

A review of gastrolith function with implications for fossil vertebrates and a revised classification

OLIVER WINGS



Wings, O. 2007. A review of gastrolith function with implications for fossil vertebrates and a revised classification. *Acta Palaeontologica Polonica* 52 (1): 1–16.

Misleading interpretations of “gastroliths” in fossil taxa have complicated the use of this term in palaeontology. This paper reviews the definitions and ascribed functions of gastroliths. According to the suggested definition, gastroliths are hard objects within the digestive tract of animals—without specification of the mechanisms that are responsible for their accumulation. To further improve definitions, the origin-based terms “bio-gastrolith”, “patho-gastrolith”, and “geo-gastrolith” are introduced. The term “exolith” is introduced for isolated clasts with a possible history as geo-gastroliths. Hypotheses about the function of stomach stones in fossil and extant taxa are reviewed, discussed and supplemented with new research. Trituration and mixing of foodstuff are the generally accepted functions of gastroliths in many vertebrates, including birds. In contrast, ballast provided by swallowed stones is considered to be of limited importance for buoyancy in aquatic animals. Other functional hypotheses include mineral supply and storage, stomach cleaning, maintenance of a beneficial microbial gut flora, destruction of parasites and alleviation of hunger. Accidental ingestion of sediment, either by being mistaken for prey, by being attached to it, during playing or due to pathological behaviour, is considered to be common. Different functions may overlap in various taxa.

Key words: Gastroliths, stomach stones, gastrolith function, palaeobiology, ingesta, vertebrates, digestion, digestive tract.

Oliver Wings [wings@web.de], Institut für Paläontologie, Universität Bonn, Nussallee 8, D-53115 Bonn, Germany; present address: Institut für Geowissenschaften, Universität Tübingen, Sigwartstr. 10, D-72076 Tübingen, Germany.

Introduction

Knowledge of stones in the digestive tract of animals reaches back to prescientific times: e.g., grit use in birds (Spallanzani 1785) or African crocodile myths (Neill 1971). Stubbes (1668), in the oldest reference to crocodile stomach stones, proposed that they had a digestive function. After Mayne (1854) had introduced the term “gastrolith” into science, it was subsequently used for crustaceans (Huxley 1880) and a pathologic gastric calculus (Anonymous 1892). Wieland (1906), without mentioning the former publications, extended the meaning of gastroliths to swallowed stones in fossil and extant vertebrates, reporting worn and polished quartz pebbles associated with plesiosaurs and sauropod dinosaurs, as well as stomach stones in extant lizards, alligators and birds.

Since then, the term “gastrolith” has been incongruently applied across palaeontology, biology and medicine to a large variety of stones or concretions found in the digestive tract of invertebrates and vertebrates (Figs. 1, 2), creating considerable confusion (e.g., Frizzell and Exline 1958). Furthermore, several researchers have ascribed specific functions to gastroliths without critically testing their hypotheses. Therefore, it is extremely difficult to interpret stomach stones in fossils, although they are potentially important evidence for palaeoecology, diet, and behaviour.

This paper is the first review of the gastrolith literature as a whole. It consists of two parts. The first part—“Terminology” presents a revised nomenclature by clarifying defini-

tion and separating existing interpretations with new functional terms. The second part—“Gastrolith function” utilises these terms in discussing and representing new data on gastrolith function and distribution with inconsistencies and palaeobiological problems highlighted.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; HLMD, Hessisches Landesmuseum Darmstadt, Germany; IPB, Institut für Paläontologie der Universität Bonn, Germany; LS, Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany (specimen currently deposited in Landesamt für Denkmalpflege Rheinland-Pfalz, Mainz); MNA, Museum of Northern Arizona, Flagstaff, USA; MWC, Museum of Western Colorado, Grand Junction, USA; NHMS, Naturhistorisches Museum Schleusingen, Germany.

Terminology

Existing definitions of “gastrolith”.—Definitions of the term “gastrolith” are rather broad, having been used to describe several types of “stones” associated with the digestive tract, each with a different functional origin. Dictionary definitions are limited to a few characteristics that do not reflect the distribution of stomach stones within animals. For example, a high polish is often attributed to gastroliths (Bates and Jackson 1980; Manley 1991, 1993; Jackson 1997; Allaby and Allaby 1999), but is rarely found on stomach stones in extant birds

(Wings 2004; Wings and Sander 2007). Definitions also are often restricted to occurrences within specific groups of animals (e.g., crustaceans, Huxley 1880; reptiles, Jackson 1997).

Definitions commonly include proposed functions of the stones, such as grinding food (Gove 1971; Bates and Jackson 1980; Morris 1992; Farlow and Brett-Surman 1997; Currie and Padian 1997; Jackson 1997; Allaby and Allaby 1999) or buoyancy control in aquatic animals (Jackson 1997), although many of these suggestions are not verified or tested. Other definitions include taphonomical and sedimentological components (Challinor 1974; Wyatt 1986) which are not essential for describing gastroliths in general and should be avoided.

To illustrate these problems in more detail, a selection of previous definitions are discussed here. The term “gastrolith” was introduced by Mayne (1854) as: “Gastrolithus—a stone or calculus in the stomach” (Soanes and Stevenson 2004). Unfortunately, this simple definition was not given priority by later authors. For example, Huxley (1880: 29) used the term solely in connection with crustaceans: “... there are commonly to be found at the sides of the stomach two lenticular calcareous masses, which are known as »crabs’-eyes«, or gastroliths.”

Skoczylas (1978: 606) also provided a very simple definition for gastroliths: “When the objects swallowed remain in the stomach, they are called gastroliths.” It includes all foreign objects in the digestive tract including hard-to-digest food items. While the occurrence of most of the gastroliths—especially intentionally ingested stones—is normally restricted to the stomach, the entire digestive tract of vertebrates can contain gastroliths (personal observation on ostriches).

As a general term for stones transported by biological agents, Johnson (1993) introduced the term bioclast. He incorporated not only gastroliths, but also “biofacts”, modified stones carried or externally transported by animals (e.g., chimpanzee tools, Boesch and Boesch 1981), and “bioports”, unmodified stones carried, externally transported, or moved by animals (e.g., birds of prey, apes and rodents, Johnson 1993). The term bioclast is regularly used in carbonate petrography for fossils seen in thin sections (Flügel 2004) and hence should not be used for biologically transported stones. Also, the need for such a general term is rather limited since gastroliths and biofacts are not commonly found together and it is likely that the functions of internally and externally carried stones will be different.

In summary, most existing definitions are impractical or too specific. A useful definition for geoscientists and biologists should contain as many applicable criteria as possible without any assumptions. It should not mention physical characteristics (e.g., roundness or polish), as they limit the applicability of the definition, or contain restrictions regarding specific groups of animals. A limitation of the definition to vertebrates also should be avoided, as it would omit sediment and concretions found in arthropods. Lastly, a definition should not be limited by implied functions, because they are still unclear in some groups and interdependencies between proposed functions might exist. To be practical, the definition should be faithful to the literal meaning of “gastrolith”, encompassing all stones and stone-like objects in the stomach.

A new definition for gastrolith.—Because it is impossible to determine the retention time of pebbles in the digestive tract of wild animals, all stones found in the digestive tract should be called gastroliths. This implies that a separation between gastroliths with a real function and accidentally swallowed objects is not feasible. The method by which gastroliths exit the body (excretion, regurgitation or post-mortem release) is not relevant for the definition.

Literal implementation of the term gastrolith—“stomach stone”—would exclude all particles of sand size and smaller, but small sediment particles are commonly found in small species and juveniles, where they fulfil the same function as stones in large animals (Best and Gionfriddo 1991). Furthermore, sand may have been derived from sandstone taken in as clasts, but disintegrated in the stomach. The minimum grit size (with a maximum diameter of less than 0.2 mm, Best and Gionfriddo 1991) found in small bird species must be considered when the minimum size of gastroliths is defined. The standard grain size border between silt and sand at 0.063 mm (e.g., Flügel 2004) is suggested in order to separate gastroliths from sediment swallowed due to clearly geophagical behaviour. This artificially set grain size limit improves clarity of definition, even if similar functions behind geophagical and lithophagical behaviour cannot always be excluded. Gastroliths typically possess a size between 0.1% and 3% of the body length of the animal (Wings, unpublished data), but it is not useful to define a minimum proportion of gastrolith size to body size, since even very small particles may have important functions in large animals. Since the term gastrolith is widely used for natural and pathological concretions, these objects must be included in any definition.

A new universal definition is proposed here: “gastrolith”—a hard object of no caloric value (e.g., a stone, natural or pathological concretion) which is, or was, retained in the digestive tract of an animal.

Gastroliths are larger than 0.063 mm in diameter, occur regularly in several groups of invertebrates (e.g., crustaceans) and vertebrates (e.g., certain archosaurs, pinnipeds), and can perform several functions, most importantly food trituration, as in herbivorous birds. The physical characteristics of gastroliths, especially roundness and surface texture, are strongly dependent on their function and other factors such as rock type, retention time, and abrasion rate in the stomach.

Categories of gastroliths regarding their origin.—Differences occur in geological, biological, and medical definitions of gastroliths. In vertebrate palaeontology gastroliths are always swallowed stones (Figs. 1C–F, 2). To the contrary, invertebrate biologists understand gastroliths as stomach concretions formed in crustaceans and used for mineral storage (e.g., Scheer 1964; Fig. 1A). Some vertebrate biologists, veterinarians and pathologists define gastroliths as pathological, stone-like concretions which were formed by swallowed and felted hair or vegetable fibres in the stomach of herbivorous mammals such as bezoar goats (the so-called “bezoar stones”, Elgood 1935), llamas (Hänichen and Wiesner 1995) or humans (e.g., Allred-Crouch and Young 1985; Fig. 1B).

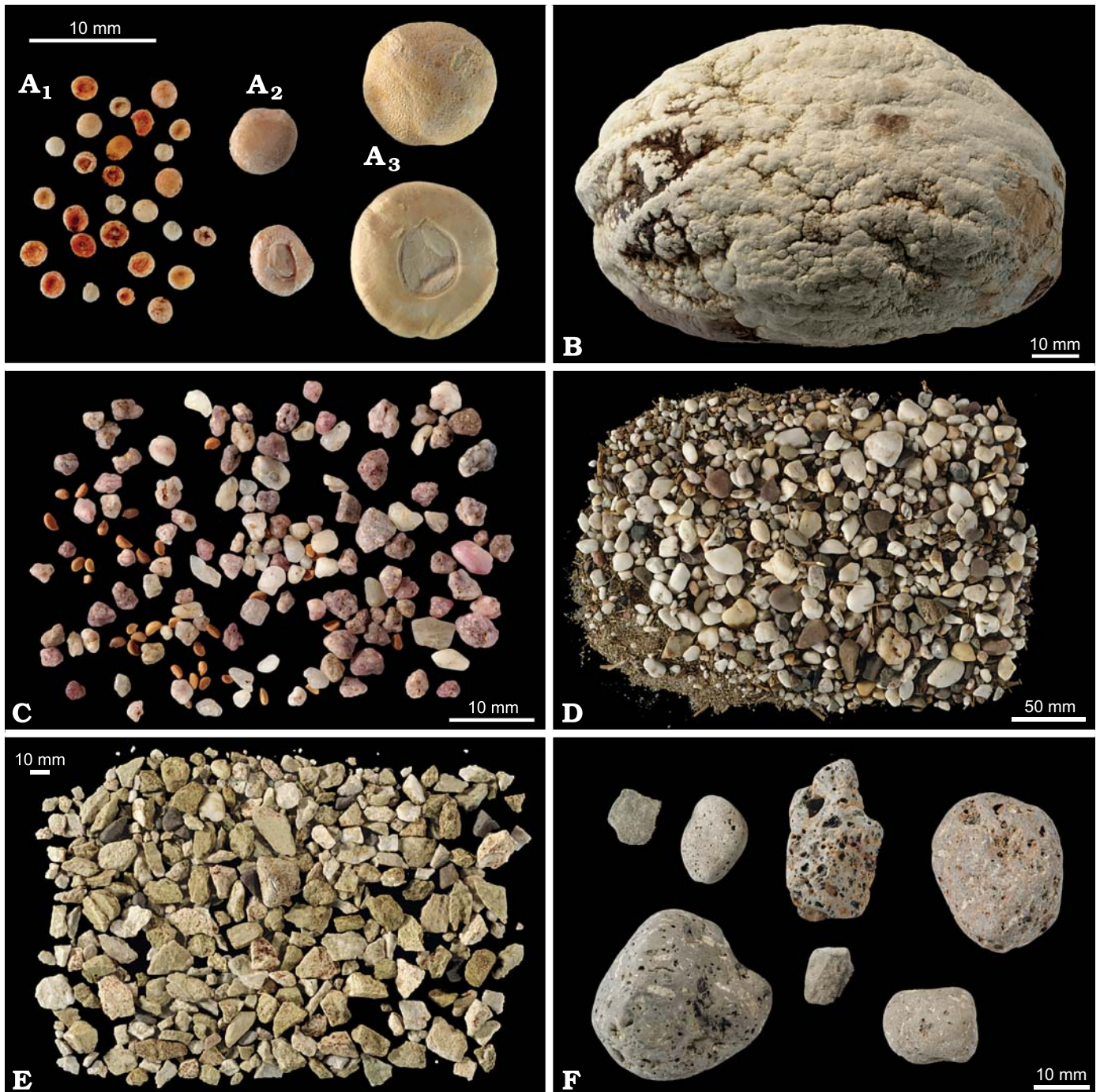


Fig. 1. Examples for gastroliths in extant animals. **A.** Bio-gastroliths of three different taxa of crustaceans. **A₁**, Mexican dwarf orange crayfish (*Cambarellus*) (IPB R566); **A₂**, blue crayfish (*Procambarus*) (IPB R567); **A₃**, yabby (*Cherax*) (IPB R568). **B.** A patho-gastrolith from a prehensile-tailed porcupine (*Coendou*) (IPB R569), held in captivity in Wilhelma Zoo in Stuttgart/Germany. This patho-gastrolith shows the impression of the inner stomach wall. It did fill the complete stomach and presumably caused the death of the animal due to starving. **C.** Set of geo-gastroliths of a ptarmigan (*Lagopus*) (IPB R570). **D.** Set of geo-gastroliths of an ostrich (*Struthio*) (IPB R571). **E.** Set of geo-gastroliths of an alligator (*Alligator*) (IPB R572). **F.** Set of geo-gastroliths of a northern elephant seal (*Mirounga*) (IPB R573).

Finally, some geologists call all isolated polished pebbles in fine-grained sediments gastroliths (Stokes 1987). Except for the latter, all different meanings of the term gastrolith are well-established, widely distributed and used often in their field of science. Completely new terms would probably not be accepted by the scientific community. Nevertheless, the mis-

leading and contradicting definitions cause confusion if mixed up (Frizzell and Exline 1958). Unfortunately, later authors never differentiated between the separate origin and function of gastroliths, even though more specific terms should be used.

Frizzell and Exline (1958) suggested the terms “crustacean gastrolith” and “saurian gastrolith” to avoid confusion.

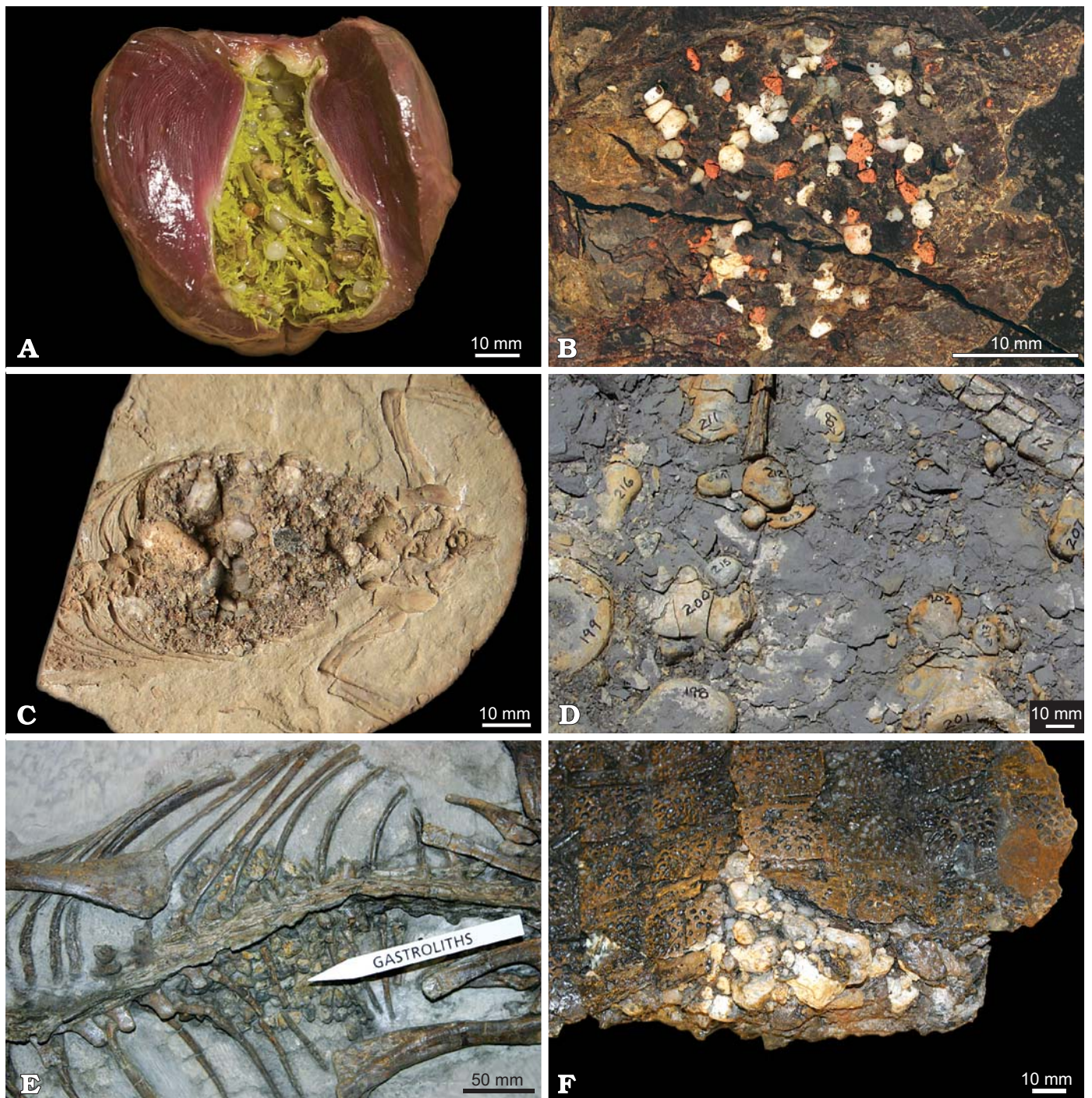


Fig. 2. Examples for *in situ* gastroliths in vertebrates. **A.** Cut-open gizzard of an extant capercaillie (*Tetrao*) from Russia during dissection (gastroliths: IPB R574). Strong muscles surround the gizzard which contains the gastroliths and plant matter which has been ground. **B.** Gastrolith cluster in the Oligocene galliform bird *Palaeortyx* from Enspel/Germany (PW 2005/5023a-LS). **C.** Cluster of gastroliths with variable grain sizes in the aquatic tangasaurid *Hovasaurus* from the Upper Permian Sakamena Formation of southern Madagascar (NHMS WP1499). **D.** Field photo of an undescribed plesiosaur skeleton with gastroliths from the Upper Cretaceous Tropic Shale of Glen Canyon National Recreation Area, Utah/USA (MNA V10046). **E.** Cluster of ≥ 112 gastroliths in the ceratopsian dinosaur *Psittacosaurus* from the Lower Cretaceous Ondai Sair Formation of Ussuk/Mongolia (AMNH 6253). **F.** Gastrolith cluster in the fossil alligatoroid *Diplocynodon* from the Eocene of Messel/Germany (HLMD Me 7493).

While “crustacean gastrolith” would be acceptable as these accretions are only known from crustaceans, the term “saurian gastrolith” is inaccurate, as it suggests that swallowed pebbles are exclusively associated with reptile remains, whereas in reality, they are known from several groups of an-

imals, including mammals. For a more general and accurate distinction, the origin of gastroliths should be included in the name.

To differentiate between the fundamentally different biological and palaeontological meanings of gastroliths, it is

proposed to use the following suitable prefixes for the term “gastrolith”:

- “bio-gastrolith” for non-pathological invertebrate concretions (Fig. 1A)
- “patho-gastrolith” for pathological stones formed in the stomach (Fig. 1B)
- “geo-gastrolith” for swallowed sediment particles such as pebbles and grit (Figs. 1C–F, 2).

“Stomach stones” can be used as a general synonym for gastroliths, without any separation into bio-, patho-, and geo-gastroliths. When geo-gastroliths are deposited in a gizzard, “gizzard stones” (e.g., Milton and Dean 1995; Twigg 2001) can be used as a synonym. “Grit” is often used for geo-gastroliths in birds (e.g., Gionfriddo and Best 1999). “Crop stones” was used for geo-gastroliths in some older publications (e.g., Forbes 1892), but this term is misleading and should be abandoned as the stones are normally situated in the stomach.

Introduction of the term “exolith”.—Many exotic stones with unknown provenance and transport mechanism are called “gastroliths” (Stokes 1987). This term should be restricted to true gastroliths and not be used for stones that are not associated with fossil vertebrates and that cannot be identified unambiguously. Other existing names for clasts in fine-grained sediments with unknown origin and transport mechanism are “foreign stones”, “extraneous stones”, “erratics”, “dropstones” and “exotic stones” (e.g., Bennett et al. 1996).

Among these existing terms, “erratic” is probably the most exact one. Erratic is defined as: “... a stone which has been transported and deposited by some agent other than those which have laid down the fine sediment in which it occurs” (Hawkes 1951: 18) and hence originally not restricted to transport by ice. The same applies to the term “dropstone” (Bennett et al. 1996). However, the terms “erratic” and “dropstone” have the disadvantage of commonly being used in connection with transport by ice, and the terms “erratics” or “erratic boulders” have been available for many years now but were never accepted for all types of stones in question.

Highly polished stones, out of depositional context and not occurring with bone material, are common in some formations (e.g., Stauffer 1945). They are especially common in dinosaur-rich, fine-grained sediments like those of the Cedar Mountain Formation (Stokes 1987). They could have been transported into the deposits as dropstones by several rafting agents (e.g., tree roots) or by hyperconcentrated flows (Zaleha and Wiesemann 2005) and are not *a priori* gastroliths. Consequently, such stones should not be called “gastroliths” (even if they may represent former gastroliths), but should be addressed with another term.

Stokes (1942) noted the improbability of the idea that all isolated stones in the Late Jurassic Morrison Formation are gastroliths. He suggested to abandon the term “gastrolith” in favour of a non-committal designation as long as a connection between dinosaurs and these stones is not proven and proposed the name “Morrison stones” (Stokes 1942). Fortunately, this term was not used by later authors, since such stones are not restricted to the Morrison Formation. While

this was acknowledged later (Stokes 1987), no new term lacking stratigraphical specificity was suggested.

For a better characterisation of isolated clasts, a new term is introduced here which can be applied to any exotic rock of unknown origin in all fine-grained sediments from different depositional environments and of different compositions: “exolith”—an exotic rock in fine-grained sediments which may show a high polish and which potentially (but not necessarily) was a former gastrolith. Etymology from the Greek: *exos*—from outside, *lithos*—stone

Definition of geophagy and lithophagy.—Voluntary and purposeful ingestion of sediment particles by animals can be divided into two groups, lithophagy and geophagy, which have not been properly separated until now (e.g., Skoczylas 1978). Lithophagy describes the deliberate consumption of stones. These stones become gastroliths after their ingestion. Geophagy is the consumption of soil and is known from reptiles, birds, and mammals. These soils, rich in clay, salt or fat, serve mainly as a food supplement for the supply of specific minerals or for medical purposes (Jones and Hanson 1985; Beyer et al. 1994; Abrahams and Parsons 1996; Klaus and Schmid 1998; Diamond et al. 1999; Setz et al. 1999).

Geophagy is often used synonymously with lithophagy (e.g., Skoczylas 1978) and is hence addressed here. Even if the grain size border for the classification of the two habits is probably continuous, geophagy should be separated from lithophagy because the reasons behind both behaviours are generally different. It is suggested that lithophagy should be separated from geophagy by using a grain size limit of 0.063 mm (sand/silt grain size border), as with the definition of the term “gastrolith”. Larger sediment particles are ingested due to lithophagy, whereas the intake of smaller material is being ascribed to geophagy.

Gastrolith function

On the following pages, each proposed function is reviewed and discussed briefly. Several hypotheses are poorly supported by data and are not generally accepted by the scientific community, but also are discussed briefly for the sake of completeness.

Trituration of ingesta.—Trituration of foodstuff using geo-gastroliths is best known in birds, and the functional role of teeth is often ascribed to bird gastroliths (Ziswiler and Farnier 1972). In birds, swallowed food is soaked with stomach juices in the proventriculus (glandular stomach); following this, rhythmic muscular contractions of the gizzard macerate hard food items with the help of gastroliths. The disintegration of large food items and therefore the contact area for digestive enzymes are both increased by gastrolith action (Sokol 1971). Without gastroliths, the bird gizzard also tends to retain fibrous material that can cause partial or complete constipation (Thomas et al. 1977).

Extensive studies on stomach contents of carrion crows (*Corvus corone*), hooded crows (*Corvus cornix*), and rooks

(*Corvus frugilegus*) have shown that the number of gastroliths is halved during summer due to a predominantly insectivorous diet in these months (Röriq 1900a). An increase in the number of gastroliths in faeces of dunnocks (*Prunella modularis*) also correlates with a change in diet from insects to both seeds and insects (Bishton 1986), implying a constant excretion rate of gastroliths from the digestive tract. This has been interpreted as an indication for the assistance of gastroliths in the grinding of vegetable matter (Bishton 1986).

While some authors doubt the effectiveness of gastroliths on food trituration in birds (e.g., Walton 1984), since not all individuals of a given species are alleged to contain stones; studies have shown that gastroliths are always present in numerous galliform bird taxa as well as in ratites (e.g., Jacobi 1900; Röriq 1900b; Gionfriddo and Best 1999; Wings 2003, 2004). Gastroliths also are known from avian fossils such as the basal ornithurine bird *Yanornis* (Zhou et al. 2004) and the galliform bird *Palaeortyx* (Mayr et al. 2006; Fig. 2B).

The question as to whether gastroliths are essential for survival of birds that possess them is controversial. In snow-rich winters, when access to grit is not available, grain-eating birds may starve to death with food-filled stomachs (Wacquand-Geozelles 1892; Siivonen 1963). However, the general conclusion regarding gastrolith function in grain-feeding birds is that grit is dispensable, but supports more effective grain digestion (Mangold 1927a). Digestibility of food to birds may be increased by 10% following addition of grit to the diet (Duke 1986). Mangold (1927b) reported an increase of digestibility of food to domestic chickens of approximately 25–30%.

In fishes, mullets (Mugilidae) have a strong muscular stomach and probably use deliberately ingested sand and mud to triturate their ingesta (Thomson 1966). A macerating function has also been proposed for sand and gravel found in several insectivorous and omnivorous lizards (Johnson 1966; Sokol 1971). Sharp gastroliths may be helpful for penetrating the exoskeletons of certain arthropods in the stomachs of animals which do not chew their food.

Several authors have suggested the utilisation of gastroliths in the physical breakdown of food in the stomach of pinnipeds (e.g., Mathews 1929; Spalding 1964). This has been speculated to be dangerous in marine tetrapods, because crushing of hard or chitinous food remains like cephalopod beaks, sucker rings and hooklets could produce sharp splinters small enough to pass into the intestine (Taylor 1993). However, birds are capable of swallowing and breaking down sharp objects like chert or glass without any damage to the digestive tract (Jacobi 1900; Gillette 1994; Wings, personal observations on ostriches 2003). Furthermore, vigorous collisions of gastroliths during gastric contractions were observed with contrast radiography and fluoroscopy in Australian sea lions (*Neophoca cinerea*) (Needham 1997), suggesting indeed a triturative or mixing function. The stones also might have acted as a sieve by retaining larger food particles in the stomach (Needham 1997).

Digestive help is the most frequent suggestion for gastrolith function in fossil vertebrates (e.g., Currie 1997). Gastroliths in stereospondyl amphibians are believed to have been swallowed for food processing (Warren 2000) and while this

also has been the most widely accepted hypothesis for gastrolith function in sauropod dinosaurs (e.g., Christiansen 1996), recent research revealed that it is not supported by sedimentological, taphonomical and palaeobiological evidence (Wings 2003, 2004, 2005; Wings and Sander 2007). Only a small percentage of sauropod finds contain gastroliths and the amounts, size, surface structure and composition of unambiguous sauropod gastroliths speak against their use for trituration of foodstuff. However, the gastrolith clusters of some derived theropod dinosaurs such as *Sinornithomimus* and *Caudipteryx* compare well with those of birds, suggesting that a gastric mill evolved in the avian stem lineage (Kobayashi and Lü 2003; Wings and Sander 2007).

Mixing of foodstuff.—The mixing of foodstuff by gastroliths occurs by necessity together with trituration. In ostriches, which mainly feed on grass (Wings 2004), the stones mix the food content and prevent the blocking of the pyloric sphincter with agglutinated balls of grass. The fact that ostriches without access to stones die of constipation (Ralph Schumacher, personal communication 2000) emphasises not only the triturative function but also the vital mixing function of the stones.

Gillette (1992, 1994, 1995) proposed a mixing function for sauropod gastroliths. He suggested that stones in sauropods “may have served primarily for creating and maintaining turbulence in the fluids of the capacious alimentary tract, churning food and digestive juices for thorough chemical digestion” (Gillette 1992). As recent studies have shown (Wings 2003, 2004), gastroliths in herbivorous birds are directly embedded in the pulped food and not surrounded by stomach fluids (Fig. 2A), and the number of stones present in the stomach regions of sauropod finds would have been too small for effective processing of foodstuff either by trituration or by mixing (Wings and Sander 2007).

Mineral supply.—Geophagy in many taxa has presumably evolved for mineral supplementation (Setz et al. 1999). Proving mineral uptake from ingested stones is difficult; however, the abrasion of the stones in the gizzard unquestionably releases minerals which are then available for metabolic uptake. All vertebrates have mineral requirements that are usually fulfilled by food intake, but deficiency symptoms and nutritional diseases such as a disturbed bone metabolism may be responsible for gravel ingestion (e.g., in turtles, Dennert 1997, 2001).

Birds provide exemplary studies of the connection between gastroliths and mineral uptake. With the exception of the high calcium need of egg-laying birds, most other mineral requirements of birds are similar to those of mammals (Fisher 1972). Mineral requirements of birds can be divided into chemical elements required for structural purposes (Ca, P), elements required for metabolic homeostasis (Na, K, Cl), and trace elements (Mg, Mn, Zn, Fe, Cu, Mo, Se, I, Co, Cr) (Fisher 1972).

Limestone is an excellent source of calcium. This rock type is widely distributed and is easily soluble in the stomach acid. It has been known for centuries that a good supply of calcium carbonate (as limestone or shells) is beneficial to bone growth and eggshell production in chickens (e.g., Mangold 1927a). Nesting pheasant hens (*Phasianus colchicus*)

even appear to have the ability to selectively ingest limestone (Harper 1964). However, most gastroliths are composed of quartz varieties. In birds, the silica supply from disintegration of quartz pebbles in the stomach was discussed by Mangold (1927a), who concluded that the slow abrasion on the surface of the pebbles could not meet the need of the body for silica. In contrast, recent experiments on ostriches have shown that stones undergo relatively fast abrasion in gizzards, with quartz gastroliths 2 cm in diameter being completely destroyed after one year (Wings and Sander 2007). In any case, physiological requirements for silica are very low and are virtually always met by silica contained in the diet (Marcus Clauss, personal communication 2004).

Trace elements that cause the colour of common quartz gastroliths cannot play an important part in mineral supply because the erosion rate is still too low to release significant amounts of trace elements. However, this is not the case for gastroliths of other rock types. Bialas et al. (1996) reported that—in addition to their trituration function—feldspar gastroliths provide birds with potassium and calcium. Greywacke contains—beside quartz—feldspar, potassium, magnesium, iron and many other minerals useful for birds (Bialas et al. 1996). In order to meet metabolic requirements, many herbivorous animals need additional salt (NaCl) to supplement their diet. Elephants, for instance, grind up complete stones and excavate extensive caves in search for salt (Redmond 1991; Lundberg 2003), and groundhogs (*Marmota*) regularly eat sand and gravel for the same reason (Weeks and Kirkpatrick 1978).

It would certainly be useful to compare the quantities of minerals provided by gastroliths with the mineral uptake from diet and the physiological requirements of certain gastrolith-using species in a future study. Except for calcium, the proven importance of gastroliths as a source of minerals is rather limited.

Stomach cleaning.—The direct ingestion and use of small quantities of gastroliths (excluding indirect consumption of grit through avian prey) is well known in various birds of prey (Cade 1982; Fox 1995). The small stones (4–20 mm in diameter) consumed by raptorial birds on a regular basis, are specifically referred to as “rangle” (Bruce in press). Birds of prey may pick up rangle any time during the day and typically retain it overnight. The stones are ingested separately from food and are regurgitated in a group the following day, before feeding (Fox 1995). The stones seem to help clean the stomach, removing mucus, grease, and any excess of cuticle of koilin lining (Fox 1976, 1995), and possibly have a purging function in the digestive tract (Bruce in press). Stones used as rangle are typically well-rounded, with a slightly textured surface (Fox 1995), but may also be polished (Cade 1982). Stones are rarely found in regurgitated pellets, and if so, they are usually smaller and sharper than rangle and represent accidentally swallowed gastroliths of prey animals such as quails or pigeons (Fox 1995). Gastroliths in nesting cormorants (*Phalacrocorax*) and divers (*Gavia*) are also thought to be used for stomach cleaning (Fox 1976).

Fox (1995) believed that the only common denominator for taxa using gastroliths for stomach cleaning was a carnivorous diet, often with a high fat content. Indeed, pinnipeds commonly regurgitate their gastroliths (e.g., Fleming 1951; Marlow 1975), and the stones may also facilitate regurgitation of indigestible parts (Baker 1956; King 1983). Penguins also frequently regurgitate stones together with parts of their prey (e.g., Murphy 1936; Spletstoeser and Todd 1999; Hocken 2005). In these taxa, gastroliths might provide a critical mass needed for complete regurgitation of the stomach contents. A closely related hypothesis is the use of gastroliths to remove objects obstructing the oesophagus, as discussed for seals by Waite (2000).

The rare occurrence of gastroliths in sauropod dinosaurs (Wings 2004; Wings and Sander 2007) permits speculation about a similar function in these giant herbivores. Perhaps small amounts of stones were ingested by sauropods in order to remove unwanted remains of foodstuff, such as natural resins, from the digestive tract.

In summary, the hypothesis that gastroliths help birds of prey to cleanse their stomach is plausible. This function is more unlikely in pinnipeds, since their gastroliths are commonly retained for several weeks (Bryden 1999), and it is mere speculation for other taxa.

Secretion of stomach juices.—Gastroliths also may enhance digestion by further stimulating the secretion of digestive fluids (Humboldt 1852; McIntosh et al. 1962), and may help to build up secretions to make swallowing easier (Fox 1976). While it is plausible that gastroliths influence the secretion rate of digestive juices in certain taxa, there is no supporting evidence for this *ad hoc* hypothesis from any gastrolith study on extant animals. The magnitude of pH fluctuation due to dissolution of calcareous gastroliths in the stomach also is unclear.

Mineral storage.—Bio-gastroliths, also called “crab’s eyes”, are known from several groups of crustaceans such as crabs (e.g., McCarthy and Skinner 1977) and crayfish (e.g., Travis 1960). Bio-gastroliths are a bio-mineral formed by specialised areas of the stomach epithelium (gastrolith discs) during premoulting stages (McCarthy and Skinner 1977). These deposits are composed mainly of calcium carbonate with a small proportion of organic material including proteins and carbohydrates (Tsutsui et al. 1999). They are presumed to serve as storage for minerals resorbed from the old exoskeleton. After ecdysis, these minerals will subsequently be utilised in calcification of the new exoskeleton. A similar storage function is not plausible for gastroliths known from vertebrates because calcareous geo-gastroliths are being dissolved very quickly (Wings and Sander 2007).

Hydrostatic function.—The use of stones as ballast is a well-established hypothesis for gastrolith function in aquatic animals. Even South American native tribes believed that crocodilians “like to augment their weight” with stones (Humboldt 1852), and as early as in the 19th century the idea was discussed in the scientific literature. While Humboldt (1852) stated this to be an “absurd hypothesis” for crocodilians, Murray and Renard

(1891) reported that sealers commonly believed that stones act as ballast in pinnipeds and penguins. Since then, many detailed but contradictory publications both for (e.g., Taylor 1993) and against (e.g., Baker 1956) gastroliths as help in buoyancy control appeared, with no apparent consensus.

Compensation of positive buoyancy is easier to accomplish by ingestion of gastroliths than by pachyostosis, the thickening of bone tissue. Rocks have a higher density than bones (see Taylor 1993 for details), and bone growth requires more time and has great metabolic costs, whereas stones can be swallowed and regurgitated rapidly. Disadvantages include the limited availability of suitable stones, the space occupied in the digestive tract, and possible constipation.

A strong case was proposed in a comprehensive study by Cott (1961) on *Crocodylus niloticus*. Cott (1961) suggested that the increase of specific gravity provided by gastroliths makes it easier to stay underwater and draw struggling prey under the surface. The stones may also help maintain a neutrally buoyant position within the water column (Storrs 1993). Gastroliths accumulate in the gut, ventral and posterior to the lungs: their position tends to elevate the anterior end of floating crocodiles and stabilises them against rolling (Cott 1961). Stoneless juveniles must use limb movements to prevent rolling (Seymour 1982). Gastroliths also may increase the useable pulmonary volume and O₂ storage available to submerged crocodiles, resulting in extending diving times by about 12% (Seymour 1982), though this hypothesis was never tested explicitly.

The hypothesis that stones in marine mammals are used as ballast to aid in diving (Murray and Renard 1891) as well as for balancing and buoyancy control, received considerable support in the pinniped literature. For instance, a study on South American sea lions (*Otaria flavescens*) revealed a positive correlation between gastrolith mass and body length, which was interpreted as an indication that gastroliths could be involved in buoyancy control (Alonso et al. 2000).

Using gastroliths to correct position in the water would be a useful adaptation especially during fasting, when thickly covered with blubber, when sleeping, or when swimming upside down (Harrison and Kooyman 1968). However, as stated by these authors, the relatively small amount of stones would hardly exert a significant effect in stabilising the body, increasing momentum, stemming the tide or currents, resisting waves, increasing drag, and any other activity where ballast might be advantageous.

Taylor (1994) discussed the complex interactions between hydrodynamic and hydrostatic buoyancy control involving factors such as body composition, lung volume, locomotion style, speed, and diving depth. Taylor (1993) suggested a correlation between the presence of gastroliths, their use for buoyancy control, and the mode of locomotion in aquatic animals. Because of the common occurrence of gastroliths in predatory underwater “flyers” (penguins, otariid pinnipeds, and plesiosaurs, but note the absence of gastroliths in Chelonioidae), and the presumed absence of gastroliths in taxa like phocid pinnipeds, which have their hind limbs modified to act as caudal fins (Taylor 1993), a locomotor function, presumably in buoyancy control was suggested (Taylor 1994). Un-

derwater “flyers” may be highly adapted to invoke density variation with water depth, particularly at low speeds, by exploiting the flexibility and efficiency of gastroliths to provide enhanced hydrostatic control efficiency (Taylor 1994).

Reports of the gastrolith presence in underwater “flyers” were reviewed by Taylor (1993). New studies on sea lions (e.g., Needham 1997; Alonso et al. 2000), penguins (e.g., De Villiers and De Bruyn 2004; Hocken 2005) and plesiosaurs (e.g., Cicimurri and Everhart 2001) confirmed the presence of gastroliths in these taxa. However, several gastrolith occurrences are known from undulatory swimmers, i.e., ichthyosaurs (Cheng et al. 2006), a mosasaur (Wings personal observations 2002), cetaceans (Nemoto and Nasu 1963; Gaskin and Cawthorn 1967; Brodie 1989; Kussakin et al. 2001) and the walrus (*Odobenus rosmarus*) (e.g., Allen 1880; Nelson and Johnson 1987; Gjertz and Wiig 1992). While many of these reports may be attributed to accidental ingestion as suggested by Taylor (1993), gastroliths in seals are far more common than noted by Taylor. Among members of Phocidae, gastroliths have been found in bearded seals (*Erignathus barbatus*) (Burns 1981; Hjelset et al. 1999), harp seals (*Phoca groenlandica*) (Nordøy 1995; Lucas et al. 2003), hooded seals (*Cystophora cristata*) (Lucas et al. 2003), Weddell seals (*Leptonychotes weddellii*) (Dearborn 1965; Clarke and MacLeod 1982), northern elephant seals (*Mirounga angustirostris*) (Anthony 1924; Condit and Le Boeuf 1984; Webb et al. 1998), southern elephant seals (*Mirounga leonina*) (Laws 1956; Ling and Bryden 1981; Bryden 1999; Waite 2000; Carlini et al. 2001), crabeater seals (*Lobodon carcinophaga*) (Perkins 1945; Lowry et al. 1988) and leopard seals (*Hydrurga leptonyx*) (Hall-Aspland and Rogers 2004).

While many seals retain gastroliths during their terrestrial moulting season (Bryden 1999), they do not always regurgitate the stones before returning to sea (e.g., Nordøy 1995), suggesting a possible function of gastroliths in water. In some studies, a high percentage of examined seals possessed gastroliths. Laws (1956) reported that 84% of 139 southern elephant seal stomachs contained sand and stones. In another study on this species, 37 out of 40 animals older than six months carried gastroliths, with a mean total gastrolith mass as high as 2.4 kg (range 0.0–8.6 kg) (Bryden 1999). The low occurrence of gastroliths in seals caught with gill nets may be due to regurgitation when the seals struggle in panic to escape from capture (Nordøy 1995). Additionally, gastrolith masses in seals are often very high (i.e., >10 kg, Mohr 1952; Ling and Bryden 1981; Webb et al. 1998). It is hence difficult to attribute their gastroliths always to accidental intake as suggested by Taylor (1993). The most parsimonious explanation for the presence of gastroliths in most Phocidae is a similar function as in Otariidae. If ballast provided by gastroliths does play a role in sea lions, it is highly plausible that stones in seals fulfil the same function, thus contradicting the idea of dependence between occurrence of gastroliths and mode of locomotion in water as suggested by Taylor (1993, 1994).

Taylor (1994) suggested that animals are most likely to use hydrodynamic buoyancy control when they are diving deep or when they contain little gas, or both. Knowledge of

diving behaviour in aquatic vertebrates has increased immensely in the past 20 years. It is now known that elephant seals usually feed at depths between 200 and 800 m, but have been known to reach depths of nearly 1600 m; hunting Weddell seals dive at depths of 50 to 600 m and Emperor penguins hunt between depths of 50 and 500 m (Kooyman and Ponganis 1998 and references therein). Hooded seals frequently dive to depths between 100–600 m (Folkow and Blix 1999). Southern elephant seals commonly perform foraging dives ranging in depth from 200 to 1100 m (Hindell et al. 1991), and while depths of presumed foraging dives of harbour seals were typically between 5 and 100 m, they can dive as deep as 481 m (Eguchi and Harvey 2005).

Lactating New Zealand sea lions (*Phocarcos hookeri*), have been reported to be the deepest- and longest-diving otariids. They routinely reach depths of 120 m, with a maximum depth of 474 m (Gales and Mattlin 1997). New Zealand fur seals (*Arctocephalus forsteri*) are the deepest diving fur seal species reported thus far, with a maximum recorded dive depth of 274 m and a typical diving depth between 30 and 74 m (Mattlin et al. 1998). In the Washington State area, USA, juvenile Steller sea lions (*Eumetopias jubatus*) dived to a mean depth of 39 m, a mean maximum depth of 145 m, and an absolute maximum depth of 328 m (Loughlin et al. 2003).

These examples show that there is no well defined difference in the diving depths of phocid and otariid pinnipeds and because taxa of both groups routinely dive deeper than 100 m, both should be more inclined to the use of hydrodynamic buoyancy (Taylor 1994). The idea that sea lions use gastroliths for buoyancy control because of their mode of locomotion, and that the presence of gastroliths in seals is merely accidental, must be rejected. In all known cases of gastroliths in aquatic animals, there is still doubt regarding the ballast hypothesis. It is clear that all swallowed objects in aquatic animals influence buoyancy. This especially applies to gastroliths which significantly increase the mass and specific density of the animal. It usually does not apply to food items that temporarily increase the mass of the animal without changing its overall density. The important question is: do swallowed objects have major importance for the diving and uplift behaviour of the animals or is their influence negligible?

From amphibians to reptiles to mammals there is a progressive increase in the complexity of the lung interior with increasing lung surface area (Schmidt-Nielsen 1997). In mammals, including some diving taxa such as porpoise, manatee, and whales, the average total lung volume is 46 ml kg⁻¹ or 4.6% of the body volume (Schmidt-Nielsen 1997). More precisely, the diving lung volumes of marine mammals range from 27 ml kg⁻¹ in Weddell seals, through 35 ml kg⁻¹ in Californian sea lions (*Zalophus californianus*), 54 ml kg⁻¹ in sperm whales (*Physeter macrocephalus*), and 81 ml kg⁻¹ in Atlantic bottlenose dolphins (*Tursiops truncatus*) (Kooyman and Ponganis 1998 and references therein). In human lungs, “dead space” is one third of total volume at rest, but only one-twentieth during exercise (Schmidt-Nielsen 1997). The tidal volume is between 500 and 3000 cm³ (Schmidt-Nielsen 1997). This means, as divers know, that 15–30 N of buoyancy is available in human

lungs without any forceful breathing. Consequently, normal breathing could equal about 3% of the body weight (about 2% in pinnipeds), a value much higher than the mean percentage of gastrolith masses known from aquatic animals (maximum: 1% of body mass in crocodiles, Cott 1961). These values show that the ballast provided by gastroliths is only a fraction of the buoyancy changes achieved by breathing.

This simple calculation is in agreement with a computational model for *Alligator mississippiensis* (Henderson 2003), which investigated the influence of gastroliths on crocodilian buoyancy and showed that the relatively small amounts of gastroliths in aquatic tetrapods are insignificant for buoyancy and stability, concluding that the lungs are the fundamental agent for hydrostatic buoyancy control. Similar three-dimensional computational models demonstrated that a stable, floating equilibrium could have been achieved by plesiosaurs without gastroliths (Henderson 2006). In gastrolith-bearing plesiosaurs, substantial lung deflation (50%) combined with impractically large amounts of gastroliths (5% of body weight) would have been required for initiate sinking. Because of that, the hypothesis that gastroliths were for control of buoyancy was rejected (Henderson 2006). However, gastroliths equal to 1% of body weight in the elasmosaurid plesiosaur *Thalassomedon* model were effective at suppressing buoyant oscillations of the neck when at the surface and minimising instability when fully immersed at ten meters depth (Henderson 2006). The models developed by Henderson (2003, 2006) also have potential for investigating the complex relationship between animal weight, blubber content, stone weight, food contents, and uplift via air-filled lungs in pinnipeds.

On the one hand, several arguments speak against a major influence of gastroliths on buoyancy control: (1) not all individuals of a given taxon have gastroliths, which could be expected if the stones have a critical physiological function; (2) within a given taxon, the range of masses of gastrolith sets of individual animals varies greatly; (3) the floating posture in crocodilians and turtles is mainly controlled by the relative position of head and body; (4) food intake could destroy the balance between stones and uplift. On the other hand, gastroliths might well serve as a short term solution to buoyancy adjustment because there are large variations in body composition and—consequently—in buoyancy during the annual cycle in aquatic tetrapods such as pinnipeds (Carlini et al. 2001). This could explain the irregular occurrence within seals and sea lions. Gastroliths might also be useful to adjust the average buoyancy of the animal, allowing to conveniently vary the buoyant force around that point by lung volume changes.

In conclusion, the issue of hydrostatic function of gastroliths in aquatic vertebrates remains unsettled. If a physiological use of gastroliths for buoyancy control is present, its importance is limited and possibly associated with other functions. For example, it is possible that animals relying on gastroliths for grinding food may have evolved positive buoyancy to compensate for the weight of the stones (Taylor 1993). Future experiments and observations on living tetrapods are necessary to clarify the influence of gastroliths for buoyancy control in aquatic animals.

Other ballast arguments.—Ballast arguments were not only suggested for aquatic animals but also for terrestrial tetrapods. Wade (1989) believed that gastroliths of prosauropods may have been essential as ballast, similar to the heavy distal end of the pubis of many theropods. In prosauropods, the pubis retained a primitive broad, concave surface to the main body cavity. A potential gizzard must have been placed posterior in the gut, so that when the animal reared up, the gizzard rested on the pubis and brought the centre of gravity back and down (Wade 1989). Wade (1989) postulated that the presence of the stones may have been critical for bipedally balancing the relatively long and strongly-built fore-bodies. Wade (1989) also suggested that gastroliths in sauropods may have had a double function: the stones primarily served as grinding agents for food and secondarily as ballast for rearing up. As gastroliths are not regularly found in sauropodomorph dinosaurs (Wings 2004), this hypothesis is unlikely. Furthermore, their limited weight relative to that of the body of significantly less than 0.1% (Wings 2003; Wings and Sander 2007) renders any balancing function implausible.

The presence of gastroliths in the maniraptoran theropod dinosaur *Caudipteryx* was used as an argument that weight reduction was not a significant selective pressure for theropods in the direct lineage leading to birds (Garner et al. 1999). This argument is not valid, since gastroliths are present in numerous birds with lightly built skeletons. Songbirds (Passeriformes) are excellent flyers and commonly utilise gastroliths (Gionfriddo and Best 1999). In summary, gastroliths used primarily as ballast in non-aquatic animals are highly implausible.

Ingestion due to pathological reasons or nutritional diseases.—Stress-induced behaviour is believed to be responsible for stone swallowing in captive animals, especially in stressful environments such as zoos. Gastroliths in iguanas, crocodiles, and hogs were attributed to pathological ingestion (Whittle and Everhart 2000). Large amounts of gravel in turtles are also considered to be pathological (Rhodin 1974). The swallowing of foreign objects by ostriches was attributed to stress (Sambras 1995; Kösters et al. 1996), an idea which has never been tested. Generally, evidence for pathological behaviour is hard to confirm. For instance, ostriches commonly swallow shiny objects, such as metal pieces (Deeming and Bubier 1999). Since it is implausible that all ostriches are suffering from stress, this behaviour can not be considered pathological and may have other reasons (e.g., shiny metallic objects could be mistaken for insects, Huchzermeyer 1998).

Gastroliths found in hogs (Beal 1904) may be the result of a monotonous diet. The hogs may have ingested the stones due to boredom or in search for some essential nutrients which were absent in their normal food. Overall, pathological gastrolith ingestion is considered to be a phenomenon of captive animals and exceptionally rare in wild animals.

Destruction of parasites.—Destruction of parasites has been proposed as a gastrolith function for pinnipeds (Hamilton 1933; Emery 1963) which often have parasitic nematode worms in their stomach. However, recent studies revealed that the presence of gastroliths is not correlated to the pres-

ence of stomach parasites in sea lions (Alonso et al. 2000) and in seals (Lucas et al. 2003). The purposeful ingestion of sand or earth after parasite infestation of turtles was reported by several authors and summarised by Dennert (2001). The concurrent presence of gastroliths and parasitic nematodes also was reported from some individuals of the crocodylians *Paleosuchus palpebrosus* (Medem 1958) and *Alligator mississippiensis* (Delany et al. 1988). Because there is no close correlation between parasitic infestation and lithophagical behaviour, this hypothesis remains unverified.

Establishment of a normal intestinal microbial flora.—Maintenance of a beneficial microbial gut flora has been suggested for lithophagy in the herbivorous lizards *Iguana iguana* and *Ctenosaura pectinata* (Sokol 1971) and also briefly mentioned by Taylor (1993) as possible reason for swallowing of stones in lizards and chelonians. Coprophagy is commonly found in vertebrates and does not only provide a method for obtaining nutrients (Soave and Brand 1991), but also supplies animals with beneficial microbes (Troyer 1982). It is possible that some taxa ingest sediment with attached desired symbiotic microorganisms for the same reason. However, no study has been conducted yet to confirm this suggestion.

Alleviation of hunger and preservation of stomach shape.—The idea that gastroliths are swallowed by hungry animals “to keep the stomach in shape” was first suggested for crocodylians (Catesby 1731; Owen 1742). The idea is also found among people of Madagascar (Decary 1950), and was repeatedly suggested for crocodylians and pinnipeds (e.g., Shaw 1802; Pitman 1931; Laws 1956). Gastroliths may provide bulk during periods of fasting. They may function simply as stomach filler and perhaps help to overcome hunger periods (Shaw 1802). This hypothesis was used to explain irregular occurrences of stones, especially in pinnipeds (e.g., Howell 1930). The stomachs of seals indeed contain sand and small stones more often in summer, during fasting season, than in spring or autumn, and some seals were observed to ingest stones on land and regurgitate them before departure (Laws 1956, 1984). Pinnipeds may therefore use stones as a sort of gastric “chewing gum” (Howell 1930) to prevent atrophy of the stomach. Gastroliths may relieve the hunger pains of pinnipeds during prolonged fasting in the breeding season, during lactation, and while moulting (Harrison and Kooyman 1968). The hypothesis that pinnipeds swallow stones to simply fill the stomach and overcome “hunger pangs” was invoked again for southern elephant seals *Mirounga leonina* (Bryden 1999).

Jacobi (1900) believed that several crow species have more gastroliths during the winter months in order to suppress hunger. During winter, generally more individuals had stones and the amounts of stones were higher, independently of food composition (insects *versus* plant material) (Jacobi 1900).

Neither hypothesis, whether alleviation of hunger or preservation of stomach shape, has ever been tested for any taxon, and their validity remains doubtful since similar behaviour is not known for other carnivorous taxa, even when they fast (e.g., snakes and lizards, Secor and Phillips 1997). Furthermore, mechanoreceptors, which can be stimulated by gastro-

liths, only have a partial contribution to the control of appetite: chemoreceptor feedback, which is not influenced by the stones, is just as important (e.g., Ralston 1983; Forbes 1996).

Accidental ingestion.—Accidental intake can occur because of sediment attached to prey, or because a prey item itself contains gastroliths. For example, bottom feeding fishes commonly contain sand and gravel in their digestive tract. Gastroliths have been found in taxa of Clupeidae (Massmann 1963), Salmonidae (Pontius and Parker 1973), Galaxiidae (Cadwallader 1975), and Cichlidae (Turner and Grimm 1991). A gastrolith with a mass of 1 kg was reported from a halibut, and its presence was ascribed “to reckless eating, not foresight” (Thompson 1919: 157). In the fossil record, verifiable accidental ingestion of gastroliths with prey is rarely known. Hundreds of stones were found among the scattered vertebrae of the large Cretaceous shark *Cretoxyrhina mantelli* (Moodie 1912) and interpreted as consumption of gastrolith-bearing prey (probably a plesiosaur, Shimada 1997). However, because no plesiosaur remains were found with the shark (Shimada 1997), this hypothesis remains unconfirmed.

An interesting case is the presumed accidental ingestion of crustacean bio-gastroliths by fishes and cormorants (Scott and Duncan 1967). Among extant amphibians, gastroliths were ingested incidental to the capture of food by two species of newts (*Taricha*) (Packer 1961). Gastroliths in an extant monitor lizard, *Varanus griseus*, might have been derived from its bird prey items, but were, in this instance (Wiman 1916), considered too big to have been derived from a bird.

Accidentally ingested extraneous matter, such as grass, stems and small pebbles, is known from the insectivorous lizard *Sceloporus olivaceus* (Kennedy 1956) and the carnivorous lizard *Gambelia wislizenii* (Knowlton and Thomas 1936). Sand in the alimentary tract of the snakes *Storeria dekayi*, *Carphophis amoenus*, and *Cemophora coccinea* was probably derived from the alimentary tract of earthworms that had been eaten. The presence of sand in the hind gut of these snakes and their empty stomach (Hamilton and Pollack 1956) indicates no special function of the sand in the stomach. Sand and grit in the gizzards of birds that have been consumed by snakes passes the digestive tract of the latter (Skoczylas 1978). Ingestion of organisms like snails and amphibians, covered in mucus with attached sand and gravel, are another source of gastroliths in snakes (Voris 1966; Skoczylas 1978). Small stones and plant remains reported from the digestive tract of rattlesnakes were probably also ingested accidentally (Klauber 1982). Sand and mud in a leatherback turtle (*Dermochelys coriacea*) was most likely ingested accidentally while the animal was feeding in shallow water, became trapped, and attempted to reach deeper water again (Den Hartog and Van Nierop 1984).

Crocodylians often swallow prey that has sand and gravel adhering to blood and flesh. For example, gastroliths in *Crocodylus niloticus* were regarded as most probably swallowed accidentally during feeding (Welman and Worthington 1943; Decary 1950). Plant material frequently found in crocodylian stomachs (e.g., Delany and Abercrombie 1986)

also indicates accidental intake and may partially be explained as ingested stomach contents of herbivorous prey. Plants and roots found in *Alligator mississippiensis* may have been picked up when feeding on aquatic animals or during burrowing (Giles and Childs 1949).

A large number of pebbles found in Pleistocene cave sediments have been interpreted as gastroliths released from pellets of snowy owls (Mühlhofer 1935). Rare occurrences of sand and gravel, mostly combined with the remains of gastrolith-bearing prey, are known from extant raptorial birds such as the osprey (*Pandion haliaetus*), hobby (*Falco subbuteo*), peregrine falcon (*Falco peregrinus*) and short-eared owl (*Otus brachyotus*) (Rörig 1906). Low numbers of stones found with theropod dinosaurs, e.g., *Baryonyx* (Charig and Milner 1997) or *Allosaurus* (Ayer 2000), can be interpreted as accidental intake.

Accidental ingestion of stones by sea lions preying on octopuses that have stones grasped in their tentacles was suggested (Sleptsov 1950), but rejected later because no stones were found in stomachs of harbour seals, which frequently preyed on octopuses (Spalding 1964). Leopard seals (*Hydrurga leptonyx*) are known to swallow intact penguin stomachs with gastroliths (Hall-Aspland and Rogers 2004). Accidental intake of gastroliths has also been reported in sperm whales (Gaskin and Cawthorn 1967) and gray whales (Kusakin et al. 2001). Among terrestrial mammals, gastroliths are known from carnivores such as stoats (*Mustela*) (Taylor and Tilley 1984) and omnivores such as black bears (*Ursus americanus*) (Bennett et al. 1943).

Accidental or purposeful swallowing of pebbles while playing is a good explanation for the presence of stomach stones in young animals of different taxa which are regularly observed to play with objects like sticks or pebbles. Playing was suggested as a factor in stomach stone acquisition for pinnipeds and captive porpoises, which often pick up, play, and sometimes swallow stones in their tank (Emery 1963). Pinniped pups were observed to play with small stones while still being suckled (Harrison and Kooyman 1968). The swallowing could be a practice for later hunting of prey.

Accidental intake is the best explanation for the presence of gastroliths in many fish, lizard, turtle, archosaur, and mammal species. However, the bigger the stones and the greater their number, the less plausible is accidental intake. To identify accidental ingestion, it also is important to consider the size of the skull and the oesophagus in comparison to the stones.

Stones mistaken as prey.—The intentional ingestion of an incorrectly recognised object is documented from egg-eating snakes, e.g., *Elaphe obsoleta*, which have swallowed artificial eggs (stone, wood, china) placed under brooding hens (Holt 1919; Smith 1953; Gans 1953). A swallowed egg-shaped cosmetic jar was reported by Kennedy and Brockman (1965). The swallowing of wood and stones by crocodylians also was assumed to be a result of mistaking them for snails and crabs (e.g., Pitman 1941), and the consumption of sand, stones or kelp could reflect a form of displacement behaviour in dehydrated or starving seals, which may have ingested

these objects as a source of water in case of absence of snow and ice (Lucas et al. 2003). In general, ingestion of stones mistaken as prey is considered to be rare.

Nest building.—The use of stones for moa nest building was considered a possibility for isolated stone clusters (commonly interpreted as moa gastroliths, Twigg 2001; Worthy and Holdaway 2002) in New Zealand (Whittle and Everhart 2000). The animals incorporated stones, which possibly represent gastroliths, in the construction of the nest. Further support for the nest building hypothesis comes from two fossil egg sites. A locality called “Young Egg” contains crushed eggs, microvertebrate remains and “gastroliths” up to 1 cm in diameter (MWC 122; Whittle and Everhart 2000). Unfortunately, no other details are provided. The second locality is an Upper Jurassic theropod dinosaur egg site near Lourinhã, Portugal, where one alleged gastrolith was found among eggs (Mateus et al. 1998).

Whittle and Everhart (2000) did not discuss whether the stones were considered to be real gastroliths, or if they were normally used for nest building but sometimes swallowed accidentally, or if they were just carried in the beak of the birds or in the mouth of dinosaurs, respectively. Extant penguins, for example, regurgitate gastroliths both at the nest site and with their chicks’ feed (Hocken 2005). Penguins also commonly use stones in nest building (e.g., Murphy 1936). However, many stones at nest sites might have been carried in the beaks/mouths of animals and are hence no gastroliths. The small number of stones in theropod nests may alternatively represent accidentally ingested gastroliths (see Wings 2004 for a list of gastrolith-bearing theropod taxa) that were regurgitated during feeding the offspring.

Thermoregulation.—The presence of gastroliths in *Psittacosaurus*, a basal ceratopsian dinosaur with well-established oral grinding capacities (You and Dodson 2004), gave rise to another hypothesis about their function: thermoregulation (Anton 2001). The hypothesis is based on the greater thermal conductivity that clasts exhibit compared to water and body tissues. A thermodynamic model showed that swallowing stones could have increased the rate of conductive heat transfer in *Psittacosaurus* by two or three times (Anton 2001). The author’s arguments have not yet been fully published, but obvious issues which would need to be resolved are different specific heat capacities of rocks and body tissue, and the length of the period during which the stones are contained in the digestive tract.

Theoretically, it is useful for ectothermic animals to swallow heated stones to heat up faster themselves. However, the specific heat capacity of quartz ($c_p=0.740 \text{ J g}^{-1} \text{ K}^{-1}$) is more than four times lower than the specific heat capacity of the animal body ($c_p=3.345 \text{ J g}^{-1} \text{ K}^{-1}$) (Schmidt-Nielsen 1997; Waples and Waples 2004). To heat up the body tissue of a 12 kg *Psittacosaurus* (Seebacher 2001) from 20°C to 30°C, as much as 18 kg of stones with a temperature of 60°C would have been needed. Swallowed stones cannot be much hotter because of the resulting damage to the digestive tract at higher temperatures. Consequently, an animal swallowing

hot stones to increase its body temperature would hence end up with very high amounts of gastroliths, but without a substantial gain in body heat.

Furthermore, any advantage gained from higher thermal conductivity due to ingested gastroliths would have been balanced or possibly exceeded by the rapid cooling down of the gastroliths once solar heat was no longer available. The shorter period that gastrolith-bearing animals required to cool down could have actually been a disadvantage compared to competing species or predators. The scenario would only be reasonable if the gastroliths were regurgitated as soon as they have reached body temperature. Such behaviour is not known for any extant taxon nor supported by fossil finds. It appears to be implausible.

Summary

A summary of proposed gastrolith functions in vertebrates and their likelihood is presented in Table 1. The most commonly proposed functions are related to the digestive system. Crushing, grinding, and mixing of foodstuff in the gizzard is the accepted gastrolith function in many birds. Mineral uptake is a welcome side effect of abrasion and dissolution of gastroliths in the gastro-intestinal tract. While a stimulation of gastric juice secretion by gastroliths is difficult to prove, stomach cleaning with stones seems to be important in some taxa.

It is clear that not all gastroliths have a physiological function. Accidental intake is relatively common in species with particular feeding habits (e.g., carnivorous taxa or ant-eaters). A low percentage of gastrolith-bearing individuals within a taxon indicates that gastroliths were accidentally ingested or fulfil a function that is not critical for survival (e.g., Gionfriddo and Best 1999; Cheng et al. 2006).

Table 1. Hypotheses for causes of deliberate and accidental lithophagy in vertebrates. See text for discussion.

Intake	Function	Status	
Deliberate ingestion	Digestive aid	Trituration of foodstuff	plausible
		Mixing of foodstuff	plausible
		Mineral supplement	plausible
		Stomach cleaning	plausible
		Secretion of stomach juices	controversial
	Ballast / hydrostatic function	controversial	
	Pathological reasons	controversial	
	Nutritional diseases	controversial	
	Destruction of parasites	controversial	
	Establishment of a normal intestinal microbial flora	controversial	
	Relief of hunger pangs and preservation of stomach shape	controversial	
	Nest building	implausible	
	Thermoregulation	implausible	
Accidental ingestion	Material is attached to swallowed prey	plausible	
	Prey contains gastroliths	plausible	
	Material is mistaken as prey	plausible	
	During playing with objects	plausible	

Several gastrolith functions may operate concurrently. For example, aquatic animals may swallow stones primarily for digestion, but the stones may also serve as ballast, and limestones will be dissolved and supply minerals to the organism. In terrestrial herbivores, gastroliths also often fulfil several functions at once, such as grinding and mixing of foodstuff and the supply with minerals. However, it is difficult to distinguish the importance of combined functions without further research. While all gastroliths are ballast when swimming in water, their influence on buoyancy control in aquatic animals is considered to be limited. Nevertheless, the function of the stones in crocodilians and pinnipeds is not yet understood. Perhaps crocodilian gastroliths are completely the result of accidental intake or were mistaken as prey. Again, the need for more information should be fulfilled by future research. Additional functions of these stones might be identified by further investigations. Perhaps hypotheses similar to those postulated for the function of soil ingested during geophagy may become important, including adsorption of plant toxins and tannins, counteraction of gastric upsets or diarrhoea, antacid action of clays or adjustment of stomach pH, tactile sensations in the mouth, tradition, or as a source of iron to counteract anaemia caused by parasitic infestations (Setz et al. 1999).

Acknowledgements

I would like to thank Paul Barrett (Natural History Museum, London, UK), Marcus Clauss (Institut für Veterinärmedizin, Universität Zürich, Switzerland), Denver Fowler (Montana State University, USA), Walter Joyce (Yale Peabody Museum, New Haven, USA), Ute Richter (Niedersächsisches Landesmuseum, Hannover, Germany), Martin Sander (Institut für Paläontologie, Universität Bonn, Germany) and Daniela Schwarz (Naturhistorisches Museum Basel, Switzerland) for reviews of the manuscript. Walter Joyce also helped in locating rare literature. I acknowledge Christopher Whittle (Colorado Springs, USA) for his bibliography about gastroliths which served as a superb starting point for the literature search and Wolfgang Gerber (Universität Tübingen, Germany) for his help with some photographs. Sven Gehrmann (Hannover, Germany) and Kurt Mack (Riegelsberg-Walpershofen, Germany) donated the bio-gastroliths (Fig. 1A), and Wolfram Rietschel (Stuttgart, Germany) donated gastroliths from Wilhema Zoo animals (Fig. 1B, F). For the permission to use their photographs, I am grateful to Markus Poschmann and Michael Wuttke (Landesamt für Denkmalpflege Rheinland-Pfalz, Mainz, Germany) (Fig. 2B) and to Rebecca Schmeisser (Museum of Northern Arizona, Flagstaff, USA) (Fig. 2D). I am thankful to Annette Richter for allowing me to finish the draft during my trainee position at the Niedersächsisches Landesmuseum, Hannover. The reviews of David Gillette (Museum of Northern Arizona, Flagstaff, USA) and Michael A. Taylor (National Museums of Scotland, Edinburgh, UK) substantially improved the submitted manuscript. Initial funding was provided by the Graduiertenförderung Nordrhein-Westfalen, the Graduiertenkolleg "Evolution und Biodiversität in Raum und Zeit", and the Jurassic Foundation. Current financial support is provided by the German Research Foundation (DFG PF 219/21-2). "Tilly Edinger Award" money of the Paläontologische Gesellschaft has been used to cover publication costs.

References

Abrahams, P.W. and Parsons, J.A. 1996. Geophagy in the tropics: a literature review. *The Geographical Journal* 162 (1): 63–72.
 Allaby, A. and Allaby, M. 1999. *A Dictionary of Earth Sciences*. 619 pp. Oxford University Press, Oxford.

Allen, J.A. 1880. *History of North American Pinnipeds*. 785 pp. U.S. Geological and Geographical Survey, San Francisco.
 Allred-Crouch, A.L. and Young, E.A. 1985. Bezoars—when the "knot in the stomach" is real. *Postgraduate Medicine* 78: 261–265.
 Alonso, M.K., Crespo, E.A., Pedraza, S.N., Garcia, N.A., and Coscarella, M.A. 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin* 98: 250–263.
 Anonymus. 1892. A gastrolith in man. *The Lancet* 139 (3566): 43.
 Anthony, A.W. 1924. Notes on the present status of the northern elephant seal, *Mirounga angustirostris*. *Journal of Mammalogy* 5: 145–152.
 Anton, J.A. 2001. Thermo-powered ceratopsians? A thermodynamic model proposing another role for gastroliths. *Journal of Vertebrate Paleontology* 21 (Supplement to No. 3): 28–29.
 Ayer, J. 2000. *The Howe Ranch Dinosaurs*. 96 pp. Sauriermuseum Aathal, Aathal.
 Baker, A.A. 1956. The swallowing of stones by animals. *The Victorian Naturalist* 73 (6): 82–95.
 Bates, R.L. and Jackson, J.A. 1980. *Glossary of Geology*. 749 pp. American Geological Institute, Falls Church.
 Beal, W.J. 1904. Stomach stones. *Science* 20 (517): 722.
 Bennett, L.J., English, P.F., and Watts, R.L. 1943. The food habits of the black bear in Pennsylvania. *Journal of Mammalogy* 24: 25–31.
 Bennett, M.R., Doyle, P., and Mather, A.E. 1996. Dropstones: their origin and significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 121: 331–339.
 Best, L.B. and Gionfriddo, J.P. 1991. Characterization of grit use in cornfield birds. *Wilson Bulletin* 103 (1): 68–82.
 Beyer, W.N., Connor, E.E., and Gerould, S. 1994. Estimates of soil ingestion by wild-life. *Journal of Wildlife Management* 58: 375–382.
 Bialas, T., Hell, P., and Slamecka, J. 1996. Untersuchung von Magensteinen bei Fasanen und Rebhühnern. *Zeitschrift für Jagdwissenschaft* 42 (1): 36–40.
 Bishton, G. 1986. The diet and foraging behaviour of the Dunnock *Prunella modularis* in a hedgerow habitat. *Ibis* 128: 526–539.
 Boesch, C. and Boesch, H. 1981. Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. *Journal of Human Evolution* 10: 585–593.
 Brodie, P.F. 1989. The white whale—*Delphinapterus leucas* (Pallas, 1776). In: S.H. Ridgway and R.J. Harrison (eds.), *River Dolphins and the Larger Toothed Whales*, 119–144. Academic Press, London.
 Bruce, T. (in press). Observations of stone-eating in two species of neotropical falcons (*Micrastur semitorquatus* and *Herpetotheres cachimans*). *Journal of Raptor Research* 41 (1).
 Bryden, M.M. 1999. Stones in the stomachs of southern elephant seals. *Marine Mammal Science* 15: 1370–1373.
 Burns, J.J. 1981. Bearded seal—*Erignathus barbatus*. In: S.H. Ridgway and R.J. Harrison (eds.), *Seals*, 145–170. Academic Press, London.
 Cade, T.J. 1982. *The Falcons of the World*. 188 pp. Collins, London.
 Cadwallader, P.L. 1975. Occurrence of gravel in the stomachs of two New Zealand stream-dwelling fish (note) *New Zealand Journal of Marine and Freshwater Research* 9: 101–103.
 Carlini, A.R., Márquez, M.E.I., Ramdohr, S., Bornemann, H., Panarello, H.O., and Daneri, G.A. 2001. Postweaning duration and body composition changes in southern elephant seal (*Mirounga leonina*) pups at King George Island. *Physiological and Biochemical Zoology* 74 (4): 531–540.
 Catesby, M. 1731. *The Natural History of Carolina, Florida, and the Bahama Islands: Containing the Figures of Birds, Beasts, Fishes, Serpents, Insects, and Plants: Particularly the Forest-Trees, Shrubs, and Other Plants, not Hitherto Described, or Very Incorrectly Figured by Authors*. 100 pp. Printed at the expence of the author, London.
 Challinor, J. 1974. *A Dictionary of Geology*. 350 pp. University of Wales Press, Cardiff.
 Charig, A.J. and Milner, A.C. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum Geology Series* 53 (1): 11–70.
 Cheng, L., Wings, O., Chen, X., and Sander, M. 2006. Gastroliths in the Triassic ichthyosaur *Panjiangsaurus* from China. *Journal of Paleontology* 80: 583–588.
 Christiansen, P. 1996. The evidence for and implications of gastroliths in sauropods (Dinosauria, Sauropoda). *Gaia* 12: 1–7.
 Cicimurri, D.J. and Everhart, M.J. 2001. An elasmosaur with stomach contents and gastroliths from the Pierre Shale (late Cretaceous) of Kansas. *Transactions of the Kansas Academy of Science* 104 (3–4): 129–143.
 Clarke, M.R. and MacLeod, N. 1982. Cephalopod remains in the stomachs of eight Weddell seals. *British Antarctic Survey Bulletin* 57: 27–31.

- Condit, R. and Le Boeuf, B.J. 1984. Feeding habits and feeding grounds of the northern elephant seal. *Journal of Mammalogy* 65: 281–290.
- Cott, H.B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society of London* 29 (4): 211–358.
- Currie, P.J. 1997. Gastroliths. In: P.J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*, 270. Academic Press, San Diego.
- Currie, P.J. and Padian, K. 1997. *Encyclopedia of Dinosaurs*. 869 pp. Academic Press, San Diego.
- De Villiers, M.S. and De Bruyn, P.J.N. 2004. Stone-swallowing by three species of penguins at sub-Antarctic Marion Island. *Marine Ornithology* 32: 185–186.
- Dearborn, J.H. 1965. Food of the Weddell seals at McMurdo Sound, Antarctica. *Journal of Mammalogy* 46: 37–43.
- Decary, R. 1950. *La faune malgache: son rôle dans les croyances et les usages indigènes*. 236 pp. Payot, Paris.
- Deeming, D.C. and Bubier, N.E. 1999. Behaviour in natural and captive environments. In: D.C. Deeming (ed.), *The Ostrich. Biology, Production and Health*, 83–104. CABI Publishing, Cambridge.
- Delany, M.F. and Abercrombie, C.L. 1986. American alligator food habits in northcentral Florida. *Journal of Wildlife Management* 50: 348–353.
- Delany, M.F., Woodward, A.R., and Kocheil, I.H. 1988. Nuisance alligator food habits in Florida. *Florida Field Naturalist* 16: 90–96.
- Den Hartog, J.C. and Van Nierop, M.M. 1984. A study on the gut contents of six leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British waters and from the Netherlands. *Zoologische Verhandlungen Leiden* 209: 1–36.
- Dennert, C. 1997. *Untersuchungen zur Fütterung von Schuppenechsen und Schildkröten*. 189 pp. Unpublished Ph.D. thesis. Tierärztliche Hochschule, Hannover.
- Dennert, C. 2001. *Ernährung von Landschildkröten*. 144 pp. Natur und Tier Verlag, Münster.
- Diamond, J., Bishop, K.D., and Gilardi, J.D. 1999. Geophagy in New Guinea birds. *Ibis* 141: 181–193.
- Duke, G.E. 1986. Alimentary canal: secretion and digestion, special digestive functions, and absorption. In: P.D. Sturkie (ed.), *Avian Physiology*, 289–302. Springer Verlag, New York.
- Eguchi, T. and Harvey, J.T. 2005. Diving behavior of the Pacific harbor seal (*Phoca vitulina richardii*) in Monterey Bay, California. *Marine Mammal Science* 21: 283–295.
- Elgood, C. 1935. A treatise on the bezoar stone. *Annals of Medical History* 7: 73–80.
- Emery, K.O. 1963. Organic transportation of marine sediments. In: M.N. Hill (ed.), *The Sea. Ideas and Observations on Progress in the Study of the Seas*, 776–793. Wiley Interscience, New York.
- Farlow, J.O. and Brett-Surman, M.K. (eds.) 1997. *The Complete Dinosaur*. 752 pp. Indiana University Press, Bloomington.
- Fisher, H. 1972. The nutrition of birds. In: D.S. Farner and J.R. King (eds.), *Avian Biology*, 431–469. Academic Press, London.
- Fleming, C.A. 1951. Sea lions as geological agents. *Journal of Sedimentary Petrology* 21 (1): 22–25.
- Flügel, E. 2004. *Microfacies of Carbonate Rocks: Analysis, Interpretation and Application*. 976 pp. Springer, Berlin.
- Folkow, L.P. and Blix, A.S. 1999. Diving behaviour of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. *Polar Biology* V22 (1): 61.
- Forbes, H.O. 1892. On the recent discovery of the remains of extinct birds in New Zealand. *Nature* 45: 416–418.
- Forbes, J.M. 1996. Integration of regulatory signals controlling forage intake in ruminants. *Journal of Animal Science* 74: 3029–3035.
- Fox, N. 1976. Rangle. *Raptor Research* 10: 61–64.
- Fox, N. 1995. *Understanding the Bird of Prey*. 375 pp. Hancock House, Surrey, B.C.
- Frizzell, D.L. and Exline, H. 1958. Crustacean gastroliths from the Clairborn Eocene of Texas. *Micropaleontology* 4: 273–280.
- Gales, N.J. and Matlin, R.H. 1997. Summer diving behaviour of lactating New Zealand sea lions, *Phocartos hookeri*. *Canadian Journal of Zoology* 75: 1695–1706.
- Gans, C. 1953. A further note on the regurgitation of artificial eggs by snakes. *Herpetologica* 9: 183–184.
- Garner, J., Taylor, G., and Thomas, A. 1999. On the origins of birds. *Proceedings of the Royal Society B: Biological Sciences* 266: 1259–1266.
- Gaskin, D.E. and Cawthorn, M.W. 1967. Diet and feeding habits of the sperm whale (*Physeter catodon* L.) in the Cook Strait Region of New Zealand. *New Zealand Journal of Marine and Freshwater Research* 2: 156–179.
- Giles, L.W. and Childs, V.L. 1949. Alligator management of the Sabine National Wildlife Refuge. *Journal of Wildlife Management* 13: 16–28.
- Gillette, D.D. 1992. Form and function of gastroliths in sauropod dinosaurs. *Geological Society of America, Rocky Mountain Section, 45th annual meeting. Abstracts with programs* 24 (6): 14.
- Gillette, D.D. 1994. *Seismosaurus, the Earth Shaker*. 205 pp. Columbia University Press, New York.
- Gillette, D.D. 1995. True grit. *Natural History* 104 (6): 41–43.
- Gionfriddo, J.P. and Best, L.B. 1999. Grit use by birds—a review. *Current Ornithology* 15: 89–148.
- Gjertz, I. and Wiig, Ø. 1992. Feeding of walrus *Odobenus rosmarus* in Svalbard. *Polar Record* 28 (164): 57–59.
- Gove, P.B. 1971. *Webster's Third New International Dictionary of the English Language, Unabridged*. 2662 pp. G. & C. Merriam Co., Springfield, Massachusetts.
- Hall-Aspland, S.A. and Rogers, T.L. 2004. Summer diet of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biology* 27 (12): 729–734.
- Hamilton, J.E. 1933. The southern sea lion, *Otaria byronia* (De Blainville). *Discovery Reports* 8: 269–318.
- Hamilton, W.J. and Pollack, J.A. 1956. The food of some colubrid snakes from Fort Benning Georgia. *Ecology* 37: 519–526.
- Hänichen, T. and Wiesner, H. 1995. Erkrankungen- und Todesursachen bei Neuweltkameliden. *Tierärztliche Praxis* 23 (5): 515–520.
- Harper, J.A. 1964. Calcium in grit consumed by hen pheasants in east-central Illinois. *Journal of Wildlife Management* 28 (2): 264–270.
- Harrison, R.J. and Kooyman, G.L. 1968. General physiology of the Pinnipedia. In: R.J. Harrison, R.C. Hubbard, R.S. Peterson, C.E. Rice, and R.J. Schusterman (eds.), *The Behavior and Physiology of Pinnipeds*, 211–296. Appleton-Century-Crofts, New York.
- Hawkes, L. 1951. The erratics of the English Chalk. *Proceedings of the Geologist's Association* 62: 257–268.
- Henderson, D.M. 2003. Effects of stomach stones on the buoyancy and equilibrium of a floating crocodilian: a computational analysis. *Canadian Journal of Zoology* 81: 1346–1357.
- Henderson, D.M. 2006. Floating point: a computational study of buoyancy, equilibrium, and gastroliths in plesiosaurs. *Lethaia* 39: 227–244.
- Hindell, M.A., Slip, D.J., and Burton, H.R. 1991. The diving behavior of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia, Phocidae). *Australian Journal of Zoology* 39: 595–619.
- Hjelset, A.M., Andersen, M., Gjertz, I., Lydersen, C., and Gulliksen, B. 1999. Feeding habits of bearded seals (*Erignathus barbatus*) from the Svalbard area, Norway. *Polar Biology* 21: 186–193.
- Hocken, A.G. 2005. Necropsy findings in yellow-eyed penguins (*Megadyptes antipodes*) from Otago, New Zealand. *New Zealand Journal of Zoology* 32: 1–8.
- Holt, E.G. 1919. *Coluber* swallowing the stone. *Copeia* 76: 99–100.
- Howell, A.B. 1930. *Aquatic Mammals; their Adaptations to Life in the Water*. 338 pp. Thomas, Springfield-Baltimore.
- Huchzermeyer, F.W. 1998. *Diseases of Ostriches and Other Ratites*. 296 pp. Agricultural Research Council, Onderstepoort Veterinary Institute, Onderstepoort.
- Humboldt, A.v. 1852. *Personal Narrative of Travels to the Equinoctial Regions of America*. 521 pp. Henry G. Bohn, London.
- Huxley, T.H. 1880. *The Crayfish*. 371 pp. Kegan Paul, London.
- Jackson, J.A. 1997. *Glossary of Geology*. 769 pp. American Geological Institute, Alexandria.
- Jacobi, A. 1900. Die Aufnahme von Steinen durch Vögel. *Arbeiten aus der Biologischen Abtheilung für Land- und Forstwirtschaft am Kaiserlichen Gesundheitsamte* 1: 223–254.
- Johnson, D.L. 1993. Dynamic denudation evolution of tropical, subtropical and temperate landscapes with three tiered soils: toward a general theory of landscape evolution. *Quaternary International* 17: 67–78.
- Johnson, D.R. 1966. Diet and estimated energy assimilation of three Colorado lizards. *American Midland Naturalist* 76: 504–509.
- Jones, R.L. and Hanson, H.C. 1985. *Mineral Licks, Geophagy, and Biogeochemistry of North American Ungulates*. 301 pp. Iowa State University Press, Ames.
- Kennedy, J.P. 1956. Food habits of the rusty lizard *Sceloporus olivaceus* Smith. *Texas Journal of Science* 8: 328–349.
- Kennedy, J.P. and Brockman, H.L. 1965. Stomach stone in the American All-

- gator, *Alligator mississippiensis* Daudin. *British Journal of Herpetology* 3: 201–203.
- King, J.E. 1983. *Seals of the World*. 240 pp. British Museum (Natural History), London.
- Klauber, L.M. 1982. *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*. 350 pp. University of California Press, Berkeley.
- Klaus, G. and Schmid, B. 1998. Geophagy at natural licks and mammal ecology: a review. *Mammalia* 62: 481–497.
- Knowlton, G.F. and Thomas, W.L. 1936. Food habits of Skull Valley lizards. *Copeia* 1936: 64–66.
- Kobayashi, Y. and Lü, J.-C. 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica* 48: 235–259.
- Kooyman, G.L. and Ponganis, P.J. 1998. The physiological basis of diving to depth: birds and mammals. *Annual Review of Physiology* 60: 19–32.
- Kösters, J., Hornung, B., and Korbel, R. 1996. Straußenhaltung aus der Sicht des Tierarztes. *Deutsche tierärztliche Wochenschau* 103 (3): 100–104.
- Kussakin, O.G., Sobolevskii, Y.I., and Blokhin, S.A. 2001. *A Review of Benthos Investigations on the Shelf of the Northeastern Sakhalin*. 91 pp. Sakhalin Energy Investment Company Ltd., Vladivostok.
- Laws, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.) II. General, social and reproductive behaviour. *Falkland Islands Dependencies Survey, London Scientific Reports* 13: 1–88.
- Laws, R.M. 1984. Seals. In: R.M. Laws (ed.), *Antarctic Ecology*, 621–715. Academic Press, London.
- Ling, J.K. and Bryden, M.M. 1981. Southern elephant seal *Mirounga leonina* Linnaeus, 1758. In: S.H. Ridgway and R.J. Harrison (eds.), *Seals*, 297–327. Academic Press, London.
- Loughlin, T.R., Sterling, J.T., Merrick, R.L., Sease, J.L., and York, A.E. 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). *Fishery Bulletin* 101: 566–582.
- Lowry, L.F., Testa, J.W., and Calvert, W. 1988. Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. *Polar Biology* 8 (6): 475–478.
- Lucas, Z., Daoust, P.-Y., Conboy, G., and Brimacombe, M. 2003. Health status of harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) on Sable Island, Nova Scotia, Canada, concurrent with their expanding range. *Journal of Wildlife Diseases* 39: 16–28.
- Lundberg, J. 2003. Speleogenesis of the Mount Elgon “Elephant Caves”, Kenya. *Geological Society of America. Abstracts with Programs* 35 (6): 422.
- Mangold, E. 1927a. Die Bedeutung von Steinchen und Sand im Hühnermagen. *Archiv für Geflügelkunde* 1: 145–152.
- Mangold, E. 1927b. Über die Bedeutung der Steinchen im Hühnermagen. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*: 20–21.
- Manley, K. 1991. Two techniques for measuring surface polish as applied to gastroliths. *Ichnos* 1: 313–316.
- Manley, K. 1993. Surface polish measurement from bona fide and suspected dinosaur gastroliths and wave and stream transported clasts. *Ichnos* 2: 167–169.
- Marlow, B.J. 1975. The comparative behaviour of the Australian sea lions *Neophoca cinerea* and *Phocarctos hookeri* (Pinnipedia: Otariidae). *Mammalia* 39: 159–230.
- Massmann, W.H. 1963. Summer food of juvenile American shad in Virginia waters. *Chesapeake Science* 4: 167–171.
- Mateus, I., Mateus, H., Antunes, M.T., Mateus, O., Taquet, P., Ribeiro, V., and Manuppella, G. 1998. Upper Jurassic theropod dinosaur embryos from Lourinhã, Portugal. *Memórias da Academia de Ciências de Lisboa* 37: 101–109.
- Mathews, L.H. 1929. The natural history of the elephant seal, with notes on other seals found at South Georgia. *Discovery Reports* 1: 233–256.
- Mattlin, R.H., Gales, N.J., and Costa, D.P. 1998. Seasonal dive behaviour of lactating New Zealand fur seals (*Arctocephalus forsteri*). *Canadian Journal of Zoology* 76: 350–360.
- Mayne, R.G. 1854. *An Expository Lexicon of the Terms, Ancient and Modern, in Medical and General Science*. 1504 pp. J. Churchill, London.
- Mayr, G., Poschmann, M., and Wuttke, M. 2006. A nearly complete skeleton of the fossil galliform bird *Palaeortyx* from the late Oligocene of Germany. *Acta Ornithologica* 41: 129–135.
- McCarthy, J.F. and Skinner, D.M. 1977. Proecdysial changes in serum ecdysone titers, gastrolith formation, and limb regeneration following molt induction by limb autotomy and/or eyestalk removal in the land crab, *Gecarcinus lateralis*. *General and Comparative Endocrinology* 33: 278–292.
- McIntosh, J.I., Slinger, S.J., Sibbald, I.R., and Ashton, G.C. 1962. Factors affecting the metabolizable energy content of poultry feeds. 7. The effects of grinding, pelleting and grit feeding on the availability of the energy of wheat, corn, oats and barley. 8. A study on the effects of dietary balance. *Poultry Science* 41: 445–456.
- Medem, F.J. 1958. The crocodylian genus *Paleosuchus*. *Fieldiana Zoology* 39: 227–247.
- Milton, S.J. and Dean, W.R.J. 1995. Gizzard stones and food selection by free-range ostrich: implications for management. *East Coast Producers Association* January–February 1995: 4–7.
- Mohr, E. 1952. *Die Robben der Europäischen Gewässer*. 283 pp. Verlag Paul Schöps, Frankfurt/Main.
- Moodie, R.L. 1912. The “stomach stones” of reptiles. *Science* 35 (897): 377–378.
- Morris, C.G. 1992. *Academic Press Dictionary of Science and Technology*. 2432 pp. Academic Press, San Diego.
- Mühlhofer, F. 1935. Beobachtungen an Gastrolithen diluvialer und rezenter Waldhühner; der Mensch der letzten Eiszeit als Anbauer von Gramineen. *Verhandlungen der zoologisch-botanische Gesellschaft in Wien* 85: 141–144.
- Murphy, R.C. 1936. *The Oceanic Birds of South America*. 1245 pp. Macmillan, New York.
- Murray, J. and Renard, A.F. 1891. *Report of the Deep Sea Deposits*. 525 pp. Her Majesty’s Stationary Office, London.
- Needham, D.J. 1997. The role of stones in the sea lion stomach: investigations using contrast radiography and fluoroscopy. In: M.A. Hindell and C.M. Kemper (eds.), *Marine Mammal Research in the Southern Hemisphere*, 164–169. Surrey Beatty & Sons, Chipping Norton.
- Neill, W.T. 1971. *The Last of the Ruling Reptiles, Alligators, Crocodiles, and Their Kin*. 486 pp. Columbia University Press, New York.
- Nelson, C.H. and Johnson, K.R. 1987. Whales and walrus as tillers of the sea floor. *Scientific American* 256 (2): 74–81.
- Nemoto, T. and Nasu, K. 1963. Stones and other aliens in the stomachs of sperm whales in the Bering Sea. *The Scientific Reports of the Whales Research Institute* 17: 83–91.
- Nordøy, E.S. 1995. Gastroliths in the harp seal *Phoca groenlandica*. *Polar Research* 14 (3): 335–338.
- Owen, C. 1742. *An Essay Towards a Natural History of Serpents: in Two Parts*. 240 pp. Printed for the author, sold by John Gray, London.
- Packer, W.C. 1961. Feeding behavior in adult *Taricha*. *Copeia* 1961: 351–352.
- Perkins, J.E. 1945. Biology at Little America III, the west base of the United States Antarctic Service Expedition 1939–1941. *Proceedings of the American Philosophical Society* 89: 270–284.
- Pitman, C.R.S. 1931. *A Game Warden Among his Charges*. 329 pp. Nisbet, London.
- Pitman, C.R.S. 1941. About crocodiles. *Uganda Journal* 8 (3): 89–114.
- Pontius, R.W. and Parker, M. 1973. Food habits of the mountain whitefish *Prosopium williamsoni* (Girard). *Transactions of the American Fisheries Society* 102: 764–773.
- Ralston, S. 1983. Factors in the control of feed intake of horses and ponies. *Neuroscience and Biobehavioral Reviews* 7: 465–470.
- Redmond, I. 1991. *The Elephant Book*. 48 pp. Overlook Press, Woodstock.
- Rhodin, A.G.J. 1974. Pathological lithophagy in *Testudo horsfieldi*. *Journal of Herpetology* 8: 385–386.
- Rörig, G. 1900a. Die Krähen Deutschlands in ihrer Bedeutung für Land- und Forstwirtschaft. *Arbeiten aus der Biologischen Abtheilung für Land- und Forstwirtschaft am Kaiserlichen Gesundheitsamte* 1: 285–400.
- Rörig, G. 1900b. Magenuntersuchungen land- und forstwirtschaftlich wichtiger Vögel. *Arbeiten aus der Biologischen Abtheilung für Land- und Forstwirtschaft am Kaiserlichen Gesundheitsamte* 1: 1–85.
- Rörig, G. 1906. Magenuntersuchungen heimischer Raubvögel. *Arbeiten aus der Kaiserlichen Biologischen Anstalt für Land- und Forstwirtschaft* 5 (5): 237–265.
- Sambraus, H. 1995. Federpicken beim Afrikanischen Strauß in Gefangenschaftshaltung. *Tierärztliche Umschau* 50: 108–111.
- Scheer, B.T. 1964. *Animal Physiology*. 409 pp. Wiley, New York.
- Schmidt-Nielsen, K. 1997. *Animal Physiology: Adaptation and Environment*. 612 pp. Cambridge University Press, Cambridge.
- Scott, D. and Duncan, K.W. 1967. The function of freshwater crayfish gastroliths and their occurrence in perch, trout and shag stomachs. *New Zealand Journal of Marine and Freshwater Research* 1: 99–104.
- Secor, S.M. and Phillips, J.A. 1997. Specific dynamic action of a large carnivorous lizard, *Varanus albigularis*. *Comparative Biochemistry and Physiology—Part A: Molecular & Integrative Physiology* 117: 515–522.

- Seebacher, F. 2001. A new method to calculate allometric length-mass relationships of dinosaurs. *Journal of Vertebrate Paleontology* 21: 51–60.
- Setz, E.Z.F., Enzweiler, J., Solferini, V.N., Amendola, M.P., and Berton, R.S. 1999. Geophagy in the golden-faced saki monkey (*Pithecia pithecia chrysocephala*) in the Central Amazon. *Journal of Zoology* 247: 91–103.
- Seymour, R.S. 1982. Physiological adaptations to aquatic life. In: C. Gans and F.H. Pough (eds.), *Biology of the Reptilia*, 1–41. Academic Press, London.
- Shaw, G. 1802. *General Zoology*. 312 pp. G. Kearsley, London.
- Shimada, K. 1997. Paleoecological relationships of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli* (Agassiz). *Journal of Paleontology* 71: 926–933.
- Siivonen, L. 1963. Die Schneemenge als überwinterungsökologischer Faktor. *Sitzungsberichte der Finnischen Akademie der Wissenschaften* 1962: 111–125.
- Skoczylas, R. 1978. Physiology of the digestive tract. In: C. Gans and K.A. Gans (eds.), *Biology of the Reptilia*, 589–717. Academic Press, London.
- Sleptsov, M.M. 1950. Concerning the biology of the far-eastern sea lion. *Izvestiia TINRO* 32: 129–133.
- Smith, H.M. 1953. Case history of a snake with an irregurgitable artificial egg. *Herpetologica* 13: 102.
- Soanes, C. and Stevenson, A. 2004. *Concise Oxford English Dictionary*. 1708 pp. Oxford University Press, Oxford.
- Soave, O. and Brand, C.D. 1991. Coprophagy in animals: a review. *Cornell-Veterinarian* 81: 357–364.
- Sokol, O.M. 1971. Lithophagy and geophagy in reptiles. *Journal of Herpetology* 5: 69–71.
- Spalding, D.J. 1964. Comparative feeding habits of the fur seal, sea lion, and harbour seal on the British Columbia coast. *Bulletin of the Fisheries Research Board of Canada* 146: 1–52.
- Spallanzani, L. 1785. *Herrn Abt Spallanzani's Versuche über das Verdauungs-Geschäfte des Menschen, und verschiedener Thier-Arten; nebst einigen Bemerkungen des Herrn Senebier*. 442 pp. Verlag der Dykischen Buchhandlung, Leipzig.
- Spletstoesser, J. and Todd, F.S. 1999. Stomach stones from emperor penguin *Aptenodytes forsteri* colonies in the Weddell Sea. *Marine Ornithology* 27: 97–100.
- Stauffer, C.R. 1945. Gastroliths from Minnesota. *American Journal of Science* 243 (6): 336–340.
- Stokes, W.M.L. 1942. Some field observations bearing on the origin of the Morrison "gastroliths". *Science* 95: 18–19.
- Stokes, W.M.L. 1987. Dinosaur gastroliths revisited. *Journal of Paleontology* 61 (6): 1242–1246.
- Storrs, G.W. 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. *American Journal of Science* 293-A: 63–90.
- Stubbes, D. 1668. An enlargement of the observations, formerly published numb. 27, made and generously imparted by that learn'd and inquisitive physician, Dr. Stubbes. *Philosophical Transactions (1665–1678)* 3 (36): 699–709.
- Taylor, M.A. 1993. Stomach stones for feeding or buoyancy? The occurrence and function of gastroliths in marine tetrapods. *Philosophical Transactions of the Royal Society of London. Series B* 341: 163–175.
- Taylor, M.A. 1994. Stone, bone or blubber? Buoyancy control strategies in aquatic tetrapods. In: L. Maddock, Q. Bone, and J.M.V. Rayner (eds.), *Mechanics and Physiology of Animal Swimming*, 151–161. Cambridge University Press, Cambridge.
- Taylor, R.H. and Tilley, J.A.V. 1984. Stoats (*Mustela erminea*) on Adele and Fisherman Islands, Abel Tasman National Park, and other offshore islands in New Zealand. *New Zealand Journal of Ecology* 7: 139–145.
- Thomas, G.J., Owen, M., and Richards, P. 1977. Grit in waterfowl at the Ouse Washes, England. *Wildfowl* 28: 136–138.
- Thompson, W.F. 1919. Halibut eats large rock. *California Fish and Game* 5: 157–158.
- Thomson, J.M. 1966. The grey mullets. *Oceanography and Marine Biology* 4: 301–335.2
- Travis, D.F. 1960. The deposition of skeletal structures in the Crustacea. I. The histology of the gastroliths skeletal tissue complex and the gastroliths in the crayfish, *Oconectes (cambaus) verilis* Hagen—Decapoda. *Biological Bulletin* 118: 137–149.
- Troyer, K. 1982. Transfer of fermentative microbes between generations in a herbivorous lizard. *Science* 216: 540–542.
- Tsutsui, N., Ishii, K., Takagi, Y., Watanabe, T., and Nagasawa, H. 1999. Cloning and expression of a cDNA encoding an insoluble matrix protein in the gastroliths of a crayfish, *Procambarus clarkii*. *Zoological Science* 16: 619–628.
- Turner, G.F. and Grimm, A.S. 1991. The diet of *Oreochromis lidole* (Trewavas) and other chambo species in Lakes Malawi and Malombe. *Journal of Fish Biology* 39: 15–24.
- Twigg, J. 2001. *Differentiating moa gizzard stones*. 118 pp. Unpublished M.Sc. thesis, University of Auckland, Auckland.
- Voris, H.K. 1966. Fish eggs as the apparent sole food item for a genus of sea snake, *Emydocephalus* (Krefft). *Ecology* 47: 152–154.
- Wacquant-Geozelles, S. v. 1892. Kleinere Mitteilungen. *Ornithologische Monatsschrift* 17: 43–44.
- Wade, M. 1989. The stance of dinosaurs and the Cossack dancer syndrome. In: D.D. Gillette and M.G. Lockley (eds.), *Dinosaur Tracks and Traces*, 73–82. Cambridge University Press, Cambridge.
- Waite, E.R. 2000. II. B Narrative of sub-Antarctic cruises; the vertebrate land fauna. In: P.D. Shaughnessy (ed.), *Antarctic Seals, Whales and Dolphins of the Early Twentieth Century: Marine Mammals of the Australasian Antarctic Expedition 1911–14, and the British, Australian and New Zealand Antarctic Research Expedition 1929–31*, 18–23. Australian Antarctic Division, Department of the Environment and Heritage, Kingston, Tasmania.
- Walton, K.C. 1984. Stomach stones in meadow pipits *Anthus pratensis*. *Bird Study* 31: 39–42.
- Waples, D.W. and Waples, J.S. 2004. A review and evaluation of specific heat capacities of rocks, minerals, and subsurface fluids. Part 1: minerals and nonporous rocks. *Natural Resources Research* 13: 97–122.
- Warren, A. 2000. Secondary aquatic tetrapods of the Upper Permian and Mesozoic. In: H. Heatwole and R.L. Carroll (eds.), *Amphibian Biology*, 1121–1149. Surrey Beatty & Sons, Chipping Norton.
- Webb, P.M., Crocker, D.E., Blackwell, S.B., Costa, D.P., and Boeuf, B.J. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology* 201: 2349–2358.
- Weeks, H.P. Jr. and Kirkpatrick, C.M. 1978. Salt preferences and sodium drive phenology in fox squirrels and woodchucks. *Journal of Mammalogy* 59: 531–542.
- Welman, J.B. and Worthington, E.B. 1943. The food of the crocodile (*Crocodilus niloticus* L.). *Proceedings of the Zoological Society of London. Series A* 113: 108–112.
- Whittle, C.H. and Everhart, M.J. 2000. Apparent and implied evolutionary trends in lithophagic vertebrates from New Mexico and elsewhere. In: S.G. Lucas and A.B. Heckert (eds.), *Dinosaurs of New Mexico. New Mexico Museum of Natural History and Science Bulletin* 17: 75–82.
- Wieland, G.R. 1906. Dinosaurian gastroliths. *Science* 23 (595): 819–821.
- Wiman, C. 1916. Blocktransport genom Saurier. *Geologiska Föreningens i Stockholm Förhandlingar* 38: 369–380.
- Wings, O. 2003. The function of gastroliths in dinosaurs—new considerations following studies on extant birds. *Journal of Vertebrate Paleontology* 23 (Supplement to No. 3): 111A.
- Wings, O. 2004. *Identification, distribution, and function of gastroliths in dinosaurs and extant birds with emphasis on ostriches (Struthio camelus)*. 187 pp. Published Ph.D. thesis, The University of Bonn, Bonn. (Accessible online at <http://nbn-resolving.de/urn:nbn:de:hbz:5N-04626>)
- Wings, O. 2005. Taphonomy, gastroliths, and the lithophagic behavior of sauropodomorph dinosaurs. *Journal of Vertebrate Paleontology* 25 (Supplement to No. 3): 131A.
- Wings, O. and Sander, P.M. 2007. No gastric mill in sauropod dinosaurs: new evidence from analysis of gastrolith mass and function in ostriches. *Proceedings of the Royal Society B: Biological Sciences* 274 (1610): 635–640.
- Worthy, T.H. and Holdaway, R.N. 2002. *The Lost World of the Moa: Prehistoric Life of New Zealand*. 718 pp. Indiana University Press, Indiana.
- Wyatt, A. 1986. *Challinor's Dictionary of Geology*. 374 pp. University of Wales Press, Cardiff.
- You, H.-L. and Dodson, P. 2004. Basal Ceratopsia. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 478–493. University of California Press, Berkeley.
- Zaleha, M.J. and Wiesemann, S.A. 2005. Hyperconcentrated flows and gastroliths: sedimentology of diamictites and wackes of the upper Cloverly Formation, Lower Cretaceous, Wyoming, U.S.A. *Journal of Sedimentary Research* 75: 43–54.
- Zhou, Z., Clarke, J.A., Zhang, F., and Wings, O. 2004. Gastroliths in *Yanornis*: an indication of the earliest radical diet-switching and gizzard plasticity in the lineage leading to living birds? *Naturwissenschaften* 91 (12): 571–574.
- Ziswiler, V. and Farner, D.S. 1972. Digestion and the digestive system. In: D.S. Farner and J.R. King (eds.), *Avian Biology*, 343–430. Academic Press, London.