

Short Note



Bacteria meet the “titans”: horizontal transfer of symbiotic microbiota as a possible driving factor of sociality in dinosaurs

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INTRODUCTION

For a long time after their discovery, and their subsequent recognition as a formal group by Sir Richard Owen in 1842, dinosaurs were considered as heavy and clumsy big lizards, with an aggressive or solitary attitude. However, since the early 1970s, a real revolution in the field of paleontology has completely changed the classic iconography of these extinct vertebrates, providing a quite different and more exciting framework for reconstructing their paleobiology. This interpretive revolution, evocatively dubbed the “Renaissance of Dinosaur Studies” by Colbert (1997), led authors, beginning with Robert Bakker and John Ostrom, to study and consider this animal group under completely new and cutting edge perspectives (e.g., Bakker, 1968, 1971, 1972, 1975, 1978, 1986; Ostrom, 1969, 1974; Bakker & Galton, 1974; Romano et al., 2016b). During subsequent decades, within the framework of a second “golden age” of dinosaur studies, numerous new species have been described from both Laurasia and Gondwana, and a complex, multi-dimensional picture of the physiology, evolution and behavior of dinosaurs has emerged.

Surprisingly, many of the possible indirect inferences about the biology and complex behavior of various groups of dinosaurs came from a discipline that had long remained in the shadows, and had been considered incidental compared with research on body fossils: ichnology, i.e. the study of the life traces of an organism. For dinosaurs, this includes study of footprints and trackways, but also of burrows, coprolites (fossil dung), eggs and nesting sites. In recent decades a new multidisciplinary approach to paleoichnology has shown the enormous inferential power of fossil traces, throwing light on biological and behavioral aspects, not obtainable by studying the bony material. In particular, the study of fossil footprints in numerous vertebrate groups (from basal tetrapods to dinosaurs and synapsids sensu lato) provided novel inferences on the behavior, type of locomotion, and biomechanics, and in various fields of their biology, such as physiology, type of metabolism, and ecological requirements (e.g., Thulborn & Wade, 1979; Farlow, 1981; Thulborn, 1981, 1982; Lockley, 1994; Avanzini, 1998; Lockley et al., 1998, 2003; Gierliński

et al., 2009; Bernardi & Avanzini, 2011; Avanzini et al., 2012; Petti et al., 2014; Sacchi et al., 2014; Bernardi et al., 2015; Citton et al., 2015, 2017; Romano et al., 2016a; Romano & Citton, 2017).

In the context of behavior, one of the most important inferences drawn from trace fossils relates to the possibility of gregariousness and complex social interrelations in some groups of dinosaurs. Parallel trackways, especially of herbivorous dinosaurs (e.g., Bakker, 1968; Currie, 1983; Ostrom, 1985; Leonardi, 1989; Pittman & Gillette, 1989; Barnes & Lockley, 1994; Lockley et al., 1994; Lockley, 1995; Matsukawa et al., 1997; Cotton et al., 1998; Matsukawa et al., 1999; Day et al., 2004; Castanera et al., 2012; Lockley et al., 2012; Piñuela et al., 2016), often referable to individuals of different sizes (and thus, presumably, ages), indicate that, as observed in many extant large-sized continental mammals, some clades of dinosaurs lived in groups and moved together as large herds.

One of the earliest described and most impressive cases of inferred complex social structure in herbivorous dinosaurs comes from the famous nesting site from the Upper Cretaceous Two Medicine Formation of Montana (Fig. 1), where 15 one-meter-long specimens of the hadrosaur *Maiasaura peeblesorum* Horner & Makela, 1979 were found together in a nest-like structure (Horner & Makela, 1979). Since then, other sites have been described, in which numerous individual herbivorous dinosaurs were found buried together in mass mortality assemblages, some of them again associated with nesting sites, but others representing social agglomerations maintained for some years after birth (e.g., Coria, 1994; Qi et al., 2007; Zhao et al., 2007, 2014; Mathews et al., 2009; Fastovsky et al., 2011; Hone et al., 2014).

In contrast, the extent to which carnivorous dinosaurs (especially those of medium to large size) were social animals is more controversial (Currie, 1998; Lockley & Matsukawa, 1999; Lingham-Soliar et al., 2003; Roach & Brinkman, 2007; Currie & Eberth, 2010; Moreno et al., 2012; Ibiricu et al., 2013; Getty et al., 2015; Funston et al., 2016). If plant-eating dinosaurs were more gregarious than meat-eaters, is there any particular process or factor that might have prompted a greater tendency to group behavior in herbivorous dinosaurs?



Fig. 1 - Reconstruction of a nesting site of the hadrosaur *Maiasaura peeblesorum* Horner & Makela, 1979. In the foreground, a juvenile hadrosaur ingests the feces of its mother, to acquire the bacteria necessary to break down and metabolize cellulose and fibrous plant tissues. In the background, an adult *Maiasaura* lays eggs in the nest. Artwork by Davide Bonadonna (<http://www.davidebonadonna.it>).

SOCIAL BEHAVIOR, HERBIVORY AND GUT MICROBIOTA

Traditionally, evidence for group behavior of plant-eating dinosaurs of the kind mentioned above (i.e., large nesting sites, mass mortality assemblages of conspecific individuals both consisting of juveniles only and of animals at differing ontogenetic stages), and tracksites showing multiple individuals moving in the same direction have been interpreted in terms of anti-predator strategies (physical defense in the case of adults, confusion of potential predators by juveniles running away in different direction, or even “swamping” predators with a substantial number of potential victims), or greater success in finding and sharing of food resources (e.g., Kobayashi & Lu, 2003; Varricchio, 2011; Hone et al., 2014). However, there may be a similarly important factor that enhanced evolutionary fitness, leading to numerous independent appearances of sociality in herbivorous dinosaurs.

Extant herbivorous vertebrates are not genetically provided with the enzymes needed to break down and metabolize cellulose and other fibrous plant tissues (McBee, 1977; Mackie et al., 2004; Lombardo, 2008; Hong et al., 2011; Yuan et al., 2015). Herbivores therefore usually host in their guts symbiotic bacterial populations, whose microbes are able to digest cellulose and hemicellulose (Yuan et al., 2015); bacteria hydrolyze and ferment plant polymers, turning these otherwise indigestible materials into nutrients for the host animal (Mackie et al., 2004; Lombardo, 2008). As indicated by overall body structure in extant and fossil tetrapods,

herbivorous taxa are generally characterized by a broad trunk region, leading to a typical barrel-shaped body to host bulk, and very long digestive tracts. Such a gut structure permits longer processing of vegetable material and also provides optimum pH conditions for symbiotic gut microbiomes (Suess, 2000; Reisz & Suess, 2001).

At present, about 80% of extant mammals are herbivores, with primary consumers found in every mammal lineage (Ley et al., 2008). Such evolutionary success is very likely linked to the coevolution for millions of years between microbiota and host, leading to several phylogenetically independent appearances of herbivory in all vertebrate groups (e.g., mammals, birds and reptiles; see Romano, 2017 and references therein).

At birth or hatching, herbivores are completely sterile with regard to microbes, so they must acquire the microbiota necessary for nutrition directly from parents (i.e., they must be “infected” by the gut bacterial population of older conspecifics), largely through ingestion of feces of their relatives that contain the microsymbionts (see Romano, 2017 and references therein). How can this need for symbiotic bacteria be related to the emergence and evolutionary success of sociality in vertebrates?

MICROBIOTA SHARING AS A TRIGGER FOR SOCIALITY IN HERBIVOROUS DINOSAURS

In large nesting sites, excrement is sure to be deposited, and it may even be used as a building material in the construction of nests, as in many birds

today. Therefore, large nesting sites obviously provide numerous opportunities for the gut-associated microbiota to be transmitted from one generation to the next. Young individuals that remain associated for long periods after hatching similarly “enjoy” many opportunities to pass microbes among themselves, leading to a homogenization and stabilization of the internal bacterial ecosystem of the young-of-the-year (Fig. 1). Similarly, animals that move about in large herds, featuring individuals of different sizes and ages, have broad possibilities for horizontal exchange of beneficial symbiotic microbes among individuals of the same group.

As initially suggested by Troyer (1982), and later developed by Lombardo (2008), the need (especially in herbivores) to transmit symbiotic microbial communities would be one of the most important factors for the repeated, independent appearance of social behavior among vertebrates. We therefore revive the hypothesis first succinctly proposed by Troyer (1982) and Rogers (1985) about thirty years ago that precisely the need to pass the beneficial gut microbiota from generation to generation may have been one of the main factors which led to the emergence of complex social interactions in dinosaurs (at least in the herbivorous and omnivorous clades).

This hypothesis has been largely ignored in the subsequent literature as a possible driving factor of sociality in dinosaurs. However, the numerous new skeletal assemblages of hadrosaurids and ceratopsids, as well as the many tracksites suggesting group movements on the part of herbivorous dinosaurs, may well reflect species-specific strategies for inter-generational transmission of symbiont microbiomes.

In recent decades, the symbiont microbiome found in nearly all groups of hosts, has increasingly been shown to be crucial for the host’s fitness, in some cases proving to be essential for host survival. Among the various beneficial effects for the host, gut microbiota prevent the invasion by pathogens by stimulating the immune system, are able to extract nutrients and thus the energy necessary for the host, and can also promote the tissue differentiation (Costello et al., 2012).

According to some studies, the whole vertebrate adaptive immune system evolved precisely in relation to an increasingly complex symbiosis with microbial communities (Wang et al., 2015). In humans, it has been experimentally shown how an alteration of the typical microbial communities can lead to serious clinical disorder such as obesity, inflammatory disease (especially in mouth and skin), malnutrition, coronary and heart disease and diabetes (Fava et al., 2006; Wen et al., 2008; Costello et al., 2012).

New concepts such as the holobiont (an indissoluble ensemble of microbiome and host) and hologenome (the combined genotype of symbiotic microbes and host) are currently debated in molecular biology and in macroevolutionary theory (e.g., Bordenstein & Theis, 2015; Doolittle & Booth, 2017; O’Malley, 2017; Romano, 2017; Webster, 2017). In fact, following the pioneering studies by Zilber-Rosenberg & Rosenberg (2008), natural selection has been inferred to act not simply on the organism as a monad, but on the whole holobiont as a new “unit of natural selection”, thus evoking the stimulating perspective of coevolution between systematically

unrelated organisms. Thus, perhaps the time has come in studies on the biology and evolution of dinosaurs, for the microbiome and its impact on fitness to be taken into account. Here, we have discussed and revised the hypothesis, first proposed by Troyer and Rogers in the 1980s, that selection pressure leading to exchange horizontally bacteria among individuals of different ages triggered a growing sociality in herbivorous dinosaurs. This hypothesis has been ignored in subsequent studies regarding a greater sociality in herbivorous dinosaurs, interpreted mainly in terms of greater success in searching for and sharing of food resources and anti-predator strategies. We hope that this contribution may reopen a discussion on the subject, and that new experimental research programs (for example by studying bacteria preserved in coprolites) may shed light on this very intriguing aspect of the behavior and evolution of dinosaurs.

It is sobering to think that microscopic beneficial bacteria, invisible to the human eye, may have acted as internal pilots driving even the social evolution of titans weighing as much as 80 tons.

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