

Plesiosaur Day, New Walk Museum, Leicester
18th November 2004

Revised Schedule.

1. Welcome by Arthur Cruickshank
2. Franziska Grossman - Plesiosaurs from the Posidonia Shale of S. W. Germany.
3. Adam S. Smith - The cladistic analysis of plesiosaurs.

Coffee

3. Denis Parsons - The Somerset plesiosaur.
4. Mark Evans - Current research (Presented by Arthur Cruickshank)

Lunch

5. Richard Forrest - Morphometric and statistical methods of analysing plesiosaur vertebral columns.
6. Richard Forrest - Introduction to the Lincoln plesiosaur.

Tea

7. Brief presentation and commentary on some plesiosaur gastroliths by Mike Everhart.
8. Open forum for discussion

The meeting closed at about 17:00

Present and attending:- Dave Martill, Darren Naish, Arthur Cruickshank, Franziska Grossmann, Denis Parsons, Mark Evans, Richard Forrest, Adam S. Smith.

Apologies from:- Leslie Noè, Marcela Gomez and David Brown.

Some notes on the meeting

My thanks to Darren Naish for his notes which contributed substantially to this account.

Franziska Grossman reviewed her recent work on the Toarcian plesiosaurs of the German Posidonia Shale. Though some of the data presented here was also spoken about at SVPCA 2004 (also held in Leicester), there was much new information. 14 plesiosaur specimens are known from this unit, only five of which have been described. Using skull morphology, tooth ornamentation and limb proportions, Franziska was able to show that *Plesiosaurus brachypterygius* and *P. guilelmiimperatoris* could be distinguished on numerous features. The former is heterodont with symmetrical tooth ornamentation, has a snout that appears constricted in dorsal view, and exhibits proportionally shorter limbs compared to body length than *P. guilelmiimperatoris*. *P. guilelmiimperatoris* lacks a constricted snout, exhibits asymmetrical tooth ornamentation, and has limbs that are c. 25% of body length

(compared to c. 20% in *P. brachypterygius*). Inclusion of these two taxa within a cladistic analysis shows that neither is close to *P. dolichodeirus*, and thus neither really belongs to the genus *Plesiosaurus*. A new generic name is needed for *P. brachypterygius*, and it appears to be close to (thought not congeneric with) *Occitanosaurus* and *Microcleidus*. Meanwhile, *Seeleyosaurus holzmadensis* White 1940 seems to be a junior synonym of *P. guilelmiimperatoris* meaning that *Seeleyosaurus* is the correct generic name for this taxon.

The recent description of a third ostensible Posidonia Shale taxon, *Plesiopterys wildii* O'Keefe 2004 for specimen SMNS 16812, has added a new facet to Franziska's research. Franziska argued that some of O'Keefe's conclusions on the morphology of this specimen were debatable, and in fact the animal does not appear to be a distinct taxon but a juvenile specimen of *P. guilelmiimperatoris*. What does appear to be a third taxon is present and is represented by a single near-complete juvenile specimen (SMNS 51945). With a total length of about 3.5 m this taxon would clearly have reached a larger adult size than either of the other Posidonia species. Its proportions are also quite different from those of *P. guilelmiimperatoris* and *P. brachypterygius* but its mangled skull meant that Franziska wasn't able to accurately determine its affinities. Given that the specimen consists of an otherwise complete skeleton this assertion is debatable to say the least! Other areas that Franziska hopes to look at in future concern palaeoecology and the reconstruction of plesiosaur musculature.

Adam Smith discussed controversy and consensus in plesiosaur phylogeny, covering the affinities of polycotyliids, the topology of elasmosaurids and the affinities of the 'southern weirdos' (viz, *Aristonectes*, *Kaiwhekea* and kin). By correcting and recoding parts of O'Keefe's (2001) analysis Adam produced a modified, though largely similar, tree. However, the main focus of his research was producing a novel analysis of plesiosauroids based on characters coded from the literature. In view of one of Franziska's assertions it was interesting that *Plesiopterys* grouped as the sister-taxon to *P. guilelmiimperatoris*. *Occitanosaurus*, *Microcleidus* and *Brancaosaurus* formed successive outgroups to an elasmosaurid-polycotyliid-cryptoclidid clade, and polycotyliids were found to be closer to cryptoclidids than to elasmosaurids. Adam also looked at the rate of skeletal character acquisition in plesiosauroids across time. The rate of evolution appears to be slow and constant for most of the Jurassic, but with marked conservatism and notably slow rates of innovation during the Cretaceous among some lineages.

Adam is to start work soon on *Rhomaleosaurus cramptoni* at Dublin.

Mark Evans was unable to present the talk he had planned for the meeting. Arthur Cruickshank stepped in and presented Mark's data. This included the latest work on the new Pliensbachian specimen discovered by Pete Blake and on reconstructing the skull of *Muraenosaurus*. The Pliensbachian animal is enigmatic, and when included in cladistic analyses not only does it appear in various places on the cladogram, but it can cause significant reordering of the structure of the tree depending on which characters are used and how they are weighted. The skull has been painstakingly reconstructed (by Mark) from numerous tiny fragments.

The newest reconstruction of the new *Muraenosaurus* specimen shows that this animal was equipped with a fairly tall, robust skull quite unlike the shallow, gracile skull as reconstructed by Andrews (1913). A prominent ridge on the frontals may have strengthened the skull and the jugal, rather than being the large subrectangular block reconstructed by Andrews, was a small element.

Dennis Parsons of Somerset County Museum gave an account of what might be the best plesiosaur specimen ever discovered. Found at the Bridgwater Bay National Nature Reserve (a SSSI), the museum was informed of the specimen in October 2003 by Nick Collard, a local fisherman, and a rescue excavation carried out. The fossil was exposed on the beach surface, which was being actively eroded and whole layers of shale were being lifted and removed by wave action. Time really was of the essence. Three joints running through the specimen made excavation precarious, especially given that one joint ran through the forelimbs perpendicular to the specimen's long axis, but things did go as planned and the entire specimen (together with associated ammonites and other samples) was successfully collected. It was transported to the museum where it was washed in fresh water for two weeks before being taken to the NHM and carefully dried under controlled conditions. At an early stage, it was realised that there was a shortage of both geological conservators and plesiosaur specialists. Fortunately, Dennis contacted Mark Evans and Richard Forrest, and a good working relationship soon emerged. While a lot of money is needed to prepare, conserve and display the specimen (c. £21,000), its preparation has been arranged and is due to start in January 2005.

Richard Forrest discussed the different mechanisms plesiosaurs use to stiffen the neck, the variability seen in the shape and number of cervical vertebrae, and the different 'zones' seen in the necks of assorted taxa. There is a consensus in the community that plesiosaurs kept their necks rather stiff: they did not coil, bend or lift their necks to a great degree. Employing a few of his famous 'forrestograms', Richard reinforced his earlier work on E-type and M-type necks. M-types (the 'M' stands for *Muraenosaurus* and/or *Mauisaurus*) have zygapophyses that are raised dorsally on the neural arch relative to those of other plesiosaurs while

E-types (E = elasmosaurid) have interlocking neural spines and low zygapophyses in contact with the centra.

He also introduced a specimen collected in 1906 and held at Lincoln Museum which may be a new species of *Microcleidus*. It includes a nearly complete neck, a partial pectoral girdle and forelimb, and dorsal vertebrae that exhibit some very unusual taphonomy. The cervical series is very well preserved and substantially complete, and shows detail of structures such as the lateral keels on the centra which may indicate patterns of muscle distribution in the neck. It shows how the centra of such long-necked taxa were very closely fitting, with hardly any room for intervertebral discs. This is not the case in rhomaleosaurs where there is room for substantial intervertebral structures.

An interesting discussion led by **Arthur Cruickshank** followed. The New Zealand 'elasmosaur' *Mauisaurus* differs from other elasmosaurs in their rod-like fused prezygapophyses which contribute to the stiffness of the neck. Cervicalisation of dorsal vertebrae appears to be a significant mechanism in the elongation of plesiosaurs necks. The distribution of binocular-shaped cervical centra was discussed, and the suggestion made that these are found only in the 'southern weirdos' – the rather aberrant upper Cretaceous Cryptoclidids such as *Kaiwhekea* and *Aristonectes*.

Richard Forrest presented **Mike Everhart's** photographs of gastroliths showing conchoidal fractures, which formed part of his talk at the 2004 SVP meeting. Mike has suggested that the fractures may be the result of high pressures within the digestive tract. There was a general consensus that it was more probable that the fracture pattern was incurred pre-ingestion. Another aspect of Mike's work on gastroliths is the investigation of their geological and geographical origin. This would be of considerable interest, as it would reveal aspects of plesiosaur behaviour and ecology not accessible by other methods.

Arthur closed the meeting by discussing the 'plesiosaur research renaissance' that has occurred since the 1970s. When, back in the '70s, Mike A. Taylor started a DPhil on plesiosaur heads he was discouraged by one senior palaeontologist on the grounds that there was no work worth doing specimens would not be made available, and/or that it was all taken up anyway by other workers.. It should be noted that Bev Halstead did not share this view, and instead shared his enthusiasm and his specimens. As Mike and others were to go on to show, this view was a rather grotesque misrepresentation and even today there are huge problem areas that require lots of work.

Additional Contributions

From Adam Morrell, Richmond Marine Fossil Museum, Australia

Email 9/12/2004

Something that I am really interested in is the origin of the Cretaceous clades – especially the Elasmosauridae. My focus is on the Early Cretaceous (Aptian/Albian) elasmosaurids from Australia. Only one skeleton has been described previously (Persson, 1960) and it was described as a “relatively” short-necked form, with a “primitive” Jurassic-grade pectoral girdle (without the intercoracoid foramen typical of the later Cretaceous elasmosaurids). As such, it formed a good evolutionary intermediate between Jurassic forms such as *Muraenosaurus* and Cretaceous forms such as *Hydrotherosaurus*.

However, examination of the type material and comparison with other, much more complete material from the same horizon shows the above description to be inaccurate. The Australian form did have a well-developed intercoracoid vacuity and long neck (~60 vertebrae), as well as many other characters of later Cretaceous elasmosaurids, such as broad epipodials and an anterodistal “knee” in the humerus. All of the characters that are typical of the Late Cretaceous forms had already evolved by the late Aptian. This is not really a surprise if earlier Cretaceous forms such as *Brancasaurus* and *Callawayasaurus* are taken into account.

This brings me to the debate about the phylogeny of the elasmosaurids. Traditionally, Jurassic long-necked forms such as *Microcleidus* and *Muraenosaurus* have been viewed as early elasmosaurids, near the base of a clade leading to the North American and New Zealand Late Cretaceous forms such as *Elasmosaurus* and *Mauisaurus*. Brown's (1981; 1993) familial diagnoses for the Elasmosauridae define the synapomorphies for the group as having elongate and numerous cervical vertebrae, with platycoelous articulations, lateral longitudinal keel, etc.

Then there's the alternative view that seems to have first been raised by Bakker in 1993 (although never acknowledged in the literature, seemingly for various reasons). In this argument, there has been much convergence between plesiosaur clades and the “elasmaur” bodyplan has evolved independently multiple times, with the Cretaceous long-necked forms representing a distinct clade from the Jurassic one(s). This was further developed and tested by Carpenter, O'Keefe, etc. based on mainly on more “reliable” cranial characters. If this is the case, then Brown's familial diagnosis is a list of homoplasies.

This is an interesting debate, and one that I hope my research will be able to offer insight into. Although my specimens were already highly derived by the end of the Early Cretaceous, I'm hoping to identify some plesiomorphic characters that will be able to link the Cretaceous group

with other plesiosaur families, whether these are the Jurassic long-necked taxa or otherwise.

What I don't understand is why this debate doesn't seem to crop up in much of the literature. Many workers in Europe (and even Australia) continue to describe new "elasmosaurid" specimens from the Jurassic, or describe Cretaceous taxa based on comparison to forms such as *Muraenosaurus* and Brown's diagnosis. These articles never even discuss the alternative view, despite mounting evidence for it.

Do you have any idea why this is? Is there some fundamental disagreement in the palaeontological community with the argument for a polyphyletic Elasmosauridae? Certainly, there have never been any definitive arguments to support separate origins of Jurassic and Cretaceous long-necked clades. O'Keefe's 2001 phylogeny left the Cretaceous elasmosaurs hanging off an unresolved trichotomy. And even if the Cretaceous elasmosaurs did share a close relationship with other Cretaceous clades such as the polycotylids (as suggested by Carpenter), then this would not preclude forms such as *Muraenosaurus* or cryptoclidids from being ancestral to the Cretaceous group.

Or are people just continuing to describe new specimens and not worrying about higher-level taxonomy while the phylogeny of the Plesiosauria is in a state of flux?

For my part, I'm focusing on the phylogeny of the Cretaceous Elasmosauridae. This was certainly an incredibly conservative group, with very little change in the last 50 million years of the Cretaceous. There have been attempts at cladistic analyses of the Elasmosauridae in the past but they weren't comprehensive. When some initial analyses placed taxa such as *Muraenosaurus* outside of the Elasmosauridae, characters such as the presence of a long neck were actually weighted to put them back inside the clade.

My work is focusing on postcranial characters, of which there are very few to differentiate between the Cretaceous specimens. I'm playing around with morphometric techniques and multivariate stats to try and identify new characters in the proportions of elements. Despite what appear to be major proportional differences between specimens (which are often noted in the literature), my preliminary results are showing very little differentiation between specimens. This was a very morphologically conservative group. This has interesting functional implications, which can be further investigated through character correlations in the phylogeny. If the shared features of Jurassic and Cretaceous long-necked forms are the result of convergence, then the similarities in proportions are remarkable, including the proportions of the limbs, etc. This indicates strong functional constraints for this bodyplan. Whatever the purpose of the elongated neck, it must have been very useful to have lasted the length of the Jurassic and Cretaceous, despite the obvious physical disadvantages it must have conveyed to swimming ability and overall fitness.

But then there are subtle differences in the form of the neck and some other elements, so there probably was some specialisation within the overall bodyplan. I've also been trying to develop some multivariate stats to compare changes in the proportions of vertebral centra along the vertebral column. As you probably well know, there are certainly some distinct patterns and differences between taxa. I guess it shows up so well in elasmosaurs because there's so much differentiation along the vertebral column, even within the dorsal series, especially when compared to other plesiosaurs.

Anyway, I have a lot of material to get through here. Over 100 elasmosaurid specimens have been collected from Australia, mostly labeled as "*Kronosaurus*" in museum collections. Colin McHenry realized what they were but has never had a chance to do anything with them. There are about 10 reasonably complete postcranial skeletons to work with, as well as a couple of skulls. A huge part of my thesis will be just raw specimen descriptions.

From Colin McHenry - Plesiosaurs down under - a quick overview

This is just a list of current research that I'm aware of. Adam Morrell has given an account of his work elsewhere in this document – after so many years of confusion about what's going on with our elasmosaurs, I'm looking forward to him sorting things out. **Chris Glen** (UQ, currently in final stages of Ph.D. looking at hind limbs in birds) did a undergraduate project on a partial specimen of a smaller, 'Leptocleidus' grade animal from Queensland, and he's presently writing that up for publication. **Ben Kear** is producing a series of interesting finds through the South Australian Museum, and **Troy Myers** is about to commence a general study on the palaeoecology of the Australian marine reptile communities through James Cook University. I'm told that **Tony Thulborn** and **Mary Wade** are close to publishing their long awaited paper on the spectacular 'Richmond pliosaur' (an early polycotyloid). **Alex Cook** at the Queensland Museum continues to dabble in the remarkable plesiosaur fossils under his care, and I'm writing up my thesis on *Kronosaurus* and hope to finish at the end of this year. I don't know what happened to **Natalie Schroeder**'s work on 'Eric'.

Obviously, plesiosaur work in Australia is almost exclusively focused on the remarkable Early Cretaceous deposits of the Great Artesian Basin. Three dimensional preservation is commonplace in the nodular limestone of the Basin, and this provides insights into anatomical features that can be hard to interpret in the 'roadkill' specimens of the more famous Jurassic plesiosaurs from Europe. Set against this is the huge area to be covered (the Basin is one of the largest geological structures in the world), and the almost total lack of good exposure – the latter a result of our 'billiard table' topography and low rainfall. Still, plesiosaurology is inching forward, with a combination of new finds and careful examination of the museum collections. A key aspect to future collection is establishing good relationships with the rural communities of the Basin – these are the people who find most of the material, and we only get to study it if they feel like telling us about it. In exchange, we do what we can to help those communities benefit from 'fossil based' tourism.

As a window into the Early Cretaceous radiation of various plesiosaurs, I think the importance of the Australian material will become more widely appreciated as the current crop of descriptions are published. As Adam Morrell has suggested for the elasmosaurs, I think that the extent of general plesiosaur radiation during the Early Cretaceous has been underestimated by most authors, and I suppose the simple reason for this is that Early Cretaceous marine sediments are rare in Europe and North America – the anglophone literature thus far concentrates on the various Jurassic radiations and of course upon the Upper Cretaceous. It will be very interesting to see if the pattern we are seeing in the Australian Early Cretaceous plesiosaurs is paralleled in rocks of this age elsewhere in the world.

I am unable to offer any summary of plesiosaurology in Australia without mentioning the difficulties faced by its practitioners. Australia is currently a very unfriendly place for any kind of science – investment in the tertiary sector continues to decrease and science funding is at an all time low. The situation in palaeontology is even worse – vertebrate palaeontologists at universities and museums are retiring without being replaced, and whilst I don't know exactly how many vertebrate palaeontologists have permanent employment in research positions at universities and museums in the country overall, I guess the number would be five or less. There is currently no-one in the country who is both allowed to officially supervise a PhD on plesiosaurs and who is qualified to do it. In the current climate, those people of the above list who have recently gained employment and/or research grants in the field are to be heartily congratulated.

This year, CAVEPS (the Australian/NZ VP meeting) is in South Australia, and hopefully a few of us will be able to catch up over a beer. However, in general isolation is a big issue, both within Australia and between us and the rest of the world. If there are any plans to implement an email list or a web discussion board, I'm sure it would be a great help for us.

Mike Everhart –Sternberg Museum of Natural History, Fort Hays State University, Kansas, USA

Other topic suggestions:

What were they eating? (let's pay special attention to stomach contents and a possible change in habits from the Jurassic through the Cretaceous)

An old, yet unanswered question: What was the role of gastroliths? ...do they occur regularly in any group besides elasmosaurs? What is their earliest occurrence?

What can we say regarding the range / mobility of elasmosaurs from the probable source of their gastroliths versus where their remains are found? (Elasmosaurs found in western Kansas are several hundred kilometers from the nearest sources of such stones)

When did pliosaurs go extinct worldwide? Our last pliosaur in Kansas (*Brachauchenius*) dates from the Middle Turonian.

From Mike Taylor – National Museums of Scotland.

Selected comments:

I should also observe that I found it a surprisingly difficult job doing a recent limbs review paper with Hans Thewissen (I did the tetrapods other than mammals). Although I managed to 'use up' most of my remaining unpublished functional morphological thinking, and clear that side of my desk, so to speak, I did not enjoy doing this paper, as I found, rather counterintuitively, that the marine reptiles were by far the most difficult part. I came to feel that one of the problems with plesiosaur (and marine reptile generally) work is that the swimming side of matters is sometimes - not always, but sometimes - being taken that bit too far. And, in fairness, I have to say that I now find my 1987 ichthyosaur swimming paper horribly simplistic.

I was left feeling that if I ever have the opportunity and the time I would like to collaborate with a real modern hydrodynamics expert to give all this marine reptile swimming stuff a good critical review.

MAT plesio projects 29.9.04

In press

J. G. M. Thewissen and M. A. Taylor. Aquatic adaptations in amniotes [limbs]. In B. K. Hall (ed.) *From Fins to Flippers*. University of Chicago Press.

Already 'started' but still in gestation – if sometimes the blastocyst is under delayed implantation ...

M. A. Taylor, A. R. I. Cruickshank and L. F. Noè. Design for torsion in tetrapod skulls: the case of twist-feeding pliosaurs (Plesiosauria: Reptilia). (This discusses the use of geodesic lines of tension and compression, and how they are not pure helices but are modified by beam loadings.)

M. A. Taylor, L. F. Noè and perhaps G. W. Storrs. The marine reptile fauna from the lowermost Lias (Rhaetian, Late Triassic, and Hettangian, Lower Jurassic) of Street, Somerset. Also published and in press/preparation, papers on various collectors of Street marine reptiles.

M. A. Taylor. Bristol Institution ichthyosaur and taxonomic problems of *Ichthyosaurus latimanus*.

In the longer term

M. A. Taylor. A review of Scottish marine reptile material as acquired by NMS in recent years – mostly fragmentary and mostly Upper Jurassic (and much of it not plesiosaurian). Likely to produce lots of worthy but short, even it'sy bitsy, papers - nothing very revolutionary at first glance.

Proposed MSc student project with Mike Benton

Dorset County Museum plesiosaur (?pliosaur) with gastroliths.

Leslie Noè - The Sedgwick Museum.

The cranial descriptions of the three genera I covered in my thesis are nearing completion for publication;

Working with Mike Taylor on the Street fauna;

The elasmosaur neck and salt gland papers are close to completion;

Work is continuing on the new pliosaur genus here in the Sedgwick and in Oxford;

I'm close to tracking down the lost holotype of *Cryptoclidus*.

Also areas that to me seem to be critical for further research are:

The origin and early evolution of the group;

Developing a rigorous and generally accepted phylogeny (via cladistics or other methods);

Elucidating the reasons for the various morphological changes seen in the group through time;

Development of robust models of locomotion for individual taxa, leading into a wider understanding within and across the group.

Marcella Gomez – Cambridge University

Working on the detailed description of the cranial anatomy of the Colombian beast, and commencing the preparation of the post-crania;

David Brown – Newcastle University Dental School

I will not be embarking on any new plesiosaur research, but before I retire (in 8 years!!) I aim to publish just 2 papers which have been partly prepared for a long time. These are:

1. A description of the small elasmosaurid plesiosaur in Hugh Miller's Reptile Bed from the Isle of Eigg.
2. A description of the skull of the holotype specimen of *Microcleidus homalospondylus* (BMNH 36184), which I prepared rather a long way back and for which I have done all the detailed drawings.

Some unanswered questions and potential areas for research.

Plesiosaur ancestry

There is 30 million year ghost lineage before the first plesiosaurs are recorded in the Rhaetian of Southern Britain.

Comment from Colin McHenry: There's an extensive series of Mesozoic marine sediments, all the way from Saudi Arabia, through Iraq and Iran, and into Afghanistan. Tony Thulborn and Tom Rich looked at the Saudi Arabian stuff back in the 70's - early Upper Triassic - they stopped at 6 places on a four day drive and found stuff in every location. Lots of 'nothosaur indet' stuff. It's crying out for some decent work..

European Cretaceous plesiosaurs

Fragmentary plesiosaur specimens are held in museum collections such as the Booth Museum, Brighton, the Natural History Museum, the Yorkshire Museum, Dorking Museum and others. Apart from Andrews (1922) account of *Leptocleidus superstes* no papers have been published on this material since the 19th century and although fragmentary, these specimens may help clarify the taxonomic relationships.

Kimmeridge Clay plesiosaurs.

Although the Callovian Oxford Clay contains perhaps the best known of all plesiosaur faunas, that of the slightly more recent Kimmeridge Clay is sparsely studied. Specimens from this formation have been assigned to Callovian taxa, but usually on the basis of fragmentary material and inadequate taxonomic analysis. Inspection of collections both in public and private hands suggests that the diversity of this fauna was greater than that of the Oxford Clay.

Leslie Noè is working on the clarification of the taxonomic and nomenclatural issues for the plesiosaurs from this fauna (Noè, Smith & Walton 2004).

The status of genus *Kimmerosaurus* (Brown 1981), needs to be resolved. It has been suggested (Brown, Milner & Taylor, 1986) that it is synonymous with *Colymbosaurus*, and this suggestion is supported by Adam Smith's cladistic analysis (above) .

Lower Cretaceous plesiosaurs.

Brancaesaurus brancai (Wegener 1914) is of uncertain phylogenetic status, and much in need of detailed revision. Little material from the Lower Cretaceous has been described, though it is known from the marine Aptian/Albian in Colombia and other parts of South America, Madagascar and the marine Albian in Alberta and Montana . Pat Druckenmiller is working on the north American material.

General

Comment from Colin McHenry: Can we cook up a standard methodology of anatomical description? An anatomical model for the Plesiosauria doesn't exist. We need a model that we can use as a reference point for descriptions, including anatomical nomenclature. We don't have one. You say pectoral, I say prothoracic. After nearly 200 years, the anatomical nomenclature of plesiosaurs is just about as messy as the taxonomy. It needs standardising.

Taxonomy

The degree of homoplasy we find in the cladistic analyses is so high that we need to think very carefully about what they are telling us. An understanding of biomechanics in plesiosaurs is needed to resolve some taxonomic issues. There is also the need for development of a more robust character set including better post-cranial characters, and a better understanding of ontogenetic variation.

Behaviour

Comment from Mike Everhart: What were they eating? Let's pay special attention to stomach contents and a possible change in habits from the Jurassic through the Cretaceous.

Gastroliths

Comment from Mike Everhart: An old, yet unanswered question: What was the role of gastroliths? Do they occur regularly in any group besides elasmosaurs? What is their earliest occurrence? What can we say regarding the range / mobility of elasmosaurs from the probable source of their gastroliths versus where their remains are found? (Elasmosaurs found in western Kansas are several hundred kilometers from the nearest sources of such stones)

Comment from Mike Taylor: And someone might want to point out that nobody has quite successfully (in my view) refuted my argument of gastroliths used in ballast (whether for trimming or overall buoyancy or for enabling an increased lung volume is perhaps debatable). A related problem seems to be that that some- but not all! - people confuse weight in air (in which gastros make a relatively small contribution) with weight in water (where they make a very large contribution as most of the animal is effectively the density of water and so weightless).

Having said that, Don Henderson's buoyancy-sceptical croc buoyancy paper (Canadian Journal of Zoology 2004) is very interesting and must be taken seriously, although he focuses on what to me is the limiting condition of surface swimming, and vice versa. I'd also draw attention to Oliver Wings's papers and website, and Mike Everhart's Oceans of Kansas site. And Mike's point about the distribution of gastroliths in plesiosaurs is also crucial, if it helps point to fundamentally different lifestyles for the subgroups. More widely than gastroliths: given the convergence in lifestyle in other groups (e.g. penguin/otariid), can we

not expect convergence and parallelism within plesiosaurs – which also ties in with what others here are saying?

Richard Forrest

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