Quantifying long loop variability in Recent terebratulide brachiopods and its implications for species delimitation in the fossil record

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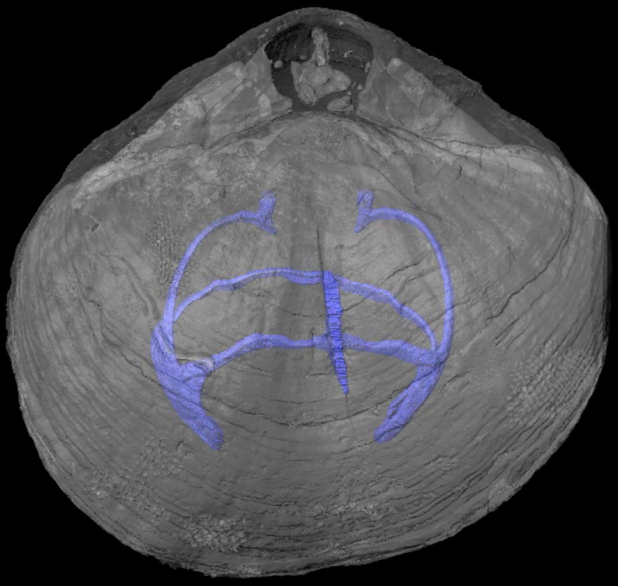
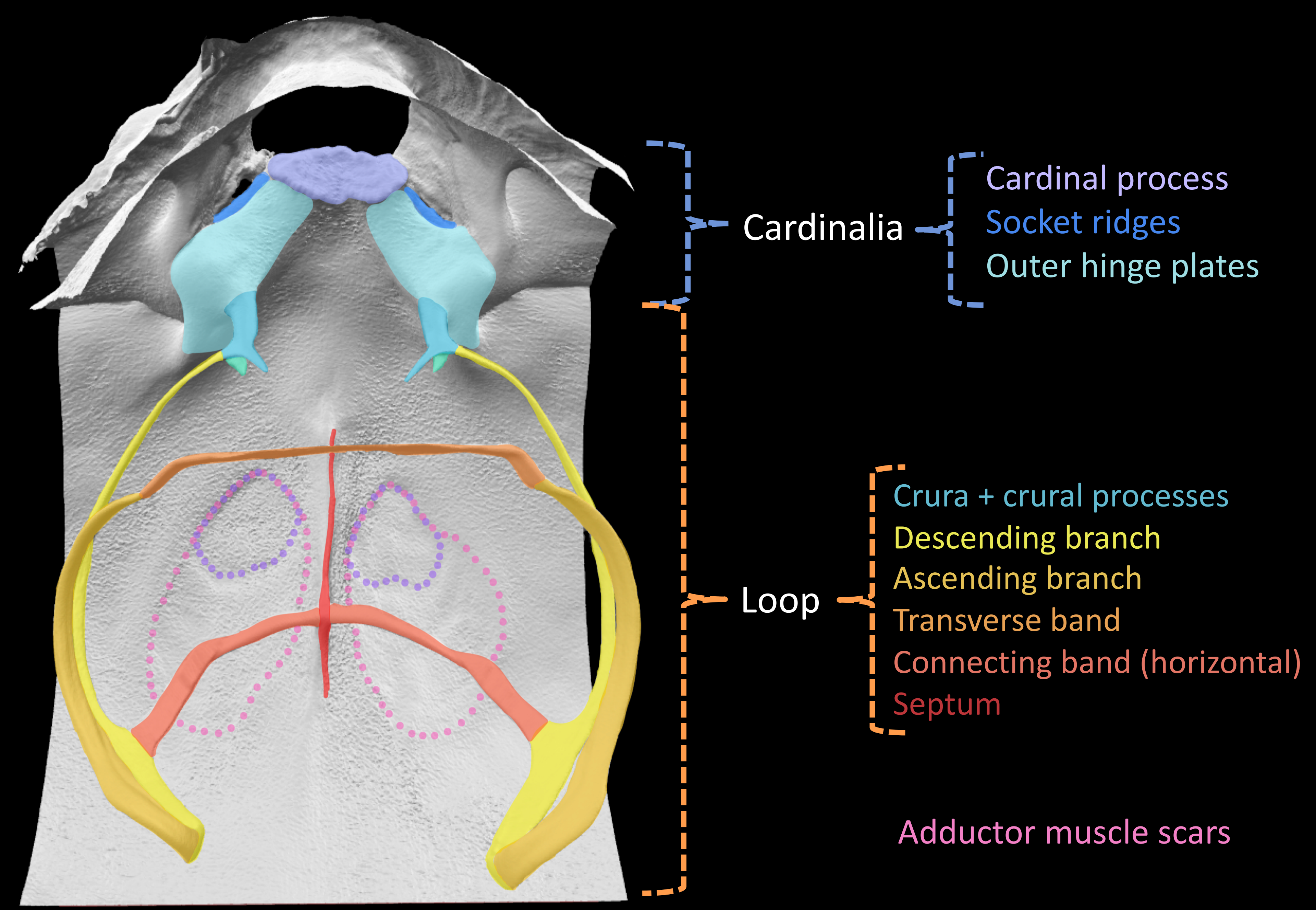
Brachiopods and their long loops

- One of the most diverse and abundant marine invertebrates in the fossil record.
- The loop is a calcareous structure that supports the lophophore.
- Important morphological character.
  - Phylogeny, taxonomy, ontogeny



Terebratalia transversa



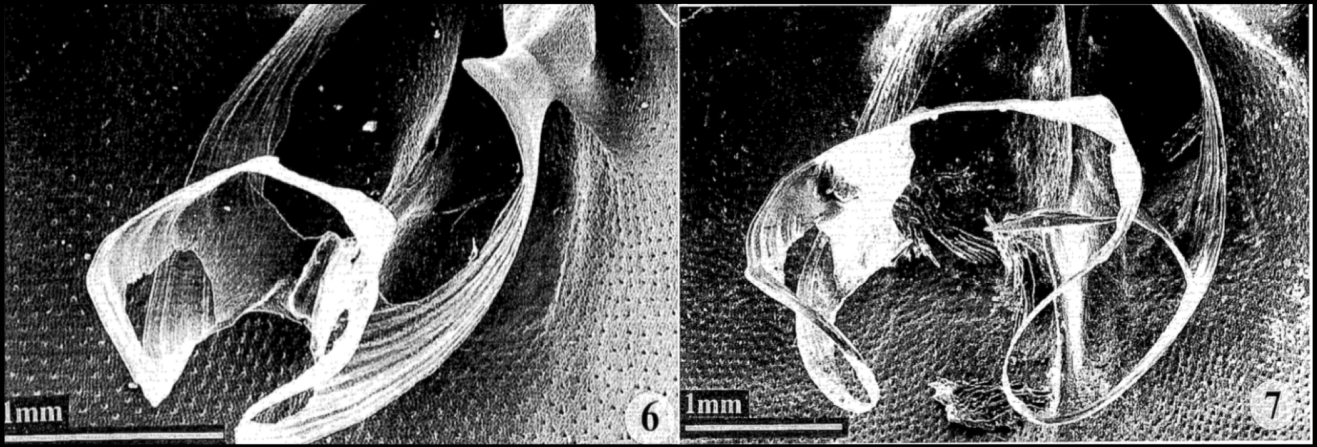
Cardinalia
Cardinal process
Socket ridges
Outer hinge plates
Loop
Crura + crural processes
Descending branch
Ascending branch
Transverse band
Connecting band (horizontal)
Septum
Adductor muscle scars

Studying loop morphology and variability

- Long loops are geometrically complex.
- How can we study them?
  - Illustrations
  - Photographs
  - SEM
  - Serial sections
  - CT scans

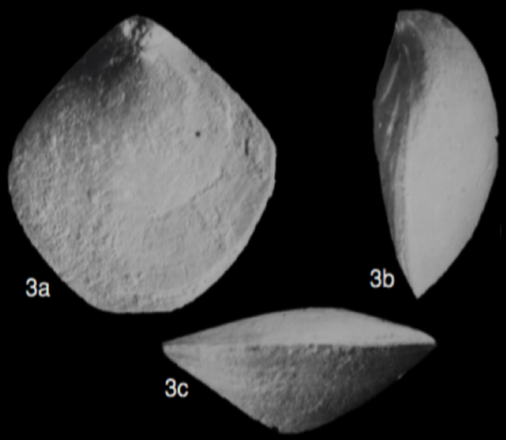
Laqueus erythraeus

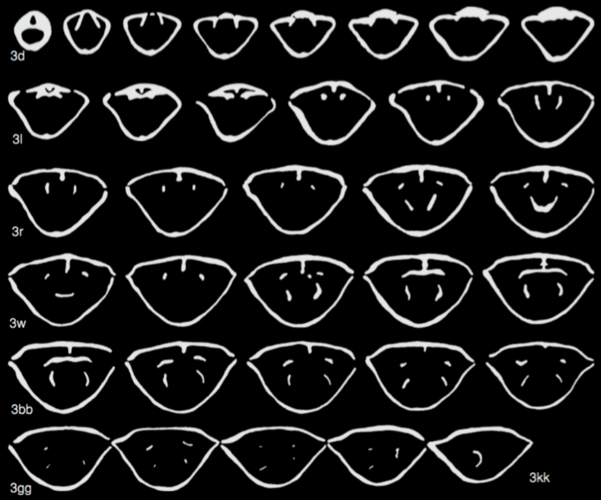
SEM

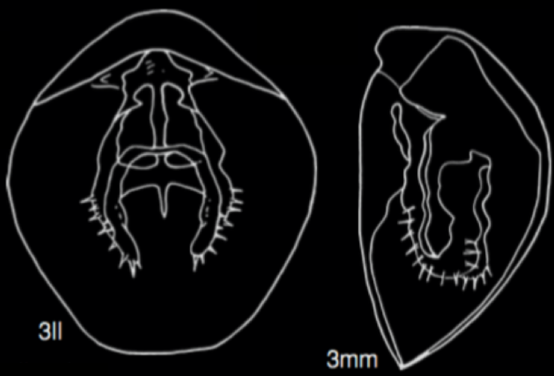


Pictothyris (taken from Saito, 1996)

Fossil specimen → Serial sections → Loop reconstruction



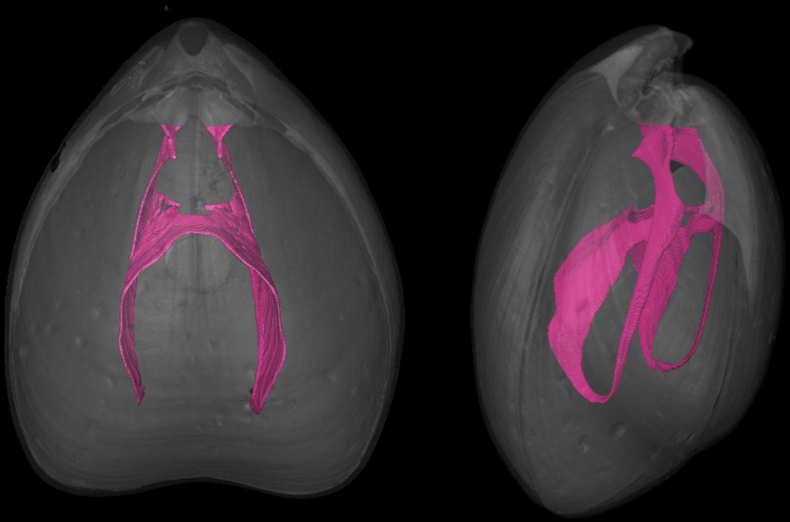




Terebrataliopsis, Cretaceous brachiopod (modified from Smirnova, 1962; Muir-Wood, 1956)

- To fully capture shape and variability in quantitative manner, it is necessary to work with 3D reconstructions.

  – CT scanning and 3D geometric morphometrics



L. quadratus, Japan

Research question and big picture

- Is it possible to discriminate species based on loop morphology?
  - Recent brachiopods
- What about in the fossil record?
  - Can we translate what we observe in extant specimens to fossils?
- Correspondence between named species in Recent and fossil record

D. occidentalis

Terebratalia occidentalis?

Species

- Three genera from Order Terebratulida
  - *Terebratalia*, *Dallinella*, *Laqueus*
- North Pacific distribution
- Some with problematic taxonomic history

Terebratalia transversa,
Tacoma Narrows, WA

Terebratalia transversa,
Friday Harbor, WA

Dallinella occidentalis,
Catalina Island, CA

Species

Laqueus

L. erythraeus
Catalina Island, CA

L. erythraeus
Monterey Bay, CA

L. blanfordi
Japan

L. quadratus
Japan

L. rubellus
Japan

Methods

3D isosurface models
- From CT scans
- Amira

Landmark and semilandmark registration
- Based on proposed landmark schemes
- Stratovan Checkpoint

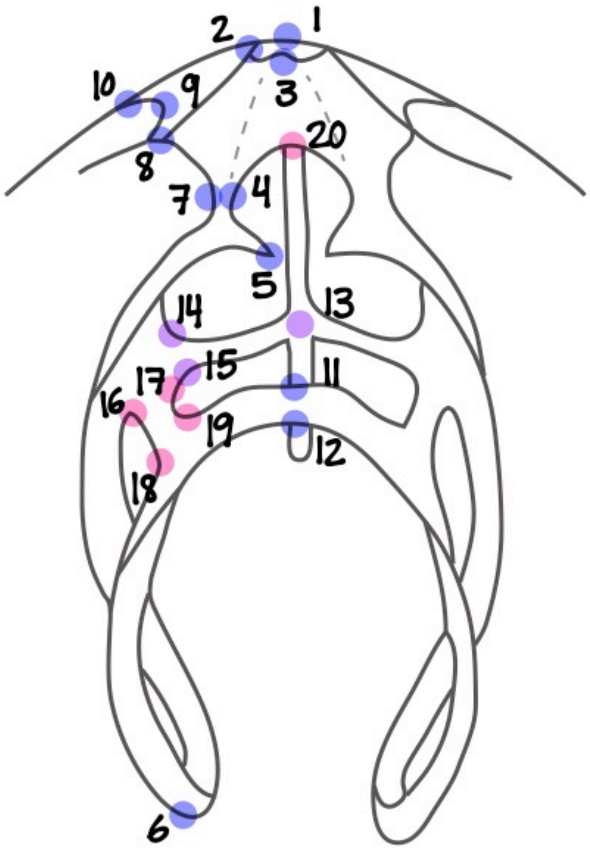
Landmark superimposition
- Generalized Procrustes Analysis
- Semilandmark sliding using bending energy

Ordination Methods
- Principal Component Analyses (PCA)
- Canonical Variate Analyses (CVA) and between-group PCAs

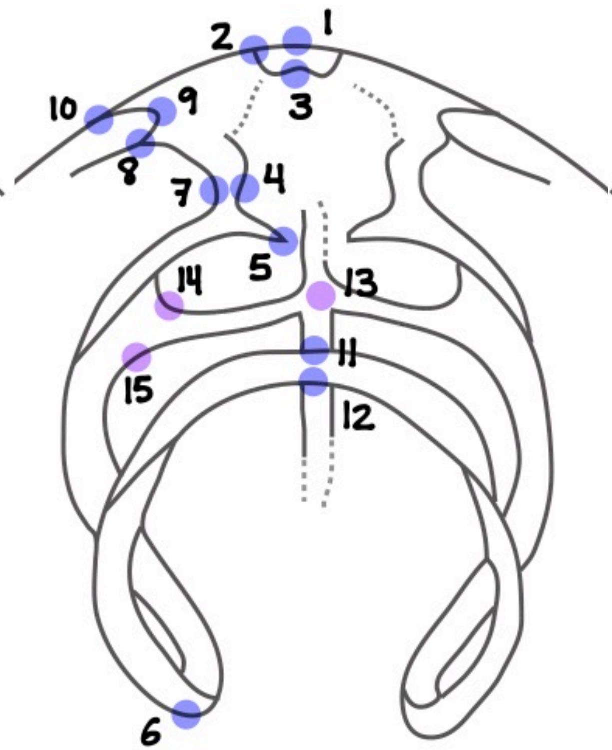
Statistical methods
- Procrustes ANOVA

R packages geomorph and Morpho

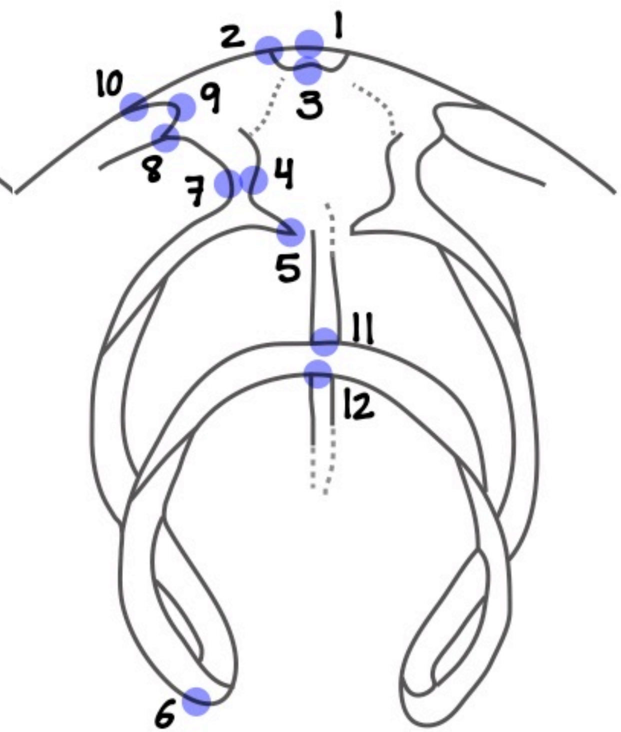
Landmark schemes



Bilateral loop
e.g. *Laqueus*

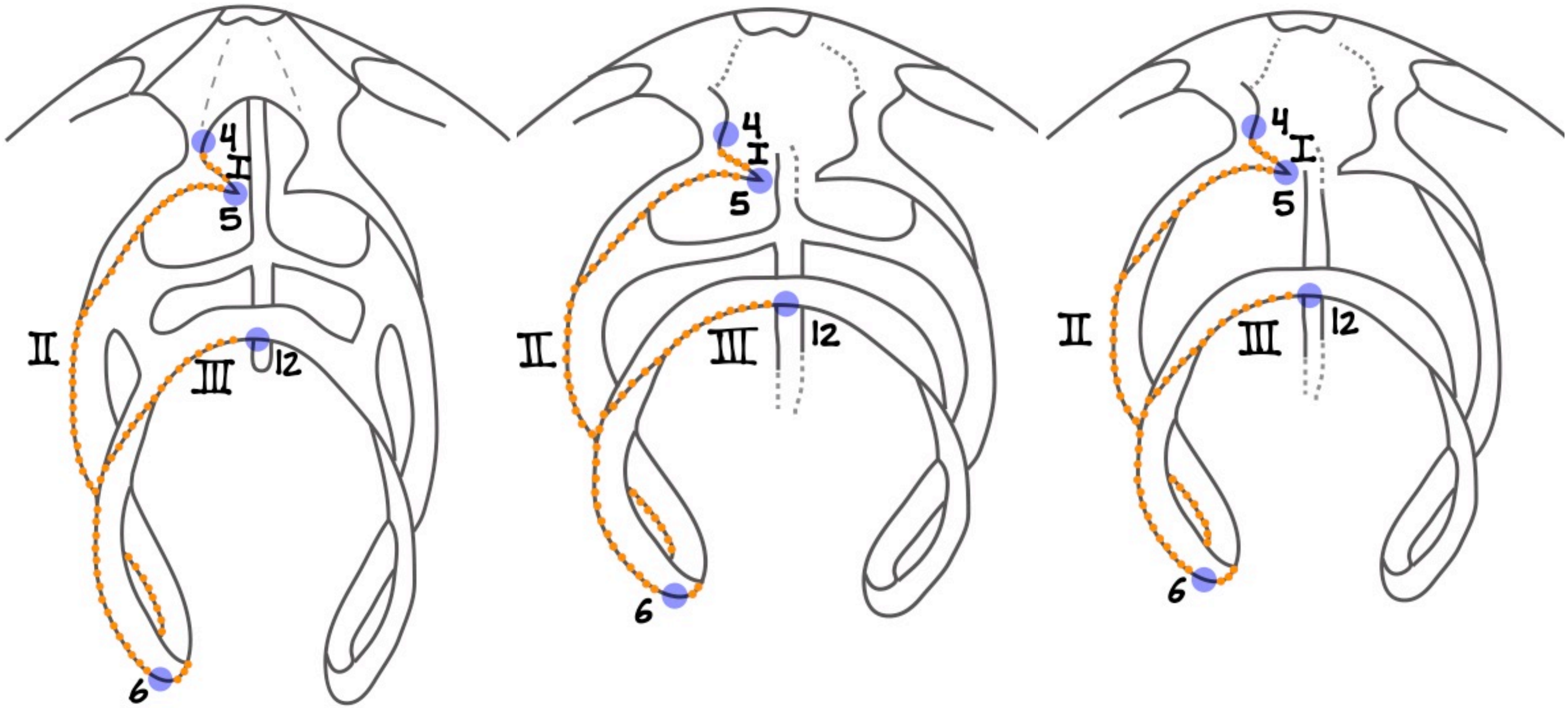


Trabecular loop
e.g. *Terebratalia*



Teloform loop
e.g. *Neothyris*

Semilandmark scheme

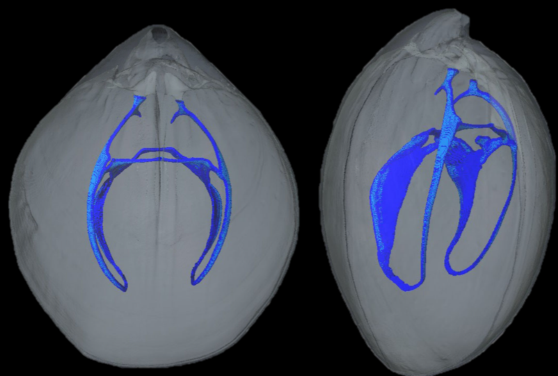


Bilateral loop
e.g. *Laqueus*

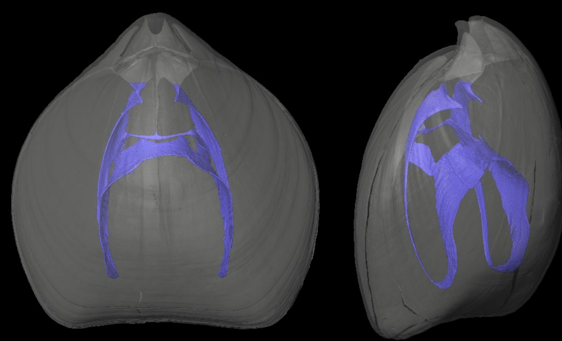
Trabecular loop
e.g. *Terebratalia*

Teloform loop
e.g. *Neothyris*

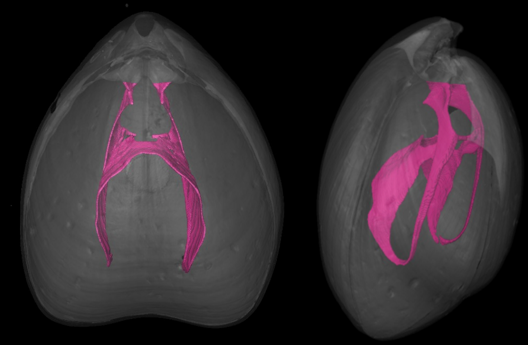
Isosurface models



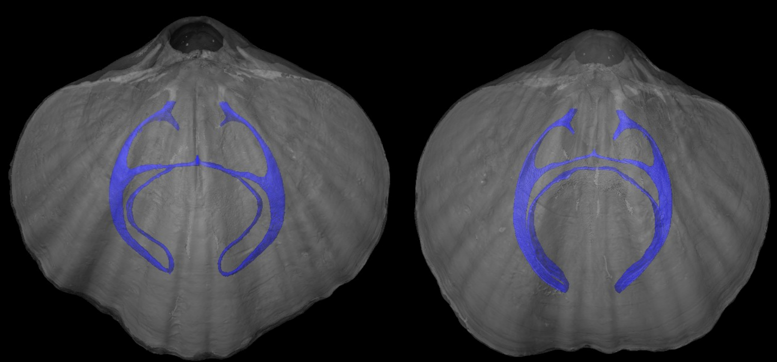
L. erythraeus , Catalina Island, CA



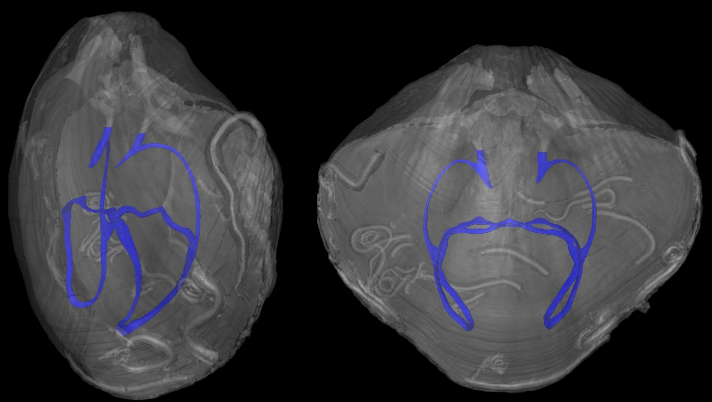
L. blanfordi, Japan



L. quadratus, Japan



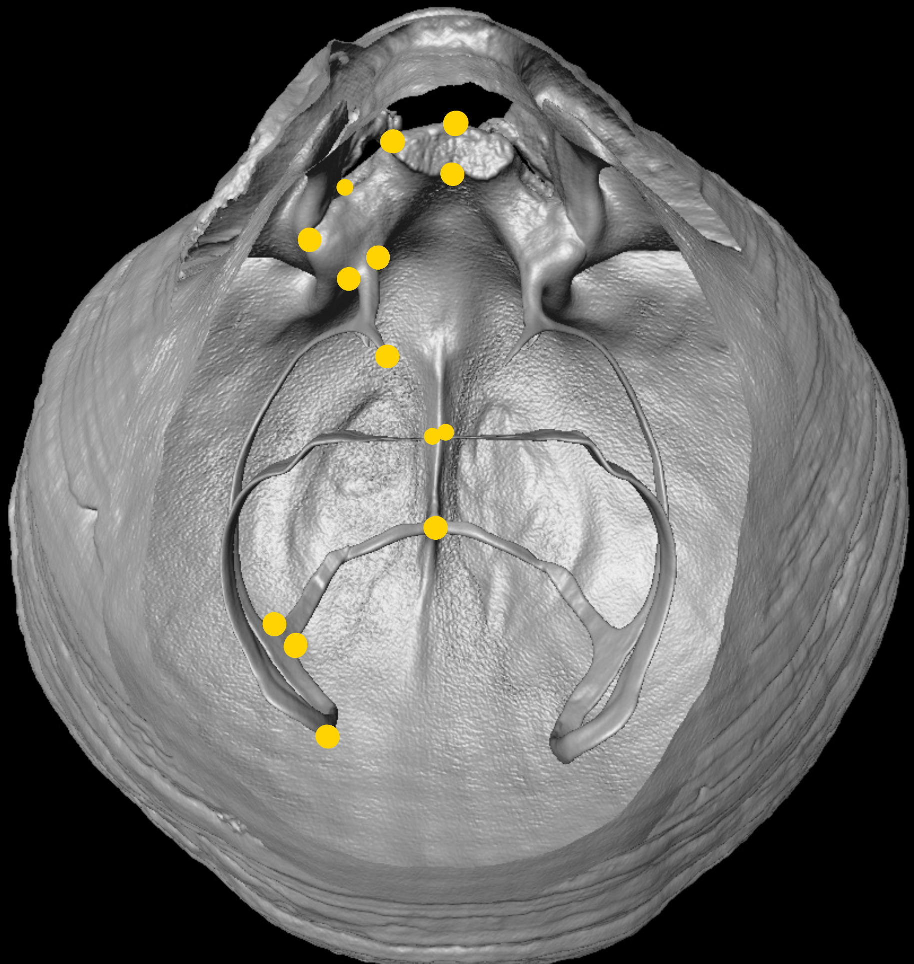
D. occidentalis, Catalina Island, CA



T. transversa, Tacoma Narrows, WA

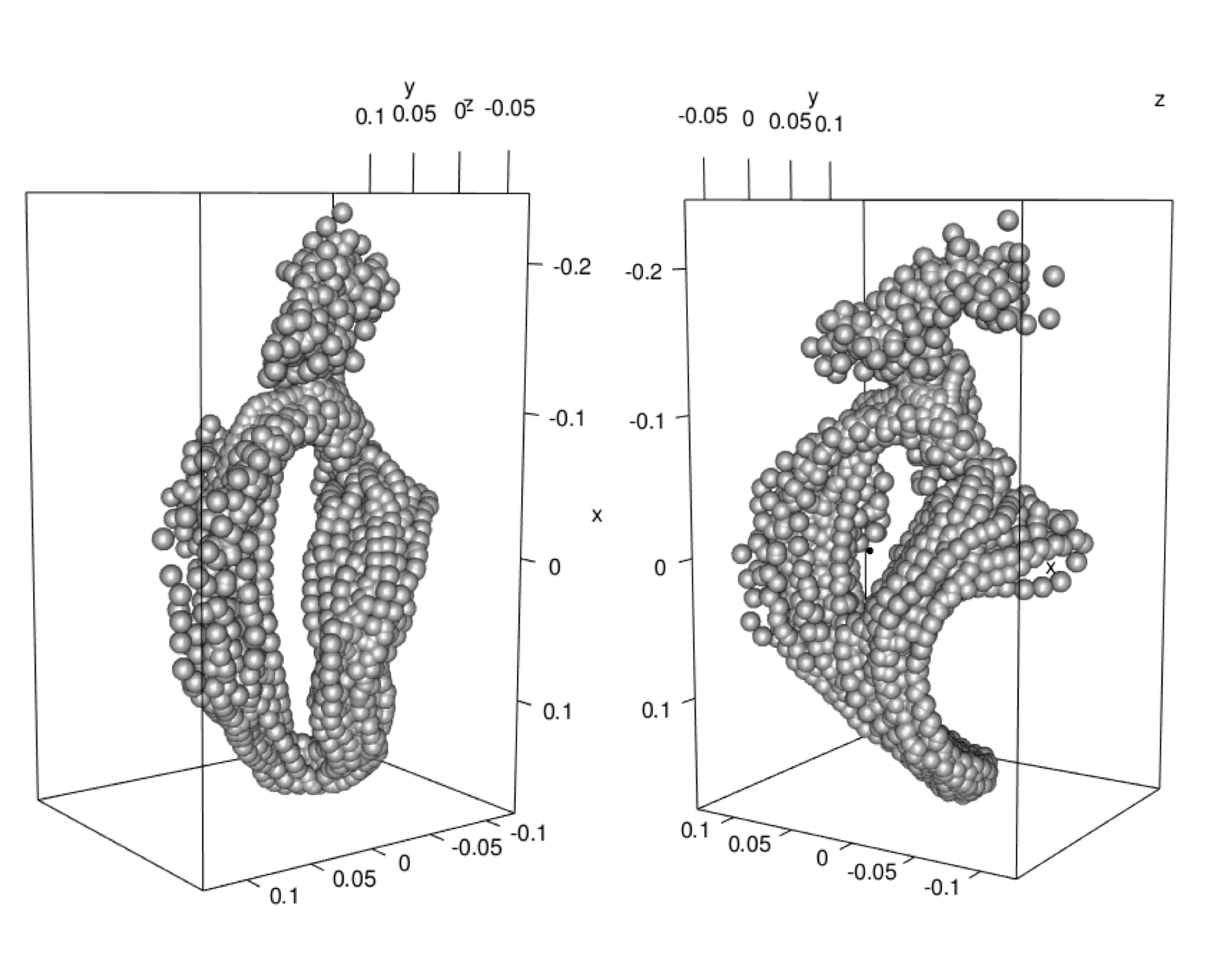
Landmark registration

Stratovan Checkpoint



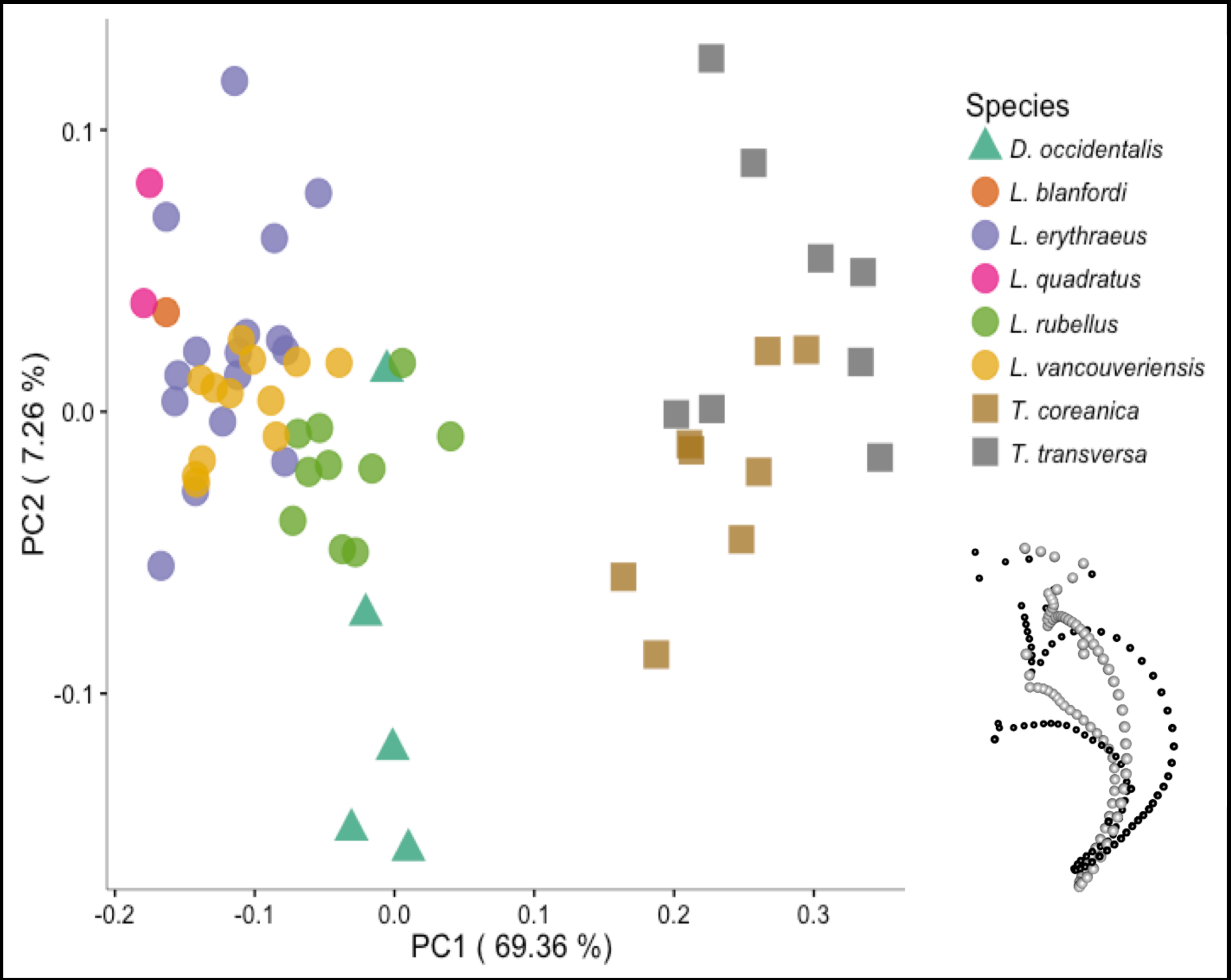
T. transversa

Landmark superimposition

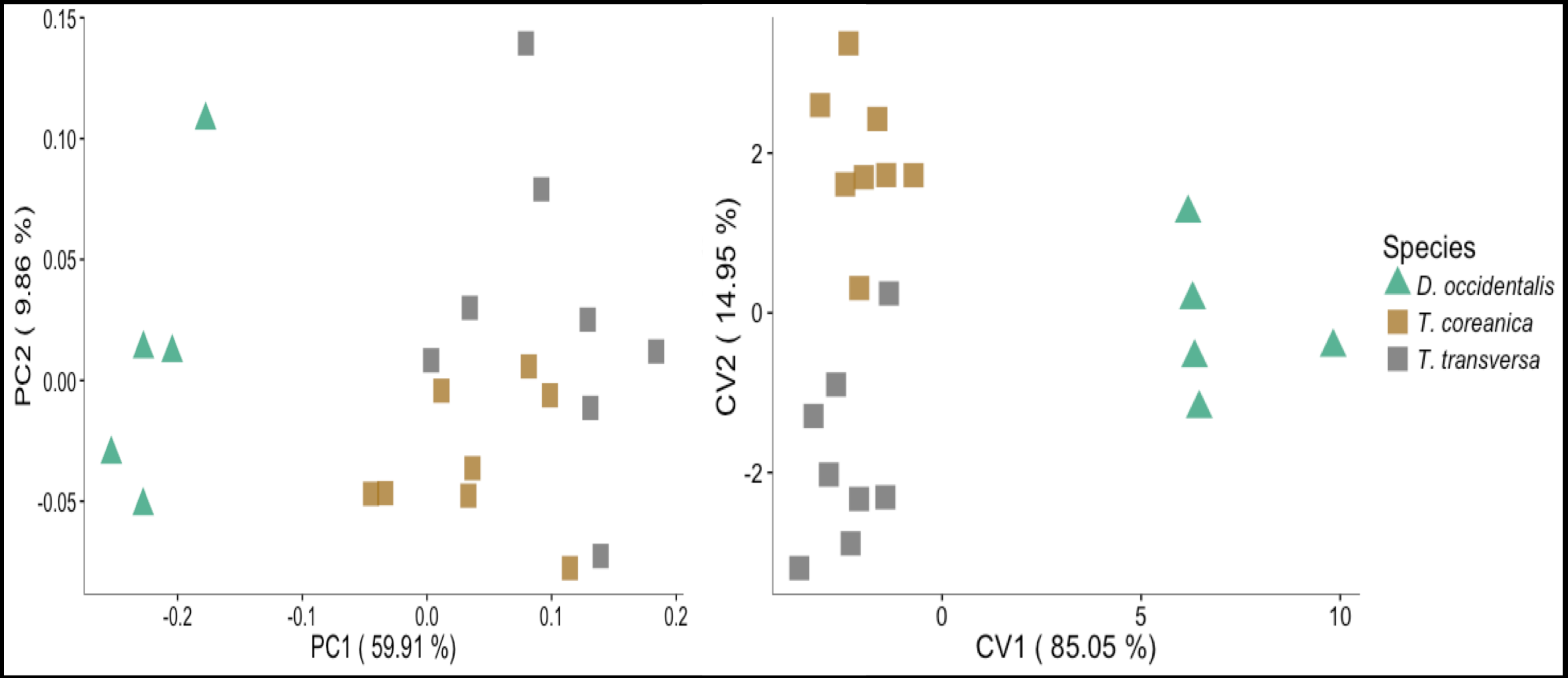


50 specimens, 15 landmarks, 69 semilandmarks

Exploring general pattern of variability



PCA and CVA for *Dallinella* and *Terebratalia*



Maximizes between-group differences relative to within-group covariation

Cross-validated classification result (CVA):

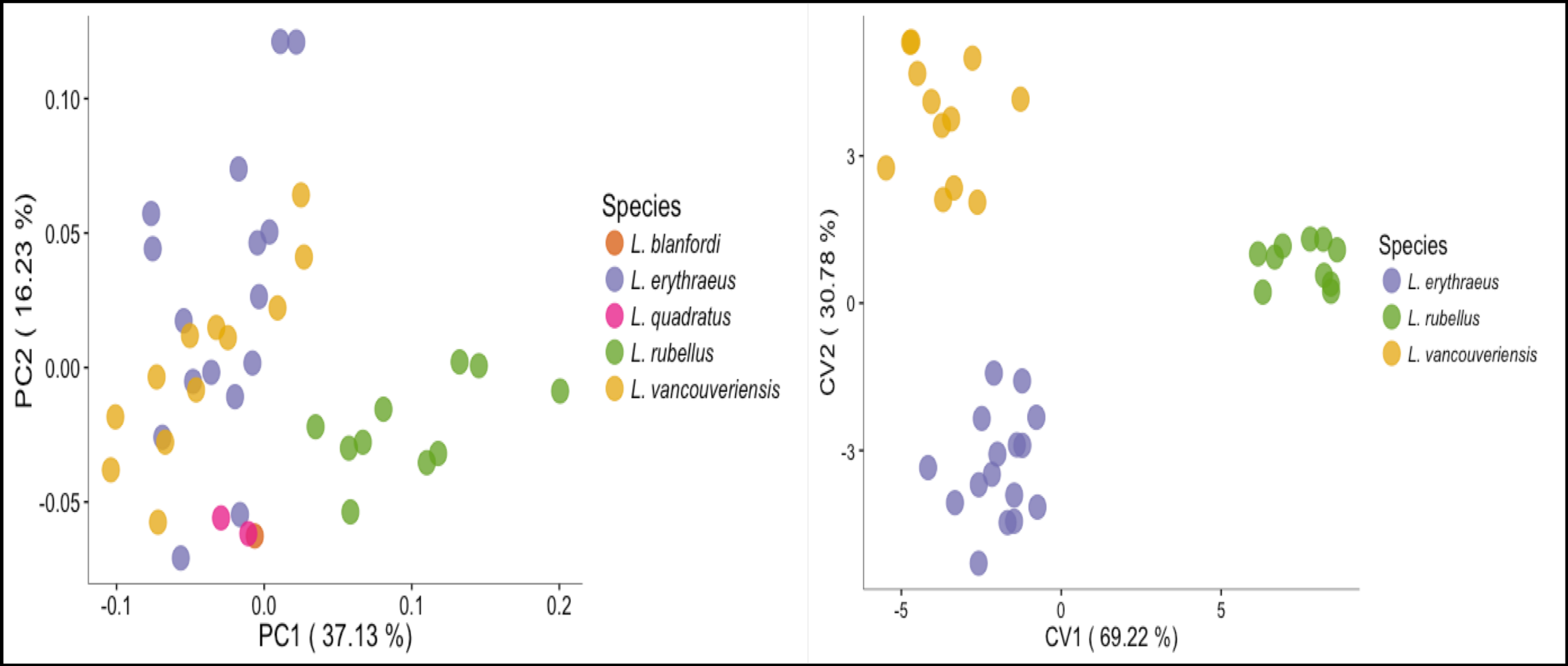
	D. occidentalis	***T. coreanica***	***T. transversa***
D. occidentalis	5 (100%)	0	0
T. coreanica	0	7 (87.5%)	1 (12.5%)
T. transversa	0	2 (25%)	6 (75%)

Overall classification accuracy: 85.71%

Procrustes ANOVA: *Dallinella* and *Terebratalia*

- Is shape dependent on size?
  - No, size does not have a statistically significant impact on shape (p=0.15).
- Do species differ in shape?
  - Yes, species are statistically different (p=0.001).

PCA and CVA for *Laqueus*



Classification result (CVA):

	L. erythraeus	*L. vancouveriensis*	*L. rubellus*
L. erythraeus	16 (100%)	0	0
L. vancouveriensis	0	12 (100%)	0
L. rubellus	0	0	10 (100%)

Overall classification accuracy: 100%

Procrustes ANOVA: *Laqueus*

- Is shape dependent on size?
  - Yes, size has statistically significant impact on shape (p=0.001).
- Do species differ in shape?
  - Yes, species are statistically different (p=0.001).

Summary

- Is it possible to discriminate species based on loop morphology?
  - Yes, each species has a statistically distinct loop.
    - Although species of *Terebratalia* seem to be harder to tell apart, possibly due to its highly variable loops.
  - Each species cluster together in shape space.

- CT technology plays an important role in understanding geometrically complex structures like loops.

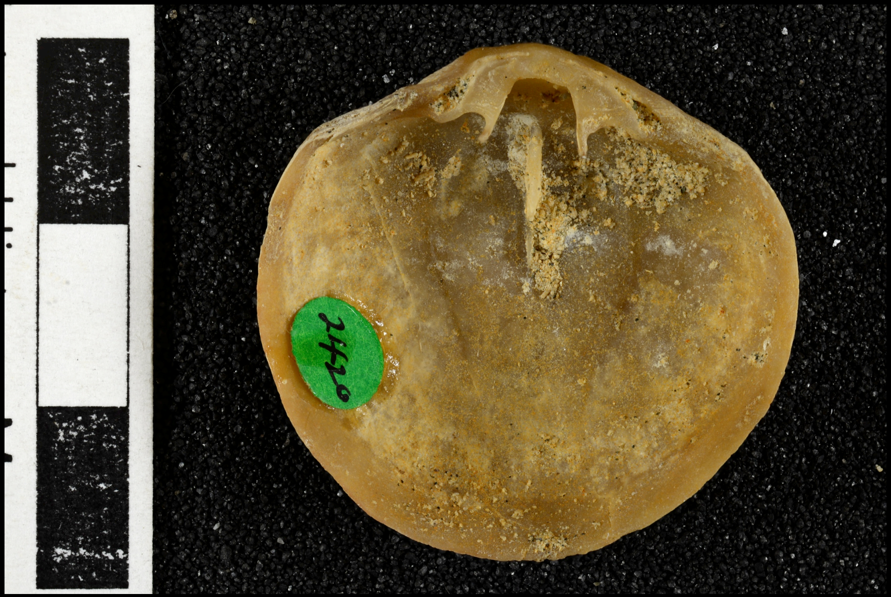
Future directions

- Since loops are rarely preserved in the fossil record, how can we apply these results to fossil specimens? CT scanning of fossils? YES.
- Is there correspondence between loop shape and shell shape?
  - Outline analyses of Recent specimens + loops
  - Outline analyses of fossil (Cenozoic) specimens
- Include genetic data.

Fossils!

- Thanks Invert Paleo Coll. at NHM!

Terebratalia transversa



Laqueus vancouveriensis

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