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INTRODUCTION

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TBI, not just for humans

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Abstract

Traumatic brain injury (TBI) is a major cause of death that can develop into long-term disability, causing significant healthcare burden. The last decade has shown laudable advancements in disease characterization, but challenges remain in injury prevention and in understanding the link between TBI and chronic neurodegenerative disease. Historically, animal models have been crucial in untangling molecular mechanisms of injury, but difficulties in translation have resulted in a lack of applicable therapies. The ongoing search for treatment has overlooked the potential of animals that experience repeated, high-velocity head impacts as part of their natural behavior. Addressing this gap could improve our understanding of acute and chronic effects of head injury and potential protective mechanisms. TBI, not just for humans is a thematic issue covering an array of topics surrounding brain injury and non-model species. Topics include a paleontological perspective of head-hitting in extinct species, a historic perspective on head-hitting animals and TBI, non-model animals in biomedicine, anatomical descriptions of exotic head-hitters like helmeted hornbills and muskoxen, and a molecular investigation of resilience pathways against brain injury in woodpeckers. Since prehistory, humans have observed animals hitting heads and wondered whether it resulted in brain injury. Using evidence-based approaches rooted in biology, we may better understand our own brain injuries by studying the animals that regularly engage in such behaviors. The untapped potential of non-model species should be recognized and integrated into the field as we continue to search for solutions to the neurodegeneration crisis.

KEYWORDS
animal models, comparative neuroanatomy, head trauma, neurodegeneration, translation

1 | BACKGROUND

Many species experience repeated, high-velocity head impacts as part of their natural behavior during mating rituals, aggression, communication, prey capture, or predator evasion. Scientists have been fascinated by these “natural engineers” for centuries—ranging from Richard Waller's, 1716 descriptions of woodpecker tongues (Waller, 1716) to the 1970s fascination with “why woodpeckers don't get headaches” (May et al., 1976). However, as reviewed by Ackermans and colleagues (Ackermans, 2023, 2025; Ackermans et al., 2021) and Tobiansky and colleagues (Tobiansky et al., 2021), past literature demonstrates that research on head impacts in such animals has mainly focused on their skulls, rather than the brain. Thus, the assumption arose that these head-hitting animals used a variety of theoretical morphological, physiological, or behavioral mechanisms to avoid sustaining brain injuries, a claim both lacking in hard data and an appreciation for evolutionary trade-offs. Additionally, there is a growing database of species that naturally develop chronic neurodegenerative conditions with age (Takaichi et al., 2021; Youssef et al., 2016). Very few studies focus on the biomechanics, anatomy, and physiology of naturally occurring brain damage in non-model species. However, in recent years, researchers have sought to better understand these natural behaviors that may have the potential to provide improved solutions for human injury.

In humans, traumatic brain injury (TBI) has the highest incidence of all neurological disorders and is a major cause of death across the world (Dewan et al., 2018). Over 200,000 hospitalizations occur for nonfatal TBI annually, of which 43% develop long-term disability (Corrigan et al., 2010). Even a single TBI increases the risk of developing a neurodegenerative disease (NDD) such as chronic traumatic encephalopathy (CTE), Alzheimer's disease (AD), and Parkinson's disease (PD) (Gardner & Yaffe, 2015). Additionally, repetitive TBI can triple that risk in certain populations such as contact-sport athletes (Lehman et al., 2012), although the association between TBI and NDDs is difficult to study and thus poorly understood (Gardner & Yaffe, 2015).

Mechanism of injury, pathophysiology, and measures of mental outcomes of severe TBI have been investigated, indicating a long-term differential effect of severe TBI years after injury (Hoofien et al., 2001). In the last decade, there have been key areas of advances in TBI management, including improved protocols for neurointensive care, improved evidence base for surgical intervention, and development of novel pharmaceutical therapies (Khellaf et al., 2019). Indeed, TBI characterization and outcome prediction have benefitted from the use of neuroimaging, biomarkers, and genomics (Maas et al., 2022). However, TBI remains a heterogenous and complex pathology that often requires an individualized approach (Khellaf et al., 2019), and challenges remain in TBI prevention, prognostic predictors, and NDD detection, as well as developing strategies for better understanding chronic disease onset and reduction (Maas et al., 2022).

The main limiting factors of studying TBI in humans include the relatively unknown biological mechanisms of disease, variability of injury type, location, severity, and outcome, as well as comorbidities with an aged target population, and high complexity at every level from genes to behavior (Alves et al., 2019). As such, model animals like rodents have been essential in advancing clinical knowledge (Dawson et al., 2018), as they have the advantage of being relatively homogenous, which reduces experimental variability between and within studies. However, this homogeneity can also be a disadvantage insofar as a lack of diversity can limit our understanding of a heterogenous disease and can hinder the development of new approaches (Hale, 2019). In addition, rodent models have historically had poor predictive value for human therapies due to anatomical and physiological differences (Alves et al., 2019; Dawson et al., 2018; Vink, 2018), and despite being the main models used to study specific pathophysiologies of TBI and NDDs, rodents are unable to naturally develop chronic NDD conditions. Modeling TBI through experimental simulation—such as a weight-drop experiment—is highly replicable but its accuracy in replicating human injury is limited (Xiong et al., 2013). Additionally, despite TBI being a high risk for chronic disease development, experimentally induced post-TBI pathology is rarely explored long term in animal models due to experimental constraints (Osier et al., 2015). Some of these limitations stand to be addressed by diversifying the pool of study organisms.

Diversity is where the potential of non-model organisms truly shines. A century ago, August Krogh posited that for every biological problem, there is a species best suited to study it (Krogh, 1929). This "Krogh's Principle" is now complemented by the "Inverse Krogh Principle," which argues that every animal is inherently worth studying for its own unique biological solutions (Clark et al., 2023). By investigating species at the extremes of physical experience, we can uncover mechanisms of resilience, such as specialized neuroimmune responses or unique meningeal clearance (Beatty et al., 2024), that could lead to better management of human-relevant neurological pathologies such as TBI and CTE. Our hope for this thematic issue is to consider non-model species when investigating anatomical, behavioral, experimental, and other aspects of brain-related pathologies. While these non-model species might not offer a perfect replacement for standard models, a thorough investigation of their anatomical and neurobiological properties benefits multiple fields by offering a broader comparative lens.

2 | OVERVIEW OF THIS THEMATIC ISSUE

This thematic issue was inspired by a symposium entitled "TBI, not just for humans" organized at the 2023 International Congress of Vertebrate Morphology (ICVM) in Cairns, Australia, and supported by The Anatomical Record. The symposium aimed to unite researchers working with unconventional animal models of TBI under the same roof (ICVM, 2023) (Figure 1). With this meeting, and subsequently this thematic issue, we highlight state-of-the-art research in an emerging field and seek to streamline field-specific terminology, methodology, and collaborative strategies.

In this thematic issue, we have grouped seven publications along the theme of "TBI, not just for humans" (Figure 2). This includes two reviews, two commentaries, and three research publications covering a vast array of non-human and non-model species.

From a social science perspective, Hollin (2024) sets the stage by challenging our philosophical assumptions. Here, he provides a critical commentary on the "irreducible vagueness" of unconventional models like woodpeckers. He challenges researchers to consider what we are truly modeling—protective mechanisms, or the natural history of trauma—and addresses the ethical complexities of studying neurodegeneration in charismatic species often linked to human sporting culture.

Another perspective on the history of headbutting explores human thought through art and scientific literature, focusing mainly on bovids (e.g., bighorn sheep) and woodpeckers. In "A history of thought on brain injury in head-hitting animals," Ackermans (2025) chronicles the hypotheses surrounding brain injury and head-hitting in animals from prehistoric times to the modern era,

FIGURE 1 Presenters at the "TBI, not just for humans" symposium as part of the 2023 International Conference of Vertebrate Morphology (ICVM) in Cairns, Australia. Top image: From left to right: Gregory Hollin, Brigid Maloney, Joy Reidenberg, Nicole Ackermans, Ryan Earley, Grace Bollinger, Cassidy McColl. Bottom image: Sketches of the symposium speakers and details about their talks. From left to right: Greg Hollin, Joy Reidenberg, Nicole Ackermans, Ryan Earley, Grace Bollinger, and Cassidy McColl. Art by Catherine Williams.

FIGURE 2 A collage of the various animals that perform head-impact behavior, as covered in the symposium and this thematic issue. Clockwise: Woodpeckers pecking, helmeted hornbills clashing in flight, muskoxen headbutting, mangrove rivulus fish jumping, and Pachycephalosaurids flank-butting. Art by Tara Barnes-Tompkins © 2025.

providing historical context for the current state of the field. This review delves into why some might think that "woodpeckers don't get headaches" and how such common sayings came to be. The result is a detailed, and oft entertaining storyline that reveals two main realms of thought: those who assume that woodpeckers and bovids are naturally protected from brain injury, and those who acknowledge the real potential for brain injury in these species. The field thus summarized, Ackermans provides suggestions for how to most effectively combine approaches from different disciplines to advance the study of these species in future efforts.

In a similar vein, Woodruff and Ackermans (2024) review the expansive literature on "headbutting through time" in dome headed fossil taxa, presenting behavioral hypotheses from the perspective of a paleontologist and that of an extant species anatomist. They demonstrate how combative behavior has a long and rich history in the vertebrate fossil literature, not just in Dinosauria, but also in Therapsida and Mammalia. Ultimately, they correct some misnomers by proposing more cohesive terminology to describe headbutting and discuss the possibility and implications of whether brain injury might be induced by headbutting in extinct taxa.

This issue also addresses the challenges of species translation and brain injury. James Smoliga (2024) offers a necessary critique of "woodpecker biomimicry," pointing out decades of methodological errors, including the widely cited but likely erroneous 1500 g impact value attributed to woodpeckers (actual values are more likely between 400 and 1200 g [Van Wassenbergh et al., 2022]). He also questions whether avian biology can ever truly be mapped onto human sports safety equipment. Yet, he concludes that the potential for discovery from these species remains high, as the rest of this thematic issue shows.

In turn, Ackermans and Reidenberg (2025) provide a needed empirical approach by exploring the more internal anatomical implications of headbutting in bovids. The authors investigate the anatomical function of digitiform impressions in the bovid brain cavity and their relationship to headbutting. In addition, they provide an anatomical description of the muskox brain cavity for the first time. Examining the endocranial roughness index (ERI) across 59 bovid species revealed no correlation to headbutting, suggesting much more work, and possibly more precise techniques, are needed to better understand this topic. They remind us that protection may not be where we expect it.

In seeking to understand resilience to impact forces, Beatty et al. (2024) investigate avian meninges and their associated vasculature (MAV), a structure that protects the brain and helps to remove cellular waste after damage. Specifically, they compared the transcriptome of the MAV between the Downy Woodpecker (*Dryobates pubescens*) and a similarly sized, non-drumming species that shares an ecological niche, the Tufted Titmouse (*Baelopholus bicolor*). This work lays the groundwork for research in the physiology of head impacts and comparative neuroprotection. Importantly, this paper is also the first exploration of any bird's meningeal transcriptome.

Also investigating bird head impacts, Schindler et al. (2024) examine the Helmeted Hornbill (*Rhinoplax vigil*), an endangered bird that headbutts noisily mid-flight. Specifically, the authors describe the craniofacial joint between the bird's bony keratin casque and the braincase that allows a hinge-like rotation. The authors investigate the paradox of a prokinetic mobile joint in a bird that performs violent head-clashing. Findings indicated that, rather than absorbing shock, the hornbill's craniofacial joint is exceptionally reinforced to "hit harder," relying on a reinforced osteological architecture of the cranium that might mitigate damage, thereby clarifying its function in the hornbill's ecology. Mirroring recent discoveries in woodpeckers, this work confirms that such craniofacial specializations function as force-multipliers rather than dampers, fundamentally refuting the long-held assumption of biological shock absorption (Van Wassenbergh et al., 2022).

In conclusion, by investigating these non-model species, we move toward a systems-level understanding of neurotrauma that integrates evolution, anatomy, and potential molecular resilience. While these organisms may not be exact human analogs for head trauma, they offer a diverse toolkit and the missing heterogeneity for reimagining neuroprotection and neurodegeneration beyond the laboratory rodent.

AUTHOR CONTRIBUTIONS

Daniel J. Tobiansky: Writing – original draft; writing – review and editing; visualization; investigation; conceptualization. **Joy S. Reidenberg:** Investigation; writing – original draft; writing – review and editing; visualization; conceptualization. **Nicole L. Ackermans:** Conceptualization; writing – original draft; writing – review and editing; project administration; investigation; visualization; funding acquisition.

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