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# TAXONOMY AND FAUNAL AFFINITY OF LATE CARNIAN - RHAETIAN CONODONTS IN THE SOUTHERN CHICHIBU BELT, SHIKOKU, SW JAPAN

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*Riassunto.* Vengono descritti in questo articolo conodonti provenienti dai calcari pelagici del Carnico terminale - Norico medio e dalle selci stratificate del Norico superiore - Retico della sezione di Hisaidani, Chichibu Belt meridionale, Shikoku, Giappone sudoccidentale. Viene discussa la tassonomia dei generi *Metapolygnathus* Hayashi, *Ancyrogondolella* Budurov, *Mockina* Kozur e *Misikella* Kozur & Mock. Sono proposte tre nuove specie: *Mockina sakurae* n. sp. e *M. shamiseni* n. sp. del Norico medio e *M. hisaidaniensis* n. sp. del Norico superiore.

L'affinità della fauna di Hisaidani è abbastanza orientata in senso tetidiano. L'associazione a conodonti di età Norica inferiore e media è dominata da *Ancyrogondolella spatulata* (Hayashi), mentre verso l'alto, nel Norico medio e superiore sono presenti taxa della provincia pacifica. La presenza di tre nuove specie suggerisce anche un provincialismo che caratterizza la situazione pre-accrezione del plateau Izanami da cui derivano le successioni rocciose di Hisaidani.

*Abstract.* Conodonts from the latest Carnian - Middle Norian pelagic limestone and Late Norian - Rhaetian bedded chert-section at Hisaidani, southern Chichibu Belt, Shikoku, SW Japan, are described. Taxonomy of conodont-genera *Metapolygnathus* Hayashi, *Ancyrogondolella* Budurov, *Mockina* Kozur and *Misikella* Kozur & Mock is discussed. Middle Norian *Mockina sakurae* n. sp., *M. shamiseni* n. sp. and Late Norian *M. hisaidaniensis* n. sp. are described.

The affinities of the Hisaidani - fauna are rather Tethyan. The Early - Middle Norian conodont-association at Hisaidani is dominated by *Ancyrogondolella spatulata* (Hayashi). Towards the Middle and Late Norian, affinities with Pacific taxa are present. The three new species provide also a provincial character that typifies the pre-accretionary Izanami plateau from which the rocks of Hisaidani were derived.

## Introduction.

Late Triassic conodont taxonomy has for a long time been confusing. Different authors publishing at short intervals around 1968 have generated problems of priorities, e.g. Mosher (July 1968) establishing the genera *Paragondolella* and *Epigondolella* almost simultaneously with Hayashi (March 1968) establishing the genus *Metapolygnathus*. Priority of the genus *Metapolygnathus* Hayashi, however, does not resolve its use and interpretation, which still differs from author to author. The overlap of definitions requires a revision, to which the present study attempts to contribute. The ideas presented in the present study reflect the consensus, reached on the occasion of a meeting with Dr. S. Hayashi in September 1999 in his hometown Omama. At this occasion Hayashi's original material was widely discussed and compared with SEM-figures of more recent publications.

The conodonts described in this paper were obtained from 20 samples, collected in 50 m of continuous carbonates and bedded chert, in the Hisaidani (Hisai-Valley), Tokushima Prefecture, Shikoku, SW Japan.

## Geological and stratigraphical setting in SW Japan

SW Japan consists of a complex orogenic belt that is presently divided by the Median Tectonic Line (MTL) into the Inner Zone to the north and the Outer Zone in the south. MTL can be followed from Kyushu, crossing Shikoku into Honshu. The N to S younging accretionary complexes (ACs) of both zones is accreted to the Yangtse block (Figs. 1a-b). The Outer Zone, south of the MTL, consists of several belts (Fig. 1b).

The Sambagawa-Mikabu Greenstone Belt, consisting of Jurassic - Cretaceous ACs, is presently exposed between MTL and the northern Chichibu Belt. The Chichibu Super-Belt consists of the Jurassic ACs of the northern and southern belts. The Permian Kurosegawa AC which separates the former into its northern and southern belts overrides it. The southern

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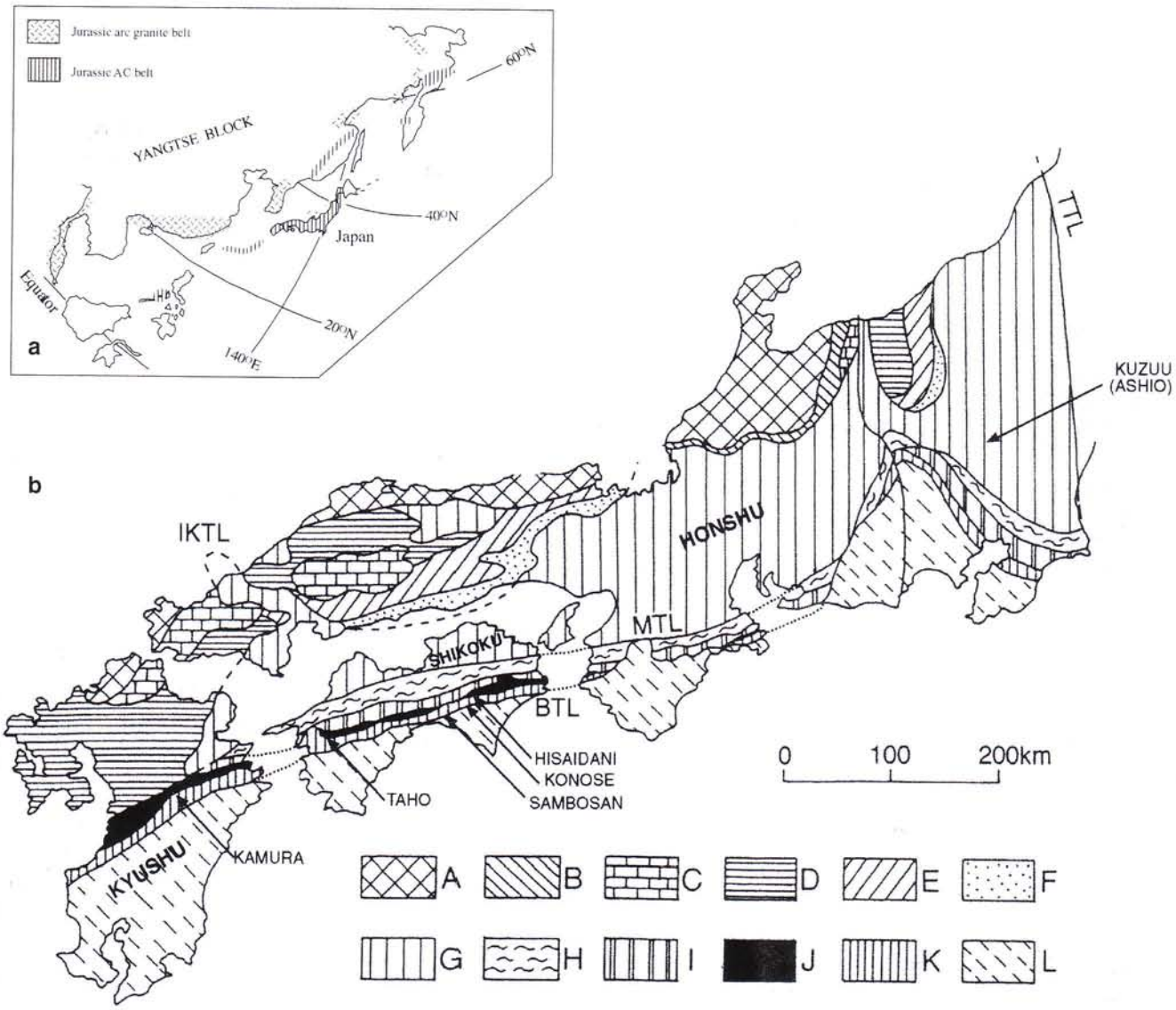



Fig. 1. - Location maps: (a) Generalized position of Japan; (b) Geologic outline map of SW Japan with location of sections mentioned in the text: A, Hida; B, Marginal Hida; C, Akiyoshi; D, Sangun; E, Maizuru; F, Ultra-Tamba; G, Mino-Tamba-Ashio Belts of the Inner Zone; H, Sambagawa-Mikabu Greenstone; I, Northern Chichibu; J, Kurosegawa; K, Southern Chichibu; L, Shimanto belts of the Outer Zone. MTL, Median; IKTL, Ishigaki-Kuga; TTL, Tanakura tectonic lines.

Chichibu Belt, overrides the Cretaceous Shimanto Super-Belt and is separated from it by the Butsuzo Tectonic Line (BTL). The southern Chichibu Belt has a number of carbonate and bedded chert successions.

### The triassic conodont bearing limestones in the southern Chichibu AC of SW Japan

In the southern Chichibu AC of Kyushu and Shikoku, Triassic conodonts were obtained from limestone blocks at Kamura, Taho and Hisaidani (Figs. 2, 3).

Kamura (Watanabe et al. 1979; Koike 1996) (Fig. 2)

At Kamura (Miyazaki Prefecture, Takachiho town, Kyushu), Griesbachian *Hindeodus parvus, Isarcicella isarcica, Neogondolella carinata*, Dienerian *Neospathodus dieneri*, Smithian *Neospathodus conservativus*, Late Spathian *Neospathodus homeri* and earliest Anisian *Chiosella timorensis* define a lower sequence. A hiatus separates the lower sequence from the late Ladinian middle sequence that yields *Sephardiella mungoensis*. A lower Carnian hiatus truncates the middle sequence. The upper sequence encompasses late Carnian *Metapolygnathus polygnathiformis*, early Norian *Ancyrogondolella spatulata*, middle Norian *Mockina multidentata* and late *Norian Mockina bidentata*.

Taho (Koike 1979, 1996) (Fig. 2)

In the Shirokawa town (Ehime Prefecture, Shikoku) at the village of Taho-kamigumi, the Griesbachian *Hindeodus parvus* and *Isarcicella isarcica*, Dienerian *Neospathodus kummeli* and *N. dieneri*, Smithian *N. conservativus*, Spathian *N. triangularis*, *N. homeri*

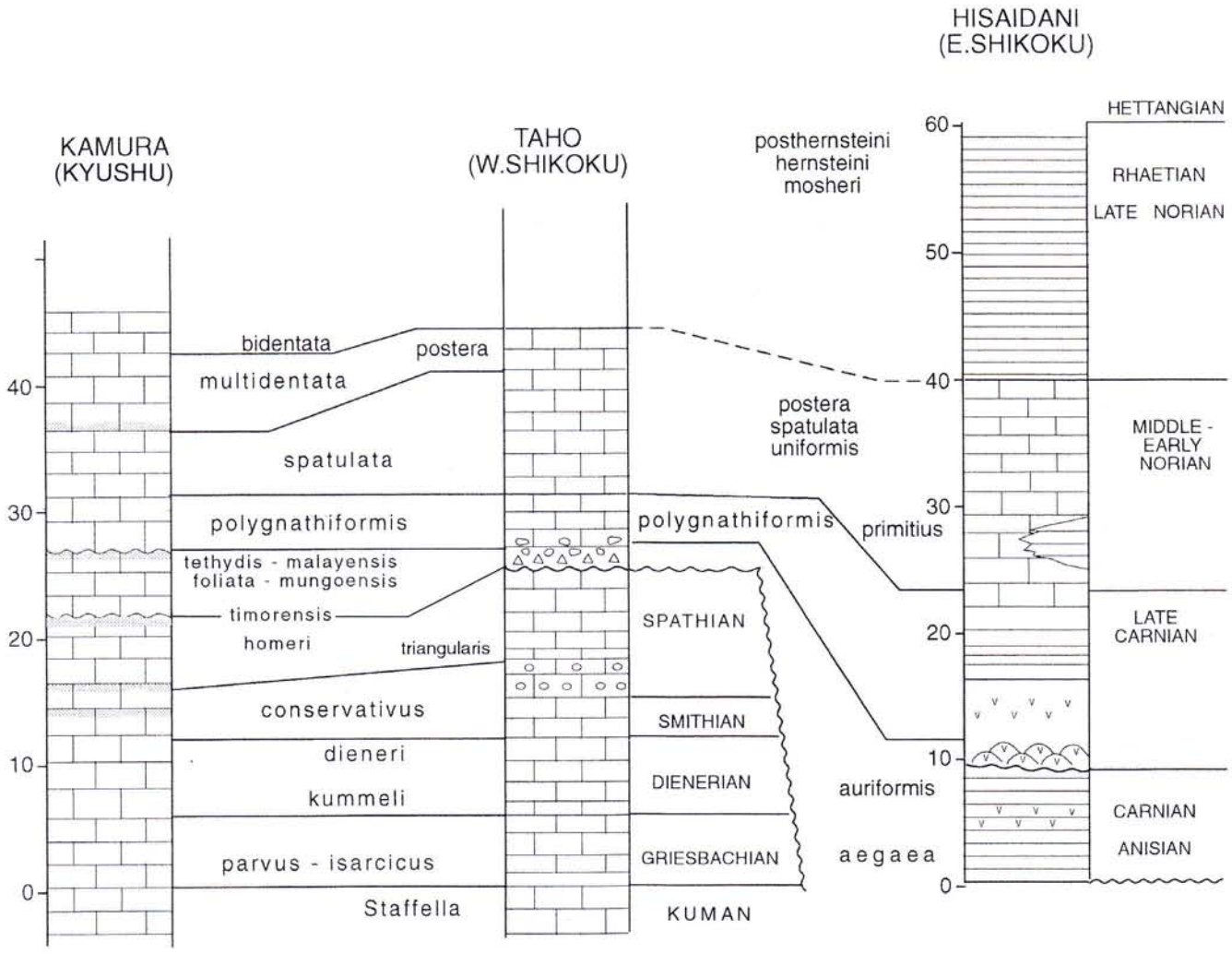



Figure 2. Conodont bearing carbonates in southern Chichibu accretionary complexes.

and Anisian *Chiosella timorensis* define a lower interval. The "mixed breccia" follows, that yields conodonts representing Middle Triassic and early Carnian zones. Upper Carnian *Metapolygnathus nodosus*, lower Norian *Ancyrogondolella spatulata* and middle Norian *Mockina postera* represent the overlying interval.

Hisaidani (Ishida 1987) (Fig. 3)

In the southern Chichibu AC of Shikoku, the Hisaidani canyon (Kito village, Tokushima Prefecture) exposes greenstones covered by a Triassic (late Carnian-Rhaetian) to Jurassic (Hettangian - Kimmeridgian) bedded-chert sequence with intercalation of some limestone beds. At Hisaidani, on both sides of the river, sections I, II, IV and VI represent a continuous sequence, sections II and IV being partly correlative.

*Lower part*: (Sections I, VI) Consists of late Carnian bedded cherts with acid and basaltic tuffs. The greenstone at the base of section I consist of pillow basalt and pillow breccia, followed by bedded chert with tuffs (8 m).

*Middle part*: (Sections II, IV) Consists of late Carnian - middle Norian (26 m) pelagic micrites alternating with bedded chert.

*Upper part*: (Sections II, IV) Consists of upper Norian - Rhaetian bedded chert (26 m), followed by Jurassic Hettangian bedded chert (10 m).

The late Carnian age of the upper 3 m of section VI is based on the occurrence of *Metapolygnathus* aff. *auriformis* from the horizon 47. The Carnian-Norian boundary is set in section I, horizon 18, by the concurrent occurrence of *Metapolygnathus primitius*, *M. polygnathiformis* and *M.* aff. *permicus*. The top of the limestone sequence in both sections II (horizon 23) and IV (horizon 33) is condensed, yielding *Metapolygnathus primitius*, lower Norian *Ancyrogondolella spatulata, A.* cf. *triangularis* and middle Norian *Mockina postera* and *M.* cf. *elongata*. *Ancyrogondolella spatulata*, represents one third of recorded specimens.

The late Norian - Rhaetian bedded cherts contain no conodonts until the first appearance of *Misikella hernsteini*, 12 m above the top of the limestone succession in section II (horizon 2), and of *M. hernsteini, M.* cf. *longidentata* and *Mockina* aff. *Mosheri*, 19 m above top of

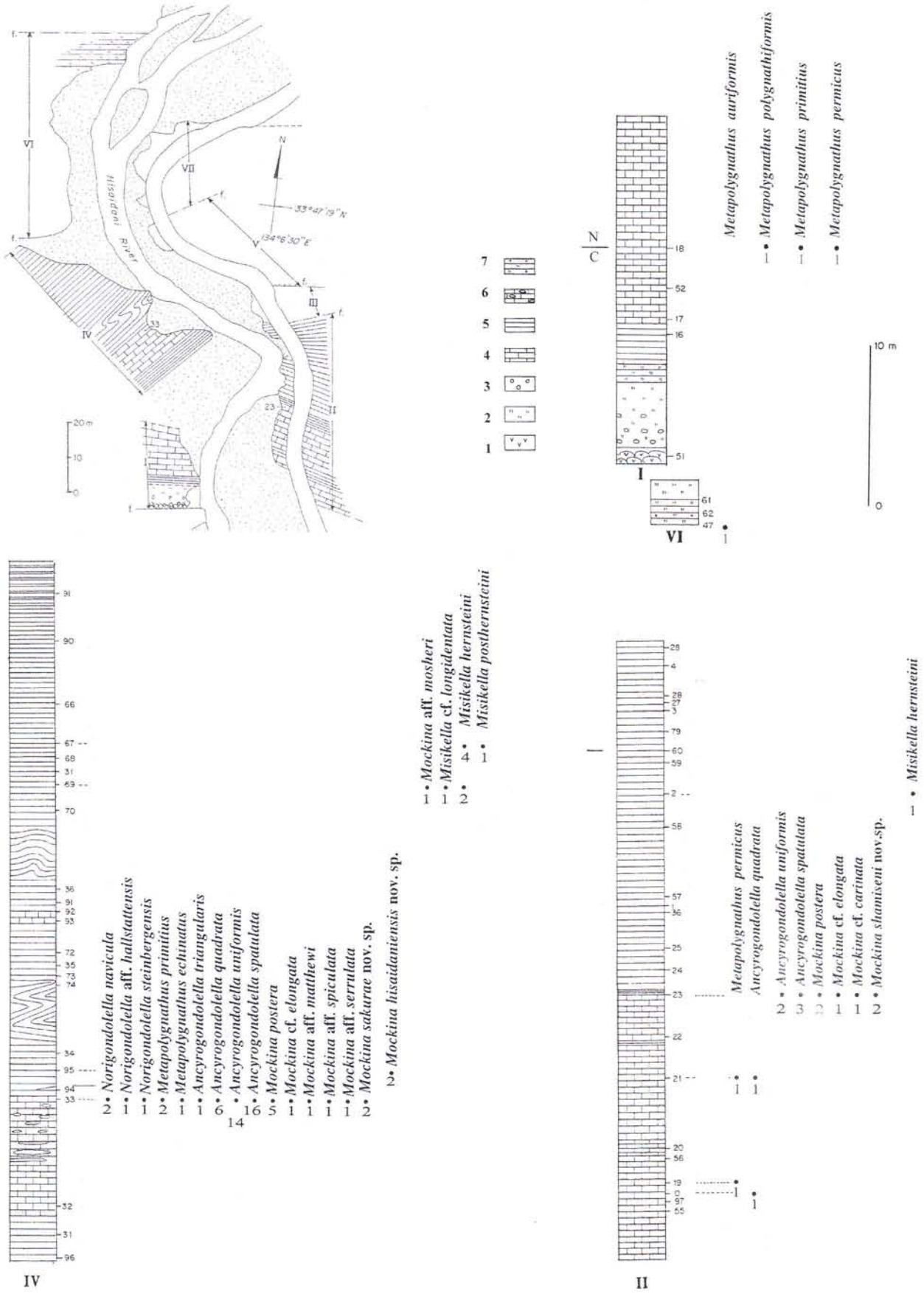



Figure 3. Lithology, samples and faunal distribution at Hisaidani: (a) Location sketchmap; b) Sections I and VI; (c) Section II; Section IV. 1: pillow lava; 2: basaltic tuff; 3: pillow breccia; 4: limestone; 5: bedded chert; 6: nodular chert in limestone; 7: chert and acid tuff.

the limestone succession in section IV (horizon 69). Further 3 m can be attributed to the Rhaetian, based on the occurrence of *Misikella hernsteini* and *M. posthernsteini* in section IV (horizon 67).

## Paleontology

Late Triassic conodonts are classified into a number of genera, that have been the subject of different and divergent interpretations. First Hayashi (1968) established the genus *Metapolygnathus*, encompassing the species *M. communisti* (type), *M. linguiformis* and *M. noah*. He further listed under the genus *Gladigondolella*, the species *G. abneptis* (Huckriede) and the new variations *G. abneptis echinata, G. abneptis nodosa, G. abneptis permica* and *G. abneptis spatulata*. The attribution of these species to the genus *Gladigondolella* was based on the centrally located basal pit. Later, Hayashi (1987) put these forms to *Metapolygnathus* as *M. echinatus, M. nodosus, M. abneptis permicus* and *M. spatulatus*.

The genus *Metapolygnathus* Hayashi has priority over the genera *Epigondolella* Mosher (type *E. abneptis*) and *Paragondolella* Mosher (type *P. excelsa*). Orchard (1983, 1991a, 1991b) extended the definition of *Metapolygnathus* Hayashi as to include a large spectrum of species, from *nodosus, zoae, lindae, samueli, stephanae, polygnathiformis* and *communisti* to *reversus, primitius* and *pseudoechinatus*, limiting the use of *Paragondolella* Mosher (1968) to pre-Carnian species. He used *Neogondolella* Bender & Stoppel (1965) for the Norian forms *navicula, hallstattensis* and *steinbergensis*, and followed Mosher (1968) in his interpretation of *Epigondolella*, introducing several species.

Koike (1982), who only recognizes the genera *Neogondolella* and *Epigondolella*, holds a different view. One has, however, to consider that the taxon *Metapolygnathus* Hayashi has priority over the taxon *Paragondolella* Mosher, as agreed upon by Mosher (1973).

Budurov (1977), Budurov & Sudar (1990) and Buryi (1996) limit the definition of *Metapolygnathus* to bifid morphs derived from evolved *Paragondolella*, using the taxon *Ancyrogondolella* Budurov (1972: type *A. triangularis*) for extreme bifid forms.

For Hirsch (1994), in an attempt to avoid the ambivalent use of *Metapolygnathus*, the *Paragondolella* may include everything Orchard (op. cit.) called *Metapolygnathus* and *Ancyrogondolella* all bifid morphs put by Orchard (op. cit.) into *Epigondolella*. The genus *Epigondolella* stands then for atavistic unilobal middle - late Norian forms only. Indeed, according to Mosher (1968, p. 936), *Epigondolella*, in its "earliest ontogenic stages shows no platform development and bears a pit located terminally", which means that middle - late Norian species remain within the 'juvenile' stages of the genus. However, an additional difficulty arises in maintaining the genus *Epigondolella* in such restricted definition, when its type, *abneptis*, has itself ceased to exist, being split into several species. Therefore, all forms included by Hirsch (1993) into *Epigondolella* can conveniently be attributed to the genus *Mockina* Kozur (1989).

The Norian forms, formerly attributed to *Paragondolella* or *Neogondolella* were put into the genus *Norigondolella* Kozur (1990).

The following taxa were identified:

*Norigondolella navicula*
*Norigondolella* aff. *hallstattensis*
*Norigondolella steinbergensis*
*Metapolygnathus* aff. *auriformis*
*Metapolygnathus polygnathiformis*
*Metapolygnathus primitius*
*Metapolygnathus echinatus*
*Metapolygnathus permicus*
*?Metapolygnathus* sp.
*Ancyrogondolella triangularis*
*Ancyrogondolella quadrata*
*Ancyrogondolella uniformis*
*Ancyrogondolella spatulata*
*Mockina postera*
*Mockina* aff. *postera*
*Mockina* cf. *elongata*
*Mockina* aff. *matthewi*
*Mockina* aff. *spiculata*
*Mockina* aff. *serrulata*
*Mockina* aff. *mosheri*
*Mockina* cf. *carinata*
*Mockina sakurae* n. sp.
*Mockina hisaidaniensis* n. sp.
*Mockina shamiseni* n. sp.
*Misikella hernsteini*
*Misikella* cf. *longidentata*
*Misikella posthernsteini*

In the present authors view the descriptive aspects of platform conodonts include the following parameters:

A. Platform. (1) The platform length extends over the entire unit, however narrow (eg. *Neogondolella, Paragondolella, Norigondolella*). (2) The platform is reduced and a free blade is developed (*Metapolygnathus, Ancyrogondolella, Mockina*).

B. Denticulation. Denticulation of the carina can consist of straight or posteriorly inclined denticles. The position of the main cusp is always above the pit of the basal cavity and can be (1) posterior, (2) central or (3) more anterior.

C. Ornamentation. Ornamentation of the oral side of the platform varies from (1) "naked" as in *Neogondolella* and *Paragondolella*, to (2) nodes bordering the platform as in *Metapolygnathus* or (3) sharp denticles as in *Ancyrogondolella* and *Mockina*, the transition between nodes and denticles defining generic criteria (sensu Orchard 1991a).

D. Basal cavity/groove. The lower surface morphology is important in conodont taxonomy. It encompasses a basal cavity, which varies in size, from narrow elongated groove to a cavity of varying depth. A basal pit, which varies in position, shape and size occurs within this cavity, located below the main cusp of the conodont. We distinguish the following types:

(1) cavital. A large and deep basal cavity that also forms the pit, encompassing most of the unit, e.g. in *Neospathodus*. Iterations of the cavital neospathid morph are observed in *Nicoraella, Mosherella, Cavitella, Misikella*.

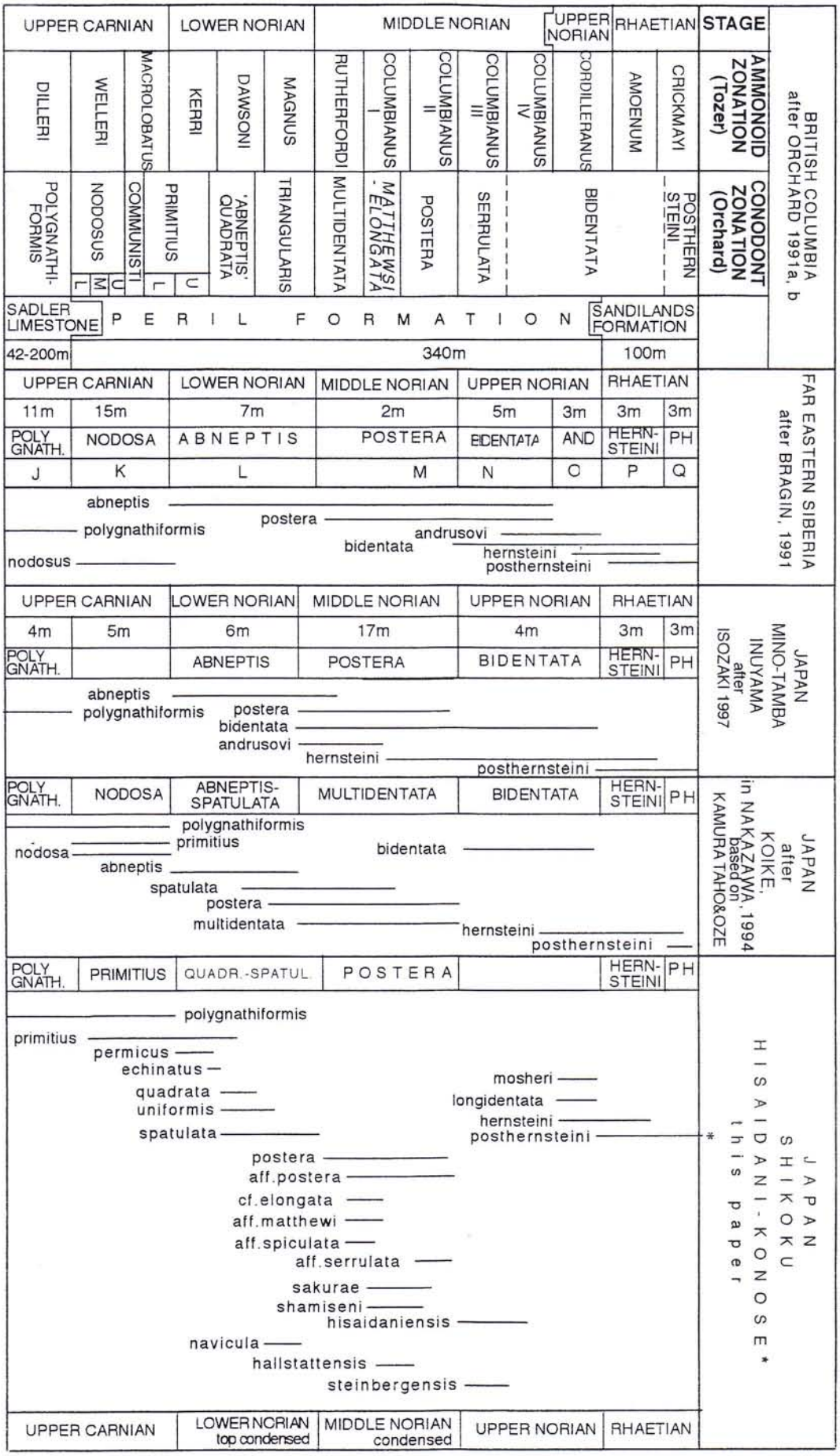



Table 1. Stratigraphic correlation of allochthonous Upper Triassic in British Columbia, the Siberian Far East and Japan.

(2) ellipsoid. As in '*Polygnathus*', the genera *Gladigondolella*, *Sephardiella* and *Mockina* have an elongated, narrow, relatively shallow basal cavity, with a small ellipsoid pit, the position of which may differ. In highly matured specimens of *Sephardiella*, the broadening of the platform may encompass a splitting of the basal groove.

(3) loop. The basal cavity is relatively narrow and shallow, broadening into a "spoon-like" deepening, containing the pit, surrounded by a loop. Characteristic in *Gondolella*, it is found in the genera *Neogondolella*, *Paragondolella*, *Metapolygnathus* and *Norigondolella*. In advanced evolutionary stages of the genera *Paragondolella* and especially *Metapolygnathus*, the broadening of the platform produces the splitting of the basal cavity into bifid grooves.

(4) spatuliform (triangular). Is characterized by a straight posterior edge of the basal cavity, giving it a "deltaic" shape, observed in both genera *Metapolygnathus* and *Ancyrogondolella*. Spatuliform cavities represent a transition between loop (unilobate) and bifid (bilobate) types.

(5) bifid. The development of a bifid basal cavity (splitted groove, bifurcated or bilobate), is a feature already observed in an initial stadium in adult elements of highly evolved *Sephardiella*, *Paragondolella* and *Metapolygnathus*. It is related with the triangular broadening of the posterior platform edge, reaching its highest development in the genus *Ancyrogondolella*.

In the following systematic descriptions, we limit synonymy to the original type and reference to a well-illustrated paratype. The material including holotypes and paratypes of new species is housed in the TKUTC (Tokushima University Triassic Conodonts) collection. Numbers include horizon followed by specimen number.

## Genus *Metapolygnathus* Hayashi, 1968 (Emend.)

1968 *Metapolygnathus* Hayashi, p. 72.

1968 *Paragondolella* Mosher, p. 938.

Type species. *Metapolygnathus communisti* Hayashi, 1968, p. 72, pl. 3, figs. 11a-c.

Remarks. In agreement with the emended diagnosis by Mosher (1973) and expanding Hayashi's original diagnosis, *Metapolygnathus* can be defined as having (1) a free blade, (2) a high anterior carina and (3) a loop-like basal cavity. However, this shape varies from a simple loop (*excelsus*, *foliatus* and early *polygnathiformis*) to spatuliform (*triangular*) shapes, characterized by a straight posterior edge of the cavity, giving it a "deltaic" shape. In advanced (late Carnian) specimens of *M. polygnathiformis* this may represent a transition between the loop and bifid types. The latter development of a split, bifurcated or bilobal groove, results in a triangular broadening of the posterior edge of the platform. The latest Carnian *M. nodosus* Hayashi and *M. primitius* (Mosher) have well-developed nodes around the platform edges. The latest Carnian and/or Early Norian *M. permicus* Hayashi and *M. stephanae* Orchard have loop-like basal cavities, a large free blade, a few platform denticles and a pronounced constriction of the platform (violin-shaped) in the former, few nodes and a slightly constricted platform in the latter.

### **Metapolygnathus polygnathiformis**

(Budurov & Stefanov, 1965)

Pl. 1, Figs. 1a-c.

1965 *Paragondolella polygnathiformis* Budurov & Stefanov, p.118-119, pl. 3, figs. 3-7.

1974 *Metapolygnathus polygnathiformis* - Eicher & Mosher, p.736-737, pl. 1, figs. 27, 28, 30, 34, 39, 40; pl. 2, fig. 6.

1991a *Metapolygnathus* ex. gr. *polygnathiformis* - Orchard, p. 176, pl. 4, figs. 1,3,4.

Remarks. A small specimen (18-1/1) has a width/length ratio of 1/3, and a free-blade/length ratio of 2/5. The round to subquadrate posterior edge of the platform, the loop-like basal cavity, the arched posterior end of the unit and the number of denticles (8) on the carina as well as a naked platform, relates this specimen to early forms of *Metapolygnathus polygnathiformis*.

### **Metapolygnathus primitius** (Mosher, 1970)

Pl. 1: Fig. 2a-c, Figs. 3a-c.

1970 *Epigondolella primitia* Mosher, p. 740-41, pl. 110, figs. 7-13, 16,17.

1991b *Metapolygnathus primitius* - Orchard, p.317, pl.1, figs.13-15.

Material. 5 specimens, 33-2/7, 33-1/8, 21-1/9, 21-1/21 and 18-1/2.

Description. The length varies from 600 $\mu$m to 1100 $\mu$m. Width varies from 1/3 of length in the smaller specimen, to nearly 1/4 in the larger one. The free blade is nearly half the length of the unit in the specimens of horizon 33, and only 1/3 in the specimen of horizon 18. The aboral side varies from slightly convex to concave posterior edge of the triangular base, becoming bifid in the larger specimen. Oral side is slightly quadrate with a concave indentation. A slight constriction may characterize the platform. The carina has at least 7 slightly fused and rather low denticles. The platform is bordered by up to 14 nodes.

Age. According to Orchard (1991b) *Metapolygnathus primitius* (Mosher) straddles the Carnian - Norian boundary.

### **Metapolygnathus echinatus** Hayashi, 1968

Pl. 1: Figs. 4a-c.

1968 *Gladigondolella abneptis echinatus* Hayashi, p. 68-69, pl. 2, fig. 1.

1990 *Epigondolella echinata* - Budurov & Sudar, (partim) p. 215-216,

pl. 4, figs. 14-16, 20-22.

Measurement. One adult specimen (33-2/44) of over 500 μm. The W/L ratio is about 1/2. The free-blade is about 1/3 of total length.

Remark. *M. echinatus* is regarded as a juvenile synonym of *M. communisti* by Kozur (1989).

### **Metapolygnathus permicus** Hayashi, 1968

Pl. 1, Figs. 5a-c, 6a-c, 7a-c.

1968 *Gladigondolella abneptis* var. *permica* Hayashi, p. 69, pl. 2, fig. 3.
1973 *Epigondolella permica* - Krystyn, pl. 5, fig. 2.
1977 *Metapolygnathus permicus* - Budurov, pl. 5, figs. 27-29 (holotype after Hayashi, 1968).
1987 *Metapolygnathus abneptis permica* - Hayashi, pl. 4, fig. 10.

Remarks. In its original diagnosis, Hayashi (1968) describes a subsymmetrical to symmetrical, elongate, arched unit. The aboral side has a narrow groove, ending in a slit like pit, surrounded by a loop. The carina has 8 denticles and the platform is naked, thought its edges may be upturned. It also has a typical 'violin' shaped constriction. 3 juvenile specimens (18-1/16; 21-1/30, 19-1/13) have strong affinities with the holotype. The W/L ratio is about 1/3 in juveniles. The shape of the posterior end of the platform is round to quadrate. The aboral side varies from amygdaloid to subquadrate, the basal cavity coincides with the holotype.

### **Metapolygnathus** aff. **auriformis** (Kovacs, 1977)

Pl. 2, Figs. 1a-c.

1977 *Gondolella auriformis*, Kovacs, p. 78-79, pl. 1, figs. 4-5; pl. 2, fig. 1; Pl. 3, fig. 1; pl. 8, fig. 1.
1986 *Gondolella auriformis*, Kovacs, pl. 6, fig. 2.

Description. One specimen (47-2/15) in section VI, has affinities to this species. It is small, with a width of 100 μm, a length of 250 μm and a free blade of 140 μm. The oral side is unilobal and has a loop-like pit, the platform is triangular and slightly V-shaped and constricted. The carina bears 7 inclined denticles and the platform is upturned on one side.

### ? **Metapolygnathus sp.**

Pl. 2, Figs. 2a-c.

Remarks. A few specimens in horizon 21 have still primitive features of unilobal basal cavities and narrow strong reduced platforms. Some affinities remind forms like *M. stephanae*, a taxon that straddles the Carnian - Norian boundary. Our specimens however have rather denticles than nodes that board the platform. One specimen (21- 2/13) has a length of 670 μm. Its W/L ratio is 1/4 and its free blade is nearly 1/2 of total length. The unilobal basal cavity and the posteriorly narrowing platform as well as the small number of denticles (8) reveal affinities to *Metapolygnathus stephanae* Orchard, thought the platform bears two rather stout denticles. The preservation of our material is not good enough to establish a new taxon.

## Genus *Ancyrogondolella* Budurov, 1972

Type species. *Ancyrogondolella triangularis* Budurov, 1972, p. 855, pl. 1, figs. 3-6.

Revised Diagnosis. The genus encompasses a free blade, a bifid basal cavity and sharp denticles around the platform.

Remarks. Budurov (1972) established *Ancyrogondolella* for extremely bifid triangular forms, attributed formerly to *Metapolygnathus*, a view also shared by Buryi (1996). Hirsch (1993) extended the array of the genus *Ancyrogondolella* to a wider range of species, including also *M. primitius*, *A. quadrata*, *A. spatulata* and *A. triangularis*. *Ancyrogondolella* differs from *Metapolygnathus* by having sharp platform denticles instead of nodes. This criterion was first used as differentiation between *Metapolygnathus* and *Epigondolella* (Orchard, 1983).

### **Ancyrogondolella triangularis** Budurov, 1972

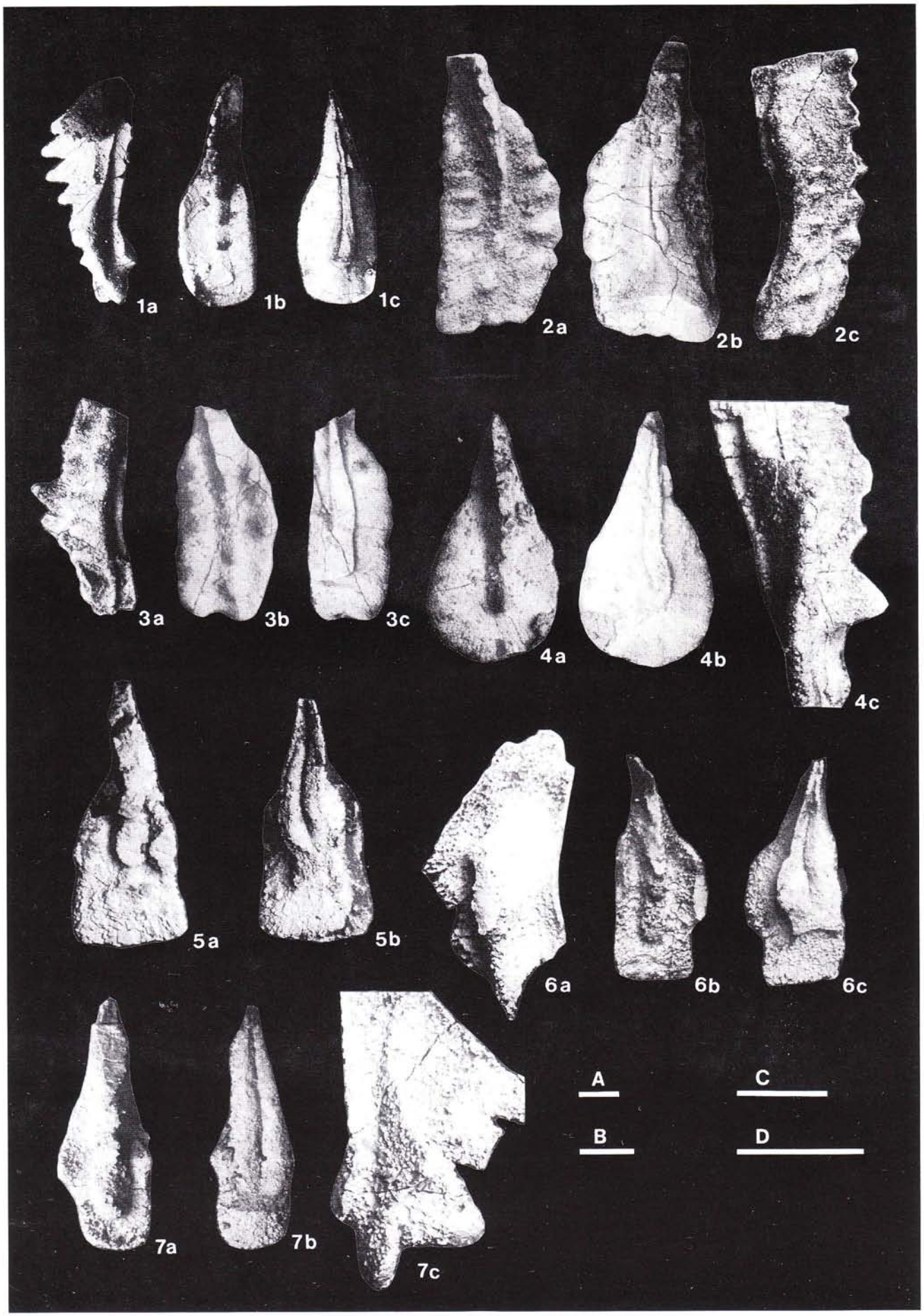
Pl. 2: Figs. 3a-c.

1972 *Ancyrogondella triangularis* Budurov p. 855, pl.1, fig. 3-6
1991b *Epigondolella triangularis triangularis* (Budurov), Orchard, p.315, pl. 3, figs. 7-9.

PLATE 1

SEM photographs of conodonts from the Hisaidani sections. All scale bars indicate 100 μm.
The material is deposited in the collections of Tokushima University Triassic Conodonts (TKUTC).

Fig. 1a, b, c - *Metapolygnathus polygnathiformis* (Budurov & Stefanov). a: lateral view; b: oral view; c: basal view. All scale bar B. Section I, Horizon 18. TKUTC18-1/1.
Fig. 2a, b, c - *Metapolygnathus primitius* (Mosher). a: oral view; b: basal view; c: lateral view. All scale bar A. Section IV, Horizon 33. TKUTC33-2/7.
Fig. 3a, b, c - *Metapolygnathus primitius* (Mosher). a: lateral view; b: oral view; c: basal view. All scale bar B. Section IV, Horizon 33. TKUTC33-1/8.
Fig. 4a, b, c - *Metapolygnathus echinatus* (Hayashi). a: oral view, scale bar B; b: basal view, scale bar B; c: lateral view, scale bar C. Section IV, Horizon 33. TKUTC33-2/44.
Fig. 5a, b - *Metapolygnathus permicus* (Hayashi). a: oral view; b: basal view. All scale bar C. Section I, Horizon 18. TKUTC18-1/16.
Fig. 6a, b, c - *Metapolygnathus permicus* (Hayashi). a: lateral view, scale bar D; b: oral view, scale bar C; c: basal view, scale bar C. Section II, Horizon 21. TKUTC21-1/30.
Fig. 7a, b, c - *Metapolygnathus permicus* (Hayashi). a: oral view, scale bar C; b: basal view, scale bar C; c: lateral view, scale bar D. Section II, Horizon 19. TKUTC19-1/13.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Remarks: One specimen (33-1/11) in the Hisaidani section has dimensional relations that match the species. It is characterized by a relatively small unit of 500 μm, a broad triangular platform of 250 μm and a free blade of 150 μm. Oral side is triangular and the basal cavity clearly bilobate or bifid. The carina bears 7 denticles, the anterior ones slightly fused. The triangular platform is bordered by 10 sharp denticles, but lacks the typical radiation of denticles originating from the carina, as in Budurov (1972: fig. 1) and in Orchard (1991b) *triangularis triangularis* hypotype GSC 95273 (pl. 3, figs. 7-9). The present specimen is wider than *triangularis uniformis* (Orchard, 1991b, pl. 3. figs. 1-3).

Age. Early Norian.

### **Ancyrogondolella quadrata** (Orchard, 1991)

Pl. 2: Figs. 4a-c, 5a-c, 6a-c, 7a-c, 8a-c.

1991b *Epigondolella quadrata* Orchard, p. 311, pl. 2, figs, 1-3, 7-9, 10-12.

Material. Eight specimens (0-1/20, 21-2/2, 33-8/2, 33-1/33, 33-1/43, 33-1/14, 33-8/9, 33-1/19) correspond to the dimensional relations of the species.

Description. The average size is around 700 μm. The width to length ratio varies from 1/4 to 1/3, whereas the ratio free-blade to length varies from 1/3 to 1/2. The aboral side shows triangular to quadrate shape with bifid basal cavity. The oral side is quadrate to round. The carina bears up to 11 denticles. The platform is ornamented with up to 15 sharp peripheral denticles. This provides the Hisaidani specimens with a strong affinity to the specimen illustrated by Orchard (1991b: pl. 2, figs. 10, 12)

Age. Early Norian.

### **Ancyrogondolella uniformis** (Orchard, 1991)

Pl. 3: Figs. 1a-c, 2a-c, 3a-c, 4a-c.

1991b *Epigondolella triangularis uniformis* Orchard, p. 315, pl. 3, figs. 1-3.

Material. 16 specimens from correlative horizon 33 in section IV (33-3/2, -12/8, -8/16, -1/1, -7/10, -2/5, -6/40, -8/7, -8/15, -8/1, -4/51, -1/27, -4/31, -8/12) with horizon 23 in section II (23-2/2, -2/3).

Description. Length varies from 400 to 850 μm. Ratio width to length varies from 1/2 in smaller specimens to 1/3 in larger specimens. The ratio between free blade and length varies from 1/3 to 1/2 with exceptions of 1/6. The aboral side is triangular to round, sometimes quadrate, always bilobal or bifid. Oral side varies from quadrate to triangular or round. The carina has up to 11 denticles. The platform has up to 14 denticles.

Remarks. One specimen, 18-1/5 (horizon 18) has dimensions and general features, that fit into the taxon, only differing from it by a much smaller number of denticles (7) on the carina and on the platform (4).

Age. Early Norian.

### **Ancyrogondolella spatulata** (Hayashi, 1968)

Pl. 3: Figs. 5a-c, 6a-c, 7a-c; Pl. 4: Figs. 1a-c, 3a-c, 5a-c.

1968 *Gladigondolella abneptis* var. *spatulata* Hayashi, p. 69, pl. 2, fig. 5.
1991b *Epigondolella spatulata* - Orchard, p. 312, pl. 2, figs. 4-6, 11.

Material. The large number of specimens referred to this species originates the correlative horizons 23 (section II) and 33 (section IV): (23-2/13, -1/32, -1/23), (33-7/1, -6/58, -7/8, -8/14, -2/27, -4/3, -6/1, -8/5, -8/20, -4/6, -8/6, -8/8, -7/21, -8/17, -8/18, -8/19).

Description. Length varying from 420 to 850 μm. Ratio width to length averages 1/2 with extremes from 1/3 to over 2/3. The ratio of the free blade to the length varies strongly from rather exceptional 1/6 to 2/3, with average of 1/3 to 1/2. Aboral side has shapes varying from quadrate to triangular, sometimes piriform and exceptionally subround. The basal cavity is always bilobal but may vary from strongly bifid to exceptionally subround to quadrate. The oral side varies from quadrate to triangular, subround shapes are exceptional. The carina bears up to 11 denticles. The platform has a varying number of denticles 4 -13. Some specimens (33-7/21, 33-8/5, 33-4/3) have 'radiating' denticles from the carina and have well defined denticles on both sides of the platform, near mid-length where a slight constriction gives a piriform shape. The posterior end of the platform may also be slightly concave.

PLATE 2

SEM photographs of conodonts from the Hisaidani sections. All scale bars indicate 100 μm.

Fig. 1a, b, c - *Metapolygnathus* aff. *auriformis* (Kovacs). a: lateral view; b: oral view; c: basal view. All scale bar C. Section VI, Horizon 47. TKUTC47-2/15.

Fig. 2a, b, c - *?Metapolygnathus* sp. a: oral view; b: basal view; c: lateral view. All scale bar B. Section II, Horizon 21. TKUTC21-2/13.

Fig. 3a, b, c - *Ancyrogondolella triangularis* Budurov. a: oral view; b: basal view; c: lateral view. All scale bar B. Section IV, Horizon 33. TKUTC33-1/11.

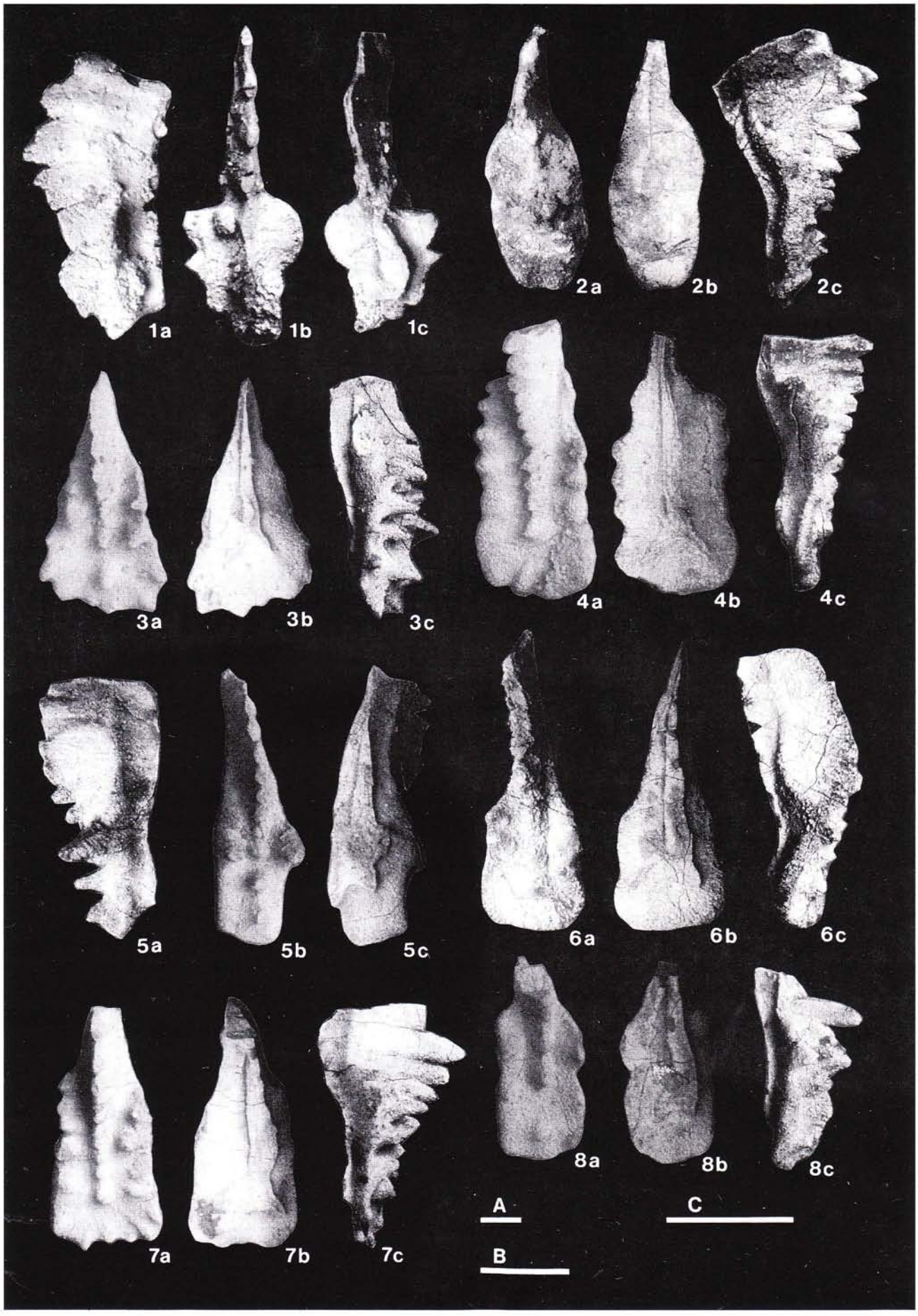
Fig. 4a, b, c - *Ancyrogondolella quadrata* (Orchard). a: oral view; b: basal view; c: lateral view. All scale bar B. Section IV, Horizon 33. TKUTC33-1/33.

Fig. 5a, b, c - *Ancyrogondolella quadrata* (Orchard). a: lateral view; b: oral view; c: basal view. All scale bar B. Section IV, Horizon 33. TKUTC33-1/43.

Fig. 6a, b, c - *Ancyrogondolella quadrata* (Orchard). a: oral view; b: basal view; c: lateral view. All scale bar B. Section II, Horizon 21. TKUTC21-2/2.

Fig. 7a, b, c - *Ancyrogondolella quadrata* (Orchard). a: oral view; b: basal view; c: lateral view. All scale bar A. Section IV, Horizon 33. TKUTC33-8/2.

Fig. 8a, b, c - *Ancyrogondolella quadrata* (Orchard). a: oral view; b: basal view; c: lateral view. All scale bar B. Section IV, Horizon 33. TKUTC33-1/14.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Age. Early Norian.

## Genus *Mockina* Kozur, 1989

Type species: *Tardogondolella abneptis* postera Kozur & Mostler, 1971, p. 14-15, pl. 2, figs. 4-6.

Revised Diagnosis. The genus has a free blade, a unilobal basal cavity, with tendency to an ellipsoid shape, an elliptic pit and sharp denticles around the platform.

Remarks. Forms presently included into *Mockina* were first included into *Polygnathus abneptis* by Huckriede (1958), who already mentioned the presence of sharp denticles around the platform. For Mosher (1968) all forms described by Huckriede as *P. abneptis* belong into the genus *Epigondolella*. Kozur & Mostler (1971) established the variation *Tardogondolella abneptis postera*. Hirsch (1993) limited the use of *Epigondolella* to forms having an unilobal aboral side, regarding the reappearance of an ellipsoid basal cavity in Middle - Late Norian conodonts as an atavistic feature. Buryi (1996), aware of this atavism, mentioned the 'rudimentation' of *Epigondolella postera*.

### **Mockina postera** (Kozur & Mostler, 1971)

Pl. 4, Figs. 2a-c, 4a-c, 6a-c.

1971 *Tardogondolella abneptis postera* Kozur & Mostler, p. 14-15, pl. 2, figs. 4-6.
1983 *Epigondolella postera* - Orchard, p.186-188, figs. 15 P-R.

Material. A small number of specimens (33-1/17, -1/42, -6/31 and 23-1/35, -1/36) are related to *E. postera*.

Remarks. The size, which is in average clearly smaller than that of species attributed to *Ancyrogondolella*, varies from 320 - 670 μm. The ratio between width and length varies from 1/3 to less than 1/2 and that of free blade to length is 1/3 to 1/ 2 as well. The posterior end of the platform varies from rounded to lancet-shaped. The aboral side is unilobal, sometimes amygdaloid. The basal cavity is rather centrally located. The carina has up to 10 denticles, the cusp being rather central and not very pronounced. In our material, the oral side of the unit consists of a platform bearing 3 lateral denticles.

Age. Middle Norian.

### **Mockina** aff. **postera** (Kozur & Mostler, 1971)

Pl. 4, Figs. 7a-c, 8a-c.

Remarks. Specimen 33-8/3 has a nearly subquadrate platform edge, much broader than the rounded - lancet shaped one in *M. postera*. Its basal cavity is more symmetrical and broader and is subquadrate to loop-shaped. The number of denticles is similar, thought the platform has only 2 stout denticles. Specimen 33-8/13 is smaller (380 μm) and has a width/length ratio of nearly 1/2 and a free-blade/length ratio of 1/3. Its platform edge is also subquadrate, the oral side is unilobal. These specimens cannot be regarded as belonging to the same species, thought they have many affinities.

### **Mockina** cf. **elongata** (Orchard, 1991)

Pl. 5: Figs. 1a-c, 2a-c.

*1991b Epigondolella elongata* Orchard, p. 308, pl. 4, figs. 4-6, 15-21.

Remarks. Two small specimens (23-1/26 and 33-8/11) in correlative horizons are slightly more elongate than *M. postera*, and resemble therefore *M. elongata*. With a length of 440 μm, a width to length ratio of 1/3 to less than 1/2 and a free-blade to length ratio of 1/4 to 1/2, these specimens still do not reach the 'stretched' shape of the holotype. The posterior edge of the platform is round to lancet shaped. The aboral side is well unilobate and the pit is more central than in *E. postera*, thought not as much as in the holotype of *M. elongata*. The carina, bearing up to 9 denticles, is only half the figure of the holotype, the platform yields 1 or 2 denticles on each side. A fragmental specimen 21-1/18 is smaller but has similar width, length and free-blade ratios, its aboral side has a posterior, more loop-like basal cavity. It may represent a juvenile specimen.

Age. Middle Norian.

### **Mockina** aff. **matthewi** (Orchard, 1991)

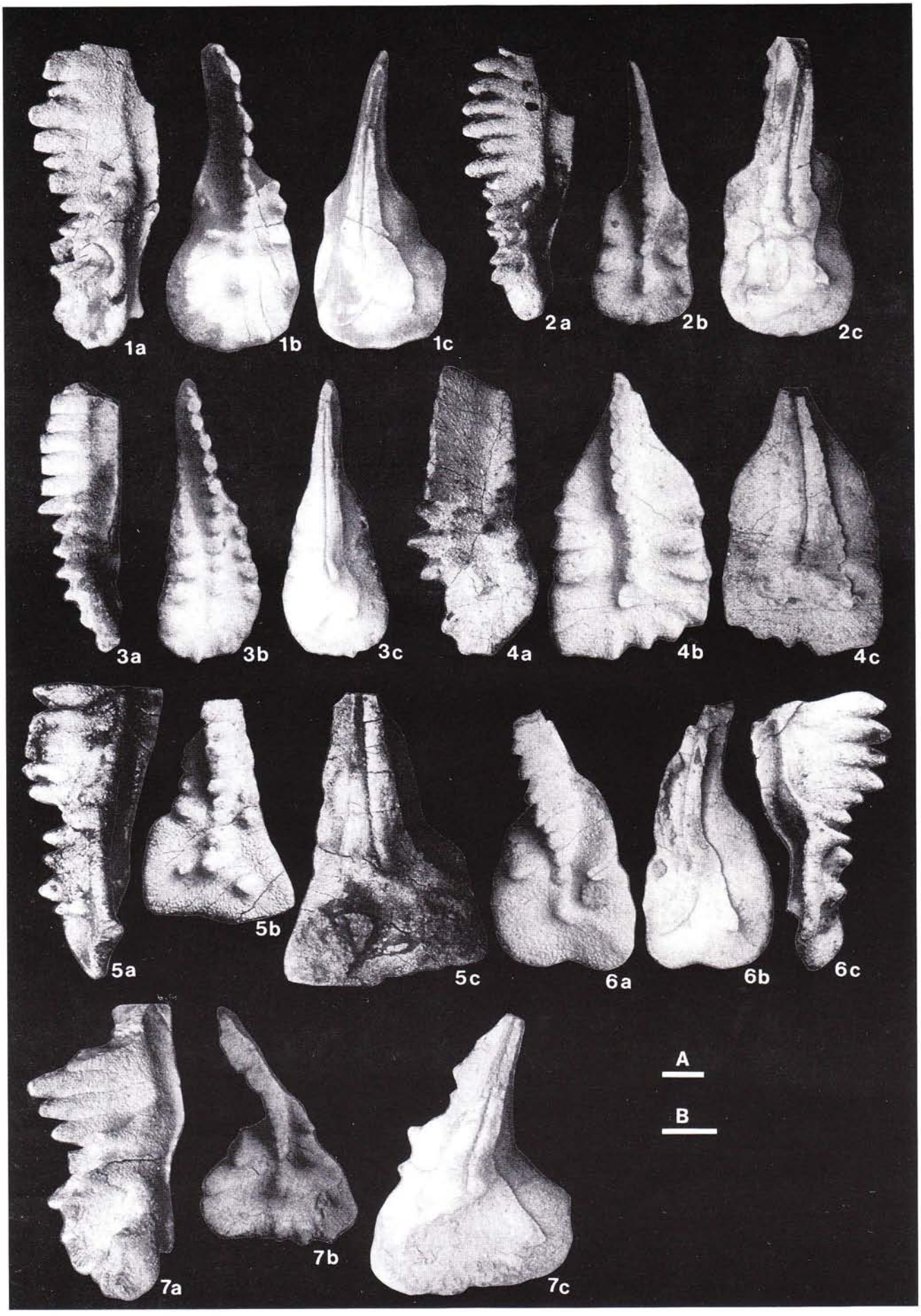
Pl. 5: Figs. 3a-c.

1991b *Epigondolella matthewi* Orchard, p. 309, pl. 4, figs. 8-10.

PLATE 3

SEM photographs of conodonts from the Hisaidani sections. All scale bars indicate 100 μm.

Fig. 1a, b, c - *Ancyrogondolella uniformis* (Orchard). a: lateral view; b: oral view; c: basal view. All scale bar B. Section IV, Horizon 33. TKUTC33-8/1.
Fig. 2a, b, c - *Ancyrogondolella uniformis* (Orchard). a: lateral view; b: oral view; c: basal view. All scale bar A. Section IV, Horizon 33. TKUTC33-4/51.
Fig. 3a, b, c - *Ancyrogondolella uniformis* (Orchard). a: lateral view; b: oral view; c: basal view. All scale bar A. Section IV, Horizon 33. TKUTC33-3/2.
Fig. 4a, b, c - *Ancyrogondolella uniformis* (Orchard). a: lateral view; b: oral view; c: basal view. All scale bar B. Section IV, Horizon 33. TKUTC33-7/10.
Fig. 5a, b, c - *Ancyrogondolella spatulata* (Hayashi). a: lateral view scale bar B; b: oral view, scale bar A; c: basal view, scale bar B. Section IV, Horizon 33. TKUTC33-7/21.
Fig. 6a, b, c - *Ancyrogondolella spatulata* (Hayashi). a: oral view; b: basal view; c: lateral view. All scale bar B. Section IV, Horizon 33. TKUTC33-4/3.
Fig. 7a, b, c - *Ancyrogondolella spatulata* (Hayashi). a: lateral view, scale bar B; b: oral view, scale bar A; c: basal view, scale bar B. Section IV, Horizon 33. TKUTC33-2/27.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Remarks. Specimen 33- 8/4 has a length of 540 μm, a width /length and free blade/length ratios of 1/3. The posterior end of the platform is subquadrate to round. The aboral side is unilobal and resembles the holotype. The carina is different from that in the holotype. Divided into an anterior process bearing 6 denticles and a posterior process, behind the cusp, the Hisaidani specimen has only 1 poorly pronounced denticle, leaving the posterior end without any process, whereas the holotype has three rather stout denticles, reaching the end of the platform. The platform has 3 denticles on one side and 2 on the other.

Age. Probably middle Norian.

### **Mockina** aff. **spiculata** (Orchard, 1991)

Pl. 5: Figs. 4a-c.

1991b *Epigondolella spiculata* Orchard, p. 312-313, pl. 3, figs. 10, 14-15.

Description. Specimen 33-5/43, 500 μm long, has a width/length ratio of 1/3 and a similar free-blade /length ratio. The posterior end of the platform is rather lancet-shaped. Basal cavity is unilobal and amygdaloid. The carina, that reaches the posterior edge of the unit, bears 9 denticles, the stout last denticle being projected posteriorly. The platform is asymmetric and bordered by 2 denticles on one side and 3 on the other side.

Remarks. Slightly smaller than the holotype, the present specimen also differs by having a more posterior basal cavity and a smaller number of denticles on the platform than the holotype.

Age. Middle Norian.

### **Mockina** aff. **serrulata** (Orchard, 1991)

Pl. 5, Figs. 5a-c.

1991b *Epigondolella serrulata* Orchard, p. 311-312, pl. 5, figs. 12, 14-18.

Description. Specimen 33-7/26 is 700 μm long and both width/length and free-blade/length ratios are over 1/4. The edge of the platform is linguiform, M-shaped. The aboral side is unilobal and the basal cavity is linguiform to amygdaloid. The pit is central. The carina consists of a continuous row of 14 denticles, and reachs the posterior end. The carina is followed posteriorly by 3 isolated lower denticles that seem to bifurcate out of the main row. The platform bears 4 denticles on one side and 2 on the other side. It differs from the holotype by a smaller width/length ratio as well as by the apparent bifurcation of the carina denticles. Also the disposition of the platform denticles is not the same.

### **Mockina** aff. **mosheri** (Kozur & Mostler)

Pl. 5: Figs. 6a-c.

1971 *Tardogondolella mosheri* Kozur & Mostler, p. 15.

1991b *Epigondolella mosheri* - Orchard, p. 309-310, pl. 4, figs, 11, 13-14.

Remarks. Specimen 69-1/15 is small (320 μm) and narrow, having a width/length ratio of 1/4. The free blade/length ratio is 1/3. The unilobal unit is lancet-shaped. The denticles are damaged but the platform edge bears 2 stout denticles. The specimen before us has certain affinities with *E. mosheri*.

Age: Presumably latest Norian, together with *Misikella hernsteini*.

### **Mockina** cf. **carinata** (Orchard, 1991)

Pl. 5, Figs. 7a-c.

1991b *Epigondolella carinata* Orchard, p. 308, pl. 5, figs. 4-5, 10.

Remarks. Specimen 23-1/18 has a medium length of 500 μm and width/length as well as free-blade/length ratios of 2/5. The unilobate unit is slightly constricted and has a subrounded posterior margin. The denticles of the carina are fused and the platform bears 4 denticles. The preservation of our specimen is too poor to make a clear comparison but its basal cavity most resembles that of *M. carinata*.

### **Mockina sakurae** n. sp.

Pl. 6, Figs. 1a-c, 2a-c.

Derivation of the name. From the cherry tree blossoms, traditional symbol of Japan.

PLATE 4

SEM photographs of conodonts from the Hisaidani sections. All scale bars indicate 100μm.

Fig. 1a, b, c - *Ancyrogondolella spatulata* (Hayashi). a: lateral view, scale bar A; b: oral view, scale bar B; c: basal view, scale bar B. Section IV, Horizon 33. TKUTC33-6/1.

Fig. 2a, b, c - *Mockina postera* (Kozur & Mostler). a: oral view, scale bar C; b: basal view, scale bar C; c: lateral view, scale bar D. Section II, Horizon 23. TKUTC23-1/36.

Fig. 3a, b, c - *Ancyrogondolella spatulata* (Hayashi). a: oral view; b: basal view; c: lateral view. All scale bar B. Section IV, Horizon 33. TKUTC33-4/6.

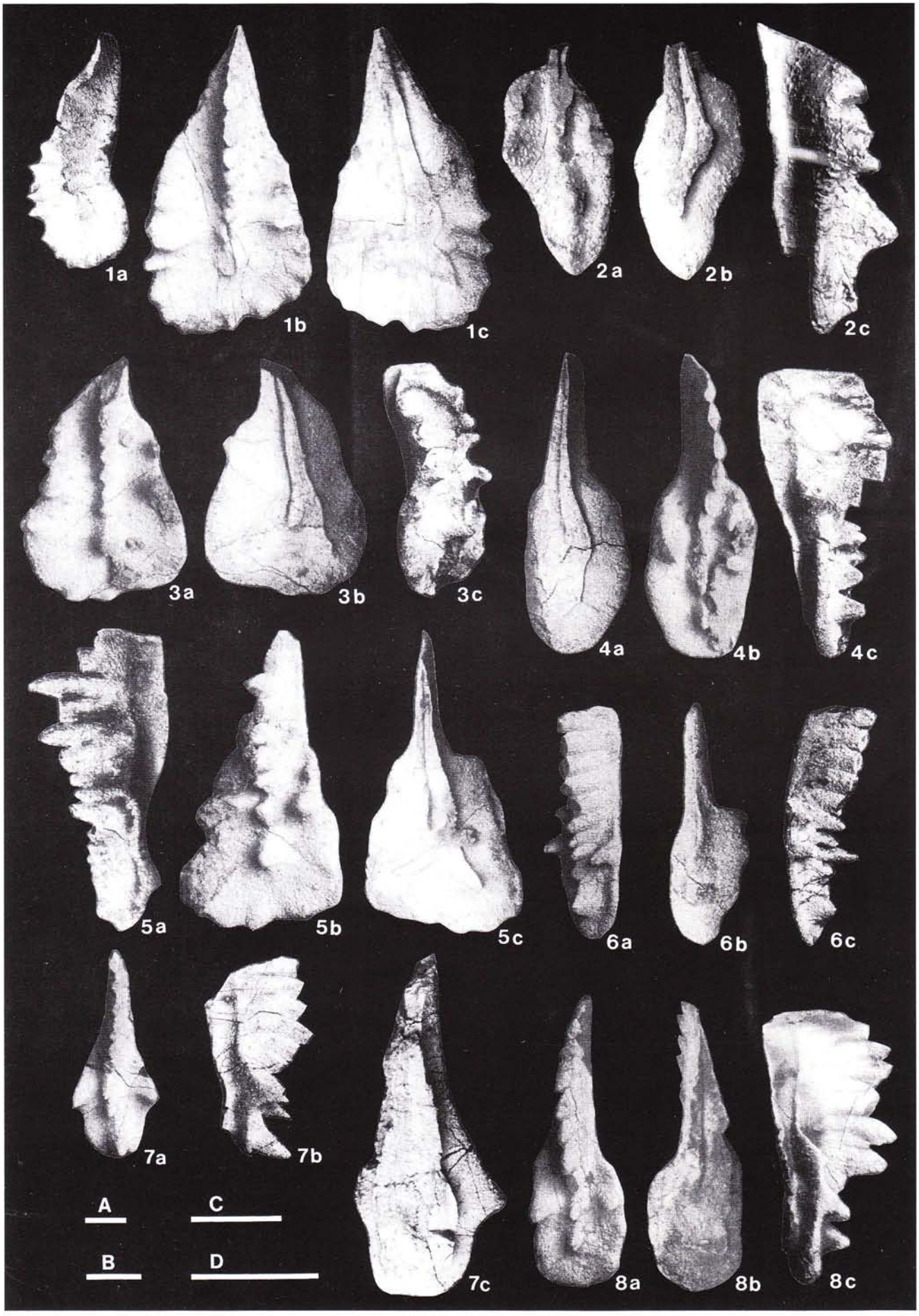
Fig. 4a, b, c - *Mockina postera* (Kozur & Mostler). a: basal view; b: oral view; c: lateral view. All scale bar B. Section IV, Horizon 33. TKUTC33-1/42.

Fig. 5a, b, c - *Ancyrogondolella spatulata* (Hayashi). a: lateral view; b: oral view; c: basal view. All scale bar B. Section IV, Horizon 33. TKUTC33-8/8.

Fig. 6a, b, c - *Mockina postera* (Kozur & Mostler). a: oral view; b: basal view; c: lateral view. All scale bar B. Section IV, Horizon 33. TKUTC33-1/17.

Fig. 7a, b, c - *Mockina* aff. *postera* (Kozur & Mostler). a: oral view, scale bar B; b: lateral view, scale bar B; c: basal view, scale bar C. Section IV, Horizon 33. TKUTC33-8/13.

Fig. 8a, b, c - *Mockina* aff. *postera* (Kozur & Mostler). a: oral view; b: basal view; c: lateral view. All scale bar B. Section IV, Horizon 33. TKUTC33-8/3.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Holotype. Specimen 33-6/51, from Hisaidani, Shikoku, Japan. Paratype. Specimen 33-7/11.

Diagnosis. Lancet shaped unilobate medium sized unit with short free blade and strongly posteriorly inclined denticles.

Description. Length 550 μm (holotype) - 500 μm (paratype). Width/length ratio of 1/3 and free blade/length ratio varying from 1/10 to 1/5. Basal cavity is amygdaloid. Carina bears 7 posteriorly strongly inclined denticles, even more inclined in the posterior process. The platform has 4 stout denticles.

Comparison. *Mockina sakurae* has less platform-denticles than *M. slovakensis* (Kozur).

It differs from *M. englandi* (Orchard) by a shorter free blade and a smaller amount of denticles on the carina. It differs from both taxa by its especially strong backward inclination of its denticles.

Age. Presumably middle Norian.

### **Mockina hisaidaniensis** n. sp.

Pl. 6, Figs. 3a-c, 4a-b.

Derivation of the name. From the type locality, the Hisaidani-valley, Shikoku, Japan.

Holotype. Specimen 95-1/19. Paratype: Specimen 95-1/26.

Diagnosis. Asymmetric, unilobate, small sized unit, with well developed free blade, strongly narrowing lancet shaped posterior end and rather stout strongly posteriorly inclined denticles, elliptic at base. Platform asymmetric with 2 denticles on the larger side, one or none on the other.

Description. Small sized units of 250 μm (holotype) to 150 μm (paratype). Width/length and free-blade/length ratios of 1/3 to 2/5. The posterior end of the platform is strongly narrowing and lancet shaped. The carina bears 7 or 9 posteriorly inclined rather stout denticles. The denticles have an elliptic base. Asymmetric shaped platform, the larger side bearing up to two denticles, the other side one or none. The subsymmetric to asymmetric aboral side is unilobal and has an elongated amygdaloid basal cavity.

Comparison. Some affinities exist among *M. hisaidaniensis* n. sp., *M. mosheri* and *M. bidentata*. The number of denticles on the platform of *M. hisaidaniensis* recalls the former, whereas the proportions of the unit resemble the latter. *M. hisaidaniensis* n. sp. is generally wider than both. *M. hisaidaniensis* n. sp. differs from *M.* cf. *elongata* by its amygdaloid basal cavity, not reaching the posterior end of the unit, and the absence of twisting of the keel. The inclination of the denticles of *M. hisaidaniensis* n. sp. is very characteristic.

Age. Presumably late Norian.

### **Mockina shamiseni** n. sp.

Pl. 6, Figs. 5a-c, 6a-e.

Derivation of the name. From the shape of a traditional Japanese three string instrument.

Holotype. Specimen 23-2/7. Paratype. 23-1/52.

Diagnosis. Asymmetric, unilobate, small sized unit, with well developed free blade, subround shaped posterior end and rather stout posteriorly inclined denticles. Platform asymmetric with 2 denticles on the larger side, one stout denticle on the other.

Description. The relatively small units, 330 μm (holotype) to 390 μm (paratype), have width/length ratio of 2/5 whereas the free-blade/length ratio is nearly 1/2.

The subround shape of the posterior platform margin and the inclination of the up to 8 denticles of the carina characterize *Mockina shamiseni* n. sp. The aboral side has an unilobate basal cavity. The platform is wider towards the middle part of the unit, where it bears one and two denticles.

Comparison. *Mockina shamiseni* n. sp. resembles in its general shape *M. postera* as well as *M. permicus*. But *M. shamiseni* n. sp. is less symmetric than the former, and its posterior end is more rounded. *M. shamiseni* n. sp. differs from the latter by its relatively sharp denticles on the flat, upward-pointing platform edge, and by showing no constriction of the posterior part of the platform and no initial stage of bifurcation of the basal cavity (as e.g. *Metapolygnathus permicus*, in Budurov 1977, p. 33, fig. 1). The latter has also clear grooves siding the carina, which *M. shamiseni* n. sp. has not. *M. shamiseni* n. sp. further differs from *M. postera* and *M. permicus* by the inclination of the denticles of the carina.

Age. Presumably middle Norian.

## Genus *Norigondolella* Kozur, 1990

1990 *Norigondolella* Kozur, p. 127-131.

Type species. *Paragondolella navicula steinbergensis* Mosher, 1968, p.939, pl. 117, figs. 13-22.

Remarks. Mosher (1968) has observed the reap-

PLATE 5

SEM photographs of conodonts from the Hisaidani sections. All scale bars indicate 100 μm.

Fig. 1a, b, c - *Mockina* cf. *elongata* Orchard. a: oral view; b: basal view; c: lateral view. All scale bar C. Section II, Horizon 23. TKUTC23-1/26.

Fig. 2a, b, c - *Mockina* cf. *elongata* Orchard. a: lateral view; b: oral view; c: basal view. All scale bar B. Section II, Horizon 33. TKUTC33-8/11.

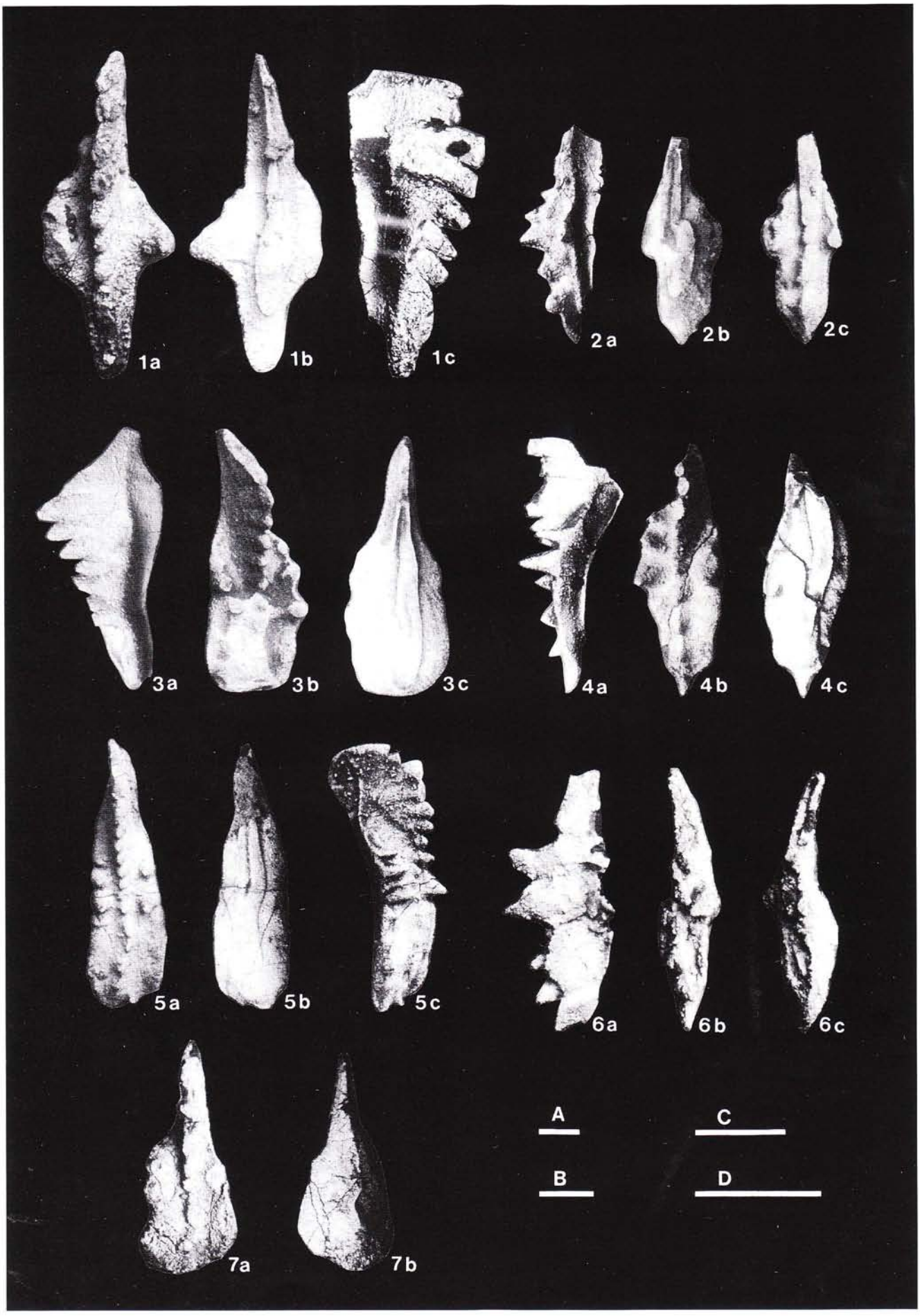
Fig. 3a, b, c - *Mockina* aff. *matthewi* Orchard. a: lateral view; b: oral view; c: basal view. All scale bar B. Section IV, Horizon 33. TKUTC33-8/4.

Fig. 4a, b, c - *Mockina* aff. *spiculata* Orchard. a: lateral view; b: oral view; c: basal view. All scale bar B. Section IV, Horizon 33. TKUTC33-5/43.

Fig. 5a, b, c - *Mockina* aff. *serrulata* Orchard. a: oral view; b: basal view; c: lateral view. All scale bar A. Section IV, Horizon 33. TKUTC33-7/26.

Fig. 6a, b, c - *Mockina* aff. *mosheri* Kozur & Mostler. a: lateral view; b: oral view; c: basal view. All scale bar C. Section IV, Horizon 69. TKUTC69-1/15.

Fig. 7a, b, - *Mockina* cf. *carinata* Orchard. a: oral view; b: basal view. All scale bar B. Section II, Horizon 23. TKUTC23-1/18.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parition of '*Gondolella*'-type conodonts from a platformless ancestor at different stages e.g. the Pennsylvanian G. denuda Clark & Mosher. Kozur (1990) has mentioned such reiterations in the Triassic. Hirsch (1993) has shown that the frequent Triassic reiterations of platformless neospathid morphs are related to paedomorphism, due to the stress caused by global eustatic sealevel changes; these periodically initiate gondolellid lineages. In the case of the Norian species "*navicula, hallstattensis* and *steinbergensis*" a derivation from a lineage of *Metapolygnathus communisti*, previously discussed by Kozur (1990) and admitted by Hirsch (1993), seems unlikely and a cavital platformless ancestor, e.g. *Neocavitella* Budurov & Sudar (1990) far more plausible.

**Norigondolella navicula** (Huckriede, ANNO)

Emend. after Koike, 1982

Pl. 7, Figs. 1a-c, Fig. 2.

1982 *Neogondolella navicula* - Koike, p. 23, pl. 2, figs. 26-27.

Description. The relatively large unit (1000 μm) is narrow (width/length ratio of 1/4) and has a subquadrate to loop-like flared basal cavity, with a deep loop-like posterior pit. The over 13 denticles of the carina are rather fused.

Remarks. The two specimens (33-7/18, -1/29) are clearly included into the taxon depicted by Koike (1982) from Taho. There is a problem concerning the use of the specific name of *N. navicula*. The holotype of this simple form of gondolelloid platform conodont, originally believed to range from Anisian to Norian, is Carnian (Huckriede 1958, p. 148). Most Middle Triassic and Carnian morphs of *navicula* are now included in various species of the genera *Paragondolella* and/or *Metapolygnathus*. Kozur (1990) established the genus *Norigondolella* based on *N. steinbergensis* (Mosher 1968), including the species navicula into this genus. Koike (1982, p. 23) wrote that "The specimens referred to this species by many authors based on the material from Middle Triassic strata should be discriminated, because the range of *Neogondolella navicula* (Huckriede) is restricted in the Norian".

The similarity between the Norian morph and older forms is due to neoteny (sensu Hirsch 1994), a phenomenon of reccurence of ancestral morphologies in younger strata, under environmental stress.

Age. Early Norian.

**Norigondolella aff. hallstattensis** Mosher, 1968

Pl. 7, Figs. 3a-c.

1968 *Paragondolella navicula hallstattensis* Mosher, p. 939, pl. 117, figs. 6-12.

Description. Specimen 33-8/12 is rather small (550 μm) and broad (200 μm) and has a free blade of 200 μm. The quadrate flared basal cavity has a posterior, relatively deep pit. The posterior margin of the platform is round to subquadrate. The strongly reticulated platform is constricted before its posterior third. The carina is high anteriorly (free-blade) whereas its posterior end does not reach to the edge, but is represented by a low, single isolated cusp. The anterior part of the arched unit of our specimen is damaged. A slight furrow runs on both sides of the carina.

**Norigondolella steinbergensis** (Mosher 1968)

Pl. 7: Figs. 4a-c.

1968 *Paragondolella navicula steinbergensis* Mosher, p. 939 - 940, pl. 117, figs. 13-22.
1990 *Norigondolella steinbergensis* - Kozur, p. 128-129, figs. 1A-F.

Remarks. The broken specimen 33-2/49 can be attributed to the taxon. The remnant is 400 μm long, but being very narrow (170 μm) the unit may have attained 3 times that length. The basal pit consists of a large, deep loop. Denticles of the carina are low and strongly fused, except for the posterior cusp, which shows the typical projection of the holotype.

Genus *Misikella* Kozur & Mock, 1974

(Emend. herein)

1974 *Misikella* Kozur & Mock, p. 135-136.
1989 *Axiothea* Fåraeus & Ryley, p. 1258.

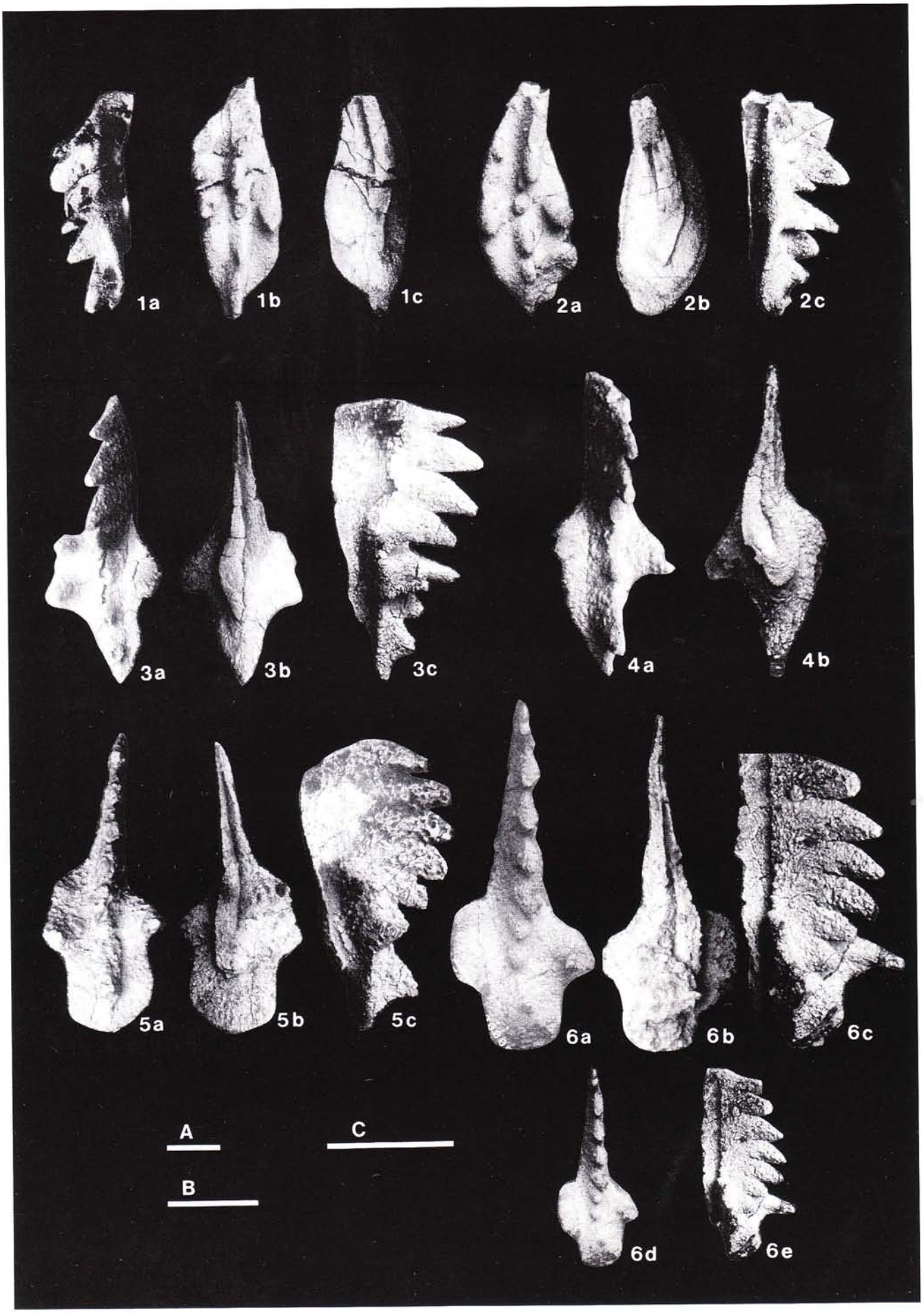
Type species. *Misikella longidentata* Kozur & Mock, 1974, p. 136-137, pl. 1, figs. 4-5.

Revised Diagnosis. Gondolellid multielement apparatus. Cavitate Pa element is platform-less. Ramiform elements are in the number of three (in type) or more.

Remarks: Platformless cavital elements occurring during the Carnian - Rhaetian interval have been attributed to the following taxa: *Mosherella* (late Ladinian -

PLATE 6

SEM photographs of conodonts from the Hisaidani sections. All scale bars indicate 100 μm.
Fig. 1a, b, c - *Mockina sakurae* n. sp. Paratype. a: lateral view; b: oral view; c: basal view. All scale bar A. Section IV, Horizon 33. TKUTC33-7/11.
Fig. 2a, b, c - *Mockina sakurae* n. sp. Holotype. a: oral view; b: basal view; c: lateral view. All scale bar A. Section IV, Horizon 33. TKUTC33-6/51.
Fig. 3a, b, c - *Mockina hisaidaniensis* n. sp. Holotype. a: oral view; b: basal view; c: lateral view. All scale bar B. Section IV, Horizon 95. TKUTC95-1/19.
Fig. 4a, b - *Mockina hisaidaniensis* n. sp. Paratype. a: oral view; b: basal view. All scale bar C. Section IV, Horizon 95. TKUTC95-1/26.
Fig. 5a, b, c - *Mockina shamiseni* n. sp. Holotype. a: oral view; b: basal view; c: lateral view. All scale bar B. Section II, Horizon 23. TKUTC23-2/7.
Fig. 6a, b, c, d, e: *Mockina shamiseni* n. sp. Paratype. a: oral view, scale bar B; b: basal view, scale bar B; c: lateral view, scale bar B; d: oral view, scale bar A; e: lateral view, scale bar A. Section II, Horizon 23. TKUTC23-1/52.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early Carnian), *Neocavitella* (late Ladinian, early Carnian, late Carnian, middle Norian), *Misikella* (middle Norian - Rhaetian), *Parvigondolella* and *Axiothea* (late Norian - Rhaetian). The Carnian - middle Norian taxon *Neocavitella* is morphologically different from *Misikella* (type *M. longidentata*) which first appeared in the middle Norian.

In their diagnosis of *Misikella*, Kozur & Mock (1974, p. 136) clearly stated that their taxon consists of a single element. Furthermore, confusion was generated by the establishment of the late Norian taxon *Parvigondolella* (type *P. andrusovi*), for which no apparatus is mentioned at all. Emended by Fåhraeus & Ryley (1989) to a tetramembrate apparatus, *Misikella* was considered to be distinct from the late Norian - Rhaetian bimembrate *Axiothea* (type *A. hernsteini*).

The genus *Axiothea* including typical gondolellid ramiform elements (Fåhraeus & Ryley 1989) was thus primarily established for a multi-element apparatus distinct from *Misikella longidentata* Kozur & Mock (1974). The multi-element apparatus may often not be preserved, as it occurs in the Hisaidani section. However, the discovery at Konose, a valley to the West of Hisaidani (E. Shikoku), by Ishida (1998), of a pentamembrate multi-element (Pa, M, Sa, Sb and Sc) of *Misikella posthernsteini* (Ishida 1998), widely similar to the apparatus of *Misikella longidentata* sensu Fåhraeus & Ryley (1989) definitely extends the definition of *Misikella* to a pentamembrate taxon, that includes forms previously attributed to *Axiothea*.

**Misikella hernsteini** (Mostler, 1967)

Pl. 7, Figs. 5-10.

1967 *Spathognatodus hernsteini* Mostler, p 182, fig. 1.
1974 *Misikella hernsteini* - Kozur & Mock, p. 135-136, pl. 1, figs. 6-7
1989 *Axiothea hernsteini* - Fåhraeus & Ryley, p. 1258, pl. 1, figs. 4-6.

Material. Seven specimens of *Misikella hernsteini* were recovered from the horizons 69, 67 and 2: 69-2/25, -2/16; 67-1/45, -1/4, -1/13, -1/24 and 2-1/2.

Remarks. The unit may reach 160 μm and the width/length ratio varies from over 1/4 to 2/5, with an average around 1/3. The units have the strongly inflated eye-shape, produced by a large and deep basal cavity. The number of denticles is 3.

Age. Late Norian to Rhaetian.

**Misikella** cf. **longidentata** (Kozur & Mock, 1974)

Pl. 7, Figs. 11-12.

1974 *Misikella longidentata* Kozur & Mock, p. 136-137, pl. 1, figs. 4-5.
1989 *Misikella longidentata* - Fåhraeus & Ryley, p. 1256-1258, pl. 1, figs. 11-15.

Remarks. Two specimens (69-2/17, -1/17) resemble the Pa element of the taxon. The short unit is 90 μm long and 30 μm wide. The cavital base is slightly quadratic. The damaged unit may have 3 denticles.

Age. Late Norian.

**Misikella posthernsteini** (Kozur & Mock, 1974)

Pl. 7: Fig. 13.

1974 *Misikella posthernsteini* Kozur & Mock, p. 247-248, textfigs. 1-4.
1979 *Misikella posthernsteini* - Gazdzicki et al., pl. 5, figs. 1-2.
1991b *Misikella posthernsteini* - Orchard, pl. 5, fig. 21.
1989 *Axiothea posthernsteini* - Fåhraeus & Ryley, p. 1260, pl. 1, figs. 7, 9.

Remarks. Specimen 67-1/32, corresponds well to *Misikella posthernsteini*. It has a length of 140 μm, and a width of 90 μm. The cavital basal cavity has a concave posterior end, continued in the characteristic groove that distinguishes the posterior cusp. Denticles, 3 in number, are inclined posteriorly. Since the illustrations of the holotype in the paper 1974 are poor, we refer to Gazdzicki et al. (1979, pl. 5, figs. 1-2) and Orchard (1991b, pl. 5, fig. 21).

Age: Rhaetian.

## Comparison with the Upper Triassic in other areas

The Upper Triassic stratigraphy of the allochtho-

PLATE 7

SEM photographs of conodonts from the Hisaidani sections. All scale bars indicate 100 μm .

Fig. 1a, b, c - *Norigondolella navicula* (Huckriede). Posterior half of the specimen. a: lateral view; b: oral view; c: basal view. All scale bar A. Section IV, Horizon 33. TKUTC33-7/18.

Fig. 2 - *Norigondolella navicula* (Huckriede). Posterior half of the specimen. Basal view, scale bar A. Section IV, Horizon 33. TKUTC33-1/29.

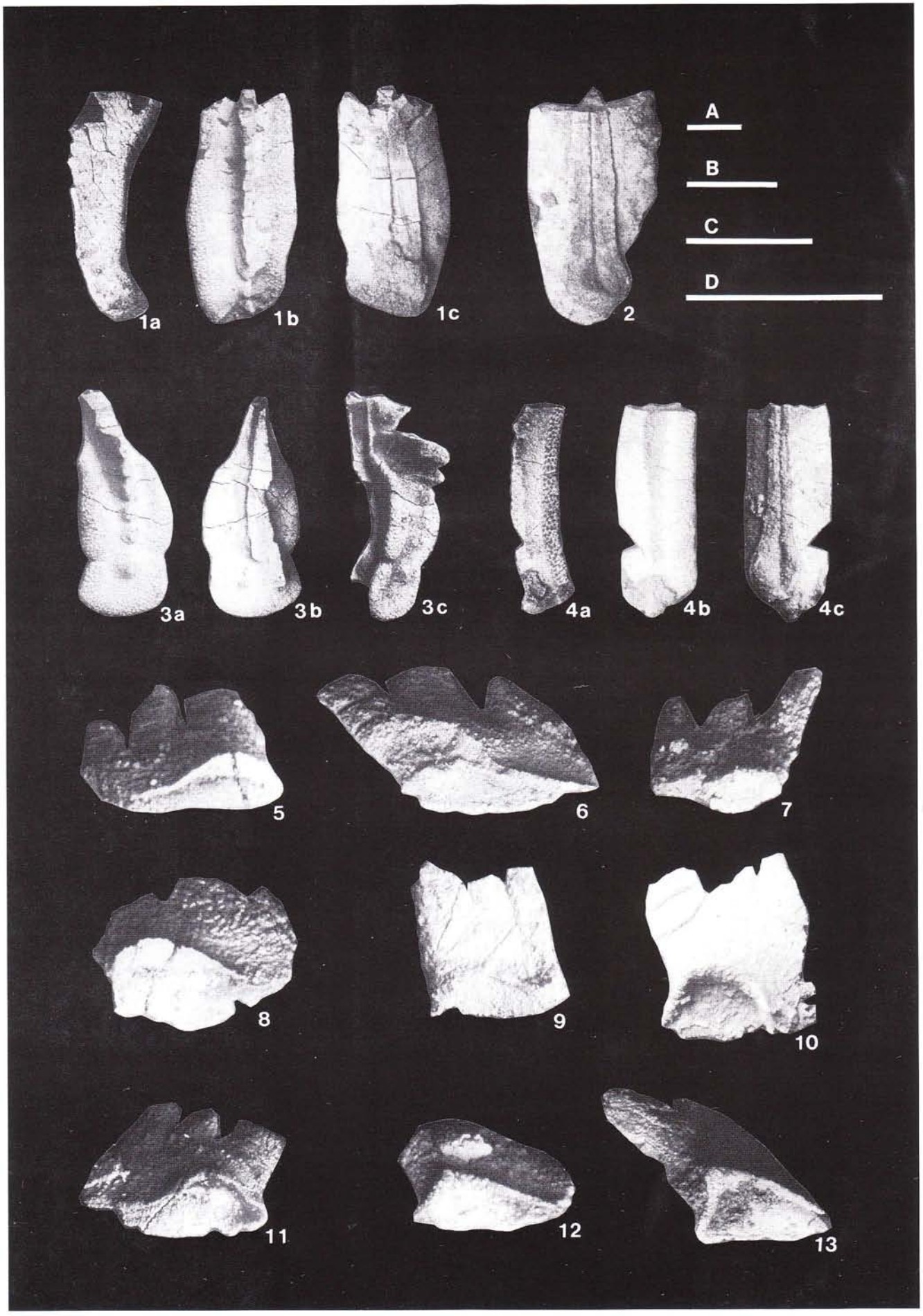
Fig. 3a, b, c - *Norigondolella* aff. *hallstattensis* Mosher. a: oral view; b: basal view; c: lateral view. All scale bar A. Section IV, Horizon 33. TKUTC33-8/12.

Fig. 4a, b, c - *Norigondolella steinbergensis* Mosher. Posterior half of the specimen. a: lateral view; b: oral view; c: basal view. All scale bar A. Section IV, Horizon 33. TKUTC33-2/49.

Fig. 5 - 10 - *Misikella hernsteini* (Mostler). 5-Lower lateral view, scale bar D. Section IV, Horizon 67. TKUTC67-1/45. 6- Lower lateral view, scale bar C. Section IV, Horizon 69. TKUTC69-2/25. 7- Lower lateral view, scale bar C. Section IV, Horizon 69. TKUTC69-2/16. 8 - Lower lateral view, scale bar D. Section IV, Horizon 67. TKUTC67-1/13. 9- Lateral view, scale bar C. Section IV, Horizon 67. TKUTC67-1/24. 10 - Lower lateral view, scale bar C. Section II, Horizon 2. TKUTC2-1/2.

Fig. 11-12 - *Misikella* cf. *longidentata* (Kozur & Mock). 11 - Lower lateral view, scale bar C. Section IV, Horizon 69. TKUTC69-1/17. 12 - Lower lateral view, scale bar D. Section IV, Horizon 69. TKUTC69-2/17.

Fig. 13 - *Misikella posthernsteini* (Kozur & Mock). Lower lateral view, scale bar B. Section IV, Horizon 67. TKUTC69-1/32.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nous terranes in British Columbia, of the Siberian Far East and the other areas in Japan is compared with the studied Hisaidani succession (Table 1).

### A. British Columbia, (Canada).

The Kunga Group (Wrangell terrane, Haida Gwaii or Queen Charlotte Islands) includes the over 500 m thick late Carnian - Norian carbonate Sadler and Peril formations, topped by *Monotis* beds. They are overlaid by the sandstones with limestone nodules of the Sandilands Formation, 100 m of which are uppermost Norian - Rhaetian (Sutherland-Brown 1968; Orchard 1991a). In NE British Columbia, biochronologically well-constrained Late Triassic conodont assemblages occur, calibrated with ammonoids (Orchard 1991 b).

The Carnian - Norian boundary is apparently within the primitius Zone, whereas a clear differentiation seems to exist between early Norian triangularis Zone and the middle Norian multidentata Zone with no overlap of early and middle Norian taxa. The late Norian is defined by the advanced forms of *Mockina* (bidentata Zone). The late Rhaetian crickmayi Zone is defined by *Misikella posthernsteini* (Orchard 1991b).

### B. Primoriye, Khabarovsk and Sakhalin (Siberian Far East, Russia).

Bragin (1991) in his composite profile and faunal distribution chart provides a summary of the stratigraphy of the Siberian Pacific terranes. The nearly 50 m thick upper Carnian - Rhaetian section consists of bedded chert and tuffs. The Carnian is relatively thick, due to these volcanic tuffs. It encompasses zones J and K, respectively *Metapolygnathus polygnathiformis* and *M. nodosus*. The Norian is subdivided by conodonts into zones L, M, N and O, respectively *abneptis, postera, bidentata* and *andrusovi*. Concurrent ranges of these taxa suggest that further identifications as e.g. of taxa described in British Columbia, may clarify this biostratigraphic zonation. The uppermost Norian zone O yields *M. hernsteini*, which ranges into the Rhaetian zone P. The lower Rhaetian conodont zone P encompasses *M. posthernsteini*, which also defines the upper Rhaetian Zone Q.

### C. Japan.

Stratigraphic distribution charts of conodonts and radiolarians in the Upper Triassic bedded cherts of the Mino-Tamba Belt were established at Inuyama and Hozugawa (Matsuda & Isozaki 1991; Isozaki & Matsuda 1980). The Carnian -Norian boundary can be set at the base of *A. abneptis*.. Within the Norian interval, the ranges of *Ancyrogondolella "abneptis", Mockina postera* and *M. bidentata overlap*. The concurrent range of all or some of these taxa with *Misikella hernsteini* differs from section to section. However, Upper Norian and Rhaetian can be defined by the range of *Mockina bidentata* and *Misikella posthernsteini* respectively. We may have some reservations concerning the identification in the Inuyama section of *Parvigondolella andrusovi* and *M. bidentata* respectively and suspect that some of the specimens may be very small and possibly not fully mature.

The overlap of early and middle Norian taxa *A. spatulata, M. postera* and *M. multidentata* below the first appearance of *M. bidentata* was already observed by Koike (1979a, p.37, table 4) and seems to represent a feature common to the low latitude Tethys. The concurrent range during the middle Norian of *"A. abneptis", A. spatulata, M. postera* and *M. multidentata* was also reported by Gazdzicki et al. (1979, table 1, p. 87) as well as by Kovacs & Kozur (1980, table 2).

Koike (1979, 1981) and Nakazawa et al. (1994) have summarized the conodont zonation in Japan, including Mino-Tamba and Chichibu belts. According to these studies, the Carnian - Norian boundary can be set at the last occurrence of *Metapolygnathus nodosus* and *M. polygnathiformis*. The Norian interval is defined by the zones of *Ancyrogondolella quadrata, A. spatulata, Mockina multidentata, M. postera* and *M. bidentata*.

As in the Tethys, in the Chichibu and Mino-Tamba belts, *Ancyrogondolella* and *Mockina* overlap during the middle Norian. In the Siberian sections, middle Norian *Mockina* ranges into the upper Norian. In both Siberian and Japanese sections the genera *Mockina* and *Misikella* overlap only shortly. This strongly contrasts the Pacific Wrangellia terrane, in which early and middle Norian taxa do not overlap but late Norian taxa may range into the Rhaetian.

In the Hisaidani section I, horizon 18 *Metapolygnathus primitius* occurs concurrently with *M. polygnathiformis* and *M. permicus*, suggesting the Carnian - Norian boundary. It is not possible at Hisaidani to reach higher resolution within the condensed horizons. In section IV, horizon 33, at the top of the limestone succession, *Metapolygnathus primitius, A. quadrata, A. spatulata* and *Mockina postera* occur. Within bedded cherts, *Misikella hernsteini* and *M. posthernsteini* are concurrent, all the way up to the uppermost Triassic horizon, suggesting an age, still older than the latest Rhaetian.

## Conclusion

From genus *Neogondolella* Bender & Stoppel (1965), with a platform that covers the entire length of the unit, the gradual development, through *Paragondolella*, of a free blade defines the genus *Metapolygnathus* Hayashi,1968.

Primitive Carnian forms that were attributed by Orchard (1991) to the genus *Metapolygnathus* have

almost full platforms. A free blade, known to have already developed in Ladinian *Sephardiella*, represents a basic criterion for Carnian *Metapolygnathus*, early Norian *Ancyrogondolella* and middle - late Norian *Mockina*, until not much of a platform is left. Iterations of "quasi" *Neogondolella* occur in late Carnian *Metapolygnathus* and Norian *Norigondolella*.

The evolutionary process of latest Triassic conodonts seems to be paced by heterochrony, which is expressed in the simplification of the platform element. In the latest Norian, two platform genera were still present, *Norigondolella* and *Mockina*. Latest Norian - Rhaetian platformless multi-elements are attributed to the taxon *Misikella*.

The affinities of the Hisaidani fauna is rather Tethyan, though towards the middle and late Norian, affinities with Pacific taxa are present. Three new species provide a provincial character, which may define the Izanami plateau (Hirsch & Ishida, in press) where the rocks of Hisaidani were derived from.

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