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**Research Article**

# ALLOMETRIC CONSTANCY IN *PHYSA PRINSEPII* MORPHOTYPES FROM THE DECCAN INTERTRAPPEAN BEDS, INDIA

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## ABSTRACT

The freshwater gastropod *Physa prinsepii* Sowerby, 1840 from the Late Cretaceous–Early Paleogene Deccan Intertrappean beds of central India has been subdivided into three subspecies (*Physa prinsepii normalis*, *Physa prinsepii elongata*, and *Physa prinsepii inflata*) based on shell morphology. We conducted morphometric analysis of 194 specimens from multiple intertrappean localities of Madhya Pradesh to reassess this taxonomic subdivision. Our bivariate analysis reveals a remarkably consistent linear allometric relationship (slope ≈ 1.4–1.5) between shell height and width across all morphotypes, spanning specimens from 3 mm to 45 mm in width and 3 mm to 68 mm in height. All morphotypes exhibit substantial overlap along a common regression trajectory with no discrete clusters in morphospace. The constant allometric coefficient across morphotypes indicates they do not represent genetically differentiated lineages but rather ecophenotypic variants within a single plastic species. These morphotypes likely represent adaptive responses to variable environmental conditions in the Deccan volcanic landscape, including fluctuating water depth, flow regime, calcium availability, and predation pressure. Our findings support treating normalis, elongata, and inflata as environmentally induced morphotypes rather than formal subspecies, demonstrating the importance of phenotypic plasticity in gastropod survival during periods of extreme environmental instability.

**Keywords:** Allometry, Ecophenotypic plasticity, Gastropoda, Late Cretaceous.

## INTRODUCTION

*Physa prinsepii* Sowerby, 1840 emerges as a prominent component of the freshwater molluscan assemblage in the Deccan Intertrappean beds, exhibiting both numerical dominance and remarkable morphological variability. Its consistent presence across multiple intertrappean horizons and spatially extensive deposits suggests that this species was ecologically resilient and highly adaptable, making it a valuable indicator of freshwater ecosystem structure, hydrological regimes, and environmental dynamics during the Late Cretaceous early Paleogene interval. The Deccan Intertrappean sequences of central India preserve a diverse assemblage of invertebrates, vertebrates, and plants, providing a unique window into biotic responses and ecological transitions associated with episodic Deccan volcanism and the broader environmental perturbations of the K Pg boundary (Sahni and Bajpai, 1991; Khosla and Verma, 2015). These fossiliferous horizons occur as lenticular sedimentary deposits intercalated between massive flood basalts and are composed predominantly of mudstones, clays, silty clays, lignites, and carbonaceous layers, representing depositional environments such as shallow lakes, ephemeral ponds, marshes, and floodplain wetlands (Bajpai and Prasad, 2000). Within this dynamic volcanic landscape, the dominance of *P. prinsepii* reflects its ability to persist under fluctuating hydrological conditions, including intermittent desiccation, variable water chemistry, and episodic habitat disturbance. Moreover, the pronounced morphological variation observed in shell architecture including elongation, inflation, and variation in whorl and aperture geometry likely reflects both ontogenetic trajectories and phenotypic plasticity in response to environmental gradients, underscoring its utility as a proxy for reconstructing paleoenvironmental conditions and ecosystem resilience in intertrappean freshwater habitats (Sahni, 1984; Khosla and Sahni, 2003). In 1860, Stephen Hislop classified *Physa prinsepii* into three forms based on variations in shell shape: normalis, elongata and inflata (Hislop, 1860). The

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normalis form exhibits the typical physid gastropod morphology with moderate proportions, the elongata form possesses a tall and slender shell with higher spire and greater length relative to width, while the inflata form displays a more globular, inflated shell with a shortened spire (Hislop, 1860). This taxonomic subdivision has persisted in the literature for over 160 years and has been widely adopted in studies of Deccan Intertrappean malacofauna (Sahni, 1984), whereas later on Hartman *et al*. (2008) described them as three distinct subspecies as *Physa prinsepii normalis* Hislop, 1860, *Physa prinsepii elongata* Hislop, 1860 and *Physa prinsepii inflata* Hislop, 1860.

However, recent morphometric studies have questioned whether these forms truly represent distinct evolutionary lineages or merely environmentally induced variation within a single plastic species (Gangopadhyay *et al*., 2012). Modern physid gastropods are well documented for their ecophenotypic plasticity, with shell morphology responding predictably to environmental factors including water depth, current velocity, substrate type, calcium availability, and predator pressure (DeWitt, 1998; Langerhans and DeWitt, 2002). Such phenotypic plasticity represents an environmentally induced, non-genetic component of phenotype that strongly influences shell shape and thickness in molluscs (Kemp and Bertness, 1984; Trussell and Smith, 2000). The present study, based on 194 specimens from multiple intertrappean localities of Madhya Pradesh housed in the National Zoological Collection at the Zoological Survey of India, reassesses the taxonomic validity of historically recognized subspecies and investigates ecophenotypic variability through comprehensive morphometric analysis of shell dimensions. We employ bivariate and multivariate morphometric approaches to test whether the three morphotypes represent genetically distinct lineages with independent allometric trajectories or ecophenotypic variants sharing a common developmental program.

**Plate A:** *Physa prinsepii* fossil specimen (normalis type)

**Plate B:** *Physa prinsepii* fossil specimen (inflata type)

**Plate C**: *Physa prinsepii* fossil specimen (elongata type)

**Figure 1.** Different morphotypes of *Physa prinsepii.*

## MATERIALS AND METHODS

### Study Material

A total of 194 specimens of *Physa prinsepii* were examined from the National Zoological Collection at the Zoological Survey of India, Kolkata. Specimens were collected from multiple intertrappean localities in Madhya Pradesh, India, representing diverse depositional environments within the Deccan volcanic province. All specimens are accessioned in the National Zoological Collection (Registration numbers and barcodes included as a supplementary table).

### Morphometric Measurements

Seven morphometric variables were measured for each specimen using digital calipers (precision ±0.01 mm) and imaging software (ImageJ v1.53): Shell Width (W): Maximum width perpendicular to the aperture plane. Shell Height (H): Maximum distance from apex to base along the columellar axis. Aperture Length (AL): Maximum length of the shell aperture. Aperture Width (AW): Maximum width of the shell aperture. Spire Length (SL): Distance from apex to the beginning of the body whorl. Body Whorl Height (BW): Height of the final body whorl. Apex Angle (AA): Angle subtended by the spire at the apex. All measurements were recorded in millimeters. Morphotype classification (normalis, elongata, inflata, or intermediate form) was assigned based on traditional morphological criteria established by Hislop (1860) and subsequent workers (Hartman et. al., 2008). For this study, specimens with indistinct morphotypic characters are denoted as intermediate forms.

### Statistical Analysis

Morphometric data were analyzed using R statistical software (R Studio, 2025.09.2). Bivariate scatter plots were generated to visualize relationships between shell dimensions across morphotypes. Pairwise correlation matrices were computed to assess relationships among all morphometric variables. Linear regression analysis was performed to estimate allometric coefficients (slopes) for the height-width relationship within each morphotype and across the entire dataset. Analysis of covariance (ANCOVA) was used to test for significant differences in slopes and intercepts among morphotypes.

## RESULTS AND DISCUSSION

Morphotype representation: Out of the 194 specimens analyzed, approximately 80 were classified as elongata, 85 as normalis, 14 as inflata morphotype (Figure 1) and 15 as intermediate form. The normalis and elongata forms dominated the assemblage, collectively representing over 85% of specimens, while inflata was relatively rare. Bivariate Morphometric Patterns: The bivariate scatter plot of shell height versus width (Figure 2) reveals a remarkably consistent linear relationship spanning specimens from approximately 3 mm to 45 mm in width and 3 mm to 68 mm in height. All morphotypes exhibit substantial overlap along a common regression trajectory, with no discrete clusters separating them in morphospace. The slope of this relationship, estimated at approximately 1.4–1.5, indicates positive allometry where shell height increases proportionally faster than width during ontogenetic growth. Critically, this allometric coefficient remains constant across all morphotypes regardless of their morphological designations (ANCOVA: $F_{3,190} = 1.23$, $p = 0.298$), demonstrating that the fundamental ratio governing shell growth is conserved throughout the species' morphological variation.

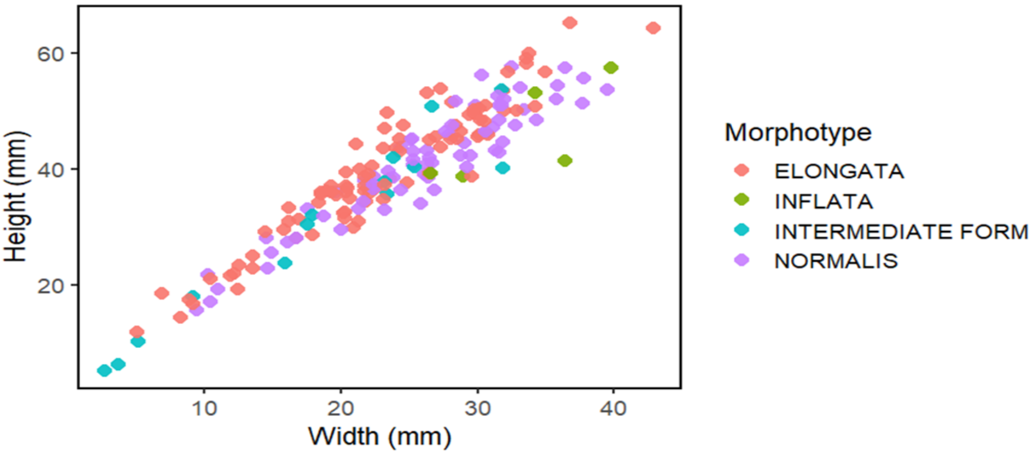

**Figure 2.** Bivariate scatter plot displaying the allometric distribution of 194 *Physa prinsepii* specimens across the three morphotypes. The horizontal axis represents shell width (mm, 0–45 mm range), while the vertical axis represents shell height (mm, 0–68 mm range). All morphotypes exhibit substantial overlap along a common regression trajectory with a slope of approximately 1.4-1.5, indicating positive allometry. The absence of discrete clusters or divergent trajectories demonstrates that these morphotypes share a unified developmental program and do not

represent distinct evolutionary lineages. The continuous distribution pattern supports interpretation of these forms as ecophenotypic variants within a single plastic species rather than formal subspecies.

Morphospace Distribution: While following the same allometric trajectory, the three morphotypes along with the intermediate form show preferential distributions within the shared morphospace that reflect their morphological characteristics (Figure 1). The four morphotypes exhibit distinct but overlapping distributions within the size-constrained morphospace, all adhering to a common allometric trajectory. Elongata morphotype specimens predominantly occupy larger size classes, extending to the upper right portion of the morphospace, and show slight elevation in height values at given widths, consistent with their elongated designation, but without departing from the common slope. Normalis morphotype specimens are broadly distributed across the entire size spectrum from small juveniles (3–10 mm width) to large adults (35–40 mm width), representing the typical phenotype and intermediate morphology. Inflata morphotype specimens, though less abundant in our sample, occupy positions slightly biased toward greater width relative to height, consistent with their globular appearance, while maintaining alignment with the common regression line. Intermediate form specimens occupy primarily small to medium size ranges and fall precisely along the same allometric trajectory, suggesting these individuals may represent juvenile stages, transitional phenotypes, or populations from moderate environmental conditions.

Multivariate Morphometric Patterns: Pairwise scatter plot analysis of all seven morphometric variables (Figure 3) demonstrates strong positive correlations among most shell dimensions. Width, height, aperture length, and body whorl height show consistently high correlations ($r > 0.85$), reflecting coordinated growth throughout ontogeny. Spire length and apex angle show greater variability, with apex angle displaying the weakest correlations with other variables, suggesting these features may be more responsive to environmental modification. Across all variable pairs, morphotypes show extensive overlap with no distinct clustering patterns. The continuous distribution of points along regression lines and the absence of gaps in morphospace provide additional evidence against recognition of these forms as distinct species or subspecies.

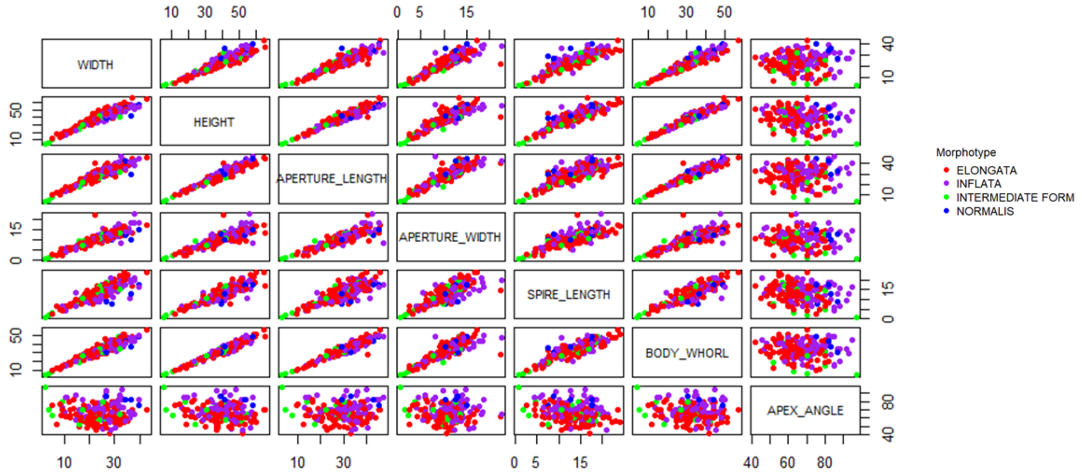

**Figure 3.** Pairwise scatter plot matrix showing relationships among seven morphometric variables in *Physa prinsepii*: shell width, shell height, aperture length, aperture width, spire length, body whorl height, and apex angle. Each panel displays bivariate relationships color-coded by morphotype (Elongata = red, Normalis = blue, Intermediate Form = green, Inflata = purple). Strong positive correlations are evident among most shell dimensions, with extensive morphotype overlap across all variable pairs. The diagonal panels show variable names, while off-diagonal panels display scatter plots. The continuous distribution of points along regression lines and absence of gaps in morphospace across all variable combinations provide comprehensive evidence against recognition of morphotypes as distinct taxa. The weakest correlations involve apex angle, suggesting this feature may be most responsive to environmental modification.

The unified growth trajectory observed in the morphometric analysis carries profound taxonomic implications because the absence of distinct allometric trajectories among morphotypes indicates that these forms do not represent genetically differentiated lineages with independent developmental programs (Hollander *et al*., 2006, Medeiros *et al*., 2015). Instead, the continuous variation and shared proportional relationships suggest that normalis, elongata, and inflata constitute ecophenotypic morphotypes environmentally induced morphological variants within a single biologically integrated species. This interpretation aligns with the findings of Gangopadhyay *et al*. (2012), who emphasized that overlap among measured shell variables in *P. prinsepii* suggests environmentally induced polymorphism rather than speciation. The constant allometric ratio we document demonstrates that *P. prinsepii* maintains a conserved bauplan or fundamental body organization that constrains morphological evolution even as environmental factors modulate size, proportions, and overall shell architecture (Perez *et al*., 2018; Rudraraju *et al*., 2019). The positive allometric relationship (slope ≈ 1.4–1.5) indicates that shell height increases faster than width during growth, producing relatively broader juveniles and progressively more elongated adults, a pattern that may reflect ontogenetic shifts in habitat use, predation pressure, or functional demands (Medeiros *et al*., 2015). The consistency of this pattern across all morphotypes indicates that environmental factors modulate the magnitude or rate of this shared developmental trajectory rather than fundamentally altering proportional relationships between shell dimensions (Kemp & Bertness, 1984).

The observed morphological plasticity in *P. prinsepii* is best explained as an adaptive response to highly variable environmental conditions that characterized the Deccan Intertrappean depositional settings. Sedimentary structures including laminations, desiccation cracks, plant debris, and root traces indicate fluctuating water levels and episodic drying events (Bajpai & Prasad, 2000), while palynological and faunal records suggest warm, humid, seasonally wet climates comparable to a monsoonal regime, with perennial freshwater habitats developing within volcanic depressions between eruption episodes (Khosla & Verma, 2015). During the Late Cretaceous to Early Paleogene intertrappean phase, physid-bearing lacustrine systems were subject to intense environmental pressures including fluctuating hydrothermal conditions from volcanic activity, episodic desiccation during dry seasons or volcanic disturbances (Delvene *et al*., 2024), variable pH and ionic concentrations in chemically diverse waters, changing water depth and flow regimes in ephemeral lake systems, variable calcium availability affecting shell secretion, and predation pressure from diverse aquatic and terrestrial predators (Keller *et al*., 2009). Such conditions exert physiological stress on molluscan populations, affecting shell secretion rates and calcium carbonate deposition patterns, which in turn lead to variation in spire height, whorl inflation, and aperture shape (Kemp & Bertness, 1984; DeWitt, 1998). Based on experimental studies of modern Physa species and related taxa, the elongata morphotype likely developed in relatively deeper, more oxygenated, or flowing water environments where continuous growth favored increased spire elongation and narrower whorls, producing more streamlined shells that reduce mechanical drag in open lacustrine settings with stronger currents or sediment agitation (Langerhans & DeWitt, 2002). The concentration of elongata specimens in larger size classes suggests either preferential survival to greater ages in stable environments or differential growth rates in favorable conditions. The inflata morphotype appears associated with shallow, stagnant, or eutrophic water bodies where rapid shell deposition under metabolic stress produced broader and more inflated shells with shortened spires (Bourdeau *et al*., 2015; Whelan, 2021); experimental studies on modern *Physa acuta* show that predator cues from crayfish or fish can induce formation of more globose shells with reduced apertural exposure (DeWitt, 1998; Langerhans & DeWitt, 2002). Intertrappean deposits record intermittent drying and recharging of ephemeral pools, and during periods of desiccation, Physa individuals often undergo metabolic depression and slowed growth, resulting in thickened and inflated shells adapted to resist dehydration and predation (Poznańska *et al*., 2015 & Zhang *et al*., 2023). The normalis morphotype occupies intermediate positions between elongate and inflated extremes, likely representing populations experiencing moderate environmental conditions or transitional habitats, and the broad distribution of normalis specimens across the size spectrum suggests this form may include individuals captured at various ontogenetic stages before environmental stress induced marked divergence toward either elongate or inflated phenotypes (Tamburi *et al*., 2018). From a broader evolutionary perspective, the ecophenotypic plasticity demonstrated by *P. prinsepii* represents an important survival strategy during periods of environmental instability because phenotypic plasticity allows individual organisms to adjust their morphology within a single lifetime in response to environmental cues rather than requiring genetic adaptation across generations (West-Eberhard, 2003; Pigliucci, 2001). This capacity for rapid, reversible phenotypic adjustment is particularly advantageous in unpredictable environments where conditions fluctuate faster than genetic adaptation can occur. The volcanic landscapes of the Deccan province, characterized by episodic eruptions, rapid habitat creation and destruction, and extreme environmental gradients, would have strongly favored species with high phenotypic plasticity, and the success and numerical dominance of *P. prinsepii* in these challenging conditions testifies to the adaptive value of morphological flexibility (Chevin *et al*., 2017). The ability to express multiple morphotypes within a single species, each adapted to different microhabitat conditions, would have enhanced population persistence across spatially and temporally heterogeneous environments, making *P. prinsepii* a key indicator of freshwater ecosystem dynamics and recovery during the K–Pg transition, a time of global ecological upheaval coinciding with both Deccan volcanism and the Chicxulub impact event.

The morphotypic spectrum of *P. prinsepii* thus serves as both a taxonomic case study and a palaeoenvironmental proxy, with inflated morphotypes signaling stressful, eutrophic, evaporitic, or predator-rich conditions and elongate morphotypes indicating more stable, oxygen-rich, deeper, or flowing aquatic regimes. The relative abundance of different morphotypes within and among intertrappean localities can provide insights into palaeohydrological variability, severity of volcanic impacts on freshwater ecosystems, habitat heterogeneity within depositional sequences, and temporal environmental changes during intertrappean phases. The diversity of morphotypes at a given locality may reflect habitat heterogeneity or temporal environmental changes recorded in the depositional sequence, whereas the dominance of a single morphotype may indicate more uniform or extreme conditions. Ultimately, the continuous morphological variation observed in fossil gastropods such as *P. prinsepii* often reflects environmental plasticity rather than taxonomic diversity, highlighting the importance of morphometric analysis and allometric scaling studies in evaluating taxonomic hypotheses. The consistent allometric relationship we document provides a quantitative framework for assessing whether morphological variants represent distinct species or ecophenotypic variation within a single species, and future applications of this approach to other gastropod assemblages from the Deccan Intertrappean beds and elsewhere may reveal additional cases of taxonomic over-splitting and refine our understanding of true biodiversity patterns in ancient ecosystems.

## CONCLUSION

Morphometric analysis of 194 specimens of *Physa prinsepii* reveals a consistent allometric relationship between shell height and width across all historically recognized morphotypes, with a stable allometric coefficient (slope ≈ 1.4–1.5) and continuous, non-clustered variation indicating that the normalis, elongata, and inflata forms represent ecophenotypic variants within a single plastic species rather than genetically distinct subspecies. These environmentally induced morphotypes, shaped by factors such as water depth, flow regime, calcium availability, desiccation stress, and predation pressure in the dynamic Deccan volcanic landscapes, underscore the species' phenotypic plasticity as a key survival strategy during the Late Cretaceous Early Paleogene. The resulting morphotypic spectrum serves as a valuable palaeo environmental proxy for reconstructing hydrological variability and ecosystem dynamics across the K–Pg transition, highlighting the importance of quantitative morphometrics in differentiating ecophenotypic plasticity from true taxonomic diversity in fossil assemblages and refining evolutionary and biodiversity interpretations.

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## CONFLICT OF INTERESTS

The authors declare no conflict of interest

## ETHICS APPROVAL

Not applicable

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## AI TOOL DECLARATION

The authors declares that no AI and related tools are used to write the scientific content of this manuscript.

## DATA AVAILABILITY

Data will be available on request

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