

GASTROLITHS IN THE TRIASSIC ICHTHYOSAUR *PANJIANGSAURUS* FROM CHINA

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INTRODUCTION

GASTROLITHS (stomach stones) are frequently reported in association with plesiosaur remains, especially elasmosaurids (e.g., Brown, 1904; Williston, 1904; Welles and Bump, 1949; Darby and Ojakangas, 1980; Everhart, 2000; Cicimurri and Everhart, 2001). Stones are also known from several other fossil and modern aquatic vertebrates, including fishes (Dapples, 1938; Thomson, 1966; Trewin, 1986), penguins (Emery, 1963; Stonehouse, 1967; Boswall and MacIver, 1975), crocodilians (Cott, 1961; Neill, 1971; Keller and Schaal, 1992), and pinnipeds (Fleming, 1951; Mohr, 1963; Bryden, 1999).

However, gastroliths are very rarely reported in ichthyosaurs, despite the fact that a large number of articulated skeletons are known from this clade. Some ichthyosaurs show preserved gut contents (e.g., Pollard, 1968; Keller, 1976; Kear et al., 2003), and sand is occasionally found in the gastric area of ichthyosaurs (R. Wild, personal commun., 2000; Wings, personal obs.). Gastroliths with grain sizes >2 mm are only known from two specimens: the one described in detail here and a complete but undescribed skeleton from the famous Upper Jurassic Solnhofen Limestone of Germany (Taylor, 1993; Wings, personal observation). The German specimen is probably referable to the genus *Nannopterygius* Huene, 1922, so far only known from England. The specimen is preserved as a slab, which is on exhibit at the Jura-Museum, Eichstätt, Germany, and a counterslab, which is accessioned to the collections of the Staatliches Museum für Naturkunde, Karlsruhe, Germany.

A description of the stones found in the perfect holotype specimen (Museum of the Yichang Institute of Geology and Mineral Resources # TR00001) of *Panjiangsaurus epicharis* described by Chen and Cheng (2003) (Fig. 1) is important not only because of the scarcity of ichthyosaurian gastroliths, the find is also relevant for the interpretation of gastrolith function. *Panjiangsaurus epicharis* is possibly a junior synonym of *Guizhouichthyosaurus tangaie* (Yin et al., 2000) from the same region and horizon. Likewise, *Cymbospondylus asiaticus*, which was described from two skulls by Li and You (2002), probably also represents the same species. However, these taxonomic questions are not the focus of the current paper. There are at least eight sufficiently prepared skeletons of *Panjiangsaurus* and *Guizhouichthyosaurus* Yin, Zhou, Cao, Yu, and Luo, 2000 combined, including the missing holotype of *Guizhouichthyosaurus*, two specimens on display at the Museum of the Yichang Institute of Geology, Yichang, Hubei Province, two in situ specimens at the Woo Long Gong National Geological Park, Guanling County, two in the collections of the City of Guanling, and one more at the museum of the Dragon Palace Cave, Anshun County, Guizhou Province, China. All except the holotype of *Guizhouichthyosaurus* were personally examined and none except the specimen described here show any evidence of stones in their gut region.

METHODS

Because most of the gastroliths are still in situ in the rib cage of the specimen, a special approach was taken to document the

physical characteristics of all the preserved gastroliths as precisely as possible. More than 100 stones were prepared out from the main in situ clusters A and B (Fig. 1) of the skeleton, of which 84 stones were completely isolated and the others were retained in small groups held together by matrix. Except for one stone, which was prepared mechanically, acid was used to free the stones from the matrix. The isolated stones were weighed, as were the detached groups of stones. To estimate the mass of the in situ pebbles, their volumes were estimated using data for length, width, and height. The estimated volumes were multiplied with respective densities of the in situ pebbles to gain mass data. To crosscheck the results, the same amount of pebbles from modern environments with a similar shape, size, and rock type were weighed. For the final estimate of in situ pebble mass, we used the mean value of both results. Finally, the estimate of total gastrolith mass was obtained by adding the in situ mass estimate to the measured mass of the isolated stones and stone groups.

Length, width, and height of the isolated pebbles were also measured to calculate sphericity, using the method described by Dobkins and Folk (1970). Pebbles still embedded in the specimen were measured in all available dimensions.

Three isolated gastroliths (one from cluster A and two from cluster B) were chosen for SEM examinations. The samples were sputtercoated with gold and examined with a Camscan MV 2300 SEM. Pictures were taken at a different magnification and compared to the results of Whittle and Onorato (2000).

DESCRIPTION OF THE GASTROLITH CLUSTERS AND THE GASTROLITHS

Panjiangsaurus epicharis was a large ichthyosaur: the total length of the holotype is 5.4 m. The specimen is exposed in right lateral view with the skull embedded in ventrolateral view (Fig. 1). The rib cage is preserved in articulation. Two clusters of gastroliths (cluster A and cluster B) are associated with the posterior region of the rib cage. Ventrally to the rib cage, the specimen shows numerous gastralia, representing the disarticulated gastral basket (Fig. 1). The specimen is embedded in a dark gray micrite. Through weathering, the dark gray micrite has become light gray. The gastrolith clusters have a matrix that differs from the surrounding rock and consists of crystalline calcite.

The gastroliths in cluster A (Fig. 2.1), located approximately 23.5 cm anterior to the pelvic girdle, cover the distal parts of some ribs, thus lying outside of the body cavity; those in cluster B are situated near the middle of the dorsal vertebral column, between some right and left ribs (Fig. 2.2). Between the two clusters, there are several isolated stones in gaps between ribs. Cluster A covers approximately 175 cm², while cluster B covers approximately 113 cm². The preserved thickness of cluster A is about 3.5 cm, whereas the preserved thickness of cluster B is 2.4 cm. Consequently, the volume of stones in cluster A is higher than the volume in cluster B. One hundred and sixty-nine gastroliths can be counted in the clusters in situ. However, because many additional stones remain hidden in the clusters, the total number of stones is probably as high as several hundred. There is no

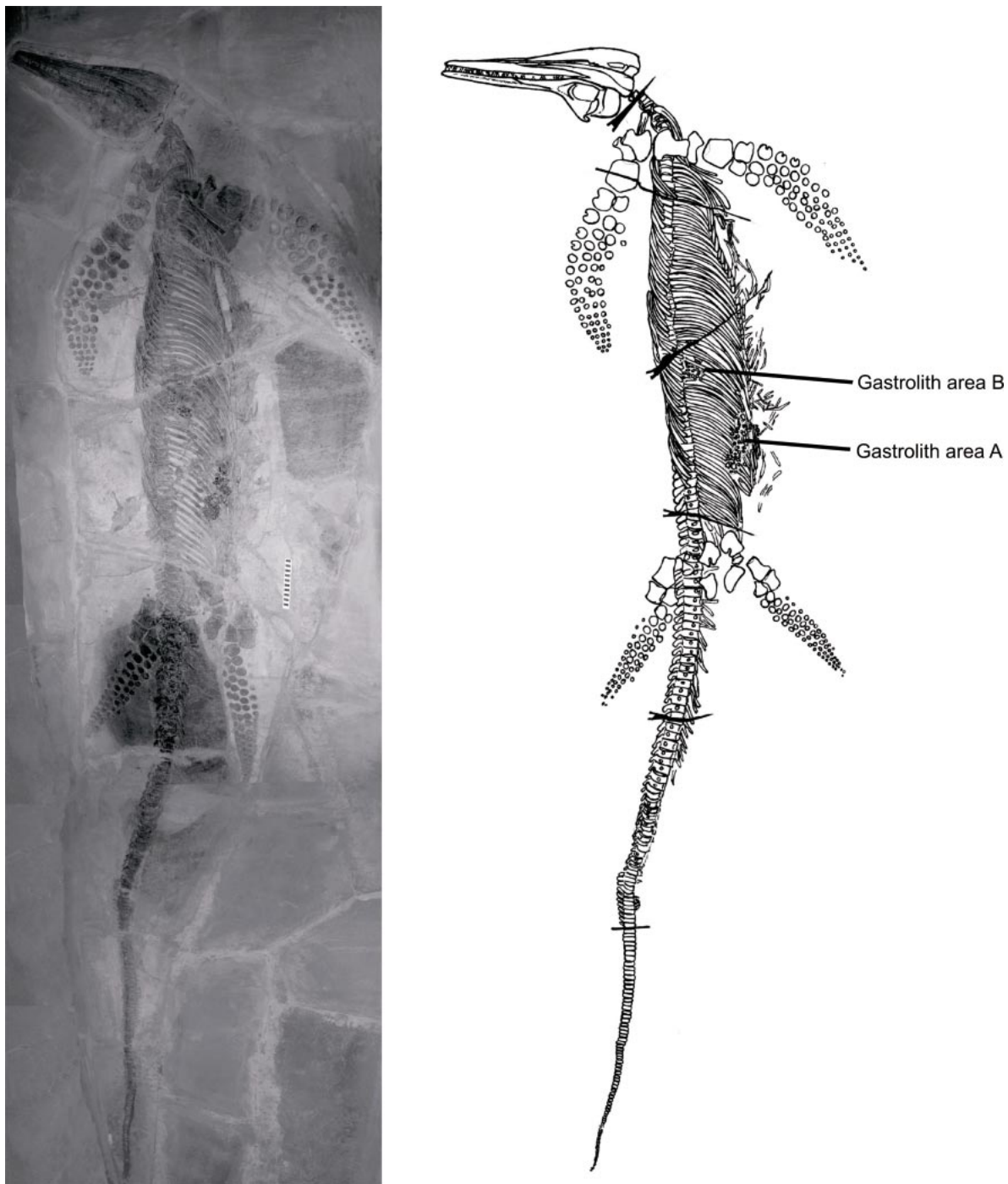


FIGURE 1—Photograph and drawing of the holotype of *Panjiangsaurus epicharis* Chen and Cheng, 2003 (Museum of the Yichang Institute of Geology TR00001) with associated gastroliths. The stones can be seen in two distinct clusters (A and B). Scale bar: 20 cm.

appreciable difference in the size and shape of the stones between the clusters.

The length of the majority of the stones ranges from 0.6 to 2.0 cm. The maximum length is 3.7 cm, the minimum length is 0.6 cm. The grain size distribution of 157 *Panjiangsaurus* gastroliths can be found in Figure 3. The stones are normally subrounded to rounded; however, some pebbles are very rounded or subangular, respectively. Some pebbles were broken up into smaller fragments by postmortem processes.

The gastroliths in both clusters have a similar lithology. Most of the pebbles are composed of quartzite and siliceous rock which were derived from strongly silicified and recrystallized carbonate rocks. Some stones show calcite-filled veins, which do not continue into the calcite matrix of the clusters. Some stones are composed of quartzitic sandstone.

The mean sphericity of the 84 isolated pebbles is 0.575 with a standard deviation of 0.176 and a median of 0.561. The isolated gastroliths have a combined mass of 183.9 g. The mass of the

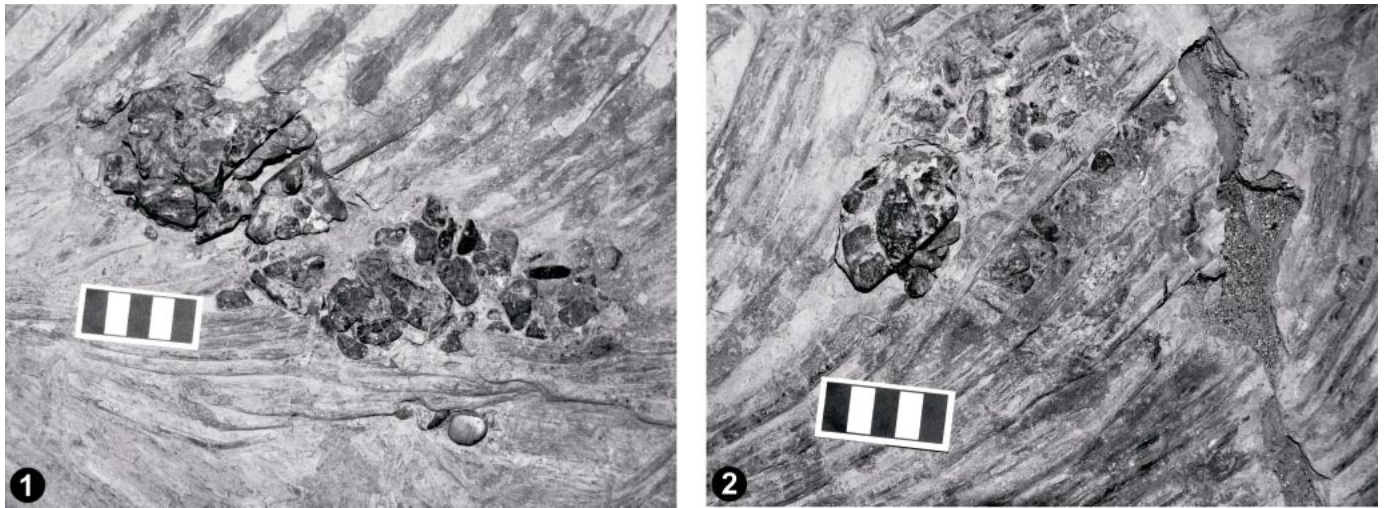


FIGURE 2—Photographs of the gastrolith clusters in the holotype of *Panjiangsaurus epicharis*. 1, The cluster anterior to the pelvic girdle (cluster A). 2, The cluster ventral to the mid-dorsal vertebral column (cluster B). Scale bars: 5 cm.

visible in situ gastroliths is estimated at 310 g. The total mass of all preserved gastroliths is estimated to be close to 1 kg.

The majority of the pebbles have a discoid or bladed shape (Fig. 4). The dull and macroscopically smooth surface of the pebbles is similar in all gastroliths (Fig. 5.1–5.3). Some stones are pitted; however, the majority shows a rather smooth surface structure. Several pebbles have a resinous to greasy polish. Microscopic examination of the pebbles with the SEM shows a rather rough microtexture (Fig. 6). Some shallow pits are visible with a width of around 100–200 μm . No grooves or furrows were found on the three gastroliths studied in the SEM.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENT

The holotype of *Panjiangsaurus epicharis* was found near Xiaowa Village, Xinpu Township, Guanling County, China (Chen

and Cheng, 2003), in the lower Carnian Xiaowa Formation (Chen and Wang, 2002). The other specimens mentioned above also come from Guanling County and from the same horizon. The Xiaowa Formation is a series of more than 130 m of impure marine carbonates. The transition between this formation and the underlying Zhuganpo Formation is conformable. The Xiaowa Formation is unconformably overlain by the Laishike Formation. The Xiaowa Formation is divided into three members. The Lower Member consists of thin-bedded medium to dark gray micrites, and bioclastic micrites, intercalated with organic-rich black shales. It contains iron-manganese and abundant manganese nodules. Fossil marine reptiles, crinoids, bivalves, and ammonoids were found in the Lower Member. The Middle Member consists of gray medium-thickness beds of sandy limestones and marls, intercalated with calcitic mudstones. There are few crinoids, bivalves, ammonoids, and other fossils in the Middle Member. The Upper Member is composed of thin gray limestones. Fossils are rare in

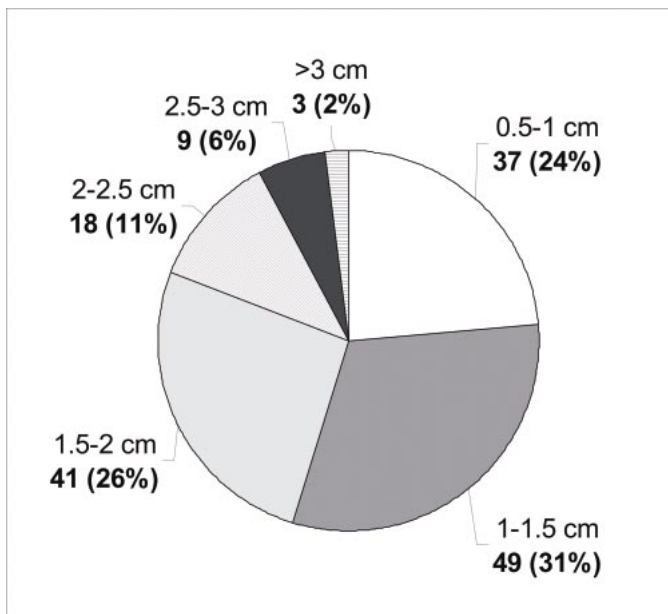


FIGURE 3—The greatest dimension of 157 gastroliths from the holotype of *Panjiangsaurus epicharis*, arranged according to grain size classes. Bold indicates numbers of stones in each of the grain size classes and their percentage of the complete set of 157 measured gastroliths.

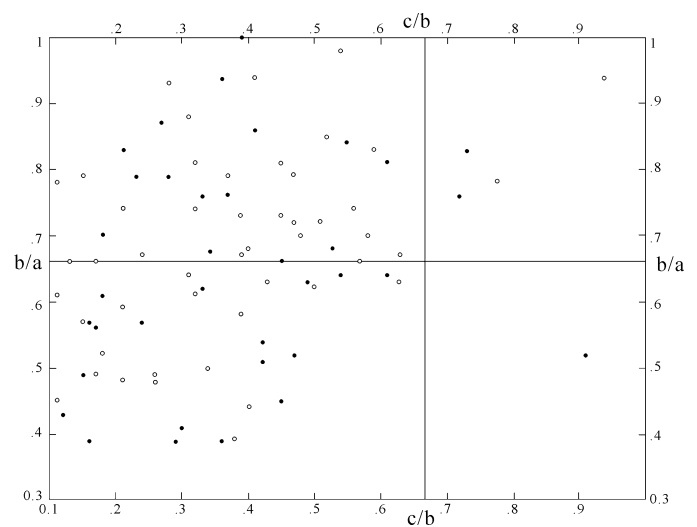


FIGURE 4—Shapes of 84 gastroliths isolated from the holotype of *Panjiangsaurus epicharis* based on Zingg's (1935) classification of ratios of three perpendicular dimensions: a = long axis, b = intermediate axis, c = short axis. Hollow dots represent gastroliths from cluster A; filled dots represent gastroliths from cluster B.



FIGURE 5—Close-up photographs of three gastroliths. 1, Pitted specimen (from cluster B); 2, gastrolith with generally rough surface (from cluster B); 3, gastrolith with macroscopically smooth surface next to a rib (from cluster A). Scale bars in cm.

this member. Previously, the Xiowa Formation was also known as the Wayao Formation, the Wayo Member of the Falang Formation, and the lower Falang Formation (for a review of the history of stratigraphic nomenclature, see Wang et al., 2002; Chen and Cuny, 2003). In the strata of the Lower Member of the Xiaowa Formation, horizontal lamination is well developed. Lithology and structure indicate a low energy subtidal environment of deposition with anoxic bottom waters. Because sea level fell at the end of the Middle Triassic, most of South China was subaerially exposed. Only the area of southwestern Guizhou had marine deposition (Liu, 1996; Wang et al., 2001, 2002, 2003a, 2003b; Chen et al., 2003). The plants *Ctenozamites sarrani*, which indicate a hot-wet climate, and *Equisetites arenaceus*, which preferred

warm habitats near rivers, are well preserved in the Guanling Biota (Meng et al., 2002, 2003). This suggests that the environment was a stagnate basin with a connection to the Tethys.

DISCUSSION

Taphonomy and sedimentology.—The holotype of *Panjiangsaurus epicharis* is a perfectly preserved, complete, and articulated skeleton. Similarly high degrees of articulation are characteristic of the other specimens of *Panjiangsaurus* referred to above that do not preserve gastroliths. The perfect preservation of the holotype of *Panjiangsaurus* implies that the carcass drifted for only a short time before sinking to the seafloor, and that decomposition gases did not refloat the carcass. Furthermore, the in

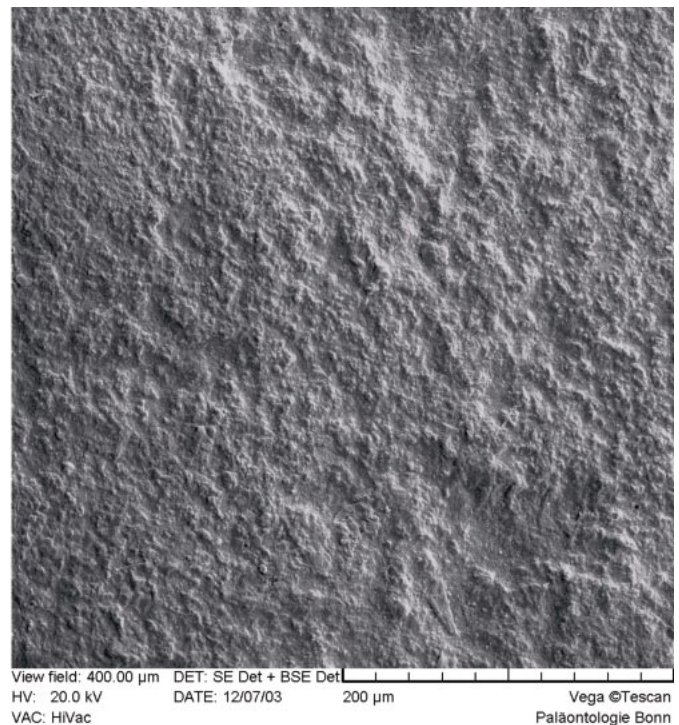
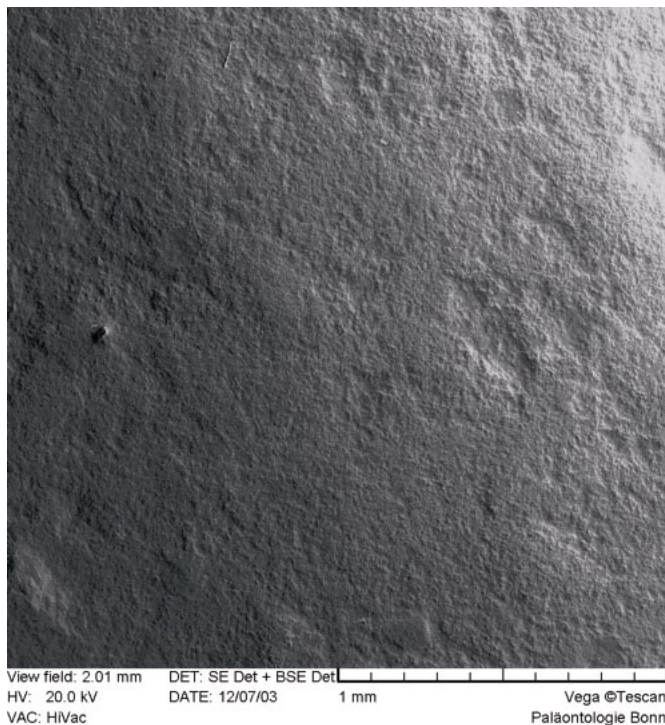


FIGURE 6—SEM micrographs of a gastrolith from cluster A at different resolutions. A micro-rough surface is visible on both pictures, groove marks are absent. The specimen is macroscopically rather smooth (similar to Fig. 5.3).

situ preserved gastralia prove the absence of serious disruption of the carcass due to decomposition gases. A very short drifting time of the carcass is in agreement with the experimental data of Wings (2003) which show that gastroliths can be separated from drifting ostrich carcasses as early as three to six days after death.

However, the two clusters of stones are puzzling. It is implausible that the stones were stored in two parts of the digestive tract since no extant vertebrate group shows such an anatomical distribution of gastroliths. It cannot be ruled out that one of the clusters caused congestion of the intestines, resulting in the death of the animal.

A postmortem separation of the stones into two clusters is also possible. First, the carcass floated for a short time at the sea surface, abdomen upward and back downward. Second, after scavenging or rupture of the abdominal cavity, the carcass sank straight to the seafloor. Some organs, including a few gastroliths (cluster B), were still in the abdomen. Parts of the digestive tract, including most gastroliths (cluster A), moved outside of the abdomen during sinking, possibly driven by mild release of decomposition gases. These parts outside of the skeleton came to rest next to the carcass. Alternatively, the specimen contained indeed two clusters of gastroliths and sank immediately to the seafloor, without a floating phase, because decomposition gas production was insufficient to overcome water pressure. In either case, the preservation of gastrolith cluster A together with the skeleton indicates that the carcass must have reached the seafloor rather rapidly and was quickly embedded (Wings, 2003).

The source area of the gastroliths is unknown. The absence of similar rock types in the embedding sediments is evidence that they originated some distance from the locality of discovery. Although the mean sphericity of the pebbles of 0.575 is almost identical to that of the high energy beach pebbles described by Dobkins and Folk (1970), the size range observed by these authors was much greater than that of the *Panjiangsaurus* gastroliths (the largest stone being only 3.66 cm in length). Also, the standard deviation of the sphericity of the gastroliths (0.176) is considerably higher than the standard deviation of beach pebbles (0.087). Nevertheless, the similarity in sphericity to beach pebbles might indicate that the ichthyosaur obtained the stones from beach environments. The significantly higher standard deviation of the gastroliths shows that they were not well sorted as opposed pebbles commonly observed in beach environments (Darby and Ojankangas, 1980). This may suggest that the gastrolith originated from beaches of different grain size. Plesiosaur gastroliths, however, have generally a higher sphericity of 0.717 (Darby and Ojankangas, 1980) and 0.736 (Everhart, 2000), and are usually interpreted as having had a fluvial origin.

The SEM observations clearly show that gastroliths in the *Panjiangsaurus* skeleton do not possess groovelike features as reported by Whittle and Onorato (2000) for other gastroliths. However, a surface modification of the gastroliths due to preparation of the cluster with acid cannot be ruled out, although the rock types present do not react with acid. The results suggest that an unambiguous identification of gastroliths by counting the abundance of pits, grooves, and smooth areas is generally doubtful.

Function.—Taylor (1993) summarized most earlier reports of gastroliths in aquatic vertebrates and concluded that the function of gastroliths in marine tetrapods is buoyancy control. However, this hypothesis is still controversially debated. Many researchers believed that the gastroliths in Mesozoic marine reptiles aided in food trituration (Seeley, 1877; Brown, 1904) similar to those of herbivorous birds (Gionfriddo and Best, 1999; Wings, 2004).

The hypothesis that *Panjiangsaurus epicharis* swallowed gastroliths to cancel out positive buoyancy, prevent tail-heaviness while floating, and control a tendency to roll about the longitudinal axis, as proposed for Nile crocodiles (*Crocodylus niloticus*)

by Cott (1961), is rather implausible (Wings, 2004). Furthermore, the hypothesis of buoyancy control using gastroliths in crocodilians was recently rejected based on computer modeling of buoyancy with and without gastroliths (Henderson, 2003). In addition, the rather low total mass (approximately 1 kg) of the stones in the holotype skeleton of *Panjiangsaurus* is limiting their possible influence as ballast in such a large animal with an estimated body mass of up to 1,000 kg (Everhart, 2000; Motani, 2001).

CONCLUSIONS

Gastroliths were only found in this one specimen of *Panjiangsaurus epicharis*, and taphonomic differences are unlikely to have been responsible for their absence in the other specimens. Because a function of the gastroliths as digestive help or as ballast cannot be argued for, accidental intake in this one specimen is the most plausible explanation. The ingestion could have occurred in attacks on bottom-living fishes and cephalopods or during active hunting in which the prey sought shelter at the beach or on the seafloor. Alternatively, the stones could have been ingested by the ichthyosaur as part of one or several prey items. However, the Xiaowa Formation vertebrate fauna, mainly ichthyosaurs and thalattosaurs as well as rare placodonts (Yin et al., 2000; Wang et al., 2003a, 2003b), has not produced any other marine reptile skeleton with gastroliths despite that a minimum of about 80 complete skeletons is known (Sander, personal observation). Because the bottom was lifeless during deposition of the Xiaowa Formation, the occurrence described here suggests that the individual had acquired the stones, or the prey containing them, many kilometers away, probably in more shallow or coastal waters.

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