

Mg/Ca ratios in stressed foraminifera, *Amphistegina gibbosa*, from the Florida Keys

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Abstract

Since 1991, significant proportions of *Amphistegina* populations in the Florida Keys and elsewhere have exhibited stress symptoms that include loss of symbiont color ('bleaching'), anomalous shell breakage and reproductive damage. Previous studies of other taxa have reported elevated Mg/Ca ratios in tests from pollution-stressed foraminiferal populations. The purpose of this study was to test the hypothesis that anomalous shell breakage in stressed *Amphistegina gibbosa* is the result of loss of control of calcification, resulting in elevated concentrations of Mg that weaken the crystal structure of the test.

Analysis of Mg and Ca concentrations in *A. gibbosa* tests, using an Inductively-Coupled Plasma Mass Spectrometer, revealed normal Mg/Ca (2–5 mol%) in all specimens analyzed, including normal specimens collected in 1982 (prior to the onset of the stress event), and both normal and broken specimens collected quarterly from afflicted populations in 1996. Analysis of specimens from the high Mg calcite taxon, *Archaias angulatus*, revealed Mg/Ca of 10–14 mol%. This study, which presents an ICP-MS procedure that can be used to assess Mg/Ca in individual foraminifera, does not support the hypothesis that shell breakage in stressed *Amphistegina* results from disruption of calcification at the ionic level. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Organisms secrete carbonate shells and skeletons which have distinctive mineralogies and compositions. Within the Class Foraminifera, the structure, mineralogy and chemical composition of shells, commonly called tests, is the basis for taxonomic classification at the ordinal level (Loeblich and Tappan, 1987; Sen Gupta, 1999). Among benthic foraminifera that secrete calcite tests, the amount of Mg incorporated within the calcite ranges from 0 to 15 mol% (Scoffin, 1987). Tests that contain more than

5 mol% MgCO₃ are classified as high-magnesium calcite, whereas tests containing less than 5 mol% MgCO₃ are classified as low-magnesium calcite (Scoffin, 1987).

The energy required to secrete and maintain a calcium carbonate shell or skeleton is a function of the degree to which seawater is saturated with respect to calcium carbonate (Morse and MacKenzie, 1990). In warm shallow seas with normal to slightly elevated marine salinities, Mg interferes with calcite precipitation. As a result, such environmental conditions geochemically favor the precipitation of aragonite or high magnesium calcite.

Foraminiferal assemblages tend to taxonomically and mineralogically reflect the relative carbonate

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saturation state of an environment (e.g. Murray, 1973; Sen Gupta, 1999). Agglutinated species are more common in waters that are undersaturated with respect to CaCO_3 , such as in hyposaline estuaries and in the deep sea. Members of the Order Miliolida, with hi-Mg calcite tests, tend to be particularly abundant in shallow tropical carbonate reef and shelf environments, where seawaters are supersaturated with respect to CaCO_3 . Members of the low-Mg calcite-secreting Bulminida and Rotaliida are found in a wide range of environments, although these taxa are much less prevalent in hyposaline, hypersaline and deep-sea environments (e.g. Murray, 1973; Sen Gupta, 1999).

Members of the genus *Amphistegina* are Rotaliida and, as such, are characterized by tests composed of highly ordered low-Mg calcite crystals that are precisely arranged optically (Debenay et al., 2000). In 1991, a previously unknown malady was discovered in live populations of *A. gibbosa* in the Florida Keys (Hallock et al., 1993) and has subsequently been seen in *Amphistegina* spp. worldwide (Hallock, 2000). The primary symptom is loss of symbiont color ('bleaching'), which has been cytologically documented as resulting from the digestion of the diatom endosymbionts, accompanied by disintegration of the host's organelles and cytoplasm (Talge and Hallock, 1995).

The second most common symptom seen in *Amphistegina* populations exhibiting loss of symbiont color is anomalous test breakage. Commonly 10–30% of the live individuals in afflicted populations exhibit some degree of test breakage or evidence of breakage and repair (Toler and Hallock, 1997). In addition to breakage and repair, which commonly results in test abnormalities, congenital abnormalities such as conjoined twins and test deformities are also common in the afflicted populations (Hallock et al., 1995; Toler and Hallock, 1997). Similar abnormalities are common in asexual broods produced in the laboratory by *A. gibbosa* specimens collected from stressed populations.

The calcification process of *A. gibbosa* is a highly ordered process that results in the production of a low-Mg calcite test in a highly Ca and Mg saturated environment that thermodynamically favors the precipitation of high-Mg calcite or aragonite crystals. Thus, *A. gibbosa* must expend energy to control magnesium influx and incorporation.

Yanko and Kronfeld (1992, 1993), as cited in Yanko et al. (1994, 1998), postulated that morphological abnormalities, which are commonly found in tests from pollution-stressed benthic foraminiferal populations, may be related to incorporation of higher concentrations of Mg and other elements from the seawater into their tests. Mg can be incorporated into the calcite crystal lattice at calcium ion sites, which then affect the morphology of the crystal and its growth (Zhang and Dawe, 2000). The rate at which the calcite is precipitated can also be inhibited by the presence of Mg. The calcite precipitation rate is reduced proportionally to the ratio of Mg to Ca in the solution (Morse and Mackenzie, 1990).

The purpose of the research reported here was to address the possibility that test damage in *Amphistegina* results from loss of control of the calcification process. If excess Mg enters the calcium pool, that could cause an increase in the Mg/Ca and disruption of the orientation of the calcite crystals produced, resulting in weaker tests more prone to breakage. The work presented here compares the Mg/Ca in normal and damaged *A. gibbosa*, as well as in normal specimens of a high-magnesium calcite foraminifer, *Archaias angulatus*, collected from the same samples.

2. Methods

2.1. Specimens analyzed

Only foraminiferal specimens collected live, as indicated by visible symbiont color (e.g. Hallock et al., 1986a) were analyzed for this study. Four types of foraminiferal specimen were analyzed:

- (a) unbroken specimens of *Amphistegina gibbosa* collected from Elbow Reef in 1982;
- (b) unbroken specimens of *A. gibbosa* collected from Conch Reef in 1996;
- (c) broken specimens of *A. gibbosa* collected from Conch Reef in 1996; and
- (d) unbroken specimens of *A. angulatus* collected from Conch Reef in 1996.

The 1996 specimens were collected during quarterly (March, June, September, and December) sampling at Conch Reef. Collection methods are

described in Hallock et al. (1995). Sea-surface temperature data for nearby Molasses Reef for 1996 were obtained from the SEAKEYS data set (website: <http://www.coral.noaa.gov/cman/>).

2.2. Sample preparation

Individuals were cleaned using 10% NaOCl, rinsed several times with ultrapure water and then air-dried. Single dry individuals were placed in 15 ml polypropylene centrifuge tubes with screwcaps and dissolved overnight in 10 ml of a 1% HNO₃ solution containing 20 ppb each of Be and Sc, which was prepared from 1000 ppm single element solutions (SPEX, Metuchen, NJ). Occasionally 15 ml was used for especially large individuals of *Archaias*. The next morning the solutions were shaken by hand and no visible residue remained.

The solutions were analyzed for Mg and Ca with a Fisons PQS Inductively-Coupled Plasma Mass Spectrometer (ICP-MS). They were introduced into the ICP-MS with a Meinhard-type concentric glass nebulizer and a double-pass (Scott-type) spraychamber water-cooled to 1°C. After mass calibration and tuning of the instrument, the formation of oxide and double-charged ions was monitored with a 25 ppb Ce solution. MO⁺ and M²⁺ peaks were always found to be stable at less than 1% of the corresponding M⁺ peak.

A 1% HNO₃ solution was run before and after the calibration line, to serve as a blank and to rinse the instrument after the highest standard. In addition, a 1% HNO₃ wash solution was aspirated after each autosampler position. All standard and sample solutions were injected in triplicate.

2.2.1. Magnesium

Magnesium has three isotopes, ²⁴Mg, ²⁵Mg and ²⁶Mg, with natural abundances of roughly 80, 10 and 10%, respectively. In view of the sometimes very high Mg content of the sample solutions (up to 1000 ppb), only the ²⁵Mg and ²⁶Mg signals were used to limit count rates. Potential isobaric interferences include ⁹Be¹⁶O, ¹²C¹³C, ²⁴MgH and ⁵⁰Ti²⁺ on ²⁵Mg, and ¹⁰B¹⁶O and ²⁵MgH on ²⁶Mg. B and Ti were not present in the sample solutions at high enough concentrations to cause a problem and, while Be was present as an internal standard, oxide and

double-charged ions are in any case strongly suppressed by the spray-chamber temperature.

The organic matter content of the sample solutions was also low and in several test runs, interference from the C dimer was found to be significant only for ¹²C¹²C on ²⁴Mg. Contributions from Mg hydrides were hard to quantify, since ²⁶MgH, the only Mg hydride that does not overlap with another Mg isotope, is interfered with by abundant ²⁷Al. However, results based on the ²⁵Mg and ²⁶Mg signals were usually sufficiently similar (see below) that interference from Mg hydrides was deemed insignificant.

Eggins et al. (1997) have shown that on the Fisons PQ2 + ICP-MS, mass-dependent loss of sensitivity with time during a run ('instrumental drift') can be highly non-linear, with evidence for a strong minimum around mass 20–30 (their Fig. 1). It should be noted that the behavior of the response curve around this minimum appears locally symmetrical. Instrumental drift was, therefore, corrected by interpolating between two internal standards (⁹Be and ⁴⁵Sc) which were chosen to be an approximately equal number of masses away from the two Mg isotopes, on either side. This choice was especially convenient since ⁴⁵Sc is also recommended by Le Cornec and Corrège (1997) as a suitable internal standard for the analysis of Ca (see below).

Mg concentrations were calculated from a regression of three standard solutions of 75, 150 and 225 ppb, which were prepared from a 1000 ppm single-element solution (SPEX, Metuchen, NJ). Sample solutions with concentrations exceeding that of the highest standard were rerun after 2–4-fold dilution with milli-Q water. Occasionally, concentrations of these diluted solutions would still exceed that of the highest standard, but insufficient solution was left for further dilutions.

Concentrations based on the ²⁵Mg and the ²⁶Mg signal were mostly equal within 3%, except for samples whose concentration exceeded that of the highest standard (5–10%). The final Mg concentration was taken as the average of these two values. The total amount of Mg (in ng) was then calculated by multiplying with the volume of the solution, taking into account any additional dilutions. Accuracy and precision are estimated to be about 2% for most samples, but about 5% for the lowest (10–20 ppb)

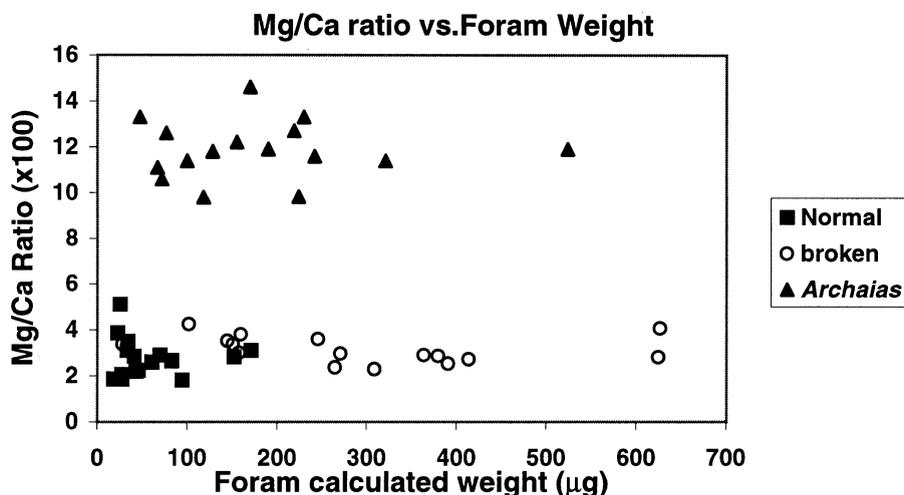


Fig. 1. Plot of Mg/Ca values against calculated mass of each foraminifer analyzed for *Archaias angulatus* and *Amphistegina gibbosa* the Florida Keys.

and highest (>500 ppb) concentrations. Procedural blanks were less than 0.1 ppb.

2.2.2. Calcium

Ca was analyzed using a modification of the method of Le Cornec and Corrège (1997). Briefly, five standards containing 2, 4, 8, 12 and 16 ppm Ca were prepared from a 1000 ppm single element solution (SPEX, Metuchen, NJ). Each standard solution also contained 20 ppb Sc. The exact Ca and Sc concentrations of the standards and the Sc concentration of the solution that was used to dissolve the foraminifera were determined gravimetrically. The $^{43}\text{Ca}/^{45}\text{Sc}$, $^{48}\text{Ca}/^{45}\text{Sc}$ and $^{43}\text{Ca}/^{48}\text{Ca}$ ratios of each standard and sample solution were measured by ICP-MS. Mass bias in the $^{43}\text{Ca}/^{45}\text{Sc}$ and $^{48}\text{Ca}/^{45}\text{Sc}$ ratios was corrected by normalizing to a $^{43}\text{Ca}/^{48}\text{Ca}$ mass ratio of 0.64674 (T. Corrège, pers. comm.), using an exponential mass fractionation law (Russell et al., 1978). Each ratio was subsequently normalized to a Sc concentration of 20.0 ppb.

Linear regression of the corrected, normalized $^{43}\text{Ca}/^{45}\text{Sc}$ and $^{48}\text{Ca}/^{45}\text{Sc}$ ratios of the standards vs Ca concentration yielded regression coefficients $r^2 > 0.9997$. Ca concentrations in the sample solutions were determined from their corrected, normalized $^{43}\text{Ca}/^{45}\text{Sc}$ and $^{48}\text{Ca}/^{45}\text{Sc}$ ratios using these calibration lines. Values based on these two ratios were always equal within 0.1% and the average was taken as the

final Ca concentration. The total amount of Ca (in μg) was then calculated by multiplying with the volume of the solution. Accuracy and precision are estimated to be about 1–2%. Procedural blanks are estimated to be on the order of 1 ppb.

3. Results

Using the ICP-MS technique, we determined Mg/Ca for unbroken and broken specimens of *A. gibbosa* and unbroken *A. angulatus*. Mg/Ca measurements were plotted against the calculated mass of each foraminiferal specimen analyzed (Fig. 1). *A. gibbosa* specimens collected before the stress event showed Mg/Ca values of 0.02–0.04 mol/mol (Mean = 0.03, SD = 0.006, $n = 6$). Unbroken *A. gibbosa* collected in 1996 had Mg/Ca of 0.02–0.06 mol/mol (Mean = 0.03, SD = 0.006, $n = 13$) similar to the pre-event forams. The visually broken *A. gibbosa* also had similar Mg/Ca of 0.02–0.05 mol/mol (Mean = 0.03, SD = 0.006, $n = 13$). Mg/Ca in high Mg-calcite tests of *A. angulatus* was 0.10–0.15 mol/mol (Mean = 0.12, SD = 0.013, $n = 13$). A Kruskal–Wallis one-way non-parametric analysis of variance was performed and showed that there were significant differences between the three groups ($\chi^2 = 34.205$, $df = 2$, $P < 0.0001$). Wilcoxon matched pairs test showed

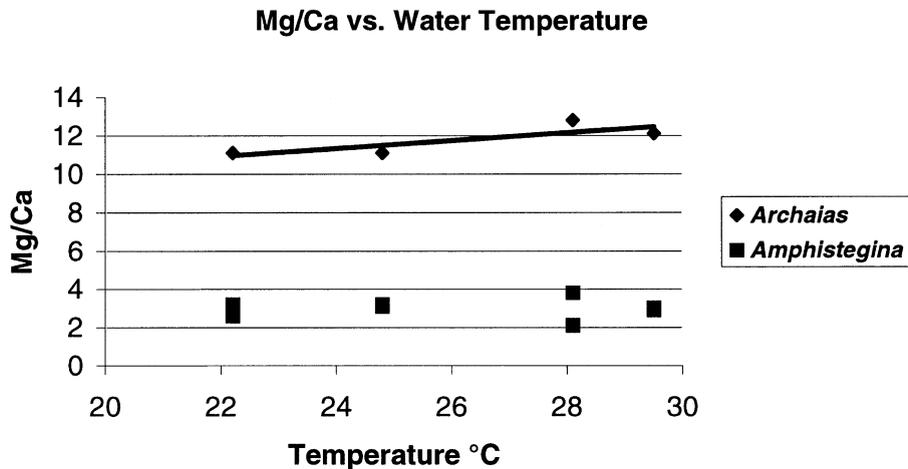


Fig. 2. Comparison of Mg/Ca values and water temperature during quarterly collection of *Archaia angulatus* and *Amphistegina gibbosa* from Conch Reef, Florida Keys. Line shows the linear regression for *Archaia* ($y = 0.21x + 6.4$, $r = 0.81$).

the significant difference to be between *A. gibbosa* (both normal and broken) and *A. angulatus* ($\alpha = 0.05$, $P = 0.0004$). The size bias of specimen among test groups of *A. gibbosa* (Fig. 1) was due to sample availability. During bleaching stress, healthy *A. gibbosa* were typically found only in small size classes (Williams et al., 1997).

Mean Mg/Ca for *Archaia* and for unbroken and broken *Amphistegina* were plotted against mean monthly temperature for March, June, September and December 1996 (Fig. 2). The data showed no statistically significant effect (Kruskal–Wallis ANOVA by ranks, $df = 4$, $N = 48$, $p = 0.96$).

4. Discussions

The rationale for this research was twofold. The first was the hypothesis presented by Yanko and Kronfeld (1992, 1993), as cited in Yanko et al. (1994, 1998), that deformed tests in rotaliid (low Mg calcite) foraminifera from pollution-stressed environments may have elevated Mg/Ca. The second reason is more complicated, and relates to both the test anomalies observed in *A. gibbosa* since 1991 and the high saturation state of warm, subtropical Atlantic seawater, which should thermodynamically promote geochemical precipitation of high Mg-calcite (Morse and Mackenzie, 1990).

Since 1991, *A. gibbosa* from the Florida Keys have exhibited high percentages of test abnormalities, both developmental and as a result of breakage and repair (Toler and Hallock, 1997). Sometimes it is difficult to tell the difference, for breakage at an early stage of development can result in what the observer might classify as a ‘deformity’.

In the warm shallow-marine environments in which *A. gibbosa* live and calcify, aragonite and high-Mg calcite are the predominate forms of CaCO_3 . To build a test of low-Mg calcite, the protist must actively exclude Mg from the crystal lattice. Knowing this, we postulated that if the foraminifer is losing some control of the calcification process, the calcite may precipitate closer to equilibrium with the environment, meaning that it would incorporate extra Mg. Furthermore, if the Mg/Ca is altered, the calcite produced would be structurally weaker, thus explaining the increase in breakage.

However, the resulting data show that broken *A. gibbosa* specimens do not incorporate more Mg than normal specimens. No significant difference was shown among the normal, broken and pre-event *A. gibbosa*. The mean Mg/Ca for all *A. gibbosa* analyzed was 0.030 mol/mol (SD = 0.006) for $n = 32$.

Bleaching stress, including anomalous shell breakage in *Amphistegina* spp., appears to be related to photic stress (Hallock et al., 1986b,

1995, 2000), and not to water-borne pollution. Therefore, our findings do not conflict with the Yanko and Kronfeld (1992, 1993) hypothesis, which related specifically to shell deformities in pollution-stressed populations. Our results only indicate that the physiological dysfunction responsible for shell breakage in the foraminifera that we examined does not appear to be related to the mechanism responsible for deformities in pollution-stressed foraminifera examined by Yanko and Kronfeld (1992, 1993). Furthermore, those investigators employed microprobe analysis, measuring Mg/Ca at multiple locations within individual shells, while our analyses examined whole shells. However, the size bias between normal and broken shells in our study (Fig. 1) supports the robustness of our conclusion of no difference among the *A. gibbosa* test groups. As Talge and Hallock (1995) demonstrated, bleaching is a progressive, degenerative intracellular process that first appears in intermediate-sized individuals (diameters 0.6–0.8 mm), and is most strongly manifested in larger individuals (>1 mm). Thus, if Mg/Ca incorporation was affected, that too should be most observable in the large, heavily damaged specimens. Our analyses revealed that Mg/Ca ratios in *A. gibbosa* shells remained consistent regardless of size or damage.

Mg/Ca did not vary significantly within the temperature range of 22–29°C for either *A. gibbosa* or *A. angulatus* (Fig. 2). Data points for *Archaias* are suggestive of a trend, though more measurements would be needed to statistically verify a relationship.

Lea (1999) reported Mg/Ca for tests of deep, cold water benthic foraminifera to be in the range of 0.005–0.01 mol/mol. Our data show that tests of a shallow-dwelling, warm water species, *A. gibbosa* have Mg/Ca approximately three times higher. Our Mg/Ca data for both species fall within the range reported by Scoffin (1987) for benthic foraminifera, 0–0.15 mol/mol. Chave (1954) reported a value of 5.1 MgCO₃ weight percent for *Amphistegina* living at 23°C and 14.5 weight percent MgCO₃ for *Archaias* at 23°C using data taken on a X-ray spectrometer. Our mean values converted to weight percent MgCO₃ are 1.8 for *Amphistegina* and 7.5 for *Archaias*.

4.1. Hypotheses for anomalous test breakage

If incorporation of excess Mg is not occurring in the tests of *A. gibbosa*, what are the other possible explanations for the anomalous incidences of test breakage in populations exhibiting bleaching stress? Three possible mechanisms have been postulated from ongoing research on these stressed populations:

- (a) Mg interference with crystal formation;
- (b) reduced amounts of organic matter in the tests of *Amphistegina* suffering from symbiont loss (Toler and Hallock, 1997);
- (c) increased susceptibility to predation (Hallock et al., 1999).

The extent of control organisms have over their skeletal mineral composition is unknown. It has been suggested that one such mechanism of control is to regulate the amount of magnesium in the solution from which the calcification is occurring (Kitano et al., 1976). The presence of magnesium modifies the morphology of calcite crystals. There does not appear to be a relationship between changes in crystal morphology and magnesium content on the crystal surfaces (Zhang and Dawe, 2000). The presence of excess magnesium in the pool, though not necessarily more magnesium incorporation, can result in precipitation of triangular crystals, rather than rhombohedral ones (Zhang and Dawe, 2000). Triangular shaped crystals may weaken the test structure making the foraminifera more susceptible to breakage.

Unknown characteristics of the organic matrix may have a similar influence. When in vitro experiments were run to investigate the effects of organic matrix proteins extracted from *A. gibbosa* on calcium carbonate crystals, triangular crystals were only formed in the presence of the matrix proteins extracted from damaged foraminifera (Toler et al., 1995).

In *Amphistegina* with weakened tests, the organic matrix of the tests also appears to be compromised. The organic matrix consists of glycosaminoglycans, which provide structural integrity to the test, as well as of two broad classes of proteins (Weiner and Erez, 1984; Langer, 1992). Of particular importance are serine and glycine-rich proteins, which provide tensile strength to the test (Robbins and Brew, 1990). Cytological studies of *A. gibbosa* specimens exhibiting

symbiont loss revealed evidence of starvation, as well as reduction or absence of endoplasmic reticulum and Golgi bodies (Talge and Hallock, 1995), which are essential to protein synthesis (Langer, 1992). Toler and Hallock (1997) found that broken tests in *A. gibbosa* exhibiting symbiont loss are visually deficient in organic matrix. They suggested that simply the lack of organic matrix, which is essential for tensile strength, might render tests more susceptible to breakage.

Finally, *A. gibbosa* stressed by symbiont loss are more susceptible to predation by *Floresina amphiphaga*, than healthy individuals (Hallock and Talge, 1994; Hallock et al., 1999). This predator bores into the tests of its victims, extracting cytoplasm from one or more chambers. Although *Floresina* predation does not cause test breakage, inability of the stressed *A. gibbosa* to defend themselves from boring may indicate their inability to fend off other predators such as small arthropods, which can break tests (Hallock et al., 1999). Whether *Amphistegina*'s natural defenses against predation are chemical, physical, or some combination is unknown and is a prime topic for future research.

The processes by which shell morphology, deposition and maintenance can be disrupted by environmental stresses, including symbiont loss and pollution, are virtually unknown. The hypotheses presented in this paper should be further explored, as should other possible factors contributing to shell breakage and deformities. If the physiological mechanisms that are disrupted by specific environmental stresses can be determined, such knowledge should enhance the use of foraminifera as environmental indicators, particularly in areas where shell deformities or breakage are common.

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