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Naturwissenschaften
The Science of Nature

ISSN 0028-1042

Naturwissenschaften
DOI 10.1007/s00114-012-0917-1

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A drowned Mesozoic bird breeding colony from the Late Cretaceous of Transylvania

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Received: 14 March 2012 / Accepted: 11 April 2012
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Abstract Despite a rapidly improving fossil record, the reproductive biology of Mesozoic birds remains poorly known: only a handful of undisputed, isolated Cretaceous eggs (some containing embryonic remains) are known. We report here the first fossil evidence for a breeding colony of Mesozoic birds, preserved at the Late Cretaceous (Maastrichtian) Oarda de Jos (Od) site in the Sebeş area of Transylvania, Romania. A lens of calcareous mudstone with minimum dimensions of 80 cm length, 50 cm width and 20 cm depth contains thousands of tightly packed, morphologically homogenous eggshell fragments, seven near-complete eggs and neonatal and adult avialan skeletal elements. Eggshell forms 70–80 % of the matrix, and other fossils are entirely absent. The bones exhibit clear characters of the Cretaceous avialan clade Enantiornithes, and the eggshell morphology is also consistent with this identification. Both taphonomy and lithology show that the

components of this lens were deposited in a single flood event, and we conclude that it represents the drowned remains of a larger enantiornithine breeding colony, swamped by rising water, washed a short distance and deposited in a shallow, low-energy pond. The same fate often befalls modern bird colonies. Such a large concentration of breeding birds suggests aquatic feeding in this species, augments our understanding of enantiornithine biology and shows that colonial nesting was not unique to crown birds.

Keywords Avialae · Enantiornithes · Eggs · Oology · Nesting behaviour · Hatching

Introduction

Despite a dramatic improvement in the number of fossil birds known from the Mesozoic over the last decade, our understanding of egg morphology and nesting behaviour in Mesozoic birds remains sparse. Just a handful of Mesozoic taxa are known from embryonic remains (Elzanowski 1981; Schweitzer et al. 2002), and even less are associated with egg shell and/or complete eggs (Grellet-Tinner and Norell 2002; Mikhailov 1996; Schweitzer et al. 2002; Zhou and Zhang 2004). Of particular note, a single unhatched enantiornithine egg, containing the remains of a clearly precocial embryo (with well-developed primary feather tracts), has been described from the Early Cretaceous of China (Zhou and Zhang 2004). Nothing is known about the breeding behaviours of Mesozoic birds; In this paper, we present a remarkable eggshell, egg and bone accumulation from the Late Cretaceous of Transylvania, Romania (Vremir 2010) (Fig. 1), that provides the first direct evidence for colonial breeding in Cretaceous birds. This fossil accumulation—termed here the Od accumulation (Oarda de Jos)—is a lens

Communicated by: Robert Reisz

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Fig. 1 The Od accumulation (Late Cretaceous: Sebeș, Romania): **a** map showing the location of the Od site (star), **b** two of the seven partial enantiornithine eggs from the upper layer, **c** matrix supported mudstone

in the upper layers of the lens, **d** shell-supported material from lower portions of the lens. Scale bars are 1 cm

of calcareous mudstone composed of thousands of morphologically homogenous eggshell fragments associated with a number of near-complete eggs ($n=7$), complete and identifiable bird bones ($n=12$) and numerous indeterminate bone fragments ($n\sim 50$; the entire lens was collected in pieces and is now housed in the Transylvanian Museum Society museum, Cluj-Napoca, Romania as EME V.314) (Fig. 1b–d). The accumulation was collected from the basal fluvio-paludal part of the Od outcrop in the Maastrichtian Sebeș Formation, which outcrops about 100 km from the city of Cluj-Napoca in western Romania (Vremir 2010; Fig. 1a).

In parts of the Od calcareous lens, 70–80 % of the rock is formed by eggshell fragments (Fig. 1d). The remainder is a calcareous matrix representing a floodplain limestone facies (Codrea and Dica 2005; Codrea et al. 2010; Csiki et al. 2010; Therrien et al. 2002; Vremir 2010). As we discuss, the bones, eggshell fragments and near-complete eggs all appear to belong to the same avialan taxon (a member of the Cretaceous clade Enantiornithes).

Geology and taphonomy

Continental outcrops of the Maastrichtian Sebeș Formation occur in the southwestern part of the Transylvanian sedimentary basin (including the well-known “Râpa Roșie” or Red Cliffs)

(Vremir 2010). The most productive vertebrate localities are distributed along the southwestern part of the Transylvanian Basin in the vicinity of the town of Sebeș (Codrea and Dica 2005; Codrea et al. 2010; Csiki et al. 2010; Vremir 2010; Fig. 1a). The calcareous lens described here comes from the middle section of the Sebeș Formation, characterised by laterally extensive sandy channel fills of a meandering fluvial system, silty crevasse splays, locally developed ponded calcareous mudstones with thin coal layers and extensive brownish-red fine overbank deposits (Vremir 2010; Fig. 2).

Few associated skeletal remains have been collected from the Sebeș Formation. Ornithopod hind limb elements, a partial lizard skeleton, a partially articulated medium-sized azhdarchid pterosaur and the dromaeosaurid *Balaur bondoc* (Csiki et al. 2010; Vremir 2010) all come from the reddish overbank sediments (Fig. 2).

The Od accumulation itself comprises a distinct calcareous lens, collected almost in entirety from above the reddish overbank mudstone mentioned above. Palaeocurrent data associated with the accumulation show a northeast flow direction (i.e. almost perpendicular to the outcrop face; Fig. 2a) and bone, egg and eggshell preservation in the accumulation is consistent with a very short transport distance from a river bank or sandbar into a small, shallow pond trapped by rising water: All bones are unabraded, and seven almost complete eggs are preserved. A seasonal, tropical monsoonal climate

Fig. 2 **a** The Oarda de Jos vertebrate locality (Od.A1 and A2), Maastrichtian, Sebeş Formation (after Vremir 2010, modified) **b** the Od site in the Sebeş river

with long dry periods followed by short, wet bursts has been inferred for the Maastrichtian in this region (Therrien et al. 2002; Therrien 2005; Vremir 2010). Periodic floods, sometimes extreme, have also been demonstrated based on sedimentological evidence (Therrien et al. 2002).

Much smaller but similar avialan eggshell-supported limestone accumulations have been described from the contemporaneous Hațeg Basin of Transylvania (Van Itterbeeck et al. 2004) and from the Paleocene of the Clarks Fork Basin, Wyoming (Bowen and Bloch 2002). The sedimentology and

interpretation of these limestones are very similar (Therrien et al. 2002; Therrien 2005), the differences being the smaller size of the Wyoming specimens and structure of the fossil assemblage from Sebeş: as far as can be determined, the Od accumulation is monospecific.

Description

Cursory examination of the Od accumulation reveals it to be a consolidated mass of literally thousands of brown-grey eggshell fragments, tightly packed together but separated by sediment (Figs. 1c, d, 3). The quantity of eggshell fragments in the Od accumulation is astonishing and beyond normal palaeontological experience, with 70–80 % of the lens' volume formed by eggshell throughout the ca. 80×50×20-cm dimensions of the accumulation: 153 shell fragments are present in one 26-cm² section from near the base of the lens (mean exposed shell fragment length, 36 mm±0.126 SD). One of the almost complete sub-rounded eggs is 4.0×2.5 cm in dimensions and would have had a volume of around 11 cm³ (using equations in Hoyt 1979). Using these calculations as a basis, eggs occur at high density in the sample, ca. 46 whole eggs per 100 cm³.

The inner surfaces of eggshell fragments are dull and etched in places (Fig. 4e), suggesting that calcium mobilisation was advanced and that the eggs had either hatched or were destroyed late in the second half of incubation (Simkiss 2004; Board and Sparks 2004). This is corroborated by the presence of broken, jumbled juvenile bone fragments within the accumulation. Scanning electron microscopy (SEM) of the Od eggshell fragments shows that they comprise compact shell units with calcite crystals

forming two large, distinct layers that are similar in thickness (Fig. 4a), a morphology consistent with previous descriptions of ornithothoracine bird eggs (see, for e.g. Grellet-Tinner et al. 2006). Further descriptions and micro-characterisation of eggs and shells will be presented in later work.

Some of the adult bones (humerus, scapula and coracoid; Fig. 4f, g) preserve characters hypothesised in phylogenetic studies to be enantiornithine synapomorphies (i.e. dorsal margin of the humeral head concave centrally, rising ventrally and dorsally; costal surface of scapula blade with prominent, longitudinal furrow; pit between acromion and humeral articular facet on proximal end of scapula absent; coracoid with laterally compressed dorsal end and almost aligned acrocoracoid process, humeral articular surface and scapular facet) (Chiappe and Witmer 2002; O'Connor et al. 2009, 2011). The surfaces of the Od eggshells also lack marked ornamentation (Fig. 4e), a character hypothesised by some authors as a synapomorphy of Avialae with respect to other theropods (Grellet-Tinner et al. 2006; O'Connor et al. 2011); furthermore, the presence of two subequal prismatic eggshell layers (rather than three) in section (Fig. 4a) implies (based on some analyses) that these shells can be excluded from the avialan clade Ornithuromorpha (sensu Grellet-Tinner et al. 2006), consistent with our osteological enantiornithine determination (Chiappe and Witmer 2002; O'Connor et al. 2009, 2011). Note that although the phylogenetic distribution of these features is debated and may be more widespread among theropods (Zelenitsky and Therrien 2008; Jackson et al. 2010), the eggshell characters we list are consistent with our osteological identification of the Od birds.

Indeed, the Od accumulation bones correspond in morphology and dimensions with those of *Enantiornis* from Argentina (Walker 1981; Chiappe 1993; Walker and Dyke 2010), strongly suggesting that they come from the same, or a similar, taxon. The proximal section of a humerus (Fig. 4f) has a saddle-shaped head that is convex and separated from the bicipital crest by a deep, wide ligamental groove. The bicipital crest is robust, rounded, anteriorly projecting and bears a distinct but narrow pneumatic fossa (as in *Enantiornis*) (Walker and Dyke 2010); the deltopectoral crest is prominent and flat. Incipient pneumatisation of this region via a small pneumatic fossa is shared with similarly sized Argentine enantiornithines, particularly *Enantiornis* (Walker 1981; Walker and Dyke 2010). An adult scapula from the Od assemblage is robust, straight and with a well-developed, straight acromion, a medial longitudinal groove (Fig. 4g) and a depression anterior to the coracoid articulation. The dorsal end of a large coracoid from the assemblage bears a fenestra in its medial wall. All of these features are also present in *Enantiornis* (Walker 1981; Chiappe 1993; Walker and Dyke 2010). The anterior portion of a sternum,

Fig. 3 The entire Oarda de Jos calcareous lens as collected and prior to preparation of individual pieces. Scale bar is 5 cm

with non-overlapping coracoidal sulci and no spina, also fits the size range of this taxon (Fig. 4h).

In a further effort to determine the affinities of the adult bones within the assemblage, we compared them with elements described for other Late Cretaceous enantiornithines from Eastern and Central Europe. Ősi (2008) reported an enantiornithine femur and tarsometatarsus from the Santonian Csehbánya Formation of Iharkút, Hungary, as well as a number of limb elements identified as those of indeterminate avialans. Dyke and Ősi (2010) described additional Iharkút enantiornithine specimens and named the Iharkút tarsometatarsus as the new avisaurid *Bauxitornis mindsentyae*. Ősi and Buffetaut (2008) described two enantiornithine femora from Iharkút and suggested that they might be referable to *Bauxitornis*. Unfortunately, none of these elements overlap with those present in the Od accumulation. Wang et al. (2011) described two enantiornithine humeri from the Hateg Basin that differ in the shapes of their proximal ends from the element present in the Od assemblage: the caput humeri of the Od enantiornithine and *Enantiornis* is smoothly rounded, whereas in the specimens described by Wang et al. (2011) the head is raised proximally and is more angular. This may very well be a size-related difference, but more fossils will be required to test this supposition.

The Od accumulation also includes numerous smaller, broken bones. These elements are mostly indeterminate, slender, thin-walled and hollow, but a quadrate, pedal phalanges, cervical and dorsal vertebrae, proximal end of a tibiotarsus and scapula (Fig. 4c–e, g–j) are also present. Identifiable elements evidently belong to avialan theropods,

and we suggest that, because of their incomplete development and size, they all belong to neonate birds. Of these smaller elements, the scapula is robust and has a well-developed, squared-off acromion, consistent with an enantiornithine identification (Chiappe and Witmer 2002; O'Connor et al. 2009, 2011) (Fig. 4j).

Discussion

Our interpretation is that the Od accumulation represents a breeding colony of Late Cretaceous (Maastrichtian) enantiornithines. As such, it significantly augments our understanding of enantiornithine biology. Firstly, the obvious proximity of the drowned colony to a water course might suggest aquatic feeding habits for this species only because there is a consistent link between aquatic foraging and the habit of nesting on sandbars and riverbanks in extant birds. While some enantiornithines were denizens of inland, terrestrial environments, stomach contents (Sanz et al. 1996) and morphological adaptations suggest that at least some members of the group were aquatic foragers (Sanz and Buscalioni 1992). We conclude that the proximity of the Od nesting colony to water provides additional evidence for this view of aquatic enantiornithines. Nesting in close proximity to water brings the danger of flooding (Kharatinov and Siegel-Causey 1988); this is a major cause of nest mortality in extant waterfowl (Whitehead and Tschimer 1990; Flint and Grand 1996), terns (Sidle et al. 1992; Ludwig et al. 1993), plovers (Espie et al. 1998), flamingos (Brown 1957) and other birds, and can cause destruction of an entire

Fig. 4 Eggshell, some adult and neonate avialan bones from the Od accumulation: **a** SEM image of sample eggshell section with two main structural layers indicated with arrows. Scale bar is 100 μ m. Neonate avialan cervical vertebra (**b**), pedal phalanx (**c**) and dorsal vertebra (**d**) (scale bar in (**b**) and (**c**) is 2 mm, in (**d**), 1 mm). **e** Eggshell shown from the inside (*in*) and outside (*o*), alongside neonate avialan quadrate (arrow). Adult enantiornithine humerus (**f**), scapula (**g**) and sternum (**h**) (scale bars are 1 cm). Neonate avialan proximal tibiotarsus (**i**) and scapula (**j**) (scale bars are 2 mm)

colony (Brown 1957; Peresbarbosa and Mellink 2001; Poiani 2006), on occasion repeatedly during the same breeding season (Peresbarbosa and Mellink 2001). Birds continue to select these sites in future nesting seasons, partly because floods remove vegetation and increase the amount of barren ground suitable for near-water nesting (Sidle et al. 1992).

The near-complete eggs in the accumulation are bluntly pointed and slightly asymmetric in profile (Fig. 1b), similar in shape to eggs produced by modern ground-nesting birds with precocial or semi-precocial young (Mao et al. 2007). Their slightly pointed shape would have affected the pattern of heat loss (Smart 2004; Mao et al. 2007) but more likely would have both facilitated gas exchange by creating space for a large air cell (Grellet-Tinner et al. 2006; Mao et al. 2007), and allowed the eggs, just like all other bird eggs, to

lie naturally on one side, with the pore-rich, blunt end elevated (Board and Sparks 2004; Mao et al. 2007; Fig. 1b). The more complete Od eggs are at least 50 % larger than the handful of other Mesozoic ornithothoracine eggs associated with embryonic bones (Elzanowski 1981; Mikhailov 1996; Grellet-Tinner and Norell 2002; Schweitzer et al. 2002; Zhou and Zhang 2004; Grellet-Tinner et al. 2006). These observations, their broken polar regions (Fig. 1b), and the absence of any remaining bone fragments within the two near-complete eggs (Paul Tafforeau, European Synchrotron Radiation Facility, personal communication 2011), are consistent with the interpretation that they are hatched and that (like other reported Cretaceous bird eggs) they belonged to ground-nesting birds (Schweitzer et al. 2002; Mikhailov 1996; Grellet-Tinner et al. 2006): the polar region adjacent to the air cell is often

Fig. 5 Additional adult and neonate enantiornithine bones from the Od accumulation: **a** complete ulna (total preserved length, 75 mm), **b** complete tibiotarsus (total preserved length, 75 mm), **c** proximal humerus (total preserved length, 11 mm)

destroyed after hatching in gull colonies (Hayward et al. 2000), as is the case here (Fig. 1b).

The abundance of eggshell, eggs and juvenile bones (and their uniformity of preservation, implying a similar taphonomic history) that make up the assemblage suggests synchronous breeding and colonial nesting (Figs. 4 and 5). This is unsurprising: Synchronous breeding in large colonies is a widespread and successful strategy in modern birds, with the largest examples most often located at secure sites like offshore islands or sandbars surrounded by flowing water. However, large colonies present birds with the problem of feeding both themselves and large numbers of young over extended periods of time. Living birds solve this problem with strong flight and the ability to disperse across large areas in search of food. Strong flight has been suggested for some larger enantiornithines, like *Enantiornis* (cf. the Od bones) and *Martinavis*, known from fossil specimens widely separated geographically (Walker et al. 2007). The presence of possibly synchronous, colonial breeding in turn implies that the Od enantiornithines were taking advantage of seasonally abundant but localised food resources. The adult birds may have nested as early as possible, balancing the risk of flooding against the advantages of early access to this constrained resource: the colonial nesting Red-billed quelea *Quelea quelea*, for example, breeds in the second half of the rainy season when insects are most abundant (Mundy and Herremans 1997). It is unknown whether the associated adults were involved in the care of eggs, nests or juveniles, but their presence at least implies some parental care in this bird: an unhatched egg from China indicates that the young of some enantiornithines were precocial (Zhou and Zhang 2004). The Od accumulation is clear evidence that waterside colonial nesting was present in Cretaceous birds, but also that this habit was far from unique to crown birds (Neornithes).

Acknowledgments We thank E. Buffetaut, A. Clark, Z. Csiki, A. Dulai, J. Dyke, G. Grellet-Tinner, E. Hankó, R. Hebda, R. Horn, F. Jackson, E. Kurochkin, A. Ősi, J. O'Connor, P.M. Sander, P. Tafforeau, D. Varricchio, X. Wang, two anonymous reviewers, R. Reisz and S. Thatje for their help with this project and for detailed comments on the manuscript.

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