuru are shadowed. S. Primorye, which is now located next to the Amuria, was probably located rather close to Maizuru or S. Kitakami (see discussion in text).

list of fossils from the Hiraiso Formation. Later, this study was summarized by Bando (1964) with minor additional information. Nonetheless, no systematic description of these fossils was made. In addition to the fossil collections gathered in this study, we also reexamined some of the Ichikawa (1951) collection that is in the University Museum, University of Tokyo.

Sedimentology. Kamada and Kawamura (1988) and Kamada (1992) studied the sedimentary fabrics in the Hiraiso Formation in the Kamiwarizaki area, 20 km south of our study area. They recognized four types of storm-generated deposits, including amalgamated hummocky-cross-stratification (Storm Deposit Type A), hummocky-cross-stratification (Storm Deposit Type B and B′), sheet-shaped thin sandstones (Storm Deposit Type C), and turbidites (Storm Deposit Type D). Corresponding sedimentary settings for these lithofacies were then interpreted in terms of basin depths relative to normal and storm wave bases (Kamada and Kawamura, 1988).

Facies analysis and reconstruction of environmental gradient

We identified nine facies (Facies Cs, Sm, S, Ha, Hb, Hc, Hd, He, Ms) within the Hiraiso Formation (Table 1; Figure 4). Sedimentary structures indicative of storm-related deposition appear in Facies Ha–He and Ms. The thick hummocky-laminated sandstone facies (Facies Ha) is overlain by the facies consisting of discrete HCS sequences (Facies Hb and Hc). Such discrete sets of the HCS sequences become unclear upward; the lamination is destroyed by bioturbation (Facies Hd); then, each sequence becomes thinner with nearly parallel lamination (Facies He). These facies (Facies Hc–He) repeatedly appear until the undisturbed, thinly bedded siltstone facies (Facies Ms) of the basal Osawa Formation.

Storm deposits are excellent bathymetric indicators. Thus, bathymetric interpretations are made by identifying the storm deposit types (Storm Deposit Type A∼D; see the previous section) of Kamada and Kawamura (1988) in our storm-generated facies (Facies Ha∼He and Ms; Table 1). Facies Ha is dominated by the Storm Deposit Type A, i.e., amalgamated hummocky cross stratification (amalgamated HCS; Dott and Bourgeois, 1982); similarly, Facies Hb and Facies Hc are dominated by Storm Deposit Type B (HCS type) and Storm Deposit Type B′ (HCS type without lag deposits, which we call herein ''basal shelly deposits''), respectively (Figure 4); Facies He and Facies Ms are alternations of thin siltstone layers and Storm Deposit Type C (sand-sheet type) or Storm Deposit Type D (turbidite type), respectively. Therefore, judging from the interpretation by Kamada and Kawamura (1988), Facies Ha is correlated to the upper

Table 1. Descriptions of facies recognized in this study. Facies Cs, Sm, S, and Ha~He are found in the Hiraiso Formation. Facies Ms is found in the base of the Osawa Formation. Storm deposit types are after Kamada and Kawamura (1988). For depositional environment, refer to Figure 5.

Facies	Storm Deposit Types (Kamada and Kawamura, 1988)	Depositional Environment	Fossil Occurrence
Facies Cs: stratified conglomerates		fluvial?	absent?
Facies Sm: poorly-sorted, massive, micaceous sandstone		fluvial?	shell fragments
Facies S: well-sorted, massive sandstone		upper shoreface?	absent?
Facies Ha: hummocky-laminated sandstones with basal shelly deposits (amalgamated HCS)	Storm Deposit Type A	upper inner shelf	basal shelly deposits and sparse concentration of crinoid ossicles
Facies Hb: hummocky-cross-laminated sandstones with basal shelly deposits and bioturbated siltstones	Storm Deposit Type B	upper inner shelf	basal shelly deposits and sparse concentration of crinoid ossicles
Facies Hc: parallel- to hummocky-cross-laminated sandstones and bioturbated siltstones	Storm Deposit Type B′	lower inner shelf	sparse concentration of crinoid ossicles
Facies Hd: thin alternation of siltstones and entirely bioturbated sandstones		lower inner shelf to outer shelf	rare
Facies He: banded alternation of parallel-laminated sandstones and bioturbated siltstones	Storm Deposit Type C	lower inner shelf to outer shelf	rare
Facies Ms: undisturbed, striped alternation of parallel- or cross-laminated, light-gray siltstones and dark-gray siltstones	Storm Deposit Type D	outer shelf	absent

inner shelf, and Facies Hb, Hc, He, and Ms are correlated to successively deeper environments, respectively (i.e., lower inner shelf to outer shelf; Figure 5). Thus, the facies analysis clearly illustrates that the entire Hiraiso Formation and the base of the Osawa Formation constitute one major deepening-upward sequence with some minor deepening-shallowing fluctuations (Figure 4).

The occurrences of fossils are limited mostly to Facies Ha and Hb (Figure 4). Facies Ha consists of hummocky-cross-laminated fine to very fine sandstone with basal shelly deposits, in which siltstone layers are only occasionally intercalated (Figure 4). Basal shelly deposits comprise either densely or sparsely concentrated shells, occasional rip-up clasts, and sandy matrix with calcareous cement (Figure 6); they are preserved without any apparent later disturbance (e.g., bioturbation). Basal shelly deposits and siltstone layers pinch out laterally within several meters. Therefore, single discrete depositional events cannot be identified in this facies (i.e., HCS sequences are amalgamated; Dott and Bourgeois, 1982). Such amalgamation as seen in Facies Ha is thought to be the consequence of little accumulation of background sediment and/or considerable erosion of silt prior to deposition of storm sand (Dott and Bourgeois, 1982; Kamada, 1992). In contrast, Facies Hb comprises alternation of hummocky- to parallel-laminated sandstone and partially or entirely bioturbated siltstone. Therefore, discrete (idealized) HCS sequences (Dott and Bourgeois, 1982) are identified, where basal shelly

deposits constitute the base of such sequences (Figure 4). Thus, Facies Ha represents a higher energy setting than Facies Hb, or a shallower (and more proximal) sedimentary environment is inferred (Kamada, 1992).

Mode of fossil occurrence

Fossils from the Hiraiso Formation are found in two types of shell beds: 1) dense concentrations in basal shelly deposits and 2) sparse concentrations within hummocky-cross laminated sand/siltstone in HCS layers. The former type contains disarticulated bivalves, a few small gastropods, and rare crinoid ossicles. On the other hand, the latter comprises crinoid ossicles only. Shelly fossils are nearly absent in intervening siltstone layers with a few minor exceptions.

Methods of fossil study

The majority of fossil specimens of bivalves and crinoid ossicles were collected from moderately weathered rock samples as natural external molds from which silicone rubber casts were obtained; few specimens could be successfully prepared from the highly consolidated and cemented fresh sandstone samples. Although such shelly deposits are ubiquitous, relatively small numbers of fossil specimens were collected due to limited exposure of moderately weathered rocks in the studied area. In addition, casts of fine shells (less than several millimeters in diameter) and small gastropods of adequate quality for species iden-
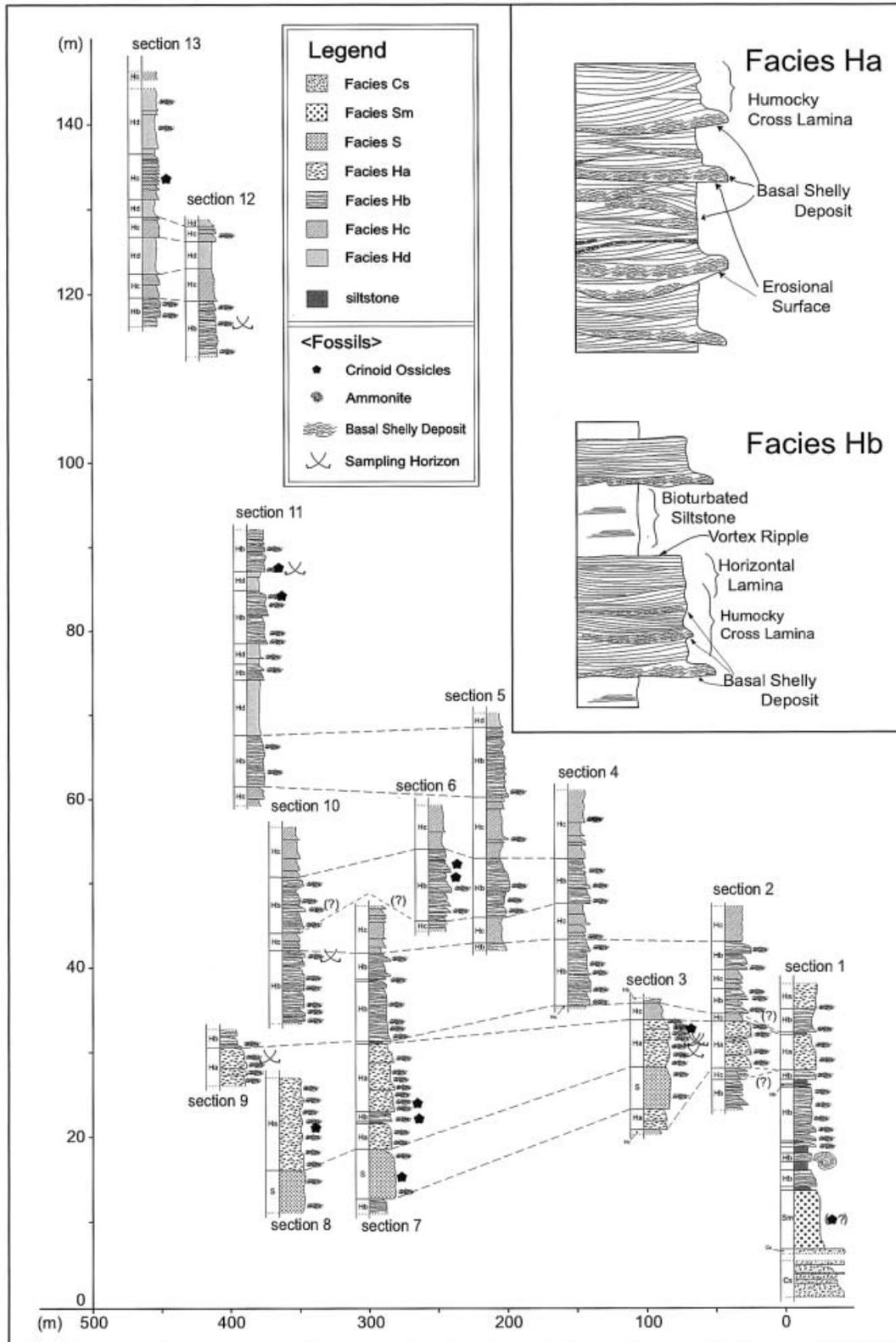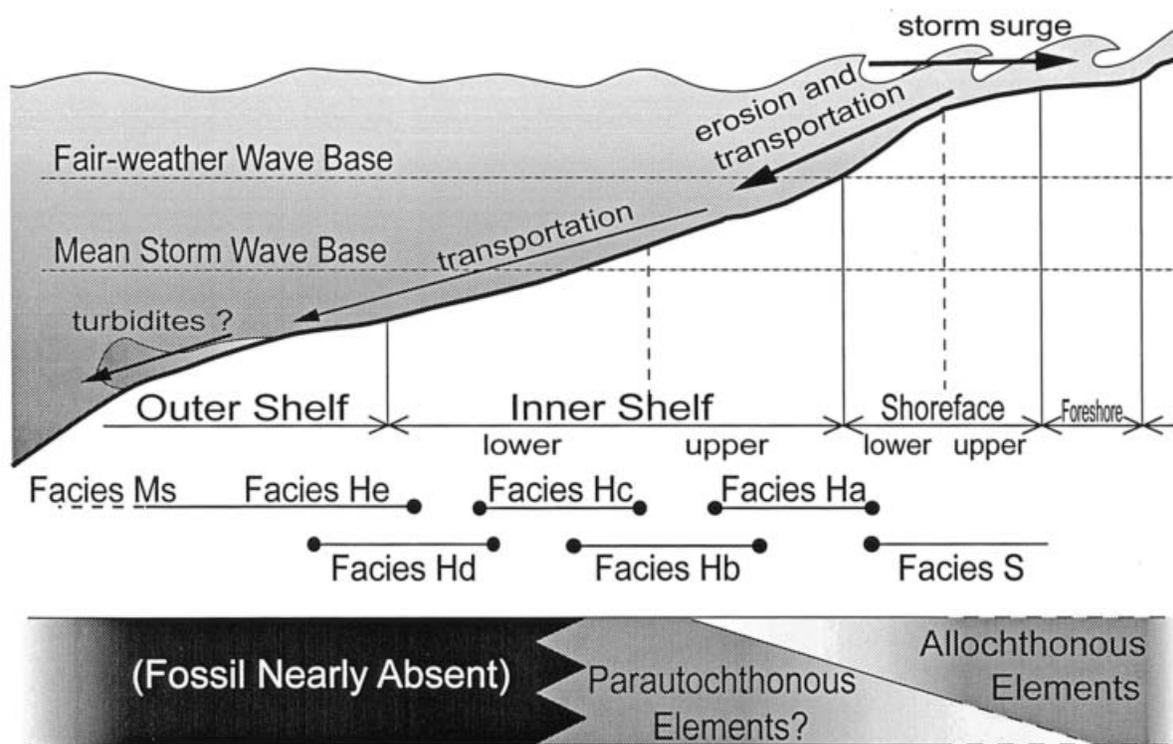
Figure 5. Schematic diagram showing transect of the continental shelf. Estimated bathymetric ranges of facies S, Ha–He, and Ms are shown. Diagram at the bottom schematically illustrates the gradual change in composition of fossil assemblages along the depth gradient.
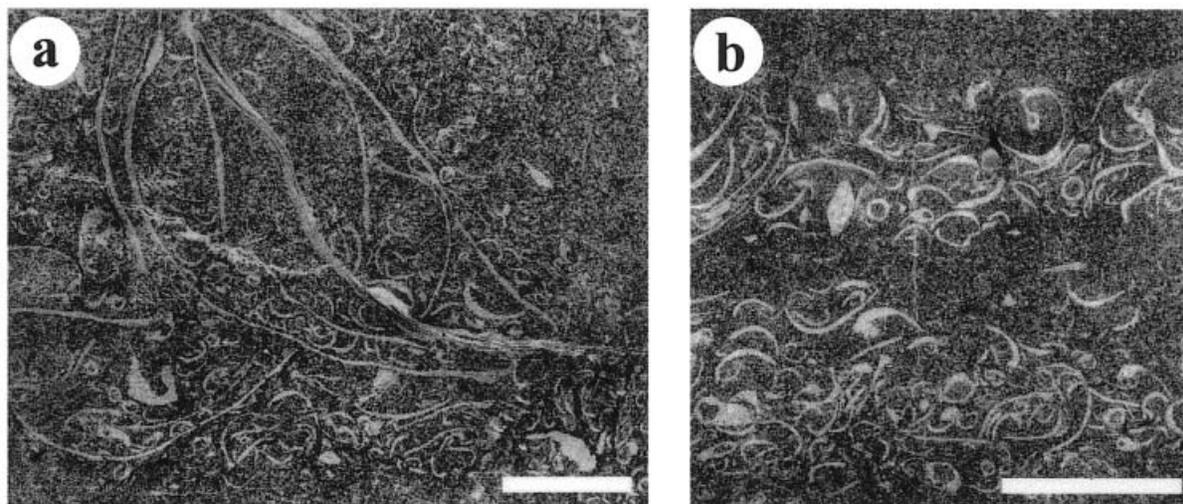

Figure 6. Cross-section of basal shelly deposits (acetate peels photographically printed onto developing papers). Typical basal shelly deposits of: ⓐ Facies Ha; and ⓑ Facies Hb. Scale bar 1 cm.

← **Figure 4.** Correlated stratigraphic sections of the Hiraiso Formation of the Hiraiso Coast. The base of the Hiraiso Formation is composed of a conglomerate layer (Facies Cs) with immediately overlying sandstone layers (Facies Sm and Facies S) that probably correspond to shoreface or shallower environments. The middle to the top of the Hiraiso Formation comprises various storm-depositional facies (Facies Ha–He and Ms), grading from shallower facies (Facies Ha) to deeper facies (Facies He) upward. Finally, it grades into further offshore facies of the base of the Osawa Formation (Facies Ms). Figures in the right-top corner are schematic diagrams of Facies Ha and Hb.

tification could not be obtained due to the fragility of the weathered sandstone. On the other hand, crinoid ossicles are preserved in finer substrates (i.e., very fine sand to silt); thus, fine details of their surface ornamentation were recovered in the silicone rubber cast.

To supplement the in situ observation of shell beds, sections of unweathered shelly deposits were slabbed and polished; details of the fabric of the shell beds were then observed in acetate peels that were photographically printed onto photographic papers (i.e., peels were treated like negative films; Figure 6).

Shell bed analysis

Observation of the polished slab sections showed that nearly all bioclasts in basal shelly deposits are bivalves with minor small gastropod shells and probable crinoid ossicles. All shells are very thin, at most 1 mm, but are unfragmented. Each shell deposit contains bivalve shells of wide size variation. The size of bivalves of Facies Ha ranges from submillimeter up to 60+mm in cross-section, with a mode of 2 mm. Those of Facies Hb range from submillimeter to 10 mm in cross-section, with a mode of 2 mm. Although size distribution varies among the shelly deposits, minute bivalves (< 4 mm) were revealed to be considerably abundant ($> 90\%$) in most of the beds. Shells are loosely to densely packed, with no obvious internal size sorting or grading. There was a tendency among large shells to be stacked concave up, indicative of repeated resuspension and fallout during turbulent storm currents (Kidwell and Bosence, 1991). All of these fabrics suggest rapid deposition as is expected for basal deposits of HCS (Dott and Bourgeois, 1982).

The nature of the basal shelly deposits varies between facies, that is, along the bathymetric depth gradient. Both abundance and thickness of shelly deposits are high in Facies Ha but significantly decrease toward deeper facies (e.g., Facies Hb). Basal shelly deposits in Facies Hb typically lack large shells (over a few centimeters) and contain occasional articulated valves. In contrast, the majority of crinoid accumulations are observed in Facies Hb. In the deeper facies, such fossil concentrations are nearly nonexistent, except for three thin sheets of shell beds within Facies Hc and Hd.

Discussion

Biostratinomy
We infer that a difference in transportational processes rather than winnowing by an in situ depositional process was responsible for the formation of these two distinct types of shelly deposits because (1) size sorting within basal shelly deposits was not observed; and (2) the size of the crinoid ossicles is significantly greater than the grain size of the matrix. This may in turn imply that the bivalves and the crinoids were derived from distinct life habitats. Nonetheless, they are treated as a single assemblage in this study because of the poor spatial resolution of habitat.

With respect to the basal shelly deposits, increasing importance of allochthonous elements in shallower facies is indicated by a morphology-based reconstruction of the habitat of *Eumorphotis iwanowi*. The large bivalve *Eu. iwanowi*, which is ubiquitous in basal shally deposits of Facies Ha, is generally thought to have attached to some hard substrates in their lifetime; its narrow and very deep byssal notch of the right valve is indicative of an epibyssate lifestyle (I. Hayami, pers. comm., 1999). Because the upper-inner shelf environments generally have a soft substrate, *Eu. iwanowi* probably represents an exotic element; their original habitat was possibly in a shallower environment with a hard substratum, such as a rocky coast. This idea is also concordant with the following observation; (1) occurrence of *Eu. iwanowi* is limited only to relatively thick basal shelly deposits of Facies Ha that are probably formed under higher energy conditions where high potential for transportation of bioclasts as large as *Eu. iwanowi* could be expected; (2) occurrence of *Eu. iwanowi* gradually decreases toward deeper facies (e.g., Facies Hb), implying that *Eu. iwanowi* lived in shallower environments. Furthermore, *Eu. iwanowi* frequently cooccurs with the medium-sized bivalve *Entolium ussuricus*, a free mobile-epifaunal species, which may reflect similar origin and similar transportation mode of *Eu. iwanowi* and *En. ussuricus* and thus may also be an allochthonous element.

An alternative explanation for the enigmatic occurrence of epibyssate *Eu. iwanowi* may be that they were attached to a *firm* substratum such as biomats (R. Twitchett, pers. comm., 2003), but not a strictly *hard* substrate such as an exhumed rock surface. We thus suggest a queer but intriguing hypothesis, that *Eu. iwanowi* was dwelling on the biomats that might have been covering the sediment in the upper-inner shelf environment during calm intervals between storm events. Indeed, the Lower Triassic is wellknown for the reappearance of normal marine stromatolites, which probably reflects reduced activity of benthic faunas (Schubert and Bottjer, 1992). Recently, Pruss *et al.* (2004) reported wrinkle structures, an evidence of microbially stabilized substrate, from storm-dominated siliciclastic settings of the Lower Triassic

Table 2. List of fossils identified in this study. The table in the middle shows occurrences of these species in three proximal localities discussed in this paper (◎: abundant; ○: common; △: rare). Fossil genera listed by Ichikawa (1951) are correlated in the right column.

| Fossils Identified in the Present Study | South Kitakami | | Southern Primorie | Maizuru | Chichibu | Fossil Genera Listed by Ichikawa (1951) |
	Facies D	Facies E				
Bivalve						
Bakevellia (Maizuria) sp. cf. *kambei* Nakazawa	◎	○	○	○		*Bakevellia, Gervellia*
Eumorphotis iwanowi (Bittner)	◎		○			*Eumorphotis*
Entolium ussuricus (Bittner)	◎		○	○		"*Pecten*"
Unionites aff. *canalensis* (Catullo)	△	○	○		○	*Anodontophoria*
Neoschizodus cf. *laevigatus* (Ziethen)		○	○	○		*Myophoria*
	?	?		○		*Nuculopsis*?
	?	?		○		*Palaeoneilo*
	?	?				*Pleurophorus*
Gastropod						
(Trochoidea; two types)	○	○				*Dentalium, Worthenia*?
Ammonoid						
Glyptophiceras? sp.	△			△		
Crinoid						
Holocrinus sp.	○	○				*Isocrinus*

beds. However, we failed to recognize any trace of biomats in the Hiraiso Formation; thus, there is no positive evidence supporting parautochthonous origin of *Eu. iwanowi*.

We thus infer considerable introduction of shells from shallower environments to the upper inner shelf, probably by offshore-directed combined flow during storm events (cf. Kamada, 1992). This hypothesis is supported by studies of modern storm sedimentation events by, e.g., Aigner (1985), who observed the introduction of shells from tidal channels or tidal flats into deeper settings and a gradual decrease of such allochthonous elements offshore. It is, therefore, impossible to distinguish between the allochthonous elements (i.e., derived from shoreface or shallower environments) and parautochthonous elements among the fossil assemblages in the basal shelly deposits (cf. Kamada, 1992). Because of the decreasing proportion of apparently allochthonous element (i.e., *Eu. iwanowi*) basinward, we may only infer that shelly deposits in deeper facies (Facies Hb) are likely to contain a higher proportion of the parautochthonous elements (i.e., derived within upper-inner shelf) than shallower facies (Facies Ha; Figure 5).

Stratigraphic variation in the taxonomic composition of the shelly deposits largely reflects the change in such biostratinomic modes with gradual deepening (i.e., proximal to distal). Given the high sedimentation rate for the Hiraiso basin (Kamada, 1992), evolution is unlikely to be a cause of the compositional variation among the shelly deposits. Thus, in the following discussion, we regard the whole collection of fossils from Facies Ha and Hb of the Hiraiso Formation as a single assemblage from the upper-shelf environment that was time-averaged over a period of relative environmental stability.

Taxonomic diversity

Very low diversity at both higher taxonomic levels and the species level apparently characterizes the Smithian shallow marine benthic fauna of S. Kitakami, even though the number of individuals preserved is remarkably large. The fossil taxa recognized from the Hiraiso Formation only include five species of bivalves, two types of gastropods (genera unknown), one crinoid, and one ammonoid (Table 2). Observations of the cross-sections are adequate to determine the higher taxonomy of the skeletal fossils (Figure 6), which affirmed that, indeed, only bivalves, gastropods, and crinoids are present.

We could only recognize five species of bivalves (one for each of five genera), although Ichikawa (1951) listed nine genera (Table 2). We suspect oversplitting and, indeed, many of these are synonymized in this study. However, species richness is probably underestimated due to sampling bias because numerous small shells (< 10 mm) could not be identified because of their poor preservation, although low variability in cross-sectional morphology among such minute valves implies that the bias might not be very significant. In addition, some of the minute valves are possibly juvenile forms. However, cross-sectional views are not reliable for species identification.

Such low species richness of bivalves is unusual in a normal marine environment, provided that the assemblage represents a wide range of environments (i.e., lower shoreface to upper inner shelf or even shallower environments). For a more conclusive dis-

Table 3. Comparison of species richness and number of higher taxa; modified after Schubert and Bottjer (1995).

		Total Species Present	Number of Higher Taxa
Permian (average)		46	9
Early Triassic (western USA)	Smithian	27	3
	Spathian	28	5
Middle and Late Triassic (average)		44	8
Early Triassic (Smithian; S. Kitakami)		9	4

cussion of the *lowness* of the fossil diversity, however, it should be compared to the fossil faunas of pre-event time (i.e., Late Permian) and the post-event time (after the end of the recovery period; i.e., Middle and Upper Triassic). Since no other example of an assemblage in shallow-marine siliciclastic settings has been well documented from immediately preceding and following times, we could only compare the taxonomic diversity of the S. Kitakami fauna to those of carbonate settings. Schubert and Bottjer (1995; p. 29) compared species richness and number of higher taxa in faunas from Permian and Early, Middle, and Late Triassic times (Table 3). Average species richness of the Permian and the Middle to the Late Triassic are 46 and 44, respectively, which is six to seven times larger than that of the S. Kitakami fauna. In addition, the number of higher taxa of the Permian and the Middle to the Late Triassic (9 and 8, respectively) also doubles that of the S. Kitakami fauna.

Diversity of the S. Kitakami fauna is similar to or even lower than those of the same time in other localities. The S. Kitakami fauna is comparable to the low-diversity Smithian fauna from the western USA (Schubert and Bottjer, 1995) and northern Italy (Twitchett and Wignall, 1996) where the faunas consist of only bivalves and gastropods. The Smithian fauna of the western USA consists of slightly different bivalve genera from those of Hiraiso and has more diverse gastropods. Significantly, however, crinoids have not been reported from the Smithian of the western USA and northern Italy only from the Spathian (Schubert *et al.*, 1992; Schubert and Bottjer, 1995; Twitchett, 1999).

Although comparison of uniquely siliciclastic S. Kitakami to other carbonate settings makes the argument less conclusive, the siliciclastic setting certainly could not be the primary factor causing the apparent low diversity of the assemblage. Many earlier Paleozoic and later Cenozoic examples assure that storm-dominated siliciclastic shallow marine environments have obviously been supportive of rich benthic faunas,

and significantly diverse fossil assemblages are thus potentially preserved in the corresponding storm-generated facies. For example, the Lower Cretaceous Miyako Group of northeast Japan preserves a total of 245 species that fall into nine higher-taxonomic groups, including foraminifers, sponge, corals, brachiopods, bivalves, gastropods, cephalopods, crinoids, echinoid, and crustacean (Hanai *et al.*, 1968). Considering the high abundance of the fossils preserved, we conclude that the observed lowness of diversity in the Hiraiso assemblage most likely reflects genuine low faunal diversity of the Smithian S. Kitakami fauna.

Low faunal diversity may be attributed to instability of the environmental conditions of the shallow shelf settings that was caused by intermittent invasion of an oxygen-depleted water mass from a deeper, but immediately adjacent, setting. Increasingly stressful conditions are inferred from the decreased intensity of bioturbation in deeper facies (e.g., Facies Hc and He) where body fossils are rare or absent; bioturbation is nearly nonexistent and laminae are preserved undisturbed in the deepest facies (i.e., Facies Ms), indicating anoxic conditions (Davis and Byers, 1989; Wignall and Hallam, 1992). In addition, the majority of bivalves from deeper facies than Facies Hb are less than 1 cm in size; there are abundant minute intact valves as small as 0.5 mm (Figure 6). Such diminished size of bivalves may be explained by oxygen depletion of the living habitat. This observation is thus concordant with the hypothesis of prolonged stressful conditions in the Lower Triassic (Hallam, 1989; Twitchett, 1999) and the superanoxic event (Isozaki, 1997; Wignall and Twitchett, 2002).

Paleobiogeography

We compared the taxonomic composition of the assemblage from S. Kitakami (i.e., the Hiraiso Formation) with other Early Triassic fossil faunas from nearby localities, including Southern Primorye (eastern Siberia, Russia; i.e., Ussuriland; hereafter S. Primorye) and the localities in the Maizuru Terrane and the Chichibu Terrane (western Japan). Clearly, these assemblages need to be reexamined from the viewpoint of paleoecology, but, nonetheless, we recognized compelling patterns of similarity among these localities.

Southern Primorye. The faunal composition of S. Primorye strongly resembles that of S. Kitakami (Bittner, 1899; Kiparisova, 1938). Both localities are characterized by very low taxonomic diversity and by a dominance of bivalves. Significantly, all the bivalves described herein are synonymous with those par-

ticularly from "outcrop (Entblössung) No. 37" in S. Primorye by Bittner (1899). In particular, the dominance of *Eumorphotis iwanowi* is characteristic to both of the localities. Occurrence of *Entolium ussuricus*, which is another of the most abundant species in S. Kitakami, is also common to S. Primorye (and to Maizuru). Although bivalves in S. Kitakami are somewhat less diverse than those of "outcrop No. 37" of S. Primorye, this is perhaps due to the poorer quality of fossil preservation at S. Kitakami.

These faunas, however, contain different minor elements. The inarticulate brachiopod *Lingula* and articulate brachiopods (*Terebratula* and *Spiriferina*) are found only in the fauna from "outcrop No. 37" of S. Primorye. In particular, the articulate brachiopods "prevailed" (Kiparisova, 1938). On the other hand, although crinoids are common in S. Kitakami, none has been reported from the entire Lower Triassic of S. Primorye. So far as the gastropods are concerned, at least a few species of Trochoidea are found in S. Kitakami; instead, the bellerophontid *Bellerophon* occurs in S. Primorye.

We suppose that this locality of S. Primorye ("outcrop No. 37") is probably contemporaneous to the Hiraiso Formation of S. Kitakami. Judging from the descriptions by Kiparisova (1938) and Bittner (1899), "outcrop No. 37" corresponds to the upper part of Horizon II of Russki Island by Kiparisova (1938). Kiparisova (1938) reported the occurrence of the ammonoid *Meekoceras* from the middle part of Horizon II and the ammonoid *Flemingites* from the overlying horizon (Horizon III). Therefore, Horizon II (i.e., "outcrop No. 37") is correlated to the Smithian, which is the same age as the Hiraiso Formation. A summary of the ammonite zones of S. Primorye appears in Kiparisova (1945, 1973).

The strong lithological resemblance between these two localities is striking. Kiparisova (1938) described Horizon II as "greenish-gray, occasionally brownish thick-bedded calcareous sandstones with lenses of shelly limestone and thin shale parting" (Kiparisova, 1938, p. 294). This description parallels that of the Hiraiso Formation; hence it probably represents a similar storm-dominated setting in a siliciclastic shallow marine environment. The bivalve community from the Hiraiso Formation is only closely related to that from Horizon II (i.e., "outcrop No. 37") and is rather different from the assemblages from other localities in S. Primorye that comprise different lithologies.

Maizuru Terrane. Nakazawa (1961) has already noted that the bivalve community of S. Kitakami is closely related to that of the Smithian siliciclastic localities in the Maizuru Terrane in western Japan (hereafter Maizuru). One notable difference is the absence of *Eumorphotis iwanowi* in Maizuru whereas it is ubiquitous in S. Kitakami. Nakazawa (1961) also noted the intimate relationship of bivalve communities between Maizuru and S. Primorye.

There again exist similar fossil assemblages and lithologies from Maizuru to those of S. Kitakami and S. Primorye. The sedimentary facies of Maizuru widely ranges from coarse- to fine-grained siliciclastic facies (Nakazawa, 1958), which apparently reflects the bathymetric gradient of the sedimentary basins. Composition of the bivalve fauna also varies along this gradient. Significantly, the assemblage from the coarser-grained facies is dominated by the bivalve species that are common to the Hiraiso Formation including *Neoschizodus* cf. *laevigatus* and *Bakevellia kambei*. On the other hand, the assemblage from the finer facies is represented by small shells such as *Palaeoneilo* and *Nuculana* (Nakazawa *et al.*, 1994) that are not recognized from the Hiraiso Formation.

Chichibu Terrane. Compositions of fossil assemblages from contemporaneous thin carbonates in Chichibu Terrane of the Outer Side of Southwest of Japan (hereafter Chichibu) are somewhat different from those from the siliciclastic localities above. Nakazawa (1971) summarized the studies of fossils from these carbonates including the Iwai Formation, the Shionosawa Limestone, the Tao Formation, the Gobangadake Formation, and the Kamura Limestone. The assemblages from the Iwai and Tao Formation consist mainly of ammonoids with some bivalves, which makes a notable contrast with rare occurrence of ammonoids from S. Kitakami, S. Primorye, and Maizuru. The other carbonates contain mainly bivalves with a few ammonoids. With respect to bivalves, *Pteria ussurica* is commonly reported from all of these carbonates whereas it is very rare in these siliciclastic facies. Likewise, *Eumorphotis iwanowi* and *Entolium ussuricus*, the dominant forms in S. Kitakami and S. Primorye, are absent from these carbonates. On the other hand, *Unionites canalensis* is common in all localities of both carbonate and siliciclastic settings except Maizuru. *Bakevellia rostrata* and *Eumorphotis multiformis*, which are abundant in the carbonates, are also reported from the siliciclastic settings except from S. Kitakami. *Leptochondria minima* is common in the carbonates and is also reported from S. Primorye.

Paleogeographic Relationship. Although only limited

paleogeographic studies are available for these localities, they were probably closely located in the Early Triassic. The Primorye region of Siberia consists of several allochthonous terranes (Shao *et al.*, 1992). Davydov *et al.* (1996) noted a significant similarity of the fusulinid fauna between Primorye and the [South] Kitakami Mountains indicating geographic proximity of these localities in the Early Triassic but a low level of similarity to adjacent regions and many other parts of the western Pacific. Kobayashi (1999) reconstructed paleogeography of the Maizuru Terrane based on foraminifera and other geographic evidence where he regarded it as a part of the eastern margin of South China in the Late Permian. It was therefore located fairly close to S. Kitakami. The Chichibu Terrane is an accreted body with seamounts, and Kobayashi (1999) located its paleogeographic position in tropical or subtropical western Panthalassa in the Permian-Triassic. The seamounts are thought to be located on a different plate from that encompassing South China and S. Kitakami. However, Kobayashi (1999) also noticed that the foraminifera of the Chichibu Terrane have some affinity to the Tethyan fauna, implying that the seamounts were not very distant from South China.

It is notable that S. Kitakami and Maizuru were both located in the equatorial region in the Early Triassic. S. Primorye could have also been located in relatively low latitudes, if it was located near S. Kitakami. Thus, all of these fossil assemblages probably represent communities from tropical shallow-marine environments.

Interpretation. Early Triassic bivalves, particularly those of the post-extinction survival interval (Erwin and Pan, 1996; Erwin, 1996), are typically dominated by eurytopic forms (e.g. Schubert and Bottjer, 1995). Indeed, all of the bivalve genera described from the Hiraiso Formation exhibit worldwide distribution. However, at the species level, they may have been more or less specialized to certain environments. These bivalve communities from the (storm-dominated) shallow marine siliciclastic settings are similar to each other but at the same time each is unique. In particular, *Eumorphotis iwanowi* and *Entolium ussuricus* are only reported from siliciclastic facies. The occurrence of *Eu. iwanowi* is restricted to only three localities, namely, S. Kitakami, S. Primorye, and South China (Yin, 1982 and 1985); this contrasts to worldwide occurrences of *Eumorphotis multiformis* (Yin, 1982 and 1985).

Some nonmolluscan taxa, such as echinoderms and (articulate) brachiopods, are regarded as ecologically

specialized forms in general. Thus, the reappearance of crinoids with resultant increase in tiering could be an indicator of a recovery in the community structure of the benthic fauna in the P/Tr mass extinction aftermath (Twitchett, 1999). For instance, in western North America, the reappearance of these taxa in the Spathian implies ecological recovery of the shallow marine benthic community (Schubert and Bottjer, 1995). A similar pattern was observed also in northern Italy where tiering increased both below and above the sediments in the Spathian (Twitchett, 1999). Considering the distinctive mode of fossil occurrence of the crinoids, compared to other shelly fossils in the Hiraiso fauna, it is possible that the crinoids could have been transported from a large distance (maybe, in an extreme case, there was a monospecific crinoid community in a distant lagoon). Therefore, does the presence of crinoid ossicles reflect true recovery in the structure of the entire shallow marine benthic community?

The occurrence of *Holocrinus* is limited only to S. Kitakami, and this may indicate that some environmental constraint prevented their colonization of nearby localities (e.g., S. Primorye). Given the high preservation potential of crinoid ossicles, preservational bias is unlikely to explain their restricted occurrence. This in turn reinforces the hypothesis that delayed recovery of the marine benthic fauna was the result of stressful environmental conditions (Twitchett and Wignall, 1996; Woods *et al.*, 1999, Twitchett, 1999).

Conclusion

The Hiraiso Formation comprises a gradation of facies that represent storm-dominated siliciclastic shelf environments of varying bathymetry. Shelly fossil assemblages are found in basal deposits of storm beds, but their occurrence is limited to those facies that represent upper inner shelf (Facies Ha and Hb). These assemblages are probably derived from a range of shallow environments and, as a whole, are time-averaged over a period of relative environmental stability. It also implies that the habitat for benthic organisms was largely restricted to settings shallower than the upper inner shelf.

Observed diversity of the shelly assemblage in both species and higher taxonomic levels is very low; it consists almost exclusively of bivalves with simple morphology. Judging from the wide range of environments that the assemblage probably represents, this apparent low diversity should indicate a genuine anomaly in the shallow marine benthic community at

the time of deposition. In deeper facies, where fossils are nearly absent, bioturbation gradually diminishes in the lower inner shelf and finally disappears in the outer shelf environment. Such patterns are most likely explained by the presence of anoxic bottom water in deeper environments. Therefore, low diversity may also have resulted from the influence of oxygen-depleted deeper water that could have occasionally invaded shallower environments, leading to fluctuations in living conditions in these shallower environments.

On the regional scale, the assemblages from similar facies of different localities resemble each other, indicating little endemism of communities. However, we recognized species-level specialization among the siliciclastic localities compared to carbonate settings.

There is only limited evidence of ecological recovery in the shallow marine benthic community of these tropical, siliciclastic settings in the Smithian. Although the occurrence of the crinoid genus *Holocrinus* may reflect the onset of the ecological recovery phase, their geographically restricted occurrence may imply that recovery was geographically limited in the Smithian. Such relative delays of ecological recovery in tropical shallow marine environments may be a consequence of low diffusivity of oxygen in tropical, hot-sea surface water that maximized the chronic impact of the superanoxic event (Isozaki, 1997; Wignall and Twitchett, 2002).

Systematic Paleontology of Bivalves
(by Y. Kashiyama)

Order Pterioida
Suborder Pteriina
Superfamily Pteriacea
Family Bakevelliidae
Genus *Bakevellia*
Subgenus *Maizuria* Nakazawa, 1959

Bakevellia (Maizuria) sp. cf. *kambei*
Nakazawa, 1959

Figure 8a–c

cf. *Gervilleia* cf. *exporrecta* Lepsius: Bittner, 1899, p. 16, pl. 3, fig 1–16.
cf. *Gervilleia exporrecta* Lepsius: Kiparisova, 1938, p. 249, pl. 5, figs. 22, 23.
cf. *Bakevellia (Maizuria) kambei* Nakazawa: Nakazawa, 1959, p. 204, pl. 2, figs. 1–12, textfig. 7.

Materials.—Two nearly complete external casts of left valves and two nearly complete external casts of right valves.

Description.—The shell is small in size (shell height 10–16 mm), strongly inequilateral, somewhat inequivalved, moderately to somewhat strongly inflated, posteroventrally elongated, and prosocline. The left valve is more broadly inflated than the right valve. The umbo is not very prominent, located in 30–40% along hinge line from the anterior end; beak salient above hinge line; hinge line straight; anterior auricle moderate to large, but only very poorly separated from the umbonal flank by a weak depression. The posterior auricle is larger and fairly defined from the disc by a broad depression along the flank of the beak elongated posteroventrally. Growth lines are smoothly continuous from the disc to the auricle.

The umbo is narrower in right valves than in left ones, with the beak salient above the hinge line. The posterior auricle is less clearly separated from the disc by a broader depression. Growth lines are less prominent or less well preserved in these specimens.

Discussion.—Although similar small fossils are abundant in sample rocks, only a few specimens are actually distinguishable. These external molds lack information of the cardinal area, including dentition. However, identification based solely on external morphology should be adequate with respect to the Early Triassic *Bakevellia*, of which dentition is more variable than the external shape (Nakazawa, 1959). Right valves of the specimens are somewhat more inflated than those of *Bakevellia (Maizuria) kambei* Nakazawa. The posterior auricles of the Hiraiso specimens are thus slightly more prominent, which invokes the form of *Gervilleia exporrecta* Lepsius decribed from S. Primorye by Kiparisova (1938). It may also be related to *Bakevellia (Maizuria) oluyamensis* Nakazawa described by Nakazawa (1959).

Occurrence.—Common in Facies Ha and Hb of the Hiraiso Formation in Hiraiso Coast.

Superfamily Pectinacea
Family Aviculopectinidae
Subfamily Aviculopectininae
Genus *Eumorphotis*

Eumorphotis iwanowi (Bittner), 1899

Figure 7

Pseudomonotis iwanowi Bittner, 1899, p. 8, pl. 1, figs 1–9.
Eumorphotis maritima Kiparisova, 1938, p. 223, 286, pl. 2, figs. 3, 6–8, 13.
Eumorphotis aff. *maritima* Kiparisova: Nakazawa, 1961, p. 259, pl. 12, figs. 25–28.

Materials.—Two nearly complete and two incomplete external casts of left valves, four nearly complete
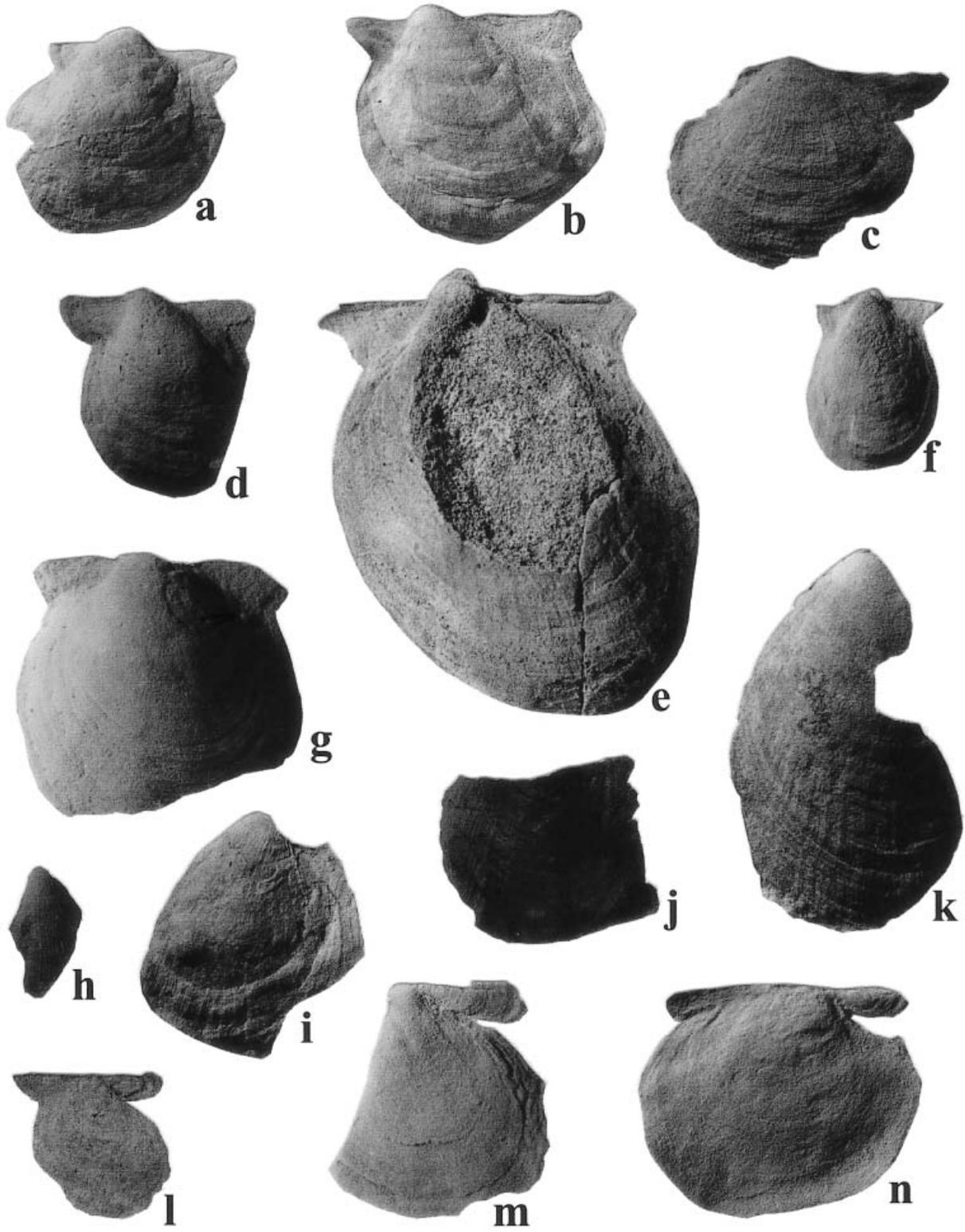
and four incomplete external molds of left valves, one external cast of a right valve, and two complete and one incomplete external molds of right valves.

Description.—The shell is relatively large in size (shell height 34–71 mm), strongly inequivalved, and inequilateral. The left valve is strongly inflated. The umbo is prominent and rounded. The beak is salient above the hinge line. The disc is strongly convex both anterodosally and dosally, but its posterior margin is slightly concave. The ventral margin is well rounded. The anterior auricle sulcus is fairly arched. The hinge line is straight and nearly equal to the shell length. The anterior auricle is trigonal, sharply separated from the disc by a steep sulcus and a moderate sinus, and convex moderately shaping a vertical section of a cone. The posterior auricle is a little larger than the anterior auricle, is not clearly separated from the umbonal flank but separated from the disc by a moderate sinus, and is nearly flat but convex close to the beak. Both auricles have straight grooves along the hinge line about 1 mm from the edge. The surface is covered with crowded and very fine radial costae and growth lines. Very fine radial costae are mostly faint due to poor preservation, are intercalated in two orders, and are commonly offset at growth lines. Growth lines are prominent and arranged in irregular intervals, forming a radially very undulant surface. The growth lines of the disc continue into the auricles.

The right valve is nearly flat. The umbo is insignificant. The disc is faintly convex around the beak but slightly concave near the margin. The anterior auricle is elongated and fan-shaped, slightly convex, and sharply separated from the disk by a narrow and very deep byssal notch. The posterior auricle is narrowly trigonal, flat, and separated from the disc by a moderate sulus and sinus. The surface is not covered by any radial ornament but has growth lines.

Discussion.—Ornamentation among specimens varys, which is probably due to postmortem abrasion. The ornamentation of molds tends to be less clear than that of casts.

The external shape and the dimension match well *Eumorphotis iwanowi* Bittner (Bittner, 1899). However, the left valve, their ornamentation in particular, more closely resembles that of *Eu. maritima* Kiparisova (Kiparisova, 1938). On the other hand, the flat-

shaped right valve that lacks radial ornamentation certainly resembles that of *Eu. iwanowi* Bittner.

Although all occurrences of the genus *Eumorphotis* that were previously reported from other Japanese localities are represented only by *Eu. multiformis* (Hayami, 1975), the Hiraiso species clearly belongs to *Eu. iwanowi* and is distinguished from *Eu. multiformis* by less prominent and low-ordering radial costae, a nearly completely flat right valve, the outlines of both auricles of the right valve, and its larger size distribution.

Occurrence.—Very common in Facies Ha of the Hiraiso Formation at Hiraiso Coast.

Family Entoliidae
Genus *Entolium*

Entolium ussuricus (Bittner), 1899

Figure 8d, e

Pecten ussuricus Bittner, 1899, p. 4, pl. 1, fig 11.
Pecten sichoticus Bittner, 1899, p. 5, pl. 1, fig 10.
Aequipcten ussuricus Kiparisova, 1938, p. 251, pl. 4, figs. 14–16.
"*Pecten*" *ussuricus* Bittner: Nakazawa, 1961, p. 257, pl. 12, figs. 10–13.

Materials.—Three nearly complete external casts of left valves and one nearly complete external cast of right valve.

Description.—The shell is moderate in size (shell height 26–28 mm), nearly equivalved, inequilateral, ovate, somewhat elongated, and prosocline. The left valve is moderately inflated. The umbo is broad but is not very prominent or rounded. The beak is not salient above the hinge line. Both anterodosal and dosal flanks are moderately convex, but both anterior and posterior flanks are rather flat. The hinge line is straight and far shorter than the shell length. The posterior auricle is a little larger than the anterior one. Both auricles are nearly flat and distinctly separated from the disc. The byssal notch is absent. The surface ornamentation is hardly observable due to poor preservation except for faint radial costae. Growth lines are not prominent.

The right valve is nearly as inflated as the left valve or slightly less inflated. Its umbo is less prominent than that of the left valve. The posterior auricle is a

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← **Figure 7.** *Eumorphotis iwanowi* (Bittner); **a~k**, left valves, models made by compound from the external casts (**a** [MM28618], **b** [MM28619], **d** [MM28621], **g** [MM28624], **i** [MM28626], **j** [MM28627], and **k** [MM28628]), and naturally occurred external molds (**c** [MM28620], **e** [MM28622], **f** [MM28623], and **h** [MM28625]); right valves, models made by compound from the external casts (**m** [MM28630] and **n** [MM28631]), and naturally occurred external molds (**l** [MM28629]). **c** and **l** are collections by K. Ichikawa. All figures ×1.0.
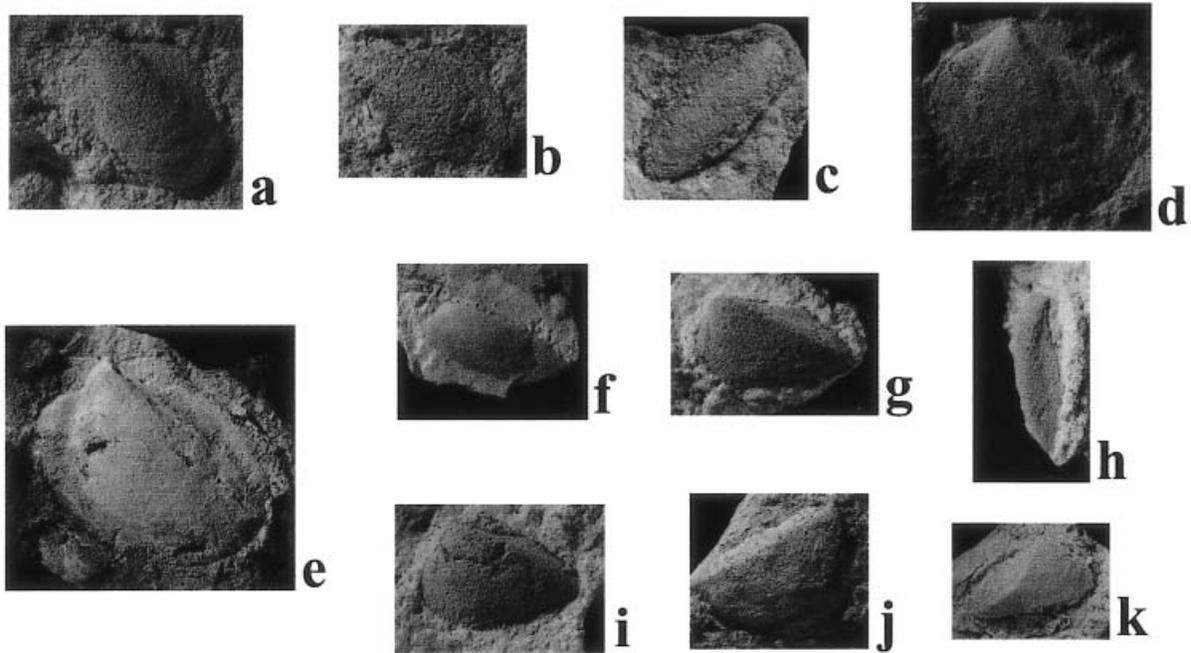
Figure 8. **a~c**, *Bakevellia (Maizuria)* sp. cf. *kambei* Nakazawa; **a** [MM28633] and **b** [MM28634], left valves; **c** [MM28635], right valve; external molds. **d** and **e**, *Entolium ussuricus* (Bittner); **e** [MM28637], left valve; **d** [MM28636], right valve; external molds. **f** [MM28638], *Unionites* aff. *canalensis* (Catullo) var. *fassaensis* (?); left valve; external molds. **g–k**, *Neoschizodus* cf. *laevigatus* (Ziethen): Nakazawa; **g** [MM28639], **h** [MM28639], and **i** [MM28640], left valves, **h** side view of **g**; **j** [MM28641] and **k** [MM28642], right valve. **a–j** are external molds; **k** is a model made by compound from the external casts. **b**, **c**, **g** (**h**), and **i** were collected by K. Ichikawa. Scale: **a** and **c** ×1.5, **b** ×2.0, **d~k** ×1.0.

little larger than the anterior auricle. The surface ornamentation is not preserved.

Discussion.—Preservation of surface ornamentation of external molds is very poor, and specimens are more or less distorted. Their morphology perfectly resembles that of *En. ussuricus* from the Maizuru Terrane described by Nakazawa (1961). They also resemble *En. ussuricus* from S. Primorye by Kiparisova (1938), except for their more prominent ornamentation, which is, however, probably a matter of preservation.

This species was assigned to *Aequipecten* Kiparisova (1938) and was later reassigned to *Eupecten* by Kiparisova (1954). Nakazawa (1961) thought that it might be a new genus and assigned it tentatively to *Pecten*. He suggested its close relationship to Entoliidae, noting that the pair of internal ridges and the smooth left valve resemble those of *Entolium*., but also a possible relationship to Amussiidae. Here, it is tentatively assigned to *Entolium* by considering the characters discussed in Nakazawa (1961).

Occurrence.—Common in Facies Ha of the Hiraiso Formation at Hiraiso Coast.

Order Unionoida
Superfamily Unionacea
Family Pachycardiidae
Genus ***Unionites***

Unionites aff. ***canalensis*** (Catullo) var. ***fassaensis*** (?)

Figure 8f

aff. *Anodontophora (Myacites) canalensis* Catullo: Bittner, 1899, p. 23, pl. 3, fig 34–38.
aff. *Anodontophora canalensis* Catullo: Kambe, 1963, p. 48, pl. 5, figs. 24, 25.
aff. *Unionites canalensis* (Catullo): Nakazawa, 1971, p. 126, pl. 24, figs. 14, 15.

Materials.—One complete, relatively well preserved external cast of left valve.

Description.—The shell is small (shell height 9 mm), relatively smooth, roughly subtrigonally outlined, weakly to moderately inflated, inequilateral, and remarkably anteroposteriorly elongated with L/H ratio of 2.2 (distorted?). The umbo is somewhat prominent, which is located in one third from the anterior end. The surface is very smooth with faint
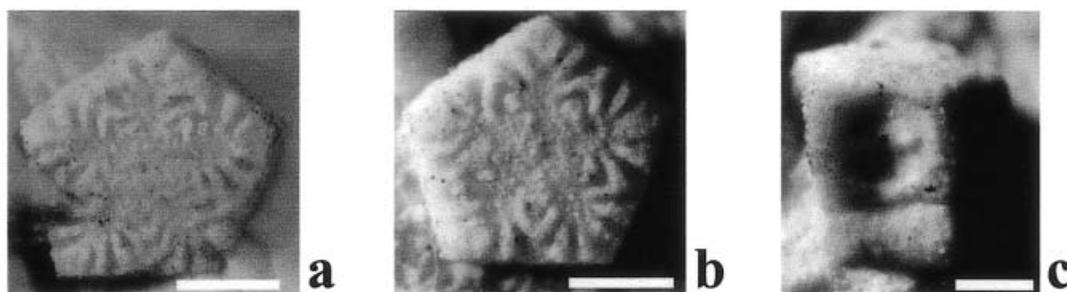
Figure 9. *Holocrinus* sp. **a** and **b**, Articular facet of internodal (symplexy), silicone rubber casts made out of the natural external molds, scale 1 mm; **c**, Lateral view of nodal and internodals, silicone rubber casts, scale 1 mm. Note that the upper surface of nodal (distal facet of nodal) shows relatively smooth, symplectial articulation.

growth lines. The dentition is not observed.

Discussion.—*Unionites canalensis* is usually distinguished from *U. fassaensis* by its trapezoidal outline and more elongated form with L/H ratio of about 1.6 to 2.0 (Kambe, 1963). This specimen has a L/H ratio of 2.2, which is significantly elongated and suggests assignment to *U. canalensis*. However, its rather smooth outline is somewhat closer to that of *U. fassaensis*. Here, it is tentatively assigned to *U. canalensis* due to very high value of L/H ratio.

Occurrence.—Facies Ha (?) and Hb of the Hiraiso Formation at Hiraiso Coast.

Order Trigonioida
Superfamily Trigoniacea
Family Myophoriidae
Genus **Neoschizodus**

Neoschizodus cf. **laevigatus** (Ziethen):
Nakazawa, 1960

Figure 8g–k

cf. *Myophoria* cfr. *laevigata* Alb.: Bittner, 1899, p. 20, pl. 3, fig 17–26.
cf. *Neoschizodus* cf. *laevigatus* (Ziethen): Nakazawa, 1960, p. 56, pl. 6, fig 21–32.

Materials.—Three complete external casts of left valves, one nearly complete external cast of a right valve, and one complete external mold of a right valve.

Description.—The shell is small (shell height 13~18 mm), equivalved, inequilateral, subtrigonal, somewhat elongated, prosocline, and moderately inflated. The umbo is prominent. The beak is orthogyrate. A diagonal ridge is developed well but less steep and sharp posteroventrally, and is strongly elongated posteriorly. The corselet is relatively narrow and depressed in the middle range. The escutcheon is narrow

and is not separated well. The surface is smooth and has faint growth lines in some specimens. The dentition is not observed.

Discussion.—External morphology is similar to *Neoschizodus* of the Maizuru Terrane, described by Nakazawa (1961), which exhibit various outlines due to deformation (Nakazawa, 1961). This may also explains the variable outlines of the specimens of Hiraiso. It probably better resembles *Neoschizodus* of the Southern Primorie (Bittner, 1899). This is, however, hard to determine because dentition was not preserved here, which is critical for classification of Myophoriidae.

Occurrence.—Common in Facies Ha and Hb of the Hiraiso Formation at the Hiraiso Coast.

Systematic Paleontology of Crinoid (by T. Oji)

Order Isocrinida
Family Holocrinidae
Genus **Holocrinus**

Holocrinus sp.

Figure 9

Isocrinus sp.: Kobayashi and Ichikawa, 1951, p. 6.
Isocrinus sp.: Tamura, 1982, p. 23, pl. 1, figs. 20 and 21.

Description.—Only columnals and cirrals were collected, and no calyces or arms have been hitherto found from the Hiraiso Formation. The columnals are small in size, ranging from 2.0 to 2.5 mm in diameter. On the articular facet there are four to five well developed adradial and marginal ridges around the petal. The cross-section is usually pentagonal but sometimes stellate. The lateral surface of the internodal is somewhat inflated, and the suture is straight and depressed. The nodals have five well developed

cirral scars. The height of the nodals is approximately 1.7 times the height of the internodals. The distal facet of the nodal has a faint articulation pattern, and is categorized as cryptosymplexic.

Remarks.—The articular facet of the columnals shows a typical *"Isocrinus"*-type articulation. Triassic genera that have such articulation are *Isocrinus* and *Holocrinus*. The genus *Holocrinus* is characterized by possessing well developed high infrabasals that can be seen from the outer surface. From Hiraiso, only columnals and cirrals were available, thus the assignment to the genus *Holocrinus* is rather tentative from a morphologic viewpoint. However, from the Early Triassic, only *Holocrinus* has been found and no reliable record of *Isocrinus* has been reported. Thus, here we assigned the material to the genus *Holocrinus*.

Previous studies on *Holocrinus? smithi* from the western United States (Schubert *et al.*, 1992) showed that the distal articular facet of nodals has relatively well developed symplexy. However, the present material from Hiraiso has cryptosymplectial articulation on the distal facet of nodals, as in most species of *Isocrinus*. Such existence of cryptosymplexy indicates that there was already differentiation of cryptosymplexy from the usual symplexy, and there was also some functional differentiation of the stalk at the distal articulation of the nodal. As early as in the Smithian, the present *Holocrinus* sp. possessed the ability to autotomize its distal stalk. This ability to discard the distal stalk enabled *Holocrinus* to relocate themselves to different places for anchorage, in the same manner as the later Isocrinidae.

The occurrence of *Holocrinus* from the Hiraiso Formation is the oldest in the world. The previous oldest *Holocrinus* was from the Virgin Limestone (Spathian) of western United States (Schubert *et al.*, 1992).

Occurrence.—Molds of *Holocrinus* skeletons are commonly found in sandstone from the middle to the upper part of the formation (Facies Ha, Hb, and Hc). The best preservation shown here came from the siltstone of the middle part of the formation (Facies Hc).

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