

Nematocyst morphology as a taxonomic tool to distinguish between *Pachyseris rugosa* and *Pachyseris speciosa*

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Abstract. Morphological similarity complicates species delimitation in *Pachyseris*, prompting the search for characters less affected by environmental plasticity. We evaluated nematocyst morphology as taxonomic tool by comparing *Pachyseris rugosa* and *P. speciosa* collected in Manado Bay, North Sulawesi, Indonesia. Coral colonies were maintained under controlled conditions and subjected to interspecific contact assays to induce discharge from mesenterial filaments. Discharged nematocysts were examined with phase-contrast microscopy, focusing on type I microbasic p-mastigophores. Despite overlap in overall nematocysts composition, statistical analyses detected significant differences ($p < 0.05$) in capsule length, capsule width, and shaft length between the two species. Because nematocyst morphology is considered more constrained genetically than skeletal features, these disparities may be comparatively robust across habitat gradients. The usefulness of nematocyst morphometry as an additional taxonomic criterion for species discrimination within the genus *Pachyseris* is supported by these findings.

Key Words: coral taxonomy, nematocyst, *Pachyseris rugosa*, *Pachyseris speciosa*, type I microbasic p-mastigophores.

Introduction. Scleractinian corals, or stony corals, display substantial variation in coloration and colony architecture, often within a single nominal species (Veron 2000; Veron et al 2016; Ghafari et al 2022). Taxonomic identification in this group has historically emphasized skeletal morphology (Veron 2000; García et al 2017; Doszpot et al 2019). Yet skeletal features including colony form and surface texture are highly plastic along environmental gradients, complicating species delimitation (Scheufen et al 2017; McWilliam et al 2018; Kramer et al 2020; Paruntu et al 2025). The wide morphological spread seen across many coral taxa frequently reflects adaptation to light, water flow, and depth (García et al 2017; Doszpot et al 2019). Although genetic background shapes morphology, local environmental interactions often generate phenotypic variability among populations that are genetically similar or even identical (Smith et al 2017; Soto et al 2018; Paruntu et al 2025).

A hallmark of cnidarians, including stony corals, is the presence of cnidae specialized intracellular organelles termed nematocysts embedded in ectodermal tissues. These organelles can rapidly eject coiled tubules when stimulated (Paruntu et al 2000; Americus et al 2020; Yue et al 2020; Paruntu et al 2023, 2025). Nematocysts reside within nematocytes and typically comprise a capsule, shaft, and tubule, together with a fluid-filled interior (Mariscal 1974; Sachkova et al 2020; Paruntu et al 2023). More than thirty distinct nematocyst types have been described across cnidarians, with classification primarily based on the form of the discharged shaft and tubule (Mariscal 1974; Paruntu et al 2022, 2025).

Dependence on skeletal traits alone has often produced misidentifications, especially where cryptic speciation and morphological convergence blur boundaries. This issue is pronounced in visually similar scleractinian genera. Within *Pachyseris*, for example,

species such as *P. rugosa* and *P. speciosa* are frequently indistinguishable in the field, creating considerable taxonomic uncertainty (Veron et al 2016). New DNA data challenges the traditional classifications of these taxa based on colony morphology, skeletal texture, and ecological distribution (Veron 2000).

P. speciosa has multiple sympatric cryptic lineages that persist, suggesting parallel evolution or morphological stasis, according to current genomic studies (Feldman et al 2022). According to Riginos et al (2024), integrated taxonomic frameworks that incorporate ecological, morphological, and genetic information are supported, and the limits of morphology-based diagnosis are reiterated.

Nematocyst morphology analysis is one method that is becoming popular in these integrative schemes; it has shown promise in distinguishing closely related coral species (Hidaka 1992). *P. rugosa* and *P. speciosa*'s relationship is still unclear; some authors support species-level differentiation based on traits like colony ridging and septal architecture (Veron 2000), while others view these forms as ecophenotypic variations influenced by hydrodynamic exposure, light, and depth (Ditlev 2003). These differing perspectives emphasize the importance of standards that are less influenced by environmental factors.

To address the complexities of taxonomy, current advancements in coral systematics prioritize integrated methods that merge both internal and external morphology along with reproductive and genetic information (Riginos et al 2024). Nematocysts are specialized stinging organelles whose size, shape, and functional diversity vary across cnidarian taxa. These internal characteristics provide biologically and ecologically informative traits and represent a valuable, yet still underutilized, source of taxonomic information when integrated with other morphological and molecular data (Technau & Steele 2011; O'Hara et al 2021). Studies on cnidarians indicate that even when external forms converge, variations in shaft morphology and capsule sizes can consistently differ across species.

Empirical and proteomic studies demonstrate that variation in nematocyst-associated venom composition and functional proteins contributes to ecological performance and adaptive success in cnidarians, as evidenced by pronounced intra- and inter-population differences in toxicity observed in reef-building corals such as *Stylophora pistillata* (Ben-Ari et al 2018; Guo et al 2022). These trends indicate that coral skeletal morphology is highly plastic and strongly influenced by environmental conditions, nematocyst-associated traits, including venom composition, may be less environmentally variable and more closely linked to genetic differentiation (van Woesik et al 2013; Ben-Ari et al 2018).

Despite this promise, nematocysts remain underapplied in coral identification. Their use may resolve cases where traditional morphological markers are inconclusive. Accordingly, this study evaluates whether quantifiable nematocyst metrics specifically capsule length, capsule width, and shaft length can deliver reliable taxonomic distinctions between *P. rugosa* and *P. speciosa*, two taxa whose external morphologies are often indistinguishable.

Material and Method

Study site and sampling. This study was conducted from May to August 2024 in Manado Bay, North Sulawesi, Indonesia. Colonies of *P. rugosa*, *P. speciosa*, and *Acropora nobilis* were collected under appropriate permits (Veron 2000; Veron et al 2016; WoRMS 2023). Samples were transported to a controlled indoor aquarium facility supplied with continuous seawater.

Coral contact experiment. Interspecific interactions were observed during nighttime to account for the nocturnal behavior of coral aggression. *A. nobilis* fragments were placed in direct contact with either *P. rugosa* or *P. speciosa*. After three hours, mesenterial filaments were observed to adhere to the target tissue, indicating nematocyst discharge.

Nematocyst collection and microscopy. Mesenterial filaments were carefully removed using pipettes and forceps, and fixed in 10% formalin-seawater solution. Nematocysts were visualized under a phase contrast microscope at 20×, 40×, and 100× magnifications. Photomicrographs were taken for morphometric analysis.

Statistical analysis. Dimensions measured included capsule length (LC), capsule width (WC), shaft length (LS), and ratios LS/LC and WC/LC. The primary focus was on undischarged type I microbasic p-mastigophores (MpMs), due to their abundance and taxonomic relevance. A T-test was conducted using Microsoft Excel to evaluate significant differences ($p < 0.05$) in nematocyst morphometrics between species.

Results

Nematocyst types observed. Both *P. rugosa* and *P. speciosa* exhibited four nematocyst types: type I MpM, type II MpM, large holotrichous isorhizas (HI), and small HI. Among these, type I MpMs were the most abundant and consistently observable in these two species (Figure 1). The other types were found only sporadically and were excluded from the quantitative analysis due to insufficient sample sizes and challenges in identification and measurement.



Figure 1. The main type of undischarged nematocyst found in *Pachyseris rugosa* and *Pachyseris speciosa* is the type I microbasic p-mastigophore (type I MpM). Scale bar: 10 μm .

Morphometric differences in type I MpMs. Significant interspecific differences were observed in the dimensions of type I MpMs (Table 1; Figure 2). On average, nematocysts from *P. rugosa* exhibited greater LC, LS, and WC than those from *P. speciosa* ($p < 0.05$), while the LS/LC and WC/LC ratios did not differ significantly ($p > 0.05$). This indicates species-level variation in absolute dimensions, though relative shape proportions remained conserved.

Table 1
Morphometric measurements of undischarged type I microbasic p-mastigophores (type I MpMs) obtained from mesenterial filaments of *Pachyseris rugosa* and *Pachyseris speciosa*

Colonies	LC (μm)	LS (μm)	WC (μm)	LS/LC	WC/LC
<i>Pachyseris rugosa</i>					
Pr1	30.05±1.26 (15)	11.90±1.00 (15)	7.92±0.68 (15)	0.40±0.03 (15)	0.26±0.02 (15)
Pr2	34.43±1.93 (15)	11.76±0.91 (15)	8.52±0.31 (15)	0.34±0.03 (15)	0.25±0.02 (15)
Pr3	34.60±1.80 (10)	13.80±0.89 (10)	7.71±0.47 (10)	0.40±0.01 (10)	0.22±0.01 (10)
<i>Pachyseris speciosa</i>					
Ps1	25.25±1.39 (15)	9.34±1.16 (15)	6.40±0.49 (15)	0.37±0.03 (15)	0.25±0.02 (15)

Ps2	31.83±2.13 (15)	12.25±0.93 (15)	7.58±0.45 (15)	0.39±0.04 (15)	0.24±0.01 (15)
Ps3	34.35±0.46 (10)	11.91±1.03 (10)	7.30±0.46 (10)	0.35±0.03 (10)	0.21±0.01 (10)

Values in parentheses represent the number of nematocysts measured. A minimum of one mesenterial filament was analyzed per coral colony. *Pr* refers to *Pachyseris rugosa*, *Ps* to *Pachyseris speciosa*; LC = capsule length, LS = shaft length, WC = capsule width. Data are presented as mean±standard deviation.

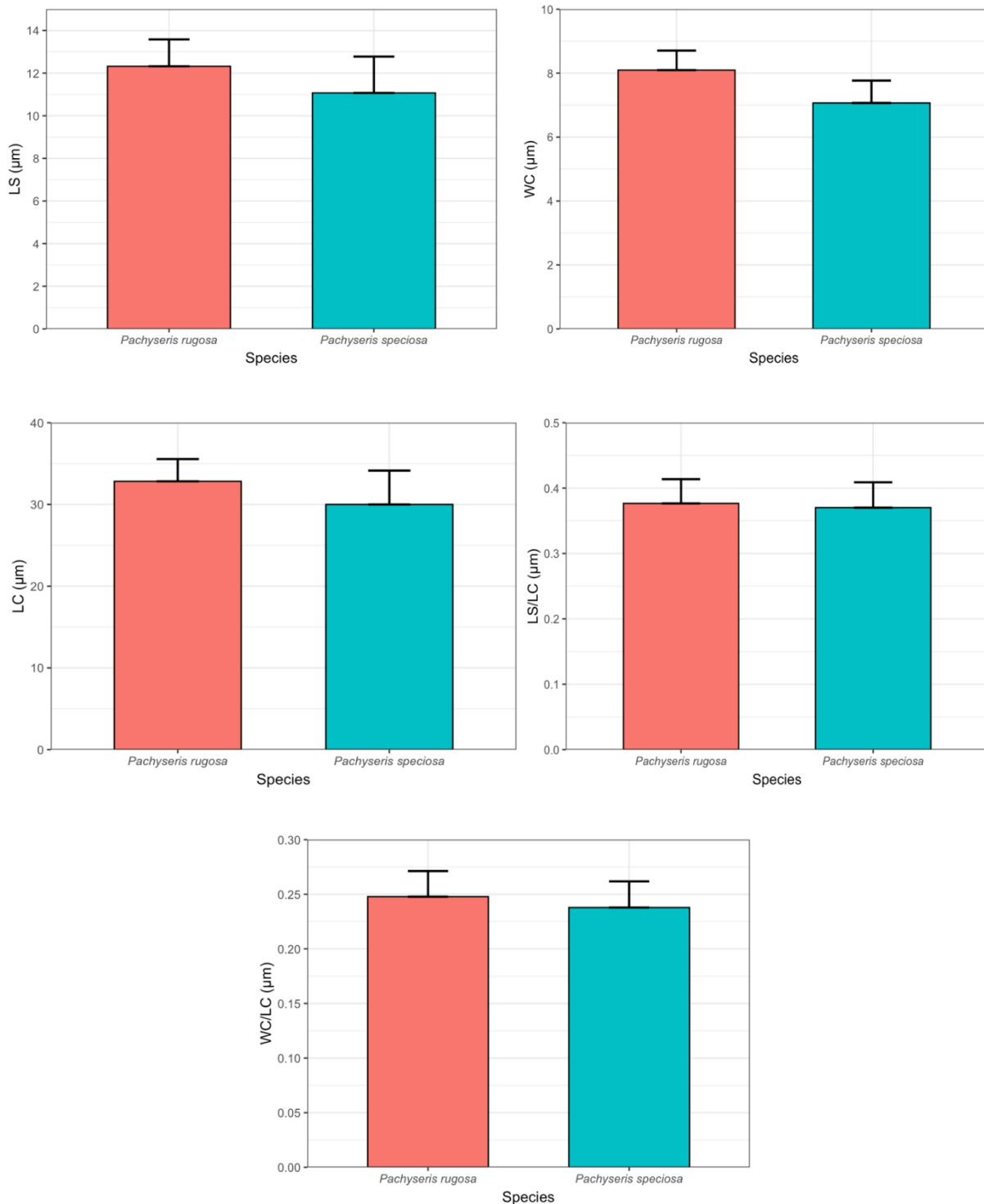


Figure 2. Comparative measurements of undischarged type I microbasic p-mastigophores (type I MpMs) from mesenterial filaments of *Pachyseris rugosa* and *Pachyseris speciosa*. LC = capsule length; LS = shaft length; WC = capsule width.

Discussion. The diagnostic utility of nematocyst morphometrics, especially measurements of type I microbasic p-mastigophores, highlights the potential of nematocyst architecture as an informative internal character for distinguishing coral species exhibiting limited skeletal disparity. This finding aligns with evolutionary and developmental frameworks that associate nematocyst structure with species-specific physiological or genetic processes (Technau & Steele 2011), and builds upon detailed morphometric descriptions of nematocyst types reported in reef-building corals (Pratama et al 2025). Although the nematocyst types of *P. rugosa* and *P. speciosa* are similar, statistically significant differences in capsule size and shaft length were found. It is likely that this divergence is due to underlying genetic evolutionary selective pressures, ecological niche partitioning, or differentiation (Nakajima et al 2016; Paruntu et al 2023).

Nematocyst development and structure are closely linked to physiological and developmental processes, nematocyst morphology may represent a biologically informative set of internal characters for species-level delimitation in scleractinian corals, potentially exhibiting greater stability than environmentally plastic skeletal traits (Technau & Steele 2011). Despite having a similar cnidom composition, *P. rugosa* and *P. speciosa* consistently differ in capsule length, capsule width, and shaft length, indicating that these patterns go beyond phenotypic plasticity and most likely indicate evolutionary divergence. These results are consistent with the taxonomic taxonomy developed by Veron (2000), which identified *P. rugosa* and *P. speciosa* as separate species according to ecological characteristics, skeletal microstructure, and colony architecture. In addition to morphological and ecological criteria, the microstructural differences in nematocyst dimensions that are shown here offer an independent line of evidence that supports their species status. The observed consistency in nematocyst morphometrics reinforces their value as internal taxonomic markers. This interpretation aligns with developmental and physiological perspectives that associate nematocyst architecture with biologically regulated processes (Technau & Steele 2011), and is further supported by species-level morphometric differentiation reported in reef-building corals (Pratama et al 2025).

Even so, the presence of all four nematocyst types in both species, coupled with the lack of significant differences in capsule-shape ratios (e.g., shaft-to-capsule length, width-to-length), lends partial credence to an alternative view. As proposed by Ditlev (2003), these taxa could represent ecophenotypic expressions molded by light regime, depth, and hydrodynamic exposure rather than discrete evolutionary lineages. If so, size differences might reflect local adaptation more than speciation. Nevertheless, the magnitude and consistency of the morphometric gaps across multiple samples argue against a purely environmental explanation and point to some heritable differentiation.

Methodologically, this study is strengthened by obtaining all measurements from undischarged capsules during controlled interspecific aggression assays, thereby minimizing artifacts linked to post-discharge deformation or preservation. Focusing on type I MpMs abundant and structurally well defined improved measurement reliability and comparability across samples. Across all colonies examined, *P. rugosa* consistently exhibited larger capsules and longer shafts than *P. speciosa*, a pattern indicative of taxonomically meaningful divergence.

Taken together, these findings contribute to the expanding body of research emphasizing the value of integrating internal microscopic traits with molecular and ecological datasets in coral systematics (Forsman et al 2009; Riginos et al 2024). Although cnidom analysis on its own may not fully resolve all instances of cryptic diversity, it represents a cost-efficient, accessible, and reproducible approach that complements both skeletal examinations and genomic methods. Its applicability to preserved material further enhances its relevance for retrospective taxonomic studies, museum collections, and long-term biodiversity assessments.

Future research should integrate nematocyst morphometric data with genomic approaches, such as RADseq or targeted gene capture, to determine whether the observed variations correspond to reproductive isolation or instead represent intraspecific polymorphism. Further examination of ontogenetic and ecological effects on nematocyst dimensions will also be critical for disentangling the relative contributions of phenotypic plasticity and genetic determination in shaping these traits.

Conclusions. The morphometric analysis of nematocysts, particularly type I microbasic p-mastigophores, proved to be a valuable supplementary tool for distinguishing *P. rugosa* from *P. speciosa*. Beyond reinforcing species-level diagnoses in morphologically similar corals, this approach also holds considerable promise for wider application in coral taxonomy and systematics.

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Conflict of interest. The authors declare that there is no conflict of interest.

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