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Evolutionary Trends in Beetle Morphology: Insights from Fossil Records

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Abstract This study delves into the evolutionary trends in beetle morphology, drawing extensively from fossil records to provide comprehensive insights. Key findings reveal significant morphological adaptations in beetles, such as the development of elytra, variations in mouthpart structures, and changes in limb morphology, which have enabled beetles to thrive in diverse ecological niches. The study also underscores the critical role of climatic changes, predation, competition pressures, and habitat adaptations in shaping these morphological traits. Case studies highlight unique insights, such as the evolution of hardened forewings and specialized feeding structures, emphasizing the intricate interplay between environmental factors and morphological evolution. By integrating fossil evidence with modern technological approaches, this study enhances our understanding of beetle evolutionary history and its broader implications for evolutionary biology.

Keywords Beetle morphology; Evolutionary trends; Fossil records; Elytra development; Morphological adaptations

1 Introduction

Beetles, belonging to the order Coleoptera, are one of the most diverse groups of animals on Earth, with over 380 000 described species and potentially millions more yet to be discovered (Cai et al., 2021). This incredible diversity makes beetles a fascinating subject for evolutionary studies. Understanding the evolutionary trends in beetle morphology is crucial. It provides insights into how beetles have adapted to various ecological niches over millions of years. Studying these trends through fossil records allows scientists to trace the lineage and diversification of beetles, offering a window into the past that can help explain present-day biodiversity (Mckenna et al., 2019).

Fossil records are invaluable in this context as they provide direct evidence of past life forms and their morphological characteristics. By examining beetle fossils, researchers can identify significant evolutionary events, such as the emergence of new species, adaptations to changing environments, and responses to mass extinction events (Smith and Marcot, 2015; Kundrata et al., 2021). These records also help in calibrating molecular phylogenies, thereby refining our understanding of beetle evolution (Mckenna et al., 2015).

This study is to synthesize current knowledge on the evolution of beetle morphology. This involves compiling and analyzing data from various studies that have utilized fossil records to understand the morphological changes in beetles over time. By providing a comprehensive overview of the evolutionary trends in beetle morphology, this study will contribute to a deeper understanding of the factors that have shaped the incredible diversity of beetles we see today. By doing so, this study aims to highlight key insights gained from these fossil records, such as the timing and drivers of major diversification events, the impact of ecological factors on beetle morphology, and the evolutionary significance of specific morphological traits.

2 Beetle Morphology: An Overview

2.1 General Morphological Characteristics

Beetles, belonging to the order Coleoptera, exhibit a highly diverse range of morphological traits, yet they share a common basic anatomy. The body of a beetle is divided into three main parts: the head, thorax, and abdomen. The head houses sensory organs such as compound eyes and antennae, as well as mouthparts adapted for various feeding habits. The thorax is segmented into three parts: the prothorax, mesothorax, and metathorax, each bearing a pair of legs. The mesothorax and metathorax also support the wings. Beetles possess two pairs of wings: the forewings, known as elytra, are hardened and serve as protective covers for the more delicate hind wings, which are used for flight (Cai et al., 2021).

The variability in beetle morphology is immense, reflecting their adaptation to a wide range of ecological niches. For instance, the hind wings of dung beetles (Scarabaeinae) show significant variation in shape, which is linked to different selective pressures and ecological roles. Similarly, the exaggerated hind legs of certain scarab beetles from the Mesozoic era suggest adaptations for springing movements and fighting (Lu et al., 2023). The elytra themselves exhibit a range of modifications, from rigid connections to partial reductions, serving various functions such as protection, thermoregulation, and even acoustic communication (Asgari et al., 2020; Goczał and Beutel, 2023).

2.2 Morphological Adaptations

Beetles have evolved a plethora of morphological adaptations that enable them to thrive in diverse habitats, diets, and behaviors. The conversion of forewings into elytra is a prime example of a morphological adaptation that has significantly contributed to the evolutionary success of beetles. Elytra provide mechanical protection, aid in water conservation, and facilitate various behaviors such as diving and burrowing (Linz et al., 2023).

Adaptations related to habitat can be seen in the structural modifications of beetle wings. For example, the hind wings of dung beetles have evolved under different selective pressures, resulting in distinct morphological patterns that are linked to their ecological roles (Bai et al., 2012). Similarly, the robust and structured hind legs of certain Mesozoic scarab beetles suggest adaptations for specific behaviors like springing and fighting, which may have been crucial for their survival and reproductive success (Lu et al., 2023).

Dietary adaptations are also evident in beetle morphology. The evolution of specialized herbivory in beetles, facilitated by the acquisition of plant cell wall-degrading enzymes through horizontal gene transfers, has led to the diversification of plant-feeding beetles. These enzymes enable the digestion of lignocellulose in plant cell walls, allowing beetles to exploit a variety of plant tissues and contributing to their adaptive radiation (Mckenna et al., 2019).

Behavioral adaptations are reflected in the morphological traits of beetles as well. For instance, the development of neoteny in net-winged beetles (Lycidae) has led to body miniaturization and structural simplification, which are linked to their unique life histories and reproductive strategies (Kusy et al., 2019). Additionally, the presence of exaggerated morphological structures, such as horns and enlarged mandibles in stag beetles, is often associated with sexual selection and intraspecific competition (Kawano, 2020).

3 Fossil Records of Beetles

3.1 Historical Context

Beetle fossils provide a rich source of information about the evolutionary history and palaeodiversity of the order Coleoptera, which is the most species-rich metazoan order with approximately 380 000 described species (Smith and Marcot, 2015). The discovery of beetle fossils has been crucial in understanding the evolutionary timeline and diversification of beetles. For instance, the study of Triassic beetles, such as those found in coprolites (Figure 1), has revealed well-preserved specimens that offer insights into early beetle evolution and their ecological interactions (Qvarnström et al., 2021). Additionally, the discovery of new beetle lineages in Eocene Baltic amber has shed light on the historical biogeography and diversification of specific beetle families.

Several major fossil sites have significantly contributed to our understanding of beetle evolution. Amber deposits, particularly from the Eocene and Cretaceous periods, have preserved a diverse array of beetle species, providing detailed morphological data that are often not available from other types of fossilization (Hsiao et al., 2021). For example, the Mid-Cretaceous Burmese amber has yielded new species of soldier beetles, enhancing our understanding of their evolutionary history and biogeographical origins. Lacustrine deposits have also been important, preserving a wide range of beetle diversity and abundance, which has been instrumental in studying the macroevolutionary history of beetles.

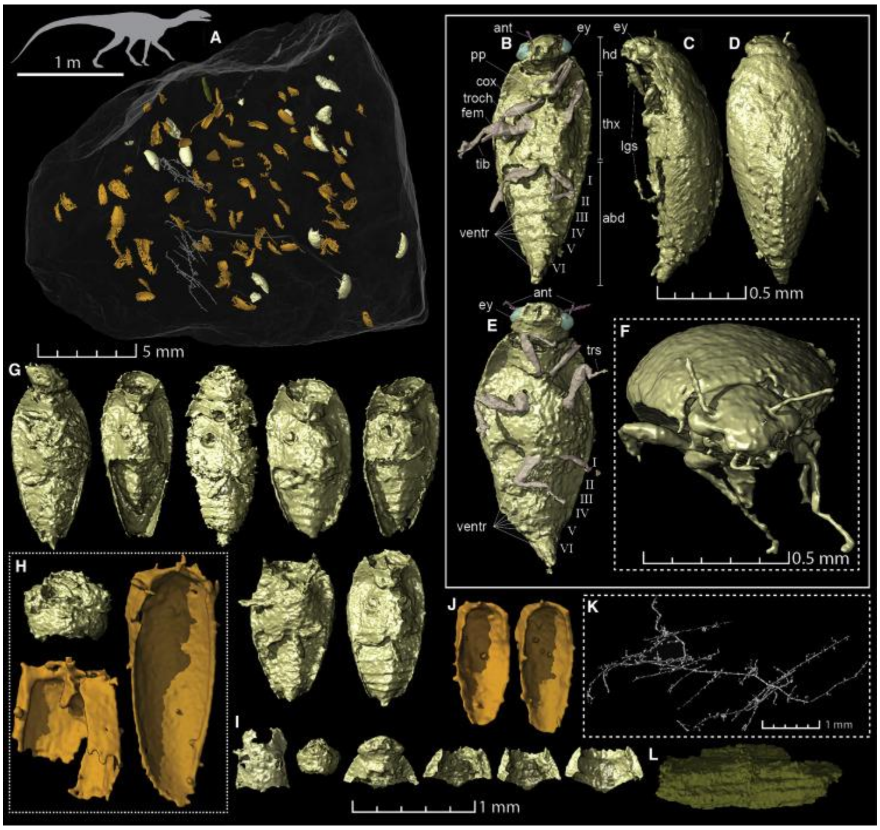

Figure 1 Contents of coprolite fragment ZPAL AbIII/3520 (Adopted from Qvarnström et al., 2021)

Image caption: (A) The coprolite rendered semi-transparent with inclusions, such as beetle remains and fibrous networks, representing fungal colonies or algae visible. Top corner: silhouette of Silesaurus opolensis, the most probable coprolite producer. (B-D) The holotype specimen of *Triamyxa coprolithica* in ventral (B), lateral (C), and dorsal (D) views. (E and F) The second complete specimen in ventral (E) and anterior (F) views. Individual ventrites are indicated by roman numerals. (G) *Triamyxa coprolithica* preserved in various degrees of disarticulation. (H) An isolated head and two elytra that do not belong to *Triamyxa coprolithica* but to slightly larger beetles that were also ingested by the coprolite producer. (I) Examples of individual remains of *Triamyxa coprolithica* (meso- and metaventrite, head, head attached to pronotum, and three pronota). (J) Two of numerous elytra of similar size and morphology attributed to *T. coprolithica*. (K) Fibrous structures interpreted as fungi or algae. (L) A possible decomposed wood fragment (Adopted from Qvarnström et al., 2021)

3.2 Methods of Studying Beetle Fossils

The study of beetle fossils employs various paleontological techniques to uncover and analyze these ancient specimens. Traditional methods include the examination of compressed fossils and the use of morphological matrices to determine phylogenetic relationships (Fikáček et al., 2020). More advanced techniques, such as synchrotron microtomography, have been used to investigate 3D-preserved beetle remains in coprolites, providing detailed insights into their morphology and phylogenetic placement. X-ray micro-computed tomography has also been employed to reconstruct the morphology of beetles obscured by opaque bubbles in amber, allowing for the identification of new species and their diagnostic characters (Kundrata et al., 2020).

Advances in technology have significantly impacted the analysis of beetle fossils, leading to more accurate and detailed reconstructions of their evolutionary history. The use of phylogenomic methods, which integrate genomic data with fossil calibrations, has refined the timescale of beetle evolution and resolved previously controversial phylogenetic relationships (Mckenna et al., 2019; Cai et al., 2021). These methods have also highlighted the importance of selecting appropriate fossil calibration points to avoid underestimating clade ages, as seen in the critique of previous studies (Toussaint et al., 2017). Additionally, the application of finite element analysis and simulations has provided new insights into the functional morphology of extinct beetle species, such as the springing movements hypothesized for a Cretaceous chafer beetle (Lu et al., 2023).

4 Evolutionary Trends in Beetle Morphology

4.1 Early Beetle Morphology

The earliest known beetle fossils date back to the late Carboniferous period, marking the origin of Coleoptera. These early beetles exhibited a range of primitive features that have since evolved significantly. For instance, the fossil record of the suborder Myxophaga, such as the mid-Cretaceous *Lepiceratus ankylosaurus*, reveals fine morphological structures that have remained relatively unchanged over millions of years, indicating a high degree of morphological stasis in some lineages (Jałoszyński et al., 2020). Early beetles like *Leehermania prorova* from the Triassic period, initially thought to be part of the Staphylinidae family, have been reclassified into the Myxophaga suborder, highlighting the complexity and diversity of early beetle forms (Fikáček et al., 2020).

In comparison to modern beetles, these ancient specimens show both similarities and differences. Modern beetles have diversified into numerous families and exhibit a wide range of specialized adaptations. For example, the reduction of antennomeres from the ancestral 11 to fewer segments in some lineages, such as the Lepiceridae, demonstrates a trend towards morphological simplification over time. Additionally, the presence of robust and structured hind legs in some Mesozoic scarab beetles, like *Antiqusolidus maculatus* (Figure 2) (Lu et al., 2023), suggests early adaptations for specific behaviors such as springing and fighting, which are less common in contemporary beetles.

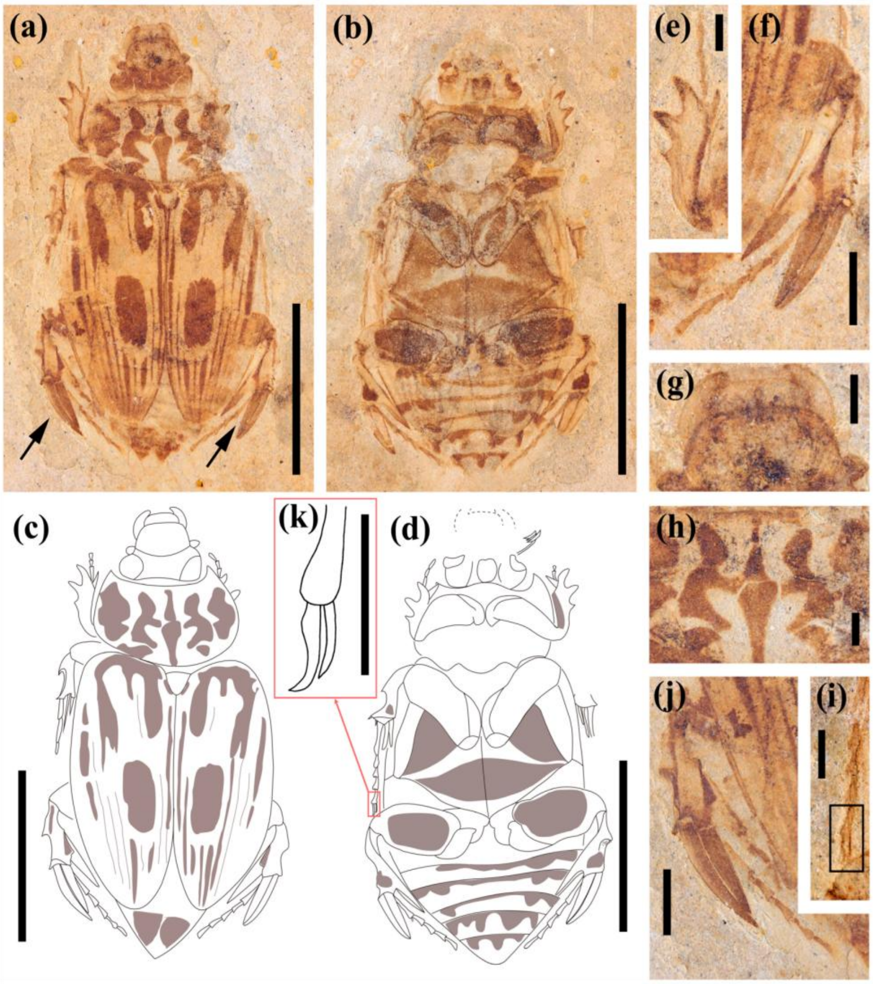

Figure 2 Photographs and line drawings of *Antiqusolidus maculatus* (Adopted from Lu et al., 2023)

Image caption: (a,c) General habitus, dorsal view; arrows indicate structured hind legs, scale 10 mm. (b,d) General habitus, ventral view, scale 10 mm. (e) Left foreleg, dorsal view, scale 1 mm. (f) Right hind leg, dorsal view, scale 2 mm. (g) Anterior part of head, dorsal view, scale 1 mm. (h) Pronotum, scale 2 mm. (i) Right mesotarsi, ventral view, rectangle indicate claws, scale 1 mm. (j) Left hind leg, dorsal view, scale 2 mm. (k) Claws of right mesotarsi, scale 1 mm (Adopted from Lu et al., 2023)

4.2 Major Morphological Changes Over Time

Key evolutionary events have significantly impacted beetle morphology. The diversification of beetles during the Mesozoic era, particularly the Jurassic and Cretaceous periods, coincided with the rise of angiosperms, leading to the co-evolution of beetles and flowering plants. This period saw the emergence of specialized herbivory, facilitated by the horizontal transfer of plant cell wall-degrading enzymes (PCWDEs) from bacteria and fungi, which enabled beetles to efficiently digest plant tissues (Mckenna et al., 2019). This adaptation was crucial for the diversification of herbivorous beetles and their subsequent radiation.

Significant morphological transformations include the development of exaggerated structures, such as the robust hind legs of *Antiqusolidus maculatus*, which likely supported unique behaviors like springing movements. Another example is the evolution of neoteny in net-winged beetles (Lycidae), where female neoteny evolved multiple times, leading to body miniaturization and structural simplification (Kusy et al., 2019). These changes reflect the diverse evolutionary pressures and ecological niches that beetles have adapted to over time.

4.3 Adaptive Radiation and Diversification

Environmental changes have played a crucial role in promoting morphological diversity among beetles. The Cretaceous Terrestrial Revolution, marked by the widespread emergence of flowering plants, provided new ecological opportunities that spurred the adaptive radiation of beetles. The codiversification of beetles and angiosperms is a prime example, where the evolution of plant-feeding habits in beetles was closely linked to the availability of new plant resources (Wang et al., 2013).

Case studies of adaptive radiation in beetle lineages include the diversification of the Chrysomeloidea superfamily, which saw the emergence of longhorn beetles (Cerambycidae) and leaf beetles, among others. The earliest known longhorn beetle, *Cretoprionus liutiaogouensis*, from the Lower Cretaceous, exhibits features characteristic of the Prioninae subfamily, indicating an early adaptation to specific ecological niches (Wang et al., 2014). Similarly, the evolutionary history of Carabid beetles (Carabidae) shows how changes in thoracic structure and locomotory adaptations have allowed them to exploit various habitats and prey types, contributing to their extensive diversification (Brandmayr, 2020).

5 Insights from Fossil Records

5.1 Patterns of Morphological Evolution

The fossil record provides a wealth of information on the evolutionary trends in beetle morphology, particularly in terms of size, shape, and structural complexity. One of the most significant morphological adaptations in beetles is the development of the elytra, or hardened forewings, which serve multiple functions including protection, thermoregulation, and aiding in flight. The evolution of elytra is believed to have occurred early in the Coleoptera lineage, likely during the Carboniferous period, through a gradual process of forewing sclerotization and the formation of inward-directed epipleura and a secluded sub-elytral space (Kusy et al., 2019; Goczał and Beutel, 2023).

In terms of size and shape, beetles exhibit a wide range of morphological adaptations. For instance, the Cetoniinae subfamily shows significant variation in body weight, which is accommodated by both size-invariant and size-dependent features in their elytra. These adaptations include chemical compositions, layered-fibrous architectures, and graded motifs that maintain biomechanical functionality across different sizes. Additionally, the reduction and modification of elytra have been observed in various beetle lineages, such as the ship-timber beetles (Lymexylidae), where fossil evidence shows a trend towards shortened elytra and exposed hindwings, dating back to the mid-Cretaceous period (Yamamoto, 2019).

Specialized morphological features such as mandibles and sensory structures have also evolved in response to ecological and behavioral pressures. For example, in the broad-horned flour beetle (*Gnatocerus cornutus*), the enlargement of mandibles for fighting has led to correlated changes in body morphology, including the reduction of elytra length (Okada and Miyatake, 2009). Similarly, the evolution of campaniform sensilla in the elytra of flying beetles has been linked to modifications in elytral mobility and shape, which vary significantly across different taxa (Frantsevich et al., 2015).

5.2 Phylogenetic Implications

Fossil evidence plays a crucial role in understanding the phylogenetic relationships among beetle lineages. The re-examination of the earliest known fossil beetle, †*Coleopsis archaica*, using advanced imaging techniques has provided new insights into the early evolution of Coleoptera. This species, belonging to an early Permian branch, exhibits primitive features such as loosely fitting elytra that cover the metathorax and abdomen in a tent-like manner, contrasting with the tightly sealed elytra of more derived beetles.

The correlation between morphological changes and genetic evolution is evident in the study of elytra development. Transcriptomic analyses have identified specific genes involved in the formation and modification of elytra, revealing that the evolution of these structures involved the co-option of exoskeleton formation pathways multiple times. This repeated co-option suggests a strong selective advantage for the elytra, contributing to the diversification and success of beetles. Furthermore, the genetic basis for the evolution of novel structures, such as the elytra, has been explored through RNA interference studies, which have identified key genes like abrupt (ab) that play a role in both conserved wing functions and the unique morphology of elytra (Ravisankar et al., 2016).

6 Case Studies

6.1 Case Study 1: Evolution of Elytra

The evolution of elytra, or hardened forewings, in beetles is a significant morphological adaptation that has contributed to their success. Elytra very likely evolved in the Late Carboniferous (Figure 1a) (Goczał and Beutel, 2023). Elytra provide protection to the delicate hindwings and the dorsal surface of the beetle's body. The development of elytra is believed to have originated from the modification of the ancestral beetle's forewings, which gradually became more sclerotized and rigid (Figure 1 b, d, f). This adaptation likely provided an evolutionary advantage by offering better protection against predators and environmental hazards.

The functional significance of elytra extends beyond protection. Elytra also play a role in reducing water loss, which is particularly advantageous for beetles living in arid environments. Additionally, the presence of elytra allows beetles to burrow into the soil or leaf litter without damaging their hindwings, facilitating their survival in various ecological niches. The study of net-winged beetles (Coleoptera: Lycidae) has shown that shortened elytra and the loss of coadaptation between the elytra and pronotum are linked to neoteny and other morphological modifications, highlighting the diverse evolutionary pathways that elytra can take (Kusy et al., 2019).

6.2 Case Study 2: Evolution of Feeding Structures

The diversification of beetle mouthparts has been a key factor in their evolutionary success, allowing them to exploit a wide range of food sources. In the dung beetle *Onthophagus taurus*, the development of mouthparts involves the functional roles of several patterning genes, including homothorax (hth), dachshund (dac), and Distal-less (Dll). These genes contribute to the development of the labium, maxilla, and labrum, with specific changes in the dac-patterning gene playing a crucial role in the transition from a short, triangular mandible adapted for chewing to an elongated, flat, and blade-like mandible suited for filter-feeding (Simonnet and Moczek, 2011).

The morphological changes in beetle mouthparts have had a profound impact on their diet and feeding strategies. For instance, the evolution of elongated mandibles in scarabaeine beetles has enabled them to adopt filter-feeding strategies, allowing them to exploit new food niches. This diversification in feeding structures has facilitated the radiation of beetles into various ecological roles, from herbivores and predators to decomposers and parasites, thereby enhancing their adaptability and survival (Simonnet and Moczek, 2011).

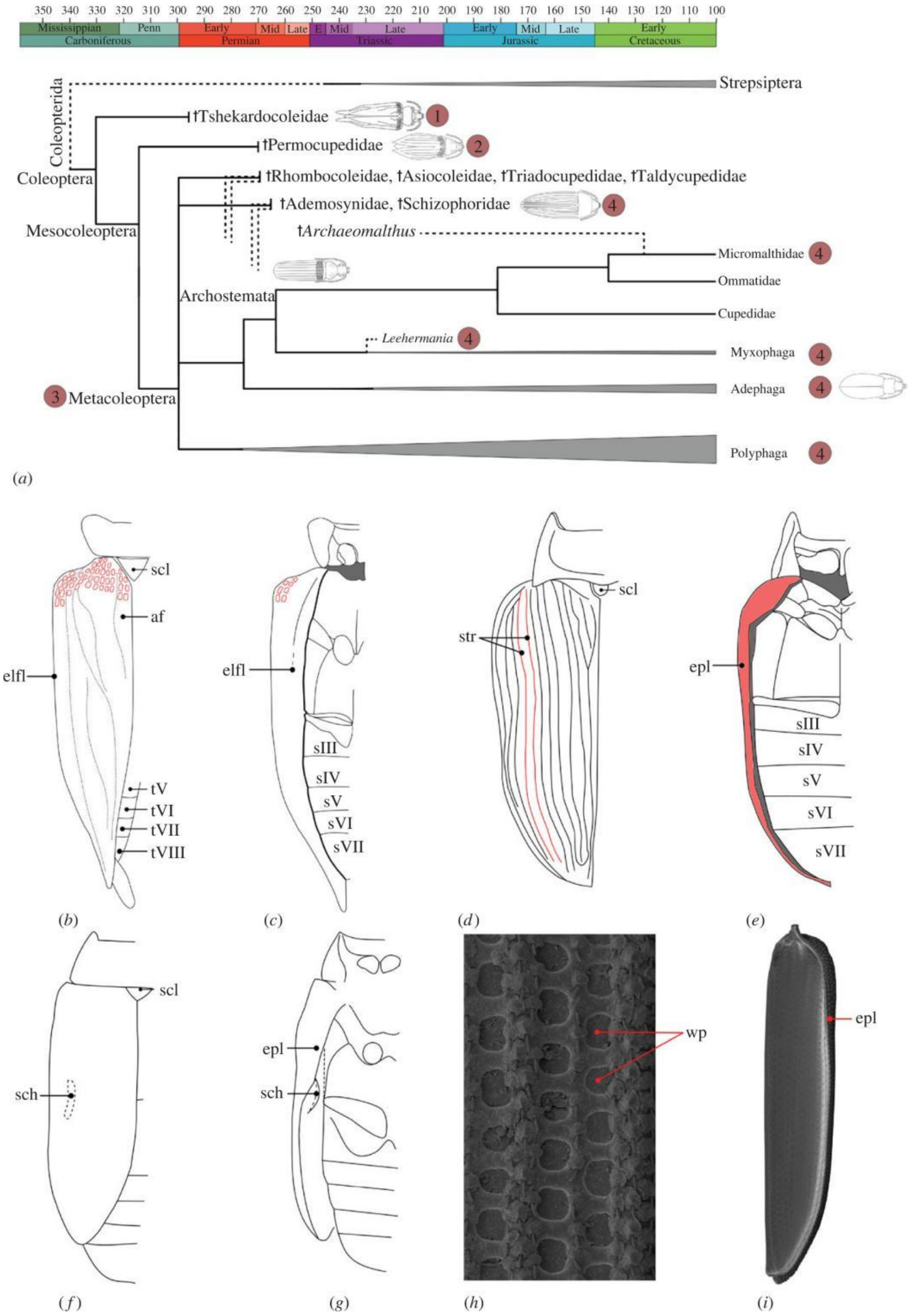

Figure 1 (a) Hypothesis for the early evolution of Coleoptera (and elytra); Numbers (1–4) indicate crucial steps in the evolution of elytra: (1) elytra distinctly surpassing the abdominal apex, lacking epipleura folded inwards, not tightly fitting with the abdomen, with partially maintained venation and window punctures—e.g. †Tshekardocoleidae; (2) elytra slightly surpassing the abdominal apex, with a parallel arrangement of longitudinal veins—†Permocupedidae; (3) elytra not surpassing the abdominal apex, tightly fitting with the abdomen, forming a secluded sub-elytral space—e.g. †Rhombocoleidae, †Taldycupedidae, all extant beetles (with few secondary exceptions); (4) elytra tightly fitting, without window punctures, smooth or with striae (or other surface patterns). Age estimates of nodes are approximations; (b,c) Reconstruction of postcephalic body of a Lower Permian beetle (†Tshekardocoleidae/†Coleopsis); (b) dorsal view; (c) ventral view (note that window punctures (in red) are present on entire elytral surface). (d,e) Postcephalic body of †*Peltosyne triassica Ponomarenko* (†Peltosynidae), (d) dorsal view, (e) ventral view. (f, g) Postcephalic body of †*Abrhadeocoleodes ooidus* Tan, Ren, Shih & Yang (†Schizophoridae), (f) dorsal view, (g) ventral view (elytron slightly extended, displaying schiza). (h,i) details of *Tetraphalerus bruchi* Heller (Archostemata, Ommatidae): (h) elytral window punctures, (i) entire elytron, epipleuron and inner surface. Abbreviations: elfl: flat lateral elytral flange, epl: infolded epipleura, str: longitudinal elytral striae, sch: schiza (ridge) of internal elytral surface, scl: mesoscutellar shield (locking device), wp: window punctures, af: anal field, t(VIII-V): abdominal tergites, s(VII-III): abdominal sternites (Adopted from Goczał and Beutel, 2023)

6.3 Case Study 3: Evolution of Limb Morphology

Beetle limb morphology has evolved to meet the demands of different ecological niches. Variations in leg structure are evident among aquatic, terrestrial, and arboreal beetles, each adaptation providing specific advantages. For example, aquatic beetles often have flattened, paddle-like legs that aid in swimming, while terrestrial beetles may have robust legs adapted for digging or running. Arboreal beetles, on the other hand, may possess legs with specialized tarsi that enhance their ability to cling to and navigate through vegetation.

The study of net-winged beetles (Coleoptera: Lycidae) provides insights into the parallel evolution of morphological traits, including limb structures. The presence of traits such as mimetic similarities and uniquely shaped terminal palpomeres in these beetles suggests that similar ecological pressures can lead to convergent evolution of limb morphology. These adaptations are crucial for survival in their respective environments, whether it be navigating through water, soil, or foliage (Kusy et al., 2019).

By examining these case studies, we gain a deeper understanding of the evolutionary trends in beetle morphology and the adaptive significance of these changes. The fossil record, combined with phylogenomic analyses, continues to shed light on the complex evolutionary history of beetles and their remarkable diversity.

7 Environmental and Ecological Influences

7.1 Impact of Climate Change

Historical climate shifts have had profound impacts on beetle morphology, influencing their evolutionary trajectories. For instance, the study on bark beetles in the Sonoran Desert highlights how past climatic changes, such as Plio- and Pleistocene-aged marine incursions, have left genetic signatures in beetle populations, indicating that abiotic factors significantly shaped their evolutionary history (Garrick et al., 2013; Cai et al., 2021). Additionally, research on forest beetles in Japan demonstrates that increased temperature and precipitation anomalies have led to divergent trends in beetle populations, with declines in evergreen coniferous forests and increases in broadleaf-coniferous mixed forests, further underscoring the role of climate change in altering beetle morphology and diversity (Evans et al., 2022). Moreover, the fossil record of northwestern European beetles reveals that climate warming during the Early Holocene significantly impacted beetle faunas, indicating that climate change has been a critical driver of morphological evolution over millennia (Pilotto et al., 2022).

7.2 Role of Predation and Competition

Biotic interactions, such as predation and competition, have also played a crucial role in the morphological evolution of beetles. The study on seed beetles, *Callosobruchus maculatus*, illustrates how host size influences larval competitiveness and associated traits, with populations evolving greater tolerance of co-occurring larvae and changes in egg size and fecundity in response to host shifts (Fox and Messina, 2018). This suggests that competition for resources within hosts can drive significant morphological adaptations. Furthermore, the research on cassidine beetles indicates that morphological divergence, such as variations in spine height and width, may be influenced by environmental gradients and possibly sexual selection, highlighting the complex interplay between biotic factors and morphological evolution (Simões et al., 2017).

7.3 Adaptations to Different Habitats

Beetles have adapted to a wide range of habitats, leading to diverse morphological changes. For example, the study on dung beetles in Mongolia shows that populations from different biomes exhibit significant variations in body shape and size, with desert-steppe populations having thinner bodies and longer heads to facilitate burrowing, and variations in body size potentially enhancing thermoregulation (Lim et al., 2020). Additionally, the research on stag beetles emphasizes the role of developmental plasticity in morphological evolution, with greater plasticity evolving as a species trait to survive in varying conditions, leading to larger size and adaptive expansion (Kawano, 2020). These adaptations to different habitats demonstrate the remarkable morphological diversity of beetles and their ability to thrive in diverse environmental conditions.

8 Future Directions and Challenges

8.1 Gaps in Current Knowledge

Despite significant advancements in our understanding of beetle evolution, several gaps remain that require further research and fossil discoveries. One major area needing attention is the incomplete fossil record, which can significantly impact our understanding of beetle diversification and biogeography. For instance, recent discoveries have pushed back the fossil record of certain beetle families, such as Silphidae, from the Eocene to the Jurassic, highlighting the need for more comprehensive fossil data to refine divergence time estimates and macroevolutionary patterns (Toussaint et al., 2016). Additionally, the fossil record of click-beetles (Elateridae) remains largely understudied, with many fossil lineages in urgent need of revision (Kundrata et al., 2021). The discovery of new fossil larvae with unique morphologies also suggests that there may be extinct larval forms or unknown larval phases in modern species that have yet to be described (Haug and Haug, 2019). Therefore, future research should focus on uncovering and analyzing new fossil specimens to fill these gaps and provide a more complete picture of beetle evolution.

8.2 Technological and Methodological Advances

The potential of new technologies in enhancing our understanding of beetle evolution is immense. Advanced imaging techniques such as X-ray micro-computed tomography (μ-CT) and cryoptychographic X-ray tomography have already proven invaluable in revealing detailed morphological structures in fossil specimens that were previously obscured (Wilts et al., 2018; Kundrata et al., 2020). These technologies allow for the reconstruction of three-dimensional models of beetle fossils, providing insights into their morphology and evolutionary adaptations. Additionally, the use of geometric morphometrics and transmission electron microscopy (TEM) has become more prominent in studying beetle morphology, enabling researchers to analyze shape variations and fine structural details with high precision. The integration of these advanced techniques with traditional paleontological methods will likely lead to more accurate reconstructions of beetle evolutionary history and the discovery of new morphological traits.

8.3 Interdisciplinary Approaches

The integration of paleontology, molecular biology, and ecology is crucial for a comprehensive understanding of beetle evolution. Phylogenomic studies, which combine genomic data with fossil calibrations, have already provided new insights into beetle phylogenetic relationships and divergence times (Cai et al., 2021). These studies highlight the importance of using large-scale genomic datasets to resolve controversial relationships and trace the evolution of key traits, such as plant cell wall-degrading enzymes (PCWDEs) that facilitated the diversification of herbivorous beetles (Mckenna et al., 2019). Furthermore, interdisciplinary approaches that incorporate ecological data can shed light on the interactions between beetles and their environments, such as the co-diversification of beetles and angiosperms. By integrating data from multiple disciplines, researchers can develop a more holistic understanding of the factors driving beetle evolution and diversification.

9 Concluding Remarks

This systematic review has thoroughly explored the evolutionary trends in beetle morphology, providing valuable insights through fossil records. Firstly, the study reveals the diversification of beetle morphological structures, including the development of elytra, changes in mouthparts, and limb morphology. These morphological adaptations have significantly impacted beetle survival and reproduction, enabling them to thrive in various ecological niches. Secondly, the research highlights the profound influence of climatic changes, predation, competition pressures, and habitat adaptations on the evolutionary trajectory of beetle morphology. By analyzing fossil records, we gain a better understanding of the timing and patterns of these evolutionary events, thus painting a comprehensive picture of beetle evolution.

Fossil records play a crucial role in understanding insect evolution. Beetle fossils provide direct evidence for studying their evolutionary history, revealing morphological changes and adaptations across different periods and environments. These fossil data not only help calibrate molecular phylogenetic trees but also offer unique perspectives on evolutionary pressures and biodiversity. By integrating fossil evidence with modern technological approaches, such as X-ray micro-computed tomography and genomic studies, scientists can more accurately reconstruct beetle evolutionary history, uncovering the complexity and diversity of insect evolution.

The future holds vast potential for research in beetle morphology and evolution. The application of new technologies, such as advanced imaging and genomic analysis, will continue to propel this field forward, enabling the discovery of more unanswered questions. Additionally, interdisciplinary approaches will further deepen our understanding of beetles and their ecosystems, revealing more about the dynamic processes of species co-evolution and environmental adaptation. Continuous exploration and research will not only provide a more comprehensive understanding of beetle evolutionary history but also offer important references for the evolutionary studies of other insect groups, thereby advancing the broader field of evolutionary biology.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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