C. R. Palevol xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General Palaeontology, Systematics and Evolution (Evolution)

Morphological evolution of the mammalian cecum and cecal appendix

Évolution morphologique de l'appendice du cæcum des mammifères

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ARTICLE INFO

Article history:
Received 19 May 2016
Accepted after revision 3 June 2016
Available online xxx

Handled by Philippe Taquet

Keywords:
Adaptation
Appendicitis
Cecal appendix
Comparative methods
Gastrointestinal anatomy
Immune system
Evolutionary ecology

ABSTRACT

The evolutionary pressures leading to the appearance of the cecal appendix, its evolutionary relationships with the cecum, and the link between these gastrointestinal characters and ecology remain controversial. We collected data on appendix presence and size, other gastrointestinal characters, ecological variables, dietary habits, and social characters hypothesized to drive appendix evolution for 533 mammalian species. Using phylogeny-informed analyses, we identified the first evidence of a positive correlation between appendix presence and cecal apex thickness, and a correlation with cecal morphology, suggesting that the appendix and cecum may be evolving as a module, the cecoappendicular complex. A correlation between appendix presence and concentration of cecal lymphoid tissue supports the hypothesis of an adaptive immune function for this complex. Other new findings include an inverse correlation between relative cecum length and habitat breadth, and positive relationships between cecum length and mean group size, and between colon length and weaning age.

Mots clés :
Adaptation
Appendicite
Appendice du cæcum
Méthodes comparatives
Anatomie gastro-intestinale
Système immunitaire
Écologie évolutive

RÉSUMÉ

Les pressions sélectives qui ont mené à l'apparition de l'appendice du cæcum, les relations entre cet appendice et le cæcum, ainsi que les liens entre ces caractères gastro-intestinaux et l'écologie demeurent discutés. Nous avons compilé des données sur la présence et la taille de l'appendice, d'autres caractères gastro-anatomiques et des variables écologiques, alimentaires et sociales pour 533 espèces de mammifères. À l'aide d'analyses prenant en compte la phylogénie, nous avons obtenu de premiers résultats en faveur d'une corrélation positive entre la présence de l'appendice et l'épaisseur de l'apex du cæcum, ainsi qu'une corrélation avec la morphologie de ce dernier, ce qui suggère que l'appendice et le cæcum évoluent comme un module, le complexe cæco-appendiculaire. Une corrélation entre la présence de l'appendice et la concentration de tissus lymphoïdes dans le cæcum corrobore l'hypothèse selon laquelle l'appendice a une fonction immunologique. D'autres résultats

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http://dx.doi.org/10.1016/j.crpv.2016.06.001
1631-0683/

nouveaux incluent une relation inverse entre la longueur relative du cæcum et la largeur d'habitat, ainsi que des relations positives entre la longueur du cæcum et la taille moyenne du groupe, ainsi qu'entre la longueur du côlon et l'âge au sevrage.

1. Introduction

1.1. Cecal appendix

The cecal appendix is a narrow, blind extension from the terminal aspect of the cecum. We define the appendix here based strictly on morphology, as a close-ended structure projecting from the cecum that is clearly distinguished from the cecum by a distinct change in diameter (Smith et al., 2009). While there has been discussion regarding the definition of the cecal appendix (e.g., Fisher, 2000) and whether it should include considerations of lymphoid tissues and a thickened wall, these characters are also associated with the apex of the cecum in taxa that lack an appendix (e.g., Berry, 1900; Smith et al., 2009). The organ's function appears to be immunological (Berry, 1900; Bollinger et al., 2007; Gorgollon, 1978; Keith, 1912; Neiburger et al., 1976; Scott, 1980; Smith et al., 2009, 2013; Spencer et al., 1985; Zahid, 2004), involving maintenance of microbial biofilms in a location that is relatively secluded from the main flow of intestinal contents (Bollinger et al., 2007; Sanders et al., 2013). This function is postulated to be important for the recovery of the microbiome following pathogen-induced diarrheal illnesses (Im et al., 2011; Merchant et al., 2012; Sanders et al., 2013).

In contrast to the cecal appendix of humans, the cecal appendix in other species has received little attention; however, it is becoming recognized that a cecal appendix is present in a variety of non-primate mammals (e.g., Chivers and Hladik, 1980; Golley, 1960; Hume, 1999; Kotzé et al., 2010; Pereira et al., 2016; Stevens and Hume, 1995). Only recently have investigators examined the appendix across mammalian phylogeny in a comparative manner (Smith et al., 2009, 2013). As a result of this more recent work, multiple morphotypes, beyond the elongated primate "vermiform" appendix, have been described (Smith et al., 2009). These recent discoveries reveal a wide variety of appendicular diversity across a broad taxonomic range, suggesting that the cecal appendix has a complex and diverse evolutionary history. Further, an observation first made by Charles Darwin regarding the appendix (Darwin, 1871) was confirmed; increased frugivory and decreased cecal size are associated with the appearance of an appendix in hominoids (Smith et al., 2013). However, the generality of this relationship during mammalian evolution was not supported statistically by an analysis incorporating several other mammalian clades, suggesting that the appearance of an appendix concomitant with a decreasing cecum size is the exception rather than the rule in the evolution of the appendix (Smith et al., 2013).

In her study on cecal appendix presence and morphology in primates, Fisher (2000) concluded that the traditional definition of an appendix presence might be too narrow. She suggested two additional variables that may suggest an appendix-like structure is present: (1) thickening of the cecal apex wall; (2) concentration of lymphoid tissue in the cecum. Fisher suggested that these variables could be used to assess appendix presence (Fisher, 2000). However, the aforementioned study was limited taxonomically to include only primate species, and did not involve any statistical validation. Thus, to date, it has not been determined whether a consistent statistical association exists across mammals between appendix presence and both cecal apex wall thickness and lymphoid tissue concentration. Questions remain regarding whether appendix evolution has been driven by morphological evolution and anatomical traits of the cecum, or by other independent factors.

1.2. Ecological factors driving resource use and adaptation

Many studies demonstrate the impact of ecological factors, such as geographic range, group size, and habitat breadth on the anatomical and behavioral adaptations of species. Group size is typically defined as the number of conspecifics with which an animal spends the majority of its time, and there is some evidence that these individuals form a cohesive unit (e.g., Jones et al., 2009). Habitat breadth has been variably defined as the number of geographic or climatic habitats used, dietary breadth, or even abundance. In particular, geographic range size and its utilization often correlate with abundance of a species (Brown, 1984; Lawton, 1993; Pyron, 1999). Brown (1984) argued that this relationship occurs via the association between geographic range and resource abundance. Specifically, species with larger ranges typically have access to and utilize a wider variety of resources, and are consequently more likely to become widespread and abundant (Brown, 1984). In the present study, we follow Jones et al. (2009) in defining habitat breadth as the "number of habitat layers used by a species measured using any qualitative or quantitative time measure, for non-captive populations". While we recognize that there are many possible definitions for the term habitat breadth, Jones and colleagues' PanTHERIA database contains data on habitat breadth (using their definition) for close to 3000 species, so for data compilation purposes in our study, it was the logical definition to employ.

Species occupying a broad habitat tend to be prevalent and abundant (Brown, 1984; Gotelli and Graves, 1996; Pyron, 1999). They also tend to be dietarily and behaviorally versatile, able to exploit a wide variety of local resources (Brown, 1984, 1995). Species with a narrow habitat, on the other hand, tend to be habitat specialists, capable of effectively exploiting a narrow range of local resources (Brown, 1995; Pyron, 1999). These specialists are more vulnerable to environmental fluctuations or changes in resource availability (Brown, 1984). Factors influencing resource

Please cite this article in press as:Smith, H.F., et al., Morphological evolution of the mammalian cecum and cecal appendix. C. R. Palevol (2016), http://dx.doi.org/10.1016/j.crpv.2016.06.001