# SHELL STRUCTURE, GROWTH, AND FUNCTIONAL MORPHOLOGY OF AN ELONGATE CRETACEOUS OYSTER

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ABSTRACT. *Konbostrea* (gen. nov.) is an aberrant oyster of the *Crassostrea* group, characterized by its dorsoventrally elongated stick-like shell. It is found in life position, perpendicular to the bedding in brackish-water muddy deposits of the Upper Turonian to Upper Coniacian, in Sakhalin and north Japan. A narrow body space is restricted to the ventral end of the shell. The ligamental area is very small, separated from the body space, and the ligament is considered to have been active only during the younger stages of growth. The adult animal most probably took advantage of the elasticity of the thin, flat, right valve to open its shell. Having reached its adult width the shell grew only in a ventral direction, at an apparently constant rate, without notable increase in the size of the body cavity. The shell is composed of an outer foliated layer which defines the structural framework of the shell, and inner chalky deposits which fill in most of the inner space. All these characteristics are thought to result from adaptation to keep up with rapid sedimentation on a soft muddy bottom. *Konbostrea* constantly grew upward, accumulating chalky deposits to maintain the body above the rising sediment surface.

*KONBOSTREA KONBO* (Hayasaka and Hayasaka, 1956), here recognized as the type species of a new genus, is an aberrant oyster characterized by an extremely elongated, stick-like left valve with a very thin right valve of the same height. The oyster typically attains a height of 1 m. The main part of its left valve is composed of massive shell, leaving no space for the soft body, which is restricted to the ventral end of the valve. The oyster is closely related to the *Crassostrea* group of the Ostreidae. When first described as *Ostrea konbo* (Hayasaka and Hayasaka 1956), its massive shell was thought to be a part of the hinge area of a huge oyster. *K. konbo* is known from Turonian and Coniacian intertidal or brackish-water deposits in southern Sakhalin (USSR), Hokkaido, and northern Honshu (Japan).

The purpose of this paper is to describe the morphology, shell structure, and growth pattern of *K. konbo*. The palaeoecology and adaptive significance of this peculiar shell will also be discussed.

Oysters of the *Crassostrea* group are suspension feeding, sessile animals which usually live on soft muddy bottoms. Suspension feeding and the sessile habit are seemingly incompatible with life on a soft muddy bottom with rapid sedimentation. The elongated shell form and gregariousness that are characteristic of the *Crassostrea* group (*Crassostrea*, *Striostrea*, and other oysters living on mud) are best understood as adaptive characters employed by these oysters to avoid burial in rapidly accumulating mud.

The stick-like shell of *K. konbo* is considered to represent an extreme example of the elongation strategy employed by these oysters (Chinzei 1982*a*; Seilacher 1984). Other examples of such elongation are seen in deeply conical forms of *Saccostrea* and *Striostrea*, in which the free valves act as lids. The development of elongated, conical shells occurs not only in bivalves, but also in other groups such as brachiopods, corals, and barnacles. However, the elongation of both valves, such as that found in *Konbostrea*, is not common. *Lithiotis* and *Cochlearites*, bivalves of isognomonid or bakevelliid affinity found in the Lower Jurassic of the Tethyan region, are analogous to *Konbostrea* in overall shell form and in shell structure (Chinzei 1982*a*). Comparison of these forms clarifies the basic adaptive and structural constraints that determined their morphologies.

The specimens used for this study are deposited in the Department of Historical Geology and Palaeontology, University Museum, University of Tokyo: Reg. nos. MM 17080 to MM 17139.

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## SYSTEMATIC PALAEONTOLOGY

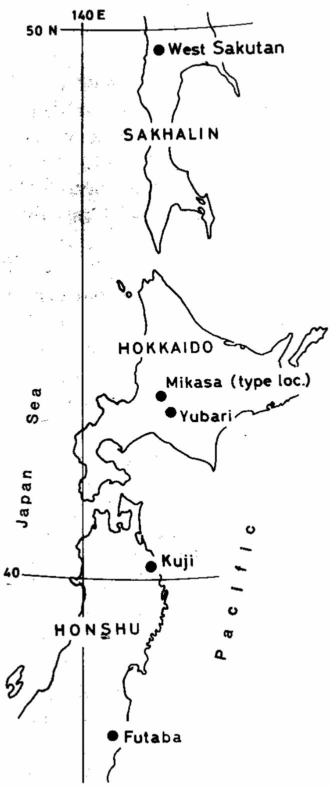
Although the oyster described here has many features in common with species of *Crassostrea* and other ostreid genera, it is unique in its extremely elongated shell form and other morphologic characters related to the elongation. As the characters described below are stable among the populations observed and are quite distinct from those of other genera, I propose to establish a monospecific new genus belonging to the Subfamily Ostreinae. The word 'konbo' means club or stick in Japanese.

### Genus *Konbostrea* gen. nov.

*Type species. Ostrea konbo* Hayasaka and Hayasaka, 1956, pp. 163, 164, pl. 12, figs. 1 and 2.

*Diagnosis.* Extremely elongated oyster; left valve very long, dorsally very thick, with anterior and posterior margins subparallel to each other; space for the soft parts with a deep umbonal cavity, located at the ventral end of the left valve; right valve of same height as left valve, flat and extremely thin except in the umbonal region; ligamental area of the adult shell separated from the dorsal margin of the body space by long cardinal area; ligament active only during the young stage.

*Comparisons. Konbostrea* has many features in common with *Crassostrea* Sacco. 1897 (*sensu* Stenzel 1971). In particular the morphology of the ligamental area is essentially the same, although it is very small relative to shell height in *Konbostrea*. The juvenile shells of the two genera are similar in outline and hinge structure, suggesting an evolutionary origin of *Konbostrea* from *Crassostrea*. The adult




TEXT-FIG. 1. Localities where *Konbostrea konbo* (Hayasaka and Hayasaka) has been recorded.

shell of *Konbostrea* differs from that of *Crassostrea* in its separation of the ligamental area from the dorsal margin of the body space. It is readily distinguishable from elongated rudistiform ecomorphs (Stenzel 1971) of *Saccostrea* Dollfus and Dautzenberg, 1920, and *Striostrea* Vyalov, 1936, by the same character.

*Localities and geologic age*. The type locality of *K. konbo* is upstream on the Sentarozawa River, Kiyozumi, Mikasa-shi, Hokkaido (Upper Turonian, the uppermost part of the Mikasa Formation of the Middle Yezo Group). The oyster is also known from: the upstream area of the West Sakutan River, on the west coast of Sakhalin (Upper Cretaceous, Hayasaka and Hayasaka 1956); the southern limb of the Hatonosu Dome, Yubari-shi, Hokkaido (Turonian Mikasa Formation, oral communication from S. Kanno): south tributary of the Edanarisawa River, Kuji-shi, Iwate Prefecture (Upper Coniacian Tamagawa Formation of the Kuji Group); Irumasawa, Ohisa, Iwaki-shi, Fukushima Prefecture (Upper Coniacian Tamayama Formation of the Futaba Group, oral communication from I. Obata, geologic age based on Obata and Suzuki 1969). All these localities except Sakhalin are in north-east Japan (text-fig. 1). The geologic ages of the oyster-bearing beds are based on the work of Matsumoto *et al.* (1982).

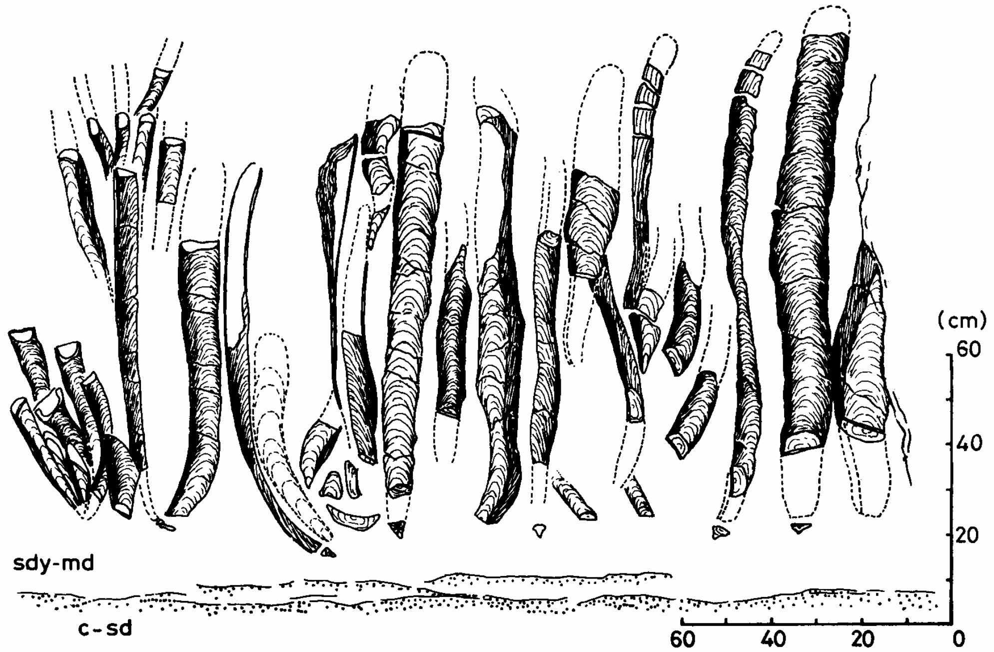
## MODE OF OCCURRENCE, INFERRED MODE OF LIFE AND POPULATION DENSITY

At the type locality, individuals of *K. konbo* are found densely crowded together, forming an oyster bed about 2 m thick. The sediment surrounding the oysters is a poorly sorted, dark grey sandy mudstone. The oysters are standing perpendicular to the bedding with their umbones pointing downward in the middle part of the bed, while they lie parallel to the bedding at the bottom and top of the bed. The upright orientation is apparently the living position of this oyster. The horizontal shells are considered to have been displaced by wave or current scouring, because most of these shells are broken, and do not show any preferred orientation, some lying with the thin valve facing down and others with it up. Several of the individuals found in life position occur as bouquet-like clusters, in which the juvenile shells radiate away from one another and then turn upward to grow parallel as adults. The oyster bed occurs as a lens within the sandy mudstone. The mudstone is overlain by fine-grained sandstone about 30 m thick, succeeded upward by ammonite-bearing mudstones. It is underlain by medium-grained to coarse-grained sandstone, 10 to 15 m thick, beneath which are thick mudstones with frequently intercalated thin coal seams. Thus the oyster bed occurs in sediments that are transitional between non-marine and marine facies.

Similar circumstances were observed at the Kuji locality. Here the oysters are crowded in dark grey, sandy mudstone 1·5 m thick, about the same height as the individual oysters. Oysters are found standing perpendicular to the bedding, their umbones pointing down in part of the exposure, and lying obliquely in the other part (text-fig. 2). Where they are oblique the shells have been broken at the same level just above the umbones, indicating that the oblique position is due to later deformation of the bed. The oyster bed is intercalated in coarse-grained, cross-laminated sandstone of the basal member of the Kuji Group. The sandstone contains coaly matter and conglomerate lenses. These have been considered to be non-marine or brackish-water deposits (e.g. Tanai 1979). In the Kuji area, *Konbostrea* is limited in its distribution to the innermost part of a triangular Cretaceous basin, 10 km wide and 15 km long, which opens toward the Pacific. Ordinary *Crassostrea* banks are found at the same stratigraphic level along the middle and outer margins of the basin. The areas of distribution of the two oysters can be sharply demarkated, for no intermediate forms between the two are found.

Upright orientation of this extremely long, narrow shell and preservation of the thin outer prismatic layer of the shells suggest that they lived with most of the shell buried in the sediment. The sediment supported the shell to keep the orientation and protected the fragile prismatic layer from erosion. The shells show no preferred orientation in the plane of the bedding. No other fossils have been found within the oyster beds or in the stratigraphically adjacent sediments except for traces of boring sponges on the surface of the oyster shells. These traces are seen on many of the well-preserved individuals.

Based on these observations the oysters are thought to have been living in intertidal or brackish




TEXT-FIG. 2. Sketch of part of a *Konbostrea* bed on the south tributary of the Edanarisawa River, Kuji-shi, north Japan (Kuji locality), showing an excavated section oblique to the bedding. Most of the *Konbostrea* shells have been broken near the umbo, and lie at about 60° to the bedding plane. sdy-md: sandy mudstone; c-sd: coarse-grained sandstone.

waters, on a muddy bottom, maintaining an upright position with most of the shell sticking into the mud. The absence of other marine fossils suggests very restricted marginal marine conditions for the habitat of *Konbostrea*.

The population density of the oysters can be measured directly where the original relative positions of the individuals are preserved. Measurements were made using the stretched line method (e.g. Ager 1963, p. 228). Along the vertical section of the bed the number of individuals falling within a one metre horizontal line was counted, and then squared to obtain the density per square metre of the horizontal surface. The density is about 350/m$^2$ (three counts: 289, 361, 400) at the type locality, and 218/m$^2$ in average (thirteen counts: observed range 144–324) at the Kuji locality where the individuals are larger than those at the type locality.

## MORPHOLOGY OF *KONBOSTREA KONBO*

### *Outlines*

*K. konbo* is characterized by a dorsoventrally elongated shell which reaches a maximum of more than 1 m in height (text-fig. 3). While the right valve is extremely thin and flat, most of the left valve is thick, with a squarish or sometimes semicircular outline in transverse cross-section. The space occupied by the soft tissues (hereafter denoted as the body space) is located at the ventral end of the left valve.

The length (distance between subparallel anterior and posterior margins, the 'width' of the gutter-shaped shell) of the left valve is 4 to 8 cm and its inflation is 3 to 4 cm in typical adult shells. One individual having a flat shape, 10 cm long and 1·5 to 2·0 cm thick, was obtained. Shell length and inflation change little or not at all towards the ventral margin. The height, on the other hand, varies considerably. It is usually 80 to 100 cm in fully grown adults. The largest individual observed at the outcrop reaches 120 cm. As the shell surrounding the body space is very fragile, because of its thinness, most adult specimens to hand are incomplete. The overall form is variable among individuals; it is generally straight, but broadly curved or sinuous shells are found quite often. Some individuals exhibit zigzag changes in growth direction. The majority of the specimens from the type locality are smaller than those from other localities. They are 50 to 70 cm high, 4 to 5 cm long, and 2 to 3 cm thick on average.

As the left valve is squarish in transverse section, the anterior and posterior walls are set off from the main surface of the valve. The main surface is flat or very gently inflated, and constitutes the 'bottom' of the gutter-shaped left valve. As both walls are usually turned inward along the commissural margin the greatest dimension measured parallel to the length axis of the left valve tends to pass through the middle part of the walls (text-fig. 3).

The right valve has nearly the same height and length as the left valve. As the length of the right valve must correspond to the maximum length of the left, the anterior and posterior margins of the former usually extend out beyond the margins of the latter. The right valve is flat, about 2 mm thick in the main part. Around the body space it is extremely thin, less than 1 mm, and flat without any cavity or depression for the soft body. It is thick in the umbonal region. Just behind the ligamental area of the right valve the outer layer is padded by a substantial inner layer about 1 cm thick in most specimens (see text-fig. 6).

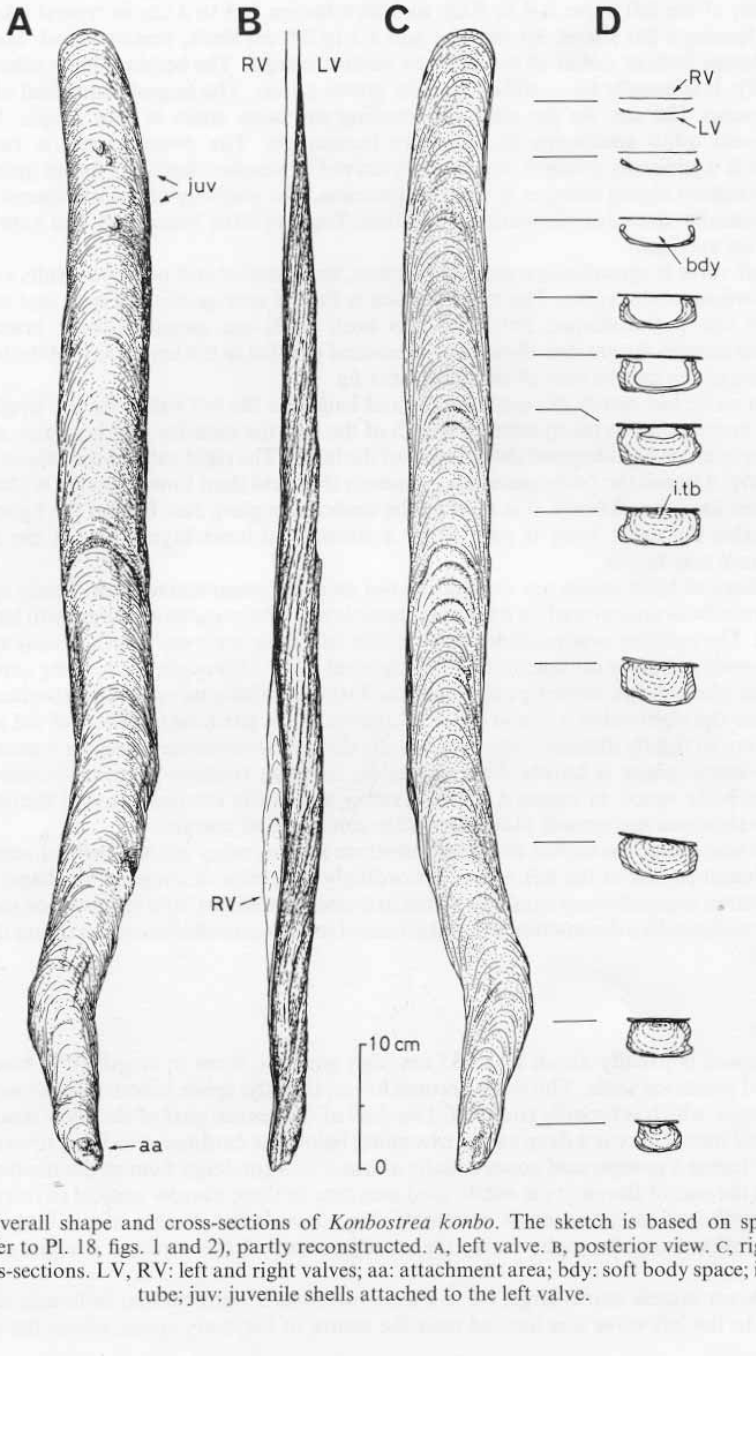
The surfaces of both valves are undulating but smooth, ornamented with closely spaced growth lines. Their surfaces are covered by a thin prismatic layer. The margins of the growth lamellae are not imbricated. The anterior and posterior walls of the left valve are rough, with closely spaced growth squamae running slightly oblique to the commissural plane. Throughout the long cardinal area the commissural plane is flat, forming a cardinal platform, on which no apparent structure is visible. In all specimens the right valve is found attached tightly to the cardinal platform of the left valve. The two valves are so tightly attached, they are usually difficult to separate along the commissural plane. The commissural plane is hardly distinguishable, even on transverse cross-sections of the shell. Around the body space, in contrast the two valves are not in contact, leaving the ventral margin gaping. No chomata are present along the entire commissural margin.

*K. konbo* was initially attached to a hard substrate such as other oyster shells or stones, cemented by the umbonal region of the left valve. Accordingly the umbo is irregular in shape, although the attachment area is usually very small, 1 to 2 cm in diameter, and has little influence on the overall shell outline. Juvenile shells are sometimes found attached to the outer shell surface around the body space of the adult.

### *Body Space*

The body space is usually about 25 to 35 cm high and 4 to 6 cm in length. It is box-shaped with anterior and posterior walls. The walls become lower, thus the space becomes shallower, toward the ventral margin, which is broadly rounded. The shell of the central part of the body space is very thin, usually 1 to 2 mm. There is a deep cavity extending below the cardinal area back towards the umbo. This cavity forms a compressed cone, usually about 2 to 3 cm deep, 5 cm at the maximum. In some individuals the end of the cavity is subdivided into two or three narrow conical cavities. As the shell above the umbonal cavity becomes extremely thin towards the margin of the body space, and is hardly separable from the right valve, the configuration of the cardinal margin of the space is uncertain.

The adductor muscle scar is large, 1·5 to 2·0 cm in diameter, semicircular or lunate, dorsoventrally elongated. In the left valve it is located near the centre of the body space, where the shell becomes

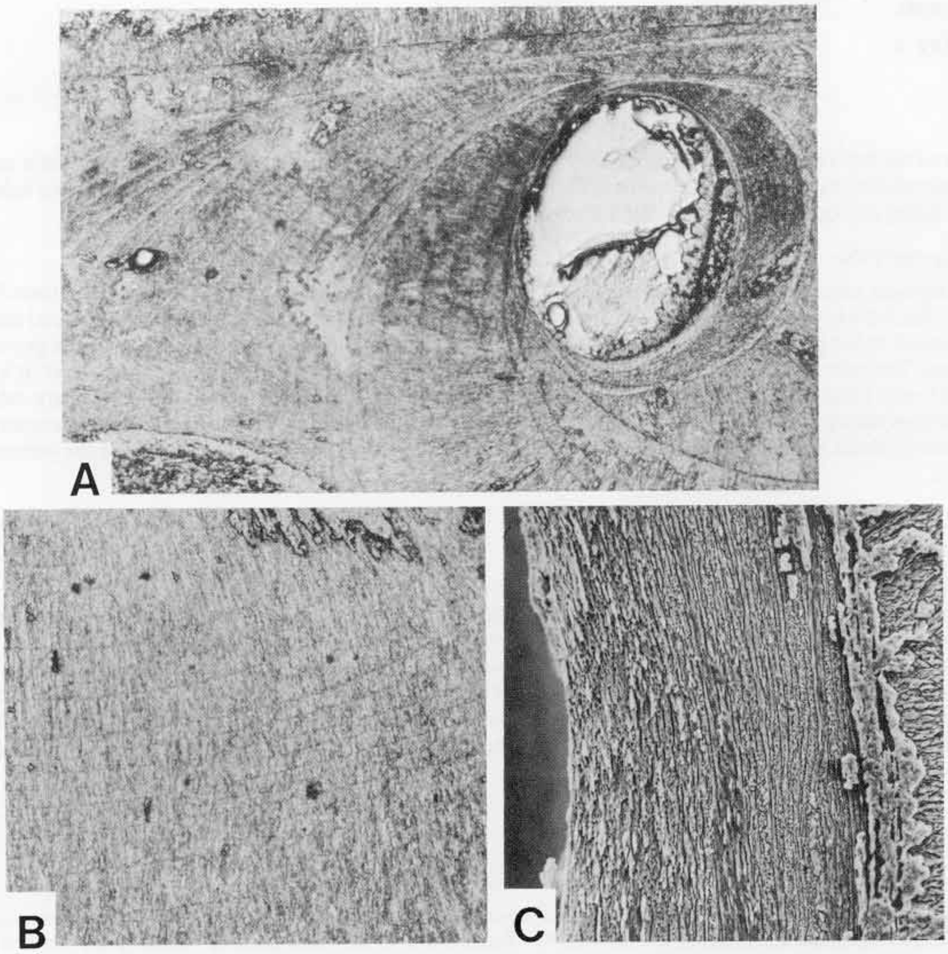



TEXT-FIG. 3. Overall shape and cross-sections of *Konbostrea konbo*. The sketch is based on specimen UT MM17080 (refer to Pl. 18, figs. 1 and 2), partly reconstructed. A, left valve. B, posterior view. C, right valve. D, transverse cross-sections. LV, RV: left and right valves; aa: attachment area; bdy: soft body space; i.tb: internal tube; juv: juvenile shells attached to the left valve.

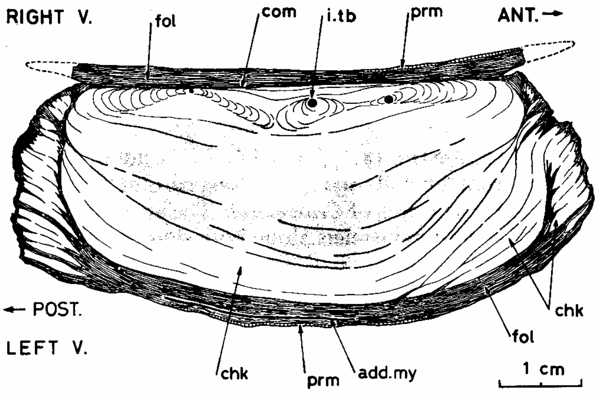
abruptly thin. In some young individuals the scar is shallowly depressed, and the surface is tilted more or less dorsally. In the right valve, however, the scar is not observable even on well-preserved specimens, probably because of the thinness of the shell.

*Ligamental Area*

The shell has a small ligamental area adjacent to the umbo (Pl. 18, figs 3 and 4). In the adult shell the ligamental area is about 1 to 2 cm high, separated from the body space by a long cardinal area. The structure of the ligamental area is similar to that of young stages of *Crassostrea*. The area consists on the right valve of a central resilifer, with narrow, indistinct bourrelets along both sides. The resilifer




TEXT-FIG. 4. Internal tube of the left valve. A, optical photograph of a cross-section around the tube, × 25. B, optical photograph of the chalky deposits near the internal tube showing regular growth lines, × 25. C, SEM showing the foliated layer around the wall of the tube and surrounding chalky deposits, × 270. The section polished and etched by weak acid.




TEXT-FIG. 5. Transverse cross-section of the left valve of *Konbostrea konbo* (specimen UT MM17082 from the Kuji locality). ANT., POST.: anterior and posterior sides; add.my: sparry calcite layer probably replacing the adductor myostracum; chk: chalky deposits; com: commissure plane; fol: foliated layer; i.tb: internal tube; prm: prismatic layer.

pit of the left valve is deeply excavated. The resilifer is well inflated, and its supporting buttress is very high relative to the size of the resilifer. Thus the growth trend of the ligamental areas of the two valves is highly oblique to the general direction of the shell elongation (see text-fig. 6).

### *Internal Tube*

A striking structural feature seen on cross-sections of the left valve is a narrow internal tube (text-fig. 4). The tube is continuous from the conical end of the body space to just behind the ligamental area. Viewed in longitudinal sections, it passes through the chevron-shaped turning point of the growth lines. The tube is 0·5 to 1·0 mm in diameter, and its inner surface is coated by a foliated layer, 0·1 to 0·15 mm thick (text-fig. 4). In specimens where the umbonal cavity is subdivided, there are tubes corresponding to the number of conical spaces. As the tube is now void or filled with transparent sparry calcite, it appears to have been hollow or filled with soft tissue during the life of the animal.

## SHELL MICROSTRUCTURE

### *General Features*

When the thick left valve is observed in cross-section, two distinctly different parts are visible, a lamellar outer layer and porcellaneous inner material (text-fig. 5). The outer layer constitutes the bottom of the box-shaped left valve and its anterior and posterior walls. The walls are composed of foliated material, with intervening porcellaneous lenses. Growth lines are observable in the lenses. The inner part of the left valve consists mainly of massive porcellaneous material with sparsely spaced growth lines. The porcellaneous part is considered originally to have been very porous chalky material. No aragonitic layer is seen on the surface of the ligamental area. The surface of the ligament

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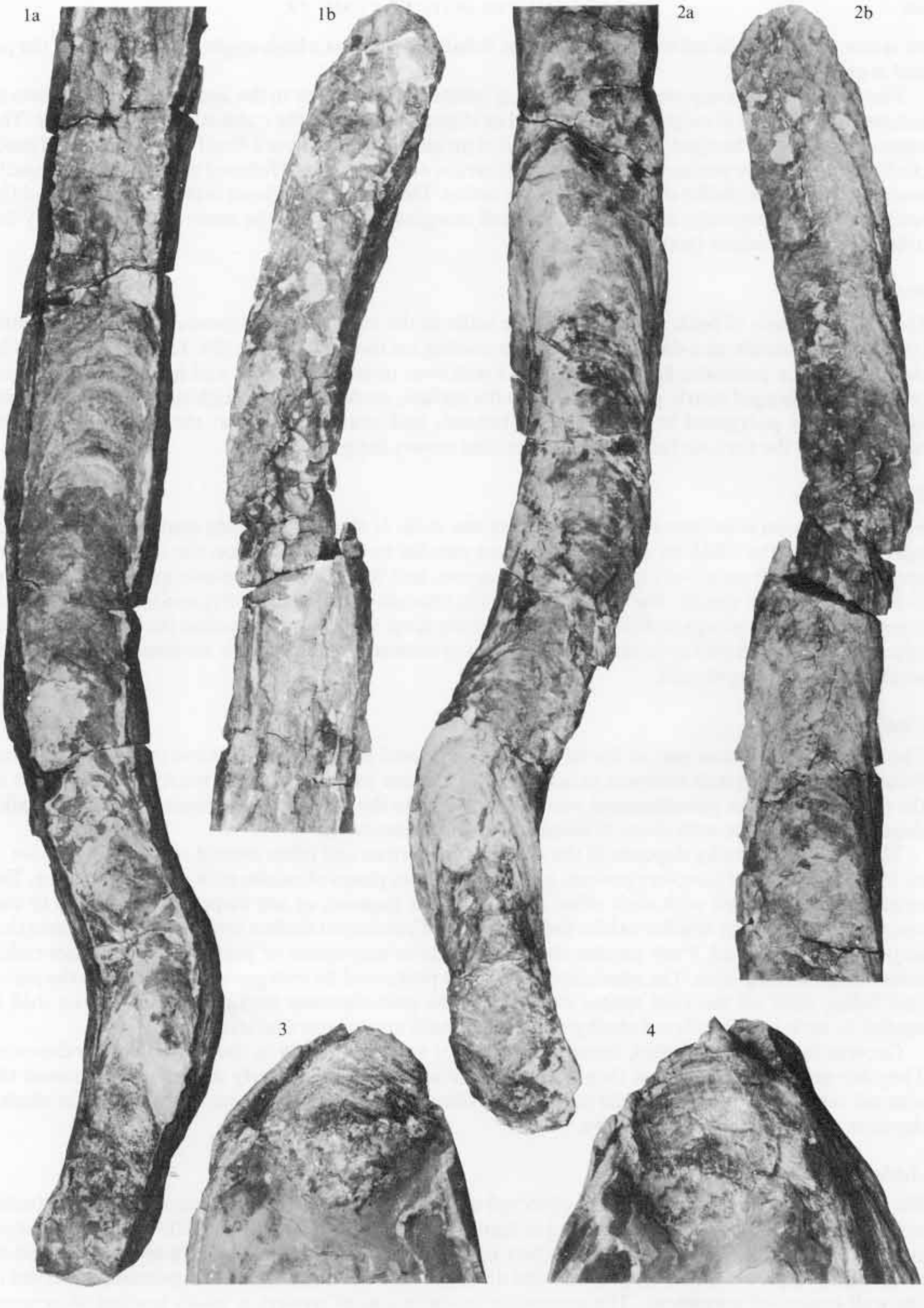
EXPLANATION OF PLATE 18

Figs. 1–4. *Konbostrea konbo* (Hayasaka and Hayasaka, 1956), Kuji, north-west Japan, Upper Coniacian. 1*a*, *b*, University Museum, Tokyo, UT MM17080. Right valve *a*, umbonal part; *b*, ventral part). Surface is unwhitened to show areas of dark colour where it is covered by the prismatic layer, × 0·42. 2*a*, *b*, left valve of same specimen as fig. 1, × 0·42. 3, UT MM17081. Ligamental area of adult right valve. In this specimen the area below the resilifer is covered by part of the inner layer of the left valve, × 0·82. 4, Ligamental area of left valve of same specimen as fig. 3. The inner layer below the ligament pit is peeled off and attached to the right valve shown in fig. 3 × 0·82.




CHINZEI, *Konbostrea konbo* (Hayasarka and Hayasarka, 1956) pit is composed of foliated material. Here, the foliation stands at a high angle to the surface of the pit and is gently arcuate.

The right valve is composed simply of a thin foliated layer, except in the umbonal region. Sheets of foliated material are arranged nearly parallel or slightly oblique to the outer surface of the valve. The umbonal region of the right valve is composed of an outer foliated layer 1·0 to 1·5 mm thick, and inner chalky deposits. The surface of the ligamental area is also made up of foliated material which rapidly wedges out into the chalky deposits below the umbo. The inner chalky layer is thickest just behind the resilifer. It thins ventrally and toward the shell margins, thus filling the inner space formed by the inflation of the resilifer (text-fig. 6).

*Prismatic Layer*

The outer surfaces of both valves, except the walls of the left valve, are covered by a thin prismatic layer which is visible as a dark grey or brown coating on the shell surface (Pl. 18, figs. 1 and 2). The thickness of the prismatic layer is 0·15 to 0·3 mm over most of the right and left valves. Prismatic crystals are arranged nearly perpendicular to the surface, each straight or slightly curved. The prisms are irregularly polygonal in section, often twisted, and sharp or blunt at the end. Growth lines subparallel to the shell surface are visible, cutting across the prisms.

*Foliated Layer*

Foliated material constitutes the outer part of the shell. It also forms a thin coating of the internal tube. Seen with the SEM on a fractured surface parallel to the shell surface, the outer foliated layer appears to be built up of very long, lath-like, narrow, and thin crystals of calcite, arranged in parallel to form compound sheets. The orientation of the crystals changes abruptly, and sheets of different orientation either overlap or abut one another at the same level. In cross-section the lath-like crystals appear as tabular blocks or layers. Differences in orientation of the crystals are seen on SEMs of the section, etched by weak acid.

*Chalky Deposits*

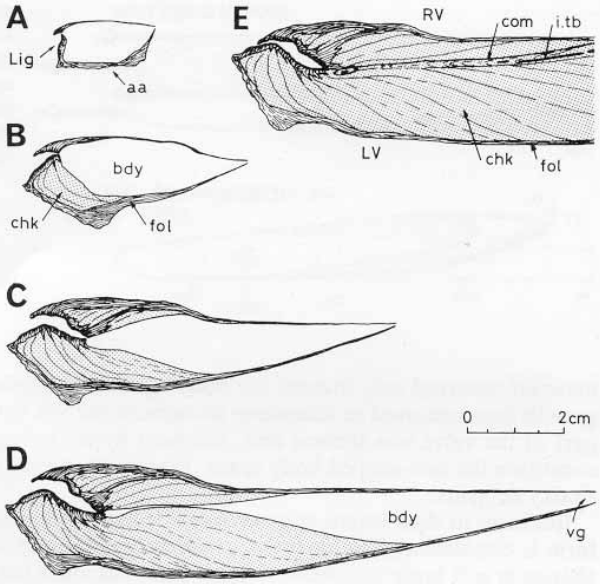
The inner porcellaneous part of the left valve is composed of irregular prismatic or granular calcite. Prismatic calcite crystals intersect at acute angles and are usually arranged nearly perpendicular to the growth lines. The porcellaneous part of the *K. konbo* shell is inferred to represent altered chalky deposits, comparable with those of fossil and living *Crassostrea*.

The white, soft chalky deposits in the shell of *Crassostrea* and other ostreid species (e.g. Taylor *et al.* 1969; Stenzel 1971) are very porous, composed of thin plates of calcite with much void space. The calcite plates interlock with each other in an irregular manner, or are disposed subparallel to one another, connected by smaller calcite flakes. In fossil *Crassostrea* shells a series of different alteration states can be observed, from porous chalky deposits to aggregates of parallel or sometimes radial calcite prisms and grains. The alteration apparently proceeded by overgrowth of calcite on the plates and flakes, until all the void spaces were filled. The porcellaneous part of the *Konbostrea* shell is similar to such heavily altered chalky deposits, in both crystal size and structure.

Growth lines appear as thin, dense aggregates of smaller crystals in the altered chalky deposits. They are generally sparse, but they become more numerous and clearly distinguished around the internal tube, where these deposits last formed. Growth lines are visible also in the lenticular chalky deposits of the walls of the left valve.

*Adductor Myostracum*

No aragonitic myostracum has been observed directly in *Konbostrea.* The position of the adductor myostracum in the left valve is suggested in many individuals by a narrow vein filled with transparent sparry calcite, within the foliated layer (text-fig. 5). The posterocentral position of this vein and its length are comparable with the position and diameter of the adductor muscle impression observed in the well-preserved specimens. The aragonitic myostracum of oysters is easily leached in general,




TEXT-FIG. 6. Ontogenetic change in the shell form of *Konbostrea konbo*, restored by tracing successive growth lines of specimen UT MM17083 from the Kuji locality. A, juvenile stage before accumulation of the chalky deposits. B, start of accumulation of chalky deposits in the left valve. C, later stage of the active ligament. D, final stage of the active ligament; the ligament is barely connected with the soft body space, but the ventral end cannot now be closed without bending because of obstruction by the mound of the chalky deposits behind the ligamental area. E, longitudinal cross-section of the ligamental region of the specimen from which restorations A to D were made. LV, RV: left and right valves; aa: attachment area; bdy: soft body space; chk: chalky deposits; com: commissural plane; fol: foliated layer; i.tb: internal tube; lig: ligamental area; vg: ventral gape.

leaving a cavity (e.g. Stenzel 1971, p. N981). The space filled with sparry calcite is seen in many specimens of *Konbostrea* at the same position, so it may be confidently interpreted as the trace of the formerly aragonitic myostracum. No such trace is seen in the right valve, probably due to the extreme thinness of its myostracum. The inferred myostracum of the left valve is located very close to the shell surface, the shell thickness outside it being usually less than 1 mm. The foliated layer outside the myostracum is weakly undulating, in contrast to the smooth, parallel sheets inside it.

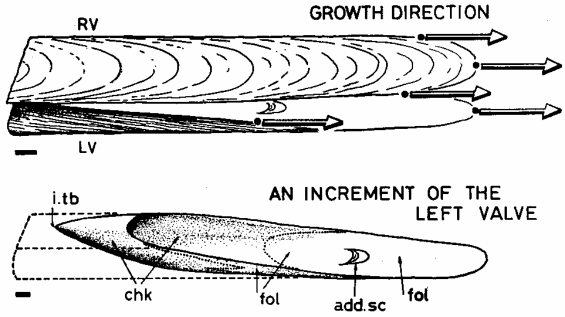
## GROWTH AND FUNCTIONAL MORPHOLOGY OF *KONBOSTREA KONBO*

### *Growth Pattern*

Growth sequences were restored based on well-preserved shells, and the examination of transverse and longitudinal cross-sections of the umbones and cardinal areas. Growth lines indicate the pattern of accretion of successive shell layers. During the early stages of the growth the shell does not show the characteristic features of *Konbostrea*. Juvenile shell growth seems to occur more or less isometrically, although the overall shell shape is extremely variable, as in typical *Crassostrea*. Adult shells are here defined as those which possess the characteristics of the genus, noted above.

Juvenile left valves, 1 to 2 cm high, found attached to adults, usually have semicircular or mytiliform outlines, with elevated umbonal areas and dorsal margins, similar to those of juvenile shells of *Crassostrea*. The juvenile stages are largely composed of foliated shell material (text-fig. 6A). Accumulation of chalky deposits inside the left valve begins when the shell height reaches about 3 to 5 cm. The young stage of the right valve is characterized by its inflated resilifer, and thin, spatular shell which extends to the ventral margin (text-fig. 6B, C, D). Accretion of chalky deposits within the right valve ends with the appearance of the umbonal cavity in the left valve. Up to this point the body space rises smoothly toward the ligamental area, and there is no umbonal cavity. At this point the ligamental area begins to recede from the body space which migrates away from it as they become separated by the chalky deposits. This occurs when the shell height attains 15 to 20 cm.

Longitudinal cross-sections of the cardinal area of the adult left valve show that accretion of shell




TEXT-FIG. 7. Growth of adult *Konbostrea konbo*, showing growth vector (arrow) around the margin, and schematic form of a unit increment of the left valve. RV, LV: right and left valves; add.sc: adductor scar; chk: chalky deposits; fol: foliated layer; i.tb: internal tube. Scale bars 1 cm.

material occurred only around the body space. The sequence of the shell formation restored from growth lines observed in transverse sections of the left valve (text-fig. 5) is as follows. The thin, flat part of the valve was formed first, followed by the anterior and posterior walls which built up to constitute the box-shaped body space. Finally the dorsal part of the body space was filled with the chalky deposits.

Increases in shell length and maximum inflation are negligible in most specimens, once the adult form is established. The shell frequently becomes more slender ventrally than it is dorsally. Little change in soft body size seems to have occurred, once the adult stage was reached. In order for the shell to grow straight, growth vectors around the entire margin must have been nearly identical, parallel to the long axis of the shell (text-fig. 7). A single shell increment has a slipper-like form, similar to the outline of the body space.

*Growth Rate*

In some bivalves such as *Mercenaria*, *Meretrix*, and *Spisula* the shell growth rate can be measured directly from daily growth lines (Pannella and MacLintock 1968; Koike 1980; Jones 1983), or it can be inferred from probable annual layers (e.g. Stenzel 1971; Chinzei 1982*a*). In *Konbostrea*, no such reliable 'clock' has been found to measure the growth rate of this bizarre shell.

Regular growth lines are visible in the chalky deposits around the internal tube, and in the chalky lenses of both walls in the left valve (text-fig. 4). The interval of these growth lines measured along the longitudinal axis of the shell, in the direction of growth, is about 0·8 to 1·2 mm. The increments are nearly the same in the tube area and both walls, reaffirming the equality of growth rates over the entire growth surface. The values do not vary much between younger and older shells or between parts of an adult individual, suggesting a relatively constant growth rate throughout life, beyond the juvenile stage. There remains a possibility, however, that the oysters adjusted their growth rate to accord with the sedimentation rate. It is not known what kind of environmental periodicities are reflected by these rhythmic increments. They are far larger than the daily growth increments of ordinary bivalves, including adult living *Crassostrea* shells, although growth rates of chalky deposits have not been determined. In any case, the chalky deposits and the outer shell layers must be growing at the same rates.

The shells of *C. gigas* (Thunberg, 1793) that live in Japanese waters grow up to 10 to 15 cm in height during the first two years (0·15 to 0·2 mm/day), after which growth becomes very slow. In a brackish lagoon in Hokkaido, adult shells more than 15 years old as observed by fishermen, are 17 to 27 cm in height in one area, while shells about 20 years old attain a height of 15 to 22 cm in another area (Chinzei 1982*b*). The growth rate thus varies greatly among individuals and according to locations, even in the same habitat. Based on these figures, however, a growth rate of roughly 1 cm per year can be estimated for adult oysters. Accordingly, I am inclined to regard the growth rate of the adult *Konbostrea* as having been of the order of 1 or 2 cm per year, by comparison with that of *C. gigas*. This would mean that the 1 m high individuals of *Konbostrea* were probably several tens to a hundred years old. Such an age is not unreasonable. In *Crassostrea* species, individuals over 30 years old are common (Galtsoff 1964). Stenzel (1971, P. N1016) recorded two examples in which the annual layers indicate ages of more than 43 and 47 years.

*Mechanism of opening and closing the shell*

The ligamental area is continuous with the body space during the juvenile stage, until the shell height reaches about 15 to 20 cm (text-fig. 6). The ligament must have retained its function throughout this stage of development. Thereafter, the ligamental area is separated from the body space by the chalky deposits of the cardinal area.

Quite apart from the fact that it could no longer grow, there are other indications that the ligament ceased to be employed to open the adult shell. As the margin of the left valve is slightly oblique to the commissural plane, as defined by the cardinal area, closure of the shell by rotation of the valves about the hinge is geometrically impossible. Field observations indicate that *K. konbo* lived with its shell largely buried in muddy sediment, in an upright position. A small ligament located near the umbo could surely not have been effective in opening a 1 m long shell buried in the mud. If the shell had opened about a hinge located near the umbo, sediment would have become jammed between the two valves. However, in all specimens examined, the valves are found tightly attached, with no exotic material between them. The valves became fused together after the filling in of the earlier occupied body space and became rigidly united. It is concluded that the ligament served no further purpose for opening the adult shell and was abandoned.

The ventral margins of the valves had to gape in order for the shell to grow straight. If the valves had been in contact, one of them would have had to curve as the shell grew, so that the entire shell would have been curved (refer to text-fig. 7). On the other hand the shell retained a large adductor muscle, by which the valves were evidently closed.

Judging from these features, it is postulated that the elasticity of the flat, thin, right valve was employed to open the shell. When the adductor muscle contracted the flexible right valve bent towards the left and the shell closed. When it relaxed the elastic valve returned to its straight, flat form and the shell opened. The thinness and flatness of the shell are basic requirements for the elastic bending. The shell structure of the valve, composed of outer prismatic and inner foliated layers, is analogous to that of pinnids and other bivalves which bend their valves in closing and open elastically (Chinzei 1982*a*). It has not been ascertained whether conchiolin-rich flexible lamellae were present along the margin of the body space as in many of the oysters (Stenzel 1971, p. N977).

Observation of well-preserved adult shells shows that the gape between the two relaxed valves at the ventral margin is about 1 to 2 cm (text-fig. 3). As the length of the body space is approximately 30 cm, a rotation of 2° to 4° would be needed to close the valves. It is not unreasonable to suppose that the right valve could bend to this extent.

Along the cardinal platform the two valves are tightly fused together. They are difficult to separate on this commissural surface. The adhesion of the valves would be important to ensure bending of the right valve near the dorsal margin of the body space. The early Jurassic bivalves *Lithiotis* and *Cochlearites* also used the elasticity of their thin free valves to open their shells. In these genera, reinforced fulcra controlled the bending of the valves. As its valves were tightly fused, *Konbostrea* did not need to reinforce the cardinal margin of the body space to constitute a definitive fulcrum, which indeed is lacking.

## CONCLUSION: THE ADAPTATION OF *KONBOSTREA* TO LIFE ON A SOFT MUDDY BOTTOM

*K. konbo* lived on a muddy bottom in intertidal or brackish water, burying its shell largely in the sediment and maintaining an upright position. The characteristics of this oyster are summarized as follows.

1. The shell is extremely elongated with space for the soft body restricted to the ventral end of the left valve. The right valve is thin, flat, and the same height as the left valve.

2. The shell is composed of a relatively thin foliated layer constituting the box-shaped outer part, and porous chalky deposits that largely fill the interior space.

3. Adult shell growth occurred only in a ventral direction, producing a long, stick-like shell, while the size of the soft body changed very little. Increments measured along the long axis of the shell suggest that the growth rate was substantially constant throughout the adult stage.

4. The ligament was active only during the early stages of shell growth. Later the oyster most probably utilized the elasticity of the thin, flat, right valve to open the shell, which was closed by action of the adductor muscle.

All these features can be explained as consequences of the adaptation of *Konbostrea* to life on a soft muddy bottom in an area of rapid sedimentation. Sediments accumulated rapidly in an intertidal or brackish mud flat. The rate of sedimentation around oyster shells is usually very high compared with that on the open muddy bottom because their own faecal products accumulate around the shells (e.g. Lund 1957), and the shells exposed above the bottom act as a sediment trap (Galtsoff 1964). In order to keep up with the rapidly accumulating sediment, *Konbostrea* grew dominantly in a ventral direction, forming the stick-like shell, to maintain the soft tissues at or above the sediment surface.

The surface foliated layer provided the structural framework of the shell and gave it the strength to withstand mechanical and chemical destruction. The inner chalky deposits are thought to have served to fill up the interior space of the shell, maintaining the soft body close to the rising sediment surface. Porous chalky matter was evidently adequate for this purpose, it could be deposited quickly, and provided for economy of material. It also provided lightweight shell, which is advantageous to an animal living on a soft bottom. The chalky deposits in living oyster shells have been thought to be used in an analogous manner to smooth out the inner contours of the shell (Medcof 1944; Korringa 1951). My observation that in *C. gigas* these deposits appear predominately along the margin of the shell, filling the inner depressions of the surface plication, supports this interpretation.

As chalky deposits accumulated between the ligamental area and the body space the ligament was left behind in the mud, and lost its function. The thick umbonal part of the right valve remained attached to the left valve, while its thin ventral margin grew upward, keeping pace with the left valve. In this situation, use of the elasticity of the flat, thin right valve is thought to be the only possible means by which the shell could have opened. The functional hinge, i.e. the bending point of the right valve, was separated from the anatomical hinge, and moved upward with the soft body.

The early Jurassic bivalves *Lithiotis problematica* Gümbel, 1871 and *Cochlearites loppianus* (Tausch, 1890), found in the Tethyan region, are similar in basic shell morphology and shell structure to *Konbostrea* (Chinzei 1982*a*). They are characterized by stick-like attached valves 30 to 50 cm high, and thin, flat free valves of the same height. The body spaces are also located at the ventral ends of these shells. Their shells are composed of compact outer layers and porous fillings of the interior. Further, the ligament was active only during the young stage in *Cochlearites*, and was lacking or vestigial in *Lithiotis*. These species probably used the elasticity of their thin valves to open their shells. These features are all comparable to those of *Konbostrea*. However, as they were composed of aragonite, and as *Lithiotis* was attached by its right valve, they are not oysters. Benini and Loriga (1977) established a new suborder Lithiotina of the Pterioida for these bivalves. The two species are probably related to the Isognomonidae (Chinzei 1982*a*) or Bakevelliidae (Seilacher 1984) of the Pteriacea. The two species lived in a lagoonal facies, with their long shells stuck down into the mud, keeping an upright position. Similar shell forms and shell structures of *Konbostrea*, *Lithiotis*, and *Cochlearites* constitute a striking example of evolutionary convergence of different taxa, resulting from their adaptation to similar modes of life.

The other type of shell elongation seen among the oysters is represented by cone-shaped ecomorphs in species of *Saccostrea* (Stenzel 1971, p. N1134). The principal difference between this cone-shaped elongation and that of the stick-shaped *Konbostrea* results from the manner by which shell elongation is accomplished. In the cone-shaped shells, upward growth occurs at the ventral margin of the ligamental area. The ligamental area and the ligament grow upward in association with the upward migration of the soft body, as one valve is elongated. The ligament may remain active for opening the shell throughout the life of the animal. The morphologic consequence is a lid-like free valve of a reduced size. Characteristic cone-shaped morphologies are seen among bivalves of diverse taxa, such as some species of *Crassostrea* and other ostreid genera, the unionacean *Etheria* (Yonge 1953), hippuritids and other rudists (e.g. Perkins 1969), as well as in richthofeniid (e.g. Rudwick 1961) and scacchinellid (Williams and Rowell 1965, p. H125) brachiopods, although the ecologic conditions to which they adapt are not always similar.

Another common feature of these cone-shaped animals is seen in the internal structures of the conical valves. The interior of the valve is typically largely empty, being closed off by thin, vaulted partitions. Such structures are comparable in function to the loose chalky material of *Konbostrea*, *Lithiotis*, and *Cochlearites*. These structures serve to close off the lower part of the shell and support the soft body at the upper end of the shell.

It may not be mere coincidence that similar internal structures occur in shells with conical elongation. This becomes apparent when they are compared with the loose chalky structure commonly utilized by animals with stick-shaped elongation. The comparison suggests that only some combinations of external morphology and internal structure can be employed by these animals. Elongation between the ligamental area and the body space may only be possible for those animals which are able to secrete chalky deposits to fill up the shell interior. For animals possessing partitions, a stout outer structure is necessary to support these thin partitions. The growing ligamental or hinge area of the conical animals has the function of supporting the partitions. The mode of shell elongation seems to determine the type of internal supports developed within the shell.

Although *Lithiotis* and *Cochlearites* have reinforced commissural platforms in their attached valves (Chinzei 1982*a*), they do not have partitions. On the other hand, *Crassostrea nippona* (Seki, 1934), which lives in open waters off the coast of Japan, often exhibits cone-shaped elongation with internal partitions, although this species also commonly precipitates chalky deposits. The possibility of other mechanical or physiological constraints on their morphogenesis merits further study.

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