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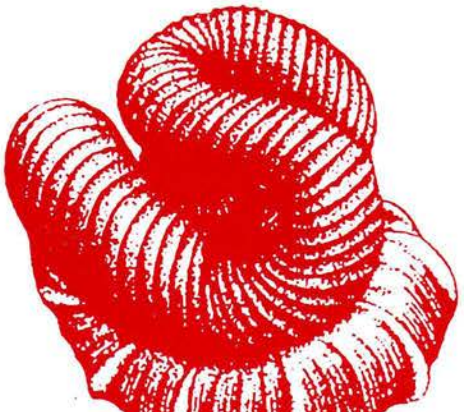

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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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1. Origin of high-rank groups of organisms

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Abstract. It is outlined how seemingly fundamental differences between high-level groups such as phyla and classes may have been introduced in fairly simple and rapid ways. Examples of such ways are development of endosymbiosis, heterochrony involving change of adult mode of feeding with associated changes of basic life habits and body plan, development of asymmetry, and turning upside-down. The latter modification has resulted in fundamental misinterpretations of so-called deuterostomes (or notoneuralians). The basal deuterostomes, the hemichordates, are much more similar to protostomes than text-book authors have been willing to admit. In fact, it is difficult to understand why they are at all considered as deuterostomes. For instance, protostome characteristics found in hemichordates include a main nerve cord on the ventral side, a circum-oesophageal nerve ring, a larva surprisingly similar to a protostome trochophora, blood circulation in the same direction as in protostomes, and (in all pterobranchians and many enteropneusts) schizocoelic formation of the coelom. New consideration of morphologies and life postures indicates that deuterostomes (notoneuralians) are not upside-down compared with protostomes (gastroneuralians). Instead, it is vertebrates that are upside-down compared with all other animals, including other deuterostomes. Fossils very poorly reveal the changes in body plans, but at least indicate that in general these changes are of (at least) Cambrian age. The oldest known group with vertebrate-type orientation is the conodonts.

Key words: Body plan, deuterostomes, evolution, heterochrony, macroevolution

Introduction

Attempts to trace in the fossil record evolutionary steps leading to new major groups of organisms usually have been in vain. New classes, phyla and divisions tend to occur abruptly, with an appreciable internal diversity virtually from the beginning. This is the characteristic result of the Cambrian fossil explosion (or biotic radiation), in which many of our extant animal phyla and classes made their first appearance (even though their lineages may have been present earlier, represented by animals with an older body plan). It is also characteristic of many later radiations, for instance of flowering plants in the Early Cretaceous and of placental mammals in the Late Cretaceous and Early Tertiary. The common occurrence of such geologically sudden appearances and radiations has seldom been taken at face value. Instead, there has been a tendency to postulate long preceding intervals with successive slow evolution of group characters. Thus, the rise of a high-rank group has been seen as a long series of additions of lower-rank groups until the necessary anatomical and morphological changes have been performed. When classes and phyla form in this way it will conceivably be a matter of hundreds of millions of years. This can be exemplified by the transition from typical reptiles to full-fledged mammals, which took some 200 million years. In many cases, however, there is no sign of any prolonged formative period. There is rather reason to believe that transitions were very swift, as in the Cambrian radiation event.

It can be mentioned that molecular differences have been used to indicate an original radiation of coelomate animals 1,200 million years ago (Wray *et al.* 1996). This estimation was based on extrapolation backwards of Phanerozoic evolutionary rates. However, when time for earlier splits, including that between eubacteria and archaebacteria, is allowed for, the age of the same radiation is estimated to be 'only' 670 million years (Doolittle *et al.* 1966).

Progress in the fields of endosymbiosis, ontogeny with heterochrony, and molecular genetics has revealed evolutionary processes which may lead—and apparently have led—to the development of new body plans, i.e., new fundamental designs. The interesting thing is that very little of genetic modification is needed—no macromutation or hopeful monster—and that the processes may be completed virtually instantaneously on the geological time scale. It should be noted that lineages leading to extant phyla may have been separated well in advance of the appearances of new body plans. Fossils and molecules therefore may indicate different dates for the origins of groups.

This contribution will concentrate on deuterostomes after a short look at other organisms. The suggested modes of group origination are only examples.

Endosymbiosis

It now appears to be generally accepted textbook knowledge that most eukaryotic cells contain modified bacteria as endosymbiotic organelles (cf. for instance Margulis 1970; Taylor 1980, 1994). One interesting category of endosymbionts is the coloured plastids, including the chloroplasts, which obviously stem from coloured bacteria. It is quite clear that such coloured bacteria have come to form endosymbionts not only once, but several times. The host organisms were protozoans. Thus there has been a repeated transition between two of the kingdoms that have been recognized of old: the Animalia and the Plantae, or in somewhat newer terms, the Protozoa and the Algae. It has been suggested that the chloroplasts of red algae stem from cyanophytes, those of green algae and land plants from prochlorophytes. There even seem to be cases where a protozoan has turned into an alga not by engulfing a coloured bacterium, but a eukaryotic alga. The result is something like a biological Russian doll, with the largest cell engulfing smaller cells which in turn had engulfed still smaller cells. One such group of complex organisms are the cryptomonads (Ludwig and Gibbs 1985; Douglas *et al.* 1991).

The endosymbiotic phenomenon could not have been detected on fossil material by palaeontologists. The stratigraphic control on its origination is vague at most, but most endosymbiosis events presumably took place in the Precambrian.

Heterochronic origins of animal phyla

In many marine coelomates the larva and adult lead two entirely different modes of life. Whereas the adult is benthic and may have one or the other mode of feeding and locomotion, the larva is pelagic and swims and feeds with the aid of cilia. Also many adult coelomates use cilia for feeding. Some of these collect their food directly from the water. Brachiopods, bryozoans, phoronids, endoprocts and pterobranchians (graptolites) are typical examples, with cilia situated on tentacles. Others collect at least part of their food from the sediment surface, although again with their cilia. In this category we find sipunculids, among others.

The question now is how these animals have developed their adult mode of feeding. We can first note that the tentaculated ciliary feeders belong to the most derived (most highly developed) of the three groups or levels of bilaterian animals, the three being acoelomates, pseudocoelomates and coelomates. Therefore there is every reason to believe that tentaculate ciliary feeding is a derived mode of feeding in adult bilaterian animals.

One way to develop ciliary feeding in adults with ciliary-feeding larvae certainly would be by heterochronic retention of such feeding into the adult (Figure 1). Since heterochronic changes by themselves need to involve only minor genetic changes, they can reasonably occur in very short time. Logically, therefore, a shift to tentacle-feeding from grazing, mud-eating or hunting could lead to a tentaculate phylum from something fundamentally different within a million years, and presumably within a very much shorter time, perhaps even 1000 years or less.

Two groups are particularly instructive in this regard. The first of them is the Endoprocta (Figure 1). An endoproct is virtually a trochophora larva on a stalk. The only characters in an endoproct that do not fit into such a larva are the stalk attachment and the reproduction ability (for instance Hyman 1951). Thus, we can easily believe that paedomorphic heterochrony made its adult characters unlike that of any other group, and particularly unlike that of the immediate ancestor, thus creating endoprocts as a discrete phylum. Since the endoproct characters are those of coelomate larvae, endoprocts are coelomates by affinity (although not by construction), not pseudocoelomates. This is also borne out by the pattern of egg cleavage, which is most similar to that of annelids and similar animals.

The second instructive group is the Phoronida (for instance Hyman 1959). Phoronid larvae are typical coelomate planktic larvae with three transverse bands of cilia. One of the bands develops tentacles in the larva already before it settles on the sea bottom, and the adult tentacles develop from the same ciliary band. This demonstrates the continuity in equipment and feeding method from larva to adult.

Endoprocts and phoronids differ fundamentally in detail. For instance, the tentacles develop from a preoral ciliary band, the prototroch, in endoprocts, but from a postoral band, the metatroch, in phoronids. The message is the same, however: a fundamentally new animal, a new phylum, could be shaped by simple heterochrony.

Twisting

Another class of processes leading to new groups is twisting, that is, deformation of the body symmetry. The gastropods provide an interesting example of this simple change behind high-level taxonomic separation (Peel 1987, pp. 305-306). The diagnostic difference between gastropods and their ancestors, the monoplacophorans, is that the latter are bilaterally symmetrical, whereas in the former the shell with its enclosed soft-parts is rotated 180° on the foot. The evolutionary process is echoed in the embryology of the individual gastropod: the small larva is symmetrical, but at one stage the rotational torsion starts. It can start suddenly and be completed within minutes. Maybe it is a mechanical instability that causes the torsion, and did so when it was evolutionarily invented. The torsion gives gastropods a great advantage compared with monoplacophorans: the mantle cavity is shifted anteriorly and gives the animal the possibility to hide inside its shell.

Modern echinoderms, and even most fossil ones, have a nice pentameric symmetry. Their larvae are bilaterally symmetrical. Certainly their ancestors were symmetrical also as adults. There is general agreement that pentameric symmetry was reached via a stage with asymmetry *distorting* the ancestral bilateral asymmetry. This is so during ontogeny, and we know of many asymmetric forms from the Palaeozoic. Some of them reclined on their sides on the bottom. This is the case with the 'carpoids'. It is possible, even most probable, that the forms leading to pentameric echinoderms

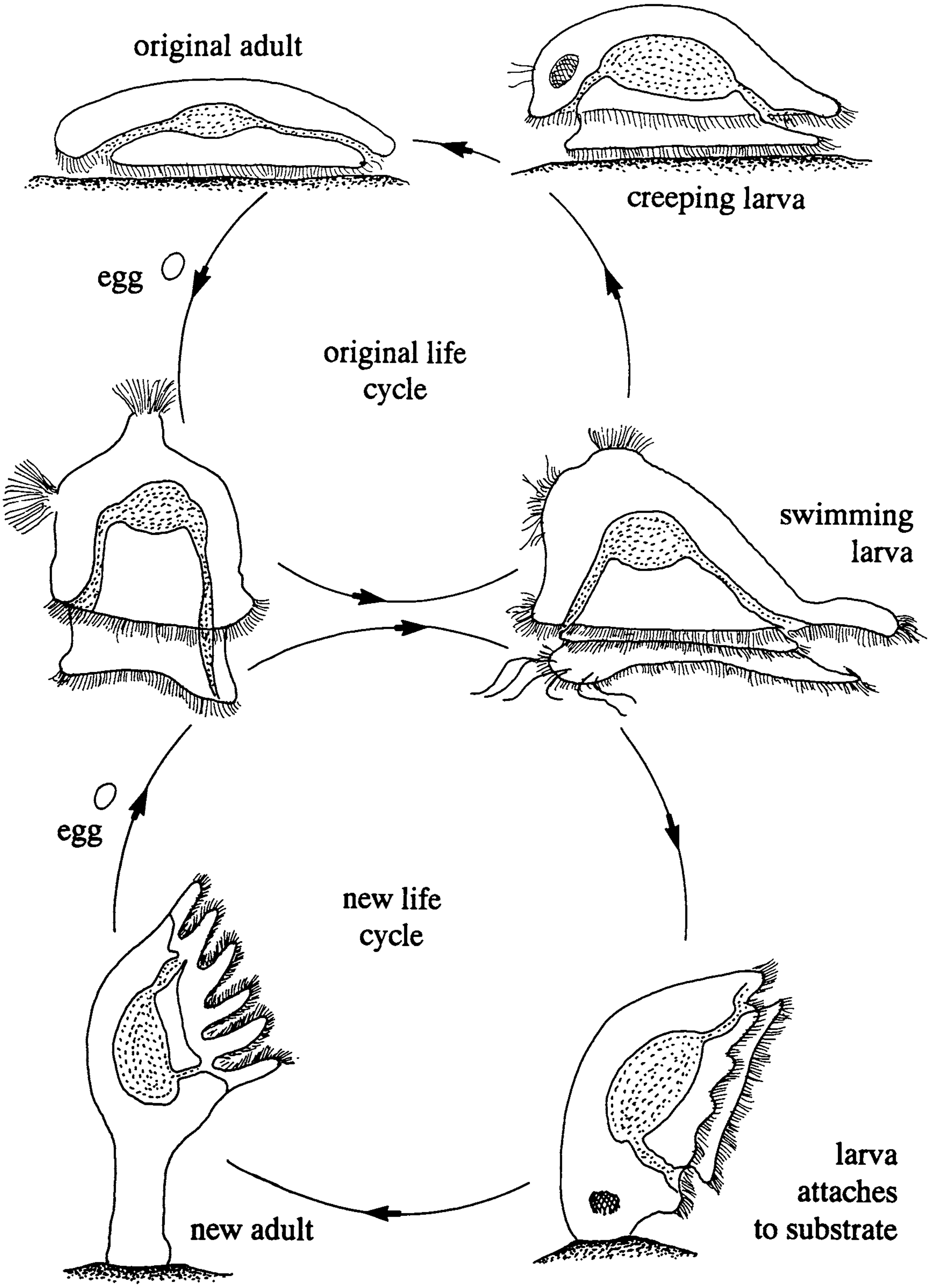

Figure 1. Endoprocta as an example of possible origination of new phyla by heterochrony. The original life cycle is supposed to have had an adult with features of flatworms, molluscs and several types of marine larvae. By prolonging the larval type of feeding into the adult there would have been a need to extend the ciliary band along tentacles to enhance the efficiency. A sessile mode of life would be optimal. It is easy to understand that the shift from the primary to the secondary life cycle would be fairly abrupt, and that the functional and morphological changes involved would remodel the adult so that relationships would be obscured - and so a new phylum would be born.

were attached. 'Carpoids', including 'calcichordates', being asymmetric recliners, may therefore represent blind ends in evolution. In any case, echinoderms provide still another example of new body plans created by small means, presumably with little genetic change and in short time.

Deuterostomes (notoneuralians)

The constructional gap between vertebrates and their relatives on one side, and 'protostomes' (or gastroneuralians) on the other, has long disturbed attempts to compare the two groups. As a result, the phylogenetic and evolutionary relationships have been poorly understood and hotly debated.

As the names indicate, students have thought that in protostomes/gastroneuralians the mouth has a primary position and the central nervous system is ventral. In deuterostomes/notoneuralians the mouth would have a secondary position and the central nervous system would be dorsal (for instance Nielsen 1995). In the following I occasionally use the terms *neural side* and *cardial side* when the terms dorsal and ventral may be confusing or irrelevant.

One attempt to understand the origination of the vertebrates has been to start from a protostome that was turned upside down, so that the originally ventral nerve cord became dorsal in vertebrates. An early proponent of this idea was Etienne Geoffroy St. Hilaire (1822), who suggested that the vertebrate origin was among the arthropods. Other mostly 19th Century authors (F. Leydig, C. Semper, A. Dohrn and A. Naef, see Nübler-Jung and Arendt 1994) have tried to find an origin among annelid-type worms also by means of dorsoventral inversion. In the 20th Century, W. Patten (1912) has been intrigued by the idea of inversion. He believed in a derivation from chelicerate arthropods. However, on the whole the idea of inversion has had only a limited number of proponents. In reality, most zoologists have considered the idea to be of entirely historical interest.

Recently, however, there has been brought impressive molecular evidence that indicates, or rather proves, that vertebrates in fact are upside-down in comparison with 'protostomes'. It started with a contribution by Arendt and Nübler-Jung (1994; see also 1996), where they demonstrated that genes controlling dorsoventral patterning of embryos show close correspondences between vertebrates and insects. The striking difference is that a gene complex (the *achaete-scute* complex) influencing neuronal precursor cells *ventrally* in insects (*Drosophila*) influences the same type of cells *dorsally* in vertebrates (*Xenopus*). In the other direction, *decapentaplegic*-related genes affect mesoderm and ectoderm dorsally in insects and ventrally in vertebrates. Holley *et al.* (1995) found that the *sog* (*short gastrulation*) gene, expressed in the region of the ventral nerve cord in insects, corresponds to the *chordin* gene, that is expressed in the mid-dorsal area in vertebrates, around the dorsal nerve cord. De Robertis and Sasai (1996) added further substance to the idea of inversion. Arendt and Nübler-Jung (1996) also demonstrated a close longitudinal correspondence between the brains of insects and vertebrates, both in gene control and in functional respects. These hard facts demonstrate that zoologists have been completely misled in producing our current view of the differences between protostomes and deuterostomes.

The new understanding of how a vertebrate must be oriented in order to be correctly compared with a protostome has prompted an attempt to see what this implies for other deuterostomes (Bergström, Viehweg and Naumann in prep.) Are all so-called deuterostomes 'upside-down' in comparison with protostomes, or only vertebrates, or some intermediate-sized assemblage? Between which groups did the inversion occur? How could this influence our ideas of protostome-deuterostome relationships?

We can first state that enteropneusts, cephalochordates and vertebrates are the only deuterostome groups with a dorsoventral life orientation that can be compared with that of protostome worms, molluscs and arthropods. It simply has no sense to compare pentaradiate echinoderms or sessile groups with a U-shaped gut with ordinary worms, since dorsal and ventral cannot be defined in a comparable way. In search for the solution of the orientation problem, I was struck by the fact that cephalochordates (amphioxus) tend to rest on their neural side, that is, upside down as the text-books see it. This raised two immediate questions: are they upside down in their life posture, or are they in textbook drawings? And if the textbook drawings are upside-down, what are the implications for our anatomical comparisons with other animals, such as the hemichordates?

Anatomy, function and relationships

In this approach I am not suggesting any bold new ideas on the relationship between phyla. The deuterostomes, as delimited here, are what they are in most textbooks: hemichordates, echinoderms and chordates. There are strong reasons to believe that these groups are closely related. These reasons are well known and need not be repeated here.

I am not suggesting that any one group evolved from any other group such as they are delimited today. For example, I do not believe that vertebrates evolved from modern cephalochordates, but from a common ancestor which had already achieved important derived characters, such as segmentation of musculature and nerve system. This means that the ancestor was able to swim, as are also modern cephalochordates, if only in short darts.

It is worth noting that all preceding steps on the evolutionary ladder within the deuterostomes—pterobranchs, enteropneusts, urochordates, cephalochordates—include ciliary feeding but not active search for food, and no eyes are involved in feeding. Vertebrates, on the other hand, have well-developed sensory organs including eyes for orientation, and they search their food actively, not by ciliary feeding. Therefore it is a logical conclusion that vertebrates have come into being by a radical shift of *habits. As in* cases referred to above, we see this shift also in the ontogeny, since larval lampreys live and feed just as the amphioxus.

This is not unique to vertebrates. Function is intimately tied to body plans. We must therefore expect evolution to have produced similar solutions over and over again. Repeated heterochronic retention of ciliary feeding resulting in a number of tentaculate phyla was mentioned above as one example. Unfortunately many scientists are so impressed by one or the other individual similarity that they overlook the overwhelming amount of parallel and convergent evolution that is clearly evident from the mosaic distribution of characters among animals.

Nielsen (1995) has produced one of the latest phylogenetic trees. His tree is founded on a series of hypothetical ancestral stages, partly larval, for which there is no evidence. His guiding idea is that two types of larval ciliary feeding, downstream and upstream food collecting, defines two phylogenetic groups. It is obvious that upstream ciliary collecting is closely tied to mesotroch ciliary feeding. This combination is found in brachiopods, phoronids, bryozoans, echinoderms, pterobranchs and enteropneusts, all ciliary feeders as adults. Endoprocts, which have prototroch ciliary feeding, have a downstream collecting system, like echiurids, annelids, nemerteans and molluscs, which are not ciliary feeders as adults. A downstream collecting system appears to be primitive among coelomates. Whenever animals have shifted to mesotroch ciliary feeding there appears also to have been a shift to upstream collecting. I do not understand why this is so, nor does Nielsen indicate any understanding of the phenomenon. There is no reason whatsoever that upstream collecting should not have evolved several times, and there is no justification for using downstream and upstream collecting systems to distinguish phylogenetic groups. Nielsen's results are not in line with either modern molecular phylogeny or molecular genetics. For instance, the very striking resemblance in genetic steering of morphogenesis between insects and vertebrates (Arendt and Nübler-Jung 1994, 1996; Holley *et al*. 1995) demonstrates that it is unreasonable to distinguish the Protostomia and Deuterostomia as two main groups, and unreasonable to regard ctenophores as a twig on the deuterostome branch.

There is also in Nielsen's approach the common tendency to generalize, and to give protostomes and supposed deuterostomes characters which they do not have, or that only some of them have. For instance, Nielsen (1994, Table 19) claims that phoronids, pterobranchs, enteropneusts, urochordates and cephalochordates have a dorsal central nervous system, and that pterobranchs, which lack a pelagic larva, have dipleurula-like ciliary bands. As stated elsewere, in many ciliary feeders there is no possibility to distinguish between dorsal and ventral sides, and regarding pterobranchs, enteropneusts, and apparently also cephalochordates, Nielsen is clearly incorrect (see below).

Enteropneusts, protostomes and the central nervous system

Vagile protostomes tend to have at least one ventral nerve cord, or a pair. An anterior part of it embraces the oesophagus. Although deuterostomes are said to have their central nervous system dorsally rather than ventrally, enteropneusts in fact have a well-developed ventral nerve cord, from the anterior end of which commissures rise to embrace the oesophagus and join the (occasionally hollow) 'brain' tube in the mesosoma (Figure 2). There is also a dorsal nerve cord, but it is the ventral cord that is the thickest and that is in close association with the longitudinal musculature. It is notable that there is one or more dorsal (and lateral) cords also in certain protostome groups, such as the flatworms, nematodes and nemertines.

The central nervous system of enteropneusts is therefore typically protostomian in its character. It is commonly said that the hollowness of the 'brain' is found elsewhere only in chordates but no chordate has a hollow nerve tube on the cardial side of the body. Arendt and Nübler-Jung (1996, p. 258) have rightly pointed out the true character of the enteropneust nervous system. It is obvious that enteropneusts are not upside-down in comparison with protostomes. Since they have a ventral mouth and a circum-oesophageal nerve commissure, it would appear to be a mistake to call them deuterostomes. Their mouth is most probably where it has always been in their ancestors, technically they are protostomes, whether or not they are related to vertebrates. And they are gastroneuralians, since the central nervous system is dominantly ventral.

Enteropneusts and chordates

The circum-oesophageal commissure is generally lost in chordates, but there is still a nerve ring in appendicularians (Urochordata), even if there is no longer any brain on the cardial side (Olsson *et al*. 1990). The existence of a nerve ring is most important for the comparison between hemichordates and chordates. If the central nervous system is used to compare appendicularians with enteropneusts, it appears that the neural (dorsal) side of the former must correspond to the neural side of the latter, that is, the side that is considered as ventral in text-books. This is at odds with conventional wisdom, according to which the neural (dorsal) side of vertebrates, and therefore the neural side of appendicularians and other urochordates, corresponds to the cardial (dorsal) side of enteropneusts.

On the whole, however, urochordates are too derived to be conveniently compared with enteropneusts. Cephalochordates (amphioxus) can be more rewarding. When amphioxus is placed with its neural (biologically ventral, but conventionally dorsal) side down, a series of similarities with enteropneusts are apparent (Figures 2, 3, 4). First, the main part of the central nervous system is down in both. The direction of blood circulation is the same, and conforms also with the general protostomian pattern. On the upper side, both cephalochordates and enteropneusts have a pair of folds, called metapleural folds in the former, genital folds in the latter. In amphioxus (but not generally in vertebrates), the metapleural folds are interconnected by a transverse fold closing an atrial space around the pharynx. Between the folds are the pharyngeal tremata (gill pores), although in adult cephalochordates the individual tremata have disappeared and there is a single atrial opening posteriorly. The anus is on the upper side both in cephalochordates and in the larval tailed enteropneust (and in pterobranchs). In cross section,

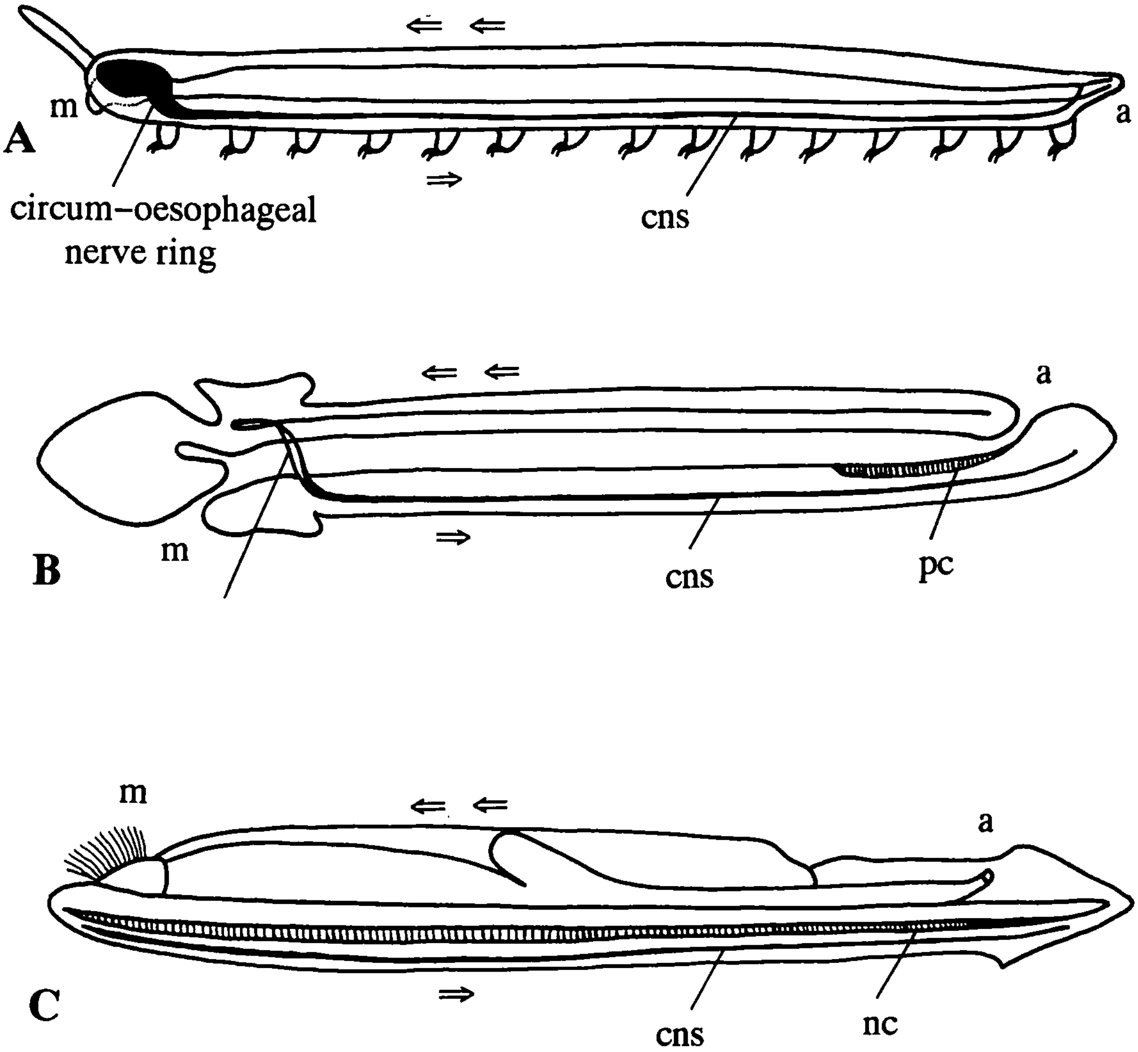

Figure 2. Central nervous system and blood circulation in protostomes (A) and deuterostomes (B, C). A, Onychophora; B, Enteropneusta (with anus in semi-larval position); C, Cephalochordata (amphioxus). With amphioxus oriented as in nature, there is a basic similarity throughout. The main blood circulation is forwards on the dorsal side, backwards on the ventral side. The main stem of the central nervous system is ventral; in the anterior end there is a circum-pharyngeal ring except in amphioxus. The absence in amphioxus appears to be a secondary condition, since such a ring is known from urochordates (*Oikopleura*). The dorsal position of the anus in amphioxus has its counterpart in hemichordates (pterobranchians and larval enteropneusts).

there are paired longitudinal muscles in the lower part of the animal, whereas the reproductive organs are situated in the upper part. Between the gut and the nerve cord is the notochord. Correspondingly there is in some enteropneust species a pygochord (for instance in species of *Balanoglossus*; cf. Figures 2, 3). This pygochord likely functions as a skeleton. The endostyle (and its derivatives), so characteristic of chordates, may correspond to the preoral ciliated organ of enteropneusts.

This impressive, and previously unexpected, list of similarities indicates that chordates may have their origin among animals very similar to extant enteropneusts. With swimming habits, there would be no need for a proboscis, and the animal would immediately be much more ampioxus-like (although lacking, for instance, muscular segmentation). However, many readers may wonder how it would have been possible for sluggish bottom-living enteropneust-like animals to develop swimming powers and pelagic habits. Actually, whereas many enteropneusts are deposit-feeders, others are able to collect food directly from the water, and the species *Glandiceps hacksi* has been observed swarming at the surface in shallow water, feeding on phytoplankton (Brusca and Brusca 1990, p. 853).

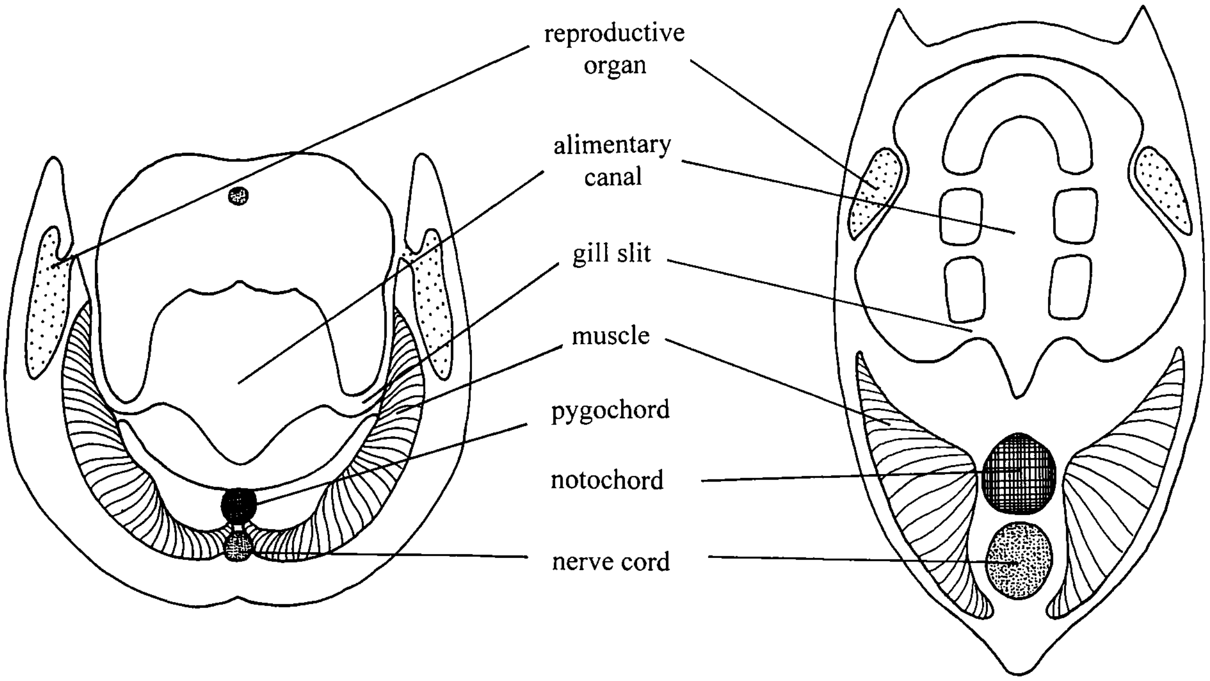

Figure 3. Idealized cross sections through A, enteropneust (Hemichordata) and B, amphioxus (Cephalochordata). Both are oriented as in nature, which means that the amphioxus is upside-down in comparison with textbook illustrations. There is a close correspondence in several structures and organs : pharynx with gill slits, paired dorsal 'wings' containing gonads (called genital wings for simplicity; in amphioxus, their technical term is metapleural folds), ventrally situated longitudinal muscles, main stem of central nervous system ventrally, and a stiffening rod (pygochord and notochord) between gut and nerve stem. The enteropneust musculature is usually poorly developed, but is massive in species of *Saccoglossus*. The enteropneust pygochord is not widely distributed, but occurs in species of *Balanoglossus*.

Filter-feeding cephalochordates, macrophagous vertebrates

We have to accept that we must orient amphioxus with its neural side down when we compare its anatomy with that of protostomes and enteropneusts. Since this is also the way it lives, it would be no problem, but for one thing : doing this, we place them upside-down in comparison with vertebrates, and we can hardly accept instead to place a fish or a mammal upside-down in order to facilitate comparison. However, we have localized the place in the evolutionary tree where reorientation must have occurred : it is inside the chordate tree, after cephalochordates (amphioxus) branched off. Vertebrates obviously are the only upside-down deuterostomes, the only real Notoneuralia.

Cephalochordates have several peculiarities of their own, but they are also similar to vertebrates in many respects, for instance in having a segmented musculature. One difference, however, is that they lack eyes, whereas vertebrates have a pair of anterior eyes. They have light-sensitive spots in the central nervous system which helps them determine the correct burrowing depth, but they cannot spot their food, and they do not need to because they are still filter-feeders like most hemichordates and urochordates. On the contrary, vertebrates find their food actively by the use of sensory organs including eyes.

How could a change from a passive filter-feeding organism to a macrophagous swimmer come about? How does the reversal of body posture fit in, if at all?

We do not know why a change came about. For the moment we just have to accept that it did. For an active localization of its food the original vertebrate apparently needed eyesight, since eyes were developed. Eyes most easily may develop from the light-sensitive nerve cord. For a primitive chordate without a circum-oesophageal ring and a cardial-side component of the brain, this means that the eyes take their origin below rather than above the mouth. For food search along the bottom this situation is inconvenient. The simplest way to solve the problem would be a reversal of body posture. We can now see that nature found this solution. Reversal would shift the mouth to the new ventral side. It is of course possible that the order of events was just opposite, with reversal preceeding eye development.

How likely is it that a swimming proto-vertebrate would be able to shift to an upside-down life? We can get some idea from a study of living amphioxus. My own observations of *Branchiostoma lanceolatum* indicate that it easily turns around when it meets a hindrance, such as aquarium glass. It turns immediately 180°, and does not swim on its side.

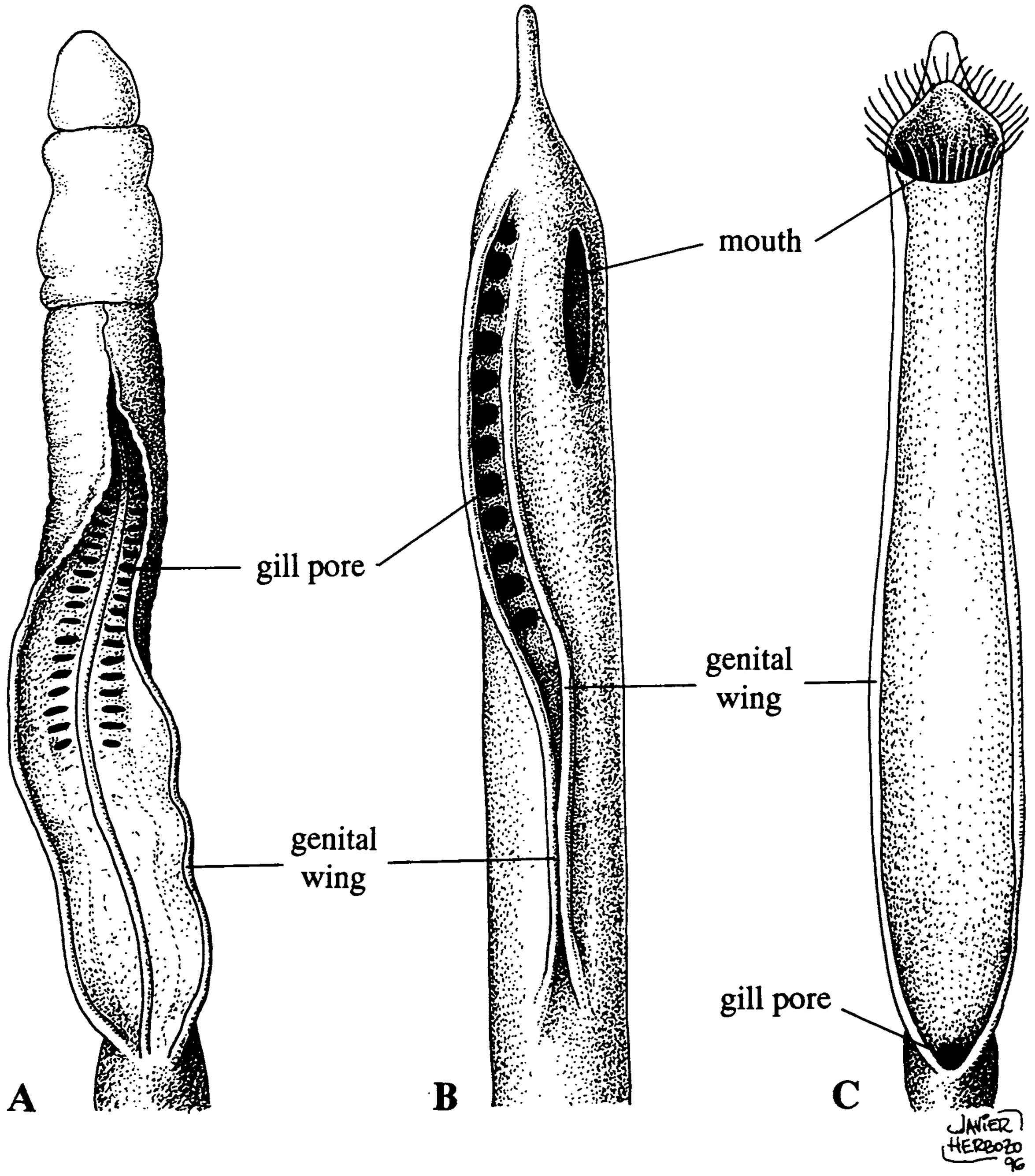

Figure 4. Ventral views of anterior body parts of enteropneusts (Hemichordata) and amphioxus (Cephalochordata). A, The enteropneust *Balanoglossus,* cardial (dorsal) side. B-C, Larval and adult amphioxus *(Branchiostoma),* cardial (so-called ventral) side. Note the general similarity, partly disguised by asymmetry in the larval amphioxus and loss of individual gill pores in adult amphioxus. The genital wings of the enteropneust are similar to the metapleural folds in amphioxus and similarly enclose the gill pores. A, modified from Ruppert & Barnes (1994); B-C, modified from Herdman (in Harmer and Shipley 1932).

After a second or two, it turns over again—and then over again. When hiding in the bottom shell sand, it usually rests with the neural side down, but in exceptional cases it appears to be the other way around. To amphioxus, therefore, one or the other side up does not mean any impossible difference.

We have some idea on when it happened. The great radiation within coelomate phyla started around 540-530 million years ago, at the beginning of the Cambrian. The oldest known cyclostomes lived during the Early Ordovician and are slightly less than 500 million years ago; they had eyes. The conodont animals must have belonged to the vertebrate side of the evolutionary tree (see below). The oldest definite conodont animals we know of lived during the Late Cambrian, some 505 million years ago. Inversion and the vertebrate eye thus are some 505-530 million years old.

Embryology

Reversing the adult means that also the egg and embryo have to be turned around 180°. Surprisingly, the edges closing the neural tube then must be considered as the lips of the urmund. In urochordates the definite mouth forms at the neuropore, that is, just at the anterior end of the urmund. *This makes urochordates indistinguishable from protostomes in this allegedly profound character* (Figure 5).

In cephalochordates and vertebrates the situation is more derived because of a secondary displacement of the mouth. However, it is notable that the nasal sack still forms from the neuropore, and that this sack is continuous with the gut in hagfish. Could it be the original mouth? Arendt and Nübler-Jung (1996, p. 258) found neural evidence that it corresponds to the original mouth, and thought that the functional mouth in vertebrates is a new penetration.

This is of course possible, but from a functional point of view it appears likely that the new mouth in one way or another has evolved from the old. We know that in many enteropneusts the pharynx is divided into upper and lower portions by lateral infoldings of the pharynx wall. The upper channel leads water to the pharyngeal tremata ('gill' pores), while the lower channel conveys food backwards to the midgut. A similar division could have separated the anteriormost part of the vertebrate forebears into an upper nasopharyngeal tube and a lower mouth cavity, both opening posteriorly into the pharynx. This appears to be the situation that is still present in myxinids (hagfishes), while in petromyzontids the upper tube is closed at the rear to form a nasal sack.

The situation in cephalochordates is less easy to interpret. Ontogenetically the definitive mouth forms as a new opening on the left side of the head, only to move later to the upper (so-called ventral) midline. This shift serves two purposes. First, it 'has to' move from its original position on the lower (so-called dorsal) midline to let the notochord grow to the anterior end of the animal, where it serves as a support during burrowing. Second, for an animal concealed in the bottom sediment its position should be as high as possible, thus on the upper side. As for vertebrates it appears most

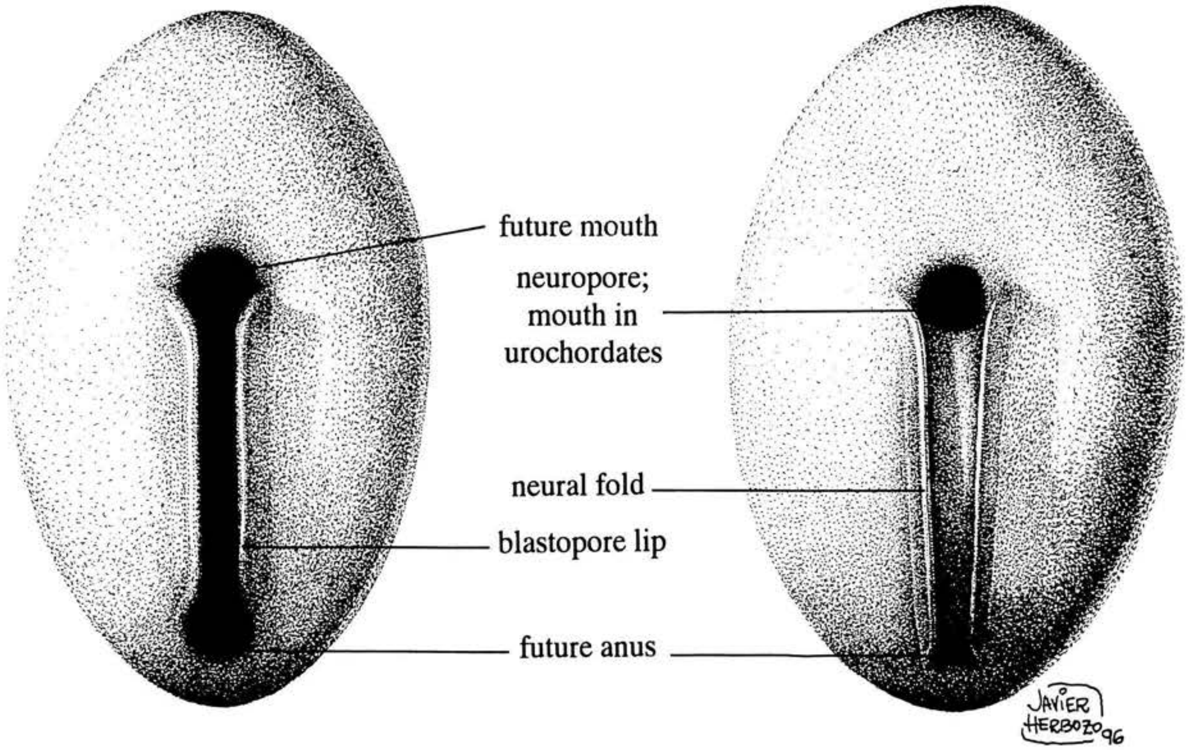

Figure 5. Idealized views of embryos from the neural side: left, protostome; right, urochordate deuterostome. In a protostome the future mouth is said to be formed by or at the anterior end of the closing blastopore, although there are numerous exceptions. The ventral nerve cord forms along the fused blastopore lips. In a deuterostome the central nerve cord similarly forms along a pair of fused folds, which in urochordates extend between the future mouth and anus. The similarity between the two embryo types is striking, but has not been appreciated because students 'knew' they were looking at opposite sides of the embryos.

likely that the mouth is not a completely new opening from an evolutionary point of view, but has shifted position. It may have moved over the anterior tip of the animal. If so, the lateral formation of the mouth may be a later adaptation, perhaps to lying down on one side, or to rotational swimming in the larvae for more effective ciliary feeding.

Fossil deuterostomes

Apart from echinoderms and vertebrates, no deuterostome group has yielded fossils useful for softpart reconstruction. The only other group that is abundant as fossils is the graptolites, to which the two genera of living pterobranchians should be counted. Unfortunately the Palaeozoic graptolites are known only from their colonial skeletons.

The Lower Cambrian Chengjiang fauna of China has yielded the worm-like animal *Yunnanozoon lividum.* In their original description, Hou *et al.* (1991) regarded it as slug-shaped. Bolder interpretations and reconstructions have been issued since. Dzik (1995) and Chen *et al.* (1995) suggested that the animal is a deuterostome, the segmented bands being myomeres of the type found in cephalochordates and vertebrates. I hesitate to accept this interpretation. There are several reasons for this. For instance, the supposed myomeres lack the V-shape characteristic of segmented chordates. They are also notably dark, which is difficult to explain if they were myomeres. It is even more remarkable that there is occasionally a small overlap between adjoining 'segments'. Such an overlap is hardly compatible with the idea that the 'segments' are massive muscle blocks. At the edge the 'segment' in front occasionally stands out a little over the successive one. These features indicate that the 'segments' are not muscle blocks at all, but sclerites in the skin of the animal. Such sclerites are unknown in marine deuterostomes. It can be added that the supposed gills have a ventral position, whereas the gill pores in deuterostomes (other than vertebrates) have a decidedly dorsal position. Moreover, Shu *et al.* (1996) pointed out that the supposed notochord is filled with gut contents.

Shu *et al.* (1996) recently described *Cathaymyrus diadexus* from the Chengjiang fauna as a cephalochordate. The single fossil specimen preserves a possible alimentary canal, a possible notochord, a possible pharynx perhaps with gill slits, and transverse bands that are interpreted as myomeres. No fins are visible. According to the authors the animal is judged to be a relative of amphioxus. This is not obvious from the illustrations. Additional material is needed before any well founded judgement on the significance of this fossil can be made.

The Middle Cambrian *Pikaia gracilens* is more easily accepted as a chordate. It has the general appearance of an eel larva (Figure 6A). It appears to be segmented and to have typically V-shaped myotomes, a key character of cephalochordates and vertebrates. However, as long as it is unknown if it has eyes or jaws (teeth) it cannot be decided if it is a cephalochordate or a vertebrate. This diminishes its value in the discussion. It does not seem to be a conodont animal, since it is likely that the conodont teeth would be easily preservable and visible. On the other hand, the absence of shell sand in the Burgess Shale indicates that its mode of life was different from that of modern cephalochordates.

These fossils apparently can not give us much information about the origin and early evolution of deuterostome groups.

The conodont animals, or conodontophorids, are now known to have had a pair of eyes and a body musculature divided into V-shaped myomeres (Figure 6B ; Purnell 1995). It is quite obvious that they are segmented chordates. The possession of eyes and teeth demonstrates that they were

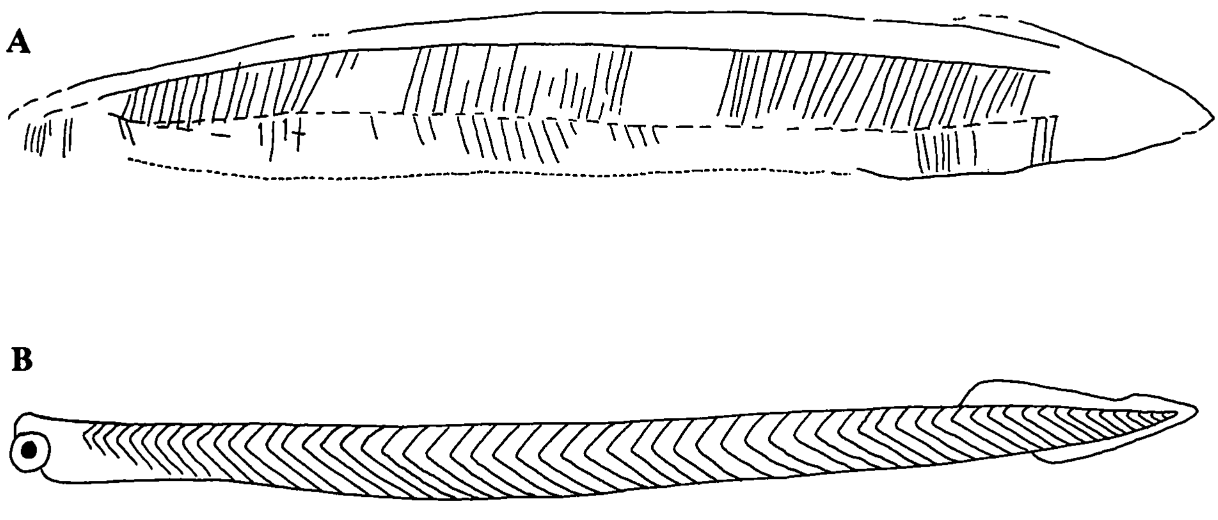

Figure 6. Fossil segmented chordates, both oriented with the neural side up. A, *Pikaia gracilens,* a possible amphioxus relative from the Middle Cambrian Burgess Shale. Length about 4 cm. Drawn from Conway Morris (1982, Pl. S). B, *Clydagnathus windsorensis,* a conodont animal from the Carboniferous of Scotland. Its eyes reveal that it belongs to the vertebrate lineage. Length about 4 cm. Simplified from Purnell (1995, Figure 1).

not ciliary feeders, but hunters. This gives us the possibility to say that they were not cephalochordates, but belonged to the vertebrate side of the evolutionary tree. The oldest true conodonts are from the Late Cambrian. However, they were preceeded already in the Early and Middle Cambrian by so-called protoconodonts and paraconodonts, which are considered by many specialists to be ancestral to the conodonts (see for instance Bengtson 1976, 1983; Andres 1981; Dzik 1991).

Echinoderms are differentiated into some 20-25 classes. The classes are so distinct that it is generally almost impossible to be sure of interrelationships. Four subphyla have been distinguished. One of them, the Homalozoa (the carpoids), include asymmetric to superficially bilaterally symmetric forms which rested with one side on the bottom. The other three phyla include more or less pentameric forms. The subphylum Asterozoa (with seastars and brittlestars) includes forms with true arms, that is, extensions of the body that contain organs such as gonads. The remaining subphyla, the Crinozoa and Echinozoa, consist of a variety of classes and are difficult to define. The basic similarities between pterobranchs (graptolites) and echinoderms makes it most likely that the latter have evolved from a pterobranch-like ancestor. However, nothing of that transition is preserved. As indicated above, a key to understanding the origination of echinoderms is the formation of asymmetry in association with a new mode of attachment (which was presumably lost in the Homalozoa). Another key invention is that of a calcitic endoskeleton. This made it possible for the animals to grow to much larger size than before. The presence of a calcareous skeleton apparently makes a pre-Cambrian origin of the echinoderm body plan impossible. Virtually without exception, calcareous skeletons occur first in the Cambrian. One reason may be that the dissolved oxygen content was too low to form them. Rhoads and Morse (1971) have shown that at present, with an atmospheric oxygen ratio below 10% acids produced by anaerobic glycolysis will dissolve calcareous skeletons. Still, echinoderms with a calcitic skeleton were around already in the Early Cambrian.

Fossils which have been used frequently in attempts to explain vertebrate origins are the so-called calcichordates (for instance Jefferies *et al.* 1987; Jefferies 1988; Woods and Jefferies 1992), more or less irregular to bilaterally symmetric forms with echinoderm-type calcitic skeleton. Most authors regard them as echinoderms forming the class Stylophora within the sub-phylum Homalozoa. According to the calcichordate hypothesis, concavities on the inner side of the skeleton housed a well-developed nervous system with a surprisingly large brain, and similarities with vertebrates include a tail (by other students considered to be a tentacle). The theory is considered controversial. It appears to be immensely more difficult to derive a cephalochordate-vertebrate origin from a 'calcichordate' than from an enteropneust. How, for instance, to evolve a muscular tail swinging sideways around a central endoskeleton from a vertically swinging pulling tool with, functionally speaking, a peripheral exoskeleton?

Deuterostomes a separate branch?

With the understanding of vertebrate inversion—and only vertebrate!—the discussion on 'protostomes' and 'deuterostomes' (or 'gastroneuralians' and 'notoneuralians') can be seen in a new light. There do not seem to exist any deuterostomes, in the sense that they should be animals with a newly formed mouth unrelated to the anterior end of the urmund. On the contrary, urochordate embryology demonstrates that the definitive mouth is formed exactly at the anterior end of the urmund. In this respect, 'deuterostomes' are 'protostomes'.

Of all the groups which now and then have been referred to as 'deuterostomes' or 'notoneuralians', only the vertebrates qualify as 'notoneuralians' in the sense that they have their neural side up (except in the upside-down swimming fish *Synodontis batensoda*). When other chordates are illustrated in the same posture, it is only by convention.

Hemichordates have a typical protostomian arrangement of their central nervous system, including an anterior dorsal part connected by a (fairly diffuse) circum-oesophageal ring with a posterior ventral nerve cord. Among chordates, some urochordates have a circum-oesophageal ring (as noted above), but the post-oesophageal nerve cord dominates strongly. Since no part of the central nervous system appears to be missing (Arendt and Nübler-Jung 1996), the oesophagus appears to have moved forwards through the central nervous system with a resulting displacement of the brain from the cardial to the neural side of the body.

The textbooks repeat the characters said to be typical of deuterostomes. One such character is the mode of coelom formation, which should be enterocoelous. There is in fact much variation. For instance, pterobranchs have schizocoelous coelom formation, some enteropneusts are schizocoelous, others enterocoelous, echinoderms are usually enterocoelous, but some ophiuroids are schizocoelous, urochordates virtually lack coelom, etc. The enterocoelous condition of deuterostomes apparently is a myth, and the variation indicates that the mode of coelom formation has little if any bearing on animal relationships.

The idea that there is a typical 'deuterostomian' larva is also a myth. It is true that enteropneust larvae and certain echinoderm larvae are similar to each other (except for the mode of swimming!), but these are exceptions among the 'deuterostomes'. It is also true that these larvae are similar to trochophoras and trochophora-like larvae, said to be typical of 'protostomes' (Figure 7). In particular, the larvae of enteropneusts, molluscs and annelids share a rotating motion around their longitudinal axis during swimming. Echinoderm larvae do not.

Comparisons of genetic steering mechanisms (Arendt and Nübler-Jung 1994, 1996; Holley *et al.* 1995; De Robertis and Sasai 1996) demonstrate great affinities between 'deuterostomes' and advanced 'protostomes', such as arthropods. Other protostomes (pseudocoelomates, flatworms) are distinctly further apart. There is fairly good agreement in molecular phyletic trees that this is so (for instance, Turbeville *et al.* 1992; Smothers *et al.* 1994; Bergström 1994; Doolittle *et al.* 1996). Winnepenninckx and Backeljau (1996)

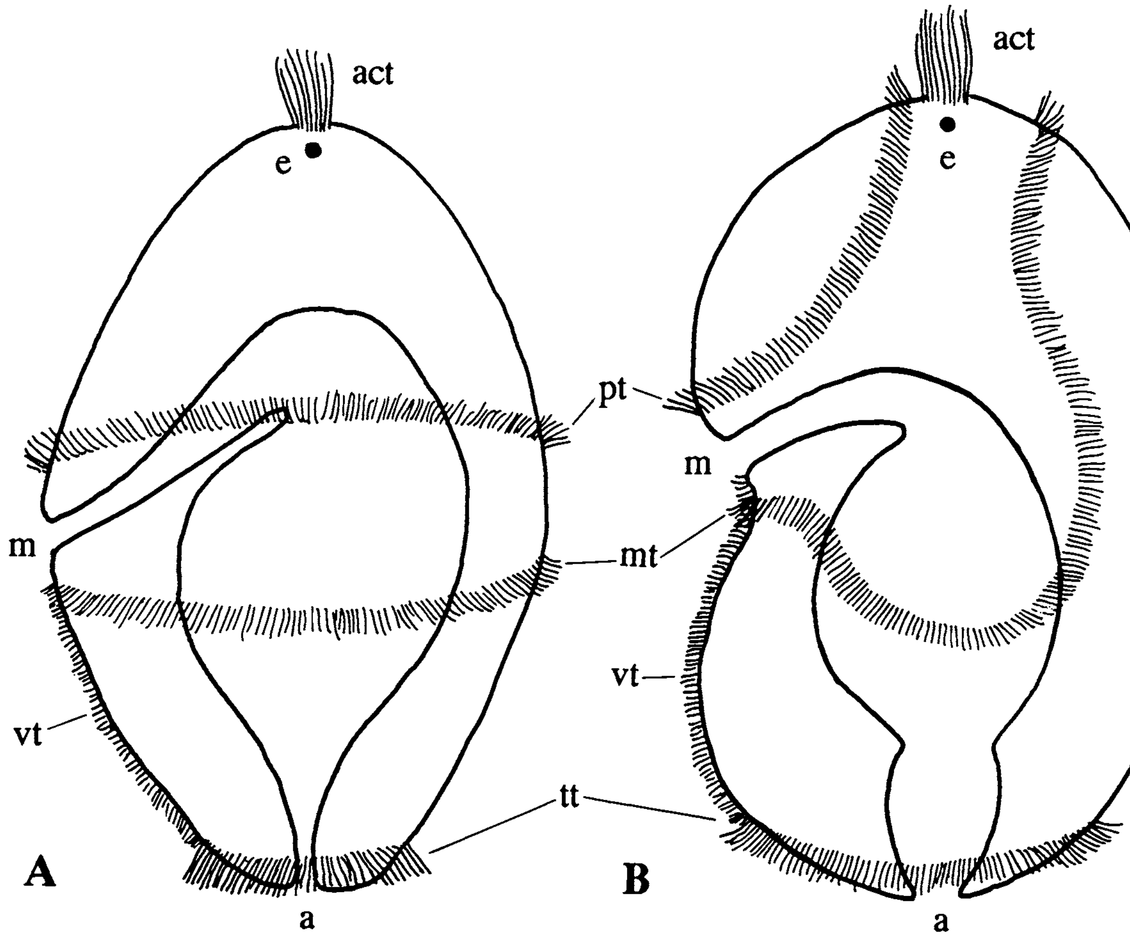

Figure 7. Comparison between typical idealized 'protostome' and 'deuterostome' larvae. A, the 'protostome' trochophora. B, the 'deuterostome' tornaria, present in enteropneusts. Except for the course of the two anterior ciliary bands (prototroch and metatroch), the two larval types are very similar. The similarities even include a rotating mode of swimming, unique to these larvae. Text-book authors, however, conventionally claim that these larvae are utterly dissimilar. a, anus; act, apical ciliary tuft; e, apical eye; m, mouth; mt, metatroch; pt, prototroch; tt, telotroch; vt, ventral ciliary band or neurotroch.

tried different tree-making approaches and molecular models on 18S rRNA and found that these greatly influence the result. However, in 16 presented trees out of 16, deuterostomes were derived from protostomes, although from almost all possible positions. In other words, although there is no agreement on the branching details of the evolutionary tree, *there is general agreement that deuterostomes are derived from protostomes.*

There remains no evidence whatsoever to regard 'deuterostomes' ('notoneuralians') as being anything else than derived 'protostomes'. There are in fact very strong arguments against the old idea that 'protostomes' and 'deuterostomes' are two main branches of the animal kingdom. 'Deuterostomian' characters such as enterocoelous coelom, radial egg cleavage, indeterminate egg cleavage, ciliary feeding and functionally associated oligomery, and upstream collecting ciliary feeding appear to be end products in protostome evolution. These characters are irregularly distributed among phyla.

Having said this, I want to emphasize that hemichordates, echinoderms and chordates belong together in a natural group. Even if the name Deuterostomia is a misnomer (like so many other names), this is of no significance for the practical use of the name. It does not cover the same groups as Nielsen's Notoneuralia, and his Neorenalia is just a younger and unnecessary synonym.

Conclusion

A major conclusion is that high-level systematic units, including classes and phyla, may have formed through simple processes involving only small genetic changes. This indicates that classes, and particularly phyla, may have originated as fast as species. Processes include the formation of endosymbiosis in protists, and both heterochrony, torsion and body reorientation in metazoans.

Among metazoans, most of the dramatic changes appear to have happened in the Cambrian.

Although many zoologists still see protostomes and deuterostomes more or less as sister-groups, there is general agreement among scientists dealing with molecular comparisons that deuterostomes are derived from protostomes.

The Deuterostomia are greatly misunderstood, since textbooks tend to overemphasize certain derived features. In fact, however, primitive deuterostomes, notably hemichordates, have series of protostomian characteristics, such as schizocoel, ventrally positioned central nervous system with an anterior circum-oesophageal ring, vascular system with identical direction of circulation, and a pelagic larva that has great similarities with a molluscan and annelid trochophora. The striking differences between 'typical' deuterostomian and protostomian features are a result of the conventional upside-down orientation of chordates in virtually all comparative studies.

Parallellism and convergence in evolution are much more common phenomena than usually recognized. For instance at the phylum level this has repeatedly resulted in ciliary feeding, segmentation etc, yielding superficial similarities which often have prompted systematists to recognize superphyla such as Articulata and Tentaculata.

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Appendix: Outline of deuterostome classification

Deuterostomian superphylum

HEMICHORDATA Bateson, 1885, emend. Fowler, 1892
  Graptolithina Bronn, 1846 = Pterobranchia Lankester, 1877
  Enteropneusta Gegenbaur, 1870
  Xenoturbellida Westblad, 1949

ECHINODERMATA de Brugière 1789
 HOMALOZOA Whitehouse, 1941 (= Carpoidea Jaekel)
  Homostelea Gill and Caster, 1960
  Homoiostelea Gill and Caster, 1960
  Stylophora Gill and Caster, 1960 (= Calcichordata Jefferies)
  Ctenocystoidea Robison and Sprinkle, 1969
CRINOZOA Matsumoto, 1929 (8 classes)
ASTEROZOA Haeckel in Zittel, 1895 (1 or 2 classes)
ECHINOZOA Haeckel in Zittel, 1895 (perhaps 6 classes)

CHORDATA
 UROCHORDATA (TUNICATA)
  Appendicularia (Larvacea)
  Doliolariacea (or as Doliolida under Thaliacea ?)
  Tunicata (with tunic)
  Ascidiacea, sea squirts
  Thaliacea, salpa
CEPHALOCHORDATA or ACRANIA
 Leptocardia
VERTEBRATA (CRANIATA)
 Several classes including Conodontophorida

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2. Ethological interpretation of the trace fossil *Zoophycos* in the Hikoroichi Formation (Lower Carboniferous), southern Kitakami Mountains, Northeast Japan

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Abstract. **The trace fossil *Zoophycos* was newly discovered in the lower part of the Hikoroichi Formation (Lower Carboniferous) distributed in the southern Kitakami Mountains, Northeast Japan. It consists of a helically coiled spreite, in which black-colored, chevron-shaped lamellae occur in cross section as an internal structure. Apart from the absence of distinct pellets and axial shaft, morphological features of the Hikoroichi *Zoophycos* are similar to those of *Zoophycos* known from Tertiary deep-sea sediments.**

X-ray diffractional analysis and microscopic observation in thin section revealed that the black material of the lamellae in the spreite appears to be derived from a higher level as a result of downward conveyor activity by tracemakers. This inference and morphological similarity to Tertiary specimens imply that the black material in the spreite of the Hikoroichi *Zoophycos* is probably of fecal origin, although there is no compelling evidence such as pellets. According to this interpretation, the producing animals of the Hikoroichi *Zoophycos* fed in surface and/or subsurface sediments and deposited fecal matter deep in sediment, as did *Zoophycos* from Pliocene deep-sea sediments of the Boso Peninsula, Central Japan. Such feeding and excretory styles in the *Zoophycos* producer may have already been achieved by at least the Early Carboniferous and have remained unchanged over a long peroid.

Key words : Ethology, Hikoroichi Formation, Japan, Lower Carboniferous, trace fossil, *Zoophycos*

Introduction

Zoophycos, a complex spreiten structure with several kinds of forms, is known as one of the most striking ichnofossils and has been reported from the worldwide post-Cambrian marine sediments (Seilacher, 1967a, 1967b ; Bischoff, 1968 ; Plička, 1968 ; Lewis, 1970 ; Simpson, 1970 ; Häntzschel, 1975 ; Ekdale, 1977 ; Wetzel and Werner 1981 ; Crimes, 1987 ; Bromley, 1990 ; Bryant and Pickerill, 1990 ; Olivero, 1994). In the post-Cretaceous, it occurs mainly in deep-sea sediments deposited at bathyal and/or hadal depths (eg., Seilacher, 1967a ; Ekdale, 1977 ; Ekdale and Bromley, 1983, 1984a, 1984b, 1991 ; Wetzel, 1981, 1983, 1987, 1991 ; Frey and Pemberton, 1984 ; Frey and Bromley, 1985 ; Bottjer *et al.,* 1987 ; Kotake, 1989 ; Frey *et al.,* 1990 ; Wetzel and Wijayananda, 1990). In contrast, the Paleozoic *Zoophycos* is found mainly in the sediments of shallower settings, such as delta, nearshore, and shelf environments (eg., Osgood, 1970 ; Loring and Wang, 1971 ; Osgood and Szmac, 1972 ; Marintsch and Finks, 1978 ; Miller and Johnson, 1981 ; Chaplin, 1982 ; Miller, 1984, 1991 ; Miller and Knox, 1985 ; Bjerstedt, 1988a, 1988b ; Bryant and Pickerill, 1990). Many authors have discussed its origin and interpreted it to be a product of feeding or foraging behavior by a worm-like, infaunal deposit-feeder. In contrast, I proposed a different model on the origin of *Zoophycos* : the animals of *Zoophycos* appear to represent surface deposit-feeders which ingested surface and/or subsurface sediments (Kotake, 1989, 1990, 1991, 1992, 1993, 1994).

During field studies of the Lower Carboniferous Hikoroichi Formation distributed in the southern Kitakami Mountains, Northeast Japan, A. Kaneko discovered a number of well-preserved specimens of *Zoophycos* in the lowermost interval of the formation. As a result of field observations following the initial recognition of *Zoophycos,* it was revealed that *Zoophycos* is a common ichnofossil in the lower part of the Hikoroichi Formation.

This article reports the first discovery of the trace fossil *Zoophycos* in Paleozoic strata in Japan. The purposes of this paper are (1) to describe the morphology and mode of occurrence of the Hikoroichi *Zoophycos* and to compare them to those of the North American specimens from the same age, (2) to deliberate on the origin of the Hikoroichi *Zoophycos,* and (3) to examine whether or not the mode of the feeding and excretory styles of the Tertiary *Zoophycos*-producer is applicable to that of the Paleozoic one.

Geologic and sedimentologic background of the *Zoophycos*-bearing interval in the Hikoroichi Formation

The Lower Carboniferous Hikoroichi Formation, which is distributed in the southern Kitakami Mountains (Figure 1), consists of shale, tuffaceous shale, fossiliferous or tuffaceous sandstones, limestone, and tuff. It is subdivided into four stratigraphic units (H-1 to H-4 Members in ascending order) (Kawamura, 1983). The trace fossil *Zoophycos* was found in the H-1 Member in the Chyoanji area and the overlying H-2 Member in the Onimaru area (Figure 1C). In this paper, I follow Kawamura's stratigraphic division.

The *Zoophycos*-bearing interval of the H-1 Member consists mainly of bluish gray tuffaceous shale (10 to 40 cm thick) with interbedded tuffaceous sandstone (less than 3 cm thick), fossiliferous sandstone (less than 5 cm thick), and gray or black shale (less than 5 cm thick). On the other hand, the H-2 Member is well exposed in a cliff at the Onimaru Quarry, west of Hikoroichi (Figures 1, 2). There it comprises mainly alternating beds of thin tuffaceous sandstone (mostly 1 to 2 cm thick), tuffaceous shale (1 to 10 cm thick), and black shale (2 to 20 cm thick) in associated with beds of fossiliferous sandstone (mostly 1 to 2 cm thick) and tuff (less than 7 to 8 cm thick) (Figures 2, 3). In particular, the lower part of the H-2 Member represents a sequence of well-sorted, bluish gray tuffaceous shale with thin tuffaceous sandstone beds (Figures 2, 3).

In the Hikoroichi Formation, *Zoophycos* usually occurs in tuffaceous shale overlying tuffaceous sandstone (Figures 4, 5). Throughout the sandstone bed and the overlying *Zoophycos*-bearing tuffaceous shale, a complete Bouma sequence is occasionally visible (Figure 5B). The basal portion of each sandstone bed exhibits several kinds of erosional structures which may have been produced during deposition of the sandstone. In contrast, black shale lacks any sedimentary structures of hydraulic origin and contains body fossils such as brachiopods, cephalopods, bryozoan fragments, and disarticulated crinoid stems. A series of sedimentary structures recognized in the tuffaceous sandstone and the overlying tuffaceous shale strongly suggests that they are of turbidity current origin. On the other hand, the black shale probably was deposited under low-energy, stable bottom conditions below the storm wave-base.

Usually an incompletely bioturbated, mottled fabric transition zone is recognizable between the black shale and tuffaceous shale, both of which occupy the uppermost part of a single turbidite unit (Figures 4, 5). The thickness of this zone varies between 1 cm and 10 cm. In this zone, the mottled background fabric contains a diverse association of biogenic sedimentary structures, including *Chondrites*, *Phycosiphon*, *Planolites*, *Scalarituba*, *Teichichnus*, *Thalassionoides*, and *Zoophycos* (Figures 4, 5). In most cases, these trace fossils are crosscut by the black spreiten of *Zoophycos*. The upper portion of the transition zone is more heavily bioturbated than the lower part. Judging from the ichnofabrics in the transition zone, the zone appears to be a product of reworking and mixing activities by benthic organisms during deposition of mud. In contrast, there is no apparent evidence of biogenic activity in either the sandstone or the lower part of tuffaceous shale.

These lithological aspects suggest a low-energy off-shore environment related to the influx of turbidity currents for the Hikoroichi basin at the *Zoophycos*-bearing interval, although Kawamura (1984) assumed shallow, temperate, and high-energy conditions above the wave-base as a background situation.

Morphology of *Zoophycos*

General characteristics

The ichnogenus *Zoophycos* usually includes two basic forms; helicoidal form and planar form (Seilacher, 1967b; Häntzschel, 1975). The former is characterized by a three-dimensional morphology and consists of a lobate, spirally coiled spreite around the central portion or axial shaft (Figure 6). The latter consists of a planar spreite developed along the bedding plane (Figure 7). In both forms, the marginal tunnel sharply bounds the spreite and the spreite-bearing host rock (Häntzschel, 1975).

In the spreite of helicoidal form, there are two kinds of lamella structures; major and minor lamellae (eg., Bischoff, 1968; Simpson, 1970). The major lamellae spirally radiate from the axial portion of the spreite (Figure 6A). On the other hand, the minor lamellae branch off the major lamella at an acute angle (10 to 35 degrees). In vertical section these two lamellae show chevron-shaped, lunate, or meniscate structures. In contrast, the spreite of the planar form *Zoophycos* has only a single lamella structure, which is less complex than that of the helicoidal form (Figure 7).

Zoophycos from the Hikoroichi Formation

In the case of *Zoophycos* from the Hikoroichi Formation, the spreite usually is arranged in parallel to the bedding plane, but toward the central portion it becomes inclined at an acute angle of 20 to 30 degrees to the bedding plane (Figure 5C). This fact indicates that the Hikoroichi *Zoophycos* is of helicoidal form. No distinct axial shaft, however, was found in the specimens examined.

The thickness of the spreite ranges from 1 mm or less to approximately 4 mm. In a cross section, the spreite is made of black sheets or systematically arranged chevron-shaped lamellae in a light-colored host rock (Figures 5, 8). In plan view, on the other hand, they are composed of densely packed lamellae of black sediment in blue-gray rock (Figure 9). The Hikoroichi specimens lack pellets in the spreite, which are often preserved in the Tertiary and Quaternary *Zoophycos* (Ekdale, 1977; Wetzel and Werner, 1981; Kota-

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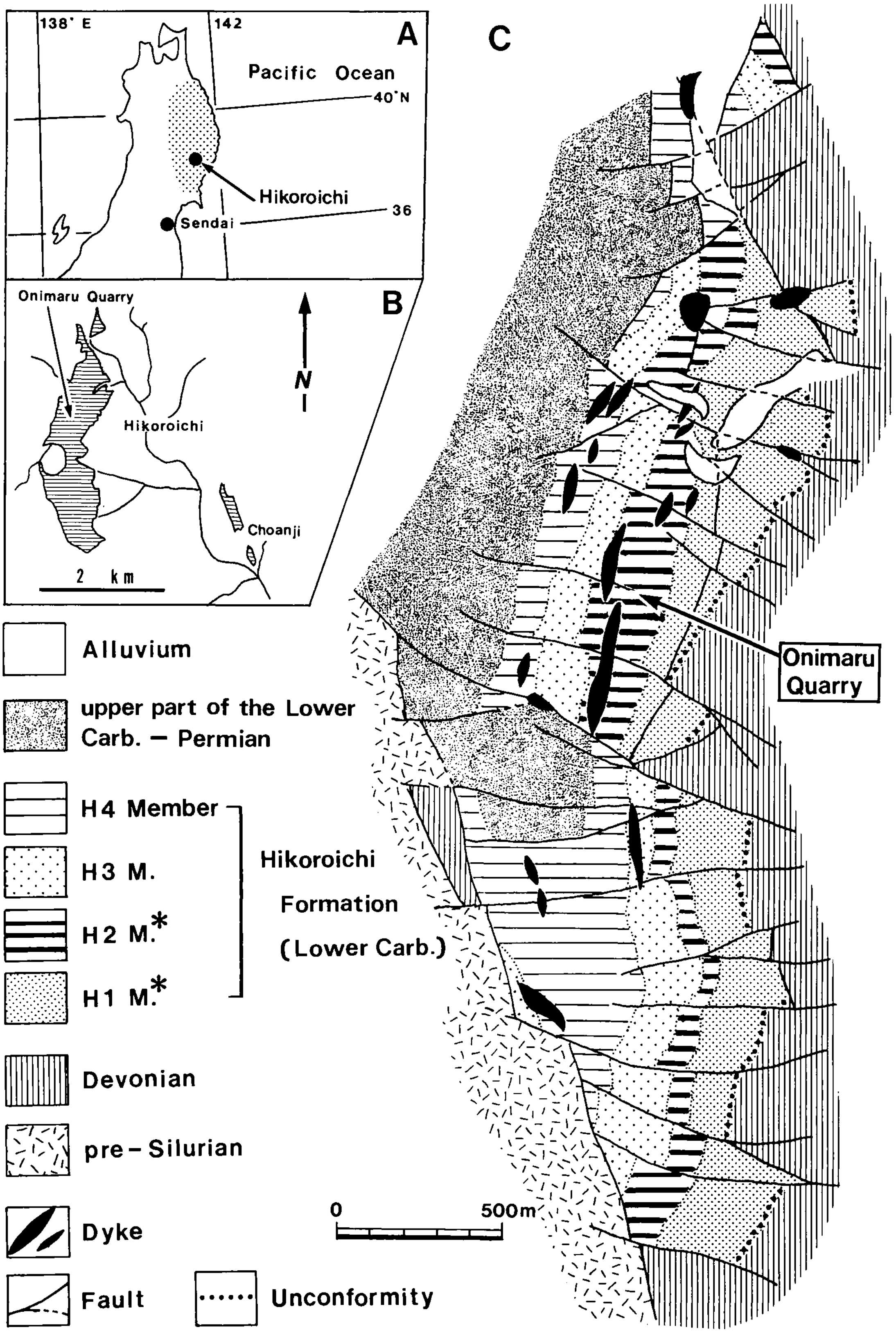
Figure 1. Fossil locality maps. **A**: Index map showing the Hikoroichi area in the Kitakami Mountains (dotted). **B**: Map showing the distribution of the Hikoroichi Formation in the Hikoroichi and Choanji areas. **C**: Geologic map of the Hikoroichi Formation in the Hikoroichi area. The geologic map was simplified from Kawamura (1984). Asteriks indicate *Zoophycos*-bearing stratigraphic units in the formation.


A
138° E
142
Pacific Ocean
40°N
Hikoroichi
36
Sendai
B
Onimaru Quarry
N
Hikoroichi
Choanji
2 km
C
Onimaru Quarry
Alluvium
upper part of the Lower Carb. – Permian
H4 Member
H3 M.
H2 M.*
H1 M.*
Hikoroichi Formation (Lower Carb.)
Devonian
pre-Silurian
Dyke
Fault
Unconformity
0
500m

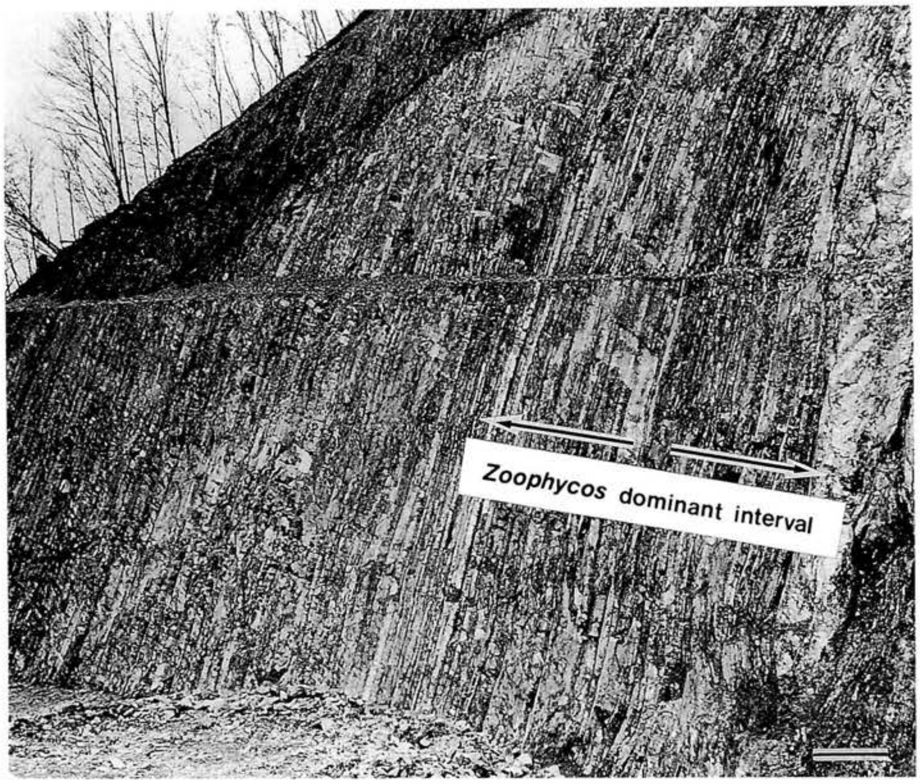


Figure 2. Outcrop photograph of the *Zoophycos*-bearing interval in H-2 Member of the Hikoroichi Formation exposed at a cliff of the Onimaru Quarry (Figure 1). Scale bar=1 m.

ke, 1989, 1991, 1992, 1993, 1994 ; Ekdale and Lewis, 1991 ; Fu and Werner, 1994). A well-defined marginal tunnel is seen at the outer edge of the spreite (Figure 5C).

The Hikoroichi *Zoophycos* occurs in the upper part of a tuffaceous shale and the overlying transition zone, but it is absent in both the black shale and the lower part of turbidite units such as TU_1 and TU_2 (Figures 4, 5). In the lithological units TU_4 and TU_5, sharply defined black *Zoophycos*-spreiten are visible and stand out against the lighter-colored surrounding rock which is characterized by the sparsity of other trace fossils (Figures 5, 8). In the transition zone, by contrast, the *Zoophycos*-spreiten are vague in outline in comparison with those occurring in the underlying tuffaceous shale (Figure 5C).

These lines of evidence suggest that the *Zoophycos* producer probably occupied the deepest tier within the sediment while the other tracemakers concurrently inhabited shallower tiers. Alternatively, the *Zoophycos* producer simply represents the latest stage of bioturbation activity in a stratum produced by discontinuous sedimentation.

As described in the previous literature, some Paleozoic *Zoophycos* seem to differ from the post-Mesozoic specimens in their overall morphology and internal structural features. Indeed, the three-dimensional morphology of the Pennsylvanian *Zoophycos* reconstructed by Miller (1991) is apparently different from that of the post-Mesozoic specimens (Figure 10). Furthermore, Chaplin (1982) and Miller (1991) pointed out that Paleozoic specimens of *Zoophycos* are characterized by wider morphological variations than the post-Mesozoic representatives (Figure 11).

In contrast, apart from the absence of pellets and a distinct axial shaft, morphological features of the Hikoroichi *Zoophycos* are more similar to those of *Zoophycos* from Tertiary deep-sea sediments than to those of the Paleozoic specimens reported by Chaplin (1982) and Miller (1991) (Table 1).

Origin of black material in spreite

The spreite of the Hikoroichi *Zoophycos* is filled with black material. Lithologically, the material superficially resembles the black shale overlying the spreite-bearing bluish-gray tuffaceous shale. Based on well-preserved specimens taken from the lower part of the H-2 Member at the Onimaru Quarry (Figures 2, 3), the component material among the black shale, spreite-bearing bluish gray tuffaceous shale, and the black material in the spreite were compared to one another in order to determine the origin of the black material.

Methods

X-ray diffraction analysis of the three kinds of sediment samples was accomplished to determine the mineralogical composition. Samples (1 g to 2 g each) were taken from three different portions in a single slab (Figure 12). Because the *Zoophycos*-spreite consists of alternating lamellae of black material and bluish-gray host tuffaceous shale (Figures 5C, 8, 9), it is difficult to completely isolate only the black portion from the spreite. Since contamination with particles originating in the tuffaceous shale portion is unavoidable, the black material dominant portion in the spreite (Figure 12) was used in the present analysis to diminish contamination as much as possible.

In addition, thin sections of the spreite and surrounding host rock were examined to compare microfacies, grain size, and component material between them.

Results

The x-ray diffraction profile of the bluish-gray tuffaceous shale markedly differs in the relative abundance of chlorite, feldspar and quartz from those of the black shale and black material in the spreite (Figure 13). The profiles of black shale and the black material in the spreite closely resemble each other, and they are characterized by the predominance of quartz. Chlorite is more abundant in the black spreite material than in the black shale. This presumably is due to the incomplete isolation of the tuffaceous shale. The bluish-gray tuffaceous shale, by contrast, is rich in chlorite and feldspar but is poor in quartz. Chlorite in the black shale appears to have derived from the bluish-gray tuffaceous shale as a result of reworking and mixing activities by benthic organisms during deposition of muddy sediments.

Microscopic observation revealed that the spreite-bearing bluish-gray tuffaceous shale consists mostly of clay-sized particles, in which no bioclasts were found. In contrast, component materials of the black sediment in the spreite and black shale closely resemble one another in grain size (ranging from clay to medium-grained sand) and are much coarser than the spreite-bearing host rock (Figure 8). In rare cases, fine to medium sand-sized bioclasts, which are dominant in the black shale, are contained in the black portion in the spreite.

These data strongly suggest that the black sediment in the spreite of the Hikoroichi *Zoophycos* originated in the black shale just above the spreite-bearing horizon.

Discussion

Most previous authors believed that the *Zoophycos* producer systematically moved through the substrate to search for and ingest organic matter for food (Bischoff, 1968; Simpson, 1970; Häntzschel, 1975; Ekdale, 1977; Wetzel and Werner, 1981; Ekdale and Lewis, 1991). In other words, the component material of the fillings in the spreite in this interpretation originated in the sediment at the site of spreite emplacement. However, Ekdale and Bromley (1983) pointed out that some *Zoophycos* occurring in the Danish Cretaceous chalk were filled with sediments derived from a higher

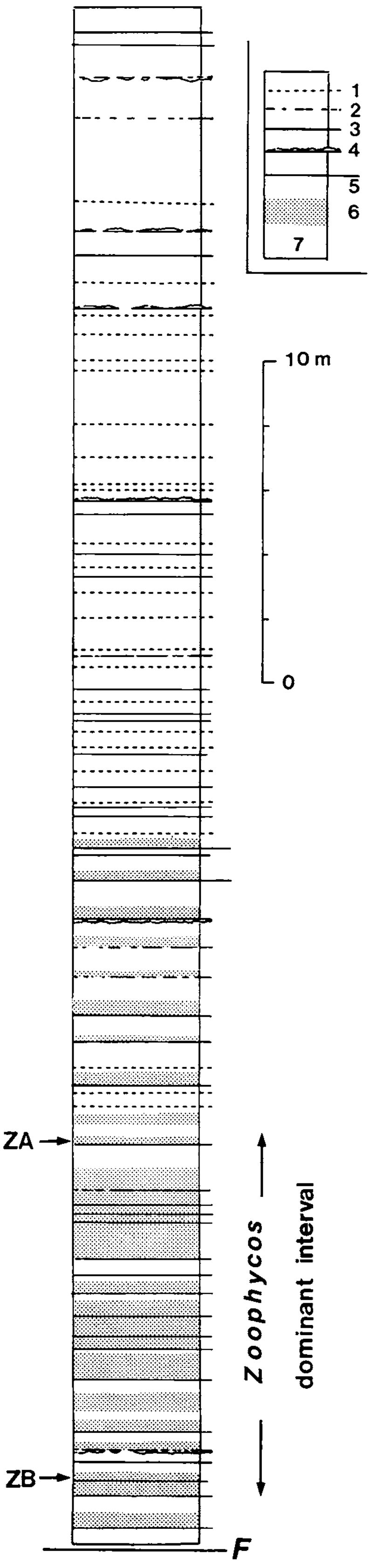


Figure 3. Columnar section of H-2 Member of the Hikoroichi Formation exposed at the Onimaru Quarry. The *Zoophycos*-bearing rock samples for this study are indicated by arrows ZA and ZB. 1 : sandstone bed less than 0.5 cm thick, 2 : sandstone bed between 0.5 cm and 1 cm thick, 3. sandstone bed between 1 cm and 2 cm thick, 4 : sandstone bed more than 2 cm thick, 5 : tuff, 6 : tuffaceous shale, 7 : shale.

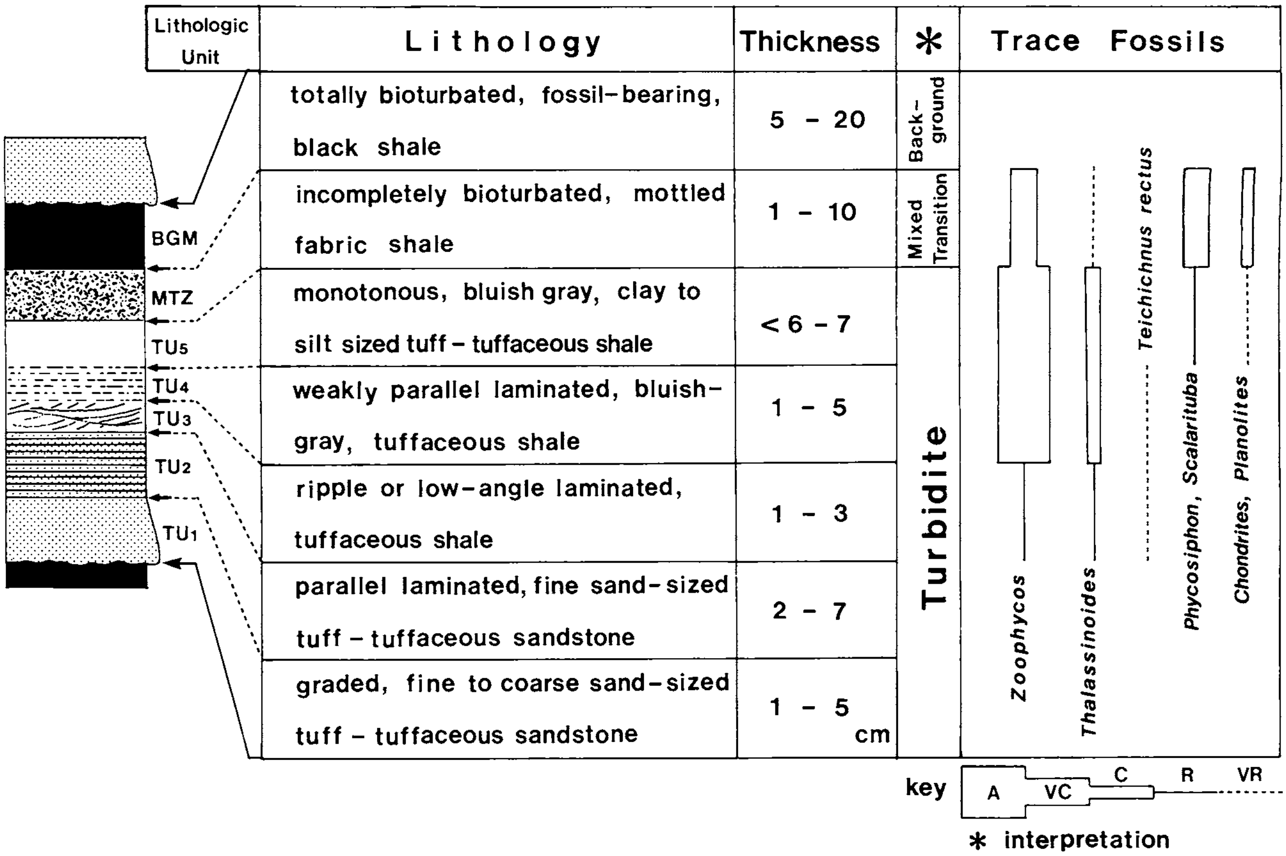


Figure 4. Lithological characteristics of the *Zoophycos*-bearing bed and tiering patterns of *Zoophycos* and related trace fossils in H-2 Member of the Hikoroichi Formation. BGM : background mud, MTZ : mixing transition zone, TU : lithological unit in a single turbidite bed, Key : A=abundant, VC=very common, C=common, R=rare, VR=very rare.

level.

Based on *Zoophycos* in Pliocene deep-sea sediments (Shiramazu Formation) of the Boso Peninsula, central Japan, I proposed another interpretation, that *Zoophycos* was produced by the excretory behavior of a deposit-feeder, which fed on surface and/or subsurface nutrient sediment at the sea floor and deposited its fecal matter deep in sediment (Kotake, 1989, 1991, 1992, 1993, 1994). This interpretation emphasizes that sediment in the spreite is of fecal origin and was derived from the sediment surface through the feeding and excretory process of the producer.

As mentioned above, mineralogical and microscopic observations suggest that the *Zoophycos* from the Hikoroichi Formation is a product of downward conveyor activity by its producer. This interpretation is consistent with that for the *Zoophycos* from the Pliocene deep-sea sediments of the Boso Peninsula. The morphological similarity between the Hikoroichi *Zoophycos* and the Pliocene specimens, furthermore, proves that the black sediment in the spreite of the Hikoroichi *Zoophycos* is probably of fecal origin.

This interpretation suggests a functional similarity in feeding and excretory styles of the producers of *Zoophycos* in the Hikoroichi and Shiramazu Formations. It is assumed that the producer of the Hikoroichi *Zoophycos* segregated the feeding and excretory places in Early Carboniferous time and retained such an ethological style until at least the latest Tertiary.

Based on specimens of *Zoophycos* found in Devonian and Pennsylvanian strata deposited in shallow marine settings, Miller (1991) considered that the material filling in the spreite was transported downward from the overlying layer or sediment surface by the tracemaker activity. This is consistent with my interpretations for Tertiary *Zoophycos* from the Boso Peninsula and the Carboniferous specimens from the Hikoroichi Formation. However, Miller (1991) did not clarify whether or not the material in the spreite was of fecal origin. This is because these specimens lack the direct evidence, such as identifiable pellets. Furthermore, it might also be difficult to apply the feeding and excretory model based on the Boso Tertiary *Zoophycos* to the Devonian and Pennsylvanian specimens illustrated by Miller (1991) because of the presence of morphological and structural dissimilarities between them. Thus, it may not be easy to judge whether or not the material filling in the spreite of the Devonian and Pennsylvanian *Zoophycos* examined by Miller (1991) was of fecal origin.

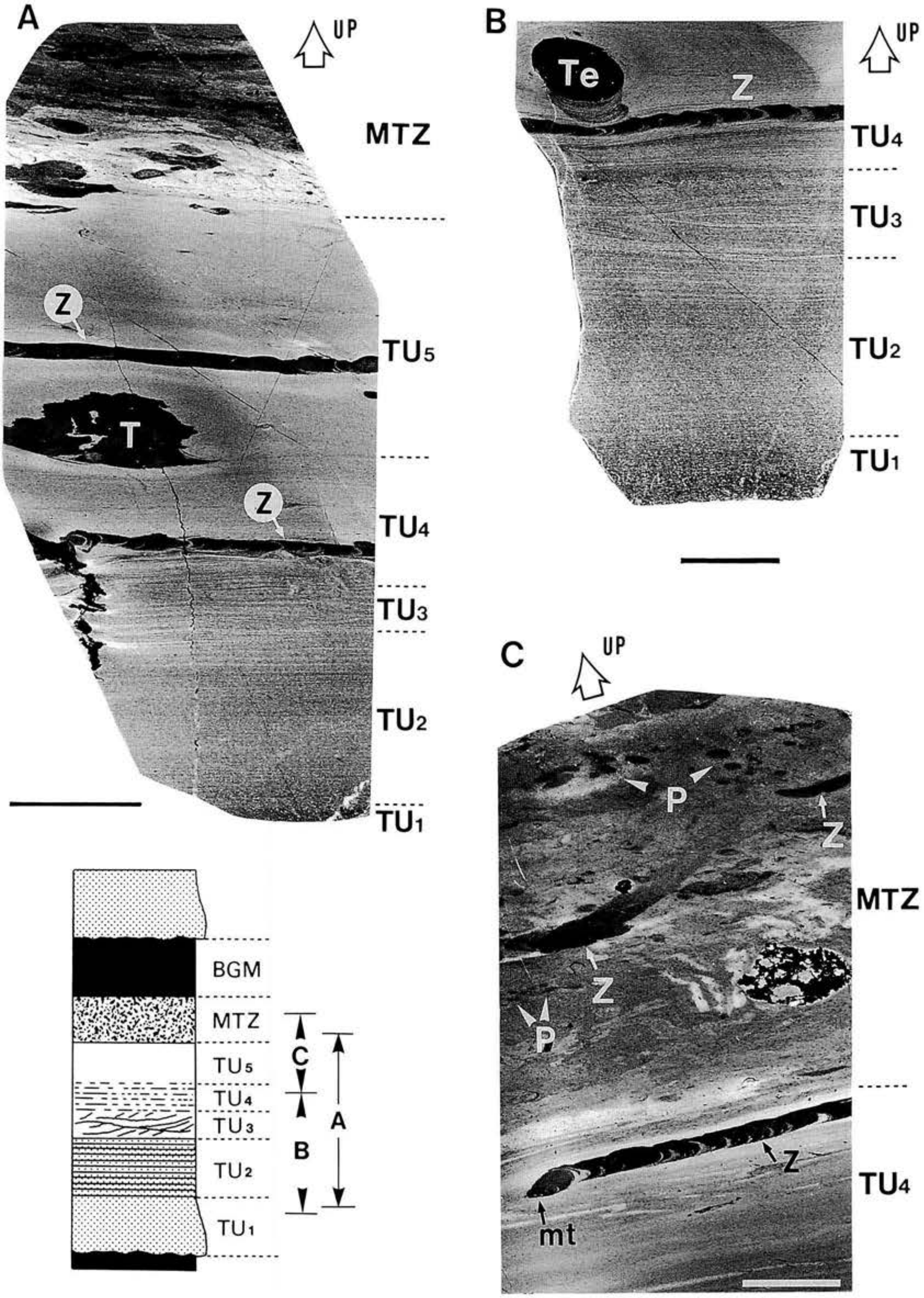


Figure 5. Specimens of the Hikoroichi *Zoophycos* on the polished surface of slabs. Note that the well-preserved, sharply defined *Zoophycos* spreiten (Z) are restricted to the lithological units in TU$_4$ and MTZ. Specimens A and C and specimen B were collected from the horizon ZB and ZA in Figure 3, respectively. Z: *Zoophycos*, T: *Thalassinoides*, Te: *Teichichnus rectus*, P: *Phycosiphon incertum*, mt: marginal tunnel. Scale bars = 2 cm (A), 1 cm (B, C).

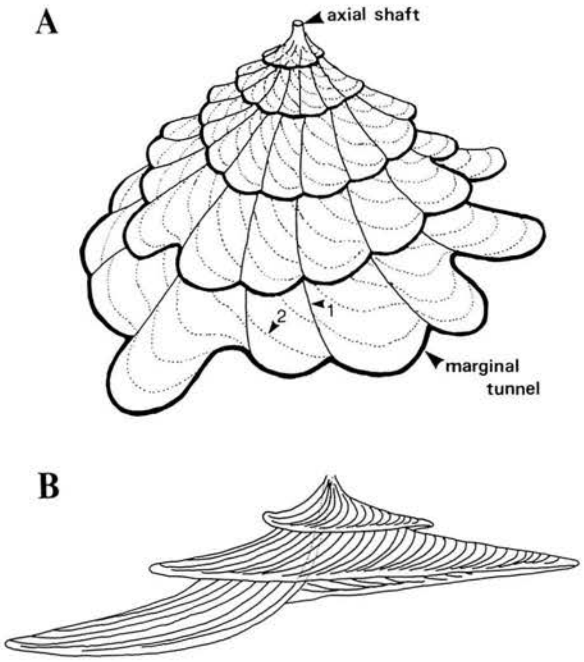


Figure 6. General morphology of the helicoidal form of *Zoophycos.* This form is characterized by a spirally coiled spreite around the axial shaft (A) or central portion (B). B is modified after Sarle (1906). Arrows 1 and 2 indicate major and minor lamellae, respectively.

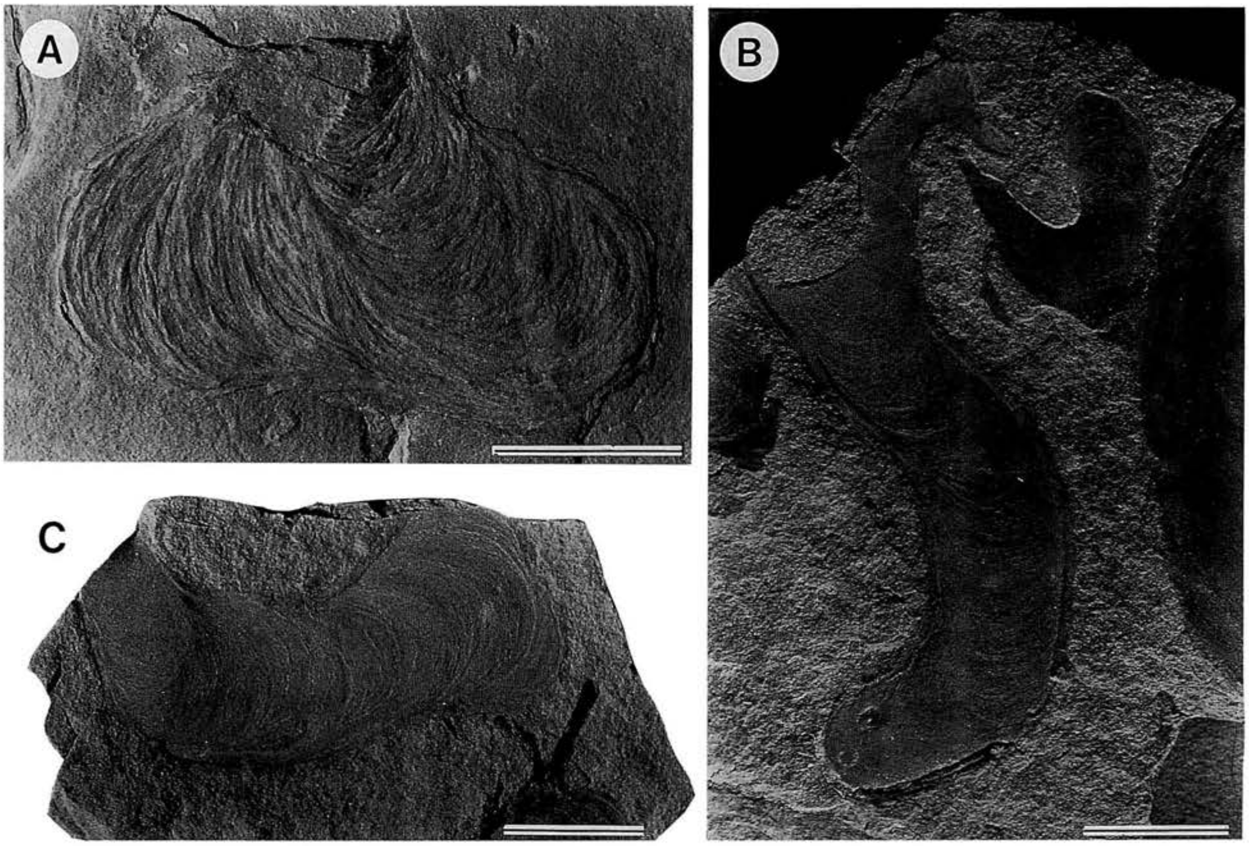


Figure 7. Plan view of the selected specimens of the planar forms of *Zoophycos* from the Mississippian Borden Formation distributed in the northeastern part of Kentucky, U.S.A. This form represents wide morphological variations ranging from the simple type (A) to the extremely lobate type (B, C). Scale bars = 4 cm (A), 3 cm (B, C).

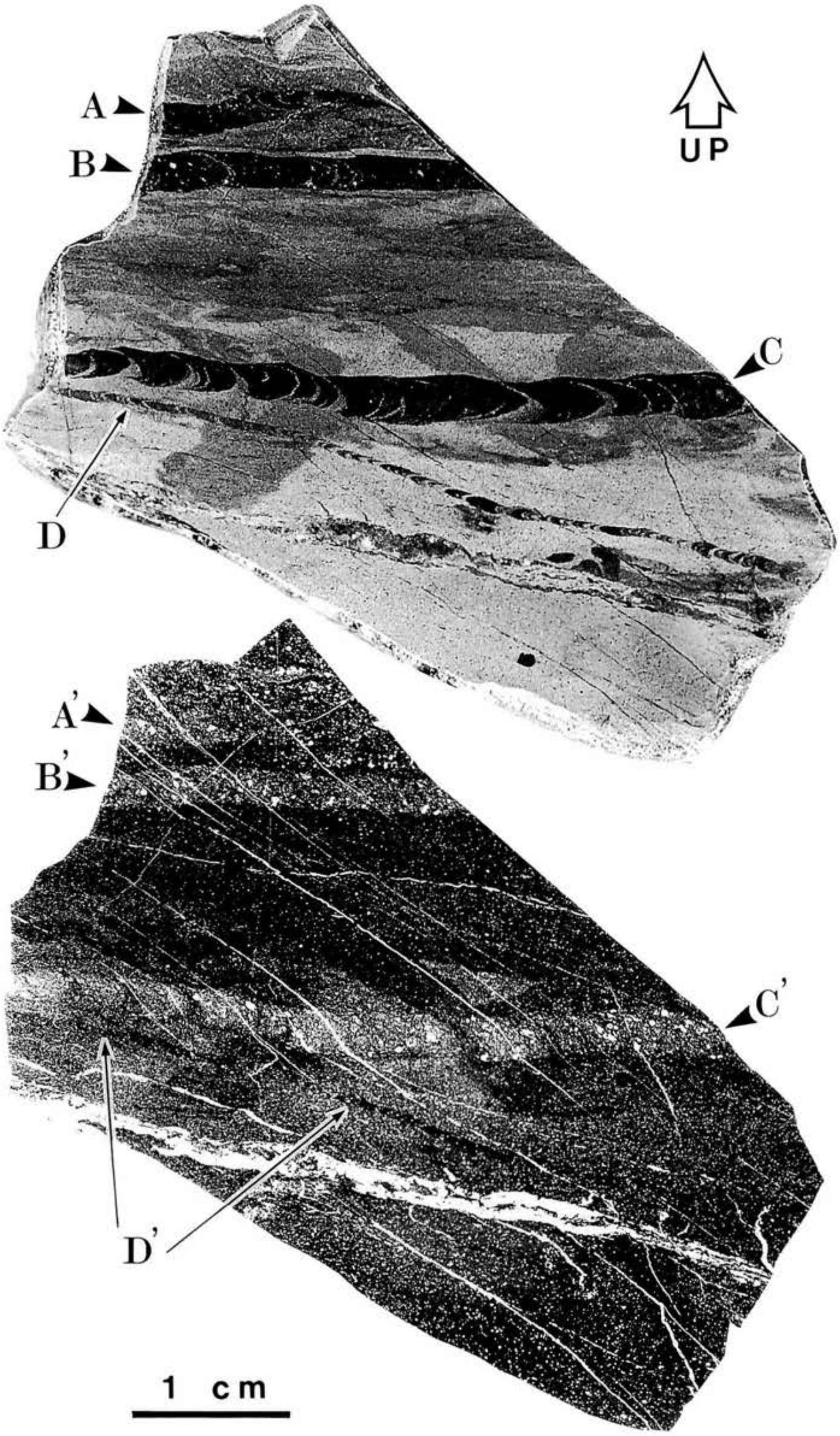


Figure 8. Cross-sectional view of the polished specimens of a *Zoophycos*-bearing slab (upper) and thin section of the same specimen (lower). Four spreiten (A-D, A′-D′) are visible. Component material in the black fill in the spreite represents ill-sorted, coarser grains in comparison with those of the spreiten-bearing rock. This specimen was collected from the horizon ZB (see Figure 3).

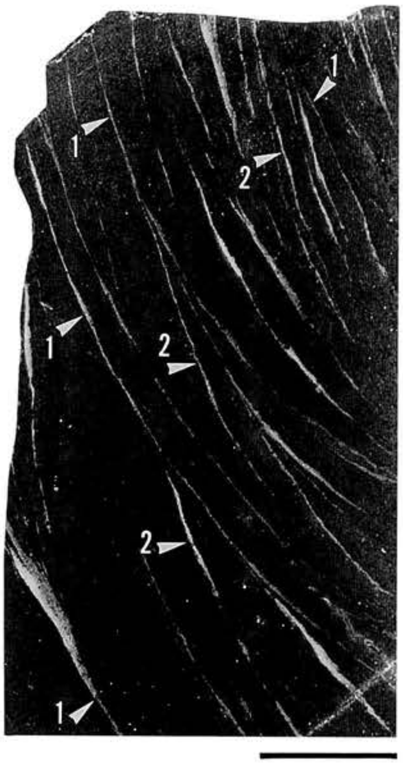


Figure 9. Plan view of polished surface of the spreite of *Zoophycos* from the Hikoroichi Formation. Arrows 1 and 2 indicate major and minor lamellae, respectively. These lamellae, consisting of light host rock, stand out against the dark-colored spreite fill sediments. Scale bar=1 cm.

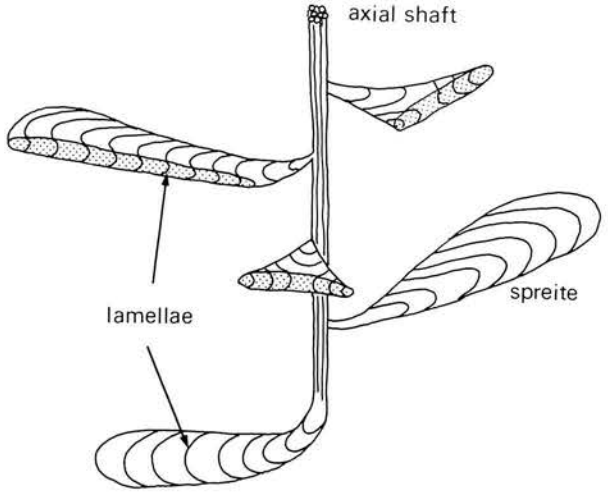


Figure 10. Three-dimensional morphology of the Pennsylvanian *Zoophycos* consisting of some axial shafts with planar spreiten. Meniscate lamellae are present in vertical section of the spreiten (stippled portion). Modified after Miller (1991, fig. 8).

As stressed in this paper, the morphological characteristics of the Japanese Paleozoic *Zoophycos* from the Hikoroichi Formation more closely resemble those of the Tertiary specimens in the Boso deep-sea sediments than do those of hithertho described Paleozoic specimens in North America (eg., Miller and Johnson, 1981 ; Chaplin, 1982 ; Marintsch and Finks, 1982 ; Miller, 1991). This fact demonstrates that the Hikoroichi *Zoophycos* has a different ethology from most Paleozoic *Zoophycos* occurring in shallow-water settings. Indeed, Miller (1991) interpreted wide morphological variations

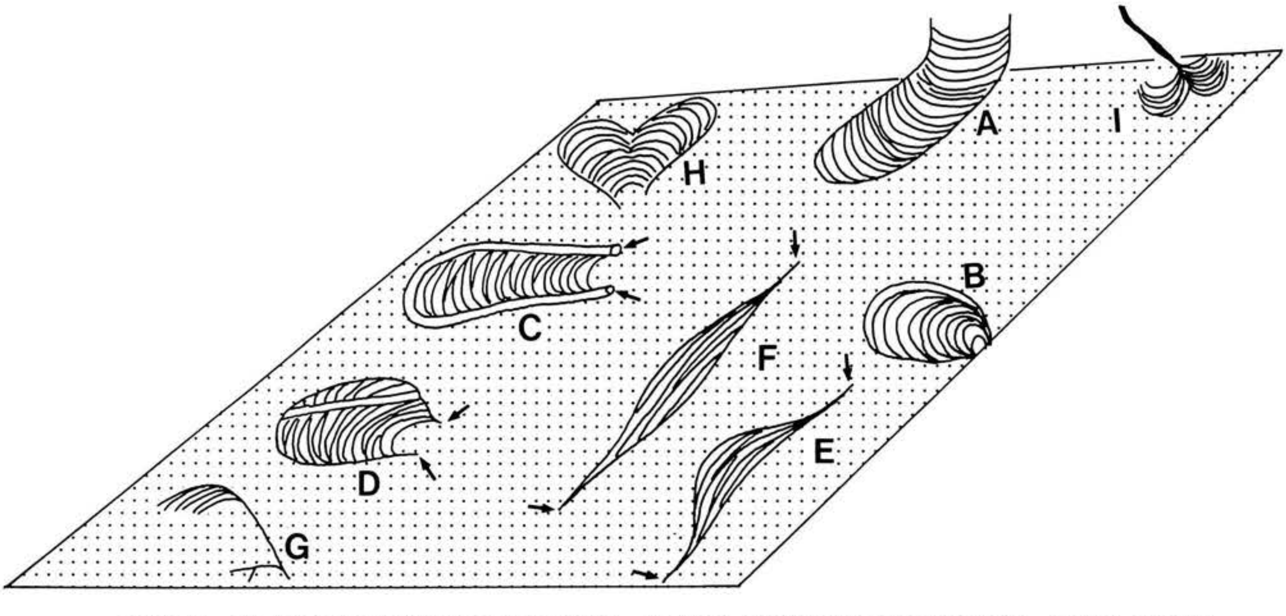


Figure 11. Morphological variations of *Zoophycos* occurring in Devonian storm deposits. Arrows indicate termination points. Modified after Miller (1991, fig. 6).

Table 1. Comparison of morphological characteristics between Tertiary and Lower Carboniferous *Zoophycos*. Morphological data on the North American Paleozoic *Zoophycos* obtained from the Mississippian and Pennsylvanian specimens of Kentucky and Tennessee.

Comparative *Zoophycos* specimens	type of form	type of lamellae	axial shaft	marginal tunnel	fecal pellet	regularity of internal structures
J.T. DS. *Zoophycos*	helicoidal	major & minor	Pr	Pr	Pr	high
J.P. *Zoophycos* (Hikoroichi *Zoophycos*)	helicoidal	major & minor	N	Pr	None	high
N.A.P. *Zoophycos*	helicoidal & planar	major >> minor	N>>Pr	N>>Pr	None	poor

N>>P indicates that both type is present but N is the major form.
T : Tertiary, DS : Deepsea, J : Japanese, P : Paleozoic, N.A. : North American
Pr : present, N : none

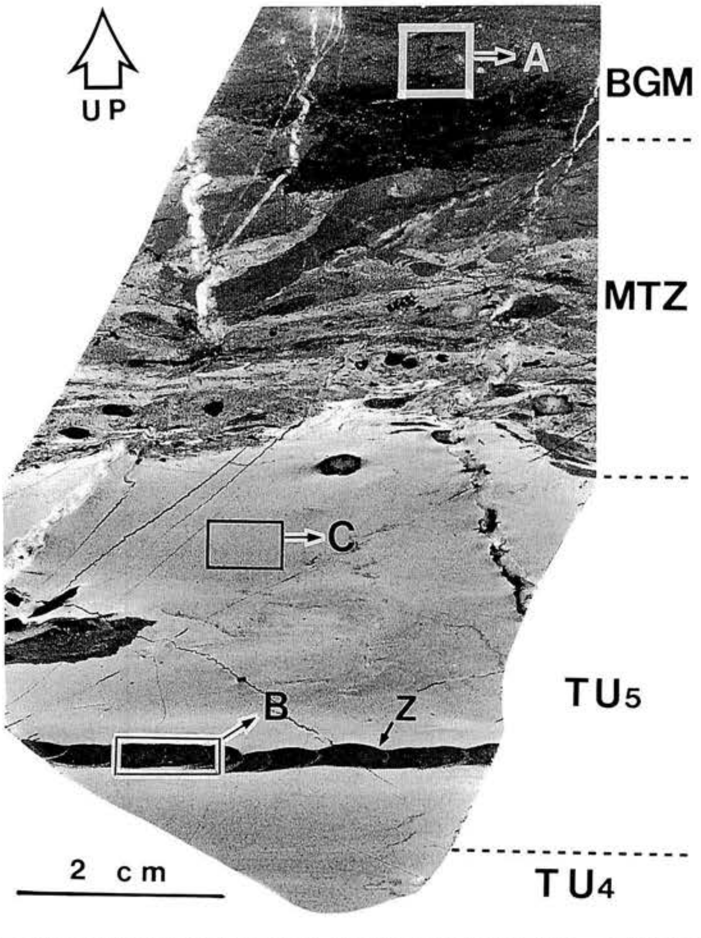


Figure 12. Cross-sectional feature of the typical *Zoophycos*-bearing rock. A to C indicate the sites where samples were taken for determination of the mineralogical composition by mean of x-ray diffractional analysis. This specimen was collected from the horizon ZB in Figure 3. A : intensely bioturbated black shale, B : spreite of *Zoophycos*, C : bluish-gray tuffaceous shale.

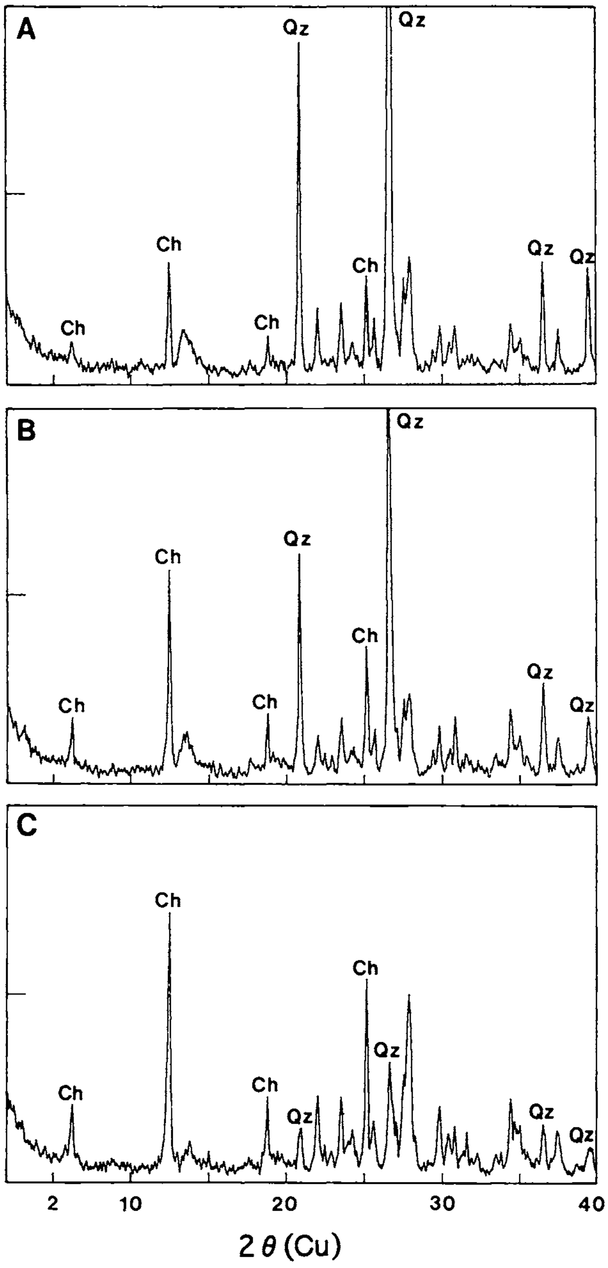


Figure 13. X-ray diffractional patterns of the bioturbated black shale (A), black material in *Zoophycos*-spreite (B), and *Zoophycos* spreite-bearing host rock (C). Ch : Chlorite, Qz : Quartz. See Figure 12 for analytical portions of A-C.

of *Zoophycos* in the Devonian and Pennsylvanian shallow-marine sediments as being due to the variability of the producer's behavior in response to changeable environmental conditions such as salinity, sedimentation rate, heterogeneity of food material on and/or within sediments. Following her interpretation that the *Zoophycos*-producers could switch their behavior in response to change in environmental conditions, the Hikoroichi specimens characterized by a three dimensional morphology and few morphological variations might be a product of a specialized behavior of a producer that lived in a more stable habitat.

The inverted conveyor model, by which the *Zoophycos*-producer fed on sediment at the seafloor and deposited its own fecal matter deep in sediment, appears to explain the origin of the *Zoophycos* in the Hikoroichi Formation. However, implicit application of this feeding and excretory model to all specimens from different ages and localities is still debatable, because other workers believe that the producer of *Zoophycos* is an infaunal deposit-feeder, which ingested organic matter at a level deep within the sediment (eg., Wetzel, 1991 ; Ekdale and Lewis, 1991 ; Fu and Werner, 1994 ; Fu *et al.*, 1994), and/or that the *Zoophycos* structure might represent bacterial gardening by the producer (*sensus* Seilacher, 1977, 1990 ; Bromley, 1991). Apart from the works by Miller (1984, 1991), furthermore, little discussion has been given to the origin and significance of the morphological variation of the Paleozoic *Zoophycos*. Consequently, any comprehensive interpretation of the origin of *Zoophycos* based on many specimens from various depositional settings of different ages is needed not only to evaluate the utility and limitation of these models, but also to consider the evolution of feeding and excretory behavior of the *Zoophycos* animals.

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3. A cyclic mode of shell growth and its implications in a Late Cretaceous heteromorph ammonite *Polyptychoceras pseudogaultinum* (Yokoyama)

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Abstract. *Polyptychoceras*, a Cretaceous heteromorph ammonite genus, is characterized by a trombone-like shell called a "hamitoid" shell. In order to clarify the shell-forming mechanism, a large sample, which consists of more than 320 specimens of *P. pseudogaultinum* (Yokoyama) obtained from the Upper Santonian of Hokkaido, was biometrically analyzed. Besides the shell coiling, cyclic changes of growth pattern are recognized by the analyses of the shell ornamentation, the relative growth rate of shell height, and the distance between septa. Intermittent shell growth, which was also deduced from the ontogenetic stage distribution in the population samples, is probably the cause of such peculiar shell coiling. Also, we carried out some computer simulations to reconstruct hydrostatically the ontogenetic change of the living attitude of *P. pseudogaultinum*. It is suggested that the rate of absolute shell growth possibly depends on the living attitude of this ammonite in the water column; the shell grows slowly when the shell aperture faces upward, and grows rapidly when the aperture faces in other directions. It is likely that every individual of this ammonite spent most of its life time with an upward-facing aperture.

Key words: Heteromorph ammonite, mode of growth, mode of life, *Polyptychoceras pseudogaultinum* (Yokoyama), Upper Cretaceous

Introduction

Ammonites, a dominant cephalopod group during Jurassic and Cretaceous times, changed their shell form in various ways in order to adapt themselves to the environment. Heteromorph ammonites were especially diversified and showed various kinds of shell shape in the Late Cretaceous, the last phase of ammonites' prosperity. *Polyptychoceras* Yabe, 1927, belonging to the diplomoceratids, is one of the most conspicuous heteromorph genera and is characterized by a trombone-like "hamitoid" shell; several straight shafts run in parallel, successive shafts being connected with a U-shaped semi-whorl. This genus was probably derived from *Scalarites*, presumably a founder of the Diplomoceratidae, and *Eubostrychoceras*, a nostoceratid, is probably the ancestor of that family (Matsumoto, 1967). The two-dimensional shell coiling as observed in the diplomoceratids generally originated from the three-dimensional shell coiling of nostoceratids in the Late Cretaceous (probably Turonian) (Matsumoto, 1967; Ward, 1976).

Several species of *Polyptychoceras* occur in the Santonian and Campanian of Hokkaido and Sakhalin (Matsumoto, 1984; Verchangin *et al.*, 1965). *Polyptychoceras* and some allied genera of the Diplomoceratidae achieved worldwide distribution, because there are some reliable records of occurrence from other provinces in the Upper Santonian and Lower Campanian, *e.g.* Vancouver Island in Canada (Whiteaves, 1903) and Barra do Dande in Angola (Howarth, 1965). In the Early Santonian and earlier, however, the occurrences of such primitive genera as *Scalarites* and *Rhyoptychoceras* and early species of *Polyptychoceras* are restricted to the Far East province. Early diversification of the Diplomoceratidae is thus suggested from the fossil records in the Far East province. This province is, therefore, important in order to document the evolutionary process of the Diplomoceratidae.

The fossils of *Polyptychoceras* usually occur in fragments in calcareous nodules of the Upper Yezo Group, Hokkaido, Japan. Previous descriptive studies of *Polyptychoceras* have mostly been based on incomplete or fragmentary specimens (Yokoyama, 1890; Jimbo, 1894; Yabe, 1927; Matsumoto, 1984). A peculiar life mode of *Polyptychoceras* was imagined by Matsumoto and Nihongi (1979); they may have lived in schools at the bottom and sometimes in dead shells of large ammonites. In their argument, however, it was not discussed why the peculiar shell form of *Polypty-*

choceras was advantageous.

A hamitoid shell morphology like that of *Polyptychoceras* appeared at least three times in independent clades (i.e. ptychoceratids, hamitids and diplomoceratids). It is, of course, regarded as morphological convergence probably related to a similar mode of life.

The purpose of this study is to clarify the mode of growth of *Polyptychoceras* by analyzing biometrically the ontogenetic change of shell form. The material is *Polyptychoceras pseudogaultinum* (Yokoyama) which occurs abundantly in the Upper Yezo Group. We also attempt reconstructions of living attitude through growth in the water column, and interpret the mode of life from the relationship between the growth and the reconstructed living attitude. Such an approach would make clear how the hamitoid shell morphology was adaptive to a certain mode of life in the Late Cretaceous seas.

Material and method

The Upper Yezo Group in the reaches of Kotanbetsu River contains numerous fossiliferous calcareous nodules in which

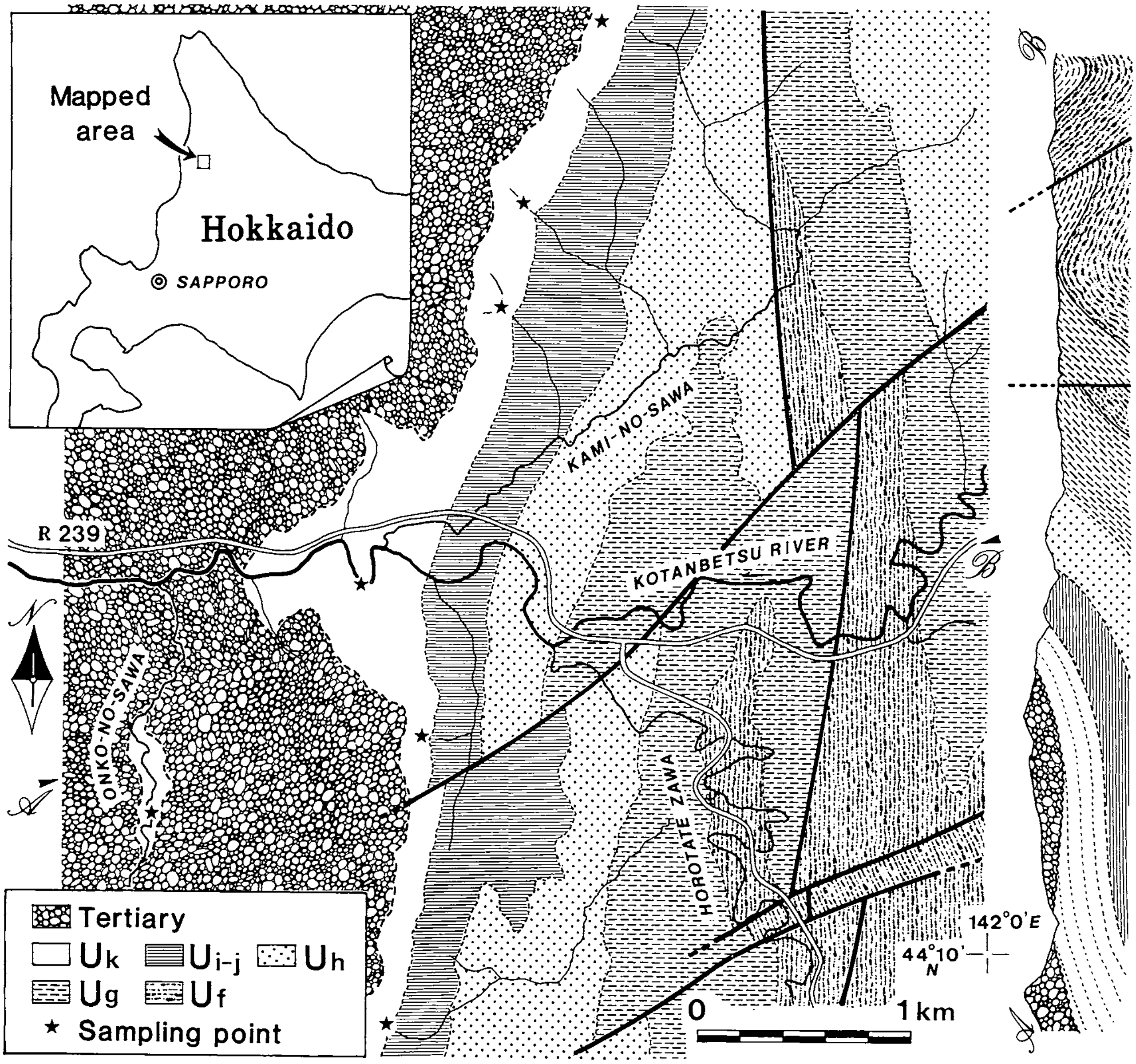

Figure 1. Sampling points shown on geologic map of Kotanbetsu area, Tomamae province, Hokkaido. The Upper Yezo Group in this area was divided into five members, Uf-Uk (Tanaka, 1963). All the localities of *Polyptychoceras pseudogaultinum* (Yokoyama) are in Uk member, Upper Santonian. A useful population sample was obtained from the inlier of this member at Onko-no-sawa.

Polyptychoceras occurs abundantly (Figure 1). In order to collect specimens of *Polyptychoceras* and to clarify their stratigraphic occurrence, we surveyed this area in the field seasons of 1992-1994. Layers of the Upper Yezo Group in this area, generally have north-south strikes and are tilted to the west, though some foldings are recognized in the eastern part. This group is unconformably covered by Tertiary sedimentary rocks in the western part of this area. The Upper Yezo Group is mainly composed of dark gray sandy siltstones and contains many intercalations of tuff and sandstone layers. Tanaka (1963) and Tanabe et al. (1977) defined twelve members (Ua-Ul) in this group, and *Polyptychoceras pseudogaultinum* occurs particularly in Uk, one of the uppermost members. This ammonite is usually contained in a cluster, and sometimes occurs gregariously in calcareous nodules. We treated a total of 323 specimens of *P. pseudogaultinum* in this study. A large population sample of this species was obtained from the Onko-no-sawa valley where the Uk member is locally exposed as an inlier. Several smaller samples were obtained from the main stream of Kotanbetsu River, tributaries of Kami-no-sawa, and a western tributary of Horotate-zawa. All specimens are kept in the University Museum, University of Tokyo with register numbers with the prefix UMUT. MM. We use consecutive specimen numbers with prefix H- or S- throughout this paper, and their correlation with register numbers is shown in the Appendix Table.

Perfectly preserved specimens give us important information concerning the ontogenetic change of shell growth and shell ornamentation. Such specimens of *Polyptychoceras pseudogaultinum* are extremely rare, while fragmentary specimens occur very abundantly in this area. We had to analyze its ontogenetic change by connecting imperfect specimens. An idealized shell form of *Polyptychoceras pseudogaultinum* is reconstructed, and terms for every part are defined as shown in Figure 2. An adult shell is composed of five shafts and four turns connecting two adjacent shafts.

In order to clarify the general shell morphology and its intraspecific variation, we mainly used a slide caliper and a binocular. For observation of the septate phragmocone, several specimens were cut along the median plane. The linear distance between adjacent septa was measured by a profile projector (Nikon, V-12). Some specimens showing early shell morphology were observed and measured by scanning electron microscope (SEM, Jeol JSM-5200). For SEM observation, the polished surface cut along the median plane was etched with 5 percent acetic acid for a half to two minutes. For the computer simulation, programs written in N88-BASIC were run on a personal computer (NEC PC-9801RA) printing to an ink-jet printer (Canon, BJ-130J).

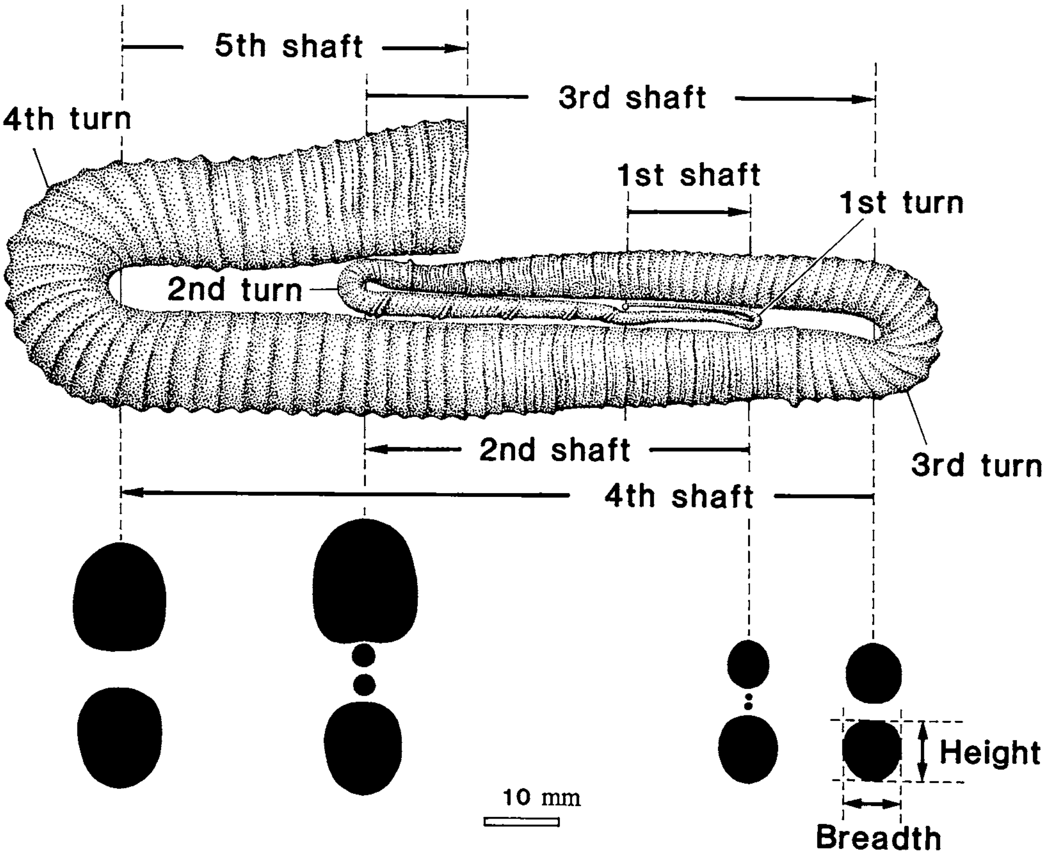

Figure 2. Schematic illustration of *Polyptychoceras pseudogaultinum* (Yokoyama).

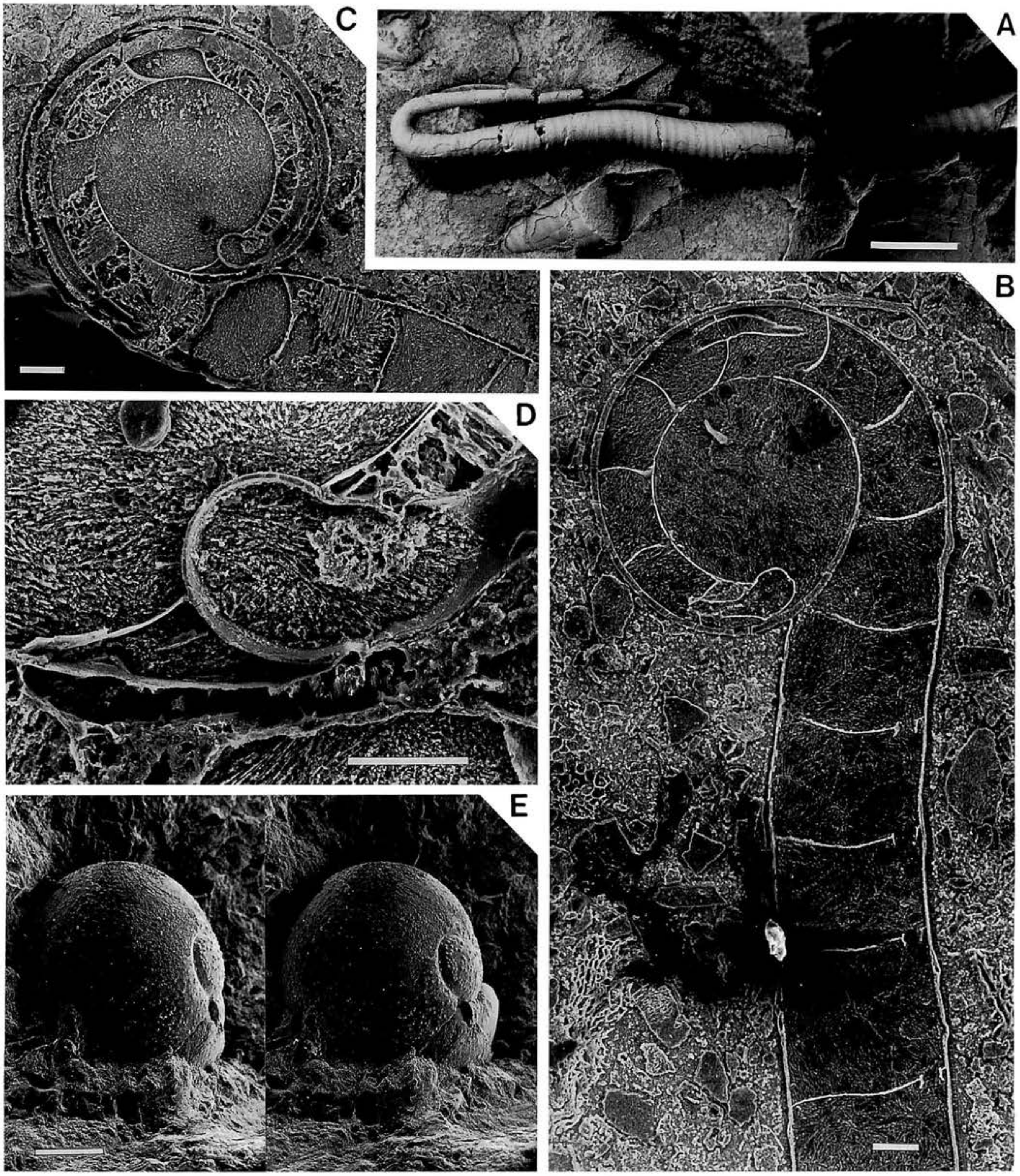

Figure 3. Early shell morphology of *Polyptychoceras* spp. **A**. Younger shell of *Polyptychoceras* sp. containing an almost complete ammonitella, and following first shaft, S-199. **B**-**E**. Microstructure of embryonic shell of *P. pseudogaultinum* (Yokoyama), **B** : S-205, **C, D** : S-204, **E** : outer wall of ammonitella, S-203 (stereographic pair). Scale bars : 5 mm for A, 100 μm for **B** and **C**, 50 μm for **D**, and 200 μm for **E**.

General morphology and remarks

Protoconch and early shell morphology

Ammonitellas of the Diplomoceratidae are in general rarely preserved. Hayakawa (1988) reported several ammonitellas of *Polyptychoceras* sp. from the Santonian of the Upper Yezo Group. We obtained some early shells of *P. pseudogaultinum* in which the ammonitella is followed by a straight shaft (=first shaft). By SEM observation along the median plane, the main structural elements of the ammonitella such as the primary varix, protoconch, prosiphon, caecum and proseptum were recognized (Figure 3). The microstructure of the embryonic shell of *P. pseudogaultinum* is somewhat similar to that of the Lytoceratina, though the size of the ammonitella is considerably smaller. The ammonitella in this species is about 0.7 mm in diameter, whereas in the Lytoceratina it generally ranges between 1.1 mm to 1.4 mm (Tanabe and Ohtsuka, 1985). It is characterized by a relatively short, arcuate prosiphon and a siphuncular tube rapidly shifting to the ventral margin. The nepionic constriction and accompanying primary varix, by which the ammonitella stage is terminated, appear at about 320 degrees from the beginning of the first whorl, and is followed by the first shaft. The shell height rapidly increases just after the nepionic constriction (Figure 3).

Tuberculate microornament is observable in some of these specimens. Homologous textures have been described by Bandel *et al.* (1982) and Tanabe (1989) in several other superfamilies of Ammonoidea. According to their arguments, these textures were secreted probably by the interior gland cells of the mantle margin and indicate that the ammonitella was enclosed by the reflected mantle lobe. Namely, the ammonitella stage of these ammonites was endocochliate. The Turrrilitaceae, in which *Polyptychoceras* is included, possibly shared a similar mode of life until the nepionic constriction was formed.

Doguzhaeva and Mutvei (1989, 1993) suggested that *Ptychoceras*, an Early Cretaceous ammonite showing convergent shell form to *Polyptychoceras*, had an internal or semi-internal shell. The grounds of their argument are 1) the mechanical truncation of the phragmocone terminus and 2) the existence of an external coating layer which is secreted probably on the shell surface by an epithelium. In *Polyptychoceras pseudogaultinum*, however, no evidence indicating an endocochliate shell has been obtained throughout the post-embryonic growth stages.

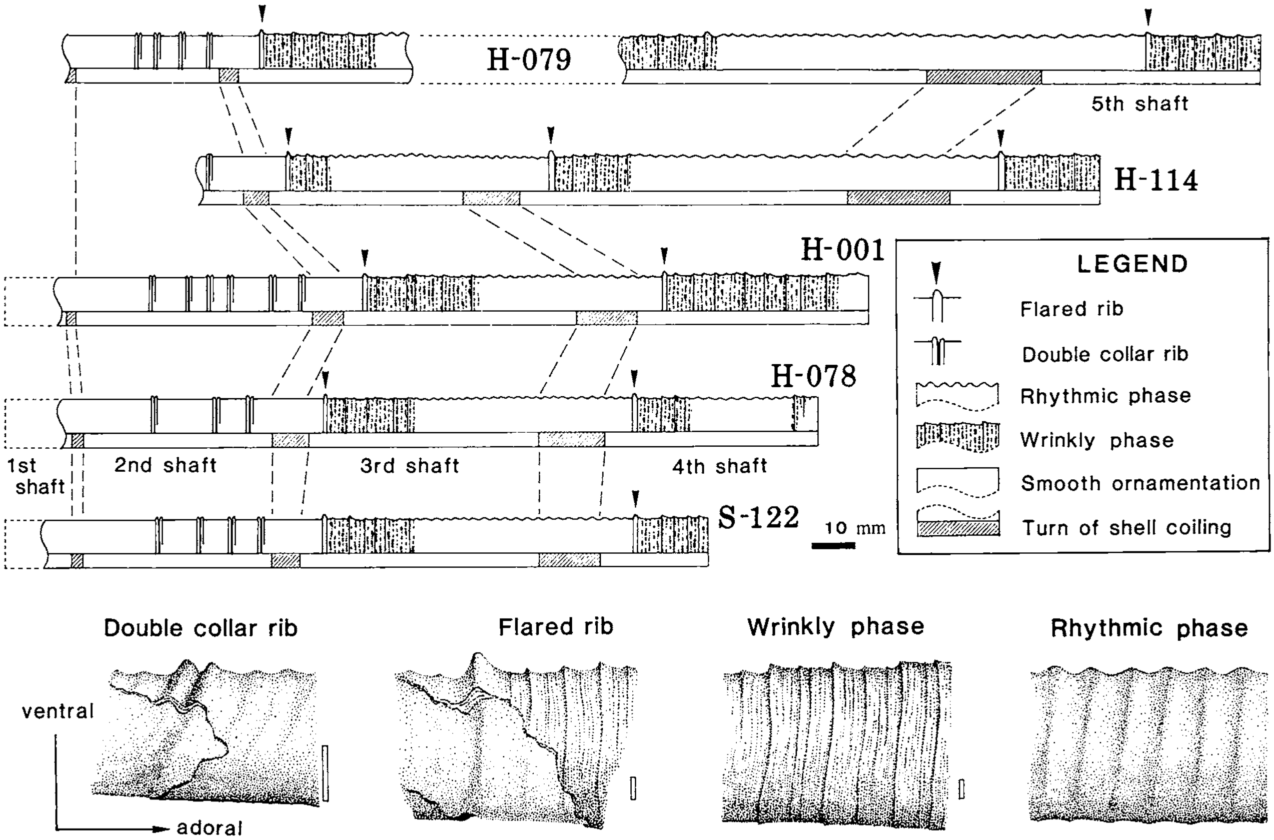

Figure 4. Schematic diagram showing the cyclic change of shell surface ornamentation throughout growth. Two phases of ornamentation appearing alternately are recognized after the second turn. The wrinkly phase which is initiated from a flared rib appearing near the beginning of the new shaft, gradually changes into the rhythmic phase during the earlier half of shaft. Each scale bar (open rectangle) on the right of the illustration indicates 1 mm.

On *Polyptychoceras subquadratum* (Yokoyama)

Polyptychoceras pseudogaultinum (Yokoyama) was established on the basis of some young specimens showing the second to the third shafts, the transverse section of which is nearly circular. In the same paper, Yokoyama (1890) described *Polyptychoceras subquadratum* (Yokoyama) from the same locality of the Urakawa area, southern Hokkaido. The latter species was established on the basis of a single fragmentary specimen showing a nearly adult growth stage having a subquadrate transverse section. In the samples examined, the larger specimens, which are usually fragments, always show the characteristics of *P. subquadratum* (i.e. subquadrate cross section), whereas almost all the younger specimens are clearly identified with *P. pseudogaultinum*. Actually, these larger specimens may look as if they belong to a different species from *P. pseudogaultinum*, because the shell shape is considerably different, and because the sample shows bimodal size distribution. However, a few well-preserved specimens reveal that the difference between the two "species" is only due to ontogenetic change within a single species (Figures 14, 15). We therefore treat *P. subquadratum* as a synonym of *P. pseudogaultinum*, and all the samples examined are regarded as belonging to a single species, *P. pseudogaultinum* (syntypes: *Ptychoceras pseudo-gaultinum* Yokoyama, 1890, *Palaeontographica*, vol. 36, p. 181, pl. 20, figs. 1-3; synonymy: *Anisoceras subquadratum* Yokoyama, 1890, *Palaeontographica*, vol. 36, p. 182, pl. 20, fig. 4). Though these two names were established in the same paper, we designate *P. pseudogaultinum* as the name of this species, because *P. pseudogaultinum* has more frequently appeared in literature (e.g. Yabe, 1927; Shimizu, 1935; and Matsumoto, 1984). Moreover, the type specimens of *Polyptychoceras haradanum* (Yokoyama) and *Polyptychoceras subundulatum* (Yokoyama), both of which were established also in the same paper (Yokoyama, 1890), are possibly includable in the intraspecific variation of *P. pseudogaultinum*.

Ontogenetic change of surface ornamentation

Polyptychoceras shows a periodically changing pattern of surface ornamentation. Since the ammonite shell is formed by accretionary growth, the tempo and mode of growth at every growth stage must be recorded in the commarginal ornamentation on the shell surface.

Polyptychoceras pseudogaultinum has two kinds of characteristic ribs (double collar ribs and single flared rib), which occur periodically at definite stages of the shell growth (Figure 4). The double collar ribs appear at first near the trisecting point of the second shaft at which the adjacent first shaft terminates, and occurs periodically until the end of the second shaft. The number and the position of the double collar ribs are variable among the examined specimens. The flared rib appears just after the shell turning point of every stage except for a point just after the first turn. While the flared rib is relatively clear in the third and fourth shafts, it is not very clear or sometimes unobservable in the fifth shaft. The shell is thickened at these ribs, and the aperture at these stages probably become a little narrower.

The shell growth of *P. pseudogaultinum* is divided into two major stages by the first appearance of the flared rib which is observed just after the beginning of the third shaft (Figure 4). In the earlier stage, several double collar ribs periodically develop and weak striae are observed between them. In the later stage, a cyclic switch of two ornamentation phases corresponds to the shell coiling. The first or wrinkly phase of ornamentation is characterized by slightly notched ribs occurring at irregular intervals and by numerous weak striae between them. This phase usually starts from the flared rib and continues for about one-third of the shaft. The notched ribs gradually change to the simple ribs. The second or rhythmic phase of ornamentation is characterized by the simple ribs occurring at regular intervals. This phase continues to the end of the next turn and is terminated by the next flared rib.

The obliquity of transverse ribs also changes cyclically throughout growth. More or less prorsiradiate ribs are observed through the later half of the second shaft and near the end of each shaft, while rursiradiate or rectiradiate simple ribs are formed during each turn and the early part of the following shaft. The change of rib obliquity is, though, rather obscure in the fourth shaft.

Shell height and shaft length

The shell height at the beginning of every shaft and the shaft length were measured in all the specimens if these values were measurable. The mean values of shell height from the second to fifth shafts are 1.58 mm, 3.78 mm, 8.41 mm, and 16.50 mm, respectively. The standard deviation of

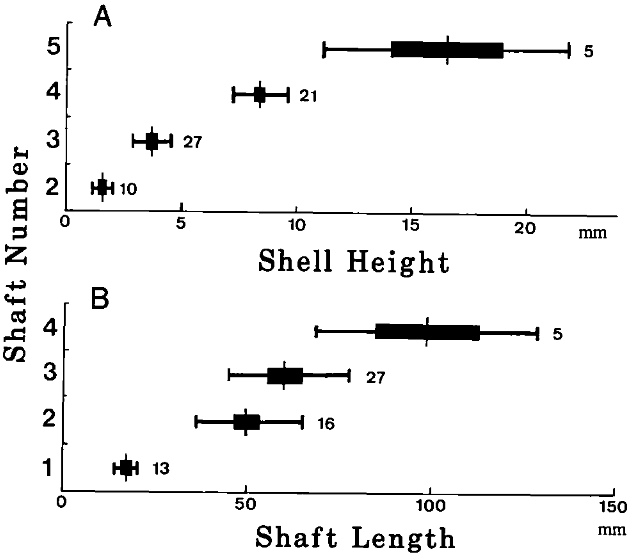

Figure 5. Diagrammatic figures showing the average and intraspecific variation of shell height and shaft length. Shell height is measured at the beginning of every shaft excluding the first shaft. Horizontal bar, solid rectangle and number on the right indicate presumable distribution range of 95% of the population (1.96 times of standard deviation), 95% confidence range of mean value (1.96 times of standard error), and the sample size, respectively.

these measurements are relatively small except for the fifth shaft. The mean values of shaft length from the first shaft to the fourth shaft are 17.86 mm, 51.06 mm, 61.50 mm and 97.87 mm, respectively (Figure 5). The first shaft length is indirectly estimated by the shape of the second shaft as mentioned below, because in no specimen is the first shaft perfect. Unlike the shell height, standard deviation of shaft length is generally large except for the first shaft.

These results indicate that the variation of shell form is fairly wide in the growth stages after the second shaft. The shaft length does not increase proportionally either with the progression of the shaft number or with the shell height. The second shaft is relatively longer than other shafts. This may be a common characteristic feature in the genus *Polyptychoceras.*

Estimation of missing shaft length

P. pseudogaultinum usually grows in parallel with the previous shaft. When the shell passes the origin of the previous shaft, the growth direction temporarily slightly shifts to the dorsal side but soon recovers its original direction. Therefore, the length of earlier shaft can often be estimated by the shape of the later shaft, even if the earlier shaft is missing. The second shaft commonly bends slightly at about 20 mm after the first turning point. This probably means a release from the constraint of the first shaft. Actually, an ammonitella situated just near the bending part of the second shaft is observed in well preserved specimens of a related species (Figure 3A). As to *P. pseudogaultinum,* a relatively long first shaft, which is merely 2.3 mm shorter than the expected first shaft, is preserved in one of our

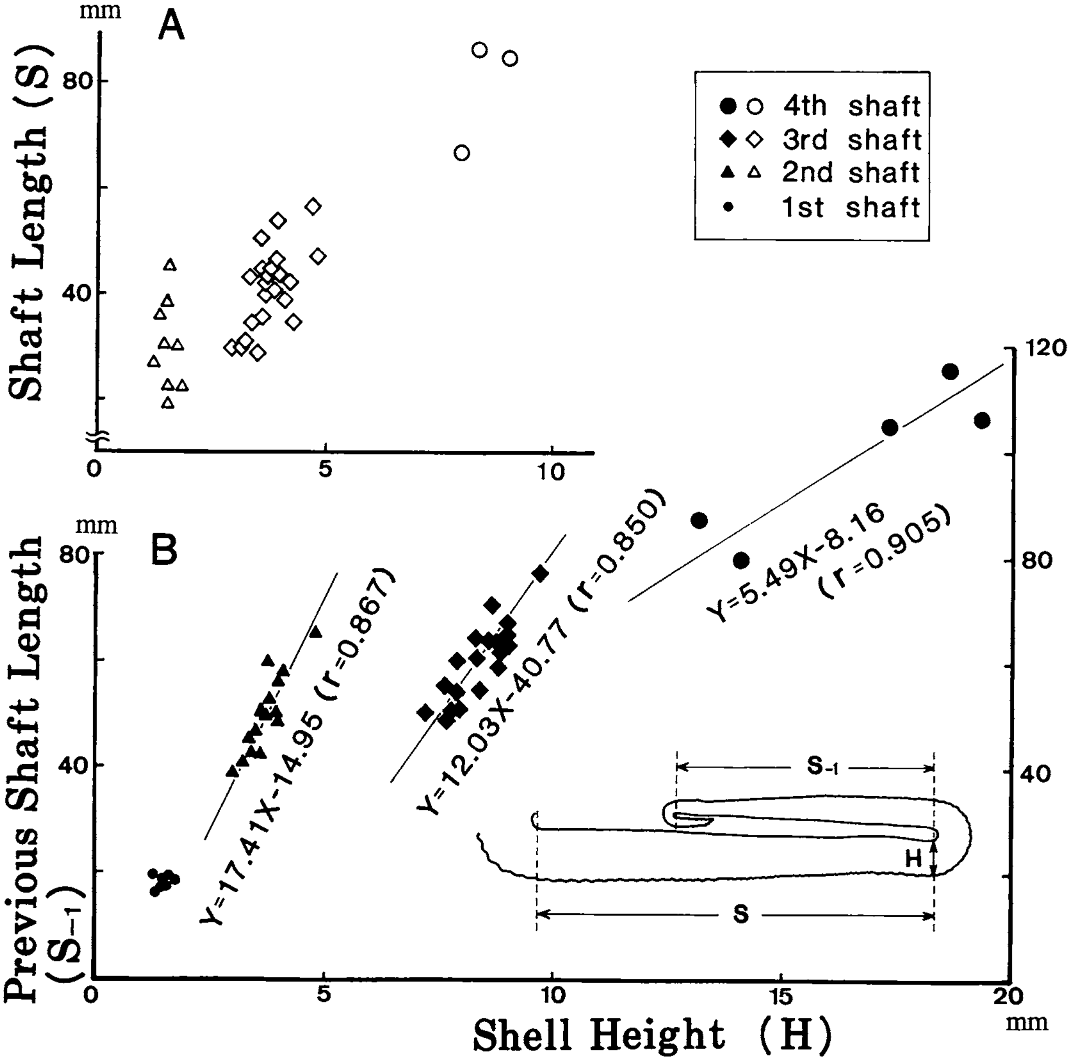

Figure 6. Scatter diagrams showing the relationship of the shaft length versus the shell height measured at the beginning of the shaft. Positive correlation between the shell height and the previous shaft length is significantly recognized (B), while the correlation between the shell height and the current shaft length is rather obscure (A). Regression line is also shown with the correlation coefficient (r), when the correlation is significant.

specimens (S-194). The shell height at the earliest point of this specimen is 0.32 mm. Since the shell height measured just after the nepionic constriction in this species is generally about 0.31 to 0.35 mm, it is reasonable to consider that the bending point of the second shaft indicates the impression of the protoconch. As a result, the first shaft length can be estimated as the distance between the end of the first turn and the bending point of the second shaft. The intraspecific variation is very small about the first shaft length estimated in this way (Figure 6B).

The shell length would be the most adequate and feasible parameter to compare the same growth stages between specimens. Since every specimen of *P. pseudogaultinum* examined in this study is more or less incomplete, the missing part of the shell must be reconstructed in order to analyze biometric data statistically. The mean values can hardly be employed for the estimation of the missing shaft length because of the large intraspecific variation. So we examined the correlation between the shell height and the shaft length (Figure 6A). No obvious correlation is, however, recognized between the shell height measured at the beginning point of each shaft and corresponding shaft length. The length of the previous shaft is, however, positively correlated to the shell height (Figure 6B). Therefore, the length of the previous shaft can be estimated by the shell height and this relationship, even if the earlier shell is missing.

Further biometric analyses

Relative growth between height and total shell length

Relative shell growth pattern in normally coiled ammonites is usually shown by the shell diameter (or whorl height), breadth and umbilicus measured in various stages along the transverse section. However, this method cannot be applied to heteromorph ammonites at all. The ontogenetic growth of the shell height should be measured relative to the total shell length. The total shell length is defined as the distance from a protoconch to a point of a certain growth stage represented by the track of the apertural center. This definition is also applied to the phragmocone length (from protoconch to the last septum).

The relative growth patterns between the shell height and the shell length in four specimens are shown in Figure 7. Morphology of the earlier shell is observable in two of the four specimens (H-038 and H-078). Relatively advanced growth stages, from the third turn to the early part of the fifth shaft, are observed in the other two specimens (S-108 and H-114). These growth patterns are combined by standardizing the third turn. These four specimens are concordant with each other in the growth pattern, showing cyclic oscillation of whorl height. The height grows slowly at an almost constant rate until the earlier half of the second shaft, but then the rate gradually decreases. Unlike the earlier stage, the height grows rapidly during the earlier halves of the third

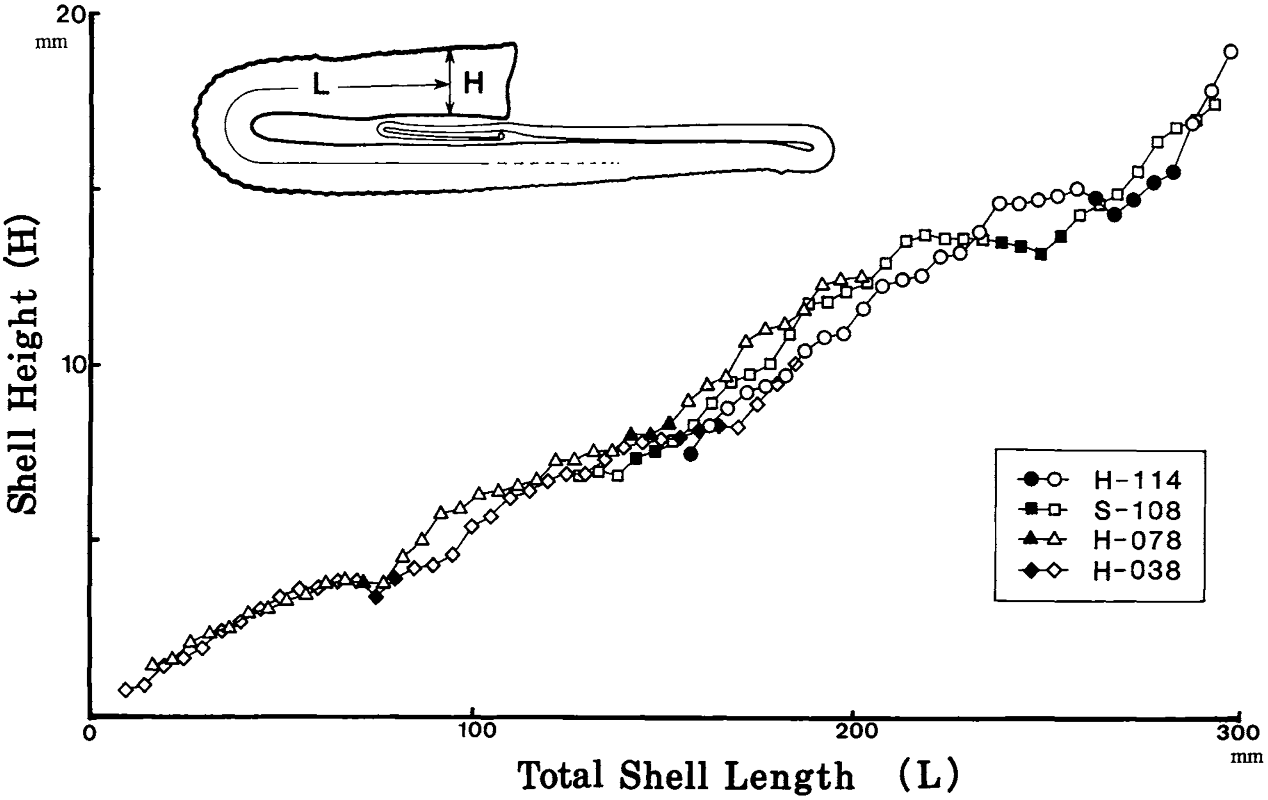

Figure 7. Relative growth between the total shell length and the shell height. Solid symbols indicate the data obtained at the turning part of shell. Shell height rapidly increases during the earlier half of every shaft.

and following shafts. Then the growth rate gradually decreases during the later half of the shafts, and this feature continues until the end of the following turn. Such periodic changes of growth rate are observed until the fifth shaft.

The shape of the transverse section of the shell changes during ontogeny (Figure 2). The section is almost circular until the middle part of the third shaft. It gradually becomes oval during the growth of the third shaft and finally subquadrate in the later stages.

Relative length between phragmocone and total shell

Every ammonite shell consists of a body chamber and a septate phragmocone. The soft part filling in the body chamber advances adorally with growth, and a new septum is formed behind the soft part. The life mode of an ammonite would have been hydrostatically controlled by the total average density of the whole ammonite body. If the density was higher than that of sea water, the ammonite could not stay in the water column without active swimming, because the buoyant force is not enough to cancel the gravity. Conversely, if the density of an ammonite was positively buoyant, the ammonite would be forced to float on the surface. In order to maintain a mode of life suspended in the water column, like extant *Nautilus*, the total average density of the ammonite had to be neutrally buoyant in sea water.

The relative volume of phragmocone to the whole ammonite body must be constant so as to maintain neutral buoyancy, if the ammonite keeps a constant density of phragmocone during growth. The relative volume of phragmocone is roughly expressed by the ratio between the phragmocone length and total shell length (P/T), if the expansion rate of the shell aperture is nearly constant with growth. The P/T ratio was actually measured in twenty-one specimens showing various growth stages (Figure 8).

The P/T ratio is almost constant throughout various growth stages of the fourth shaft and ranges approximately from 0.57 to 0.61. Younger specimens, however, have relatively short phragmocones. Although relatively little data was obtained for other stages, the ratios are similar to the values measured in the fourth shaft. Consequently, the ratio is roughly 0.6 and is almost invariable throughout growth except for the youngest stage. The value is nearly equivalent to or slightly smaller than the ratios of normally coiled and other heteromorph ammonites (Okamoto, 1996).

In *Polyptychoceras pseudogaultinum,* the expansion rate of the shell aperture is not constant, as shown by the cyclic change of shell height during growth. If the species needs to maintain a total average density so as to achieve neutral buoyancy, for example, the P/T ratio may also change slightly with growth. So we classified the data into two groups by the growth stages; the open circles in Figure 8 indicate that the shell aperture is situated in the later half of the shaft whereas the solid ones indicate that the shell aperture is in the other part. However, no significant difference was detected between the two groups.

Interval of septa throughout growth

The interval between septa becomes rapidly shortened in many ammonites when they reach the fully mature stage. If a stagnation or break of shell growth has occurred during ontogeny, similar shortening of septal distance may appear in the phragmocone. We measured the distance between two adjacent septa together with corresponding phragmocone length.

Because the specimens examined are more or less frag-

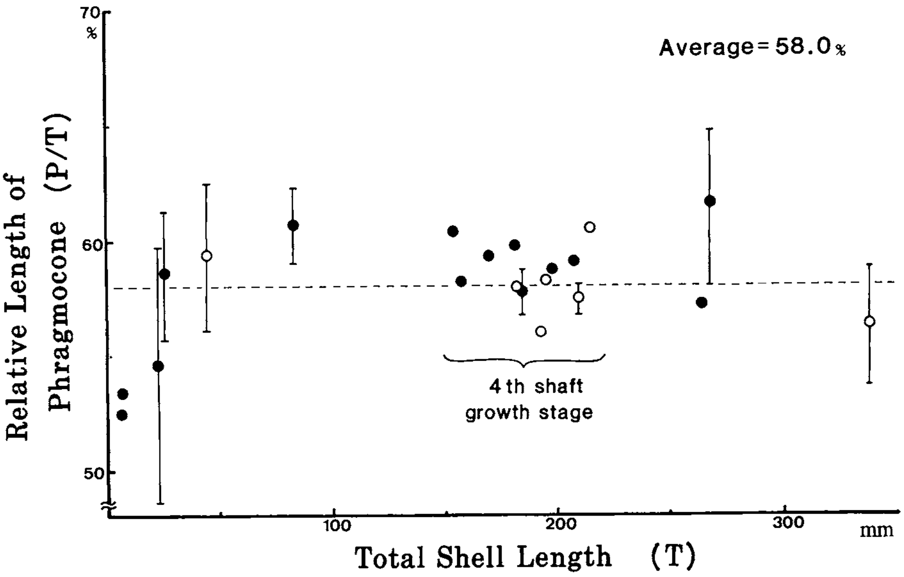

Figure 8. Diagrammatic figure showing the length of phragmocone relative to the total shell length. Vertical bars indicate the presumable range of error owing to the indirect estimation of missing shell length. Solid and open circles stand for specimens with the shell aperture situated in the earlier and later halves of shaft, respectively. The P/T ratio seems to be almost invariable throughout growth except for the two youngest specimens.

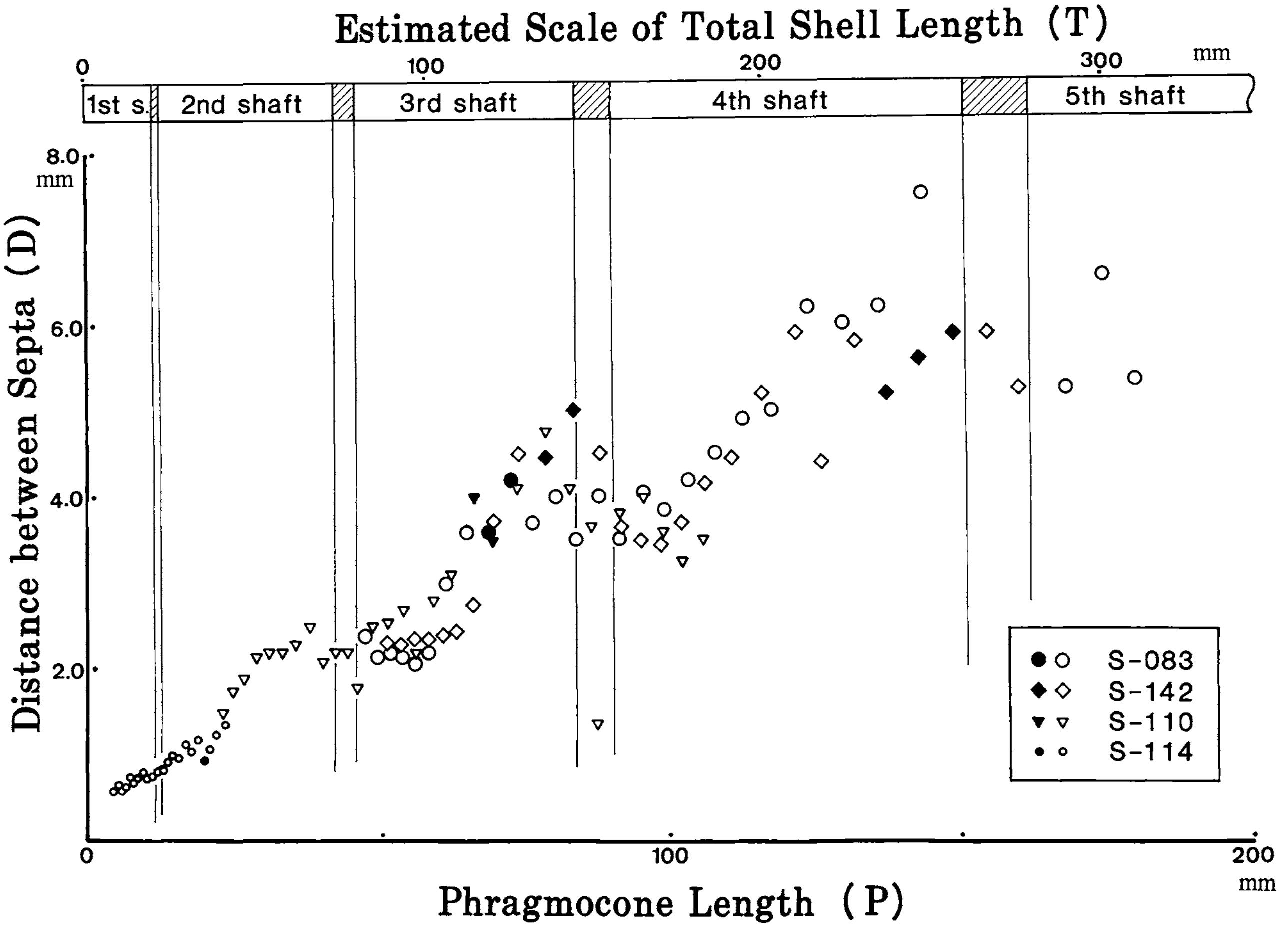

Figure 9. Diagrammatic figure showing the ontogenetic change of distance between septa. Solid symbols indicate the values measured in the turning parts of shell. Estimated length of total shell corresponding to the phragmocone length is also entered on this diagram. The distance between septa rapidly increases when the shell aperture is in the later half of the shaft.

mentary, the developmental change of the septal distance cannot be measured in a single specimen. The septal distance is actually measured on the cross section cut along the median plane. Its ontogenetic change is synthetically shown by connecting four specimens (S-083, S-142, S-110 and S-114) in Figure 9. In this diagram, the lower horizontal axis shows the phragmocone length, and the vertical axis shows the distance between septa. The progressive stages, in which the distance increases more or less rapidly, appears at 20-30 mm, 60-80 mm and 110-140 mm in phragmocone length. These stages are followed by some stagnant stages in which the septal distance is nearly constant. Though this biometric analysis shows that the progressive and stagnant stages alternately appear throughout the ontogeny, the relation to the position of septa is not obvious.

The cyclic change of the septal distance is well demonstrated in relation to the shell aperture. A scale of total shell length estimated from the phragmocone length and P/T ratio is also shown in Figure 9. The progressive stage of the distance between septa corresponds well to the growth stage where the shell aperture is located in the middle part or later half of every shaft.

Population analysis (Distribution of growth stage)

If the fossils are collected at random, the sample indicates the distribution of growth stages in a fossil population. As to normally coiled ammonites, the growth stage is usually shown by the total revolution angle until the shell aperture. In *Polyptychoceras pseudogaultinum,* however, the growth stage has to be shown by the shaft number and relative position of the shell aperture in the shaft.

A total of 71 specimens with complete apertures was examined, and the frequency distribution is shown in Figure 10B. The intervals of horizontal axis corresponding to every shaft were standardized so as to increase proportionally to the corresponding shell height. Three peaks which appear in the earlier parts of the third to fifth shaft are recognized in this diagram, although the sample size is not sufficient owing to the infrequent preservation of the shell aperture. This method bears some difficulties in requiring randomness of observed sample. For example, full-aperture specimens having only one shaft (without turn and ammonitella) were

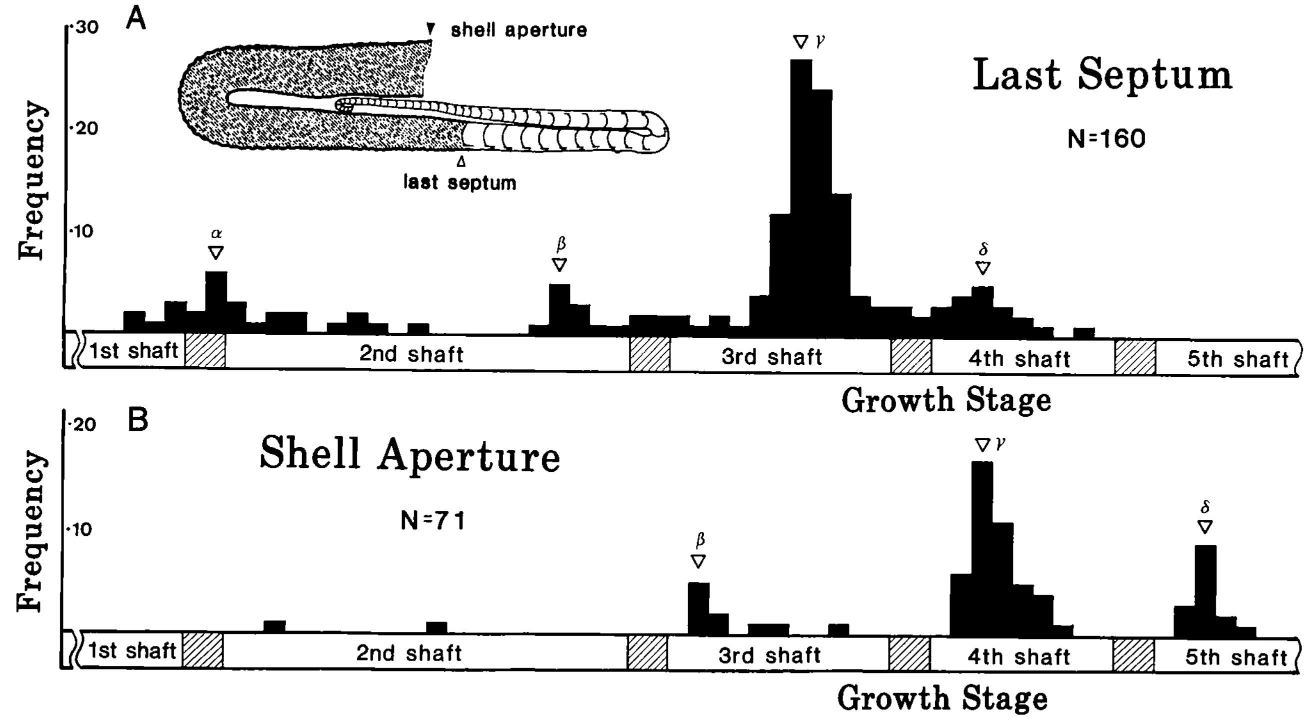

Figure 10. Histograms showing the distribution of the last septum and shell aperture in all the measurable specimens. Horizontal scale for the growth stage is proportionally divided by the corresponding shell height. Obliquely lined rectangle indicates turning part of shell. Three peaks in the histogram 10B for the shell aperture, reffered to β, γ and δ, appear just after every turning point of shell. Three of the four peaks appearing in the histogram 10A for the last septum surely correspond to those for the shell aperture.

not counted, because the growth stage cannot be determined in such specimens ; and such specimens could have originated more frequently from individuals having a long last shaft. The full-aperture specimens being younger than the second turn stage are extremely rare, while such young shells are very common in the samples.

To offset the difficulty mentioned above, we also analyzed the stage distribution of the last septum. In some cases, the shaft length was estimated from the shell height and the relationships shown in Figure 6. A total of 160 specimens with the last septum was examined (Figure 10A). Though the peaks are somewhat broad, three peaks appear between the later half of the second shaft and earlier half of the fourth shaft. They correspond well with the peaks observed in the analysis of full-aperture specimens (Figure 10B). They appear near the end of the second turn, near the midpoint of the third shaft, and near the beginning of the fourth shaft. These data indicate that the effect of the biased sampling is relatively small except for the younger stages. Additionally we detected another peak which appears around the first turn.

While the peaks in the frequency distribution of the shell aperture are quite sharp and occur at a regular interval corresponding to the pattern of shell coiling, the peaks of the last septum are somewhat obscure. The position of the last septum must be related to the position of shell aperture, the P/T ratio, and the length of each shaft. The P/T ratio is stable among specimens and is also nearly constant throughout the ontogeny (Figure 8), whereas the shaft length is quite variable among specimens (Figures 5, 6). This may be the reason why the position of the last septum is so dispersed in the population sample.

Discussion

Mode of shell growth

If the specimens examined in Figure 10 are regarded as a result of random sampling, the concentration at some definite growth stages is possibly caused by uneven rate of mortality or uneven rate of shell prolongation. The latter cause is more likely, if the data of relative growth and other shell morphologic features are considered.

The mortality rate may change during ontogeny. Though the actual mortality rate of *P. pseudogaultinum* is unknown, a roughly constant mortality rate may be expected within a relatively short growth interval, e.g. within the growth of a single shaft. If this assumption is valid, the uneven and cyclic distribution of growth stages as shown in Figure 10 suggests periodic change of growth rate. It is likely that individuals of *P. pseudogaultinum* temporally ceased or stagnated their shell prolongation at the beginning of every shaft marked by the flared rib (except for the first and second shafts). The shell growth probably gradually accelerated during the earlier half of shaft, and the later half of shaft and turn must be formed rapidly. Moreover, the truncated distribution of growth stage shown in Figure 10B indicates that an abrupt reduction of growth rate and its gradual recovery occur in the sequence of the cyclic growth.

The aforementioned periodic changes of the enlarging rate of shell height and surface ornamentation also support the cyclic growth mode of *P. pseudogaultinum.* The cyclic oscillation of the increasing rate of the shell height appears to correlate negatively (but significantly) with that of shell prolongation. It is reasonable to consider that the growth of soft parts is proportionate to the increase of the volume of body chamber. The observed rapid increase of shell height may compensate for the slow prolongation of shaft so as to keep an increasing rate of body chamber volume. The cyclic changes of the surface ornamentation may also be influenced by the rate of shell prolongation. The wrinkly phase characterized by the appearance of several irregular, notched ribs and numerous striae in between indicates the stagnation of shell prolongation, whereas the rhythmic phase characterized by the normal transverse ribs occurring at regular intervals is probably accompanied by rapid shell prolongation. The distance between septa also shows a cyclic change during growth. The stages showing wide septal intervals probably correspond to the promotional stages of shell prolongation. Judging from all the observation of specimens and from the result of biometric analyses, the most believable growth pattern of *Polyptychoceras pseudogaultinum* would be summarized as follows.

The first shaft, which directly follows the ammonitella, reaches about 2 cm in length. Then the shell turns back tightly and the second shaft is formed along the existing first shaft in parallel. This shaft bends slightly near the beginning of the first shaft and shows a weak sigmoidal curve just like that protecting the protoconch and ammonitella. Rather rapid and constant shell growth is presumable until this stage. Double collar ribs appear characteristically in the later half of second shaft, suggesting temporal pauses of shell growth. They are prorsiradiate and accompanied by slight narrowing of the shell aperture. The double collar rib seems to have the function of reinforcement of the aperture and protection of the body chamber filled with soft parts. The broad, first peak of the last septum shown in Figure 10A suggests the decline of the rate of shell prolongation during the later half of second shaft. The flared rib is usually formed periodically at definite position. It appears near the beginning of the third and later shafts, and probably shows the beginning of the stagnant interval of shell growth. Unlike the flared rib, the ornamentation of this interval characterized by the notched ribs and fine irregular striae in between does not indicate pauses of shell growth, but means slow shell prolongation. This phase occupies one third or sometimes almost the first half of each shaft. While the rate of shell prolongation is significantly decreased, the soft part may grow constantly during this interval. The rapid enlargement of shell aperture (height) at this phase may resolve the shortage of space for the soft part. The rate of enlargement of the shell aperture becomes lower during the later halves of shafts, while the growth rate of shell prolongation gradually recovers. Toward the end of this phase, the surface ornamentation composed of the notched ribs and weak striae gradually changes to simple ribs developed at regular intervals. Then the wrinkly phase of surface ornamentation is followed by the rhythmic phase. The sequence of the growth cycle is usually terminated by a flared rib appearing at the beginning of the next shaft.

Specimens showing either the last septum or shell aperture situated in the second shaft are not abundant, and specimens growing until the fifth shaft are also rare. If we ignore possible bias from geologic and diagenetic factors, the stage distribution of the present sample suggests that *P. pseudogaultinum* grows rapidly in the early stage, and that the fifth shaft represents the ultimate growth stage.

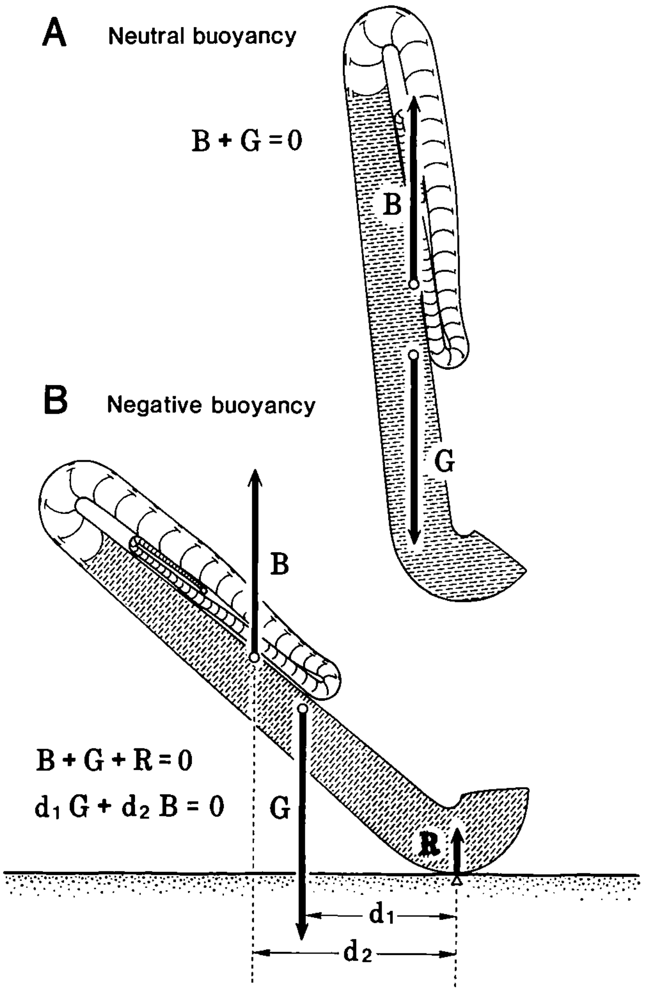

Figure 11. Reconstructions of the living attitude of ammonite. Vectors **B**, **G** and **R** show buoyant force, gravitational force, and resistant force, respectively. Under the condition of neutral buoyancy the center of gravity (the origin of vector **G**) is situated just below the center of buoyancy (the origin of vector **B**). When the ammonite is negatively buoyant, the living attitude is determined so as to keep a balance of moments acting on the circumference of the tangential point (origin of vector **R**).

Figure 12. Result of computer simulations of living attitude under the assumption of suspended mode life in water column (i.e. the buoyancy is equivalent with gravity). Solid triangle indicates the boundary between the phragmocone and body chamber.

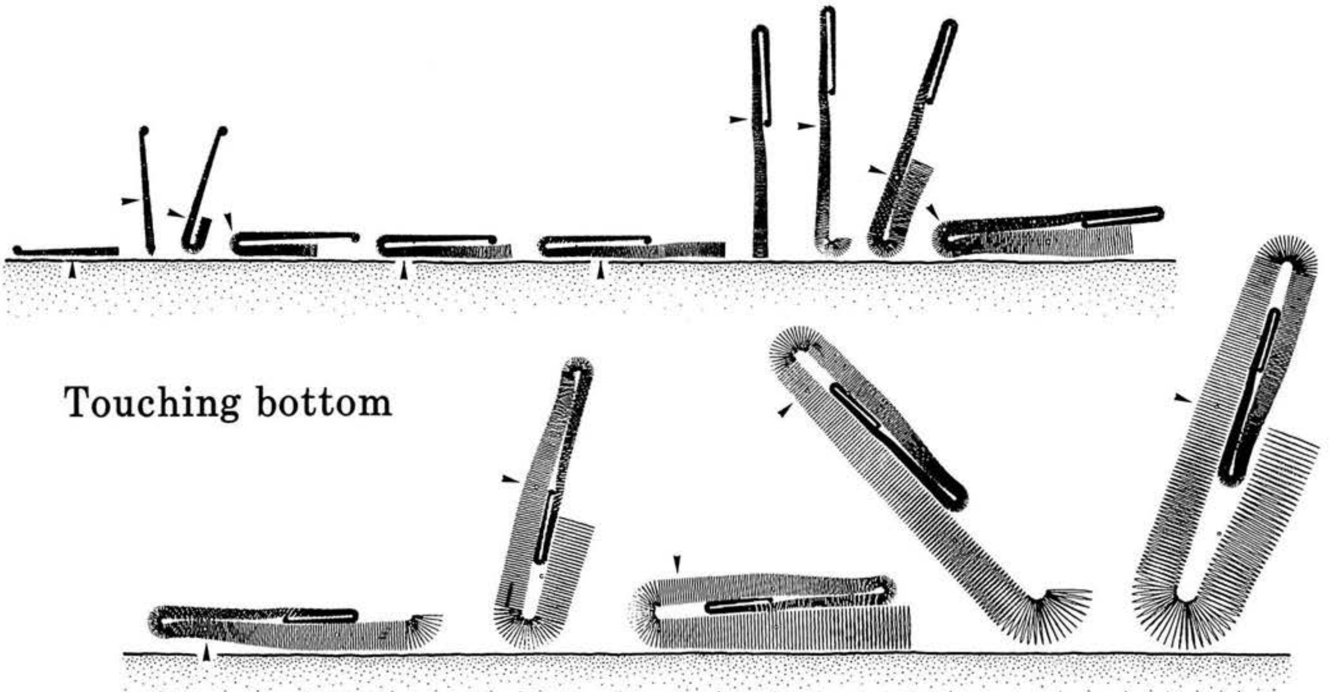

Figure 13. Result of computer simulations of living attitude on the assumption that the ammonite was lightly touching the bottom (i.e. the gravitational force acting on the ammonite body is 1.1 times larger than the buoyant force, and the density of phragmocone is 0.6 g/cm^3). Solid triangle indicates the boundary between the phragmocone and body chamber.

Reconstruction of living attitude

Heteromorph ammonites in general seem to have changed their living attitude during growth according to the aberrant changes of shell coiling. In order to estimate the living attitude of *P. pseudogaultinum* and its ontogenetic change, we carried out computer simulations based on the excellent hydrostatic concept of Trueman (1941). The detailed procedure of this simulation basically follows the method mentioned by Okamoto (1988a, b). The living attitude of ammonites is hydrostatically determined by the distribution of the center of buoyancy and the center of gravity, because the buoyant and gravitational forces act on these centers (Figure 11). Therefore, the living attitude of ammonites is related not only to the shell coiling pattern but also to the share of the phragmocone in the whole ammonite shell. The ratio of the phragmocone length to the total shell length (P/T) is chosen as 0.6 throughout the computer simulation of hypothetical shell growth. The ratio of the gravitational force to the buoyant force (G/B) is also required for the calculation. Since the actual G/B ratio is unknown, two possible cases, i.e. neutral buoyancy and slightly negative buoyancy for the whole ammonite body, are assumed in this study. The two conditions, of course, correspond to nektoplanktic and benthic life modes. The results of simulations are as follows (see also Figures 12, 13).

Neutral buoyancy: The G/B ratio is assumed to be 1.0 throughout this simulation (Figure 12). The gravitational vector must have the direction from the center of buoyancy to the center of gravity. The living attitude is reconstructed so as to situate the center of gravity just below the center of buoyancy (Figure 11A). Under this condition, *P. pseudogaultinum* is suspended in the water column and changes its living attitude in succession. Note that the aperture faces upward when it is situated at the earlier half of each shaft (except for the first shaft), while the direction of the aperture becomes nearly horizontal or downward when it is situated at other part of the shell.

Negative buoyancy: The G/B ratio is hydrostatically chosen as 1.1 throughout this simulation (Figure 13). This assumption means that the total average density is about 1.13 g/cm^3. Under this condition, the shell of *P. pseudogaultinum* had to touch the sea bottom lightly. Because many damage scars suggesting attacks by crustaceans are observed on the shells, this species possibly lived near the sea bottom. Since gravity does not balance with buoyancy in this case, the resistant upward force acting at the tangential point between the shell and sea floor must compensate for the surplus weight. The living attitude can be determined so as to keep a balance of moments acting on the circumference of the tangential point. Under this condition, an attitude of stably lying down on the sea bottom is repeatedly reconstructed throughout growth stages. Until the second turn, the shell starts turning when the attitude changes to an upright posture and the aperture faces downward. At the third and the fourth turn, the turning starts slightly before the stage when the aperture faces downward.

As the result of these simulations, the living attitude shows cyclic changes throughout growth. Though the presumable change of the living attitude is somewhat different between two conditions, the reconstructed living attitude usually shows upward growth direction in the earlier half of every shaft. These stages correspond well with the growth stagnation presumed by the analyses of relative shell growth, shell ornamentation and frequency distribution of growth stages. Consequently, *Polyptychoceras pseudogaultinum* seems to have preferred a living attitude showing an upward growth direction, and to have maintained such a life orientation for most of the time throughout its growth.

Further speculation about shell coiling

One of the authors (T.O.) pointed out that some heteromorph ammonites possibly regulate their shell coiling by referring to some information such as direction of gravity. The meandrous coiling of *Nipponites,* a Late Cretaceous nostoceratid heteromorph, has been explained by the "growth direction regulatory hypothesis", in which *Nipponites* alternately switched three modes of shell coiling so as to maintain its growth direction within a preferable range (Okamoto, 1988c). Some other cases also suggest that the shell coiling of ammonites is *a posteriori* determined (Merkt, 1966 ; Okamoto, 1992).

Here, we also pointed out that the shell coiling of *Polyptychoceras* was possibly influenced by the change of growth direction. The great variability of shaft length and existence of some aberrant individuals (Figure 15-7, 8) suggest that the shell coiling is not determined rigidly under genetic control. *Polyptychoceras* perhaps had a rather wide range of preferred growth direction which ranges from nearly horizontal to upward vertical. Usually, the shell runs straight while the growth direction is preferable. Shell turning seems to occur when the growth direction becomes downward, so as to recover a more preferable direction of the aperture. The condition in which the ammonite was lightly touching the sea bottom is more likely for interpreting the shell coiling of *Polyptychoceras* by this hypothesis, because the growth direction changes more rapidly to an unfavorable state when the new shaft attains a certain length.

Theoretical approaches by using computer simulations of shell coiling seem to elucidate the process of growth and morphogenesis of this heteromorph ammonite.

Conclusion

In order to interpret the peculiar shell formation of *Polyptychoceras,* more than 320 specimens of *P. pseudogaultinum* were analyzed by various methods of biometry, population analysis and theoretical morphology. It is concluded that the peculiar shell morphology of *P. pseudogaultinum* is related to the intermittent growth pattern and to the cyclic change of living attitude. Namely, the shell grows slowly

Figure 14. *Polyptychoceras pseudogaultinum* (Yokoyama). All figures natural size. **1-12.** From Onko-no-sawa, **13-15.** From Kami-no-sawa, Kotanbetsu, Tomamae Province, Hokkaido, 1 : H-049, 2 : S- 124, 3 : H-038, 4 : S-148, 5 : H-076, 6 : H-001, 7 : S-146, 8 : H-078, 9 : S-125, 10 : S-065, 11 : S-147, 12 : S-123, 13 : H-114, 14 : T-027, and 15 : T-028.


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when the aperture faces upward and grows quickly when the aperture faces other directions. Various kinds of cyclic morphologic changes observed during growth can be reasonably interpreted with this hypothesis. The sudden increase of shell height occurs in several stagnant stages of shell prolongation and enables the body to grow continuously. The periodic flared rib occurring near the beginning of every shaft suggests the start of the stagnation interval. The notched ribs characteristically develop during the intervals. Thus, the changes of shell ornamentation reflect the mode of growth, which is related to the change of living attitude.

In this study, we cannot necessarily elucidate the shell-forming mechanism of *P. pseudogaultinum* or the adaptive significance of such an aberrant shell form. We merely have made clear the characteristics of the shell growth of this ammonite which are probably controlled by its life orientation in sea water. The peculiar mode of shell coiling was possibly caused by the cyclic change of growth direction, which must be strongly constrained by the existing shell geometry. The validity of such hypotheses should be checked by a theoretical approach using some computer simulations of shell coiling. The changing process of shell geometry throughout the phylogeny of *Polyptychoceras* and its ancestors is possibly reconstructed by analogous approaches.

Acknowledgments

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Figure 15. *Polyptychoceras pseudogaultinum* (Yokoyama). All figures natural size. **1.** From Kami-no-sawa, **2-9.** from Onko-no-sawa, Kotanbetsu, Tomamae Province, Hokkaido. 1: H- 114, 2: H-079, 3: H-080, 4: S-126, 5: S-122, 6: S-108, 7: H-007, 8: H-088, and 9: S-163.

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Appendix table. Correlation between the consecutive specimen numbers and register numbers.

Register No. [UMUT MM-]	Sample No.	Consecutive specimen No.
19877 a-c	K1001p-1	H.068-070
19878 a-d	K9000p-2	H.049-052
19879	K9000p-4	H.048
19880 a-g	K9000p-6	H.042-047, H.054
19881 a-d	K9000p-7	H.038-041
19882	K9000p-9	S.203
19883	K9000p-17	H.053
19884	K9000p-21	H.055
19885 a-b	K9000p-30	H.060-061
19886 a-c	K9000p-31	H.065-067
19887	K9000p-32	H.071
19888	K9000p-33	H.107
19889 a-b	K9000p-34	H.110, H.121
19890 a-d	K9000p-35	S.197-198, S.204-205
19891	K9009c	H.059
19892 a-c	K9011a	H.102-104
19893 a-f	K9011b	S.041-046
19894 a-e	K9011d	H.028-032
19895 a-d	K9011e	H.024-027
19896 a-c	K9011g	H.035-037
19897	K9011h	H.034
19898	K9011j	H.033
19899 a-e	K9011k	H.019-023
19900 a-c	K9012b	H.001-003
19901 a-d	K9012e	H.004-007
19902	K9012g	H.018
19903 a-e	K9012j	H.008-012
19904 a-e	K9012n	H.013-017
19905	K9110a	H.064
19906	K9111b	H.074
19907 a-c	K9111d	H.056-058
19908	H6101p-3	H.072
19909 a-d	92KT1004p-1	H.091-093, H.095
19910 a-g	92KT3142p-1	H.113-119
19911	92KT3522p-1	H.109
19912 a-d	92KT3707p-1	S.009, S.011, S.117, S.121
19913	92KT3713p-1	H.108
19914	92KT8563p-1	H.120
19915 a-b	92KT8566p-1	H.111-112
19916	92KT9008p-1	H.105
19917	92KT9008p-2	H.106
19918 a-h	92KT9029c	H.075-080, H.126-127
19919 a-e	92KT9029d	H.082-086
19920 a-e	92KT9029g	S.091-095
19921 a-b	92KT9029u	S.015, S.202
19922	92KT9029v	S.113
19923 a-c	92KT9029w	S.032-033, S.074
19924 a-i	92KT9029p-2	S.026-029, S.106, S.110-111, S.119-120
19925	92KT9031p-1	H.081
19926 a-f	92KT9031p-2	H.096-101
19927	92KT9031p-3	S.010
19928 a-b	92KT9035a	S.030-031
19929 a-d	92KT9035p-1	H.087-090
19930 a-i	92KT9035p-2	S.020-025, S.176-178
19931 a-d	92KT9606p-1	S.076, S.114-116
19932 a-b	92KT9611p-1	S.118, S.142
19933 a-e	93KT9019p-1	S.016-019, S.179
19934 a-c	93KT9030b	S.143-145
19935 a-v	93KT9030c	S.012-014, S.037-038, S.096-097, S.103-105, S.159-170
19936 a-w	93KT9030d	S.122-141, S.180, S.188-189
19937 a-g	93KT9030e	S.181-185, S.200-201
19938 a-d	93KT9030f	S.056-059
19939	93KT9030g	S.069
19940 a-b	93KT9030h	S.108-109
19941 a-v	93KT9030k	S.146-158, S.186-187, S.190-196
19942 a-n	93KT9030l	S.039-040, S.070-072, S.082-090
19943 a-e	93KT9030n	S.060-064
19944 a-e	93KT9030q	S.051-055
19945 a-d	93KT9030r	S.047-050
19946	93KT9030u	S.075
19947 a-d	93KT9030w	S.065-068
19948	93KT9030x	S.073
19949 a-n	93KT9035a	S.001-004, S.034-036, S.077-081, S.112, S.175
19950 a-n	93KT9035b	S.005-008, S.098-102, S.107, S.171-174
19951	95HB4014p-2	S.199
SKIPPED NUMBERS :		H.062-063, H.073, H.094, H122-125

All specimens are identified with *P. pseudogaultinum* except for S.199.

Hokkaido 北海道, Horotate-zawa 幌立沢, Kami-no-sawa 上の沢, Kotanbetsu 古丹別, Onko-no-sawa オンコの沢, Tomamae 苫前, Urakawa 浦河

Paleontological Research, vol. 1, no. 1, pp. 47-54, 3 Figs., April 30, 1997

4. Late Gzhelian (Carboniferous) to early Asselian (Permian) non-ammonoid cephalopods from the Taishaku Limestone Group, Southwest Japan

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Abstract. The non-ammonoid cephalopod fauna described here was collected from the upper Gzhelian-lower Asselian (Upper Carboniferous to Lower Permian) hydrozoan-algal buildups in the Taishaku Limestone Group, Southwest Japan. The fauna consists of four orthocerids: *Michelinoceras* ? sp., *Bogoslovskya miharanoroensis* sp. nov., *Geisonocerina* ? sp., *Lopingoceras hayasakai* sp. nov.; two nautilids: *Parachouteauoceras bingoense* gen. et sp. nov., *Parachouteauoceras* ? sp.; and a bactritid: *Bactrites* sp. *Parachouteauoceras* is most similar to *Chouteauoceras*, but unlike the latter has a lobated aperture. The occurrence of *Bogoslovskya miharanoroensis* represents one of the latest records of the genus in the world. This fauna is important because it adds some new data to a poorly known Late Carboniferous-Early Permian non-ammonoid cephalopod fauna.

Key words: Asselian, Bactritida, Gzhelian, Nautilida, Orthocerida, Taishaku Limestone Group

Introduction

The non-ammonoid cephalopods of the Taishaku Limestone Group, Southwest Japan, were first noticed by Hayasaka and Nishikawa (1963) who reported the orthocerid species *Orthoceras* cf. *adrianense* Gemmellaro in an oral presentation (Koizumi, 1975). Of the fauna, only three specimens were kept back for future examination. Recent studies, as described by Niko *et al.* (1993), show that the specimens are referable to a bactritid and represent a new species, *Aktastioceras nishikawai.* An additional seven species belonging to the Orthocerida, Nautilida and Bactritida are described and figured herein from the upper Gzhelian to lower Asselian part of the Taishaku Limestone Group. This report adds some new data to a poorly known non-ammonoid cephalopod fauna in the vicinity of the Carboniferous-Permian boundary, and will provide a basis for future biostratigraphic and paleobiogeographic studies.

All specimens used for the study are housed in the paleontological collections of the Department of Earth and Planetary Sciences, Nagoya University (ESN).

Geologic setting and occurrence

The Taishaku Limestone Group, located in the northeastern part of Hiroshima Prefecture, is a thick Carboniferous to Permian greenstone-limestone sequence occurring in the Akiyoshi Terrane in the Inner Zone of Southwest Japan. Hase *et al.* (1974) conducted a detailed facies analysis of the Taishaku Limestone Group and interpreted that it was formed as a table reef complex on the submarine volcanic mound. In Miharanoro, Hiba-gun, Hiroshima Prefecture (Figure 1), Upper Carboniferous to Lower Permian hydrozoan-algal reef complexes are well developed, forming a reef core facies in the Taishaku Limestone Group. The Upper Carboniferous to Lower Permian sequence of the Taishaku Limestone Group in Miharanoro is divided into the following six fusulinacean zones (Ozawa and Hirakawa, MS): in ascending order, these are the *Triticites ozawai-Carbonoschwagerina morikawai* Zone, *Triticites contractus* Zone, *Pseudoschwagerina muongthensis* Zone, *Pseudoschwagerina miharanoensis* Zone, *Pseudofusulina vulgaris* Zone, and *Pseudofusulina kraffti* Zone. The stratigraphic horizon of *Aktastioceras nishikawai* belongs to the *Pseudoschwagerina miharanoensis* Zone, indicating a late Asselian age. On the other hand, fossil localities of the present non-ammonoid cephalopods are in the *Triticites contractus* Zone, which coincides with the *Carbonoschwagerina minatoi-Daixina* cf. *robusta* Zone (upper Gzhelian) and the *Sphaeroschwagerina fusiformis* Zone (lower Asselian) of the Akiyoshi Limestone Group (Ozawa and Kobayashi, 1990).

The cephalopods described herein were collected by the

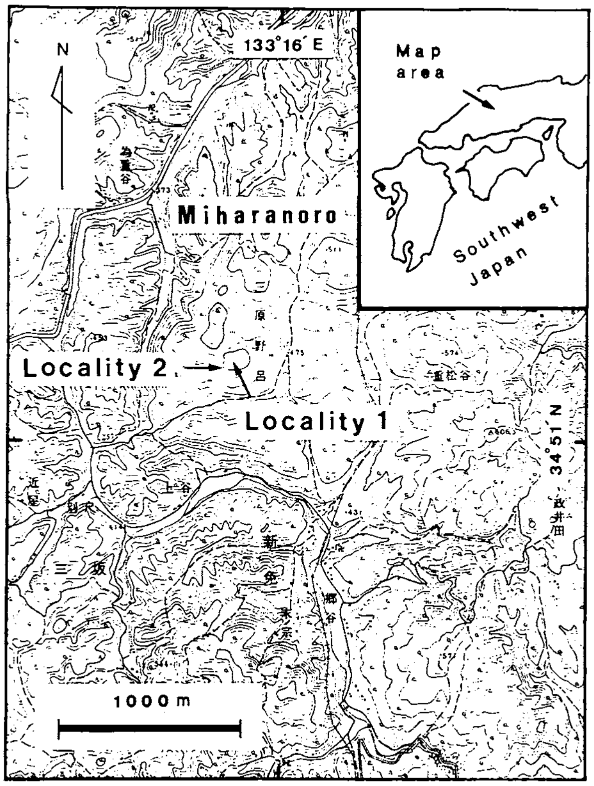

Figure 1. Part of topographic map "Tojo", 1 : 25,000 quadrangle of Geographical Survey Institute, showing fossil localities in Miharanoro, Hiroshima Prefecture.

junior author from bioclastic limestones in channellike depressions of the *Triticites contractus* Zone. In the channel-fill sediments, they occurred along with ammonoids, gastropods, pelecypods, brachiopods, and foraminifers.

Systematic paleontology

Class Cephalopoda Cuvier, 1797
Subclass Nautiloidea Agassiz, 1847
Order Orthocerida Kuhn, 1940
Superfamily Orthocerataceae M'Coy, 1844
Family Orthoceratidae M'Coy, 1844
Subfamily Michelinoceratinae Flower, 1945
Genus ***Michelinoceras*** Foerste, 1932

Type species.—*Orthoceras michelini* Barrande, 1866.

Michelinoceras ? sp.

Figures 2-14—16

Description.—Smooth-surfaced orthocones with gradual shell expansion, circular cross section; largest specimen (ESN 2593) of phragmocone 3.9 mm in adoral diameter; sutures straight, transverse; siphuncle central, composed of orthochoanitic necks and cylindrical connecting rings.

Discussion.—This description is based on three poorly preserved phragmocones of probably immature portions. Judging from the siphuncular structure, they may represent a species of *Michelinoceras*. However, there is no denying the possibility that the specimens are apical shells of associated *Geisonocerina* ? sp. (this report) until better material is recovered.

Material and occurrence.—ESN 2593-2595 from Locality 1.

Genus ***Bogoslovskya*** Zhuravleva, 1978

Type species.—*Bogoslovskya perspicua* Zhuravleva, 1978.

Bogoslovskya miharanoroensis sp. nov.

Figures 2-1—9

Diagnosis.—Species of relatively large *Bogoslovskya* with distant, very narrow ribs; cameral ratio approximately 3-4; siphuncular position midway between center and margin in adoral shell.

Description.—Shells relatively large for genus, orthoconic with circular cross section, largest specimen (ESN 2590) of phragmocone reaches approximately 25 mm in diameter; angle of shell expansion moderate, 4-5 degrees; surface ornamentation consists of distant, very narrow ribs, weakly sinuate, slightly toward aperture on antisiphuncular side, rib index (number of ribs per length of corresponding shell diameter) 13-17, interribs space flat, smooth; septa moderately deep forming straight, transverse sutures; cameral length short for genus, cameral ratio (diameter/length) 3.2-4.1; siphuncle very narrow, maximum external diameter of septal neck/shell diameter 0.03 in holotype, siphuncular position submarginal, but shifts midway between center and margin in adoral shell, minimum distance of siphuncular axis from shell surface per shell diameter in dorsoventral section 0.19 in immature shell (9.5 mm in diameter) of paratype (ESN 2589), increases to 0.26 adorally (20 mm in diameter); length of septal necks moderately long for genus, approximately 1.8 mm at shell diameter of 21 mm, gently tapering orthochoanitic with weak auxiliary deposits in funnel-shaped septal foramen; connecting rings not preserved; no camer-

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Figure 2. **1-9.** *Bogoslovskya miharanoroensis* sp. nov., 1-4 : holotype, ESN 2586, 1, side view of siphuncular side, ×2, 2, lateral view, siphuncular side on right, ×2, 3, septal view of apical end, ×2, 4, dorsoventral polished section, arrow indicates siphuncular position, ×3, 5, 6 : paratype, ESN 2587, 5, lateral view, siphuncular side on left, ×2, 6, dorsoventral thin section, details of siphuncular structure, note auxiliary deposits, ×10, 7 : paratype, ESN 2589, septal view of apical end, ×2, 8 : paratype, ESN 2591, lateral view, siphuncular side on right, ×2, 9 : paratype, ESN 2590, lateral view, siphuncular side on left, ×2. **10-13.** *Geisonocerina* ? sp., 10-12 : ESN 2596, 10, side view, ×2, 11, septal view, ×2, 12, longitudinal polished section, ×3, 13 : ESN 2597, side view, ×2. **14-16.** *Michelinoceras* ? sp., ESN 2593, 14 : side view, ×4, 15 : septal view of apical end, ×4, 16 : longitudinal thin section, ×4.


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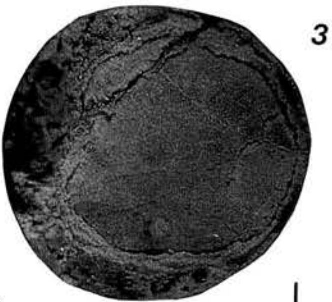
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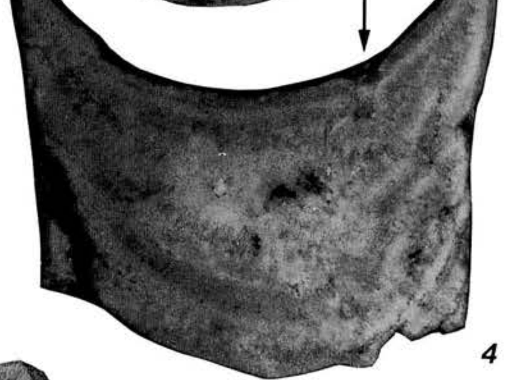
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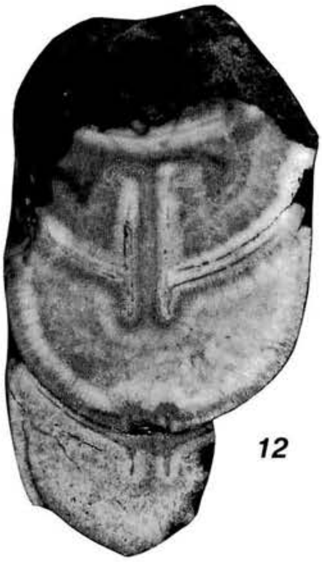
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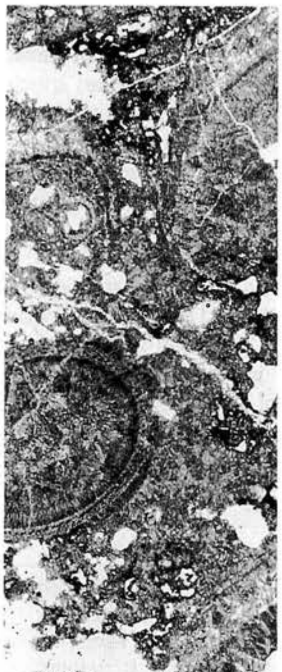
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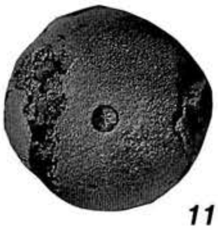
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al deposits detected.

Discussion.—The possession of surface ribs of *Bogoslovskya miharanoroensis* sp. nov. clearly distinguishes it from all other known species of the genus. The range of *Bogoslovskya* was previously restricted to the Middle to Late Devonian of the Urals (Zhuravleva, 1978) and the Middle Carboniferous of the Akiyoshi Limestone Group (Niko *et al*., 1995). Thus, this late Gzhelian to early Asselian species represents the youngest record of the genus.

Etymology.—The specific name is derived from the type locality name Miharanoro.

Material and occurrence.—Holotype, ESN 2586, incomplete phragmocone, 22.5 mm in length; five paratypes, ESN 2587-2591, incomplete phragmocones, are surely, and a specimen, ESN 2592, is questionably, assigned to this species. All specimens from Locality 1.

Family Geisonoceratidae Zhuravleva, 1959
Genus **Geisonocerina** Foerste, 1935

Type species.—*Orthoceras wauwatosense* Whitfield, 1882.

Geisonocerina ? sp.

Figures 2-10—13

Description.—Orthocones with gradual shell expansion, circular cross section; surface ornamentation consists of distinct transverse lirae, adorally indicating weak sinuations; largest specimen (ESN 2597) of phragmocone reaches approximately 16 mm (reconstructed) in diameter; septa thick, deeply concave, forming straight, transverse sutures; siphuncle central; septal necks long, orthochoanitic, but slightly dilated terminally; connecting rings cylindrical.

Discussion.—This description is based on two fragmentary phragmocones. They are not sufficiently well preserved to identify more precisely, but lack of periodic thickening of the lirae suggests this species probably belongs to *Geisonocerina* rather than *Geisonoceras* Hyatt, 1884.

Material and occurrence.—ESN 2596, 2597. In addition, a specimen (ESN 2598) is questionably assigned to this species. All specimens from Locality 1.

Superfamily Pseudorthocerataceae Flower and Caster, 1935
Family Pseudorthoceratidae Flower and Caster, 1935
Subfamily Spyroceratinae Shimizu and Obata, 1935
Genus **Lopingoceras** Shimanskiy in Ruzhentsev, 1962

Type species.—*Orthoceras lopingense* Stoyanow, 1909.

Lopingoceras hayasakai sp. nov.

Figures 3-1—7

Diagnosis.—Annulated orthocones with conspicuous surface lirae, annulations have subangular profile; cameral deposits episeptal-mural, hyposeptal; endosiphuncular deposits form continuous lining.

Description.—Annulated orthocones with gradual shell expansion, angle approximately 3-4 degrees; cross section of shell circular; largest specimen (ESN 2600) of phragmocone reaches approximately 10 mm (reconstructed) in diameter; annulations relatively low, subangular profile in longitudinal section, bearing weak lateral sinus; annulations and interspaces of annulations ornamented by conspicuous lirae that run parallel with annulation, salient forms over injured portion of shell as repaired; sutures straight, transverse; septal curvature moderate, cameral ratio approximately 2.2 in holotype; there are usually two annulations in single camera; siphuncle subcentral, shifts slightly dorsally from center, septal necks short, suborthochoanitic to weakly cyrtochoanitic, 0.45 mm in length in holotype, connecting rings subcylindrical with constrictions at septal foramen and weak dorsal inflations, maximum external diameter of connecting rings/shell diameter in each segment of holotype approximately 0.2; cameral deposits episeptal-mural, hyposeptal; endosiphuncular deposits well developed, form thick continuous lining on siphuncular wall, thicker in venter than dorsum.

Discussion.—Generic assignment of the species is tentative at present. A combination of surface annulations and conspicuous lirae relates the form to *Reticycloceras* Gordon, 1960, but the possession of hyposeptal deposits in the species clearly separates them. *Lopingoceras* Shimanskiy in Ruzhentsev (1962) is based on an Upper Permian species from Dzhul'fa, of which species has an annulated orthocone. The distinguishing feature of *Lopingoceras* is angularity of outline of annulations, and the present species shears this morphology. Although the structure of deposits is unknown in the generic type species, we consider that the present species probably belongs to *Lopingoceras.*

Shimanskiy (1954, pl. 7, figs. 6a-v) referred a species from the lower Asselian of the southern Urals to *Cycloceras laevigatum* M'Coy (1844, pl. 2, fig. 3), which was described from the Lower Carboniferous of Ireland. With the exception of a somewhat larger angle of shell expansion (approximately 6 degrees), the Russian species is very likely closely related to *Lopingoceras hayasakai* sp. nov. *Cycloceras* was defined on an internal mold of a body chamber by M'Coy

Figure 3. **1-7.** *Lopingoceras hayasakai* sp. nov., 1-4: holotype, ESN 2599, 1, ventral view, ×2, 2, lateral view, venter on right, ×2, 3: dorsoventral thin section, venter on left, note subangular profile of annulations, ×4, 4, details of siphuncular structure, note thick continuous lining of endosiphuncular deposits, ×10, 5-7: paratype, ESN 2600, 5, lateral view, venter on right, ×2, 6, dorsal view, ×2, 7, septal view of apical end, venter down, ×2. **8-11.** *Bactrites* sp., ESN 2607, 8: ventral view, ×2, 9: lateral view, venter on right, ×2, 10: dorsal view, ×2, 11: septal view of apical end, venter down, ×2. **12-15.** *Parachouteauoceras bingoense* gen. et sp. nov., 12-14: holotype, ESN 2601, 12, lateral view, note color markings through ammonium chloride coating, ×3, 13, ventral view, ×3, 14, septal view of apical end, venter up, ×3, 15: paratype, ESN 2602, lateral view with complete embryonic shell, ×3. **16-18.** *Parachouteauoceras* ? sp., ESN 2604, 16: lateral view, ×3, 17: ventral view, ×3, 18: septal view of apical end, venter up, ×3.


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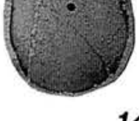
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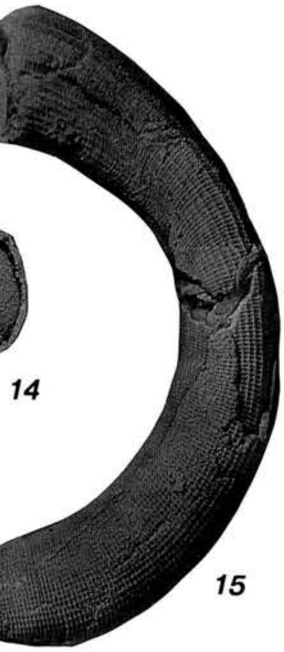
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(1844), thus the diagnosis of the genus calls for nothing further than an annulated orthocone with low angles of expansion. Sweet (1964) properly stated that "no species other than the type species should be referred to *Cycloceras* until its type is better known". This problem is still unsolved.

Etymology.—The specific name refers to the late Dr. Ichiro Hayasaka, a pioneer in the study of the Paleozoic nautiloids of Japan.

Material and occurrence.—Holotype, ESN 2599, incomplete phragmocone, 20.1 mm in length; paratype, incomplete phragmocone, ESN 2600. Both from Locality 2.

Order Nautilida Agassiz, 1847
Superfamily Trigonocerataceae Hyatt, 1884
Family Trigonoceratidae Hyatt, 1884
Genus ***Parachouteauoceras*** gen. nov.

Type species.—*Parachouteauoceras bingoense* sp. nov.

Diagnosis.—Like *Chouteauoceras* but differs in possession of lobed peristome with linguiform ventral sinus, ventrolateral saddle, dorsolateral sinus, dorsal saddle.

Etymology.—The generic name is derived from the Greek *para*, meaning near, and *Chouteauoceras.*

Parachouteauoceras bingoense sp. nov.

Figures 3-12—15

Diagnosis.—As for the genus.

Description.—Loosely coiled, gyrocones losing contact; whorl section weakly compressed, width/height ratio ranges from 0.90 to 0.97 in holotype, venter and flanks slightly convex with subangular ventral shoulders, dorsum broadly rounded; adoral end of body chamber of holotype reaches 8.6 mm in height; embryonic shell weakly inflated in dorsoventral direction, with cone-shaped primary shell; most inflated portion of embryonic shell 5.3 mm in height, 4.7 mm in width, giving a ratio of 0.89; surface ornamentation consists of numerous longitudinal ridges and growth lines; growth lines nearly transverse, producing a latticework in embryonic shell; later growth lines indicate lobed peristome of deep linguiform ventral sinus, rounded ventrolateral saddle, shallow dorsolateral sinus, broadly rounded dorsal saddle; sutures transverse with broadly rounded lateral lobes, dorsal and ventral saddles; siphuncle small, subcentral, slightly shifts to venter; preserved color markings consist of 7 or 8 relatively wide bands, which run parallel with peristome, in ventral shoulder to ventrolateral position on holotype.

Discussion.—The gyroceraconic shells with a compressed whorl section, the longitudinal surface ridges, and rounded lateral lobes in the sutures of *Parachouteauoceras bingoense* gen. et sp. nov. suggest a relationship to the trigonoceratid genus *Chouteauoceras* Miller and Garner, 1953. *Chouteauoceras* is a rare genus which embraces the type species *C. americanum* (Miller and Furnish, 1938, pl. 48, figs. 4-6) from Missouri and some other species questionably assigned to the genus from North America, Belgium and Ireland. All occurrences are in the Lower Carboniferous. *Parachouteauoceras* can be distinguished from *Chouteauoceras* by its peristome shape. The growth lines of *Chouteauoceras* indicate a transverse peristome with weak lateral saddles.

Apogonoceras remotum Ruzhentsev and Shimanskiy (1954, pl. 11, figs. 8a, 8b; only known species and the type species of the genus) from the Artinskian of the southern Urals has a shell shape generally similar to *Parachouteauoceras bingoense,* but has nearly straight sutures in the adoral shell and a somewhat subtriangular whorl section. The peristome shape of *Apogonoceras* is unknown.

Etymology.—The specific name is derived from Bingo, which is the historic province name of the region in which the type locality lies.

Material and occurrence.—Holotype, ESN 2601, incomplete phragmocone with apical body chamber, 25.5 mm in length; two paratypes, ESN 2602, 2603, apical phragmocones. All specimens from Locality 2.

Parachouteauoceras ? sp.

Figures 3-16—18

Description.—Loosely coiled juvenile phragmocones losing contact; whorl section compressed, ovoid, width/height ratio 0.90; shell height reaches 4.9 mm in largest specimen ESN 2604; surface ornamentation consists of weak longitudinal ridges and growth lines indicating ventral sinus; sutures nearly transverse; siphuncle subcentral.

Discussion.—This species is represented by two fragmentary phragmocones of juvenile portion. The specimens differ from *Parachouteauoceras bingoense* gen. et sp. nov. (this report) in smaller shell size in the corresponding shell portion. The lack of adult shells of this species leaves doubt upon assignment to *Parachouteauoceras.*

Material and occurrence.—ESN 2604, 2605 from Locality 1.

Subclass Bactritoidea Shimanskiy, 1951
Order Bactritida Shimanskiy, 1951
Family Bactritidae Hyatt, 1884
Genus ***Bactrites*** Sandberger, 1843

Type species.—*Bactrites subconicus* Sandberger, 1843.

Bactrites sp.

Figures 3-8—11

Description.—Orthocones with gradual shell expansion, angle approximately 3.5 degrees, circular cross section; largest specimen (ESN 2607) of phragmocone reaches 11.5 mm in diameter; transverse lirae of surface ornamentation slightly sinuate, very fine, closely spaced; sutures straight, transverse with ventral lobe, siphuncle relatively large, ventral margin in position.

Discussion.—This species resembles most closely *Bactrites costatus* Mapes (1979, pl. 31, figs. 7-9, 13) from the upper Virgilian of Texas in having closely spaced surface lirae. *Bactrites costatus* differs from the present species in its larger angle (5-7 degrees) of shell expansion.

Material and occurrence.—Based on two phragmocones: ESN 2606 from Locality 1, and ESN 2607 from Locality 2.

Acknowledgments

The second author is deeply indebted to Mitsuaki Hirakawa and Akihiko Shioe, former post-graduate students of the Hyogo University of Teacher Education, for their kind help in sampling.

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5. Permian cephalopods of Kurosawa, Kesennuma City in the Southern Kitakami Massif, Northeast Japan

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Abstract. **Permian nautiloids and ammonoids are described from the middle part of the Ochiai Formation distributed in the Kurosawa district of northern Kesennuma City, Southern Kitakami Massif, Northeast Japan. The nautiloids are *Tainoceras, Pleuronautilus* and *Stearoceras*. One new species, *Tainoceras carinatum*, is proposed. The ammonoids are *Jilingites, Stacheoceras, Timorites, Pseudagathiceras, Propinacoceras* and *Eumedlicottia*. *Jilingites kesennumensis, Timorites takaizumii* and *Pseudagathiceras ornatum* are newly proposed species. Based on the stratigraphic distribution of *Timorites, Jilingites* and *Pseudagathiceras*, and the stratigraphic relationship between the cephalopod horizon and *Lepidolina*-bearing limestones, the cephalopod-bearing formation of Kurosawa is considered to be correlatable with the upper Capitanian.**

Key words: Capitanian, *Helicoprion*, Kesennuma, Kitakami Massif, Permian cephalopod

Introduction

Permian strata are widely distributed in the northern district of Kesennuma City, Southern Kitakami Massif, forming a large synclinorium, the axis of which trends NS and plunges to the south. They are divided into the Nakadaira, Ochiai and Nabekoshiyama Formations, in ascending order (Ehiro, 1977). These formations are roughly correlated with the Lower Permian Sakamotozawan Series, Middle Permian Kanokuran Series to the middle part of the Upper Permian Toyoman Series, and upper Toyoman Series, respectively. They have been studied stratigraphically and paleontologically for 100 years, and many Middle Permian brachiopods and molluscs have been described from the upper part of the lower Ochiai Formation. Uppermost Permian fossils such as *Colaniella parva* and *Palaeofusulina* sp., in association with brachiopods and pelecyoods, have also been found (Tazawa, 1975; Ishii *et al.*, 1975) from the Nabekoshiyama Formation.

Araki (1980) reported the occurrence of a chondrichthyes, *Helicoprion* sp., from sandy shale of the middle part of the Ochiai Formation, which crops out at a tributary of the Kurosawa River in the Kamiyasse district, northern Kesennuma. He also collected some cephalopods from a horizon slightly lower than that of *Helicoprion.* These horizons were correlated with the upper part of the Kanokuran Series based on a preliminary study of the cephalopod fauna (Araki, 1980). The upper Kanokuran Series is generally correlated with the upper Maokouan of South China and with the Capitanian of North America. These cephalopods, however, have not been described previously, nor have been known other index fossils near the fossil locality.

Recently, the present authors studied stratigraphically the Permian strata in and around the Kurosawa River and collected some additional cephalopods from Araki's locality and other new localities with the assistance of Yukihiro Takaizumi. The present paper describes the cephalopods from the middle part of the Ochiai Formation distributed in the catchment area of the Kurosawa River and discusses the age of the fauna.

Geologic settings

The Ochiai Formation in the Kamiyasse district is composed mainly of shales, except for the upper part of the lower part (Toyazawa Member). In this member, distributed in the upper tributaries of the Shigejizawa River (Figure 1), sandstones and impure limestones predominate. It yields diverse fossils such as fusulinids, brachiopods, bryozoans, crinoids and molluscs. *Monodiexodina matsubaishi* (Fujimoto), which is a characteristic fusulinid of the lower part of the Kanokuran Series, dominates in the lower to middle part of the member. The upper part of the member yields such fusulinids as *Verbeekina, Pseudodoliolina* and *Lepidolina* (Tazawa, 1976), which characterize the upper Kanokuran.

The middle part of the Ochiai Formation, consisting mainly of massive sandy shales and shales with rare thin sandstone interbeds, is widely distributed in the Kurosawa River and its tributaries. In a horizon about 400 m above the top of the Toyazawa Member, thin lenticular limestones with maximum

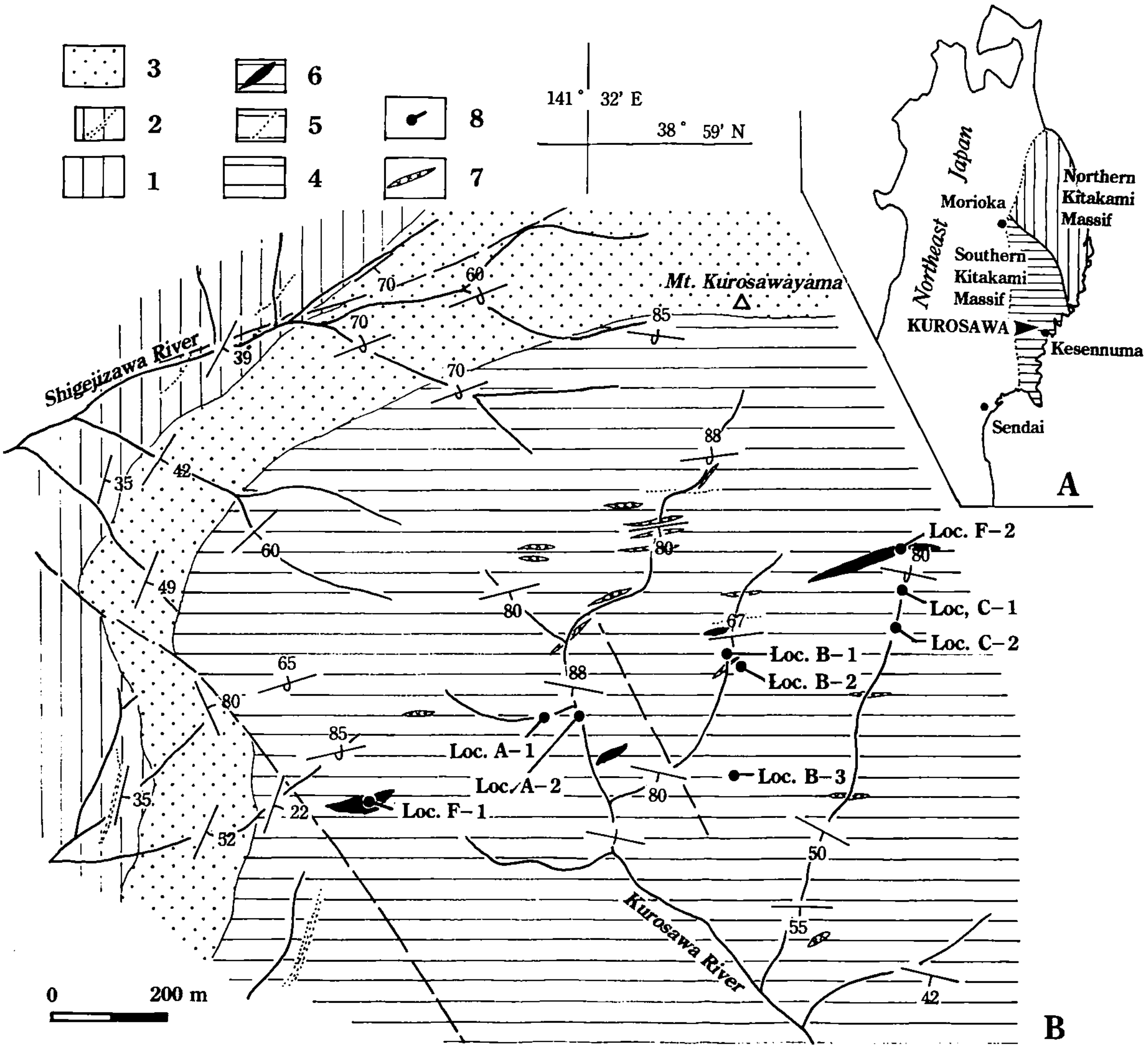


Figure 1. Index map (A) and geologic map of the Kurosawa district, northern Kesennuma, Southern Kitakami Massif, Northeast Japan (B). **1-2.** lower part of the Ochiai Formation (1: shale, 2: sandstone). **3.** Toyazawa Member of the Ochiai Formation (sandstone, limestone, shale and conglomerate). **4-6.** middle part of the Ochiai Formation (4: shale, 5: thin sandstone, 6: limestone). **7.** porphyrite. **8.** fossil localities.

thicknesses of 5 to 20 meters are intercalated at some localities (Figure 1B). They yielded fusulinids, *Lepidolina* sp. (Loc. F-1 in Figure 1B) and *Verbeekina* sp. (Loc. F-2). The relationships between these limestone lenses and surrounding shales is uncertain. The latter are not calcareous. This points to a possibility that these limestone lenses are not *in situ* but are exotic blocks derived likely from lower horizons.

Shales in the middle part of the Ochiai Formation are almost barren of fossils, but some cephalopods, together with a few brachiopods and gastropods, have been collected at some localities (Loc. A-1 to C-2 in Figure 1B). Among these are Loc. B-1 and B-2 which yielded abundant cephalopods. Examination led to the discrimination of the following forms.

Locality A-1: *Propinacoceras* sp.

Locality A-2: *Eumedlicottia primas* (Waagen)

Locality B-1: *Tainoceras carinatum* sp. nov., *Pleuronautilus* sp., *Jilingites kesennumensis* sp. nov., *Timorites takaizumii* sp. nov., *Pseudagathiceras ornatum* sp. nov., *Propinacoceras* sp.

Locality B-2: *Tainoceras* sp., *Pleuronautilus* sp., *Stacheoceras* sp., *Timorites*? sp., *Propinacoceras* sp., *Eumedlicottia primas* (Waagen)

Locality B-3: *Stearoceras* sp.

Locality C-1: *Timorites takaizumii* sp. nov.

Locality C-2: *Tainoceras* sp.

Ammonoid locality A-1 is stratigraphically about 100 m lower than that of *Lepidolina*-bearing lenticular limestone. The ammonoid *Eumedlicottia* from Loc. A-2 at a horizon about 20 m higher than that of Loc. A-1 was collected from a large loose shale block on the river bed. Cephalopod horizons at Loc. B-1, B-2 and B-3 are about 80-90, 110-120 and 300 m above the limestone lenses, respectively. The locality of *Helicoprion* is near Loc. B-2 and is stratigraphically 30-40 m higher than that of the latter. Cephalopods of Loc. C-1 and C-2 were both collected from floats on the river floor, possibly derived from shales little above *Verbeekina*-bearing limestone.

Faunal consideration

The cephalopod fauna of Kurosawa comprises three genera of nautiloids and six of ammonoids. *Timorites* is abundant in the fauna and more than 20 specimens are at hand. *Propinacoceras* is the next most common. Specimens of the other genera are rarer, one to four specimens each. *Jilingites* and *Pseudagathiceras* are described here from Japan for the first time.

Cephalopod genera of Kurosawa, except for *Jilingites, Timorites* and *Pseudagathiceras,* have rather long stratigraphic ranges. *Jilingites bidentus* Liang, which is the type species and only known representative of the genus, occurs in the Middle Permian (Wordian) Fanjiatun Formation of Jilin, North China (Liang, 1982). The Kurosawa species of *Jilingites* is closely similar to the Chinese species.

Species of *Timorites* are characteristic of the Permian ammonoid Equatorial Provinces (Ehiro, 1996), and have been reported from the upper Middle Permian (Capitanian) formations in the Tethyan province from such places as Timor, Japan, Far Eastern Russia, South China and the Himalayan region of China, and Texas, U.S.A, and Coahuila, Mexico, in North America. They are also known from Upper Permian Dzhulfian formations in the Kitakami Massif (Ehiro *et al.*, 1986), Transcaucasia and Central Iran (Zhou *et al.* 1989).

According to Miller (1944), five species of *Pseudagathiceras* are known from Wordian formations of Timor, Sicily and Coahuila. The Kurosawa species of *Pseudagathiceras* closely resembles the Coahuila species in the shape of shells and the presence of prominent ventrolateral spines.

Based on the occurrence of *Timorites,* the ammonoid-bearing horizons of Kurosawa, especially B-1 and B-2, are correlatable with somewhere in the interval from the Capitanian to Dzhulfian. On the other hand, the associated *Jilingites* and *Pseudagathiceras* suggest that the age of the fauna is not younger than Wordian, although their stratigraphic ranges are less certain. The horizons of B-1 and B-2 are a little higher than those of limestone lenses, which yield Capitanian fusulinids such as *Lepidolina* and *Verbeekina,* although there is a possibility that the limestone lenses are not *in situ*. No typical Dzhulfian ammonoids, such as araxoceratids and advanced xenodiscids, have been collected from these horizons. Therefore, the age of the cephalopod fauna and of *Helicoprion* sp. from Kurosawa is considered to be late Capitanian as presumed by Araki (1980), not Dzhulfian.

Systematic description

Specimens described in this paper are kept in the Institute of Geology and Paleontology, Tohoku University, Sendai (IGPS).

Subclass Nautiloidea Agassiz, 1847
Order Nautilida Agassiz, 1847
Superfamily Tainocerataceae Hyatt, 1883
Family Tainoceratidae Hyatt, 1883
Subfamily Tainoceratinae Hyatt, 1883
Genus ***Tainoceras*** Hyatt, 1883

Type species.—Nautilus quadrangulus McChesney, 1868

Tainoceras carinatum sp. nov.

Figures 3-2a, b

Material.—A fragmentary specimen, IGPS coll. cat. no. 103114, collected from Loc. B-1 by Y. Takaizumi.

Diagnosis.—Tainoceras having lateral ribs and carinated ventrolateral shoulders.

Descriptive remarks.—About one third of the outer volution, the diameter of which is estimated to attain 45 mm, was examined. The conch is thickly discoidal and evolute in outline, with a large and deep umbilicus. It is slightly wider than high, and has flat sides, which very slightly converge toward the broadly rounded venter. The umbilical shoulder

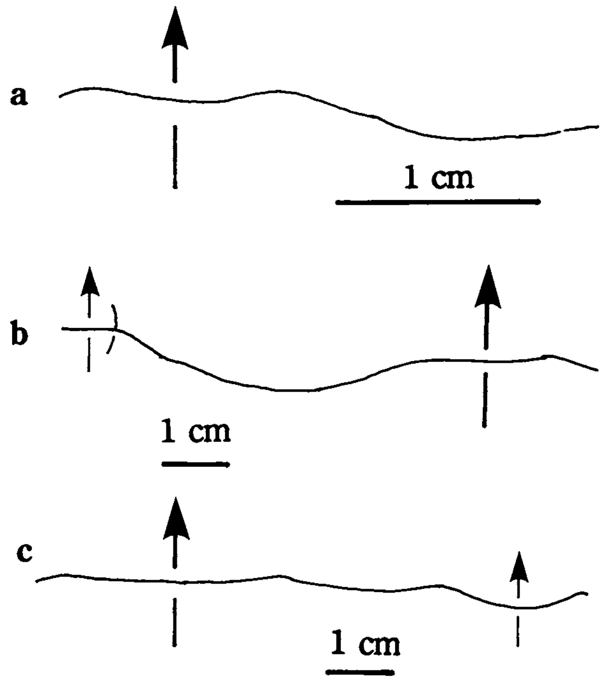


Figure 2. Suture lines of nautiloids from the Ochiai Formation. **a.** *Tainoceras* sp., IGPS coll. cat. no. 103115. **b.** *Pleuronautilus* sp., IGPS coll. cat. no. 103116. **c.** *Stearoceras* sp., IGPS coll. cat. no. 103118.

is acutely rounded and ventral shoulder is edged with a fine keel. The flanks have rather fine but strong radial ribs, which are straight throughout their length. They extend from the umbilical to ventral shoulder and are nodose at the ventral end. There are two rows of nodes, which characterize the genus *Tainoceras,* on the venter. The suture is unknown.

In having straight and fine lateral ribs, the present species somewhat resembles *Tainoceras noetlingi* Frech (Frech, 1911, p. 106, pl. 16, fig. 1) and *T. noetlingi subglobosa* Reed (Reed, 1931, p. 51, pl. 7, fig. 5) from the Salt Range and *T. orientale* (Kayser) from South China (Kayser, 1883, p. 163, pl. 14, fig. 2). The Kurosawa species, however, has a larger umbilicus than the Salt Range and Chinese species. Moreover, the carinated ventral shoulders, though the keels are very fine, are unique in the present species and distinguishes it from all

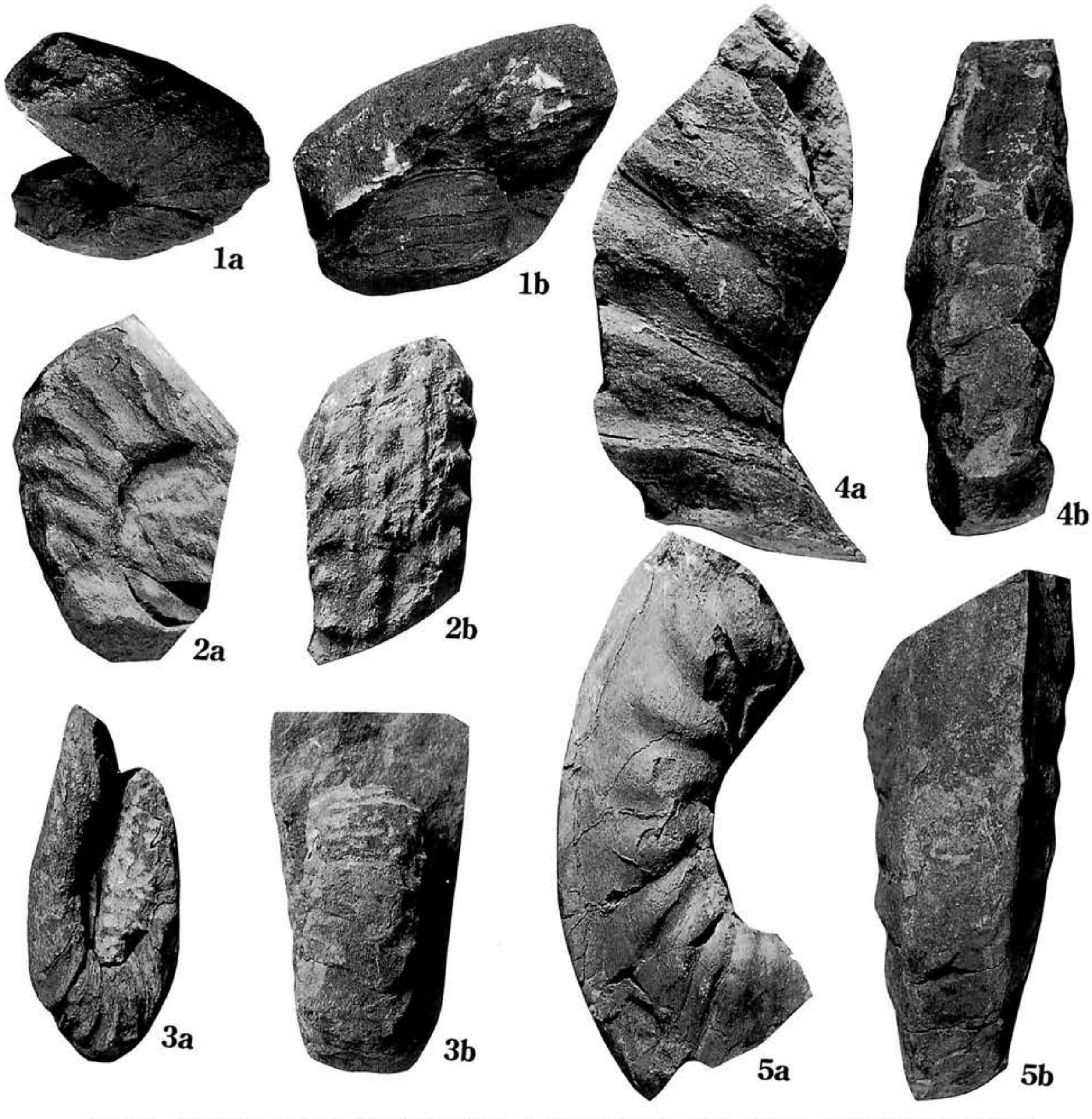


Figure 3. Nautiloids from the Ochiai Formation. **1.** *Stearoceras* sp., IGPS coll. cat. no. 103118, lateral (a) and ventral (b) views, ×0.9. **2.** *Tainoceras carinatum* sp. nov., IGPS coll. cat. no. 103114 (Holotype), lateral (a) and ventral (b) views, ×1.1. **3.** *Tainoceras* sp., IGPS coll. cat. no. 103115, lateral (a) and ventral (b) views, ×1. **4, 5.** *Pleuronautilus* sp., 4 : IGPS coll. cat. no. 103117, lateral (a) and ventral (b) views, ×0.65, 5 : IGPS coll. cat. no. 103116, lateral (a) and ventral (b) views, ×0.75.

other species of the genus *Tainoceras.*

Etymology.—From the carinated form of the ventrolateral shoulders.

Tainoceras sp.

Figures 2-a; 3-3a, b

Material.—A deformed specimen, IGPS coll. cat. no. 103115, collected from Loc. C-2 by M. Ehiro.

Description.—The conch is flattened dorsoventrally due to tectonic deformation. It is moderately evolute and may be thickly discoidal in outline. The whorl section is subrectangular with broadly rounded sides which converge toward the convex venter. The flanks bear radial ribs extending from the umbilical to ventral shoulder. There is a pair of rows of nodes on the venter, though not so visible owing to tectonic flattening.

The suture is simple and nearly straight, but with a shallow and wide lateral lobe.

Subfamily Pleuronautilinae Hyatt, 1890
Genus ***Pleuronautilus*** Mojsisovics, 1882

Type species.—*Pleuronautilus trinodosus* Mojsisovics, 1882

Pleuronautilus sp.

Figures 2-b; 3-4, 5

Materials.—Two fragmental specimens, IGPS coll. cat. no. 103116, collected at Loc. B-1 by M. Ehiro, and IGPS coll. cat. no. 103117, at Loc. B-2 by H. Araki.

Descriptive remarks.—The conch attains more than 100 mm in diameter. It is evolute and considered to be thickly discoidal in outline with a large and deep umbilicus. The umbilical wall is steep and umbilical shoulder is acutely rounded. The flat to slightly convex sides converge toward the venter. The wide venter is flat and the ventral shoulder is edged. The cross section of the conch is subtrapezoidal. The flanks are ornamented with broad and strong radial ribs. They extend from the umbilical wall to the outer third of the flank or to the ventral shoulder, and are widest and highest just above the umbilical shoulder. The suture consists of a very shallow ventral lobe, a small ventrolateral saddle and a wide and shallow lateral lobe.

Broad and strong ribs on the flanks are unique in the present species, but the material is too incomplete to represent any type of taxa.

Superfamily Trigonocerataceae Hyatt, 1884
Family Grypoceratidae Hyatt in Tittel, 1900
Genus ***Stearoceras*** Hyatt, 1893

Type species.—*Endolobus gibbosus* Hyatt, 1891

Stearoceras sp.

Figures 2-c; 3-1a, b

Material.—One specimen, IGPS coll. cat. no. 103118, collected from Loc. B-3 by M. Ehiro.

Description.—The specimen is involute in outline, with an almost closed umbilicus. It attains a diameter of more than 50 mm. The side of it is broadly rounded and the venter is slightly convex with rounded ventral shoulders. The cross section of the whorl is subtrapezoidal and depressed dorsoventrally in outline, but its depressed form is partly due to tectonic flattening. The surface of the conch is smooth. The suture lines are simple, forming a broad and shallow ventral lobe, a low ventrolateral saddle and a broad and shallow lateral lobe. The dorsal lobe is somewhat deep

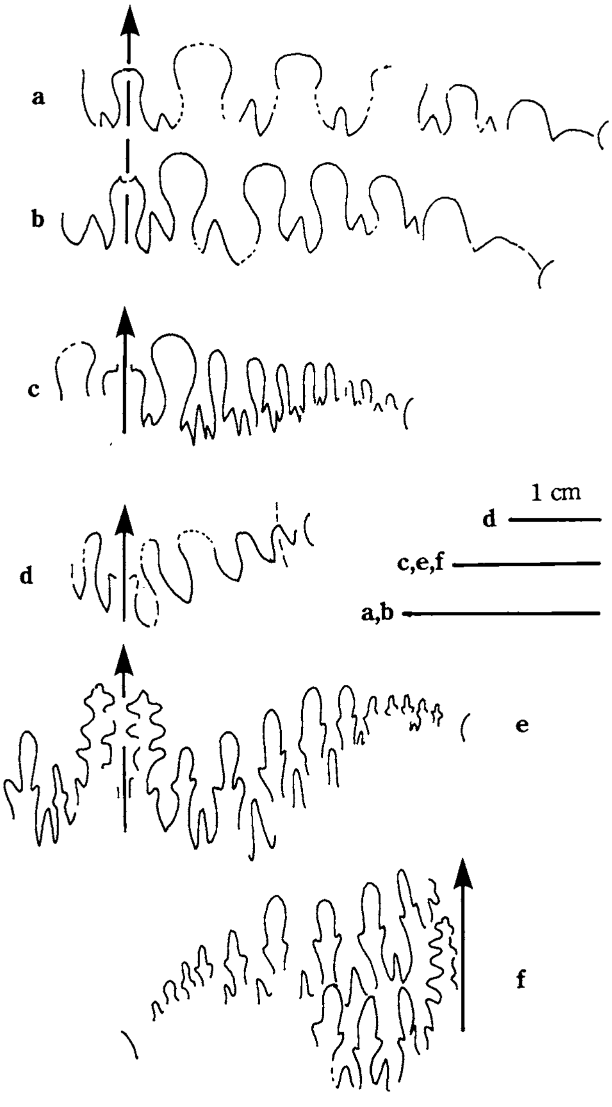


Figure 4. Suture lines of *Jilingites, Stacheoceras, Pseudagathiceras* and *Eumedlicottia* from the Ochiai Formation. **a, b.** *Jilingites kesennumensis* sp. nov., a: IGPS coll. cat. no. 103119 (Holotype), b: IGPS coll. cat. no. 103121. **c.** *Stacheoceras* sp., IGPS coll. cat. no. 103123. **d.** *Pseudagathiceras ornatum* sp. nov., IGPS coll. cat. no. 103136. **e, f.** *Eumedlicottia primas* (Waagen), e: IGPS coll. cat. no. 103142, f: IGPS coll. cat. no. 103143.

compared with the others.

Subclass Ammonoidea Agassiz, 1847
Order Goniatitida Hyatt, 1884
Suborder Goniatitina Hyatt, 1884
Superfamily Marathonitaceae Ruzhentsev, 1938
Family Marathonitidae Ruzhentsev, 1938
Subfamily Jilingitinae Liang, 1982
Genus ***Jilingites*** Liang, 1982

Type species.—*Jilingites bidentus* Liang, 1982

Jilingites kesennumensis sp. nov.

Figures 4-a, b; 5-1, 4, 5

Materials.—Holotype: IGPS coll. cat. no. 103119, collected from Loc. B-1 by Y. Takaizumi. Paratypes: IGPS coll. cat. no. 103120, by Y. Takaizumi and IGPS coll. cat. no. 103121, by M. Ehiro, both from Loc. B-1, and IGPS coll. cat. no. 102122, from Loc. B-2 by H. Araki.

Diagnosis.—*Jilingites* with a small but deep umbilicus. The surface of the living chamber is ornamented by fine radial growth lines.

Description.—The shell is involute and thickly lenticular in outline. It is moderately large and attains a diameter of 54 mm. The umbilicus with a steep umbilical wall is small but deep. The sides of the conch are broadly convex and converge towards the venter. The venter is broadly rounded, but acutely rounded on the adoral part of the body whorl. The whorl cross section is subtriangular, with rounded umbilical and ventral shoulders. The surface of the phragmocone may be smooth, but on the living chamber of the holotype there are faint sigmoidal growth lines.

The suture consists of a broad bifid ventral lobe, four bifid lateral lobes and a pointed small umbilical lobe on the umbilical shoulder. All saddles are rounded.

Comparison.—The Kitakami species of *Jilingites* closely resembles *J. bidentus* Liang (Liang, 1982, p. 651, text-figs. 6a-b, pl. 1, figs. 10-13) reported from the Wordian Fanjiatun Formation of Jilin, North China in the shape of the conch and suture. The former, however, differs from the latter in having a deeper umbilicus and ornamented living chamber.

Etymology.—The specific name is derived from Kesen-

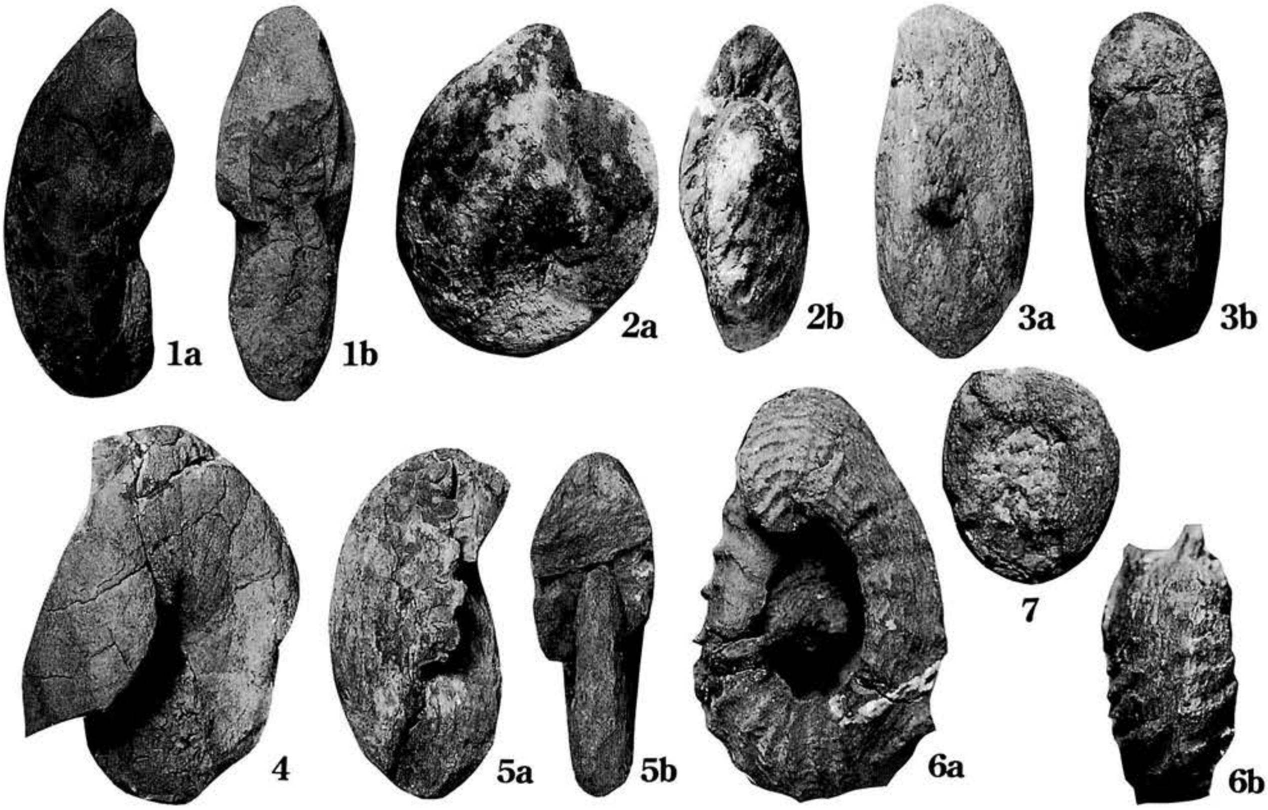


Figure 5. *Jilingites, Stacheoceras* and *Pseudagathiceras* from the Ochiai Formation. All figures approximately natural size unless otherwise stated. **1, 4, 5.** *Jilingites kesennumensis* sp. nov., 1: IGPS coll. cat. no. 103122, lateral view (a) and cross section (b), 4: IGPS coll. cat. no. 103119 (Holotype), lateral view, 5: IGPS coll. cat. no. 103120, lateral (a) and ventral (b) views. **2, 3.** *Stacheoceras* sp., 2: IGPS coll. cat. no. 103124, lateral (a) and ventral (b) views, 3: IGPS coll. cat. no. 103123, lateral (a) and ventral (b) views. **6, 7.** *Pseudagathiceras ornatum* sp. nov., 6: IGPS coll. cat. no. 103135 (Holotype), lateral (a) and ventral (b) views, ×1.6, 7: IGPS coll. cat. no. 103136, lateral view, ×1.5.

numa City, where it was collected.

Superfamily Cyclolobaceae Zittel, 1895
Family Vidrioceratidae Plummer and Scott, 1937
Genus **Stacheoceras** Gemmellaro, 1887

Type species.—*Stacheoceras mediterraneum* Gemmellaro, 1887

Stacheoceras sp.

Figures 4-c ; 5-2, 3

Materials.—IGPS coll. cat. nos. 103123 and 103124, from Loc. B-2 collected by H. Araki.

Description.—The conch is involute, subglobular to sublenticular in outline, with a closed umbilicus. One specimen (no. 103124) is tectonically flattened laterally. The phragmocone attains a diameter of 42 mm. The sides are convex and the venter is broadly rounded with rounded ventral shoulders. The shell surface may be smooth. The suture consists of a large bifid ventral lobe and many lateral lobes. The first lateral lobe is primarily bifid and each of its prongs is also bifid. The other lateral lobes are trifid.

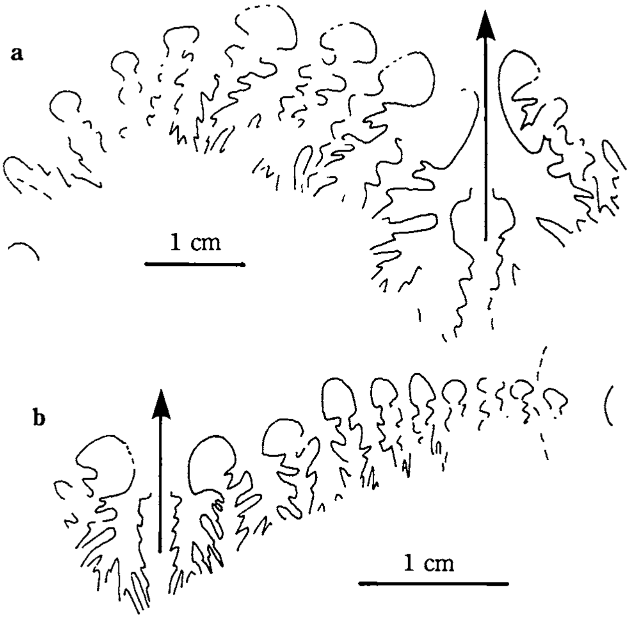


Figure 6. Suture lines of *Timorites takaizumii* sp. nov. from the Ochiai Formation. **a.** IGPS coll. cat. no. 103125 (Holotype), **b.** IGPS coll. cat. no. 103132.

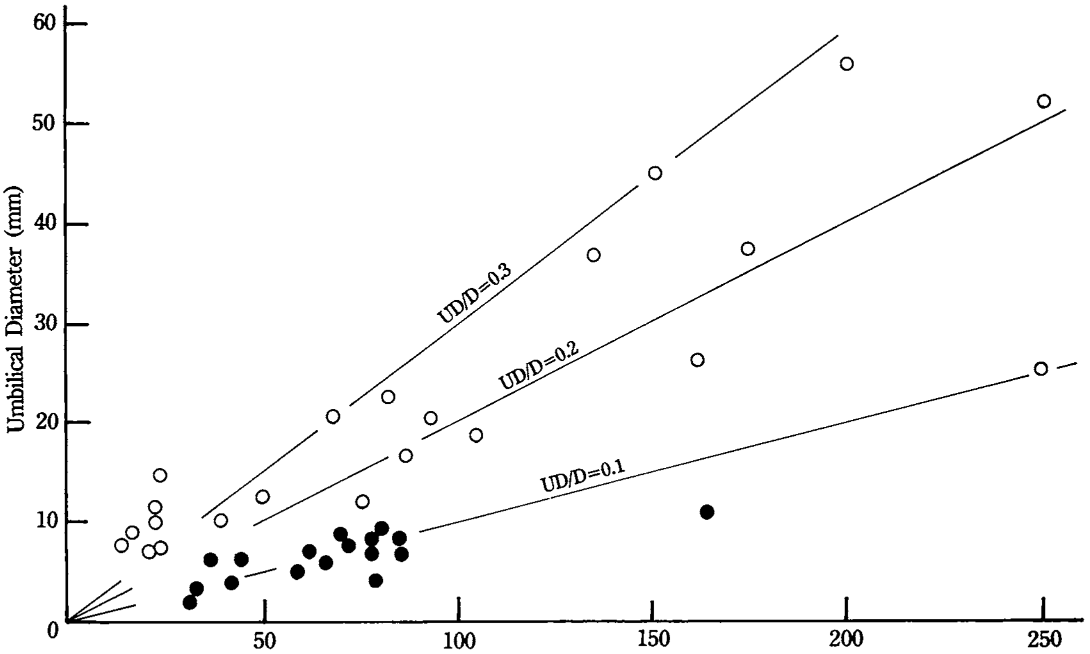


Figure 7. Umbilical diameter/shell diameter ratios of Timorites. Filled circles are *Timorites takaizumii* sp. nov. Open circles other known species of *Timorites* : *T. curvicostatus* Haniel (Haniel, 1915), *T. gemmellaroi* (Haniel) (Haniel, 1915), *T. giganteus* Sheng (Sheng, 1988), *T. intermedium* (Wanner) (Wanner, 1932 ; Ehiro *et al*., 1986), *T. markevichi* Zakharov (Zakharov in Kotlyar *et al*., 1989), *T. schucherti* Miller and Furnish (Miller and Furnish, 1940), *T. sigillarius* Ruzhentsev (Ruzhentsev, 1976), *T. sinensis* Sheng (Sheng, 1984), *T. striatus* Haniel (Haniel, 1915), *T. yunnanensis* Liang (Liang, 1983), *T. uddeni* Miller and Furnish (Miller and Furnish, 1940).

Family Cyclolobidae Zittel, 1895
Genus **Timorites** Haniel, 1915

Type species.—*Timorites curvicostatus* Haniel, 1915

Timorites takaizumii sp. nov.

Figures 6-a, b; 8-1—5

Materials.—Holotype: IGPS coll. cat. no. 103125, collected from Loc. B-1 by M. Ehiro. Paratypes: IGPS coll. cat. no. 103126-103132, collected by M. Ehiro, IGPS coll. cat. nos. 103133 and 103134, collected by Y. Takaizumi, all from Loc. B-1.

Diagnosis.—*Timorites* with an almost smooth shell surface and a very small umbilicus.

Description.—The holotype is fairly large, estimated to be more than 250 mm in diameter. Paratypes are moderately large, usually measuring 70 to 85 mm in diameter. The conch is involute and subglobular in outline. It is compressed laterally, but the ratios of width to height of conch vary from 0.3 to 1.0 due to tectonic deformation. Because the outer whorl embraces completely inner whorls in the adult stage, the ratios of umbilical diameter to shell diameter become smaller with increasing height. They are nearly equal or less than 0.1 in mature specimens as shown in Figure 7. The umbilical wall is almost perpendicular and the umbilical shoulder is acutely rounded. The convex sides grade round into a rounded venter. The shell surface is ornamented with fine, weakly sigmoidal growth lines in a few specimens, but smooth in many specimens. The living chamber is about a volution in length.

The sutures are not so well preserved, but are characteristic of *Timorites* as shown in Figure 6.

Comparison.—The Kurosawa species of *Timorites* is easily distinguished from the other species by having a very small umbilicus and nearly smooth shell surface, except for slight growth lines. The umbilical diameter of the present species is about 10 percent of the shell diameter or smaller, while those of the others are larger than 15 percent at a diameter smaller than 200 mm (Figure 7).

Etymology.—The specific name is given in honor of Mr. Yukihiro Takaizumi, who collected many cephalopod fossils from Kurosawa.

Superfamily Adrianitaceae Schindewolf, 1931
Family Adrianitidae Schindewolf, 1931
Genus **Pseudagathiceras** Schindewolf, 1931

Type species.—*Agathiceras* (*Doryceras* ?) *wichmanni* Haniel, 1915

Remarks.—*Pseudagathiceras* was established by Schindewolf (1931) based on *Agathiceras* (*Doryceras* ?) *wichmanni* Haniel described from the Basleo beds of Timor and was regarded as valid by Miller (1944) and Ruzhentsev (1962). On the other hand, Miller *et al.* (1957) considered that *Pseudagathiceras* is congeneric with *Doryceras* established by Gemmellaro (1887). The present authors agree with Miller (1944) and Ruzhentsev (1962), and treat *Pseudagathiceras* as a distinct genus, because the species referable to the genus *Pseudagathiceras* have a considerably larger umbilicus and one or two more external lobes than do the species of *Doryceras*. The Coahuila species *P. difuntense* Miller and *P. spinosum* Miller have two rows of prominent spines on the ventrolateral shoulder at full maturity.

Pseudagathiceras ornatum sp. nov.

Figures 4-d; 5-6, 7

Materials.—Two specimens, both from Loc. B-1: IGPS coll. cat. no. 103135 (holotype), collected by Y. Takaizumi, and IGPS coll. cat. no. 103136, collected by M. Ehiro.

Diagnosis.—A large *Pseudagathiceras* with prominent lateral ribs, ventral spines and a wide umbilicus.

Description.—The conch is subdiscoidal, moderately evolute and widely umbilicate. Holotype is moderately large in size, attaining a diameter of 35 mm in the deformed state, and at the adoral end its umbilical diameter is 15 mm. The venter is broadly rounded and the sides, which converge toward the venter, are also rounded. The whorl is depressed in outline. The surface of the conch is marked by rather prominent longitudinal lirae, and at maturity it is ornamented by radial ribs and two rows of ventrolateral nodes or spines, but the nodes or spines are not so visible on the apertural half of the last whorl. The small paratype has longitudinal lirae and transverse constrictions. The suture is poorly preserved on the paratype, consisting there of some rounded lateral saddles and pointed lateral lobes.

Comparison.—In having prominent lateral ribs and two rows of ventrolateral spines, the present species resembles the Coahuila species, *Pseudagathiceras difuntense* Miller (Miller, 1944, p. 101, plate 29, figs. 6-12) and *P. spinosum* Miller (Miller, 1944, p. 103, plate 29, figs. 1-5). The former is, however, considerably larger than the latter two. It is also distinguished in having more prominent lateral ribs and a larger umbilicus.

Etymology.—The specific name is derived from its remarkable shell ornamentation.

Figure 8. *Timorites takaizumii* sp. nov. from the Ochiai Formation. **1.** Holotype, IGPS coll. cat. no. 103125, lateral (a) and ventral (b) views of phragmocone, ×0.68, ventral view (c) of phragmocone, ×0.47, cross section (d) of living chamber, ×0.42, and lateral view (e) of living chamber, ×0.33. **2.** IGPS coll. cat. no. 103126, lateral (a) and ventral (b) views, ×0.9. **3.** IGPS coll. cat. no. 103133, lateral (a) and ventral (b) views, ×0.78. **4.** IGPS coll. cat. no. 103132, lateral view, ×0.9. **5.** IGPS coll. cat. no. 103130, lateral view, ×1.1.

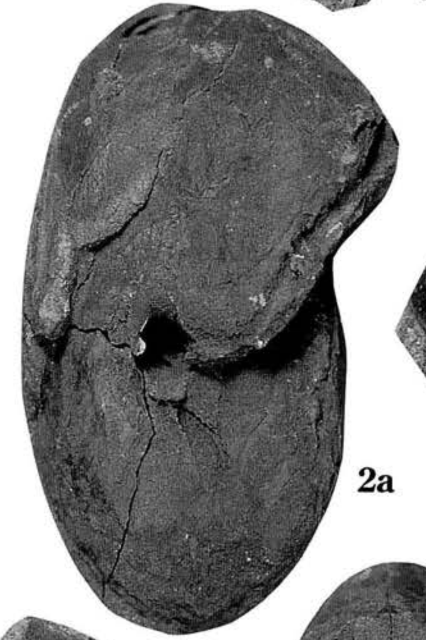
1a

1b

1c

1d

1e



2a

3a

4

5

2b

3b

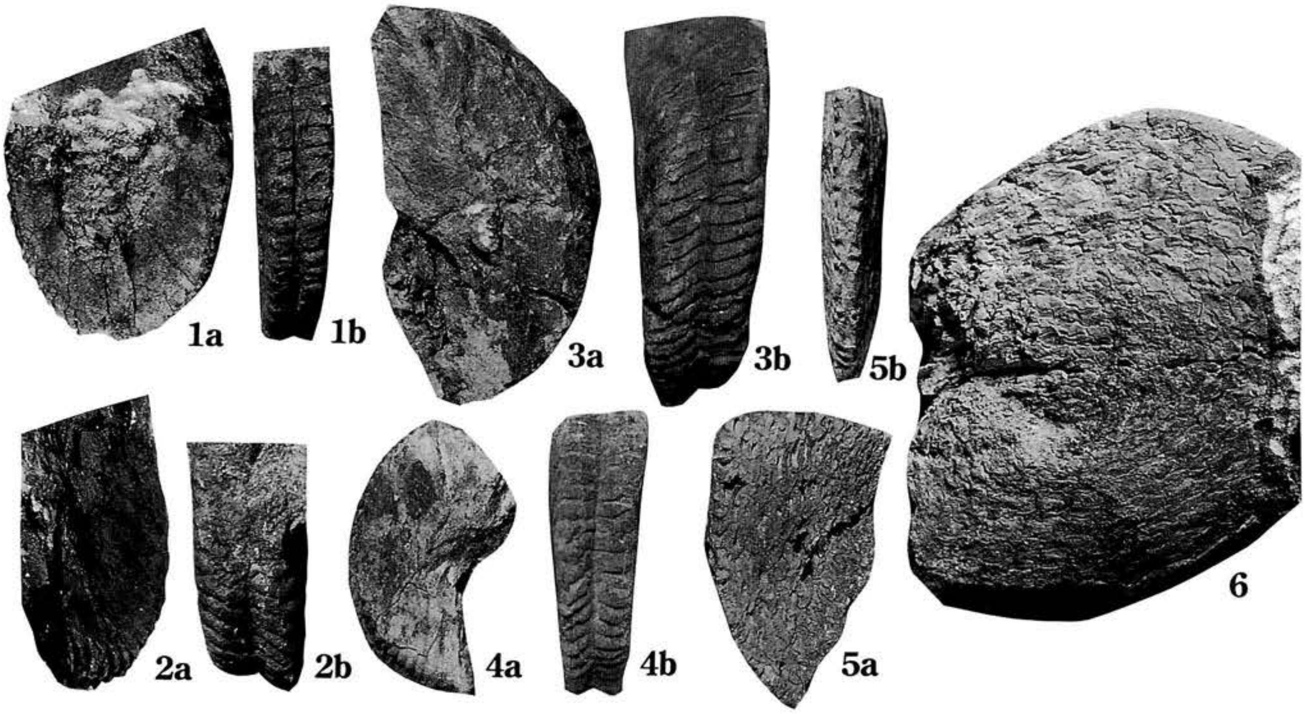


Figure 9. *Propinacoceras* and *Eumedlicottia* from the Ochiai Formation. All figures approximately natural size. **1-4.** *Propinacoceras* sp., 1 : IGPS coll. cat. no. 103141, lateral (a) and ventral (b) views, 2 : IGPS coll. cat. no. 103138, lateral (a) and ventral (b) views, 3 : IGPS coll. cat. no. 103137, lateral (a) and ventral (b) views, 4 : IGPS coll. cat. no. 103139, lateral (a) and ventral (b) views. **5, 6.** *Eumedlicottia primas* (Waagen), 5 : IGPS coll. cat. no. 103142, lateral (a) and ventral (b) views, 6 : IGPS coll. cat. no. 103143, lateral view.

Order Prolecanitida Miller and Furnish, 1954
Superfamily Medlicottiaceae Karpinsky, 1889
Family Medlicottidae Karpinsky, 1889
Genus ***Propinacoceras*** Gemmellaro, 1887

Type species.—Propinacoceras beyrichi Gemmellaro, 1887

Propinacoceras sp.

Figures 9-1—4

Materials.—IGPS coll. cat. no. 103137-103140, collected from Loc. B-1 by M. Ehiro, and IGPS coll. cat. no. 103141, from Loc. B-2 collected by H. Araki.

Description.—The conch is involute and thinly discoidal in outline, with a very small umbilicus. The sides are flat and almost parallel, but slightly converge toward the umbilicus. The venter is also flat, but bears two rows of prominent nodes or short ribs, which are separated by a median groove. The umbilical and ventral shoulders are acutely rounded. The suture is only poorly preserved in some specimens and its details cannot be observed.

Genus ***Eumedlicottia*** Spath, 1934

Type species.—Medlicottia bifrons Gemmellaro, 1887

Eumedlicottia primas (Waagen)

Figures 4-e, f ; 9-5, 6

Sageceras primas Waagen, 1879, p. 39, pl. 2, figs. 7a-c
Medlicottia primas Waagen. Noetling, 1904, p. 355, pl. 17, figs. 1-1b, pl. 19, fig. 1.

Materials.—Two specimens, IGPS coll. cat. no. 103142, collected from Loc. A-2 by M. Ehiro, and IGPS coll. cat. no. 103143, from Loc. B-2 by H. Araki.

Descriptive remarks.—The conch is involute and thinly discoidal to sublenticular in outline, with a closed umbilicus. The phragmocone attains a diameter of at least 65 mm. The flanks are slightly convex and converge toward the venter. The venter is narrow and grooved, with keeled ventrolateral shoulders. The shell surface is smooth.

The suture forms a deep and narrow ventral lobe, a high and narrow ventrolateral saddle, and many lateral and auxiliary saddles and lobes. There are many secondary lobes in the ventrolateral saddle. Ten to eleven saddles, which have notches at midheight on each wing, and subdivided lobes are on the flanks.

In having a smooth shell surface and complex sutures, especially many notched saddles, the present specimens are identified with *Eumedlicottia primas* (Waagen).

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Paleontological Research, vol. 1, no. 1, pp. 67-75, 6 Figs., April 30, 1997

6. A new species of the extinct shrew *Paenelimnoecus* from the Pliocene of Yinan, Shandong Province, northern China

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Abstract. A new species of a small allosoricine shrew from Late Pliocene cave deposits in Yinan County is described under the name *Paenelimnoecus chinensis*, and its systematic position is discussed. Detailed description of the species reveals morphological characters that distinguish it from the known species of *Paenelimnoecus*. Comparisons with the known species indicate close relationships between this new species and *P. pannonicus* from the Pliocene of Europe. Owing to lack of reliable Pliocene records in the literature, *P. chinensis* first demonstrates the Pliocene distribution of *Paenelimnoecus* in East Asia, although this genus was very recently described from the Late Miocene of Inner Mongolia. It is inferred that *Paenelimnoecus* was widely distributed from Europe to north China across the northern part of Eurasia in the Late Pliocene.

Key words : New species, north China, *Paenelimnoecus*, Pliocene, shrew

Introduction

Paenelimnoecus is a small allosoricine shrew, which is known mainly from the Miocene and Pliocene of Europe. The taxonomy of the genus was greatly confused until the revision by Reumer (1984). He concluded that the generic names *Petenyiella*, *Suncus*, *Pachyura* and *Allopachyura* previously used for this shrew were untenable, and that the generic name *Paenelimnoecus* was appropriate for the shrew.

In China, Cai (1987) referred a small soricid mandible from the lower part of the Nihewan beds to *Paenelimnoecus* sp. This was the only record of the genus hitherto known in East Asia, but unfortunately, his unillustrated description is too simple to confirm the generic allocation of the mandible. Recently, Storch (1995) described a new species of *Paenelimnoecus* from the Late Miocene of Inner Mongolia, which indicates its distribution in East Asia during Late Miocene time.

Pliocene cave deposits recovered on the Qipanshan Hill near Xingtunzhi in Yinan County have yielded a great number of mammalian remains, which include two forms of shrew with striking difference in size. The larger form, *Lunanosorex lii*, was already described in our preceding paper (Jin and Kawamura, 1996b), while the smaller form is assignable to a new species of *Paenelimnoecus* and is described herein. The specimens of this species comprise a skull, a mandible, and maxillary and mandibular fragments, which were obtained from Layer 6 of the cave deposits. A geological account of the deposits is given in Jin and Kawamura (1996b).

Terminology and measuring method

Jin and Kawamura (1996a) provided the terminology and measuring method for a soricid skull, mandible and dentition, which are also used herein. Measurements were taken by using a measurescope (Nikon : MM-11) with an electric digital counter (Nikon : CM-65).

Systematic paleontology

Order Insectivora Bowdich, 1821
Family Soricidae Gray, 1821
Subfamily Allosoricinae Fejfar, 1966
Genus ***Paenelimnoecus*** Baudelot, 1972

Remarks.—We follow the conclusion of Reumer (1992), in which this genus is allocated to the subfamily Allosoricinae instead of to the Limnoecinae, Crocidurinae, Soricinae, or Crocidosoricinae.

Paenelimnoecus chinensis sp. nov.

Figures 1-6

Holotype.—Right mandible with first lower incisor, P_4, M_1 and M_2 (V10814, 1).

Paratype.—Fragmentary skull with left P^4, M^1 and M^2 (V10814, 2).

Referred specimens.—A left maxilla with P^4, M^1 and M^2 (V10815, 1); a right maxilla with P^4, M^1 and M^2 (V10816); a left maxillary fragment with P^4 (V10815, 3); a right mandibular fragment with M_2 (V10815, 2).

Repository.—All the specimens described are stored in the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing.

Geographic and geologic distribution.—Known only from the locality of Yinan; Late Pliocene.

Name derivation.—*chinensis*, denoting its occurrence in China.

Diagnosis.—A *Paenelimnoecus* species with four alveolar pits for upper antemolars between first upper incisor and P^4; teeth pigmented red to orange; infraorbital foramen ranging from the position above paracone of P^4 to that above mesostyle of M^1; lacrimal foramen opening above post-ectoflexus of M^1; alveolus of first lower incisor ending below protoconid of M_1; mental foramen positioned below hypoflexid of M_1; upper facet triangular; interarticular area very short and narrow; lower facet rectangular with no emargination on its lower margin, and its lingual protrusion weaker than in *P. micromorphus, P. crouzeli* and *P. repenningi*; lower sigmoid notch narrow dorsoventrally in lateral view; first lower incisor with very weak serration on its cutting edge, and without buccal cingulum; M_1 and M_2 completely lacking entoconid and entoconid crest; overlap of M_2 on M_1 weak relative to *P. pannonicus*.

Description.—

Skull: In lateral view, the rostrum extends almost straight forward (Figure 1B) in contrast to *Sorex* where it is strongly bent anteroventrally. The lateral wall of the rostrum is weakly depressed above the alveoli of the antemolars. The infraorbital foramen is a large oval depression ranging from the position above the paracone of P^4 to that above the mesostyle of M^1 (Figure 2A). Two small foramina open in the depression near its anterior margin. The posteroventral corner of the depression is almost right-angled. A slender vertical bar separates the lacrimal foramen from the depression. The foramen has a round outline, and is placed above the post-ectoflexus of M^1. The anterior margin of the orbit is almost vertical and situated above the pre-ectoflexus of M^2. The rostral part of the bony palate is broader and

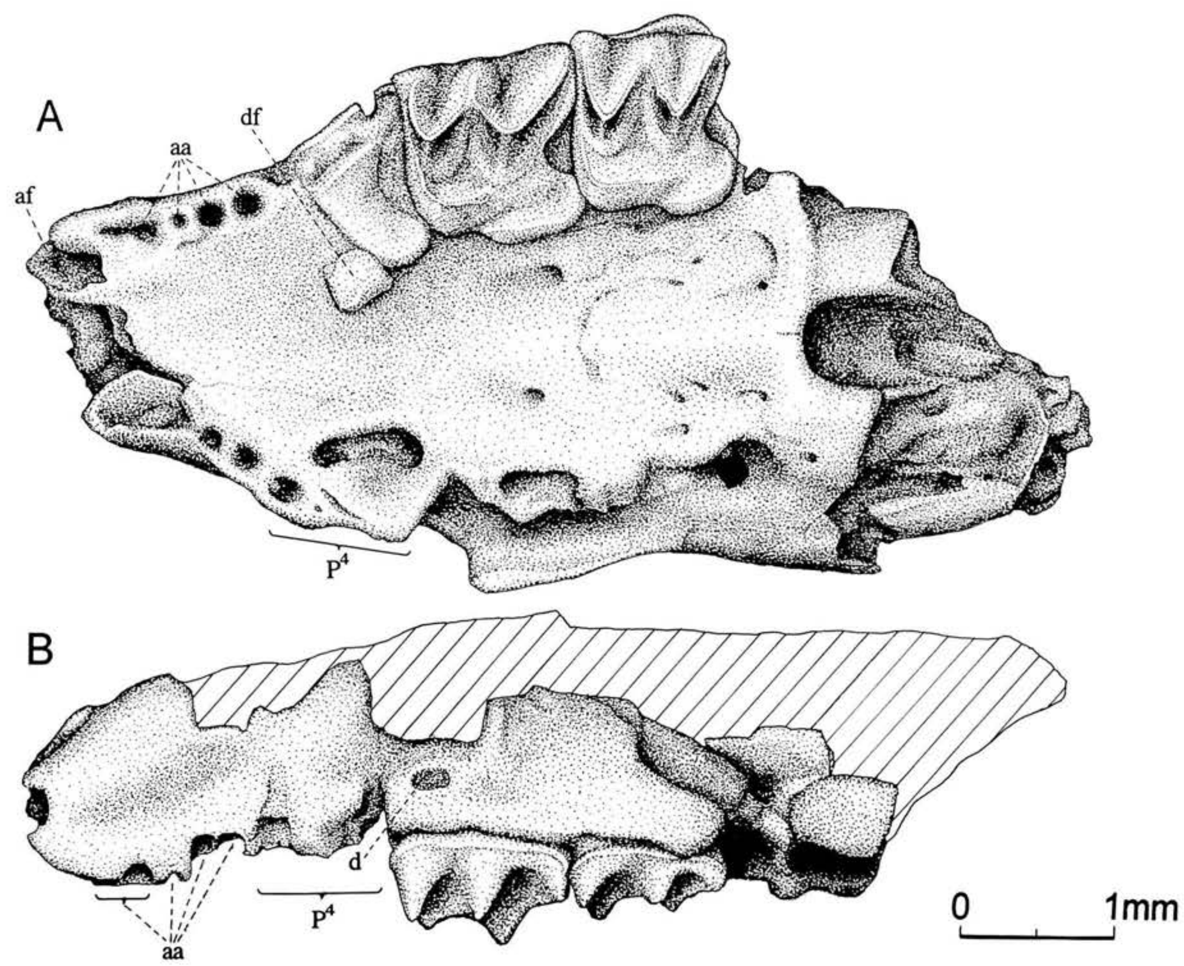

Figure 1. *Paenelimnoecus chinensis* sp. nov. Fragmentary skull with left P^4, M^1 and M^2 (paratype; V10814, 2). **A**: palatal view, **B**: left lateral view. **aa**: alveolar pits for antemolars, **af**: alveolar pit for first upper incisor, **d**: depression probably formed by the damage of the maxillary wall, **df**: displaced fragment of P^4, $\mathbf{P^4}$: alveolus of P^4.

shorter than that of *Sorex* (Figure 1A). Four alveolar pits for antemolars are present between the first upper incisor and P⁴. The most anterior alveolus has a gourd-shaped outline larger posteriorly, and with a marked central constriction. It is considered to be the alveolus of A¹ and A², in accordance with Rzebik-Kowalska's interpretation (1990). The second discrete alveolus is round, and is much smaller than the preceding one. The third and fourth are of nearly the same size, and have round outlines. They are much larger than the second. Of the alveoli of P⁴, the anterior and lingual ones are observable on the right side of the bony palate of V10814, 2 (Figure 1A). The former has a round outline, and is nearly the same size as the fourth antemolar alveolus. The lingual one is a large curved depression, elongated anteroposteriorly, with anterior and posterior ends being deep pits. The posterior palatal foramina open lingually to the position between the hypocone and the posterior margin of M¹. The bony palate is elevated along its posterior margin to form a low transverse ridge. The mesopterygoid fossa is observed behind this ridge. The anterior margin of the fossa is arcuate.

P⁴: The occlusal outline is a rounded trapezoid with its posterior margin markedly emarginated. The parastyle is a low, small conical cusp placed at the anterobuccal corner of the crown, where it forms a distinct protrusion of the anterior margin of the crown. The paracone, the highest cusp in the crown, is separated from the parastyle by a distinct notch. A high sharp ridge extending from the paracone to the posterobuccal corner of the crown is obtusely V-shaped in occlusal view. This ridge and the paracone is stained red to orange, whereas other parts of the crown are not pigmented. The protocone is a small conical cusp on the middle of the anterior margin of the crown. It is lower and smaller than the parastyle. A ridge connecting the protocone to the parastyle is slender and distinct in V10815, 3 (Figure 3A), while it is broad and indistinct in V10816 and V10815, 1 (Figures 2B and 3B). A low blunt ridge, into which the hypocone is merged, runs along the lingual margin of the crown. The anterior tip of the ridge is separated from the protocone by a broad shallow valley. In the valley, a supplementary low cusplet is observed in V10815, 1 (Figure 3B), but it is absent in V10815, 3 and V10816. On the buccal face of the crown, there is a weak cingulum in V10815, 1 and V10815, 3, whereas no cingulum is present in V10816.

M¹ and M²: The occlusal outline is roughly a broad oblong with its posterior margin strongly emarginated. The ectoloph is stained red to orange, while the remaining part of the crown is unpigmented. The paracone is situated near the anterior margin of the crown. This cusp is much lower and smaller than the metacone in M¹, while the differences between them are slighter in M². The mesostyle is rather conical and not completely merged into the ectoloph. At a position somewhat lingual to the apex of the mesostyle, the ridge extending from the paracone meets that from the metacone. A slender flange extends from the posterior base of the metacone to that of the metastyle along the posterior margin of the crown. The pre-ectoflexus is much smaller than the post-ectoflexus in M¹, while the two are

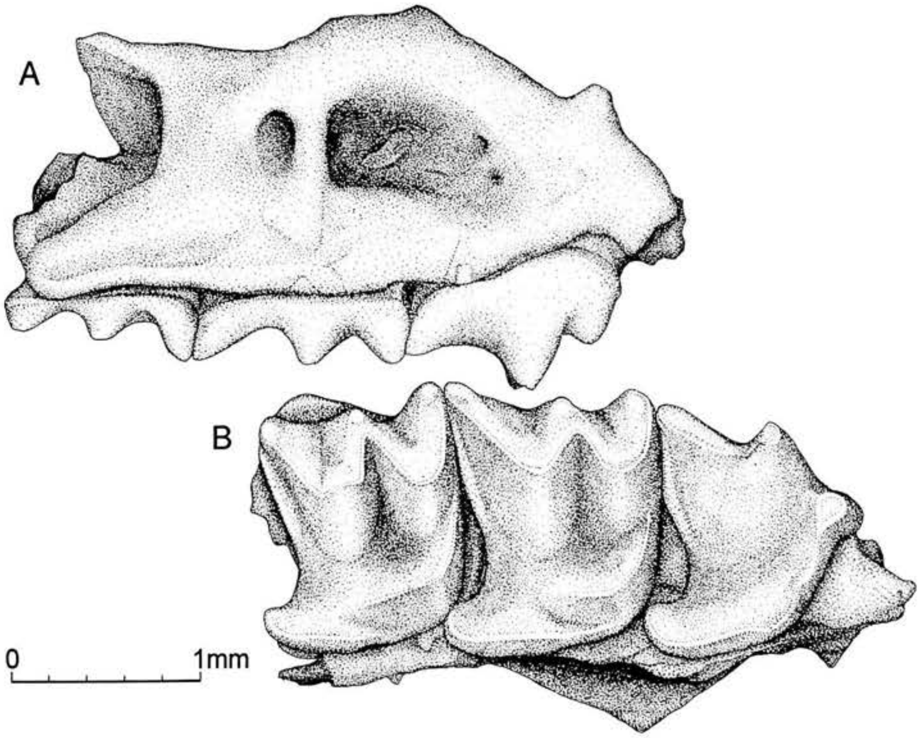

Figure 2. *Paenelimnoecus chinensis* sp. nov. Right maxilla with P⁴, M¹ and M² (V10816). **A**: right lateral view, **B**: palatal view.

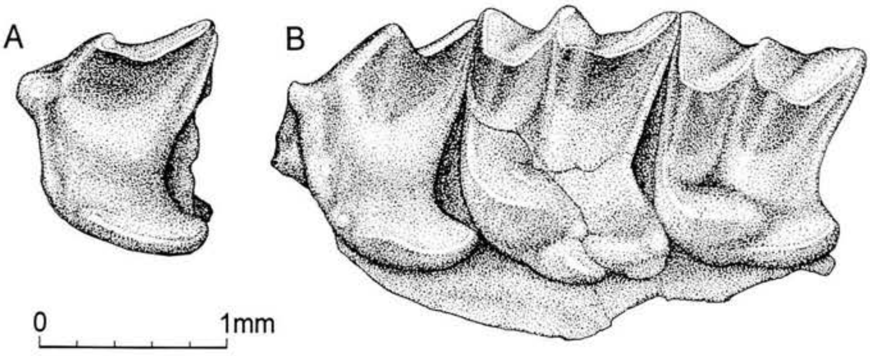

Figure 3. *Paenelimnoecus chinensis* sp. nov. **A**: left maxillary fragment with P^4 in palatal view (V10815, 3), **B**: left maxilla with P^4, M^1 and M^2 in palatal view (V10815, 1).

nearly the same size in M^2. On the buccal face of the crown, no cingulum is present in V10815, 1 and V10816, but there is a weak cingulum in V10814, 2 (Figure 1B). The protocone, situated near the anterior margin of the crown, is much lower than the ectoloph. From the protocone, a distinct ridge extends buccally along the anterior margin of the crown, and another ridge extends straight posteriorly. The latter ridge is separated from the lingual base of the metacone, and thereby the trigon basin is continuous with the talon basin. The hypocone is indistinct and merged into

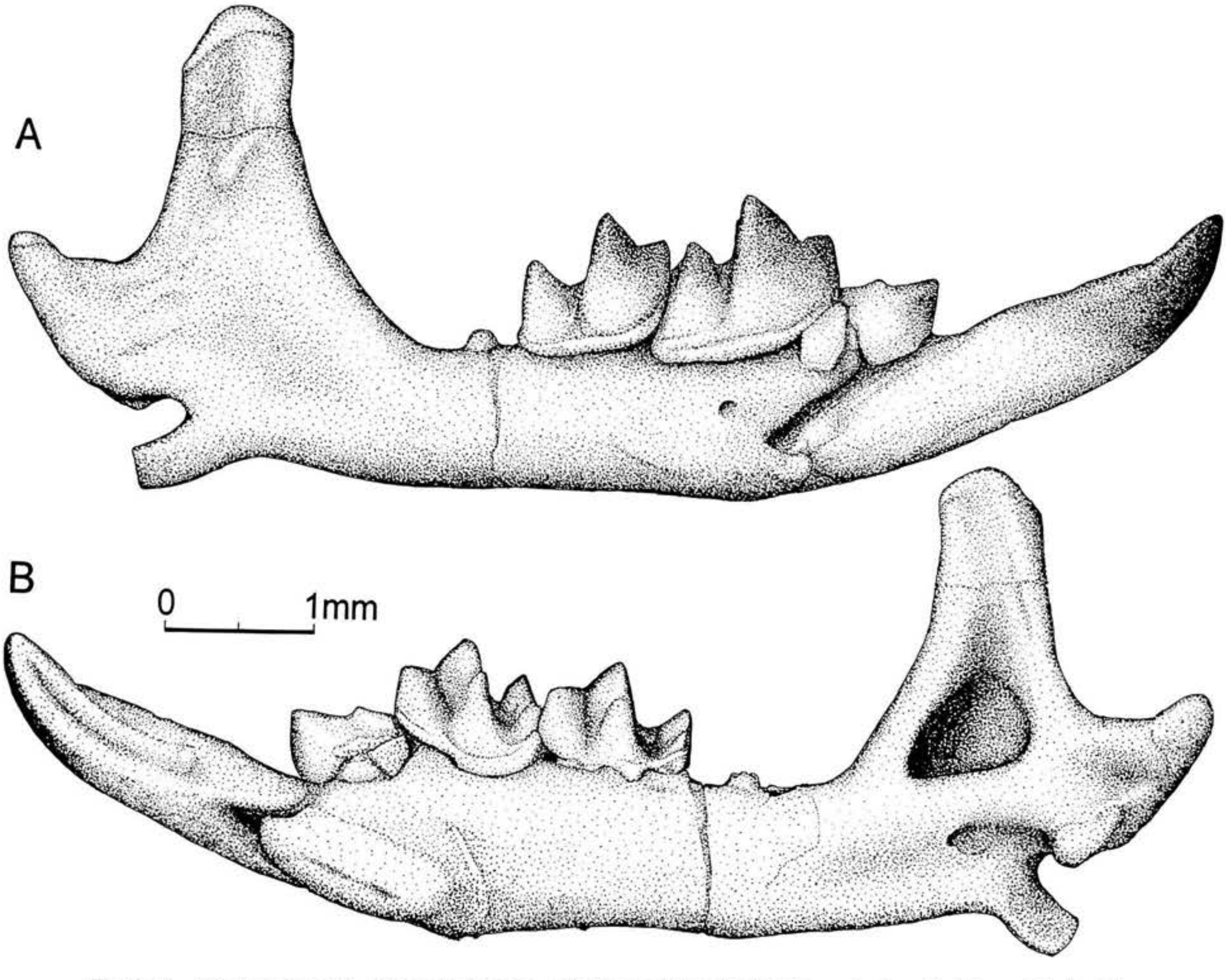

Figure 4. *Paenelimnoecus chinensis* sp. nov. Right mandible with first lower incisor, P_4, M_1 and M_2 (holotype: V10814, 1). **A**: buccal view, **B**: lingual view.

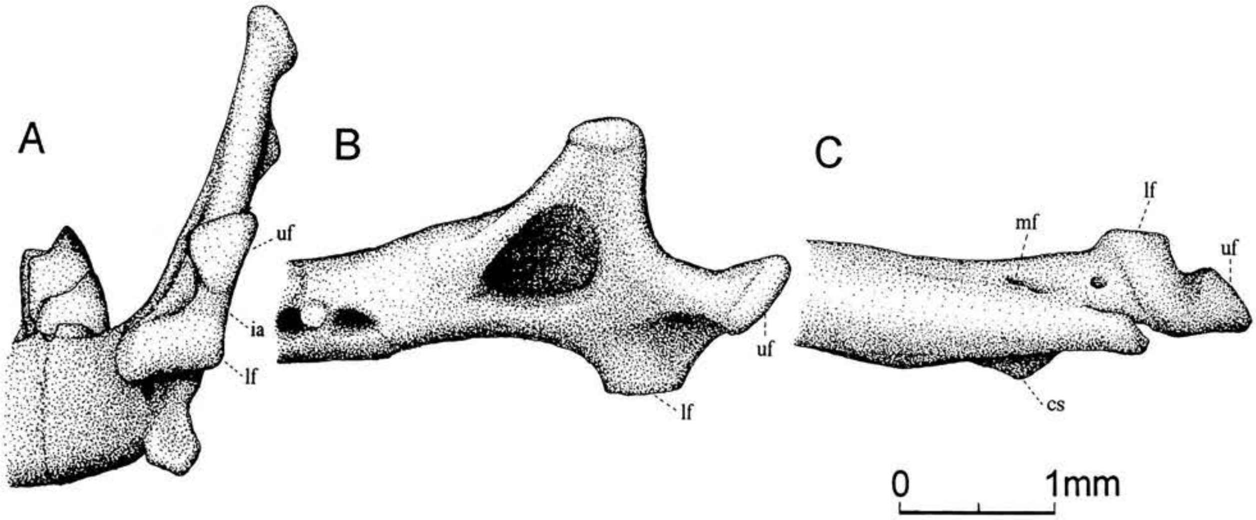

Figure 5. *Paenelimnoecus chinensis* sp. nov. Ascending ramus of the holotype (V10814, 1). **A** : posterior view, **B** : dorsal view, **C** : ventral view. **cs** : coronoid spicule, **ia** : interarticular area, **lf** : lower facet, **mf** : mandibular foramen, **uf** : upper facet.

a low ridge running along the posterior half of the lingual margin of the crown. This ridge is almost parallel to the above-mentioned posterior ridge of the protocone. These two ridges are separated by a shallow valley continuous with the talon basin.

Mandible : The horizontal ramus is slender and delicate, and has an almost straight lower margin in lateral view. It shows nearly the same height from front to rear in buccal view, whereas it attains its maximum height below M_1 in lingual view (Figure 4). The alveolus of the lower incisor ends below the protoconid of M_1. The mental foramen is small, and opens below the hypoflexid of M_1. The symphysis forms an elliptical swelling, with a central groove elongated anteroposteriorly, and terminates below the metaconid of M_1. The morphology of the ascending ramus is generally similar to that of *Sorex*. The deflection of the ascending ramus toward the buccal side is relatively slight (Figure 5A), to the same extent as in *Sorex*. The tip of the coronoid process is thickened to form a rounded surface with no depression. The coronoid spicule is well developed, and situated at midheight of the coronoid process. The external temporal fossa is clearly observed between the tip of the process and the spicule, but is indistinct below the spicule. The upper sigmoid notch is slightly emarginated ventrally in lateral view. There is no pterygoid spicule. The upper pterygoid fossa is broadly excavated on the dorsolingual face of the condyle, and forms a strong lingual emargination of the interarticular area. In posterior view, this area is very short, and much narrower than the upper facet (Figure 5A). The buccal margin of the area is straight. The upper facet is triangular in posterior and ventral views, and a narrow ellipse in dorsal view (Figures 5A-C). The lower facet is rectangular in posterior and ventral views, and protrudes lingually far beyond the lingual tip of the upper facet. Its lower margin is straight and not emarginated dorsally in posterior view

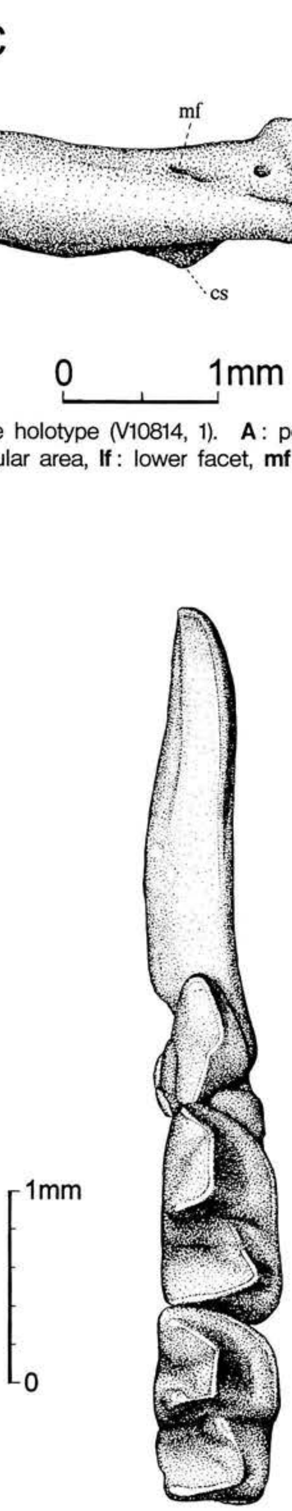

Figure 6. *Paenelimnoecus chinensis* sp. nov. Dentition of the holotype in occlusal view (V10814, 1).

(Figure 5A). In dorsal and ventral views, its lingual margin is rather straight and not pointed lingually (Figures 5B and 5C). The lower facet can be seen from the buccal side (Figure 4A). A small foramen is observed just anterior to the lower facet (Figure 5C). The lower sigmoid notch is deeply emarginated into the ascending ramus, and is narrow dorsoventrally in lateral view. The internal temporal fossa is very large and deep, and exhibits a rounded triangular shape. Its basal margin lies nearly on the same level as the upper margin of the horizontal ramus. The mandibular foramen is relatively small, and opens below and somewhat anterior to the middle of the basal margin of the internal temporal fossa. It extends anteriorly, and is not connected to the internal temporal fossa. The lingual face of the angular process is depressed to form the lower pterygoid fossa.

First lower incisor: The crown is relatively long and extends straight forward in dorsal view (Figure 6). Its anterior part is stained red to orange. The tip of the crown is somewhat upturned. In the specimen observed (holotype only), this tooth seems to be somewhat displaced anteriorly on the buccal face of the horizontal ramus. Judging from the posterior end of the alveolus of this tooth, the original position of the posterior margin of its crown is probably below the protoconid of M_1. The cutting edge undulates very weakly, possibly corresponding to the weakly "monocuspulate" or "bicuspulate" character states of Reumer (1984). No cingulum is observed along the posterior margin of the crown. There is a shallow broad groove on the lingual face of the crown.

P_4: Both lingual and buccal faces of the crown are damaged. The main cusp with orange pigmentation is situated at the anterior tip of the crown. From the cusp, a ridge extends posterobuccally and gradually descends to the middle of the crown, where it turns posterolingually and rises slightly to form another cusp without pigmentation. From this cusp, the ridge descends again in the same direction and extends to the posterior margin of the crown. The ridge therefore exhibits a broad V-shape in occlusal view (Figure 6), and is notched between the cusps in lateral view (Figure 4). A broad indistinct valley occurs on the lingual side of the ridge.

M_1 and M_2: The occlusal outline is trapezoidal. The buccal face of the ectolophid is stained orange. The paraconid at the anterior tip of the crown is remote from the protoconid, and the ridge between them is strongly notched. In occusal view, the posterior half of this ridge is parallel to the lingual margin of the crown (Figure 6). On the other hand, the metaconid is situated near the protoconid (especially in M_1), and the notch in the ridge between them is much weaker. The metaconid is more conical than other main cusps. The hypoflexid is deep (especially in M_2), and almost reaches the buccal cingulum. A ridge extending anterolingually from the hypoconid attaches to the posterior face of the protoconid, and steeply descends toward the

Table 1. Measurements of *Paenelimnoecus chinensis* sp. nov.

Element	Parameter	V10814, 2	V10815, 1	V10815, 3	V10816	V10814, 1	V10815, 2
P^4	BL	—	1.18	1.16	1.14	—	—
	LL	—	0.80	0.73	0.80	—	—
	PE	—	0.65	0.58	0.71	—	—
	W	—	1.14	1.19	1.27	—	—
M^1	BL	1.19	1.05	—	1.16	—	—
	LL	1.23	—	—	1.13	—	—
	PE	0.88	—	—	0.94	—	—
	AW	1.32	—	—	1.30	—	—
	PW	1.45	—	—	1.42	—	—
M^2	BL	1.06	1.02	—	1.05	—	—
	LL	1.17	1.04	—	1.12	—	—
	PE	0.87	0.84	—	0.89	—	—
	AW	1.31	1.25	—	1.31	—	—
	PW	1.26	1.23	—	1.26	—	—
Mandible	LMH	—	—	—	—	3.32	—
	HC	—	—	—	—	2.94	—
	LUF	—	—	—	—	0.61	—
First lower incisor	L	—	—	—	—	2.95	—
M_1	L	—	—	—	—	1.20	—
	TRW	—	—	—	—	0.60	—
	TAW	—	—	—	—	0.65	—
M_2	L	—	—	—	—	1.12	—
	TRW	—	—	—	—	0.70	—
	TAW	—	—	—	—	0.62	0.65

Abbreviations AW: anterior width, BL: buccal length, HC: height of the coronoid process, L: length, LL: lingual length, LMH: length from the mental foramen to the uppermost point of the lower margin of the ascending ramus, LUF: length of the upper facet, PE: length to the posterior emargination, PW: posterior width, TAW: talonid width, TRW: trigonid width, W: width. For detailed explanation see Jin and Kawamura (1996a).

protoconid. The hypoconulid (entostylid in Reumer, 1984) is a ridgelike cusp, which is lower than the hypoconid. The ridge between them is weakly notched. There is neither entoconid nor entoconid crest, so that the talonid basin opens broadly to the lingual side. The buccal cingulum is well developed and not undulated, while the lingual one is weak in M_1 and indistinct in M_2. In buccal view, the anterior part of M_2 overlaps the posterior end of M_1 (Figure 4A). In lingual view, the lower margin of the crown is arcuate ventrally, more extremely so in M_1 than in M_2 (Figure 4B).

Measurements.—The measurements of the teeth and mandible are given in Table 1. As regards M^1 and M^2, the PE index of Reumer (1984) is calculated in order to quantify the degree of the posterior emargination (PE index= $\{(LL+BL)/2PE\}-1$). Values for M^1 are 0.37 in V10814, 2 and 0.22 in V10816, while those for M^2 are 0.28 in V10814, 2 and 0.22 in V10815, 1 and V10816.

Systematic position.—The specimens described above have the following diagnostic characters: the upper facet triangular; the interarticular area very short; entoconid and entoconid crest completely absent; the ridge connecting the paraconid to the protoconid long, and its posterior half parallel to the longitudinal axis of the mandible; the metaconid placed near the protoconid. These coincide with the diagnostic characters of the tribe Allosoricini given by Reumer (1984), and are applicable to the subfamily Allosoricinae of Reumer (1992), who dropped the tribal treatment he used previously. The present specimens are therefore referred to Allosoricinae. According to Reumer (1992), the subfamily comprises only two genera, *Allosorex* and *Paenelimnoecus*. The detailed description of *Allosorex* given by Fejfar (1966) indicates that this genus differs greatly in much larger size, a unique shape in the ascending ramus (coronoid process very short and strongly deflected buccally; upper pterygoid fossa very large; lower facet placed very anteriorly, etc.), and in having the teeth unpigmented, the lower incisor strongly upturned in its apical part, the lower molars without cingula and with the protoconid placed much nearer to the metaconid, and M_1 larger relative to M_2.

On the other hand, the morphological characters of the maxillae, mandibles and teeth of *Paenelimnoecus* hitherto described (Engesser, 1979, 1980; Reumer, 1984, 1992; Rzebik-Kowalska, 1990) are consistent with those of the present specimens. This justifies their allocation to the genus *Paenelimnoecus*.

Reumer (1992) listed four species for the genus, and gave their temporal ranges. They are: *P. micromorphus* (Doben-Florin, 1964) from the Early Miocene, *P. crouzeli* Baudelot, 1972 from the Middle Miocene, *P. repenningi* (Bachmayer and Wilson, 1970) from the Late Miocene, and *P. pannonicus* (Kormos, 1934) from the Pliocene.

Doben-Florin (1964) and Ziegler (1989) described and figured the morphology of *P. micromorphus*. The present specimens are distinguishable from *P. micromorphus* in having the mental foramen positioned more posteriorly, the alveolus of the lower incisor ending more posteriorly in buccal view, the condyle with remarkable lingual emargination (the condyle of *P. micromorphus* with buccal emargination as stated by Ziegler, 1989), the lingual protrusion of the lower facet weaker, the lower margin of the lower facet not emarginated dorsally, the lower sigmoid notch much narrower in lateral view, the mandibular foramen positioned more anteriorly, the lower incisor without cingulum (buccal cingulum is present in *P. micromorphus*, judging from fig. 3 of Pl. 5 in Ziegler, 1989), and the teeth distinctly pigmented. In addition to these, the infraorbital and lacrimal foramina seem to be placed more anteriorly in the specimens.

On the basis of the illustrations and descriptions in Engesser (1979, 1980) and Reumer (1992), *P. crouzeli* resembles *P. micromorphus* in the position of the mental foramen and that of the alveolus of the lower incisor, and in the morphology of the lower facet and lower sigmoid notch. These characters therefore distinguish the present specimens from *P. crouzeli*. Furthermore, the present specimens are distinct from *P. crouzeli* in having the coronoid process slenderer and less stout, the interarticular area narrower, and the internal temporal fossa smaller.

The descriptions and illustrations of *P. repenningi* given by Bachmayer and Wilson (1970, 1978) indicate that the present specimens differ from *P. repenningi* in having the teeth clearly pigmented, the posterior border of the infraorbital foramen positioned more anteriorly, the anterior margin of the coronoid process sloping down more gently (in *P. repenningi*, it makes a near-right angle with the horizontal ramus), in the buccal shape of the condyle (in *P. repenningi*, the lower facet distinctly protrudes ventrally), and in having the lower sigmoid notch much narrower in lateral view. The buccal view of the fragmentary skull of *P. repenningi* is illustrated in Bachmayer and Wilson (1978; Pl. 1, fig. 3), where three antemolars are observable. In the figure, the most anterior and middle ones are much larger than the most posterior one. This possibly suggests that *P. repenningi* has a different alveolar pattern from the present specimens.

The morphological characters of *P. pannonicus* given by Reumer (1984) and Rzebik-Kowalska (1990) are compared with those of the present specimens. The specimens are distinguished from *P. pannonicus* in having the lacrimal foramen positioned more anteriorly, an additional alveolar pit for upper antemolars probably indicating the presence of an additional antemolar, the interarticular area narrower in relation to the width of the upper facet, the lower incisor with a less serrated cutting edge, and weaker overlap of M_2 on M_1 (thereby the posterior face of the hypoconid is not concave in M_1). Moreover, the pigmentation of the teeth seems heavier (red to orange) than in *P. pannonicus* (light orange, according to Reumer, 1984).

Additionally, the Late Miocene species *P. obtusus* recently described by Storch (1995) is compared with the present specimens on the basis of his description and figures. The specimens are clearly distinct from *P. obtusus* in having somewhat larger size; P^4 and M^1 with much stronger posterior emargination; the coronoid process not leaning anteriorly; the mandibular condyle with stronger lingual emargination, with a narrower interarticular area and with a triangular upper facet; the lower sigmoid notch much narrower; and M_1 and M_2 with more roundish occlusal outlines, with buccal cingula sloping posteriorly and with no entoconid.

The specimens are therefore different from all the known species of *Paenelimnoecus.* We can conclude that they represent a new species of the genus, which we name *P. chinensis.*

Discussion.—Among the *Paenelimnoecus* species hitherto described, the information on skulls and upper teeth is poor or absent for the Early and Middle Miocene species *P. micromorphus* and *P. crouzeli.* It is therefore impossible to discuss the relationships among the two species and *P. chinensis* on the basis of these parts. On the other hand, the morphology of mandibles is comparable among all the species of the genus. *P. micromorphus* and *P. crouzeli* are distinct from *P. chinensis* in the anterior position of the mental foramen and that of the alveolus of the lower incisor, in the morphology of the lower facet (with strong lingual protrusion and emargination on its lower margin), and in having a much broader lower sigmoid notch. According to Bachmayer and Wilson (1970), a Late Miocene species, *P. repenningi,* has the position of the mental foramen near that in *P. chinensis,* but it is distinct from *P. chinensis* in the morphology of the ascending ramus (morphology of its anterior border, lower condyle and lower sigmoid notch). The other Late Miocene species, *P. obtusus,* clearly differs from *P. chinensis* in having the coronoid process leaning anteriorly and lower sigmoid notch much broader, and in the morphology of the condyle (oval upper facet, much weaker lingual emargination and broader interarticular area).

The difference in mandibular morphology between *P. chinensis* and the Pliocene *P. pannonicus* is less than that between *P. chinensis* and the above-mentioned Miocene species. The mandible of *P. chinensis* is similar to that of *P. pannonicus* in the position of the mental foramen and that of the alveolus of the lower incisor, and in the morphology of the ascending ramus (narrow lower sigmoid notch, weak lingual protrusion of the lower facet and no emargination on its lower margin, and curvature of the anterior margin of the ramus). *P. chinensis* is therefore considered to be closely related to *P. pannonicus.*

Our recognition of *P. chinensis* confirms the existence of *Paenelimnoecus* in East Asia during Late Pliocene time. In the Early Miocene, this genus appeared in Europe, and survived there until the Late Pliocene. In East Asia, the genus first appeared in the Late Miocene, which is indicated by *P. obtusus* from Inner Mongolia. *P. obtusus* is not a direct ancestor of *P. chinensis,* because there is great morphological difference between them. *P. chinensis* was possibly derived from a form close to the European species, *P. pannonicus,* while the lineage of *P. obtusus* had possibly become extinct before the Pliocene. It is inferred that the ancestor of *P. chinensis* migrated from Europe in the Early Pliocene, and speciated into *P. chinensis.* Again in the Late Pliocene *Paenelimnoecus* was widely distributed from Europe to north China across the northern part of Eurasia. Such a distribution pattern in Pliocene time is also inferred for another soricid genus, *Beremendia* (Jin and Kawamura, 1996a).

Conclusions

Small shrew remains from Late Pliocene cave deposits of Yinan County are assigned to a new species of the genus *Paenelimnoecus* and named *P. chinensis.* This species is characterized by pigmented teeth, four alveolar pits for upper antemolars, anteriorly positioned infraorbital and lacrimal foramina, posteriorly positioned alveolus of the lower incisor, posteriorly positioned mental foramen, short and narrow interarticular area, rectangular lower facet with weak lingual protrusion, narrow lower sigmoid notch, absence of buccal cingulum in the lower incisor and weak serration on its cutting edge, and weak overlap of M_2 on M_1. These characters distinguish *P. chinensis* from the known species of the genus, *P. micromorphus, P. crouzeli, P. repenningi, P. obtusus* and *P. pannonicus.* Of these known species, the morphological difference from *P. chinensis* is smallest for the Pliocene species, *P. pannonicus.* It is therefore inferred that *P. chinensis* originated from a form close to *P. pannonicus* of the Late Miocene or the Early Pliocene. *P. chinensis* confirms the distribution of *Paenelimnoecus* in East Asia during the Late Pliocene. In this time, *Paenelimnoecus* was widely distributed from Europe to north China across the northern part of Eurasia.

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Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on January 25, the JSP Standing Committee enacted the following changes to its membership.

New members elected ;
Kiyotaka Asami,
Kyoko Hagino,
Satoshi Hanagata,
Manabu Ishino,
Masao Kametaka,
Mieko Kanai,
Shungo Kawagata
Yoshinori Kumazawa,
Yoshihiko Nakayama,
Hotaka Ohba,
Masato Ohwada,
Teruo Ono,
Ryo Saito,
Kimiko Sato,
Wonn Soh,
Hikaru Uno,
Mohamed Zakhera.

Resigned members ;
Yoshihiro Goto,
Kumiko Nishiyama.

Deceased members ;
Yoshimichi Kagawa.

Palaeontological Society of Japan (JSP) Council Actions

During its meeting on January 29, the JSP Council enacted the following changes to its membership.

New fellow members ;
Youichi Azuma,
Michiharu Goto,
Kiichiro Hachiya
Keisuke Inoue,
Shinji Isaji,
Kennichi Kanazawa,
Naotomo Kaneko,
Kaoru Kashima,
Naoki Kohno,
Akihiro Koizumi,
Fumio Ohe,
Chikao Kurimoto,
Hiroshi Kurita,
Isao Motoyama,
Naoki Nemoto,
Tateo Shiraishi,
Katsumi Ueno.

The Palaeontological Society of Japan has revitalized its journal. Now entitled **Palaeontological Research**, and published preferably in English, its scope and aims have entirely been redefined. The journal now accepts and publishes any international manuscript meeting the Society's scientific and editorial standards. In keeping with the journal's new target audience the Society has established a new category of membership (**Subscribing Membership**) which, hopefully, will be especially attractive to new and existing overseas members. The Society looks forward to receiving your applications. Thank you.

APPLICATION FOR OVERSEAS MEMBERSHIP TO THE PALAEONTOLOGICAL SOCIETY OF JAPAN

1. NAME: ______________________________
Title Last (Surname) First (Given name) Middle Initial

2. POSTAL ADDRESS: ______________________________
____
____

3. TELEPHONE AND FAX (please include country code if known):
TEL ______________________________
FAX ______________________________
country code area code number

4. E-MAIL: ______________________________

5. MEMBERSHIP CATEGORY (please check one):
☐**Full Member** receives four issues of **Paleontological Research** .... **8,500 JP Yen**
and two issues of **Kaseki** (a Japanese language journal of paleontology)
in a year and all privileges of the Society including voting rights and
conference programs
☐**Subscribing Member of PR** receives four issues of .... **6,000 JP Yen**
Paleontological Reasearch in a year
(Current JP Yen is 0.008 U.S. $)

6. METHOD OF PAYMENT (Please check one box):
☐I enclose a bank draft made payable to the PSJ.
☐I will remit/have remitted the above amount on ____________ JP Yen through my bank to the account of JPS, a/c #062-0211501, The Bank of Tokyo-Mitsubishi, Kasuga-cho Branch, Tokyo.
☐I agree to pay the amount of ____________ JP Yen by my credit card.
☐Master ☐VISA ☐American Express
☐Diners Club ☐Access ☐Euro
Card Account Number ☐☐☐☐ ☐☐☐☐ ☐☐☐☐ ☐☐☐☐
Signature (required) ____________ Card Expiration ____________

7. SIGNATURE ____________ DATE ____________

8. MAIL TO: Palaeontological Society of Japan
c/o Business Center for Academic Societies, Japan
5-16-9 Honkomagome, Bunkyo-ku, Tokyo, 113 Japan

A GUIDE FOR PREPARING MANUSCRIPTS

PALEONTOLOGICAL RESEARCH is dedicated to serving the international community through the dissemination of knowledge in all areas of paleontological research. The journal publishes articles, normally not exceeding 24 pages, and short notes, normally less than 4 pages. Manuscripts submitted are subject to review and editing by reviewers and a language editor. A condition of acceptance for all manuscripts is that they have not been published and will not be submitted nor published elesewhere. Manuscripts accepted for publication will generally be published in order of submission. Authors submit three copies of their manuscript for editorial review. After review, two copies of the revised manuscript are to be returned for copy editing.

Text: Paleontological Research is intended to be read by an international audience, therefore it is particularly critical that language be clear and concise. Though manuscripts in French and German may occasionally be accepted (with abstract and captions for illustrations and tables also provided in English), English is strongly favored as the language of international scientific communication. For manuscripts prepared in English, either British or American usage in style, words and spelling is acceptable. Use SI (Systeme International d'Unités) units wherever possible.

Text should be typed always in double space on one side of opaque white paper of not less than either 210×280 mm (A4 size) or 8 1/2×11 inches in the following order.

Cover sheet. Cover sheet should contain (1) full name, address, phone number and fax number of the author taking responsibility for the galley proofs, (2) running title composed of less than 40 characters, and (3) the numbers of tables and figures.

Title page. Title of the paper, names of authors and their professional affiliations with addresses (or residential address, if an author is unaffiliated). Titles are to be brief and simple. Spell out one or more of the authors' first names.

Abstract. Abstract should be a condensation and concentration of the essential qualities of the paper. All the papers, including Short Notes, are to be accompanied by an abstract not exceeding 500 words. New taxonomic or stratigraphic names should be mentioned in the abstract.

Key words. Select keywords (not more than six words or phrases) which identify the most important subjects covered by the paper and arrange them in alphabetical order.

Main text. Use three or fewer levels of heading. No footnotes are to be used. Bibliographical references are to be identified by citing the authors' names, followed, in parentheses, by the date of publication, with a page number if desired. All citations must have a corresponding entry in the reference list.

The typical format for arrangement of systematic paleontology can be learned from current issues of the Journal. All descriptions of new taxa must include a diagnosis, and, as appropriate, stratigraphic and geographic indications, designation of a type or types, depository information, and specification of illustrations. In synonymies use an abbreviated form of the reference, consisting only of authors of reference, date of publication, and number of pages, plates, figures and text-figures referring to the organism or organisms in question.

References. Heading for the bibliography can be either "References cited" or "References." Entries are to be listed alphabetically. No abbreviations will be used in article and book titles. Journal titles are written out, not abbreviated. Series, volume, and number or part are to be given, with the appropriate word abbreviated in each case ("ser.", "vol.", etc.; see the next page for examples).

Illustrations: All illustrations, including maps, geologic sections, and half-tone illustrations (including "plates") are to be called figures and must be numbered in the same sequence as they are first cited in the text. Citations of illustrations in the text are to be spelled out in full (e.g., Figure 2 or Figure 2.1). Figure captions are to be typed separately. Plan the illustrations so that they take up either the entire width of the printed page (170 mm) or the width of one column (80 mm). Originals should not be smaller than the final intended size for printing. No foldouts will be accepted. Mark all originals clearly with authors' names and figure number. Photographs of all specimens except sections must be illuminated from the upper left side, as is conventional.

Manuscripts on disk: Authors are encouraged to deliver final, revised manuscript copy on disk, but disks should be sent only after the paper has been accepted. Both 5.25 and 3.5 inch disks with the text in a recent version of Word Perfect or Microsoft Word are acceptable. Be sure to specify, in a covering note, the hardware and the word-processing package used.

Galley proofs and offprints: Galley proofs will be sent to authors about one month before the expected publication date and should be returned to the Editors within 3 days of receipt. The authors are responsible for reading the first galley proof. Minor changes submitted by the author will be permitted while a paper is in galleys, but a charge will be made for substantial alterations.

The authors receive free of charge 50 offprints without covers. Additional copies and covers can be purchased and should be ordered when the proofs are returned.

Charges: If a paper exceeds 24 printed pages, payment of page charges for the extra pages is a prerequisite for acceptance. Illustrations in color can also be published at the authors' expense. For either case, the Editors will provide information about current page charges.

Return of published figures: The manuscripts of the papers published will not be returned to the authors. However, figures will be returned upon request by the authors after the paper has been published.

Ager, D.V., 1963: *Principles of Paleoecology*, 371 p. Magrwhill Co., New York.

Barron, J.A., 1983: Latest Oligocene through early Middle Miocene diatom biostratigraphy of the eastern tropical Pacific. *Marine Micropaleontology,* vol. 7, p. 487-515.

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Burckle, L.H., 1978: Marine diatoms. *In*, Haq, B.U. and Boersma, A. *eds., Introduction to Marine Micropaleontology*, p. 245-266. Elsevier, New York.

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Koizumi, I., 1972: Marine diatom flora of the Pliocene Tatsunokuchi Formation in Fukushima Prefecture. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series,* no. 86, p. 340-359.

Kuramoto, S., 1996: Geophysical investigation for methane hydrates and the significance of BSR. *Journal of the Geological Society of Japan,* vol. 11, p. 951-958. (*in Japanese with English abstract*)

行事予定

○1997年の第146会例会は6月28日（土）・29日（日）に豊橋市自然史博物館で開催の予定です。6月28日午前にロシア科学アカデミー古生物学研究所の研究者2名による記念講演会を，午後にシンポジウム「古生物学と博物館」を行う予定です。一般講演の申し込みの締め切りは5月10日です。

○日本地質学会第104年学術大会（福岡）は，日本古生物学会ほかの参加した連合学術大会となります。日本古生物学会は10月10日にシンポジウムを実施いたします。シンポジウムの課題は3月末日に決定されますので，今後のご案内をご覧下さい。

○1998年年会・総会は1998年1月30日（金）～2月1日（日）に，神奈川県立生命の星・地球博物館で開催予定です。シンポジウム企画案を募集しております。企画案の締め切りは6月中旬，一般講演の申し込み締め切りは12月5日です。

第146回例会までの申込先：〒169-50 東京都新宿区西早稲田1-6-1
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1998年年会からの申込先：〒240 横浜市保土ケ谷区常盤台79-2
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