Two distinct growth stages of a deep-sea, giant white clam, "Calyptogena" soyoae, and its allied species

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Abstract: Two distinct growth stages, the immature- and the adult stages, are recognized in a Japanese giant white clam, "Calyptogena" soyoae Okutani. In the immature stage, the mode of living is endobiotic, a "subumbonal pit" exists on the hinge plate, and the relative length of hinge ligament to the shell length is small. In the adult stage, both valves become detached in the umbonal region, so that the subumbonal pit cannot become enlarged in its original position and is extended posteroventrally towards showing a white chalky area on the nympha. After the mode of living changes to semi-epibiotic, the shell shape and the ligament length change abruptly. Nevertheless, the growth of the ligament slows until the shell attains its near adult size, and then it grows rapidly with shell growth. Such abrupt post nemic change in the shell morphology and mode of living in the present species is comparable to the metamorphosis in other invertebrate animal groups, and similar abrupt post nemic changes can also be found in some other bivalves. The hinge structure of the type species of the genus Calyptogena, C. pacifica, are quite different from those of "C." soyoae, and the present species is more closely related to Akebiconcha kawamurai and "C." laubieri.

1. Introduction

In a previous paper dealing with the identity of two Japanese giant white clams, Akebiconcha kawamurai Kuroda, 1943 and "Calyptogena" soyoae Okutani, 1957, the presence or absence of the "subumbonal pit", which is a newly named, hollow structure on the hinge plate, was recognized as one of the discriminating characteristics for these two species (Horikoshi, 1986). At that time, both a small, young specimen (Holotype) and larger, adult (and/or gerontic) specimens were available for Akebiconcha kawamurai, but only adult specimens of Calyptogena soyoae were studied. Subsequently, the junior author (J.H.) collected several smaller, younger specimens of "C." soyoae, during a dive of the submersible "Shinkai 2000" (JAMSTEC), and reported briefly on their life habit (Hashimoto et al., 1987; 1989). These young specimens were collected near a colony of adult shells of "C." soyoae. To our surprise, these smaller younger specimens were found to bear a subumbonal pit on their hinge plate.

The smaller, younger specimens are different from larger, adult or gerontic specimens not only in the hinge morphology and shell sizes, but also in their mode of living, or life habit. The life habit of younger individuals is entirely endobiotic, protruding only the tip of their siphons from the sediment surface, in contrast to that of the adult (gerontic) individuals which is semi-epibiotic, exposing the posterior half of their shells on the sea floor. Along with the change of life habit, the length of the ligament relative to the shell length becomes larger.

Such changes take place rather abruptly, and are considered to be a kind of metamorphosis, and two distinct growth stages can be recognized as the immature- and the adult (gerontic) stages.
Comparing the hinge morphology of the present species with that of smaller specimens of *Calyptogena pacifica* Dall, 1891, which is the type species of the genus, we briefly discuss the classification of "Calyptogena group" in the family Vesicomyidae.

### 2. Materials and method

Four specimens of the smaller younger shell of "Calyptogena" soyoeae were collected by a grab sampler (20 × 20cm) during the Dive 228(9/VI/1986 : Jun Hashimoto) of the submersible, "Shinkai 2000" Japan Marine Science and Technology Center (JAMSTEC). The location of the collecting site was off Hatsu-shima (a small island off Ito City, Shizuoka Prefecture), in the northwestern part of Sagami Bay, and the precise position was 35° 00.1’ N, 139° 13.6’ E (1150m). Colour photographs showing the mode of living of the smaller, young individuals were taken through a window of the submersible.

Several adult specimens were collected by the manipulator of the submersible during two other dives, (Dive 225, 2/VI/1986: Suguru Ohta, and Dive 226, 3/VI/1986: Hitoshi Sakai) in practically the same locality : 34°59.9’ N, 139°13.6’ E(1170m).

A figure showing the mode of living of endobiotic, small-sized individuals was sketched from a colour photograph published by Hashimoto et al., 1987 (photo 4 : p.49). A pencil drawing of the hinge part was drawn using a binocular microscope (NIKON SMZ-10) with a camera lucida of drawing-tube type.

### 3. Life habit of smaller, younger shells

It is now well known that larger individuals of "Calyptogena" soyoeae, inhabiting the sediment bottom, always expose their posterior portion out of the sediment surface (Okutani and
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Egawa, 1985; HoriKoshi, 1986, 1989: pl.1, fig.1, etc.). In contrast, smaller, younger specimens were found to be buried entirely within the sediment, with only the tip of their siphons protruding (Fig.1). Although both the inhalent and exhalent siphons are recognized in some individuals, one of the two orifices is more prominent with a circular shape in some others. This is thought to be the inhalent siphon, if we take into account the general shape of siphons of the larger, adult individuals observed in the laboratory on board the mother ship of submersible, “Natsushima” (HoriKoshi, unpublished observation).

The spatial distribution of smaller, younger individuals is rather dense, if not gregarious, within a small limited area. About ten individuals were found in an area of about $15 \times 30$ cm, and practically no other individual was found in the surrounding area photographed (see Fig.1). Judging from the photograph, the surface of the seafloor seems to be covered by fine grained sediment at this site.

4. Shell shapes of immature and adult stages

The shape in outline of immature shells of “Calyptogena” soyoeae is rather elliptical, though that of the second largest specimen among four individuals becomes somewhat longer (Fig.2b) than that of the smallest one (Fig.2a). On the other hand, the outline of the smallest specimen among semiphibiotic adult shells shows the shape of the normal adult shell of this species (Fig.2c), being elongate and slightly contracted in the middle of the ventral margin.

The shape of the immature specimen of Akebiconcha kawamurai is also elliptical in outline (Fig.2d), but it is higher than that of “C.” soyoeae, being more roundish.

5. Hinge structure of smaller, young specimens

Terminology of the hinge elements: For the terminology of hinge elements see Fig.3.

Subumbonal pit: In all of the four specimens examined the “subumbonal pit”, a hollow structure just beneath the umbo (HoriKoshi, 1987), was found on the hinge plate directly behind the posteriormost dental element in both the right and left valves. In the smallest, or youngest, individual, the pit is small but deep, and is clearly demarcated from the hinge plate by its distinct margin (Pl.1, fig.1). The shape of the pit differs somewhat from that of Akebiconcha kawamurai of an equivalent growth stage (HoriKoshi, 1987: fig.4a), being longer antero-posteriorly and narrower dorso-ventrally in the present species.

In the second largest or oldest individuals among the four smaller, younger specimens, however, the ventral margin of the pit spread out ventrallywards, and becomes shallower along its ventral margin (Pl.1, fig.2). In this respect, the present species, “C.” soyoeae, is quite different from an allied species, Akebiconcha kawamurai. In the latter species, the pit is still deep and well demarcated even in full grown, adult specimens (HoriKoshi, 1987, fig.4b), and it becomes larger and shallower with ill-defined ventral margin, only when the shell attains gerontic age (HoriKoshi, 1. c., fig.4c).

In larger, adult and/or gerontic specimens of “C.” soyoeae, the right and left valves become detached in their umboal region (HoriKoshi, 1987: fig.5). Consequently the subumbonal pit can not become enlarged any more in its original position on the hinge plate, and its postero-ventral extension runs posteriorwards on the nympha along the ventral hode of the hinge ligament. Such an extended part of the pit can be recognized as a white, chalky area covered by yellowish membrane, as was pointed out in a previous paper (HoriKoshi, 1988: p.254).

Dental elements: The morphology of dental
Fig. 3. Terminology of hinge elements of “Calyptrigena” (Horikoshi, 1989b: fig. 1). Dental elements of left valve (left side in the figure): 2a = ramus-2a = anterior ramus of subumbonal tooth; 2b = ramus-2b = posterior ramus of the same tooth; 4b = tooth-4b = postero dorsal cardinal tooth; Right valve (right side fig.): 1 = tooth-1 = ventral (central) tooth; 3a = ramus-3a = anterior ramus of subumbonal (dorsal) cardinal tooth; 3b = ramus-3b = posterior ramus of the same tooth. a.e. = anterior edge of ramus 3b; a.1.1.1. = anterior lamellar layer of ligament (“cardinal ligament”); d.p. = distal portion of dental element; ex.a.1.1.1. = extension of anotier lamellar layer of ligament, investing internal shell surface under the coverage of periostracum; ext.3a = extension of ramus-3a; f.(i.1.) = fibrous (inner) layer of hinge ligament; h.1. = hinge ligament; h.pl. = hinge plate; l.(u.).l. = lamellar (outer) layer of hinge ligament; p.e. = posterior edge of ramus-3b; per. = periostracum hanging freely from shell margin; p.fus. = point of fusion of periostracum; p.p. = proximal portion of dental element; r.l.m. = roofing of lamellar membrane covering subumbonal pit; t.s. = top surface of dental element; v.s. = ventral surface of hinge ligament.

Elements are also different in smaller, younger specimens from those of larger, adult (gerontic) specimens. In the right valve (see Pl.1.fig.1a, 2a), the top surface of the posterior ramus of the subumbonal (dorsal) cardinal tooth (3b) is clearly grooved, and furnished with a rather sharp ridge along either edge, anterior and posterior. Such features of this dental element (3b) are similar to those of the same dental element of Akebicichna kawamurae, especially to those of a smaller, young specimen (holotype) of that species (Horikoshi, 1987: fig. 4a). On the other hand, the shape of the anterior ramus (3a) is rather similar to that of the larger, adult (gelontic) specimens of the present species, “C.” soyoae. It is extended anteriorwards from the proximal part of the posterior ramus (3b) nearly pararell to the dorsal margin of the hinge plate, covering and concealing the proximal part of the ventral (central) tooth (1).

In the left valve (Pl.2, fig.1b), both anterior and posterior rami of the subumbonal tooth (2a, b) are also different from those of the larger, adult specimens. The posterior edge of the anterior ramus (2a) stands erect from the hinge plate, so that it looks more ordinary hinge tooth-like than plate-like, and it abuts against the posterior ramus (2b) at more proximal part of the rami than in the larger specimens, leaving an open, spacious socket in between them. In these respects, the morphology of the anterior ramus (2a) of the smaller, young specimens is somewhat more similar to that of Akebicichna kawamurae than that of adult specimens of the same species “C.” soyoae.

The posterior ramus (2b) has a blunt point of the posteroventral corner of the ramus and has a small ridge that branches out towards the anteroventral corner, so that the distal part of the ramus looks as if the ramus is bifurcated at its distal extremity.

The postero dorsal cardinal tooth (4), however, is not much different from that of the larger specimens. It is laminate or plate-like, and it leans anteriorwards hanging over the socket between this tooth (4) and the ramus 2b.
6. Abrupt changes in ligamental length during growth

A remarkable change was found between relative lengths of the hinge ligament in the smaller, younger specimens and those in the larger, adult specimens.

In the case of the smaller, younger specimens bearing the subumbonal pit on the hinge plate (Fig. 4a: small solid circles), the ligamental length shows a linear relationship to the shell length, and the least squares line shows a good fit (Regression line A in the same figure). In the case of the larger, adult specimens without the subumbonal pit (open circles), the regression line shows entirely different trend (Line B). In this case, however, the points show a much wider scattering than in the case of smaller specimens. Closer inspection of the graph reveals that there are two categorically different groups among the individuals of the larger, adult specimens. One group consists of relatively small to larger individuals with short ligament of around 30 mm in length, and the other group includes still larger individuals with longer ligament of around 35 mm. If we obtain the least squares line separately for these two groups (Lines B' and B''), each of them shows a good fit.

This means that, just after the mode of living changes from endobiotic to semiepiphytic, both the shell length and the ligamental length become longer rather abruptly. So that a clear gap is seen in the ligamental length between the largest individual of the endobiotic, smaller specimens (21.7mm in shell of 82.9mm long) and the smallest individual of the semi epiphytic, larger specimens (28.0mm in shell of 87.4mm). However, the growth of the hinge ligament slows until the shell attains to near adult size, and then it grows rapidly with shell growth.

Such abrupt changes in hinge morphologies (dental elements, subumbonal pits and ligamental length) as well as a change in the mode of living suggest that the smaller, younger specimens and the larger adult specimens can be recognized as two distinct growth stages, the immature- and adult (plus gerontic) stages.

It is interesting to know that a similar features in the growth of the hinge ligament can be found in another species of the allied group of "Calypogena", "C." laubieri Okutani et Mé- tivier, 1986, as described briefly elsewhere (Horikoshi, 1989). In that species, two distinct growth stages were also recognized, and similar regression lines of the hinge growth were obtained (Fig. 4b). In this case, however, the regression lines of both the immature and the adult (gerontic) stages are clearly recognized (A and B’), but the number of individuals of adult (gerontic) stage examined was so few that the transient regression line B’ could not be obtained.

7. Hinge structures of Calypogena pacifica Dall

Ligamental structure: The type species of the genus Calypogena, C. pacifica Dall, lacks the subumbonal pit, so that the proximal part of the hinge ligament with calcified fibrous layer is not destroyed by the formation of the pit and still remains under the beak, if not fully functional (Pl.1, fig.4a). A horny ligamental membrane forms a roof-like bridge between both valves in the subumbonal region posteriorly from the point of fusion (anterior) of the periostracum, covering and connecting the anterodorsal margin of the right and left valves. The membrane seems to become detached progressively from the proximal surface of the hinge along with the growth of the shell as in C. soyouae (Horikoshi, 1987, p. 254 and fig. 5). During this process of detachment, the membrane invades the hinge area including the proximal portions of the dental elements ventrally parallel to the dorsal margin as in C. kahoi Okutani et Mé-tivier, 1986 (Horikoshi, 1988b: p.155, pl.4, figs.5,6), leaving a vacant area in between the line of attachment of this membrane and the ventral surface of the hinge ligament. The posterior end of this membrane abuts against the ventral surface of the hinge ligament at some distance posterior from the proximity of the hinge ligament situated beneath the beak. Through such an invasion, the proximal part of the dental elements are concealed by the ligamental membrane, and the area of concealment is broader in the older, larger specimen in the type materials (compare Bossi’s (1986) fig.16 to fig.17). Along the ventral border of
this area of invasion, a deposit of shelly substance forms a slightly raised edge along the dorsal brim of the hinge plate, as in *C. kaikoi* (Horikoshi, 1989b: p.155).

**Dental elements of right valve:** The dental elements in the present material (see pl.1, fig.4a) are almost identical to those of the samller individual in the type materials (Okutani, 1966: pl. 27, fig. 3; Boss, 1968: figs.16,19). The posterior ramus of the subumbonal (dorsal) cardinal tooth (3b) is much broader than that of "C. soyoae. The top surface is slightly concave, but both anterior and posterior edges are sharply ridged. The anterior ramus (3a) is well developed, running parallel to the anterodorsal margin of the shell, and has a blunt point on its distal end. Its ventral edge is rather sharp forming a weak ridge, and is continuous to the anterior edge of the posterior ramus (3b), describing a sharp curve at the corner of the junction of the anterior and posterior rami.

The ventral (central) tooth (1) runs obliquely from beneath the beak. It has two blunt points on its distal end, which looks as if it is bifurcated. The proximal part is obsolete, sinking diagonally into the hinge plate, and is concealed by the dorsal tooth (3a,b). A posteriorly radiating nymphal callosity looks as if it is a subobsolete, ridge-like dental element (cf. Boss and Turner, 1980: p. 163). A space between the posterior edge of the posterior ramus 3b and this ridge-like nymphal callosity forms a deep groove with a flattish bottom.

**Dental elements of left valve:** The posterior
A slender shelly callous runs along the ventral edge of the anterior ramus (2a), crosses the top surface of the posterior ramus (2b) and bends ventralwards forming nearly a right angle along the posterior edge of the posterior ramus. Such a structure seems to be rather normal in this species, since an almost indential calous can be recognized in a photograph showing the details of the dentition of one of the type specimens (syntype) (Boss, 1968, fig.19).

The posterodorsal cardinal tooth (4) radiates from beneath the beak obliquely, but its proximal part is concealed by shelly substance deposited along the dorsal brim of the hinge plate mentioned above. This tooth (4) stands far apart from the ramus (2b), forming a broad socket in between these dental elements, so as to form a spacious socket for the very broad posterior ramus (3b) of the dorsal tooth of the right valve.

8. Discussion

In "Calyptogena" soyoae, changes in the life habit, in the morphology of hinge structures and in the relative hinge length are rather abrupt, and are thought to take place rapidly within a rather short period of time. Such sudden changes remind us metamorphosis during the growth of some invertebrates. In some bivalves, e.g. mytilids, a distinct growth stage, called the "nepioconch" stage, is known between the larval stage (prodissococonch stages I, II) and the adult (dissococonch) stage. The nepioconch of mytilids is very small (ca. 1000 μm) and often has been confused with prodissococonch (Ockelmann, 1983). In some other bivalves, such as corbulids, the nepioconch can be recognized easily with the naked eye as a distinct apical shell (Wrigley, 1946; Cox, 1969:fig.83). It is much larger than the prodissococonch (protoconch), and its actual length is 7-8 mm in a 24-25mm long shell of Corbula (Anisocorbula) erythrodon Lamark (Horikoshi, unpublished data).

According to Wrigley (1946), one more stage can be recognized in between the nepioconch and adult stages, and was named "mesoconch" in the fossil Plicatula (Cox, 1.c.; fig.54, 1). In a living species of the same genus, P. muricata Sowerby (ca. 25 mm in height), the mesoconch (7-8 mm in height) is considered to be the shell of the sessil

Fig 4a,b. Relationships between the shell length and the length of hinge ligament in "Calyptogena" soyoae (a; above) and "C" laubieri (b; below). Small solid circles indicate immature individuals and large empty circles adult shells. For further explanation see text.
stage, which is firmly attached or cemented to the hard substratum, because it shows xenomorphic sculpture (cf. Stenzel, 1971, p. N 1021) especially on the mesocone of the lower (right) valve, which forms an attachment area. The adult shell becomes virtually free-lying, and shows idiomorphic or automorphic sculpture furnished with spiny ridges (HoriKoshi, unpublished observation).

The most striking example can be found in pectinid genera Hinnites (Cox, I.c.: fig. 84: 3b) and its allied genus Classadoma (Barnard, 1986). The early stage shells (ca. 20 mm in height in H. coralinus Sowerby, and ca. 20-30 mm in C. giganteus: HoriKoshi, unpublished data) are Chlamys-shaped until they become appressed or attached to the substratum, and then in the later stage the shell grows irregularly like Spondylus. It is interesting to find that the size of the early stages is similar in different species or genera, regardless of different full grown sizes in the later stage (The younger stage is ca. 25 mm in height even in an European, fossil species, H. crispus (Brocchi); measured from photographs illustrated in Cox, I.c., fig. 84: 3a, b). The changes in shell morphology and life habit between the two distinct stages, the immature and adult stages of the present species, “C.” soyoae, are another striking example of abrupt postneanic changes in a bivalve. Changes in the physiology and functional anatomy, if any, are hoped to be studied in future.

As for the taxonomical relationship of the present species, “Calyphtogena” soyoae, it is now clear that this species can not be regarded as a member of Calyphtogena Dall, 1891 in the strict sense. It is rather closely related to Akebiconica Kuroda, 1943 as suggested by Okutani (1966). Another close relative seems to be Archivesica, and we are inclined to concur with Keen’s (1969: p. N664) opinion to put together Archivesica Dall, 1908 and Akebiconica into a single group outside Calyphtogena in the family Vesicomyidae. A new large-sized form (ca. 14 cm in length) has recently been collected from Iheya Sea Mount, west of Okinawa by dredging of German Vessel “Sonne” (H. Sakai) and by diving of the Japanese subsensible “Shinkai 2000” (S. Ohta). This is closely related to “C.” soyoae, lacking the subumbonal pit in the adult stage and the proximal parts of dental elements are exposed on the outside of the shell. A newtaxon of the genus group (perhaps a subgeneric one) should be established for these two species.

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References
海大大型二枚貝シロウリガイ “Calyptogena” soyoae
及びその近縁種における明確な2生長段階

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要旨：地下湧水に伴い、硫化物が生じた海大大型二枚貝シロウリガイに、“未成段階”と“成段段階”との明確な2段階が認められた。成段段階では生活型が半外生的であるのに対し、未成段階段階では全内生性で堆積物内に潜入し、水管の先端のみを海底に露出する。“成段段階”は成段段階の殻体には見られない近縁種アケビガイ *Akebiconcha kawamurae* との区別点になるが、未成段階段階には明らかに存在する。成段段階に移行すると、本種の特徴として、両殻の殻頂部分が左右に離れれて来て絞帯膜の形で接合し、絞帯の咬み合わせがゆるめ、殻頂下洞は原位置で拡大する事が不可能となり、歯丘上に黄帯色の腹を帯びた白亜質の領域として後方に延長する。絞帯の形態は生長段階で著しく異なり、未成段階段階ではむしろアケビガイに類似した点が多い。Calyptogena 属の模式種は成段段階段階はなく、絞帯も全く異なり、本種とは異なる属のレベルで異なる。絞帯帯長は、未成段階段階では成長と共に増大する。半外生性の成段段階に移行する際には絞帯帯長も速やかに増大するが、その後絞帯の成長は足踏みし、絞帯長がほぼ成長度に達した後に再び絞帯長が増大する。同様な傾向は、近縁種テリウシュシロウリガイ *C. laubieri* にも見られた。成段段階段階の移行は、他の動物での事例を思わせるが、二枚貝類には、この様な未成段階後 (*postmeanic*) の変態が2、3 知られている。