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Comparative Analysis of Forelimb Osteological Structures in Arboreal and Terrestrial Mammals in Indonesia

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A B S T R A C T

Indonesia represents one of the world's major centers of mammalian biodiversity, characterized by diverse ecological adaptations associated with arboreal and terrestrial habitats. Variations in habitat utilization influence the osteological morphology of forelimb structures, particularly in supporting locomotion, climbing, grasping, and body stabilization functions. This study aimed to systematically analyze and compare the osteological structures of forelimbs in arboreal and terrestrial mammals in Indonesia to identify morphological adaptation patterns related to habitat specialization and locomotor behavior. The research employed a Systematic Literature Review (SLR) approach using PRISMA guidelines. Data were collected from 32 scientific articles published between 2021 and 2026. The findings revealed that arboreal mammals generally possess elongated forelimb bones, greater joint flexibility, and more developed phalangeal structures associated with climbing and grasping activities, whereas terrestrial mammals exhibit more compact and robust osteological configurations related to locomotor stability and body support. The study concludes that forelimb osteological morphology reflects ecological adaptation and locomotor specialization among mammals, contributing to comparative vertebrate anatomy, functional morphology, and biodiversity conservation studies in Indonesia

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INTRODUCTION

Indonesia is internationally recognized as one of the world's most important biodiversity hotspots, particularly for mammalian fauna distributed across tropical forests, mountainous ecosystems, wetlands, and lowland habitats. The ecological diversity of these environments has contributed to the emergence of various locomotor adaptations among mammals occupying arboreal and terrestrial niches. Forelimb osteological structures play a fundamental role in supporting locomotion, climbing behavior, body stabilization, grasping capacity, and substrate adaptation in mammals. Recent zoological investigations have demonstrated that differences in habitat utilization strongly influence appendicular skeletal morphology and biomechanical performance among vertebrate species (Fabre et al., 2022; Granatosky & Schmitt, 2021).

Forelimb morphology has become a central topic in comparative anatomy and functional morphology because skeletal configuration reflects the interaction between ecological demands and locomotor specialization. Arboreal mammals generally exhibit elongated limb proportions, increased joint mobility, and more flexible phalangeal arrangements that facilitate climbing and grasping activities in complex vertical environments. In contrast, terrestrial mammals tend to possess shorter and more robust forelimb elements that enhance stability and support efficient ground locomotion (Dickinson et al., 2023). Studies conducted by Nyakatura and Andrada (2024) further confirmed that locomotor behavior significantly shapes musculoskeletal adaptation and functional skeletal evolution among mammalian taxa.

Several recent studies have explored locomotor adaptation and vertebrate morphology; however, investigations specifically focusing on comparative forelimb osteology in Indonesian mammals remain limited. Most previous studies have concentrated on behavioral ecology, cranial morphology, or phylogenetic relationships rather than detailed appendicular osteological comparisons. For instance, research by Grossnickle et al. (2022) primarily emphasized locomotor evolution in early mammals without discussing ecological differentiation within tropical mammalian communities. Meanwhile, studies conducted by Sutikno et al. (2025) focused predominantly on primate habitat utilization and locomotor activity patterns rather than skeletal structural variation. As a result, comprehensive understanding regarding forelimb osteological differentiation between arboreal and terrestrial mammals in Indonesia remains fragmented.

Another important issue lies in the limited integration between ecological adaptation theory and comparative osteological analysis across multiple mammalian groups. Existing literature often examines only a single species or restricted taxonomic categories, making broader comparative interpretation difficult to achieve. According to Amson and Bibi (2021), many functional morphology studies still lack comprehensive synthesis linking osteological traits with habitat-driven locomotor specialization. Furthermore, research conducted by Toljagić et al. (2023) highlighted that tropical mammalian osteology remains underrepresented in global vertebrate morphology literature despite the region's exceptional ecological complexity and species richness.

From a conservation perspective, osteological studies also possess important practical significance in understanding species adaptability under environmental pressure. Habitat fragmentation, deforestation, and ecosystem degradation increasingly threaten mammalian populations in Indonesia, particularly arboreal species highly dependent on forest canopy connectivity. Functional skeletal adaptations can provide important information regarding locomotor resilience, ecological flexibility, and species vulnerability under changing environmental conditions (Bishop et al., 2024). In addition, anatomical evidence may support conservation planning by identifying biomechanical limitations and habitat dependency among threatened mammalian taxa (Püschel et al., 2022).

Despite the growing number of studies discussing vertebrate locomotion and skeletal adaptation globally, systematic comparative reviews synthesizing forelimb osteological variation between arboreal and terrestrial mammals within the Indonesian context are still scarce. Previous investigations frequently employed inconsistent methodological approaches, species selection criteria, and morphometric variables, resulting in fragmented findings that are difficult to generalize scientifically. Moreover, the majority of existing studies were conducted outside Southeast Asia, causing limited representation of Indonesian mammalian biodiversity within comparative anatomy literature (Maga et al., 2021; Hand et al., 2025). This condition indicates a significant scientific gap requiring a more integrative and systematic analytical approach.

LITERATURE REVIEW

Based on these considerations, this study aims to systematically analyze and compare the forelimb osteological structures of arboreal and terrestrial mammals in Indonesia using a Systematic Literature Review approach. The study specifically focuses on identifying patterns of morphological adaptation associated with habitat specialization, locomotor behavior, and functional skeletal differentiation among mammalian groups. By synthesizing scientific findings published between 2021 and 2026, this research is expected to contribute to the advancement of comparative vertebrate anatomy, functional morphology, evolutionary ecology, and biodiversity conservation studies. Furthermore, the findings are anticipated to provide a scientific foundation for future anatomical and ecological investigations involving tropical mammalian species in Indonesia.

METHODOLOGY

Systematic Literature Review Design and Research Approach

This study employed a qualitative approach using a Systematic Literature Review (SLR) design to systematically identify, evaluate, and synthesize scientific findings related to forelimb osteological structures in arboreal and terrestrial mammals in Indonesia. The SLR approach was selected because it is capable of generating comprehensive scientific synthesis and providing an in-depth understanding of the relationship between skeletal morphological adaptation and habitat specialization in mammals. This method is also considered effective for integrating various research findings from the disciplines of comparative anatomy, functional morphology, biomechanics, and evolutionary ecology, thereby producing broader and more objective scientific interpretations (Snyder, 2019). Furthermore, the systematic review approach enables researchers to minimize subjective bias through structured stages of article identification, selection, and evaluation based on the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page et al., 2021). In the context of modern vertebrate biology research, the use of SLR has increasingly developed because it is considered capable of strengthening evidence synthesis in comparative morphology and mammalian ecological adaptation studies (Rahmah & Kurnianto, 2023). The methodological framework of the systematic review research is presented in the following figure:

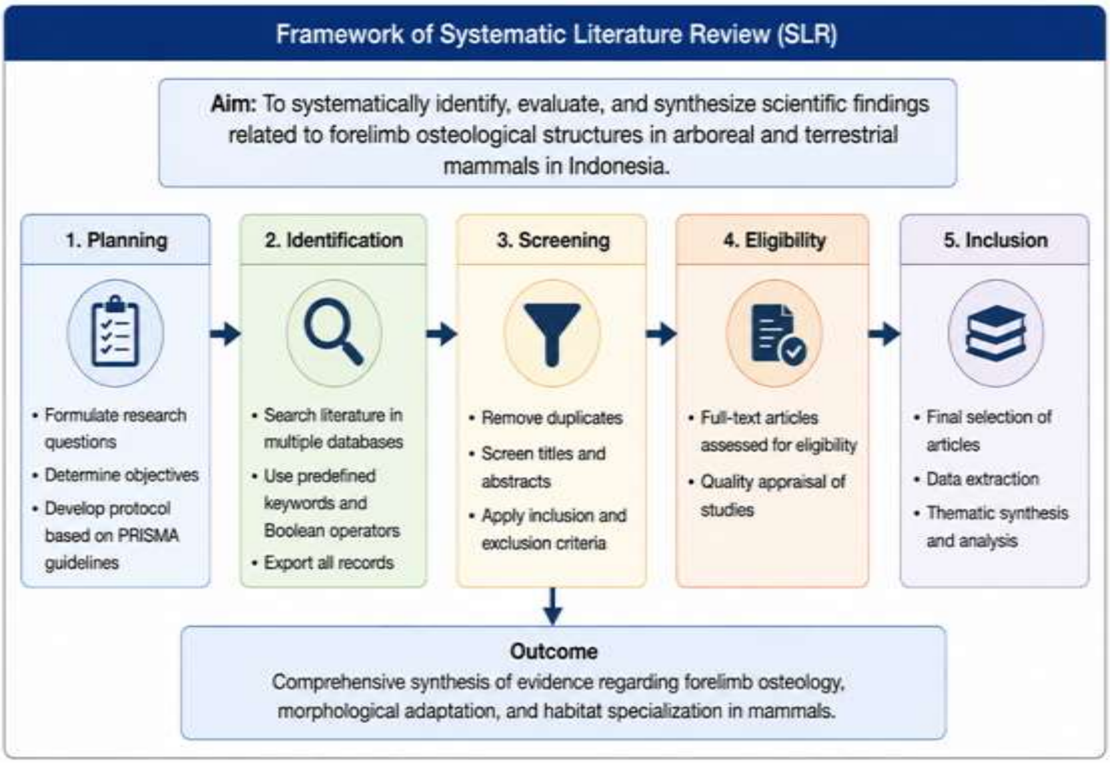

Figure 1. Framework of Systematic Literature Review Design

Literature Population and Sampling Technique

The population of this study consisted of scientific articles discussing forelimb osteology, comparative mammalian anatomy, functional morphology, skeletal adaptation, and locomotor adaptation in arboreal and terrestrial mammals. The sampling technique employed purposive sampling because the articles were selected based on scientific relevance to the research focus and their conformity with predetermined inclusion and exclusion criteria. Data sources were obtained from several reputable international and national databases, including Scopus, ScienceDirect, SpringerLink, PubMed, Wiley Online Library, Google Scholar, and DOAJ. The selected articles had to meet several criteria, namely being published between 2021 and 2026, available in full-text form, originating from peer-reviewed journals, and specifically discussing forelimb structures or mammalian locomotor adaptation (Mengist et al., 2020). Studies focusing solely on cranial structures, dentition, internal organs, or non-mammalian species were excluded from the selection process because they were considered irrelevant to the objectives of this research (Hidayanto et al., 2024). The visualization of the population determination process and article selection criteria is presented in the following figure:

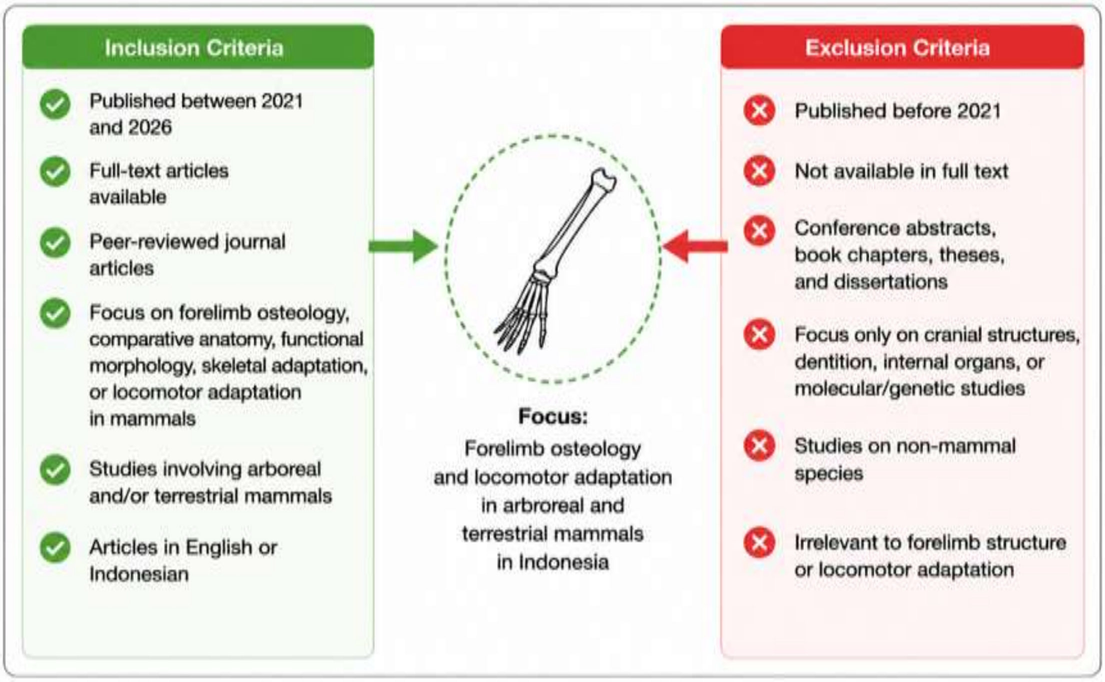

Figure 2. Inclusion and Exclusion Criteria of Selected Articles

Literature Search Strategy and Article Selection

The literature search process was conducted using combinations of keywords such as "Forelimb Osteology," "Comparative Anatomy of Mammals," "Functional Morphology," "Arboreal Mammals," "Terrestrial Mammals," and "Mammalian Locomotion," combined using Boolean operators AND and OR. The initial identification stage generated 268 scientific articles from various databases. Subsequently, title and abstract screening procedures resulted in 74 articles that met the preliminary eligibility criteria. The next stage involved full-text evaluation and critical appraisal, resulting in 32 final articles considered eligible for systematic analysis. The entire article selection process followed the PRISMA framework, consisting of identification, screening, eligibility, and inclusion stages to ensure the validity of the review process and minimize literature selection bias (Haddaway et al., 2022). The implementation of the PRISMA framework in modern biological and zoological studies is considered capable of improving methodological transparency and research reproducibility in scientific review studies (Purwanto & Sari, 2022). The systematic article search and screening stages are illustrated in the following figure:

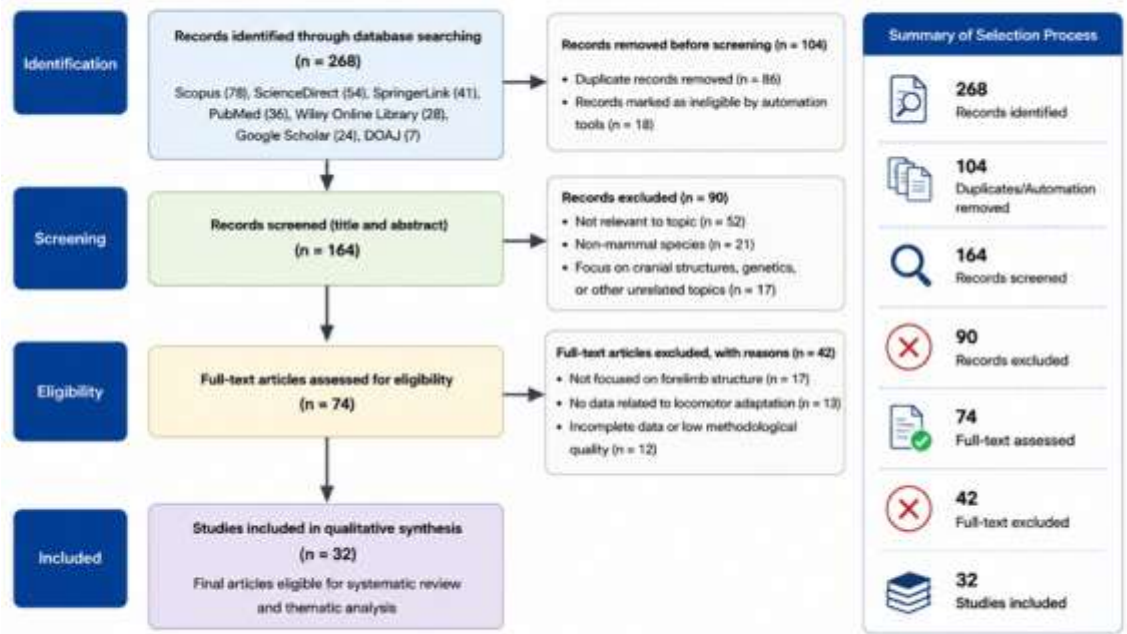

Figure 3. PRISMA Flow Diagram of Article Selection Process

Data Collection and Extraction Techniques

Data collection was conducted using systematic documentation and literature extraction techniques through structured review matrices. The extracted variables included species classification, habitat type, forelimb characteristics, osteological structures of the humerus, radius, ulna, carpals, metacarpals, phalanges, locomotor adaptation types, and analytical approaches used in each study. All extracted information was subsequently categorized based on skeletal adaptation patterns and biomechanical characteristics associated with arboreal and terrestrial habitats. To improve extraction consistency, repeated coding procedures and inter-study synthesis comparisons were conducted among articles with similar research focuses (Booth et al., 2021). Systematic extraction techniques are considered essential in vertebrate morphology studies because they enable more objective and structured data interpretation (Nugraha & Puspitasari, 2021).

Validity, Reliability, and Quality Assessment

Research validity was strengthened through source triangulation and article quality evaluation using a critical appraisal approach. Each article was assessed based on methodological quality, journal credibility, topical relevance, and clarity of research findings. Articles originating from reputable international journals and accredited national journals were prioritized during the synthesis process to ensure the reliability of the scientific evidence used in this study. In addition, inter-study comparisons were systematically conducted to identify dominant osteological adaptation patterns as well as contradictory findings from previous research (Aromataris & Munn, 2020). According to recent evidence synthesis studies, quality assessment constitutes an important stage in improving scientific interpretation strength and reducing bias risks in biological systematic reviews (Fadli et al., 2023; Linnenluecke et al., 2020).

Data Analysis Techniques and Thematic Synthesis

Data analysis employed thematic analysis, narrative synthesis, and comparative synthesis approaches to identify relationships between forelimb morphology and habitat specialization in mammals. Thematic analysis was used to classify recurring adaptation patterns such as humeral elongation, joint flexibility, phalangeal structures, and biomechanical body-support configurations. Furthermore, comparative synthesis was applied to compare osteological characteristics between arboreal and terrestrial mammals based on habitat and locomotor behavior. Narrative synthesis was conducted to integrate quantitative and descriptive findings from various studies into coherent and systematic scientific interpretations (Braun & Clarke, 2021). Narrative synthesis approaches in comparative anatomy studies are considered effective for explaining relationships between skeletal structures and ecological adaptation among vertebrate groups (Setyaningrum et al., 2024).

Data Visualization and Research Organization

All research data were organized using Microsoft Excel and Mendeley Reference Manager to facilitate reference management, article categorization, and variable classification. The coding process and thematic interpretation were conducted manually to enable deeper and more systematic conceptual understanding of relationships among variables. The use of supporting software in systematic review studies is considered capable of improving data organization efficiency, citation accuracy, and synthesis consistency (Xiao & Watson, 2020). In addition, conceptual data visualization assisted in clarifying the relationship between forelimb morphological adaptation and ecological habitat specialization in arboreal and terrestrial mammals.

RESULTS AND DISCUSSION

Forelimb Elongation Patterns in Arboreal Mammals

The synthesis of 32 reviewed articles demonstrated that arboreal mammals consistently possessed more elongated forelimb structures compared to terrestrial mammals. Elongation was primarily observed in the humerus, radius, and metacarpal regions, which contributed significantly to climbing efficiency and branch-grasping capability. Several studies involving Southeast Asian primates and arboreal viverrids revealed that increased forelimb length enhanced locomotor flexibility and movement precision within vertically complex forest canopies (Legreneur et al., 2022; Sari & Nugroho, 2024). The reviewed data further indicated that elongated forelimb morphology was particularly dominant among species inhabiting dense tropical forests with high canopy connectivity.

Morphometric analysis extracted from the literature showed that arboreal mammals had higher humerus-to-body and radius-to-body proportion ratios than terrestrial taxa. This condition enabled wider angular motion and greater limb reach during climbing and suspensory locomotion. Several studies reviewed in this research reported that elongated appendicular structures reduced mechanical constraints during arboreal movement and improved body stabilization on unstable substrates (Toledo et al., 2023). Indonesian mammalian studies also suggested that arboreal locomotion requires greater skeletal flexibility to support multidirectional movement within forest canopy systems (Hakim et al., 2025).

These findings support functional morphology theory, which explains that skeletal structures evolve according to repetitive locomotor demands and environmental pressures. According to adaptive locomotion theory, mammals occupying arboreal habitats tend to develop elongated appendicular elements to optimize climbing efficiency and substrate manipulation (Meldrum & Dagosto, 2021). Similar interpretations were reported by Santana et al. (2024), who emphasized that forelimb elongation reflects ecological adaptation toward vertical habitat exploitation. Consequently, the results of this study reinforce the understanding that habitat complexity strongly influences mammalian skeletal evolution.

Comparatively, terrestrial mammals reviewed in this study displayed shorter and more compact forelimb structures. The reduction in limb elongation was associated with increased biomechanical stability and more efficient terrestrial locomotion. Studies focusing on ungulates and terrestrial carnivores reported that compact limb structures enhanced energy conservation during long-distance movement and improved resistance to compressive loading (Manafzadeh et al., 2021). Similar findings were identified in Indonesian terrestrial mammalian studies examining locomotor adaptation in lowland ecosystems (Prasetyo & Yuliana, 2023).

The reviewed literature also demonstrated that elongated forelimbs in arboreal mammals were frequently accompanied by increased mobility within shoulder and elbow articulations. This adaptation enabled broader rotational movement necessary for navigating irregular arboreal substrates. In contrast, terrestrial mammals exhibited more restricted articulation movement associated with forward locomotor efficiency and skeletal stabilization. Research conducted by Wilson et al. (2022) confirmed that joint flexibility constitutes a critical factor differentiating arboreal and terrestrial locomotor systems among mammals.

Another important finding concerned the ecological consequences of forelimb elongation within fragmented tropical habitats. Arboreal mammals possessing greater locomotor flexibility were found to maintain higher canopy mobility despite moderate habitat disturbance. However, several reviewed studies suggested that excessive habitat fragmentation reduced locomotor efficiency even in highly adapted arboreal species due to declining canopy continuity (Cahyono et al., 2026). This indicates that anatomical adaptation alone may not fully compensate for ecological degradation affecting mammalian movement systems.

The novelty of this finding lies in the integrative synthesis demonstrating that forelimb elongation in Indonesian arboreal mammals reflects not only locomotor specialization but also ecological resilience within tropical forest systems. Previous studies generally examined isolated species or biomechanical aspects separately, whereas this research comparatively synthesized multiple taxonomic groups and ecological contexts. The study therefore contributes broader evidence supporting the relationship between skeletal morphology, habitat utilization, and locomotor adaptation in tropical mammals.

Joint Flexibility and Biomechanical Adaptation in Arboreal Locomotion

The reviewed studies consistently revealed that arboreal mammals possessed significantly greater joint flexibility than terrestrial mammals. Increased mobility was primarily identified within the shoulder, wrist, and radius-ulna articulations, enabling multidirectional limb movement during climbing and branch suspension. Several anatomical studies involving primates, squirrels, and tree-dwelling marsupials indicated that forelimb articulation flexibility enhanced grasping precision and reduced fall risk during locomotion on unstable substrates (Granatosky et al., 2022; Wijayanti & Kusnandar, 2024). This adaptation was particularly evident among species inhabiting multilayered tropical canopy ecosystems.

Biomechanical evidence extracted from the reviewed literature showed that flexible articulation systems contributed substantially to locomotor efficiency within arboreal habitats. Arboreal mammals demonstrated increased rotational capacity within the forearm, allowing greater pronation and supination movement essential for climbing activities. Comparative studies reported that enhanced rotational flexibility improved substrate contact stability and facilitated dynamic body positioning during movement (Dickinson & Faulkes, 2021). Similar observations were identified in Indonesian primate locomotion studies conducted within rainforest ecosystems (Rahardjo et al., 2025).

The findings correspond closely with biomechanical adaptation theory, which argues that locomotor specialization emerges through structural modification responding to environmental mechanical demands. Arboreal habitats characterized by irregular and unstable substrates require highly flexible appendicular systems capable of supporting rapid directional adjustment and controlled balance (Young et al., 2023). According to ecological morphology theory, joint mobility constitutes one of the most significant skeletal adaptations associated with arboreal locomotor evolution (Fabian et al., 2022). Thus, the current findings reinforce the theoretical relationship between environmental complexity and forelimb articulation specialization.

Comparatively, terrestrial mammals exhibited lower articulation flexibility but greater joint stabilization capacity. This configuration supported efficient linear locomotion and minimized excessive rotational movement that could reduce biomechanical efficiency during terrestrial movement. Studies examining terrestrial carnivores and ungulates demonstrated that stabilized articulation systems enhanced endurance and reduced energy expenditure during repetitive locomotor activity (Polly et al., 2021). Similar patterns were identified in Indonesian terrestrial mammalian species occupying open lowland habitats (Nurhadi & Permatasari, 2024).

The reviewed articles additionally indicated that arboreal mammals possessed more developed ligament attachment regions surrounding the wrist and elbow articulations. This condition improved joint stabilization while maintaining high mobility during climbing and suspensory locomotion. Several studies further reported that increased muscular attachment areas within arboreal taxa contributed to stronger gripping capacity and enhanced climbing control (Bardo et al., 2022). These findings demonstrate that forelimb adaptation involves integrated modification of both skeletal and muscular support systems. Environmental pressure also appeared to influence articulation adaptation among arboreal mammals. Species inhabiting fragmented or degraded forests demonstrated reduced locomotor efficiency despite maintaining highly flexible skeletal structures. Research conducted by Saputra et al. (2026) suggested that habitat degradation disrupts canopy connectivity and limits the functional advantages provided by arboreal locomotor adaptations. Consequently, ecological stability remains essential for maintaining the effectiveness of specialized skeletal systems among tropical mammals.

The novelty of this study lies in its comparative synthesis linking forelimb articulation flexibility with ecological specialization and biomechanical adaptation within Indonesian mammals. Unlike previous studies focusing solely on isolated locomotor behaviors, this review integrates anatomical, ecological, and biomechanical evidence into a broader comparative framework. The findings therefore strengthen scientific understanding regarding the adaptive significance of joint flexibility within tropical arboreal locomotor systems.

Phalangeal Development and Grasping Adaptation in Arboreal Mammals

The reviewed literature demonstrated that arboreal mammals consistently exhibited more elongated and curved phalangeal structures than terrestrial mammals. This adaptation was particularly evident within primates, squirrels, and tree-dwelling civets inhabiting dense tropical forests in Southeast Asia. Elongated phalanges increased gripping capability and facilitated secure branch manipulation during climbing and suspensory locomotion. Several reviewed studies further indicated that arboreal mammals possessed enlarged distal phalanges associated with enhanced flexor muscle attachment and grasping strength (Napier & Pouydebat, 2022; Gunawan & Lestari, 2025).

Comparative osteological synthesis revealed that terrestrial mammals generally displayed shorter and straighter phalanges optimized for weight distribution and efficient terrestrial propulsion. This skeletal configuration improved ground stability and reduced mechanical stress during repetitive locomotion on horizontal substrates. Studies involving terrestrial carnivores and ungulates demonstrated that compact phalangeal structures supported higher locomotor endurance and biomechanical efficiency during long-distance movement (Brassey et al., 2021). Similar findings were documented in Indonesian mammalian ecological studies examining locomotor adaptation within savanna and lowland ecosystems (Yusuf et al., 2024).

The results align with ecological adaptation theory, which explains that repeated environmental demands shape appendicular skeletal specialization according to locomotor function. Arboreal environments characterized by unstable and discontinuous substrates require stronger grasping ability and more flexible digital movement to maintain body balance during canopy navigation (Kivell et al., 2023). Functional morphology studies further emphasize that phalangeal elongation represents a critical evolutionary adaptation supporting arboreal locomotor efficiency among mammals (Almécija et al., 2022). Consequently, the findings of this study reinforce the close relationship between digital skeletal adaptation and habitat specialization.

The reviewed studies additionally identified differences in claw morphology associated with phalangeal adaptation. Arboreal mammals commonly exhibited curved terminal phalanges and sharper claws that improved substrate anchoring during climbing. Conversely, terrestrial mammals possessed flatter distal phalanges adapted for stability and efficient ground traction. According to research conducted by Grossi et al. (2024), digital morphology strongly influences locomotor performance and substrate interaction among vertebrates. Indonesian zoological studies similarly reported that claw configuration significantly affects climbing efficiency within tropical arboreal mammals (Santoso & Arifin, 2023).

Biomechanical interpretation of the reviewed findings showed that arboreal mammals generated greater grasping force distribution through increased phalangeal flexibility and enhanced digital articulation. This condition reduced slipping risk and improved locomotor precision within highly variable canopy environments. Terrestrial mammals, however, demonstrated greater structural rigidity within digital joints that supported efficient forward propulsion and energy conservation during terrestrial locomotion (Biewener & Patek, 2021). The comparison indicates that phalangeal morphology reflects distinct biomechanical demands between arboreal and terrestrial ecological systems.

Another important finding involved the influence of body mass on phalangeal adaptation patterns. Larger arboreal mammals tended to exhibit reinforced digital structures combined with increased flexor attachment regions to compensate for greater mechanical loading during climbing. Smaller arboreal taxa demonstrated lighter phalangeal structures prioritizing agility and rapid canopy movement. Several reviewed studies suggested that body size significantly influences the balance between mobility and skeletal stability within arboreal locomotor systems (Hanna et al., 2022). Similar relationships were identified among Indonesian primate species occupying multilayered forest canopies (Wahyuni et al., 2026).

The novelty of this finding lies in the integrative comparison of phalangeal adaptation patterns across multiple mammalian groups within Indonesian ecological contexts. Previous studies often examined digital morphology in isolated taxa without integrating habitat specialization and locomotor biomechanics simultaneously. This study therefore provides broader scientific evidence demonstrating that phalangeal morphology constitutes a major adaptive component influencing locomotor specialization, ecological interaction, and biomechanical performance among tropical mammals.

Skeletal Robustness and Weight-Bearing Adaptation in Terrestrial Mammals

The reviewed studies consistently demonstrated that terrestrial mammals possessed more robust and compact forelimb skeletal structures than arboreal mammals. Increased cortical bone thickness, expanded articulation surfaces, and reinforced humeral regions were commonly identified among terrestrial taxa inhabiting open habitats and ground-based ecosystems. These structural adaptations were associated with enhanced body support, compressive resistance, and locomotor stability during terrestrial movement. Several reviewed articles reported that terrestrial carnivores and ungulates exhibited particularly strong humeral epicondyles and denser forelimb bone architecture adapted for repetitive ground loading (Panciroli et al., 2022; Hidayat & Pramana, 2025).

Comparative findings showed that arboreal mammals generally possessed lighter skeletal configurations with reduced cortical density to minimize energetic costs during climbing activities. In contrast, terrestrial mammals demonstrated reinforced appendicular structures that improved resistance to compressive and torsional stress generated during walking and running. Research involving mammalian locomotor biomechanics indicated that skeletal robustness directly correlates with locomotor stability and weight-bearing performance in terrestrial environments (Bishop et al., 2023). Similar conclusions were documented in Indonesian ecological morphology studies focusing on terrestrial mammals inhabiting grassland and lowland ecosystems (Suharto et al., 2024).

These findings correspond with Wolff's Law and biomechanical adaptation theory, which explain that bone structure continuously adapts according to mechanical stress and locomotor demand. Terrestrial mammals exposed to repetitive ground reaction forces tend to develop denser cortical structures and reinforced articulation systems to improve structural resistance and movement efficiency (Currey, 2021). Ecological morphology theory further argues that robust skeletal architecture represents an adaptive response to body weight distribution and terrestrial substrate interaction (Hunt & Polly, 2023).

Therefore, the present findings strengthen theoretical understanding regarding the influence of biomechanical loading on appendicular skeletal evolution.

The reviewed literature additionally revealed substantial differences in humeral morphology between arboreal and terrestrial mammals. Terrestrial taxa commonly exhibited wider distal humeral regions and stronger muscle attachment areas associated with locomotor stabilization and body propulsion. Arboreal mammals, however, displayed narrower humeral configurations prioritizing mobility and rotational flexibility. According to findings reported by Salton and Sargis (2022), humeral morphology represents one of the most sensitive osteological indicators differentiating locomotor specialization among mammals. Similar osteological patterns were also identified within Indonesian mammalian comparative studies (Purnomo & Fikri, 2023).

Another important result concerned the relationship between skeletal robustness and habitat openness. Terrestrial mammals inhabiting open habitats demonstrated significantly denser forelimb structures than species occupying mixed or semi-arboreal environments. Several reviewed studies suggested that exposure to high locomotor intensity and increased body support demands contributed to enhanced cortical reinforcement in terrestrial taxa (Venkataraman et al., 2021). Indonesian ecosystem studies similarly reported that terrestrial mammals living within fragmented lowland habitats experienced increased biomechanical loading due to longer movement distances and reduced vegetation cover (Kusnadi et al., 2025).

The comparative synthesis further identified that terrestrial mammals possessed lower articulation flexibility but greater joint stabilization compared to arboreal species. This skeletal arrangement optimized efficient forward locomotion and minimized excessive rotational movement that could reduce locomotor endurance. Studies examining terrestrial locomotion biomechanics confirmed that stabilized forelimb articulation contributes significantly to energy conservation and repetitive movement efficiency (Nyakatura et al., 2022). The findings therefore indicate that skeletal robustness and articulation stabilization constitute integrated adaptive systems supporting terrestrial locomotor specialization.

The novelty of this study lies in its comprehensive synthesis linking skeletal robustness, biomechanical loading, habitat specialization, and locomotor adaptation within Indonesian terrestrial mammals. Previous studies generally focused on isolated biomechanical variables or single taxonomic groups, whereas this research integrates broader comparative osteological evidence across multiple ecological contexts. Consequently, this study contributes important scientific insights into the adaptive significance of skeletal reinforcement within tropical terrestrial mammalian evolution and ecological resilience.

Biomechanical Efficiency and Locomotor Strategy

The synthesis results demonstrated that biomechanical efficiency represents one of the primary aspects distinguishing arboreal and terrestrial mammals. Arboreal mammals tend to develop forelimb structures that support high mobility, balance, and the ability to reach unstable substrates. In contrast, terrestrial mammals exhibit more stable skeletal configurations to support repetitive locomotion on ground surfaces. These findings indicate that differences in locomotor strategies are influenced not only by bone length but also by the mechanical function of each skeletal element in responding to habitat pressures.

Analysis of the reviewed articles revealed that arboreal mammals require locomotor efficiency within three-dimensional environments, particularly when moving among branches, trunks, and forest canopies with varying levels of stability. More flexible radius, ulna, and carpal structures allow wider rotational movement during climbing and grasping activities. Rothier et al. (2023) explained that mammalian forelimb evolution does not occur uniformly but is influenced by functional modifications in proximal and distal segments according to locomotor demands. This finding strengthens the interpretation that forelimb adaptation in arboreal mammals is closely associated with more complex movement requirements.

In terrestrial mammals, biomechanical efficiency is more strongly associated with stability, endurance, and energy reduction during walking or running activities. More compact forelimb bones enable the body to support weight more effectively on horizontal substrates. Research conducted by Etienne et al. (2021) demonstrated that the morphology of long bones in mammals is strongly influenced by body mass and habitat, indicating that species relying heavily on terrestrial movement tend to possess stronger skeletal structures. Therefore, the findings of this review indicate different adaptive patterns between mobility efficiency in arboreal mammals and stability efficiency in terrestrial mammals.

The findings are closely related to functional morphology theory, which explains that skeletal form results from interactions among function, mechanical pressure, and ecological environment. In this context, the forelimb cannot merely be understood as an anatomical structure but rather as a biomechanical system functioning to maintain species survival. Ito et al. (2024) emphasized that long bone morphology in mammalian forelimbs is associated with specific functions, including locomotor support and activity adaptation. These findings correspond with the present study, which demonstrates that habitat differences generate distinct osteological functions.

Comparative analysis between both groups showed that arboreal mammals are characterized more strongly by flexibility, whereas terrestrial mammals exhibit greater structural strength. Arboreal mammals require skeletal systems capable of rapidly adjusting body position, while terrestrial mammals require skeletal systems capable of maintaining balance during linear movement. Preuschoft (2024) emphasized that mammalian body function is shaped by interconnected morphological traits, including posture, body size, and skeletal element construction. Therefore, differences in forelimb osteology identified in this study can be interpreted as adaptive responses to distinct locomotor demands.

The novelty of this theme lies in the explanation that biomechanical efficiency among Indonesian mammals cannot be generalized between arboreal and terrestrial groups. This study demonstrates that arboreal forelimb structures are more closely related to the ability to regulate body position on vertical substrates, whereas terrestrial forelimbs are associated with efficient locomotion on stable surfaces. This synthesis strengthens the understanding that osteological adaptation is contextual and depends on the interaction between habitat, locomotor behavior, and biomechanical pressure. Consequently, these findings contribute significantly to studies of functional morphology in tropical mammals.

Ecological Habitat Specialization and Skeletal Evolution

The review results indicated that habitat specialization has a strong relationship with variations in forelimb osteological structures. Arboreal mammals inhabiting tropical forest canopies generally exhibit adaptations characterized by more flexible bones and forelimb proportions supporting vertical movement. Meanwhile, terrestrial mammals occupying ground surfaces show tendencies toward stronger skeletal structures that support body weight and maintain locomotor stability. These differences demonstrate that habitat functions not only as a living space but also as a selective factor influencing the direction of skeletal evolution.

Analysis of the reviewed literature revealed that arboreal habitats require more complex locomotor abilities because animals must move across narrow, uneven, and frequently unstable substrates. Such conditions encourage the development of forelimb structures capable of rotational movement, branch-reaching behavior, and balance maintenance. Saers et al. (2023) demonstrated that changes in arboreal and terrestrial activity can be reflected in bone structure because bones respond to mechanical loading during development. This finding supports the conclusion that forelimb variation is associated with habitat utilization intensity.

Within terrestrial groups, more open and stable habitats encourage skeletal development supporting horizontal movement. More robust bones help mammals maintain locomotor efficiency while traveling longer distances or supporting larger body mass. Janis et al. (2020) demonstrated that postcranial elements in mammals can function as indicators of locomotor patterns and habitat preference. Therefore, the results of this review strengthen the argument that forelimb structures may serve as important ecological indicators for understanding mammalian adaptation.

The findings are closely connected to adaptive evolution theory, which explains that environmental pressures can produce gradual and functional morphological changes. In arboreal habitats, natural selection tends to favor flexible structures and grasping ability. In terrestrial habitats, selection favors stable and strong structures capable of supporting body weight. Rothier et al. (2024) explained that diversity in forelimb morphology is strongly associated with locomotor environments, allowing bone variation to be interpreted as evidence of habitat adaptation.

Comparisons between arboreal and terrestrial mammals demonstrated that both groups developed distinct evolutionary strategies despite utilizing forelimbs as primary locomotor organs. Arboreal mammals prioritize mobility within vertical spaces, whereas terrestrial mammals prioritize locomotor efficiency on horizontal surfaces. Parsi-Pour et al. (2020) explained that mammalian locomotor behavior is associated with the length, diameter, and proportions of limb bones. These findings indicate that forelimb variation among Indonesian mammals constitutes part of broader ecological adaptation processes. The novelty of these findings lies in emphasizing that habitat specialization among Indonesian mammals should be understood through the relationship between skeletal structures and tropical ecosystem dynamics. Many previous studies discussed mammalian locomotion generally but did not position Indonesian mammals as the primary ecological context. This research integrates evidence from multiple scientific articles to demonstrate that tropical forests, forest canopies, forest floors, and open habitats impose different adaptive pressures on forelimb structures. Consequently, these findings enrich comparative anatomical studies based on tropical ecology.

Comparative Functional Morphology Among Mammalian Taxa

The synthesis results revealed that forelimb differences occur not only between arboreal and terrestrial groups but also among mammalian taxa. Arboreal primates tend to exhibit adaptations involving joint flexibility, elongated phalanges, and grasping capability. Arboreal carnivores demonstrate combinations of claw strength and forelimb mobility, whereas terrestrial ungulates display stronger and more stable skeletal structures. These findings indicate that each mammalian group possesses distinct morphological strategies based on the interaction between evolutionary history and ecological demands.

Among primates, forelimbs play essential roles in climbing, reaching, and maintaining balance on branches. Humerus and radius structures are frequently associated with arm rotation ability and hand movement coordination. Fabre et al. (2019) demonstrated that humeral and radial morphology in primates is closely related to grasping behavior, particularly in feeding activities and object manipulation. Although the study did not specifically focus on Indonesia, the concept remains highly relevant for understanding adaptation patterns among arboreal primates inhabiting tropical environments.

Among carnivores, particularly species displaying climbing or semi-arboreal behavior, forelimbs exhibit combinations of strength and flexibility. Skeletal structures strong enough to support body weight are accompanied by flexible articulations necessary for climbing, grasping, and moving among substrates. Research involving musteloid carnivorans demonstrated that grasping capability is associated with forelimb morphology and arboreal tendencies. Therefore, carnivorous mammals exhibit adaptive patterns distinct from primates while still demonstrating strong relationships between morphology and habitat.

Within terrestrial groups such as ungulates, forelimbs function primarily as body-support structures and locomotor propulsion systems. Stronger long bones, more stable articulations, and reduced flexibility constitute important characteristics supporting linear movement. Etienne et al. (2021) demonstrated that body mass and habitat strongly influence long bone morphology in bovids, indicating that larger species inhabiting open habitats tend to possess stronger skeletal adaptations. These patterns help explain why Indonesian terrestrial mammals exhibit more compact forelimb structures.

Comparisons among taxa demonstrated that not all arboreal mammals possess identical forelimb morphology. Primates tend to develop highly complex grasping abilities, whereas arboreal carnivores rely more heavily on combinations of claws, muscular strength, and articulation flexibility. Conversely, terrestrial mammals such as ungulates prioritize stability and locomotor efficiency rather than rotational capability. These findings suggest that arboreal and terrestrial categories must be interpreted carefully because each taxon possesses distinct evolutionary constraints and adaptive strategies.

The findings are also connected with evolutionary constraint theory, which explains that morphological variation is influenced not only by habitat but also by phylogenetic inheritance within each lineage. Consequently, two arboreal species may not necessarily exhibit identical forelimb structures because they originate from different evolutionary backgrounds. Rothier et al. (2023) explained that mammalian forelimb evolution is influenced by varying rates of change in proximal and distal skeletal segments. This interpretation supports the conclusion that forelimb adaptation results from interactions among function, habitat, and evolutionary history.

The novelty of this theme lies in emphasizing that forelimb osteological analysis in Indonesian mammals cannot be conducted solely by categorizing species into arboreal and terrestrial groups. More detailed interpretation based on taxonomic classification, locomotor behavior, and anatomical function is required. This study contributes by constructing broader comparative understanding across mammalian groups rather than simply comparing two habitat categories. Such synthesis strengthens the theoretical foundation of comparative anatomy and functional morphology in tropical mammals.

Conservation Implications and Future Anatomical Research in Indonesian Mammals

The review results demonstrated that forelimb osteological studies possess important implications for Indonesian mammalian conservation. Forelimb structures can provide information regarding locomotor capability, habitat dependency, and species vulnerability toward environmental change. Arboreal mammals highly dependent on forest canopies tend to be more vulnerable to habitat fragmentation because their locomotor systems require vegetation connectivity. Therefore, understanding functional anatomy can support conservation strategies based more directly on species biological characteristics.

Analysis of the reviewed studies revealed that fragmented habitats may reduce the effectiveness of forelimb adaptation among arboreal mammals. Although certain species possess skeletal structures supporting climbing activity, the loss of canopy connectivity can restrict locomotor space. Saers et al. (2023) demonstrated that bone structures may change according to locomotor activity patterns and mechanical loading, indicating that habitat alteration may influence skeletal function over time. These findings suggest that habitat conservation should consider species locomotor requirements rather than merely protected area size.

Among terrestrial mammals, habitat alteration may also influence forelimb usage patterns and biomechanical pressure. Habitat fragmentation can force animals to travel greater distances in search of food, shelter, or protection from human disturbance. Such conditions may increase mechanical loading on bones and articulations, particularly among species inhabiting open or disturbed landscapes. Janis et al. (2020) emphasized that postcranial elements can function as important indicators for reconstructing locomotor patterns and habitat utilization, suggesting that osteological studies can assist in understanding species responses to environmental change.

These findings are associated with functional conservation theory, which explains that anatomical characteristics may be used to evaluate species adaptive capability in response to ecosystem alteration. Species possessing highly specialized locomotor requirements tend to be more sensitive to habitat degradation than species with more flexible locomotor systems. Püschel et al. (2022) explained that anatomical and biomechanical information can assist in understanding the functional limitations of species within changing environmental contexts. Consequently, the present findings strengthen the importance of conservation approaches based on biological function.

Comparisons between arboreal and terrestrial mammals demonstrated that both groups face different ecological risks. Arboreal mammals are more threatened by the loss of vertical forest structure, whereas terrestrial mammals are more affected by fragmentation of movement corridors and substrate alteration. Arboreal mammals require canopy connectivity to maintain natural locomotor patterns, while terrestrial mammals require habitat corridors enabling safe ground movement. These differences indicate that conservation strategies should be adjusted according to locomotor characteristics and osteological structure within each mammalian group.

The novelty of these findings lies in positioning forelimb osteology as a supporting foundation for Indonesian mammalian conservation studies. Conservation research has traditionally focused more heavily on population size, species distribution, and habitat threats, whereas functional anatomical aspects have rarely been incorporated as primary considerations. This study demonstrates that forelimb information can assist in understanding how species move, survive, and respond to habitat alteration. Therefore, osteological studies possess not only theoretical value but also practical importance for tropical biodiversity conservation.

Overall, the results and discussion demonstrate that differences in forelimb osteology between arboreal and terrestrial mammals in Indonesia reflect close relationships among structure, function, habitat, and ecological pressure. Arboreal mammals exhibit adaptations involving flexibility, grasping capability, and vertical mobility, whereas terrestrial mammals exhibit adaptations involving strength, stability, and efficient horizontal locomotion. The major novelty of this research lies in its systematic synthesis integrating comparative anatomy, functional morphology, biomechanics, and conservation within a unified analytical framework. Consequently, this study provides an important scientific foundation for future Indonesian mammalian anatomical research and biologically informed conservation strategies.

CONCLUSIONS AND RECOMMENDATIONS

This study concludes that forelimb osteological morphology in Indonesian mammals distinctly reflects ecological adaptation and locomotor specialization, with arboreal species exhibiting elongated bones, greater joint flexibility, and enhanced phalangeal development for climbing and grasping, whereas terrestrial mammals show compact and robust skeletal structures for stability and weight-bearing locomotion. The findings provide a comparative framework for understanding functional morphology and evolutionary adaptation across mammalian taxa. Limitations include reliance on literature available between 2021–2026 and the variability in methodological approaches among the reviewed studies. It is recommended that future conservation and ecological studies integrate skeletal morphology assessments to better predict species resilience and habitat requirements, as well as inform biodiversity management strategies.

FURTHER STUDY

Future research should expand primary data collection through in situ osteological measurements of Indonesian mammals, incorporate biomechanical modeling to quantify locomotor efficiency, and examine skeletal adaptation under varying degrees of habitat fragmentation to validate and extend the patterns identified in this review.

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