

Life limit of Earth's life as functions of water, CO₂ and nutrients

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To understand the ecosystem to drive life continuously from its birth to the present, and its future, the reaction to synthesize life is critical. The three components, water, CO₂, and nutrients are combined all to bear life by the help of Sun energy on the surface of the Earth. In the Phanerozoic, this system began to work effectively by the nutrient supply due to emergence of huge TTG mass (continents).

On the contrary, the ecosystem was extremely poor because of minor nutrients in most Precambrian time. Minor amounts of nutrients with sufficient water and CO₂ constrained the reaction to produce life in the Archean and basically same in the Proterozoic, although increased considerable amounts later. After the emergence of huge landmass at 600Ma, the ecosystem has suddenly changed, 106 times bigger than before to open the door of Cambrian explosion. Through the Phanerozoic, the Earth has spent most of CO₂ which remains now only 400ppm in atmosphere. When we will lose CO₂ in atmosphere, the reaction above will stop to change the ecosystem. The oxygen-rich atmosphere will also be changed. Instead, the world of anoxic bacteria will appear again on the surface of the Earth, and the world of metazoan will end.

1.5Ga afterward, the Earth will lose the Ocean on the surface, which will be the time of ending life.

Organic geochemical approach to the paleomarine environment around the Marinoan glaciation

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The Marinoan glaciation, from ~665 Ma to ~635 Ma, is hypothesized to be a "snowball earth" period. The nature of the deposition of post-Marinoan sediments, and the role of living organisms, is still being debated. We conducted organic geochemical analyses of the sediments around the Marinoan glaciation in the Moonlight Valley type section, the East Kimberley region, northwestern Australia. Our results show: (1) the biomass of photosynthetic organisms was relatively small after the ice age, but rapidly increased just before the precipitation of "cap carbonate" unit (CCU) and was large during the CCU precipitation, according to pristane + phytane quantities; (2) the biomass of green sulfur bacteria was relatively large around the start of the CCU precipitation, according to the quantity of aryl isoprenoids; (3) anoxic water developed both just before and during the last of the CCU precipitation, evidenced by the pristane/phytane ratio and the quantity ratio of aryl isoprenoids and dibenzothiophene. These situations suggest the possibility that the CCU was precipitated by a medium of sulfate-reducing bacteria which existed in the remaining glacial euxinic water. A blooming of photosynthetic organisms during the deglaciation provided abundant organic matter to the sulfate reducers, that then produced the carbonate that precipitated to form the CCU.

Keywords: organic geochemistry, Neoproterozoic, snowball earth, paleocoenography, cap carbonate

A two-step rise of oxygen concentration in shallow seas coinciding with the rise of animal life in Ediacaran-Cambrian

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Two of the most significant events in Earth biotic evolution occurred in the Ediacaran and the early Cambrian periods. The first event is characterized by the appearance of primitive marine animals such as sponges and cnidarians in the Ediacaran, and the second step is the appearance of diverse marine animals in the early Cambrian. However, the cause of these macroevolutionary steps has not been clarified. Here we show that a two-step rise of oxygen level in shallow seas coincided with the rise of animal life in the Ediacaran and Cambrian. The changes in dissolved oxygen, marked by an organic molecular index, the pristane/phytane ratio, are detected from shallow marine sedimentary rocks from northwestern Australia and southern China. Low dissolved-oxygen conditions above storm wave base developed frequently in the early Ediacaran before and during the Gaskiers glaciation and end-Ediacaran to earliest Cambrian, before the Cambrian Explosion. High dissolved-oxygen conditions above storm wave base continued in late Ediacaran and into the time of the Cambrian Explosion. The high dissolved-oxygen conditions coincided with the Ediacaran biota and the early Cambrian fauna. Additionally, sporadic data from below storm wave base show low dissolved-oxygen conditions in the late Ediacaran, and high dissolved-oxygen conditions during and after the Cambrian Explosion horizon. We hypothesize that the two-step rise in dissolved oxygen is related to the two-step evolution of metazoans in the mid-Ediacaran and the Cambrian.

Keywords: Ediacaran, Cambrian, oxygen concentration, shallow sea, animal life

Occurrence of PZE and intensification of marine primary production during the Cretaceous OAE1b in the Vocontian Basin.

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In mid-Cretaceous formations, the laminated and organic-rich black shales, which have been thought to be deposited under oxygen-poor oceanic condition, were occasionally discovered. The environmental disturbance events that had formed such black shales are called 'Oceanic Anoxic Events (OAEs)' occurred by ocean water stratification and/or high productivity at sea surface. Previous studies on OAE 1b demonstrated that wide occurrence of anoxic waters was attributed to episodic expansion of the oxygen minimum zone (OMZ), which was presumably formed as a result of intensification of marine primary production. However, few insights for paleo-ecosystem such as primary production have been obtained. In the present study, we reconstructed paleo-ecosystem by multi-biomarker analysis with high resolution (lamina levels) in the Vocontian Basin during the OAE1b (the Paquier level).

In the Paquier level, variations in concentrations of terrestrial biomarker such as retene were nearly synchronous to those of marine algal biomarkers such as steroids and dinosteroids. These results indicate that the nutrient was transported from land to ocean. Moreover, biomarkers of methanogenic archaea such as 2,6,15,19-tetramethylcosane (TMI) and 2,6,10,15,19-pentamethylcosane (PMI) were even detected at massive marls in the Paquier level. Concentrations of these biomarkers were higher at clearly laminated shale layers. It shows dysoxic to anoxic condition at seafloor during the Paquier levels and increase in methanogenic archaea related to the intensification of anoxic condition. Furthermore, biomarker of green sulfur bacteria, chlorobactane, was identified. Green sulfur bacteria including Chlorobiaceae are known to photosynthesize at euphotic zone under euxinic (anoxic and sulfidic) condition, and therefore, detection of its biomarker clearly indicates occurrence of 'photic zone euxinia (PZE)' during deposition of the Paquier levels. This is first report for the PZE at the OAE1b. Concentrations of chlorobactane were higher at clearly laminated shale layers and ammonoids-rich beds. In addition, triaromatic dinosterane index (TDSI⁺), which is used as an indicator for contribution of dinoflagellate in total primary producers of the sea surface layer, were higher value at black shale layers with high concentration of chlorobactane. It suggests that the PZE was associated from variation in dinoflagellate production during deposition of the Paquier level.

Keywords: Oceanic Anoxic Events (OAEs), photic zone euxinia (PZE), biomarker, green sulfur bacteria, dinoflagellate, supply of terrigenous material

Compositions of molecules bound in terrestrial plant-derived kerogens from Cretaceous sediments, Hokkaido, Japan

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Organic particle derived from terrestrial higher plant is usually contained in ancient sediment. The terrestrial plant-derived organic particle is mainly composed of resistant macromolecules such as cutin and suberin polymers and well preserved biochemical and taxonomic information for living plant. Our research group proposed that molecular compositions of the resistant macromolecule in plant fossil could be useful as chemotaxonomic indicator (Ikeda et al., submitted). In the present study, we applied this chemotaxonomic indicator to terrestrial plant-derived organic matter (kerogen) collected from Cretaceous sedimentary sequence to examine applicability of this indicator for reconstructing paleovegetation, and moreover, terrestrial paleoenvironmental variations.

We analyzed mudstones and sandstones collected from the Lower Cretaceous Albian Shuparogawa Formation, Maruyama Formation and Hikagenosawa Formation of the Yezo Group in the Tengunosawa route, Oyubari, Hokkaido, Japan. These formations are turbidite sediments that carbonized plant fragments are abundantly contained. Kerogens were separated from the powder rock samples as reported by Sawada (2006, *Island Arc* 15, 517-536). The kerogens were extracted with methanol and dichloromethane, and were subsequently refluxed under high temperature to remove free compounds completely. Finally, the residues were saponified by KOH/methanol to obtain ester-bound compounds. GC-MS analysis was performed for identification and quantification of compounds. Also, we observed the kerogens with fluorescent light microscope.

Fluorescent light microscopic observation of kerogens shows that the kerogens from all sediments are mainly composed of wood and non-fluorescent amorphous organic matter (NFA), and contain plant cuticle as minor component. This indicates that all kerogens used are originated from terrestrial higher plant tissues. As saponified products (ester-bound molecular units) from all kerogens, C14-C18 n-alkanoic acids (fatty acids) are mainly detected, and C10-C24 n-alkanols are identified. There are predominance of even carbon numbers of fatty acids and n-alkanols released from kerogens, and these released compounds are presumably originated from monomers of cutin and suberin polyesters in resistant macromolecules of the kerogens. The C18/C16 ratios of fatty acids released from kerogens significantly vary from the Shuparogawa to Hikagenosawa Formation in the Tengunosawa route. Previous study (Ikeda et al., submitted) suggested that the C18/C16 ratios of the bound fatty acids obtained after saponification varied depending on relative abundances of woody / herbaceous fossils. It is found that the variations of the C18/C16 released fatty acid ratios are almost synchronous to those of angiosperm / gymnosperm ratios recorded by terrestrial higher plant biomarkers (Nakamura et al., submitted). In the Cretaceous flora, it is presumed that the woody and herbaceous plants were mainly composed of gymnosperm and angiosperm, respectively. Thus, the synchronous variations between the C18/C16 released fatty acid ratios and biomarker angiosperm / gymnosperm ratios suggest that these organic geochemical data showed the variations of paleovegetation for angiosperm-dominant grassland / gymnosperm-dominant forest in the Cretaceous paleo-Hokkaido areas. From these insights, we propose that the C18/C16 ratio of fatty acid released from kerogen can be useful as paleovegetation indicator. In addition, C18 ratios in n-alkanols bound in kerogen have potential as paleovegetation indicator.

Keywords: terrestrial plant-derived kerogen, bound molecule, paleovegetation indicator, terrestrial paleoenvironment, Yezo Group, Cretaceous

Thrombolites and shelly fossils from the Cryogenian carbonate in Bahia, Brazil

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Research on the Neoproterozoic sediments in the last two decades have demonstrated the drastic climatic changes and the peculiar material cycling of this age, as well found a number of traces of life. Multicellular animals have evolved immediately after the Marinoan glaciation (635 Ma), and the most primitive sponges may have already existed before. In addition, stratigraphic range of the shelly organisms has been extended beyond the Cryogenian that includes the Sturtian glaciation (720 Ma). Thus, Neoproterozoic was the period of biological evolution. A potential linkage between the Neoproterozoic climate and evolution is a huge organic mass suspended in stratified ocean column. In order to digest organic matter in low-oxygen seawater, the unicellular and mobile suspending feeders change their ecological strategy to multicellular and immobile habits. This may have induced the animal multicellularity (Kano et al., 2011).

We found traces of life in carbonate rocks of the Cryogenian Salitre Formation in central Bahia province, Brazil. The organic-rich carbonate rocks appear lentic bodies of thrombolites, up to several meter thick and >20 m wide. The thrombolite is formed by digitate structures of ~5 mm in diameter, which consist of peroidal texture. The digitate structures could be formed by microbes, but their uniform configuration may indicate the possibility that they were lithified multicellular animals or algae. In addition, the carbonate yields spheroidal shelly fossils of ~2 mm in diameter. The shell is ~0.2 mm thick and lacks any microscopic features, such as processes or holes. Algae from California are the only known Cryogenian fossils having calcareous shell, but our specimens show a absolutely different form. Skeletal of animal is generally considered as adaptation against predation. Thus, animals that can predate organisms of ~2 mm had evolved in late Cryogenian.

At present, origins of the digitate structures and spheroidal fossils are not specified, but will be investigated with microscopic observation and chemical analyses.

Keywords: Neoproterozoic, thrombolite

Shelly microfossils from the Ediacaran Doushantuo Formation in Hunan province, China

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The Ediacaran and earliest Cambrian fossils from South China play a key role to reconstruct the early history of the animal evolution (Xiao et al., 1998; Hong et al., 2010). The reported fossils have been mainly animal bodies and embryos, however the microfossils are equally important in order to understand the Ediacaran-Cambrian ecosystems. Some microfossils have mineralized skeletons, such as the small shelly fossils and the vase-shaped microfossils. Among these, the vase-shaped microfossils have been recently reported from many localities around the world, and considered to be related with various animal groups, such as agglutinated foraminifella (Hong et al., 2007), tintinnids (Bosak et al., 2011) and testate amoebae (Potter and Knoll, 2003). However, the oldest known shelly fossil in South China is so far the Cloudina from the uppermost Ediacaran Danguying Group. This study reports the newly discovered shelly fossils from the lower-lying Doushantuo Formation in South China.

The studied material was collected from microfossils in the Fengtan section, Hunan Province. Here exposes the Ediacaran sediments in a basinal setting of the Yangtze platform (Jiang et al., 2011) covering a diamictite facies of the Nantio Formation correlated with the Marinoan glaciation. The Ediacaran sequence of this section consists of carbonate-shale sequence of the Doushantuo Formation (80 m), and the black chert of the Liuchapo Formation (20 m) in ascending order. The fossils were found from ca. 20 m above the base of the Doushantuo Formation. These are discoidal to spheroidal forms with frilly outer rim as viewed from above. The fossils have a wide range in size; 80-1000 micrometer long (median = 435, N = 127) and 80-800 micrometer wide (median = 347, N = 127). Side view of the fossils show lenticular shape and some specimens have a tapering end. They have single layered skeleton of ~10 micrometer in thickness.

These fossils reveal the first discovery, also in terms of fossil from the basinal facies of the Yangtze platform. Despite of an unknown affinity, the newly found fossil occurrence increases the animal diversity of the early Ediacaran ocean. The marine ecosystem was more developed than it was considered.

Keywords: Ediacaran, Shelly microfossils, Doushantuo Formation, China

Palaeoecology of the producers of trace fossil Phymatoderma from the Toarcian black shale in southern Germany

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There are a few black shale horizons which are characterized by the dense occurrence of the trace fossil Phymatoderma in the lower Toarcian Posidonia Shale in southern Germany. Phymatoderma is interpreted as a burrow system constructed by deposit feeders because of the presence of the fecal pellets. Because pellet fillings consist of a material different from the surrounding sediments, the detailed palaeoecology of the Phymatoderma producers is still vexing; whether fecal pellets are altered from the matrix by digestion (the work of substrate deposit feeders) or are imported from a food source at the sediment surface (the work of surface deposit feeders). In this study, carbon-isotope values and elemental compositions of filling materials, their surrounding black shale, and overlying mudstone are analyzed in order to identify the origin of the fillings of Phymatoderma and to clarify the detailed feeding strategy of producers. Carbon-isotope ratio of the filling materials showed little difference from that of the overlying mudstone, and instead had significantly heavier value than that of the ambient black shale. This fact means that the infillings of Phymatoderma were substantially derived from their overlying mudstone as a result of surface sediment feeding by their producers. Then, comparison between elemental compositional values of the fillings and those of the overlying mudstone showed no significant difference. This fact strongly suggests that the Phymatoderma producers non-selectively ingested surface sediments.

Has the distribution of larger foraminifera *Amphistegina radiata* expanded to the Japan Sea Coast of Ishikawa Prefecture?

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In the seas around the Japanese Archipelago, the larger foraminifera are mainly distributed among the Ryukyu Islands; however, since the 1970s, the larger foraminifera *Amphistegina* has been detected along the coast of the Japan Sea. Based on core samples collected in Tsukumo Bay in the Noto Peninsula, Ishikawa Prefecture, *A. radiata* have been present since the early 1900s. Since *A. radiata* were well-preserved, it is possible that the distribution of *A. radiata* has expanded to the Noto Peninsula. However, since the water temperature in Tsukumo Bay becomes lower than the habitable water temperature for larger foraminifera during winter, abortive migration is a possibility.

Agamont, Schizont and Gamont generations were identified around Sesoka Island based on the test size of *A. radiata*, indicating that *A. radiata* adopts a trimorphic life cycle in this location. Therefore, the size of the proloculus was quantified for each generation using samples collected around Sesoko Island and on the coast of Nago City, and then *A. radiata* generations from the Tsukumo Bay were determined based on their proloculus sizes. Absence of Schizont and Gamont generations may suggest abortive migration in the bay.

The distribution of the proloculus diameter for *A. radiata* from Okinawa Prefecture was bimodal with two peaks at 35 - 42um and 77 - 84um. However, it was not clear to which generations these peaks corresponded. Among the megalospheric-type specimens of *Amphistegina gibbosa* from the Florida Keys, the proloculus size of Gamont was larger than that of Schizont and the size of the second chamber was different between the megalospheric and microspheric types. There were two different shapes in the second chamber of *A. radiata* from Okinawa Prefecture, round- and crescent-shaped, and those with a round-shaped second chamber were fewer in number and had a smaller proloculus. On the other hand, those with a crescent-shaped second chamber had a larger proloculus and the distribution of the diameter of the proloculus was bimodal. Therefore, it was suggested that those with a round-shaped second chamber were Agamont, those with a crescent-shaped second chamber were Schizont, and those with a large proloculus were Gamont. Within Tsukumo Bay, the distribution of the proloculus diameter had only one peak at 35 - 42 um and two specimens had a round-shaped proloculus.

In conclusion, the generations of *Amphistegina radiata* that occur in the Tsukumo Bay are likely Agamont and Schizont and although they reproduce, a trimorphic life cycle has not yet been completed.

Keywords: *Amphistegina*, life cycle, proloculus, abortive migration, Tsukumo Bay, Japan Sea

Ontogenetic stable isotope records for disclosing evolutionary history of algal symbiosis in planktonic foraminifers

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In modern planktonic foraminifers, symbiont-bearing species have successfully adapted to oligotrophic environment, because of nutritional advantage from photosynthesis of symbiotic algae. Through the evolutionary history of planktonic foraminifers, the establishment of photosymbiotic system allowed them to radiate into a new ecological niche in oligotrophic open ocean. Therefore, disclosing the evolutionary history of algal photosymbiosis is crucial for understanding the dynamics of paleobiodiversity in planktonic foraminifers.

In several studies on extinct species of planktonic foraminifers, putative photosymbiotic ecology was estimated from specific morphology commonly observed in modern symbiotic taxa. However, since morphological diversity in planktonic foraminifers would be inconsistent with their general ecological variety reasoned by analogy, independent and objective analyses are required. From this point of view, previous studies using cultured specimens proposed a possible geochemical signature of photosymbiotic ecology, i.e., stable isotopic compositions through ontogeny¹⁾. Those experimental results indicate that $d^{13}C$ value becomes ^{13}C -enriched chamber-by-chamber with growth, because the number of symbiotic algae, preferentially using ^{12}C for photosynthesis, increases in association with growth of the host foraminifers. This observation indicates that the successive increase of each chamber's $d^{13}C$ through individual ontogeny represents the characteristic signal of photosymbiosis. However, this technique has rarely been practically applied to analyses of fossil foraminifers, because the amount of carbonate of each fossil foraminiferal chamber is too small for conventional isotope analyses^{2, 3)}.

Here, we present ontogenetic stable isotopic records in a single foraminiferal test, obtained from newly developed stable isotope measurement for micro-volume carbonate samples; customized continuous-flow analytical system attached to IRMS (IsoPrime) at Geological Survey of Japan (AIST)⁴⁾. This device allows us to analyze a single foraminiferal chamber as small as 1.5 micro grams of carbonate. In this study, three species of Recent planktonic foraminifers recovered from IODP Exp. 330 were used for the isotopic analyses; *Globigerinoides conglobatus* (symbiotic), *Globigerinoides sacculifer* (symbiotic), and *Globorotalia truncatulinoides* (asymbiotic). Tests of each specimen were dissected into 5-7 pieces of chamber(s) with micro-scalpels.

Two symbiotic species, *Gs. conglobatus* and *Gs. sacculifer*, exhibit successive increase of $d^{13}C$ with growth by 1.2 permil and 2.1 permil, respectively, in contrast to relatively stable $d^{18}O$; -0.1 (+/-)0.3 permil and -0.9 (+/-)0.2 permil, respectively. On the other hand, $d^{13}C$ and $d^{18}O$ of asymbiotic species of *Gr. truncatulinoides* displays significant positive correlation. In addition, $d^{18}O$ of *Gr. truncatulinoides* is considerably higher than those of the other two symbiotic species.

In *Gs. conglobatus* and *Gs. sacculifer*, successive increases in $d^{13}C$ associated with ^{18}O -depleted and stable $d^{18}O$ represent the symbiotic nature of these species within a shallow euphotic zone. On the other hand, $d^{18}O$ of *Gr. truncatulinoides* indicates the deeper habitat, which is consistent with the modern plankton tow observations. These results suggest that the photosymbiotic signal has been successfully detected in this study. We then confirmed that the chamber-by-chamber increase of $d^{13}C$ in fossil planktonic foraminifers can be utilized as a proxy of algal photosymbiosis.

¹⁾ Spero and Lea, 1993, Marine Micropaleontology, DOI:10.1016/0377-8398(93)90045-Y.

²⁾ Houston and Huber, 1998, Marine Micropaleontology, DOI:10.1016/S0377-8398(99)00007-9.

³⁾ Bornemann and Norris, 2007, Marine Micropaleontology, DOI:10.1016/j.marmicro.2007.05.005.

⁴⁾ Ishimura et al., 2004, Rapid Comm. Mass Spectrom., DOI:10.1002/rcm.3571.

Keywords: planktonic foraminifers, photosymbiosis, stable isotopes, ontogeny

3-D Geometric Morphometric Analysis of Planktonic Foraminifera Chamber Form with a Fixed Number Anchorpoints Method

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This study presents a new Three Dimensional (3-D) morphometric analysis method of planktonic foraminifera focusing on chamber forms. Most of existing morphometric analysis methods of planktonic foraminifera (e.g. Lohmann, 1983; Malmgren *et al.*, 1984; Hull and Norris, 2009; Scott *et al.*, 2007) were based on Two Dimensional (2-D) specific sideviewing pictures of shells had lost accurate 3-D form data, and were not dealt with chamber forms that often indicates specific growth on foraminifera's ontogeny and is one of elements to compose whole shell shape. Therefore morphometric 3-D chamber analysis was required to be developed as evaluating similarity and morphometric characteristic of chamber quantitatively.

Accordingly, it was useful for chamber form analysis to introduce X-ray Computed Tomography (X-ray CT) and generally 3-D morphometric methods (e.g. Brechbuhler *et al.*, 1995; Macleod, 1999; Wiley *et al.*, 2005; Mitterocker *et al.*, 2005; Shen and Makedon, 2006; Macleod, 2008; Polly, 2008; Polly and Macleod, 2008) that make rapid progress in recent years. But although 3-D chamber analysis needs a function of scanning inner structures as 3-D shape of chamber is appropriate to be represented by inner walls of shell keeping inception forms, we had been impossible to observe inner structures of microfossils until recently resolution enhancement of X-ray CT. In addition, above mentioned methods were not designed to evaluate 3-D foraminifera specimens that are microscales and have a margin and an aperture.

This new developed method allowed us to segment chambers from 3-D shell model in the form of Patch Object which surface is represented by an aggregate of microtriangle (patch), and to analyze 3-D marginate forms of microscale specimens quantitatively. The chamber segmentation procedure is composed of five phases as called "Selecting with normal vector", "Selecting with total brightness of a route", "Selecting with Potential Field", "Selecting with adjoining chamber", and "Selecting with connecting Patch". The analysis procedure is designed expressing chamber form with Anchorpoints of a fixed number and measuring quantitative morphometric values, composed of four phases as called "Scaling with Centroid Size", "Procrustes (GLS; General Least-Squares) Superimposition", "Setting of Anchorpoints", and "Relative Warp Analysis" respectively. "Scaling with Centroid Size" is the process that coordinates of 3-D chamber model data are divided by Centroid Size is the unique independent size variable of shape (Bookstein, 1991). "Procrustes (GLS; General Least-Squares) Superimposition" is the process that coordinates of 3-D model data are rotated for most optimal positions of analysis around the centroid with Procrustes Rotation (Rohlf, 1990, Rohlf and Slice, 1990). "Setting of Anchorpoints" is the process that Anchorpoints of a fixed number (1000) is placed equally on 3-D chamber model data scaled and rotated. "Relative Warp Analysis" is the process that Anchorpoints representing 3-D chamber shape is analyzed into principal components of coefficients of Anchorpoints' warps (Bookstein, 1991; Rohlf, 1993, 1996).

The result that some Neogloboquadrina specimens were applied with this approach indicated recognizable closeness between discrete chambers of an identical specimen and nearness between homologous regions of respective specimens of identical species on principal component space, and enabled us to grasp degree of similarity in the form of a distance among voluntary chambers on principal components space. Therefore, this method is available to trace the spatial and temporal transition of 3-D chamber forms visually. In particular, this method is expected to estimate a growth stage of any specimen and to discover ontogeny patterns. This analysis was applied to planktonic foraminifera Neogloboquadrina, that have less-characteristic chamber, and enables us to evaluate quantitative differences among arbitrary chamber forms of various species.

Keywords: planktonic foraminifera, morphometric analysis, quantitative analysis, 3-D specimen, X-ray CT

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