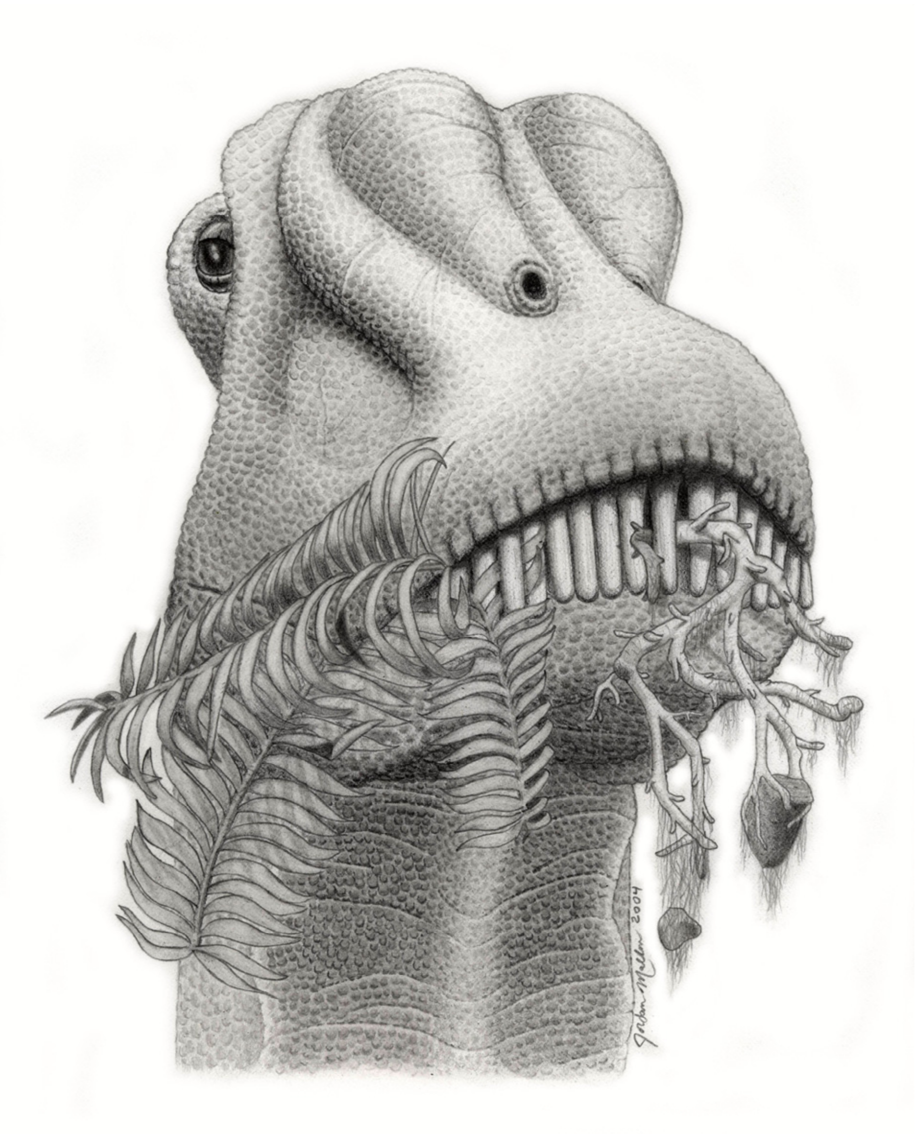
IDENTIFICATION, DISTRIBUTION, AND FUNCTION OF GASTROLITHS IN DINOSAURS AND EXTANT BIRDS WITH EMPHASIS ON OSTRICHES (*STRUTHIO CAMELUS*)

Dissertation
zur
Erlangung des Doktorgrades (Dr. rer. nat.)
der
Mathematisch-Naturwissenschaftlichen Fakultät
der
Rheinischen Friedrich-Wilhelms-Universität Bonn

vorgelegt von
Oliver Wings
aus
Sangerhausen

Bonn 2004



Diplodocid sauropod accidentally ingesting gastroliths while feeding on a cycad.

IDENTIFICATION, DISTRIBUTION, AND FUNCTION OF GASTROLITHS IN DINOSAURS AND EXTANT BIRDS WITH EMPHASIS ON OSTRICHES (*STRUTHIO CAMELUS*)

Dissertation

zur

Erlangung des Doktorgrades (Dr. rer. nat.)

der

Mathematisch-Naturwissenschaftlichen Fakultät

der

Rheinischen Friedrich-Wilhelms-Universität Bonn

vorgelegt von

Oliver Wings

aus

Sangerhausen

Bonn 2004

Angefertigt mit Genehmigung der Mathematisch-Naturwissenschaftlichen Fakultät der Rheinischen Friedrich-Wilhelms-Universität Bonn

1. Referent: Privat-Dozent Dr. Martin Sander
2. Referent: Professor Dr. Jes Rust

Tag der Promotion: 02.12.2004

Dedicated to Claudia. Thanks for everything.

French proverb: “Il a un estomac d’autuche!” (literally: He has the stomach of an ostrich!)
means: He can tolerate everything!

Geheimnisvoll am lichten Tag
Läßt sich Natur des Schleiers nicht berauben,
Und was sie deinem Geist nicht offenbaren mag,
Das zwingst du ihr nicht ab mit Hebeln und mit Schrauben.
JOHANN WOLFGANG VON GOETHE, Faust. Erster Teil (Szene Nacht)

TABLE OF CONTENTS

PREFACE

Despite of hundreds of papers and more than 150 years of research, the problems of gastrolith function and identification in the fossil record are far from being solved. Therefore, this dissertation project was conceived and a broad approach with consideration of many geological and biological factors was envisaged. The restricted timeframe of a dissertation did not allow the comprehensive study of the numerous fossil species from different clades with gastroliths. Consequently, I decided to concentrate on dinosaurs, with a focus on sauropodomorphs, an especially interesting clade because of their gigantism and their physiological adaptations.

Since an examination of fossil gastroliths alone would have left too many uncertainties, modern gastroliths from several vertebrate clades were included in this study. Because the function of gastroliths is best researched in birds and the closest modern equivalent to gastroliths-bearing dinosaurs are ratites, I focused on ostriches.

I did not focus on aquatic lithophagic clades such as plesiosaurs, pinnipeds, and crocodilians. However, since gastroliths in these groups offer new insights into avian and dinosaurian gastroliths, basic facts about gastroliths in aquatic animals are included where appropriate.

The chapters comprise:

- An overview about gastroliths with the focus on dinosaurs and extant vertebrates (including taxon lists of gastrolith-bearing dinosaurs and extant birds). This chapter is intended as introduction.
- A review of the definitions of gastroliths used in biology, medicine, and paleontology and suggestions for new terms for more exact descriptions. This chapter also reviews all hypotheses about the function of gastroliths.
- A study of stomach contents of free-ranging farm ostriches in Germany (n=135) and South Africa (n=212) with a focus on the gastroliths. The results are the most comprehensive study ever conducted on extant ratite gastroliths.
- The description and interpretation of a taphonomical experiment addressing the release of gastroliths from ostrich carcasses and its implications for the fossil record. This chapter is already published, in the Journal of Taphonomy in 2003.

- An analysis of the taphonomy of gastroliths. The processes which could lead to the loss of gastroliths are discussed and the fossil record of the most important groups of lithophagic vertebrates is reviewed. A new classification system for the authenticity of gastroliths is introduced.
- A field study and literature review of the presence of gastroliths in Upper Jurassic sauropods at several important dinosaur localities.
- The description of an experiment to simulate a bird gastric mill and a discussion of the implications for identification of fossil gastroliths.
- Suggestions for potential projects for future research on gastroliths.

ABSTRACT

Gastroliths (stomach stones) are known from many extinct and extant vertebrate clades and are potentially useful for paleobiological interpretations. This dissertation investigates the identification, function, distribution, and taphonomy of gastroliths with a focus on those of dinosaurs, including extant birds.

The terms bio-gastroliths, patho-gastroliths, and geo-gastroliths are suggested as more precise descriptions involving the origin of the stones. A review of the literature reveals that trituration and mixing of ingesta is an accepted function of gastroliths in many vertebrates (particularly in birds), whereas the influence of gastroliths on buoyancy in aquatic animals appears to be negligible. Accidental ingestion of sediment is considered to be common, as is the overlap of numerous functions.

The results of a study on German (n=135) and South African (n=212) free-ranging farm ostriches (*Struthio camelus*) indicate that ostriches ingest stones of greatly varying size. Adult animals typically hold one kilogram of stones in their stomach. On average, each stomach contained several thousand gastroliths with a grain size >1 mm. The mean gastrolith mass is very similar in both populations and constitutes about 1% of the mean body mass. Gastrolith mass is not significantly correlated with gender, age, season, and food contents by weight. Quartz is the predominating mineral type among ostrich gastroliths.

The taphonomic processes that may lead to the loss of gastroliths are discussed and the fossil record of the most important groups of lithophagic vertebrates (tangasaurids, crocodilians, sauropodomorph and theropod dinosaurs including birds) is reviewed. Experimental results show that gastroliths can be set free from ostrich chick carcasses with a body weight <12 kg after relatively short periods (3-6 days) in a hot and arid climate and that a separation in an aquatic environment is likely caused by prolonged floating of the carcass. A new classification of gastroliths is introduced that scales their presumed authenticity. The scale ranges from 1 (cluster of stones in the abdominal area of the skeleton) to 6 (surface finds of isolated, rounded and occasionally polished stones without associated bones).

Sedimentological and taphonomic evidence from several classic Upper Jurassic sauropod dinosaur localities shows that there are very few sauropod finds with unambiguous gastroliths. The scarcity of stones in the fine-grained sediments of most of these localities suggests that only a small number of sauropods possessed gastroliths. The occurrence of a gastric mill as seen in birds is not supported by the taphonomic evidence for sauropods. Without an association with fossil bone, there is no convincing evidence that exotic stones (exoliths) represent former gastroliths. It is more plausible that most of the surface-collected exoliths are weathering relicts of stratigraphically younger conglomerate layers.

An experiment was conducted that simulated a bird gastric mill in a rock tumbler using stones, water, plant material (grass), hydrochloric acid, and pepsin. The forces and the abrasion rate in the artificial gizzard were lower than in a real ostrich gizzard. After the end of the experiment six months later, the stones exhibited a total weight loss of 22.4%. Stomach juices and phytoliths contained in the grass had no visible effect on stone surface development. Given that no polish formed due to continuous abrasion, other causes, such as wind abrasion and diagenesis, should be considered for the polish sometimes observed on fossil gastroliths.

Finally, future research on gastroliths in crocodilians, pinnipeds, Permian tangasaurids, insectivorous species (e.g., anteaters) and other taxa is suggested. The distribution of gastroliths in extant and fossil members of Dinosauria is listed in appendices.

ZUSAMMENFASSUNG

Gastrolithen (Magensteine) sind von vielen ausgestorbenen und heutigen Wirbeltiergruppen bekannt und daher potentiell nützlich für paläobiologische Interpretationen. Diese Dissertation behandelt die Identifikation, Funktion, Verbreitung und Taphonomie von Gastrolithen mit Schwerpunkt auf Dinosaurier- und Vogelgastrolithen.

Zur präziseren Abgrenzung von Gastrolithen werden die Begriffe Bio-Gastrolithen, Patho-Gastrolithen und Geo-Gastrolithen vorgeschlagen. Sie enthalten Hinweise auf den Ursprung der jeweiligen Steine. Ein Literaturüberblick zeigt, dass die Zerkleinerung und Durchmischung der Nahrung die anerkannte Erklärung der Funktion von Gastrolithen bei vielen Wirbeltieren (insbesondere bei Vögeln) ist, wohingegen bei aquatischen Tieren der Einfluss von Gastrolithen auf den Auftrieb im Wasser vernachlässigbar scheint. Versehentliches Verschlucken von Sediment kann häufig als Erklärung für die Präsenz von Gastrolithen dienen. Auch eine Überlagerung verschiedener Funktionen ist möglich.

Die Ergebnisse einer Studie an freilaufenden Farmstraußen aus Deutschland (n=135) und Südafrika (n=212) zeigen, dass die Größe der von Straußen verschluckten Steine sehr stark schwankt. Adulte Tiere haben im Durchschnitt ein Kilogramm Steine in ihrem Magen und jeder Magen enthält durchschnittlich mehrere tausend Gastrolithen mit einer Korngröße >1 mm. Das mittlere Gastrolithengewicht ist in beiden Populationen nahezu gleich und beträgt etwa 1% des mittleren Körpergewichts. Das Gastrolithengewicht ist nicht signifikant mit Geschlecht, Alter, Jahreszeit und dem Gewicht der Nahrung korreliert. Quarz ist das dominierende Gestein bei Straußengastrolithen.

Die taphonomischen Prozesse die zum Verlust von Gastrolithen führen können, werden ebenso diskutiert wie der Fossilbericht der wichtigsten Gruppen lithophager Wirbeltiere (Tangasauride, Krokodilier, sauropodomorphe und theropode Dinosaurier, Vögel). Experimente zeigen, dass Gastrolithen aus Kadavern von Straußenküken mit einem Körpergewicht <12 kg in heißen und ariden Klimata bereits nach relativ kurzen Zeiträumen (3-6 Tage) freigesetzt werden können und dass eine Separation in aquatischer Umgebung aufgrund des anhaltenden Aufschwimmens der Tierleiche wahrscheinlich ist. Eine neue Klassifikation von Gastrolithenfunden, geordnet nach ihrer vermutlichen Authentizität, wird vorgeschlagen. Die Skala reicht dabei von 1 (Ansammlungen von Steinen im abdominalen Bereich von Skeletten) bis 6 (Oberflächenfunde von isolierten, gerundeten und gelegentlich polierten Steinen ohne assoziierte Knochen).

Die sedimentologischen und taphonomischen Gegebenheiten verschiedener klassischer Sauropodenfundstellen aus dem Oberjura zeigen, dass es nur sehr wenige Sauropodenfunde mit eindeutigen Gastrolithen gibt. Die Seltenheit von Steinen in den feinkörnigen Sedimenten der meisten dieser Lokalitäten deutet darauf hin, dass nur eine kleine Anzahl von Sauropoden überhaupt Gastrolithen hatte. Die Idee einer „Magenmühle“ wie sie von Vögeln bekannt ist, wird bei Sauropoden daher nicht durch taphonomische Fakten gestützt. Ohne eine Assoziation mit fossilen Knochen gibt es keine überzeugenden Beweise, dass exotische Gerölle (Exolithen) frühere Gastrolithen darstellen. Es ist wahrscheinlicher, dass die meisten der von der Oberfläche abgesammelten Exolithen Verwitterungsreste von stratigraphisch jüngeren Konglomeratlagen sind.

Mit Hilfe einer Trommelmaschine, Steinen, Pflanzenmaterial (Gras), Salzsäure und Pepsin wurde ein Experiment zur Simulation der „Magenmühle“ bei Vögeln durchgeführt. Die Kräfte und die Abrasionsrate in diesem künstlichen Muskelmagen waren geringer als in einen echten Straußenmagen. Als das Experiment nach sechs Monaten beendet wurde, betrug der gesamte Gewichtsverlust der Steine 22,4%. Magensäfte und im Gras enthaltene Phytolithen hatten keinen sichtbaren Effekt auf die Entwicklung der Gesteinsoberfläche. Da durch die kontinuierliche Abrasion keine Politur entstehen konnte, sollten andere Gründe wie Windabrasion oder Diagenese als Ursache für die Politur, die zuweilen an fossilen Gastrolithen beobachtet werden kann, in Betracht gezogen werden.

Zukünftige Forschung an Gastrolithen von Krokodiliern, Pinnipediern, permischen Tangasauriden, insektivoren Arten (z.B. Ameisenfresser) und anderen Wirbeltiergruppen wird empfohlen. Die Verbreitung von Gastrolithen bei heutigen und fossilen Vertretern der Dinosauria ist in Appendices aufgelistet.

GENERAL ACKNOWLEDGEMENTS

All the people I am in debt to are listed in the acknowledgements of each chapter. However, since this work is the result of several years of research, I would like to thank some people without which this thesis would not be in the present state.

I am very thankful to my advisor Martin Sander for his recognition and interest in the topic and his constant support during the progress of my research. Walter Joyce donated much time for discussions and the supply of literature. Denver Fowler is given my thanks for fruitful discussions and his company in the field. Claudia Trögl supported my work in most diverse ways, among others, preparing of illustrations, measuring data, financial and moral support. I would like to thank numerous people for literature hints regarding rare and sometimes obscure publications, but especially Christopher Whittle who kindly supplied his bibliography about gastroliths which served as an excellent starting point for my literature search. Ralf Schuhmacher from the Straussenfarm Gemarkenhof made the main research on living ostriches in Germany possible. Adriaan Olivier was very helpful during my research on South African ostriches. I thank Mike Everhart for providing samples, introducing me to a number of outcrops in Kansas and for our stimulating discussions. Annette Broschinski allowed me to finish the writing during my trainee position at the Landesmuseum Hannover.

I am grateful to all the people who gave an introduction or any other kind of advise for and during field work in Argentina, Germany, Portugal, and the USA, particularly Ken Carpenter, Dan Chure, Karen Cloward, Mike Everhart, John Forster, Michael Leschin, Spencer Lucas, Octavio Mateus, Oliver Rauhut, Karsten Sommerwerk, Ken Stadtman, and Glenn Storrs.

Jordan Mallon kindly lend his drawing skills for the cover illustration. Marcus Clauss proof-read the complete thesis and made suggestions for last-minute changes. Jes Rust and Wolfgang Böhme kindly agreed to be on my board of examiners.

Furthermore, I want to thank my parents and friends for their steady support and interest. Financial support was provided by the “Graduiertenförderung Nordrhein-Westfalen”, the Graduiertenkolleg “Evolution und Biodiversität in Raum und Zeit”, the Jurassic Foundation, and my parents. Last not least many thanks to all the countless paleontologists and interested lay-man world-wide, for the useful discussions, the supply of references as well as material, and all the other help. It was delightful.

CHAPTER I: Gastroliths – An overview

An earlier version of this compilation was written with Phillip J. Currie for the second edition of the "Encyclopedia of Dinosaurs" but never published. Since it is an up-to-date review of dinosaur gastroliths, I have decided to add it here as an introduction.

Stones kept within the digestive tract of living animals and inside the abdominal area of fossil animals are referred to as gastroliths, a term derived from the Greek words gastir (=belly, stomach) and lithos (=stone), and colloquially referred to as "stomach stones" or "gizzard stones". Unfortunately, the term gastroliths has also been applied towards biogenic carbonate concretions found in some crustaceans and some pathological concretions that form out of food remains and residual stomach fluids in the stomachs of extant mammalian herbivores like camelids. To most vertebrate paleontologist, gastrolith only refers to stones, which have been naturally ingested during a behavior known as lithophagy. Among fossil and living amniotes, stomach stones are most commonly found in plesiosaurs, pinnipeds (seals and sea lions), and several clades of archosaurs (e.g., crocodilians, dinosaurs (Appendix I), ratites, songbirds, and galliform birds (Appendix II)) (Baker, 1956; Whittle and Everhart, 2000).

Despite the widespread opinion, gastroliths are not necessarily linked to a certain function (Wieland, 1906). Accordingly, although several groups of extant birds swallow small pebbles and sand grains to mechanically break down hard or coarse food in the muscular gizzard ("gastric mill"), this is not necessarily the only possible use of gastroliths. The gastroliths of many swimming vertebrates may function as ballast for buoyancy control by increasing the animal's overall density and lowering its center of gravity (Currie, 1981; Taylor, 1993, though see Henderson, 2003, for an opposing opinion). Many other hypotheses regarding their functions have been formulated, such as a relief of hunger pangs, ingestion by mistake, mineral supply, detoxification of ingested toxic food, extermination of intestinal parasites, play instinct, and pathological behavior. However, none of these have been sufficiently tested.

Because the pattern of gastrolith occurrence is extremely patchy in the fossil record, it is very difficult to decisively identify the function of gastroliths in dinosaurs. Indeed, only seldom are fossils found that contain enough gastroliths relative to the calculated body mass of the animal to support the notion of a digestive function, as seen in extant birds. Among those species that exhibit gastroliths, only some individuals are actually found with them. There is no clear correlation between the morphology and arrangement of teeth of a species and the presence of gastroliths. Finally, especially among larger dinosaurs, the association of stones with a particular skeleton is often conjectural, because most early excavators provided little information as to the location of these pebbles in relation to the skeleton. The situation is very different for some aquatic reptiles, such as crocodilians (Troedsson, 1924; Weigelt, 1927; Berckhemer, 1928; Langston and Rose, 1978; Keller and Schaal, 1992) and long-necked plesiosaurs (Williston, 1904; Darby and Ojakangas, 1980; Everhart, 2000; Sato and Storrs, 2000) which predominantly preserve gastroliths directly inside their articulated rib cages.

In spite of the long list of dinosaur finds with purported gastroliths (Appendix I), only few can withstand rigorous testing. This may be due to poor collection records or taphonomical processes. However, some fossil sites, like the Upper Jurassic alluvial fan deposits at Lourinhã (Portugal), yield several different dinosaur species with gastroliths. Stomach stones are consistently reported for three clades of non-avian dinosaurs: sauropodomorphs (Christiansen, 1996), psittacosaurids, and the maniraptoriform theropods *Sinornithomimus dongi* (Kobayashi and Lü, 2003) and *Caudipteryx zoui* (Ji et al., 1998).

More than two dozen sauropod fossils are known to have had gastroliths, and one of the best documented examples was found in the abdominal region of the diplodocid sauropod *Seismosaurus hallorum* (Gillette, 1994). In total, more than 240 gastroliths were recovered from the excavation, the largest of which with a diameter of roughly 10 cm. Nevertheless, this amount of gastroliths – the largest ever reported from a dinosaur – would not have been sufficient to support a gastric mill as seen in extant birds (Wings, 2003; Wings and Sander, in preparation). In the case of all sauropodomorphs, the ingested stones might have been swallowed accidentally or for mineral uptake (Wings and Sander, in preparation). Because some sauropods such as diplodocids and titanosaurids had thin, pencil-like teeth and an only minimal capability of processing food in their mouths (Calvo, 1994), their exact food processing thus still remains a mystery.

The presence of stones in the abdominal cavities of specimens of *Psittacosaurus mongoliensis* (Osborn, 1924) and *Psittacosaurus mazongshanensis* (Xu, 1997) is difficult to understand. Although not as highly developed as in neoceratopsians, psittacosaurs nevertheless had relatively sophisticated dental batteries that must have accomplished most of the mechanical food processing. Perhaps their food was extremely resistant, or the stones were swallowed primarily for other reasons like mineral supply. However, all of these hypotheses must be considered *ad hoc* until additional evidence is discovered.

In the theropods *Sinornithomimus dongi* and *Caudipteryx zoui*, there is consistent evidence for the use of gastroliths in trituration of foodstuff (Wings, 2003; Wings and Sander, in preparation). Gastroliths occasionally found within the body cavities of other dinosaurs (e.g., other theropods or ornithischians) probably had no important function or were acquired *post mortem* during burial.

The appearance of gastroliths is highly variable and extremely complex processes change their look. Some of the stones have a distinctive, highly polished surface, which has previously been attributed to physical movements within the digestive tract, abrasion from plant matter, especially phytoliths, and the action of digestive acids and enzymes. Recent research (see chaper III) has shown that the abrasion rate of gastroliths in extant bird gizzards is too high to develop polish. Ostrich gastroliths, for example, have a dull surface and show no differences to river gravel (Wings, 2003). Furthermore, stomach juices as well as phytoliths have very limited influence on gastrolith surface texture (see chapter VII). Isolated pebbles also may be polished by processes other than a gastric mill, like sandblasting by winds. As such, and in spite of several attempts (Manley, 1991; Manley, 1993; Whittle and Onorato, 2000), no unambiguous method has been found yet to identify isolated pebbles as gastroliths.

The designation of exotic stones as gastroliths was discussed for more than hundred years (Stokes, 1987). Highly polished stones, which are out of the context of depositional dynamics and occur found without any relationship to bone material, are common in dinosaur fossil-rich, fine-grained sediments like those of the Morrison Formation. They could be transported into the deposits as dropstones on rafting agents (tree roots, ice, etc.) and should not be considered gastroliths *a priori*. Consequently, such stones should be addressed as “exoliths”, a term that is proposed in chapter II, meaning isolated exotic stone in a fine-grained matrix.

References

Baker, A.A., 1956. The swallowing of stones by animals. The Victorian Naturalist, 73(6): 82-95.

Berckhemer, F., 1928. Untersuchungen über die Meerkrokodile des schwäbischen oberen Lias (Diskussionsbemerkung). Paläontologische Zeitschrift, 10: 63.

Calvo, J.O., 1994. Gastroliths in sauropod dinosaurs. Gaia, 10: 205-208.

Christiansen, P., 1996. The evidence for and implications of gastroliths in sauropods (Dinosauria, Sauropoda). Gaia, 12: 1-7.

Currie, P.J., 1981. *Hovasaurus bolei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeontologica Africana, 24: 99-163.

Darby, D.G. and Ojakangas, R.W., 1980. Gastroliths from an Upper Cretaceous plesiosaur. Journal of Paleontology, 54(3): 548-556.

Everhart, M.J., 2000. Gastroliths associated with plesiosaur remains in the Sharon Springs Member of the Pierre Shale (late Cretaceous), Western Kansas. Transactions of the Kansas Academy of Science, 103(1-2): 58-69.

Gillette, D.D., 1994. *Seismosaurus*, the Earth Shaker. Columbia University Press, New York, 205 pp.

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(8): 1346-1357.

Ji, Q., Currie, P.J., Norell, M.A. and Ji, S.-A., 1998. Two feathered dinosaurs from northeastern China. Nature, 393(6687): 753-761.

Keller, T. and Schaal, S., 1992. Crocodiles: large ancient reptiles. In: S. Schaal and W. Ziegler (Editors), Messel. An Insight into the History of Life and of the Earth. Clarendon Press, Oxford, pp. 109-118.

Kobayashi, Y. and Lü, J.-C., 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. Acta Palaeontologica Polonica, 48(2): 235-259.

Langston, W.J. and Rose, H., 1978. A yearling crocodilian from the Middle Eocene Green River Formation of Colorado. Journal of Paleontology, 52(1): 122-125.

Manley, K., 1991. Two techniques for measuring surface polish as applied to gastroliths. Ichnos, 1(4): 313-316.

Manley, K., 1993. Surface polish measurement from bona fide and suspected dinosaur gastroliths and wave and stream transported clasts. Ichnos, 2(2): 167-169.

Osborn, H.F., 1924. *Psittacosaurus* and *Protiguanodon*: two Lower Cretaceous iguanodonts from Mongolia. American Museum Noviates, 127: 1-16.

Sato, T. and Storrs, G.W., 2000. An early polycotylid plesiosaur (Reptilia : Sauropterygia) from the Cretaceous of Hokkaido, Japan. Journal of Paleontology, 74(5): 907-914.

Stokes, W.M.L., 1987. Dinosaur gastroliths revisited. Journal of Paleontology, 61(6): 1242-1246.

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-Biological Sciences, 341(1296): 163-175.

Troedsson, G.T., 1924. On Crocodilian Remains from the Danian of Sweden Ohlson. Lunds Universitets Arsskrift, 20(2): 1-75.

Weigelt, J., 1927. Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung. Max Weg, Leipzig, 227 pp.

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 (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin, pp. 75-82.

Whittle, C.H. and Onorato, L., 2000. On the origins of gastroliths determining the weathering environment of rounded and polished stones by scanning-electron-microscope examination. In: S.G. Lucas and A.B. Heckert (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin, pp. 69-74.

Wieland, G.R., 1906. Dinosaurian gastroliths. Science, N.S., 23(595): 819-821.

Williston, S.W., 1904. The stomach stones of the plesiosaurs. Science, N.S., 20(October 28, 1904): 565.

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. and Sander, P.M., in preparation. Gastrolith function in dinosaurs reconsidered: No evidence for gastric mills in sauropods.

Xu, X., 1997. A new psittacosaur (*Psittacosaurus mazongshanensis*, sp. nov.) from Mazongshan Area, Gansu Province, China. In: Z. Dong (Editor), Sino-Japanese Silk Road Dinosaur Expedition. China Ocean Press, Beijing, pp. 48-67.

CHAPTER II: A review of gastrolith function and a revised classification

Abstract

Hard objects within the digestive tract of animals are called gastroliths, without specification of the mechanism that is responsible for their accumulation. This paper reviews the differences that exist between the definitions of gastroliths used in biology, medicine, and paleontology. The terms bio-gastroliths, patho-gastroliths, and geo-gastroliths are suggested for more exact descriptions involving the origin of the stones.

Hypotheses about the function of gastroliths are reviewed and discussed. The trituration and mixing of foodstuff is the accepted function of gastroliths in many vertebrates, including birds. Ballast provided by swallowed stones is considered to be of negligible importance for buoyancy in aquatic animals. Among plausible hypotheses for gastrolith function are mineral supply and mineral storage, the maintenance of a beneficial microbial gut flora, the destruction of parasites, or the alleviation of hunger. However, accidental ingestion of sediment is considered to be common, either by being mistaken for prey, by being attached to it, during playing, or due to pathological behavior. It is plausible that several functions overlap in specific taxa, e.g., gastroliths in herbivorous birds serve as grinding and mixing agent but also as mineral source (e.g., limestones for calcium supply).

Introduction

While the term “gastrolith” was introduced by Mayne (1854) “Gastrolithus - a stone or calculus in the stomach”, the knowledge about stones in certain animals is much older. The grit use in birds was of particular interest to early natural historians (Spallanzani, 1785), and the stones in crocodile stomachs are included in many African myths (Neill, 1971). Stubbes (1668), the oldest reference mentioning the stomach stones in crocodiles, already proposed that the stones had a digestive function. Huxley (1880) used the term gastroliths in connection with crustaceans: “There are […] found at the sides of the stomach, two lenticular calcareous masses, which are known as ‘crabs-eyes’, or gastroliths.” Finally, 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 with plesiosaurs and sauropod dinosaurs, as well as stomach stones in extant lizards, alligators, and birds.

Since 1906, the term “gastrolith” has been applied to a large variety of stones or concretions found in the digestive tract of invertebrates and vertebrates, thereby creating some confusion.

Several researchers have ascribed a specific function to gastroliths without a critical test of their hypotheses, which further complicates scientific communication. Therefore, I feel that it is necessary to clarify definitions of relevant terms and to separate the existing interpretations with new functional terms.

In the last centuries, many hypotheses were suggested for the function of gastroliths, some of which are tested herein. A review of the ideas for gastrolith function helps to understand their distribution in fossil and extant taxa and might solve some paleobiological problems. An additional goal of this paper is to increase awareness regarding the variety of possible gastrolith functions.

Terminology

Existing definitions for gastrolith

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) and bioports (unmodified stones carried, externally transported, or moved by animals). A good example for biofacts are stones used by chimpanzees (Boesch and Boesch, 1981). Several kinds of animals are known to carry stones externally, for instance buzzards, vultures, kites, eagles, apes, and rodents. For more details, see Johnson (1993) and references therein. Unfortunately, the term bioclast is preoccupied with a different meaning in carbonate petrography and should therefore not be used. Also, the need for such a general term is rather limited since, for example, gastroliths and biofacts are not commonly found together.

Since the term “gastrolith” was used for the description of several types of “stones” in context with the digestive tract of animals, each of which with a different formation history, the definitions are rather diverse. Most definitions in dictionaries and glossaries are limited to some characteristics and do not reflect the distribution of stomach stones within animals. For instance, a high polish is often attributed to gastroliths (e.g., Bates and Jackson, 1980; Jackson, 1997; Allaby and Allaby, 1999), but is rarely found on stomach stones of extant birds (Wings and Sander, in preparation). Also, definitions are often restricted to occurrences within only certain clades of animals (e.g., crustaceans, Huxley, 1880; or reptiles, Jackson, 1997) and do not represent the reported distribution of stones in animals.

Commonly, definitions contain proposed functions of the stones, such as grinding food (Bates and Jackson, 1980; Currie and Padian, 1997; Farlow and Brett-Surman, 1997; Jackson, 1997; Allaby and Allaby, 1999; Anonymous, last time accessed: 2001a; Anonymous, last time accessed: 2004) or buoyancy in aquatic animals (Jackson, 1997). Many functions in certain taxa are not proven, and a general definition should therefore not be restricted to a specific function. Taphonomic and sedimentological issues are integrated in other definitions (Challinor, 1974; Wyatt, 1986). Since such issues are not essential to describe the term, they also should be avoided.

In summary, most existing definitions are impractical. A useful definition should contain as much applicable criteria as possible without many assumptions. Therefore, a definition for gastroliths should not mention the physical characteristics such as roundness and polish of stones as they limit the applicability of the definition. The same is true for restrictions regarding specific groups of animals. Also, a limitation of the definition to vertebrates should be avoided, as it would leave out the sediments and concretions found in crustaceans and insects. Last but not least, a definition should not be limited by implied functions of the stones, because gastrolith function in some clades is still unclear and because interdependencies between proposed functions might exist. To be practical and easy to understand, the definition should closely lean on the meaning of the word gastrolith, covering all stones and stone-like objects in the stomach.

Skoczylas (1978) gave a very simple definition for gastroliths: “When the objects swallowed remain in the stomach, they are called gastroliths.” This definition is almost acceptable. It, however, includes all foreign objects including hard-to-digest food items, while a definition of gastrolith should be restricted to geological material of sand size and larger or to concretions formed within the animal, respectively. The entire digestive tract of vertebrates can contain gastroliths. However, the occurrence of most of the gastroliths, especially the not accidentally ingested stones, is restricted to the stomach.

Historically, the first definition is “Gastrolithus - a stone or calculus in the stomach: a gastrolith“ cited from the Oxford English Dictionary (Anonymous, last time accessed: 2001b), the original publication is possibly Mayne (1854). This definition should be used with priority.

Suggested new definition for gastrolith

As it is impossible to determine the retention time of pebbles in the digestive tract of dead animals, all stones found in the digestive tract should be called gastroliths. This implies that a separation of gastroliths with a real function and accidentally swallowed objects is not feasible. The way of extraction of the gastroliths (via excretion or regurgitation or post-mortem) is not relevant for the definition.

The literal implementation of the term gastroliths – stomach stones – would exclude all particles of sand size and smaller. However, such a limit is rather artificially set, since small sediment particles are commonly found in small species and juveniles, respectively, where they fulfill the same function as stones in large animals. The minimum grit found in many small bird species (sometimes reaching 0.1 mm, e.g., Best and Gionfriddo, 1991) must be included and a new minimum size of the particles should be defined. The standard grain size border between silt and sand at 0.063 mm is suggested. 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: Gastroliths are hard objects of no caloric value (for instance, stones, natural and pathological concretions) which are or were kept in the digestive tract of animals and have a minimum diameter of 0.063 mm. Gastroliths occur regularly in several clades of invertebrates (e.g., crustaceans) and vertebrates (e.g., archosaurs, pinnipeds) and can serve several functions, most importantly food trituration as in birds. The physical characteristics of gastroliths, especially roundness and surface texture, are strongly depended on the function of the stones and other factors such as rock type, retention time, or abrasion rate in the stomach.

Categories of gastrolith regarding their origin

Until now, the term gastrolith is applied to several fields of geological, biological, and medical sciences with different definitions, causing problems in the understanding between biologists and paleontologists, for instance. Whatever exact definition might be applied, in paleontology gastroliths are always swallowed stones. To the contrary, most biologists understand gastroliths as stomach concretions formed in crustaceans and used for mineral storage. Some crustacean species reabsorb calcium from the old cuticle and deposit it in gastroliths (Scheer, 1964).

Also, some vertebrate biologists, veterinarians, and pathologists define gastroliths as pathological, stone-like concretions which were formed by swallowed and felted hair or vegetable fibers in the stomach of herbivorous mammals like the bezoar goat or the llama. Such stones are also called "bezoar stones" (e.g., Elgood, 1935).

Finally, some geologists call all isolated polished pebbles in fine-grained sediments gastroliths. 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 misleading and contradicting definitions cause confusion if mixed up. Frizzell and Exline (1958) already realized that the different meanings of the word gastrolith create misunderstandings. Unfortunately, later authors never bothered to differentiate between the separate origin and function. Therefore, more specific term should be used.

Frizzell and Exline (1958) suggested the terms "crustacean gastrolith" and "saurian gastrolith" to avoid confusion. While "crustacean gastrolith" would be acceptable (but rather long) because the accretions are only known from crustaceans, the term "saurian gastrolith" is inaccurate, as it suggests that swallowed pebbles are exclusively associated with reptile remains. However, they are known from several groups of animals, including many birds and mammals. For a more general and accurate distinction, the origin of the gastroliths should be used for the name.

To differentiate between the fundamentally different biological and paleontological meanings of gastroliths, it is proposed to use suitable prefixes for the term "gastrolith". Suggested are:

- **bio-gastrolith** for non-pathological invertebrate concretions
- **patho-gastrolith** for every pathological stone formed in the stomach.
- **geo-gastrolith** for swallowed pebbles and grit. When these pebbles are deposited in a gizzard (muscular stomach used for trituration of foodstuff), "gizzard stones" can be used as a synonym. Another rather rarely used term for geo-gastroliths is "belly boulders". "Grit" is often used for geo-gastroliths in birds. "Crop stones" was sometimes used in older publications for geo-gastroliths. This term is very misleading because the stones are normally situated in the gizzard. Hence, the term should not be used anymore.

The use of these somewhat longer terms should at least be mentioned in the abstract and keywords of scientific publications to ease the classification of the paper to the reader. "Stomach stones" can be used as a general description for gastroliths, without any separation into bio-, patho-, and geo-gastroliths.

Introduction of the term "exolith"

I am aware of the difficulties of introducing a new sedimentological term for a phenomenon known for a long time, especially since some generally established terms do exist. Existing names for clasts in fine-grained sediments with unknown origin and transport mechanism are "foreign stones", "extraneous stones", "erratics", "dropstones", and "exotic stones".

Among the existing terms, “erratics” is probably the most exact one. An acceptable definition is “An erratic is 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). This definition is hence not restricted to transport by ice. However, the terms erratic and dropstone have the disadvantage of commonly being used only in connection with glacial processes. Furthermore, the terms “erratics” or “erratic boulders” have been available for many years now but were never accepted for all types of stones in question.

The existence of these terms notwithstanding, many exotic stones with an unknown provenience and transport mechanism are called “gastroliths”. This term should be restricted to true gastroliths and therefore should not be used for stones which are not associated with fossil vertebrates and which can therefore not be identified unambiguously. This designation of exotic stones as gastroliths was discussed for more than one hundred years (Stokes, 1987). The need for naming exotic pebbles in fine-grained sediments without implying a special way of transportation was already realized by Stokes (1942). He suggested the name “Morrison stones” based on their occurrence in the Jurassic Morrison Formation of western USA. The term was fortunately not used by later authors, since the pebbles are not restricted to the Morrison Formation.

Highly polished stones, which are out of the context of depositional dynamics and occur without any relationship to 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. They could have been transported into the deposits as dropstones by several rafting agents (tree roots, ice, etc.) and are not *a priori* gastroliths. Consequently, such stones should not be called “gastrolith” (even if they could represent former gastroliths) but should rather be addressed with another term. Stokes (1942) noted the improbability of the fact that all these isolated stones in the Morrison Formation are gastroliths. He thought it would be “advisable to abandon the term “gastrolith” in favor of some non-committal designation” as long as the “connection between the dinosaurs and these highly polished pebbles” is not proven. Later, Stokes (1987) rejected his own suggestion “Morrison stones” (analogous to “Gobi stones”) because of the wide distribution of such stones in other formations. However, Stokes did not introduce a new term with no stratigraphical limitation.

For a better characterization of isolated clasts, a new term is proposed here:

> **Exolith** – an exotic rock in fine-grained sediments which may show a high polish and which potentially (but not necessarily) was a former gastrolith.

This term is meant to replace the term “gastrolith” which is often used incorrectly in its geological meaning. The onomastic origin of exolith is “exos” (from outside), which is already used in sedimentology in exotic blocks or pebbles, and “lithos” (stone). “Exolith” can be applied to any exotic rock of unknown origin in all fine-grained sediments from different depositional environments and of different compositions.

Definition of geophagy and lithophagy

The behavior of voluntary and purposeful ingestion of sediment particles by animals can be divided into two groups: geophagy and lithophagy, which have not been properly separated until now (e.g., Skoczylas, 1978). Geophagy is the consumption of soil and is known from reptiles, birds, mammals, and even from people of specific nations. These soils, rich in clay, salt, or fat, serve as a food supplement for the supply of specific minerals or for medical purposes. For an overview of existing literature and possible functions of ingested soil, see for instance Setz et al. (1999), Beyer et al. (1994), and Jones and Hanson (1985). Since geophagy is restricted to soil and therefore does not cover the consumption of stones, the term is not relevant for this study, but is mentioned to separate it from lithophagy.

If the grain size of the swallowed sediment reaches sand size (0.063 mm), the consumption should be called lithophagy. Geophagy is often synonymous with lithophagy (e.g., Skoczylas, 1978). Yet, even if the grain size border for the classification of the two habits is continuous, geophagy should be separated from lithophagy because the reasons behind both behaviors are generally different.

Lithophagy describes the deliberate consumption of stones. The stones become gastroliths after their ingestion. It is suggested to separate lithophagy from geophagy by using minimum sand grain size (0.063 mm) as the minimum grain size of the ingested material.

Gastrolith function

Early on, the stomach stones of many different clades of vertebrates stirred scientific interest, and many hypotheses about the function of the stones developed. The first report of gastroliths in crocodilians is more than 330 years old (Stubbes, 1668), and despite continuous studies during the last centuries, many questions about gastrolith function still remain unanswered. On the following pages, each proposed function is reviewed and discussed briefly. Some hypotheses are rather absurd, not supported by any data, and are not generally accepted by the scientific community. However, they are also discussed briefly for the sake of completeness.

Trituration of ingesta

The trituration of foodstuff using gastroliths is best researched in birds, and the functional role of teeth is often ascribed to the gastroliths of all birds (Ziswiler and Farner, 1972). In birds, the swallowed food is soaked with stomach juices in the proventriculus (glandular stomach) and after that, 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 is increased by this use of gastroliths (Sokol, 1971). Without gastroliths, the bird gizzard also tends to retain fibrous material which can cause a partial or complete constipation (Thomas et al., 1977).

A increase in the number of gastroliths in feces of dunnocks (*Prunella modularis*) correlates with a change in diet from insects to both, seeds and insects (Bishton, 1986). This has previously been interpreted as an indication for an assistance of gastroliths in the grinding of vegetable matter (Bishton, 1986).

However, there are also authors who completely doubt the effect of gastroliths on the trituration of food in birds (e.g., Walton, 1984) since not all individuals of a given species allegedly contain stones. Several studies have shown that gastroliths are always present in several galliform birds as well as in ratites (e.g., Gionfriddo and Best, 1999; Wings, 2003, and see chapter III).

The question if 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 (Wacquant-Geozelles, 1892). However, the general conclusion of the gastroliths function in grain-feeding birds is that the stones are not indispensable to life but support a more effective grain digestion (Mangold, 1927a). The digestibility in birds may be increased by 10% by addition of grit (Duke, 1986). Mangold

(1927b) even reported an increase of digestibility in 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 also was proposed for sand and gravel found in several insectivorous and omnivorous lizards (Johnson, 1966; Sokol, 1971).

In marine tetrapods, trituration of ingesta with gastroliths has been speculated to be dangerous, because the 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 and pointy objects like chert or glass without any damage to the digestive tract (Jacobi, 1900; Gillette, 1994, and Wings, personal observations on ostriches 2003), possibly by shifting the stomach contents in case of danger of injuries. Perhaps marine tetrapods are able to do the same. Examinations of pinniped feces might clarify this issue. In any case, several authors believed in the utilization of gastroliths in the physical breakdown of food in the stomach of pinnipeds (e.g., Mathews, 1929; Spalding, 1964).

A digestive help is also the most frequent suggestion for gastroliths found in fossil vertebrates (e.g., Currie, 1997). Gastroliths in stereospondyl amphibians are believed to have been swallowed for food processing (Warren, 2000). Especially for sauropodomorph dinosaurs this has previously been the most widely excepted hypothesis (e.g., Christiansen, 1996). However, recent research revealed that this hypothesis is not supported by sedimentological, taphonomical, and paleobiological evidence (Wings, 2003; Wings and Sander, in preparation; and see chapters III-VII): only a small percentage of sauropod finds contained gastroliths and the amounts, the size, the surface structure, and the composition of unambiguous sauropod gastroliths speak against their use for trituration of foodstuff.

Mixing of foodstuff

The mixing of foodstuff by gastroliths occurs by necessity together with trituration. In examined ostriches, mainly feeding on grass (see chapter III), the stones mix the food content and prevent the blocking of the pyloric sphincter with agglutinated balls of grass. The fact that ostriches which have no access to stones die of constipation (Ralf Schuhmacher, pers. comm. 2000) emphasizes 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; Wings and Sander, in preparation; and see chapter III), gastroliths in herbivorous birds are directly embedded in the pulped food and not surrounded by stomach fluids, and the number of stones present in the stomach regions of sauropod finds would be too small for effective processing of foodstuff either by trituration or by mixing.

Mineral supply

Geophagy of many taxa has presumably evolved for mineral supplementation (Setz et al., 1999). To prove 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. Deficiency symptoms and nutritional diseases such as a disturbed bone metabolism may be responsible for gravel ingestion (e.g., of turtles, Dennert, 1997; Dennert, 2001).

Birds are a good clade to exemplarily study the connection between gastroliths and mineral uptake. Except for the high calcium need of egg-laying birds, most other mineral requirements of birds are similar to those of mammalian species (Fisher, 1972). Gastroliths-bearing birds can use abraded mineral material from the gastroliths. The mineral requirements of birds can be divided into structural elements (Ca, P), homeostatic elements (Na, K, Cl), and trace elements (Mg, Mn, Zn, Fe, Cu, Mo, Se, I, Co, Cr)(Fisher, 1972). Among the trace elements, the largest amounts are needed of magnesium, manganese, zinc, and iron. On the other hand, cobalt is required only as a part of the vitamin B_{12} molecule. For the exact values of the mineral requirements see Fisher (1972) and the references therein.

Limestone is an excellent source of calcium. This rock type is widely distributed on Earth, and it is easily soluble in the acidic stomach environment. It has been known for centuries that a good supply with calcium carbonate (as limestone or shells) is beneficial to good bone growth and eggshell production in chickens (Mangold, 1927a). Nesting pheasant hens (*Phasianus colchicus*) even have the ability to selectively ingest limestone (Harper, 1964). However, most gastroliths are composed of quartz varieties. In birds, the supply with silica due to chemical solution of quartz pebbles in the stomach was discussed in Mangold (1927a). He concluded that the slow abrasion on the surface of the pebbles could not meet the need of the body for silica. However, recent experiments on ostriches have shown that quartz gastroliths are undergoing a fast abrasion in gizzards (Wings and Sander, in preparation); questioning the conclusions of Mangold (1927a) regarding silica. Furthermore, the physiological requirements for silica are very low and are virtually always met by silica contained in the diet (M. Clauss, pers. comm. 2004).

The trace elements which cause the color of the common quartz gastroliths can not play an important part in the mineral supply because the erosion rate of quartz is too low to set free significant amounts of trace elements. Bialas et al. (1996) reported that feldspar gastroliths provide birds, in addition to their trituration function, with potassium and calcium. Greywacke contains - beside quartz - feldspar, potassium, magnesium, iron, and many other minerals useful for birds (Bialas et al., 1996). Many herbivorous animals, not only birds, need an additional salt (NaCl) supply to their diet to meet their metabolic requirements. Elephants, for instance, grind up complete stones in search for salt (Redmond, 1991).

It is certainly useful to compare the quantities of minerals provided by gastroliths with the mineral uptake with diet and the physiological requirements of certain gastrolith-using species in a future study. I expect, however, that except for calcium, the importance of gastroliths as a source of minerals is rather limited.

Secretion of stomach juices

Gastroliths also 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.

Mineral storage

Bio-gastroliths, also called “crab eyes”, are known from several clades of crustaceans such as crabs (e.g., McCarthy and Skinner, 1977) or crayfish (e.g., Travis, 1960). Bio-gastroliths are a bio-mineral formed by specialized areas of the stomach epithelium (gastrolith discs) during premolting stages (McCarthy and Skinner, 1977). These deposits are composed mainly of calcium carbonate and contain a small amount 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 exdysis, these minerals will subsequently be utilized in calcification of the new exoskeleton. A similar function is not plausible for any gastroliths known from vertebrates.

Hydrostatic function

The idea of the ballast function for gastroliths in aquatic animals is rather old. Even 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) suggested stones as a ballast to aid in diving in Pinnipedia. Since then, many in-depth but yet contradicting reviews (e.g., Baker, 1956, who believed that the "ballast" theory is fundamentally impossible) and studies (e.g., Taylor, 1993, who believed in gastroliths having an important role in buoyancy control) were carried out, with no apparent consensus.

A strong case was provided by the comprehensive study of Cott (1961) on *Crocodilus niloticus*. Cott (1961) suggested that the increase of specific gravity provided by gastroliths makes it easier to stay underwater and to draw struggling prey under the surface. Gastroliths are supposed to form a ballast, important for the stabilization of swimming animals (Cott, 1961). The stones may then help maintain a neutrally buoyant position within the water column (Storrs, 1993). Gastroliths accumulate in the gut, ventral and posterior to the lungs, therefore their position tends to elevate the anterior end of floating crocodiles and stabilizes them against rolling (Cott, 1961). Stoneless juveniles must use limb movements to prevent rolling (Seymour, 1982). Gastroliths were also suggested to increase the useable pulmonary volume and O_2 storage available to submerged crocodiles, resulting in extending diving times by about 12% (Seymour, 1982). This hypothesis was never tested explicitly.

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

Taylor (1993) suggested a correlation between the presence of gastroliths, their use for buoyancy control, and the mode of locomotion in aquatic animals. Underwater "flyers", such as plesiosaurs, penguins, and otariids, commonly have gastroliths, although others do not (Chelonioidea). However, my surveys of the literature and visits to various collections have also produced several gastrolith occurrences in undulatory swimmers (ichthyosaurs, one mosasaur, cetaceans). Gastroliths are especially common in phocid seals. While many seals hold stones during their terrestrial molting season (Bryden, 1999), seals do not always regurgitate the stones before returning to sea (Nordøy, 1995). This independence of gastrolith occurrence from body form and locomotor habit is in contrast to the suggestions of Taylor (1993).

Murray and Renard (1891) believed that stones in marine mammals serve as a ballast to aid in diving. This hypothesis together with the balancing and buoyancy hypotheses has received much support in the pinniped literature. Using gastroliths to correct the 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 Harrison and Kooyman (1968), the relatively small amount of stones would hardly exert an significant effect in stabilizing the body, increasing momentum, stemming the tide or currents, resisting waves, increasing drag, and any other activity where ballast might be advantageous.

Thus, 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 applies to gastroliths, which significantly increase the mass and specific density of the animal, as well as food items which temporarily increase the mass of the animal but do not change the overall density of the animal. The important question is, however, do these objects have any importance for the diving and uplift behavior of the animals or is their influence negligible? Conversely, Taylor (1993) noted that it can be argued that animals relying on gastroliths for grinding food may have evolved positive buoyancy to compensate for the weight of the stones.

From amphibians to reptiles to mammals there is a progressive increase in the complexity of lung interior and increasing lung surface area. In mammals, the lung volume is 4.6% of the body volume. In human lungs, the dead space is one third of total volume at rest, but only one-twentieth during exercise. The tidal volume is between 500 and 3000 cm^3 (Schmidt-Nielsen, 1997). This means, as divers know, that 1.5 to 3 kg of buoyancy is available in human lungs without any forceful breathing. Consequently, normal breathing could equal about 3% of the body mass, a value much higher than the mean percentage of gastrolith masses known from aquatic animals (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 and I therefore consider the effect of stabilizing etc. to be negligible.

This simple calculation is in agreement with the computational model of Henderson (2003) for *Alligator mississippiensis*, in which he 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, whereas the lungs are the principle agent for hydrostatic buoyancy control. The model developed by Henderson (2003) also has the potential of investigating the complex relationship between animal weight, blubber content, stone weight, food contents, and uplift via air-filled lungs in pinnipeds.

Beside that, several arguments speak against the proposed ballast function: 1) Not all animals of a species have gastroliths as it should be expected with a critical physiological demand. 2) The range of masses of gastrolith sets known within a taxon varies greatly (e.g., Bryden, 1999). 3) Buoyancy in crocodilians and turtles is mainly controlled by the relative position of head and body. 4) Every food intake would change the balance between stones and uplift. For animals with their activities restricted to the water column (e.g., plesiosaurs), buoyancy compensation with stones would be rather insignificant, as their position within the water column varies greatly.

In conclusion, if a physiological use of gastroliths as ballast indeed is present, its importance is limited. The issue of the hydrostatic function of gastroliths in aquatic vertebrates nevertheless remains unsettled. Future experiments and observations on living tetrapods are necessary to finally solve this problem.

Other ballast arguments

Ballast arguments were not only suggested for aquatic animals but also in terrestrial animals. For instance, Wade (1989) believed that the 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. The 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 center 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 (see chapter VI), this hypothesis is implausible. Furthermore, their limited weight relative to that of the body of less than 0.03% renders any balancing function implausible (Wings and Sander, in preparation).

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. Good examples are songbirds (Passeriformes), which are excellent flyers and commonly utilize gastroliths. Gastroliths used primarily as ballast in non-aquatic animals is considered to be a highly implausible scenario.

Ingestion due to pathological reasons

Stress-induced behavior is believed to be the reason for pebble swallowing in captive animals, especially in stressful environments such as zoos. Gastroliths in iguanas, crocodiles, and pigs were attributed to pathological ingestion (Whittle and Everhart, 2000). Overly 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 (Sambraus, 1995; Kösters et al., 1996), an idea which never has been tested. Generally, evidence for pathological behavior is hard to confirm. For instance, ostriches show commonly the behavior of swallowing shiny objects, such as metal pieces (Deeming and Bubier, 1999). Since it is implausible that all ostriches are suffering from stress, this behavior can not be considered pathological and may have other reasons (e.g., shiny metallic objects could be mistaken for insects, Huchzermeyer, 1998). Overall, pathological gastrolith ingestion is considered to be very rare in wild animals.

Nutritional diseases

Gastroliths found in hogs (Beal, 1904) may be the result of a monotonous diet. Perhaps the hogs ingested the stones due to boredom or in search for some essential nutrients with were absent in their normal food. There are few reports of similar behavior in other vertebrate clades, making this reason of gastrolith intake rather uncommon.

Destruction of parasites

Destruction of parasites was proposed as a gastrolith function for pinnipeds (Hamilton, 1933; Emery, 1963) which often have parasitic nematode worms in their stomach. The purposeful ingestion of sand or earth after parasite infestation of turtles was reported by several authors and summarized by Dennert (2001). The concurrent presence of gastroliths and parasitic nematodes was reported from some individuals of the crocodilians *Paleosuchus palpebrosus* (Medem, 1958) and *Alligator mississippiensis* (Delany et al., 1988). However, because there is no tight correlation between parasitic infestation and lithophagical behavior, this hypothesis remains unverified.

Establishment of a normal intestinal microbial flora

Maintenance of a beneficial microbial gut flora was 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. Since coprophagy is commonly found in vertebrates and does not only provide a method for obtaining nutrients (Soave and Brand, 1991) but also supplies the animals with beneficial microbes, it may be possible that some taxa use sediment and the attached 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 crocodilians (Catesby, 1731-43; Owen, 1742). This idea is also found among people of Madagascar (Decary, 1950), and was repeatedly suggested for crocodilians 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 the irregular occurrence of stones, especially in pinnipeds (e.g., Howell, 1930). Indeed, the stomachs of seals contain sand and small stones more often in summer, during fasting season, than in spring or autumn (Laws, 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 during the breeding season, during lactation, and while moulting (Harrison and Kooyman, 1968). Recently, 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 the reason why several crow species have more stones in the stomach during the winter times is to suppress hunger. He argued that in winter, there are generally more individuals which have stones and that the amount of stones is higher, independently of food composition (insects versus plant material).

Both hypotheses, alleviation of hunger and preservation of stomach shape, were never tested in any taxon, and their validity remains doubtful since similar behavior is not known from other carnivorous taxa, even when they fast (e.g., snakes or lizards, Secor and Phillips, 1997). Furthermore, mechanoreceptors, which can be stimulated by gastroliths, do 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 sediment is attached to prey or because a prey item itself contained gastroliths. 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). Verifiable accidental ingestion of gastrolith with prey is rarely known from the fossil record. Hundreds of stones were found within the scattered vertebrae of a large Cretaceous shark *Cretoxyrhina mantelli*, reported by Moodie (1912) and interpreted as the consumption of gastrolith-bearing prey (Shimada, 1997). This *Cretoxyrhina* individual presumably ingested a plesiosaur which contained gastroliths. However, because plesiosaur remains were not found with the shark (Shimada, 1997), this hypothesis remains unconfirmed. Gastroliths in an extant *Varanus griseus* may have been derived from its bird prey, but were considered too big to have been derived from a bird captured by this monitor (Wiman, 1916).

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 preyed upon. 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.

The sand and gravel in the gizzards of birds that have been preyed upon reach the digestive tract of snakes when the birds are swallowed (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). The small stones reported from rattlesnakes (Klauber, 1972) were probably ingested accidentally, as well as the plant remains.

Sand and mud in a leatherback turtle (*Dermochelys coriacea*) was probably ingested accidentally while the animal was feeding in shallow water (Den Hartog and Van Nierop, 1984). Den Hartog and Van Nierop (1984) presented a scenario, where the turtle was trapped by low tide in shallow water. Sand and mud were involuntarily taken in during the attempts to reach deeper water again (Den Hartog and Van Nierop, 1984).

Crocodiles often swallow prey that has sand and gravel adhering to blood and flesh. For example, all stones in some specimens of *Crocodilus niloticus* were most likely swallowed accidentally during feeding (Welman and Worthington, 1943; Decary, 1950). Accidental ingestions in crocodilians is also indicated by plant material frequently found in stomachs. Plants and roots found in alligators, *Alligator mississippiensis,* may have been picked up when feeding on aquatic animals or during burrowing (Giles and Childs, 1949). In the insectivorous lizard *Sceloporus olivaceus*, extraneous matter such as grass, stems, and small pebbles also were regarded as accidentally ingested (Kennedy, 1956).

A large number of pebbles found in Pleistocene cave sediments were 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 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 which have stones grasped in their tentacles was suggested (Sleptsov, 1950), but rejected later because stones are not found in stomachs of harbour seals which frequently prey on octopuses (Spalding, 1964).

Accidental intake is the best explanation for the presence of gastroliths in many fish, lizard, turtle, and archosaur species. However, the bigger the stones and the larger their number, the less plausible is accidental intake. It is important to consider the size of the skull and the esophagus in comparison to the stones.

Stones mistaken as prey

This is the intentional ingestion of an incorrectly recognized object. It is documented from egg-eating snakes, e.g., *Elaphe obsoleta*, which have swallowed artificial eggs (stone, wood, china) placed under brooding hens (Holt, 1919; Gans, 1953; Smith, 1953). A swallowed egg-shaped cosmetic jar was reported by Kennedy and Brockman (1965).

The swallowing of wood and stones by crocodilians was assumed to be a result of mistaken as prey (mistaken as snails and crabs) (e.g., Pitman, 1941). The ingestion of stones mistaken as prey is considered to be rare.

Playing

Accidental or purposeful swallowing of pebbles while playing is considered to be a good explanation for young animals of different taxa which regularly are observed to play with objects like sticks or pebbles. Playing was suggested among other functions 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 and acquire them even while still being suckled (Harrison and Kooyman, 1968). The swallowing could be interpreted as practice for the later hunt for prey. As it is not possible to corroborate this hypothesis, this reason for swallowing is closely associated with the accidental intake.

Nest building

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

Whittle and Everhart (2000) did not discuss if the stones are considered to be real gastroliths, 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. Since regurgitation of gastroliths for nest building is not reported from extant birds, it is unlikely that the fossil stones represent former gastroliths. However, since an unambiguous identification of gastroliths is not possible, isolated stones might be carried in beaks/mouths of animals. In that case, the stone would not represent gastroliths. Alternatively, I propose that the stones in theropod nests are gastroliths which were regurgitated during feeding the offspring.

Thermoregulation

The presence of gastroliths in *Psittacosaurus*, a dinosaur with well-established oral grinding capacities and the capability of stones to store heat more efficiently than living tissue 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 tissue, respectively. An employed thermodynamic model showed that swallowing stones could have increased the rate of conductive heat transfer in *Psittacosaurus* by two or three times (Anton, 2001). Theoretically, it is therefore useful for exothermic animals to swallow heated stones to heat up faster themselves. However, any advantage would be consumed by the rapid cooling down of the stones once solar heat is not available. The shorter time to cool down would be an actual disadvantage compared to other competing species or predators. The scenario would only be reasonable if the stones are regurgitated every day as soon as they reach body temperature. However, such a behavior is not known from any extant clade of animals and considered to be highly implausible.

Memorial of events

Two different myths exist about stones in crocodilians. Relatively common is the legend that crocodiles swallow one stone annually to count and remember their birthdays. This is believed by some inhabitants of Arabia (Williston, 1904), Africa (Williston, 1914; Villiers, 1958), and India (D' Abreu, 1915). The second legend is even more sensational: Some inhabitants of Africa believed that crocodiles swallow a stone for every human they eat (Neill, 1971).

Both legends are, of course, not correct and do therefore not need to be discussed in any detail. There are many reports of older crocodiles without gastroliths as well as zoo specimens with high numbers of gastroliths and no reported human kills (e.g., Neill, 1971).

Admiration of semi-precious gemstones

Polished semi-precious stones were found in dune deposits in New Zealand and interpreted as moa gastroliths (Hayward, 1978). Hayward suggested that "… the moa, was roaming the countryside searching for semi-precious gemstones (such as agate, opal, chalcedony, chert, jasper) which it proceeded to collect and tumble polish in its gizzard before coughing them up to admire …". This function was proposed *ad hoc* and can not be proven. Regurgitating of stones in herbivorous birds is rarely reported, the semi-precious stones were probably not carefully selected by the moas, and it is highly implausible that the birds might have admired the gastroliths, even if extant ostriches are attracted by shiny objects. In the gizzard, gastroliths are mixed with foodstuff, any regurgitation would therefore also contain a large amount of plant material covering the stone surface for some time. Since such a behavior is not reported from any modern bird, there is no reason to believe that moas had such a weird habit.

Conclusions

A summary of proposed gastrolith functions in vertebrates and their likelihood can be found in Table 1. The most commonly proposed functions are related to the digestive system. Crushing or grinding of food in the gizzard is the accepted gastrolith function in many birds. Stimulation of gastric juice secretion was also proposed (Fox, 1976). Mineral uptake is a welcome side effect of erosion and dissolution of gastroliths in the gastro-intestinal tract.

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 species indicate that the gastroliths were accidentally ingested or fulfill a function that is not critical for survival (e.g., Gionfriddo and Best, 1999; Cheng et al., in revision).

Accumulation of several gastrolith functions is possible. For instance, 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 might often fulfil several functions at once, such as grinding and mixing of foodstuff and the supply with minerals. However, it is very difficult to distinguish the importance of combined functions without further extensive experiments.

While all gastroliths are ballast when swimming in water, their influence on buoyancy control in aquatic animals is considered to be minimal. 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 mistaken as prey. Again, the real need for more information should be fulfilled by future research.

Additional functions of these stones might turn up in the light of future research. Perhaps similar to hypotheses that were postulated for the function of soil ingested during geophagy: mineral supplementation, adsorption of plant toxins and tannins, counteraction of gastric upsets or diarrhea, 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 Marcus Clauss, Walter Joyce, Ute Richter, and Martin Sander for improvements of the manuscript. Walter Joyce also helped locating rare literature. Christopher Whittle kindly supplied his bibliography about gastroliths which served as a superb starting point for my literature search. I am thankful to Annette Broschinski for allowing me to finish the draft during my trainee position at the Landesmuseum Hannover. Initial funding was provided by the Graduiertenförderung Nordrhein-Westfalen, the Graduiertenkolleg “Evolution und Biodiversität in Raum und Zeit”, and the Jurassic Foundation.

References

Allaby, A. and Allaby, M., 1999. A Dictionary of Earth Sciences. Oxford University Press, Oxford, 619 pp.

Anonymous, last time accessed: 2001a. Academic Press Dictionary of Science and Technology. online version: http://www.harcourt.com/dictionary/.

Anonymous, last time accessed: 2001b. Oxford English Dictionary. http://dictionary.oed.com/.

Anonymous, last time accessed: 2004. Merriam-Webster Online Dictionary. online version: http://www.m-w.com/netdict.htm.

Anton, J.A., 2001. Thermo-powered ceratopsians? A thermodynamic model proposing another role for gastroliths. Society of Vertebrate Paleontology, Sixty-first annual meeting; abstracts of papers., 21; 3 Suppl.: 28-29.

Ayer, J., 2000. The Howe Ranch Dinosaurs/Die Howe Ranch Dinosaurier. Sauriermuseum Aathal, Aathal, 96 pp.

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. American Geological Institute, Falls Church, x+749 pp.

Beal, W.J., 1904. Stomach stones. Science, 20(517): 722.

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 [Investigations of gizzard stones among partridge and pheasants]. 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.

Bryden, M.M., 1999. Stones in the stomachs of southern elephant seals. Marine Mammal Science, 15: 1370-1373.

Catesby, M., 1731-43. 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. Together with their descriptions in English and French. To which, are added observations on the air, soil, and waters: with remarks upon agriculture, grain, pulse, roots, &c. To the whole, is perfixed a new and correct map of the countries treated of. Printed at the expence of the author, London.

Challinor, J., 1974. A Dictionary of Geology. University of Wales Press, Cardiff, xvii+350 pp.

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., in revision. Gastroliths in the Triassic ichthyosaur *Panjiangsaurus* from China. Journal of Paleontology.

Christiansen, P., 1996. The evidence for and implications of gastroliths in sauropods (Dinosauria, Sauropoda). Gaia, 12: 1-7.

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 (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 270.

Currie, P.J. and Padian, K., 1997. Encyclopedia of Dinosaurs. Academic Press, San Diego, 869 pp.

D' Abreu, E.A., 1915. Note on the "mugger" *Crocodilus palustris*; contents of their stomachs, folklore, etc. Journal of the Bombay Natural History Society, 23(4): 780.

Decary, R., 1950. La faune malgache: son role dans les croyances et les usages indigenes. Payot, Paris, 1-236 pp.

Deeming, D.C. and Bubier, N.E., 1999. Behaviour in natural and captive enviroments. In: D.C. Deeming (Editor), The Ostrich. Biology, Production and Health. CABI Publishing, Cambridge, pp. 83-104.

Delany, M.F., Woodward, A.R. and Kochel, 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: Dermochelidae) from British waters and from the Netherlands. Zoologische Verhandelingen Leiden, 209: 1-36.

Dennert, C., 1997. Untersuchungen zur Fütterung von Schuppenechsen und Schildkröten. Ph.D. Thesis, Tierärtzliche Hochschule, Hannover, 189 pp.

Dennert, C., 2001. Ernährung von Landschildkröten. Natur und Tier Verlag, Münster, 144 pp.

Duke, G.E., 1986. Alimentary canal: secretion and digestion, special digestive functions, and absorption. In: P.D. Sturkie (Editor), Avian Physiology. Springer Verlag, New York, pp. 289-302.

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 (Editor), The Sea. Ideas and Observations on Progress in the Study of the Seas. 3: The Earth Beneath the Sea. History. Wiley Interscience, New York, pp. 776-793.

Farlow, J.O. and Brett-Surman, M.K., 1997. The Complete Dinosaur. Indiana Univ. Press, Bloomington, 752 pp.

Fisher, H., 1972. The nutrition of birds. In: D.S. Farner and J.R. King (Editors), Avian Biology. 2. Academic Press, London, pp. 431-469.

Forbes, J.M., 1996. Integration of regulatory signals controlling forage intake in ruminants. Journal of Animal Science, 74(12): 3029-3035.

Fox, N., 1976. Rangle. Raptor Research, 10(2): 61-64.

Frizzell, D.L. and Exline, H., 1958. Crustacean gastroliths from the Clairborn Eocene of Texas. Micropaleontology, 4: 273-280.

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 of London. Series B, Containing Papers of a Biological Character, 266: 1259.

Giles, L.W. and Childs, V.L., 1949. Alligator management of the Sabine National Wildlife Refuge. Journal of Wildlife Management, 13(1): 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. Columbia University Press, New York, 205 pp.

Gillette, D.D., 1995. True grit. Natural History, 104(6): 41-43.

Gionfriddo, K.P. and Best, L.B., 1999. Grit use by birds - a review. Current Ornithology, 15: 89-148.

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.

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 (Editors), The Behavior and Physiology of Pinnipeds. Appleton-Century-Crofts, New York, pp. 211-296.

Hawkes, L., 1951. The erratics of the English Chalk. Proceedings of the Geologist's Association, 62(4): 257-268.

Hayward, B.W., 1978. Moas; New Zealand's first rockhounds; evidence from Kawerua. Tane (Auckland University Field Club, Journal). Auckland, New Zealand., 24: 159-171.

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(8): 1346-1357.

Holt, E.G., 1919. *Coluber* swallowing the stone. Copeia, 1919(76): 99-100.

Howell, A.B., 1930. Aquatic Mammals; their Adaptations to Life in the Water. Thomas, Springfield-Baltimore, xii+338 pp.

Huchzermeyer, F.W., 1998. Diseases of Ostriches and Other Ratites. Agricultural Research Council, Onderstepoort Veterinary Institute, Onderstepoort, 296 pp.

Humboldt, A.v., 1852. Personal Narrative of Travels to the Equinoctial Regions of America, 2. Henry G. Bohn, London, vi+521 pp.

Huxley, T.H., 1880. The Crayfish. International Science Series, 28: 347.

Jackson, J.A., 1997. Glossary of Geology. American Geological Institute, Alexandria, xii+769 pp.

Jacobi, A., 1900. Die Aufnahme von Steinen durch Vögel. Arbeiten aus der Biologischen Abtheilung für Land- und Forstwirthschaft 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(2): 504-509.

Jones, R.L. and Hanson, H.C., 1985. Mineral Licks, Geophagy, and Biogeochemistry of North American Ungulates. Iowa State University Press, Ames, x+301 pp.

Kennedy, J.P., 1956. Food habits of the Rusty Lizard *Sceloporus olivaceus* Smith. Texas Journal of Science, 8(3): 328-349.

Kennedy, J.P. and Brockman, H.L., 1965. Stomach stone in the American Alligator, *Alligator mississippiensis* Daudin. British Journal of Herpetology, 3(8): 201-203.

Klauber, L.M., 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. University of California Press, Berkeley, xxx+1533 pp.

Kösters, J., Hornung, B. and Korbel, R., 1996. Straußenhaltung aus der Sicht des Tierarztes. Deutsche tierärztliche Wochenschau, 103(3): 100-104.

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 (Editor), Antarctic Ecology. 2. Academic Press, London, pp. 621-715.

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.

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.

Mayne, R.G., 1854. An Expository Lexicon of the Terms, Ancient and Modern, in Medical and General Science. J. Churchhill, London.

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(2): 278-292.

Medem, F.J., 1958. The crocodilian genus *Paleosuchus*. Fieldiana Zoology, 39(21): 227-247.

Moodie, R.L., 1912. The "stomach stones" of reptiles. Science, 35(897): 377-378.

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.

Murray, J. and Renard, A.F., 1891. Report of the deep sea deposits. Challenger Expedition, 321, 323, 324 pp.

Neill, W.T., 1971. The Last of the Ruling Reptiles, Alligators, Crocodiles, and Their Kin. Columbia University Press, New York, xx+486 pp.

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. Printed for the author, sold by John Gray, London, xxiii+240+index pp.

Pitman, C.R.S., 1931. A Game Warden among his Charges. Nisbet, London, xvi+329 pp.

Pitman, C.R.S., 1941. About crocodiles. Uganda Journal, 8(3): 89-114.

Ralston, S., 1983. Factors in the control of feed intake of horses and ponies. Neuroscience and Biobehavioral Reviews, 7(4): 465-470.

Redmond, I., 1991. The Elephant Book. Overlook Press, Woodstock, 48 pp.

Rhodin, A.G.J., 1974. Pathological lithophagy in *Testudo horsfieldi*. Journal of Herpetology, 8(4): 385-386.

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. Wiley, New York, XI + 409 pp.

Schmidt-Nielsen, K., 1997. Animal physiology: adaptation and environment. Cambridge University Press, Cambridge, viii, 607 pp.

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(4): 515-522.

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 chrysochephala*) in the Central Amazon. Journal of Zoology, 247: 91-103.

Seymour, R.S., 1982. Physiological adaptions to aquatic life. In: C. Gans and F.H. Pough (Editors), Biology of the Reptilia. Volume 13. Academic Press, London, pp. 1-41.

Shaw, G., 1802. General Zoology, Volume 3, Part 1. Amphibia. G. Kearsley, London, viii+312 pp.

Shimada, K., 1997. Paleoecological relationships of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli* (Agassiz). Journal of Paleontology, 71(5): 926-933.

Skoczylas, R., 1978. Physiology of the digestive tract. In: C. Gans and K.A. Gans (Editors), Biology of the Reptilia. Volume 8, Chapter 6. Academic Press, London and New York, pp. 589-717.

Sleptsov, M.M., 1950. Concerning the biology of the far-eastern sea lion. Investiia Tikhookeanskogo N.-I. Instituta Rybnogo Khoziaistva i Okeanograffi [TINRO], 32.

Smith, H.M., 1953. Case history of a snake with an irregurgitable artificial egg. Herpetologica, 13: 102.

Soave, O. and Brand, C.D., 1991. Coprophagy in animals: a review. Cornell-Veterinarian, 81(4): 357-364.

Sokol, O.M., 1971. Lithophagy and geophagy in reptiles. Journal of Herpetology, 5(1-2): 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. Versuche über das Verdauungsgeschäft des Menschen und verschiedener Tierarten. Ueberf., Leipzig, 18-24 pp.

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(2453): 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 publisht numb. 27, made and generously imparted by that learn'd and inquisitive physitian, 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(1296): 163-175.

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.

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(1): 137-149.

Tsutsui, N., Ishii, K., Takagi, Y. and al., 1999. Cloning and expression of a cDNA encoding an insoluble matrix protein in the gastroliths of a crayfish, *Procambarus clarkii*. Zoological Science, 16(4): 619-628.

Twigg, J., 2001. Differentiating Moa Gizzard Stones. M.Sc. Thesis, University of Auckland, Auckland, 118 pp.

Villiers, A., 1958. Tortues et Crocodiles de l'Afrique noire. Institute Francaise d'Afrique Noire, Initiations Africaines, Dakar, 354 pp.

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. Ornithologische Monatsschrift, 43.

Wade, M., 1989. The stance of dinosaur and the cossack dancer syndrome. In: D.D. Gillette and M.G. Lockley (Editors), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 73-82.

Walton, K.C., 1984. Stomach stones in meadow pipits *Anthus pratensis*. Bird Study, 31: 39-42.

Warren, A., 2000. Secondary aquatic temnospondyls of the Upper Permian and Mesozoic. In: H. Heatwole and R.L. Carroll (Editors), Amphibian Biology. Surrey Beatty & Sons, Chipping Norton, pp. 1121-1149.

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(1-2): 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 (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 75-82.

Wieland, G.R., 1906. Dinosaurian gastroliths. Science, 23(595): 819-821.

Williston, S.W., 1904. The stomach stones of the plesiosaurs. Science, 20(513): 565.

Williston, S.W., 1914. Water Reptiles of the Past and Present. University of Chicago Press, Chicago, viii+251 pp.

Wiman, C., 1916. Blocktransport genom Saurier. Geologiska Föreningens i Stockholm Förhandlingar, 38(5): 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. and Sander, P.M., in preparation. Gastrolith function in dinosaurs reconsidered: No evidence for gastric mills in sauropods.

Worthy, T.H. and Holdaway, R.N., 2002. The Lost World of the Moa: Prehistoric Life of New Zealand. Indiana University Press, Indiana, 718 pp.

Wyatt, A., 1986. Challinor's Dictionary of Geology. University of Wales Press, Cardiff, xviii+374 pp.

Ziswiler, V. and Farner, D.S., 1972. Digestion and the digestive system. In: D.S. Farner and J.R. King (Editors), Avian biology. Volume 2. Academic Press, London, pp. 343-430.

Tables

Intake	Function		Status
Deliberate ingestion	Digestive aid	Trituration of foodstuff	very plausible
		Mixing of foodstuff	very plausible
		Mineral supplement	very 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 & preservation of stomach shape		controversial
	Nest building		implausible
	Thermoregulation		implausible
	Memorial of events		implausible
	Admiring of semi-precious gemstones		implausible
Accidental ingestion	Material is attached to swallowed prey		very plausible
	Prey contains gastroliths		very plausible
	Material is mistaken as prey		very plausible
	During playing with objects		very plausible

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

CHAPTER III: Amounts and composition of gastroliths in farm ostriches (*Struthio camelus*)

Abstract

The stomach contents of free-ranging farm ostriches in Germany (n=135) and South Africa (n=212) were sampled with the focus on the gastroliths. The results show that ostriches are very flexible regarding the amount and grain size of gastroliths. The mean mass of gastroliths in adult ostriches is higher than reported in the existing literature (Johnson, 1990; Milton et al., 1994). Adult animals have about one kilogram of stones in the stomach. On average, each stomach contained several thousand stones. While there is no significant correlation between body mass and gastrolith mass of individuals among the German as well as the South African farm ostriches, the mean mass is very similar: in both groups gastroliths constitute about 1% of the body mass. Natural amounts of food contents were only found in the stomachs of German ostriches because South African birds fast before slaughtering. The gastrolith mass in German farm ostriches is not significantly correlated with food contents, gender, age, and season. The rock types of gastroliths are strongly dominated by varieties of quartz, the most resistant material which is abundantly available in the ostrich habitats.

Introduction

Grit and gastroliths (stomach stones) are essential for the digestive system of most herbivorous birds, and many studies have concentrated on poultry grit (Gionfriddo and Best, 1999). However, no comprehensive study about gastroliths in ostriches (*Struthio camelus*) was conducted until now. This is surprising considering the economic interest in ostriches with a farming history for more than 120 years as well as the scientific interest in the largest living bird. With moas and elephant birds, fossil ratites also constitute the largest birds that ever existed, and research on gastroliths from extant ratites might help to answer paleobiological questions about these fossil birds.

Furthermore, the digestive process and physiology of ratites is not only relevant to the entire bird clade, but has also implications for the fossil record, especially dinosaurs. Some aspects such as the abrasion rate of rock types in bird gizzards have never been studied until now, but can give valuable information about the lifestyle of birds (e.g., the migrational habits via rock type composition of gastroliths). The ornithological literature in general is poor in quantitative studies that relate the grit content to other parameters such as body mass or nutrition. Last but not least, the data could help ostrich farmers to understand and fulfill the gastrolith needs of their birds. The research was conducted on farm ostriches and not on wild ostriches because of easily available sample material that was abundant enough for statistical analysis.

Anatomy and physiology of the digestive tract

This paragraph is intended to give a short overview of the digestive tract of ostriches. For a detailed insight into the anatomy of the ostrich, see for example Bezuidenhout (1999). Ostriches, like other ratites, do not have a crop (Shanawany and Dingle, 1999). The oesophagus ends in a sac-like proventriculus where approximately 300 openings of proventricular glands provide the secretion of gastric juice during the transport of the food into the gizzard (Stevens and Hume, 1995; Bezuidenhout, 1999). Distally, the proventriculus opens into the biconvex ventriculus or gizzard which fulfills maceration, trituration, and pumping of ingesta with the help of gastroliths (Stevens and Hume, 1995). The gizzard is surrounded by strong muscles which contract several times a minute. The gizzard is lined with koilen, a horny material consisting of protein and carbohydrates. In many bird species, the koilen is molted periodically (Stevens and Hume, 1995). The exit from the gizzard, the pyloric orifice, is guarded by the pyloric valve which is particularly prominent in the ostrich (Thomson, 1964). This can be explained by the large particles of grit and pebbles in the gizzard (Thomson, 1964). The duodenum leaves the gizzard on the right and is approximately 800 mm long. The two caeca are approximately 900 mm in length and the rectum (or colon) is approximately 16 m long. The length and masses of the various parts of the gastro-intestinal tract is depended on the dietary fiber content in the food of the ostrich (Baltmanis et al., 1997). The mass of the gizzard (full and empty) is higher in a moderate fiber diet than in a low fiber diet (Baltmanis et al., 1997).

Diet and digestion

The ostrich is a selective feeder, preferring soft annual herbs and grasses, both moist (70% water) and rich in crude protein (24% of dry mass) (Milton and Dean, 1995a). If no annual plants are available, ostrich feed on flowers, new leaves, and soft shoot tips of some grasses, shrubs and trees (Milton and Dean, 1995a). In dry conditions with only dead grass and scattered shrubs, ostriches rely on uprooting and swallowing the bases of grass tufts or strip off the remaining leaves of shrub branches. Ostriches avoid strongly smelling and very salty plants in their diet.

Detailed information about the digestion in ostriches can be found elsewhere (Cilliers and Angel, 1999). Ostriches lack cellulase to digest plant fiber and have therefore to rely on plant fiber fermentation, similar to all other herbivorous land vertebrates. This implies a slow passage of digesta. The efficiency of the digestion in ostriches is comparable with that of large herbivorous mammals (Milton et al., 1994). Also, the mean ingesta retention time in ostriches is similar to that in ruminants. Ostriches are without doubt the best post-gastric fiber fermenters among birds (Cilliers and Angel, 1999). 38% of cellulose and 66% of hemicellulose is degraded (Swart, 1988).

In birds, serviceable grit is not evacuated from the stomach with the bolus, but retained (Thomson, 1964). A certain quota of grit is kept even when the stomach is completely free of food (Thomson, 1964). Birds are lithophagic and geophagic. While the main function of the ingested non-food material is trituration of foodstuff, fine-grained material is occasionally ingested, presumably in order to rectify mineral deficiencies in the bird's diet (Jones and Hanson, 1985).

Existing data about gastroliths in ratites

Gastroliths are already known from the geologically oldest struthioform bird, *Palaeotis weigelti*, found in the Eocene fossil deposit Geiseltal in Germany (Ernst et al., 1996). Among the very large ratite species which recently went extinct, gastrolith use is exceptionally well documented for several moa species in New Zealand (e.g., Anderson, 1989; Twigg, 2001; Worthy and Holdaway, 2002), and also well established for the ostrich-sized mihirungs *Genyornis* in Australia (Stirling, 1900; Rich, 1990). To my knowledge, no occurrence of gastroliths associated with elephant birds *Aepyornis* in Madagascar is known. Yet, a parsimonious interpretation of the digestive tract of ratites demands that gastroliths existed in elephant birds too, and there are authors who mentioned gastroliths in these birds without providing evidence (e.g., Johnson, 1993).

While the presence of gastroliths is well documented for all extant ratites (Hoyo et al., 1992), detailed studies are very rare. Apart from ostriches, some research has been conducted on emu gastroliths (Davies, 1978; Webb, 1994). Most reports of ostrich gastroliths also have been rather anecdotally. No comprehensive study of ostrich gastroliths had been conducted to date. Only very little data is published at all and partially hidden in works of other context (e.g., Johnson, 1990).

Garrod and Darwin (1872) reported approximately two liters of stones and several coins in the stomach of a zoo ostrich; the stones were mostly pea sized. Three to four kg sand and gravel, two iron keys, 17 copper nails, 20 iron nails and other objects were reported from the stomach contents of an ostrich kept in a zoo (Wiman, 1916). This is the largest mass of non-foodstuff stomach contents found in the ostrich literature.

Johnson (1990) briefly reported data for five ostriches, probably from Kenya. He obviously made a typographical error with the weight of the stones of ostrich No. 1, given as 855 kg. Given the high number of stones and judging from the published photo, the correct weight must have been 855 g. Unfortunately, no age or body mass of the ostriches is given, limiting the usefulness of the data. Lithologies included pure quartz, feldspar, obsidian, chert and others (Johnson, 1990).

Some publications for ostrich farmers do contain information about gastroliths. The amount of daily ad lib food intake of farm ostriches is approximately 2.5 kg (Kreibich and Sommer, 1994). The gizzard of an adult animal contains, beside the food, 1.5 kg stones (Kreibich and Sommer, 1994). The size of pebbles supplied to young chicks should be half the size of the claw on the big toe (Huchzermeyer, 1998).

Milton and Dean (1995a; 1995b) examined over 100 kg of stomach contents of wild ostriches but did not mention how many individuals they sampled. On average, their sampled ostrich gizzard contained about 500 g of stones (total range 200-1000 g) with general sizes between 1 and 29 mm and a size preference of 5-15 mm. Ostriches seem to prefer white quartz pebbles and find them even on the dark mudstone soils of the Karoo. In an ambiguous figure, it was intended to show that subadult birds with an age of 6-12 month take smaller stones than do adults (Milton and Dean, 1995a; Milton and Dean, 1995b). Until now, this study was the most detailed research on ostrich gastroliths. However, the number of examined individuals may not have been high enough to reach the recommended size for an analysis with high statistical significance (Reed et al., 1971).

Material and Methods

Free-ranging farm ostriches from Germany and South Africa were sampled (see appendix III). Samples of 135 German ostriches were collected between November 2000 and May 2003. Most of these ostriches were raised in large enclosures with a total size of approximately 20 hectares on the farm “Gemarkenhof” near Remagen (coordinates: 50°34’N lat., 7°11’W long.). Data about age (in month) and gender were collected from all German birds. The body mass was weighed for a few of the birds and later estimated to the nearest 5 kg by the farmer (R. Schuhmacher).

Gender was collected for a part of the South African birds, body masses were always weighed shortly after death. The German and the South African birds were able to swallow pebbles *ad libitum* before slaughter (personal observations, 2000-2003, and Olivier, pers. comm. 2003).

The South African birds were sampled because of their more natural habitat compared to that of the German ones. The material was collected during slaughtering of ostriches in an abattoir of the Klein Karoo Co-operative in Oudtshoorn, Klein Karoo, between 31st of January 2003 and 14th of February 2003. The birds originated from several farms in the Klein Karoo basin. All slaughtered birds receive a tag number for unique identification. Because of hygiene restrictions, the gastrointestinal tract of the animals is processed in another room, separated from the main process line. It was therefore not possible to handle the stomach contents and to note the tag number simultaneously. Hence, the tag numbers were noted by an employee of the abattoir and attached to the removed gastrointestinal tract. After the stomach was opened and the tag number collected, the stomach contents were placed in a plastic bucket for later processing. Six to 24 ostriches were sampled each day. A total number of 212 animals was sampled, the gender was determined for 145 of these animals.

Approximately one out of ten birds regurgitated stones (usually only small pebbles) during death throes (personal observations, 2003). In the abattoir, this is supported by the immediate insertion of the body into the conveyor line in an upside-down position, with feet pointing to the ceiling and the head pointing to the floor. Because the slaughtering process is rapid (usually more than one animal is processed each minute), it was not possible to collect the stomach contents with the same accuracy as in Germany. It is likely that some stones might have been lost during opening of the stomach as well as during transfer into the bucket. However, the maximum mass of the lost stones was visually estimated at <10 g, approximately less then 1% of the total gastrolith mass.

The South African ostriches are not supplied with food for one to two days before slaughtering, but always have access to water. Hence, many animals have high amounts of water in the stomach, but little plant material. A considerable amount of stomach liquids was lost during opening of the stomachs. A separation between the contents of the proventriculus and the gizzard was not appropriate for the South African birds. A random sample test had shown that the absence of food greatly enhanced the mobility of the gastroliths between proventriculus and gizzard and created an abnormal situation. The German birds, on the other hand, are considered to have provided more natural samples of stomach contents because the animals were selected and separated from the other birds in their breeding group only a few minutes before slaughtering. The advantage of the South African birds lies in the exactly determined body mass and a somewhat more “natural” habitat. It should be noted that in both groups only healthy animals were sampled.

The stomach contents of all animals were weighted and then washed with water until all the plant matter was separated from the gastroliths. The stones were dried in the sun and their mass (Fig. 1), estimated number, and size were analyzed in relation to amount of foodstuff, body mass, gender, age, and season. Sieves were used to separate five different grain size fractions: <2 mm, 2-4 mm, 4-8 mm, 8-20 mm, and >20 mm within the gastroliths of German farm birds but not for the South African birds.

The number of gastroliths in specific grain sizes also was examined. Because of the high number of sampled stomachs, the high number of gastroliths in each of these stomachs, and limited time for examination, only a representative mass of stones in each grain size was counted.

To gain a representative cross section, gastroliths from six animals which could not be used in the main data set because of missing information like gender and age, were combined. A comparison with the gastroliths used in the main data set ensured that the stones were typical in size, rock type, and other features. After that, a specific amount of gastroliths from each size fraction was weighed, the rock type was determined macroscopically (Table 1), and the stones were counted. This data was used later to determine the mean mass of a single gastrolith in each grain size (Table 2). The number of gastroliths was then calculated for the grain size fractions 2-4 mm, 4-8 mm, and 8-20 mm from the German farm birds.

Correlation analysis after Pearson was utilized to test the significance of relationships between the gastrolith mass and other parameters such as body mass, gender, or age. The dependence on factors like season or gender was tested with One-Way ANOVA (significance level: 0.05). All samples are available for future research at the Institute of Paleontology at the University of Bonn, Germany.

Results

Ostriches from Remagen, Germany

Most of the sampled birds were young adults, between 12 and 19 month old. Additionally, some breeding birds with ages of up to five years were sampled. No juvenile birds were sampled. The mean body mass is 97 kg ± 12.5 kg (S.D.) (range 60-140 kg; n=135).

The diet of the German farm ostriches consists mainly of grass, straw, oats, and granulate composed of 100% vegetable matter (mostly lucerne). Some animals had wooden branches and sticks in the stomach, very few foreign objects such as metal pieces were found in others.

The mean ratio of food to stones in the complete stomach (proventriculus and gizzard combined) of German farm ostriches is 1:0.31 (S.D.=1:0.12; range 1:0.08 to 1:0.68; n=135). In the gizzard, the mean ratio is 1:1.39 (S.D.=1:0.73; range 1:0.06 to 1:4.77; n=135). The mean mass of the complete stomach contents, including the gastroliths, is 3.6 kg ± 1.6 kg (S.D.) (range 0.7-11.2 kg; n=135). The mean mass of gastroliths in the complete stomachs of German farm birds was 1021 g ± 410 g (S.D.) (range 232-2306 g; n=135) (Fig. 1). There was no significant difference (p=0.26) in the mean gastrolith masses of male (1057 g ± 437 g (S.D.); n=74) and female birds (978 g ± 373 g (S.D.); n=61). Gastrolith masses in the proventriculi (mean=294 g ± 300 g (S.D.); n=135) and the gizzards (mean=727 g ± 274 g (S.D.); n=135) of the same birds are not significantly correlated (p=0.83). Ingesta mass (stomach contents minus gastroliths) is not significantly correlated with the gastroliths mass (p=0.13).

There is no significant correlation between body mass and gastrolith mass (p=0.06) and between the body mass and the complete stomach contents (p=0.48). There also is no significant correlation between the age and the gastrolith mass (p=0.85). The proportion of mean gastrolith mass relative to mean body mass was 1.05%.

The mean gastrolith mass for the months January to March (n=34) was 1033 g ± 424 g (S.D.), for April to June (n=28) 1096 g ± 383 g (S.D.), for July to September (n=27) 987 g ± 428 g (S.D.), and for October to December (n=46) again 987 g ± 412 g (S.D.). The One-Way ANOVA test (significance level: 0.05) showed that there were no significant differences between the gastrolith masses in each quarter of the year (p=0.69).

Rock type composition

The ostrich farm is situated in the Middle Rhine region near Remagen. The gravels which serve as ostrich gastroliths belong to the main terrace level of the river Rhine and were deposited mainly during the Pleistocene (Semmel, 2002). Today, the river gravel is deeply weathered and incorporated in a normal soil sequence. The ostriches pick their gastroliths from the soils exposed in their pastures.

The composition of the gravel is very varied: quartz, sandstones, vulcanites, and other rocks from the catchment area of the Rhine and its feeders. The percentage of weathering resistant components (vein quartz, quartzite, siliceous shales) increases with the terrace age: lower terrace 20-35%, middle terrace 30-40%, main terrace 50-60% (Meyer and Stets, 1996).

Beside the Rhine gravel, anthropogenic material such as glass, building materials and metal pieces might be available on the ostrich pastures. However, the occurrence of these materials was rare, as all the enclosures are carefully controlled for anthropogenic items.

The most common rock types among the gastroliths were vein quartz, quartzite, chert, and anthropogenic glass (Fig. 2). The rest of the stones was composed of a large variety of sedimentary, magmatic, and metamorphic rocks found along the upper reaches of the Rhine. Among others, basalts, conglomerates and siltstones were found. Several rocks were also silicified, especially shales (lydite) and siltstones. No limestones were found in the stomachs. The only relatively soft rock in the smaller grain size classes was an eroded fragment of an anthropogenic brick. Except for the chert abundance in the larger fraction, rock type composition was almost identical in the grain size classes 4-8 mm and 8-20 mm.

Grain size distribution and number of gastroliths

The largest mass of stones was most commonly found in the 8-20 mm fraction, second most common was the grain size 4-8 mm (Fig. 3). Interestingly, the grain size 2-4 mm was rather rare, whereas the sand fraction (<2 mm) was highly variable. The mass of pebbles with a size >20 mm was also highly variable. The mean number of gastroliths in the grain size classes 2-4 mm, 4-8 mm, and 8-20 mm was a total of 1793 ± 993 (S.D.) (calculated range 279-5649; n=135). The gastrolith proportions between the proventriculi and the gizzards were recorded. The results show clearly that the majority of the gastroliths is normally situated in the gizzard (Fig. 4).

Ostriches from the Klein Karoo, South Africa

The diet of the farm ostriches from South Africa is very varied, depending on the farmer’s choice, but lucerne granulate and several grain types are commonly used. Foreign objects, including sharp glass bottle necks and even a Swiss army pocket knife with an open blade, as well as wooden sticks were found in some stomachs. Age was not available for the South African ostriches, but most of the birds are generally slaughtered as subadults at 12-14 months of age (A. Olivier, pers. comm. 2003). The mean body mass was 83.8 kg ± 7.9 kg (range 62.5-108.4 kg; n=212).

The mean mass of the complete stomach contents of South African farm birds, including the gastroliths, was 1.26 kg ± 0.50 kg (S.D.) (range 0.23-3.48 kg; n=212). The mean gastrolith mass in the stomachs was 870 g ± 335 g (S.D.) (range 156-2880 g; n=212) (Fig. 1).

Interestingly, the foodstuff mass (stomach contents minus gastroliths) is, in contrast to the German birds, most highly significant correlated with the gastroliths mass ($p<0.001$).

There was no significant difference ($p=0.70$) in the mean gastrolith masses of male (858 g ± 318 g (S.D.); n=73) and female birds (881 g ± 371 g (S.D.); n=72). A random sample (n=26) showed that the mean gastrolith masses in the proventriculi (259 g ± 242 g (S.D.)) and the gizzards (660 g ± 317 g (S.D.)) of the same birds were not significantly correlated ($p=0.15$).

There was no significant correlation between body mass and gastrolith mass ($p=0.38$) and between the body mass and the complete stomach contents ($p=0.21$). The proportion of mean gastrolith mass relative to mean body mass was 1.04%.

Discussion and Conclusions

Occurrence of gastroliths

Gastroliths were present in all examined stomachs. However, there were large differences in the quantities. The large variations in the gastrolith mass and food content mass in the sample group is consistent with other reports of gizzard/gastrolith studies in birds (e.g., Ayeni et al., 1983). There is most likely a very large difference between the optimal amount and the minimum number of gastroliths required for the trituration process. Furthermore, it is possible that birds which usually have limited access to suitable pebbles will swallow more stones at any given opportunity than they actually need and “cache” stones in the gizzard. This hypothesis could explain the infrequent cases (16 out of 135; 12%) among the German farm birds where the proventriculus contained more stones than the ventriculus (Fig. 4). However, while most birds seem to know the necessary amount of stones by instinct, in some cases pathological behavior cannot be ruled out. There are individuals (not sampled) which swallow more stones than they actually can handle. For example, a farm ostrich was found dead with the entire stomach and even the esophagus completely filled with stones (R. Schuhmacher, pers. comm. 1999). This behavior is relatively common with ostrich chicks (A. Olivier, pers. comm. 2003).

Amounts of gastroliths

The capacity of adult ostrich stomachs (proventriculus and gizzard) was given at approximately 2.5 kg (Kreibich and Sommer, 1994) and 4.5-5.5 kg fresh mass (Milton et al., 1994), respectively. However, my results show that the maximum capacity of an ostrich stomach is over 11 kg, including 869 g gastroliths. On the other hand, this maximum amount of 11.2 kg is far above the average (3.6 kg). In the complete stomach, stones constitute on average of about a third of all contents (1:0.31).

In the ostrich study by Milton et al. (1994), the gastrolith mass varied in subadults (mean=444 g ± 130 g (S.D.)) and adults (mean=646 g ± 266 g (S.D.)) and averaged 0.83% of body mass. In the German ostriches, the stones had a mean mass of 1021 g, in the subadult South African farm ostriches of 870 g and were therefore considerably higher than in the Milton et al. study as well as in the data provided by Johnson (1990) (Table 3). However, the mean gastrolith mass was lower than the 1.5 kg stones reported by Kreibich and Sommer (1994). On average, gastroliths constituted in both ostrich groups about 1% of the body mass in both ostrich groups. Yet, the minimum of 156 g and the maximum of 2880 g show the wide spectrum of possible gastrolith masses.

The ratio of food to stones in the ventriculus of 20 ostriches examined by Milton et al. (1994) was 1:1.0. Unfortunately, the farm ostriches studied by me were not completely suitable for an examination of the relationship between gastroliths and food because of their dependence on provided food. Within the German farm ostriches, there was on average less foodstuff by mass than stones in the gizzard (1:1.39 on a wet weight basis).

The reasons why there was no correlation between the gastrolith mass and other parameters like age, gender, body mass etc. are unknown. On one hand, intake of gastroliths is possibly mainly controlled by individual preferences of the birds. On the other hand, it is likely that with samples from a greater range of body masses, at least a good correlation between the body mass and the gastrolith mass would be noticeable.

There is also no significant connection between gastrolith mass and season. This is a contrast to wild crows which have more stones in the stomach during the winter months (Jacobi, 1900). Jacobi argued that, in winter, there are generally more individuals which have stones and that the amount of stones is higher regardless of the food composition (insects and plant material, respectively). The hypothesis that the larger amounts of stones help to suppress hunger (Jacobi, 1900) may indeed be correct, since the ostriches have no higher amounts of gastroliths in winter, but are also always provided with sufficient food. Yet, farm ostriches as a somewhat non-natural group are only of limited help in solving this question.

In the German birds with representative amounts of foodstuff in the stomach, there is no significant correlation to the gastroliths. This is to be expected, of course, because of discontinuous feeding. That the foodstuff of South African ostriches is significantly correlated with the gastroliths mass ($p<0.001$) is possibly an artifact of starvation. As noted earlier, only very little plant matter was found in the stomachs beside water and stomach liquids.

Rock type composition

It is reported from South African ostriches that they swallow selectively white quartz pebbles (M. Jarvis, pers. comm. 2003). Hence, some ostriches seem to prefer stones of a certain size or of a special color (Fig. 5a-d) and may therefore actively select special rock types. However, experiments on German ostriches showed that most ostriches swallow all rock types without any selection (Wings, unpublished data). Therefore, one would expect to find a representative cross section of the rock types in the habitat among the gastroliths. However, the real "selection" happens in the gizzard, where soft rocks are quickly eroded and carbonates become dissolved (Wings and Sander, in preparation). The most durable rock types, commonly quartz varieties, resist even the high mechanical erosion in the gizzard for the longest time and therefore accumulate in the gizzard (Wings and Sander, in preparation). Siliceous rocks formed approximately 90% of the gastroliths in German ostriches. Compared to the normal rock type composition of Rhine River gravels with a maximum of siliceous rocks of 60%, a clear increase is apparent.

Grain size composition

The distribution of gastrolith grain sizes shows that ostriches are very flexible in utilization of stones of different sizes. While most of them seem to prefer stones in the range of 8-20 mm, they can even utilize sand-sized grit or stones >20 mm (Fig. 5b). The large amounts of sand show that even this small grain size is swallowed intentionally. If it would represent ground-down pieces of larger gastroliths, the amount found in each stomach should be more consistent. Instead, some stomachs contained more than 50% sand and others less than 5%. Additionally, the low amounts of sand found in some stomachs had another composition (darker color, less quartz) than the large amounts of sand in other stomachs. This could indicate that the darker sand represented either ground-down gastroliths or the natural sand fraction in the habitat. This sand had most likely been swallowed accidentally together with grass roots and attached to stones and feces. The large amount of white quartz sand found in other stomachs of German birds was very similar in appearance to the sand provided to the animals for plumage care and most plausibly originated from this source.

The reasons why individual birds prefer different grain sizes remains unclear. There is no obvious correlation to gender, age, body mass, breeding group, and season. A correlation with food was not conducted because as farm birds, all animals had a rather similar diet and the diet was not known precisely, respectively. A hypothesis suggested to explain the variance in gastrolith grain size composition is that the natural supply of stones of certain sizes is depleted in some enclosures and that the birds shift to other grain sizes. But perhaps the grain sizes are indeed controlled by the individual taste of each bird, and some samples from South African birds support this hypothesis (Fig. 5a, 5b).

The general scarcity of the grain size class 2-4 mm could be a result of preferred excretion by the ostriches. Perhaps this grain size class is too rare to be ingested intentionally and too small to be of any use in the trituration of foodstuff. Since uptake of stones is continuous (personal observations 2000-2003), the excretion of rock material must happen continuously too. Preliminary research on feces from German ostriches showed that the maximal size of excreted gastroliths is indeed in the grain size class 2-4 mm (Wings, unpublished data).

The high numbers of stones in each of the examined masses ensures that the calculated mean masses are significant. Since all animals had the same rock types as gastroliths, there was no large difference in the specific density of the stones and therefore in the mass of pebbles from each grain size. Using the mean mass of gastroliths from each grain size, it is possible to estimate the total number of stones in all sampled stomachs from the same region.

The mean masses of individual gastroliths in different grain size classes are very different. This implies that the total number of stones in the stomach is strongly depended on the grain size distribution. This is also evident in Fig. 5a and Fig. 5b: a few large cobbles can amount to the same mass as thousands of very small stones. Since not all grain size classes were included in the calculation, the total amount of pebbles is always higher than calculated, and if the sand fraction is added to the count, the total number of stones is rising by thousands of grains. In this case, each stomach has several thousand grains and stones, respectively, in the stomach.

Foreign objects

The abundance and size of foreign objects in captive ostrich stomachs is remarkable. The swallowing of strange items is often interpreted as abnormal behavior because of missing access to stones (e.g., Stokes, 1987). As the ostriches have unlimited access to stones on the farms, the reason for this behavior must be different. Most objects have an unusual shape or are colorful and/or bright. The most probable reasons could be the objects being mistaken for insects (Huchzermeyer, 1998), urge to play, or pathological behavior.

Milton and Dean (1995a; 1995b) reported that sharp objects such as nails, wire, coins and broken glass frequently cause stomach lesions. This observation is not supported by my own research. Most examined gizzards were intact, even when sharp or pointy objects such as a pocket knife with an open blade or large glass fragments were found in the stomach. Large objects were mostly found in the proventriculus, where no major movement of the stomach contents occurs. Stomach lesions were found very rarely compared to the finds of sharp objects in the stomachs.

Milton et al. (1994) reported mammal bones and teeth in 5 out of 20 examined stomachs. No bones or teeth were found in the German and South African farm ostrich material. This could be caused by the availability of skeletal remains. In the limited areas of the enclosures, skeletal remains are less abundant than in the vast open regions in southern Africa.

Usability of the data as reference values

The presented dataset is the largest examination of stomach contents and gastroliths in ratites ever endeavored. The number of 135 examined German animals and 212 South African animals is significantly above the recommended minimum number of 120 samples for an estimation of normal range with accuracy (Reed et al., 1971). After Reed et al. (1971), 120 is the smallest number of sample values that permit 90% confidence intervals for the endpoints of the normal range. Therefore, the presented data has a high scientific value especially as reference data for comparisons with other vertebrates. The data also has great potential to be used for comparison with vertebrate fossils, especially dinosaurs (Wings, 2003; Wings and Sander, in preparation).

Some possible factors of influence for the choice of nutrition were not controlled or observed, such as weather or climate. It is likely that for other ratite species, different ostrich age groups, regions with a different geology or climate, and especially with a different diet, some restrictions to the validity of the presented data might apply. However, the obvious similarity between the gastroliths of ostriches living in South Africa and Germany suggests that at least the influence of climatic factors is rather limited.

Acknowledgements

I am very thankful to my Ph.D. advisor Martin Sander for his constant support during my research. Ralf Schuhmacher from the Straussenfarm Gemarkenhof made the main research on living ostriches in Germany possible. Adriaan Olivier was very helpful during my research on South African ostriches and organized the study on ostriches in the Klein Karoo Co-operative. I also would like to thank Kerstin Athen for reviewing the results of the statistical analyses. Marcus Clauss commented on a draft of the manuscript. Claudia Trögl helped with the preparation of some samples and the counting of the gastroliths. Financial support was provided by a scholarship of the “Graduiertenförderung Nordrhein-Westfalen”. The

Graduiertenkolleg “Evolution and Biodiversity in Space and Time” in Bonn is gratefully acknowledged for funding the research in South Africa.

References

Anderson, A., 1989. Prodigious birds. Moas and moa-hunting in prehistoric New Zealand. Cambridge University Press, New York, 238 pp.

Ayeni, J., Olowo-Okorun, M.O. and Aire, T.A., 1983. The biology and utilization of helmet quinea-fowl (*Numida meleagris galeata* Pallas) in Nigeria. III Gizzard weights and contents. African Journal of Ecology, 21: 11-18.

Baltmanis, B.A., Blue-McLendon, A. and Angel, C.R., 1997. Effect of diet on the ostrich gastrointestinal tract size. American Ostrich (Research Issue), April: 17-19.

Bezuidenhout, A.J., 1999. Anatomy. In: D.C. Deeming (Editor), The Ostrich. Biology, Production and Health. CABI Publishing, Cambridge, pp. 13-49.

Cilliers, S.C. and Angel, C.R., 1999. Basic concepts and recent advances in digestion and nutrition. In: D.C. Deeming (Editor), The Ostrich. Biology, Production and Health. CABI Publishing, Cambridge, pp. 105-128.

Davies, S.J.J.F., 1978. The food of emus. Australian Journal of Ecology, 3: 411-422.

Ernst, G., Kohring, R. and Rehfeld, U., 1996. Gastrolithe aus dem Mittel-Cenomanium von Baddeckenstedt (Harzvorland) und ihre paläogeographische Bedeutung für eine prä-ilsedische Harzinsel. Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg, 77: 503-543.

Garrod, A.H. and Darwin, F., 1872. Notes on an ostrich lately living in the society's collection. Proceedings of the Scientific Meetings of the Zoological Society of London for the Year 1872, 1872: 256-363.

Gionfriddo, K.P. and Best, L.B., 1999. Grit use by birds - a review. Current Ornithology, 15: 89-148.

Hoyo, J.d., Elliott, A. and Sargatal, J., 1992. Handbook of the Birds of the World, 1: Ostrich to Ducks. Lynx Editions, Barcelona, 696 pp.

Huchzermeyer, F.W., 1998. Diseases of Ostriches and Other Ratites. Agricultural Research Council, Onderstepoort Veterinary Institute, Onderstepoort, 296 pp.

Jacobi, A., 1900. Die Aufnahme von Steinen durch Vögel. Arbeiten aus der Biologischen Abtheilung für Land- und Forstwirthschaft am Kaiserlichen Gesundheitsamte, 1: 223-254.

Johnson, D.L., 1990. Biomantle evolution and the redistribution of earth materials and artefacts. Soil Science, 149: 84-102.

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.

Jones, R.L. and Hanson, H.C., 1985. Mineral Licks, Geophagy, and Biogeochemistry of North American Ungulates. Iowa State University Press, Ames, x+301 pp.

Kreibich, A. and Sommer, M., 1994. Straußenhaltung. Landwirtschaftsverlag, Münster-Hiltrup, 215 pp.

Meyer, W. and Stets, J., 1996. Das Rheintal zwischen Bingen und Bonn. Sammlung geologischer Führer , 89. Gebr. Borntraeger, Berlin, XII , 386 pp.

Milton, S.J. and Dean, W.R.J., 1995a. Gizzard stones and food selection by free-range ostrich: implications for management. East Coast Producers Association, January-February 1995: 4-7.

Milton, S.J. and Dean, W.R.J., 1995b. Why ostriches swallow stones, Prince Albert Friend, Prince Albert, pp. 7.

Milton, S.J., Dean, W.R.J. and Siegfried, W.R., 1994. Food selection by ostrich in southern Africa. Journal of Wildlife Management, 58(2): 234-248.

Reed, A.H., Henry, R.J. and Mason, W.B., 1971. Influence of statistical method used on the resulting estimate of normal range. Clinical Chemistry, 17(4): 275-284.

Rich, P.V., 1990. *Genyornis newtoni* Stirling and Zietz, 1896. A mihirung. In: P.V. Rich and G.F.v. Tets (Editors), Kadimakara: Extinct Vertebrates of Australia. Princeton University Press, Princeton, pp. 188-194.

Semmel, A., 2002. Rheinisches Schiefergebirge. In: H. Liedtke and J. Marcinek (Editors), Physische Geographie Deutschlands. Justus Perthes Verlag, Gotha, pp. 466-481.

Shanawany, M.M. and Dingle, J.H., 1999. Ostrich production systems. FAO Animal Production and Health Paper; 144. Food and Agriculture Organization of the United Nations, Rome, xi, 256 pp.

Stevens, C.E. and Hume, I.D., 1995. Comparative Physiology of the Vertebrate Digestive System. Cambridge University Press, 400 pp.

Stirling, E.C., 1900. The physical features of Lake Callabonna. Memoirs of the Royal Society of South Australia, 1(2): i-xv.

Stokes, W.M.L., 1987. Dinosaur gastroliths revisited. Journal of Paleontology, 61(6): 1242-1246.

Swart, D., 1988. Studies on the hatching growth and energy metabolism of ostrich chicks *Struthio camelus* var. *domesticus*. Ph.D. Thesis, University Stellenbosch, South Africa, 170 pp.

Thomson, A.L., 1964. A New Dictionary of Birds. McGraw-Hill, New York, 928 pp.

Twigg, J., 2001. Differentiating Moa Gizzard Stones. M.Sc. Thesis, University of Auckland, Auckland, 118 pp.

Webb, C., 1994. Lithic assemblage formation in semi-arid Australia: the role of emu gastroliths. Journal of Archaeological Science, 21(2): 145-152.

Wiman, C., 1916. Blocktransport genom Saurier. Geologiska Föreningens i Stockholm Förhandlingar, 38(5): 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. and Sander, P.M., in preparation. Gastrolith function in dinosaurs reconsidered: No evidence for gastric mills in sauropods.

Worthy, T.H. and Holdaway, R.N., 2002. The Lost World of the Moa: Prehistoric Life of New Zealand. Indiana University Press, Indiana, 718 pp.

Tables

Size	**Mass [g]**	**Rock type**	**Number of stones**
4-8 mm	200	total	623
		vein quartz	473
		chert	2
		glass	18
		quartzite	55
		other rock types	75
8-20 mm	1000	total	527
		vein quartz	346
		chert	24
		glass	4
		quartzite	75
		other rock types	78
Total amount			
4-8 and 8-20 mm	1200	total	1150
		vein quartz	819
		chert	26
		glass	22
		quartzite	130
		other rock types	153

Table 1. Count of stones for each rock type in the 4-8 mm and 8-20 mm grain size fraction and in total from both fractions in a sample from Remagen, Germany.

Size range	Sampled mass [g]	Number of stones	Mean mass of single gastrolith [g]
2-4	50	1072	0.047
4-8	200	623	0.321
8-20	1000	527	1.898

Table 2. Number of stones in each grain size fraction and calculation of mean mass of a single gastrolith in a sample from Remagen, Germany.

Sample no.	**Total number of stones**	**Total stone weight in gram**	**Long axis of the largest stone in mm**
Masai Ostrich No. 1	5,000	855	16.5
Masai Ostrich No. 2	2,856	707	18.1
Masai Ostrich No. 3	9,128	991	19.0
Masai Ostrich No. 4	3,108	433	19.1
Masai Ostrich No. 5	436	117	21.7

Table 3. Ostrich gastrolith data reported by Johnson (1990).

Figures

Fig. 1. Histograms of the gastroliths masses of a South African as well as a German group of free-range farm ostriches. Both groups exhibit a significant normal distribution of data. While the South African birds were some month younger and therefore had a lower mean body mass, the proportion between gastrolith mass and body mass is almost identical in both group.

Fig. 2. Rock type composition of sampled gastroliths material from German farm ostriches. The circular charts show the sampled grain sizes 4-8 mm and 8-20 mm as well as the combined number of samples from both grain sizes (4-20 mm). The differences in composition are minimal, siliceous rock types comprise more than 80% of all rocks.

Fig. 3. Gastroliths grain size distribution in German farm ostriches. Note the irregular distribution of the grain size classes and the small proportion of grain size class 2-4 mm. The animals are sorted in chronological order of sampling.

Fig. 4. Relative amount of gastroliths in the proventriculus and gizzard of German farm ostriches. Note that despite of the great variability in the distribution, the majority of all gastroliths is situated in the gizzard. The animals are sorted in chronological order of sampling.

Fig. 5. Photos of different sets of gastroliths from South African farm ostriches (all scales are 2 cm). Figures a and b show extreme differences in the size of gastroliths: while the first animal preferred stones with a maximum size of approximately 1 cm, the second preferred very few stones, but many of cobble size. Figures c and d show, on the other hand, clear differences in color, while the first animal obviously preferred bright white stones, the latter had mostly dark pebbles in the stomach. A similar variation in the preferred grain size and/or color was found in some of the German ostriches.

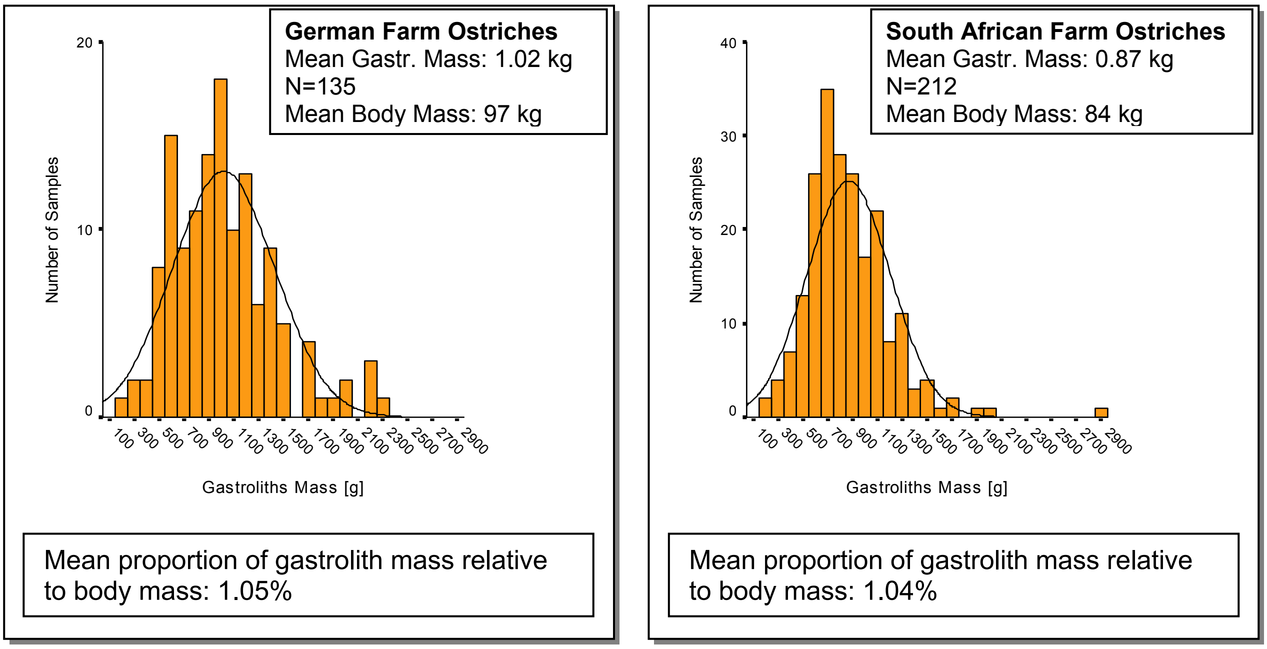
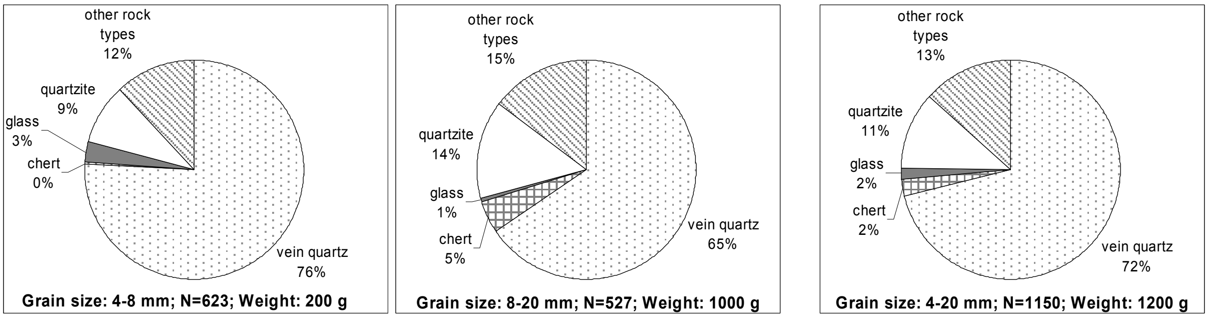

German Farm Ostriches
Mean Gastr. Mass: 1.02 kg
N=135
Mean Body Mass: 97 kg
Number of Samples
0
10
20
100
300
500
700
900
1100
1300
1500
1700
1900
2100
2300
2500
2700
2900
Gastroliths Mass [g]
Mean proportion of gastrolith mass relative to body mass: 1.05%
South African Farm Ostriches
Mean Gastr. Mass: 0.87 kg
N=212
Mean Body Mass: 84 kg
Number of Samples
0
10
20
30
40
100
300
500
700
900
1100
1300
1500
1700
1900
2100
2300
2500
2700
2900
Gastroliths Mass [g]
Mean proportion of gastrolith mass relative to body mass: 1.04%

Fig. 1



Grain size: 4-8 mm; N=623; Weight: 200 g

Grain size: 8-20 mm; N=527; Weight: 1000 g

Grain size: 4-20 mm; N=1150; Weight: 1200 g

Fig. 2

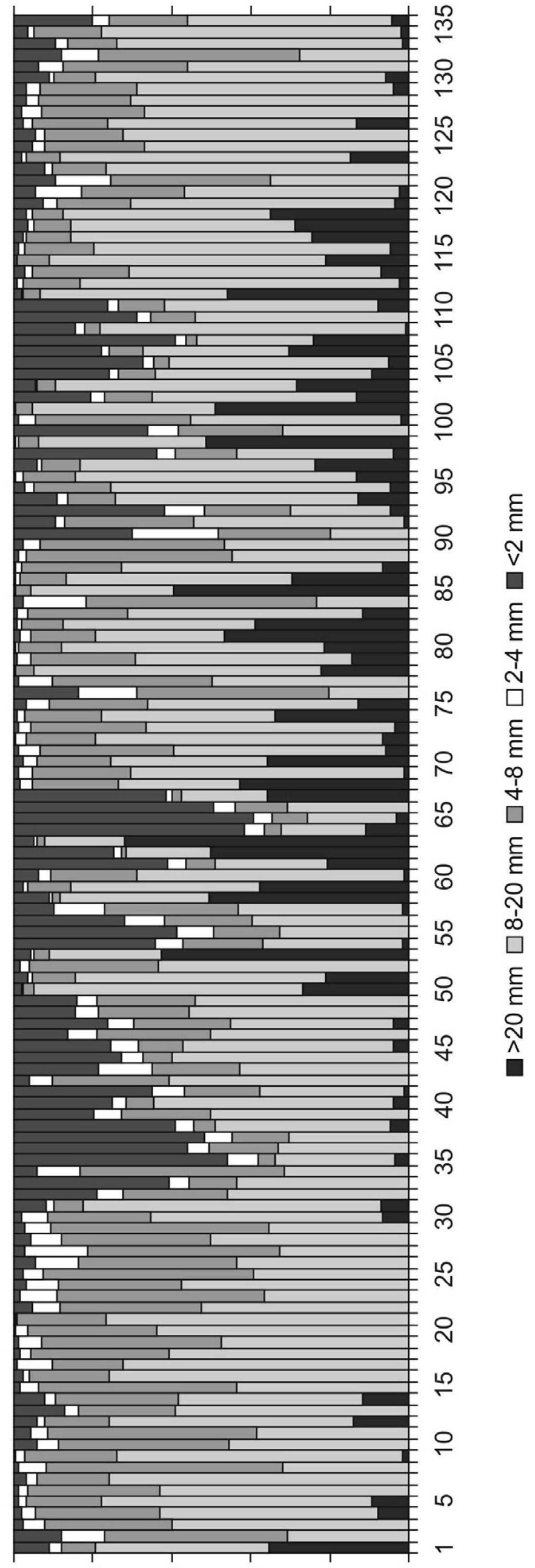

100%
80%
60%
40%
20%
0%
1
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
105
110
115
120
125
130
135
■ >20 mm
▨ 8-20 mm
▨ 4-8 mm
□ 2-4 mm
■ <2 mm

Fig. 3

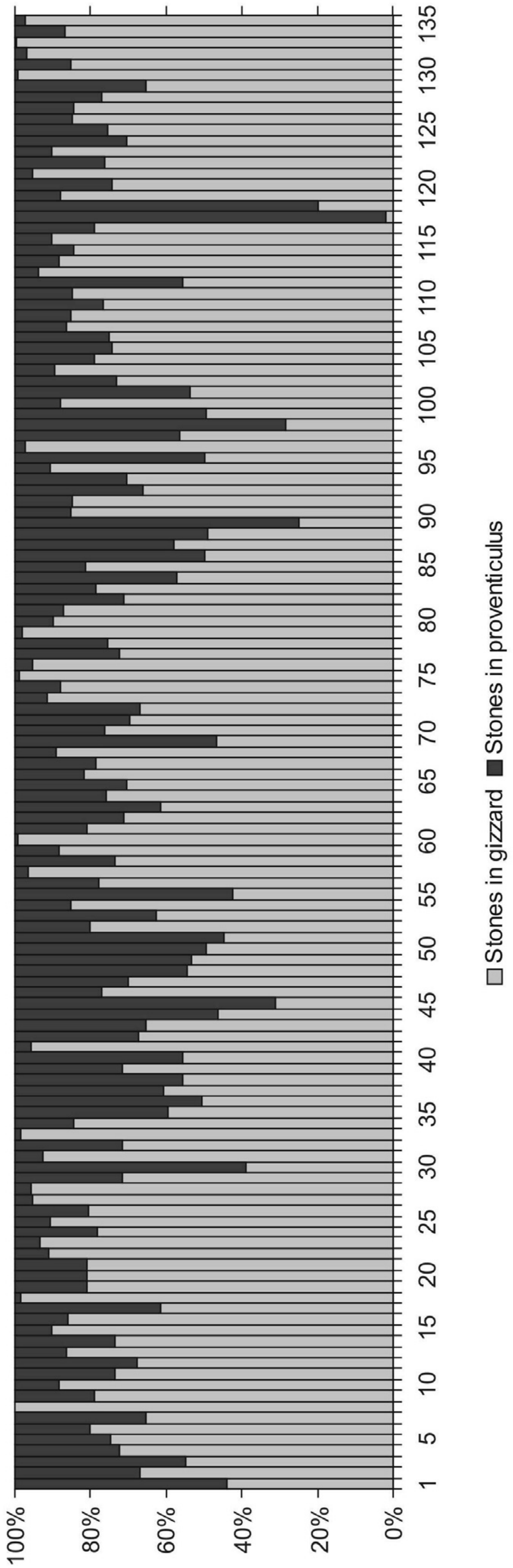

100%
80%
60%
40%
20%
0%
1
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
105
110
115
120
125
130
135
Stones in gizzard
Stones in proventiculus

Fig. 4

Fig. 5

CHAPTER IV: Observations on the release of gastroliths from ostrich chick carcasses in terrestrial and aquatic environments

Abstract

The decomposition of two ostrich (*Struthio camelus*) chicks (body masses 2.1 kg and 11.5 kg) was observed in a terrestrial and an aquatic setting, respectively, in a hot and arid climate with temperatures ranging from 25-40°C. Special attention was given to the observation of the release of gastroliths from the body cavity. The results show that the gastroliths can be set free from carcasses with a body weight <12 kg after relatively short periods (3-6 days), and that a separation in an aquatic environment is likely because of prolonged floating of the carcass.

Introduction

Gastroliths, stomach stones, are known to occur in many fossil and extant vertebrate clades including some birds (Whittle and Everhart, 2000, and see chapter I and references therein). Despite this common occurrence, the taphonomy of fossil skeletons associated with gastroliths has received little attention in the past and the release processes of gastroliths from recent carcasses are largely unstudied. Furthermore, only a small number of taphonomic studies has concentrated on recent bird bone assemblages and none of them discussed gastroliths (Bickart, 1984; Oliver and Graham, 1994; Davis and Briggs, 1998).

This is unfortunate because there are many interesting questions concerning the taphonomy of gastroliths, for example: How long does it take until the stones are released? Can the gastroliths exit an articulated carcass? What are the different effects of terrestrial and aquatic environments on gastrolith deposition? During a research project on ostrich gastroliths in cooperation with the Klein Karoo Co-operative Ltd. in Oudtshoorn, South Africa, I conducted a preliminary experiment on freshly dead ostrich chicks to address these issues.

Experimental setting

The carcasses of two ostrich chicks were deposited in Oudtshoorn (Klein Karoo, Republic of South Africa) on the same day they died from bacterial infections beginning an experiment that ran for six days. The daily temperature during the duration of the experiment ranged from 25 to 45°C. Both carcasses were exposed to dry heat in direct sunlight for most of the day and no rainfall occurred during the experiment. The smaller carcass with a body mass of 2.1 kg was placed on the ground (Fig. 1a). On the third day, this carcass was lifted at the right leg, resulting in a disruption of the carcass and exposure of the body cavity (Fig. 1b). This was done in order to study the condition of the internal organs and stomach contents at this stage of decomposition.

The second carcass with a body mass of 11.5 kg was deposited in a 200 liter barrel of freshwater with the ventral side oriented upwards (Fig. 2a). The carcass was turned sideward after three days (Fig. 2b) in order to place the complete carcass in the barrel.

On the second day, a white woven plastic bag was placed under the smaller carcass to increase the ability to distinguish it from the ground and for easier removal of the remains after the experiment was terminated. Admittedly, this was an unnatural situation, but the effect of this bag on the distribution of invertebrate scavengers on the carcass was considered to be negligible since most maggots derived from flying insects and the bag caused no barrier for terrestrial insects. Since the experiments were merely concerned with the taphonomical behavior of gastroliths, no special attention was given to the species or size of the maggots in the carcass.

Observations

The decay of the smaller chick progressed more rapidly than that of the larger one. Most of the flesh of the smaller chick was consumed by maggots after three days. Decomposition gases were rather limited. The thin neck dried out during the first day, and would have prevented any oral exit of stomach contents had the carcass been moved. The remaining flesh “liquidized” to some extent, permitting a potential release of the stomach contents through other “exit” sites. When the right leg of the carcass was lifted after three days, all internal organs had been disintegrated and were almost completely consumed by maggots. However, the stomach contents, including the gastroliths, were still arranged in a cluster and not dispersed over the entire body cavity. Because of the high temperatures, the remaining soft tissues dried out very quickly during the next days of the experiment, mummifying the carcass and preserving the gastroliths in the gastric cavity (Fig 1c). At the end of the experiment, the carcass showed the phenomenon of adherence to the ground (respectively to the underlying bag) observed by Bickart (1984).

The larger chick carcass floated in the water until the experiment was terminated (Fig. 2a-2c). Few maggots were observed, and they seemed to have been restricted to that part of the carcass above the water line. Unfortunately, the gizzard position could not be controlled visually during the experiment because of wet feathers that covered most of the carcass skin.

The esophagus and anus were swollen and therefore did not permit the exit of decompositional gases, which expanded the body and facilitated carcass floatation. While the amount of the gases decreased during the next days, (visible as less tension of the skin), there was still a considerable amount of gas left in the carcass at the experiment's end (Fig. 2b, 2c). When the experiment was terminated and the barrel emptied, all gastroliths were found in isolation at the bottom of the barrel and detached from the carcass, while all skeletal remains were still articulated and floating.

Discussion

Experiment in terrestrial environment

In general, there tends to be an overall increase in rate of decay with rising temperature (Swift et al., 1979). However, the rapid disintegration of the smaller carcass used in these experiments was not only due to the environmental setting. Disintegration also depended on body size: smaller animals contain less flesh, warm up faster and are more quickly consumed by maggots. In a less arid and cooler environment, the carcass would not have been mummified but rather would have completely disintegrated. An already mummified carcass would probably be transported in water in one piece. The stones would therefore remain in the carcass until it was soaked with water again and disintegrated. After that, the heavy gastroliths would sink to the bottom.

It is likely that carcasses buried autochthonously in a terrestrial environment (e.g., by wind-transported sediments) would have any existing gastroliths preserved *in situ.* The same pattern is predicted to occur if "terrestrial" carcasses are embedded by water-transported sediments without prior transport by water. This is the case if water velocity is too low to transport the carcass or the gastroliths.

Experiment in aquatic environment

Gastroliths are the densest and heaviest parts of a carcass and therefore tend to be the first parts to separate from a floating body. As discussed by Schäfer and Craig (1972), bird carcasses do not initially sink to the bottom, as do the carcasses of fish, reptiles, and mammals. This is because air stored in bird quills, between the down feathers and in their pneumatized long bones prevents sinking. In addition, their skin probably largely prevents their guts from falling out quite some days after death. Nevertheless, as soon as a breach in the body cavity appears, the heavy gastroliths will exit the carcass and drop to the bottom. Schäfer and Craig (1972) reported that many bird carcasses found on beaches and in dunes still have gastroliths *in situ.* This is an indication of short transportation times or death in a terrestrial environment.

Without specific information about the environment and the temperatures, the decay process of a herring gull *(Larus argentatus)* was described by Schäfer and Craig (1972): four days after death, maggots were visible in the parts above the water line; after 13 days, all skeletal elements above the water were bare of musculature and connective tissue; after 27 days, the carcass was still afloat but the hind limbs and the sternum had fallen off; after 38 days, the carcass sank to the bottom; and after 65 days, the carcass remained articulated on the bottom, without any parts floating up again. A broadly similar pattern of disarticulation was reported for some of the coot *(Fulica americana)* carcasses observed by Oliver and Graham (1994)

General discussion

Neither of the carcasses reported on here, or those in previous experiments on birds (Bickart, 1984; Oliver and Graham, 1994; Davis and Briggs, 1998), burst due to extensive generation of decompositional gases. Thus, it is likely that strong "explosion-like" disruptions of carcasses, with a potential for propulsive transport of body contents beyond the carcass, are rare in birds, and are probably restricted to much larger carcasses.

During previous examinations of other ostrich carcasses, I observed that the koilin lining layer of the gizzard can be separated from the stomach muscles after several minutes to hours. Thus, I assume the same for the two carcasses observed in this experiment. This detachment of the koilin layer is probably caused by the acidic environment in the stomach. Yet, the large muscles around the gizzard still protect the gastroliths for a considerable period before the release of its contents. In the absence of maggots, the stomach is very resistant to putrification, as shown for ranids and bufonids (Wuttke, 1983), which do not even have muscular stomachs. In such cases, the gastroliths would either exit the body cavity with the stomach, or, if the opening in the carcass is too small, remain in the body cavity until the stomach is putrefied and eventually sets the isolated stones free itself. However, the stomach muscles represent valuable nutrition for maggots and are therefore rapidly consumed within a few days, allowing the fast separation of gastroliths.

Conclusions

Although the results presented here are very preliminary, they still allow a few generalizations about different taphonomic patterns of gastrolith release in terrestrial and aquatic environments.

Generally, the release of gastroliths in small animals in hot climates is very fast, both, in aquatic and terrestrial environments. In aquatic environments there is a greater chance that the stones will be separated from the skeleton due to prolonged floating of the decaying carcass without the already detached gastroliths. However, numerous well-preserved skeletons with gastroliths are known from aquatic fossil deposits, such as the marine Cretaceous formations in North America (plesiosaurs, e.g., Welles and Bump, 1949; Darby and Ojakangas, 1980; Taylor, 1993) or the Eocene lake sediments of Messel in Germany (crocodilians, e.g., Keller and Schaal, 1992; Koenigswald, 1998). At these fossil sites, vertebrates are mostly articulated, indicating a short drifting time of the carcasses. It is plausible that a tougher skin or, in the case of the crocodiles, osteoderms delayed the release of the gastroliths. This idea is further corroborated by the very rare occurrence of gastroliths in fossil birds from the lacustrine deposits of Messel (G. Mayr, pers. comm. 2003) as opposed to crocodiles from the same locality, which generally have gastroliths preserved *in situ* (own observations and W. v. Koenigswald, pers. comm. 2003).

All observations and conclusions are only valid for finds lacking indications of scavenging. Scavengers are a primary agent of carcass degradation (Davis and Briggs, 1998) and scavenging animals often commence consumption of a carcass on its abdomen (e.g., Weigelt, 1989), thus altering the position of the gizzard with the potential of complete removal of the gastroliths. With this in mind, a comprehensive discussion of the taphonomical and sedimentological processes altering the fossil record of gastroliths is forthcoming (see chapter V).

Acknowledgements

I would like to thank Dr. Adriaan Olivier from the Klein Karoo Co-operative Ltd. in Oudtshoorn, Republic of South Africa, for supplying the carcasses and permitting the experiments on the property of the Cooperative. Annalisa Gottmann, Dr. Martin Sander, and Lars Schmitz commented on earlier drafts of the manuscript and considerably improved the manuscript. The Graduiertenkolleg “Evolution und Biodiversität in Raum und Zeit” in Bonn is gratefully acknowledged for funding the research in South Africa.

References

Bickart, K.J., 1984. A field experiment in avian taphonomy. Journal of Vertebrate Paleontology, 4(4): 525-535.

Darby, D.G. and Ojakangas, R.W., 1980. Gastroliths from an Upper Cretaceous plesiosaur. Journal of Paleontology, 54(3): 548-556.

Davis, P.G. and Briggs, D.E.G., 1998. The impact of decay and disarticulation on the preservation of fossil birds. Palaios, 13(1): 3-13.

Keller, T. and Schaal, S., 1992. Crocodiles: large ancient reptiles. In: S. Schaal and W. Ziegler (Editors), Messel. An Insight into the History of Life and of the Earth. Clarendon Press, Oxford, pp. 109-118.

Koenigswald, W.v., 1998. Magensteine eines Krokodils. In: W.v. Koenigswald and G. Storch (Editors), Messel - Ein Pompeji der Paläontologie. Thorbecke Verlag, Sigmaringen, pp. 40-41.

Oliver, J.S. and Graham, R.W., 1994. A catastrophic kill of ice-trapped coots: time-averaged versus scavenger-specific disarticulation patterns. Paleobiology, 20(2): 229-244.

Schäfer, W. and Craig, G.Y., 1972. Ecology and palaeoecology of marine environments. University of Chicago Press, Chicago, xii, 568 pp.

Swift, M.J., Heal, O.W. and Anderson, J.M., 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, xii, 372 pp.

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(1296): 163-175.

Weigelt, J., 1989. Recent Vertebrate Carcasses and their Paleobiological Implications. University of Chicago Press, Chicago, i-xviii and 1-188 pp.

Welles, S.P. and Bump, J.D., 1949. *Alzadasaurus pembertoni*, a new elasmosaur from the Upper Cretaceous of South Dakota. Journal of Paleontology, 23(5): 521-535.

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 (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 75-82.

Wuttke, M., 1983. Aktuopaläontologische Studien über den Zerfall von Wirbeltieren. Teil I: Anura. Senckenbergiana lethaea, 64(5/6): 529-560.

Figures

Fig. 1a. Terrestrial setting, first day of the experiment. The small ostrich chick carcass with swollen body cavity is lying on the ground.

Fig. 1b. Terrestrial setting, fourth day of the experiment. Most of the flesh has already been consumed by maggots. Note the visible stomach contents including gastroliths as brown mass in the centre of the picture.

Fig. 1c. Terrestrial setting, sixth day of the experiment. The carcass had completely dried out, forming a solid mass and preserving the gastroliths *in situ.*

Fig. 2a. Aquatic setting, second day of the experiment. The large ostrich chick carcass floating with the ventral side up in the water barrel. Note the swollen body cavity, filling most of the barrel's diameter. The carcass had easily fit in the barrel the day before.

Fig. 2b. Aquatic setting, fourth day of the experiment. The carcass was turned to a lateral position (left leg is visible) in order to place all body parts in the barrel. Until then, the legs were still situated beyond the barrel margin and could have potentially stopped the carcass from sinking. The carcass is still intact and floating.

Fig. 2c. Aquatic setting, sixth day of the experiment. The carcass started to macerate, but all bones are still connected and floating. The experiment was ended on this day, the barrel was emptied and all the gastroliths were found separated from the carcass on the bottom of the barrel.

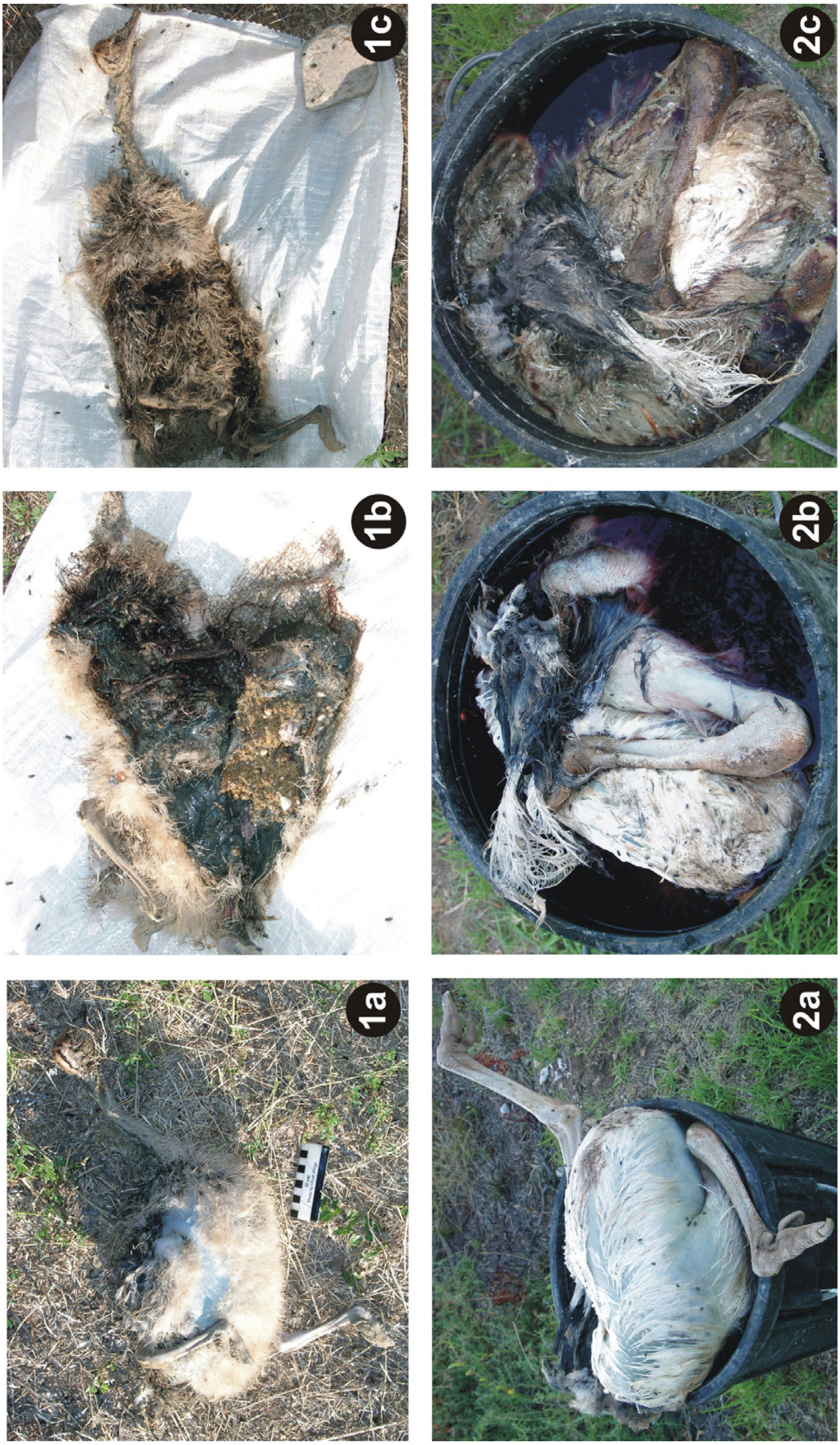


Fig. 1a-2c.

CHAPTER V: Review of the taphonomy of gastrolith-bearing vertebrates and a new classification for gastrolith finds

Abstract

Gastroliths (stomach stones) are known from many extant and extinct vertebrate clades and are potentially useful for paleobiological interpretations. However, the connection between bones and gastroliths in the fossil record is not always evident. Therefore, processes which could lead to the loss of gastroliths from the body but also to the coincidental association of gravel with vertebrate remains are reviewed. The separation modes for bones and gastroliths comprise active behaviors in the living animal (regurgitation and defecation) as well as several post-mortem processes, including the transport of bones and/or stones by other animals (scavengers) and water transport as well as the selective destruction of stones or bones (mainly the latter). The importance of transport by water in marine and fluvial systems is also discussed. The fossil record of the most important groups of lithophagic vertebrates is reviewed in regard to taphonomy and sedimentology in order to develop a generalized pattern of gastrolith distribution and preservation. Examples of fossil gastrolith-bearing taxa include tangasaurids, crocodilians, sauropodomorph as well as non-avian theropod dinosaurs, and birds. The occurrence pattern of gastroliths within the fossil record shows that associated gastroliths are especially abundant in stagnant aquatic environments. A simple classification system for the authenticity of gastroliths is introduced. The scale ranges from 1 (cluster of stones in the abdominal area of the skeleton) to 6 (surface finds of isolated, rounded and occasionally polished stones without associated bones).

Introduction

The analysis of fossil stomach contents is difficult in general. Complications include the identification of small amounts of partly digested food, the discrimination between food and unintentionally swallowed particles, the possibility that the food contents are the result of a non-typical feeding situation or that the stomach contents were subject to fossil or recent contamination (Richter, 1988). These problems do not only apply to food items but also to other stomach contents including gastroliths (stomach stones). Gastroliths are known from many extinct vertebrate clades (Whittle and Everhart, 2000, see also chapter I and II). Unfortunately, the identification of isolated gastroliths is very difficult and often impossible

(Wings, in preparation-b). This implies that the sedimentological and taphonomic situation of presumed gastrolith-bearing skeletons is important.

The following sedimentological and taphonomic factors support the interpretation of stones found in association with vertebrate remains as genuine gastroliths:

- Found *in situ*
- Fine-grained matrix which lacks such clasts elsewhere (low energy deposits)
- Clustering of the stones
- Association with articulated skeletons
- Preservation in an anatomically correct position, preferably within the ribcage

For example, recent research has shown that not all sauropodomorphs possessed gastroliths (see chapter VI), and it has been argued that most sauropod gastroliths are plain river gravel (Calvo, 1994; Lucas, 2000). The factors above, however, indicate in several cases that gastroliths are the most parsimonious explanation for the stones.

Authentic gastrolith deposits without associated bones

Because there is no unambiguous identification method (Wings, in preparation-b), it is difficult to identify isolated stones as authentic gastroliths. However, a few examples are known. In a Pliocene lake deposit in South Australia, scattered stones as well as clusters of gastroliths were found within complete skeletons of the large flightless bird *Genyornis newtoni*, as well as isolated on the surface of the clay-pans (Stirling, 1900). Because of the lack of another transport mechanism and the evidence of gastroliths associated with bones, Stirling (1900) suggested that all of the stones are gastroliths and were transported by the birds. The gastroliths occurred at various places in the fossil lake and were not naturally present in the embedding fine-grained strata (Stirling, 1900). The parent rock of these gastroliths was narrowed to the great Central Australian Plain Formation (Stirling, 1900). Finds of supposed moa gastroliths are also known from several areas of New Zealand (Anderson, 1989; Twigg, 2001). Johnson (1993) believed that bird gastroliths are commonly included as residual elements in soils.

The regurgitation of gastroliths by Hooker's sea lion (*Zalophus hookeri*) (Fleming, 1951), suggests that pinniped gastroliths can be locally important as clasts moved long distances from their source. The stones, which can have a total weight of several kilograms, are deposited in a compact cluster, or are splattered over an area of a few square meters due to violent shaking of the head during regurgitation (Fleming, 1951). Pinnipeds also accumulate stones in large numbers in coastal beds, e.g., forming a gravel lag deposit at the Snares Islands south of New Zealand (Fleming, 1951).

Non-gastrolith deposits of exotic rocks

There can be no certainty if exotic stones represent former gastroliths. Isolated polished exotic clasts in fine-grained sediments from Lower Cretaceous formations in the western USA are often believed to represent dinosaur gastroliths (Stokes, 1987). However, the scarcity of unambiguous dinosaur gastroliths makes this implausible (see chapter VI).

Transport mechanisms of clasts

Beside the obvious transport in aquatic environments, there are several other mechanisms by which clasts can be transported. These transport modes are especially important for the interpretation of isolated exotic clasts.

Several authors have discussed and summarized the possibilities of clast transport (Emery, 1963; Etzold and Maus, 1990; Bennett et al., 1996). The main transport modes for isolated clasts are: ice drift (icebergs or ice sheets in seasonally frozen aquatic environments), vegetational rafting (mainly in tree roots or attached to seaweed), vertebrates, gravitational processes (outrunner blocks), and projectiles (mainly volcanic ejecta).

Only transport by vertebrates is discussed in this study. Such transport is not necessarily limited to gastroliths. Clasts can also be transported externally with or without modifications. For a discussion of terms and examples see Johnson (1993) and chapter II.

Simple external transport is known from several birds of prey (buzzards, vultures, kites, eagles) and different clades of mammals (primates, rodents, and others) (Lawick-Goodall, 1970; Beck, 1980; Boesch and Boesch, 1981; Boesch and Boesch, 1984; Johnson, 1989). For example, transport of sediment by birds as contamination on dirty feet and feathers is known (Emery, 1963). Apes use and modify stones as tools and can transport these over some distance (Boesch and Boesch, 1981). Anthropogenic transport, for instance as ship’s ballast or coal clinker waste, should also be considered as a possible source in recent sediments (Bennett et al., 1996). Nevertheless, gastroliths are by far the most common form of vertebrate clast transport and are the focus of this paper.

Separation mechanisms for gastroliths and bones

Separation during lifetime

Regurgitation

While crocodilians are able to regurgitate, this has been reported very rarely (Fisher, 1981). Abel (1935) stated that stressed birds, snakes, and lizards are able to regurgitate as well. Hayward (1978) also mentioned that a number of birds are known to regurgitate or cough up the grit or small stones from their gizzards. He gives no reference or example for this statement. Personal observations and discussions with veterinarians, hunters, and farmers revealed that regurgitation in herbivorous birds is very rare. Only carnivorous birds regurgitate on a regularly basis, but these species do not typically utilize gastroliths.

The only vertebrate group where regurgitation of gastroliths is regularly reported are pinnipeds (e.g., Fleming, 1951). Regurgitation is common in sea lions. *Phocarctos*, e.g., was observed to regurgitate up to 20 gastroliths at a time and these stones were later clearly visible in small piles on the sand of the breeding beach (Marlow, 1975). *Neophoca* and *Phocarctos* are in a standing position while they regurgitate and are rarely lying prone. One animal was observed to regurgitate underwater, while lying in a rock pool (Marlow, 1975). Regurgitation during swimming was not observed. Involuntarily loss of gastroliths under stress was suggested by Taylor (1993) for marine tetrapods. The loss might aid in adding positive buoyancy in an emergency. However, there is no recorded evidence for such behavior, and the change in buoyancy can be considered minimal (see chapter II).

Defecation

Modern tetraonid birds (grouses) defecate stones when exposed to a excess of grit or excrete the grit involuntarily when fed with coarse food such as hard twigs (Porkert and Höglund, 1984). Furthermore, the excrements of moas are assumed to have contained stones. Chapman (1884) reported finds of generally three or four white exotic quartz pebbles and proposed their origin from moa excrement. In the feces of free ranging farm ostriches, no sediment particles larger than 4 mm in diameter were detected (Wings, unpublished data), whereas their stomachs commonly contain stones with a size of up to a few centimeters (see chapter III).

Fossil coprolites with gastroliths are extremely rare and are only attributed to crocodilians. Coprolites with gastroliths from the Eocene crocodile *Diplocynodon* were found in the Geiseltal lignite in Germany (Weigelt, 1927). Furthermore, one out of 22 coprolites of *Asiatosuchus nanliengensis* found in Paleocene sediments of Nanhsiung, China, contained some pebbles mixed with the otherwise pure dung (Young, 1964).

In summary, a loss of “working size” gastroliths during life by regurgitation or defecation is possible, but does not occur on a regular basis, except in pinnipeds. Ground-off pieces of gastroliths are probably lost continuously, but are difficult to detect in coprolites. At least in birds, the stones are usually kept in the gizzard until they are totally eroded and too small to be of use in the trituration of food (see chapter III).

Post-mortem separation

Gastroliths can be can be destroyed or separated from the bones in several scenarios:

- Disintegration of the bones by scavenging or weathering (before final burial)
- Removal of the digestive tract including gastroliths by scavengers
- Transport of bones or stones by other animals or by water
- Diagenetic destruction of bones or of gastroliths
- Complete erosion of the bone material after exposure of the fossil

The post-mortem transport of gastroliths into the vicinity of the carcass can be caused by scavengers or sedimentological processes, but also by rupturing of the ventral body cavity due to the build up of decomposition gases.

Denudation processes can move selected sediments including bones and gastroliths. The processes include cryoturbation, bioturbation by various animals and by trees, and transport by water or ice.

Predation, scavenging, and reuse

Evidence from tooth marks on sauropod bones suggest that theropods were scavenging selectively (Matthew, 1908; Borsuk-Bialynicka, 1977; Buffetaut and Suteethorn, 1989; Hunt et al., 1994b). Recent scavengers usually start in the pelvic area of a carcass, especially in the anal region, where the easiest access to the nutritious internal organs is granted (Weigelt, 1989). It is probable that Mesozoic scavengers also concentrated on feeding on the body parts with the highest nutritional values: the ventral body cavity in the pubic area and the femora (Hungerbühler, 1998; Michelis, 2003). For example, an almost surgical dissection of the pelvis and individual vertebrae is known from prosauropod (Hungerbühler, 1998) and iguanodontid skeletons (Maxwell and Ostrom, 1995).

It is known from extant birds that scavengers or raptors ingest the complete stomach of their prey. Rörig (1903; 1906; 1909) examined the stomach contents of more than 4000 raptor birds from Germany and found gastroliths in less than 0.5% of all birds. The presence of plant material in some stomachs as well as occasionally preserved gizzards of the preyed-upon bird indicate that the gastroliths were often swallowed accidentally with the prey (Rörig, 1903).

Given the evidence of theropod teeth and tracks near sauropod remains, it is possible that large theropod scavengers may have swallowed the stomach with all contents and therefore left no evidence of gastroliths near the carcass. However, this is unlikely to be the case for very large amounts of gastroliths. For a functioning gastric mill, several hundred gastroliths would be needed for each sauropod. A total removal of the intact gizzard from the burial site or a complete swallowing of its content is unlikely. Therefore, complete articulated skeletons, especially those with preserved gastralia, should also have associated gastroliths.

If large theropods removed the complete gizzard from scavenged sauropod carcasses, accidentally swallowed gastroliths should be relatively common in theropod coprolites and in articulated skeletons. Yet, studies conducted on coprolites (e.g., Chin et al., 1998) and most of the large theropod skeletons showed no preserved gastroliths. The gastrolith record from large theropods like *Allosaurus* or *Tyrannosaurus* is very limited and mostly consists of single stones (Currie, 1997; Ayer, 2000). Furthermore, mass assemblages of theropod remains in predator traps, such as the Cleveland-Lloyd-Dinosaur-Quarry with at least 44 individuals of *Allosaurus* (Smith, 1997), produced virtually no gastroliths (Stokes, 1985). The Portuguese allosauroid *Lourinhanosaurus antunesi* which has at least 35 associated gastroliths (Mateus, 1998) is the only carnivorous theropod specimen worldwide that supports the hypothesis of theropods removing sauropod gastroliths.

Because of observations of regurgitation of the indigestible food remains in extant birds of prey, it can be argued that the theropod scavengers regurgitated the gastroliths soon after the food was digested. However, it is unlikely that all excavated theropod specimens died in exactly the same stage after regurgitation. Furthermore, we would expect to find such regurgitated clusters of stones in fine-grained sediments, especially in the vicinity of scavenged skeletons. Since such clusters are generally exceptionally rare in terrestrial sediments, random regurgitation is not plausible. It may be possible that regurgitation occurred near rivers (perhaps combined with drinking) and that the regurgitated stones might therefore be masked among normal river gravel. However this is speculative and does not explain the almost complete absence of gastroliths in theropod skeletons. Because of the lack of studies on the scavenging techniques on recent large carcasses with a gizzard, speculation will remain.

A reuse of gastroliths from carcasses by other individuals of the same taxon because of a general scarcity of suitable stones is considered to be implausible. A detailed discussion of this argument can be found in chapter VI.

Destruction of bones or stones by weathering and diagenesis

Bones are susceptible to destruction by weathering and diagenesis, in contrast to resistant gastroliths which are commonly composed of quartz. Most bones decompose beyond recognition in 10 to 15 years, and bones of small animals are especially susceptible to fast destruction (Behrensmeyer, 1978). A selective diagenetic destruction of gastroliths is hypothetically possible for certain rock types such as limestone, soft mudstone, and sandstone. However, a destruction of gastroliths composed of vein quartz (the most common rock type of gastroliths), is unlikely.

Aquatic transport

Taphonomic processes in an aquatic environment often eliminate gastroliths before burial (Taylor, 1993). Besides scavenging, aquatic transport is the most important process for the separation of gastroliths and bones and is therefore discussed in detail.

Marine transport

Gastroliths should be particularly well preserved in those animals that sank directly to the seafloor after death. In anoxic bottom water, these carcasses may not float to the surface (Schäfer, 1962), therefore having a better chance for fossilization. Scavengers, such as crocodiles, can also prevent the later rise of the carcass to the surface if they tear into carcasses and release accumulations of putrefactive gases (Weigelt, 1989). In normal waters, however, decomposition produces enough gas to cause the flotation of carcasses. Later, scavenging or rupturing of the body cavity releases the gas, causing the sinking of the carcass to the seafloor again. After the body cavity is open, it is likely that the stomach contents (and hence any gastroliths) would become separated from the carcass. If the stomach walls are still intact, the mass should be deposited on the sea-floor as a cluster, otherwise the stones may sink down individually. A fossil example of these processes is the plesiosaur specimen discussed by Everhart (2000). Buffetaut (1979) illustrated a fossil marine crocodilian with a disrupted body cavity and a stone cluster lying to one side, an indication that the carcass had come to a rest with its stomach hanging out (Taylor, 1993).

The drifting of vertebrate carcasses in different aquatic environments should be discussed briefly. It is appropriate to separate fluvial, lacustrine, and marine drifting. In rivers, drifting occurs normally for limited distances, often with several breaks in between. Only during flood events are carcasses transported fast and for long distances. Drifting in lakes is less interrupted, but winds can push the carcass to the shore, prohibiting sinking to the lake bottom. Marine drifting is slightly prolonged by the higher density of the salt water, although this factor may not have any measurable influence on floating behavior. On the other hand, higher waves may cause a more rapid sinking of the carcass.

The strong dermal armor of crocodilians allows a relatively long drifting time. Weigelt (1989) described an approximately two month old carcass of a large alligator where putrefying gases had finally caused the skin to burst. In the photograph (plate 26/C in Weigelt, 1989), no major damage or disarticulation is visible on the body, suggesting that gastroliths would still have been in place. Mummified carcasses, reported for instance for *Alligator mississipiensis* by Weigelt (1989), would also preserve gastroliths. Mummification is also relevant for large dinosaur carcasses (e.g., in hadrosaurs, Czerkas, 1997). Coe (1980) showed in a photograph of a comparably sized elephant cadaver on the East African savannah that quick desiccation (within three weeks after death) is possible even with large carcasses. Other examples are mummified carcasses of the Australian sea lions, *Neophoca cinerea* and *Phocarctos hookeri*, which are sometimes found on shore (Marlow, 1975). They often contain gastroliths and squid beaks in the stomach region of the carcass or on the ground underneath skeletons (Marlow, 1975).

Carcasses of seals, dolphins, and whales, animals with a similar body size to dinosaurs and plesiosaurs, can float several weeks before sinking (Schäfer, 1962). Even if the application of data from marine mammals might be of limited use for dinosaurs (Buffetaut, 1994), it indicates that dinosaurs could have drifted for long distances across the sea before they sunk to the bottom. This is supported by the fact that dinosaurs have been found in marine deposits (Buffetaut, 1994), for example the type specimen of *Niobrarasaurus coleii* (Nodosauridae) from the Cretaceous of the Western Interior Sea (Carpenter et al., 1995).

Fluvial transport of bones and gastroliths

The Hjulström diagram (e.g., Reineck and Singh, 1980) gives values for the mean flow velocity needed to mobilize, transport, and deposit stones of a certain size (Fig. 1). The flow velocity needed to transport bones is more variable. It is dependent on many factors such as density of the bone, shape, size, and post-mortem changes (e.g., by weathering). Richmond and Morris (1998) used an equation to estimate the flow velocity needed to transport dinosaur bones (Fig. 2). Despite the fact that Richmond and Morris (1998) did not take bone shape into account, their equation is used here to compare the flow velocities of bones with those of stones.

First, the fine grain fractions such as sand and grit will be removed with mean flow velocities of below 100 cm/s, a velocity, where the transportation of bones just starts. This means that all small grains might have been removed while all bones are still intact.

Second, if the minimum grain size commonly observed for gastroliths is estimated at 3 cm, significant higher flow velocities of 200 cm/s are needed to mobilize the stones. At this velocity, even large sauropod bones are moved, indicating transport of large dinosaur bones in conjunction with stones 3 cm in size. Subsequent deposition of bones together with stones is therefore possible, and these stones do not necessarily represent gastroliths. This has to be considered for some localities producing high numbers of isolated bones and stones (e.g., Dry Mesa Dinosaur Quarry).

Third, stones with more than 6 cm in size need very high flow velocities (above 300 cm/s) to be eroded. Such high velocities would easily transport very large sauropod bones. It is also possible that at velocities above 200 cm/s, all bones are mobilized but the stones are still in place. However, clusters of large stones in fluvial sediments are not common in dinosaur-rich strata, making this hypothesis implausible.

In contrast to the data of Richmond and Morris (1998), Fiorillo (1990) used data from Behrensmeyer (1975) and Korth (1979) to demonstrate that compact as well as porous bones with a length of 19 cm have a hydraulic equivalent of spheroidal quartz clasts with 10 cm in diameter. Compact bones of 9 cm length correlate with stones 3.5 cm in size whereas porous bones with 9 cm in length correspond with 2 cm stones (Fiorillo, 1990). If this model is correct, all large sauropod bones would still be present while the gastroliths are eroded by high energy currents.

All considerations are only valid for isolated bones. Bones still connected by muscles and tendons, partly covered by sediment, and carcasses not completely immersed in the river would need higher current velocities. Furthermore, the sediment suspension-load of a river increases the specific density and therefore may increase the carrying capacity of the fluid at a set velocity, allowing the mobilization of heavier objects than predicted from experimental studies.

For first hand observations of bone and stone transport in rivers, an experiment was conducted in the river Sieg near Bonn, Germany. Fresh chicken bones (rib cage and long bones) were used in the experiment. Bones and gravel of variable grain sizes (sand and small pebbles; <2-4 mm in size) were placed in a small river channel with a flow rate of approximately 175 cm/s. This velocity was calculated from the time that several swimming pieces of wood needed to cover a defined distance in the river. The bed of the river consisted mainly of cobble-sized stones, but also contained sediment in the pebble and sand fraction. The experiment was carried out in two parts. First, the bones and gravel were placed individually in the water current and the transport was recorded. Second, gravel was put inside the ribcage of the chicken and any changes in transport were studied.

It was observed that isolated long bones were not transported well in the current. Rather, they sank down to the bottom and nestled between cobbles. The trunk was transported fairly well and rolled over the surface rocks. During the second part of the experiment, the sand and pebbles inside the rib cage, simulating gastroliths in a heavily decayed carcass, were removed in a few seconds from the rolling carcass. However, once outside the trunk, the pebbles did not move anymore and even the largest fraction of the sand was deposited directly on the riverbed. Totally isolated trunk bones showed a different behavior: small ribs were almost floating in the water and transported with maximum current speed.

A conclusion from the experiment is that a large surface as well as a more angular shape of an object allows greater force of the flow velocity and therefore an easier transportation of the objects. Bones have a much lower density compared to rocks (specific density of bone: 1.47 g/cm^3, specific density of quartz: 2.65 g/cm^3) and are much more easily transported. Large isolated bones are much less likely to be transported than small and fragile bones (isolated or still connected in the trunk). The transport of chicken bones correlates to fine sand, not the regular gastroliths size of the living animals (2-5 mm). These results may not be completely transferable to other vertebrate groups such as crocodilians or dinosaurs because of the thin and hollow nature of bird bones.

This preliminary experiment does not present any proof for or against the connection between large fossil bones and associated stones. However, it seems possible that the transportation of large dinosaur bones correlated with the transportation of the stones associated with the bones. Further studies with large bones of modern animals (elephant, giraffe) should be conducted to reveal exact correlating sizes of bones and stones.

Post-mortem accumulation with bones

While separation of stones from bones by sedimentary processes appears likely, the reverse process is also possible. Stones might have been transported to the carcass by another medium. It is known from recent bird carcasses that wind-blown sand can enter a carcass from the ventral side, filling the abdominal and thoracic cavities (Schäfer and Craig, 1972). While such carcasses are normally easily recognized because the sediment in the body cavity is similar with the embedding matrix, the decrease in current velocity caused by the carcass may also accumulate sediment not found in the vicinity. The correct identification of sediment in carcasses which were transported following death is difficult. However, the subsequent transport is presumably a very rare event given the high mass of sediment-filled carcasses.

Larger carcasses may also act as sediment traps. Clarke and Pascoe (1985) reported an accumulation of sand and stones within the body cavity of a Risso's Dolphin (*Grampus griseus*) carcass stranded on a rocky shore. However, under normal conditions, the high-energy waves or currents needed to move stones into the carcass would either transport the same grain sizes around the carcass or cause the fast disintegration of the carcass, making its fossilization unlikely. The only plausible scenario for fossilization would be an infill by high-energy waters and a subsequent drop in water energy followed by final burial. Such a scenario is considered to be rare.

Another possibility for accumulations of stones with bones could be an authigenic origin of the stones. Chert for instance can form during diagenetic processes. Anyhow, such rocks should be clearly identifiable.

Taphonomic evidence from gastrolith-bearing fossil taxa

Some examples from the fossil record of gastrolith-bearing vertebrates are discussed to illustrate the taphonomic pattern of gastroliths. The discussed taxa represent groups where gastroliths are commonly reported and are not intended to embody a complete compilation. The results are summarized in Table 1.

Tangasaurids and other reptiles from Madagascar

Small Tangasauridae and other reptiles from the Upper Permian Sakamena Formation of Madagascar (*Hovasaurus*, *Barasaurus*, *Claudiosaurus*) frequently show large amounts of pebbles and sand in their abdominal region (Currie, 1981 and personal observations on approximately 20 specimens). All the specimens are preserved in finely laminated siltstone nodules. The abdominal cavity was the center of nodule formation (Currie, 1981). While the head and the tail of the larger *Hovasaurus* specimens are often not preserved, specimens of the smaller *Barasaurus* are completely enclosed in the nodules.

Hovasaurus specimens are commonly reported with large amounts of rounded and dull siliceous pebbles preserved in the body cavity (Piveteau, 1955; Currie, 1981; Baloge and Dutuit, 1982; Currie, 1982). More than 300 specimens of *Hovasaurus* are known and only two of them have no stones in the abdomen (Currie, 1981).

The frequency and abundance of pebbles in several taxa of small vertebrates from the Sakamena Formation is difficult to explain. While a special sedimentological process is implausible, a similar lifestyle could well be the reason. To some extent, the ingested grain sizes appear to be species-specific. On one hand, *Hovasaurus* gastroliths appear to be dominated by sand (0.5-2 mm) (Currie, 1981). On the other hand, sand size particles are rare in *Barasaurus* (personal observation on specimens in the Staatliches Museum für Naturkunde, Stuttgart, the Staatliches Museum für Naturkunde, Karlsruhe, the Carnegie Museum, Pittsburgh, and the Schloßmuseum Bertholdsburg, Schleusingen).

The gastrolith clusters do not always have the same position in the *Barasaurus* skeletons (personal observations). Stones can be found throughout the entire body cavity. This might be an indication that the carcasses were embedded in a state of advanced decomposition where the internal organs had already disintegrated but the body cavity was still held together by strong skin. Similar cases are reported from extant amphibians (Wuttke, 1983).

Extant and fossil crocodilians

Recent crocodiles are often reported to have gastroliths in their stomachs (e.g., Brander, 1925; Deflines, 1925; Dharmakumarsinhji, 1952; Corbet, 1960; Cott, 1961; Brazaitis, 1969; Peaker, 1969; Neill, 1971; Pooley and Gans, 1976; Webb et al., 1982; Hutton, 1987; Davenport et al., 1990). Unfortunately, the vast majority of the literature concerning gastroliths in crocodiles is anecdotal and scientifically superficial. Additionally, the function of crocodilian gastroliths has never been unambiguously clarified, thus complicating our understanding of gastrolith distribution in the fossil record. The most plausible hypotheses are ballast (e.g., Cott, 1961; but see Henderson, 2003), digestive help (e.g., Davenport et al., 1990), or accidental ingestion (e.g., Webb et al., 1982).

However, a few principles of gastrolith distribution in crocodiles are apparent. Davenport (1990) demonstrated that juvenile *Crocodylus porosus* deliberately ingest small stones and other available hard material. X-radiographs revealed that the stones were concentrated in a small area at the bottom of the stomach of unfed animals, but became dispersed throughout the stomach contents after a meal (Davenport et al., 1990). Stomachs of captive animals do often contain anthropogenic materials like coins, glass, broken pottery, bits of plastic, and tire-tube caps (Brazaitis, 1969). Large animals contained stones more frequently than juveniles (Cott, 1961). Individuals in stone-free habitats acquire stones later in life than youngsters living in areas where adequate amounts of stones are present (Cott, 1961). Of 153 examined individuals of *Crocodylus johnstoni*, 88.2% contained stones (Webb et al., 1982). Mean stone weight and the number of stones both increased with body length.

Teeth and bones of crocodilians are abundant in the fossil record. If the majority of extant crocodilians have gastroliths, it could be assumed that fossil crocodilian gastroliths are also common. However, this is not the case. Fossil crocodilian gastroliths are restricted to a few localities, usually low energy deposits, where they can be very abundant in articulated skeletons (e.g., Messel). Fossil gastroliths are absent from nearly all isolated crocodilian bone material.

Unambiguous finds of fossil crocodilians with gastroliths are known from several localities in Germany: Rott (Meyer, 1857), Messel (Keller and Schaal, 1992), Geiseltal (Weigelt, 1933; Weigelt, 1934; Ernst et al., 1996; Hellmund, 2001), and Holzmaden (Hölder, 1955; Urlichs et al., 1979). The gastroliths usually consist of quartz stones which are not related to the fine-grained matrix. Another articulated crocodilian with some small subrounded quartz and mica fragments in the abdominal area was reported from calcareous shales of lacustrine origin in the Green River Formation (Eocene) of Colorado (Langston and Rose, 1978).

Articulated skeletons of marine crocodilians, e.g., *Steneosaurus* from the Toarcian Posidonia shale, often contain gastroliths (e.g., Etzold and Maus, 1990). A partial skeleton of *Hyposaurus* with gastroliths is known from a Cretaceous fine-grained glauconite marl in New Jersey (Denton et al., 1997).

In summary, crocodilian gastroliths are commonly associated with articulated skeletons in fine-grained sediments and are virtually absent from all finds with isolated crocodilian remains.

Plesiosauria

The fine-grained matrix of the marine sediments in which plesiosaur remains usually occur makes identification of the gastroliths easy. Most, if not all, elasmosaurs had gastroliths whereas the short-necked, large-headed pliosaurs have rarely been reported with any significant number of gastroliths (Storrs, 1993). Many skeletons have gastroliths in an autochthonous position inside the rib cage (e.g., *Terminonatator ponteixensis*, Sato, 2003). For example, in an articulated skeleton of *Styxosaurus snowii* (formerly *Alzadasaurus pembertoni*), 253 quartzite gastroliths with a total mass of 8249 g were found immediately in front of the pelvic girdle in a concentrated area about 76 cm square and 18 cm deep (Welles and Bump, 1949). A weathered and therefore mostly displaced (only the right pelvic and pectoral paddles were relatively undisturbed) specimen of *Styxosaurus* sp. had gastroliths associated with rib fragments in the area of the central axis (Darby and Ojakangas, 1980). A photo shows a cluster of stones next to an articulated paddle.

Seeley (1877) reported approximately 9 liters of ovate and rounded stones, between 6 and 50 mm in diameter, found in the lower dorsal region of a *Mauisaurus gardneri*, the largest British plesiosaur find known at that time. Riggs (1939) described a *Hydralmosaurus serpentinus* (formerly *Elasmosaurus serpentinus*) specimen with gastroliths. The pectoral and pelvic girdles and the left paddle were articulated, whereas the vertebrae and most of the ribs were disarticulated. The stones were described as “scattered about the coracoid bones and the anterior parts of the paddle, several of them overlying the bones and indented into them” (Riggs, 1939). However, a photo taken during the excavation shows a defined cluster of stones between the paddle and the coracoid. In an almost complete, opalized specimen of the pliosaurid *Leptocleidus* sp., remains of teleost vertebrae were found inside the gut along with rounded gastroliths (Long, 1998). Cicimurri and Everhart (2001) reported a fish bone hash together with gastroliths and gastralia concentrated in a 1 by 2 meter area just behind the pectoral girdle of a nearly complete skeleton of an elasmosaurid plesiosaur. Other stomach contents associated with plesiosaur gastroliths were reported by Brown (1904) as well as by Martin and Kennedy (1988).

Heuvelmans (1968) stated that “sauropterygians would sink as soon as they died” because of the additional ballast from gastroliths. This idea is not plausible – the decaying gases would have produced enough uplift to more than compensate for the gastrolith mass (see chapter IV). To explain incomplete plesiosaur remains (the described specimen consists of two vertebrae, some ribs, gastralia, and 47 gastroliths), Everhart (2000) developed a plausible “bloating and floating” scenario on the basis of observations of modern marine mammal carcasses by Schäfer and Craig (1972). The elasmosaur specimen described by Everhart (2000) was a case of a floating carcass rupturing and spilling out bones and gastroliths. However, the plesiosaur fossil record suggests that sinking of the complete carcass was the normal case.

Sauropodomorph dinosaurs

Several sauropod and a few prosauropod dinosaurs have been found with associated gastroliths. The number of stones is usually low, in most cases below ten. A detailed description and review of the finds can be found in Christiansen (1996), in Whittle and Everhart (2000), and in chapter VI. The depositional environment is usually a floodplain, the sediments range from cross-bedded sandstones representing former riverbeds to fine-grained pond deposits in the overbank facies. Gastroliths are arranged along fluvial channels (e.g., *Seismosaurus*, Gillette, 1994; Lucas, 2000; Wings, in preparation-a) or found as clusters in low energy environments (e.g., *Cedarosaurus*, Sanders et al., 2001).

Taphonomic theory suggests that large animals may potentially be overrepresented in the fossil record (e.g., Behrensmeyer et al., 1979). On the other hand, the probability of preservation of complete specimens declines with larger size due to sedimentological, diagenetic and erosional processes. A very large carcass is less likely to be moved into a depositional environment with high sedimentation rates and has lower chances of being buried and protected from scavenging and weathering (Hunt et al., 1994a). Complete sauropod skeletons are exceedingly rare (Dodson, 1990) and are only known from a fraction of the 90 valid genera (McIntosh, 1990).

Gastroliths are elements of a carcass which are most easily separated due to either scavengers or post-mortem transport. However, autochthonous embedded skeletons should have a higher percentage of preserved gastroliths than skeletons from fluvial sediments. Such patterns are not noted in the sauropodomorph record, implying that the absence of gastroliths in most sauropodomorphs is not a taphonomic artifact (see chapter VI).

Theropod dinosaurs

There are two theropod taxa which are commonly found with gastroliths preserved *in situ*: the ornithomimid *Sinornithomimus* (Kobayashi et al., 1999; Kobayashi and Lü, 2003) and the basal oviraptorosaur *Caudipteryx* (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000). All fourteen well-articulated skeletons of *Sinornithomimus dongi* from China were found with clusters of gastroliths (Kobayashi et al., 1999; Kobayashi and Lü, 2003). A very similar taphonomic pattern can be observed in all described *Caudipteryx* skeletons which were found in fine-grained lake deposits of China (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000). The well-articulated skeletons show preserved gastralia and well-defined clusters of gastroliths within the body cavity.

In large theropods, however, gastroliths are rare and often consist of very few stones or just one isolated stone per specimen, e.g., *Allosaurus* (Ayer, 2000) or *Baryonyx* (Charig and Milner, 1997), probably indicating accidental intake. An exception is the holotype and only specimen of the allosauroid *Lourinhanosaurus antunesi*, with three small bone fragments (interpreted as food remains) and a minimum number of 35 gastroliths which form a cluster in the rib cage ventral to the eleventh dorsal vertebra (Mateus, 1998).

Fossil birds with focus on ratites

Gastroliths associated with fossil birds are known from Early Cretaceous to Quaternary sediments. Examples are the recently extinct solitaire (*Pezophaps solitaria*) (Newton and Clark, 1879) and dodo (*Raphus cucullatus*) (Fuller, 2000), the Early Cretaceous bird *Yanornis* (Zhou et al., 2004), the Miocene pelicaniform bird *Protoplotus beauforti* (Lambrecht, 1931) and the Miocene grebe *Thiornis sociata* (Lambrecht, 1933). Most are solitary individuals containing gastroliths deposited in low energy environments such as lakes. However, the best examples of bird gastroliths from the fossil record are those of ratites.

Many very large ratite species are recently extinct, such as the moas of New Zealand, the elephant birds of Madagascar, and mihirungs of Australia. Among these fossil species, gastroliths are exceptionally well documented for moas (see below), and are also known from mihirungs (Stirling, 1900; Rich, 1990). I have found no occurrence of gastroliths associated with elephant birds in the descriptive publications of *Aepyornis*. However, some authors have mentioned gastroliths in elephant birds, but did not cite the source of their information (e.g., Johnson, 1993), and a parsimonious interpretation of the digestive tract of ratites suggests that *Aepyornis* also had gastroliths.

Evidence for gastroliths is exceptionally good in several moa species. Many authors report skeletal remains associated with stones. See Anderson (1989), Twigg (2001), and Worthy and Holdaway (2002) for overviews. Three major habitats are known to have preserved authentic moa gastroliths: caves, swamps, and dunes. The swamp deposits were subject to seasonal drought and flooding, and therefore possibly only irregular visitation spots (Deevey, 1955). Quickly changing conditions may have also caused the entrapment of the moas (Twigg, 2001). The moa skeletons embedded in swamp deposits often contain not only gastroliths but the complete stomach contents with plant matter (e.g., Simmons, 1968; Burrows et al., 1981). Caves may have been used for shelter, but were probably in most cases places of accidental death (Twigg, 2001). Birds fallen into karst fissures may have been embedded *in situ* or may have been moved by water dispersion within the cave systems. Quarternary and Holocene sand dunes may have once been covered by forest and provided a habitat for the moa as well as a depositional setting for post-mortem burial (Twigg, 2001). However, authenticated moa gastroliths from these paleoenvironments represent only a small fraction of most moa gastroliths collections (Twigg, 2001). The majority of material consists of supposed gastroliths collected without any associated skeletal remains. Moa gastroliths have been found on raised beach terraces, mountain ridges, in loess, in rock shelters, as well as by lakes and rivers (Twigg, 2001). Hamilton (1892) reported clusters of moa gastroliths and plant matter without associated bones. Only one “decalcified” bone fragment was found with large amounts of pebbles (Hamilton, 1892). Interestingly, the moa gastroliths are mostly found in pockets or clusters; scattered stones are an exception.

Forbes (1892) reported moa skeletons found in two localities in the province of Otago. At the first locality, some of the large number of individuals had associated stomach contents (gastroliths and grass) as a cluster beneath the sternum. The stones, mostly white quartz, are smooth, rounded and a few cm in size (Forbes, 1892). He also states that the stones were mingled with the bones, and that an abundance of small gastroliths covered the surface when the first bones were found. The total amount of the gastroliths was “more than a cart-load”. No similar stones were found in the surrounding sediments without associated bones. At Glenmark, the second reported locality, articulated moa skeletons with gastroliths also covered by the sterna were found (Forbes, 1892).

In a Pliocene lake deposit in South Australia, several clusters of gastroliths were found within complete skeletons of the mihirung *Genyornis newtoni* (Stirling, 1900). In fact, clusters of stones at the soil surface led to the discovery of the skeletons. The skeletons were found by the presence of circular surface patches of stones, consisting of coarse sand and small siliceous pebbles with a smooth surface (Stirling, 1900). Stirling (1900) did not explicitly report any bird remains without associated gastroliths. The stones occurred scattered or in groups at various places in the fossil lake and were not naturally present in the embedded strata but were transported by the birds (Stirling, 1900). The associated gastroliths had an average mass of 0.4 kg and were often resting on the top surface of the sternum (Rich, 1990). The origin of the rock types was the great Central Australian plain formation (Stirling, 1900). No plant matter was found with *Genyornis* specimens (Rich, 1990).

The taphonomy of *Genyornis* as well as the other vertebrates from the lake deposit suggest that the animals were not transported by floods, but died *in situ* (Stirling, 1900). They may have been trapped in boggy places near waterholes, died from poisoned water or exhaustion (Stirling, 1900). However, miring on an unpredictable lake surface is considered to be the most likely scenario (Rich, 1990).

Fragmentary bird remains are relatively common in the Eocene fossil lagerstätte Geiseltal, but most of them cannot be identified. However, a well preserved specimen of the crane-sized flightless palaeognathous ostrich (Houde, 1986) *Palaeotis weigelti* (Geiseltal Museum Halle

4362) from the Eocene Geiseltal deposits in Germany, is the oldest record of gastroliths in ratites and the only bird from the Geiseltal with associated gastroliths. The specimen has four associated gastroliths reaching a maximum length of 2 cm (Ernst et al., 1996). *Diatryma*, a giant cursorial bird frequently found in the Geiseltal, had no gastroliths (H. Haubold, pers. comm. 2003). This is consistent with *Diatryma*'s supposed predatory way of life.

Interestingly, no gastroliths were reported from another articulated specimen of *Palaeotis weigelti* (Senckenberg Museum Frankfurt ME 1578) found in the Eocene Messel Pit in Germany (Peters, 1988). However, it is not clear if gastroliths were originally preserved with this specimen because all the matrix had been removed (including any possibly existing gastroliths) during preparation (G. Mayr, pers. comm. 2003). Among all other Messel birds, only two passeriform birds have been preserved with small amounts of sand in the body cavity (G. Mayr, pers. comm. 2003).

Evidence for bird gastroliths, presumably without any directly associated bones of the gastroliths-bearing animals, comes from cave deposits near Merkenstein in Austria (Mühlhofer, 1935). The majority of the isolated pebbles are interpreted as deposited as pellets of snowy owls. A comparison of the pebbles with recent galliform birds (*Tetrao* and *Lagopus*) supported the interpretation as former gastroliths (Mühlhofer, 1935). Another report of isolated gastroliths comes from Holocene and Pleistocene loess and peat deposits in Alaska which contain scattered grains of quartz but no bird bones (Hoskin et al., 1970). The grains were interpreted as bird gastroliths because of their rock type, size, roundness and polish (Hoskin et al., 1970). However, they have never been unambiguously identified as gastroliths.

Discussion and Conclusions

Classification of gastrolith finds

The term gastrolith is used to describe stones in a variety of taphonomic situations from isolated stones to *in situ* positions in articulated skeletons. This wide variety of scenarios makes it difficult to evaluate the importance of certain finds. A classification of gastroliths according to their sedimentological and taphonomical characteristics as well as their documentation may help to apply a standard for the description of new specimens. Such a classification should not only provide valuable information about the taphonomic history of the specimen, it also should help to easily identify significant gastrolith finds. It should contain all possible taphonomic scenarios and should be easy to apply and understand. Such information provides a basis for assessing the potential value of gastroliths as a source of paleobiological and taphonomic data.

A descriptive categorization of gastroliths based on practical observations of existing finds is proposed here (Table 2). The new classification separates six categories (Fig. 3-6), ranging from clusters of stones in articulated skeletons (category 1) to surface collected stones without associated bone remains (category 6). The only fully reliable taphonomic situation for gastrolith identification is category 1, when the stones are still enclosed in the rib cage (Fig. 3, 4). In all other situations, different transport mechanisms for the stones (and therefore a non-gastrolithic origin) are possible. For example, strong fluvial currents could have deposited stones in a carcass belonging to category 2. Category 6 has the lowest probability to represent authentic gastroliths. While the categories 1 and 2 comprise autochthonous and allochthonous specimens, stones in the categories 3 to 6 do always have an allochthonous origin.

Occurrence pattern of gastroliths within the fossil record

The identification of stones as former gastroliths is strongly dependent on the grain size of the surrounding sediment. In coarse sediments like conglomerates, gastroliths will most likely be overlooked, but in fine-grained sediments isolated clasts can easily be recognized.

The presence of avian gastroliths found *in situ* in bird fossils is consistent with taphonomic observations on recent carcasses. Many recent bird carcasses found on beaches and in dunes still contain gastroliths (Schäfer and Craig, 1972). The isolated finds of supposed moa gastroliths make a destruction of bone material and a sole survival of the gastroliths plausible for other taxa, including dinosaurs. Chapman (1884) reported dozens of finds of moa gastroliths, most of which were nevertheless associated with bones. While clusters of suspected moa gastroliths without associated bones are common, there are virtually no finds of autochthonous bones without associated gastroliths. Most exceptions can be explained by the slaughtering of birds by Maori hunters (Chapman, 1884).

The total mass of the gastroliths in *Genyornis* is small for a ratite similar in size to a large moa (Rich, 1990). Perhaps a fraction of the gastrolith mass was not preserved because of its small grain size: sand could have been blown away by wind. Another hypothesis is that the habitat was barren of other suitable stones for the birds.

Isolated bird gastroliths without associated bones are rare in the fossil record. This might be caused by collection bias or the lack of identification, but it is nevertheless a striking contrast to the exoliths (see chapter II) in dinosaur-rich sediments in the western USA which are commonly interpreted as gastroliths (see chapter VI).

Sauropodomorphs and moas are often compared because of their relatively small heads compared to body size (Bakker, 1980). Their gastrolith record, however, is very different.

While gastroliths associated with moa remains are common, stones associated with sauropodomorphs are exceptional rare. The depositional environment (e.g., moas miring in swamps versus sauropods transported in rivers) cannot completely explain this discrepancy. Several sauropodomorphs have been found in autochthonous settings, e.g., in the Howe Quarry (see chapter VI) or in the German *Plateosaurus* sites (Sander, 1992). The lack of gastroliths in autochthonous sauropods indicates the true absence of gastroliths in sauropods (see chapter VI).

Completeness of skeletal remains

Presumably, most gastroliths are destroyed or transported as a consequence of taphonomic processes prior to final burial. However, more research is needed to understand these processes. Preliminary research on gastrolith release from carcasses has shown that gastroliths can be separated from bird carcasses while all bones are still articulated (see chapter IV). Therefore, gastroliths should occur rarely in skeletons that were transported prior to burial or that are partly disarticulated.

The presence of gastralia can be an important indication for the post-mortem loss of gastroliths. Obviously, the taphonomic and diagenetic destruction of gastralia would be much easier than the destruction of gastroliths (e.g., easier transport by water and scavengers, dissolution of bone). Therefore, it can be hypothesized that gastroliths must be more common than gastralia and that for instance all sauropodomorphs (which were commonly believed to have gastroliths) should indeed have gastroliths when gastralia are present. This is not the case. Among sauropods, gastralia are exceptionally rare. Only one specimen of *Apatosaurus* has been shown to possess a full set of gastralia (Filla and Redman, 1994), but even these bones were recently interpreted as sternal ribs (Claessens, 2004). However, this specimen had no associated gastroliths. On the other hand, Michelis (2003) reported abundant gastralia from the Howe Quarry and also one cluster and more than 15 isolated gastroliths. Perhaps the vertical burial of the Howe Quarry sauropods provided the special conditions for the preservation of the gastralia (Michelis, 2003). That such a position would preserve gastroliths is also indicated by *Cedarosaurus* (Sanders et al., 2001).

The rare preservation of gastralia in sauropods contrasts the prosauropod record. In prosauropods, gastralia are more common than gastroliths (Sander, 1992; Claessens, 2004). Hence, the common presence of prosauropod gastralia is another indication that these animals did not have gastroliths, which should normally be preserved if the rather delicate gastralia are fossilized. In summary, there is no obvious correlation between the presence of gastroliths and gastralia in sauropodomorphs, but the presence of gastralia without associated gastroliths is an indication for the absence of gastroliths in the living animal.

The influence of the depositional environment

Within terrestrial sediments, the likelihood of preservation of gastroliths in association with vertebrate remains is relatively low due to scavenging and sedimentological processes discussed elsewhere. An exception to this rule is the record of mired animals (i.e., moas) that died *in situ* and were not scavenged. In low energy environments without extensive scavenging and with relatively fast burial, gastroliths have a high chance of being preserved *in situ*. Mummification is another excellent mechanism to preserve gastroliths.

Vertebrate fossils from stagnant marine depositional environments are often complete and large numbers of skeletons from certain clades (e.g., crocodilians, plesiosaurs) show associated gastroliths. There are generally a high number of gastrolith-using taxa preserved within Konservatlagerstätten. Messel, for instance, records beside the crocodilians mentioned above also two types of ant-eating mammals (*Eomanis* and *Eurotamandua*) with gastroliths (Koenigswald et al., 1981; Storch and Richter, 1992). This can be expected since complete animals are often preserved with soft tissues and stomach contents. It is peculiar, however, that virtually no gastrolith-bearing bird has been found in Messel. Since fossil birds with gastroliths have been found in lacustrine sediments (e.g., Zhou et al., 2004) this is probably an indication for the true absence of gastroliths in the bird species known from Messel. The otherwise common gastrolith occurrence within the Messel deposits might represent the actual gastrolith distribution within the ecosystem.

In summary, gastroliths in association with vertebrate remains are mainly restricted to stagnant aquatic environments: lacustrine, marine, or even swampy habitats. Fluvial environments have also produced several gastrolith-bearing skeletons (especially dinosaurs), but the total number of finds is generally much lower than in the other aquatic depositional settings. That this pattern is not an artifact caused by the lower number of gastroliths-using taxa preserved in fluvial sediments can be concluded from the fossil record of crocodilians, which are abundant in many fluvial (e.g., the Morrison Formation) as well as lacustrine (e.g., Messel) sediments but preserve gastroliths only in the latter.

Acknowledgements

This research is an essential part of my Ph.D. thesis. I am very grateful to my advisor Dr. Martin Sander for his constant support during my studies. I want to thank Denver Fowler and

Walter Joyce for stimulating discussions and their help to locate rare literature. Claudia Trögl helped with the chicken bone experiment in the river Sieg. Jonathan Codd, Mike Everhart, Denver Fowler, Martin Sander, and Lars Schmitz commented on early drafts of the manuscript. Financial support was provided by the "Graduiertenförderung Nordrhein-Westfalen", the Graduiertenkolleg "Evolution und Biodiversität in Raum und Zeit", the Jurassic Foundation, and my family.

References

Abel, O., 1935. Vorzeitliche Lebensspuren. Gustav Fischer, Jena, xv+644 pp.

Anderson, A., 1989. Prodigious birds. Moas and moa-hunting in prehistoric New Zealand. Cambridge University Press, New York, 238 pp.

Ayer, J., 2000. The Howe Ranch Dinosaurs/Die Howe Ranch Dinosaurier. Sauriermuseum Aathal, Aathal, 96 pp.

Bakker, R.T., 1980. Dinosaur heresy - dinosaur renaissance: why we need endothermic archosaurs for a comprehensive theory of bioenergetic evolution. In: D.K. Thomas and E.C. Olson (Editors), A Cold Look at the Warm-Blooded Dinosaurs. AAAS Selected Symp. no. 28. Westview Press, Boulder, pp. 351-505.

Baloge, P.A. and Dutuit, J.M., 1982. *Hovasaurus ranohirensis*, nouvel eosuchien de Madagascar. C. r. Séanc. Acad. Sci. Paris, 294: 683-686.

Beck, B.B., 1980. Animal Tool Behavior. Garland STPM Press, New York.

Behrensmeyer, A.K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolph, Kenya. Bulletin of the Museum of Comparative Zoology, 146(10): 473-578.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology, 4(2): 150-162.

Behrensmeyer, A.K., Western, D. and Dechant-Boaz, D.E., 1979. New perspectives in vertebrate paleoecology from a Recent bone assemblage. Paleobiology, 5: 12-21.

Bennett, M.R., Doyle, P. and Mather, A.E., 1996. Dropstones: their origin and significance. Palaeogeography, Palaeoclimatology, Palaeoecology, 121(3-4): 331-339.

Bird, R.T., 1985. Bones for Barnum Brown: Adventures of a Dinosaur Hunter. Texas Christian Univ. Press, Fort Worth, 225 pp.

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.

Boesch, C. and Boesch, H., 1984. Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. Primates, 25: 160-170.

Borsuk-Bialynicka, M., 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. Palaeontologica Polonica, 37: 1-64.

Brander, D., 1925. Stones in crocodile's stomach. Field, 146: 537.

Brazaitis, P., 1969. The occurrence and ingestion of gastroliths in two captive crocodilians. Herpetologica, 25(1): 63-64.

Brown, B., 1904. Stomach stones and food of plesiosaurs. Science, 20(501): 184-185.

Buffetaut, E., 1979. The evolution of the crocodilians. Scientific American, 241(4): 124-132.

Buffetaut, E., 1994. The significance of dinosaur remains in marine sediments: an investigation based on the French record. Berliner Geowissenschaftliche Abhandlungen, E, 13: 125-133.

Buffetaut, E. and Suteethorn, V., 1989. A sauropod skeleton associated with theropod teeth in the Upper Jurassic of Thailand: remarks on the taphonomy and palaeoecological significance of such associations. Palaeogeography, Palaeoclimatology, Palaeoecology, 73: 77-83.

Burrows, C.J., McCulloch, B. and Trotter, M.M., 1981. The diet of moas based on gizzard contents samples from Pyramid Valley, North Canterbury, and Scaifes Lagoon, Lake Wanaka, Otago. Records of the Canterbury Museum, 9(6): 309-336.

Calvo, J.O., 1994. Gastroliths in sauropod dinosaurs. Gaia, 10: 205-208.

Carpenter, K., Dilkes, D. and Weishampel, D.B., 1995. The Dinosaurs of the Niobrara Chalk Formation (Upper Cretaceous, Kansas). Journal of Vertebrate Paleontology, 15(2): 275-297.

Chapman, F., 1884. Notes on moa remains in the Mackenzie Country and other localities. Transactions and Proceedings of the New Zealand Institute, 17: 172-178.

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.

Chin, K., Tokaryk, T.T., Erickson, G.M. and Calk, L.C., 1998. A king-sized theropod coprolite. Nature, 393(6686): 680-682.

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.

Claessens, L.P.A.M., 2004. Dinosaur gastralia: origin, morphology, and function. Journal of Vertebrate Paleontology, 24(1): 89-106.

Clarke, M.R. and Pascoe, P.L., 1985. The stomach contents of a Risso's dolphin (*Grampus griseus*) stranded at Thurlestone, South Devon. Journal of the Marine Biological Association of the United Kingdom, 65: 663-665.

Coe, M., 1980. The role of modern ecological studies in the reconstruction of paleoenvironments in sub-Saharan Africa. In: A.K. Behrensmeyer and A.P. Hill (Editors), Fossils in the Making. Univ. Chicago Press, Chicago, pp. 55-71.

Corbet, P.S., 1960. The food of a sample of crocodiles (*Crocodilus niloticus*) from lake Victoria. Proceedings of the Zoological Society of London, 133(4): 561-572.

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., 1981. *Hovasaurus bolei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeontologica Africana, 24: 99-163.

Currie, P.J., 1982. The osteology and relationships of *Tangasaurus mennelli* Haughton (Reptilia, Eosuchia). Annals of the South African Museum, 86: 247-265.

Currie, P.J., 1997. Gastroliths. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 270.

Czerkas, S.A., 1997. Skin. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 669-675.

Darby, D.G. and Ojakangas, R.W., 1980. Gastroliths from an Upper Cretaceous plesiosaur. Journal of Paleontology, 54(3): 548-556.

Davenport, J., Grove, D.J., Cannon, J., Ellis, T.R. and Stables, R., 1990. Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*. Journal of Zoology (London), 220(4): 569-592.

Deevey, E.S., 1955. Paleolimnology of upper swamp. Records of the Canterbury Museum, 6(4): 291-344.

Deflines, E., 1925. Contenu de l'estomac d'un Crocodile. Cercle Zoologique Congolais, 2(3): 112.

Denton, R.K., Jr., Dobie, J.L. and Parris, D.C., 1997. The marine crocodilian *Hyposaurus* in North America. In: J.M. Callaway and E.L. Nicholls (Editors), Ancient Marine Reptiles. Academic Press, San Diego, pp. 375-397.

Dharmakumarsinhji, K.S., 1952. Large stone in stomach of crocodile. Journal of the Bombay Natural History Society, 50(4): p. 950.

Dodson, P., 1990. Sauropod palaeoecology. In: D.B. Weishampel, P. Dodson and H. Osmolska (Editors), The Dinosauria. University of California Press, Berkeley, pp. 402-407.

Emery, K.O., 1963. Organic transportation of marine sediments. In: M.N. Hill (Editor), The Sea. Ideas and Observations on Progress in the Study of the Seas. 3: The Earth Beneath the Sea. History. Wiley Interscience, New York, pp. 776-793.

Ernst, G., Kohring, R. and Rehfeld, U., 1996. Gastrolithe aus dem Mittel-Cenomanium von Baddeckenstedt (Harzvorland) und ihre paläogeographische Bedeutung für eine prä-ilsedische Harzinsel. Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg, 77: 503-543.

Etzold, A. and Maus, H., 1990. Exotische Blöcke und Gerölle im schwäbischen Lias. Jh. geol. Landesamt Baden-Württemberg, 32: 63-91.

Everhart, M.J., 2000. Gastroliths associated with plesiosaur remains in the Sharon Springs Member of the Pierre Shale (late Cretaceous), Western Kansas. Transactions of the Kansas Academy of Science, 103(1-2): 58-69.

Filla, J.B. and Redman, P.D., 1994. *Apatosaurus yahnahpin*: A preliminary description of a new species of diplodocid dinosaur from the Late Jurassic Morrison Formation of southern Wyoming, the first sauropod dinosaur found with a complete set of "belly ribs". In: G.E. Nelson (Editor), Wyoming Geological Association, 44th Field Conference, Guidebook, pp. 159-178.

Fiorillo, A.R., 1990. Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland County, Montana, U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecology, 81: 281-311.

Fisher, D.C., 1981. Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth. Palaeobiology, 7(2): 262-275.

Fleming, C.A., 1951. Sea lions as geological agents. Journal of Sedimentary Petrology, 21(1): 22-25.

Forbes, H.O., 1892. On the recent discovery of the remains of extinct birds in New Zealand. Nature, 45: 416-418.

Fuller, E., 2000. Extinct Birds. Oxford University Press, Oxford, 398 pp.

Gillette, D.D., 1994. *Seismosaurus*, the Earth Shaker. Columbia University Press, New York, 205 pp.

Hamilton, A., 1892. Notes on moa gizzard stones. Transactions and Proceedings of the New Zealand Institute, 24: 172-175.

Hayward, B.W., 1978. Moas; New Zealand's first rockhounds; evidence from Kawerua. Tane (Auckland University Field Club, Journal). Auckland, New Zealand., 24: 159-171.

Hellmund, M., 2001. Magensteine von Crocodiliern in der mitteleozänen Braunkohle des ehemaligen Tagebaues Mücheln-Westfeld (Geiseltal, Sachsen-Anhalt, Deutschland). Hallesches Jahrbuch für Geowissenschaften, Reihe B, Beiheft 13: 77-99.

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(8): 1346-1357.

Heuvelmans, B., 1968. In the Wake of the Sea-Serpents. Hart-Davis, London, 675 pp.

Hölder, H., 1955. Ein Jurakrokodil mit Magensteinen. Aus der Heimat, 63(6): 84-88.

Hoskin, C.M., Guthrie, R.D. and Hoffman, B.L.P., 1970. Pleistocene, Holocene and recent bird gastroliths from interior Alaska. Arctic, 23(1): 14-23.

Houde, P., 1986. Ostrich ancestors found in the Northern Hemisphere suggest new hypothesis of ratite origins. Nature, 324(6097): 563-565.

Hungerbühler, A., 1998. Taphonomy of the prosauropod dinosaur *Sellosaurus*, and its implications for carnivore faunas and feeding habits in the Late Triassic. Palaeogeography, Palaeoclimatology, Palaeoecology, 143: 1-29.

Hunt, A.P., Lockley, M.G., Lucas, S.G. and Meyer, C.A., 1994a. The global sauropod fossil record. Gaia, 10: 261-279.

Hunt, A.P., Meyer, C.A., Lockley, M.G. and Lucas, S.G., 1994b. Archeology, toothmarks and sauropod dinosaur taphonomy. Gaia, 10: 225-231.

Hutton, J.M., 1987. Growth and feeding ecology of the Nile crocodile *Crocodylus niloticus* at Ngezi, Zimbabwe. Journal of Animal Ecology, 56(1): 25-38.

Ji, Q., Currie, P.J., Norell, M.A. and Ji, S.-A., 1998. Two feathered dinosaurs from northeastern China. Nature, 393(6687): 753-761.

Johnson, D.L., 1989. Subsurface stone lines, stone zones, artifact-manuport layers, and biomantles produced by bioturbation via pocket gophers (*Thomomys bottae*). American Antiquity, 54: 370-389.

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.

Keller, T. and Schaal, S., 1992. Crocodiles: large ancient reptiles. In: S. Schaal and W. Ziegler (Editors), Messel. An Insight into the History of Life and of the Earth. Clarendon Press, Oxford, pp. 109-118.

Kobayashi, Y. and Lü, J.-C., 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. Acta Palaeontologica Polonica, 48(2): 235-259.

Kobayashi, Y., Lu, J.-C., Dong, Z.-M., Barsbold, R., Azuma, Y. and Tomida, Y., 1999. Herbivorous diet in an ornithomimid dinosaur. Nature, 402: 480-481.

Koenigswald, W.v., Richter, G. and Storch, G., 1981. Nachweis von Hornschuppen bei *Eomanis waldi* aus der "Grube Messel" bei Darmstadt (Mammalia, Pholidota). Senckenbergiana Lethaea, 61: 291-298.

Korth, W.W., 1979. Taphonomy of microvertebrate fossil assemblages. Annals of Carnegie Museum, 48: 235-285.

Lambrecht, K., 1931. *Protoplotus beauforti* ng n.sp., ein Schlangenhalsvogel aus dem Tertiär von W.-Sumatra. Wetenschappelijke Mededeelingen. Dienst. van den Mijnouw in Nederlandsch-Indie, 17: 15-24.

Lambrecht, K., 1933. Magensteine (Gastrolithen), Handbuch der Palaeornithologie. Verlag von Gebrüder Borntraeger, Berlin, pp. 817-821.

Langston, W.J. and Rose, H., 1978. A yearling crocodilian from the Middle Eocene Green River Formation of Colorado. Journal of Paleontology, 52(1): 122-125.

Lawick-Goodall, J.v., 1970. Tool-using in primates and other vertebrates. In: D.S. Lehrmann, R.A. Hinde and E. Shaw (Editors), Advances in the Study of Behavior. 3. Academic Press, New York, pp. 195-249.

Long, J.A., 1998. Dinosaurs of Australia and New Zealand and other animals of the Mesozoic era. University of New South Wales Press, Sydney, 188 pp.

Lucas, S.G., 2000. The gastromyths of "*Seismosaurus*," a Late Jurassic dinosaur from New Mexico. In: S.G. Lucas and A.B. Heckert (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 61-68.

Marlow, B.J., 1975. The comparative behaviour of the Australian sea lions *Neophoca cinerea* and *Phocarctos hookeri* (Pinnipedia: Otariidae). Mammalia, 39(2): 159-230.

Martin, J.E. and Kennedy, L.E., 1988. A plesiosaur from the late Cretaceous (Campanian) Pierre Shale of South Dakota: a preliminary report. Proceedings of the South Dakota Academy of Science, 67: 76-79.

Martin, R.E., 1999. Taphonomy. A Process Approach. Cambridge Paleobiology Series. Cambridge University Press, Cambridge, 508 pp.

Mateus, O., 1998. *Lourinhanosaurus antunesi*, a new Upper Jurassic allosauroid (Dinosauria: Theropoda) from Lourinhã, Portugal. Memórias da Academia de Ciências de Lisboa, 37: 111-124.

Matthew, W.D., 1908. *Allosaurus*, a carnivorous dinosaur, and its prey. American Museum Journal, 8(1): 2-5.

Maxwell, W.D. and Ostrom, J.H., 1995. Taphonomy and paleobiological implications of *Tenontosaurus-Deinonychus* associations. Journal of Vertebrate Paleontology, 15(4): 707-712.

McIntosh, J.S., 1990. Sauropoda. In: D.B. Weishampel, P. Dodson and H. Osmolska (Editors), The Dinosauria. University of California Press, Berkeley, pp. 345-401.

Meyer, H.v., 1857. Beiträge zur näheren Kenntnis fossiler Reptilien. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1857: 532-543.

Michelis, I., 2003. Vergleichende Taphonomie des Howe Quarry's (Morrison Formation, Oberer Jura), Bighorn County, Wyoming, USA. Ph.D. Thesis, University of Bonn, Bonn, 324 pp.

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.

Neill, W.T., 1971. The Last of the Ruling Reptiles, Alligators, Crocodiles, and Their Kin. Columbia University Press, New York, xx+486 pp.

Newton, E. and Clark, J.W., 1879. On the osteology of the solitaire (*Pezophaps solitaria,* Gmel.). Philosophical Transactions of the Royal Society of London, 168: 438-451.

Peaker, M., 1969. Active acquisition of stomach stones in a specimen of *Alligator mississippiensis* Daudin. British Journal of Herpetology, 4(4): 103-104.

Peters, D.S., 1988. Ein vollständiges Exemplar von *Palaeotis weigelti* (Aves, Palaeognathae). In: J.L. Franzen and W. Michaelis (Editors), Der eozäne Messelsee - Eocene Lake Messel. Courier Forsch.Inst. Senckenberg. 107, pp. 223-233.

Piveteau, J., 1955. Traité de Paléontologie, 5. Masson, Paris, 1110 pp.

Pooley, A.C. and Gans, C., 1976. The Nile Crocodile. Scientific American, 234(4): 114-119, 122-124.

Porkert, J. and Höglund, N., 1984. Zur Regulierung des Gritgehalts im Magen der Tetraoniden. Zeitschrift für Jagdwissenschaft, 30: 81-88.

Reineck, H.-E. and Singh, I.B., 1980. Depositional Sedimentary Environments. Springer, Berlin, 549 pp.

Rich, P.V., 1990. *Genyornis newtoni* Stirling and Zietz, 1896. A mihirung. In: P.V. Rich and G.F.v. Tets (Editors), Kadimakara: Extinct Vertebrates of Australia. Princeton University Press, Princeton, pp. 188-194.

Richmond, D.R. and Morris, T.H., 1998. Stratigraphy and cataclysmic deposition of the Dry Mesa dinosaur quarry, Mesa County, Colorado. Modern Geology, 22: 121-143.

Richter, G., 1988. Problems in the analysis of stomach contents of Eocene mammals from the Messel oil-shale layers. Courier Forschungsinstitut Senckenberg, 107: 121-127.

Riggs, E.S., 1939. A specimen of *Elasmosaurus serpentinus*. Field Museum of Natural History, Geological Series, 6(25): 385-391.

Rörig, G., 1903. Untersuchungen über die Nahrung unserer heimischer Vögel, mit besonderer Berücksichtigung der Tag- und Nachtraubvögel. Arbeiten aus der Biologischen Abtheilung für Land- und Forstwirthschaft am Kaiserlichen Gesundheitsamte, 4(1): 51-120.

Rörig, G., 1906. Magenuntersuchungen heimischer Raubvögel. Arbeiten aus der Kaiserlichen Biologischen Anstalt für Land- und Forstwirtschaft, 5(5): 237-265.

Rörig, G., 1909. Magen- und Gewölluntersuchungen heimischer Raubvögel. Arbeiten aus der Kaiserlichen Biologischen Anstalt für Land- und Forstwirtschaft, 7(4): 473-520.

Sander, P.M., 1992. The Norian Bonebeds of central Europe and their taphonomy. Palaeogeography, Palaeoclimatology, Palaeoecology, 93: 255-299.

Sanders, F., Manley, K. and Carpenter, K., 2001. Gastroliths from the Lower Cretaceous sauropod *Cedarosaurus weiskopfae*. In: D.H. Tanke and K. Carpenter (Editors), Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie. Indiana University Press, Bloomington & Indianapolis, pp. 166-180.

Sato, T., 2003. *Terminonatator ponteixensis*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Saskatchewan. Journal of Vertebrate Paleontology, 23(1): 83-103.

Schäfer, W., 1962. Aktuo-Paläontologie nach Studien in der Nordsee. Kramer, Frankfurt/M., 666 pp.

Schäfer, W. and Craig, G.Y., 1972. Ecology and palaeoecology of marine environments. University of Chicago Press, Chicago, xii, 568 pp.

Seeley, H.G., 1877. On *Mauisaurus Gardneri* (Seeley), an elasmosaurian from the base of the Gault at Folkstone. Quarterly Journal of the Geological Society of London, 33: 541-547 and plate l3.

Simmons, D.R., 1968. Man, moa and the forest. Transactions of the Royal Society of New Zealand, General, 2(7): 115-127.

Smith, J.B., 1997. Cleveland-Lloyd Dinosaur Quarry. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 126-128.

Stirling, E.C., 1900. The physical features of Lake Callabonna. Memoirs of the Royal Society of South Australia, 1(2): i-xv.

Stokes, W.M.L., 1985. The Cleveland-Lloyd-Dinosaur Quarry: Window to the Past, 1985-0-576-423. .U.S. Dept. of the Interior, Bureau of Land Management, Washington, 27 pp.

Stokes, W.M.L., 1987. Dinosaur gastroliths revisited. Journal of Paleontology, 61(6): 1242-1246.

Storch, G. and Richter, G., 1992. The ant-eater *Eurotamandua*: a South American in Europe. In: S. Schaal and W. Ziegler (Editors), Messel. An Insight into the History of Life and of the Earth. Clarendon Press, Oxford, pp. 211-215.

Storrs, G.W., 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. American Journal of Science, 293-A: 63-90.

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(1296): 163-175.

Twigg, J., 2001. Differentiating Moa Gizzard Stones. M.Sc. Thesis, University of Auckland, Auckland, 118 pp.

Urlichs, M., Wild, R. and Ziegler, B., 1979. Fossilien aus Holzmaden. Stuttgarter Beiträge zur Naturkunde, Serie C, 11: 1-34.

Webb, G.J.W., Manolis, S.C. and Buckworth, R., 1982. *Crocodylus johnstoni* in the McKinlay River area, N.T., part 1: variation in the diet, and a new method of assessing the relative importance of prey. Australian Journal of Zoology, 30(6): 877-899.

Weigelt, J., 1927. Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung. Max Weg, Leipzig, 227 pp.

Weigelt, J., 1933. Die Biostratonomie der 1932 auf der Grube Cecilie im mittleren Geiseltal ausgegrabenen Leichenfelder. Nova Acta Leopoldina (N.F.), 1(2,3): 158-174.

Weigelt, J., 1934. Die Geiseltalausgrabungen des Jahres 1933 und die Biostratonomie der Fundschichten. Nova Acta Leopoldina (N.F.), 1(4/5): 552-600.

Weigelt, J., 1989. Recent Vertebrate Carcasses and their Paleobiological Implications. University of Chicago Press, Chicago, i-xviii and 1-188 pp.

Welles, S.P. and Bump, J.D., 1949. *Alzadasaurus pembertoni*, a new elasmosaur from the Upper Cretaceous of South Dakota. Journal of Paleontology, 23(5): 521-535.

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 (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 75-82.

Wings, O., in preparation-a. Gastroliths or river gravel? The authenticity of *Seismosaurus* (Sauropoda, Dinosauria) stomach stones revisited.

Wings, O., in preparation-b. The identification of gastroliths: potentials and limits.

Worthy, T.H. and Holdaway, R.N., 2002. The Lost World of the Moa: Prehistoric Life of New Zealand. Indiana University Press, Indiana, 718 pp.

Wuttke, M., 1983. Aktuopaläontologische Studien über den Zerfall von Wirbeltieren. Teil I: Anura. Senckenbergiana lethaea, 64(5/6): 529-560.

Young, C.-C., 1964. New fossil crocodiles from China. Vertebrata PalAsiatica, 8(2): 189-210.

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.

Zhou, Z.-H. and Wang, X.-L., 2000. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China. Vertebrata PalAsiatica, 38(2): 111-127.

Zhou, Z.-H., Wang, X.-L., Zhang, F.-C. and Xu, X., 2000. Important features of *Caudipteryx* – evidence from two nearly complete new specimens. Vertebrata PalAsiatica, 38(4): 241-254.

Tables

Clade	**Frequency of bones**	**Frequency of gastroliths**	**Taphonomy: Frequency of category 1 cases**	**Most Common Depositional environment**	**Orientation during embedding and transport prior to burial**
Elasmosaurid plesiosaurs	High	High	Very high	Shallow marine	Often autochthonous in stagnant bottom waters
Crocodilians	Very high	Low	Generally low, but very high in the lake deposits from Messel	Lacustrine and river deposits; shallow marine forms known	Scavenging and transport common
Sauropod dinosaurs	High	Very low	Very low	Floodplain deposits	Scavenging and fluvial transport common, miring also known
*Sinornithomimu*s (Theropoda)	High (in specific sites)	Very high	Very high	Lake deposits?	After sinking of carcasses, quick burial on lake bottom?
Caudipteryx (Theropoda)	High (in specific sites)	Very high	Very high	Lake deposits	After sinking of carcasses, quick burial on lake bottom
Moas	High	High	High	Swamps, beaches, caves	Miring caused upright position
Hovasaurus	High	Very high	Very high	Great variety of aquatic settings	Settled probably upright in the mud

Table 1. The pattern of gastrolith occurrence in selected vertebrate taxa. All these vertebrate groups are common in the fossil record and often have associated gastroliths. The frequencies of occurrences were estimated from the literature. See text for details.

Category	Description	Examples from the fossil record
1	The stones are found as a cluster in the abdominal area, formerly occupied by the gastrointestinal tract, respectively in the closed ribcage of relatively complete, articulated skeletons; the documentation is complete and conclusive.	*Caudipteryx* (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000); *Cedarosaurus* (Sanders et al., 2001); *Sinornithomimus* (Kobayashi et al., 1999; Kobayashi and Lü, 2003); *Yanornis* (Zhou et al., 2004)
2	The stones are found near articulated bone material as a cluster or dispersed, but not necessarily in the abdominal cavity; documentation is available.	*Barosaurus* (Bird, 1985); *Seismosaurus* (Gillette, 1994)
3	The gastroliths are associated with isolated bones, documentation is available.	Sediments in the Dry Mesa Dinosaur Quarry (see chapter VI)
4	The stones are found as a cluster; accompanying skeletal remains are not known or not documented, but bones are present elsewhere in the strata.	Elasmosaurid plesiosaur discussed by Everhart (2000)
5	The stones are found *in situ* in the sediment. They are isolated, rounded and may be polished. Their lithology does not concur with the sediment matrix. No skeletal remains are associated, but the strata may contain bones elsewhere.	Lower Cretaceous sediments in the western USA (Stokes, 1987)
6	The stones exhibit the same features as in category 5, but are surface collected rather than found *in situ*.	Lower Cretaceous sediments in the western USA (Stokes, 1987)

Table 2. Taphonomic classification of gastroliths finds. See text for details.

Figures

Fig. 1. The Hjulström diagram with an enhanced detail showing the relationship between the stone size commonly regarded for gastroliths and the current velocity required for erosion, transport, and deposition (redrawn from Martin, 1999).

Fig. 2. Bone volume plotted against flow velocity (from Richmond and Morris, 1998). For details of equation, etc., see original reference.

Fig. 3. Example for gastrolith category 1: The Lower Cretaceous sauropod *Cedarosaurus* with a cluster of gastroliths *in situ* (from Sanders et al., 2001). For detailed discussion of the find see Sanders et al. (2001) and chapter VI.

Fig. 4. Another example for gastrolith category 1: The Lower Cretaceous theropod *Caudipteryx* of which several articulated skeletons with gastroliths were found in fine-grained lake deposits (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000). The figure has been modified from Ji et al. (1998), the gastrolith clusters are enhanced.

Fig. 5. Example for gastrolith category 2: The Upper Jurassic sauropod *Barosaurus* (Bird, 1985). The field note sketch shows that the bones are not completely articulated but still associated. The gastroliths (black dots) were found as a cluster next to the pubis and a rib. The figure has been modified from Michelis (2003).

Fig. 6. Another example for gastrolith category 2: The Upper Jurassic sauropod *Seismosaurus* (Gillette, 1994). The field sketch (from Gillette, 1994) shows the distribution of bones and stones at the *Seismosaurus* locality. The first cluster was found in the pelvic area, whereas the other stones were dispersed along sandstone channels.

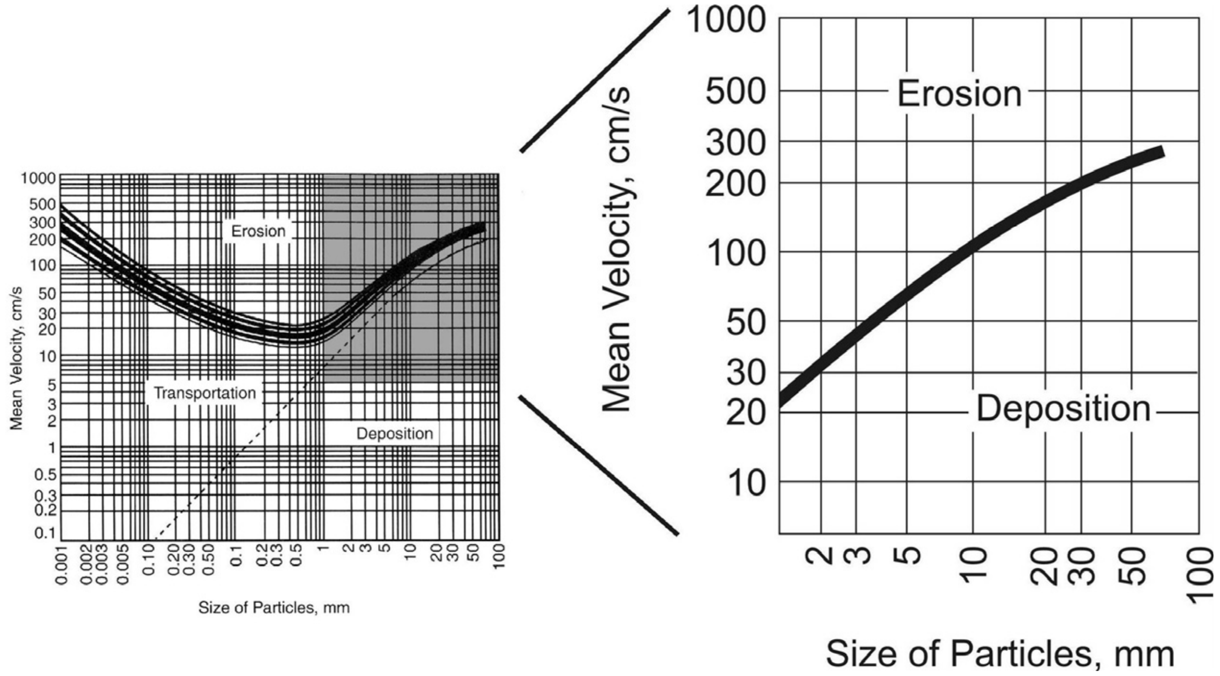

Mean Velocity, cm/s
1000
500
300
200
100
50
30
20
10
5
3
2
1
0.5
0.3
0.2
0.1
Erosion
Transportation
Deposition
0.001
0.002
0.003
0.005
0.10
0.20
0.30
0.50
0.1
0.2
0.3
0.5
1
2
3
5
10
20
30
50
100
Size of Particles, mm
Mean Velocity, cm/s
1000
500
300
200
100
50
30
20
10
Erosion
Deposition
2
3
5
10
20
30
50
100
Size of Particles, mm

Fig. 1.

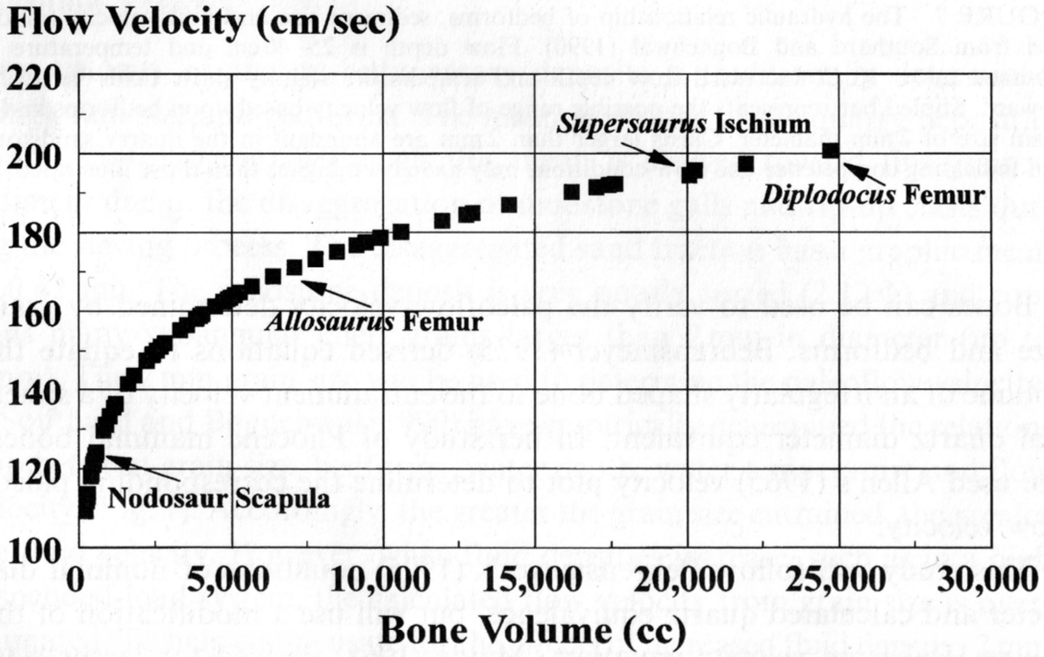

Flow Velocity (cm/sec)
220
200
180
160
140
120
100
0
5,000
10,000
15,000
20,000
25,000
30,000
Bone Volume (cc)
Supersaurus Ischium
Diplodocus Femur
Allosaurus Femur
Nodosaur Scapula

Fig. 2.

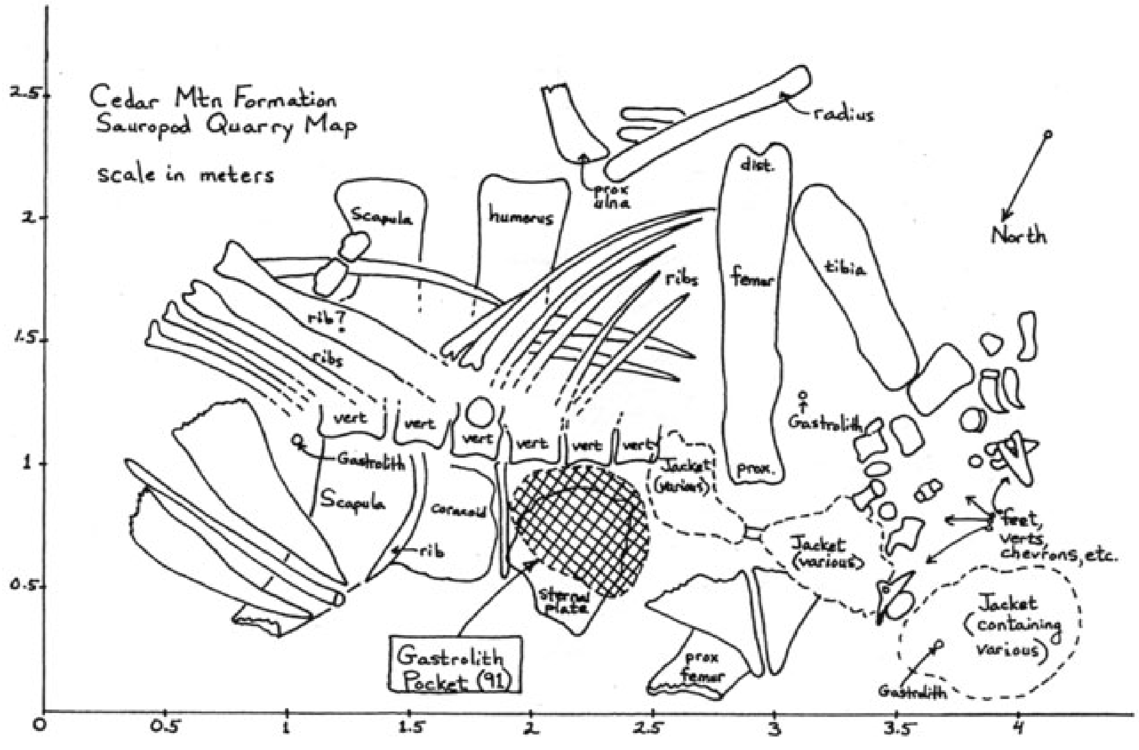
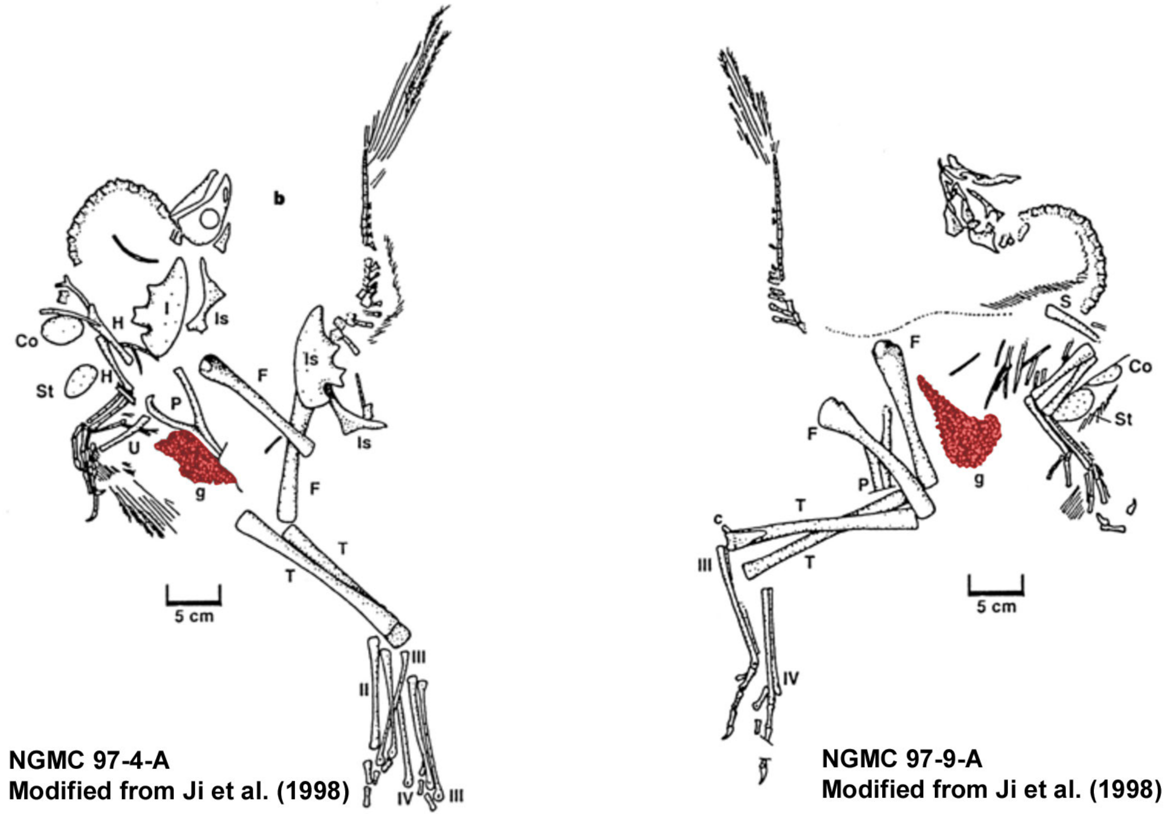

Cedar Mtn Formation
Sauropod Quarry Map
scale in meters
2.5
2
1.5
1
0.5
radius
prox ulna
Scapula
humerus
dist.
femur
prox.
tibia
North
ribs
rib?
ribs
vert
vert
vert
vert
vert
vert
Gastrolith
Scapula
Coracoid
rib
Sternal plate
Gastrolith Pocket (91)
Jacket (various)
Jacket (various)
Gastrolith
feet, verts, chevrons, etc.
Jacket (containing various)
Gastrolith
prox femur
0
0.5
1
1.5
2
2.5
3
3.5
4

Fig. 3.



NGMC 97-4-A
Modified from Ji et al. (1998)

NGMC 97-9-A
Modified from Ji et al. (1998)

Fig. 4.

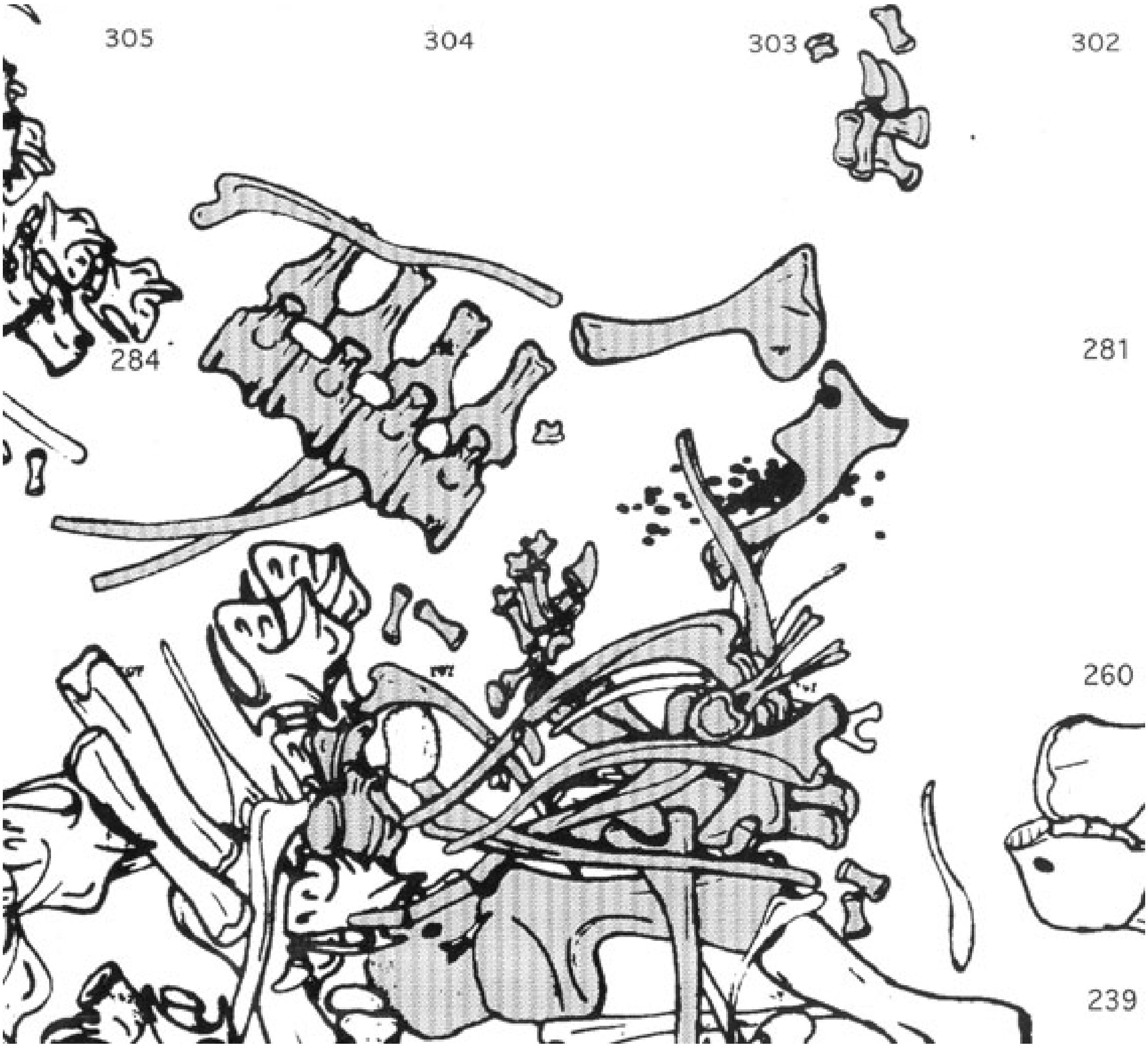


Fig. 5.

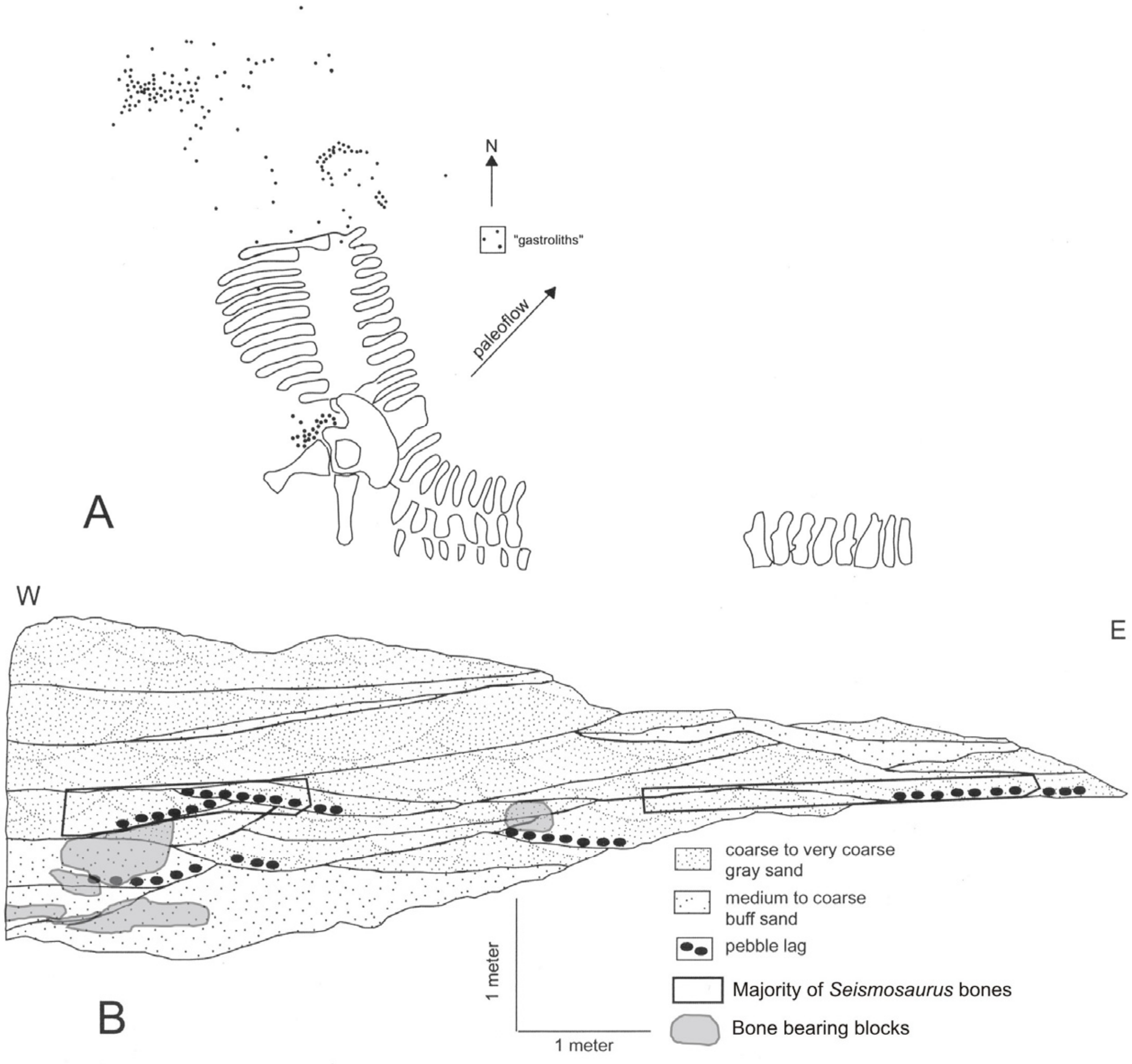

N
"gastroliths"
paleoflow
A
W
E
coarse to very coarse gray sand
medium to coarse buff sand
pebble lag
Majority of *Seismosaurus* bones
Bone bearing blocks
1 meter
1 meter
B

Fig. 6.

CHAPTER VI: Are gastroliths scarce in sauropod dinosaurs? Paleobiological, taphonomical, and sedimentological evidence from field work in Upper Jurassic dinosaur localities

Abstract

The sedimentological and taphonomical evidence from several classical Upper Jurassic sauropod dinosaur localities (Cleveland-Lloyd Dinosaur Quarry, Dry Mesa Dinosaur Quarry, Carnegie Quarry/Dinosaur National Monument, Howe Quarry, Como Bluff, and Bone Cabin Quarry) is reviewed in regard to the occurrence of suspected sauropod gastroliths and exotic clasts (exoliths). The results are compared with authentic finds of sauropod gastroliths (*Seismosaurus* and *Cedarosaurus*) as well as with other Upper Jurassic dinosaur sites.

There are very few sauropod finds with unambiguous gastroliths. The scarcity of pebbles in the fine-grained sediments of most of the localities suggests that only a small number of sauropods possessed gastroliths. The occurrence of a gastric mill in all sauropods is not supported from the taphonomical evidence. Exoliths which are abundant in the Lower Cretaceous of the western USA are virtually absent in Upper Jurassic sediments. Without an association to fossil bone, there is no convincing evidence that such clasts represent former gastroliths. It is more plausible that most of the surface-collected stones are weathering relicts of former conglomerate layers.

Introduction

One of the most interesting and enigmatic issues in the paleobiology of dinosaurs is the process of digestion and nutrition in sauropods. Because of their weak dentition, it is often assumed that all sauropods utilized gastroliths (stomach stones) in a gastric mill (Bakker, 1986; Currie, 1997). However, the authenticity of such gastroliths in sauropods is still debated.

On one hand, stones were indeed found with a variety of sauropods (see appendix I and for example Christiansen, 1996; Gillette, 1994; Janensch, 1929a; Sanders et al., 2001). On the other hand, given the abundance of reasonably complete sauropod fossils world-wide, the scarcity of associated gastroliths is striking and raises the question if their absence can be explained by taphonomical processes alone. This results in two opposing viewpoints regarding sauropod gastroliths: one group of authors who ignore most of the finds (e.g., Calvo, 1994; Lucas, 2000); and another group who firmly believe in the presence of gastroliths and a taphonomical bias (e.g., Christiansen, 1996).

The main aim of this study is to determine how common sauropod gastroliths are in the fossil record. Exoliths (stones which are not related to local sediments regarding rock type and size and may represent former gastroliths, see chapter II) are also considered. Such exotic stones are common in Lower Cretaceous sediments but are very rare in Upper Jurassic sediments (Stokes, 1987). The solution of the problem therefore appears to be the frequency of gastroliths occurrence in the classical Morrison Formation (Upper Jurassic) dinosaur localities in the western USA.

Methods

For this study I have visited documented gastrolith sites, classical North American outcrops of Upper Jurassic and Lower Cretaceous strata (Fig. 1), as well as some Jurassic sauropod localities world-wide. Additionally, I studied the taphonomy of numerous sauropod finds regarding a potential association of gastroliths and the possible reasons for their absence. Field work and first hand observations were conducted at many Morrison sites, including the Carnegie Quarry in the Dinosaur National Monument, Cleveland-Lloyd Dinosaur Quarry, Como Bluff and Bone Cabin Quarry, Dry Mesa Dinosaur Quarry, Howe Quarry, and Howe Stephens Quarry. These sites were complemented with Jurassic localities near Lourinhã in Portugal and in the Chubut region in Argentina.

The fieldwork focused on the comparative study of available sediments, the sauropod finds at these localities, their taphonomy, and the prospection for exotic stones in and around the quarries. The taphonomy of *in situ* sauropod bones at Dinosaur National Monument was studied regarding possible gastrolith loss.

Literature data was collected for the Tendaguru sauropod finds in Tanzania. Visits in relevant museum collections (American Museum of Natural History, College of Eastern Utah Prehistoric Museum Price, Denver Museum of Natural History, New Mexico Museum of Natural History, Carnegie Museum Pittsburgh, Staatliches Museum für Naturkunde Stuttgart, Sauriermuseum Aathal, Yale Peabody Museum) were necessary to study the available gastrolith material and the general bone preservation at each site. The study of loan material (e.g., Tendaguru gastroliths from the Museum für Naturkunde Berlin) amended the research. The available old field notes and publications about the quarries were studied regarding sedimentology, taphonomy, and fauna lists.

Other fossil vertebrate skeletons with gastroliths have shown that the stones are often preserved in the body cavity or at least in close association with the bone (see chapter V and for example: Currie, 1981; Darby and Ojakangas, 1980; Sanders et al., 2001; Whittle and

Everhart, 2000). Hence, the null hypothesis is that if all sauropod dinosaurs required stomach stones for food processing, as suggested by many authors (e.g., Bakker, 1986; Currie, 1997), then many relatively complete skeletons should have associated gastroliths. Autochthonous and parautochthonous skeletons in fine-grained sediments are especially relevant for such observations. Thus, a special focus was given to localities which produced articulated or well-associated sauropod skeletons. Furthermore, the field sites and the collection material of two of the best sauropod dinosaurs with gastroliths preserved *in situ* were examined: *Seismosaurus* and *Cedarosaurus*.

It is important to distinguish between true gastroliths and exoliths. The exoliths commonly found on the surface of the strata in question, are frequently polished and were believed to represent the gastroliths of sauropods where all bone material has been destroyed (Bakker, 1986) and hence are often called “gastroliths” by laymen (Stokes, 1942; Stokes, 1987). However, because the name “gastroliths” comprises an *a priori* assumption (there is no evidence that these stones are indeed former gastroliths), the name should not be applied to these exotic stones (Wings, in preparation-a). Because other terms like “dropstones” or “erratics” were not used until now for the exotic stones in question, the new term “exolith” was proposed in chapter II. Exoliths are defined as stones which are not in agreement with the hydrodynamic characteristics of the embedding sediment, e.g., stones in a fine-grained matrix. Exoliths could have been, but not necessarily are, gastroliths.

To set the framework and to understand the context between stratigraphy, sedimentology, taphonomy, taxonomy, and the appearance of gastroliths and exoliths, detailed descriptions of the localities were compiled. The localities are discussed in alphabetical order and the data is summarized in Table 1.

Carnegie Quarry, Dinosaur National Monument (DNM)

The quarry face of the Dinosaur National Monument (DNM) Quarry, located near Vernal in Utah, provides an excellent possibility to study several articulated sauropods finds *in situ*. Like many other dinosaur localities in the Morrison Formation, the DNM sediments were formed by fluvial channel deposits (e.g., Fiorillo, 1994; Lawton, 1977). The main bone layer is composed of channels with sand and grit-sized sediments, described in detail by Lawton (1977). Fiorillo (1994) characterized the sediment as a coarse, partially conglomeratic sandstone. In marginal areas, olive-green to violet siltstones which are separated from the sandstones by an erosional surface, possibly represent the river banks (Michelis, 2003).

Initially, it was estimated that the remains of approximately 60 dinosaurs were deposited during 3 or 4 depositional cycles (Dodson et al., 1980; Fiorillo, 1994). Later, Chure (1997) reported several hundred dinosaurs belonging to 10 genera. Among them, a number of reasonably complete skeletons of *Camarasaurus*, as well as those of *Dryosaurus* and *Camptosaurus,* were found. After each cycle, a hiatus with a drop of the current energy and partly with the drying out of the channel occurred (Lawton, 1977). Evidence for scavenging can only be found on very few bones.

The articulation of the skeletons varies greatly. Isolated bones to complete articulated skeletons are known (Dodson et al., 1980; Lawton, 1977). Less heavy skeletal elements drifted further and some elongated bones are deposited parallel to the water currents (Lawton, 1977). The bones show only little weathering (stage 0 and 1 sensu Behrensmeyer, 1978; Fiorillo, 1994, and Wings, personal observations on the DNM specimens at the Carnegie Museum, Pittsburgh, 2002).

Gastroliths and exoliths are completely absent from the Carnegie Quarry (personal observations 2002; D. Chure, pers. comm. 2002). No stones were found associated with several rather complete skeletons, including the Carnegie Museum and USNM *Camarasaurus* skeletons as well as the Carnegie *Dryosaurus* and *Camptosaurus* (D. Chure, pers. comm. 2002). The total absence of “anything that might be called gastroliths” from the large accumulation of bones at DNM was already noted by Stokes (1942).

The examination of the sediments around the bones in the quarry face did not reveal any potential gastroliths. Furthermore, field work in the Upper Jurassic outcrops near DNM has not produced any pebbles in the size commonly assumed for sauropod gastroliths (>3 cm in diameter). The largest siliceous pebble discovered in the sediment layer which contained the richest bone deposits was approximately 25 mm in length. Nevertheless, pebbles of this size are exceptionally rare, as the vast majority of the siliceous pebbles in the conglomeratic sandstones has a diameter below 10 mm. However, larger (up to 10 cm in diameter) angular to rounded reworked mudstone and limestone clasts were also reported, indicating a rather short transport distance (Lawton, 1977; Michelis, 2003).

Cleveland-Lloyd-Dinosaur-Quarry (CLDQ)

The CLDQ is located in Emery County, Utah and can stratigraphically be assigned to the lower part of the Brushy Basin Member of the Morrison Formation. Most of the bones were found in uniform calcareous smectitic mudstone layers (Richmond and Morris, 1996). A personal examination of the outcrop revealed no signs of channel deposits or any exoliths in the mudstone layers. The only pebble-rich stratum in the vicinity is the basal conglomerate of the Cedar Mountain Formation, stratigraphically situated several meters above the quarry.

Seventy five percent of the dinosaur remains from CLDQ belong to the theropod *Allosaurus* (Madsen, 1976). Sauropod remains are relatively rare: only two or three individuals of *Camarasaurus*, and some elements belonging to possibly more than one non-camarasaurid sauropod were found (Madsen, 1976). The theropod-dominated fauna of the CLDQ indicates its taphonomic origin as a predator or scavenger trap (Dodson et al., 1980). While drinking or hunting at a floodplain pond, the dinosaurs became entrapped in the cohesive and adhesive mud (Richmond and Morris, 1996). The site was also considered a spring-fed pond or seep where the animals sank into the volcanic ash-rich mud before scavenging could take place (Bilbey, 1999). For more information, the reader is referred to several detailed studies about the CLDQ (e.g., Bilbey, 1998; Bilbey, 1999; Richmond and Morris, 1996).

During the removal of 10,000 bones from various species at the CLDQ, only two exotic stones were noted by Stokes (1987) and described as “not typical gastroliths” (possibly an indication for a lack of polish). The repository of the two exoliths is unknown.

Como Bluff and Bone Cabin Quarry

Due to the similarity of depositional environments and their geographical proximity, Como Bluff and the Bone Cabin Quarry (BCQ), both located in northern Wyoming, are discussed together. The sediments represent the upper part of the Morrison Formation (Schmude and Weege, 1996). Unfortunately, no general synopsis of the sedimentology and taphonomy of Como Bluff and the BCQ has yet been published. New excavations by Western Paleontological Laboratories, Inc. in the BCQ area will supply more sedimentological and taphonomical data for the interpretation (K. Cloward, pers. comm. 2003).

The sediments are smectitic claystones, sandstones (occasionally chert-rich), and horizons of caliche, while non-swelling shales dominate in the upper parts of the Morrison Formation (Wings, personal observations 2002). The base of the Cloverly Formation starts with a prominent chert pebble conglomerate.

Como Bluff represents a complex fluviatile and lacustrine floodplain with a seasonal wet-dry cycle (Dodson et al., 1980). The depositional environment of the BCQ can also be characterized as a braided river system with seasonal flooding as well as periods of drought or a dry season. The flooding is interpreted as not catastrophic but more typical of high water run off after storms and similar events (K. Cloward, pers. comm. 2003).

The bones are not confined to a specific layer but can occur in neighboring channels. While the exact number of sauropod individuals found at Como Bluff is unclear, at least five types of sauropods have been identified (Breithaupt, 1997b). A short synopsis about the rich vertebrate fauna of the BCQ (including 44 sauropods) can be found in Breithaupt (1997a). The finds consist of mostly rather complete individuals, usually juveniles. The specimens are not scattered over large areas but are rather confined. The sediments in a part of the BCQ West area were probably deposited by normal river flows. They contain numerous shed teeth from crocodiles, allosaurids, and sauropods together with heavily eroded and possibly redeposited bones. Many teeth were trapped behind and underneath the larger bones (K. Cloward, pers. comm. 2003). In other areas of the BCQ, the discovery of skin impressions of a stegosaur, fragile skull parts from pterosaurs, and articulated crocodile scutes indicates a very rapid burial with a subsequent dry period after the event and little disturbance (K. Cloward, pers. comm. 2003).

It is interesting that scavenging was repeatedly reported from both sites. Matthew (1908) was the first who reported “scored and bitten off” bones of some herbivorous dinosaurs including an incomplete ?*Apatosaurus* skeleton. Toothmarks on sauropod bones found in the Bone Cabin Quarry probably indicate a late stage scavenging (Hunt et al., 1994). This involves that articulated portions of sauropod carcasses were exposed long enough to allow extensive alteration by theropods (Hunt et al., 1994).

Bakker (1986) also reported the association of sauropod bones and carnosaur teeth from Como Bluff. During recent excavations in the BCQ area, very little evidence of predation was discovered on the bones (K. Cloward, pers. comm. 2003). Only one femur of a camarasaurid sauropod appeared to have been scavenged. No gastroliths were found *in situ* with the articulated skeletons that were recently excavated, and no exoliths were found in the channel lag material, or isolated on the surface of the relevant strata.

Dry Mesa Dinosaur Quarry (DMDQ)

DMDQ is located on the Uncompaghre Plateau, Mesa County, western Colorado, and is stratigraphically situated in the Brushy Basin Member of the Morrison Formation. The fluvial deposits consist of a broad sandstone channel incised into mudstones representing overbank deposits (Britt and Curtice, 1997) or, in an alternative interpretation, a lacustrine zeolite lithofacies (Richmond and Morris, 1998). The so-called “Christmas Tree Conglomerate”, a colorful pebble-rich very coarse- to medium-grained sandstone, is found stratigraphically 1 m below the quarry floor (Richmond and Morris, 1998). The depositional environment may have been a relatively straight bedload system (Richmond and Morris, 1998).

An immense accumulation of well-preserved bones was found at the base of crossbeds at the bottom of the river channel (Britt and Curtice, 1997). The bone accumulation has possibly resulted from a mass mortality of dinosaurs during a major drought and a subsequent cataclysmic flash flood, with high flow velocities around 200 cm/s (Richmond and Morris, 1998). Geological and taphonomical characteristics show that the transport distance of the bones prior to burial was mainly short and that the bones represent an autochthonous accumulation (Richmond and Morris, 1998). Only in some cases, taphonomy suggests a long transport distance in fast flowing channels of water (K. Stadtman, pers. comm. 2003).

The DMDQ has produced an exceptionally high number of bones (>4000 elements) and yielded the most diverse dinosaur fauna from any quarry in the Morrison Formation (Britt and Curtice, 1997). Most bones are isolated and cannot be assigned to specific individuals. Some articulated vertebral column segments and one partially articulated juvenile diplodocid were discovered. In two instances, posterior dorsal vertebrae, pelvic bones, and several caudal vertebrae were found in articulation (K. Stadtman, pers. comm. 2003).

The minimum number of sauropod individuals found in the DMDQ is estimated to be more than 20. There are more than five valid sauropod genera represented, including *Diplodocus*, *Apatosaurus*, *Supersaurus* (not disputed in print, may be a giant *Diplodocus*), cf. *Barosaurus*, *Camarasaurus*, *Brachiosaurus*, and *Haplocanthosaurus.* Another genus, *Dystylosaurus,* may not be valid but has not been disputed to date in print (K. Stadtman, pers. comm. 2003).

During 30 years of excavation in the DMDQ, about 500–600 exoliths have been found randomly in the bone deposit (K. Stadtman, pers. comm. 2003). A part of these stones is retained in the collections of Brigham Young University in Provo, Utah. The bone deposit was somewhat bowl shaped, and is up to 1.5 m in depth in the center where collecting started. In the early years of work, exoliths were more common than in the thinned horizons worked now. However, stones have never been found in relation to an articulated skeleton. Also, there has never been a cluster found. Pebbles found *in situ* in the sediments always exhibit a high polish and are mostly composed of chert. The most common exolith size is around 4 cm, but the collections at Brigham Young University also include smaller sizes (K. Stadtman, pers. comm. 2003).

A personal search for exoliths in the area revealed no pebbles in the outcrop and on the surface of the excavation dumps. The siliceous clasts in the conglomeratic parts of the sandstone channels are much smaller (maximum sizes around a few mm) than any exoliths in the collections. Only clay balls occurring occasionally in the sandstones can reach a few centimeters in size.

Howe Quarry

The Howe Quarry is situated in the Bighorn Basin near Greybull, Wyoming, and represents strata of the Morrison Formation with an estimated age of 145.7 Ma (Michelis, 2003).

The bones were found in shales, mudstones, and siltic sediments. The main bone-producing stratum was an olive-green, inhomogeneous mudstone of variable thickness (Michelis, 2003). All these sediments represent water flows of insufficient energy to transport the heavy sauropod carcasses (Ayer, 2000; Michelis, 2003). The most plausible scenario is an autochthonous origin of the assemblage with the sauropods having been trapped in sticky sediments (Ayer, 2000; Michelis, 2003). Michelis (2003) proposed a selective process where it was only the physically weakened animals that were mired in the mud of a waterhole within a levee of the river.

Scavenging is indicated by abundant theropod (*Allosaurus*) teeth and tracks, whereas direct evidence such as tooth marks is very rare (Michelis, 2003). Predators and scavengers were probably also responsible for some disarticulation of the skeletons. The weathering of the bones prior to burial was very limited (weathering stages 0 or 1, Behrensmeyer, 1978), showing a fast burial or mummification (Michelis, 2003). The weathering period before burial is estimated at no more than three to four years, but was usually much less (Michelis, 2003). Some 2400 bones of at least 25 partial sauropod skeletons were found, with the genus *Barosaurus* dominating the fauna. Bird (1985) reported 64 gastroliths, found as a single cluster in the abdominal area of a *Barosaurus* skeleton (Fig. 2, 3). These stones were sent to the American Museum of Natural History in New York, but could not be located during a recent visit to the collections (Michelis, pers. comm. 2000). Michelis (2003) reported at least 15 exoliths found *in situ* during new excavations in the How Quarry in 1990 and 1991. Another interesting specimen is a single quartz pebble that was found embedded in a carbonized patch in the sandstone matrix with a size of approximately 2 cm (Fig. 4). The carbonized material may represent former herbaceous stomach contents. All stones retrieved during the new excavations are stored in the Sauriermuseum Aathal in Switzerland. During field work by the author in 2002, exotic pebbles were found only on the surface in the vicinity of the quarry. An examination of the quarry walls revealed no appropriate pebbles *in situ*.

Howe Stephens Quarry

In the vicinity of the Howe Quarry, some other dinosaur sites were found. These sites, collectively named Howe Stephens Quarry (HSQ), are about 450 m away from the original Howe Quarry and stratigraphically some meters above the latter. The HSQ represents a different taphonomy. Most commonly found are channel sandstones, often containing plant debris. The site is interpreted as fluvial deposits formed during a catastrophic flood which may have transported the carcasses for some distance before their final deposition (Ayer, 2000). The carcasses were then covered rapidly by river sediments (Ayer, 2000).

The HSQ also yielded an enormous concentration of articulated skeletons: at least ten different dinosaur specimens were found (Ayer, 2000). Two relatively complete articulated sauropods were found without any associated gastroliths (K. Siber, pers. comm. 2001). Another solitary sauropod skeleton was found in fine-grained crevasse splay sediments of the HSQ “A-Pit” (Michelis, 2003), indicating again very low transport velocity of the water.

In the sediments at the excavation sites, only about a dozen exoliths and gastroliths have been recovered and preserved in the Sauriermuseum Aathal (Ayer, 2000). Among them is the *Allosaurus* specimen “Big Al Two”, having preserved probable stomach contents including a relatively large gastrolith (Ayer, 2000). In contrast to the rareness of exoliths *in situ*, hundreds of exoliths can be found on the surface at certain spots in the vicinity of the two quarries (Ayer, 2000 and personal observation, 2002). However, they are most probably a result of long term weathering from conglomerates in the uppermost Morrison Formation and especially in the Cloverly Formation (H.J. Siber, pers. comm., 2002) or may represent weathered remains of glacial deposits.

Additional sites

Five additional sites will be discussed briefly for supplementary information about authentic sauropod gastrolith finds and sauropod lagerstätten similar in depositional environment and age. For comparison with the North American sites, three other regions rich in Jurassic sauropod fossils were chosen: Lourinhã in Portugal, the Chubut province in Argentina, and Tendaguru in Tanzania. Together with Lourinhã, the North American *Cedarosaurus* site and *Seismosaurus* site provided excellent verification for sauropod gastrolith existence.

Cedarosaurus site

A set of 115 clasts with a total mass of 7 kg and a total volume of 2703 cm^3 was associated with the holotype skeleton of the brachiosaurid *Cedarosaurus weiskopfae* in the Yellow Cat

Member of the Cedar Mountain Formation (Lower Cretaceous) of eastern Utah (Sanders et al., 2001).

The embedding sediment was a maroon mudstone without inclusions or lenses of other materials, indicating a low energy flood-plain environment. The gastroliths are composed of cherts, sandstones, siltstones, and quarzites. Many stones show a metallic (probably hematite) coating. The skeletal position indicates that the carcass came to rest in an upright position with the gastroliths preserved *in situ* (Sanders et al., 2001). All but three of the stones were found in a cluster covering an area of approximately 0.5 x 0.5 x 0.25 m (Fig. 5). The gastroliths are stored in the Denver Museum of Natural History.

Seismosaurus site

This locality (Morrison Formation, Brushy Basin Member) near San Ysidro, New Mexico, has exemplary importance as an association of a sauropod and possible gastroliths. The *Seismosaurus* case is a typical example for common problems of the identification of gastroliths in fluvial environments and is discussed in more detail elsewhere (chapter V and Wings, in preparation-b). More than 240 stones were found in direct association with the semi-articulated holotype skeleton of *Seismosaurus* and interpreted as gastroliths (Gillette, 1994).

The supposed gastroliths from this locality were well documented and used for several follow-up studies (e.g., Manley, 1993). However, the interpretation of the stones as gastroliths was questioned by Lucas (2000), who interpreted them as stream-deposited cobbles in a channel lag deposit. Nevertheless, a reinvestigation of the sedimentological and taphonomical situation indicates that gastroliths are the most parsimonious explanation for the clasts (Wings, in preparation-b).

Two clusters of the stones were identified (Fig. 6). Some stones were found within the rib cage in contact with ribs and vertebrae, a few gastroliths close to the rib cage were “crudely aligned and in serial contact, as though held in place by soft tissue before burial” (Gillette, 1992). All gastroliths are composed of chert and quartzite. The matrix of all gastroliths was a fluvial sandstone with a medium to coarse grain size (Gillette, 1991). Except for the gastroliths, no pebbles or gravel occurred in the section containing the fossil bones (personal observations, 2002). The bones and gastroliths of *Seismosaurus* are stored in the New Mexico Museum of Natural History in Albuquerque.

Lourinhã, Portugal

Lourinhã is situated in the Lusitanian Basin in western Portugal. The coastal exposures of distal alluvial fan sediments yield many vertebrate fossils, including more than 70 individuals from seven sauropod species (O. Mateus, pers. comm. 2003). The general geological setting and details of the facies types, which are rather similar to the Morrison Formation, were described by Hill (1989). At least three sauropods had associated gastroliths (O. Mateus, pers. comm. 2003), including one of the best examples world-wide for sauropod gastroliths: almost one hundred stones were found in close association with vertebrae of the holotype of *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus, 1999). All sauropod gastroliths are stored in the Museu da Lourinhã, Portugal.

My field work in 2000 at Lourinhã has revealed overall similar depositional settings to the North American Morrison Formation: exoliths are present, but are exceptionally rare. During ten days of field work, including many hours of prospecting along the sea cliffs, only two isolated pebbles were found *in situ*. No bone material was found in the vicinity.

Chubut, Argentina

The fine-grained clastic sediments of the Cañadón Asfalto Formation (Middle Jurassic) and the Cañadón Calcareo Formation (Upper Jurassic) in the Chubut province, Argentina, have produced at least 12 and 4, respectively, partly associated sauropod skeletons (O. Rauhut, pers. comm. 2003). No gastroliths were discovered with any of these skeletons (O. Rauhut, pers. comm. 2003) and virtually no exoliths were found during three weeks of prospection in the relevant strata (Wings, personal observations 2001).

Tendaguru, Tanzania

The Upper Jurassic beds of Tendaguru in Tanzania consist of three horizons of terrestrial marls alternating with marine sandstones (Janensch, 1929a; Maier, 1997). The sauropod genera *Brachiosaurus*, *Barosaurus*, *Dicraeosaurus*, *Janenschia*, and *Tendaguria* were found (Bonaparte et al., 2000; Janensch, 1929b; Maier, 1997) in stages of disarticulation ranging from incomplete skeletons to solitary bones, indications for carcass decay and port-mortem transport are common (Heinrich, 1999). The minimum number of sauropods is given as 23 by Heinrich (1999), but could be well above 50 (M. Sander, pers. comm. 2003). Janensch (1927; 1929a) reported very few associated gastroliths from a *Barosaurus* and a *Dicraeosaurus* specimen. During several years of intensive prospection and excavation in the region, a total number of only 13 clasts was reported (Janensch, 1929a). Some of the 13 clasts, which are preserved at the Museum für Naturkunde in Berlin, are concordant with the exolith definition (see chapter II). Gastroliths are therefore exceptionally rare in the Tendaguru region.

Interpretation and Discussion

Among the examined North American localities and specimens, there is conclusive evidence (fine-grained matrix without similar pebbles, direct association with bone, pebbles deposited as clusters) for genuine gastroliths in *Seismosaurus*, *Cedarosaurus*, and one *Barosaurus* from the Howe Quarry. Furthermore, as allometric comparison with birds has shown (Wings, 2003; Wings and Sander, in preparation), the 600 isolated stones from DMDQ might have been just enough to support gastrolith-supported trituration of foodstuff in the gizzard of a single medium-sized sauropod. This indicates an overall extremely rare occurrence of sauropod gastroliths.

These facts lead to the question if the absence of gastroliths could be an artifact of special sedimentological and taphonomical circumstances. There are several plausible reasons for gastroliths absence in most sauropod finds although the living animals possessed them:

1) Material not recognized, recorded, nor collected
2) Loss under stress or during death
3) Postmortem removal by:
    a. scavengers
    b. sedimentological processes
    c. diagenetic processes
    d. other sauropods

Alternatively, the true absence of gastroliths must be considered.

The general processes which could cause a separation of the remains of the gastrolith-bearing animal and the gastroliths are discussed in detail in chapter V. Therefore, only a short summary, adapted to the relevant field sites, is presented here.

1) Material not recognized, recorded, nor collected

The absence of gastroliths from the historic excavations could be the result of the excavation crews simply not recognizing or collecting them. However, it is unlikely that especially the Carnegie crews at DNM would not have recognized a cluster of stones as gastroliths. The first discussion about gastroliths in sauropods in the journal *Science* (Brown, 1907; Cannon, 1906; Wieland, 1906) had already been published when the Carnegie quarry at DNM was discovered in 1909.

The absence of gastroliths associated with, for example, the dinosaur skeletons found at Como Bluff and CLDQ cannot be absolutely confirmed, because poor field notes do not allow a detailed reconstruction. Yet, at least at CLDQ it is not very plausible that the absence of gastroliths is a consequence of collection bias, since Stokes, one of the excavation managers of the initial excavations, was very interested in the gastroliths problem (e.g., Stokes, 1942; Stokes, 1987).

It is generally rather doubtful that clusters of pebbles and stones associated with articulated sauropod skeletons were not reported by early researchers. Moa remains associated with gastroliths were already commonly reported at the end of the 19th century (e.g., Chapman, 1884; Hamilton, 1891). Also in the 19th century, clusters of stones in fine-grained sediments were recognized as important exotic rocks, even if not hypothesized as possible gastroliths (Jukes-Browne and Hill, 1887). Therefore, it is very likely that at least large clusters of exotic pebbles (which would be expected if the stones had a gastric function in dinosaurs) associated with dinosaur bones would have been noted by early researchers. The rare occurrence of gastroliths associated with sauropod remains also is encountered in the recent excavation record, making it likely that during early excavations the gastrolith density was indeed as low as indicated by the collected material.

Perhaps gastroliths were overlooked because of unusual grain sizes. For example, the only possible gastroliths material in the DNM quarry would have been the conglomeratic sandstones with clasts in sizes <25 mm. But while pebbles of this grain size are used as gastroliths in many large bird species, their exclusive use as gastroliths in the large dinosaurs found at DNM is highly unlikely, since there is generally a correlation between animal size and gastroliths size in living animals (Gionfriddo and Best, 1999; Wings and Sander, in preparation).

The explanation that so few exoliths were found during the author’s field work at the localities because the stones have been extensively collected by geologists and layman, as stated by Minor (1937) for the area around Rigg’s Dinosaur Hill (Morrison Formation, near Fruita, Colorado), cannot account for all exolith absence. Early publications report that the Morrison Formation has generally very few exoliths (Stokes, 1942). Stokes (1987) noted that at DNM and CLDQ, “gastroliths” (exoliths) are abundant in the overlying Lower Cretaceous Cedar Mountain Formation. It is furthermore plausible that exoliths found on the surface are weathering relicts from former conglomerates. The abundance of surface pebbles in the Howe Quarry area can also be explained by glacial input.

2) Loss under stress or during death

The loss of gastroliths under stress or during prolonged death throes is commonly suggested (e.g., Gillette, 1994; Janensch, 1929a). However, the loss of all stones is not plausible. In no extant gastroliths-bearing species, such behavior was ever recorded. Furthermore, this hypothesis could explain the absence of gastroliths in a few individuals, but not in the vast majority of the sauropods, especially in those animals whose rapid deaths are attributed to catastrophic events.

3a) Postmortem removal by scavengers

Signs of scavenging (e.g., Como Bluff) suggest that the gastroliths might have been commonly transported and dislocated by scavengers. These gastroliths should then have been deposited in sediments near the sauropod carcasses or must have been swallowed by the carnivores with carcass flesh. However, exoliths are not specifically abundant near sauropod fossils and the overall absence of gastroliths in theropod skeletons and in predator-rich dinosaur sites such as the CLDQ makes this hypothesis implausible. This issue will be discussed in detail in another publication (see chapter V).

3b) Postmortem removal by sedimentological processes

Recent studies have shown that gastroliths release from carcasses can be a fast process (see chapter IV). Consequently, transport processes in aquatic environment could potentially separate gastroliths from an otherwise complete carcass. However, transport processes can be completely ruled out with autochthonous skeletons in low energy environments. Most transport processes would also affect the bones and not just the gastroliths and should be visible in the taphonomic record. A prolonged transport of carcasses might be indicated by poorly preserved bones. Such poorly preserved bones from classical Upper Jurassic dinosaur localities, such as DNM, cannot be found in the relevant collections (personal observations, Wings, 2003). Nevertheless, the overall excellent preservation of bones in the collections may result from a collection bias, as poorly preserved bones were probably not collected during the first excavations. For DNM for instance, the maximum time period for the formation of the bone bed was calculated at 19 years (Fiorillo, 1994). During that time, the bones could have been transported to the bone bed from several sources. They can originate from river banks, from reworked river channels upstream, or from locally reworked sediments (Michelis, 2003). In all cases, if the skeletons had decayed or were scavenged before their final transport, a loss of the gut contents is probable. However, the exceptionally complete *Camarasaurus* skeleton with preserved skull at DNM indicates a very short transportation of at least one skeleton, and the complete burial of such a carcass with all stomach contents in place is plausible.

The gastrolith record in the Howe Quarry (one cluster of 64 stones belonged to a single specimen; beside that, only 15 stones were associated with skeletal remains of 24 autochthonous individuals) raises the question if any gastroliths might have been removed from the site. During the flood events which covered up the carcasses at Howe Quarry, the soft tissues would have been decayed, therefore preventing any gizzards to float off. A complete mummification of the gut contents and a later transport of the gastroliths in the river is not likely. Although the mummified skin found at several places in the Howe Quarry permits such a scenario, complete mummified carcasses were not found (Michelis, 2003). Even if the gizzards would have been mummified, the combined weight of the gastroliths would have made water transport difficult. Another reason why most gastroliths should be still preserved in the Howe Quarry are large bones that were standing upright in the mudstones. During burial, these bones have been prevented that any items, including small bones, were carried away (Michelis, 2003). Most gastroliths should therefore also have been trapped between these bones.

While the total absence of gastroliths at DNM and at Como Bluff/BCQ could be a result of unusual fluvial sedimentological processes (e.g. short periods of high energy currents), the absence of exoliths at CLDQ, an autochthonous site, is another indication that gastroliths were not present in all sauropods.

3c) Postmortem removal by diagenetic processes

A selective diagenetic dissolution (e.g., by pH changes in the ground water) of the gastroliths is very unlikely. Most gastroliths are composed of quartz, a highly resistant material which also commonly forms the embedding matrix (sandstones, siltstones, and claystones) of the fossils.

3d) Postmortem removal by other sauropods

The fine-grained sediments in the Morrison Formation indicate that stones suitable as gastroliths were rare in the habitat of the Upper Jurassic sauropods. Therefore, a hypothetical scenario can be developed, where gastroliths have been utilized again and again by succeeding generations of sauropods until they were too small to be of use in the putative gastric mill. In situations where a carcass was exposed to weathering for 5-10 years, there might have been numerous opportunities for the stones to be picked up by other sauropods.

Anyhow, some arguments speak against this scenario. If sauropods migrated over extended distances (Paul, 1997), they could easily fulfill their demand for pebbles in suitable sediments. The abrasion of resistant quartz pebbles is relatively low in bird gizzards, and the stones survive several month in the stomach as shown in experiments on ostriches (Wings and Sander, in preparation). If the stones had a similar function in sauropods, the animals would have survived some months without the need to replenish the stones.

Furthermore, such behavior has not been reported from any extant species in the wild. On one hand, observations on free-ranging farm ostriches, which had unlimited access to pebbles in their habitat, have shown that the birds do not accept gastroliths from the stomach contents of slaughtered ostriches for several weeks (R. Schuhmacher, pers. comm. 2003). On the other hand, preliminary research conducted by the author on ten day old ostrich chicks which had no former access to grit shows that the chicks accept former ostrich gastroliths if the stones are clean. Consequently, sauropods may have accepted former gastroliths as their own gastroliths if the stones were exposed for several months or years and if there was a limited sedimentary supply of stones. Nevertheless, this "reuse hypothesis" cannot explain the absence of stones in articulated and quickly buried skeletons.

True absence of gastroliths

After eliminating all other reasons, the true absence of gastroliths is the most parsimonious interpretation for the majority of the sauropods from the investigated sites. Furthermore, the isolated gastroliths might not derived from dinosaur carcasses but from other vertebrate clades. For instance, while the sedimentological situation at DMDQ suggests that gastroliths are the most plausible explanation for the isolated clasts in the sandstones, their assignment to sauropod dinosaurs is uncertain. Beside dinosaur remains, many other vertebrate fossils are found in the DMDQ including a crocodilian (Britt and Curtice, 1997). Since crocodilians do often possess gastroliths (e.g., Cott, 1961; Whittle and Everhart, 2000) and are found as fossils with gastroliths in their body cavity (see chapter V), the isolated stones could also belong to this clade.

Conclusions

The taphonomy of complete articulated and/or autochthonous sauropod skeletons in low-energy sediments allows the conclusion that only very few sauropods possessed small masses of gastroliths. An estimate of the number of sauropod individuals with associated gastroliths shows that they at most comprise 2-4% of all sauropods found at the North American localities discussed. If other sauropod-rich sites are added to the statistic (Chubut, Tendaguru, Lourinhã), this number remains constant at around 4%. This astonishing low number is, beside the results from allometric comparison of gastrolith mass and body mass in birds and sauropods (Wings and Sander, in preparation), yet another argument that gastroliths were not essential for food processing in sauropod dinosaurs.

Exotic pebbles which can be found on the surface of the sediments in some other Morrison outcrops are not necessarily former gastroliths. It is more plausible that most of them are weathering relicts of conglomerate beds.

Acknowledgements

This research is an integral part of my Ph.D. thesis, and I am very grateful to my supervisor M. Sander for his constant advice and support. D. Fowler is thanked for fruitful discussions and his great company in the field. W. Joyce helped in locating rare literature. M. Everhart, M. Sander, and L. Schmitz critically commented on the manuscript.

I am very grateful to all the people who gave a field introduction or any other kind of advice before and during field work in Argentina, Portugal, and the USA, particularly J. Bussen, K. Carpenter, D. Chure, K. Cloward, A. Elder, M. Everhart, J. Forster, M. Leschin, S. Lucas, O. Mateus, O. Rauhut, H.J. Siber, K. Stadtman, and G. Storrs. K. Cloward (Western Paleo) also provided much valuable information about the BCQ. For help during my ostrich gastrolith research which clarified many ideas about sauropod gastroliths, I wish to thank A. Olivier and R. Schuhmacher.

The Jurassic Foundation funded my field work in the USA. Additional financial support was provided by the “Graduiertenförderung Nordrhein-Westfalen”, the Graduiertenkolleg “Evolution und Biodiversität in Raum und Zeit”, and my family.

References

Ayer, J., 2000. The Howe Ranch Dinosaurs/Die Howe Ranch Dinosaurier. Sauriermuseum Aathal, Aathal, 96 pp.

Bakker, R.T., 1986. The Dinosaur Heresies. William Morrow, New York, 481 pp.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology, 4(2): 150-162.

Bilbey, S.A., 1998. Cleveland-Lloyd dinosaur quarry - age, stratigraphy and depositional environments. Modern Geology, 22: 87-120.

Bilbey, S.A., 1999. Taphonomy of the Cleveland-Lloyd Dinosaur Quarry in the Morrison Formation, Central Utah - a lethal spring-fed pond. In: D.D. Gillette (Editor), Vertebrate Paleontology in Utah. Miscellaneous Publication. Utah Geological Survey, pp. 121-133.

Bird, R.T., 1985. Bones for Barnum Brown: Adventures of a Dinosaur Hunter. Texas Christian Univ. Press, Fort Worth, 225 pp.

Bonaparte, J.F., Heinrich, W.-D. and Wild, R., 2000. Review of *Janenschia* WILD, with the description of a new sauropod from the Tendaguru beds of Tanzania and a discussion on the systematic value of procoelous caudal vertebrae in the sauropoda. Palaeontographica Abt. A, 256(1-3): 25-76.

Bonaparte, J.F. and Mateus, O., 1999. A new diplodocid, *Dinheirosaurus lourinhanensis* gen. et sp. nov., from the Late Jurassic beds of Portugal. Revista del Museo Argentino de Ciencias Naturales, 5(2): 13-29.

Breithaupt, B.H., 1997a. Bone Cabin Quarry. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 80-81.

Breithaupt, B.H., 1997b. Como Bluff. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 135-137.

Britt, B.B. and Curtice, B.D., 1997. Dry Mesa Quarry. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 196-197.

Brown, B., 1907. Gastroliths. Science, 25(636): 392.

Calvo, J.O., 1994. Gastroliths in sauropod dinosaurs. Gaia, 10: 205-208.

Cannon, G.L., 1906. Sauropodan gastroliths. Science, 24(604): 116.

Chapman, F., 1884. Notes on moa remains in the Mackenzie Country and other localities. Transactions and Proceedings of the New Zealand Institute, 17: 172-178.

Christiansen, P., 1996. The evidence for and implications of gastroliths in sauropods (Dinosauria, Sauropoda). Gaia, 12: 1-7.

Chure, D.J., 1997. Dinosaur National Monument. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 179.

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., 1981. *Hovasaurus bolei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeontologica Africana, 24: 99-163.

Currie, P.J., 1997. Gastroliths. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 270.

Darby, D.G. and Ojakangas, R.W., 1980. Gastroliths from an Upper Cretaceous plesiosaur. Journal of Paleontology, 54(3): 548-556.

Dodson, P., Behrensmeyer, A.K., Bakker, R.T. and McIntosh, J.S., 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. Paleobiology, 6(2): 208-232.

Fiorillo, A.R., 1994. Time resolution at Carnegie Quarry (Morrison Formation: Dinosaur National Monument, Utah): implications for dinosaur paleoecology. Contributions to Geology, University of Wyoming, 30(2): 149-156.

Gillette, D.D., 1991. Paleoecological significance of gastroliths in a dinosaur excavation site. Geological Society of America, Rocky Mountain Section. Abstracts with programs, 23(4): 24.

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. Columbia University Press, New York, 205 pp.

Gionfriddo, K.P. and Best, L.B., 1999. Grit use by birds - a review. Current Ornithology, 15: 89-148.

Hamilton, A., 1891. Moa gizzard stones. New Zealand Journal of Science, 1: 269-270.

Heinrich, W.-D., 1999. The taphonomy of dinosaurs from the Upper Jurassic of Tendaguru, Tanzania (East Africa), based on field sketches of the German Tendaguru expedition (1909-1913). Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, 2: 25 -61.

Hill, G., 1989. Distal alluvial fan sediments from the Upper Jurassic of Portugal: controls on their cyclicity and channel formation. Journal of the Geological Society, London, 146: 539-555.

Hunt, A.P., Meyer, C.A., Lockley, M.G. and Lucas, S.G., 1994. Archeology, toothmarks and sauropod dinosaur taphonomy. Gaia, 10: 225-231.

Janensch, W., 1927. Ueber Magensteine bei Dinosauriern aus Deutsch-Ostafrika. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1926: 34-36.

Janensch, W., 1929a. Magensteine bei Sauropoden der Tendaguru-Schichten. Palaeontographica, Supplement, VII(2): 135-144.

Janensch, W., 1929b. Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru-Expedition. Palaeontographica, Supplement, VII(2): 1-34.

Jukes-Browne, A.J. and Hill, W., 1887. On the lower part of the Upper Cretaceous Series in West Suffolk and Norfolk. Quarterly Journal of the Geological Society of London, 43: 544-598.

Lawton, R., 1977. Taphonomy of the dinosaur quarry, Dinosaur National Monument. Contributions to Geology, University of Wyoming, 15: 119-126.

Lucas, S.G., 2000. The gastromyths of "*Seismosaurus*," a Late Jurassic dinosaur from New Mexico. In: S.G. Lucas and A.B. Heckert (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 61-68.

Madsen, J.H., 1976. *Allosaurus fragilis*: A revised osteology. Utah Geological & Mineral Survey, Bulletin, 109, 163 pp.

Maier, G., 1997. Tendaguru. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 725-726.

Manley, K., 1993. Surface polish measurement from bona fide and suspected dinosaur gastroliths and wave and stream transported clasts. Ichnos, 2(2): 167-169.

Matthew, W.D., 1908. *Allosaurus*, a carnivorous dinosaur, and its prey. American Museum Journal, 8(1): 2-5.

Michelis, I., 2003. Vergleichende Taphonomie des Howe Quarry's (Morrison Formation, Oberer Jura), Bighorn County, Wyoming, USA. Ph.D. Thesis, University of Bonn, Bonn, 324 pp.

Minor, W.C., 1937. Dinosaur gizzard stones. Rocks and Minerals, 12(8): 229-231.

Paul, G.S., 1997. Migration. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 444-446.

Richmond, D.R. and Morris, T.H., 1996. The dinosaur death-trap of the Cleveland-Lloyd Quarry, Emery County, Utah. The Continental Jurassic, Museum of Northern Arizona Bulletin, 60: 533-545.

Richmond, D.R. and Morris, T.H., 1998. Stratigraphy and cataclysmic deposition of the Dry Mesa dinosaur quarry, Mesa County, Colorado. Modern Geology, 22: 121-143.

Sanders, F., Manley, K. and Carpenter, K., 2001. Gastroliths from the Lower Cretaceous sauropod *Cedarosaurus weiskopfae*. In: D.H. Tanke and K. Carpenter (Editors), Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie. Indiana University Press, Bloomington & Indianapolis, pp. 166-180.

Schmude, D.E. and Weege, C.J., 1996. Stratigraphic relationship, sedimentology, and taphonomy of Meilyn: A dinosaur quarry in the basal Morrison Formation of Wyoming. Museum of Northern Arizona Bulletin, 60: 547-554.

Schwartz, H.L. and Manley, K., 1992. Geology and stratigraphy of the *Seismosaurus* locality, Sandoval County; New Mexico. New Mexico Geology, 14(2): 25-30.

Stokes, W.M.L., 1942. Some field observations bearing on the origin of the Morrison "gastroliths". Science, 95(2453): 18-19.

Stokes, W.M.L., 1987. Dinosaur gastroliths revisited. Journal of Paleontology, 61(6): 1242-1246.

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 (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 75-82.

Wieland, G.R., 1906. Dinosaurian gastroliths. Science, 23(595): 819-821.

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., in preparation-a. Exoliths and their sedimentological interpretation.

Wings, O., in preparation-b. Gastroliths or river gravel? The authenticity of *Seismosaurus* (Sauropoda, Dinosauria) stomach stones revisited.

Wings, O. and Sander, P.M., in preparation. Gastrolith function in dinosaurs reconsidered: No evidence for gastric mills in sauropods.

Tables

Locality	**Stratigraphy**	**Depositional environment**	**Sedimentology**	**Taphonomy**	**Origin of carcasses**	**Amount of material**	**General diversity**	**Sauropod diversity**	**No. of sauropod individuals**	**No. of gastroliths/ exoliths**
Carnegie Quarry, Dinosaur National Monument	Morrison Fm., Brushy Basin Member	River channels	Coarse sandstone, in parts conglomeratic	Carcasses washed together, articulated skeletons are abundant	Allochthonous – parauthochtonous	Some 5000 bones, 60 - 300 Dinosaurs	High	4 genera	>20	0
Cleveland-Lloyd Dinosaur Quarry	Morrison Fm., Brushy Basin Member	Water hole, oxbow lake	Mudstone	Miring in mud	Autochthonous	10000 disarticulated bones of at least 70 individuals	Medium	3 valid genera, maximum 6 genera	10	2?
Como Bluff/Bone Cabin Quarry	Upper part of the Morrison Fm.	River channels	Fine-grained sandstones and claystones	Isolated skeletons and articulated skeletons washed together	Allochthonous– parauthochtonous	Thousands of bones (only in BCQ approx. 69 partial skeletons)	High	5 genera	Como Bluff: unknown BCQ: 44	Como: 0 BCQ: 0
Dry Mesa Quarry	Morrison Fm., Brushy Basin Member	River channels	Conglomeratic sandstones	Bones washed together, mainly disarticulated skeletal elements	Allochthonous	More than 4000 mainly isolated skeletal elements	Very high (highest in the Morrison Fm.)	5 genera	>20	500-600
Howe Quarry	Morrison Fm. (145,7 Ma)	Water hole, oxbow lake	Siltstone, in parts sandy	Miring in mud	Autochthonous	More than 4000 bones of at least 25 animals	Low	3 genera	25	64
Cedarosaurus site	Cedar Mountain Fm., Yellow Cat Member	Floodplain with low water energy	Mudstone	Isolated skeleton resting on its belly	Parautochthonous - autochthonous	Isolated skeleton	Isolated find	1 genus	1	115
Seismosaurus site	Morrison Fm., Brushy Basin Member	River channels	Sandstone	Partly preserved isolated skeleton	Parautochthonous	Isolated skeleton	Isolated find	1 genus	1	>240

Table 1. Summary of information for selected quarries. For references and discussion see text.

Figures

Fig. 1. Studied dinosaur localities in the western USA. The surrounding line represents the extension of the Morrison Formation. Abbreviations: BCQ – Bone Cabin Quarry; CLDQ – Cleveland-Lloyd Dinosaur Quarry; DMDQ – Dry Mesa Dinosaur Quarry; DNM (CQ) – Dinosaur National Monument (Carnegie Quarry); Howe Q & HSQ – Howe Quarry and Howe Stephens Quarry;. The dark bones represent sites where gastroliths have been found in association with bones. Modified from Dodson et al. (1980).

Fig. 2. Photograph of the gastroliths find in the Howe quarry. Next to a *Barosaurus* pubis and an elongated bone, probably an abdominal rib, the cluster of 64 stones is visible. From Bird (1985).

Fig. 3. Section of R.T. Bird's Howe Quarry map showing the *Barosaurus* bones (grey) as well as the gastroliths (black dots) seen in the photograph in Fig. 2. The numbers in the map define the original excavation squares. The bones of the *Barosaurus* individual were still partly articulated. From Michelis (2003).

Fig. 4. Carbonized material with a single gastrolith from Howe Quarry. The presence of plant matter surrounding the clast is interpreted as evidence for former stomach contents. This is specimen number D18-15 in the Sauriermuseum Aathal, scale in cm.

Fig. 5. *Cedarosaurus* site field sketch, the gastrolith cluster is clearly visible. Three isolated gastroliths were dispersed throughout the skeleton. From Sanders et al. (2001).

Fig. 6. Distribution of bones and stones at the *Seismosaurus* locality (A) and cross-section of the quarry (B). Note that bone-bearing blocks occurred below the first pebble lag and that there are two concentrations of gastroliths. A defined cluster was found in the pelvic area, whereas the majority of the stones was dispersed in the area north of the bone material. Modified from Lucas (2000), and including information from Gillette (1994) (in A) and Schwartz and Manley (1992) (in B).

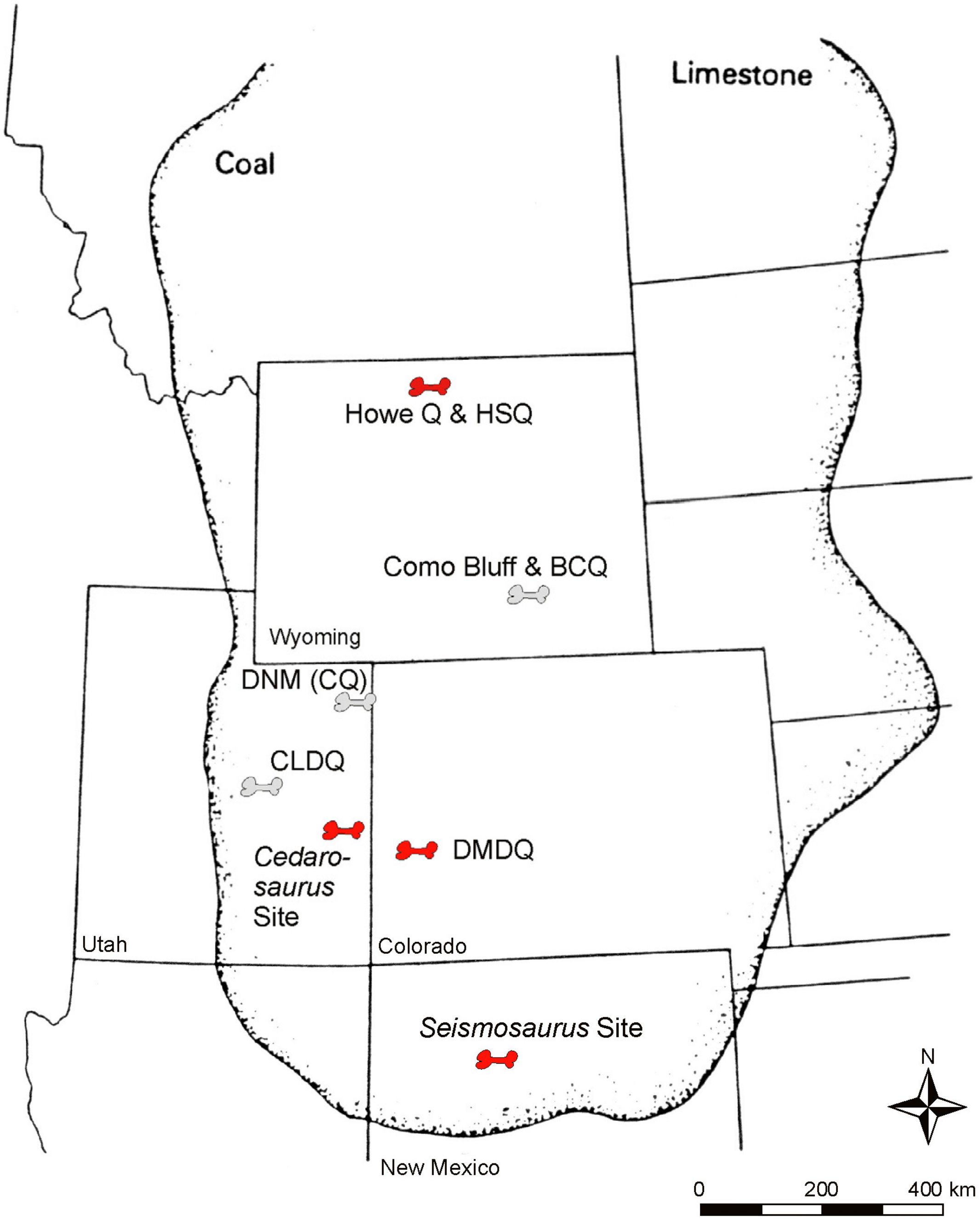

Limestone
Coal
Howe Q & HSQ
Como Bluff & BCQ
Wyoming
DNM (CQ)
CLDQ
Cedaro-saurus Site
DMDQ
Utah
Colorado
Seismosaurus Site
N
New Mexico
0
200
400 km

Fig. 1.

Fig. 2.

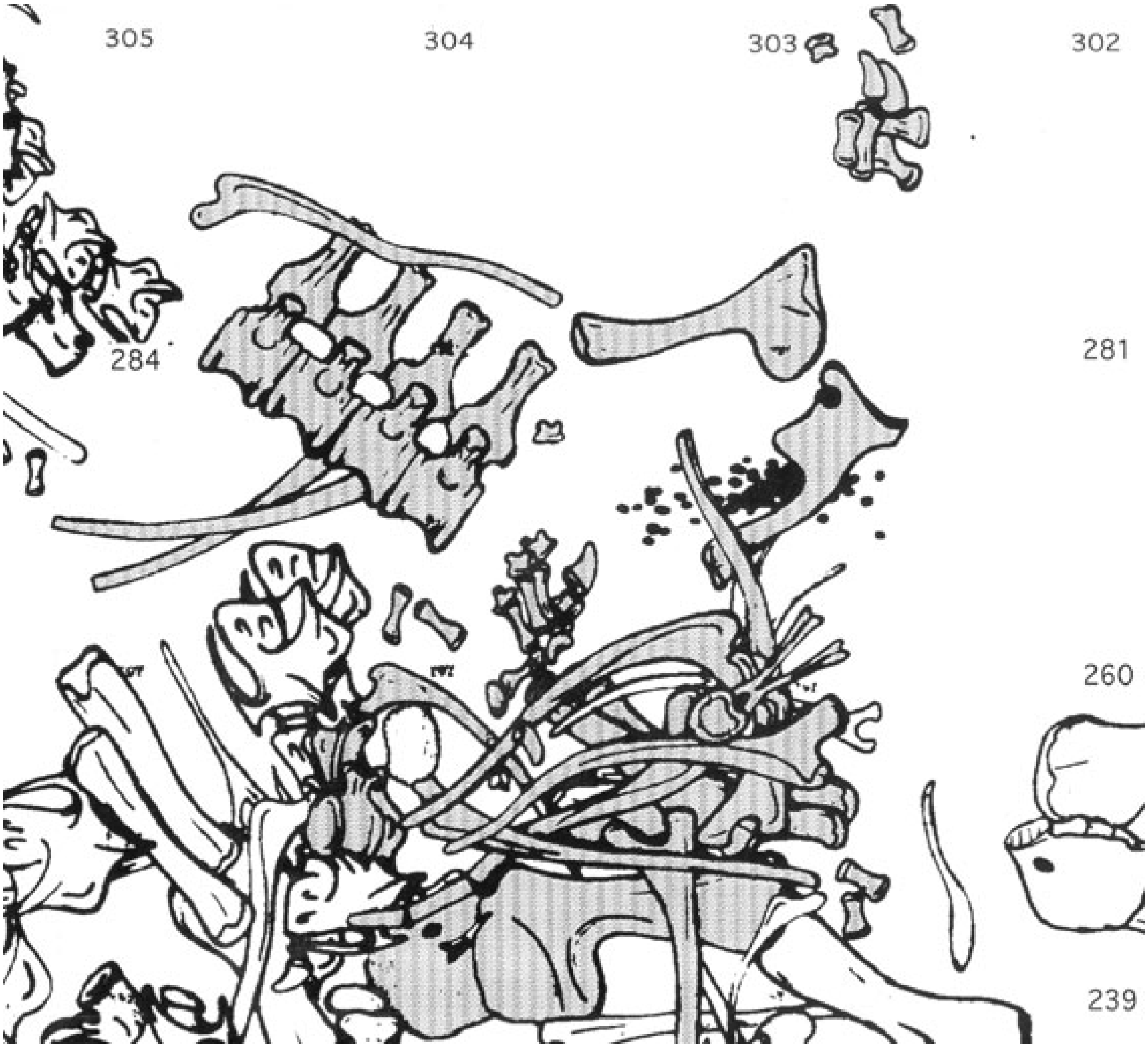


Fig. 3.

Fig. 4.

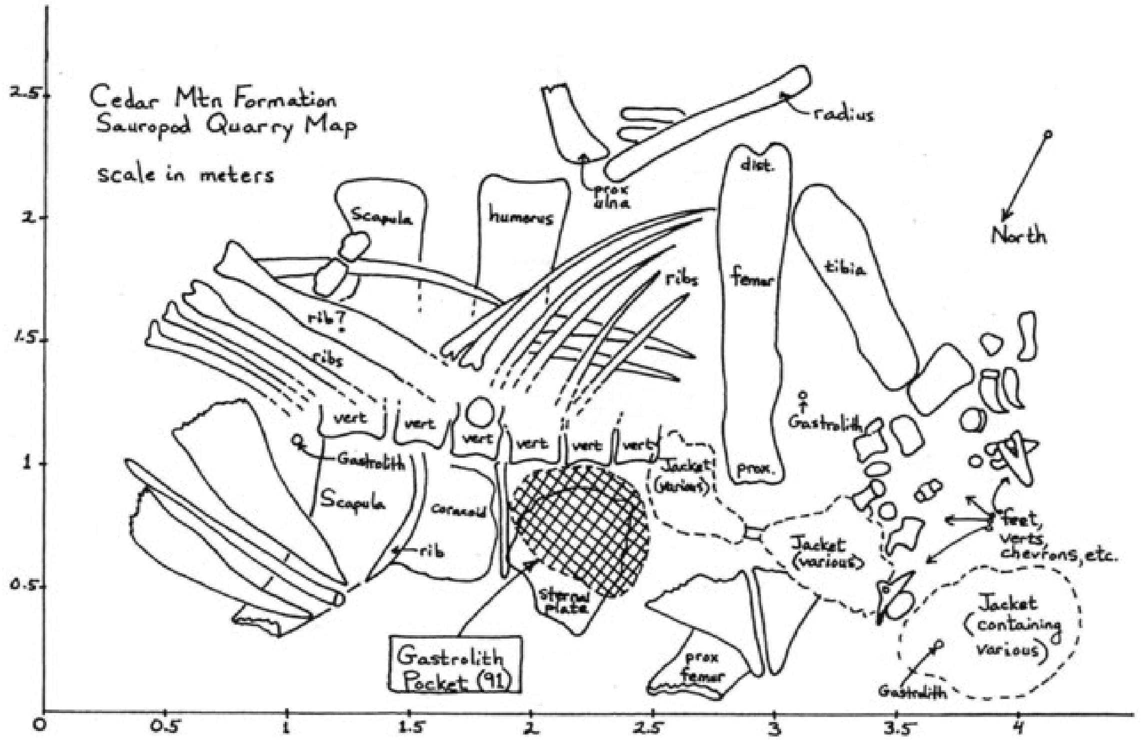

Cedar Mtn Formation
Sauropod Quarry Map
scale in meters
2.5
2
1.5
1
0.5
0
0.5
1
1.5
2
2.5
3
3.5
4
Scapula
humerus
prox ulna
radius
dist.
femur
prox.
tibia
North
ribs
rib?
ribs
vert
vert
vert
vert
vert
vert
Gastrolith
Scapula
coracoid
rib
sternal plate
Gastrolith Pocket (91)
Jacket (various)
Gastrolith
Jacket (various)
feet, verts, chevrons, etc.
Jacket (containing various)
Gastrolith
prox femur

Fig. 5.

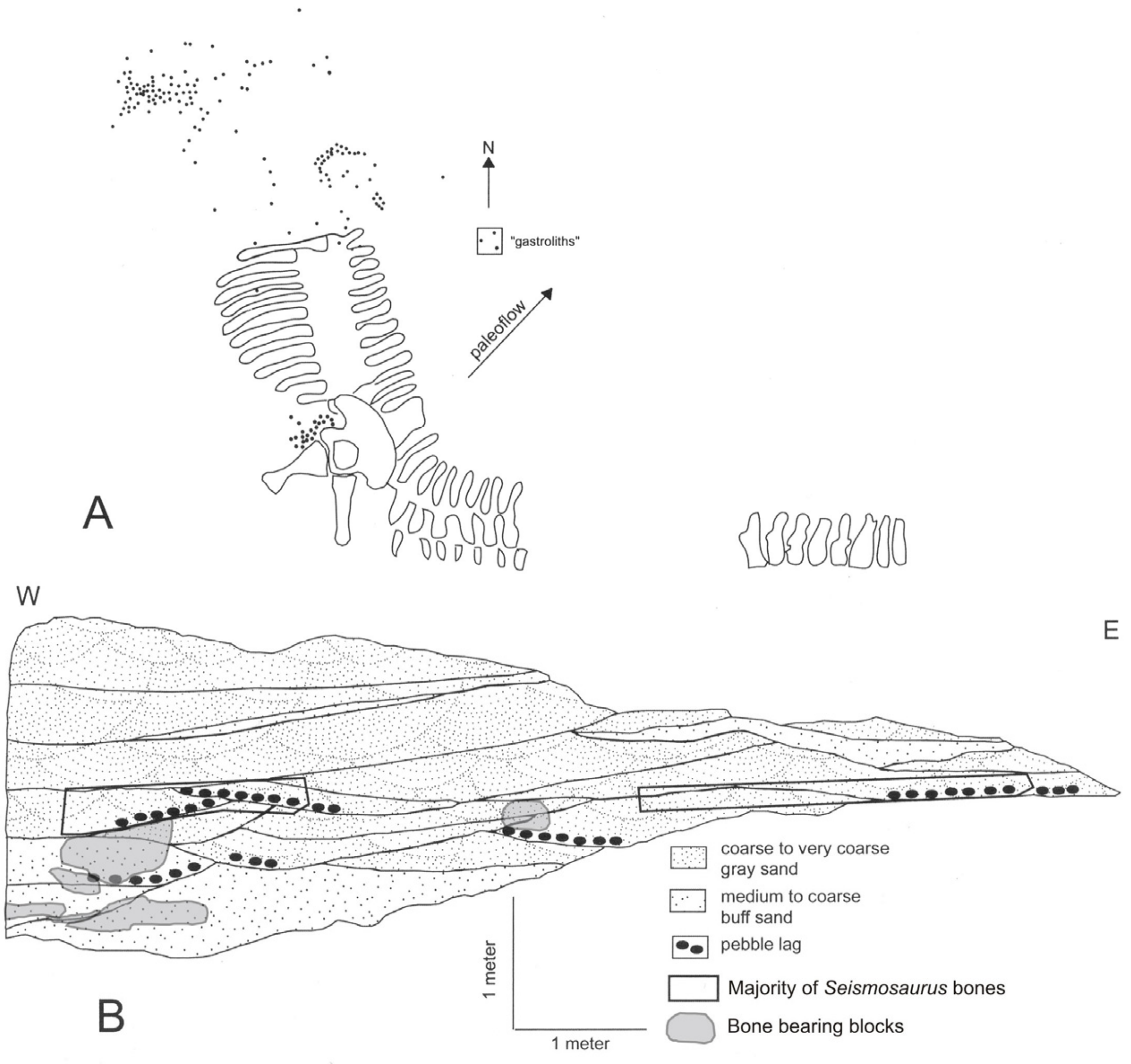

N
"gastroliths"
paleoflow
A
W
E
coarse to very coarse gray sand
medium to coarse buff sand
pebble lag
Majority of *Seismosaurus* bones
Bone bearing blocks
1 meter
1 meter
B

Fig. 6.

CHAPTER VII: A simulated bird gastric mill and its implications for fossil gastrolith authenticity

Abstract

A rock tumbler, stones, water, plant material, hydrochloric acid, and pepsin were used to simulate a bird gizzard, an "artificial stomach". The experiment was conducted in order to study the abrasion rate and the influence of stomach juices and foodstuff on gastrolith surface development and lasted for six months. Each week, the stomach was supplied with fresh grass and stomach juices. After the end of the experiment, the stones had a total weight loss of 22.4%, with softer rock types showing a higher abrasion rate. No polish had formed on the surface of the stones due to continuous abrasion of the surface. The phytoliths within the grass as well as stomach juices had no visible effect on stone surface development. They did not enhance polish nor caused any pitting on the stone surface. The major cause for rock abrasion was the contact between the moving stones. A comparison with authentic ostrich gastroliths showed that the forces and therefore the abrasion rate in the artificial stomach were lower than in a real ostrich gizzard. However, the abrasion rate was still too high to maintain or develop surface polish. If the polish occasionally seen on fossil gastroliths was indeed caused by the stomach environment, this implies a very low abrasion rate not observed in extant bird gizzards and the "artificial gizzard". Since stomach juices and hard plant matter including phytolith-rich tissue cannot have played an important role in this polish formation, other origins of polish such as wind polish or a diagenetic origin should be considered for fossil gastroliths.

Introduction

Gastroliths, stomach stones, occur in a variety of fossil and extant vertebrates including non-avian dinosaurs, crocodilians, and birds (see chapter I, II, and V). However, if gastroliths are separated from the skeletal remains, their unambiguous identification is extremely difficult. For gastrolith identification, it is important to understand and document the surface alteration of stones in the digestive tract. Because of the limited availability of suitable data and the resulting poor understanding of processes which influence pebbles in the gastric environment, new experiments were conducted. The goal of the experiments was to gain a general idea of the importance of factors influencing the abrasion of stones in the stomach and especially the formation of polish on gastrolith surfaces. Among these factors are stomach fluids (acid and enzymes), amount of plant matter, and type and force of movement. Attention was paid that the conditions of the experiment were approximating real stomach conditions as much as possible. Especially the addition of acid and enzymes improved the authenticity of the simulation compared to previous experiments (Chatelain, 1991; Moore, 1998).

The investigations of Moore (1998) and Moore et al. (1998) were conducted in order to study the effect of gastroliths on the breakdown of grass in geese gizzards (Moore, 1998; Moore et al., 1998). The artificial gizzard used in their experiments was modelled with two types of gizzard muscle morphology: asymmetric muscles generated a translational movement, whereas symmetric muscles generated a compressional movement (Moore et al., 1998). Unfortunately, the surface alteration of the gastroliths used during the experiments was never studied (Moore, 1998).

Experimental research on gastrolith identification was conducted by Chatelain (1991) who used stream-abraded pebbles in tumbling experiments with conifer and cycad foliage as abrasive material. His preliminary analyses indicated that a highly polished, grid like pattern of fine scratches was imprinted upon the originally dull surface texture. Unfortunately, no details of the experiment were given (Chatelain, 1991).

Material and Methods

A rock tumbler was used as a simplified substitute of a gizzard (Fig.1). The intended purpose of such tumblers is to polish semi-precious stones. The machine is built with a sealed rubber compartment and has relatively soft walls with longitudinal grooves. The rubber is hence a rather rough, but appropriate alternative for the gastric wall. The cylindrical rubber compartment was continuously moved by a small electric motor, except during refilling times.

Fresh cut perennial rye grass (*Lolium perenne*) was used as plant material for the experiment because of its mechanical resistance, high contents of phytoliths, and its importance in the diet of free-range ostriches on German farms. Gastroliths of these German farm ostriches were used for comparison (see chapter III). To facilitate and quicken the task of simulating the stomach environment, hydrochloric acid (HCl) and pepsin in concentration significantly higher in concentration than in gastric juices of birds were used for the simulated stomach juices. Freshly secreted gastric juice contains about 0.5% HCl and the stomach of vertebrates has commonly a pH around 2 (Schmidt-Nielsen, 1997). In living animals, the stomach juices are constantly secreted and replaced. In the experiment, the stomach juices and the “food” were replaced once a week. During replacement, a fraction of the digested plant matter was discarded and exchanged for a constant amount of fresh ingredients.

The artificial stomach was set up in March 2001 and run continuously at room temperature for six months. Initially, the stomach was loaded with 113 g fresh-cut grass, 375 g stones, 3 g pepsin dissolved in 100 ml tap water, and 25 ml of 10% HCl. Each week, 20 g grass, 1 g pepsin in 5 ml tap water, and 10 ml of 10% HCl were added. To test the maximum amount of plant matter that can be processed, different amounts of ingredients were used during three weeks. In the 6th week, 50 g grass, 1.5 g pepsin in 5 ml tap water, and 10 ml of 10% HCl were added. In the 7th week, 60 g grass, 3 g pepsin in 5 ml tap water, and 30 ml of 10% HCl were added. In the 8th week, no grass (the large amounts added in the two weeks before were not yet disintegrated), 1 g pepsin in 5 ml tap water, and 10 ml of 10% HCl were added. In the following weeks the normal ingredients (20 g grass, 1 g pepsin in 5 ml tap water, and 10 ml of 10% HCl) were added until the experiment was terminated.

The rock samples used in this experiment were small, randomly selected river pebbles from the Rhine River (mainly composed of vein quartz, quartzite, sandstone, lydite) (Fig. 2a, 2b). These stones were chosen for comparability with ostrich gastroliths from a farm in the region (see chapter III). There, the ostriches graze on pastures situated on the Middle Pleistocene terrace of the Rhine River. Additionally, several larger stones were selected purposefully. Three stones had artificial surfaces and shapes, respectively: two polished standard quartz samples (black and white), previously polished in a rock tumbler, as well as one rock-sawed granite cube with one polished face and an edge length of 2 cm. Additionally, some cherts and silicified mudstones, respectively, were added because such stones develop the highest luster found among ostrich gastroliths (Wings, unpublished data). The size of all used stones was comparable to the genuine ostrich gastroliths.

To investigate the influence of the rubber walls of the tumbler on the surface development of the pebbles, a second sequence of the experiment was conducted. Similar pebbles were put in the tumbler together with tap water, but without stomach juices and plant matter, and also tumbled for six months. To test if gastroliths indeed increase the digestive efficiency, the tumbler also was loaded only with grass and stones and run for another week.

After the end of the experiments, the changes of the surface texture of stones (river gravel, artificially polished stones, rock cubes) from both experiments were examined via close-up photography, stereo light microscopy, and scanning electron microscopy using a Camscan MV 2300. Ostrich gastroliths, including similar artificially polished quartz samples, were used for comparison.

Results

In the environment of aggressive stomach juices and exposed to continuous grinding, the plant material was pulped and disintegrated within a few days after feeding. All stones in both experiments showed high mechanical erosion (Fig. 2b, 3). However, the abrasion rate was considerably higher in the experiment without plant matter and stomach juices as evident from the granite sample (Fig. 3). The total weight of the stones after the experiment with the artificial stomach was 291.0 g. This is a weight loss of 84 g, or 22.4%, respectively. As expected, softer rocks such as sandstones show a generally higher abrasion rate than hard rocks such as vein quartz. Sharp edges on all the stones were eroded. The standard granite cube sample in the artificial stomach experienced a weight loss of 3.4 g (15.3%). The identical sample in the tumbler with water only, lost much more mass: 10.1 g (45.3%).

The artificially polished samples lost their luster in both experiments. On the other hand, some of the chert and lydite samples, which initially had a dull surface, developed a weak resinous luster. No significant difference was found between the surfaces of stones from the two experiments in any of the stone types.

While the original standard sample was highly polished (Fig. 4a), the sample from the artificial stomach shows equal abrasion without any major surface features such as scratches or pitting (Fig. 4b). Most of the polish is abraded. This is also a strong contrast to another standard sample which stayed for 24 hours in an ostrich gizzard and is heavily and irregularly scratched (Fig. 4c).

In the preliminary experiment using only grass and stones in the tumbler, the stones were not able to triturate the grass but were rather enclosed in the ball formed by the plant material.

Discussion and Conclusions

The most significant difference between the experimental setting and a gizzard is the type of movement: while a stone in a gizzard is subject to strongly fluctuating forces from defined directions (mainly direct and lateral compression), a stone in a rock tumbler is in constant movement, by uplift in the grooves of the rubber-lined drum and a short fall once the position in the groove becomes unstable. The total forces are thus probably weaker and more equally distributed than in a gizzard.

The observation that the abrasion of rocks was stronger in the experiment without plant matter indicates that soft plant matter served as a buffer between the stones. Less contact between the stones means less abrasion.

The formation of a weak luster on some cherts is similar to the luster found on shingle from chert beaches (personal observations on German and English beaches) which shows that this luster is not a result of specific conditions in the gizzard. The largest fraction of the polished pebbles interpreted as dinosaur gastroliths (Stokes, 1987) is represented by vein quartz. However, these lithologies did not develop any polish in the artificial stomach. This is evidence that phytoliths do not enhance the formation of polish on gastrolith surfaces. The enzymatic reaction of pepsin has no visible effect on the gastroliths but caused the fast disintegration of plant material. The highly acidic environment had no effect on the selected stones, but would have caused the fast dissolution of limestones. Microscopic examination revealed that the number and depth of scratches on the experimental “gastroliths” is smaller than on ostrich gastroliths. This indicates that forces in the tumbler are generally much lower than in a gizzard as suggested earlier.

In summary, although the forces and therefore the abrasion rate in the artificial stomach were lower than in a real ostrich gizzard, the abrasion rate was still too high to maintain or develop any stone surface polish. Phytoliths from normal grass did not enhance polish, but plant matter slowed down the abrasion in the tumbler. This was also supported by the preliminary experiment with only grass and stones in the tumbler, where the stones did not triturate the grass at all. The efficiency of real gastroliths is therefore directly correlated to the presence of gastric juices.

Implications for fossil gastrolith authenticity can be drawn from the experiment. If gastrolith polish was caused inside a dinosaur stomach, this implies a very low abrasion rate unknown from extant bird gastroliths and not reproducible in a simulation. Stomach juices and hard plant matter, including phytolith-rich material, do not play an important role in polish formation. No pitting of gastrolith surface is caused by stomach acids.

Therefore, I suggest that other ways of gastrolith polish formation than continuous movement in a gizzard must be considered. If the stones were indeed polished in a stomach, they must have been retained for a longer period and experienced very little movement or movement of low energy, not comparable to extant bird gizzards.

In a normal rock tumbler, polish is formed by the movement of the stones in a liquid composed of very fine abrasives and water. Perhaps also the polish on the alleged dinosaur gastroliths was formed by totally different processes, such as wind polish or diagenetic polish (Wings, in preparation).

Acknowledgements

This paper is a part of my Ph.D. thesis. I would like to thank my advisor Martin Sander for the steady support of my studies. Georg Oleschinski is acknowledged for his help taking photographs and Olaf Dülfer for taking care of the artificial stomach during my absence for field work. I received financial support from the "Graduiertenförderung Nordrhein-Westfalen", the Graduiertenkolleg "Evolution und Biodiversität in Raum und Zeit", and my family.

References

Chatelain, E., 1991. Surface textures on gastroliths as a key to origin: vertebrate gastric mills or stream abraded gravels. Georgia Academy of Science, 68th annual meeting - Bulletin of the Georgia Academy of Science, 49(1): 35.

Moore, S.J., 1998. Use of an artificial gizzard to investigate the effect of grit on the breakdown of grass. Journal of Zoology, 246: 119-124.

Moore, S.J., Lill, C.A. and Sanson, G.D., 1998. Functional morphology of the gizzard of the domestic goose: design of an artificial gizzard. Journal of Zoology, 246: 111-117.

Schmidt-Nielsen, K., 1997. Animal physiology: adaptation and environment. Cambridge University Press, Cambridge, viii, 607 pp.

Stokes, W.M.L., 1987. Dinosaur gastroliths revisited. Journal of Paleontology, 61(6): 1242-1246.

Wings, O., in preparation. The identification of gastroliths: potentials and limits.

Figures

Fig. 1. View into the rubber-lined drum of the rock tumbler ("artificial stomach") after seven weeks of operation and one week after the last addition of fresh ingredients. The plant matter is totally disintegrated due to mechanical and chemical treatment. The result is a sludge in which the stones are embedded (not visible). The inner diameter of the drum is 10 cm.

Fig. 2a. The stones used in the artificial stomach before the experiment. Several stones in the upper right of the picture possess a very high luster due to preexisting polishing. Other stones exhibit sharp corners and edges.

Fig. 2b. The stones used in the artificial stomach after the experiment. No high luster is preserved, all stones possess a rather dull surface. Very few stones (black specimens in the center) show a slightly higher luster compared to the pictures before the experiment (resinous). All sharp edges are now rounded. Some pebbles are considerably smaller than at the start of the experiment.

Fig. 3. Rock-sawed cubes of the granite standard sample used in the experiment. The left stone is a original sample used for the tests (weight: 22.3 g), the second stone from the left was moved for approximately 180 days in the artificial stomach (weight: 18.9 g), the second from the right was moved for approximately 180 days in the tumbler filled only with water (weight: 12.2 g), the stone on the right was retrieved from an ostrich gizzard after 50 days (weight: 10.7 g). Note that the abrasion in the ostrich gizzard was, despite of the shortest time of abrasion, higher than in both experiments. The abrasion in the artificial stomach was the lowest.

Fig. 4a. Close-up photograph of an unaltered standard quartz sample in the polished state. Note the smooth surface and the high luster.

Fig. 4b. Close-up picture of a standard quartz sample after six months in the artificial stomach. Note the even abrasion without any major surface features such as scratches or pitting. This indicates a constant but low energy abrasion. This is in strong contrast to the surface texture seen on a similar pebble derived from an ostrich gizzard (Fig. 4c).

Fig. 4c. Standard quartz sample after 24 hours in an ostrich gizzard. Note the deep scratches in the surface. No pitting is visible. The differences in surface structure compared with the unaltered sample (Fig. 4a) and a similar sample from the simulated bird gastric mill (Fig. 4b) are obvious. The scratches indicate the strong lateral movement in the ostrich gizzard.

Fig. 1.

Fig. 2a.

Fig. 2b.

Fig. 3.

Fig. 4a.

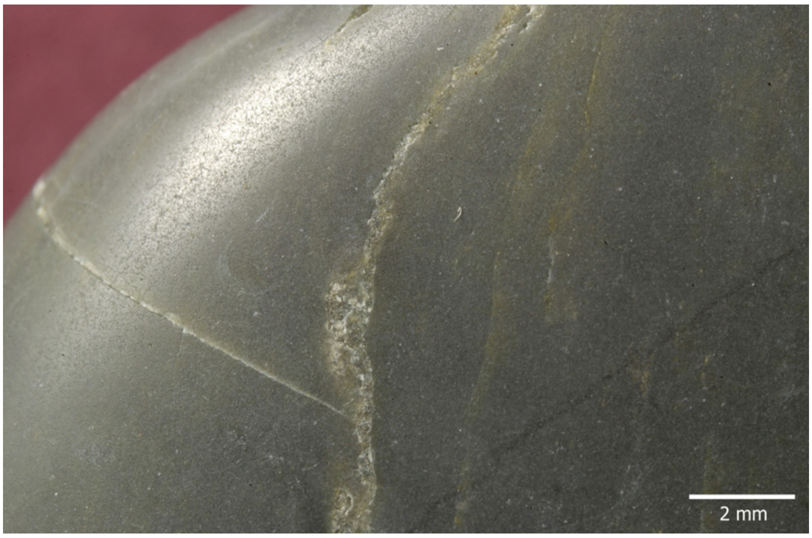


Fig. 4b.

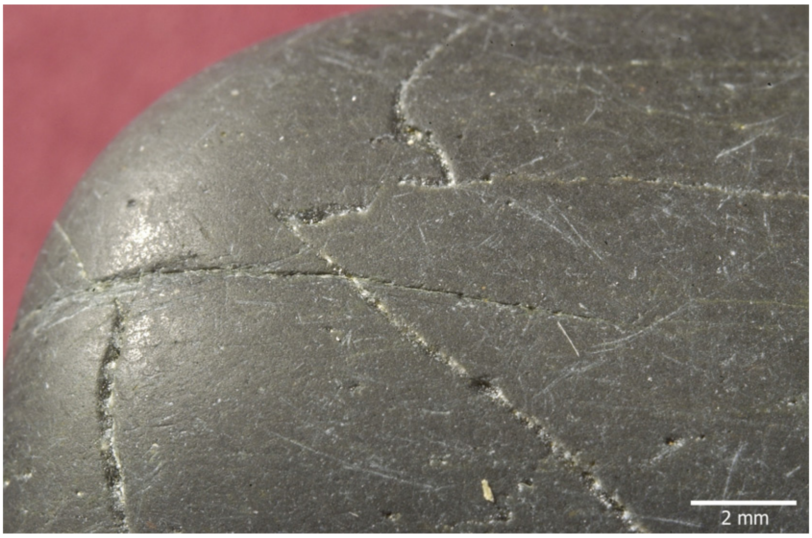


Fig. 4c.

CHAPTER VIII: Suggested future research on gastroliths

Several aspects of gastroliths in living animals and the fossil record still need attention. The following part lists the most fundamental research needed to understand gastroliths function and occurrence. The topics are listed in order of their importance and practicability.

Crocodilian gastroliths

Research on a group of gastrolith-bearing aquatic vertebrates is particularly rewarding for crocodiles and I have therefore planned to carry out this research within the next years. Although there also exists much literature about gastroliths in extant crocodilians, most of it is anecdotal and scientifically superficial. Therefore, I have planned to carry out new research on wild and farm crocodiles in Australia, France, South Africa, Florida/USA, as well as in German zoos. Experiments will be conducted to revise the existing hypotheses for gastrolith function. In particular, possible interactions between the assumed functions will be investigated. Furthermore, simple-structured experiments, which already have proven their practicability during the experiments conducted on ostriches, will be executed on the crocodilians. They can be repeated or developed as necessary. A detailed comparison of the results from these experiments on crocodiles with the experimental results from my ostrich research will be conducted.

At the moment, cineradiographic studies on the digestion of alligators are conducted at Harvard University in cooperation with Leon Claessens. These cine-x experiments are comparable to the experiments reported by Bakker (1986) and Whittle and Ross (unpublished data), respectively, and are carried out to clarify the possible digestive role of crocodilian gastroliths.

Complete articulated skeletons with associated gastroliths are available for some fossil crocodilians. The crocodilians from the Eocene Messel site are particularly interesting because of their abundance and superb preservation. Research on this material will permit the direct comparison between living and fossil representatives of the same lithophagic vertebrate clade. This is especially interesting because the functional morphology of extant crocodilians is very similar to fossil species, and living representatives can be examined with relatively little efforts. Hence, this also offers the possibility for a case study to investigate possible changes of gastrolith preservation within the complete vertebrate fossil record.

Pinniped gastroliths

Pinnipeds are one of the three extant clades of vertebrates (the other two are crocodilians and birds) which regularly swallow stones (Baker, 1956; Whittle and Everhart, 2000, and see chapter II). Despite several scientific publications (e.g., Emery, 1941; Marlow, 1975; Laws, 1984; Taylor, 1993; Nordøy, 1995; Bryden, 1999), the function and the distribution of pinniped gastroliths is still unknown. That other marine vertebrates in the fossil record utilized stomach stones, for example plesiosaurs (Brown, 1904; Darby and Ojakangas, 1980; Everhart, 2000; Bartholomäus et al., 2004) or ichthyosaurs (Cheng et al., in revision) emphasizes the importance of gastroliths in extant marine vertebrates.

The extensive research conducted on gastroliths in extant birds and on dinosaur fossils (see previous chapters) allows to employ statistical analyses to any retrieved pinniped gastroliths for the first time. While research on living pinnipeds would certainly improve our knowledge on gastroliths function in aquatic animals and could probably settle the long-lasting discussion about the function of the stones in pinnipeds, this research can be problematic because of animal welfare regulations, large amount of travel necessary, and the inconsistent occurrence of gastroliths in seals and sea lions.

Therefore, I suggest basic research to approach the question of gastrolith function. Stomach contents of dead pinnipeds stored at research institutes in Europe and North America will be examined. Any existing gastroliths will be collected and used for ongoing analyses. These analyses will include:

- Total mass of gastroliths/comparison to body mass of animal
- Physical characteristics such as size, mass, and shape of gastroliths
- Rock type composition and possible origin
- Surface structure (some typical stones are to be wrapped individually directly after the stomach is opened and the unaltered surfaces can be examined using scanning electron microscopy)

This data will help to understand the occurrences of gastroliths in extant marine mammals and will allow new insights into the fossil record of gastroliths in marine vertebrates.

Permian vertebrates

Especially the species known from the Permian of Madagascar (*Tangasaurus*, *Barasaurus*, *Hovasaurus*) are interesting. The relationship between body mass and gastrolith mass as well as gastrolith size is important for our understanding of the phylogenetic position of these tetrapods and the gastrolith function in aquatic vertebrates. The available fossil material of these species is large enough for a major study and similar sized extant amphibians and reptiles can be studied for comparison.

Insectivorous species

This research should compare gastroliths occurrence and physical characteristics of the stones in several different clades of insectivorous vertebrates. Any correlation between gastroliths mass and body mass in insectivores would be especially interesting. Lizards, birds, pangolins, and echidnas should be sampled because they have been reported to carry gastroliths. The results from extant animals should be compared with fossil specimens, like the pangolins found in the Eocene lake deposits of Messel/Germany.

Psittacosaurus and *Caudipteryx*

Distribution and function of gastroliths in *Psittacosaurus* and *Caudipteryx* may help to understand the taphonomical filter in dinosaurs in general. *Psittacosaurus* is one of the few dinosaur species were gastroliths occur commonly. However, as many specimens are stored in private collections throughout the world, a comprehensive study may be difficult. The Chinese material of *Caudipteryx* may more easily be accessible.

Taphonomy studies

The decay process of large bird (e.g., ostriches) and crocodile carcasses should be observed in different sedimentological environments over a period of several months. Scavenging should be documented with an emphasis on the gizzard: is the gizzard swallowed as a whole or triturated before swallowing? What happens to the stones? If stones are separated from the guts, in which area around the carcass are they deposited?

References

Baker, A.A., 1956. The swallowing of stones by animals. The Victorian Naturalist, 73(6): 82-95.

Bakker, R.T., 1986. The Dinosaur Heresies. William Morrow, New York, 481 pp.

Bartholomäus, W.A., Reich, M., Krüger, F.J., Ansorge, J. and Wings, O., 2004. Das Liefergebiet der Magensteine von Baddeckenstedt. Bochumer geowissenschaftliche Arbeiten, 4: 103-131.

Brown, B., 1904. Stomach stones and food of plesiosaurs. Science, 20(501): 184-185.

Bryden, M.M., 1999. Stones in the stomachs of southern elephant seals. Marine Mammal Science, 15: 1370-1373.

Cheng, L., Wings, O., Chen, X. and Sander, M., in revision. Gastroliths in the Triassic ichthyosaur *Panjiangsaurus* from China. Journal of Paleontology.

Darby, D.G. and Ojakangas, R.W., 1980. Gastroliths from an Upper Cretaceous plesiosaur. Journal of Paleontology, 54(3): 548-556.

Emery, K.O., 1941. Transportation of rock particles by sea-mammals. Journal of Sedimentary Petrology, 11(2): 92-93.

Everhart, M.J., 2000. Gastroliths associated with plesiosaur remains in the Sharon Springs Member of the Pierre Shale (late Cretaceous), Western Kansas. Transactions of the Kansas Academy of Science, 103(1-2): 58-69.

Laws, R.M., 1984. Seals. In: R.M. Laws (Editor), Antarctic Ecology. 2. Academic Press, London, pp. 621-715.

Marlow, B.J., 1975. The comparative behaviour of the Australian sea lions *Neophoca cinerea* and *Phocarctos hookeri* (Pinnipedia: Otariidae). Mammalia, 39(2): 159-230.

Nordøy, E.S., 1995. Gastroliths in the harp seal *Phoca groenlandica*. Polar Research, 14(3): 335-338.

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(1296): 163-175.

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 (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 75-82.

Whittle, C.H. and Ross, F.D., An x-ray observation of crocodilian digestion (*Alligator mississippiensis*), and a review of the literature about stomach stones in large reptiles. unpublished manuscript.

APPENDIX I: Compilation of records of gastroliths in non-avian dinosaurs

SAURISCHIA

Theropoda

Allosaurus	(Ayer, 2000)
Baryonyx	(Charig and Milner, 1997)
Caudipteryx	(Ji et al., 1998)
Lourinhanosaurus	(Mateus, 1998)
Nqwebasaurus	(De Klerk et al., 2000)
Sinornithomimus	(Kobayashi et al., 1999; Kobayashi and Lü, 2003)
Podokesaurus	(Talbot, 1911)
Poekilopleuron	(Eudes-Delongchamps, 1838)
Syntarsus	(Whittle and Everhart, 2000)
Tyrannosaurus	(Currie, 1997)

Sauropodomorpha

Prosauropoda

Ammosaurus	(Whittle and Everhart, 2000)
Massospondylus	(Bond, 1955; Raath, 1974; Cooper, 1981; Galton, 1990)
Sellosaurus	(Huene, 1932; Galton, 1973; Galton, 1990)

Sauropoda

Apatosaurus	(Cannon, 1906; Wieland, 1906)
Barosaurus	(Brown, 1941)
Barosaurus africanus	(Janensch, 1929)
Barosaurus lentus	(Bird, 1985)
Brachiosaurid sauropod	(pers.comm., S. Hutt 2001)
Cedarosaurus	(Tidwell et al., 1999)
Chubutisaurus	Museo Paleontólogico Egidio Feruglio in Trelew/Argentina (pers. obs.)
Dicraeosaurus	(Janensch, 1929)
Dinheirosaurus	(Dantas et al., 1993; Dantas et al., 1998; Bonaparte and Mateus, 1999)
aff. *Rebbachisaurus*	(Calvo, 1994)
Seismosaurus	(Gillette, 1994)
Sonorasaurus	(Gillette et al., 1990; Ratkevich, 1998)
Vulcanodon	(Dodson, 1997)

ORNITHISCHIA

Ceratopsia

Psittacosaurus	(Osborn, 1924; Brown, 1941; Sereno, 1990; Xu, 1997)

Ankylosauria

Galtonia	CEU Dinosaur Museum in Price/Utah (pers. obs.)
Panoplosaurus	(Carpenter, 1990; Carpenter, 1997)

Stegosauria

"Near … stegosauroid dinosaur bones" (Brown, 1907)

Iguanodontia

Iguanodon	(Rivett, 1953; Rivett, 1956; Hölder and Norman, 1986)

Hadrosauridae

Edmontosaurus ("*Claosaurus*")	(Brown, 1907)

References:

Ayer, J., 2000. The Howe Ranch Dinosaurs/Die Howe Ranch Dinosaurier. Sauriermuseum Aathal, Aathal, 96 pp.

Bird, R.T., 1985. Bones for Barnum Brown: Adventures of a Dinosaur Hunter. Texas Christian Univ. Press, Fort Worth, 225 pp.

Bonaparte, J.F. and Mateus, O., 1999. A new diplodocid, *Dinheirosaurus lourinhanensis* gen. et sp. nov., from the Late Jurassic beds of Portugal. Revista del Museo Argentino de Ciencias Naturales, 5(2): 13-29.

Bond, G., 1955. A note on dinosaur remains from the Forest Sandstone (Upper Karoo). Occasional Papers of the National Museum of Southern Rhodesia, 2(20): 795-800.

Brown, B., 1907. Gastroliths. Science, 25(636): 392.

Brown, B., 1941. The last dinosaurs. Natural History, 48: 290-295.

Calvo, J.O., 1994. Gastroliths in sauropod dinosaurs. Gaia, 10: 205-208.

Cannon, G.L., 1906. Sauropodan gastroliths. Science, 24(604): 116.

Carpenter, K., 1990. Ankylosaur systematics: Example using *Panoplosaurus* and *Edmontonia (Ankylosauria: Nodosauridae)*. In: K. Carpenter and P.J. Currie (Editors), Dinosaur Systematics: Approaches and Perspectives. University Cambridge Press, Cambridge, pp. 281-298.

Carpenter, K., 1997. Ankylosaurs. In: J.O. Farlow and M.K. Brett-Surman (Editors), The Complete Dinosaur. Indiana University Press, Bloomington and Indianapolis, pp. 307-316.

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.

Cooper, M.R., 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life, and phylogenetic significance. Occasional Papers of the National Museums of Rhodesia, 6(10): 689-840.

Currie, P.J., 1997. Gastroliths. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 270.

Dantas, P., Freitas, C., Azevedo, T., Galopim de Carvalho, A.M., Santos, D., Ortega, F., Santos, V., Sanz, J.L., Silva, C.M.d. and Cachao, M., 1998. Estudo dos Gastrólitos do Dinossaurio *Lourinhasaurus* do Jurássico Superior Português. Actas do V Congresso Nacional de Geologia, 84(1): A87-A89.

Dantas, P., Freitas, C., Azevedo, T., Sanz, J.L., Galopim de Carvalho, A.M., Santos, D. and Santos, V., 1993. Sauropod gastroliths study from Upper Jurassic of Lourinhã region (western Portugal), Res. Comunic. "Premier Congrès Européen de Paléontologie" [First European Palaeontol. Congress 7-9 July]. European Paleontol. Ass., Lyon, pp. 34.

De Klerk, W.J., Forster, C.A., Sampson, S.D., Chinsamy, A. and Ross, C.F., 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. Journal of Vertebrate Paleontology, 20(2): 324-332.

Dodson, P., 1997. Paleoecology. In: P.J. Currie and K. Padian (Editors), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 515-519.

Eudes-Delongchamps, M., 1838. Mémoire sur le *Poekilopleuron bucklandi*, grand saurien fossile, intermédiare entre les crocodiles et les lezards. Mémoires de la Societe Linneenne de Normandie, 6: 37-146.

Galton, P.M., 1973. On the anatomy and relationships of *Efraasia diagnostica* (v. Huene) n. gen., a prosauropod dinosaur (Reptilia: Saurischia) from the Upper Triassic of Germany. Paläontologische Zeitschrift, 47: 229-255.

Galton, P.M., 1990. Basal Sauropodomorpha - Prosauropoda. In: D.B. Weishampel, P. Dodson and H. Osmolska (Editors), The Dinosauria. University of California Press, Berkeley, pp. 320-344.

Gillette, D.D., 1994. *Seismosaurus*, the Earth Shaker. Columbia University Press, New York, 205 pp.

Gillette, D.D., Bechtel, J.W. and Bechtel, P., 1990. Gastroliths of a sauropod dinosaur from New Mexico. Journal of Vertebrate Paleontology, 10(3, Suppl.): 24a.

Hölder, H. and Norman, D.B., 1986. Kreide-Dinosaurier im Sauerland. Naturwissenschaften, 73: 109-116.

Huene, F.v., 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Monographien zur Geologie und Palaeontologie, 1(4): XIII+361.

Janensch, W., 1929. Magensteine bei Sauropoden der Tendaguru-Schichten. Palaeontographica, Supplement, VII(2): 135-144.

Ji, Q., Currie, P.J., Norell, M.A. and Ji, S.-A., 1998. Two feathered dinosaurs from northeastern China. Nature, 393(6687): 753-761.

Kobayashi, Y. and Lü, J.-C., 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. Acta Palaeontologica Polonica, 48(2): 235-259.

Kobayashi, Y., Lu, J.-C., Dong, Z.-M., Barsbold, R., Azuma, Y. and Tomida, Y., 1999. Herbivorous diet in an ornithomimid dinosaur. Nature, 402: 480-481.

Mateus, O., 1998. *Lourinhanosaurus antunesi*, a new Upper Jurassic allosauroid (Dinosauria: Theropoda) from Lourinhã, Portugal. Memórias da Academia de Ciências de Lisboa, 37: 111-124.

Osborn, H.F., 1924. *Psittacosaurus* and *Protiguanodon*: two Lower Cretaceous iguanodonts from Mongolia. American Museum Noviates, 127: 1-16.

Raath, M.A., 1974. Fossil vertebrate studies in Rhodesia: Further evidence of gastroliths in prosauropod dinosaurs. Arnoldia, 7(5): 1-7.

Ratkevich, R., 1998. A new Cretaceous brachiosaurid dinosaur from Southern Arizona. The Journal of the Arizona-Nevada Academy of Science, 31(1): 71-82.

Rivett, W.H.E., 1953. Saurian remains from the Weald Clay at Ockley, Surrey. South Eastern Naturalist, 58: 36-37.

Rivett, W.H.E., 1956. Reptilian bones from the Weald Clay. Proceedings of the Geological Society of London, 1540: 110-111.

Sereno, P.C., 1990. Psittacosauridae. In: D.B. Weishampel, P. Dodson and H. Osmolska (Editors), The Dinosauria. University of California Press, Berkeley, pp. 579-592.

Talbot, M., 1911. *Podokesaurus holyokensis*, a new dinosaur from the Triassic of the Connecticut Valley. American Journal of Science, 31(4): 469-479.

Tidwell, V., Carpenter, K. and Brooks, W., 1999. New sauropod from the Lower Cretaceous of Utah, USA. Oryctos, 2: 21-37.

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 (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 75-82.

Wieland, G.R., 1906. Dinosaurian gastroliths. Science, 23(595): 819-821.

Xu, X., 1997. A new psittacosaur (*Psittacosaurus mazongshanensis*, sp. nov.) from Mazongshan Area, Gansu Province, China. In: Z. Dong (Editor), Sino-Japanese Silk Road Dinosaur Expedition. China Ocean Press, Beijing, pp. 48-67.

APPENDIX II: Compilation of records of gastroliths in extant bird species

While this list is far from being complete, it is aimed to be the most comprehensive list of lithophagic birds yet published. Probably most species mentioned in the existing literature are included. Because the minimum grain size for gastroliths was not determined or defined in some publications, all species with sediment (including mud) in the digestive tract are listed.

The cited references are not complete: several species are the topic of many papers, e.g., the Ring-necked Pheasant or the House Sparrow. Cited is mostly the oldest reference found, not necessarily the most significant reference. The systematic classification follows Cracraft (1988), Sibley and Ahlquist (1990), Hoyo et al.(1992), and Mindell et al. (1997).

Struthioniformes

Struthionidae (Ostriches)	
Struthio camelus (Ostrich)	(see chapter III)
Rheidae (Rheas)	
Rhea americana (Greater Rhea)	(Hoyo et al., 1992; Whittle and Everhart, 2000)
Casuariidae (Cassowaries)	
Casuarius bennetti (Dwarf Cassowary)	(Hoyo et al., 1992)
Apteryidae (Kiwis)	
Apteryx australis (Brown Kiwi)	(Reid et al., 1982)
Dromaiidae (Emus)	
Dromaius novaehollandiae (Larger Emu)	(Hoyo et al., 1992)

Tinamiformes

Tinamidae (Tinamous)	
Eudromia elegans (Elegant Crested Tinamou)	(Hoyo et al., 1992)
Nothoprocta pentlandii (Andean Tinamou)	(Hoyo et al., 1992)
Crypturellus soui (Little Tinamou)	(Hoyo et al., 1992)
Tinamus guttatus (White-thoated Tinmou)	(Hoyo et al., 1992)

Galliformes (Domestic Fowl and Game Birds)

Phasianidae	
Colinus virginianus (Northern Bobwhite)	(Gionfriddo and Best, 1996)
Coturnix coturnix (Common Quail)	(Jacobi, 1900; Mangold, 1927)
Coturnix pectoralis (Stubble Quail)	(McKeown, 1934)
Falcipennis canadensis (Spruce Grouse)	(Pendergast and Boag, 1970)
Gallus domesticus (Domestic Chick)	(Lambrecht, 1933; Hogstad, 1988)
Numida meleagris (Helmeted Guinea-Fowl)	(Ayeni et al., 1983)
Perdix perdix (Common partridge)	(Jacobi, 1900; Lambrecht, 1933) (Mangold, 1927; Weigand, 1980)
Phasianus colchicus (Pheasant)	(Mangold, 1927; Lambrecht, 1933)
Synoicus sordicus (Sombre Brown Quail)	(Mathews, 1909)
Synoicus ypsilophorus (Brown Quail)	(White, 1917)
Turnix castanonota (Chestnut-backed Quail)	(White, 1917)
Turnix maculosa (Red-backed Quail)	(Mathews, 1909)
Turnix melanotus (Black-backed Quail)	(White, 1917)
Turnix velox (Little Quail)	(Mathews, 1909)
Tetraonidae	
Lagopus lagopus (Whillow Ptarmigan)	(Norris et al., 1975)
Lagopus leucurus (White-Tailed Ptarmigan)	(May and Braun, 1973)
Lagopus scoticus (Red Grouse)	(Thomson, 1964)
Bonasa bonasia (Hazel Grouse)	(Jacobi, 1900; Porkert and Höglund, 1984)
Tetrao urogallus (Western Capercaillie)	(Jacobi, 1900; Mangold, 1927; Lambrecht, 1933; Porkert and Höglund, 1984)

Tetrao tetrix (Black Grouse, Blackgame)	(Jacobi, 1900; Mangold, 1927; Lambrecht, 1933; Porkert and Höglund, 1984)
Megapodidae	
Leipoa ocellata (Malleefowl)	(Booth, 1986; Kentish and Westbrooke, 1994)
Meleagrididae	
Meleagris gallopavo (Wild Turkey)	(Lambrecht, 1933; Schorger, 1960)

Anseriformes (Ducks, Geese, Swans)

Anatidae (Waterfowl)	
Amazonetta brasiliensis (Brazilian Teal)	(Whittle and Everhart, 2000)
Anas acuta (Pintail)	(Schäfer, 1962; Thomas et al., 1977)
Anas castanea (Chestnut Teal)	(Norman and Brown, 1985)
Anas clypeata (Shoveler)	(Thomas et al., 1977)
Anas crecca (Teal)	(Thomas et al., 1977)
Anas (*Querquedula*) *gibberifrons* (Grey Teal)	(McKeown, 1934; Norman and Brown, 1985)
Anas platyrhynchos (Mallard)	(Thomas et al., 1977; Trost, 1981)
Anas penelope (Wigeon)	(Thomas et al., 1977)
Anas rhynchotis (Australian Shoveler)	(Norman and Brown, 1985)
Anas strepera (Gadwall)	(Thomas et al., 1977)
Anas superciliosus (Black Duck)	(McKeown, 1934)
Anas superciliosa (Pacific Black Duck)	(Norman and Brown, 1985)
Anser arvensis brachyrhynchus (Pink-footed Goose)	(Schäfer, 1962; Thomson, 1964)
Anser canagicus (Emperor Goose)	(Eisenhauer and Kirkpatrick, 1977)
Anser domesticus (Domestic goose)	(Lambrecht, 1933)
Anser fabalis (Bean Goose)	(Schäfer, 1962)
Aythya affinis (Lesser Scaup)	(Whittle and Everhart, 2000)
Aythya australis (Hardhead)	(Norman and Brown, 1985) (McKeown, 1934)
Aythya ferina (Porchard)	(Thomas et al., 1977)
Aythya fuligula (Tufted Duck)	(Thomas et al., 1977)
Biziura lobata (Musk Duck)	(McKeown, 1934; Norman and Brown, 1985)
Branta leucopsis (Barnacle Goose)	(Schäfer, 1962)
Chenonetta jubata (Maned Duck)	(McKeown, 1934; Norman and Brown, 1985)
Coscoroba coscoroba (Coscoroba Swan)	(Whittle and Everhart, 2000)
Cyanochen cyanopterus (Blue-winged Goose)	(Whittle and Everhart, 2000)
Cygnus cygnus (Whooper Swan)	(Thomson, 1964)
Cygnus olor (Mute Swan)	(Owen and Cadbury, 1975; Thomas et al., 1977)
Cygnus columbianus (Bewick's Swan)	(Owen and Cadbury, 1975; Thomas et al., 1977)
Histrionicus histrionicus (Harlequin Duck)	(Vermeer, 1983)
Malacorhynchus membranaceus (Pink-eared Duck)	(Norman and Brown, 1985)
Melanitta nigra (Black Scoter)	(Schäfer, 1962)
Mergus merganser (Common merganser)	(Jacobi, 1900)
Mergus serrator (Red-breasted merganser)	(Jacobi, 1900)
Oxyura australis; (Blue-billed Duck)	(Norman and Brown, 1985)
Plectropterus gambensis (Spur-winged Goose)	(Halse, 1983)
Somateria mollissima (Common Eider)	(Whittle and Everhart, 2000)
Stictonetta naevosa; (Freckled Duck)	(Norman and Brown, 1985)
Tachyeres sp. (Steamer Duck)	(Whittle and Everhart, 2000)
Tadorna rufitergum (White-headed Shieldrake)	(White, 1917)
Tadorna tadornoides; (Australian Shelduck)	(Norman and Brown, 1985)

Piciformes (Woodpeckers)

Picidae (Woodpeckers)	
Jynx torquilla (Wryneck)	(Lambrecht, 1933)
Melanerpes erythrocephalus (Red-headed Woodpecker)	(Gionfriddo and Best, 1996)
Picus viridis (Green Woodpecker)	(Lambrecht, 1933)
Picoides villosus (Hairy Woodpecker)	(Lambrecht, 1933)
Dendrocopos minor (Lesser spotted Woodpecker)	(Lambrecht, 1933)

Coraciiformes (kingfishers and relatives)

Upupidae	
Upupa epops (Eurasian hoopoe)	(Jacobi, 1900; Lambrecht, 1933)

Strigiformes (Owls)

Strigidae	
Asio flammeus (Short-eared Owl)	(Rörig, 1906)

Cuculiformes (Cuckoos)

Cuculidae (Cuckoos)	
Coccyzus americanus (Yellow-billed Cuckoo)	(Gionfriddo and Best, 1996)
Cuculus canorus (Cuckoo)	(Lambrecht, 1933)

Psittaciformes (Parrots)

Cacatuidae (Cockatoos)	
Catatua galerita (White Cockatoo)	(McKeown, 1934)
Cacatua gymnopis (Bare-eyed Cockatoo)	(Mathews, 1909)
Cacatua (*Eolophus*) *roseicapilla* (Galah)	(McKeown, 1934)
Leptolophus (*Nymphicus*) *hollandicus* (Cockatiel)	(McKeown, 1934)
Psittacidae (Parrots)	
Barnardius barnardi (Ringneck (Mallee) Parrot)	(McKeown, 1934)
Psephotus haematonotus (Red-backed Parrot)	(McKeown, 1934)
Ptistes coccineopterus (Crimson-winged Parrot)	(White, 1917)
Platycercus browni (Smutty Parrot)	(White, 1917)
Platycercus flaveolus (Yellow Rosella)	(McKeown, 1934)
Polytelis swainsoni (Superb Parrot)	(McKeown, 1934)

Columbiformes (Doves and Pigeons)

Columbidae (pigeons and doves)	
Caloenas nicobarica (Nicobar Pigeon)	(Lambrecht, 1933)
Chalophaps longirostris (Long-billed Green-Pigeon)	(White, 1917)
Columba leucocephala (White-crowned Pigeon)	(Wiley and Wiley, 1979)
Columba livia (Rock Dove)	(Lambrecht, 1933; Gionfriddo and Best, 1996)
Columba palumbus (Wood Pigeon)	(Jacobi, 1900; Mangold, 1927)
Geopelia humeralis (Barred-shouldered Dove)	(Mathews, 1909)
Geopelia placida (Peaceful Dove)	(McKeown, 1934)
Geophaps smithi (Naked-eyed Partridge Pigeon)	(White, 1917)
Goura cristata (Common Crowned Pigeon)	(Lambrecht, 1933)
Lophophaps plumifera (Plumed-Pigeon)	(Mathews, 1909)
Phaps chalcoptera (Bronze-winged Pigeon)	(White, 1917)
Zenaida macroura (Mourning Dove)	(Chambers, 1963; Ward, 1964; Gionfriddo and Best, 1996)
Pteroclididae	
Syrrhaptes paradoxus (Pallas' Sandgrouse)	(Lambrecht, 1933)

Gruiformes (Cranes, Hemipodes, Gallinules)

Eurypygidae (Bustards)	
Eupodotis australis (Australian bustard)	(Cane, 1982) in (Webb, 1994)
Otidae	
Eupodotis vigorsii (Karoo Korhaan, Karoo Bustard)	(Boobyer and Hockey, 1994)
Chlamydotis Macqueenii (Maqueens Bustard)	(Lambrecht, 1933)
Otis tarda (Great Bustard)	(Lambrecht, 1933)
Tetrax tetrax (Little Bustard)	(Lambrecht, 1933)
Gruidae (Cranes)	
Grus cinerea (European Crane)	(Jacobi, 1900; Lambrecht, 1933)
Grus grus (Crane)	(Mangold, 1927)

Grus leucogeranus (Siberian Crane)	(Lambrecht, 1933)
Grus monacha (Hooded Crane)	(Whittle and Everhart, 2000)
Rallidae (Rails)	
Fulica atra (Coot)	(McKeown, 1934; Thomas et al., 1977)
Gallinula chloropus (Moorhen)	(Thomas et al., 1977)
Gallinula tenebrosa (Dusky Moorhen)	(McKeown, 1934)
Porphyrio bellus (Blue Bald-Cott)	(Mathews, 1909)
Porphyrio melanotus (Eastern Swamp Hen or Bald Cott)	(McKeown, 1934)

Falconiformes (Hawks, Eagles, Falcons, Caracaras)

Accipitridae	
Pandion haliaetus (Osprey)	(Rörig, 1906)
Falconidae	
Falco subbuteo (Eurasian Hobby)	(Rörig, 1906)
Falco peregrinus, (Peregrine Falcon)	(Rörig, 1906)

Ciconiiformes (Herons, Storks, New World Vultures and Relatives)

Ardeidae	
Notophoyx flavirostris (Piet Egret)	(Mathews, 1909)
Notophoyx novae-holladiae (White-fronted Heron)	(McKeown, 1934)
Threskiornithidae	
Plegadis falcinellus (Glossy Ibis)	(Lambrecht, 1933)
Threskiornis molucca (Australian White Ibis)	(McKeown, 1934)
Threskiornis spinicollis (Straw-Necked Ibis)	(McKeown, 1934)
Accipitridae	
Accipiter nisus (Sparrowhawk)	(Lambrecht, 1933)
Ciconidae	
Ciconia alba (White Stork)	(Lambrecht, 1933)

Passeriformes (Songbirds)

Paridae	
Parus ater (Coal Tit)	(Betts, 1955)
Parus caeruleus (Blue Tit)	(Betts, 1955)
Parus major (Great Tit)	(Betts, 1955; Royama, 1970)
Parus palustris (Marsh Tit)	(Betts, 1955)
Ploceidae (Weavers and Allies)	
Passer domesticus (House Sparrow)	(Gionfriddo and Best, 1995)
Passer hispaniolensis (Spanish Sparrow)	(Alonso, 1985)
Ploceus cucullatus (Village Weaver)	(Adegoke, 1983)
Prunellidae	
*Prunella collaris (*Alpine Accentor)	(Lambrecht, 1933)
Prunella modularis (Dunnock)	(Lambrecht, 1933; May and Braun, 1973; Martinez-Cabello et al., 1991)
Fringillidae (twinspots, firefinches, waxbills and mannikins)	
Bathilda ruficauda (Red-faced Finch)	(Hogstad, 1988)
Loxia curvirostra (Red Crossbill)	(Frost, 1985)
Munia flaviprymna (Yellow-rumped Finch)	(Mathews, 1909)
Neochmia phaeton (Crimson Finch)	(Mathews, 1909; White, 1917)
Poephilia acuticauda (Long-tailed Finch)	(Mathews, 1909)
Poephilia gouldiae (Gouldian Finch)	(Mathews, 1909)
Poephila personata (Masked Grass-Finch)	(White, 1917)
Serinus citrinella (Citril Finch)	(Frost, 1985)
Stictoptera annulosa (Black-ringed Finch)	(Mathews, 1909)
Estrildidae (twinspots, firefinches, waxbills and mannikins)	
Fringilla montifringilla (Brambling)	(Mathews, 1909)
Taeniopygia guttata castanotis (Zebra Finch)	(McKeown, 1934)
Timaliidae	
Panurus biarmicus (Bearded Tit)	(Spitzer, 1972)
Turdidae	

Catharus guttatus (Hermit Thrush)	(Gionfriddo and Best, 1996)
Turdus iliacus (Redwing)	(Soler et al., 1988a; Soler et al., 1988b)
Turdus migratorius (American Robin)	(Gionfriddo and Best, 1996)
Turdus philomelos (Song Thrush)	(Tejero et al., 1984)
Turdus viscivorus (Mistle Thrush)	(Pérez-González and Soler, 1990)
Corvidae	
Corvus brachyrhynchos (American Crow)	(Beer and Tidyman, 1942; Gionfriddo and Best, 1996)
Corvus corax (Common Raven)	(Soler et al., 1993)
Corvus cornix (Dun Crow, Hooded crow)	(Jacobi, 1900; Mangold, 1927; Lambrecht, 1933)
Corvus corone (Carrion Crow)	(Lambrecht, 1933; Soler et al., 1993)
Corvus frugilegus (Rook)	(Jacobi, 1900; Mangold, 1927; Lambrecht, 1933; Porter, 1979)
Corvus monedula (Eurasian Jackdaw)	(Jacobi, 1900; Mangold, 1927; Lambrecht, 1933; Soler et al., 1990; Soler et al., 1993)
Cyanocitta cristata (Blue Jay)	(Gionfriddo and Best, 1996)
Garrulus glandarius (Jay)	(Jacobi, 1900; Mangold, 1927; Lambrecht, 1933)
Nucifraga caryocatactes (Nutcracker)	(Lambrecht, 1933)
Pica pica (Black-Billed Magpie)	(Mangold, 1927; Lambrecht, 1933; Soler et al., 1993)
Pyrrhocorax pyrrhocorax (Red-billed Chough)	(Soler et al., 1993)
Sturnidae	
Sturnus vulgaris (Starling)	(McKeown, 1934; Thomson, 1964)
Cinclidae	
Cinclus aquaticus (European Dipper)	(Lambrecht, 1933)
Cinclus cinclus (Dipper)	(Thomson, 1964)
Motacillidae	
Anthus novaeseelandiae (Australasian Pipit)	(Garrick, 1981)
Anthus pratensis (Meadow Pipit)	(Walton, 1984)
Corcoracidae	
Corcorax melanoramphus (White-winged Chough)	(McKeown, 1934)
Tyrannidae	
Tyrannus tyrannus (Eastern Kingbird)	(Gionfriddo and Best, 1996)
Hirundinidae	
Hirundo rustica (Barn Swallow)	(Barrentine, 1980; Gionfriddo and Best, 1996)
Alaudidae	
Alauda arvensis (Sky Lark)	(Garrick, 1981)
Eremophila alpestris (Horned Lark)	(Gionfriddo and Best, 1996)
Bombycillidae	
Bombycilla cedorum (Cedar Waxwing)	(Gionfriddo and Best, 1996)
Emberizidae (Buntings, Seedeaters and Allies)	
Chondestes grammacus (Lark Sparrow)	(Gionfriddo and Best, 1996)
Emberiza calandra (Corn Bunting)	(McLelland, 1979)
Melospiza melodia (Song Sparrow)	(Gionfriddo and Best, 1996)
Passerculus sandwichensis (Savannah Sparrow)	(Gionfriddo and Best, 1996)
Passerella iliaca (Fox Sparrow)	(Gionfriddo and Best, 1996)
Pooecetes gramineus (Vesper Sparrow)	(Gionfriddo and Best, 1996)
Spizella arborea (American Tree Sparrow)	(West, 1967; Gionfriddo and Best, 1996)
Spizella passerina (Chipping Sparrow)	(Crook, 1975; Gionfriddo and Best, 1996)
Cardinalidae (Cardinals, Grosbeaks, and Allies)	
Cardinalis cardinalis (Northern Cardinal)	(Gionfriddo and Best, 1996)
Passerina cyanea (Indigo Bunting)	(Gionfriddo and Best, 1996)
Spiza americana (Dickcissel)	(Gionfriddo and Best, 1996)
Icteridae (Blackbirds, etc.)	
Agelaius phoeniceus (Red-winged Blackbird)	(Bird and Smith, 1964; Mott et al., 1972; Gionfriddo and Best, 1996)
Molothrus ater (Brown-headed Cowbird)	(Gionfriddo and Best, 1996)
Quiscalus quiscula (Common Grackle)	(Gionfriddo and Best, 1996)
Sturnella neglecta (Western Meadowlark)	(Gionfriddo and Best, 1996)
Troglodytidae	
Troglodytes aedon (House Wren)	(Mayoh and Zach, 1986; Gionfriddo and Best, 1996)

Parulidae	
Geothlypis trichas (Common Yellowthroat)	(Gionfriddo and Best, 1996)
Sylviidae	
Sylvia cinerea (Whitethroat)	(Lambrecht, 1933)
Sylvia melanocephala (Sardinian Warbler)	(Tejero et al., 1983)
Laniidae	
Lanius minor (Lesser Grey Shrike)	(Lambrecht, 1933)
Sittidae	
Sitta europaea caesia (Southern Nuthatch)	(Lambrecht, 1933)
Muscicapidae	
Erithacus rubecula (European Robin)	(Herrera, 1977)

Podicipediformes (Grebes)

Podicipedidae (Grebes)	
Podiceps auritus (Horned Grebe)	(Schäfer, 1962)
Podicipes gularis (Black-throated Grebe)	(White, 1917)
Podiceps ruficollis (Dabchick)	(McKeown, 1934; Schäfer, 1962)

Gaviiformes (Divers)

Gavidae	
Gavia arctica (Black-Throated Diver)	(Schäfer, 1962)
Gavia immer (Great Northern Diver, Common Loon)	(Lambrecht, 1933; Schäfer, 1962)
Gavia spp. (Adult diver)	(Thomson, 1964)
Gavia stellata (Red-throated Loon or Diver)	(Lambrecht, 1933)

Sphenisciformes (Penguins)

Spheniscidae	
Aptenodytes forsteri (Large Emperor Penguin)	(Sclater, 1888)
Spheniscus magellanicus (Magellanic Penguin)	(Boswall and MacIver, 1975)

Pelecaniformes (Pelicans, Frigate Birds, Gannets, Cormorants)

Phalacrocoracidae	
Phalacrocorax atriceps (Imperial Shag)	(Siegel-Causey, 1990)
Phalacrocorax brasilianus(Neotropic cormorant)	(Siegel-Causey, 1990)
Phalacrocorax magellanicus (Rock Shag)	(Siegel-Causey, 1990)
Phalacrocorax spp. (Cormorants)	(Thomson, 1964)

Charadriiformes (Gulls and Shore birds)

Charadriidae (Plovers)	(Lambrecht, 1933)
Charadrius alexandrinus (Snowy Plover)	(Schäfer, 1962)
Charadius apricarius (Golden Plover)	(Lambrecht, 1933)
Charadrius hiaticula (Common Ringed Plover)	(Schäfer, 1962)
Charadrius melanops (Black-fronted Dotterel)	(McKeown, 1934)
Charadrius vociferus (Killdeer)	(Rundle, 1982; Gionfriddo and Best, 1996)
Erythrogonys cinctus (Red-kneed Dotterel)	(Mathews, 1909; McKeown, 1934)
Lobibyx novae-hollandiae (Australian Spur-winged Plover)	(McKeown, 1934)
Lobivanellus personatus (Masked Plover)	(White, 1917)
Vanellus (*Zonifer*) *tricolor* (Banded Plover)	(McKeown, 1934)
Vanellus vanellus (Common Peewit)	(Jacobi, 1900)
Haematopodidae (Oystercatchers)	
Haematopus ostralegus (Oystercatcher)	(Schäfer, 1962)
Laridae (Gulls, Terns)	
Larus canus (Common Gull)	(Lambrecht, 1933; Schäfer, 1962)
Larus marinus (Great Black-Backed Gull)	(Schäfer, 1962)
Larus ridibundus (Black-Headed Gull)	(Lambrecht, 1933; Schäfer, 1962)
Recurvirostridae (Stilts, Avocets)	
Himantopus leucocephalus (White-headed Stilt)	(White, 1917; McKeown, 1934)

Himantopus himantopus (Black-winged Stilt)	(Serrano and Cabot, 1983)
Scolopacidae (Sandpipers)	
Calidris alpina (Dunlin)	(Worrall, 1984)
Gallinago gallinago (Snipe)	(Thomas, 1975)
Gallinago megala (Swinehoe Snipe)	(White, 1917)
Heteropygia aurita (Sharp-tailed Stint)	(Mathews, 1909)
Limosa limosa (Black-tailed Godwit)	(Schäfer, 1962)
Mesoscolopax minutus (Little Whimbrel)	(Mathews, 1909)
Numenius arquata (Curlew)	(Schäfer, 1962)
Pisobia acuminata (Sharp-tailed Stint)	(White, 1917)
Scolopax rusticola (Eurasian Woodcock)	(Koubek, 1986)
Burhinidae	
Burhinus oedicnemus oedicnemus (Stone-Curlew)	(Lambrecht, 1933)
Jacanidae (Jacanas)	
Irediparra gallinacea (Comb-crested Jacana)	(Mathews, 1909)

Phoenicopteriformes (Flamingos)

Phoenicopteridae	
Phoenicopterus roseus (Greater Flamingo)	(Lambrecht, 1933)
Phoenicopterus ruber (Flamingo)	(Thomson, 1964)
Phoenicopterus minor (Lesser Flamingo)	(Thomson, 1964)

Procellariiformes (Albatrosses and Fulmars)

Procellariidae (Shearwaters, Petrels)	
Daption capense (Cape Pigeon)	(Murphy, 1936)
Puffinus tenuirostris (Mutton-bird)	(Lewis, 1946)

Caprimulgiformes (Nightbirds)

Caprimulgidae (Nightjars & Allies)	
Caprimulgus europaeus (Eurasian Nightjar)	(Lambrecht, 1933)

References:

Adegoke, A., 1983. Diet of the village weaver, *Ploceus cucullatus*. Malimbus, 5: 79-89.

Alonso, J., 1985. Grit in the gizzard of Spanish sparrows (*Passer hispaniolensis*). Die Vogelwarte, 33: 135-143.

Ayeni, J., Olowo-Okorun, M.O. and Aire, T.A., 1983. The biology and utilization of helmet quinea-fowl (*Numida meleagris galeata* Pallas) in Nigeria. III Gizzard weights and contents. African Journal of Ecology, 21: 11-18.

Barrentine, C.D., 1980. The ingestion of grit by nestling Barn Swallows. Journal of Field Ornithology, 51(4): 368-371.

Beer, J. and Tidyman, W., 1942. The substitution of hard seeds for grit. Journal of Wildlife Management, 6(1): 70-82.

Betts, M.M., 1955. The food of titmice in oak woodland. Journal of Animal Ecology, 24: 282-323.

Bird, R.D. and Smith, L.B., 1964. The food habits of the red-winged blackbird, *Agelaius phoeniceus*, in Manitoba. The Canadian Field-Naturalist, 78: 179-186.

Boobyer, M.G. and Hockey, P.A.R., 1994. Dietary opportunism in the Karoo korhaan - consequence of a sedentary life-style in an unpredictable environment. Ostrich, 65(1): 32-38.

Booth, D.T., 1986. Crop and gizzard contents of two malleefowl. Emu, 86: 51-53.

Boswall, J. and MacIver, D., 1975. The magellanic penguin *Spheniscus magellanicus*. In: B. Stonehouse (Editor), The Biology of Penguins. Macmillan, London, pp. 271-305.

Cane, S., 1982. Bustard gastroliths in the archaeological record. Australian Archaeology, 14: 25-34.

Chambers, G.D., 1963. Corn, a staple food of doves wintering in northern Missouri. Journal of Wildlife Management, 27(3): 486-488.

Cracraft, J., 1988. The major clades of birds. In: M.J. Benton (Editor), The phylogeny and classification of the tetrapods. Systematics Association. Special Volume No. 35A. Clarendon Press, Oxford, pp. 333-355.

Crook, D., 1975. Chipping sparrows feeding grit to offspring. Wilson Bulletin, 87: 552.

Eisenhauer, D.I. and Kirkpatrick, C.M., 1977. Ecology of the emperor goose in Alaska. Wildlife Monograph, 57: 62.

Frost, M.P., 1985. Citril finches and crossbills eating minerals. British Birds, 78: 50.

Garrick, A., 1981. Diets of pipits and skylarks at Huirua Station, Tokomaru Bay, North Island, New Zealand. New Zealand Journal of Ecology, 4: 106-114.

Gionfriddo, J.P. and Best, L.B., 1995. Grit use by house sparrows: effects of diet and grit size. The Condor, 97: 57-67.

Gionfriddo, J.P. and Best, L.B., 1996. Grit-use pattern in North American birds: The influence of diet, body size, and gender. Wilson Bulletin, 108(4): 685-696.

Halse, S.A., 1983. Weight and particle size of grit in gizzards of spur-winged geese. Ostrich, 54: 180-182.

Herrera, C.M., 1977. Ecologia alimentacia del Petirrijo (*Erithacus rubecula*) durante su invernada en encinares del Sur de Espana. Doñana, Acta Vertebrata, 4: 35-59.

Hogstad, O., 1988. Foraging pattern and prey selecting of breeding bramlings *Fringilla montifringilla*. Fauna Norvegica Series C, Cinclus, 11: 27-39.

Hoyo, J.d., Elliott, A. and Sargatal, J., 1992. Handbook of the Birds of the World, 1: Ostrich to Ducks. Lynx Editions, Barcelona, 696 pp.

Jacobi, A., 1900. Die Aufnahme von Steinen durch Vögel. Arbeiten aus der Biologischen Abtheilung für Land- und Forstwirthschaft am Kaiserlichen Gesundheitsamte, 1: 223-254.

Kentish, B. and Westbrooke, M., 1994. Crop and gizzard contents of a road-dead malleefowl. The Emu, 93: 130-132.

Koubek, P., 1986. The spring diet of the woodcock (*Scolopax rusticola*). Folia zoologica, 35: 289-297.

Lambrecht, K., 1933. Magensteine (Gastrolithen), Handbuch der Palaeornithologie. Verlag von Gebrüder Borntraeger, Berlin, pp. 817-821.

Lewis, F., 1946. Feeding habits of the short-tailed shearwater (mutton-bird). The Emu, 45: 225-228.

Mangold, E., 1927. Die Bedeutung von Steinchen und Sand im Hühnermagen. Archiv für Geflügelkunde, 1: 145-152.

Martinez-Cabello, A., Soler, M. and Soler, J.J., 1991. Alimentacion del acentor comun (*Prunella modularis*) durante su invernada en el sureste de la peninsula Iberica. Ardeola, 38(2): 305-315.

Mathews, G.M., 1909. On the birds of north-west Australia. The Emu, 9(2): 53-65.

May, T.A. and Braun, C.E., 1973. Gizzard stones in adult white-tailed ptarmigan (*Lagopus leucurus*) in Colorado. Arctic and Alpine Research, 5: 49-57.

Mayoh, K.R. and Zach, R., 1986. Grit ingestion by nestling tree swallows and house wrens. Canadian Journal of Zoology, 64: 2090-2093.

McKeown, K.C., 1934. The food of birds from south western New South Wales. Records of the Australian Museum, 19(2): 113-135.

McLelland, J., 1979. Digestive system. In: A.S. King and J. McLelland (Editors), Form and Function in Birds. 1. Academic Press, New York, pp. 69-181.

Mindell, D.P., Sorenson, M.D., Huddleston, C.J., Miranda, H.C.J., Knight, A., Sawchuk, S.J. and Yuri, T., 1997. Phylogenetic relationships among and within select avian orders based on mitochondrial DNA. In: D.P. Mindell (Editor), Avian Molecular Evolution and Systematics. Academic Press, New York, pp. 211-247.

Mott, D.F., West, R.R., De Grazio, J.W. and Guarino, J.L., 1972. Foods of the red-winged blackbird in Brown County, South Dakota. Journal of Wildlife Management, 36(3): 983-987.

Murphy, R.C., 1936. The Oceanic Birds of South America. Macmillan, New York, 1245 pp.

Norman, F.I. and Brown, R.S., 1985. Gizzard grit in some Australian waterfowl. Wildfowl, 36: 77-80.

Norris, E., Norris, C. and Steen, J.B., 1975. Regulation and grinding ability of grit in the gizzard of Norwegian willow ptarmigan (*Lagopus lagopus*). Poultry Science, 54: 1839-1843.

Owen, M. and Cadbury, C.J., 1975. The ecology and mortality of swans at the Ouse Washes, England. Wildfowl, 26: 31-42.

Pendergast, B.A. and Boag, D.A., 1970. Seasonal changes in diet of spruce grouse in central Alberta. Journal of Wildlife Management, 34(3): 605-611.

Pérez-González, J.A. and Soler, M., 1990. Le regime alimentaire en automne-hiver de la grive draine *Turdus viscivorus* dans le sud-est de l'Espagne. Alauda, 58(3): 195-202.

Porkert, J. and Höglund, N., 1984. Zur Regulierung des Gritgehalts im Magen der Tetraoniden. Zeitschrift für Jagdwissenschaft, 30: 81-88.

Porter, R., 1979. Food of the rook (*Corvus frugilegus* L.) in Hawke's Bay, New Zealand. New Zealand Journal of Ecology, 6: 329-337.

Reid, B., Ordish, R. and Harrison, M., 1982. An analysis of the gizzard contents of 50 North Island brown kiwis, *Apteryx australis* Mantelli, and notes on feeding observations. New Zealand Journal of Ecology, 5: 76-85.

Rörig, G., 1906. Magenuntersuchungen heimischer Raubvögel. Arbeiten aus der Kaiserlichen Biologischen Anstalt für Land- und Forstwirtschaft, 5(5): 237-265.

Royama, T., 1970. Factors governing the hunting behaviour and selection of food by the great tit (*Parus major* L.). Journal of Animal Ecology, 39: 619-668.

Rundle, W.D., 1982. A case for esophageal analysis in shorebird food studies. Journal of Field Ornithology, 53(3): 249-257.

Schäfer, W., 1962. Aktuo-Paläontologie nach Studien in der Nordsee. Kramer, Frankfurt/M., 666 pp.

Schorger, A., 1960. The crushing of carya nuts in the gizzard of the turkey. Auk, 77: 337-340.

Sclater, P.L., 1888. Notes on the emperor penguin (*Aptenodytes forsteri*). Ibis, 6: 325-334.

Serrano, P. and Cabot, J., 1983. Gastrolitos en cigüeñuela (*Himantopus himantopus*). Doñana, Acta Vertebrata, 10: 71-76.

Sibley, C.G. and Ahlquist, J.E., 1990. Phylogeny and Classification of Birds: A Study in Molecular Evolution. Yale University Press, New Haven, 976 pp.

Siegel-Causey, D., 1990. Gastroliths assist digestion in shags. Notornis, 37: 70-72.

Soler, J.J., Soler, M. and Martínez, J.G., 1993. Grit ingestion and cereal consumption in five corvid species. Ardea, 81: 143-149.

Soler, M., Alcalá, N. and Soler, J.J., 1990. Alimentacion de la grajilla *Corvus monedula* en tres zonas del sur de Espana. Doñana, Acta Vertebrata, 17(1): 17-48.

Soler, M., Pérez-Gonzáles, J.A., Tejero, E. and Camacho, I., 1988a. Alimentacion del zorzal alirrojo (*Turdus iliacus*) durante su invernada en olivares de Jaen (sur de Espana). Ardeola, 35(2): 183-196.

Soler, M., Pérez-Gonzáles, J.A., Tejero, E. and Camacho, I., 1988b. Alimentacion del Zorzal Alirrojo (*Turdus iliacus*) durante su invernada en olivares de Jaen (sur de Espana) [Diet of the Redwing (*Turdus iliacus*) during fall in olive groves in Jaen in Spain]. Ardeola, 35(2): 183-196.

Spitzer, G., 1972. Jahreszeitliche Aspekte der Biologie der Bartmeise (*Panurus biarmicus*). Journal für Ornithologie, 113: 241-275.

Tejero, E., Camacho, I. and Soler, M., 1983. La alimentacion de la curruca cabercinegra (*Sylvia melanocephala*, Gmelin 1788) en olivares de la provincia de Jaen (otono-invierno). Doñana, Acta Vertebrata, 10(1): 133-153.

Tejero, E., Soler, M. and Camacho, I., 1984. Alimentacion del zorzal comun (*Turdus philomelos* Brehm, 1831) en olivares de la provinica de Jaén (otoño-invierno). Anales del Instituto Nacional de Investigaciones Agrarias/Ministerio de Agricultura, Pesca y Alimentación. Serie forestal, 8: 9-32.

Thomas, G.J., 1975. Ingested lead pellets in waterfowl at the Ouse Washes, England 1968-73. Wildfowl, 26: 43.

Thomas, G.J., Owen, M. and Richards, P., 1977. Grit in waterfowl at the Ouse Washes, England. Wildfowl, 28: 136-138.

Thomson, A.L., 1964. A New Dictionary of Birds. McGraw-Hill, New York, 928 pp.

Trost, R.E., 1981. Dynamics of grit selection and retention in captive mallards. Journal of Wildlife Management, 45: 64-73.

Vermeer, K., 1983. Diet of the harlequin duck in the Strait of Georgia, British Columbia. Murrelet, 64: 55-57.

Walton, K.C., 1984. Stomach stones in meadow pipits *Anthus pratensis*. Bird Study, 31: 39-42.

Ward, A.L., 1964. Foods of the mourning dove in eastern Colorado. Journal of Wildlife Management, 28(1): 152-157.

Webb, C., 1994. Lithic assemblage formation in semi-arid Australia: the role of emu gastroliths. Journal of Archaeological Science, 21(2): 145-152.

Weigand, J.P., 1980. Ecology of the Hungarian partridge in north-central Montana. Wildlife Monograph, 74: 106.

West, G.C., 1967. Nutrition of tree sparrows during winter in central Illinois. Ecology, 48: 58-67.

White, H.L., 1917. North Australian birds (observed by McLennan, W.). The Emu, 16(4): 205-231.

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 (Editors), Dinosaurs of New Mexico - New Mexico Museum of Natural History and Science Bulletin. Volume 17, pp. 75-82.

Wiley, J.W. and Wiley, B.N., 1979. The biology of the white-crowned pigeon. Wildlife Monograph, 64: 54.

Worrall, D., 1984. Diet of the dunlin, *Calidris alpina* in the Severn Estuary. Bird Study, 31: 203-212.

APPENDIX III: Raw data of ostrich examination. Part A: German farm ostriches

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Animal Age [months]	Provent Contents [g]	Provent Stones [g]	Provent >20 mm [g]	Provent 8-20 mm [g]	Provent 4-8 mm [g]	Provent 2-4 mm [g]	Provent <2 mm [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Gizzard >20 mm [g]	Gizzard 8-20 mm [g]	Gizzard 4-8 mm [g]	Gizzard 2-4 mm [g]	Gizzard <2 mm [g]	Complete Contents [g]	Complete Stones [g]	Complete >20 mm [g]	Complete 8-20 mm [g]	Complete 4-8 mm [g]	Complete 2-4 mm [g]	Complete <2 mm [g]
25.11.2000	female DM + MM	Female	110	12	1775	746	389	269	37	13	38	1035	581	83	314	77	27	80	2810	1327	472	583	114	40	118
25.11.2000	male DM+MM	Male	130	16	3747	478	0	152	202	46	78	1534	965	0	292	464	111	98	5281	1443	0	444	666	157	176
03.02.2001	3	Female	120	48	2461	564	0	390	140	20	14	1076	690	0	362	265	48	15	3537	1254	0	752	405	68	29
03.02.2001	4	Male	130	36	2594	292	0	170	100	10	12	1200	762	83	410	234	26	9	3794	1054	83	580	334	36	21
03.02.2001	2	Male	140	60	2209	321	63	200	48	5	5	1583	957	54	680	195	17	11	3792	1278	117	880	243	22	16
03.02.2001	1	Female	100	12	910	193	0	123	63	3	4	1126	787	0	495	266	18	8	2036	980	0	618	329	21	12
12.02.2001	3D+4MW	Female	90	12	1765	219	0	158	45	7	9	833	410	0	320	70	10	10	2598	629	0	478	115	17	19
12.02.2001	5M	Female	130	30	0	0	0	0	0	0	0	703	413	0	132	247	29	5	703	413	0	132	247	29	5
12.02.2001	1+2M	Male	100	12	1148	246	0	170	70	4	2	1333	923	17	679	201	22	4	2481	1169	17	849	271	26	6
19.02.2001	14+15	Male	115	15	1211	161	0	58	75	12	16	1834	1209	0	565	516	63	65	3045	1370	0	623	591	75	81
19.02.2001	10+11	Female	110	13	2750	260	0	94	136	13	17	1511	728	0	287	387	29	25	4261	988	0	381	523	42	42
19.02.2001	16+17	Male	95	14	1507	535	29	340	113	12	41	1701	1118	200	683	158	20	57	3208	1653	229	1023	271	32	98
19.02.2001	12+13	Male	100	14	2058	139	0	67	46	6	20	1641	875	0	533	201	31	110	3699	1014	0	600	247	37	130
19.02.2001	9+8	Male	95	13	1941	273	49	124	67	8	25	1470	765	73	361	254	23	54	3411	1038	122	485	321	31	79
03.03.2001	6+7	Male	110	15	691	92	0	26	58	5	3	1148	845	0	384	409	39	13	1839	937	0	410	467	44	16
23.03.2001	23+24	Female	110	60	1596	125	0	83	34	3	5	1517	775	0	599	149	12	15	3113	900	0	682	183	15	20
23.03.2001	19+20	Female	100	14	784	129	0	117	9	2	1	539	207	0	126	51	28	2	1323	336	0	243	60	30	3
23.03.2001	21+22	Female	110	48	800	15	0	6	6	1	2	1617	843	0	515	294	21	13	2417	858	0	521	300	22	15
23.03.2001	17+18	Male	140	60	1908	230	0	90	118	15	7	1755	983	0	487	434	57	5	3663	1213	0	577	552	72	12
31.03.2001	26+25	Female	130	72	1764	220	0	142	71	6	1	1518	925	0	590	304	29	2	3282	1145	0	732	375	35	3
31.03.2001	28+27	Female	110	36	2122	181	0	153	27	1	0	1270	761	0	570	183	6	2	3392	942	0	723	210	7	2
21.10.2001	5+6	Female	90	17	1537	48	0	13	19	5	11	970	479	0	263	171	32	13	2507	527	0	276	190	37	24
21.10.2001	1+2	Male	95	16	1022	55	0	23	26	6	0	1468	771	0	280	408	71	12	2490	826	0	303	434	77	12
21.10.2001	14+13	Male	90	15	2594	152	0	65	60	12	15	1048	550	0	340	159	45	6	3642	702	0	405	219	57	21
21.10.2001	11+12	Female	85	15	3890	74	0	34	28	6	6	1155	705	0	273	386	35	11	5045	779	0	307	414	41	17
21.10.2001	7+8	Male	85	13	3902	148	0	67	44	16	21	1411	610	0	263	259	69	19	5313	758	0	330	303	85	40
21.10.2001	3+4	Male	90	14	2189	25	0	5	13	3	4	1053	528	0	176	256	85	11	3242	553	0	181	269	88	15
21.10.2001	9+10	Female	90	16	1289	28	0	12	9	4	3	1243	648	0	328	246	49	25	2532	676	0	340	255	53	28
02.11.2001	1+2	Male	100	18	1366	152	0	56	76	13	7	955	382	0	134	219	21	8	2321	534	0	190	295	34	15

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Animal Age [months]	Provent Contents [g]	Provent Stones [g]	Provent >20 mm [g]	Provent 8-20 mm [g]	Provent 4-8 mm [g]	Provent 2-4 mm [g]	Provent <2 mm [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Gizzard >20 mm [g]	Gizzard 8-20 mm [g]	Gizzard 4-8 mm [g]	Gizzard 2-4 mm [g]	Gizzard <2 mm [g]	Complete Contents [g]	Complete Stones [g]	Complete >20 mm [g]	Complete 8-20 mm [g]	Complete 4-8 mm [g]	Complete 2-4 mm [g]	Complete <2 mm [g]
02.11.2001	3+4	Male	80	16	994	390	27	251	87	20	5	418	249	15	124	81	22	7	1412	639	42	375	168	42	12
09.11.2001	5+6	Male	90	15	485	43	0	16	2	2	23	3296	536	41	421	41	9	24	3781	579	41	437	43	11	47
09.11.2001	7+8	Female	85	16	1685	273	0	52	45	26	150	1372	684	0	388	206	38	52	3057	957	0	440	251	64	202
16.11.2001	9+10	Female	100	18	858	18	0	5	7	3	3	1822	1156	0	507	132	59	458	2680	1174	0	512	139	62	461
16.11.2001	11+12	Male	90	16	1971	190	0	117	47	9	17	1991	1018	0	264	576	125	53	3962	1208	0	381	623	134	70
23.11.2001	17+18	Male	100	18	2213	871	76	240	8	54	493	1935	1280	0	408	88	117	667	4148	2151	76	648	96	171	1160
23.11.2001	15+16	Female	90	15	2213	617	0	177	54	33	353	948	629	0	235	164	33	197	3161	1246	0	412	218	66	550
23.11.2001	13+14	Female	80	14	1562	269	0	73	10	24	162	820	416	0	136	87	25	168	2382	685	0	209	97	49	330
30.11.2001	23+24	Male	90	18	1581	894	14	478	83	33	286	1704	1128	79	421	29	60	539	3285	2022	93	899	112	93	825
30.11.2001	25+26	Female	80	18	4560	312	0	139	49	23	101	1322	791	0	415	201	54	121	5882	1103	0	554	250	77	222
30.11.2001	27+28	Male	95	17	5338	671	27	307	48	30	259	1582	839	32	609	57	23	118	6920	1510	59	916	105	53	377
30.11.2001	19+20	Male	100	19	515	52	0	18	27	4	3	1574	1148	14	420	205	90	419	2089	1200	14	438	232	94	422
30.11.2001	21+22	Male	90	16	746	370	0	303	40	9	18	1347	763	0	386	292	58	27	2093	1133	0	689	332	67	45
14.12.2001	3+4	Female	85	17	3644	417	0	167	94	62	94	1732	781	0	347	170	103	161	5376	1198	0	514	264	165	255
14.12.2001	5+6	Male	100	19	4376	964	0	582	62	61	259	1371	826	0	490	74	32	230	5747	1790	0	1072	136	93	489
14.12.2001	1+2	Female	100	18	5984	1009	0	567	104	76	262	1133	460	56	217	63	28	96	7117	1469	56	784	167	104	358
30.12.2001	7+8	Male	90	18	718	183	0	140	19	3	21	2804	608	0	258	207	56	87	3522	791	0	398	226	59	108
30.12.2001	11+12	Female	60	11	347	139	18	66	33	5	17	738	325	0	126	81	25	93	1085	464	18	192	114	30	110
30.12.2001	9+10	Male	85	18	991	368	0	243	51	7	67	848	441	0	206	135	42	58	1839	809	0	449	186	49	125
10.01.2002	13+14	Male	90	18	1953	303	0	168	69	17	49	875	344	0	183	92	15	54	2828	647	0	351	161	32	103
19.02.2002	7+8	Female	90	16	3385	1168	388	721	32	4	23	1738	1138	234	843	36	3	22	5123	2306	622	1564	68	7	45
16.03.2002	11+12	Female	85	16	3880	1029	118	743	122	12	34	1681	834	276	433	85	9	31	5561	1863	394	1176	207	21	65
16.03.2002	9+10	Female	90	16	2776	211	0	136	66	5	4	1389	845	0	535	277	21	12	4165	1056	0	671	343	26	16
05.04.2002	2+1	Male	110	16	4464	802	662	77	24	6	33	2135	1356	687	537	59	10	63	6599	2158	1349	614	83	16	96
05.04.2002	3+4	Female	90	16	2013	170	0	53	37	15	65	1766	987	16	357	200	63	351	3779	1157	16	410	237	78	416
12.04.2002	7+8	Female	100	18	10094	499	0	143	94	53	209	1147	370	0	142	50	27	151	11241	869	0	285	144	80	360
12.04.2002	5+6	Female	80	14	2680	254	0	99	59	28	68	2063	897	0	356	199	89	253	4743	1151	0	455	258	117	321
23.05.2002	13+14	Female	110	14	1018	25	0	8	9	4	4	1181	714	12	298	243	89	72	2199	739	12	306	252	93	76
23.05.2002	15+16	Female	100	16	2532	300	153	104	4	4	35	1353	830	419	323	17	3	68	3885	1130	572	427	21	7	103
23.05.2002	1+2	Female	80	12	1936	167	78	61	18	2	8	2174	1247	456	616	137	15	23	4110	1414	534	677	155	17	31
23.05.2002	11+12	Female	110	17	2075	7	0	0	0	1	6	1707	967	10	659	213	31	54	3782	974	10	659	213	32	60
23.05.2002	9+10	Male	90	16	3090	166	14	30	11	13	98	1357	710	168	219	51	29	243	4447	876	182	249	62	42	341
23.05.2002	7+8	Female	120	16	2365	355	220	35	4	7	89	1545	874	399	226	10	18	221	3910	1229	619	261	14	25	310

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Animal Age [months]	Provent Contents [g]	Provent Stones [g]	Provent >20 mm [g]	Provent 8-20 mm [g]	Provent 4-8 mm [g]	Provent 2-4 mm [g]	Provent <2 mm [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Gizzard >20 mm [g]	Gizzard 8-20 mm [g]	Gizzard 4-8 mm [g]	Gizzard 2-4 mm [g]	Gizzard <2 mm [g]	Complete Contents [g]	Complete Stones [g]	Complete >20 mm [g]	Complete 8-20 mm [g]	Complete 4-8 mm [g]	Complete 2-4 mm [g]	Complete <2 mm [g]
23.05.2002	5+6	Male	90	16	2388	837	739	70	6	2	20	1732	1337	823	377	35	12	90	4120	2174	1562	447	41	14	110
23.05.2002	3+4	Female	120	14	1992	339	44	7	2	24	262	1674	1071	110	293	57	49	562	3666	1410	154	300	59	73	824
26.05.2002	1+2	Female	90	15	1898	296	0	0	0	19	277	1152	707	30	229	87	31	330	3050	1003	30	229	87	50	607
26.05.2002	3+4	Female	100	15	1765	209	0	9	19	17	164	1399	942	0	344	133	49	416	3164	1151	0	353	152	66	580
26.05.2002	5+6	Female	100	15	1745	306	247	10	3	2	44	1874	1112	261	301	29	17	504	3619	1418	508	311	32	19	548
12.07.2002	5+6	Female	105	15	2657	104	0	35	53	13	3	1521	846	408	256	152	20	10	4178	950	408	291	205	33	13
12.07.2002	1+2	Male	100	14	3010	593	12	390	162	21	8	1019	518	0	382	114	17	5	4029	1111	12	772	276	38	13
12.07.2002	3+4	Female	95	16	2275	231	58	84	60	10	19	1345	749	294	304	124	22	5	3620	980	352	388	184	32	24
12.07.2002	7+8	Male	95	14	1762	245	31	141	63	8	2	1313	566	15	297	210	37	7	3075	811	46	438	273	45	9
19.07.2002	9+10	Male	90	14	1442	279	39	179	52	8	1	1293	562	18	430	96	15	3	2735	841	57	609	148	23	4
19.07.2002	11+12	Male	90	15	836	45	0	34	9	1	1	965	481	18	297	146	15	5	1801	526	18	331	155	16	6
04.08.2002	7+8	Female	90	14	1016	74	15	25	29	3	2	960	549	197	248	93	7	4	1976	623	212	273	122	10	6
04.08.2002	5+6	Female	80	17	1064	7	0	0	1	1	5	1193	619	81	332	156	35	15	2257	626	81	332	157	36	20
04.08.2002	3+4	Female	95	15	1388	11	0	1	1	2	7	789	221	0	46	112	32	31	2177	232	0	47	113	34	38
04.08.2002	1+2	Male	100	16	1879	126	0	53	57	14	2	805	328	0	173	126	26	3	2684	454	0	226	183	40	5
10.08.2002	13+14	Female	95	15	1485	364	125	231	8	0	0	1418	1119	203	848	65	3	0	2903	1483	328	1079	73	3	0
10.08.2002	9+10	Male	110	16	589	22	0	16	4	2	0	1729	1202	177	657	318	41	9	2318	1224	177	673	322	43	9
10.08.2002	11+12	Male	115	15	936	138	12	108	16	1	1	1471	1216	279	791	133	7	6	2407	1354	291	899	149	8	7
17.08.2002	1+2	Male	110	16	1661	83	24	36	13	5	5	1014	555	275	171	91	14	4	2675	638	299	207	104	19	9
17.08.2002	3+4	Female	90	17	2335	399	114	209	67	6	3	1422	995	429	471	79	10	6	3757	1394	543	680	146	16	9
17.08.2002	5+6	Male	100	15	1147	294	0	211	72	8	3	1533	1068	159	598	275	29	7	2680	1362	159	809	347	37	10
30.08.2002	5+6	Male	100	15	748	276	0	67	159	44	6	525	369	0	83	218	60	8	1273	645	0	150	377	104	14
30.08.2002	3+4	Male	100	16	766	319	228	80	10	1	0	1746	1390	790	536	56	4	4	2512	1709	1018	616	66	5	4
30.08.2002	1+2	Male	110	16	1135	647	282	304	54	6	1	822	645	99	436	98	10	2	1957	1292	381	740	152	16	3
07.09.2002	5+6	Male	95	15	3133	824	0	540	267	13	4	1505	1140	127	759	236	16	2	4638	1964	127	1299	503	29	6
07.09.2002	3+4	Male	100	16	3641	514	0	209	285	12	8	775	493	0	240	242	7	4	4416	1007	0	449	527	19	12
07.09.2002	1+2	Female	90	15	4346	1105	0	536	547	18	4	723	366	0	148	141	47	30	5069	1471	0	684	688	65	34
07.09.2002	7+8	Female	80	14	1056	51	0	8	12	10	21	568	298	0	61	88	66	83	1624	349	0	69	100	76	104
07.09.2002	11+12	Female	110	18	1668	146	11	23	6	8	98	1237	813	0	488	306	16	3	2905	959	11	511	312	24	101
07.09.2002	9+10	Female	90	14	1963	368	0	53	114	81	120	1357	725	51	223	123	32	296	3320	1093	51	276	237	113	416
22.09.2002	3+4	Female	90	14	1288	178	22	127	23	3	3	833	420	55	240	50	14	61	2121	598	77	367	73	17	64
22.09.2002	1+2	Male	90	15	949	89	0	50	15	4	20	1276	872	44	632	171	19	6	2225	961	44	682	186	23	26
05.10.2002	DM1+MM1	Male	130	84	616	262	56	186	16	3	1	859	260	13	186	53	6	2	1475	522	69	372	69	9	3

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Animal Age [months]	Provent Contents [g]	Provent Stones [g]	Provent >20 mm [g]	Provent 8-20 mm [g]	Provent 4-8 mm [g]	Provent 2-4 mm [g]	Provent <2 mm [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Gizzard >20 mm [g]	Gizzard 8-20 mm [g]	Gizzard 4-8 mm [g]	Gizzard 2-4 mm [g]	Gizzard <2 mm [g]	Complete Contents [g]	Complete Stones [g]	Complete >20 mm [g]	Complete 8-20 mm [g]	Complete 4-8 mm [g]	Complete 2-4 mm [g]	Complete <2 mm [g]
05.10.2002	DM2+MM2	Male	95	15	3604	26	0	16	2	3	5	1703	886	217	528	85	8	48	5307	912	217	544	87	11	53
29.10.2002	DM1+MM1	Male	100	18	3960	445	0	172	63	22	188	1248	577	39	236	96	26	180	5208	1022	39	408	159	48	368
29.10.2002	DM2+MM2	Male	95	16	3531	1239	742	438	50	4	5	1009	492	144	298	42	4	4	4540	1731	886	736	92	8	9
09.11.2002	DM3+MM3	Female	90	15	5550	483	0	164	102	32	185	930	470	0	139	151	41	139	6480	953	0	303	253	73	324
09.11.2002	DM5+MM5	Female	90	16	497	82	0	38	40	3	1	1018	596	13	324	227	24	8	1515	678	13	362	267	27	9
09.11.2002	DM4+MM4	Male	95	14	2693	661	447	201	10	1	2	1046	764	253	459	48	3	1	3739	1425	700	660	58	4	3
16.11.2002	3+4	Male	95	15	1919	297	18	163	39	12	65	1369	805	126	411	93	26	149	3288	1102	144	574	132	38	214
16.11.2002	1+2	Female	90	15	1928	123	73	32	4	1	13	2197	1028	252	671	51	5	49	4125	1151	325	703	55	6	62
23.11.2002	1+2	Male	95	14	1086	175	20	92	10	4	49	1122	661	59	365	68	17	152	2208	836	79	457	78	21	201
01.12.2002	DM1+MM1	Female	95	15	2192	157	16	46	4	7	84	1030	455	14	295	20	11	115	3222	612	30	341	24	18	199
01.12.2002	DM2+MM2	Female	90	15	1097	163	27	69	12	3	52	910	492	172	173	45	9	93	2007	655	199	242	57	12	145
01.12.2002	DM3+MM3	Female	90	16	1929	105	0	45	4	6	50	1417	665	186	181	19	15	264	3346	770	186	226	23	21	314
01.12.2002	DM5+MM5	Male	100	16	2348	126	0	77	3	3	43	1120	728	8	582	32	16	90	3468	854	8	659	35	19	133
01.12.2002	DM4+MM4	Male	95	16	2043	194	0	105	13	7	69	1370	636	0	345	79	24	188	3413	830	0	450	92	31	257
01.12.2002	DM6+MM6	Male	95	15	1709	83	0	30	8	3	42	984	464	43	265	56	12	88	2693	547	43	295	64	15	130
28.12.2002	DM Blatt + MM Blatt	Male	100	16	2235	248	136	101	6	1	4	973	312	121	165	18	2	6	3208	560	257	266	24	3	10
04.01.2003	DM+MM	Male	100	16	1086	57	0	42	11	1	3	1291	860	22	700	121	12	5	2377	917	22	742	132	13	8
17.01.2003	DM 01 + MM 01	Male	80	18	1354	52	0	34	12	1	5	814	391	31	248	97	8	7	2168	443	31	282	109	9	12
17.01.2003	DM2 + MM2	Male	100	19	2416	158	34	113	8	0	3	1665	869	180	609	74	3	3	4081	1027	214	722	82	3	6
25.01.2003	DM03 + MM03	Female	80	16	804	56	13	27	12	1	3	882	524	13	410	89	9	3	1686	580	26	437	101	10	6
25.01.2003	DM04+MM04	Male	95	18	1075	174	81	77	13	1	2	1347	656	123	430	80	6	17	2422	830	204	507	93	7	19
22.02.2003	1 DM + MM	Male	95	18	3537	1514	445	856	139	21	53	590	32	0	24	5	0	3	4127	1546	445	880	144	21	56
22.02.2003	2 DM + MM	Male	90	17	4209	1346	570	630	89	16	41	808	336	19	251	46	8	12	5017	1682	589	881	135	24	53
15.03.2003	6 DM + MM	Male	95	17	2200	76	0	52	10	2	12	1182	549	21	366	109	20	33	3382	625	21	418	119	22	45
15.03.2003	5 DM + MM	Male	100	18	2764	268	0	140	11	94	23	1420	770	23	427	261	25	34	4184	1038	23	567	272	119	57
29.03.2003	3+4	Male	90	16	4015	31	0	7	5	5	14	1283	622	0	222	259	86	55	5298	653	0	229	264	91	69
29.03.2003	1+2	Male	100	18	2456	171	0	133	17	4	17	1273	550	0	420	82	8	40	3729	721	0	553	99	12	57
02.04.2003	X DM + X MM	Male	90	28	2589	109	0	86	13	2	8	1709	995	163	726	82	10	14	4298	1104	163	812	95	12	22
05.04.2003	8+7	Female	90	18	6843	252	0	179	45	6	22	1288	604	0	393	174	19	18	8131	856	0	572	219	25	40
05.04.2003	5+6	Male	95	19	6335	230	0	159	36	8	27	1149	704	0	516	149	15	24	7484	934	0	675	185	23	51
12.04.2003	10+11	Female	90	20	4413	194	61	92	30	3	8	1681	1070	105	706	213	23	23	6094	1264	166	798	243	26	31
12.04.2003	14+15	Male	90	19	4509	149	0	96	41	7	5	1640	814	0	548	209	44	13	6149	963	0	644	250	51	18

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Animal Age [months]	Provent Contents [g]	Provent Stones [g]	Provent >20 mm [g]	Provent 8-20 mm [g]	Provent 4-8 mm [g]	Provent 2-4 mm [g]	Provent <2 mm [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Gizzard >20 mm [g]	Gizzard 8-20 mm [g]	Gizzard 4-8 mm [g]	Gizzard 2-4 mm [g]	Gizzard <2 mm [g]	Complete Contents [g]	Complete Stones [g]	Complete >20 mm [g]	Complete 8-20 mm [g]	Complete 4-8 mm [g]	Complete 2-4 mm [g]	Complete <2 mm [g]
12.04.2003	16+17	Male	85	19	6238	137	0	96	24	5	12	1204	463	0	327	116	14	6	7442	600	0	423	140	19	18
12.04.2003	12+13	Male	95	18	5039	440	13	293	105	12	17	1571	831	37	533	208	30	23	6610	1271	50	826	313	42	40
04.05.2003	DM1+MM1	Male	90	18	3160	6	0	0	0	0	6	1941	960	57	711	100	11	81	5101	966	57	711	100	11	87
11.05.2003	DM3+MM3	Female	90	18	4281	132	0	52	38	14	28	1300	765	0	450	245	42	28	5581	897	0	502	283	56	56
11.05.2003	DM2+MM2	Male	85	15	1498	15	0	5	3	1	6	804	484	0	133	252	45	54	2302	499	0	138	255	46	60
24.05.2003	DM4+MM4	Female	100	19	951	2	0	0	0	0	2	1157	651	11	471	82	21	66	2108	653	11	471	82	21	68
24.05.2003	DM5+MM5	Male	90	18	2829	123	0	103	11	2	7	1401	812	17	606	149	15	25	4230	935	17	709	160	17	32
31.05.2003	DM10+MM10	Female	100	24	1489	24	0	0	4	2	18	1493	857	36	457	170	37	157	2982	881	36	457	174	39	175

Appendix IV: Raw data of ostrich examination. Part B: South African farm ostriches

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Provent Contents [g]	Provent Stones [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Complete Contents [g]	Complete Stones [g]
31.01.2003	01; tag-no.: 267155	Male	86,9	906	328	2195	1669	3101	1997
31.01.2003	02; tag-no.: 264324	Male	82,9	737	499	770	622	1507	1121
31.01.2003	03; tag-no.: 263624	Female	79,8	258	101	1207	890	1465	991
31.01.2003	05; tag-no.: 264405	Female	80,9	387	57	1088	763	1475	820
31.01.2003	06; tag-no.: 577802	Male	83,1	223	9	1392	998	1615	1007
03.02.2003	01 (2); tag-no.: 101802	Unknown	83,2	143	122	1121	827	1264	949
03.02.2003	01; tag-no.: 217695	Unknown	81,5	311	246	353	268	664	514
03.02.2003	02 (2); tag-no.: 83510	Unknown	81	369	312	640	417	1009	729
03.02.2003	02; tag-no.: 103065	Unknown	93,4	122	107	1102	805	1224	912
03.02.2003	03 (2); tag-no.: 83659	Unknown	79,3	39	10	1376	954	1415	964
03.02.2003	03; tag-no.: 217342	Unknown	100,6	976	520	1178	817	2154	1337
03.02.2003	04 (2); tag-no.: 83526	Unknown	76,4	156	109	341	253	497	362
03.02.2003	04; tag-no.: 217670	Unknown	85	642	524	1178	985	1820	1509
03.02.2003	05 (2); tag-no.: 83633	Unknown	78,8	806	515	501	329	1307	844
03.02.2003	05; tag-no.: 13094	Unknown	93,8	1077	837	539	323	1616	1160
03.02.2003	06 (2); tag-no.: 999925	Unknown	89,4	167	113	910	794	1077	907
03.02.2003	06; tag-no.: 217657	Unknown	75,2	630	403	188	121	818	524
04.02.2003	01; tag-no.: 219178	Unknown	92,6	163	118	742	583	905	701
04.02.2003	02; tag-no.: 219220	Unknown	92,6	60	39	909	738	969	777
04.02.2003	03; tag-no.: 219244	Unknown	91,1	132	110	986	698	1118	808
04.02.2003	04; tag-no.: 219470	Unknown	85,2	130	48	781	546	911	594
04.02.2003	05; tag-no.: 208121	Unknown	82,2	428	246	916	627	1344	873
04.02.2003	06; tag-no.: 45550	Unknown	77,7	35	28	742	617	777	645
04.02.2003	07; tag-no.: 219527	Unknown	78,6	24	16	1069	653	1093	669
04.02.2003	08; tag-no.: 219203	Unknown	78,3	1146	691	727	350	1873	1041
04.02.2003	09; tag-no.: 219461	Unknown	79	790	618	740	523	1530	1141
05.02.2003	01G; tag-no.: 259832	Unknown	68					1613	897
05.02.2003	01P; tag-no.: 578578	Unknown	104					927	650
05.02.2003	02G; tag-no.: 259820	Unknown	76,1					754	692
05.02.2003	02P; tag-no.: 259858	Unknown	72,6					1031	772
05.02.2003	03P; tag-no.: 48311	Unknown	65,5					892	772
05.02.2003	04P; tag-no.: 259839	Unknown	75					782	695
05.02.2003	05G; tag-no.: 999500	Unknown	79,2					3114	1188
05.02.2003	05P; tag-no.: 999502	Unknown	62,5					1565	1073
05.02.2003	06P; tag-no.: 259843	Unknown	69,6					633	491
05.02.2003	07G; tag-no.: 259836	Unknown	72,4					1127	873
05.02.2003	07P; tag-no.: 48707	Unknown	74,7					1298	1002
05.02.2003	08G; tag-no.: 259860	Unknown	85,9					946	822
05.02.2003	08P; tag-no.: 259851	Unknown	75,7					1101	918
05.02.2003	09G; tag-no.: 47768	Unknown	94,8					1168	685
05.02.2003	09P; tag-no.: 18946	Unknown	76,4					764	564
05.02.2003	10G; tag-no.: 21431	Unknown	83,9					1956	1114
05.02.2003	10P; tag-no.: 24760	Unknown	74,1					1270	570
05.02.2003	11G; tag-no.: 24683	Unknown	107					805	557
05.02.2003	11P; tag-no.: 23175	Unknown	78					509	395
05.02.2003	12G; tag-no.: 13341	Unknown	80,5					1105	887
05.02.2003	12P; tag-no.: 51321	Unknown	83,8					1726	1513
06.02.2003	01; tag-no.: 223486	Unknown	87,6					959	802
06.02.2003	02; tag-no.: 999564	Unknown	93,3					1252	701
06.02.2003	03; tag-no.: 223476	Unknown	85,6					753	553
06.02.2003	04; tag-no.: 223445	Unknown	86,2					1081	611

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Provent Contents [g]	Provent Stones [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Complete Contents [g]	Complete Stones [g]
06.02.2003	05; tag-no.: 223432	Unknown	87,4					853	668
06.02.2003	06; tag-no.: 223454	Unknown	91,7					666	422
06.02.2003	07; tag-no.: 223438	Unknown	85,7					936	702
06.02.2003	08; tag-no.: 223430	Unknown	80,1					1048	696
06.02.2003	10; tag-no.: 577545	Unknown	76,5					2347	1716
06.02.2003	11; tag-no.: 577571	Unknown	97,4					1282	1094
06.02.2003	13; tag-no.: 577584	Unknown	89,4					1608	1184
06.02.2003	14; tag-no.: 577539	Unknown	76,9					994	791
06.02.2003	15; tag-no.: 231010	Unknown	108,4					1414	1198
06.02.2003	16; tag-no.: 225286	Unknown	92,2					1013	739
06.02.2003	17; tag-no.: 225297	Unknown	102,5					1050	749
06.02.2003	18; tag-no.: 225318	Unknown	95,5					1686	1487
06.02.2003	19; tag-no.: 225323	Unknown	85					1689	1452
06.02.2003	20; tag-no.: 225285	Unknown	91,3					1703	1392
06.02.2003	21; tag-no.: 225314	Unknown	83,5					1279	1129
06.02.2003	22; tag-no.: 225271	Unknown	83,6					1390	1199
06.02.2003	23; tag-no.: 225307	Unknown	100,3					753	593
06.02.2003	24; tag-no.: 225281	Unknown	75,1					541	467
07.02.2003	01; tag-no.: 222322	Female	90,3					959	784
07.02.2003	02; tag-no.: 222226	Male	91					952	743
07.02.2003	03; tag-no.: 222342	Male	78,2					1041	849
07.02.2003	04; tag-no.: 222393	Male	81,1					2020	974
07.02.2003	05; tag-no.: 222490	Male	87,4					1412	1115
07.02.2003	06; tag-no.: 222503	Female	89,3					1028	624
07.02.2003	07; tag-no.: 231893	Male	84					790	523
07.02.2003	08; tag-no.: 222391	Female	74,4					1153	839
07.02.2003	09; tag-no.: 222299	Male	91,5					1498	921
07.02.2003	10; tag-no.: 222315	Male	88,1					1619	669
07.02.2003	11; tag-no.: 222361	Male	84,6					2053	967
07.02.2003	12; tag-no.: 222246	Female	92,5					1106	786
07.02.2003	13; tag-no.: 222293	Male	72,6					1008	756
07.02.2003	14; tag-no.: 222328	Female	88,2					625	515
07.02.2003	15; tag-no.: 231860	Male	75					1933	1395
07.02.2003	16; tag-no.: 222454	Male	76,1					573	364
07.02.2003	18; tag-no.: 222343	Male	88,6					1840	1332
07.02.2003	19; tag-no.: 222238	Female	78,9					1184	920
07.02.2003	20; tag-no.: 222492	Male	81,4					806	594
07.02.2003	21; tag-no.: 222214	Male	87					1287	1041
07.02.2003	22; tag-no.: 222251	Male	86,8					1073	702
07.02.2003	23; tag-no.: 222360	Male	90,5					1268	834
07.02.2003	24; tag-no.: 222288	Female	65,6					1226	1129
10.02.2003	01; tag-no.: 249223	Male	92,3					774	624
10.02.2003	02; tag-no.: 291816	Male	74,9					754	540
10.02.2003	03; tag-no.: 249248	Female	76,8					403	307
10.02.2003	04; tag-no.: 270781	Unknown	81					832	644
10.02.2003	05; tag-no.: 249311	Male	79,1					727	492
10.02.2003	06; tag-no.: 249208	Female	85,9					1519	1072
10.02.2003	07; tag-no.: 270807	Female	78,1					1130	859
10.02.2003	08; tag-no.: 270751	Female	86,7					1175	824
10.02.2003	09; tag-no.: 262269	Male	90,9					1350	637
10.02.2003	10; tag-no.: 263321	Male	86					1541	897
10.02.2003	11; tag-no.: 263309	Male	85,5					1471	980
10.02.2003	12; tag-no.: 262267	Male	87,2					1611	1048
10.02.2003	13; tag-no.: 261991	Male	97,6					1035	702
10.02.2003	14; tag-no.: 262280	Male	85					1402	820

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Provent Contents [g]	Provent Stones [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Complete Contents [g]	Complete Stones [g]
10.02.2003	15; tag-no.: 262287	Male	86,4					1042	748
10.02.2003	16; tag-no.: 262248	Male	85,5					1237	792
10.02.2003	17; tag-no.: 262245	Female	83,6					1095	847
10.02.2003	18; tag-no.: 999653	Female	79,2					946	712
10.02.2003	19; tag-no.: 263312	Male	84,4					930	735
10.02.2003	20; tag-no.: 262216	Female	84					632	506
10.02.2003	21; tag-no.: 234181	Female	75,2					2285	333
10.02.2003	22; tag-no.: 57437	Female	98					1902	656
10.02.2003	23; tag-no.: 57362	Female	87,6					1723	561
10.02.2003	24; tag-no.: 57360	Male	86,7					2810	887
11.02.2003	01; tag-no.: 219316	Male	90,3					225	156
11.02.2003	02; tag-no.: 219218	Male	79,5					1185	755
11.02.2003	03; tag-no.: 219172	Female	79,3					676	578
11.02.2003	04; tag-no.: 219489	Male	86,9					743	497
11.02.2003	05; tag-no.: 219269	Male	86,7					1132	826
11.02.2003	06; tag-no.: 219258	Male	84,5					1506	937
11.02.2003	07; tag-no.: 45579	Female	83,9					1993	1655
11.02.2003	08; tag-no.: 219326	Male	100,3					1501	1019
11.02.2003	09; tag-no.: 91714	Female	81,5					1033	861
11.02.2003	10; tag-no.: 91671	Male	75,8					1336	696
11.02.2003	11; tag-no.: 19705	Male	87,1					689	484
11.02.2003	12; tag-no.: 999718	Male	86					878	624
11.02.2003	13; tag-no.: 91689	Male	86,2					314	240
11.02.2003	14; tag-no.: 91682	Male	85,8					1014	665
11.02.2003	15; tag-no.: 91674	Female	85,3					699	439
11.02.2003	16; tag-no.: 91667	Male	85,1					781	586
11.02.2003	17; tag-no.: 5524	Female	87,1					1054	606
11.02.2003	18; tag-no.: 77208	Female	66,6					1075	814
11.02.2003	19; tag-no.: 5776	Male	79					556	346
11.02.2003	20; tag-no.: 263710	Female	78,3					627	482
11.02.2003	21; tag-no.: 276500	Female	76,5					846	663
11.02.2003	22; tag-no.: 6715	Female	81,7					1216	1004
11.02.2003	23; tag-no.: 276706	Female	81,1					1210	977
11.02.2003	24; tag-no.: 2933	Female	78,1					567	378
12.02.2003	01; tag-no.: 98067	Male	82,8					1136	897
12.02.2003	02; tag-no.: 296795	Male	91,8					1304	1116
12.02.2003	03; tag-no.: 16075	Male	85,5					1368	888
12.02.2003	04; tag-no.: 296777	Female	84,7					1178	924
12.02.2003	05; tag-no.: 15531	Female	88,7					1492	1057
12.02.2003	06; tag-no.: 296741	Male	92,2					2406	1313
12.02.2003	07; tag-no.: 999811	Male	83,7					1172	917
12.02.2003	08; tag-no.: 206937	Female	79,1					1754	1190
12.02.2003	09; tag-no.: 296930	Male	79,2					795	629
12.02.2003	10; tag-no.: 66344	Male	83,9					1400	1036
12.02.2003	11; tag-no.: 999815	Female	85,8					1464	1115
12.02.2003	12; tag-no.: 98139	Female	84,3					1351	1023
12.02.2003	13; tag-no.: 296878	Female	84,2					984	749
12.02.2003	14; tag-no.: 296877	Male	88,5					892	736
12.02.2003	15; tag-no.: 296860	Female	94,2					788	641
12.02.2003	16; tag-no.: 12789	Male	88,7					1090	809
12.02.2003	17; tag-no.: 41901	Female	87,5					932	746
12.02.2003	18; tag-no.: 224826	Male	94,9					1746	1089
12.02.2003	19; tag-no.: 38779	Female	87,3					1581	1134
12.02.2003	20; tag-no.: 41849	Male	88,5					1780	1312
12.02.2003	21; tag-no.: 38748	Male	106,9					1561	1017

Date of Extraction	Number of Sample	Sex	Body mass [kg]	Provent Contents [g]	Provent Stones [g]	Gizzard Contents [g]	Gizzard All Stones [g]	Complete Contents [g]	Complete Stones [g]
12.02.2003	22; tag-no.: 38612	Male	82,8					1604	1022
12.02.2003	23; tag-no.: 999825	Male	96,5					2629	1945
12.02.2003	24; tag-no.: 999824	Female	94,4					1793	1335
13.02.2003	01; tag-no.: 90014	Female	86,7					835	593
13.02.2003	02; tag-no.: 90361	Male	82,7					1932	1446
13.02.2003	03; tag-no.: 999875	Female	94,7					969	610
13.02.2003	04; tag-no.: 90005	Male	85,8					977	699
13.02.2003	05; tag-no.: 90473	Female	75,2					951	800
13.02.2003	06; tag-no.: 220920	Female	75,2					575	444
13.02.2003	07; tag-no.: 220930	Female	81,2					1092	484
13.02.2003	08; tag-no.: 999878	Unknown	75,1					890	600
13.02.2003	09; tag-no.: 217276	Female	77,3					1372	860
13.02.2003	10; tag-no.: 999880	Female	71,8					939	769
13.02.2003	11; tag-no.: 97617	Male	73					1460	1060
13.02.2003	12; tag-no.: 217278	Female	76					1632	1250
13.02.2003	13; tag-no.: 217199	Female	71,6					1039	739
13.02.2003	14; tag-no.: 97557	Female	73,4					1631	1300
13.02.2003	15; tag-no.: 97571	Female	76,6					3476	2880
13.02.2003	16; tag-no.: 217179	Female	70,3					1763	1092
13.02.2003	17; tag-no.: 217174	Unknown	68,2					2306	1629
13.02.2003	18; tag-no.: 49789	Female	73,9					2134	1331
13.02.2003	19; tag-no.: 203977	Female	88					1867	1067
13.02.2003	20; tag-no.: 597970	Male	75,3					1327	1090
13.02.2003	21; tag-no.: 71538	Female	91,9					1643	1294
13.02.2003	22; tag-no.: 203863	Female	89,4					1303	909
13.02.2003	23; tag-no.: 71634	Female	92,2					1414	873
13.02.2003	24; tag-no.: 203751	Female	87,9					1843	1162
14.02.2003	01; tag-no.: 59928	Female	71					880	740
14.02.2003	02; tag-no.: 78984	Male	97,8					2105	1189
14.02.2003	03; tag-no.: 220997	Male	93,4					947	838
14.02.2003	04; tag-no.: 54319	Male	79,4					960	655
14.02.2003	05; tag-no.: 98999	Male	77,2					1025	695
14.02.2003	06; tag-no.: 98629	Female	83,1					349	305
14.02.2003	07; tag-no.: 98533	Female	75,5					1357	1146
14.02.2003	08; tag-no.: 253084	Female	79,1					878	688
14.02.2003	09; tag-no.: 37346	Female	77,7					1118	839
14.02.2003	10; tag-no.: 15842	Male	82,2					1212	677
14.02.2003	11; tag-no.: 228138	Female	92,7					1589	1119
14.02.2003	12; tag-no.: 228141	Male	80,3					995	646
14.02.2003	13; tag-no.: 3777	Female	80,1					795	554
14.02.2003	14; tag-no.: 999955	Male	82,3					1010	791
14.02.2003	15; tag-no.: 15768	Female	78,4					1074	897
14.02.2003	16; tag-no.: 37322	Female	82,3					1099	862
14.02.2003	17; tag-no.: 999958	Female	79,5					1265	1065
14.02.2003	18; tag-no.: 56495	Male	84,2					1171	884
14.02.2003	19; tag-no.: 56449	Female	77,9					1715	1315
14.02.2003	20; tag-no.: 37352	Female	84,4					1874	1053
14.02.2003	21; tag-no.: 15627	Male	82,8					1720	940
14.02.2003	22; tag-no.: 999959	Male	79,9					1067	673
14.02.2003	23; tag-no.: 3938	Female	84					1061	636
14.02.2003	24; tag-no.: 37076	Female	88,2					1542	1261