On the Origin of Morphospecies Using Bayesian Phylogenetics to Quantify the Mode of Ancestor Descendant Relationships in Paleozoic Invertebrates

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Dicellograptus

Morphotaxa in the Fossil Record

- Often, we find specimens with similar morphology, but from different localities and stratigraphic height
- We use those features to define morphotaxa that persist over geologic time



A New Era of Ancestors on Trees

• We expect to sample ancestors (especially indirect ancestors) from first principles



Proportion of species preserved (PP)

A New Era of Ancestors on Trees

- We expect to sample ancestors (especially *indirect ancestors*) from first principles
- Bayesian tip-dating and other methods let us quantify support for ancestor-descendant relationships
- Different methods seem to assign similar support

Sinornithoides young Ornithomimus_edmontonicus Erlikosaurus_andrewsi Microvenator celer Alxasaurus elesitaiensis Protopteryx_fengningensis Ingenia_yanshini Utahraptor_ostrommaysi IGM100_44_unnamedtroodontid Anchiomis huxlevi UnnamedOviraptorid Troodon formosus Compsognathus longipes Shuvuula desert Segnosaurus galbiensis Epidexipteryx_ningchengensis romaeosaurus albertensis Belplaosaurus inexpectus Patagonykus_puertai romithoides mongoliensis elecanimimus_polyodon Citipati osmolskae Khaan mckennai Archaeornithomimus_asiaticus Velociraptor_mongoliensis Sinornithosaurus millenii Eotyrannus_lengi Conchoraptor_gracilis Mei_long Gallimmus_bullatus Hagryphus giganteus Xiaotingia zhengi IndesDromaeosaurir aplocherius Caudiotervx namedDromaeosaurid Microraptor zhaoianus Garudimimus_brevipes Erliansaurus bellamanus Nanshiungosaurus brevispinus pidendrosaurus_ningchengensis Neimongosaurus yangi larpymimus_okladnikovi Unenlagia Struthiomimus_altus Bambiraptor feinberg zhousaurus_orientalis enfuciusomis sanctus Chirostenotes_pergracilis uitreraptor_gonzalezorum yrannosaurus_rex Coelurus fragilis Fanycolagreus_topwilsoni Wellnhoferia_grandis Elmisaurus rarus Nothronychus_mckinleyi Gorgosaurus libratus Falcarius utahensis Avimimus portentosus Archaeopteryx Tithographica Similicaudipteryx dasaurus_mongoliensis ncisivosaurus_gauthieri Sinovenator_changi iromitholestes langston rotarchaeoptervx robusta Oviraptor_philoceratops Dilong_paradoxus Byronosaurus_jaffei Ornitholestes hermanni Deinonychus_antirrhopus Atrociraptor marshall Zanabazar_junio Yanomis martin herizinosaurus_cheloniformis Sinrapto Sinosauropteryx_prima Sapeornis_chaoyangensis Rinchenia_mongoliensis Rahonavis_ostromi Mononykus_olecranus Jeholornis_prima Huaxiagnathus orientalis Heyuannia_huangi Deinocheirus mirificus Anserimimus_planinychus Alvarezsaurus calvoi Allosaurus Tragilis



. Lett



How often do we infer sampled ancestors in real fossil records? Which mode of differentiation is most common among persistent morphotaxa?

- Implications for our understanding of speciation, trait evolution, extent that taxonomic turnover could be inflated by pseudo-extinction
- Apply tip-dating to morphological matrices from the well-sampled marine invertebrate record
 - More than 35 pre-existing datasets; 26 examined today
 - Predominantly Paleozoic groups, such as brachiopods, graptolites, trilobites, crinoids, other echinoderms
 - Varying matrix size, taxonomic level (species vs genera), sampling schema (e.g. clade-focused vs interval focused)

Sampled-Ancestor Tip-Dating with the Fossilized Birth-Death Model in MrBayes



- Currently available tip-dating methods limited to considering taxon units as point occurrences in time
- To consider relationships among persistent morphotaxa, we treat first & last appearances as two separate taxon units, with identical morphological characters but different time of appearance
 - Functions for automating this are in R package paleotree







But this is just a single tree pulled from a very large posterior – need to measure and summarize these patterns across the posteriors







Proportion of Last Occurrences Placed as Sampled Ancestors



Paraphyletic Proportion of First-Last Pairs

The Pattern of Ancestor-Descendant Relationships

- Treating fossil morphotaxa as more than single OTUs sheds light on patterns of ancestor-descendant relationships
- Ancestor-descendant relationships considerably across different datasets
 - Effects of taxonomic practices? Sampling? Biological differences?

Thanks for listening! Questions?









'Budding'

Sigmocheilus pogonipensis-Sigmocheilus flabellifer

Pterocephalia concava-Pterocephalia sanctisabae

> Housia ovata-Housia vacuna

Parahousia subequalis-Parahousia constricta

Aphelaspis subditus-Dicanthopyge quadrata

> Aphelaspis haguei-Aphelaspis subditus

Strigambitus transversus-Strigambitus utahensis

Sigmocheilus notha-Sigmocheilus pogonipensis

Tumicephalus depressus-Housia ovata

Cernuolimbus laevifrons-Cernuolimbus depressus

Dicanthopyge quadrata-Dicanthopyge convergens

> Prehousia indenta-Prehousia alata

Dicanthopyge convergens-Dicanthopyge reductus

Aphelaspis longispina-Tumicephalus depressus

Dicanthopyge quadrata-Dicanthopyge reductus

Strigambitus utahensis-Strigambitus transversus



as Ancestor-Descendant Pair

Each pair is a stacked barplot

Dots indicate putative pairs

 Evidence for all a priori AD pairs,
& a few extra

cal3 finds very little support for anagenesis

> ➢ Given biases, perhaps entirely budding?

Bapst & Hopkins 2017



ime

The problem is, very rarely can we read the fossil record as literally as this







How do we infer the relationships among ancestors & their descendants, given the incompleteness of the fossil record?



Do morphotypes mainly arise from asymmetric cladogenetic change?





Notice that budding can look like anagenesis (but not *vice versa*) in an incomplete record



'Budding'

Gaps in Densely-Sampled **Fossil Records**



Sinoretiograptus Latest Katian

Bergstromgraptus Middle Darrwillian



- Closest relatives separated by a 15 to 20 million year gap in this lineage:
- Were the intermediates living *somewhere else*? Open ocean?

Maletz and Zhang, 2003; Vandenberg, 2003; C.E. Mitchell

In The Age Of Ancestor Inference...



- Different methods agree on placing ancestors [dinosaurs]
- Quantitative inferences agree with previous putative pairs of ancestor-descendants [trilobites]



(cal3 is an off-brand tip-dating lite)