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It is widely accepted that Mesozoic ecosystems were basically similar to Cenozoic ecosystems and it has been proposed that the role of dung-beetles in those ecosystems was identical to that of today, but the dung of dinosaurs were used as a source of food instead of the dung of mammals. While dinosaurs have been known since Triassic, Scarabeids are present in the fossil records probably since Lower Jurassic. But a very important metabolic feature of dinosaurs has not been taken into account, the connection between digestive and uro-genital systems. So here we propose the hypothesis that coprophagy in dung-beetles has been associated, since it began, with mammals.

Keywords: paleobiology; mesozoic ecosystems; coprophagy; dinosaurs; dung-beetles

Introduction

In today's ecosystems, most dung-beetles are associated with herbivorous mammals. The moment when some scarabeids changed their saproxilic diet to coprophagy (Cambefort 1991) is controversial and some authors believe that dung-beetles were associated with plant-eating dinosaurs (Krell 2006). This presumes that Mesozoic ecosystems were basically similar to Cenozoic ecosystems and that the role of dung-beetles in those ecosystems was identical to that of today, but the dung of dinosaurs were used as a source of food instead of the dung of mammals. Such extrapolations are "often unreliable especially when fossil assemblages include members of extinct clades" (Chin and Gill 1996).

Materials and methods

In this paper three hypotheses will be proposed as a result of comparing digestive systems between mammals and the clade Aves + Dinosauria.

Results

Terrestrial Cenozoic ecosystems have been dominated by vast areas of grassland, at least since the Eocene, which led to a co-radiation of herbivorous mammals and scarabeids. In these ecosystems big-sized gregarious mammals fed on pasture. Their dung was used by dung-beetles as a source of food for their larvae, mainly in three

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different ways: (1) ball formation followed by rolling away for burial in soil (telecoprids or rullers); (2) net construction directly under the dung (paracoprids or tunnellers) and (3) feeding from and reproducing directly into the dung (endocoprids or dwellers) (Bornemisszа 1969; Cambefort and Hanski 1991). Burrowed faecal material unused by larvae and the dung-beetle faeces act as a fertilizer of the soil regenerating the grassland. This energy flow among the different trophic levels of the ecosystem is rapid.

When a comparison is made between Cenozoic and Mesozoic ecosystems, a very important metabolic difference between dinosaurs and mammals has not been taken into account. It is very important that extinct dinosaurs (as extant avian dinosaurs) had a connection between digestive and uro-genital systems, converging at their end in a joint orifice: the cloaca. So they produced a mixture of faeces and excretory products. This mixture has a high percentage of nitrogenous molecules. Today birds produce this uro-digestive waste that is not very attractive to dung-beetles (probably because of its nitrogenous levels, in the form of ammonia and uric acid, and high concentration of phosporic acid, oxalic, carbonic acids and salts), so when birds nest in huge gregarious groups their dung accumulate, forming guano.

This is the case of gregarious birds nesting in sea cliffs, but normally their guano accumulations are washed by the sea. There is another very interesting example – the oil bird or guácharo (*Steatornis caripensis* Humboldt, 1817) who nests in caves in Trinidad, Venezuela, Colombia, Ecuador and Peru. These night birds feed on fruits and seeds and once in caves they regurgitate the indigestible seeds. These seeds, together with bird droppings and bird carcasses accumulate on the cave floor. Some seeds, if moisture is sufficient, sprout but seedlings die due to the perpetual darkness of the cave. Beetle fauna have been studied in the most important oil bird cave, the Cueva del Guácharo in Venezuela, where 29 beetle species have been reported (Peck and Kukalova-Peck 1989) including only one Scarabaeidae, *Anaides* cf. *fossulatus* Westwood, 1841 which is not a dung-attracted species but a feeder on decaying plant matter in seed piles. Several physical and chemical variables in the oil bird guano deposits have been studied finding that they were very rich in nitrogen (Herrera 1995).

Sampling dung beetles in Panama with pitfall traps baited with reptile faeces (Young 1981) only two species of Scarabaeidae were obtained (*Onthophagus sharpi* Harold 1875 and *Canthon moniliatus* Bates 1887) both with a wide feeding niche, and always in very small quantities in contrast of close pitfall traps baited with mammal faeces. In addition, none of these species had been reported using this reptile dung as food. So it seems that attraction of dung beetles to reptile faecal material is also low, and, in any case, the limited attraction of adult scarabeids to reptile dung does not prove that their larvae could feed and complete metamorphosis with this faecal material.

While dinosaurs are known since Triassic, Scarabeids are present in the fossil record only since Upper Jurassic of Karatau, Kazakhstan (Krell 2000, 2006; Scholtz 1990) but features that could be interpreted as adaptations for coprophagy are ambiguous. Indeed coprophagy traces are known in vertebrate coprolites (not only dinosaurs) since the Triassic, so they could not be attributed to Scarabaeidae but probably to Diptera larvae (Wahl et al. 1998). This must be the case of a dinosaur coprolite (probably produced by *Maiasaura peeblesorum* Horner and Makela, 1979) discovered in a late Campanian outcrop in Montana (Chin and Gill *op. cit*.). This coprolite shows two holes (very different sized) and, although they are interpreted as being produced by scarabeid dung-beetles, due to their small diameter they were probably more likely produced by Diptera larvae.

The oldest ichnofossil that can be interpreted, without any doubt, as the result of coprophagy behaviour in dung beetles is *Coprinisphaera* Sauer, 1955, a very common ichnofossil in South America, from Late Cretaceous-Paleocene to Pleistocene. It represents fossil dung-beetle pupal chambers (Genise et al. 2000).

Recently (Prasad et al. 2005) a study of 65–67 million year old coprolites from India, have found fossil grass phytoliths, which implies that at least five taxa of grasses (Poaceae) were present in Late Cretaceous ecosystems of Gondwana. Authors suggest that grass was an important food for Cretaceous mammals belonging to poorly known clade Gondwanatheria, known from Upper Cretaceous of Argentina, Madagascar, Tanzania and India and the Early Cenozoic of Argentina and Antarctica. The most frequent herbivorous mammal group in Cretaceous was Multituberculata, a Prototheria group. Today extant Prototheria (Ornithorhynchidae and Tachyglossidae) have cloaca, so, although Prototheria is a clearly paraphyletic group (Luo et al. 2002), Multituberculata probably also had cloaca. Thus it seems that coprophagous behaviour in dung-beetles was associated with the Theria faecal material.

If we assume that *Coprinisphaera* was present during the Late Cretaceous, association between dung-beetles and Gondwanatherians began in southern continents, previous to the extinction of large non-avian dinosaurs although coprophagy probably had a small role in ecosystems until large herbivorous mammals began their radiation in the Cenozoic (in South America Edentata could be present in Uppermost Cretaceous).

Discussion

As a result of previous information we propose the following hypotheses:

(1) Coprophagy in dung-beetles is associated, since it began, with mammals, probably since Lower Cretaceous in Gondwana.

(2) Energy flow in Mesozoic ecosystems must be slower than in Cenozoic ecosystems; dinosaur faeces were not worked and they probably accumulated, dried and hardened. They only returned to the soil when mechanical disruption (probably the rain) disaggregated them. To avoid the suffocation of the ecosystem due to the presence of this large amount of hardened dung, and as many herbivorous had gregarious behaviour, these species probably had a low density of population, which allowed the regeneration of the soil. So herbivorous dinosaurs had vast feeding areas like modern big-sized carnivorous mammals. Something similar occurs today in areas where extinction of big mammals occurred recently affecting dung-beetle population. For example, the introduction of cattle in Australia was a problem, as native coprophags were not able to process the huge quantity of faeces and the unprocessed dung was suffocating pasture systems and preventing the regeneration of grass (Bornemissza 1960).

(3) In a forest ecosystem, dung deposited on the floor has little effect on photosynthesis as the plants are mainly arboreal, while in a grassland, dung accumulated on the floor limits light penetration and therefore photosynthesis. Thus a fauna with large dinosaurs producing an accumulative layer of

dung favours a forest ecosystem instead of a grassland ecosystem. It is likely, therefore, that grass prairies, although perhaps present in the Late Cretaceous, only became dominant ecosystems once large dinosaurs became extinct.

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References

Bornemissza GF. 1960. Could dung eating insects improve our pastures? J Aust Inst Agric Sci. 26:54–56.

Bornemissza GF. 1969. A new type of brood care observed in the dung beetle *Oniticellus cinctus* (Scarabaeidae). Pedobiologia 9:223–225.

Cambefort Y. 1991. From saprophagy to coprophagy. In: Hanski I, Cambefort Y, editors. Dung beetle ecology. Princeton (NJ): Princeton University Press. p. 22–35.

Cambefort Y, Hanski I. 1991. Dung beetle population biology. In: Hanski I, Cambefort Y, editors. Dung beetle ecology. Princeton (NJ): Princeton University Press. p. 36–50.

Chin K, Gill BD. 1996. Dinosaurs, dung beetles and conifers: participants in a Cretaceous food web. Palaios 11:280–285.

Genise JF, Mangano MG, Buatois LA, Laza JH, Verde M. 2000. Insect trace fossil association in paleosols; the *Coprinisphaera* ichnofacies. Palaios 15:49–64.

Herrera FF. 1995. Las comunidades de artrópodos del guano de guácharos en la Cueva del Guácharo, Venezuela. Bol Soc Venez Espeleol. 29:39–46.

Krell FK. 2000. The fossil record of Mesozoic and Tertiary Scarabaeoidea (Coleoptera: Polyphaga). Invertebr Taxon. 14:871–905.

Krell FK. 2006. Fossil record and evolution of Scarabaeoidea (Coleoptera: Polyphaga). Coleopterists Society Monograph Number 5:120–143.

Luo Z-X, Kielan-Jaworowska Z, Cifelli RL. 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeontol Pol. 47(1):1–78.

Peck SB, Kukalova-Peck J. 1989. Beetles (Coleoptera) of an oil-bird cave: Cueva del Guácharo, Venezuela. Coleopt Bull. 43(2):151–156.

Prasad V, Strömberg CAE, Alimohammadian H, Sahni A. 2005. Dinosaur coprolites and the early evolution of grasses and grazers. Science 310(5751):1177–1180.

Scholtz CH. 1990. Phylogenetic trends in the Scarabaeoidea. J Nat Hist. 24:1027–1066.

Wahl AM, Martin AJ, Hasiotis ST. 1998. Vertebrate Coprolites and Coprophagy Traces, Chinle Formation (Late Triassic), Petrified Forest National Park, Arizona. Technical Report National Park Service/NRGRD/GRDTR-98/1, p. 144–148. Available at: http://www2.nature.nps.gov/geology/paleontology/pub/grd3_3/pefo7.htm.

Young OP. 1981. The attraction of Neotropical Scarabaeinae (Coleoptera: Scarabaeidae) to reptile and amphibian fecal material. Coleopt Bull. 35(3):345–348.