Taphonomic Biases Influencing Exceptionally Preserved *Naraoia* from the Burgess Shale

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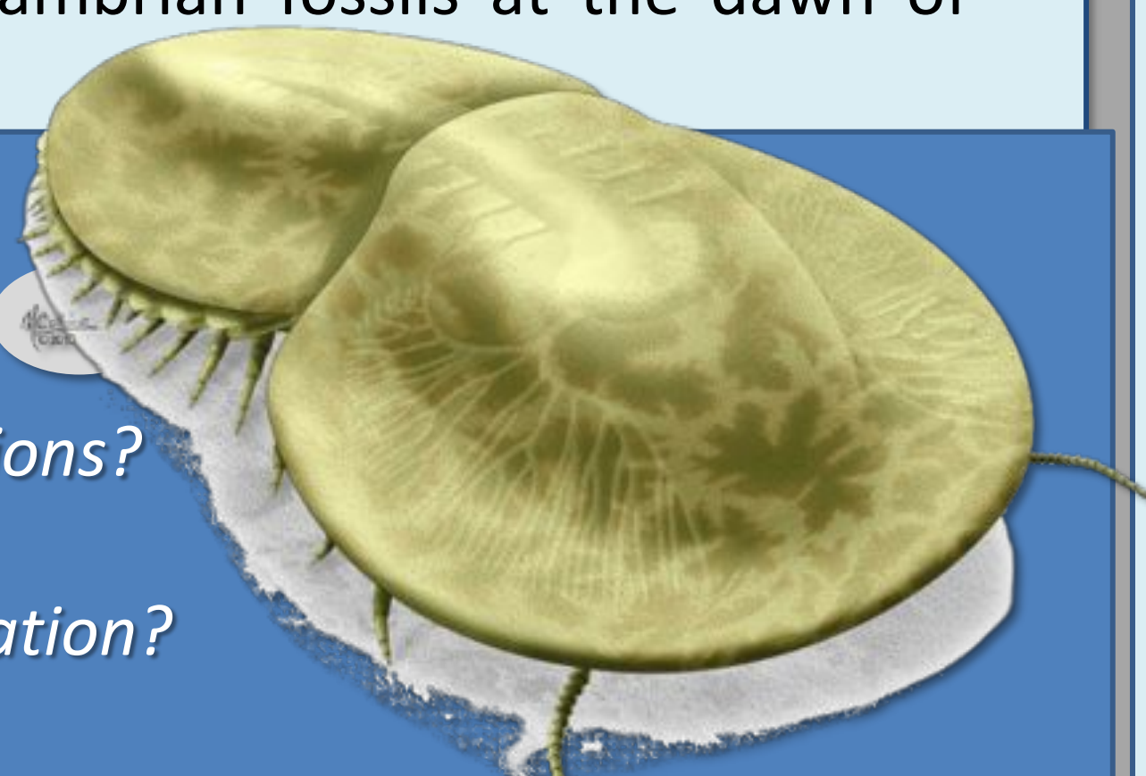
Abstract and Introduction

The identification of fossilized species relies on morphological characteristics. Accurate morphological observations must account for preservational biases because, as an organism decays and fossilizes, soft tissues are typically lost. This creates a bias towards biomineralized tissues such as shells, bones, and teeth. Cases of exceptional soft-tissue preservation, as seen in the Burgess Shale, offers unique insights into fossil morphology and diversity during the Cambrian explosion. The Burgess Shale is best known for exquisitely preserved specimens however preservation quality ranges between specimens, presumably as a result of tissue decay. *Naraoia* is a Trilobitomorph arthropod first described from the Burgess Shale by Walcott (1912). It is an ideal experimental proxy for Bugress Shale preservation because of its simple morphology, which exhibits easily defined characteristics, and its range of morphologies which may represent different preservational stages of decay. Identifying taphonimic biases influencing *Naraoia* is essential to accurately describe its true morphological variation, as well as preservational processes influencing the Burgess Shale. Understanding taphonomic processes resulting in Burgess Shale Type Preservation is vital for accurate interpretations of Cambrian fossils at the dawn of animal life.

Questions



1. *What features are reliable for species distinctions?*
2. *How does taphonomy influence species designation?*
3. *What taphonomic processes create artificial variation?*

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Methods

All 203 *Naraoia* specimens in the U.S.N.M. Collection were examined (Zhang et al. 2007). A decay series (Fig. 1) was constructed from the available range of preservation in the collection. The taphonomic index semiquantitatively assesses the preservational state of each individual. This series approximates a decay scale, which was compared to other notable characteristics such as body size, orientation to bedding plane, and presence/quality of genal spines, diverticula, caeca, gut, and appendages.

Body Size	Orientation	Genal Spines	Diverticula/Caeca
Lengths measured in mm along transverse and sagittal axes.	High variation in orientation. Identified as parallel, slightly tilted, oblique, or lateral.	Found along posterolateral margin of anterior shield.	Highly reflective. Caeca branchinto diverticula in anterior shield.
Gut	**Appendages**	**Distortion from Decay**	**Anterior Shape**
Appears as a dark "ribbon" along sagittal axis. Some exhibit 3-dimensional structure.	Appendages consist of antennae and many biramus legs. Paddle-like exopods covered with lamellae.	Forms of distortion: wrinkling of carapace, irregular/rocky texture, "rusting," inarticulation of shield margins.	Appears to have several shapes, described as sub-circular, elliptical, and spade.

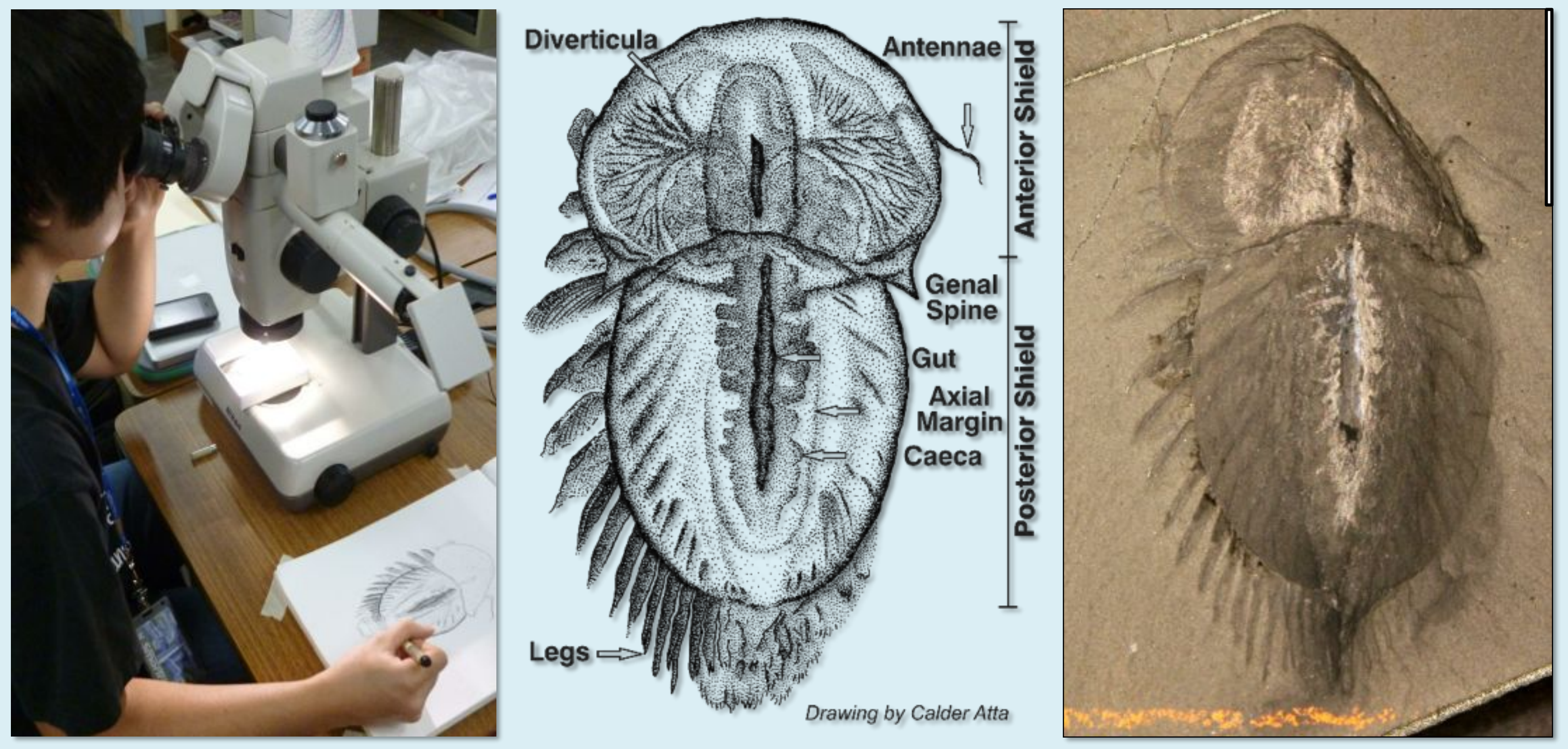

Figure 2: Left: Setup using a cameral lucida microscope, Center: Camera lucida composite illustration of *Naraoia*, from U.S.N.M. 57687, 235862, and 235888E. Right: U.S.N.M 57687.

Figure 1: The decay series from well (10) to poorly (1) preserved. The relative preservational states are shown with their taphonomic indices. Scale bars 1 cm.

Results and Discussions

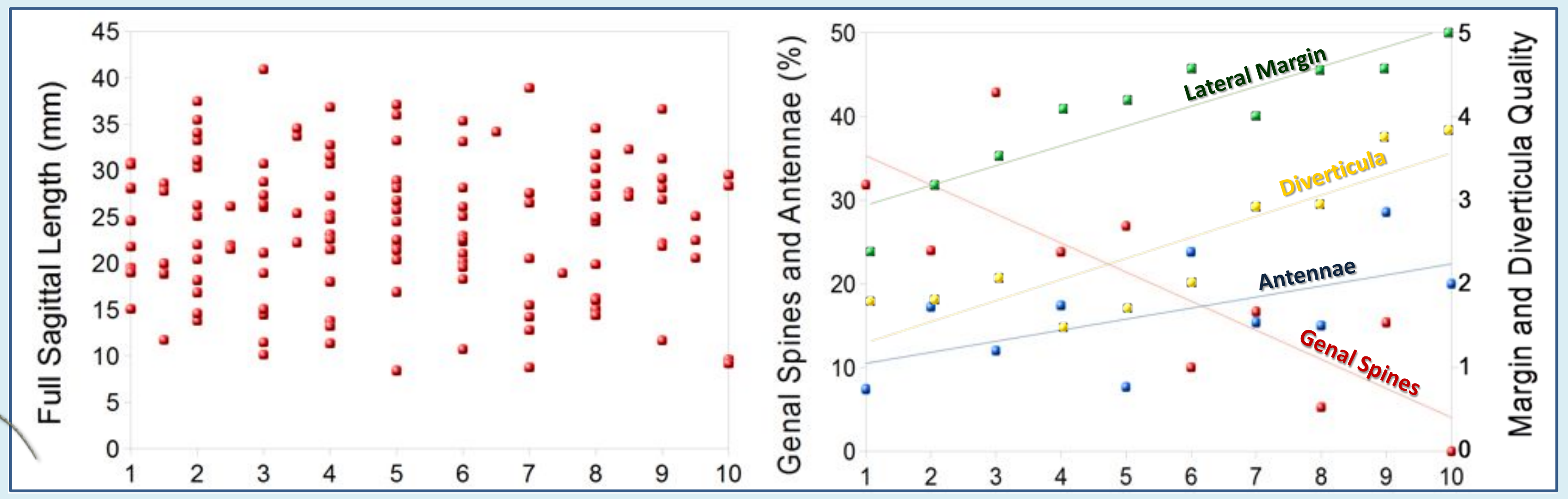

Figure 3: Left: Carapace length plotted against taphonomic index, with no obvious correlation. Right: Characters influenced by decay potted against taphonomic index.

Apatite is a principal mineral in Burgess Shale fossils, which requires sufficient phosphate to inhibit the production of calcite or aragonite. Decomposition will typically produce enough phosphorous to stimulate precipitation of apatite (Briggs 2003). The lack of correlation between body size and decay (Fig. 3 left) suggests that Naraoiids were not large enough to greatly influence the production of apatite. As such characters associated with body size, legs, gut, (presence of) diverticula and caeca are less influenced by decay.

Simonetta and Delle Cave (1975) used genal spines to distinguish a new species (*N. halia*). Whittington (1977) claimed genal spines to be a form of sexual dimorphism. Our results support a negative relationship between genal spines and preservation (Fig. 3 right). Decay may enhance preservation of certain tissues by increasing tissue permeability and creating void spaces for minerals to precipitate (Briggs 2003). Trilobite genal spines are thought to be hollow (Moore et al. 1996). If this feature remains homologous in Naraoiids, deterioration of the genal spine cuticle may enhance preservation. Based on this correlation, genal spines should not be used to identify either species or dimorphism.

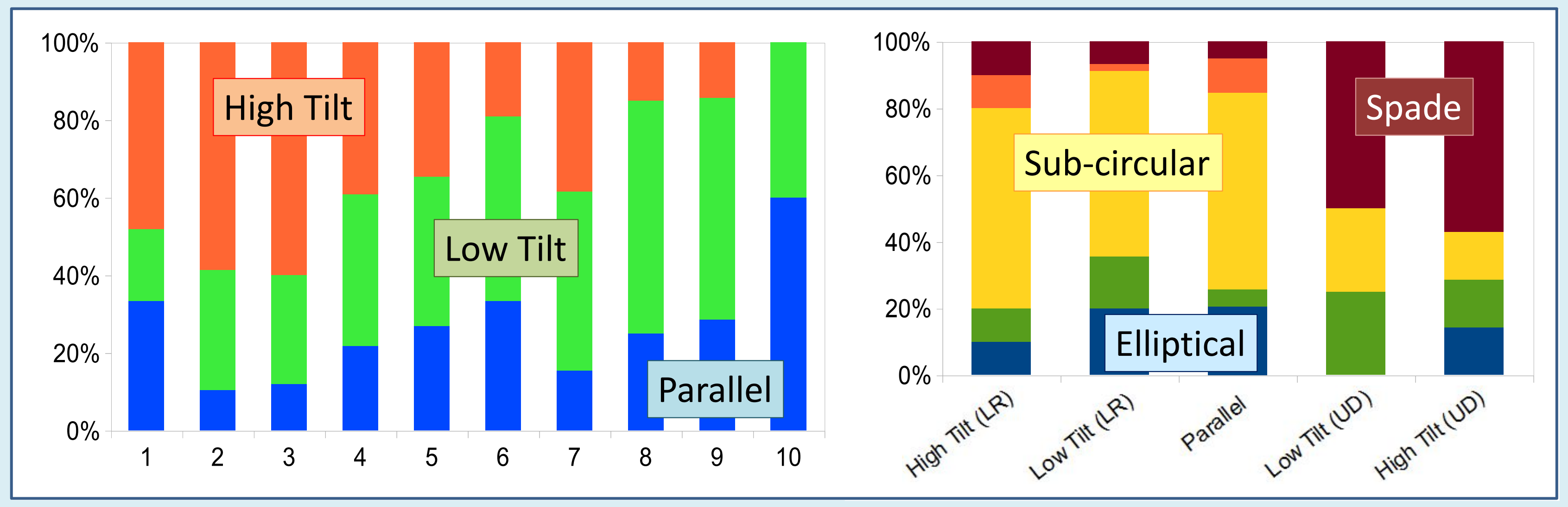

Figure 4: Left: orientation plotted against taphonomic index. Poorly preserved typically oblique. Right: Anterior shield shape vs. orientation (LR = left or right, UD = up or down).

Simonetta and Delle Cave (1975) erected *N. pammon* due to its circular anterior shield. As shown, variation in anterior shield shape is influenced by the orientation of the specimen in reference to the bedding plane (Fig. 4 left). Oblique specimens were typically poorly preserved (Fig. 4 right), possibly due to higher exposure to scavenging, diffusion of mineral producing ions, or hidden and distorted structures (Briggs 2003). Consequentially, overall shape is highly influenced by decay and orientation in substrate, and should not be used in species designation.

Further Results and Conclusions

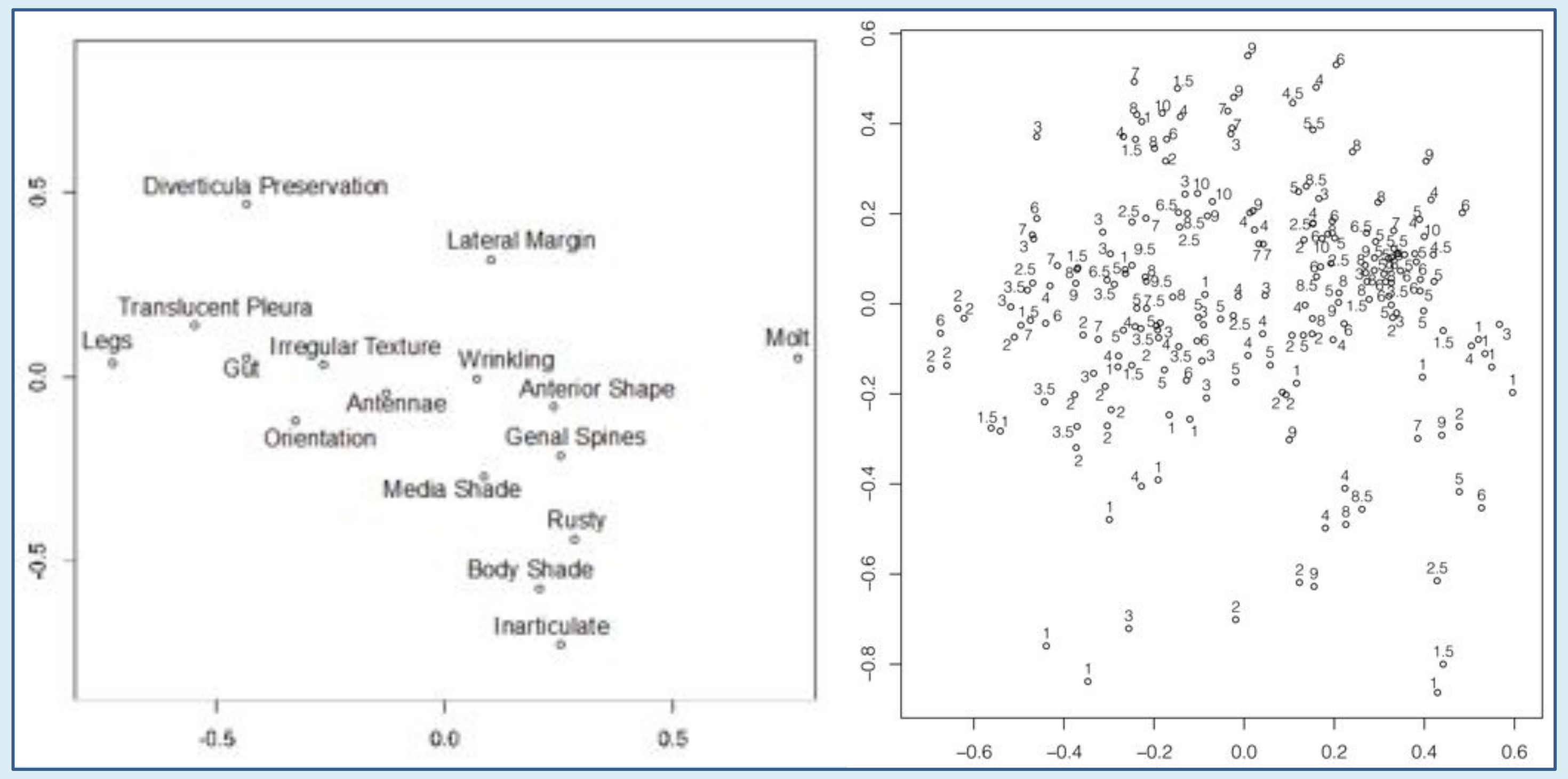

Figure 5: NMDS ordination of attributes and specimens. Left: Attribute plot showing better correlated characters as more closely spaced. Right: Specimens arranged according to attributes and labeled by decay index.

Specimens show a trend with high preservation concentrated near the upper margins, validating the decay series and revealing a decay-influenced region. Characters within the decay-influenced region are taphonomically biased, supporting our previous results (Fig. 3-4). We originally hypothesized that molts and highly decayed individuals would be indistinguishable. However, our NMDS ordination isolates molts from other decay-influenced characters. Molts are also negatively correlated to the presence of legs, supporting their validity.

What features are reliable for species designations? Characters least influenced by taphonomy are the most reliable for describing a species and its morphology. Refer to table on right.

How does taphonomy influence species designation? Species designations should avoid taphonomically biased characters. Previous species designations will require revisions as a consequence of this study.

What taphonomic processes create artificial variation? Future studies should explore decay processes in modern arthropods. An expanded study of all Burgess Shale arthropods would corroborate our results and may provide a better understanding of taphonomic processes influencing soft tissue preservation.

Reliable for Species Designation?	
Body Size	✓
Body Shape	✗
Genal Spines	✗
Diverticula	
Presence	✓
Structure	✗
Molts	✓
Lateral Margin	✗
Legs	✓
Antennae	✗
Gut	✓

Acknowledgements

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Briggs. 2003. Annual Review of Earth and Planetary Sciences 31:275-301, **More. et al**. 1996. Treatise on Invertebrate Paleontology, (O) Arthropoda 1:51-52, **Simonetta and Delle Cave**. 1975. Palaeontographica Italica, 69, p.4-5, **Walcott**. 1912. Smithsonian Miscellaneous Collections, 57:145-229, **Whittington**. 1977. Phil. Trans. of the Royal Soc. (London), B, 280:409-443, **Zhang et al**. 2007. The Paleontological Society, 81:1-52