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The fossil on the cover is an adult example (T. TAKAHASHI coll.) of Mikasaites orbicularis MATSUMOTO (subfamily Marshallitinae, family Kossmaticeratidae) from the Lower Cenomanian (Cretaceous) of the Mikasa area, central Hokkaido. (photo by M. NODA, natural size)

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740. CRETACEOUS TETRAGONITID AMMONITE JAWS: A COMPARISON WITH MODERN NAUTILUS JAWS*

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Abstract. The morphology and mineral composition of jaw apparatuses in *Tetragonites glabrus*, *Gaudryceras denseplcatum*, *G. tenuiliratum* and *G. sp.* are described. The studied material is well-preserved specimens in some calcareous nodules from the Turonian-Maastrichtian of Hokkaido and Sakhalin. The upper and lower jaws of these species consist of black outer lamella, reduced short inner lamella and covering rostra. The two lamellae are composed of carbonate apatite, and the rostra are calcareous covering. The lamellae and rostra may have been diagenetically replaced from chitin and aragonite respectively, judging from the comparison with modern cephalopod jaws. The calcareous rostra of the upper and lower jaws are analogous to rhyncholite (upper jaw) and conchorhynch (lower jaw) of modern *Nautilus* instead of coleoids in the internal microstructure, and mineral and chemical composition. These evidences suggest an analogy in feeding habits between tetragonitid ammonites and *Nautilus*, although the ammonites have larger and stronger jaws.

Introduction

Anaptychi and aptychi are often preserved in ammonoid body chambers. They have been interpreted as ammonoid opercula (e.g. Retowski, 1891; Schmidt, 1928; Trauth, 1927-1936; Nagao, 1931a-c, 1932; Fischer & Fay, 1953; Arkell, 1957; Schindewolf, 1958) or jaw apparatuses (e.g. Meek & Hayden, 1864; Kennedy & Cobban, 1976). Recently, Closs (1967a, b) discovered several examples of anaptychus (upper jaw)—radula associations within the living chambers of an Upper Carboniferous ammonoid, *Eoasianites (Gisphyrrites) rionegrensis* Closs, and Lehmann (1967, 1971b, 1979) reported in situ aptychi or anaptychi and radulae in some Jurassic ammonites. Thus, aptychi and anaptychi have been confirmed as the lower jaws of ammonites in Jurassic examples (Lehmann, 1967, 1970, 1971a, 1972, 1976, 1978, 1979; Lehmann & Weitschat, 1973; Kaiser & Lehmann, 1971). Recently Zakharov (1979) described the jaw apparatuses of Cretaceous *Tetragonites*. Lehmann *et al.* (1980) described the jaw apparatuses of Lytocerataceae. On the other hand, rhyncholite and conchorhynch were interpreted as calcified elements of nautiloid jaws (d'Orbigny, 1825; Foord, 1891; Rutte, 1962; Teichert *et al.*, 1964; Gasiorowski, 1973; Shimansky, 1962; Müller, 1974; etc.) or coleoid jaws (Biguet, 1819; Gaillardot, 1824; de Blainville, 1827; etc.), but some were considered to belong to ammonoids (Schmidt-Effing, 1972; Mundlos, 1973; Tanabe *et al.*, 1980; etc.).

Almost all cephalopods have jaw apparatuses and radulae. The taxonomic and ecological implications of jaw apparatuses in modern coleoids were studied

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by Clarke (1962), Nixon (1969) and others, and those in *Nautilus* by Okutani & Mikami (1977) and Saunders et al. (1978).

Most previous works on ammonoid jaws have been done mainly on the basis of the Jurassic materials from Europe. However, Nagao (1931a-c, 1932) reported Cretaceous aptychi and anaptychi from Hokkaido and south Sakhalin, and Trauth (1935) redescribed Nagao's *Neoanaptychus*. Kanie et al. (1978) preliminarily reported the jaw apparatuses of some Late Cretaceous ammonites from Hokkaido and Sakhalin. They recognized in some specimens that a pair of lower and upper jaws are preserved in the body chamber; calcareous coverings similar to rhyncholite and conchorhynch exist in the rostra of lower and upper jaws; the ammonite jaws are biomineralogically comparable with those of extant *Nautilus*. Furthermore, the tetragonitid jaws were interpreted to be analogous to those of *Nautilus* owing to similar feeding habit (Kanie & Tanabe, 1979; Tanabe et al., 1980).

This paper presents a description of the general morphology of the tetragonitid ammonite jaws from the Upper Cretaceous of Hokkaido and Sakhalin (Text-fig. 1), and compares them with the jaw apparatuses of modern *Nautilus* by some mineralogical analysis. On the basis of the results obtained, the tetragonitid jaws are restored.

The depositories of the specimens examined are as follows (abbreviations are shown in parentheses):

Yokosuka City Museum, Yokosuka 238 (YCM)
Department of Geology, Kyushu University, Fukuoka 812 (GK)
Department of Geology and Mineralogy, Hokkaido University, Sapporo 060 (UH)
Japanese Expert Consultation on Living *Nautilus*, c/o Yokosuka City Museum (JECOLN)
Y. Kawashita’s private collection, 2 A1-5, Tomatsu-Chiyoda-cho, Mikasa 068-22
M. Nihongi’s private collection, 8S, 22W, Chuo, Sapporo 064 (MN)
T. Takahashi’s private collection, 28-109, Hanazono-cho, Mikasa 068-22

**General morphology**

*Comparison with modern cephalopods*

*Identification of lower and upper jaws.*—The lower jaw is distinguished from the upper one by several characters (Text-figs. 2, 3), namely, the larger size of lamellae (compared with the height and width of living chambers), the broader lamella angle (angle between left and right sides of the outer lamellae) and less

Extended hood area (Clarke, 1962 for coleoids; Okutani & Mikami, 1977 and Saunders et al., 1978 for Nautilus).

Morphological comparison with modern cephalopods.—The morphological features of the tetragonitid jaws (Text-figs. 4, 7) can be correlated with those of living Nautilus rather than with those of modern coleoids. These ammonite jaws are characterized by the presence of rhyncho- lites and conchorhynchs at the anterior part of the jaws (Tanabe et al., 1980). The Nautilus jaw is also covered with rhyncholite and conchorhynchs (Text-fig. 3; Okutani & Mikami, 1977; Saunders et al., 1978). Those of coleoids, however, lack calcareous coverings visible with the naked eye (Text-fig. 2). The lower jaw of the Tetragonitidae is morphologically similar to those of Nautilus and Vam- pyroteuthis infernalis in the scarcely extended crest and lateral wall. In the Tetragonitidae the upper jaw more or less resembles the lower jaw except for the more extended wings covering the reduced short lateral walls and crest, whereas in these living cephalopods the upper and lower jaws are morphologically quite different from each other.

Description of jaw apparatuses

The jaw specimens examined are attributed to Gaudryceras and Tetragonites (Tetragonitidae: Lytoceratina). They were previously named Neoanaptychus by Nago
Text-fig. 3. Basic morphology of modern *Nautilus* jaw. L: length of lateral wall, W: length of wing, Hd: length of hood, Hi: height, B: breadth, $a$: wing (lateral wall) angle, $\beta$: jaw angle. Terminologies are mostly based on Okutani & Mikami (1977) and Saunders et al. (1978). Solid area is covered with a calcareous covering.

(1931a) and *Anaptychus* by Trauth (1935).

Family Tetragonitidae Hyatt, 1900
Subfamily Gaudryceratinae Spath, 1927
Genus *Gaudryceras* Grossouvre, 1894

Jaws of *Gaudryceras* spp.

*General characters:* The lower and upper jaws are of *Anaptychus* type. They are broader than high. Lower jaw is larger and broader than upper one. Both
lower and upper jaws are constructed by wing, hood and rostrum with calcareous covering and crest plus minor lateral wall beneath them. Wing angle ($\alpha$, angle between left and right sides of the wings; Text-fig. 7) is wide in the lower jaw.
Jaw angle (β) is obtuse; the curve between rostrum and wing margin is gentle without notch. The black lamellae are made up of apatitic mineral and covered with a thin calcite layer.

Remarks: The specific distinction of these jaws in accordance with the classification of *Gaudryceras* is difficult at present.

Upper jaw (Pl. 39, Figs. 1-3; Text-fig. 4-U)

Previously described material: The following specimens are attributable to the upper jaws of *Gaudryceras* spp.

1931c. *Neoanaptychus* sp. form 7, Nagao, p. 216, pl. 15, fig. 6.


Description: The wings are triangular and make up the greater part of the upper jaw. Wing surface is marked by concentric costae and numerous growth lines of variable prominence. The wings are slightly compressed towards the flank of the living chamber, and combine a hood at the antero-dorsal part, being narrowly flat at the dorsal part; growth lines gently concave toward anterior direction. In some specimens (e.g., Pl. 39, Fig. 1b), folds or a groove are found; wings posteriorly projected in later growth stage. Crest and lateral wall are small. Wing

<table>
<thead>
<tr>
<th>Specimen</th>
<th>W</th>
<th>Hd</th>
<th>Hi</th>
<th>B</th>
<th>α</th>
<th>β</th>
<th>Lh</th>
<th>(Hi/LH)</th>
</tr>
</thead>
<tbody>
<tr>
<td>UH3193</td>
<td>56.9</td>
<td>38.4</td>
<td>37.0</td>
<td>58.0</td>
<td>60°</td>
<td>165°</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>MN6</td>
<td>58.8+</td>
<td>41.5</td>
<td>29.2</td>
<td>40.0</td>
<td>49°</td>
<td>155°</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>GK.H8086</td>
<td>34.7</td>
<td>31.2</td>
<td>25.7</td>
<td>30.9*</td>
<td>51°</td>
<td>170°</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>R4040b</td>
<td>33.4+</td>
<td>30.7</td>
<td>27.4+</td>
<td>27.0*</td>
<td>65°</td>
<td>165°</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>GK.H3220</td>
<td>28.7</td>
<td>24.3</td>
<td>25.0+</td>
<td>32.9</td>
<td>48*</td>
<td>165°</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>GK.H8087</td>
<td>23.7</td>
<td>18.7</td>
<td>23.1+</td>
<td>—</td>
<td>—</td>
<td>135*</td>
<td>29.2 (0.64)</td>
<td></td>
</tr>
<tr>
<td>GK.H2262</td>
<td>16.5</td>
<td>14.9</td>
<td>18.8</td>
<td>14.0</td>
<td>47*</td>
<td>160°</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>UH3191</td>
<td>12.7</td>
<td>10.9</td>
<td>11.6</td>
<td>14.4+</td>
<td>87**</td>
<td>170°</td>
<td>18.9 (0.61)</td>
<td></td>
</tr>
</tbody>
</table>

Cretaceous Tetragonitid Ammonite Jaws

The rostrum projects toward the ventral side and is covered with a calcite layer. In specimen MN6 (Pl. 39, Fig. 1), the poorly preserved rostral tip fills inside of the rostrum. The rostrum, originally sharp-topped, decreases in thickness toward the wings; the outer surface of the wings is covered with a light-colored, thin (approximately 500 µm thick) calcite layer. The jaw angle is generally obtuse (135°-170°), without a notch (Table 1).

Remarks: In comparison with Gaudryceras, the upper jaw of Nautilus has less extended wings, larger lateral wall and narrower jaw angle (118°-119°). The upper jaw of Tetragonites is clearly distinguished from that of Gaudryceras in the higher, narrower and more rounded outline.

Lower jaw (Pl. 39, Figs. 4-6; Text-figs. 4-1, 5, 6-1)

Previously described material: The following specimens are attributable to the lower jaws of Gaudryceras spp.
1931c. Neoanaptychus tenuiliratus Nagao, p. 216, pl. 15, fig. 1.


Coniacian (T. Matsumoto coll.).

Description: Wings are triangular and make up the greater part of the lower jaw. Wing surface is marked by concentric costae and numerous growth lines. Wings are slightly compressed toward the side of living chamber; the hood combines wings at the antero-ventral part, being flat, occasionally folded at the ventral part (Text-fig. 4-2); growth lines gently concave toward the aperture. Wing angle is 80°-87°. Wings are made up of carbonate apatite in the specimen YCM. Ur307002.

Lateral wall is small. Thick calcareous substance (rhyncholite) covers entire lateral wall (Text-fig. 5). Lateral wall continues to rostrum at the tip of beak. The rostrum is covered with a calcareous layer forming a beak which consists of an alveolus structure of 2 mm wide at the dorsal part, though decreasing in thickness to 0.5 mm toward posterior part of the wing and hood areas (Text-fig. 6-1).

Remarks: The general morphology of the lower jaw in Gaudryceras is similar to that of Nautilus except for the longer wing, partly flattened hood, and larger

Table 2. Measurements (in mm) of lower jaw of Gaudryceras denseplicatum (†).

<table>
<thead>
<tr>
<th>Specimen</th>
<th>W</th>
<th>Hd</th>
<th>Hi</th>
<th>B</th>
<th>α</th>
<th>β</th>
<th>Lh</th>
<th>(Hi/Lh)</th>
</tr>
</thead>
<tbody>
<tr>
<td>YCM. Ur307002</td>
<td>37.8</td>
<td>25.0+</td>
<td>34.0*</td>
<td>51.0+</td>
<td>80°</td>
<td>140°</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

Symbols as in Table 1. * deformed specimen.
Yasumitsu KANIE

Text-fig. 5. Crest and lateral wall structure (arrow) of the lower jaw probably attributable to *Gaudryceras* sp., GK.H8045, from loc. As1140, the lower part of the Souashibetsu River, Ashibetsu area. Coniacian. ×2.3. Photo by K. Tanabe.

Text-fig. 6. Alveolus structure of *Gaudryceras denseplicatum* (1), YCM. Ur307002, from loc. U307p, the Ikandai Valley, Urakawa area. Lower Campanian (Tanabe et al., 1980) and *Nautilus macromphalus* (2), JECOLN.M5, from Nouméa, New Caledonia. Both are the lower jaws (dorsal views). Photos by Kanie.

Jaw angle. The lower jaw of *Tetragonites* is clearly distinguished from that of *Gaudryceras* in the greater height, narrower wing angle, and larger jaw angle.

Subfamily Tetragonitinae Hyatt, 1900

Genus *Tetragonites* Kossmat, 1895

Jaws of *Tetragonites glabrus* (Jimbo, 1894)

General characters: Lower jaw is broader than high. It is slightly larger than upper jaw. The breadth of upper jaw is approximately equal to or smaller than height. The jaw plate consists of outer lamellae (wing and hood) and inner lamellae (minor crest plus lateral wall). Wing angle (α) is wide in lower jaw. Jaw angle (β) is obtuse to rectangular; the curve between rostrum and wing margin is gentle without notch. The wing is mainly composed of apatitic mineral with a thin covering of calcite layer.

Upper jaw (Pl. 40, Figs. 1-3; Text-fig. 7-U)


Description: The wings are triangular and make up the greater part of the upper jaw. Wing surface is marked by concentric costae and numerous growth lines. Wings are slightly compressed toward the side of living chamber; the hood is flat or waved in dorsal part; growth lines concave toward the anterior part. Crest and lateral wall unclear. Wing angle is approximately 55°.

The rostrum is sharply projected toward the ventral side and covered with a thick calcareous layer (rhyngolith), decreasing the thickness toward the wing; outer surface of wings is covered with a thin (ca. 500 μm thick) calcite layer (Pl. 40, Fig. 2). The jaw angle is approximately 55° in Kawashita’s specimen, without a notch (Table 3).

Remarks: The lateral wall and crest of *Tetragonites* are reduced to a short
inner lamella as compared with those of the upper jaw of *Nautilus*.

Lower jaw (Pl. 40, Figs. 3-5; Text-fig. 7-L)

*Previously described material*: The following specimens are attributable to the lower jaws of *Tetragonites glabrus*.

1931a. *Neoanaptychus tenuilliratum* Nagao, pp. 106-109, fig. 2.

1931c. *Neoanaptychus* sp. form 5, Nagao, p. 216, pl. 15, fig. 4.
Table 3. Measurements (in mm) of upper jaw of *Tetragonites glabrus*.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>W</th>
<th>Hd</th>
<th>B</th>
<th>Hi</th>
<th>α</th>
<th>β</th>
<th>Lh</th>
<th>(Hi/Lh)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kawashita’s coll.</td>
<td>32.3</td>
<td>27.9</td>
<td>20.0*</td>
<td>28.0</td>
<td>55*</td>
<td>100*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>GK423</td>
<td>17.3+</td>
<td>13.8+</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>38**</td>
<td>(0.48)</td>
</tr>
</tbody>
</table>

Symbols as in Table 1. * deformed specimen; ** restored.

Table 4. Measurements (in mm) of lower jaws of *Tetragonites glabrus*.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>W</th>
<th>Hd</th>
<th>B</th>
<th>Hi</th>
<th>α</th>
<th>β</th>
<th>Lh</th>
<th>(Hi/Lh)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GK. H8043</td>
<td>28.9</td>
<td>23.2</td>
<td>18.9*</td>
<td>23.0*</td>
<td>—</td>
<td>135*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>GK. H8049</td>
<td>26.2</td>
<td>—</td>
<td>20.0+</td>
<td>30.9*</td>
<td>85*</td>
<td>115*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>UH3194</td>
<td>24.6</td>
<td>19.3</td>
<td>13.4</td>
<td>30.5+</td>
<td>95*</td>
<td>100*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>MN83a</td>
<td>16.6</td>
<td>10.4</td>
<td>11.0*</td>
<td>27.0+</td>
<td>95*</td>
<td>150*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>GK. H2073</td>
<td>10.0</td>
<td>10.3</td>
<td>7.2*</td>
<td>25.0*</td>
<td>70*</td>
<td>—</td>
<td>37**</td>
<td>(0.36*)</td>
</tr>
<tr>
<td>UH3194</td>
<td>14.6</td>
<td>13.4</td>
<td>7.8</td>
<td>21.0</td>
<td>90*</td>
<td>110*</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

Symbols as in Table 1. * deformed specimen; ** restored.

1931c. *Neoanaptychus* sp. form 1, Nagao, p. 216, pl. 15, fig. 2.
1931c. *Neoanaptychus* sp. form 4, Nagao, p. 216, pl. 15, fig. 3.
1935. *Anaptychus tenuiliratus* (Nagao), Trauth, pp. 452-454, pl. 14, fig. 6.


*Description:* The wings are quadrate to triangular and make up the greater part of the lower jaw. Wing surface is marked by concentric costae and numerous growth lines. Wings are gently compressed toward the side of living chamber; the hood is flat and sometimes folded at the ventral part (Nagao, 1931c, pl. 15, fig. 4); growth lines gently concave toward the anterior part. Wing angle is 90-95° (Table 4). Crest and lateral wall are small, existing as inner lamella. Thin calcite layer covers the greater part of outer surface of the wings. Wings are continuous to the rostrum at the tip of the beak (Pl. 40, Fig. 5c). The rostrum is sharp-topped, but denticles as cutting edge are not preserved; rostrum is covered with a calcite layer, the thickness of which decreases toward the posterior part of wings.
Table 5. Measurements (in mm) of jaw appofaratuses of adult *Nautilus macromphalus*.

The specimens are from of Nouméa, New Caledonia.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>W (L)</th>
<th>Hd</th>
<th>B</th>
<th>Hi</th>
<th>α</th>
<th>β</th>
<th>Lh</th>
<th>(Hi/Lh)</th>
</tr>
</thead>
<tbody>
<tr>
<td>JECOLN. up. (31.3)</td>
<td>19.0</td>
<td>17.0</td>
<td>25.3</td>
<td>33°</td>
<td>119°</td>
<td>94</td>
<td>(0.27)</td>
<td></td>
</tr>
<tr>
<td>M4 low.</td>
<td>28.9</td>
<td>19.5</td>
<td>33.0</td>
<td>24.5</td>
<td>52°</td>
<td>102°</td>
<td>(0.26)</td>
<td></td>
</tr>
<tr>
<td>JECOLN. up. (34.0)</td>
<td>21.5</td>
<td>27.2</td>
<td>23.4</td>
<td>31°</td>
<td>118°</td>
<td>93</td>
<td>(0.27)</td>
<td></td>
</tr>
<tr>
<td>M5 low.</td>
<td>29.0</td>
<td>18.3</td>
<td>30.6</td>
<td>23.7</td>
<td>51°</td>
<td>102°</td>
<td>(0.26)</td>
<td></td>
</tr>
</tbody>
</table>

W: length of wing (lower jaw), L: length of lateral wall (upper jaw), Hd: length of hood, B: breadth, Hi: height, α: wing (lower jaw) or lateral wall (upper jaw) angle, β: jaw angle, Lh: height of living chamber, as illustrated in Text-figure 3.

Table 6. Comparison of jaw size of tetragonitid ammonites and modern *Nautilus*.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Upper</th>
<th>Lower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gaudryceras</td>
<td>Hi/Lh: 0.64-0.61 (2.4-2.3)</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>W/Lh: 0.81-0.87 (2.3-2.0)</td>
<td>—</td>
</tr>
<tr>
<td>Tetragonites</td>
<td>Hi/Lh: 0.48 (1.8)</td>
<td>0.47 (1.5-1.3)</td>
</tr>
<tr>
<td></td>
<td>W/Lh: 0.27 (0.8)</td>
<td>0.19 (-)</td>
</tr>
<tr>
<td>Nautilus</td>
<td>Hi/Lh: 0.27 (1.0)</td>
<td>0.26 (1.0)</td>
</tr>
<tr>
<td></td>
<td>WL/Lh: 0.36-0.33 (1.0)</td>
<td>0.36-0.31 (1.0)</td>
</tr>
</tbody>
</table>

Hi: height, W: length of wing, L: length of lateral wall, Lh: length of living chamber. The number in parentheses is the ratio with that of *Nautilus*. *: deformed specimen.

**Remarks**: The general outline of the lower jaw of *Tetragonites* is closely similar to that of *Nautilus* except for the narrower wing angle (51-52°) and smaller size (Table 5).

**Discussion**: The upper jaw plates of tetragonitid ammonites are morphologically more similar to those of octopods than decapods, and they resemble those of *Nautilus* more closely than octopods (Text-figs. 2, 3). Namely, the crest and lateral wall of the lower jaw of *Nautilus* are shortly reduced as in tetragonitid ammonites. Meanwhile, the upper jaw of modern *Nautilus* consists of wide inner lamellae (lateral wall and crest) and shortly reduced outer lamellae (hood and wing).

The outer and inner lamellae are morphologically similar between the upper and lower jaws in tetragonitid ammonites. The ratio of jaw height to living chamber height is less than 100 percent; for example, the upper jaw of *Gaudryceras* is 61-64%; the upper jaw of *Tetragonites* is 48% and lower jaw 47%; the upper jaw of *Nautilus macromphalus* is 27% and lower jaw 26% (see Tables 5, 6).

Table 6 gives the size of the jaw apparatuses of tetragonitid ammonites in relation to the living chambers. The size of the jaw apparatuses in *Gaudryceras* is 1.7-2.4 times and in *Tetragonites* is 1.3-1.8 times as large as that of adult *Nautilus macromphalus*.

Sharp denticles are present on the alveolus structure in living *Nautilus*, but unknown in the Tetragonitidae. However, it may be due to the matter of fossilization (Text-fig. 6-2).

**Mineral composition**

The mineral composition of the jaw plates of tetragonitid ammonites was

analyzed by an X-ray powder diffraction method. The patterns are compared with those of modern coleoids by the same method. The specimens examined are the lower jaws of *Gaudryceras* sp., *Tetragonites glabrus*, *Nautilus macromphalus* and *Sepia* sp. It was found that the calcareous covering of the rostrum in *Gaudryceras* is made up of calcite (Text-fig. 8-2), whereas the black outer lamella (wing) is composed mainly of well-crystallized carbonate apatite (Text-fig. 8-1). The whole surface of the outer lamellae in *Gaudryceras* (Pl. 39, Fig. 1b) and *Tetragonites* (Pl. 40, Fig. 2) is covered with a calcite layer about 500 μm thick. The layers grades into the calcareous covering of the rostrum. The lower jaw plate of *Nautilus* consists of outer and inner lamellae, calcareous rostrum, and denticles. The former two are made up of chitin (Saunders *et al.*, 1978), but the X-ray powder diffraction studies show that almost all materials display broad bands near d=4.4 Å only as represented by Text-figure 9-2, also that of *Sepia* (Text-fig. 9-1). The calcareous covering of the rostrum is composed of aragonite (Text-fig. 9-4), but the denticles are of calcite (Text-fig. 9-3). Another test showed that a pair of the aragonitic rostra changed into calcite by heating at 300°C in half an hour (Text-fig. 9-5). The wing surface of the jaw of *Nautilus macromphalus* shows similarities with that of *Tetragonites*, a prismatic layer covers the outer surface of the wings of *Nautilus macrom-
Discussion: The wing surface of the upper and lower jaws of tetragonitid ammonites are covered with a calcite layer, approximately 500 μm in thickness. Hölder (1958) reported that a thin calcareous layer covers the outer surface of a Jurassic anaptychus, probably attributable to *Psiloceras torus* d’Orbigny. Recently, Zakharov (1979) described the calcareous covering, 100-200 μm thick, on the lamella of the lower jaw in *Tetragonites popetellis* Yabe. The outer lamellar surface (wing) of the lower jaw of modern *Nautilus* is underlain by an aragonite layer, 50-75 μm thick (Fukuda, personal comm.). Its thickness is about 1/10 of that of tetragonitids. The aragonite layer covers the inner side of broadly extended lamellae. Therefore, the upper jaw of modern *Nautilus* is mostly occupied by the inner lamellae (crest and lateral wall). The outer lamellae of the upper jaw in modern cephalopods are generally reduced in length. Both the upper and lower jaws of tetragonitid ammonites are characterized by similar morphology. The calcified denticles of the tetragonitid jaws were originally made of calcite as in *Nautilus*, the rostrum and the outer surface of wings consisted of aragonite, and the wings were made up of chitin. During the course of fossilization, the rostrum and outer surface may have changed into calcite and the wings into carbonate apatite. This suggests that aragonite has changed into calcite during diagenesis. Such a conversion of aragonite into calcite is also indicated in the septa of *Subptychoceras* sp. (specimen YCM. Ur307001) preserved in the same nodule.

Restoration of jaws

The restoration of tetragonitid ammonite jaws is undertaken on the basis of the above mentioned observations and some anatomical studies of living *Nautilus*.

Saunders *et al.* (1978) discussed the function of the calcareous coverings of the rostral part, ryncholite (upper jaw) and conchorhynch (lower jaw), in modern *Nautilus* and the extinct Nautilida. Tanabe *et al.* (1980) clarified some of the previously known fossil ryncholites and conchorhynchs belong to such Cretaceous ammonites as *Gaudryceras*, *Tetragonites*, *Zelandites* and *Neophylloceras*. Morphologically the tetragonitid ammonite jaws are most similar to those of living *Nautilus*. However, the analogous internal structure is observed between upper and lower jaws of the ammonites in contrast to the great difference in *Nautilus*. The outer lamella (wings) of the upper jaws of *Nautilus* is reduced in length and the inner lamella (lateral wall) extends broadly. The lower jaw of modern coleoids is composed of lateral wall instead of wing.

Text-fig. 10 shows the articulation system of the upper and lower jaws of *Nautilus pompilius* in a buccal mass in the anterior part of the soft body. The calcareous covering, namely ryncholite (rh) and conchorhynch (co), is shown as solid on soft X-ray photographs (Text-fig. 10), whereas the lamellae mostly made of chitin are faintly shadowed. Text-fig. 10-2 shows the articulated upper and lower jaws of *Nautilus macromphalus*. The muscle system between the upper and lower jaws of the present two species of *Nautilus* is designed in Text-figure 11 on the basis of data above mentioned and some anatomical studies. Namely, the wing and lateral wall are distinguished from the attachment muscle system on the lamellae and the existence of the calcareous covering; the outer surface of the wing is covered with a calcareous layer and the muscle attaches inside; the inner surface of the lateral wall is overlain.

by a calcareous layer and underlies the muscle attachment.

It is suggested that the articulation and muscle system of both upper and lower jaws of tetragonitids are quite different from those of living cephalopods. The attachment areas of the muscles of tetragonitids are inferred from the morphological features of the muscle-scar, though there is no information on the jaw muscle-scar. The muscle attachments of the lower jaw in tetragonitids might be inside of the wing (Text-fig. 12), because of the existence of a calcareous layer on the wing surface. The muscle of the upper jaw also attaches inside of the wings
Text-fig. 11. Anterior view of articulated upper and lower jaws of modern *Nautilus* species with jaw muscles (horizontal lines). U: upper jaw, L: lower jaw.


Based on the similar lamellar structure, therefore, the buccal mass system and morphological feature of the upper and lower jaws suggest an articulation system of the tetragonitid ammonite jaws as shown in Text-figure 13.

The feeding habits of tetragonitid ammonites which have a conchorhynch at the rostral part of the lower jaw are partly inferred from those of *Nautilus* with similar conchorhynch. Dean (1901), Bidder (1962), Haven (1972), Mikami & Okutani (1977), Kanie & Tanabe (1979), and others observed the feeding habits of living *Nautilus*. In their views, *Nautilus* mostly scavenges animals on the sea floor and rarely feed on slow moving benthos. The function of the rhyncholites and conchorhynchs to bite and cut up a prey has already demonstrated by Tanabe *et al.* (1980) through the observations of crop content remains. *Nautilus* is a slow moving animal, its maximum swimming speed being 25 cm/sec (Ward *et al.*, 1977), and usually 2.8 cm/sec (Mikami *et al.*, 1980). The tetragonitid animals with similar shells to *Nautilus* are probably also slow swimmers.

**Conclusions**

The general morphology of the jaw apparatuses of Late Cretaceous *Tetragonites* and *Gaudryceras* is described. They are of anaptychus-type, and are
often preserved in situ within the body chambers. The upper and lower jaws are distinguished from each other by differences of morphology, size, internal structure and others. The tetragonitid ammonite jaws are more similar to those of modern Nautilus than to those of coleoids especially in the existence of calcareous coverings at the rostral part.

The jaw lamellae of tetragonitid ammonites are composed of carbonate apatite, and the rostra grade into wing surface layer consisting of calcite, whereas the lamellae of modern cephalopods consist of chitin. The rostra and denticles of Nautilus jaws are made up of aragonite and calcite, respectively. The outer lamellae of modern Nautilus are overlain by very thin aragonite layers. Therefore, the ammonite jaws originally seem to have been analogous to modern cephalopod jaws in regard to mineral composition and internal structure.

Based on the similarities of jaws and shell morphology, tetragonitid ammonites are interpreted to be analogous to Nautilus in living habits. The jaw apparatuses of tetragonitid ammonites are relatively large and probably stronger in comparison with those of Nautilus.

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Müller, A. H. (1974): Über den Kieferapparat fossiler und rezenter Nautilida (Cepha-
Yasumitsu KANIE


Explanation of Plate 39


1a, b. Upper jaw probably attributed to Gaudryceras sp. a: ventral, b: lateral views. x1. MN6. Loc. the upper part of the Yubari-goenosawa, the Ikushumbetsu River, Ikushumbetsu area, central Hokkaido. Upper Yezo Group (Coniacian ?). M. Nihongi coll. (Kanie et al., 1978) 2. Lower view of the upper jaw attributed to Gaudryceras sp. x1. UH3193. Loc. the Kikumezawa, the Ikushumbetsu River, Ikushumbetsu area. Upper Yezo Group (Santonian ?). R. Saito coll. 3. Mode of occurrence of the upper jaw in Gaudryceras denseplicatum (Jimbo). x1. GK. H8087. Loc. R401ip2, the upper part of Obirashibe River, Obira area, northwestern Hokkaido. Upper Yezo Group (Lower Santonian). H. Hirano and K. Tanabe coll. 4. Upper view of the deformed lower jaw attributed to Gaudryceras sp. x2. GK. H8059. Loc. the upper part of the Kamikinenbetsu River, Obira area. Middle Yezo Group (Upper Turonian). T. Matsumoto coll. 5a-c. Upper jaw of Gaudryceras tenuiliratum Yabe. a: mode of occurrence, b: lateral, c: anterior views. a(x1), b, c(x2). UH3191. Loc. the Ikushumbetsu River, 200 m east from the junction with the Kikumezawa, Ikushumbetsu area. Upper Yezo Group (Santonian). R. Saito coll. (Nagao, 1931a, c; Tanabe et al., 1980). 6a, b. Lower jaw probably attributed to Gaudryceras denseplicatum (Jimbo). a: dorsal, b: lateral views. co: conchorhynch. x1 YCM. Ur307002. Loc. U307p, Ikandai Valley, Urakawa area, southern-central Hokkaido. Upper Yezo Group (Lower Campanian). Y. Kanie coll. (Kanie et al., 1978; Lehmann et al., 1980)

Photos, without whitening, by Kanie (1-3, 5, 6) and K. Tanabe (4).
740. Cretaceous Tetragonitid Ammonite Jaws

S. 49-55, Taf. 11.


Ashibetsu 芦別, Furenai 振内, Hakkinzawa 白金沢, Ikandai 井寒台, Ikushumbetsu 余呂別, Juhachirinpan-Ichinosawa 18林遠の沢, Kamikinenbetsu 上紀内別, Kaneobetsu 金尾別, Kikumezawa 菊面沢, Naibuchi 内渕, Nakakenbetsu 中紀内別, Obira 小平, Obirashibe 小平柴, Oyubari 大夕張, Santan 三丹, Shiyubari 主夕張, Souashibetsu 双芦別, Takishita 池下, Tomobetsu 須別, Urakawa 澪河, Yubarigoeonsawa 夕張越の沢

現代産頭足類顎器との比較研究によるテトラゴニテクトイアモンサイトの顎器：北海道・樺太の白亜紀チューネンアン～マーストリヒティアン階層の石灰質ジーコール中に保存された*Tetragonites glabrus*, *Gaudryceras denseplicatum*, *G. tenuiliratatum*, *G. sp.*の顎器の形態と顎骨組成を記載した。これらの顎器は、外ラメラ・薄小化した内ラメラと石灰質の構造部より構成されている。前者はカーボネイトアパタイト、後者はカルサイトよりなり、現生頭足類の顎器と比較検討することによって、それぞれキチンとアラゴナイトより置換されると考えられる。石灰質構造部は、内部構造の顕著、化学組成から、現生オームガイ類のリンやナトリウ (上顎)・コニコンリクト (下顎)に酷似する。これらの資料に基づいて、テトラゴニテクトイアモンサイトの顎器と口球の一部を復元した。これらのアンモンサイトの顎器は、オームガイ類よりがん大で、住居部の大きさに対する顎器の大きさの比はより大きい。この事実は、テトラゴニテクトイアモンサイトがオームガイ類に似た食生活をしていたことを示唆する。

蟹江康光
Explanation of Plate 40

Figs. 1-5. Jaw apparatuses of *Tetragonites glabrus* (Jimbo).

1a, b. Mode of occurrence (a) and lateral views (b) of upper jaw. a(×1), b(×2). GK423. Loc. Sakhalin. Horizon unknown (Upper Cretaceous). Collector unknown. 2. Lateral view of upper jaw; white calcareous covering is observable. ×1.5. Loc. the lower part of the Kaneobetsu, Oyubari area, central Hokkaido. Middle Yezo Group (Turonian). Y. Kawashita coll. (Tanabe et al., 1980).

3a, b. Mode of occurrence of lower and upper jaws (a), dorsal view of lower jaw (b). lj: lower jaw, uj: rostral part of upper jaw. a(×3/4), b(×2). GK.H2073. Loc. N143a, the lower part of the Santan, Naibuchi area, south Sakhalin. Upper part of the Miho Group (Lower Santonian). T. Matsumoto coll. (Kanie et al., 1978; Tanabe et al., 1980; Lehmann et al., 1980).

4a, b. Lateral (a) and deformed dorsal (b) views of the lower jaw. ×2. GK.H8049. Loc. R2251b, the middle part of the Nakakenbetsu River, Obira area, northwestern Hokkaido. Saku Formation (Upper Turonian). H. Hirano and K. Tanabe coll. 5a-c. Mode of occurrence (a), lateral (b) and dorsal (c) views of the lower jaw. a(×1), b, c(×2). GK. H8043. Loc. N382, the Juhachirinpan-Ichinosawa, the Naibuchi River, Naibuchi area. Upper part of the Miho Group (Santonian). T. Matsumoto coll. (Tanabe et al., 1980).

Photos, without whitening, by K. Tanabe (1b, 3-5), I. Obata (1a) and Kanie (2).
KANIE: Cretaceous tetragonitid ammonite jaws

Plate 40
Abstract. This is the fourth of our serial papers on the early Jurasssic plants in Japan. In this paper we describe Ctenozamites sarrani belonging to Pteridospermales, and Anomozamites sp. A, Otozamites fujimotoi, O. neiridaniensis sp. nov., Pterophyllum ex gr. propinquum, P. sp. A, Ptilophyllum cfr. cutchense, P. nipponicum sp. nov., P. shinadaniense sp. nov., P. sp. A and P. sp. B, all belonging to Bennettitales.

The occurrence of Ctenozamites and Ptilophyllum is the first record not only in the early Jurassic flora but also in the older Mesozoic floras in Japan.

Introduction and acknowledgements

In continuation of our previous papers (Kimura and Tsujii, 1980a, b, '81), we here describe the fossil plants belonging to the Pteridospermales and Bennettitales from the Lower Jurassic Kuruma Group and Iwamuro Formation. The details of stratigraphy of plant-bearing formations and localities were given in our first paper (Kimura and Tsujii, 1980a).

We express our sincere gratitude to Professor Emeritus Thomas M. Harris, F. R. S. of the University of Reading for his helpful suggestions and critical reading over the present manuscript. We also give our thanks to Mr. Gumpei Mori, Mr. Noriyuki Sasaki and Mr. Akihiro Kobayashi for their kind help in collecting the fossils here described.

Systematic description

Pteridospermales
Genus Ctenozamites Nathorst 1886: 122
Ctenozamites sarrani (Zeiller) Harris
Pl. 41, Fig. 1; Text-fig. 1
Ctenopteris sarrani Zeiller: Zeiller, 1903, p. 53, pls. 6-7, fig. 1, la; pl. 8, figs. 1-2 (Hongay Coal-Field, North Viet-Nam); p. 292, pl. 44, figs. 3-4 (Tai-pin-tchang, North Yunnan; corresponding possibly to the Yipinglang Group): Sze, 1956, pp. 39, 146, pl. 35, figs. 3, 3a, 4 (Upper Triassic Yanchang Group, N-China).

Ctenozamites sarrani (Zeiller) Harris: Harris, 1961, p. 170 (name): Sze et al., 1963, p. 198, pl. 58, fig. 1 (reinserted from Sze, 1956, pl. 35, fig. 3a); pl. 59, figs. 2, 3 (from Sze, 1956, pl. 35, figs. 3, 4); Li P.C., 1976, p. 126, pl. 40, figs. 5, 6 (Upper Triassic Yipinglang Group).

Material: NNW-146, 846 (counterpart)
(Nishi-Neiridani).

Description: Pl. 41, Fig. 1 shows two pinna fragments. Leaf-outline and forking of main rachis are unknown. The pinnae are more than 14 cm long and 5.2 cm wide, nearly parallel-sided and with a thick...
pinna rachis, 4 mm wide with longitudinal ribs on its surface. Segments (or pinnules) are typically rhomboidal, 2.9 cm long and 1.7 cm wide, and arising on the upper side of pinna rachis at a wide angle. The apex of segments is obtuse or rounded, its margins are entire and are flat but apical margins are sometimes reflexed. The bases of segments are not contracted. Veins are 10-11 in number at base, then forking once or twice, but the marginal ones are mostly simple. They are nearly parallel and end in the outer margin. Text-fig. 1 shows the form of typical pinnules and venation. The cuticle is not preserved.

**Distribution and occurrence:** In the Kuruma Group, a single specimen was obtained from the Negoya Formation. This species has been known from the Upper Triassic of North Viet-Nam and of North and Middle China.

**Remarks:** Our leaf corresponds in size and outline of segments (pinnules) to *Ctenozamites sarrani*. But it is somewhat different from Zeiller's original specimens of *Ctenopteris sarrani*. Differences are:

- In the original specimens, the veins are more crowded and generally forking once, and the segments arise at reduced angle and are usually directed forwards, instead of arising at wide angle in ours.

- Our leaf resembles a well-known European species, *Ctenozamites cycadea* (Berger) Schenk (references, see Harris, 1961, p. 169; 1964, p. 95). But our leaf differs from *Ctenozamites cycadea* in its large-sized segments with denser veins forking twice, instead of medium-sized segments (2 cm long and 1 cm wide, according to Harris, 1961, '64) with coarser veins (usually 6) forking once-twice in *C. cycadea*.

- *Ctenozamites cycadea* finely illustrated by Delle (1967) from the Middle Jurassic of Tkvarchelian Coal-Basin (Transcausia) and *Ctenopteris cycadea* (Brongnarti) by Yang (1978) from the Upper Triassic Daqiaoade Formation, Sichuan, are also similar in form of segments to ours, but they are distinguished from ours by their medium-sized segments with coarser veins forking once or twice. *Ctenopteris megaphylla* described by Yang (1978) from the Upper Triassic Daqiaoade Formation resembles *Ctenozamites sarrani* in form but smaller.

- *Ctenozamites usnadzei* originally described by Doludenko and Svanidze (1969) from the Callovian of Georgia and later by Barnard and Miller (1976) from the Middle Jurassic of Iran, is distinguished from ours by its rhomboidal segments typically with a free acroscopic margin and decurrent basiscopic margin, and further by its small-sized segments with 1-3 small teeth at apex.

Recently 6 new *Ctenozamites* species were described from the Upper Triassic of China by Hsü et al. (1975) and Chen and Duan (1979a, b). Among them *Ctenozamites otoeis* described by Chen and Duan (1979a) from the Upper Triassic of Yanbian, has segments of similar size to our specimen of *C. sarrani*, but they are longer and have a decurrent base. The veins are more crowded.

This is the first record of the genus *Ctenozamites* in Japan.

### Bennettitales

**Genus Anomozamites** Schimper, 1870: 140

- *Anomozamites* sp. A

**Material:** A-0558 (a single specimen).

**Remarks:** Our leaf-fragment resembles *Anomozamites major* (Brongnarti) Nathorst, and also *Pterophyllum pinnatifidum* Harris. Further material is needed for
specific determination.

Genus *Otozamites* Braun, 1842

*Otozamites fujimotoi* Kimura

Text-figs. 2a-b

*Otozamites fujimotoi* Kimura: Kimura, 1959a, p. 23, pl. 12, figs. 2-4, 6; text-figs. 12-13 (Iwamuro).


**Emended diagnosis:** (Length and apex of leaf unknown.) In middle region rachis 2 mm wide, lamina 6 cm wide but narrower in basal part of leaf. Pinnae varied in form according to their position on a leaf, attached perpendicularly to the upper side of rachis by the lower half of base, thus the upper half free, forming a distinct angle entirely covering the rachis and the lower part of opposite pinna base. Pinnae mostly elongated but the proximal ones broadly deltoid or circular in form. Elongated pinnae 3 cm long or more, nearly parallel-sided, typically 1 cm wide. Deltoid or circular pinnae 8-20 mm long or more and 10-14 mm wide, with pointed apex. Circular pinnae with rounded apex restricted to basal part of a leaf. Veins on the lower half of pinna mostly simple or once forked and parallel, but those on free angle radiating, simple or once forked. Concentration of veins about 20 per cm. (Cuticle not preserved.)

**Distribution and occurrence:** *Otozamites fujimotoi* is occasional in the Iwamuro Formation, and seems to be local.

**Comparison and remarks:** Since Kimura (1959a) described this species, only a few additional specimens were obtained. *Otozamites fujimotoi* is characterized by its varied pinnae in form, with distinct acroscopic basal angle.

*Otozamites gissaricus* illustrated by Iminov (1976) from the Middle Jurassic of Central Asia, is similar in form to ours, but *O. gissaricus* is a smaller leaf with narrower pinnae, especially on the proximal part of a leaf.

Specimens determined by Iminov (1976) from the Upper Triassic of Central Asia as *Otozamites paniricus* Prynada are distinguished from *O. fujimotoi* by its pinnae with rounded or truncated apex. *Otozamites ptilophylloides* originally described by Barnard and Miller (1976) from the Middle Jurassic of Iran is similar in pinna form to *O. fujimotoi*, but it is macroscopically distinguished from ours by its pinnae mostly with rounded apex and smaller number of veins in each pinna.

Although we still do not know the form of the whole leaf of *Otozamites fujimotoi*, we feel sure it is distinct for its varied and characteristic pinna forms with distinct acroscopic angle.

*Otozamites neiridaniensis* Kimura and Tsujii sp. nov.

Pl. 42, Figs. 1-5; Pl. 43, Figs. 1-2; Text-figs. 3a-f

*Otozamites molinianus* Zigno: Oishi, 1940, p. 333, pl. 31, figs. 3, 3a, 4 (Neiridani).

*Otozamites sp.:* Oishi, 1940, p. 336, pl. 30, fig. 5 (Neiridani).

**Material:** Holotype; NEE-095 (Higashi-Neiridani). Paratypes; NEE-065, 174, TOB-013A, B, 050B, 050B', 050C (Tobiiwadani), NNW-084 (Nishi-Neiridani), NEG-251 (Negoya). Other specimens; NE-026 and other 9 specimens (Neiridani), NEE-007 and other 64, NNW-002 and other 57, NEG-006 and other 49, DAI-004 and other 38 (Dairagawa), TOB-
Tatsuaki KIMURA and Masanori TSUJI

3a

3e 2b' 2b

3e' 2b

3d

2b''

1

2a

3f

3b 3c

4 cm
Early Jurassic Plants

004 and other 21.

*Stratum typicum:* Negoya Formation, Kuru­ma Group. *Locus typicus:* Higashi-Neiridani, Asahi-machi, Shimo-Niikawa-gun, Toyama Prefecture (see Kimura and Tsuji, 1980a, p. 342, fig. 2). *Derivatio nominis:* After the Neiridani where the holotype and many other specimens were collected.

*Diagnosis:* Leaf rather large, long and narrow, linear; length estimated at 30 cm or more, width over the middle leaf typically about 2-2.5 cm, occasionally 3.7 cm. Leaf tapering gradually to both ends. Rachis rather thin, 1 mm wide, usually concealed. Pinnae oval or short-rectangular in form, typically 1.2 cm long and 0.8 cm wide, with rounded or obtusely pointed apex, attached on the upper side of rachis by the lower two-thirds or three-fourths of their width (accordingly upper one-third or one-fourth of acroscopic basal part free), at an angle of 60-90 degrees. Acroscopic basal corner slightly auriculated but seldom covering the pinna on the opposite side of the rachis. Basiscopic basal angle slightly contracted or occasionally straight but not decurrent. Near the leaf base, pinnae becoming shorter and more deltoid but still broad, and near the leaf apex, pinnae becoming narrower. Veins arising from proximal two-thirds or three-fourths of pinna base and radiating into the acroscopic corner and the rest of pinna, branching at all levels, at a concentration of 15 per cm at base. (Petiole not known and cuticle not preserved.)

*Distribution and occurrence:* *Otozamites neiridaniensis* is abundant in the Negoya Formation and rather rare in the Shinadani Formation. A doubtful leaf-fragment is known from Neiridani.

*Comparison and discussion:* *Otozamites neiridaniensis* is characterized by its oval or short-rectangular pinnae with a rounded or obtusely pointed apex. Its auricle is developed slightly if at all and its veins are crowded.

Oishi (1940) described several leaf-fragments from Neiridani (exact locality not clear) as *Otozamites molinianus.* But our observation of his figures shows that they do not belong to Zigno's species but to *Otozamites neiridaniensis,* because in his pinnae auricles are scarcely developed. In *Otozamites molinianus,* auricles are distinctly developed (Zigno, 1883; Möller, 1903). Oishi (1940) also described a single leaf-fragment as *Otozamites* sp. from Neiridani. This specimen agrees possibly with the basal pinnae of *Otozamites neiridaniensis.*

Among 160 *Otozamites* species hitherto known from the Mesozoic plant-beds, the following species resemble ours in rectangular or triangular pinnae with rounded or obtusely pointed apex, and with not or only slightly expanded auricle:

Text-figs. 1-3. (All natural size)

1. *Ctenozamites sarrani* (Zeiller) Harris; Outline of pinnules and venation (NNW-146; counterpart of NWW-846 shown in Pl. 41, Fig. 1).

2. *Otozamites fujimotoi* Kimura. 2a: A leaf-fragment with elongated and auriculated pinnae (A-4091; counterpart of A-4090 shown in Kimura, 1959a, text-fig. 12e). 2b-b''': Deltoid and auriculate pinnae at the basal part of a leaf (A-2054; redrawn from Kimura, 1959a, text-fig. 12b, a, d, c respectively).

3. *Otozamites neiridaniensis* Kimura and Tsuji sp. nov. 3a: A medium sized leaf (NEE-095, holotype; Pl. 42, Fig. 1). 3b: Ditto, with apex (TOB-050B, paratype). 3c: A large-sized leaf (TOB-050B', paratype; Pl. 42, Fig. 2). 3d: Apical part of a broken leaf (TOB-013B, paratype). 3e-e': Pinnae, showing the venation (NEE-255). 3f: A large-sized pinnae, showing the venation (NNW-084, paratype; Pl. 43, Fig. 1).
Otozamites falsus Harris: Harris, 1949, '69; Middle Jurassic of Yorkshire. O. indosinensis Zeiller: Zeiller, 1903; Upper Triassic of North Viet-Nam. O. kondoi Oishi: Oishi, 1940; Upper part of Middle Jurassic Moné Formation, NE-Japan. O. parallelus Phillips: Harris, 1969; Middle Jurassic of Yorkshire. O. reglei (Brongniart) Saporta: Brongniart, 1828; Bartholin, 1894; Möller, 1903 (cfr. reglei); Lower Jurassic of Bornholm. O. simpsoni Harris: Harris, 1949 (regarded as O. feistmanteli Zigno), '69; Middle Jurassic of Yorkshire.

These differ as follows: Otozamites falsus has mostly rhomboid pinnae with an acute apex. O. indosinensis, O. parallelus and O. simpsoni have more elongate pinnae. Ptilophyllum khargaense (Kilpper, 1966) from the Middle Jurassic (?) of Egypt has pinnae of rather similar shape but the lower ones differ in being imbricate. The closest to our species is Otozamites kondoi but its pinnae have a nearly symmetrical base and its veins which are coarser, only fork near their origin.

Genus Pterophyllum Brongniart, 1828: 25

Pterophyllum jaegeri Brongniart described by Oishi (1931) from Tsuchizawa is not Pterophyllum but referable to Nilssonia sp. A to be described later.

**Pterophyllum ex gr. propinquum** Goeppert

Pl. 41, fig. 2; Pl. 42, figs. 6-7; Pl. 43, figs. 3-6; Text-figs. 4a-n

**Specimens from East Asia:**

*Pterophyllum propinquum* Goeppert: Oishi, 1931, p. 245, pl. 18, figs. 1-2 (Tsuchizawa, Kuruma Group): Yabe and Oishi, 1933, p. 227, pl. 34, fig. 2 (Lower-Middle Jurassic of Liaoning, NE-China): Oishi, 1940, p. 344 (remarks): Kimura, 1959b, p. 70, pl. 2, fig. 2 (Kotaki Coal-Field, Kuruma Group): Sze et al., 1963, p. 157, pl. 61, fig. 8 (reinserted from Yabe and Oishi, 1933, pl. 34, fig. 2).

*Pterophyllum aff. propinquum* Goeppert: Yabe and Oishi, 1929, p. 91, pl. 18, fig. 6 (Daedong Group, N-Korea).

For European references, see Antevs, 1919, p. 28.

**Material:** NNW-009 and other 32 specimens (Nishi-Neiridani), DAI-027 (Dairagawa), SHI-035, 040 (Shinadani), KR-087, 090 (Tsuchizawa), 4962113 (Kotaki Coal-Field), A-7535, 751124 (Iwamuro).

**Description:** Leaves are varied in size and form, but are mostly medium-sized and oblanceolate in outline. Leaves taper gradually towards the proximal end, are more than 6.5 cm long and 4 cm wide at the widest portion, and possibly contract suddenly at the apex. The rachis is rather thin, 2 mm wide. The petiole is not known. The pinnae arise at a wide angle from the lateral margins of rachis. They are rectangular, up to 2 cm long and are shorter towards the base of the leaf. The width of pinnae is variable but often about 1.2 cm; pinnae near the leaf apex are narrow. Margins of adjacent pinnae are mostly apart but are always connected to one another near the rachis by a web of lamina. The apex of pinnae is truncate in lower part of leaf, but rounded in the middle of leaf. Veins are parallel and simple or often fork once. Their concentration is typically 25 per cm at the middle of pinna. The cuticle is not preserved. Text-figs. 4a-n show varied pinna forms and venation.

**Distribution and occurrence:** This species is locally very abundant in the Negoya Formation, but rather rare in the Shinadani and Iwamuro Formations. In East Asia, this species occurs in the Lower-Middle Jurassic of NE-China and the Upper Triassic (?) of N-Korea.

**Remarks:** *Pterophyllum ex gr. propinquum* is characterized by its rectangular pinnae with an expanded base and truncated or rounded apex. Our leaves are indistinguishable from *Pterophyllum propinquum* illustrated in detail by Antevs (1919) from the Liassic Hör Sandstone, Sweden, although in our large collection, leaves with elongated pinnae such as Antevs’ pl. 3, figs. 10-12 have not been found.

The leaves regarded by Oishi (1931) as *Pterophyllum propinquum* from Tsuchizawa and by Yabe and Oishi (1929) as *P. aff. propinquum* from N-Korea are
indistinguishable from ours, although the Korean leaf is about twice as large as ours. A leaf-fragment regarded by Yabe and Oishi (1933) as *Pterophyllum propinquum* possibly from the Beipiao Group (Lower-Middle Jurassic), NE-China is similar in pinna form to ours.

*Pterophyllum* leaves with similar pinna form to ours have been described as follows:


They are distinguished from ours as mentioned below. In *Pterophyllum pinnatifidum*, pinna apices are often acuminated. In *Pterophyllum kochi*, pinna bases are not contiguous except in the apical part of leaf and are square in the middle of leaf, and slightly contracted in the proximal part of leaf. In ours, pinna bases are usually contiguous from one pinna to the next.

A little known *Pterophyllum abnorme* is distinguished from ours by its usually twice forked veins instead of simple or once forked ones in ours. In *Pterophyllum sensinovianum*, its pinnae are more elongated than those of ours.

*Pterophyllum propinquum* illustrated by Iminov (1976) from the Upper Triassic of Pamir is, in our opinion, rather close to *P. tsetzei* Schenk or to *P. subaequale* Hartz because of its large-sized leaves with more elongated pinnae.

*Pterophyllum* sp. A illustrated by Weber (1968) from the Rhaeto-Liassic of Bayreuth resembles *P. propinquum*. *Pterophyllum exhibens* originally described by Li, P. C. (1964) from the Upper Triassic Xujiahe Formation, Sichuan and later by Zhou, T. S. (1978) from the Upper Triassic Wenshan Formation, Fujian, China, is similar in its expanded pinna base, but it is distinguished by its more elongated pinnae with smaller number of veins (5-12) in each pinna.

*Pterophyllum sp. A*

*Pterophyllum sp. A* and sp. B: Kimura, 1959a, p. 24, pl. 9, figs. 2-3 (Iwamuro).

Remarks: Kimura (1959a) illustrated two *Pterophyllum* leaf-fragments as *P. sp. A* and sp. B. Our study convinced us that they are conspecific but the specimens are too poorly preserved to determine. Their cuticle is not preserved.

Text-figs. 5-6 (a-f). (All natural size, unless otherwise indicated)

5. *Ptilophyllum cfr. cutchense* Morris. 5a: A leaf-fragment, showing the venation (TE-001; Pl. 43, Fig. 7). 5b: Ditto, with apex (TE-003; Pl. 43, Fig. 8). 5b’ : Venation drawn from 5b.

6. *Ptilophyllum nipponicum* Kimura and Tsuji sp. nov. 6a: A typical leaf (NEG-720, holotype; Pl. 43, Fig. 9). 6a’ : Venation drawn from 6a. 6b: Lower part of a leaf (NNW-806, Pl. 41, Fig. 3). 6b’ : Possibly representing the basal part of 6b. 6c: Basal part of a leaf, bearing broader pinnae with truncated distal margin (NE-067, paratype). 6d: Apical part of a medium-sized leaf bearing rather remotely set pinnae (NNW-353, paratype; Pl. 41, Fig. 4). 6d’ : Venation drawn from 6d. 6e: A leaf-fragment bearing rectangular pinnae (NEE-074; Pl. 42, Fig. 8). 6e’ : Venation drawn from 6e. 6f: A leaf-fragment bearing broader and remotely set pinnae (NNW-745).
Genus *Ptilophyllum* Morris, 1840: 327

About 60 Mesozoic species have been described. Many of them have similar pinnae. Thus except the leaves with distinct morphological features, it is getting difficult to identify them depending only on their macroscopical forms. Our knowledge of the epidermis of this genus owes much to the studies of Jacob and Jacob (1954), Klappe (1965, '66), Harris (1941, '42, '46, '49, '53, '69), Doludenko (1963), Bose and Kasat (1972) and Barnard and Miller (1976).

We recognized five forms in the Lower Jurassic of Japan. This is the first record...
of this genus in the older Mesozoic floras in Japan. The phytogeographical implication on the occurrence of this genus in the Japanese Lower Jurassic will be mentioned in our later paper treating the concluding chapter of this series.

Key to the Japanese Lower Jurassic species of *Ptilophyllum*

1. Leaf large-sized, widest part over 5.4 cm .................... *P. nipponicum* sp. nov.
1'. Leaf medium-sized about 3 cm wide ................................. 2
1''. Leaf small-sized width less than 1 cm ............................... 3
2. Pinnae elongate-rectangular ............................... *P. shinadaniense* sp. nov.
2'. Pinnae elongate-oval or rectangular ............................... *P. sp. A*
3. Pinnae elongate-triangular ............................... *P. cfr. cutchense*
3'. Pinnae rhombic ............................... *P. sp. B*

*Ptilophyllum* cfr. *cutchense* Morris

Pl. 43, Figs. 7-8; Text-figs. 5a-b

Comparable specimens: *Ptilophyllum cutchense* Morris: Bose and Kasat, 1972, p. 118, pl. 1, figs. 7-10; pl. 2, figs. 14-17 (Upper Jurassic of Rajmahal Hills and Lower Cretaceous Jabalpur Series, India).

Material: TE-001, 003 (Teradani, Negoya Formation).

Description: Two small-sized leaf-fragments were obtained. The leaves are 0.8–1 cm wide with an acuminate apex as shown in Pl. 43, Fig. 7. The rachis which is partially exposed, is about 0.5 mm wide. Pinnae are attached on upper surface of rachis, closely set or imbricate, mostly attached by entire base, arising at an angle of about 60–90 degrees. Pinnae are as a whole linear, elongate-triangular, sometimes rhomboidal, sublate or ovate in form; margins are straight. Apices are usually obtuse or rounded and the basiscopic basal margin straight, slightly contracted, rounded or decurrent. Veins arise from the whole base. They are parallel, mostly simple, 5 in number on each pinna. Cuticle is not preserved.

Distribution and occurrence: This form is rare and known only from Teradani, Negoya Formation.

Remarks: Our leaves resemble closely some smaller leaves illustrated by Bose and Kasat (1972) as *Ptilophyllum cutchense*. *Ptilophyllum horridum* Roy and *P. institacallum* Bose are allied forms to *P. cutchense*. But both are distinguished from our leaves by their radiating

Text-figs. 6 (g-k)–9. (All natural size, unless otherwise indicated)

6. *Ptilophyllum nipponicum* Kimura and Tsuji sp. nov. 6g: A leaf-fragment bearing elongated pinnae with decurrent base and contracted acrosopic base (NNW-241, paratype). 6g': Venation drawn from 6g. 6h: Small-sized leaf-fragment (NNW-353, paratype). 6i: Large-sized leaf-fragment bearing broader pinnae with slightly decurrent base (NNW-241, paratype). 6j: Apical part of a leaf (NE-169). 6k: Basal part of a leaf with thick petiole of which base is expanded. Pinnae are small-sized, and with straight or slightly contracted base (NNW-111, paratype; Pl. 43, Fig. 10).

7. *Ptilophyllum shinadaniense* Kimura and Tsuji sp. nov. 7a: A part of leaf (SHI-007, holotype; Pl. 41, Fig. 5). 7b: A leaf-fragment, showing the venation (SHI-024, paratype). 7c: Ditto (SHI-019, paratype; Pl. 41, Fig. 6).

8. *Ptilophyllum* sp. A; a part of leaf (SHI-030; Pl. 43, Fig. 11). 8': Venation drawn from 8.

9. *Ptilophyllum* sp. B. 9a: A part of leaf (NEG-51; Pl. 43, Fig. 12). 9b: Ditto (A-0379). 9b': Venation drawn from 9b.
and forked veins instead of mostly simple and parallel ones.

*Ptilophyllum cantherifera* originally described by Douglas (1969) from the Lower Cretaceous of Victoria (Australia) is similar in form, but is distinguished by its pinnae attached by central basal area instead of by the entire base in ours.

Thus our leaves are most like the small-sized *Ptilophyllum cutchense*, but we here refrain from fully identifying them with this Indian species, because our leaves without cuticle are only two and incomplete.

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*Ptilophyllum nipponicum* Kimura and Tsujii sp. nov.

Pl. 41, Figs. 3-4; Pl. 42, Fig. 8; Pl. 43; Figs. 9-10; Text-figs. 6a-k

**Material:** Holotype; NEG-270 (Negoya). Paratypes; NNW-111, 241, 353, 697, 806 (Nishi-Neiridani), NE-067 (Neiridani). Other specimens; NEG-071 and other 3 specimens, NNW-004 and other 6, NEE-074 (Higashi-Neiridani), NE-169, DAI-086 (Dairagawa), IN-001, 002 (Inumatadani).

**Stratum typicum:** Negoya Formation, Kuru­ma Group. **Locus typicus:** The Negoya, Asahimachi, Shimo-Nikawa-gun, Toyama Prefecture. **Derivatio nominis:** After Nippon meaning Japan in Japanese.

**Diagnosis:** Leaf large, oblong or oblan­ceolate in form; the widest part 5.4 cm. (Whole length and leaf apex unknown.) Rachis slender 2 mm wide at the middle of leaf but 3 mm wide at the basal part. Petiole about 5 cm long with striated surface, base distinctly expanded. Pinnae varied in form according to their position on a leaf, attached on the upper side of rachis at an angle of 50-90 degrees by entire base, set closely but sometimes remotely. Middle pinnae elongate-rectangular, typically 3.5-4 cm long and 0.5-1 cm wide. Apical pinnae similar in form to those of middle ones but smaller in size. Basal pinnae typically deltoid in form, 1.5 cm long and 0.5-0.8 cm wide at base, but smaller towards the base of leaf. Acroscopic basal margin mostly rounded and basiscopic basal margin straight, slightly contracted or slightly decurrent. Apex acutely or obtusely pointed. Veins numerous, divergent, forking at all levels, 28-30 per cm in density at the middle of pinna. (Cuticle not preserved.)

**Distribution and occurrence:** *Ptilophyll­um nipponicum* is common only in the Negoya Formation.

**Comparison and discussion:** It is clear that our leaves belong to *Ptilophyllum* redefined by Harris (1969), because our acroscopic pinna base is not auriculated and the basiscopic pinna base is typically decurrent.

*Ptilophyllum nipponicum* is characterized by its large-sized leaf with elongated pinnae above and deltoid pinnae below with divergent and forked veins, and its thick petiole and expanded base.

Several *Ptilophyllum* species with large leaves have been described. *Ptilophyllum nipponicum* closely resembles *P. hirsutum* Thomas and Bancroft described in detail by Harris (1949, '69) from the Middle Jurassic of Yorkshire. But the pinnae of *Ptilophyllum hirsutum* do not have a decurrent basal margin.

*Ptilophyllum harrisi­anum* described by Kilpper (1968) from the Liassic of N-Iran has pinnae of similar size but with an auriculate acroscopic base. Kilpper's *Ptilo­phyllum zirabense* (1968) has more elong­ated pinnae.

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*Ptilophyllum shinadaniense* Kimura and Tsujii sp. nov.

Pl. 41, Figs. 5-6; Text-figs. 7a-c

**Material:** Holotype; SHI-007 (Shinadani).
Paratypes; SHI-019, 024.

*Stratum typicum*: Shinadani Formation, Kuruma Group (see Kimura and Tsujii, 1980a, p. 342, fig. 2). *Locus typicus*: The Shinadani (near Agero Village), a branch of the Dairagawa, Omi-machi, Nishi-Kubiki-gun, Niigata Prefecture. *Derivatio nominis*: After the locality, the Shinadani where the holotype and paratypes were collected.

**Diagnosis**: Leaf medium-sized, 3 cm wide. (Whole length unknown.) Pinnae arising at an angle of 65–80 degrees to the rachis, elongate-rectangular in form, typically 1.8 cm long and 3.5–4 mm wide. Width of pinnae about one-fifth its length. Pinnae straight or very slightly falcate, apex obtusely pointed, basiscopic basal angle normally decurrent but often concealed by the pinna below. Veins arising from whole base of pinna, nearly parallel, often forking once at the middle of pinna, 8–10 in number in each pinna. (Cuticle not preserved.)

**Distribution and occurrence**: *Ptilophyllum shinadaniense* is rare and known only from the Shinadani Formation.

**Discussion and comparison**: *Ptilophyllum shinadaniense* is characterized by its medium-sized elongate-rectangular pinnae with parallel veins often forking once.

*Ptilophyllum contiguum* originally described by Sze (1949) and later by Wu et al. (1980) from the Lower Jurassic Xiangxi (formerly Hsiangchi) Formation in W-Hubei, China has pinnae of similar form. But it is distinguished by its small-sized leaf (13.5 cm long and 1.6 cm wide) and fewer veins (4–6 in each pinna).

*Ptilophyllum basekgabense* originally described by Barnard and Miller (1976) from the Middle Jurassic of N-Iran has smaller pinnae (8–15 mm long and up to 3 mm wide) with fewer veins (4–5 in each pinna).

Some leaves of *Ptilophyllum caucasicum* Dolundenko and Svanidze from the Upper Jurassic of Georgia resemble *P. shinadaniense*, but others have very long and narrow pinnae (Dolundenko and Svanidze, 1969).

*Ptilophyllum boreale* (Heer) (Seward, 1917; *Zamites borealis* by Heer, 1874) from the Lower Cretaceous of Greenland is distinguished by its stout rachis and fewer veins (3–5 in number in each pinna).

*Ptilophyllum sokalense* described by Dolundenko (1963) from the Jurassic of W-Ukraine has pinnae of similar form, but their basiscopic margin is mostly straight or slightly contracted.

**Ptilophyllum sp. A**

Pl. 43, Fig. 11; Text-fig. 8, 8’

**Material**: SHI-030 (Shinadani).

**Description**: Leaf medium-sized, elongated, 2.5 cm wide over the most part; neither end known. Pinnae elongate-oval or rectangular, attached by entire base on the upper side of rachis (2 mm wide) at an angle of 60–90 degrees, 1.4 cm long and 0.5 cm wide. Acroscopic basal angles mostly rounded or slightly decurrent, apices rounded or obtusely pointed. Veins indistinct, possibly simple and parallel, not radiating, 9 in each pinna. (Cuticle not preserved.)

**Distribution and occurrence**: A single specimen was obtained from the Shinadani Formation.

**Remarks**: Our specimen is characterized by its elongate-oval or rectangular pinnae. Our specimen is distinguished from *Ptilophyllum shinadaniense* from the same locality by its shorter pinnae.

Some leaves regarded as *Ptilophyllum caucasicum* Dolundenko and Svanidze (Dolundenko and Svanidze, 1969; Dolundenko and Orlovskaja, 1976) from the Upper Jurassic of Georgia and Kazakhstan are similar in pinna form and venation to
ours, but others have very long and narrow pinnae.

**Ptilophyllum sp. B**

Pl. 41, Fig. 7; Pl. 43, Fig. 12; Text-figs. 9a-b'

*Material*: A-0379, 0456, 7564 (Iwamuro), NEG-051 (Negoya).

*Description*: Leaves small-sized, long and narrow and nearly parallel-sided, 4 mm wide. Rachis 1 mm wide but mostly concealed. Pinnae rhombic, attached by entire base at a wide angle on the upper side of rachis, closely set or imbricate, apices usually obtuse, acrospecific basal margin straight or rounded, basispecific basal margin mostly straight but sometimes slightly contracted. Veins indistinct arising from the whole base, parallel, probably simple, about 5 in each pinna. (Cuticle not preserved.)

*Distribution and occurrence*: This form occurs sparsely in the Iwamuro and Negoya Formations.

*Remarks*: Judging from the mode of pinna attachment and venation, our leaves may belong to *Ptilophyllum*. So far as we know, such small-sized leaves as ours have been described as *Ptilophyllum* or *Otozamites* as follows: *Ptilophyllum bengalense* (Oldham) Schimper: Kilpper, 1968; Liassic of N-Iran. *Otozamites abreviatus* Feistmantel: Feistmantel, 1876; Jurassic of India. *O. bengalensis* (Oldham and Morris) Schimper: Oldham and Morris, 1862 (regarded by them as Palaeozamia bengalensis); Jurassic of India. *O. bunburyanus* Zigno: Zigno, 1881; Middle Jurassic of Italy. *O. contiguus* Feistmantel: Feistmantel, 1767; Jurassic of India. *O. kilpperiana* Barnard and Miller: Barnard and Miller, 1976; Middle Jurassic of N-Iran. *O. tenuatus* (Leckensby) Harris: 1969; Middle Jurassic of Yorkshire. *O. vemavaramensis* Bose and Jain: Bose and Jain, 1967; Upper Jurassic (?) of India. Among these, our leaves are most like *Ptilophyllum bengalensis* in pinna form. But we refrain from determining it specifically because our leaves are all incomplete.

**References**


KIMURA and TSUJI: Early Jurassic plants

Plate 41


—— (1961): The form and structure of Ctenozamites cycadea, Bull. Brit. Mus. (Nat. Hist.), Geol., vol. 6, no. 6, p. 159-
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173, pls. 31-32.


— (1976) : Cycadophytes of the late Triassic and Jurassic of Middle Asia and their stratigraphic significance. 72 p., 48 pis. Ibid.


— (1959b) : Mesozoic plants from the Kotaki Coal-Field, the Kuruma Group, Central Honshu, Japan. Ibid., p. 61-83, incl. pls. 1-2.


— and —— (1980b) : Ditto. Part 2. Ibid., 120, p. 449-465, pls. 54-56.


Explanation of Plate 42

Figs. 1-5. Otozamites neiridaniensis Kimura and Tsujii sp. nov.; all figures, ×1. 1, 3. Leaves of typical size. 1; (NNE-095, holotype; Text-fig. 3a), 3; (NE-046). 2. A large-sized leaf (TOB-050B', paratype; Text-fig. 3c). 4. Basal part of a leaf (NEE-250). 5. Ditto (NEE-073).

Figs. 6-7. Pterophyllum ex gr. propinquum Goeppert; both, ×1. Leaf-fragments. 6; (NNW-073), 7; (NNW-600).

Fig. 8. Ptilophyllum nipponicum Kimura and Tsujii sp. nov.; apical part of a leaf (NEE-074; Text-fig. 6e), ×1.
KIMURA and TSUJII: Early Jurassic plants

Plate 42


Geographical names in China (with former expression in parentheses): Beipiao (Pempiao), Daqiaode, Fujian, Hubei (Hupeh), Nariwa, Neiridani, Nishi-Neiridani, Shinadani, Teradani, Tobiiwadani, Tsuchizawa, Fujian, Hubei, Liaoning, Sichuan, Taipingchang, Wengbinshan, Xiangxi, Yanbian, Yanchang, Yongren, Yunnan.

Geographical name in Korea (with former expression): Daedong (Taedong).

Explanation of Plate 43

Figs. 1-2. Otozamites neiridaniensis Kimura and Tsujii sp. nov.; both, x1. 1. A large-sized leaf-fragment with elongated pinnae (NNW-084, paratype; partly shown in Text-fig. 3f). 2. Basal part of a leaf (TOB-032).

Figs. 3-6. Pterophyllum ex gr. propinquum Goeppert; all figures, x1. Leaf-fragments. 3; (NNW-240), 4; (NNW-356B), 5; (NNW-356; Text-fig. 4j), 6; (NNW-014).

Figs. 7-8. Ptilophyllum cfr. cutchense Morris; both, x1. Unsatisfactorily preserved leaf-fragments. 7; (TE-001; Text-fig. 5a), 8; (TE-003; Text-fig. 5b).

Figs. 9-10. Ptilophyllum nipponicum Kimura and Tsujii sp. nov.; both, x1. 9. A leaf lacking both apical and basal portions (NEG-270, holotype; Text-fig. 6a, a'). 10. Basal part of a leaf with petiole of which base is expanded; upper arrow indicates a thick rachis and lower one an expanded petiole-base (NNW-111, paratype; Text-fig. 6k).

Fig. 11. Ptilophyllum sp. A; a leaf-fragment (SHI-030; Text-fig. 8), x1.

Fig. 12. Ptilophyllum sp. B; a leaf-fragment (NEG-051; Text-fig. 9a), x2.
742. JAPANESE MIocene CIRRIPED BALANUS SENDAICUS: A COMPARISON WITH TETHYAN BALANUS CONCAVUS GROUP*

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Abstract. Balanus sendaicus was described as a new species by Hatai, Masuda and Noda (1976) based on a single scutum from the Miocene Moniwa Formation, northern Honshu, Japan. However, the scutum deposited in the Saito Ho-on Kai Museum, Sendai, Japan (Hatai et al., 1976) could not be found. Tergum and shell wall, which with scutum comprise the skeletal elements, had not been described. According to my investigation of topotype materials and of materials illustrated by Hatai et al. (1976), the shell walls described and illustrated under the name of B. rostratus by Hatai et al. (1976) belong to B. sendaicus. B. sendaicus, including tergum undescribed by Hatai et al. (1976), is therefore defined in this paper. B. sendaicus is distinct from the already known taxa, as mentioned by Hatai et al. (1976). However, B. sendaicus is closely related to the extinct B. concavus sensu de Alessandri (1906), which flourished in the Mediterranean region (Tethys) from the Oligocene to Pleistocene. B. sendaicus belongs to the B. concavus species group represented by the nominal species based on having transverse septa in longitudinal (parietal) tubes of shell wall and the characteristic ornamentation of scutum. Disappearance of the B. concavus group from the Atlantic and the Mediterranean regions in Pleistocene is mysterious as mentioned by Pilsbry (1916), though "four" species belonging to the B. concavus group are living in the eastern Pacific (Newman, 1979). B. sendaicus is restricted to the Miocene, is the first fossil record of the B. concavus group from the east Asia, and indicates the presence of a connection between the Tethys and the east Asia.

Introduction

Balanus sendaicus was proposed as a new species by Hatai, Masuda and Noda (1976), based on a single scutum from the Miocene Moniwa Formation of the Sendai area of northeast Honshu, Japan. Seven new species including B. sendaicus, an already known species of B. rostratus, and an indetermined species of Balanus were described from the same locality.

Four new species including B. sendaicus were based on scuta and three new species, B. rostratus and B. sp. based on the shell walls. No tergum was described.

Fossil specimens are usually found as fragmental skeletal elements of shell wall and opercular valves, and therefore it is difficult to reconstruct the exoskeleton of a species from the mixture of fragments of several extinct species. Under these circumstances, each fragmental skeletal element, such as shell wall, scutum or tergum, has been frequently chosen as
representative of a new species. Thus in some cases, an individual consisting of three kinds of skeletal elements, may possesses three different species names. Therefore, biological study of fossil specimens of extinct species is faced with difficulties unless basic work, revealing the precise combination of skeletal elements, is done first. When a complete shell wall is discovered, it is necessary to determine whether or not opercular valves are preserved in the shell cavity.

In this paper the following points are considered: 1) Description of shell wall and tergum of *B. sellaicus*, whose original description was based on a single scutum, 2) The status of *B. sellaicus* as a previously unknown taxon, as discussed by Hatai et al. (1976), 3) The affinity of *B. sellaicus* with known species and species groups, and 4) The stratigraphic and geologic distributions in Japan and the paleoecological significance of *B. sellaicus*.

*Balanus sellaicus*, type-locality and formation

The type-locality of this species is an outcrop (Loc. 4) of the Miocene Moniwa Formation situated about 200 m south of the Oide Bridge across the Natori River, near Moniwa, Sendai City, Miyagi Prefecture, northeast Honshu, Japan. The Miocene Moniwa Formation overlies the Miocene Takadate Andesite with a clino-unconformity. *B. sellaicus* was collected from the basal part of the Moniwa Formation which consists of gravelly calcareous medium-grained sandstone containing very abundant well preserved marine fossils. Reports on brachiopods, shark teeth, fossil problematica, and on pelecypods have already been published (Hatai et al., 1973, 1974a, 1974b, 1974c, respectively). A report on cirripeds was the fifth of this series from the same locality. Besides *B. sellaicus*, shell walls but no terga of *B. rostratus*, *B. miyagensis*, *B. tohokuensis*, *B. rikuzensensis*, and *B. sp.* and scuta of *B. oidiensis*, *B. moniwaensis*, and *B. natori-anus* were described. Except for *B. rostratus* and *B. sp.*, all were proposed as new species.

Combination of skeletal elements of *B. sellaicus*

The writer has collected many well preserved fossil cirripeds from the above locality. Four species by shell walls, five species by scuta, and two species by terga were distinguished. However, the combination of these exoskeleton elements was not clear. Judging from shell size and the frequency of occurrence of each element, it was presumed that shell wall of *B. rostratus* and scutum of *B. sellaicus*, as described by Hatai et al. (1976) and a previously undescribed tergum probably constituted skeletal elements of one species. This is also supported by the fact that the following morphological characteristics of shell walls of *B. rostratus* identified by Hatai et al. (1976) are clearly different from the true *B. rostratus* proposed by Pilsbry (1916); narrow radii and oblique summits of radii. In order to confirm the above conjecture additional material was sought.

Recently some shell walls collected from the same locality, identical with *B. rostratus* of Hatai et al. (1976), were found to contain paired scuta and terga within their shell cavity. The specimen of *B. rostratus* illustrated by Hatai et al. (1976, pl. 2, fig. 2, left, and Pl. 44, Figs. 2a–c, left, in this paper) was also found to contain four opercular valves in its shell cavity (Pl. 44, Figs. 2d–g, in this paper). It is important to note that morphologically
these scuta are identical with the holotype scutum of *B. sendaiicus* (Hatai *et al.* 1976, pl. 2, figs. 9 and 10). It can, therefore, be concluded that *B. sendaiicus* is conspecific with *B. rostratus* of Hatai *et al.* (1976). However, *B. rostratus* of Hatai *et al.* (1976) is not the true *B. rostratus* in the sense of Pilsbry (1916) and the name *B. sendaiicus* should be used. As a result of the confirmation of the correct combination of skeletal elements, the taxonomic status and the affinity of *B. sendaiicus* can be discussed.

In the description of *B. sendaiicus*, Hatai *et al.* (1976) pointed out that “In the external sculpture, the present scutum resembles that of *Balanus concavus* Bronn (Pilsbry, 1916, p. 100, pl. 21, fig. 1), a Pliocene species of the British Red Crag especially in cancellated sculpture, bifurcation of the longitudinal striae, general shape of scutum,...”. Thus, owing to distinct growth ridges and longitudinal ridges or striations frequently bifurcated on external surface, scutum of *B. sendaiicus* possesses common morphological characteristics found in scuta of all members of the *B. concavus* species group. The tergum of *B. sendaiicus* described here also has a long spur and partially closed spur furrow, characteristics found in some members of the *B. concavus* group. These morphological characteristics found in *B. sendaiicus* are also present in members of the *B. perforatus* species group. However, in members of the *B. concavus* group, the external surface of scutum is heavily ornamented, the aperture is small, and the carina strongly curved. Therefore, *B. sendaiicus* is regarded as a member of the *B. concavus* group.

**Morphological comparisons of *B. sendaiicus* with the living taxa of the *B. concavus* group**

According to Newman and Ross (1976), the *B. concavus* group contains the following “five” living taxa, *B. aquila (=B. gregarius* Conrad), 1856; a senior synonym of *B. aquila* Pilsbry, 1907, see Zullo, 1964:360, 1969:6, 1979:4), *B. concavus concavus*, *B. c. mexicanus*, *B. eyerdami (=B. panamensis* Rogers, 1948; a senior synonym of *B. eyerdami* Henry, 1960, D. P. Henry, pers. comm., in Newman and Ross, 1976:102), and *B. regalis*. *B. concavus concavus* of Newman and Ross (1976) includes the two already known “*B. c. indicus*” and *B. c. sinensis* as synonyms of *B. c. concavus* (Newman and Ross, 1976). *B. c. mexicanus* lacking the transverse septa in the parietal tubes of shell wall does not belong to the *B. concavus* group in the strict sense, but is close to *B. pacificus* of the *B. perforatus* group (Newman, pers. comm.). These four extant members exclusive of *B. c. mexicanus* are living in Indo-Pacific, *B. c. concavus* in Dar-es-Salaam of Tanzania, the Persian Gulf and Hong Kong, and the other three species on the eastern Pacific. In the following paragraph, *B. sendaiicus* is compared with these four “living” taxa of the *B. concavus* group on the basis of morphology.

*B. gregarius* (Conrad), 1856 was originally described as *Tamiosoma gregaria*, a new genus and species of a rudistid pelecypod by having the peculiar, elongate, vesiculose basis. This species is the most widespread and commonly encountered barnacle in the Miocene and Pliocene formations of central and southern California and Baja California regions (Zullo, 1964, 1969, 1979). “It was not until the opercular valves were described by Woodring”, in Woodring *et al.* (1940), “that any
Table 1. List of members of the *B. concavus* group and geographic and stratigraphic ranges quoted from Newman and Ross (1976) except for *B. concavus concavus* and "*B. concavus indicus".* [Oligo.: Oligocene, Mio.: Miocene, Plio.: Pliocene, Pleisto.: Pleistocene]

<table>
<thead>
<tr>
<th>Species</th>
<th>Date</th>
<th>Location</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Balanus bloxhamensis</em> Weisbord, 1966:48</td>
<td>fossil, (Florida; Mio.)</td>
<td></td>
<td></td>
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<tr>
<td><em>B. concavus concavus</em> Bronn senus de Alessanri, 1906:295</td>
<td>fossil (Europe; Oligo.-Pleisto.)</td>
<td></td>
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</tr>
<tr>
<td><em>c. alloplax</em> Pilsbry and Olsson, 1951:200</td>
<td>fossil, (Ecuador; Oligo.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>c. chesapeakeensis</em> Pilsbry, 1916:103</td>
<td>fossil, (Maryland; Mio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>c. coosensis</em> Dall, 1909:138</td>
<td>fossil, (Oregon; Mio.)</td>
<td></td>
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<tr>
<td><em>c. dallonii</em> Davadie-Suauveau, 1952:20</td>
<td>fossil, (Algeria; Plio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>c. eorytus</em> Pilsbry, 1924:1</td>
<td>fossil, (Haiti; Mio.)</td>
<td></td>
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<tr>
<td><em>c. finchii</em> Lea, 1833:211</td>
<td>fossil, (Maryland; Mio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>c. glyptopoma</em> Pilsbry, 1916:102</td>
<td>fossil, (east USA; Mio., Panama &amp; east Mexico; Plio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>c. indicus</em> Nilsson-Cantell, 1932:2</td>
<td>living, [Dar-es-Salaam, Tanzania]</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>c. oligoseptatus</em> Kolosváry, 1961:149</td>
<td>fossil, (USSR; Oligo.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>c. proteus</em> Conrad, 1834:134</td>
<td>fossil, (east USA; Mio.-Plio.)</td>
<td></td>
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</tr>
<tr>
<td><em>c. raphanoides</em> Moroni-Ruggieri, 1952:71</td>
<td>fossil, (Italy; Plio.)</td>
<td></td>
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<tr>
<td><em>c. rarispeptatus</em> Pilsbry, 1918:186</td>
<td>fossil, (Panama; Mio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>c. rubescense</em> Seguenza, 1876:450</td>
<td>fossil, (Italy; Tertiary)</td>
<td></td>
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<tr>
<td><em>c. scutorum</em> Seguenza, 1876:74</td>
<td>fossil, (Italy; Plio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>gregarius</em> (Conrad), 1856:315</td>
<td>living, [California, 0-18 m], fossil, (central, southern &amp; Baja California; Mio.-Plio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>indicus</em> Withers, 1923:291</td>
<td>fossil, (Pakistan; Mio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>panamensis</em> Rogers, 1948:95</td>
<td>living, [Gulf of California to Pacific coast of Panama]</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>polyseptatus</em> Pilsbry, 1924:2</td>
<td>fossil, (Haiti; Mio.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>regalis</em> Pilsbry, 1916:108</td>
<td>living, [southern &amp; Baja California]</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>sendaiicus</em> Hatai, Masuda and Noda, 1976:13</td>
<td>fossil, (Japan; Mio.)</td>
<td></td>
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<tr>
<td><em>talquinensis</em> Weisbord, 1966:37</td>
<td>fossil, (Florida; Mio.)</td>
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<tr>
<td><em>vadászii</em> Kolosváry, 1949:2</td>
<td>fossil, (Europe; Mio.)</td>
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</table>

An attempt could be made to determine the affinities of this unique species." "Woodring concluded that *B. gregarius* was related to the *B. concavus* Bronn group." "Comparison of well preserved opercular valves with those of the extant Pacific coast species *B. aquila* reveals no apparent differences. The only major distinction in the two species would appear to be a tendency for the formation of elongate cellular basis in the fossils. However, this unique basis has now been discovered in extant specimens of *B. aquila* taken by the Allan Hancock Foundation off Santa Rosa Island, California. It is probable that the prevalence of elongate basis in fossils is related to past environmental conditions (warm, shallow embayments with high sedimentation rates) which are not widespread along the Pacific coast today." (Zullo, 1964:360). The morphological characteristics of this species, such as deeply sunken radii, growth ridge of scutum divided into beads by striations, and the rather narrow spur of tergum considerably close to the basiscutal angle,
Table 2. Morphological comparisons of *B. sendaicus* with the extinct *B. concavus* concavus sensu de Alessandri (1906) and the living taxa of the *B. concavus* group. O: agreed; x: disagreed. Informations on parietal tubes of shell wall in fossil European *B. c. concavus* and living *B. gregarius* are by courtesy of Newman (in press, pers. comm.).

<table>
<thead>
<tr>
<th>B. sendaicus</th>
<th>&quot;B. concavus indicus&quot;</th>
<th>&quot;B. concavus concavus&quot;</th>
<th>&quot;B. panamensis&quot;</th>
<th>&quot;B. regalis&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>surface smooth</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>radii wide</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>summits of radii oblique</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>parietal tubes with septa</td>
<td>x</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>surface strongly sculptured</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>adductor ridge weak</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>spur furrow closed</td>
<td>x</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>spur short</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>basal margin straight</td>
<td>x</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
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</table>

are different from those of *B. sendaicus*.

*B. panamensis* Rogers, 1948 [Holotype, Calif. Acad. Sci. Dept. Paleo. Type Coll. 9434; paratypes, 9435-9437] was collected from C. A. S. Loc. 32532 of Chame Point, Canal Zone, Panama. Nature of shell form, toothed orifice, internal and basal margins of scutum, external surface of tergum, and basal margin of tergum found in this species are similar to those of *B. sendaicus*. Relatively narrow radii in comparison with *B. sendaicus*, weakly sculptured external surface of scutum, and shallow and opened spur furrow of tergum found in this species are apparently distinct from those of *B. sendaicus*. Nevertheless, among the American living taxa *B. panamensis* resembles the fossil Japanese *B. sendaicus*.

*B. regalis* Pilsbry, 1916 [Holotype, USNM 43485] was described from Point Abreojos, west coast of Lower California based on shell wall without opercular valve. Rugged shell with irregularly arranged ribs of various size, extremely narrow radii, and moderately projecting and short adductor ridge of *B. regalis* distinguishes it from *B. sendaicus*. Morphological observation of opercular valves is based on samples obtained through the courtesy of Professor Newman. This species resembles *B. sendaicus* in the nature of spur furrow, parietal tubes of shell wall with transverse septa, and basal margin of tergum.

As mentioned above, the three living taxa distributed along the west coast of USA and central America are morphologically distinct from the fossil Japanese *B. sendaicus*. The morphological difference suggests the species level distinction between *B. sendaicus* and the three living taxa. Among the three living taxa, *B. panamensis* has more characters in common with *B. sendaicus* than the other two species. Thus it can be inferred that, among the living American species of the *B. concavus* group, *B. panamensis* is related to extinct *B. sendaicus*.

In Indo-Pacific area, survival of the infraspecific taxa of *B. concavus* is indicated by only three reports: Broch (1931), Nilsson-Cantell (1932) and Utinomi (1969). Their taxa were included in the *B. c. concavus* of Newman and Ross (1976). According to Newman and Ross (1976), studies on *B. c. concavus* except for the three reports mentioned above are con-
cerned with fossil materials.

In Broch’s type specimen of *B. c. sinensis* from Hong Kong, Newman and Southward “have distinguished two species, *B. reticulatus* and *B. variegatus*”. “They have concluded that *B. c. sinensis* was a junior synonym of *B. variegatus* and that *B. reticulatus* of Utinomi remains valid (Newman and Southward, pers. comm.)” (Yamaguchi, 1980: 1088).

Based on reexamination of Utinomi (1969)’s materials by Newman, *B. c. concavus* from the Persian Gulf reported by Utinomi (1969) is *Chirona cf. amaryllis* previously called *B. amaryllis*, because it does not have the parietal tubes in shell wall and has denticular ribs in inner base of parietes (Newman, pers. comm.). Therefore, the decision whether *B. c. concavus* of Newman and Ross (1976) is extant or not should be determined by reexamination of “*B. c. indicus*”.

“*B. concavus indicus*” Nilsson-Cantell, 1932 was described based on only one specimen collected from a buoy in Dar-es-Salaam, Tanzania and has been preserved in the Berlin Museum. However, the type specimen can not be found in the Museum (Newman, pers. comm.). Live “*B. c. indicus*” has not been reported since 1932. Name *indicus* is preoccupied by *B. indicus* Withers, 1932. Therefore “*B. c. indicus*” is a homonym of *B. indicus*. However, both are apparently different from each other in morphology, so a replacement name is proposed by Newman (in press, pers comm.). Therefore, “*B. c. indicus*” of taxonomically invalid name is used in this paper.

Before entering to morphological comparison of *B. c. concavus* with “*B. c. indicus*”, it will be historically reviewed on taxonomy of *B. c. concavus*. *B. concavus* was described by Bronn (1831) from the Pliocene of Andona Valley, near Asti, Piedmont, Italy (Pilsbry, 1916). However, the substance of *B. concavus* was not always clear until de Alessandri (1906)’s redescription of topotype materials.

Darwin (1854a) reported three different forms of terga under the name of *B. concavus*: 1) terga of pl. 1, figs. 4g from Coralline Crag, England (fossil) and of pl. 1, fig. 4o from Turin, Italy (fossil) having a narrow spur furrow and basal margin slightly depressed; 2) tergum of pl. 1, fig. 4k from Maryland, USA (fossil) having a very wide spur furrow and a straight basal margin; and 3) tergum of pl. 1, fig. 4m from Portugal (fossil, recent ?) having certainly opened spur furrow and basal margin slightly projected. These morphological differences are usually regarded to represent distinction of species level, therefore, it is not appropriate that those three forms of terga are summarized to a species of *B. concavus*. Darwin (1854b) also reported two different forms in terga under the name of *B. concavus*. Specimens of pl. 4, figs. 4d and 4e and specimen of pl. 4, fig. 4c in Darwin (1854b) are morphologically identical with those of pl. 1, figs. 4g and 4o and that of pl. 1, fig. 4m in Darwin (1854a) respectively.

After Darwin (1854a, b), studies of *B. concavus* have been subjected to his great influence, and three distinct forms have probably been treated as a species of *B. concavus*. This fact seems to be a main cause for the taxonomic confusion of *B. concavus*.

Revision of topotypes (pl. 16, figs. 21–25; pl. 17, figs. 1a–4b) of *B. concavus* Bronn by de Alessandri (1906) seems to be found a clue to solve the taxonomic confusion and pointed out that terga of the real *B. concavus* are identical with those of pl. 1, figs. 4g and 4o in Darwin (1854a) and of pl. 4, figs. 4d and 4e in Darwin (1854b). Therefore, *B. concavus* redescribed by de Alessandri (1906) is called *B. c. concavus* sensu de Alessandri.
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(1906) in this paper. It is interpreted that B. c. concavus of Newman and Ross (1976) contains five or more species of B. c. concavus sensu de Alessandri, “B. c. indicus”, B. c. sinensis (=B. amphitrite s. 1.), and at least two species of Balanus (?) eliminated B. c. concavus sensu de Alessandri from Darwin (1854a)’s B. concavus.

In this paper, B. concavus in the following references is considered to be identical with B. concavus concavus Bronn in the sense of de Alessandri (1906): Darwin, 1854a, p. 17 (in part), figs. 4g and 4o; Darwin, 1854b, p. 235 (in part), pl. 4, figs. 4d and 4e; de Alessandri, 1895, p. 282, pl. 2, figs. 10a—10e; Pilsbry, 1916, p. 100, pl. 21, figs. 1—1c; Davadie, 1963, p. 52, pl. 24, figs. 8—9, pl. 26, figs. 1—4, pl. 28, figs. 1a—2b; and Menesini, 1965, p. 110, pl. 28, figs. 2—6, pl. 29, figs. 1—9, pl. 30, figs. 1—4, pl. 34, figs. 7—8, pl. 35, figs. 1—2, pl. 41, figs. 3—8, pl. 42, figs. 1—8, pl. 43, figs. 1—3.

“B. c. indicus” and B. c. concavus sensu de Alessandri (1906) have common morphological characteristics, such as conical shell form, rhomboidal orifice, oblique summits of radii, external scutal surface with longitudinal striations, relative spur width for basal length of tergum, relative position of spur, shape of basal margin of tergum, etc. However, the following morphological differences are present: shell surface is smooth in “B. c. indicus”, but costated, sulcated, festooned, or with longitudinal ribs in B. c. concavus. Parietal tubes of shell wall have not transverse septa in “B. c. indicus”, but have transverse septa in B. c. concavus (Information on this shell structure is by courtesy of Professor Newman, pers. comm.). The adductor ridge is very low and short in “B. c. indicus”, but prominent, long, clear and slightly curved in B. c. concavus. Tergal surface has longitudinal striae on carinal side of “B. c. indicus”, but is longitudinally and transversally sulcated in B. c. concavus. Spur furrow is open in “B. c. indicus”, but closed in B. c. concavus. The morphological resemblances show close relationship between them, however, the morphological distinctions are usually sufficient to recognize them as different species. As mentioned above, B. c. concavus sensu de Alessandri (1906) is neither an extant species nor “B. c. indicus”, therefore, B. c. concavus is an extinct species.

B. sendaicus and B. c. concavus sensu de Alessandri (1906) closely resemble each other in their morphology. The common characteristics are conical shell shape, rhomboidal and toothed orifice, having transverse septa in parietal tubes of shell wall, striated external surface of scutum, etc. In B. sendaicus, shell wall is generally smooth, but occasionally costated in carina and carinolateral. This character resembles that of B. c. concavus. The two species, however, differ morphologically in the following characters: high, long and clear adductor ridge of scutum in B. c. concavus, but obscure in B. sendaicus; long spur length in B. c. concavus, but moderately long in B. sendaicus; and surface of tergum longitudinally and transversely sulcated in B. c. concavus, but having only weak growth lines in B. sendaicus. These morphological differences are sufficient enough to distinguish them as two distinct species. Morphological resemblance, however, suggests their close relationship.

Furthermore, when B. sendaicus and “B. c. indicus” compared on the basis of morphology, they are found to resemble each other. The conical form, rhomboidal and moderately wide orifice, smooth shell surface (in B. sendaicus, carina and carinolateral are often costated, but generally smooth), scutum with well developed growth lines and strong striae on external
surface, and crenulation of basal margin of scutum are their common character. However, they have four different characteristics: parietal tubes of shell wall have not transverse septa in “B. c. indicus”, but have the septa at upper half of shell wall in B. sendaiicus, though usually secondarily filled up with calcite as result of fossilization; the adductor ridge of scutum is very low and short in “B. c. indicus”, but obscure in B. sendaiicus; distance from basiscutal angle to spur of tergum approximately is equal to spur width in “B. c. indicus” (Henry and McLaughlin, 1975), but is 2/3 in B. sendaiicus; and the spur furrow is open in “B. c. indicus”, but partially closed in B. sendaiicus.

Thus, morphological distinction is clear and sufficient enough to separate them into two distinct species.

B. sendaiicus was described by Hatai et al. (1976) based on only one scutum (Holotype). However, the shell walls of B. sendaiicus were described under the name of B. rostratus Hoek, and the tergum was undescribed. Thus, B. sendaiicus of Hatai et al. (1976) clearly does not agree with B. sendaiicus redescribed here. However, as mentioned above, B. sendaiicus redefined here is not identical with the already known living species of the B. concavus group.

Comparison with the extinct taxa of the B. concavus group

B. bloxhamensis Weisbord, 1966 [Holotype, PRI (Paleontological Research Institution) 27408] was described from the late Miocene Choctawhatchee Formation at Jackson Bluff in Leon County, Florida. This species is based on complete shells without opercular valve, and “the V-shaped cut at the summit of the radii, the longitudinal slit dividing the radii, and the vertical ridges transversing the radii, are the distinctive characters of the shell”. These characters are distinct from those of B. sendaiicus.

B. concavus alloplax Pilsbry and Olsson, 1951 [Holotype, ANSP (Academy of Natural Sciences of Philadelphia) 18869] is represented only by opercular valves from the Oligocene age of Playa Rica, Rio Santiago, Ecuador. Shell walls without opercular valves were described from another fossil locality, Posorja, Ecuador. It is difficult whether these shell walls belong to the same subspecies, until more fossil specimens from the type locality are available. The following morphological characteristics of this subspecies are distinct from those of B. sendaiicus; scutum strongly wrinkled; tergum with “a decidedly sunken spur fasciole”; spur removed “from basiscutal angle by nearly twice width of spur”.

B. concavus chesapeakensis Pilsbry, 1916 [Holotype, ANSP 1143] is based on a complete shell having scutum and tergum from the Miocene beds of Maryland. A long and high adductor ridge in its middle part, and lateral depressor muscle pit having a strongly prominent bordering ridge, parallel to adductor ridge in B. c. chesapeakensis distinguish it from B. sendaiicus.

B. concavus coosensis Dall, 1909 [Holotype, USNM 153960] was originally described as a variety of B. tintinnabulum, based on four specimens of shell wall without opercular valves from the Miocene of Coos Bay, Oregon. As Pilsbry (1916) pointed out, B. concavus coosensis having oblique summit radii and no porous radii is not related to B. tintinnabulum. Very large specimen attaining 50 mm in greatest diameter and the relatively narrow rostrum typical of B. concavus coosensis is not found in B. sendaiicus.

B. concavus dallonii Davadie-Suaudeau,
Miocene Cirriped Balanus sendaicus

B. concavus eseptatus Pilsbry, 1924 [Holotype, USNM 352257] was described based on complete shell wall without opercular valve from the Miocene of Haiti. In B. concavus eseptatus, the radii are narrower and the orifice is larger than those of B. sendaicus.

B. concavus finchii Lea, 1833 was originally described as B. finchii Lea from the Miocene of St. Marys, Maryland. Pilsbry (1930: 432) redescribed and illustrated topotype specimens. This subspecies is distinguished from B. sendaicus by large orifice, weak growth ridges and a long, moderately well developed adductor ridge in scutum.

B. concavus glyptopoma Pilsbry, 1916 [Syntype, ANSP 1140] was described from the Pliocene Caloosahatchie Formation, Florida. The rather numerous small ribs, sometimes weak or nearly obsolete on the surface of parietes, a strong but rather short adductor ridge, and a short, widely obliquely truncated spur of this subspecies distinguish it from B. sendaicus.

B. concavus oligoseptatus Kolosváry, 1961 [Holotype preserved in Coll. Mus. Inst. Syst. Zool. Univ. Szeged] from the upper Oligocene of Kizil-Kum, USSR has level summits radii and large orifice, which are different characteristics from B. sendaicus.

B. concavus proteus Conrad, 1834 was described based on specimens from James River, Suffolk, and Yorktown, Virginia. This subspecies is characterized by strong ribs on the external shell wall, and slightly well developed adductor ridge. These morphological characteristics are not present in B. sendaicus.

B. concavus raphanoides Moroni-Ruggieri, 1952 [Holotype, Cirr. 342] from the Pliocene of Bagni of Casciana, Italy is represented by an internal mould of shell wall. The characteristic cup-shaped base, cylindrical form and wide orifice of this subspecies are not present in B. sendaicus.

B. concavus rariseptatus Pilsbry, 1918 [Holotype, USNM 324292] is based on one cluster of shell walls without opercular valves from the Miocene Gatum Formation of Panama Canal Zone. The slightly longitudinally roughened walls of characteristic of this subspecies are not present in B. sendaicus.

B. concavus rubescens Seguenza, 1874 was originally described as a variety of B. concavus from the Tertiary formation of the province of Messina, Italy. In B. concavus rubescens, the growth ridges of scutum are scarcely detectable and the longitudinal striations on external surface of scutum are weak. These morphological characteristics are distinct from those of B. sendaicus.

B. concavus scutorum Seguenza, 1876 was described as a distinct species B. scutorum from the province of Messina, Italy. The following morphological characteristics of this subspecies are different from those of B. sendaicus: surface of scutum with fine longitudinal striations; spur width nearly equal to 1/3 basal length of tergum; narrow spur furrow; distinctly prominent adductor ridge.

B. indicus Withers, 1923 [Holotype, In. 20233] was reported from the Miocene of Karachi, Mouth of the Indus. This species is distinguished from B. sendaicus by rather deeply sunken radii, narrowly spaced and weakly prominent growth ridges on scutum, and spur fasciole in tergum.

B. polyporus Pilsbry, 1924 [Holotype, USNM 352258] from the Miocene of Haiti is represented by only one shell wall specimen. The somewhat roughened wall surface and rostrum notably longer than the other plates distinguish it from B.
sendaicus.

B. talquinensis Weisbord, 1966 [Holotype, PRI 27374] was described from the Miocene Choctawhatchee Formation at Jackson Bluff in Leon County, Florida. The following morphological characteristics of B. talquinensis are distinct from those of B. sendaicus: small beads or nodules are found at the intercepts of the radial riblets with the growth ridges of scutum; adductor ridge of scutum is high and long; spur furrow of tergum is shallow and moderately wide.

B. vadaszi Kolosváry, 1949 was reported from the early Miocene of Felsőtarkány, Hungary. Compartments with narrow radii and coarse white ridges on surface and scutum without longitudinal striations on external surface of B. vadaszi are not found in B. sendaicus.

In conclusion, as mentioned above, B. sendaicus is not identical with any of the already known living and extinct taxa of the B. concavus group, and is surely a distinct species as pointed by Hatai et al. (1976). However, because B. sendaicus based on a single scutum of Hatai et al. (1976) is not entirely identical with that of this paper based on complete specimens and description given by Hatai et al. (1976) is too brief, B. sendaicus is redescribed here.

Systematic Paleontology

Superfamily Balanoidea Leach, 1817
Family Balanidae Leach, 1817
Genus Balanus Da Costa, 1778
Balanus sendaicus Hatai, Masuda and Noda, 1976

Balanus concavus Bronn: Yamaguchi, 1974, p. 218, pl. 67, figs. 9-10.
Balanus sendaicus Hatai, Masuda and Noda, 1976, p. 13, pl. 2, figs. 1 (same specimen as fig. 20), 9 (same specimen as fig. 10, Holotype, missing), 10, 14-17, 19, and 20.

Explanation of Plate 44

Balanus sendaicus Hatai, Masuda and Noda, 1976
from the Miocene Moniwa Formation

All specimens were illustrated under the name of Balanus rostratus Hoek in plate 2 of Hatai et al. (1976) and were deposited in the Saito Ho-on Kai Museum, Sendai, Japan.

[Hatai, et al.’s specimens are not accompanied with registration number.]

Fig. 1. 1a-b, shell wall (same specimen as pl. 2, figs. 1 and 20 of Hatai et al.) on gravel, ×1.
Fig. 2. 2a-c, shell walls (same specimens as pl. 2, fig. 2 of Hatai et al.) on a brachiopod shell of Coptothyris grayi miyagiensis Hatai, Masuda and Noda, 2a, ×1. 2b-c, ×2. 2d-k, opercular valves preserved in the shell cavity of shall (left) [These opercular valves were not found by Hatai et al.], ×5; 2d-e, right scutum. 2f-g, right tergum. 2h-i, left scutum [morphologically identical with Holotype (missing), pl. 2, figs. 9 and 10 of Hatai et al.], 2j-k, left tergum.

Fig. 3. 3a-b, shell wall (same specimen as pl. 2, fig. 14 of Hatai et al.) on a brachiopod shell of Coptothyris grayi miyagiensis, 3a, ×1. 3b, ×2.

Fig. 4. 4a-b, shell wall (same specimen as pl. 2, fig. 15 of Hatai et al.) on a brachiopod shell of Coptothyris grayi miyagiensis, 4a, ×1. 4b, ×2.

Fig. 5. 5a-b, shell walls (same specimens as pl. 2, fig. 19 of Hatai et al.) on a molluscan shell of Anomia sp., 5a-b, ×1.

Fig. 6. 6a-b, shell walls (same specimens as pl. 2, figs. 16 and 17 of Hatai et al.) on gravel, ×1.
Description.—General appearance.—Shell conical and smooth often with weak longitudinal ribs. Color of shell ivory yellow, frequently with very fine striations of pale reddish purple or tinted with pale reddish purple near orifice or on the shell wall. Orifice toothed.

Compartments.—Parietes very wide in rostrum and lateral. Radii wide in rostrum and lateral, and moderately wide in carinalateral and carina; summits oblique. Sheath solid. Parietal (longitudinal) tubes with transverse septa in upper half of shell wall. Parietal tubes usually secondarily filled up with calcite as the result of fossilization. Those transverse septa usually not found by soft X radiographs (Pl. 48, Figs. 15-19), although, they observable in the longitudinal thin section of shell wall (Text-fig. 1, Pl. 48, Figs. 1-3).

Base.—Calcereous.

Opercular plates.—Scutum slightly concave externally with narrowly inflected tergal segment; basal angle obliquely truncated; external surface with prominent and crenulate growth ridges and moderately prominent longitudinal ridges frequently bifurcated by the weak longitudinal striae; nodes observable at the connection between the ridges; these ridges circumscribing square depressions ("rather coarsely latticed sculpture" as pointed by Pilsbry, 1916:101); color ivory yellow; inner surface smooth on upper part; articular ridge moderately projected, reflexed and greater than 1/2 length of tergal margin; articular furrow narrow and shallow; adductor ridge weak or hardly visible; pit for adductor muscle wide and deep; pit for lateral depressor muscle wide and deep; inner surface of basal margin faintly crenulated.

Tergum flat, moderately wide with a weakly developed beak (Pl. 44, Figs. 2f–g); external surface smooth with fine growth lines; color ivory yellow, tinted with pale reddish purple near apex between spur furrow and carinal margin; basal margin of both sides of spur approximately straight; spur furrow extremely narrow in young specimens or partially closed in large specimens and slightly sunken; spur rounded at end and with several very weak projections on inner surface of basal margin; spur width approximately 1/3 length of basal margin.

Text-fig. 1. Shell structures in longitudinal sections of a rostrum (UMUT CA9686) from the Miocene Moniwa Formation (Loc. 4). Photos for Text-figs. 1a–b are shown in Pl. 48, Figs. 1-2. 1a, a parietal tube with transverse septa in a longitudinal section parallel to the parietal (longitudinal) tube. 1b, parietal tubes with transverse septa in an oblique longitudinal section. I: inner lamina, Lr: longitudinal rib, Ls: longitudinal septum, O: outer lamina, P: parietal tube, S: sheath, T: transverse septum.
or less; distance between basiscutal angle and anterior side of spur nearly equal to 1/3 length of spur width; crests for depressor muscle well developed; rest of inner surface smooth.

Stratigraphic and geographic ranges, definition of *B. c. concavus* and habitat

The straigraphic range of each member of the *B. concavus* group summarized by Newman and Ross, 1976 is shown in Table 1. The oldest record is the Oligocene of Nurri, Sardinia Is. and Capo S. Elia, Cagliari, Italy concerning *B. c. concavus* (de Alessandri, 1906), of Pomaz and God, Hungary concerning *B. c. concavus* (Kolosváry, 1943), of Buda-fork concerning *B. c. chesapeakeinsis* and *B. c. glyptopoma* (Kolosváry, 1943), and of Kizil-Kum, USSR concerning *B. c. oligoseptatus* (Kolosváry, 1943). The youngest record is the Pleistocene of Monte Mario, Roma; Civitavecchia, Palo; and Sciaccra, Sicilia Is., Italy concerning *B. c. concavus* (de Alessandri, 1895, 1906), of Pisa province, Italy concerning *B. c. concavus* (Menesini, 1965), and of Monastir, Tunisia concerning *B. c. concavus* (Davadie 1963), etc. However, most of the fossils were obtained from the Miocene and Pliocene.

There are two critical and important problems of stratigraphic distribution of the *B. concavus* group:

1) Most of *B. c. concavus* reported in the literature appear only as listed occurrence of fossil and/or have only brief morphological description without illustration. Are most of these specimens identical with *B. c. concavus* in the sense of de Alessandri (1906, pl. 16, figs. 21–25; pl. 17, figs. 1a–4b), based on reexamination of topotypes of Bronn (1831)'s *B. concavus*? The writer discussed precisely on *B. concavus* of Darwin (1854a, b) and of de Alessandri (1906) in the preceding line.

2) Geologic age-determination in Neogene and Quaternary were advanced by biostratigraphy based on planktonic micro-fossils since 1950's and by magnetostra-
tigraphy based on paleomagnetic polarity in sediments since 1970’s. Determination of the stratigraphic range of *B. concavus* requires knowledge of the precise geologic age of the sampling horizons. However, many previous studies of *B. concavus* did not incorporate the current stratigraphic method mentioned above in age-determination, because they were published before the recent advance of age-determination.

Stratigraphy of Italy, based on modern geologic views, was established after the World War II and thus the geologic ages published before the World War II will have to be compared with the advanced stratigraphy and geologic age.

Therefore, in case where these two important problems of identification or definition of species and geologic age are not concurrently solved, discussion on stratigraphic and evolutionary change of *B. c. concavus* or other members of the *B. concavus* group should be restricted until the precise range of the *B. concavus* group in Mediterranean region is summarized.

The fossils of this group were found in areas surrounding the Mediterranean, corresponding to the western part of Tethys Sea (Oligocene-Pleistocene), England (Pliocene), west Atlantic coast of North and South America (Pliocene), the east Pacific coast from California to Mexico (Miocene-Pliocene), and east Pacific coast of Peru (Pleistocene). One noteworthy result is, as pointed by Pilsbry (1916), that this group had flourished from the Miocene to Pliocene and had lived in the Atlantic and the Mediterranean region until Pleistocene, but is extinct in this region ever since, though its members continuously live on the east Pacific coast of California and Baja California at present. The disappearance of this group from the Atlantic and the Mediterranean region in Pleistocene is a mystery.

In the east Pacific region, after the closure of Panama istmus in the Miocene, three species: *B. gregarius* (=*B. aquila*, a junior synonym of *B. gregarius*), *B. panamensis*, and *B. regalis*, live in the California and Oregonian Provinces from California to Peru-Chile. They are relicts of the Tethys (Newman, 1979). *B. gregarius* is endemic to the narrow Transition Zone (about 4° in latitude) in between California and Oregonian Provinces (Newman, 1979). The nature of this “so-called 4° short-range endemism” is discussed in detail by Newman (1979).

Japanese fossil *B. sendaicus* is the first record of this species group from the western Pacific area. *B. sendaicus* were collected from several localities of northern Honshu, Japan. The geologic age is restricted to the Miocene.

*B. sendaicus* occurs in association with extinct pectinid *Chlamys kaneharai*, brachiopods and bryozoans from the type locality of this species (Loc. 4). Brachiopods are well preserved, and the majority of them are articulated. Bryozoans have fine and reticulated structure, and are also well preserved. Shells of *B. sendaicus* are chiefly found as fragmental, skeletal elements, however, some of shells are complete shell walls and in some cases opercular valves are preserved in their shell cavities. These facts seem to indicate that those fossils were not transported so far away from their habitat. Those fossils associated indicate the paleoenvironment of moderately strong water agitation. The habitat of *B. sendaicus* is also presumed from the nature of fossil assemblage and sediments at the other fossil localities of *B. sendaicus*.

**Conclusion**

The description of *Balanus sendaicus*
Hatai, Masuda and Noda (1976) was based on a single scutum, but it could not be found out in the Saito Ho-on Kai Museum, Sendai. Study of topotype materials suggests that B. sendaicus is conspecific with shell walls incorrectly identified as B. rostratus Hoek by Hatai et al. (1976). B. sendaicus, based on scuta, terga and shell walls, is distinct from the known taxa, and is a good species as proposed by by Hatai et al. (1976). B. sendaicus is redescribed on the basis of skeletal elements of the topotypes.

B. sendaicus belongs to the B. concavus group based on having transverse septa in parietal tubes of shell wall and the characteristic ornamentation of scutum and seems to have derived from the closely related B. concavus concavus Bronn sensu de Alessandri (1906) which has mainly lived in the Mediterranean region of Italy and its adjacent areas from the Oligocene to the Pleistocene.

Darwin (1854a, b)'s B. concavus includes two or more taxa which are morphologically distinct from true B. concavus concavus. Newman (in press) reexamined based on the materials of Darwin (1854a, b), and recognized three taxa including true B. concavus concavus (Newman, pers. comm.). It is difficult to decide whether or not extinct infraspecific taxa of B. concavus are distinct from the other taxa, judging from their brief descriptions and their incomplete assemblage of skeletal elements. Their taxonomic positions will be valid by the Zoological Nomenclature, however, their holotypes and topotypes are necessary to be reexamined from the modern taxonomic point of view.

Acknowledgments

The author wishes to thank Professor William A. Newman, Scripps Institution of Oceanography, who kindly read the manuscript, and provided with invaluable comments and living American species of the B. concavus group for comparative study. The author is also indebted to Professor Elena Menesini for providing invaluable informations of the European B. concavus.

Thanks are due to Professor Tetsuro Hanai, University of Tokyo for reading the manuscript and giving valuable advice. I am grateful to Dr. Paul Frydl of our Institute for the reading of the draft.

Explanation of Plate 46

Balanus sendaicus Hatai, Masuda and Noda, 1976

All specimens are topotypes from Loc. 4 of the early to middld Miocene Moniwa Formation and preserved in University Museum, University of Tokyo (UMUT).

Figs. 1-4. rostrum, ×1.2. 1a-b, (UMUT CA9649). 2a-b, (UMUT CA9650). 3a-b, (UMUT CA9651). 4a-b, (UMUT CA9652).

Figs. 5-8. lateral, ×1.2. 5a-b, left, (UMUT CA9653). 6a-b, left, (UMUT CA9654). 7a-b, left, (UMUT CA9655). 8a-b, right, (UMUT CA9656).

Figs. 9-12. carinolateral, ×1.2. 9a-b, left, (UMUT CA9657). 10a-b, left, (UMUT CA9658). 11a-b, left, (UMUT CA9659). 12a-b, right, (UMUT CA9660).

Figs. 13-16. carina, ×1.2. 13a-b, (UMUT CA9661). 14a-b, (UMUT CA9662). 15a-b, (UMUT CA9663). 16a-b, (UMUT CA9664).

Figs. 17-19. scuta. 17a-b, right, (UMUT CA9665), ×3. 18a-b, left, (UMUT CA9666). 19a-b, left, (UMUT CA9667), ×2.5.

Figs. 20-22. terga, ×2.5. 20a-b, right, (UMUT CA9668). 21a-b, right, (UMUT CA9669). 22a-b, left, (UMUT CA9670).
Text-fig. 2. Sampling localities of fossil *Balanus sendaicus*. Details for each site are given in the section Locality.

 Locality

1a-b.—Obuchi: a) cliff (40°58'55.1"N, 141°21'42.9"E) along the Oippe river, situated about 2.85 km N26°W of Obuchi, Rokkashomura, Kamikita-gun, Aomori Pref., cross-laminated coarse shell sand ("coquina"), b) cliff (40°58'55.1"N, 141°20'49.3"E) along the Oippe river, situated about 3.55 km N44°W of Obuchi; cross-laminated coarse shell sandstone ("conquina"), a–b) late Miocene Takahoko Formation.

2a-c.—Ohmagari: a) shell quarry at Arasawa (39°24'16.2"N, 140°21'4.2"E), Minami-Sotomura, Senpoku-gun, Akita Pref.; barnacle shell sand ("coquina"), b) cliff (39°21'34.1"N, 140°21'42.1"E) at Asizawa Pass of Takei, Ohmori-machi, Hiraga-gun, Akita Pref.; massive poorly sorted tuffaceous sandstone containing carbonaceous matter, c) cliff (39°22'6.5"N, 140°21'42.1"E) of left bank of creak situated about 1 km north of Loc. 2b; massive poorly sorted tuffaceous fine sandstone containing carbonaceous matter, a–c) late Miocene Sugota Formation.

3.—Ukibuta: cliff (39°18'47.8"N, 140°20'41.1"E) situated about 100 m east of Ukibuta Tunnel, Ukibuta, Higashi-Yuri-mura, Yuri-gun, Akita Pref.; poorly sorted, tuffaceous, coarse sandstone; late Miocene Sugota Formation.

4.—Sendai: cliff (type locality of *B. sendaicus*) (38°12'45.4"N, 140°47'26.9"E) situated about 200 m south of the Oide Bridge across the Natori river, Moniwa, Sendai City, Miyagi Pref.; poorly sorted, gravelly, calcareous, medium shell sandstone; early to middle Miocene Moniwa Formation.

5.—Nanao: cliff (37°2'23.5"N, 136°57'23.4"E) situated about 0.95 km N85°W of Nanao Station, Iwaya-cho, Nanao City, Ishikawa Pref.; cross-laminated conglomeratic coarse shell sandstone containing many bryozoans; late Miocene Nanao Calcareous Sandstone.

6a-b.—Mizunami: a) cliffs (35°23'32.5"N, 137°16'35.6"E) situated about 3.5 km N32°E of Mizunami Station, Dan, Mizunami City, Gifu Pref.; conglomeratic very coarse sandstone, b) cliff (35°22'25.7"N, 137°16'28.6"E) situated about 1.95 km N61°E of Mizunami Station, Sakurado, Mizunami City., a–b) late Miocene
Oidawara Formation.

References


Explanation of Plate 47

*Balanus sendaicus* Hatai, Masuda and Noda, 1976

All specimens are from various localities of the Miocene and preserved in University Museum, University of Tokyo (UMUT).

Fig. 1. Specimen from the late Miocene Takahoko Formation (Loc. 1). 1a-b, left scutum (UMUT CA9671), ×2.5.

Fig. 2. Specimen from the late Miocene Sugota Formation (Loc. 2a). 2a-b, left scutum (UMUT CA9672), ×2.5.

Figs. 3-5. Specimens from the late Miocene Sugota Formation (Loc. 2b). 3a-b, left scutum (UMUT CA9673), ×4. 4a-b, left scutum (UMUT CA9674), ×4. 5a-b, right scutum (UMUT CA9675), ×4.

Figs. 6-10. Specimens from the late Miocene Sugota Formation (Loc. 2c). 6a-b, left scutum (UMUT CA9676), ×3. 7a-b, right scutum (UMUT CA9677), ×4. 8a-b, left tergum (UMUT CA9678), ×4. 9a-b, left tergum (UMUT CA9679), ×4. 10a-b, right tergum (UMUT CA9680), ×4.

Figs. 11, 12. Specimens from the late Miocene Nanao Calcareous Sandstone (Loc. 5). 11a-b, right scutum (UMUT CA9681), ×4. 12a-b, left scutum (UMUT CA9682), ×4.

Figs. 13, 14. Specimens from the late Miocene Oidawara Formation (Loc. 6b). Coll. Mizunami Fossil Museum, Mizunami, Gifu Pref. 13a-b, left scutum (UMUT CA9683), ×2.5. 14a-b, right scutum (UMUT CA9684), ×3.


Figs. 20-22. Interlaminate figures observed in thin section parallel to the base of shell wall (Loc. 4). 20, carina (UMUT CA9685). 21, rostrum (UMUT CA9686). 22, left lateral (UMUT CA9687).
Miocene Cirriped Balanus sendaicus

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(in press): A review of extant taxa of the group of *Balanus concavus* (Cirripedia; Thoracica) and a proposal for genus-group ranks. *Crustacea.*

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(1939): Recent and fossil balanids from the north coast of South America. *Capita*
Zool., vol. 8, no. 4, p. 3-7.


--- (1918): Cirripedia from the Panama Canal Zone. Ditto, no. 103, p. 185-188.


--- (1980): A new species belonging to the Balanus amphitrite Darwin group (Cirripedia, Balanomorpha) from the late Pleistocene of Japan; An example of peripheral speciation. J. Paleont., vol. 54, no. 5, p. 1084-1101.


Explanation of Plate 48

Shell structure in longitudinal sections of a rostrum (UMUT CA9686) from the Miocene Moniwa Formation (Loc. 4).

Fig. 1. a parietal tube with transverse septa in a longitudinal section parallel to the parietal (longitudinal) tube. 1a, ×8.4. 1b, ×10.2. 1c, ×42.

Fig. 2. parietal (longitudinal) tubes with transverse septa in an oblique longitudinal section (four parietal tubes are found). 2a, ×5.8. 2b, ×10.2. 2c, ×42.

Fig. 3. parietal (longitudinal) tubes with transverse septa in an oblique longitudinal section. 3a, photos by an optical microscope of Replica film (cellulose acetate film), ×10.2. 3b-e, external and internal walls (correspond to the outer and inner laminae) of parietal tubes and transverse septa partially left the original shell structure. Interspace of the parietal tube is secondarily filled up with the calcite which contrasts with the calcite composing the transverse septa in grain size, shape and arrangement. Photos by scanning electron microscope (SEM) of the etched surface. 3b, enlargement of top of fig. 3a, ×42. 3c, ditto, ×128. 3d, ditto, ×290. 3e, ditto, ×728.
Miocene Cirriped Balanus sendaiicus


Obuchi 尾敷, Oiipe 老部, Takahoko 鷹査, Ohmagari 大曲, Arasawa 荒沢, Asizawa 芦沢, Takinoue 滝ノ上, Sugota 須郷田, Ukibuta 浮蓋, Sendai 仙台, Oide 生出, Natori 名取, Moniwa 茂庭, Mizunami 水洗, Dan 段, Sakurado 桜道, Oidawara 桜田

Balanus sendaiicus Hatai, Masuda and Noda

日本の中新世稲脚類 Balanus sendaiicus Hatai, Masuda and Noda について——テーキス海の Balanus concavus 種群と比較して——: Balanus sendaiicus は仙台付近に分布する中新世巻層から得られた殻の一部分の 1 つの捲板 (scutum) に基づいて畑井, 増田, 野田 (1976) により新種として記載された。その標本は仙台の貞藤報恩会博物館に保管されているはずだが、そこには見つけられなかった。その名前のものもとに殻の他の部分, 背板 (tergum) および周壁 (shell wall), は記載されなかった。原産地標本 (topotype) および畑井ら (1976) に図示された標本調査で、畑井らが B. rostratus として記載・示した周壁は B. sendaiicus に属す。それゆえ、本論文では畑井らによって記載されなかった背板を含め B. sendaiicus を明確にする。B. sendaiicus は畑井らの指摘の通り既知の分類群から異なる。B. sendaiicus は慮潮世から更新世に地中海海地域テーキス海に繁栄した de Alessandri (1906) の意味合いでの絶滅種 B. concavus と近縁である。B. sendaiicus は周壁の壁管 (longitudinal または parietal tubes) に直交副隔膜 (transverse septa) を持つことおよび捲板の特徴的な表面装飾によって B. concavus に代表される種群に属す。この種群に属す "4 種" が東部太平洋に生息している (Newman, 1979) けれども、大西洋・地中海地域からの B. concavus 種群の消滅は Pillsbr (1916) の指摘のようにミステリアスである。化石の日本の B. sendaiicus は、中新世に限られ、B. concavus 種群の東アジアからの最初の化石記録となり、そしてテーキス海と東アジアの間のつながりの存在を指摘する。

Postscript: After submitted, Saito Ho-on Kai Museum of Natural History (SHM) let me know on registration numbers of illustrated specimens in the plate (pl. 2) of Hatai et al. (1976). The registration numbers are as follows.

<table>
<thead>
<tr>
<th>Registration number</th>
<th>figure in Hatai et al.</th>
<th>species name in Hatai et al.</th>
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<tr>
<td>SHM, Reg. No. 22069</td>
<td>figs. 1 &amp; 20</td>
<td>Balanus rostratus</td>
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<td>22070</td>
<td>figs. 3 &amp; 4</td>
<td>B. oidensis (Holotype)</td>
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<td>figs. 5 &amp; 6</td>
<td>B. moniwaensis (Ditto)</td>
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<td>22072</td>
<td>figs. 7 &amp; 8</td>
<td>B. natorianus (Ditto)</td>
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<td>figs. 11 &amp; 22</td>
<td>B. miyagiensis (Ditto)</td>
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<td>22074</td>
<td>fig. 12</td>
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<td>fig. 18</td>
<td>B. rikuzenensis (Ditto)</td>
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<td>fig. 23</td>
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<td>figs. 13 &amp; 21</td>
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<td>figs. 9 &amp; 10</td>
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Clark and Behenken (1971) summarized "Conodont and biostratigraphy of the Permian" in Symposium on Conodont Biostratigraphy edited by Sweet and Bergström. In this paper, they mentioned that Permian System represents the "last frontier" for conodont research. Permian conodont study was the same situation in Japan.

About ten years ago, Hisaharu Igo initiated to study Permian conodonts and he succeeded to recover numerous specimens from the various sections which were dated by fusulinaceans mainly in central part of Japan. The author clarified stratigraphic as well as geographic distribution of many important species and compared with the range of the previously described species in North America and Europe. Conodonts collected from chert and compound-type are mostly excluded in this volume, but he proposed two conodont faunas and two assemblage zones in the Japanese Permian and described 44 species and subspecies from 14 genera, among which 10 species and 1 subspecies are new to science.

This volume would be indispensable for geological and paleontological libraries as well as workers who may have interests in conodontology and later Paleozoic to early Mesozoic historical geology.

Orders must be accompanied by remittance made payable to Dr. Tsugio Shuto, Editor of the Special Papers, c/o Department of Geology, Faculty of Science, Kyushu University, Hakozaki, Fukuoka 812, Japan.
PROCEEDINGS OF THE PALAEOENTOLOGICAL SOCIETY OF JAPAN

学会記事

〇1982年1月22日に東京大学で開かれた評議員会において16の委員の半数選定を行ない、西澤清長・長谷川善和の両君が定まった。1982年度賞の委員会は、会長のほか、柳川正代、木村逆明（幹事）および上記の2名、計5名で構成される。
〇同評議員会において、次の諸君の入退会、および特別委員の推薦が認められた（敬称略）。
[入退者] 竹村孝司（1981年度より）、中川嘉孝雄、金 恒幸、斎田 聡、伊藤利夫、長谷川明、松岡 稔、中川 洋、於保正正、大矢 仁、中西正夫、加藤 進、高木俊男、須田美裕、坪内均道、国府 田良樹、岡部隆一、飯村 治（18名）。
[退会者] 木村方一、石川 正、三谷勝利、平川 昌登、長谷川俊男（5名）。
〇1982年中の逝去会員は、奥津春生、中野光雄の両君であった。
〇1982年1月23日現在の会員数は、名誉会員10、特別会員193、普通会員394、在外会員45、賛助会員9、計651名である。
〇1981年9月に行なわれた地学関係5学会の協議の結果、昭和57年度の科学研究費研究助成金の分配合議員補として、東京古生物学会1委員に、増田孝一郎（本会推薦）、質問学一般1段委員に村田正三（本会推薦）、谷田 末（実の諸君が推薦された。なお、2段委員として棚井敏雅、島崎正生物1段委員として小林郁生、沖村雄二、地質学一般に田尻一雄の諸君が留任している。
〇1981年度日本古生物学会論文賞は、加瀬友喜君の“Early Cretaceous Gastropoda from the Choshi District, Chiba Prefecture, Central Japan (報告・記事118号)に、学術賞は、棚部一成君の“白亜紀アンモイイド的研究”、および松丸国原君の“第三紀大型有孔虫の研究”にそれぞれ授与された。

日本古生物学会1982年年会・総会

日本古生物学会年会・総会が1982年1月23日24日には、千葉大学教育学部を会場として開催された（参加者222名）。

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Masuda, T.
松丸国照君：第三紀大型有孔虫の研究

日本における第三紀大型有孔虫化石の研究は、歴史的にかなり古く、20世紀初頭の矢部長次博士によるorboidsの記載に始まる。1920年までに至って矢部博士と半沢正四郎博士の多くの共著論文が発表され、有孔虫研究史上、矢部・半沢時代とも称すべき活動期に入った。その後、半沢博士を主とする大型有孔虫の研究は1960年代まで続き、日本列島はもともと広く東南アジア・太平洋諸島などに関する成果は、今日でも国際的に高く評価されている。このような歴史的背景のもとに、局所富良野地域のNephrolepidinaの研究(1967)より始め松丸君は、本州各地から産する本種の詳細な記載・分類を行い、時空的分布と系統発生の傾向を論ずる好著を1971年にまとめた。それ以後、日本列島ならびに周辺諸島の既知の産地のみならず、新産地における大型有孔虫の産出層を確認し、層位の分布を明らかにする努力を続けた。

このような研究の過程で必然的に国際的に熱帯亜熱帯地域の有孔虫群との比較研究が必要となるが、このことにより関心を抱いた松丸君は、台湾・北米・ニュージーランド産の化石の研究(1968-1971)を行っている。さらに橋本英君を中心とするフィリピン・インドネシア等の地質古生物学研究グループに1973年より参加し、主として第三系の大型有孔虫の分類学的研究を担当している。このグループの代表作である「フィリピン産大型有孔虫」と題するシリーズをはじめ、多くの共著論文を発表した。

松丸君の研究対象は地理的に広範囲に及び、かつ研究活動ははほどが精力的である。1971〜1980年の間に大量有孔虫に関するものだけでも30篇を超えている。いえまでもなく、このような成果により西太平洋および東南アジア地域の大型有孔虫に関する多くの貴重な知見がもたらされた。しかしご、もう一つ注目されるのは、公表論文に海外での見地を日本列島の化石の時空的分布の再評価へ還元させる傾向のものが見出されることである。

「日本の新生代大型有孔虫群（第1部）」(1980)はまだ化石層位学的問題の一部を取り上げているにすぎないが、今後新たな資料を用いて、多様な分類学的手法・層位学的手法を駆使して、より厳密な吟味が行われれば、新生代大型有孔虫学の大きな寄与となると思われる。よって日本古生物学はここに学術賞を賜り、今後のいっそうの発展を期待するものである。
日本古生物学会特別号 No. 24

日本古生物学会特別号 No. 24 IGO, Hisaharu: Permian Conodont Biostratigraphy in Japan（50ページ，12図版，1981年12月15日発行）が出版されました（定価3900円，送料300円）。購入申込は特別号の他の号と同じく日本古生物学会特別号編集委員会（福岡市東区箱崎九州大学理学部地質学教室内）（送金先：三和銀行福岡支店普通預金口座12172；振替口座，福岡19014）にお願いします。郵送によらない直接販売は東京大学総合研究資料館（速水格）および国立科学博物館分館（藤山家徳）でも取扱います。なお，特別号バックナンバーの表題・販売価格（国内）・郵送料は本誌121号83ページにてあります（残部価値の号もありますので売り切れる前に御早めに）。

第6回 パリノロジー国際会議 (予告)

4年毎に開催されるパリノロジー国際会議（IPC）（International Palynological Conference）の第6回大会の第1回予告が到着しましたのでお知らせします。

開催場所：Calgary University, Calgary, Canada
期間：1984・8・24—30

IPCの講演区分・提出論文締切日等については1982年11月発行の第2回予告で示される。講演公式用語は英・仏語。学会に際しては内容要約・野外見学旅行案内書等が刊行される予定。野外見学旅行については下記があげられています。

1. Calgary 中心……Rocky Mountain, Banff 等
2. 航空機利用……Hay River, Norman Well 等
3. 計画中……Nova Scotia, Quebec 等

なお出席希望者の学会内容についてのアンケートなどが付いております。この予告入手希望の向は下記に御連絡下さい。

103 東京都中央区日本橋室町 3-2 C.Mビル パリノ・サーヴェイ KK 徳永重元
(Tel 03-241-4566)

第3回太平洋地域第三紀国際会議

第15回太平洋学会総会のセッションB固地地球科学と共催で開かれる。

開催場所：Dunedin University, Dunedin, New Zealand
期間：1983年2月2—4日，7日
すべての参加希望者は Pacific Science Congress, P.O. Box 6063, Dunedin, New Zealand に登録されたい。

テーマ：1）太平洋地域の年代層序体系と対比，2）地磁気層序と放射年代，3）生層序，4）古海洋と古環境，5）新第三紀の地球的事件（海水準，同位体他），6）新第三紀の諸境界

選択：会期中2日間 South Island の第三紀（130米ドル），会期後6日間 第三紀（700米ドル）
国内問合せ先：東北大学理学部地球古生物学教室 高柳洋吉
環太平洋ジオラ系第1回 Field Conference

環太平洋地域のジオラ系に関する共同研究が IGCP の正式プロジェクトとして認められ、第1回 Field Conference が行われる。
開催場所：Calgary University, Canada
期間：1982年8月9日—14日

なおこの現地討論会はモントリオールで計画されている3rd North American Paleontological Convention の後に接続されるよう計画されている。次の11のトピックに分れて討論される。
A) Ocean floor, continental margins and exotic terrains, B) Palaeogeography of sedimentary basins, C) Eustatic events and their correlations, D) Ocean currents and climatic events, E) Floral biostratigraphy, G) Macrofaunal biostratigraphy, H) Supra-regional standard zones, I) Biogeography

連絡先：Prof. G.E.G. Westermann, Dept of Geology, McMaster University, Hamilton, Ontario, Canada.
国内連絡先：305 奈良県新治郡桜村 筑波大学地球科学系 佐藤 正
## 行事予定

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<tr>
<td>第129回例会</td>
<td>北海道大学</td>
<td>1982年6月26日</td>
<td>1982年5月15日</td>
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<td>第130回例会</td>
<td>早稲田大学</td>
<td>1982年10月17日</td>
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<td>1983年年会・総会</td>
<td>東京大学</td>
<td>1983年1月22・23日</td>
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講演申込先：〒113 東京都文京区弥生 2-4-16 日本学会事務センター 日本古生物学会行事係

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○本会名許員会藤本治義君は昭和57年3月31日に逝去されました。ここに本会の発展に尽された功績を追い、謹んで哀悼の意を表します。

日本古生物学会

○日本古生物学会では過去5年間経費の節減をはかりながら皆様の会費を留置してきていますが、昨今の諸経済の高騰により今後財政が苦しくなって参りました。現在の規模の活動を続けていくには来年度会費の値上げをお願いしなければならなくなる見通ですので、お含めいただくと共に会費の完納に御協力下さるようお願いいたします。

○日本古生物学会では年会・例会をより魅力あるものにするため、シンポジウムをはじめ各種の新しい形の会合（例えば、テクニックの会合、ポスターセッション、ワークショップ、夜間小集会など）の提案を歓迎します。よい企画がありましたら早急に常務委員会でお申出下さいお願い申し上げます。

○日本古生物学会刊行の和文誌「化石」を次のように充実させる方向で検討しています。1）B5版の定期的（年2回発行）の刊行物とする（昭和57年度より実施）。2）現在の予約購読制を改め、誌代を会費に含め全会員に配布する。3）原著論文を掲載し、内容を一見充実させる。これらの実施につきましては、印刷費等に相当する会費の値上げが伴ないますので、御意見がありましたら、化石編集部または常務委員会まで早急にお申出下さい。

○1981年度に投稿原稿の校閲者として尽力された諸兄に感謝いたします。

○本年度より賞の委員会委員の半数改選にともない幹事が交代しました。1982年度中の各種の賞に関する問合せ、推薦依頼は鏡野正（東京大学理学部地質学教室）にお願いします。その他の委員の役割分担と関連先（本誌122号参照）には変更ありません。

常務委員会

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○ 文部省科学研究費補助金（研究結果刊行費）による。

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