

Stomach stones for feeding or buoyancy? The occurrence and function of gastroliths in marine tetrapods

MICHAEL A. TAYLOR

Earth Sciences Section, Leicestershire Museums, Arts and Records Service, 96 New Walk, Leicester LE1 6TD, U.K.

CONTENTS

	PAGE
1. Introduction	163
2. Occurrence of gastroliths in marine tetrapods	164
3. Correlation of occurrence of gastroliths with locomotor mode	164
4. Occurrence of gastroliths in terrestrial tetrapods	166
5. Origin, loss and taphonomy of gastroliths	166
6. Theory of gastrolith function	167
7. Observations on gastroliths in living crocodylians	168
8. Discussion	169
Appendix 1. The occurrence of gastroliths in marine tetrapods	169
References	171

SUMMARY

Gastroliths or 'stomach stones' occur frequently in some, but not all, groups of fossil and living marine tetrapods. Comparative analysis of gastrolith distribution suggests a role in buoyancy control rather than food processing. Once accidental ingestion by bottom-feeding animals is excluded, gastroliths occur in most tetrapods which 'fly' underwater with hydrofoil limbs, including plesiosaurs, penguins, and otariid pinnipeds, but not the marine chelonians. They do not usually occur in cetaceans, ichthyosaurs, mosasaurs, and odobenid and phocid pinnipeds, which swim with a caudal fin or the equivalent. Occurrence in amphibious forms is variable; crocodylians often have gastroliths, but nothosaurs and placodonts do not. The correlation of gastroliths and underwater flight is corroborated by a comparative analysis which takes phylogenetic factors into account. There is no correlation with diet. Consideration of function and occurrence in terrestrial forms suggests that the use of gastroliths in digestion would not be useful, and might even be harmful, to a carnivorous marine tetrapod. Gastroliths are more efficient than skeletal bone (as in pachyostosis) in terms of sinking force per unit of added mass or volume. As well as driftwood and ice, marine tetrapods should be considered as a potential source of erratic stones in freshwater and marine sediments. Gastroliths may have evolved by the accidental ingestion of stones, the retention into adulthood of stones used by juveniles to process insect or plant food, or as a compensatory replacement for dense bones habitually filling the stomach. Their presence or absence should be more carefully recorded and further studies should be carried out on their function.

1. INTRODUCTION

Gastroliths, or stomach stones, are pebbles and stones found in the stomachs of many freshwater, marine and terrestrial tetrapods, living and fossil. This paper is primarily about marine tetrapods. Pre-Columbian and modern Peruvians used sealion gastroliths in folk-healing (Donnan 1978). The earliest scientific report

seems to be Geoffroy Saint-Hilaire (1831, pp. 48–49), on gastroliths in a fossil crocodile, and debate on gastroliths in aquatic tetrapods began in the 1880s, based initially on otariids and plesiosaurs. Suggested functions included food processing, buoyancy control (including adjustment of floating posture and stability in rolling), elimination of internal parasites, and the alleviation of hunger (Harrison 1888; Turner 1888;

Williston 1903, 1904; Brown 1904; Lucas 1904; Wickes 1908; Wiman 1916; Emery 1941; Rand 1959; Cott 1961; Emery 1963; Harrison & Kooyman 1968; Hubbard 1968; Eastman & Coalson 1974; Darby & Ojakangas 1980; Taylor 1981; Stokes 1987; Chatterjee & Small 1989; Boucot 1990; Davenport *et al.* 1990; Riedman 1990; Storrs 1993). Most workers favour food processing (see, for example, Davenport *et al.* 1990) but there is also evidence for buoyancy control (Cott 1961; Darby & Ojakangas 1980).

The functional dilemma is that an aquatic animal changes buoyancy when it swallows a stone, even if this is for food processing. Nile crocodiles (*Crocodylus niloticus*) swallow gastroliths to cancel out positive buoyancy, prevent tail-heaviness while floating, and control a tendency to roll about the longitudinal axis (Cott 1961). However, it could be argued that the animals use the gastroliths for grinding food, and have therefore evolved positive buoyancy to compensate for the stones' weight. A third possibility is that gastroliths have a dual role in food processing and buoyancy control.

I here present a way around this problem: a study of gastrolith distribution in marine tetrapods by the comparative method (Harvey & Pagel 1991). Correlation of gastrolith distribution with diet would suggest a function in food processing, but a correlation with body form and locomotor habit would suggest a function in buoyancy control. Because every major group of marine tetrapods has radiated into a variety of feeding types, diet does not correlate well with body form, eliminating a potentially confounding cross-correlation.

I aim to show that the distribution of gastroliths in carnivorous marine tetrapods correlates well with locomotor habit. I discuss the function of gastroliths, comparing marine with terrestrial tetrapods. Finally, I outline some palaeontological, sedimentological and evolutionary implications. (I am not concerned with those 'stomach stones' which are protective calculi formed around sharp objects in the gastrointestinal cavity (see, for example, Hirsch 1986), nor those 'gastroliths' which are the regurgitated hard parts of prey (see, for example, Dixon 1971).)

2. OCCURRENCE OF GASTROLITHS IN MARINE TETRAPODS

Appendix 1 summarizes the reported distribution of gastroliths in the major groups of marine tetrapods. There are problems in using published reports, especially those not primarily concerned with gastroliths. A negative report could mean a true absence of gastroliths, failure to record their occurrence, loss under stress or during death, or the vagaries of fossilization (see § 5). It seems very likely that the occurrence of gastroliths is underreported, and that Appendix 1 is not always reliable at lower taxonomic levels. Indeed, I omit higher taxa for which the available data are clearly unreliable, such as the aigialosaurs, extinct marine lizards known from only three specimens (Carroll & deBraga 1992). However, I find that further reports do not substantially change

the pattern seen here, which can be taken as an excellent first approximation of the situation in major groups.

I omit most reports on captive animals (see, for example, Emery 1963; Mohr 1963; Kennedy & Brockman 1965; Keyes 1968; Brazaitis 1969) because of possibly unnatural behaviour (e.g. pathological feeding on debris in a common seal *Phoca vitulina* (Harrison 1888), or the lack of stones to swallow, e.g. *Alligator mississippiensis* (Kennedy & Brockman 1965)).

A confounding factor is benthic feeding. Tetrapods feeding at the sea floor often contain gastroliths, which characteristically grade into coarse gravel, sand and silt, and were presumably accidentally ingested, e.g. the sea snake *Aipysurus eydouxi*, the walrus *Odobenus*, the phocid seals *Erignathus*, *Leptonychotes* and *Lobodon*, the mysticetes *Balaena mysticetus*, *Balaenoptera acutirostrata*, and *Eschrichtia robustus*, and the odontocetes *Berardius bairdii*, *Delphinapterus leucas*, and *Physeter macrocephalus*. A further source of accidental ingestion is prey containing gastroliths (see § 5).

3. CORRELATION OF THE OCCURRENCE OF GASTROLITHS WITH LOCOMOTOR MODE

The data summarized, for major groups, in Appendix 1 suggest that the distribution of gastroliths does not correlate with any particular type or size of prey (apart from accidental ingestion with benthic prey). Marine tetrapods which are active predators often feed on a range of fish, cephalopods and other tetrapods as available (see, for example, Ridgway & Harrison 1981*a,b*, 1989; Massare 1987; Taylor 1987). The only truly marine herbivorous tetrapods are the sirenians and extinct desmostylians, which apparently lack gastroliths (the Galapagos marine iguana *Amblyrhynchus* and herbivorous birds such as ducks, geese and swans are all essentially amphibious). However, the distribution of gastroliths correlates well with locomotor mode. Three main groups are apparent.

(i) *Underwater fliers with gastroliths*

Gastroliths are common in tetrapods which swim with their limbs in a form of underwater flight, with propulsion based partly or wholly on lift rather than drag forces. These are the plesiosaurs, penguins, and otariids (Clark & Bemis 1979; Godfrey 1984, 1985; Feldkamp 1987; Alexander 1989; Riess & Frey 1991). However, marine chelonians, which 'fly' with their forelimbs (Davenport *et al.* 1984), lack gastroliths.

(ii) *Lateral undulatory swimmers, without gastroliths*

Gastroliths are not usually found in fully aquatic tetrapods propelling themselves primarily with long tails (mosasaurs and some ichthyosaurs (Massare 1988)), tail fins (other ichthyosaurs, odontocete and mysticete cetaceans (Massare 1988)) or hind feet functionally analogous to tail fins (phocid seals (Fish *et al.* 1988) and *Odobenus* (Gordon 1981)). Exceptions are usually benthic feeders. (The elephant seal *Mirounga leonina* does swallow gastroliths when coming onto land during the breeding season, perhaps to alleviate hunger; however, the animals are neither feeding nor

swimming, and vomit the stones before returning to the sea (Ling & Bryden 1981; Laws 1984).

(iii) *Amphibious forms of generally crocodile-like body plan*

These include the crocodylians, nothosaurs, placodonts and other aquatic 'diapsids'. Nothosaurs are a paraphyletic group of amphibious fossil reptiles which swam with their tails much as crocodylians, but also used their limbs to varying extents in a rowing action during swimming, rather than underwater flight (Sues 1987; Rieppel 1989; Sander 1989; Storrs 1991, 1993). The placodonts, benthic durophagous reptiles, also lacked gastroliths; some swam by lateral undulation, but others had rigid armoured bodies and swam by sculling the hind limbs (Pinna & Nosotti 1989). Of various superficially similar Triassic aquatic (amphibious) diapsids of uncertain affinities, only *Hovasaurus* regularly had gastroliths. Some nothosaurs and the diapsid *Claudiosaurus* had pachyostotic skeletons with thickened bones, which are generally regarded as an alternative means of providing ballast (de Buffrénil & Mazin 1989; Sander 1989; Storrs 1993; see § 6).

A comparative study is only valid if care is taken to exclude false correlations caused by any close phylogenetic relationship between the taxa involved and by the common inheritance of primitive characters (see Harvey & Pagel (1991) for a detailed discussion). The first problem is insignificant here, as the marine tetrapod groups set out in table 1 all evolved independently from different terrestrial or flying forms, except for the pinnipeds (see below). However, the second problem is important and each group must be discussed in turn.

The crocodylians combine laterally undulatory swimming with gastrolith-swallowing habits, both apparently primitive characters. Gastroliths commonly occur in freshwater crocodylians (e.g. *Crocodylus niloticus* (Corbet 1960; Cott 1961); *Crocodylus palustris* (D'Abreu 1915); *Diplocynodon darwini*, several specimens, Eocene, Germany (Keller & Schaal 1992); *Paleosuchus palpebrosus* and *P. trigonatus* (Medem 1958, p. 242); indeterminate crocodylian yearling, Eocene, U.S.A. (Langston & Rose 1978); but Schaller & Crawshaw (1982) found no gastroliths in 31 specimens of *Caiman crocodylus*, an observation repeated by Davenport *et al.* (1992) who suggest that this reflects a genuine difference in behaviour). These crocodylians are primarily adapted to ambush predation in shallow water, such as rivers and lakes, where gastroliths are valuable in adjusting buoyancy so that the animal can lurk just breaking the surface (Cott 1961). 'Marine' forms such as the Jurassic *Steneosaurus* seem little modified from this basic freshwater habitus and may have followed a similar way of life in shallow coastal waters, in which case they may have retained gastroliths for much the same function. It is unclear whether gastroliths occurred in the most highly adapted marine crocodylians such as the geosaurs, with reduced flipper-like limbs and tail fins; *Metriorhynchus* appears to have had gastroliths, but I have no data for the other, possibly independently evolved, groups of marine crocodylians. The marine crocodylians are, in any case, so closely related to their freshwater ances-

Table 1. *Comparative analysis of the occurrence of gastroliths and locomotor habits in major groups of marine tetrapods*

(See text for discussion. The only valid examples for comparative analysis are the taxa with both characters in the derived character state; +, gastroliths present; -, gastroliths absent; U, lateral undulation; F, underwater flight; prim., primitive.)

taxon	gastroliths	locomotor mode
Ichthyosauria	- (prim.)	U (prim.)
Plesiosauria	+ (derived)	F (derived)
Mosasauria	- (prim.)	U (prim.)
Spheniscidae	+ (derived)	F (prim.)
Otariidae	+ (derived)	F (derived)
Phocidae	- (prim.)	U (prim.)
Cetacea	- (prim.)	U (prim.)

tors that the occurrence of gastroliths can be ascribed to phylogenetic inertia or functional correlation with the overall crocodylian habitus.

The ancestral forms for most other taxa in table 1 were terrestrial carnivores (or flying, in the case of penguins), and therefore probably lacked gastroliths (see § 4). The cetaceans are apparently derived from ungulates (Gingerich *et al.* 1990; Wyss 1990) but even if the ancestral form was a herbivore, it would also lack gastroliths (see § 4). Pinnipeds share a common, probably aquatic, ancestor (Wyss 1988; Berta *et al.* 1989; Berta & Ray 1990), but phocids lack gastroliths while the otariids possess them, and it is assumed that their common ancestor also lacked gastroliths.

The primitive reptilian mode of swimming is by newt-like lateral undulation of the body and tail, with or without concurrent use of the limbs. The reptilian body plan is thus inherently amphibious (Romer 1972) and amphibious habits, or at the very least a potential for developing them, must therefore be considered primitive for reptiles. The long swimming tail of mosasaurs and primitive ichthyosaurs, and the caudal fin of later ichthyosaurs, are refinements of this basic locomotor pattern. It is an arbitrary judgement whether to break these up into discrete characters; here, I conservatively treat them as one essentially primitive character. The mammals primitively use both lateral and sagittal undulation in terrestrial locomotion (Pridmore 1992). Whereas the cetaceans use sagittal undulation, the phocids use lateral undulation (Fish *et al.* 1988). I, again conservatively, regard both as refinements of a basically primitive character state.

I exclude the marine chelonians (Cheloniidae and the leatherback turtle *Dermochelys*) from the comparative analysis as they are derived from ancestors whose chelonian body plan, with a rigid armoured body and short tail, did not allow the evolution of lateral undulation as a means of locomotion. Also, the weight of the carapace itself acts as ballast, and may substitute for this role of gastroliths. Finally, marine chelonians typically feed on sessile and slow invertebrates and plants, in contrast to the mobile prey favoured by most marine tetrapods.

The underwater flight of plesiosaurs, relying on the symmetrical beating of two pairs of 'wings', is derived relative to the basic reptilian locomotor pattern seen in their most likely relatives, the 'nothosaurs' (Sues 1987; Alexander 1989; Storrs 1991, 1993). The similar locomotion of otariid pinnipeds is also derived relative to primitive pinnipeds. The underwater flight of penguins is modified from aerial flight, a primitive character of birds generally, but has specializations for aquatic motion. I conservatively regard it here as primitive.

Thus only two groups of marine tetrapods, the plesiosaurs and the otariids, are derived in both locomotor pattern and gastrolith-swallowing habits, and are therefore strictly valid data for a comparative analysis (although a less conservative definition of penguin swimming as derived would add the penguins as a third group). Their independent evolution suggests a correlation between the two characters, but the only other major group of underwater fliers, the turtles, have a restrictive body plan and in any case have very different, slow-swimming, predatory habits. Two or even three taxa are, of course, too few for a definite conclusion, but there are simply no other taxa available. The correlation is apparently strengthened by the absence of gastroliths in forms which use lateral undulation. But, although suggestive, these cannot be accepted as strictly equivalent evidence because of the persistence of primitive character states. However, there is no general distribution of gastroliths across taxa, suggesting that their occurrence is not correlated with diet, which is indirect evidence for function in buoyancy control.

4. OCCURRENCE OF GASTROLITHS IN TERRESTRIAL TETRAPODS

The distribution of gastroliths in terrestrial tetrapods is highly relevant. These forms provide outgroups for the discussion above (see § 4) and they offer an opportunity to assess the function of gastroliths without the confounding factor of an aquatic lifestyle. In complete contrast to aquatic forms, terrestrial tetrapods with gastroliths are mostly plant-eaters, e.g. some prosauropod and some sauropod dinosaurs, a few ornithomimid dinosaurs, and gallid birds, emus (*Dromaius novaehollandiae*), rheas (*Rhea americana*), ostriches (*Struthio camelus*), mihirungs (*Genyornis*, Dromornithidae) and moas (Dinornithes) (Miller 1962; Emery 1963; Ziswiler & Farner 1972; Burrows *et al.* 1981; Herd & Dawson 1984; Coe *et al.* 1987; Farlow 1987; Galton 1985, 1987; Stokes 1987; Anderson 1989; Boucot 1990; Rich 1990), and even a beetle (Rickson *et al.* 1990). Lacking the chewing teeth of mammals and most ornithischian dinosaurs, they use gastroliths in muscular crops to triturate food, breaking open hard seeds and tough plant cell walls to release nutriment and speed up digestion and fermentation (Alexander 1991).

The few terrestrial carnivores with gastroliths are mostly insectivores. Pangolins (*Manis* and the Eocene fossil *Eomanis*), the Eocene fossil anteater *Eurotamandua*, and the aardwolf *Proteles* ingest coarse sand and

gravel, either incidentally or to help their muscular stomachs comminute and squeeze the body contents from their diet of insects (plant tissue was also found in *Eomanis* (Wiman 1916; Storch & Richter 1992a,b; Anderson *et al.* 1992)). Some lizards and terrestrial and amphibious chelonians (some probably herbivores) also ingest gravel, grit and sand, perhaps for food processing, or for its calcium content or bacterial flora (Wiman 1916; Johnson 1966; Sokol 1971; E. Frey, personal communication).

Most terrestrial carnivores, even those that feed on large prey without chewing it, lack gastroliths, even when, like theropod dinosaurs, they cannot chew their food. Meat, even swallowed in large chunks, is readily digestible, lacking the tough cell walls of plant material. Gastroliths are thus not needed for dealing with meat, nor, by inference, with fish or cephalopods. This is consistent with distributional evidence (see § 2) that gastroliths are not functionally correlated with diet in carnivorous marine tetrapods.

5. ORIGIN, LOSS AND TAPHONOMY OF GASTROLITHS

Wild animals have been reported swallowing gastroliths (e.g. *Spheniscus magellanicus* (Boswall & MacIver 1975)) and stone swallowing is also reported in captive specimens, e.g. *Alligator mississippiensis* (Peaker 1969), *Crocodylus rhombifer* and *C. acutus* (Brazaitis 1969), *C. porosus* (Davenport *et al.* 1990), and *Zalophus californianus* (Schroeder & Wegforth 1935). *A. mississippiensis* apparently eat charred pinewood knots, perhaps by mistake for stones (Holman & Case 1988). Alternatively, the predator may swallow stones inside prey, such as tetrapods, and fishes including elasmobranchs and teleosts (Janet 1891; Vaillant 1892; Dapples 1938; Emery 1963; Miles 1971; Miles & Westoll 1968; Trewin 1986). Gastroliths can be lost by vomiting, voluntarily (e.g. *Phocarcos hookeri* (Fleming 1951; Marlow 1975; Walker & Ling 1981a); *Arctocephalus pusillus* (Rand 1959)) and perhaps also involuntarily under stress, which might usefully add positive buoyancy in an emergency.

Gastroliths have been reported *in situ* in corpses of land animals, both fossil and Recent (e.g. mihirungs (Rich 1990), and moas (Burrows *et al.* 1981)) and marine animals on land (e.g. mummified carcasses of the otariids *Neophoca cinerea* and *Phocarcos hookeri* (Marlow 1975)). However, in water, the taphonomic processes by which living animals become fossils (Schäfer 1972; Martill 1985, 1987) tend to eliminate gastroliths before burial, itself a rare occurrence due to scavenging and decay. Thus gastroliths have never been reported from fossil penguins (Fordyce & Jones 1990), themselves only rarely preserved as even partial skeletons. Gastroliths are also likely to be lost during collection of specimens (see, for example, Taylor 1992a). Gastroliths would be best preserved in those animals which sank straight to the sea-floor on death. However, corpses often float at the surface, bloated with gases of decomposition, before scavenging or rupture of the abdominal cavity releases the gas, allowing the corpse to sink to the sea-floor. This would

often release the stomach contents, including any gastroliths, which then sink either individually or, occasionally, still packed together in the stomach. Buffetaut (1979, p. 125) illustrates a fossil marine crocodylian with a clump of stones lying to one side of the disrupted body cavity, as if the skeleton had come to rest with the stomach hanging out. If scavenging and decay had destroyed the bones before burial, then the gastroliths would have become the sole evidence of the skeleton. These phenomena are likely causes for the anomalous 'nests' of alien pebbles known from some fine-grained sediments (Wiman 1916; possibly the case reported by Double 1931; Hawkes 1951). The 'large stones mixed with material like rotten wood or decayed bones' reported by Jukes-Browne & Hill (1887) may represent a poorly preserved reptile skeleton, although Jukes-Browne and Hill ascribed this to driftwood.

The reverse phenomenon, of corpses accumulating stones, is much less likely. Carcasses can act as sediment traps, such as a Risso's Dolphin (*Grampus griseus*), stranded on a rocky shore, which accumulated stones and sand within its body cavity (Clarke & Pascoe 1985). However, the high-energy environments, such as littoral waves, needed to move stones also make preservation of fossil skeletons very unlikely.

Marine tetrapods are thus a potential source of anomalous erratic pebbles in Permian and later strata, especially in fine-grained marine deposits (see, for example, Woodworth & Wigglesworth 1934, pp. 19–20; Emery 1941; Miller 1962). Fleming (1951) ascribed the occurrence of erratic basalt pebbles on the Snares Islands, south of New Zealand, to transport by the sealion *Phocarcetos hookeri* over at least 130 miles. Abundant pebbles in the Upper Triassic 'Rhaetic Bone Bed' of England have been regarded as accumulated gastroliths from fish or reptiles (Burton 1867; Wickes 1904; Macfadyen 1970), but the origin of this deposit is not fully understood and the pebbles may be from a beach (D. M. Martill, personal communication). More generally, it is often impossible to determine the origin of isolated pebbles or groups which are not clearly associated with skeletal remains, if it is not possible to rule out alternative agencies of transport such as fish, drifting ice, tree roots, or algal holdfasts (see Emery (1963) and Frakes & Francis (1988) for discussion of criteria such as pebble size, composition, and context). For example, some erratics of the English Upper Cretaceous Chalk were probably transported by animals, but others are plainly too large and were presumably moved by driftwood (Godwin Austen 1857; Jukes-Browne & Hill 1887; Double 1931; Hawkes 1951).

6. FUNCTIONAL CONSIDERATIONS

Gastroliths occur in the stomach or in a subdivision of the stomach, or perhaps in a muscular region of the oesophagus (the crop). These facts do not offer any support to one function rather than another. The stomach and crop are the only locations for gastroliths used in grinding food, but they are also the most likely locations for gastroliths used as ballast.

Gastroliths are retained in the stomach or forestomach by a physical filter. The retention of large items such as cephalopod beaks and hooklets in the stomach (or part of it) shows the operation of a duodenal sphincter (McGinnis 1968) or else a more anterior sphincter between the anterior and posterior portions of the stomach or between a crop or forestomach and the stomach proper. This can be seen in living and fossil forms such as ichthyosaurs, plesiosaurs, and odontocete cetaceans (Zhuravlyev 1943; Clarke *et al.* 1970; Harrison *et al.* 1970; Keller 1976; Martin & Clarke 1986; Massare 1987; Böttcher 1989). A similar retention of gastroliths is reported in crocodylians (see § 7), the otariid *Eumetopias jubata* (McGinnis 1968), and possibly plesiosaurs (Williston 1903). The presence of a functional filter in ichthyosaurs and cetaceans, moreover, shows that their lack of gastroliths is not due to the absence of such a filter. Currie (1981), however, suggested that gastroliths in *Hovasauros* were housed in a special intestinal diverticulum.

The position of the gastroliths is important. In reptiles and birds, the stomach and crop lie ventrally so that the downwards weight of the gastroliths comes directly below the lungs which provide most of the positive buoyancy of the animal. This also helps control longitudinal posture and rolling, as in crocodylians (Cott 1961). Some reports of gastroliths in the extremely long-necked elasmosaurid plesiosaurs note the concentration of gastroliths just anterior to the pelvic girdle (see, for example, Welles & Bump 1949; Russell 1967). Although possibly a taphonomic artefact, this location would place the gastroliths posterior to the buoyant lungs, in the right place to counteract the noseheaviness caused by the neck, with its mass of muscle and bone (Taylor 1992b).

The gastroliths of aquatic tetrapods are typically stones ranging from about 5 mm to 100 mm maximum length, composed of hard rocks such as quartzite, granite and basalt. (Smaller clasts are defined as gravel or sand.) Softer rocks would be rapidly eroded. Stone gastroliths have important advantages over the alternative strategy of pachyostosis, deposition of extra bone onto the skeleton (de Buffrénil & Mazin 1989; de Buffrénil *et al.* 1990). The density of silicate rock is typically about 2700 kg m⁻³ (2650 kg m⁻³ for quartz (Stone 1987)). Calcite, slightly denser at 2715 kg m⁻³, is readily available in the form of mollusc shells as well as stone, but calcite-based rocks are rare as gastroliths, presumably because they are dissolved by stomach acids (Martill 1992). Bone is less dense, typically about 2000 kg m⁻³ (ox femur (Wainwright *et al.* 1976)); the disparity is much greater for weights in water, quartz then weighing 16 N kg⁻¹ compared with bone's 10 N kg⁻¹. Stone is thus markedly more efficient than bone in terms of added mass or volume, maximizing acceleration and minimizing drag (cf. Alexander 1977; Webb 1982).

Gaps between gastroliths do increase the apparent volume cost of adding a given mass of gastroliths. For identical spherical gastroliths, only 74% of the added volume would actually be stone (Smith 1982). However, this is probably not important. Small stones fill gaps between larger ones, and muscular agitation of

the stomach contents means that the space between the stones is functionally part of the stomach cavity, and is not 'lost' to the animal.

Pachyostosis occurs in some slow-swimming feeders on stationary benthic food, for which, presumably, locomotor efficiency is unimportant. Sirenians graze on plants, and the extinct placodont reptiles cropped benthic invertebrates. Some 'nothosaurs' (Storrs 1993) and aquatic 'diapsids', notably *Claudiosaurus* (de Buffrénil & Mazin 1989), also used bone ballast.

Stones can also be quickly swallowed and vomited to change buoyancy quickly as needed (Harrison & Kooyman 1968), and they do not bear the metabolic cost of depositing bone. Stones do have the disadvantage that they can be difficult to obtain; growing *Crocodylus niloticus* took longer to obtain their full complement of stones if they lived in stone-poor habitats (Cott 1961).

Evidence from terrestrial predators suggests that gastroliths are unnecessary for digestion (see § 3 and § 4). Aquatic tetrapods typically feed on fish, tetrapods, cephalopods without exoskeletons, shelled cephalopods whose exoskeletons have been broken and perhaps discarded, and crustaceans that are either small enough for the gut juices to macerate or large enough for the relatively coarse homodont dentitions to penetrate (Pollard 1968; Keller 1976; Taylor 1987; Massare 1987). Their food is thus more accessible to gastric juices, especially after repeated penetration by teeth and, if necessary, dismemberment (e.g. adult *Crocodylus niloticus* (Pooley & Gans 1976)). Gastroliths have, indeed, been observed associated with fragile but uncrushed prey in *Crocodylus niloticus* (Cott 1961) and plesiosaurs (Brown 1904; Darby & Ojokangas 1980; Ritchie 1991; Martill 1992).

Indeed, using gastroliths to crush food may be dangerous. Gastric acids eventually soften and destroy vertebrate bones and calcareous invertebrate shells, but have little effect on the tanned chitinous cephalopod beaks, sucker rings, and hooklets, which remain hard and sharp for much longer (e.g. modern odontocetes (Clarke 1980)). Ichthyosaurs and plesiosaurs, like modern odontocete whales and otariids, retained these chitinous residues in the stomach and periodically vomited them up, rather than pass them into the intestine, hence, presumably, the need for the retention mechanism discussed earlier (see, for example, Williston 1903; Zhuravlyev 1943; Fleming 1951; Pollard 1968; Harrison *et al.* 1970; Keller 1976; Clarke 1980; King 1983; Martin & Clarke 1986; Massare 1987; Böttcher 1989; Martill 1992). Smashing these hard parts with gastroliths would produce sharp splinters small enough to pass through into the intestine.

An apparent objection to the buoyancy control hypothesis is that at any one time many individuals lack gastroliths (e.g. otariids (Mathisen *et al.* 1962; Emery 1963; Hubbard 1968)). However, gastroliths are likely to be used facultatively to adjust for changes in buoyancy (Harrison & Kooyman 1968), and changes in the optimum depth at which the animal becomes neutrally buoyant (Taylor 1994), so that

individual animals will differ in the numbers of gastroliths which they carry. In any case, if gastroliths are essential for digestion, it is hard to see why some but not other animals in a population should lack them. However, this is precisely the situation in three species of terrestrial lizard which presumably use them for digestion (Johnson 1966).

7. OBSERVATIONS ON GASTROLITHS IN LIVING CROCODILIANS

Most studies of gastrolith function in aquatic tetrapods have been on crocodylians, with conflicting results. Cott (1961) suggested that *Crocodylus niloticus* uses gastroliths to adjust buoyancy and stability, but the presence of fragile but unpulverized prey in the stomachs implied that the gastroliths were not used for grinding food. Fisher (1981) studied young *Alligator mississippiensis*, which suffer internal injuries from broken bones in food. Prey bones and teeth are retained in the fundic portion of the stomach, until they are decalcified when they pass through to the pyloric portion, and eventually defecated largely intact. Fisher did not specifically discuss the function of gastroliths, but this observation suggests that gastroliths were not used to break up food.

Davenport *et al.* (1990) demonstrated that hatching and juvenile *Crocodylus porosus* deliberately swallow stones, their stomachs sort and retain small, dense spheroids, and gastroliths disperse throughout the stomach during digestion (see also Darby & Ojokangas (1980), for 'caiman'). They suggested that the gastroliths are probably used in conjunction with the muscular stomach wall to break down ingested prey, perhaps helping to squeeze fluids from arthropods. However, they did not show that the gastroliths were actually used to process food in any more active manner, or that their movement was anything other than a consequence of normal digestive contractions.

J. Davenport (personal communication) and E. Frey (personal communication) state that captive specimens of, respectively, *Caiman crocodilus* and *Paleosuchus* sp. had no difficulty in swimming even without gastroliths. However, it now seems that *C. crocodilus* does not normally possess gastroliths (see § 2), and I also suggest that these are possible cases of facultative buoyancy control (see § 6). Perhaps these animals have adapted over the short term (exhalation of air when swimming) or medium term (lung volume). It may be a question not of whether the animals need gastroliths to swim but of whether they need them to swim efficiently. Plainly, the function of crocodylian gastroliths is unresolved, and deserves further research.

Another example of the problem of interpreting reports of gastroliths without actual experimentation is that Schroeder & Wegeforth (1935) noted that captive otariids *Zalophus californianus* swallowed stones after feeding, and regurgitated them after digestion was complete, whereas specimens without stones fed in apparent discomfort. They suggested that the gastroliths were needed for digestion; however, this does not match the distributional evidence.

8. DISCUSSION

This paper shows a correlation of gastroliths with underwater flight in aquatic tetrapods, and a lack of correlation with diet, which suggests their use in buoyancy control. I intend to discuss elsewhere the relative merits of gastroliths against other buoyancy control strategies and why they should be linked to underwater flight (Taylor 1991, 1994). For now, it may be noted that gastroliths are indeed more efficient than bone (see §6) and have the advantage over hydrodynamic lift forces that they do not depend on the motion of the animal through the water. This predicts that animals with gastroliths are at least sometimes more dependent on relative manoeuvrability and slow swimming or even hovering. This is easily understood for ambush predators like crocodiles and elasmosaurid plesiosaurs (Massare 1988; Taylor 1992*b*) but is not at all clear for active pursuit predators such as penguins and otariids.

Gastroliths make the animal heavier and larger, and, apart from affecting acceleration and drag, must also affect any locomotor mechanism which involves transfer between gravitational potential energy and kinetic energy, such as 'porpoising' at the surface (J. Davenport, personal communication). Blake & Smith's (1988) model does indeed imply that the energetic benefits of porpoising relative to swimming underwater decrease with added mass.

Little has been said about the evolution of the regular use of gastroliths. The most obvious origin is in swallowing stones in error, perhaps when feeding on the bottom. Erickson (1982) noted that gastroliths were not recovered from a Palaeocene fossil assemblage of crocodylians, perhaps because stones were unavailable; instead, the crocodylians used bones. I suggest that any animal which habitually ate bone-laden meat would often have to carry dense bones in its stomach. Further evolution led to compensatory changes in the animal's buoyancy which would have to be balanced by swallowing stones when the animal's stomach was empty. The regular use of gastroliths could then be developed into the present flexible buoyancy control mechanism. Alternatively, juveniles were primarily insectivorous (as in young Nile crocodiles (Cott 1961)), and swallowed stones to deal with this, later retaining the stones to adulthood (however, Cott's young crocodiles were stoneless).

Surprisingly, I know of only one report of gastroliths in amphibians (the temnospondyl *Acerastea wadeae*, Early Triassic, Australia (Warren & Hutchinson 1987)) although the body form, size and presumed habits of some large extinct forms converge upon freshwater crocodiles. In any case, there have been few or no fully marine amphibians.

An interesting analogue of gastroliths is the anvil stone held by sea otters (*Enhydra lutris*) to break open invertebrates. An otter will carry the same stone during repeated dives, so it may serve also as ballast (Emery 1963), as in some human breath-hold divers.

I conclude that distributional evidence and functional considerations suggest that gastroliths are used for buoyancy control rather than food processing in

marine tetrapods, but more studies are needed on living forms. Obvious questions are the nature of buoyancy control and its short- and long-term adaptation with and without gastroliths, and whether gastroliths affect the digestibility of food. Another would be the study of microwear patterns on gastroliths, which would help identify isolated stones (cf. dinosaurian gastroliths (Johnson *et al.* 1990; Manley 1991)). I urge careful recording of the occurrence or absence of gastroliths in living and fossil aquatic tetrapods. Finally, what is the functional link, if any, between underwater flight and gastroliths?

Gastroliths are plainly not an aberrant feature of minor interest, but a potentially major adaptation to life in water. The 19th Century seal-hunters had a sailor's grasp of function and structure, yet their assessment of the otariid stomach as a 'ballast-bag' was patronizingly dismissed by scientists as a 'pretty legend' (Harrison 1888, Turner 1888). Perhaps the sealers will be proved right.

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APPENDIX 1

THE OCCURRENCE OF GASTROLITHS IN MARINE TETRAPODS

This table lists the main groups of marine tetrapods, summarizing the known or reported occurrence of gastroliths in cases where a significant proportion of living animals possess them, or a fossil skeleton is found associated with gastroliths beyond reasonable doubt. Captive animals are mostly excluded (see text).

Repository abbreviations: BMNH, Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, U.K.; DORCM, Dorset County Museum, High West Street, Dorchester, Dorset DT1 1XA, U.K.; OUM, Geological Collections, University Museum, Parks Road, Oxford OX1 3PW, U.K.; SMNK, Staatliches Museum für Naturkunde, Erbprinzenstrasse 13, Postfach 6209, D-7500 Karlsruhe 1, Germany.

(a) *Reptilia*

(i) *Chelonia*

Gastroliths are rare or unknown from marine turtles, although the mass of siliceous sponge spicules in the stomach of hawksbill turtles *Eretmochelys imbricata* could affect buoyancy (Meylan 1988; J. Davenport, personal communication).

(ii) *Squamata, Lacertilia, Mosasauria*

Many complete and near-complete specimens are known but I have not been able to trace any report of gastroliths (also S. Lingham-Soliar, personal communication; D. A. Russell, personal communication).

(iii) *Squamata, Ophidia*

Sand ingested by *Aipysurus eydouxi* when feeding on benthic fish eggs (McCarthy 1987).

(iv) *Ichthyosauria*

Very many complete and near-complete skeletons, some with gut contents, are known. Sand is occasionally found but never gastroliths (Pollard 1968; Keller 1976; M. A. Taylor, personal observation), with only two exceptions known to me: a fragment of ribcage of indeterminate ichthyosaur with small pebbles, Lower Jurassic, England (OUM J.12146), and a skeleton of ?*Nannopterygius* containing small pebbles up to 1 cm maximum dimension, Upper Jurassic, Germany (SMNK jo 50; E. Frey, personal communication).

(v) *Eosuchia, Tangasauridae*

Hovasaurus boulei and *H. ranohirensis*, Upper Permian, Madagascar; specimens of *H. boulei* usually have well developed masses of gastroliths (Currie 1981, 1982; Baloge & Dutuit 1982); *Thadeosaurus*, Upper Permian, Madagascar, occasional gastroliths (Currie 1982).

(vi) '*Nothosauria*'

Single, presumably aberrant, gastroliths in two out of many specimens of *Neusticosaurus pusillus*, Middle Triassic, Switzerland (Sander 1989); otherwise, there appear to be no reports of gastroliths in any nothosaur (Storrs 1993).

(vii) *Placodontia*

There appear to be no reports of gastroliths in placodonts (S. Nosotti, personal communication).

(viii) *Plesiosauria, Pliosauroida*

Liopleurodon, Middle Jurassic, England, at least seven gastroliths plus a considerable amount of sand and grit, possibly formed by the action of stomach acids on further gastroliths of the same calcite-cemented sandstone (Martill 1992); *Peloneustes*, Middle Jurassic, England (Andrews 1910, pp. xvi–xvii); *Rhomaleosaurus victor*, Lower Jurassic, Germany (Fraas 1910); *Rhomaleosaurus zetlandicus*, Lower Jurassic, England: single gastrolith in specimen whose intestinal cavity had ruptured (Taylor 1992a); *Rhomaleosaurus* sp. indeterminate, Lower Jurassic, Germany, partial ribcage with gastroliths, small quartz gravel and sand (Janensch 1928); unidentified pliosauroids: one skeleton, Upper Jurassic, Russia, with gravel 3 to 4 mm diameter within a mass of cephalopod hooklets, but no larger pebbles (Zhuravlyev 1943); partial skeleton, Late Cretaceous, U.S.A. (Martin & Kennedy 1988); opalized skeleton, Cretaceous, Australia (Ritchie 1991). At least one record of *Polycotylus*, Upper Cretaceous, U.S.A., by Williston (1906) refers to an elasmosaur, and there is now some doubt about Williston's (1906)

records of gastroliths in *Polycotylus* and *Trinacromerum*, Cretaceous, U.S.A. (Storrs 1993).

(ix) *Plesiosauria, Plesiosauroida, Elasmosauridae*

Alzadasaurus colombiensis, Upper Cretaceous, Colombia (Welles 1962, pp.16, 26); *Alzadasaurus pembertoni*, Upper Cretaceous, U.S.A. (Welles & Bump 1949); ?*Alzadasaurus*, Upper Cretaceous, U. S. A. (Darby & Ojakangas 1980); *Brancaosaurus brancai*, Lower Cretaceous, Germany (Wegner 1914); *Cimoliosaurus?* sp., Upper Cretaceous, Canada (Russell 1967); *Elasmosaurus morgani*, Upper Cretaceous, U.S.A. (Shuler 1950); *Elasmosaurus serpentinus*, Upper Cretaceous, U.S.A. (Riggs 1939); *Thalassomedon* n.sp., Upper Cretaceous, U.S.A. (Storrs & Langston 1993); specimen cf. *Tuarangisaurus keyesi*, Upper Cretaceous, New Zealand (Wiffen & Moisley 1986); two indeterminate elasmosaurids, Upper Cretaceous, Antarctica (Chatterjee & Small 1989); indeterminate elasmosaurid, Upper Cretaceous, England (now BMNH 47295; Seeley 1877, as *Mauisaurus gardneri*; Welles 1962).

(x) *Plesiosauria, unidentified plesiosaurs*

Single gastrolith in partial skeleton cf. ?*Plesiosaurus hawkinsi*, Triassic–Jurassic boundary, England (OUM J.10337); fragment of skeleton, Upper Jurassic, England, still embedded in matrix but showing six whitish quartzite pebbles, up to 47 mm maximum dimension (DORCM G184; Taylor & Benton 1986); partial skeleton, Lower Cretaceous, England (now BMNH R.3316; Codrington 1870, pp. 170–171); one specimen, Cretaceous, Australia (Longman 1935); partial skeleton, Upper Cretaceous, U.S.A. (Martin & Kennedy 1988); gastroliths occurring 'in nearly every instance . . . of many plesiosaurs', Upper Cretaceous, U.S.A. (Brown 1904; also see Williston (1903, 1906) and Storrs (1993)); 'most' of a number of plesiosaur specimens containing ribs and vertebrae recovered from the Mangahouanga Stream, Upper Cretaceous, New Zealand (Wiffen & Moisley 1986).

(xi) *Archosauria, Crocodilia (marine forms only)*

Metriorhynchus sp., Middle Jurassic, England, single large gastrolith in partial skeleton (Martill 1986); *Steneosaurus bollensis*, Lower Jurassic, England and Germany (Westphal 1962; Buffetaut 1979, 1982; Walkden *et al.* 1987); *Teleosaurus cadomensis*, Upper Jurassic, France (Eudes-Deslongchamps in Buffetaut 1982).

(b) *Aves*

Spheniscidae: in general, 'penguins of nearly every species . . . swallow and regurgitate pebbles in amounts which would adjust their specific gravity far beyond the range of sea water densities likely to be encountered' (Stonehouse 1967, p. 160); 'penguins, living far from known sources, commonly carry stones of a wide variety of rock types'; the stones are commonly regurgitated near the nests and picked up on returning to sea (Emery 1963). Specific citations

include *Aptenodytes forsteri* (2–10 lb, i.e. approximately 0.9–4.5 kg, of granite, quartz and volcanic rocks, Ross in Sclater 1888, p. 330) and *Spheniscus magellanicus*, which was said by sealers to vomit up stones when coming ashore and swallow them again when going to sea (Boswall & MacIver 1975).

I have been unable to obtain data on the flightless alcid and pterodromid birds and various diving birds although cormorants *Phalacrocorax auritus* have been reported to carry gastroliths (Miller 1962).

(c) *Mammalia*

(i) *Pinnipedia, Otariidae*

These commonly possess gastroliths (reviews in Keyes 1968 and Riedman 1990). *Arctocephalus australis*: 'does not normally ingest stones' in the Falkland Islands (Hamilton 1934, p. 297); *Callorhinus ursinus*: 20 kg of stones in one individual (Scheffer in Mohr 1963); 50% of 20 pups before autumn migration carry gastroliths (Keyes 1968); *Eumetopias jubata*: 'rocks', 'pebbles' and/or 'gravel', including stones of up to 12 cm diameter, up to a volume of a few hundred cubic centimetres, found in 16 of 34 taken at sea (Fiscus & Baines 1966); rocks in 61 of 114 sampled (Mathisen *et al.* 1962); *Neophoca cinerea* (Marlow 1975, Walker & Ling 1981b); *Otaria byronia*: 'in . . . practically every sea lion . . . a quantity of stones, varying in size, roughly, but not invariably, with the size of the animal', up to 1.46 kg in a 2.3 m long male (Hamilton 1934, pp. 296–297; Vaz-Ferreira 1981); *Phocarcos hookeri* (Fleming 1951; Marlow 1975; Walker & Ling 1981a); *Zalophus californianus* (Emery 1941, 1963; Scheffer & Neff 1948; Mohr 1963; Fiscus & Baines 1966).

(ii) *Pinnipedia, Odobenidae*

Odobenus rosmarus, sand and gravel 'acquired incidentally from the habitats of their prey' (Fay 1981, p. 8, 1982; Nelson & Johnson 1987).

(iii) *Pinnipedia, Phocidae*

Erignathus barbatus, sand and gravel (Burns 1981); *Halichoerus grypus*, isolated report of one piece of clinker in one specimen (Legendre 1947); *Hydrurga leptonyx*, 'gravel' in a small percentage of animals (Øritsland 1977); *Leptonychotes weddelli*, 'a variety of stones, sands and muds' found in stomachs generally, ascribed to feeding on benthic organisms (Dearborn 1965, p. 44; also Clarke & MacLeod 1982b; Øritsland 1977), but not found by Eastman & Coalson (1974); *Lobodon carcinophagus*, 'gravel' in some (Perkins 1945; Øritsland 1977); *Mirounga angustirostris* (Mohr 1963); *Mirounga leonina*, sand and small pebbles commonly ingested by animals moving onto land for the breeding season, and apparently regurgitated before departure (Matthews 1962 in Mohr 1963; Ling & Bryden 1981; Laws 1960; Laws 1984); *Phoca hispida*, one specimen (Mohr 1963); *Phoca groenlandica*, two 'pebbles' in 1 out of 25 stomachs studied (Murie & Lavigne 1991).

(iv) *Cetacea, Mysticeti*

Balaena mysticetus, pebbles sometimes ingested

when filter-feeding on benthic crustaceans (Reeves & Leatherwood 1985); *Balaenoptera acutorostrata*, occasional 'gravel and stones' (Jonsgård 1951); *Eschrichtia robustus*, silt, sand and gravel as a result of filter-feeding on benthic crustaceans (Oliver & Kvittek 1984; Wolman 1985; Nelson & Johnson 1987).

(v) *Cetacea, Odontoceti*

Berardius bairdii, pebbles when feeding on benthic forms (Balcomb 1989); *Delphinapterus leucas*, pebbles when feeding on benthic forms (Brodie 1989); *Physeter macrocephalus*, stones in a few whales, presumably accidentally ingested when feeding on benthic forms (Takahisa Nemoto & Keiji Nasu 1963; Martin & Clarke 1986; Rice 1989).

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