

COMPARATIVE ANATOMICAL ADAPTATIONS IN FLOATING, EMERGENT AND SUBMERGED AQUATIC PLANTS

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Abstract:

Aquatic plants (hydrophytes) have evolved highly specialised anatomical adaptations enabling survival across distinct ecological niches. This study presents a comparative anatomical investigation of six species from Gujarat, India (December 2025–March 2026): floating (*Eichhornia crassipes*, *Pistia stratiotes*), emergent (*Nelumbo nucifera*, *Typha latifolia*), and submerged (*Hydrilla verticillata*, *Marsilea quadrifolia*). Freehand transverse sections of roots, stems, and leaves were stained with safranin and fast green and observed under a compound microscope. Results demonstrate that aerenchyma development, vascular reduction, and epidermal modifications correlate directly with the degree of aquatic immersion. Floating plants exhibit extensive aerenchyma and epistomatic leaves; emergent plants show intermediate vascular development; submerged plants display extreme tissue reduction and lack stomata.

1. INTRODUCTION

Hydrophytes are a specialized subset of vascular plants adapted to freshwater habitats, facing extreme conditions including reduced oxygen availability, diminished light penetration, and altered nutrient dynamics (Sculthorpe, 1967). They are ecologically vital, contributing to oxygen budgets, nutrient cycling, and sediment stabilization in freshwater ecosystems (Cronk & Fennessy, 2001). The aquatic environment drives convergent evolution of tissue-level modifications, aerenchyma development, vascular reduction, and epidermal restructuring across phylogenetically unrelated taxa (Barrett, 2013).

Hydrophytes are broadly classified into three functional groups: (1) floating plants, whose photosynthetic organs rest on or above the water surface; (2) emergent plants, rooted in submerged substrate with aerial leaves and stems; and (3) submerged plants, which complete their life cycles entirely or largely below the water surface. Each group faces distinct physiological challenges and has evolved a coherent suite of anatomical solutions.

This study addresses the comparative anatomical framework of six representative species collected from five freshwater sites in Gujarat, India, contributing to the understanding of plant environment interactions along the aquatic terrestrial gradient.

1.1 Objectives

- To examine and document the anatomical organization of selected floating, emergent, and submerged aquatic plant species through microscopic analysis of transverse sections of roots, stems, and leaves.
- To compare anatomical adaptations across the three hydrophyte functional groups and identify structural modifications correlated with the ecological niche.

- To relate tissue-level specializations, aerenchyma development, vascular reduction, and epidermal modifications to the physiological demands of each aquatic habitat type.

2. MATERIALS AND METHODS

2.1 Study Area and Field Collection

Field surveys and specimen collection were conducted at five freshwater sites across Gujarat, India, between December 3, 2025, and March 20, 2026. Site selection was guided by prior knowledge of hydrophyte distribution and confirmed using satellite imagery. Geotagged photographic documentation used with GPS Map Camera application.

Table 1: Plant Species, Collection Sites, and GPS Coordinates

Species	Type	Site	GPS Coordinates
<i>Eichhornia crassipes</i> (Mart.) Solms	Floating	Site-5 VNSGU Pond	21.15°N, 72.78°E
<i>Pistia stratiotes</i> L.	Floating	Site-4 VNSGU Pond	21.19°N, 72.75°E
<i>Nelumbo nucifera</i> Gaertn.	Emergent	Site-3 Vyara	21.12°N, 73.39°E
<i>Typha latifolia</i> L.	Emergent	Site-2 Panch Pipla	21.26°N, 73.45°E
<i>Hydrilla verticillata</i> (L.f.) Royle.	Submerged	Site-3 Vyara	21.12°N, 73.39°E
<i>Marsilea quadrifolia</i> L.	Submerged	Site-1 Vajharda	21.21°N, 73.45°E

Five sites surveyed across Gujarat, India, December 2025–March 2026.

2.2 Laboratory Materials and Sectioning Protocol

Anatomical sectioning utilized sharp stainless-steel razor blades, glass microscope slides, cover slips, and standard staining reagents: safranin (2–3 min) and fast green (counter-stain, few seconds). FAA (Formalin-Acetic Acid-Alcohol) served as a preservative. Observations were made under a compound light microscope at 10× and 40× objectives, with images captured via smartphone mounted on the eyepiece.

Free-hand transverse sections were cut from fresh material, washed, stained, and mounted in water. The thinnest, most uniform sections were selected. All specimens were washed with distilled water to remove sediment before processing.

2.3 Study Species

Six species were selected: Floating, *Eichhornia crassipes* (Mart.) Solms (Water Hyacinth) and *Pistia stratiotes* L. (Water Lettuce); Emergent, *Nelumbo nucifera* Gaertn. (Sacred Lotus, *Nelumbonaceae*) and *Typha latifolia* L. (Common Cattail, *Typhaceae*); Submerged, *Hydrilla verticillata* (L.f.) Royle (*Waterthyme*, *Hydrocharitaceae*) and *Marsilea quadrifolia* L. (*Water Clover*, *Marsileaceae*).

3. RESULTS

Microscopic examination of transverse sections revealed distinct anatomical profiles for each functional group, with consistent differences in aerenchyma development, vascular tissue organization, epidermal structure, and mechanical tissue presence.

3.1 Floating Plants: *Eichhornia crassipes* and *Pistia stratiotes*

3.1.1 Root Anatomy

Transverse sections of *E. crassipes* root reveal a single-layered epidermis lacking root hairs in mature regions, followed by an extensive multi-layered cortex dominated by loosely arranged parenchyma. The cortex is traversed by conspicuous aerenchyma, large, oval to irregular air-filled lacunae, occupying a substantial proportion of cortical volume, facilitating oxygen diffusion and contributing to buoyancy. Vascular bundles are scattered in monocotyledonous fashion with reduced xylem; an endodermis with Casparian strips is present but not prominently thickened. *P. stratiotes* root sections display equally extensive cortical aerenchyma with a notably distinct endodermis, star-shaped xylem arms in a radial arrangement, a small pith, and clearly defined pericycle cells.



Fig. 1: Root T.S. of *E. crassipes* – extensive aerenchyma lacunae, cortical parenchyma (CP), scattered vascular bundles (VB). | Root T.S. of *P. stratiotes* – well-defined endodermis (En), aerenchymatous cortex, star-shaped xylem (X), phloem (P), pith (Pi). Safranin–fast green stain.

3.1.2 Stem Anatomy

The stem of *E. crassipes* is stoloniferous and parenchymatous with very large aerenchyma chambers in concentric zones, often separated only by single-cell-thick partitions, maximizing air volume relative to tissue mass. Mechanical tissues are conspicuously absent or vestigial. *P. stratiotes* has a compressed rosette stem with similarly compact aerenchymatous cortex and scattered vascular bundles.

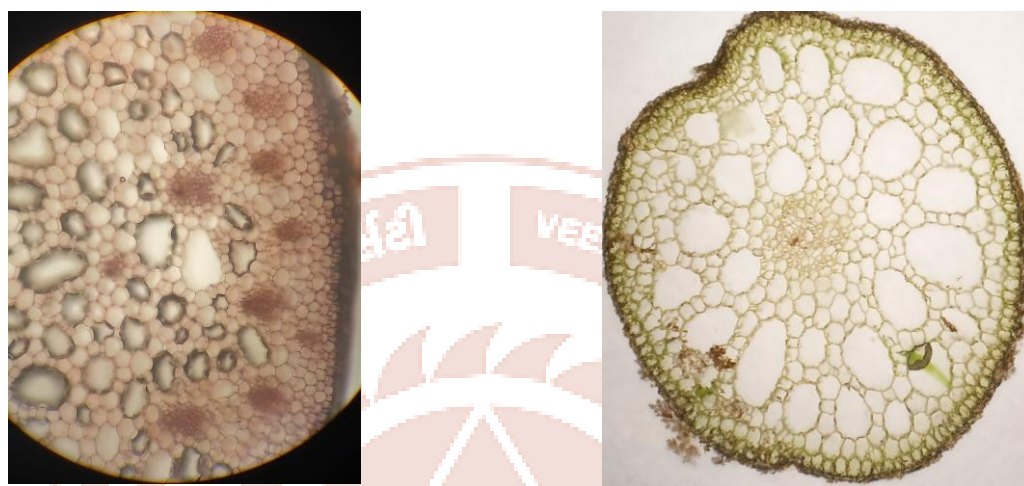


Fig. 2: Stem T.S. of *E. crassipes* – large aerenchyma chambers (Ae), thin parenchyma partitions (Pa), scattered vascular bundles (VB); no mechanical tissue. | Stem T.S. of *P. stratiotes* – regularly arranged aerenchyma lacunae (Ae), small scattered vascular bundles (VB) with minimal xylem. Safranin–fast green stain.

3.1.3 Leaf Anatomy

Leaves of *E. crassipes* bear numerous stomata on the upper epidermis (epistomatic), facilitating direct gas exchange. The mesophyll differentiates into compact palisade and loosely arranged spongy layers containing large aerenchymatous intercellular spaces. *P. stratiotes* leaves bear stellate epidermal hairs on the abaxial surface that trap air bubbles, contributing to buoyancy, with predominantly adaxial stomata and abundant chlorenchyma.



Fig. 3: Leaf T.S. of *E. crassipes* – upper epidermis (UE) with stomata (St), cuticle (Cu), palisade mesophyll (PM), aerenchyma spaces (Ae), vascular bundle (VB). | Leaf T.S. of *P. stratiotes*

– adaxial epidermis (AE) with stomata, aerenchyma-rich mesophyll (Ae), chlorenchyma (Ch), abaxial branched trichomes (Tr). Safranin–fast green stain.

3.2 Emergent Plants: *Nelumbo nucifera* and *Typha latifolia*

3.2.1 Root Anatomy

Transverse sections of *N. nucifera* root reveal a broad cortex with large oval aerenchyma spaces and notable raphide-containing idioblasts, calcium oxalate crystals serving defense and calcium storage. *T. latifolia* root sections present a distinctive spoke-like radiating aerenchyma configuration and slightly more pronounced sclerenchyma, with a clear endodermis, pericycle, and central pith.

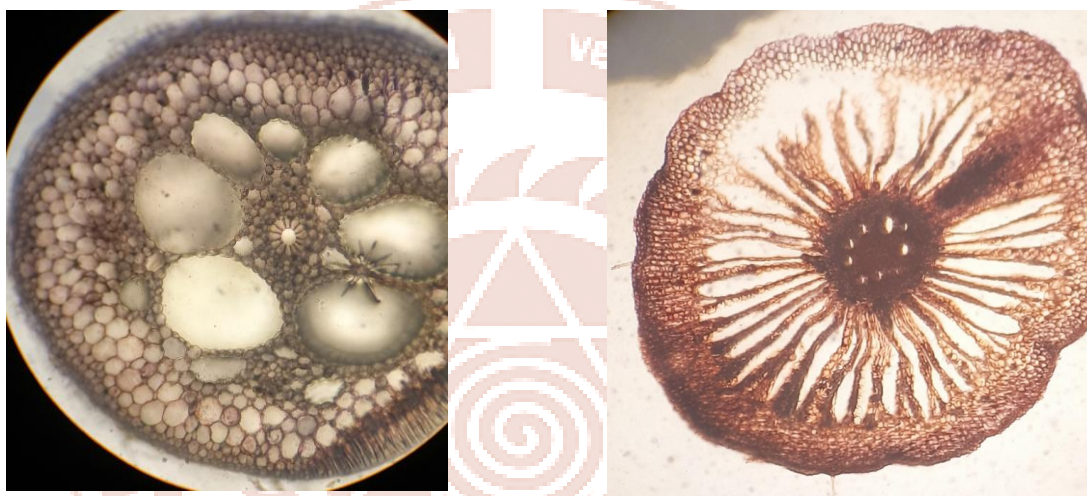


Fig. 4: Root T.S. of *N. nucifera* – large oval aerenchyma (Ae), raphide idioblasts (Ra), distinct endodermis (En), vascular cylinder (VC). | Root T.S. of *T. latifolia* – spoke-like radiating aerenchyma channels (Ae), endodermis (En), pericycle (Pc), central stele with pith (Pi). Safranin–fast green stain.

3.2.2 Rhizome/Stem Anatomy

The rhizome of *N. nucifera* shows very large macroscopically visible air chambers forming a continuous aeration network from rhizome through petiole to leaf, with raphide idioblasts in parenchymatous septa. The rhizome of *T. latifolia* is more elongated and fibrous with moderately developed cortical aerenchyma and sclerenchyma fiber strands, an intermediate characteristic between aquatic and terrestrial organization.

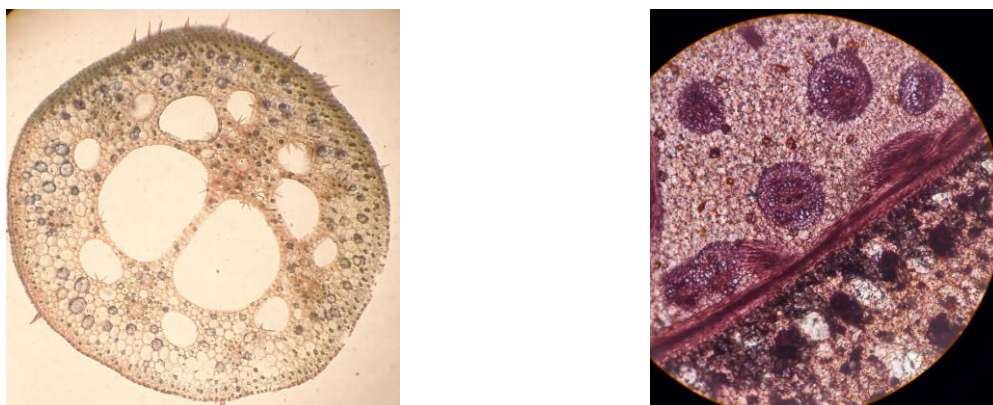


Fig. 5: Rhizome T.S. of *N. nucifera* – very large aerenchyma chambers (Ae), parenchymatous septa (PS) with raphide idioblasts (Ra), reduced vascular bundles (VB). | Stem T.S. of *T. latifolia* – cortical aerenchyma (Ae), more prominent xylem (X) in vascular bundles (VB), sclerenchyma fiber strands (Sc). Safranin–fast green stain.

3.2.3 Leaf Anatomy

Leaves of *N. nucifera* show a prominent waxy adaxial cuticle (superhydrophobic 'lotus effect'), stomata, loosely organized aerenchymatous mesophyll, raphide idioblasts, and large well-developed vascular bundles with bundle sheaths. *T. latifolia* leaves are amphistomatic (stomata on both surfaces) with more differentiated mesophyll, prominent vascular bundles, and sclerenchyma caps, the most terrestrial-like anatomy among the study species.



Fig. 6: Leaf T.S. of *N. nucifera* – adaxial epidermis (AE) with thick cuticle (Cu) and stomata (St), aerenchymatous mesophyll (Ae), raphide idioblasts (Ra), large vascular bundles (VB) with bundle sheath (BS). | Leaf T.S. of *T. latifolia* – amphistomatic epidermis, differentiated mesophyll (Me), aerenchyma (Ae), vascular bundles (VB) with sclerenchyma caps (Sc). Safranin–fast green stain.

3.3 Submerged Plants: *Hydrilla verticillata* and *Marsilea quadrifolia*

3.3.1 Root Anatomy

Roots of *H. verticillata* show a thin epidermis, narrow cortex with aerenchyma lacunae, and a greatly reduced stele with minimal xylem, consistent with their primary anchorage function. *M. quadrifolia* roots show somewhat more developed anatomy (defined endodermis, protostele-like stele) reflecting amphibious habits.



Fig. 7: Root T.S. of *H. verticillata* – thin epidermis (Ep), narrow cortex with aerenchyma (Ae), greatly reduced central stele (St) with minimal xylem. | Root T.S. of *M. quadrifolia* – cortex with moderate aerenchyma (Ae), distinct endodermis (En), protostele-like vascular cylinder (VC) with xylem (X) and phloem (P). Safranin–fast green stain.

3.3.2 Stem Anatomy

The stem of *H. verticillata* is slender with no cuticle, narrow cortex with moderate aerenchyma, and greatly reduced stele; mechanical tissue is entirely absent. Chloroplasts are present in outer cortical cells, contributing to photosynthesis through the shoot surface.

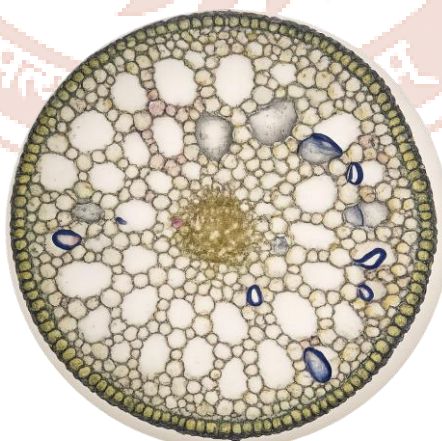


Fig. 8: Stem T.S. of *H. verticillata* – thin epidermis (Ep) without cuticle, parenchymatous cortex with aerenchyma spaces (Ae), greatly reduced central stele (St) with minimal xylem; no mechanical tissue. Safranin–fast green stain.

3.3.3 Leaf Anatomy

Leaves of *H. verticillata* entirely lack cuticle and stomata; gas exchange occurs by direct diffusion through the thin permeable surface. The mesophyll is undifferentiated with chloroplast-rich thin-walled parenchyma and a highly reduced single vascular bundle with xylem nearly absent. *M. quadrifolia* demonstrates heterophylly: aerial leaflets bear a thin cuticle and reduced stomata, whereas submerged leaflets lack cuticle and stomata entirely, a documented example of phenotypic plasticity.



Fig. 9: Leaf T.S. of *H. verticillata* – absence of cuticle and stomata; undifferentiated mesophyll (Me) of chloroplast-rich parenchyma; large intercellular spaces (IS); reduced vascular bundle (VB) with minimal xylem. | Leaflet T.S. of *M. quadrifolia* (submerged form) – absent cuticle, no stomata, undifferentiated mesophyll (Me), chloroplasts (Cl), aerenchymatous spaces (Ae), reduced vascular bundle (VB). Safranin–fast green stain.

4. COMPARATIVE ANATOMICAL ANALYSIS

The anatomical data from all six species permit systematic comparison across the three functional groups. Tables 2–3 summarize key parameters, and Figures 10 - 13 present graphical comparisons of the major adaptive features.

Table 2: Comparative Summary of Anatomical Features Across Hydrophyte Functional Groups

Feature	Floating Plants	Emergent Plants	Submerged Plants
Aerenchyma	Extensive (>60% cortex)	Moderate–extensive; continuous channels	Moderate; primarily in roots/rhizomes
Xylem Development	Poorly developed; reduced vessels	Moderately–well developed	Greatly reduced; near-vestigial
Mechanical Tissue	Greatly reduced/absent	Reduced to moderate (prominent in <i>Typha</i>)	Absent or minimal

Feature	Floating Plants	Emergent Plants	Submerged Plants
Stomata Position	Adaxial (epistomatic)	Adaxial or amphistomatic (Typha)	Absent or vestigial
Cuticle	Thin-waxy on upper surface	Present; thick and waxy in Nelumbo	Absent or vestigial
Root Development	Reduced; mainly absorptive	Well-developed; anchoring	Poorly developed; anchorage only
Stem Type	Stoloniferous / rosette	Rhizome; upright stems	Slender / creeping rhizome
Mesophyll Differentiation	Palisade + spongy present	Loosely differentiated	Undifferentiated chlorenchyma
Crystal Inclusions	Absent	Raphides in Nelumbo only	Absent
Gas Exchange Route	Stomatal (aerial)	Stomatal (aerial)	Diffusion through epidermis

Amphi. = amphistomatic; Well-dev. = well developed

Table 3: Species-Level Anatomical Feature Matrix

Species	Group	Aerenchyma	Vascular	Mech. Tissue	Stomata	Cuticle
<i>E. crassipes</i>	Floating	Extensive	Reduced	Absent	Adaxial	Waxy thin
<i>P. stratiotes</i>	Floating	Extensive	Reduced	Absent	Adaxial	Waxy thin
<i>N. nucifera</i>	Emergent	Moderate	Moderate	Moderate	Adaxial	Thick waxy
<i>T. latifolia</i>	Emergent	Moderate	Well-dev.	Prominent	Amphi.	Well-dev.
<i>H. verticillata</i>	Submerged	Moderate	Vestigial	Absent	Absent	Absent
<i>M. quadrifolia</i>	Submerged	Moderate	Reduced	Minimal	Absent*	Absent*

*In submerged leaflet form, aerial leaflets of *M. quadrifolia* show a thin cuticle and reduced stomata.

Graphical Analysis of Key Anatomical Parameters

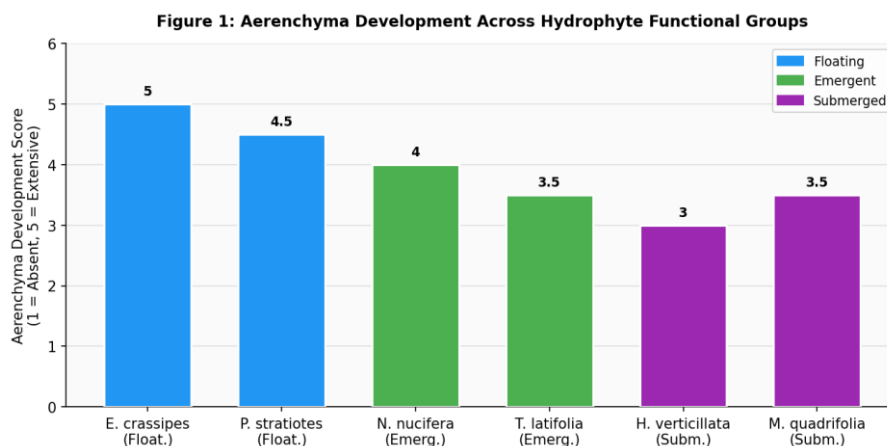


Figure 10: Aerenchyma development scores (1 = absent, 5 = extensive) across the six study species. Floating plants show the highest aerenchyma relative to cortical cross-section.

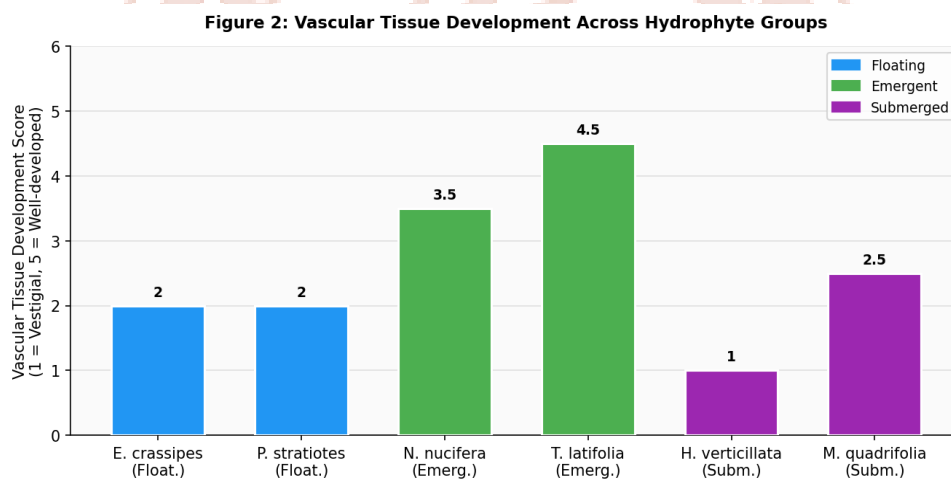


Figure 11: Vascular tissue development scores. Emergent plants, particularly *Typha latifolia*, show the most developed vascular system. *Hydrilla verticillata* shows near-vestigial xylem.

4.1 Aerenchyma: The Universal Hydrophytic Adaptation

Aerenchyma development was observed in all six species and all three organ types (root, stem, leaf), confirming its designation as the cardinal anatomical adaptation of hydrophytes. Floating plants exhibited the most expansive aerenchyma, *E. crassipes* stem sections showing air volume exceeding 60% of cortical area by estimation. Emergent plants showed moderate aerenchyma concentrated in rhizomes and petioles, forming a continuous aeration channel from soil-embedded roots to aerial leaves. Submerged plants showed aerenchyma primarily in roots and rhizomes for oxygen supply to tissues in anaerobic sediment. Geometric patterns also differed: concentric lacunae in floating species, large oval chambers in *N. nucifera*, spoke-like radiating patterns in *T. latifolia*, and smaller intercellular spaces in submerged species.

4.2 Vascular and Mechanical Tissue Gradient

A gradient of vascular tissue complexity was evident across the three groups. Emergent plants, particularly *T. latifolia*, showed the most developed vascular system, consistent with the demand for efficient water and nutrient transport to tall aerial shoots. Floating plants exhibited significantly reduced xylem, reflecting the abundance of water surrounding tissues. Submerged plants showed the greatest xylem reduction, approaching vestigiality in *H. verticillata*. Collenchyma and sclerenchyma were well represented only in *T. latifolia*; floating and submerged species showed negligible mechanical tissue, consistent with the physical support provided by water buoyancy.

4.3 Epidermal Modifications

Epidermal organization proved highly diagnostic of the functional group. Floating and emergent species with aerial leaf surfaces uniformly showed stomata concentrated on the upper epidermis and possessed varying degrees of cuticle development. In contrast, submerged species showed complete absence of stomata and cuticle, with gas exchange occurring entirely by diffusion through the permeable epidermis. This transition from epistomatic, cuticularized epidermis to permeable, unspecialized epidermis represents the clearest anatomical signature of submergence adaptation.

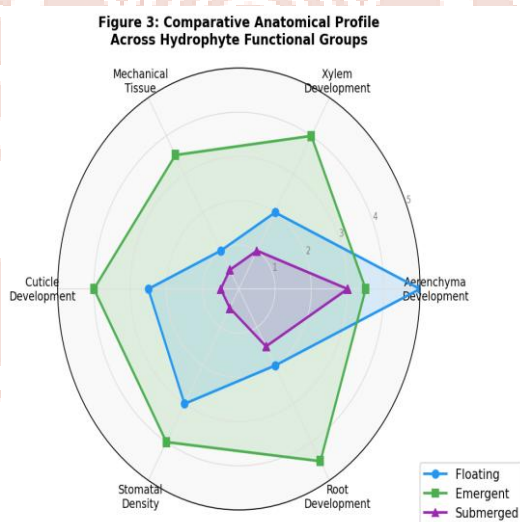


Figure 12: Radar diagram comparing anatomical profiles across the three hydrophyte functional groups. Emergent plants (green) show highest structural investment; submerged plants (purple) exhibit the most extreme anatomical reductions.

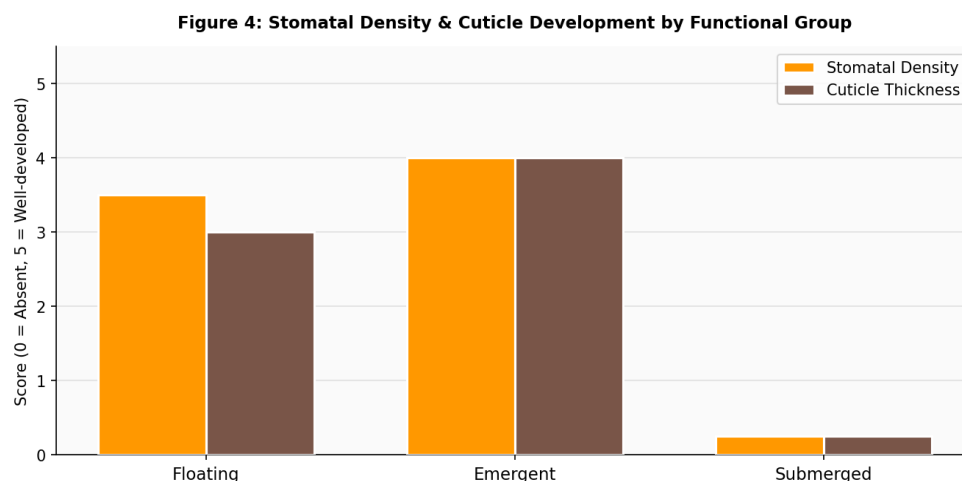


Figure 4.4: Stomatal density and cuticle development scores by functional group (0 = absent, 5 = well-developed). Both features are essentially absent in submerged plants, confirming complete reliance on diffusive gas exchange.

5. DISCUSSION

The findings of this study corroborate and extend the comparative anatomical framework established by classical and contemporary research in aquatic plant biology. The three hydrophyte functional groups represent a spectrum of structural adaptation to increasing degrees of aquatic immersion, each exhibiting a coherent suite of anatomical features optimized for its ecological niche.

The primacy of aerenchyma across all groups confirms Sculthorpe's (1967) designation of this tissue as the defining adaptation of hydrophytes. Armstrong's (2020) mechanistic emphasis on internal aeration as the key physiological challenge in waterlogged environments finds clear anatomical correlates in the present data, the continuous aerenchyma systems connecting aerial and submerged organs in both floating and emergent species constitute literal air pipelines maintaining aerobic respiration in anaerobic sediment. These findings align with Colmer's (2009) documentation of analogous aeration mechanisms in *Oryza sativa*, supporting the view that aerenchyma represents a broadly conserved solution to submerged root respiration.

The phenomenon of convergent vascular and mechanical tissue reduction across phylogenetically distant taxa, Nelumbonaceae, Typhaceae, Hydrocharitaceae, and Marsileaceae, supports Barrett's (2013) argument for convergent evolution driven by shared environmental constraints rather than shared ancestry. The gradient from *T. latifolia* (most terrestrial-like) through *N. nucifera* and floating species to *H. verticillata* (most aquatically specialized) mirrors predictions from ecological theory regarding costs and benefits of structural investment across water regimes. Crawford (2008) similarly argued that mechanical

tissue is metabolically costly and superfluous when water provides physical support, a principle clearly borne out by the near-complete absence of sclerenchyma in *H. verticillata* and the floating species.

Epidermal modifications demonstrate equally clear ecological differentiation. The complete loss of stomata and cuticle in fully submerged *H. verticillata* confirms Sand-Jensen's (2015) and Maberly's (2014) documentation of diffusion-based gas exchange in submerged macrophytes. The superhydrophobic epicuticular wax of *N. nucifera* leaves, the 'lotus effect', represents an advanced epidermal specialisation that prevents waterlogging of stomata, as documented by Wang et al. (2021). The epistomatic condition of floating-plant leaves reflects their stable interface with the atmosphere, consistent with findings by González-Méndez et al. (2021) on buoyancy and gas exchange adaptations in *E. crassipes* and *P. stratiotes*.

The presence of calcium oxalate raphides in *N. nucifera* tissues, absent in all other study species, illustrates that anatomical diversification operates at multiple scales simultaneously. Alharthi et al. (2024) and Singh (2022) similarly noted the multi-functional significance of these crystals in *Nelumbo*, encompassing anti-herbivory defense, calcium storage, and potential roles in cellular pH regulation.

Marsilea quadrifolia's heterophylly, producing anatomically distinct aerial and submerged leaflets, represents an extreme case of phenotypic plasticity within a single individual, as documented by Koga et al. (2024) and Mommer et al. (2005). This developmental flexibility allows the plant to exploit both aquatic and semi-terrestrial niches simultaneously.

In the context of contemporary environmental change, the adaptive plasticity documented by Yuan et al. (2024) and Sharma (2025), increased aerenchyma formation under stress, modified cortex thickness under pollution, suggests that the anatomical features documented here are not static endpoints but dynamic responses within a broader plasticity envelope. This has implications for predicting hydrophyte community responses to climate change, eutrophication, and pollution in the freshwater ecosystems of Gujarat and beyond. Cheng et al. (2025) further demonstrated that aerenchyma formation pathways in aquatic macrophytes are environmentally modulated, suggesting considerable scope for anatomical adjustment within individual plants.

6. CONCLUSION

This comparative anatomical study of six aquatic plant species across three functional groups demonstrates clear and systematic relationships between internal tissue organization and ecological positioning along the aquatic–terrestrial gradient.

Aerenchyma development emerged as the universal, cross-group adaptive feature, varying in extent, geometry, and distribution in accordance with the oxygen demands and buoyancy requirements of each ecological position. Vascular and mechanical tissue investment decreased progressively from emergent to floating to submerged species, reflecting reduced functional requirements in increasingly water-supported environments. Epidermal modifications, stomatal position, cuticle development, and surface permeability provided the most diagnostically clear indicators of functional group.

Species-specific features, raphide idioblasts in *Nelumbo*, amphistomatic leaves in *Typha*, and heterophyllous plasticity in *Marsilea*, illustrate that shared functional challenges are solved through both convergent and individually distinct anatomical strategies. These findings establish an anatomically coherent framework for understanding hydrophyte adaptation. Future work incorporating quantitative image analysis onto genetic sectioning and molecular investigation of aerenchyma formation pathways would further enrich this comparative framework.

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