A natural assemblage of Ellisonia sp. cf. E. triassica Müller (Vertebrata: Conodonta) from the uppermost Permian in the Suzuka Mountains, central Japan

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A natural assemblage of *Ellisonia* sp. cf. *E. triassica* Müller (Vertebrata: Conodonta) from the uppermost Permian in the Suzuka Mountains, central Japan

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Abstract. A natural assemblage of *Ellisonia* sp. cf. *E. triassica* Müller was recovered from the uppermost Permian close to the Permian-Triassic boundary in the Nabejiriyama section in the Mt. Ryozen area, Suzuka Mountains, central Japan. This natural assemblage and collections of similar ellisonids from the Taho Formation of Ehime Prefecture, southwestern Japan, demonstrate that the *Ellisonia* apparatus is composed of eight kinds of elements: breviform digyrate M, symmetrical S_0, extensiform digyrate S_1 and S_2, bipennate S_3 and S_4, and angulate P_1 and P_2 elements. The apparatus structure of *Ellisonia* is comparable to the standard 15-element plan of Carboniferous ozarkodinids and prioniodinids. The apparatus structure of the present natural assemblage is important in discussing the phylogenetic affinity of the genus *Ellisonia*.

Key words: Conodonta, *Ellisonia*, Japan, Mt. Ryozen area, Nabejiriyama section, natural assemblage, Permian and Triassic boundary

Introduction

A natural assemblage of *Ellisonia* sp. cf. *E. triassica* Müller was discovered in siliceous claystone of the Nabejiriyama (Mt. Nabejiri) section, one of the large blocks in the Nishizaka Unit, exposed in the Mt. Ryozen area, in the northernmost Suzuka Mountains, Shiga Prefecture, central Japan. The Nabejiriyama section consists of an about 4-m thickness of strata of deep-sea origin in which the Permian-Triassic boundary is present.

The apparatus of *Ellisonia* (Carboniferous-Triassic) was reconstructed as a multimembrate apparatus with two to six kinds of elements (Sweet, 1970, 1981; von Bitter and Merrill, 1983; Koike, 1990). The discovery of a natural assemblage of *Ellisonia* in the Nabejiriyama section and intensive study of ellisonids from the Taho Formation of Ehime Prefecture demonstrate that the following eight kinds of elements constitute the *Ellisonia* apparatus: breviform digyrate M, triramous alate S_0, extensiform digyrate S_1 and S_2, bipennate S_3 and S_4, and angulate P_1 and P_2 elements.

The purpose of this paper is (1) to determine the exact age of the natural assemblage, (2) to describe the arrangement of elements in the natural assemblage, (3) to compare the natural assemblage with the previously reconstructed Carboniferous to Triassic ellisonids, (4) to describe the individual elements of the natural assemblage, (5) to indicate the characteristics of the component elements of the *Ellisonia* apparatus, and (6) to discuss the phylogenetic relationships between *Ellisonia* and other taxa.

Geologic setting

The strata of the Nabejiriyama section were included in the Ryozensan Formation of the Kitasuzuka Group of Lower Permian age (Miyamura *et al.*, 1976). The Kitasuzuka Group was regarded as a Jurassic accretionary complex in the Mino Belt and divided into two tectonostratigraphic units by Yamagata (2000): the Kitasuzuka Unit composed of various-sized disrupted masses of Permian oceanic rocks of basalt and volcaniclastic rock, limestone, and chert; and the Nishizaka Unit composed of melange with mudstone matrix containing blocks of basaltic rock, limestone, chert, and sandstone. The rock of the Nabejiriyama section is one of the large blocks in the Nishizaka
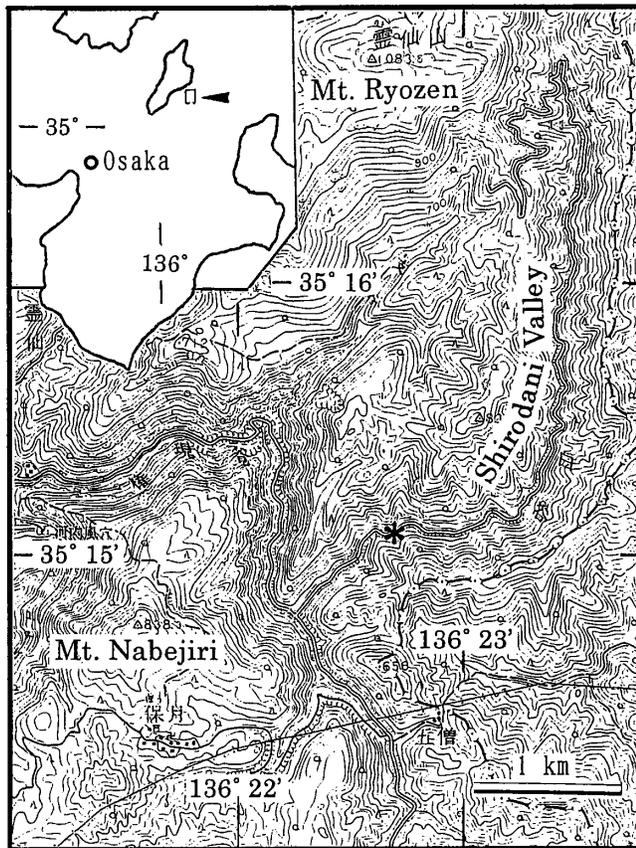
Figure 1. Map showing the fossil locality (solid asterisk) in the Nabejiriyama (Mt. Nabejiri) section (136°22′42″E, 35°15′05″N), Mt. Ryozen area of the Suzuka Mountains, Shiga Prefecture. The map is a part of 1:50,000 topographic map "Hikonetobu (N1-53-8-9, 1990)" published by Geographical Survey Institute of Japan.

Figure 2. Geological sketch map of the Nabejiriyama section at the level of 1.5 m above the road surface.

Unit. It consists of chert and claystone representing an ocean-floor sequence (Kuwahara, 1997).

The Nabejiriyama section is exposed in a road cut on the Shirodani forestry road in the Shirodani Valley, east of Nabejiriyama (Figure 1). This road cut is about 8 m long and 4 m high, where bedded chert with subordinate amounts of claystone is continuously exposed. The beds strike NNE to NS and dip 80° to 86° E or W (Figure 2).

Ishiga *et al.* (1982a) recognized two Upper Permian radiolarian zones in this section (section I): the upper *Neoalbaillella ornithoformis* and the lower *N. optima* Assemblage Zones. Kuwahara *et al.* (1998), however, pointed out that these two assemblage zones were reversed; overturned based on their studies of Late Permian radiolarians in the Gujohachiman area of the Mino Belt. This conclusion is supported by the occurrence of Middle Permian radiolarians in bedded chert
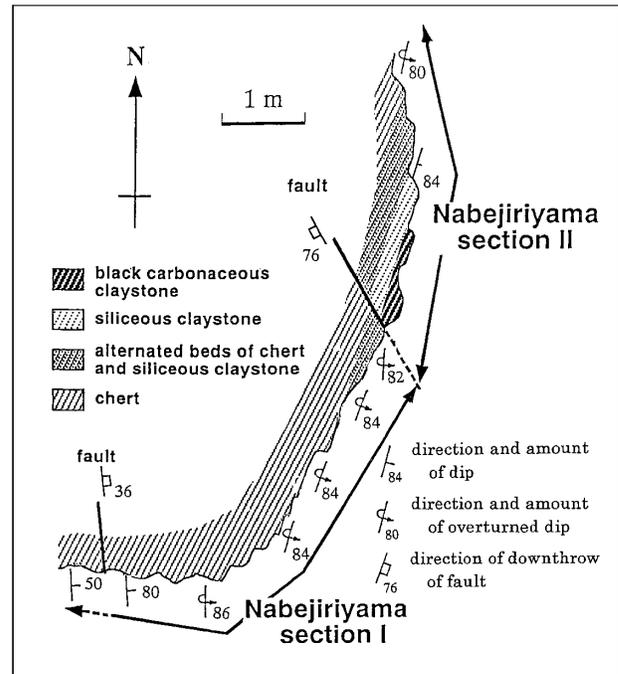
exposed about 30 m southwest of the Nabejiriyama section (Ishiga *et al.*, 1982b). Yao *et al.* (2001) studied conodonts recovered from the strata of the Nabejiriyama section I (Figure 2) and determined them to be Changhsingian in age.

One of us (S. Y.) made a detailed stratigraphic study of the Nabejiriyama section II (Figure 2) and established the succession shown in Figure 3. The lower part of the section (Beds Rz-4 to Rz-12) consists of 55-cm-thick alternating beds of gray chert and gray siliceous claystone. The upper part (Bed Rz-1 and Rz-2) is composed of 18-cm-thick black carbonaceous claystone. A particular characteristic of the sequence is that a 3-cm-thick black claystone with laminae of gray siliceous claystone (Bed Rz-3) intercalates between the lower and upper parts of the sequence (Figure 3). As will be discussed, the Permian-Triassic boundary is provisionally placed immediately above this bed.

Two of us (S. Y. and N. K.) continued to attempt to recover microfossils from the strata. As a result, a latest Permian radiolarian, *Albaillella triangularis* Ishiga *et al.*, was recovered from Bed Rz-9; latest Permian conodonts, *Neogondolella changxingensis* Wang and Wang, *N. subcarinata* Sweet, and a latest Permian to earliest Triassic conodont, *Hindeodus typicalis* (Sweet) were recovered from Bed Rz-4; the natural
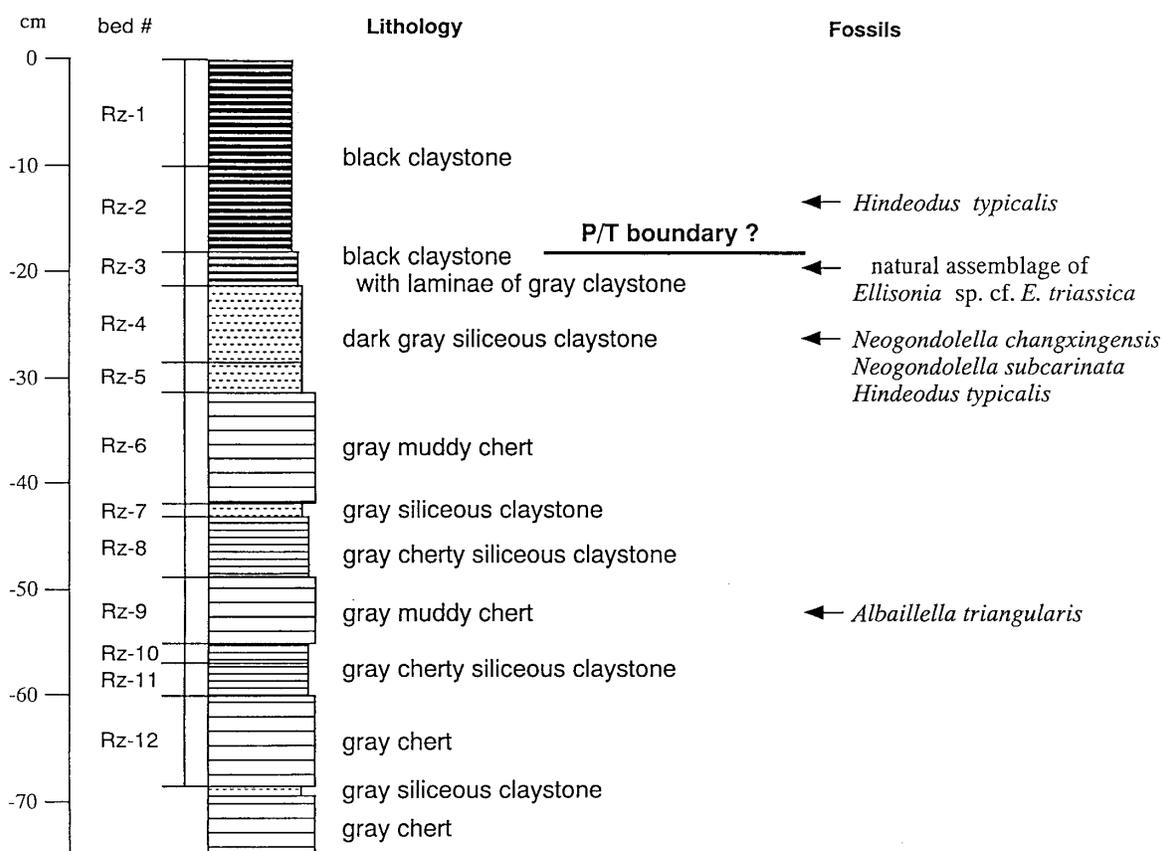
Figure 3. The Permian to Triassic sequence and horizons of the natural assemblage of *Ellisonia* sp. cf. *E. triassica* Müller, 1956 and other fossils in the Nabejiriyama section.

assemblage of *Ellisonia* sp. cf. *E. triassica* was discovered from Bed Rz-3; and *Hindeodus typicalis* was obtained from Bed Rz-2 (Figure 3).
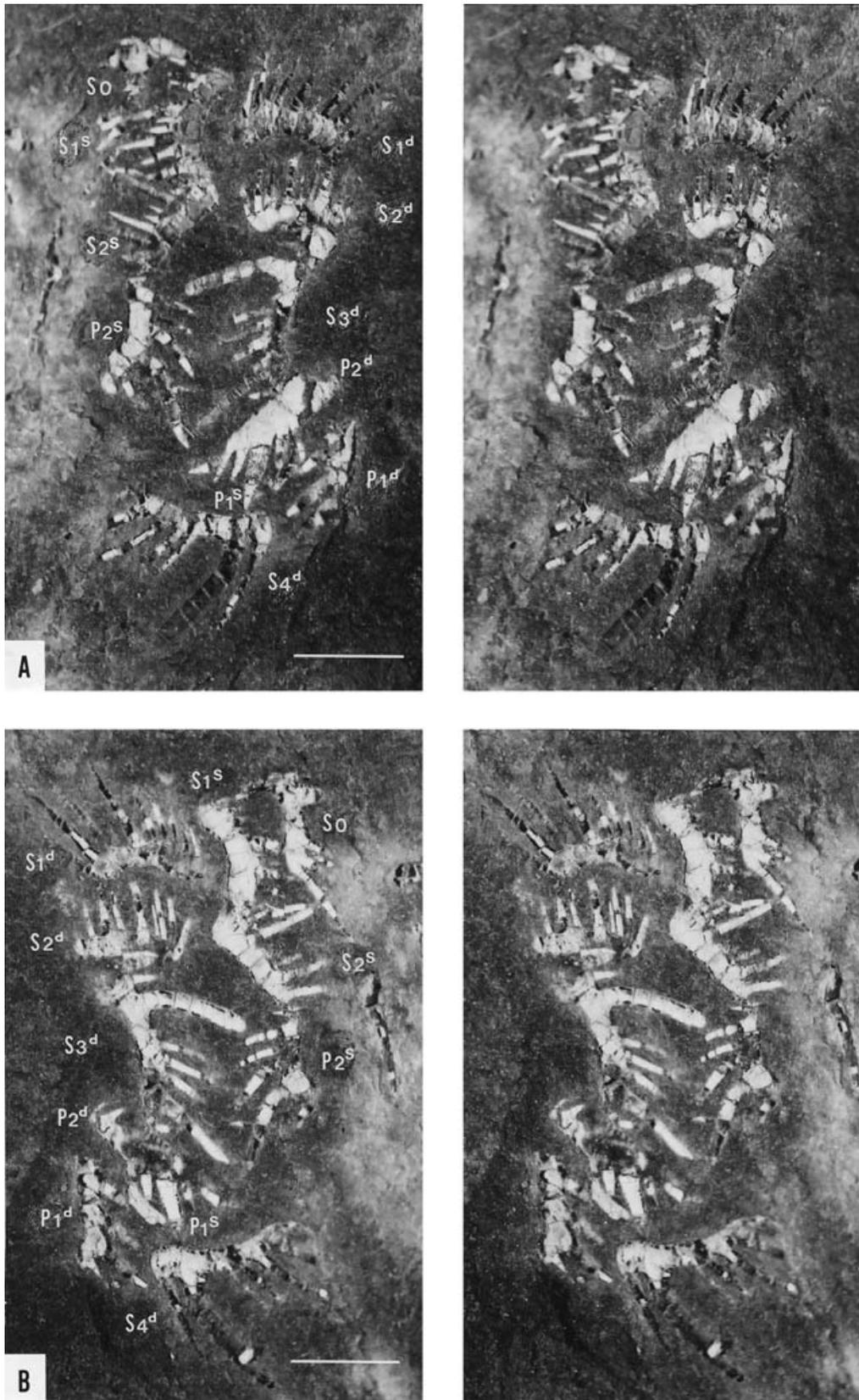
Our micropaleontological data are not entirely sufficient to settle a more detailed geochronology of this section, however, a previous study by Yamakita *et al.* (1999) causes us to conclude that this section apparently includes the Permian-Triassic boundary beds.

Yamakita *et al.* (1999) intensively studied a sequence of the uppermost Permian to the lowermost Triassic in the Ubara section of the Hukuchiyama area, in the Tamba Belt. The stratigraphic succession of the Ubara section exhibits close similarity to that of the present section. The micropaleontological evidence found in the Ubara section is noteworthy. In the Ubara section, *Hindeodus parvus* Kozur and Pjatakova was recovered from black claystone that is lithologically identical with Bed Rz-2 of the Nabejiriyama section. The gray siliceous claystone in the Ubara section, which is a correlative of Bed Rz-4 in the Nabejiriyama section, yielded a latest Permian conodont, *Neogondolella changxingensis*.

The first occurrence of *Hindeodus parvus* defines the base of the Triassic (Paull and Paull, 1994; Orchard *et al.*, 1994; Yin *et al.*, 1996). Thus, Bed Rz-2 is correlated with the Griesbachian. It is not certain, however, whether the Permian and Triassic boundary should be placed at the base of Bed Rz-2 or Bed Rz-3, because paleontological data are not sufficient to define the age of Bed Rz-3. We provisionally interpret that the base of the Triassic coincides with the base of Bed Rz-2, and the natural assemblage of *Ellisonia* sp. cf. *E. triassica* occurs immediately below the Permian-Triassic boundary.

Components of the natural assemblage

Conodonts are generally rare in the claystone of Bed Rz-3. Individual elements are found sporadically scattered on the bedding plane surface and seem to be restricted to a specific bedding plane. The only natural assemblage recovered is not well preserved due to dissolution of the surface of elements and development of fine fractures (Figure 4).
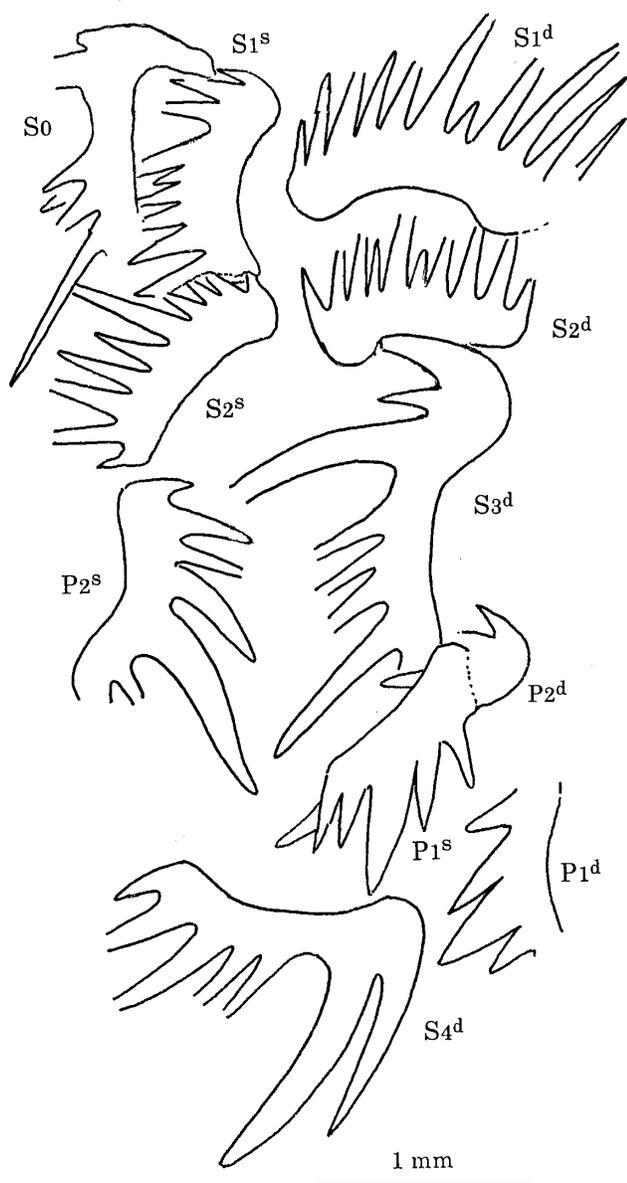
Figure 5. Drawing of the natural assemblage of *Ellisonia* sp. cf. *E. triassica* Müller, 1956; part (sample no. MPC02627).

relationships with the ozarkodinid apparatuses (e.g., Aldridge *et al.*, 1987; Purnell and Donoghue, 1998).

Of the eleven elements on the bedding plane, eight elements (apparatus nomenclature of Purnell *et al.*, 2000): the triramous S_0, extensiform digyrate S_1^s (sinistral S_1 element), extensiform digyrate S_2^s, bipennate S_3^d (dextral S_3 element), angulate P_2^s and P_2^d, and the angulate P_1^s and P_1^d, are aligned almost parallel to each other, but others (the S_1^d, S_2^d, and bipennate S_4^d elements) make an angle of about 90° with the eight elements. The S_0 element covers the S_1^s element. The anterior part of the S_2^s element is overlain by the posterior part of the S_1^s element. The S_2^d element is overlain at the tips of the denticles by the process of the S_1^d element. The P_2 elements overlie a part of the S_3^d element. The P_1 elements lie posterior of the S_3^d element and the P_1^s element overlies the P_2^d element. The S_4^d element lies posterior of the P_1 elements.

The S_3^s and S_4^s elements are most likely to lie underneath on the left side of the S_2^s and P_2^s elements. A part of the denticles and cusp of the elements are observed in those positions. The M elements are not observed. They are most likely to lie beneath on the left side of the S_0 element and on the right side of the S_1^d element.

The S_0, S_2, S_3, and S_4 elements of the natural assemblage are morphologically similar to *Ellisonia triassica*, *Lonchodina triassica*, *Hindeodella nevadensis*, and *H. raridenticulata* all first described by Müller (1956). These species were regarded the elements of the *Ellisonia triassica* apparatus by Sweet (1970, 1981, 1988). Furthermore, the P_1 and P_2 elements of the natural assemblage are also similar to the Pa and Pb elements of the *E. triassica* apparatus reconstructed from discrete elements (Figure 7). *Ellisonia triassica* and other species of *Ellisonia* previously described are reviewed in the following chapters.

Review of *Ellisonia triassica* Müller

Ellisonia triassica was proposed as the type species of *Ellisonia* by Müller (1956) for the alate S_0 element from the *Meekoceras* Zone of Smithian age in Nevada. Sweet (1970) reconstructed *E. triassica* as a multielement apparatus composed of four kinds of elements, U (*E. triassica*), LA (*Hibbardella subsymmetrica* Müller), LF (*Lonchodina triassica*), and LB (*Hindeodella nevadensis* and *H. raridenticulata*), based on the

The original alignment and the counterpart of the natural assemblage can be observed on part (MPC02627, Micropaleontology Collection, National Science Museum, Tokyo) and counterpart (MPC02628) (Figures 4A and 4B), respectively. Preservation of the natural assemblage, with weak postmortem disruption, enables direct comparison of element arrangement and recognition of homologous

← Figure 4. Stereo-pairs of the natural assemblage of *Ellisonia* sp. cf. *E. triassica* Müller, 1956. **A**. Part (sample no. MPC02627), **B**. Counterpart (sample no. MPC02628). Scale bar indicates 1 mm.
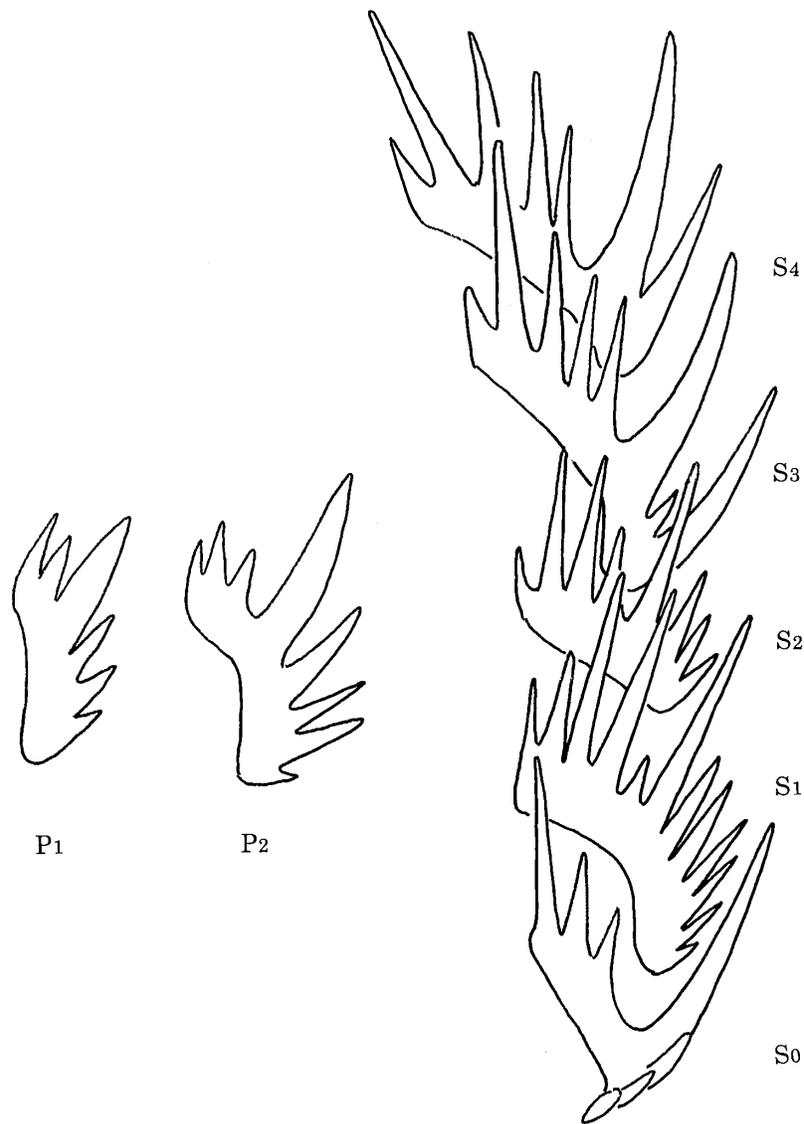
Figure 6. Partial reconstruction of the apparatus of *Ellisonia* sp. cf. *E. triassica* Müller, 1956 showing the position and arrangement of the S_0 and sinistral S and P series elements. S elements are shown in rostral-caudal axis view. P_1 and P_2 elements are shown in caudal view. The arrangement of the P_1 and P_2 elements is based on Carboniferous ozarkodinid apparatuses (e.g., Aldridge *et al.*, 1987). The terminology "rostral-caudal axis" is after Purnell and Donoghue (1998).

material from the uppermost Permian and Lower Triassic of Pakistan. Sweet (1981, 1988) subsequently concluded that the apparatus of *E. triassica* was composed of breviform digyrate M (LA element of Sweet, 1970), alate Sa (U), extensiform digyrate Sb (LF), and bipennate Sc (LB), breviform digyrate Pb, and angulate Pa elements.

Swift and Aldridge (1982) reported a prioniodinan (Pb) element of *E.* cf. *triassica* from the Upper Permian of North Yorkshire.

Von Bitter and Merrill (1983) identified three kinds of elements of *E. triassica*, Tr (Sa), Pl (M), and Hi (Sc), based on the material from the *Meekoceras* Zone in Idaho. Von Bitter and Merrill (1985) emphasized that *E. triassica* is a ramiform – only apparatus.

T. Koike, in this study, examined the apparatus of *Ellisonia triassica* recovered from the limestone core sample at 12.70–12.90 m depth in the Taho Formation. These conodont elements include *Neospathodus bransoni* (Müller), *N. conservativus* (Müller), *N. discretus* (Müller), and *N. dieneri* Sweet. The former three *Neospathodus* species are accompanied by *E. triassica* in the *Meekoceras* Zone conodont faunule from Nevada described by Müller (1956). Therefore,
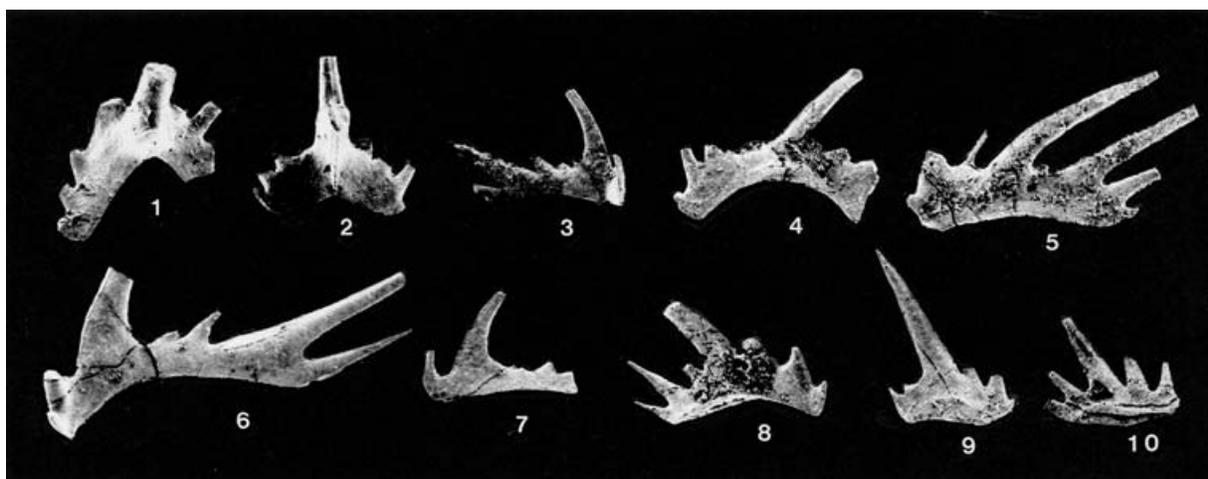
Figure 7. *Ellisonia triassica* Müller, 1956 from the Taho Formation, Shirokawa-cho, Higashiuwa-gun, Ehime Prefecture. All × 60. From carbonate in borehole at 12.70–12.90 m. **1**. M element, MPC02629. **2**, **3**. Sa (S_0) elements, MPC02630, 02631. **4**. Sb_1 (S_1) element, MPC02632. **5**. Sb_2 (S_2) element, MPC02633. **6**. Sc_1 (S_3) element, MPC02634. **7**. Sc_2 (S_4) element, MPC02635. **8**. Pb (P_2) element, MPC02636. **9**, **10**. Pa (P_1) elements, MPC02637, 02638.

the conodont faunule in drill core of Taho has almost the same element composition as that reported by Müller (1956).

As a result of the examination of the Taho conodont faunule, the following eight kinds of elements are distinguished for the *E. triassica* apparatus, M, Sa, Sb_1, Sb_2, Sc_1, Sc_2, Pa, and Pb (Figure 7). Of these elements, M, Sa, Sb, and $Sc_{1/2}$ are identical to M, Sa, Sb and Sc of *E. triassica* of Sweet (1981, 1988), respectively. Pa elements are rather different in morphology from the Pa element of *E. triassica* illustrated by Sweet (1981, 1988). Pb elements are ozarkodiniform angulate and significantly different in morphology from the breviform digyrate Pb element of *E. triassica* of Sweet (1981, 1988).

Review of Triassic species of *Ellisonia*

Koike (1990) attempted to reconstruct *E. triassica* on the basis of conodont elements from three levels of the Taho Formation and identified three kinds of elements, M (= Pb element of Koike, 1990), Sa, and Sc elements. Of the three sampled levels, levels 03 and 1113 are about 7 m below the boundary of the Smithian and Spathian and are almost identical to the conodont elements from the drill core sample. Besides the M, Sa, and Sc elements, Sb_1, Sb_2, Pa, and Pb of *E. triassica* were recently recognized in levels 03 and 1113.

Of the three sampled levels, level 103A is just below the Smithian-Spathian boundary and the conodont composition is quite different from those of levels 03,

1113, and the drill core sample. Level 103A yielded numerous elements of *Ellisonia* sp. and only a few Pa elements of *Neospathodus* sp. All elements of *E. triassica* illustrated by Koike (1990) were from level 103A. Elements illustrated on the figures of Koike (1990) and Figure 8 of this paper demonstrate that the elements identified as Sa, M and Sc are similar to those of *E. triassica* described by Müller (1956) and Sweet (1970). The Sb_1, Sb_2, Pa, and Pb elements are, however, significantly different in morphology from those of *E. triassica* (Figure 7) from Taho. The Sb_1 elements are extensiform digyrate, with a high and intensely curved unit. The Sb_2 elements are extensiform digyrate, with a high unit. The Pa and Pb elements are angulate, without a distinct cusp. Thus, the ellisonid species at level 103A should be removed from *E. triassica* and tentatively referred to *E.* sp. aff. *E. triassica* Müller in this paper (Figure 8).

A Smithian *Ellisonia* species, *E. agordina* proposed by Perri and Andraghetti (1987), has six kinds of elements, M, Sa, Sb, Sc, Pa, and Pb. These elements are characterized by having a relatively short unit with an inflated rib and blunt discrete denticles. The six kinds of elements of *E. agordina* are easily distinguished from those of *E. triassica*. It is noteworthy, however, that the individual elements of *E. agordina* and *E. triassica* are basically similar in morphology.

Consequently, the apparatuses of Triassic *Ellisonia* are composed of the following eight kinds of elements: breviform digyrate M, triramous Sa, intensely arched or curved extensiform digyrate Sb_1, gently arched extensiform digyrate Sb_2, bipennate Sc_1 and Sc_2, and
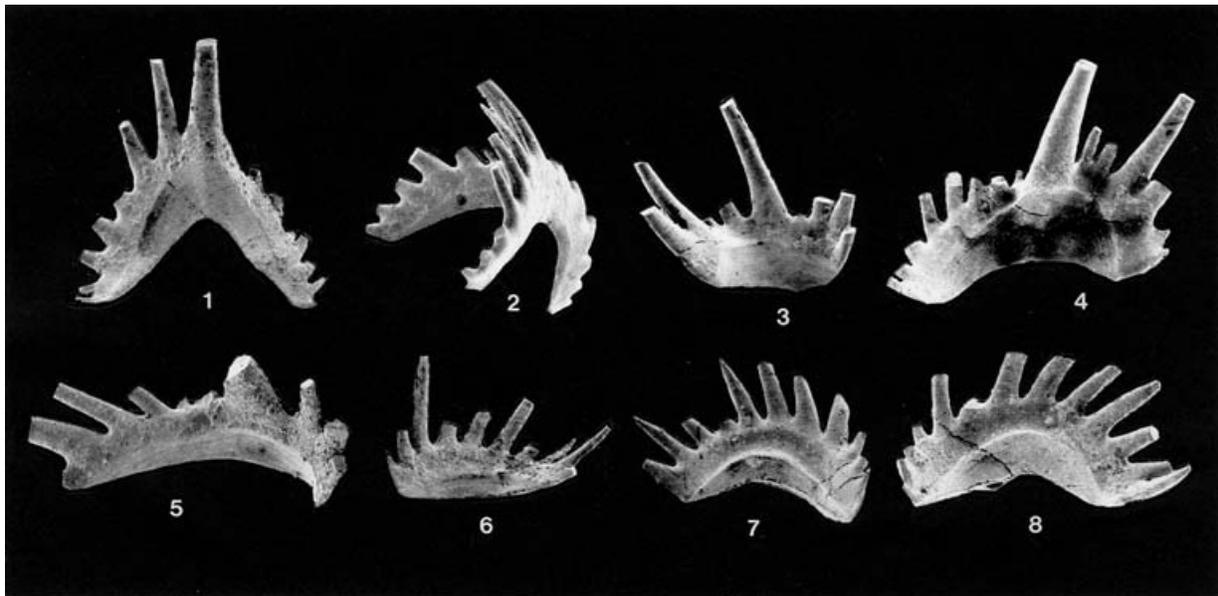
Figure 8. *Ellisonia* sp. aff. *E. triassica* Müller, 1956 from the Taho Formation, Shirokawa-cho, Higashiuwa-gun, Ehime Prefecture. All × 50. From carbonate at level 1612A just below the boundary of the Smithian and Spathian. **1**. M element, MPC02639. **2**. Sa (S_0) element, MPC02640. **3**. Sb_1 (S_1) element, MPC02641. **4**. Sb_2 (S_2) element, MPC02642. **5**. $Sc_{1/2}$ ($S_{3/4}$) element, MPC02643. **6**. Pb (P_2) element, MPC02644. **7**, **8**. Pa (P_1) elements, MPC02645, 02646.

angulate Pa and Pb. The apparatus structure of Triassic species of *Ellisonia* is comparable to the standard 15-element plan of ozarkodinids (Purnell and Donoghue, 1998; Purnell *et al.*, 2000), prioniodinids (Purnell, 1993), and gondolellids (Rieber, 1980; von Bitter and Merrill, 1998; Orchard and Rieber, 1999).

Carboniferous and Permian *Ellisonia*

Von Bitter and Merrill (1983) reconstructed Pennsylvanian species of *Ellisonia*, *E. conflexa* (Ellison) and *E. latilaminata* von Bitter and Merrill, and identified five kinds of elements, Oz (Pb), Ne (M), Tr (Sa), Pl, and Hi (Sc), in the former, and two kinds of elements, Tr (Sa) and Hi (Sc) in the latter. *Ellisonia conflexa* and *E. latilaminata* were distinguished from each other based on the following diagnosis: the former possesses a well defined basal cavity and the latter exhibits a strongly everted basal cavity in individual elements (von Bitter and Merrill, 1983).

The elements of *E. triassica* also carry an everted basal cavity, and those of the present natural assemblage *E.* sp. cf. *E. triassica* probably possess an everted basal cavity. Thus, the features of the basal cavity are different in *E. conflexa* and *E. triassica*.

The Tr (Sa), Hi (Sc), and Oz (Pb) elements of *E. conflexa* are, however, basically similar in morphology to the Sa (S_0), $Sc_{1/2}$ ($S_{3/4}$), and Pb (P_2) elements of *E.*

triassica, and *E.* cf. *E. triassica*. Furthermore, the Tr (Sa) and Hi (Sc) elements of *E. latilaminata* are also similar to the Sa (S_0) and $Sc_{1/2}$ ($S_{3/4}$) elements of *E. triassica* and *E.* sp. cf. *E. triassica*.

Orchard (1984) reported *E. conflexa* of Early Permian age from the Harper Ranch beds of southern British Columbia. He suggested that Permian *Ellisonia* sp. A of von Bitter and Merrill (1983) could be identical to *E. conflexa* and that Pennsylvanian *E. conflexa* ranged into the Early Permian.

Grayson (1990) reported *E. latilaminata* from the Middle Carboniferous in the Canyon Creek, Oklahoma. He identified six kinds of elements in *E. latilaminata*, M, Sa, Sb, Sc, Pa, and Pb. The Pa and Pb elements illustrated by him are of angulate type and basically similar in morphology to the Pa (P_1) and Pb (P_2) elements of *E. triassica* from the Taho Formation and *E.* sp. cf. *E. triassica*, respectively.

Swift and Aldridge (1982) reported *Ellisonia* spp. from the Upper Permian of North Yorkshire. Among the elements of *E.* spp., Pb (pl. 90, fig. 3) is similar to P_1 (Pb) elements of *E. triassica* from the Taho Formation and *E.* sp. cf. *E. triassica*. The M elements (pl. 90, figs. 8 and 14) differ from M of *E. triassica* and are similar to M of *E. conflexa*. As stated earlier, the prioniodinan element of *E. triassica* of Swift and Aldridge (1982) from the Upper Permian is identical to the Pb (P_2) element of *E. triassica* and *E.* sp. cf. *E.*

triassica.

Von Bitter and Merrill (1983) illustrated some elements of Late Permian ellisonids from Bororga in Russia and the Butte Mountains in Nevada. The elements shown by von Bitter and Merrill (1983) are Pl, Tr (Sa), and Hi (Sc) (Hi1 and Hi2). The Pl, Tr, and Hi1 elements are similar to M, Sa, and Sc1/2 elements of *E. triassica*, respectively.

As mentioned above, some elements of Late Permian ellisonids: Pb element (P2) of *Ellisonia triassica* and *E.* spp. of Swift and Aldridge (1982); Sa (S0) and Sc1/2 (S3/4) of *E.* sp. of von Bitter and Merrill (1983), are similar to those of the latest Permian natural assemblage from the Nabejiriyama section. Owing to a lack of information on the S1, S2, and P1 elements of the Late Permian ellisonids, it is difficult to judge how closely they relate with the natural assemblage.

Taxonomic relationships of the natural assemblage

The S0, S2, and S3/4 elements of the latest Permian natural assemblage from the Nabejiriyama section are identical to the Sa, Sb2, and Sc elements of Smithian *E. triassica* of Sweet (1981, 1988). Furthermore, the P1, P2, and S1 elements of the natural assemblage are very similar to the Pa, Pb, and Sb1 elements of Smithian *E. triassica* from the Taho Formation. A morphologic difference among them is recognized only in profile and size of P1 elements. It is not certain whether the difference is within the range of morphological variation of Pa elements of *E. triassica* or not.

Unfortunately, the M element that is one of the characteristic elements by which to distinguish *E. triassica* from Pennsylvanian and Permian species of *Ellisonia* [e.g., *E. conflexa* (Ellison)] is not observed in the present natural assemblage. Thus, the natural assemblage is referred to *E.* sp. cf. *E. triassica* Müller herein.

Sweet (1988) emphasized that the *Ellisonia* apparatus is characterized by the possession of "enantiognathiform" breviform digyrate elements in the Pb (P2) position. As mentioned above, the natural assemblage *E.* sp. cf. *E. triassica* and other species of *Ellisonia* based on discrete elements, however, have no "enantiganthiform" element in any position. Typical "enantiognathiform" elements occupy the S1 (Sb1) position in the Triassic natural assemblage of *Neogondolella* sp. (Rieber, 1980; Orchard and Rieber, 1999). Consequently, Lower Triassic *Ellisonia delicatula*, *E. gradata*, *E. robusta*, and *E. torta* proposed by Sweet (1970) as multielement species with "enantiognathiform" elements are probably gondolellids or neospathodids belonging to the Gondolellidae.

The family Ellisonidae Clark contains six genera including *Ellisonia*, which are charactrerized by angulate or digyrate elements in the Pa positions (Sweet, 1981, 1988). Permian *Merrillina* Kozur and Mock includes six or seven kinds of elements (Sweet, 1988; Swift and Aldridge, 1985). The Pa elements are basically segminate in structure. The M, Sb, and Pb elements are, however, closely similar to the M, S2, and P2 elements of *E. triassica* and *E.* sp. cf. *E. triassic*. Although the triramous Sa and bipennate Sc elements have fused denticles, they resemble the S0 and S4 elements of the *Ellisonia* species. The morphologic similarity demonstrates a close phylogenetic relationship between *Merrillina* and *Ellisonia*.

The Permian *Sweetina* Wardlaw and Collinson (Sweet, 1988) and the Early Triassic *Hadrodontina* Staesche (Staesche, 1964; Sweet, 1981, 1988; Perri, 1991), *Furnishius* Clark (Sweet, 1981, 1988), and *Pachycladina* Staesche (Staesche, 1964; Sweet, 1981, 1988; Kolar-Jurkovsek and Jurkovsek, 1996) contain extensiform digyrate Sb elements somewhat similar to the S1 or S2 elements of *Ellisonia*. Other elements in these genera are, however, quite different from those of *Ellisonia*; the Sa elements are biramous in structure in *Sweetina*, *Hadrodontina*, *Furnishius*, and *Pachycladina*; the Pb (sensu Sweet, 1988) elements are angulate in structure with a secondary row in *Hadrodontina* and are triradiate extensiform digyrate in structure in *Furnishius* and *Sweetina*.

Sweet (1988) assumed the origin of *Ellisonia* to be Mississippian *Idioprioniodus* Gunnell or a closely related genus, based on the occurrence of "enantiognathiform" elements in the Pb position. As mentioned above, "enantiognathiform" elements are not present in any position in the *Ellisonia* apparatus. Almost all kinds of elements in the *Idioprioniodus* apparatus (Baesemann, 1973; Merrill and Merrill, 1974; Sweet, 1988; Rexroad, 1993) are quite different in morphology from those of *Ellisonia*. In *Idioprioniodus*, the Pa elements are digyrate pectiniform without any posterior process and the M elements are dolabrate. Furthermore, the processes are very short in S elements. Thus, it is difficult to regard *Idioprioniodus* as an ancestral taxon of *Ellisonia*. Von Bitter and Merrill (1998) considered that *Idioprioniodus* is a likely ancestor of the Pennsylvanian *Gondolella*, based on their recognition of an evolutionary trend of reduction of the posterior process in the anguliplanate Pa elements.

The genus *Ellisonia* has been assigned to the order Prioniodinida Sweet that is characterized by digyrate elements in the P region (Sweet, 1988; Sweet and Donoghue, 2001). The well preserved apparatus of Upper Devonian *Oulodus* Branson and Mehl, recov-

ered from the gut region of a palaeoniscoid fish, comprises a single unpaired triramous Sa, single pairs of dolabrate M, digyrate Sb, Sd, Pa, and Pb, and two pairs of bipennate Sc elements (Nicoll, 1977, 1985). The Sb, Sd, Sc, Pa, and Pb elements have considerable similarity to the S_2, S_1, S_4, P_1, and P_2 elements of *E.* sp. cf. *E. triassica* and *E. triassica*, respectively.

The complete apparatus of Upper Mississippian *Kladognathus* Rexroad, recovered from the midgut of *Typhloesus wellsi* (Melton and Scott), has a pair of dolabrate M, one triramous Sa, two pairs of bipennate Sb and Sc, a pair of bipennate (modified tertiopedate) Pa, and a pair of bipennate Pb elements (Purnell, 1993). All of the elements are markedly different in morphology from those of *Ellisonia*.

The order Ozarkodinida is distinguished from the order Prioniodinida by the possession of carminate and angulate elements or their platformed analogues in P positions (Sweet, 1988; Sweet and Donoghue, 2001). Some species referring to the order Ozarkodinida contain elements similar to those of *Ellisonia*.

Silurian *Ozarkodina pirata* reconstructed by Uyeno and Barnes (1983) based on isolated elements is composed of dolabrate M, biramous Sa, extensiform digyrate Sa-b and Sb, bipennate Sc, angulate P_1 and P_2 elements. Of the seven elements, Sa-b, Sb, Sc, Pa, and Pb are similar to S_1, S_2, S_4, P_1, and P_2 elements of *E.* sp. cf. *E. triassica*, respectively.

Silurian *Ctenognathodus murchisoni* (Pander) reconstructed by Aldridge and Jeppson (1984) has breviform digyrate M, biramous Sa, arched digyrate Sb, bipennate Sc, carminate Pa, and angulate Pb elements. The Sb, Sc, and Pb elements are similar to the S_1, S_4, and P_2 elements of *E.* sp. cf. *E. triassica*, respectively.

Thus, the *E.* sp. cf. *E. triassica* and *E. triassica* apparatuses are more closely related to some taxa in the Ozarkodinida than they are to other Prioniodinida. The "digyrate" Pa elements in the Prioniodinida demonstrate various morphologic characteristics: extensiform digyrate "prioniodiniform" structure (*e.g.*, *Oulodus*); triangulate "ozarkodiniform" (*e.g.*, *Ellisonia*, *Pachycladina*), triradiate extensiform digyrate structure (*e.g.*, *Sweetina and Furnishius*); bipennate (modified tertiopedate) structure (*e.g.*, *Kladognathus*); segminate structure (*e.g.*, *Merrillina*), and segminate-like digyrate structure (*e.g.*, *Idioprioniodus*). These "digyrate" Pa elements in the Prioniodinida presumably do not necessarily represent monophyletic taxa.

Sweet and Donoghue (2001) pointed out that "some prioniodontides, a group united on possession in the P region of pastinate elements or their platformed equivalents, are more closely related to ozarkodinides than they are to other prioniodontides, that is, they share a common ancestor with ozarkodinides that they do not share with other prioniodontides."

The understanding of the phylogenic relationships between *Ellisonia* and other taxa will progress, if evolutional histories are clarified among various shaped digyrate Pa (P_1) elements; distinction is established between Pa (P_1) and Pb (P_2) elements; division of Sb elements into Sb_1 (S_1) and Sb_2 (S_2) ones is accomplished; and assessment of ramiform elements is defined at several taxonomic levels.

The genus *Ellisonia* is assigned to the order Prioniodinida herein, following the proposal of Sweet (1988), and Sweet and Donoghue (2001).

Systematic paleontology

Phylum Chordata
Subphylum Vertebrata
Class Conodonta
Subclass Conodonti
Order Prioniodinida
Family Ellisonidae
Genus **Ellisonia** Müller, 1956

Type species.—*Ellisonia triassica* Müller, 1956

Ellisonia sp. cf. **E. triassica** Müller, 1956

Figures 4, 5

Material.—A natural assemblage consisting of part and counterpart, MPC02627 and MPC02628, respectively, from Bed Rz-3 of the Nabejiriyama section in the Nishizaka Unit. They are deposited at the Department of Geology and Paleontology, National Science Museum, Tokyo.

Description.—The natural assemblage is composed of 11 elements, single pairs of angulate P_1 and P_2, a single unpaired symmetrical S_0, a pair of deeply arched extensiform digyrate S_1, a pair of gently arched extensiform digyrate S_2, and bipennate dextral S_3 and S_4 elements. The sinistral S_3 and S_4 and a pair of M elements are not observed. All elements possess large and blunt processes and bear discrete denticles.

P_1 element: Unit about 850 µm long. Anterior process relatively long and has 3 or 4 discrete denticles. Denticles tend to increase in length and inclination toward posterior. Posterior process short and carries 2 denticles. Denticle just before cusp is about 470 µm long. Cusp is about 600 µm long and blunt.

P_2 element: Anterior process about 590 µm long and carries 4 discrete denticles. Denticles relatively long, and tend to increase posteriorly in length and inclination. Posterior process about 400 µm long and

bends gently inward, and bears 2 or 3 discrete denticles. Cusp is about 890 μm long and about twice as long as denticle just before cusp.

S_0 element: Lateral and posterior processes meet at an angle of about 80 degrees in lateral view. Lateral processes stout and probably carry 2 or 3 denticles on each. Posterior process is about 690 μm long and bears 3 discrete denticles. Denticle of anterior first is short and highly isolated from cusp. Denticle on distal end is as long as posterior process. Cusp is just behind a small denticle on lateral process and probably very large.

S_1 element: Unit is deeply arched. Anterior and posterior processes about 540 μm and 560 μm long, respectively, and carry 5 denticles. Denticles on both processes gently curve inward and increase in length and inclination toward posterior. Cusp is long and slender.

S_2 element: Unit is gently arched. Anterior and posterior processes about 280 μm and 560 μm long, and carry 4 and 5 discrete denticles, respectively. Denticles on both processes tend to increase posteriorly in length and inclination. Cusp is slender and moderate in size.

S_3 element: Antero-posterior process stout and large. Anterior process more than 490 μm long, extends downward, curves strongly inward, and carries 2 or more discrete denticles. Posterior process about 1000 μm long and has 5 discrete denticles. Denticles tend to increase posteriorly in inclination and length, and about 780 μm long in anterior fourth. Cusp is more than 900 μm long.

S_4 element: Unit large and gently arched. Anterior process about 370 μm long, curves slightly inward and bears a large denticle as long as 770 μm. Posterior process about 950 μm long and bears 5 discrete denticles. Denticles long in anterior third and fourth. Cusp is about 1210 μm long.

Remarks: The S_0 element is very similar to *Ellisonia triassica*, the type species of the genus *Ellisonia*, described by Müller (1956). It is also similar to the U and Sa elements of Sweet (1970, 1981). The S_1 elements are similar to Sb_1 of *E. triassica* from the Taho Formation. The S_2 elements are identical to *Lonchodina triassica* described by Müller (1956) and the Sb element illustrated by Sweet (fig. 101-3b, 1981). The S_3 and S_4 elements are similar to each other but are apparently different in morphology of the anterior process and denticulation. The S_3 and S_4 elements are probably identical to *Hindeodella nevadensis* Müller and *H. raridenticulata* Müller described by Müller (1956), respectively. The P_2 elements are similar to the LF element of *E. triassica* illustrated by Sweet

(pl. 5, fig. 20, 1970), but significantly different in morphology from the breviform digyrate Pb element of *E. triassica* illustrated by Sweet (1981, 1988). The P_1 elements are rather different in morphology from the Pa element of *E. triassica* illustrated by Sweet (1981, 1988) in having a long cusp and 2 to 4 discrete denticles on each short anterior and posterior process. The P_1 elements are morphologically different from the Pa elements of *E. triassica* from the Taho Formation in possessing a relatively short cusp and a very large unit. The morphologic difference may taxonomically distinguish this natural assemblage from *E. triassica* to the extent that it will be assigned to a new species of *Ellisonia*. On the basis of much material, further study on the morphologic variation within Pa elements of *E. triassica* is required to settle the conclution.

References

Aldridge, R. J. and Jeppson, L., 1984: Ecological specialists among Silurian conodonts. *In*, Basset, M. G. and Lawson, J. D. *eds.*, *Autecology of Silurian organisms. Special Papers in Palaeontology*, no. 32, p. 141–149. Palaeontological Association, Oxford.

Aldridge, R. J., Smith, M. P., Norby, R. D. and Briggs, D. E. G., 1987: The architecture and function of Carboniferous polygnathacean conodont apparatuses. *In*, Aldridge, R. J. *ed.*, *Palaeontology of Conodonts. British Micropalaeontological Society Series*, p. 63–75. Ellis Horwood, Chichester.

Baesemann, J. F., 1973: Missourian (Upper Pennsylvanian) conodonts of northeastern Kansas. *Journal of Paleontology*, vol. 47, no. 4, p. 689–710.

Grayson, Jr., R. C., 1990: Canyon Creek: A significant exposure of a predominantly mudrock succession recording essentially continuous deposition from the Late Devonian through the Middle Pennsylvanian. *Oklahoma Geological Survey Guidebook* 27, p. 85–114.

Ishiga, H., Kito, T. and Imoto, N., 1982a: Permian radiolarian biostratigraphy. *News of Osaka Micropaleontologists, Special Volume*, no. 5, p. 17–26.

Ishiga, H., Kito, T. and Imoto, N., 1982b: Middle Permian

radiolarian assemblages in the Tamba district and an ad-
jacent area, Southwest Japan. *Earth Science (Chikyu Ka-gaku)*, vol. 36, no. 5, p. 272–281.

Koike, T., 1990: The conodont apparatus of *Ellisonia triassica* Müller. *Science Reports of the Yokohama National University, Sec. 2*, no. 37, p. 35–46.

Kolar-Jurkovsek, T. and Jurkovsek, B., 1996: Contribution to the knowledge of the Lower Triassic conodont fauna in Slovenia. *Razprave IV. Razreda SAZU*, vol. 37, no. 1, p. 3–21.

Kuwahara, K., 1997: Upper Permian radiolarian bio-stratigraphy. Abundance Zones of *Albaillella. News of Osaka Micropaleontologists, Special Volume*, no. 10, p. 55–75.

Kuwahara, K., Yao, A. and Yamakita, S., 1998: Reexamination of Upper Permian radiolarian biostratigraphy. *Earth Science (Chikyu Kagaku)*, vol. 52, no. 5, p. 391–404.

Merrill, G. K. and Merrill, S. M., 1974: Pennsylvanian non-platform conodonts. IIa: The dimorphic apparatus of *Idioprioniodus. Geologica et Palaeontologica*, vol. 8, p. 119–130.

Miyamura, M., Mimura, K. and Yokoyama, T., 1976: *Geology of the Hikonetobu district. Quadrangle Series, Scale 1:50,000*, Geological Survey of Japan, Tokyo. (*in Japanese with English abstract*)

Müller, K. J., 1956: Triassic conodonts from Nevada. *Journal of Paleontology*, vol. 30, no. 4, p. 818–830.

Nicoll, R. S., 1977: Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Cannig Basin, Western Australia. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics*, vol. 2, p. 217–228.

Nicoll, R. S., 1985: Multielement composition of the conodont species *Polygnathus xylus xylus* Stauffer, 1940 and *Ozarkodina brevis* (Bischoff and Ziegler, 1957) from the Upper Devonian of the Canning Basin, Western Australia. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics*, vol. 9, p. 133–147.

Orchard, M. J., 1984: Early Permian conodonts from the Harper Ranch beds, Kamloops area, southern British Columbia. *Current Research, Part B, Geological Survey of Canada*, Paper 84-1B, p. 207–215.

Orchard, M. J., Nassichuk, W. W. and Rui, L., 1994: Conodonts from the Lower Griesbachian *Otoceras latilobatum* bed of Selong, Tibet and the position of the Permian-Triassic boundary. *In* Embry, A. F., Beauchamp, B. and Glass, D. J., *eds.*, *Pangea: Global Environment and Resources: Canadian Society of Petroleum Geologists*, Memoir 17, p. 823–843.

Orchard, M. J. and Rieber, H., 1999: Multielement *Neogondolella* (Conodonta, upper Permian-middle Triassic). *Bollettino della Società Paleontologica Italiana*, vol. 37, no. 2–3, p. 475–488.

Paull, R. K. and Paull, R. A., 1994: *Hindeodus parvus*; proposed index fossil for the Permian-Triassic boundary. *Lethaia*, vol. 27, p. 271–272.

Perri, M. C. 1991: Conodont biostratigraphy of the Werfen Formation (Lower Triassic), Southern Alps, Italy. *Bollettino della Società Paleontologica Italiana*, vol. 30, no. 1, p. 23–46.

Perri, M. C. and Andraghetti, M., 1987: Permian-Triassic boundary and Early Triassic conodonts from the Southern Alps, Italy. *Rivista Italiana di Paleontologia e di Stratigrafia*, vol. 93, no. 3, p. 291–328.

Purnell, M. A., 1993: The *Kladognathus* apparatus (Conodonta, Carboniferous): Homologies with ozarkodinids, and the prioniodinid Bauplan. *Journal of Paleontology*, vol. 67, no. 5, p. 875–882.

Purnell, M. A. and Donoghue, P. C., 1998: Skeletal architecture, homologies and taphonomy of ozarkodinid conodonts. *Palaeontology*, vol. 41, pt. 1, p. 57–102.

Purnell, M. A., Donoghue, P. C. and Aldridge, R. J., 2000: Orientation and anatomical notation in conodonts. *Journal of Paleontology*, vol. 74, no. 1, p. 113–122.

Rexroad, C. B., 1993: Conodonts from coal balls in the Springfield Coal Member of the Petersburg Formation (Desmoinesian, Pennsylvanian) in southern Indiana. *Proceedings of the Indiana Academy of Science*, vol. 102, p. 83–91.

Rieber, V. H., 1980: Ein Conodonten-cluster aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kt. Tessin/Schweiz). *Annalen des Naturhistorischen Museums in Wien*, vol. 83, p. 265–274.

Staesche, U., 1964: Conodonten aus dem Skyth von Südtirol. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, vol. 119, no. 3, p. 247–306.

Sweet, W. C., 1970: Uppermost Permian and Lower Triassic conodonts of the Salt Range and Trans-Indus Range, West Pakistan, *In* Kummel, B. and Teichert, C. *eds.*, *Stratigraphic Boundary Problems, Permian and Triassic of West Pakistan. The University of Kansas, Department of Geology, Special Publications*, no. 4, p. 207–275. The University of Kansas, Kansas.

Sweet, W. C., 1981: Family Ellisonidae Clark, 1972. *In* Robinson, R. A. *ed.*, *Treatise on Invertebrate Paleontology. Pt. W. Miscellanea, Supplement 2, Conodonta*, p. W152–W154. The Geological Society of America and the University of Kansas Press, Colorado and Kansas.

Sweet, W. C., 1988: The Conodonta. Morphology, Taxonomy, Paleontology, and Evolutionary History of a Long-extinct Animal Phylum. *Oxford Monographs on Geology and Geophysics*, no. 10, 212 p. Clarendon Press, Oxford.

Sweet, W. C. and Donoghue, P. C. J., 2001: Conodonts: Past, present, future. *Journal of Paleontology*, vol. 76, no. 6, p. 1174–1184.

Swift, A. and Aldridge, R. J., 1982: Conodonts from the Upper Permian strata of Nottinghamshire and North Yorkshire. *Palaeontology*, vol. 25, pt. 4, p. 845–856.

Swift, A. and Aldridge, R. J., 1985: Conodonts of the Permian System from Great Britain. *In*, Higgins, A. C. and Austin, R. L. *eds.*, *A stratigraphic index of conodonts*, p. 228–236, British Micropalaeontological Society, Ellis Horwood, Chichester.

Uyeno, T. T. and Barnes, C. R., 1983: Conodonts of the Jupiter and Chicotte Formations (Lower Silurian), Anticasti Island, Quebec. *Bulletin of Geological Survey of Canada*, no. 355, p. 1–49.

Von Bitter, P. H. and Merrill, G. K., 1983: Late Palaeozoic species of *Ellisonia* (Conodontophorida), Evolutionary and palaeoecological significance. *Royal Ontario Museum, Life Sciences Contributions*, no. 136, p. 1–56.

Von Bitter, P. H. and Merrill, G. K., 1985: *Hindeodus, Diplognathodus* and *Ellisonia* revisited – an identity crisis in Permian conodonts. *Geologica et Palaeontologica*, vol. 19, p. 81–96.

Von Bitter, P. H. and Merrill, G. K., 1998: Apparatus composition and structure of the Pennsylvanian conodont genus *Gondolella* based on assemblages from the Desmoinesian

of northwestern Illinois, U.S.A. *Journal of Paleontology*, vol. 72, no. 1, p. 112–132.

Yamagata, T., 2000: Chaotically intermixed Permian oceanic rocks of Mino terrane, northern Suzuka Mountains, central Japan. *The Memoirs of the Geological Society of Japan*, no. 55, *In*, Kimura, K., Kojima, S., Sano, H., and Nakae, S., *eds.*, *Origin and evolution of Jurassic accretionary complexes in Japan*, p. 165–179. The Geological Society of Japan, Tokyo (*in Japanese with English abstract*)

Yamakita, S., Kadota, N., Kato, T., Tada, R., Ogihara, S., Tajika, E. and Hamada, Y., 1999: Confirmation of the Permian/Triassic boundary in deep-sea sedimentary rocks; earliest Triassic conodonts from black carbonaecous claystone of the Ubara section in the Tamba Belt, Southwest Japan. *Journal of the Geological Society of Japan*, vol. 105, no. 12, p. 895–898.

Yao, J., Yao, A. and Kuwahara, K., 2001: Upper Permian biostratigraphic correlation between conodont and radiolarian zones in the Tamba-Mino Terrane, Southwest Japan. *Journal of Geosciences, Osaka City University*, vol. 44, p. 97–119.

Yin, H., Wu, S., Ding, M., Zhang, K., Tong, J., Yang, F. and Lai, X., 1996: The Meishan section, candidate of the Global Stratotype Section and Point of Permian-Triassic boundary. *In*, Yin, H. *ed.*, *The Palaeozoic-Mesozoic boundary, Candidate of the Global Stratotype Section and Point of the Permian-Triassic Boundary*, p. 31–48, *International Geological Correlation Programme, Project no. 359, Correlation of Tethyan, Circum-Pacific and marginal Gondwanan Permo-Triassic*, China University of Geosciences Press, Wuhan.