MORPHOLOGICAL VARIATION IN SPATHIAN CONODONTS
SPATHOCRIODUS COLLINSONI (SOLIEN)
FROM THE Taho LIMESTONE, JAPAN

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ABSTRACT—The early Spathian Spatioicerioidus collinsoni (Solen) is characterized by unique ridgelike denticles on a platform and denticulated postero-lateral processes. This conodont is studied on its ontogenetic development and morphological variation based on a number of specimens from the Taho Limestone in Southwest Japan. The platform is 0.31~0.95 mm long; height to length ratios are 0.25~0.65 and decrease with increasing length; and width to height ratios are 0.22~1.12 and increase with increasing length. On the basis of the denticulation, this conodont can be morphologically subdivided into 3 forms and 7 types. The oral surface is ornamented by a web-like network or a honeycomb-like microstructure which is usually observed on the platform and denticles of pectiniform elements such as gonolekellids. The Spatioicerioidus collinsoni apparatus seems to be unimembrate and composed of a minimum pair of symmetrical elements and two or three pairs of asymmetrical elements.

Key words: Conodont, Spatioicerioidus collinsoni, Spathian, Taho Limestone, Japan, ontogeny, morphology

INTRODUCTION

Sphatocrioidus collinsoni (Solen) is one of the important conodonts as an index of the lower Spathian. This conodont has unique ridgelike denticles on the platform and denticulated postero-lateral processes which are similar to Icriodus ranging in age from the latest Silurian through Devonian.

Clark et al. (1964) first reported the occurrence of this conodont from a Meekoceras-bearing limestone in Nevada and treated it as an unidentified species which has definite affinities with the Devonian genus Icriodus. Sweet et al. (1971) illustrated this conodont obtained from Columbioceras-bearing strata in several sections of Nevada and tentatively named it Neospatriodus sp. G. According to them, this conodont is a marker of Zone 11 of their conodont biostratigraphy and represents the lower Spathian Stage.

Solen (1979) first described this conodont from the Lower Triassic Thaynes Formation of Utah and proposed a new species, Neospatriodus collinsoni.

In addition to the above-mentioned occurrences in the United States of America, this conodont has been known from the following: the Taho Limestone, Japan (Koike, 1979, 1981); the Tirolites cassianus Zone and the Amphistephanites pariasensis Zone in south Primorye, U.S.S.R. (Buryi, 1979; Zakharov and Rybalka, 1987); the Biandanshan Formation in the Anhui Province, Southeast China (Ding, 1983); the Stucky Keep Formation, Spitsbergen in the Svalbard Archipelago, Norway (Clark and Hattleberg, 1983; Hattleberg and Clark, 1984); and Kashimir, India (Budurov et al., 1988).

Fig. 1. Index map showing the location of the Taho Limestone at Tahokamigumi, Shirokawa-cho, Higashi-kuwa-gun, Ehime Prefecture, Southwest Japan.
Recently, Budurov et al. (1987) proposed a new genus, Spatioicriodus, for Neospathodus collinsoni. Their proposal is acceptable because this conodont can be easily distinguished from other forms of Neospathodus by its characteristic morphology.

Although Spatioicriodus collinsoni has been illustrated and described by many authors, any detailed morphological variation in this species has not been described. The author presents herein a result of morphological analysis of this conodont based on a number of specimens.

LOCALITY AND LITHOFACIES

The specimens treated herein were collected from the Tahoe Limestone cropping out at Tahokamigumi, Shirokawa-cho, Higashiwa-gun, Ehime Prefecture, Southwest Japan. The Tahoe Limestone at the type locality is about 40 meters thick and represents a Smithian to Norian interval (Koike, 1979, 1981). Spatioicriodus collinsoni occurs in the horizon about 15 to 17 meters above the base of this limestone.

The Spatioicriodus-bearing limestone is a massive, dark gray micrite and contains a small quantity of glauconite grains. Small gastropods, echinoid spines, fish teeth, thin-shelled pelecypods and smaller foraminifers occur with this conodont. Lithological features of this limestone indicate that the Spatioicriodus-bearing carbonate rock was deposited in a low energy and shallow water environment.

CONODONT FAUNA

Spathioicriodus collinsoni is accompanied by Neospathodus homeri (Bender), N. triangularis (Bender), Kashimirella cf. novaehollandiae (McTavish) and Xanognathus curvatus Sweet in the Tahoe Limestone. The association of Spatioicriodus homeri and N. triangularis together with S. collinsoni is also known from the western United States (Sweet et al., 1971; Solien, 1979), the Primorye region (Sikhote-Alin of U.S.S.R. (Buryi, 1979; Zakharov and Rybalka, 1987), Spitsbergen of Norway (Hatteberg and Clark, 1984) and southeastern China (Ding, 1983; Duan, 1987)).

Kashimirella cf. novaehollandiae from the Tahoe Limestone closely resembles the specimens originally described by McTavish (1973) from Western Australia. In Australia Kashimirella novaehollandiae is, however, associated with Neospathodus waageni Sweet, N. dieneri Sweet, and N. conservativus (Muller), which represent a late Smithian age.

Spathioicriodus collinsoni is accompanied by Platylvilosus asperatus Clark (Solien, 1979) in the Thaynes Formation. Platylvilosus asperatus has never been found from the Tahoe Limestone, but the ancestral form P. costatus (Staesche) occurs in a horizon about 2 meters below the Spatioicriodus-bearing horizon. Neogondolella jubata Sweet occurs in association with S. collinsoni in Utah (Solien, 1979) and Primorye (Buryi, 1979). Conodont elements referable to Neogondolella first occur in a horizon about 5 meters above the...
Spathoicriodus-bearing horizon in the Taho Limestone. The Neogondolella elements from this horizon are generally characterized by numerous high and indiscrete denticles as observed in N. jubata.

MORPHOLOGICAL CHARACTERISTICS AND VARIATION IN SPATHOICRIODUS COLLINSI

The author obtained more than 250 specimens referable to S. collinsi from approximately 20 kg of limestone samples. About 170, 50 and 30 specimens were obtained from locations 9, 10 and 1119, respectively. Spathoicriodus collinsi exhibits remarkable variations in morphology as mentioned below.

Size: A total of 122, 10 and 12 specimens from locations 9, 10 and 1119, respectively, were measured for the length, height, width of a platform, and the width and number of denticles. The measurements are illustrated in Figs. 4 to 8.

The length of a platform ranges from 0.31 to 0.95 mm in specimens from location 9. The length of a platform of specimens from locations 10 and 1119 is 0.40 to 0.95 mm and 0.34 to 0.73 mm, respectively. The range of the length is within the distribution of the length of specimens from location 9 (Fig. 4). The maximum height of a platform ranges from 0.13 to 0.35 mm (Fig. 4).

The maximum width of a platform in the anterior process measures from 0.05 to 0.35 mm (Fig. 5). The maximum width of the postero-lateral processes ranges from 0.55 to 0.72 mm in large forms with strongly expanded processes.

Shape: The platform in the anterior process is generally greatest in width near the posterior one-third or just before the anterior margin of postero-lateral processes and tapers anteriorly. However, the outline of the anterior process is considerably variable, and shows a thin, bladelike or narrow to broad platform. This feature is represented by width-to-length ratios ranging from 0.12 to 0.37. The ratios show no relation with the length of a platform and are independent of each other.

The presence of postero-lateral processes is one of the most important characteristics of this species. The postero-lateral processes are weakly developed in minute forms to a sharp edge surrounding their posterior por-

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Fig. 4. Scatter diagram showing the relationship between length and height of platform in Spathoicriodus collinsi (Solen) from the Taho Limestone. Symbols used are: (1) solid snow flakes refer to specimens from location 1119; (2) solid stars refer to those from location 10; (3) solid circles refer to those from location 9.
tion. In large forms the postero-lateral processes represent a great variety of shape as shown in Figs. 12 and 13. The outline of the processes is round to ellipsoidal or triangular, diamond to quadrangular. In some specimens a denticulated process strongly extends to the lateral, postero-lateral or antero-lateral side.

The platform is highest at the cusp and rather rapidly decreases its height anteriorly and gradually toward the posterior. The height of the platform increases with increasing length. The ratio of height to length varies greatly and ranges from 0.25 to 0.65, but tends to decrease gradually from small to large forms (Fig. 6).

In some specimens the platform in the anterior process curves out laterally. However, most specimens carry an almost straight platform. In case of the former, it is rather easy to determine whether the specimen is a left (sinistral) or right (dextral) element. In case of the latter, the determination is often very difficult.

**Denticulation:** Denticles systematically increase in number with increasing length. As shown in Fig. 7, the number of denticles ranges from 8 to 12 in small-sized forms (0.30 to 0.50 mm long), 11 to 15 in intermediate ones (0.50 to 0.70 mm long), and 12 to 17 in large ones (0.70 to 0.95 mm long). The number of denticles shown in Fig. 7 was counted along the anterior process and the outer postero-lateral process.

Denticles of many specimens are ridgelike or biserial in the central portion, and uniserial and needlelike at the anterior and posterior ends. Denticles of some specimens are laterally compressed, and sharply or bluntly pointed throughout the entire length of a platform.

The ratio of width to height of a platform ranges from
0.22 to 1.22, and shows a tendency to increase with the length increase of a platform (Fig. 8). The ratio is usually low in specimens with tipped denticles though there are some exceptions. The ratio of maximum width of ridgelike denticles to length of a platform ranges from 0.09 to 0.37. There is no tendency to increase in length.

Denticles stand erect and are slightly reclined in the posterior third of the crest. The denticles are fused for about two-thirds of the length, but in large forms they are fused for most of the length.

The cusp is present above the basal cavity or at a slightly anterior portion. It is not distinct in some specimens because it is not always larger than other denticles. The cusp is usually followed by shorter denticles. In small forms the denticles number 2 or 3. In some large specimens they attain 5 to 7. However, there is no tendency for the denticles to increase in number with increasing length of a platform.

The carina is almost straight in some specimens. In most specimens it twists postero-laterally behind the cusp at angles larger than 90°. As mentioned previously, the anterior process is almost straight and symmetrical in most specimens. Thus, it is difficult to indicate the direction of the twisted carina. In a small number of specimens, which possess an asymmetrical anterior process, the posterior carina projects outward.

In many specimens short denticles occur on the inner postero-lateral process. The denticles attain 5 to 6, and sometimes much more on the outer postero-lateral process. The row of denticles usually begins from the point where the anterior carina is out-laterally twisted, and extends toward the postero-lateral to antero-lateral side. The denticle rows on the inner and outer postero-lateral processes are brachiated off at an angle of from 60° to 180°.

The inner lateral denticle row of a specimen at hand is situated anteriorly far apart from the outer lateral denticle row (Fig. 12-52). In another specimen, nodose denticles sporadically stand at the center or near the lateral margin of postero-lateral processes (Fig. 12-50). The denticles on the outer and inner postero-lateral processes are generally sharply or bluntly pointed, but ridgelike in some large-sized specimens.

**Morphological variation in denticulation:** Specimens can be divided into three forms α, β and γ on the basis of the degree of development of ridgelike denticles. Form α is marked by having transverse ridgelike denticles in most part of a platform. Form β has narrow uniserial or a few biserial denticles in the middle portion of a platform. Form γ carries laterally compressed or laterally rounded and tipped denticles throughout the platform.

These three forms represent a great variation in denticulation. However, a certain trend can be recognized in the variation. In order to express this trend, a diagram
was constructed (Fig. 9). Types A and B are characterized by possessing a carina bending behind the cusp and projecting toward the postero-lateral side. However, the ratio of width of denticles to that of platform is more than 1 in the former and less than 1 in the latter. The morphological difference between Types A and B in the profile of the anterior process is illustrated in Fig. 10. The holotype described by Solien (1979) is identical to Form $\beta$ in Type A. Types C and D carry a row of denticles on both the outer and inner postero-lateral processes. The degree of transverse extension of denticles on a platform is high in Type C and low in Type D. In Types E and F the carina is almost straight and exhibits no lateral bend behind the cusp. Of the two types, Type F has a wider denticle row on a platform. Type G is marked by having nodelike denticles besides the carina near the posterior end of a platform. Nodelike denticles may exist on the outer and/or inner sides of postero-lateral processes.

![Fig. 10. Profile of platform and denticulation. A: Form $\alpha$, Type A. A$: Form $\alpha$, Type B. B$: Form $\beta$, Type A. B$: Form $\beta$, Type B. C$: Form $\gamma$, Type A. C$: Form $\gamma$, Type B.](image)

Microstructure: The platform surface of this conodont is ornamented with a microstructure which represents a web-like network or bears some resemblance to a honeycomb pattern. Denticles are also covered with the web-like structure. This microstructure is present not only in specimens having a broad platform but also in those having blade-like one (Fig. 11).

The web-like structure developed on the platform and denticles of this conodont is quite similar to the web-like patterns observable on the denticles and on their sides of Neogondolella sp. illustrated by von Bitter (1976, fig. 5). The honeycomb or web-like structure is characteristically developed on the platform of pectiniform elements (i.e. gondolellid and balognathid elements) (Lindstrom, 1973, von Bitter, 1976, Budurov, 1976). On the other hand, ramiform elements are usually ornamented with discontinuous striae on the denticles and cusp which die out toward the base.

Similarities of the microstructure on the oral surface of this conodont to that of gondolellid and other pectiniform elements may indicate that this conodont had the same function with those elements.

Basal field: The basal cavity is shallow and broad. A pit is present near the center of the basal cavity, and its posterior end may slightly curve toward the outer side. This attitude of the pit offers a key for the determination of orientation. A narrow groove extends anteriorly from the pit.

Apparatus structure: The Spathoicriodus collinsoni apparatus can be thought to be unimembrate. Because the ramiform and neospathodid elements occurring with *S. collinsoni* are inconstant in relative frequency, and the ramiform elements are of those types characteristic of Xaniognathus curvatus Sweet which ranges in age from Early to Late Triassic. Kashimirilla cf. novaehollandiae somewhat resembles *S. collinsoni* in having a bending carina near the posterior end, and in some cases, carrying nodulike denticles on the postero-lateral process. How-

![Fig. 9. Morphological variation in denticulation on platform and postero-lateral processes of Spathoicriodus collinsoni (Solien) from the Tahoe Limestone. Forms $\beta$ and $\gamma$ of Types E, F and G are not illustrated in this figure.](image)
ever, Kashmirirella cf. novaehollandiae has discrete and subequal sized denticles, and it is not included within the morphological variation of S. collinsoni. Furthermore, this species appears earlier than S. collinsoni in the Taio Limestone.

In Spathoicridus collinsoni at hand, the ratio of symmetrical to asymmetrical elements is 15/141 in sample 9 (Table 1). The apparatus of this conodont was probably composed of a minimum pair of symmetrical elements and 9 to 10 pairs of asymmetrical elements.

This conodont being reminiscent of a miniature elephant tooth might have functioned like a tooth.

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![Image of Spathoicridus collinsoni](image)

Table 1. Frequency distribution of morphological variation in Spathoicridus collinsoni from the Taio Limestone. Symmetry range: L; Left (sinistral) elements. R: right (dextral) elements. Frequency: symbols used are: (1) Solid circle refers to the total number of specimens from locations 9, 10 and 1119. (2) Open star refers to sample from location 10. (3) Solid star refers to that from location 1119.

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Fig. 12. Spathoiceridius collinsoni (Solien) from the Taho Limestone, 1~34, 39, 45, ×70; 35~38, 40~44, 46~53, ×60. 1, 2. Dextral element of Form γ, Type A, loc. 9, YNUC-1483. 3, 4. Ibid., loc. 1119, YNUC-1484. 5, 6. Ibid., YNUC-1485. 7, 8. Sinistral element of Form γ, Type A, loc. 9, YNUC-1486. 9, 10. Ibid., loc. 1119, YNUC-1487. 11, 12. Dextral element of Form γ, Type C, loc. 9, YNUC-1488. 13. Symmetrical element of Form a, Type E, loc. 9, YNUC-1489. 14, 15. Dextral element of Form a, Type E, loc. 9, YNUC-1490. 16. Ibid., YNUC-1491. 17. Sinistral element of Form a, Type E, loc. 9, YNUC-1492. 18, 19. Ibid., Type F, loc. 9, YNUC-1493. 20, 21. Dextral element of Form a, Type A, loc. 9, YNUC-1494. 22, 23. Ibid., Type B, loc. 9, YNUC-1495. 24, 25. Ibid., Type A, loc. 10, YNUC-1496. 26. Ibid., loc. 9, YNUC-1497. 27, 28. Sinistral element of Form β, Type A, loc. 1119, YNUC-1498. 29, 30. Dextral element of Form β, Type B, loc. 9, YNUC-1499. 31. Dextral element of Form a, Type B, loc. 9, YNUC-1500. 32, 33. Ibid., Type A, loc. 10, YNUC-1501. 34, 35. Sinistral element of Form a, Type C, loc. 9, YNUC-1502. 36. Ibid., YNUC-1503. 37. Ibid., Type D, loc. 9, YNUC-1504. 38. Dextral element of Form a, Type D, loc. 9, YNUC-1505. 39. Sinistral element of Form a, Type C, loc. 9, YNUC-1506. 40. Symmetrical element of Form a, Type E, loc. 9, YNUC-1507. 41, 42. Sinistral element of Form a, Type A, loc. 10, YNUC-1508. 43. Dextral element of Form γ, Type A, loc. 1119, YNUC-1509. 44. Dextral element of Form a, Type B, loc. 1119, YNUC-1510. 45. Sinistral element of Form γ, Type B, loc. 9, YNUC-1511. 46. Ibid., YNUC-1512. 47. Sinistral element of Form a, Type B, loc. 9, YNUC-1513. 48. Dextral element of Form a, Type B, loc. 9, YNUC-1514. 49. Ibid., loc. 1119, YNUC-1515. 50. Ibid., Type D, loc. 9, YNUC-1516. 51. Dextral element of Form γ, Type C, loc. 9, YNUC-1517. 52. Ibid., YNUC-1518. 53. Ibid., Type C, loc. 9, YNUC-1519.
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REFERENCES


Postscript

The genus *Spatioicriodus* described by Budurov, Sudar and Gunata (1987) is a junior synonym of *Icriospathodus* Krah, Kauffmann *et al.* (1983). *Spatioicriodus collinsoni* (Solien) in this paper should be referred to as *Icriospathodus collinsoni* (Solien).
