A functional and biomechanical perspective on deep time biodiversity

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Acknowledgements

Phil Anderson
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Paul Barrett
Natural History Museum, London
Ecomorphology and function

Ecology

Ecomorphology

Morphology

Genetics/Development/Environment

E.g. Losos et al. 1998 Science and many related works
Ecomorphology and function

Ecology

Ecomorphology

Low MA
fast

Mechanical advantage
ratio in lever : out lever

High MA
forceful

Morphology

Genetics/Development/Environment

Stayton 2006 Evolution
Ecomorphology and function

Ecology

Function

“Emergent functional properties”

Mechanism

Morphology

Genetics/Development/Environment

Stayton 2006 Evolution
Why should functional diversity differ from morphological diversity?

In the case of biomechanical measurements, we’re taking linear measurements from the skull; you’re essentially measuring the same thing, right?
Multiple morphologies may possess the same emergent functional property

Suction Index
Centrarchid fishes

Alfaro et al. 2004 *Evolution*
Collar & Wainwright 2006 *Evolution*
Mechanically neutral morphological variation may exist

Within neutral zone, features may adapt for a different purpose (e.g. decrease length of in-lever to flatten head without modifying suction index)

Structures can become modified for other functions whilst maintaining the original function.
H: Functional redundancy decouples morphological and functional disparity

*Functional convergence or functional diversity may go unrecognised.*

H: Functional redundancy promotes morphological evolution

*Increasing trait complexity reduces the correlation between morphological and functional diversity* (Alfaro et al. 2004)

Labrid fishes – similar jaw closing mechanisms in fish with diverse morphologies
The utility of functional and biomechanical diversity in deep time

1. Potential decoupling of morphological and functional diversity (in complex systems)

2. Recover the functional implication of changes in form on evolutionary timescales (trophic structure communities, evolution innovations, occupation new habitats, response to external drivers, rates functional evolution…)

3. Tracking evolution of measure of performance – potential agent of selection (quantified for certain traits in certain fish clades)

4. Functionally and biomechanically significant parameters can be preserved in the fossil record.
Functional morphospaces

Bellwood 2003 *Paleobiology* 29: 71-83

Functional morphospaces

Anderson 2009 *Paleobiology* 35: 321-342
Functional variation in the earliest jaws

62 Ma
Late Silurian (412) – end Devonian (359)

Gracile, fast closing jaws, with thin, pointed teeth

Robust, forceful jaws, resistant to bending

Lack dentition, large adductor muscle

Sharp tooth cusps, smaller adductor muscle

variation in the earliest jaws: Silurian to end Devonian
Mesozoic crurotarsans – mandibular biomechanical disparity

Trophic shifts and gigantism in Sauropodomorph dinosaurs
- Evidence for functional diversity between grades
- Shifts in rates of functional evolution?
- Correlation to body mass / gigantism

Cranial biomechanics underpins high sauropod diversity in resource-poor environments

David J. Button, Emily J. Rayfield and Paul M. Barrett

Selection of functional traits or characters

“The primary aim was to select structural features where variation in morphology had known functional significance, which is in turn directly related to trophic status. These structural features should be present in all taxa and preserve well, with minimal distortion. Functionally homologous features should be easily recognized and quantified, with minimal subjectivity. Furthermore, differences in morphology should have known biomechanical consequences, with a clear link between structure and performance in a range of extant forms. This performance should be directly related to feeding abilities and, if possible, trophic status in a number of extant taxa.”

Bellwood 2003
29 biomechanical characters, 62 taxa

Mechanical advantage

Skull anterior M.A.

Skull posterior M.A.

Jaw anterior M.A.

Jaw posterior M.A.

Fin/Fout
29 biomechanical characters, 62 taxa

Mechanical advantage

Adductor muscle characters

Skull anterior M.A.  Skull posterior M.A.

Jaw anterior M.A.  Jaw posterior M.A.

Stf length/skull length  Stf breadth/skull breadth

Adductor fossa length/jaw length  EMF area/jaw area

Adductor muscle angle
29 biomechanical characters, 62 taxa

**Mechanical advantage**
- Skull anterior M.A.
- Skull posterior M.A.
- Fin/Fout

**Adductor muscle characters**
- Stf length/skull length
- Stf breadth/skull breadth

**Tooth characters**
- Jaw length/jaw length
- Tooththrow length/skull length
- Tooththrow length/jaw length
- Average jaw depth/jaw
- Average jaw width/jaw
- Lateral plates present/absent

**Tooth slenderess index**
- Tooth denticles: absent/present
- Tooth battery: present/absent

**Tooth angle**
- Tooth occulsional pattern: absent/interdigitating/precision shear

**Heterodonty**
- Present/absent
- Recurved teeth: present/absent
29 biomechanical characters, 62 taxa

**Mechanical advantage**
- Adductor muscle characters
  - Stf length/skull length
  - Stf breadth/skull breadth
- Adductor muscle angle

**Cranial robusticity**
- Herbivory characters
  - Premaxillary divergence angle
  - Average jaw width/Jaw
  - Lateral plates present/absent

**Tooth characters**
- Tooth slenderness index
- Tooth denticles absent/present
- Tooth battery presence
- Articulation of tooth row on shear
- Retroarticular process/jaw length
- Quadrate condyle length/articular cotyle length
- Articular process/jaw length

- Tooth angle
- Recurved teeth present/absent
29 biomechanical characters, 62 taxa

Mechanical advantage
- Skull anterior M.A.
- Skull posterior M.A.
- Jaw anterior M.A.
- Jaw posterior M.A.

Adductor muscle characters
- Stf length/skull length
- Stf breadth/skull breadth
- Adductor fossa length/jaw length
- EMF area/jaw area
- Adductor muscle angle

Cranial robusticity
- Max jaw depth/Jaw length
- Average jaw depth/Jaw length
- Symphysis depth/Jaw length
- Average jaw width/Jaw length

Tooth characters
- Tooth slenderness index
- Tooth denticles absent/present
- Tooth battery present/absent
- Tooth occlusional pattern-absent/interdigitating/precision shear
- Toothrow length/skull length
- Toothrow length/jaw length
- Tooth angle

Herbivory characters
- Premaxillary divergence angle
- Quadrate condyle length/articular cotyle length
- Articular offset/jaw length
- Retroarticular process/jaw length
- Lateral plates present/absent
Data processing: towards a multivariate “functionspace”

• Continuous characters Z-transformed (mean = 0, SD = 1)
• Principal Coordinate Analysis (PCO) in PAST (75.3% completeness of matrix)
• Gower Similarity index (continuous and categorical variables)

Summary statistics, first 10 PC axes

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| Total | 70.18% |

Character | r values and *r²* values | p-values |
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PC1: Proxy for rel. muscle size
PC1: Rel. mandibular fen size
PC1: Premax shape

• Spearman’s Rank (PAST) to test correlation between each functional character and PC axes

PC2: MA
PC1&2: Jaw robustness
PC1: Rel. length tooth row
One-way npMANOVA of scores on all PC axes, conducted in PAST (Hammer et al., 2001)
Informal time-calibrated supertree

- Taxa dated to stage-level
- Time calibrated tree in paleotree (timePaleoPhy)
Informal supertree projected into the phylofunctionspace in R utilizing the “phytools” package (Revell, 2012).
Testing for shifts in rates of functional evolution (PC scores) and body mass.

Rate shifts: tested in MOTMOT (Thomas & Freckleton 2011). AICc score calculated using simulated data.

67 taxa from craniodental PCO

Supertree (after Gallina & Apesteguia, 2011; Whitlock, 2011; Zaher et al., 2011; Otero & Pol, 2013; McPhee et al., 2014; Wilson & Upchurch, 2009; Royo-Torres et al., 2012; D’Emic, 2012; Mannion et al., 2013 & Benson et al., 2014).
Testing for shifts in rates of functional evolution (PC scores)

Two-rate trait evolution models with enforced shifts.
Values = %age of 1000 trees with sig shifts in PC axes scores.

67 taxa from craniodental PCO

Supertree (after Gallina & Apesteguia, 2011; Whitlock, 2011; Zaher et al., 2011; Otero & Pol, 2013; McPhee et al., 2014; Wilson & Upchurch, 2009; Royo-Torres et al., 2012; D’Emic, 2012; Mannion et al., 2013 & Benson et al., 2014).
Testing for shifts in rates of functional evolution $\log(body\ mass)$

Two-rate trait evolution models with enforced shifts.
Values = %age of 1000 trees with sig shifts in PC axes scores.

101 taxa with mass estimates (mostly from Benson et al. (2014))

Supertree (after Gallina & Apesteguía, 2011; Whitlock, 2011; Zaher et al., 2011; Otero & Pol, 2013; McPhee et al., 2014; Wilson & Upchurch, 2009; Royo-Torres et al., 2012; D'Emic, 2012; Mannion et al., 2013 & Benson et al., 2014).
Summary: sauropodomorphs

1. Sauropodomorphs traverse functionspace throughout their evolutionary history.

2. Show evidence of functional convergence (titanosaurs, dicraeosaurs, rebbachisaurids)

3. Do also show evidence of functional divergence between different Morrison taxa (high diversity – resource poor environment)

4. But no evidence of shifts in rates of (a) functional evolution, and (b) body mass evolution, at key points in their evolutionary history
Concluding remarks

1. Useful tool, reasons suggested earlier (different metric, decoupling morphological and functional diversity, evolution form-function, evolution performance, data preserved in fossil record etc.)

2. Obvious, generic problems – missing data, uncertainty in phylogenetic relationships, tree dating.

   1. Extinct taxa still subject to same physical principles as extant taxa
   2. Vertebrate-wide studies suggest that material properties of tissues (bone, soft tissue) are consistent across clade – no reason to suspect large differences in material construction
   3. But extinct taxa may display body plans not evident in extant data e.g. – extreme size (sauropods); giant carnivorous bipeds (theropods)

4. Fitness benefits of functional and biomechanical traits are rarely studied in extant tetrapod populations. Most commonly performance and subsequently benefits are inferred.
Thanks to Anjali, Mike and Phil for the invite to speak at this symposium

Thank you for listening