Journal of Geek Studies

jgeekstudies.org

You're an oegopsid now: the phylogeny of squid kids from the future

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The main characters of Nintendo's 2015 video game *Splatoon* and its 2017 sequel *Splatoon* 2 are Inklings, a species of sapient cephalopod with the ability to transform between a humanoid form and a more traditional coleoid form. Also present are the Octarians: octopus descendants that take the role of enemies. Since the release of the Octo Expansion for *Splatoon* 2, the Octoling, a subspecies of Octarian with similar appearance and abilities to Inklings, has become playable. Both Inklings and Octolings are hyper-evolved descendants of modern cephalopods, having evolved after sea level rise drives humanity to extinction 12,000 years in the future.

Figure 1. Comparison between the cephalopods of *Splatoon* and real cephalopods. Clockwise from top left: an Inkling in squid form; a female Inkling in humanoid form; a male Octoling in humanoid form; an Octoling in octopus form; *Ommastrephes bartramii*; *Todarodes pacificus*; *Octopus vulgaris*; *Abralia veranyi*; *Thysanoteuthis rhombus*. (Inklings' and Octolings' official renders are a courtesy of Nintendo; other images are public domain, retrieved from Wikimedia Commons.).

Exactly which cephalopods Inklings and Octolings descended from is unknown. In-game lore posits that Inklings are descended from squids and Octolings are descended from octopuses. A previous article covering the cephalopods of *Splatoon* has suggested links to Ommastrephidae or Thysanoteuthidae for Inklings (Salvador & Cunha, 2016). Here, I set out to resolve the relationships of these cephalopods with phylogenetic analysis.

Usually, scientists would use molecular data, *i.e.*, DNA or protein sequences, to determine relationships among recent taxa. There have been numerous recent studies on the relationships of coleoid cephalopods based on molecular data (*e.g.*, Sanchez et al., 2018). However, since video game characters have no DNA, this cannot be applied here. Thus, only morphological and behavioral data can be used. Luckily, there have been morphological phylogenies of cephalopods in the past to build off of.

METHODS

To answer this question that nobody was really asking, I constructed a morphological dataset of cephalopods. This combines four previously-published morphological datasets (Young & Vechione, 1996; Voight, 1997; Lindgren et al., 2004; Sutton et al., 2016), as well as additional characters. I also added Inklings, Octolings, and nine extant squid genera to the dataset (Table 1): *Dosidicus*, *Eucleoteuthis*, *Hyaloteuthis*, *Lampdioteuthis*, *Lycoteuthis*, *Mesonychoteuthis*, *Todarodes*, *Todaropsis*, and *Watasenia*. "*Palaeoctopus pelagicus*" was removed because it isn't a cephalopod at all, but fragments of a fossil coelacanth (Schultze et al., 2010).

Table 1. List of OTUs and sources of data. Extinct taxa are denoted by the symbol (†) before the species name. New data is marked in bold. Note that inklings and octolings are fictional taxa.

Taxon	Source of morphological data
Abralia trigonura	Young & Vecchione, 1996; Sutton et al., 2015
Abraliopsis pfefferi	Lindgren et al., 2004
†*Actinosepia canadensis*	Sutton et al., 2015
Allonautilus scrobiculatus	Lindgren et al., 2004 [as *Nautilus scrobiculatus*]
Amphitretus pelagicus	Voight, 1997; Sutton et al., 2015
Ancistrocheirus lesueuri	Lindgren et al., 2004
Architeuthis dux	Lindgren et al., 2004; Sutton et al., 2015
Argonauta spp.	Voight, 1997 [*A. argo*]; Lindgren et al., 2004 [*A. nodosa*]; Sutton et al., 2015 [*A. nodosa*]
Bathypolypus arcticus	Voight, 1997; Lindgren et al., 2004
Bathyteuthis abyssicola	Young & Vecchione, 1996; Lindgren et al., 2004; Sutton et al., 2015
Batoteuthis skolops	Lindgren et al., 2004
†*Belemnotheutis antiquus*	Sutton et al., 2015
Bolitaena pygmaea	Voight, 1997 [as *Eledonella pygmaea*]
†*Boreopeltis sagittata*	Sutton et al., 2015
†*Boreopeltis smithi*	Sutton et al., 2015
Brachioteuthis sp.	Lindgren et al., 2004
Callistoctopus ornatus	Voight, 1997 [as *Octopus ornatus*]
Chiroteuthis veranyi	Lindgren et al., 2004
Chtenopteryx sicula	Lindgren et al., 2004; Sutton et al., 2015
Cirroteuthis muelleri	Voight, 1997
Cirrothauma murrayi	Lindgren et al., 2004; Sutton et al., 2015

Table 1. (cont.)

Taxon	Source of morphological data
Cistopus sp.	Voight, 1997
Cranchia scabra	Lindgren et al., 2004; Sutton et al., 2015
Cycloteuthis sirventi	Lindgren et al., 2004; Sutton et al., 2015
Discoteuthis laciniosa	Lindgren et al., 2004
†*Dorateuthis syriaca*	Sutton et al., 2015
Doryteuthis pealeii	Young & Vecchione, 1996 [as *Loligo pealei*]; Lindgren et al. 2004 [as *L. pealei*]; Sutton et al., 2015
Dosidicus gigas	**new data** (tolweb.org)
Eledone cirrhosa	Voight, 1997; Lindgren et al., 2004
Enoploteuthis spp.	Young & Vecchione, 1996 [*E. anapsis*]; Lindgren et al., 2004 [*E. leptura*]
†*Eoteuthoides caudata*	Sutton et al., 2015
Eucleoteuthis luminosa	**new data** (tolweb.org)
Filippovia knipovitchi	Lindgren et al., 2004 [as *Moroteuthis knipovitchi*]
FMNH 278064	Voight, 1997 [as FMNH 278064]
†*Geopeltis simplex*	Sutton et al., 2015
†*Glyphidopsis waagei*	Sutton et al., 2015
†*Glyphiteuthis abisaadiorum*	Sutton et al., 2015
†*Glyphiteuthis freijii*	Sutton et al., 2015
†*Glyphiteuthis libanotica*	Sutton et al., 2015
†*Glypthiteuthis minor*	Sutton et al., 2015
†*Glyphiteuthis ornata*	Sutton et al., 2015
†*Glyphiteuthis rhinopora*	Sutton et al., 2015
Gonatus antarctus	Young & Vecchione, 1996; Lindgren et al., 2004; Sutton et al., 2015
Graneledone spp.	Voight, 1997 [*G. pacifica*] ; Lindgren et al., 2004 [*G. verrucosa*]
Grimpoteuthis bathynectes	Voight, 1997
Haliphron atlanticus	Voight, 1997; Lindgren et al., 2004; Sutton et al., 2015
Hapalochlaena lunulata	Voight, 1997
Heteroteuthis hawaiiensis	Lindgren et al., 2004; Sutton et al., 2015
†*Hibolithes semisulcatus*	Sutton et al., 2015
Histioteuthis celetaria	Sutton et al., 2015
Histioteuthis corona	Lindgren et al., 2004; Sutton et al., 2015
Histioteuthis reversa	Lindgren et al., 2004
Hyaloteuthis pelagica	**new data** (tolweb.org)
Idiosepius pygmaeus	Lindgren et al., 2004; Sutton et al., 2015
Illex spp.	Young & Vecchione, 1996 [*I. illecebrosus*]; Lindgren et al., 2004 [*I. coindeti*]
Japetella diaphana	Young & Vecchione, 1996; Voight, 1997; Lindgren et al., 2004; Sutton et al., 2015
Japetella heathi	Young & Vecchione, 1996
†*Jeletzkya douglassae*	Sutton et al., 2015
†*Jeletzkyteuthis coriaceus*	Sutton et al., 2015
Joubiniteuthis portieri	Lindgren et al., 2004
†*Keuppia hyperbolaris*	Sutton et al., 2015

Table 1. (cont.)

Taxon	Source of morphological data
†*Keuppia levante*	Sutton et al., 2015
Lampadioteuthis megaleia	**new data** (tolweb.org)
Leachia atlantica	Lindgren et al., 2004
Lepidoteuthis grimaldii	Lindgren et al., 2004; Sutton et al., 2015
†*Leptoteuthis gigas*	Sutton et al., 2015
†*Loligosepia aalensis*	Sutton et al., 2015
†*Loliogsepia bucklandi*	Sutton et al., 2015
Lolliguncula brevis	Young & Vecchione, 1996
Lycoteuthis sp.	**new data** (tolweb.org)
Macrotritopus horridus	Voight, 1997
†*Marekites vinarensis*	Sutton et al., 2015
Mastigoteuthis agassizi	Lindgren et al., 2004; Sutton et al., 2015
†*Muensterella scutellaris*	Sutton et al., 2015
Muusoctopus hokkaidensis	Voight, 1997 [as *Benthoctopus hokkaidensis*]; Lindgren et al., 2004 [as *Benthoctopus* sp.]
Nautilus pompilius	Young & Vecchione, 1996; Lindgren et al., 2004; Sutton et al., 2015
Neoteuthis thielei	Lindgren et al., 2004
Octopoteuthis sicula	Lindgren et al., 2004; Sutton et al., 2015
Octopus spp.	Young & Vecchione, 1996 [*O. vulgaris*]; Voight, 1997 [*O. bimaculatus*]; Sutton et al., 2015 [*O. vulgaris*]
Ocythoe tuberculata	Young & Vecchione, 1996; Voight, 1997; Sutton et al., 2015
Ommastrephes bartramii	Young & Vecchione, 1996; Lindgren et al., 2004; Sutton et al., 2015
Onychoteuthis banksii	Young & Vecchione, 1996; Sutton et al., 2015
Opisthoteuthis agassizi	Young & Vecchione, 1996; Voight, 1997; Sutton et al., 2015
Opisthoteuthis californiana	Young & Vecchione, 1996; Voight, 1997
Opisthoteuthis sp.	Lindgren et al., 2004
Ornithoteuthis antillarum	Lindgren et al., 2004
†*Palaeoctopus newboldi*	Sutton et al., 2015
†*Palaeololigo oblongata*	Sutton et al., 2015
†*Parabelopeltis flexuosa*	Sutton et al., 2015
Pareledone charcoti	Voight, 1997
†*Phragmoteuthis bisinuata*	Sutton et al., 2015
†*Plesioteuthis prisca*	Sutton et al., 2015
†*Plesioteuthis subovata*	Sutton et al., 2015
†*Pohlsepia mazonensis*	Sutton et al., 2015
Psychroteuthus sp.	Lindgren et al., 2004
Pteroctopus tetracirrhus	Voight, 1997
Pterygioteuthis gemmata	Lindgren et al., 2004
Pyroteuthis margaritifera	Lindgren et al., 2004
†*Rachiteuthis donovani*	Sutton et al., 2015
Robsonella fontanaia	Voight, 1997
Rossia spp.	Young & Vecchione, 1996 [*R. pacifica*]; Lindgren et al., 2004 [*R. palpebrosa*]; Sutton et al. 2015 [*R. pacifica*]

Table 1. (cont.)

Taxon	Source of morphological data
Scaeurgus unicirrhus	Voight, 1997
†*Senefelderiteuthis tricarinata*	Sutton et al., 2015
Sepia officinalis	Young & Vecchione, 1996; Lindgren et al., 2004; Sutton et al., 2015
Sepiella inermis	Lindgren et al., 2004
Sepiola spp.	Young & Vecchione, 1996 [*S. atlantica*]; Lindgren et al., 2004 [*S. affinis*]
Sepioteuthis spp.	Young & Vecchione, 1996 [*S. sepioidea*]; Lindgren et al., 2004 [*S. lessoniana*]
Spirula spirula	Young & Vecchione, 1996; Lindgren et al., 2004; Sutton et al., 2015
Stauroteuthis syrtensis	Young & Vecchione, 1996; Lindgren et al., 2004; Sutton et al., 2015
Sthenoteuthis oualaniensis	Lindgren et al., 2004
Stigmatoteuthis hoylei	Lindgren et al., 2004 [as *Histioteuthis hoylei*]
Stoloteuthis leucoptera	Lindgren et al., 2004
†*Styletoctopus* aff. *annae*	Sutton et al., 2015
†*Styloteuthis convexa*	Sutton et al., 2015
Tetracheledone spinicirris	Voight, 1997
†*Teudopsinia haasi*	Sutton et al., 2015
†*Teudopsis bollensis*	Sutton et al., 2015
†*Teudopsis bunellii*	Sutton et al., 2015
†*Teudopsis jeletzkyi*	Sutton et al., 2015
†*Teudopsis subcostata*	Sutton et al., 2015
Thaumeledone guntheri	Lindgren et al., 2004
Thysanoteuthis rhombus	Young & Vecchione, 1996; Sutton et al., 2015
Todarodes spp.	**new data** (tolweb.org)
Todaropsis eblanae	**new data** (tolweb.org)
†*Trachyteuthis bacchiai*	Sutton et al., 2015
†*Trachyteuthsis covacevichi*	Sutton et al., 2015
†*Trachyteuthis hastiformis*	Sutton et al., 2015
†*Trachyteuthis nusplingensis*	Sutton et al., 2015
†*Trachyteuthis teudopsiformis*	Sutton et al., 2015
Tremoctopus violaceus	Voight, 1997
Uroteuthis chinensis	Lindgren et al., 2004 [as *Loligo formosana*]
†*Vampyronassa rhodanica*	Sutton et al., 2015
Vampyroteuthis infernalis	Young & Vecchione, 1996; Voight, 1997; Lindgren et al., 2004; Sutton et al., 2015
Velodona togata	Voight, 1997
Vitreledonella richardi	Voight, 1997
Watasenia scintillans	**new data** (tolweb.org)
Inkling	**new data** (Nintendo, 2015, 2017, 2018)
Octoling	**new data** (Nintendo, 2018)

A few species in the same genera were lumped due to either having identical codings or in the name of having more complete Operational Taxonomic Units, or OTUs (several were coded in one dataset and not the others). Most Octarians have highly unorthodox morphology compared to Inklings or Octolings, and were excluded because how do you code a tentacle with a face? The resulting dataset has 283 characters and 139 OTUs.

I ran analyses in TNT (Goboloff & Catalano, 2016) using equal weighting methodology for 2000 replicates, producing 10 trees each. I ran one analysis with no constraints and one with a "molecular backbone" – forcing the analysis to fit a certain topology corresponding to what molecular phylogenies tell us. The framework of Sanchez et al. (2018) was used for the backbone analysis. This way, the trees can be built around how certain taxa are related, while the morphological data plots where those without molecular data would be. The outgroup taxon was *Nautilus pompilius*.

RESULTS AND DISCUSSION

Surprisingly, *contra* in-game lore, Inklings and Octolings are consistently recovered as sister taxa. The two species are united by numerous features, mostly having to do with living on land and shooting ink everywhere. Feasibly, these could have evolved independently, but compared to other NPC species in the game, the similarities between these two are striking. If this is true, this may make their rivalry analogous to that which may have occurred between Neanderthals and anatomically modern humans in the Pleistocene (Finlayson & Carrión, 2007) in response to environmental change (changing sea levels and climate change, respectively). This may also explain why most Octarians are so different from Octolings – they may have *actually* descended from octopuses, and gone down a completely different evolutionary path towards sapience and land-living. It is canon that Octolings were brainwashed into serving the Octarian army, so this might imply that the Octarian-Octoling link is largely fabricated. Of course, that adds a layer of in-game cultural implications that is out of the scope of this paper.

In all analyses, both species ended up well inside Ommastrephidae, the flying squids. This fits with what we know of Inkling biology. As previously noted by Salvador & Cunha (2016), the leaping ability of Inklings in squid form ("super jump"), demonstrated in *Splatoon*, *Splatoon 2*, and *Super Smash Bros. Ultimate*, may be exapted from the tendency of flying squids to jump above the surface of water. Inklings are also bioluminescent, a trait shared with certain members of Ommastrephidae, including *Ommastrephes* itself. The unusual octopus-like form of the Octoling may be convergent evolution with Octopoda; Octolings display the same "super jump", not known in any octopods, and similar awkward terrestrial locomotion in coleoid form (in contrast to the Octarians).

But aside from being a fun and way too time-consuming exercise in phylogenetics, what does this tell us? Our results echo the suggestions of Salvador & Cunha (2016) that the design of Inklings was likely heavily influenced by ommastrephid squids that live in Japanese waters, such as *Todarodes pacificus* and *Ommastrephes bartramii*. This shows that the designers of the *Splatoon* franchise likely deliberately modeled this game's characters after specific cephalopod species (echoed in the fact that the Japanese names of several characters reference specific real-world species). Nintendo certainly knows their squids.

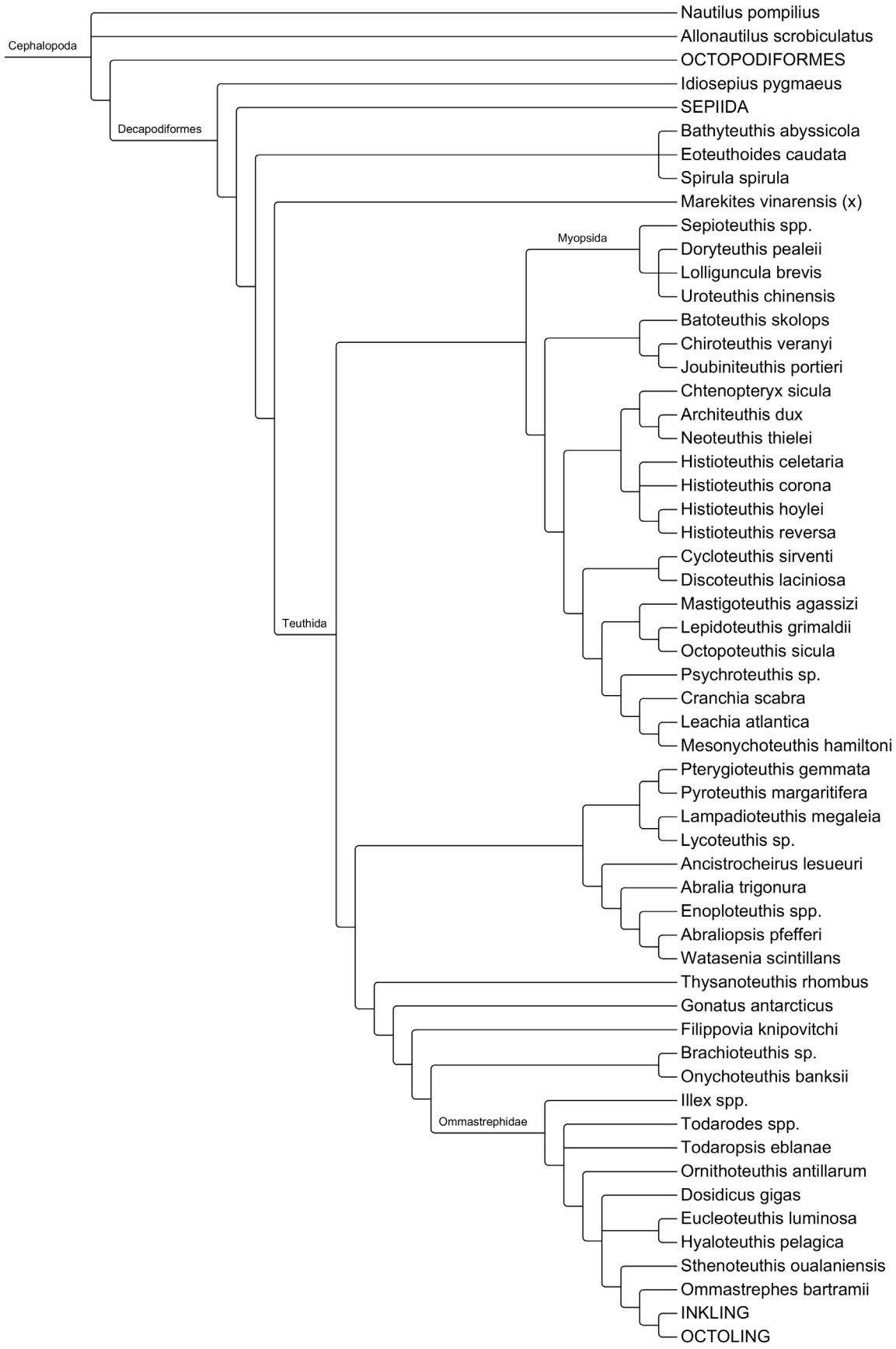

Figure 2. Strict consensus tree of the "spineless" analysis, with *Pohlsepia* removed *a posteriori* because it was unstable.

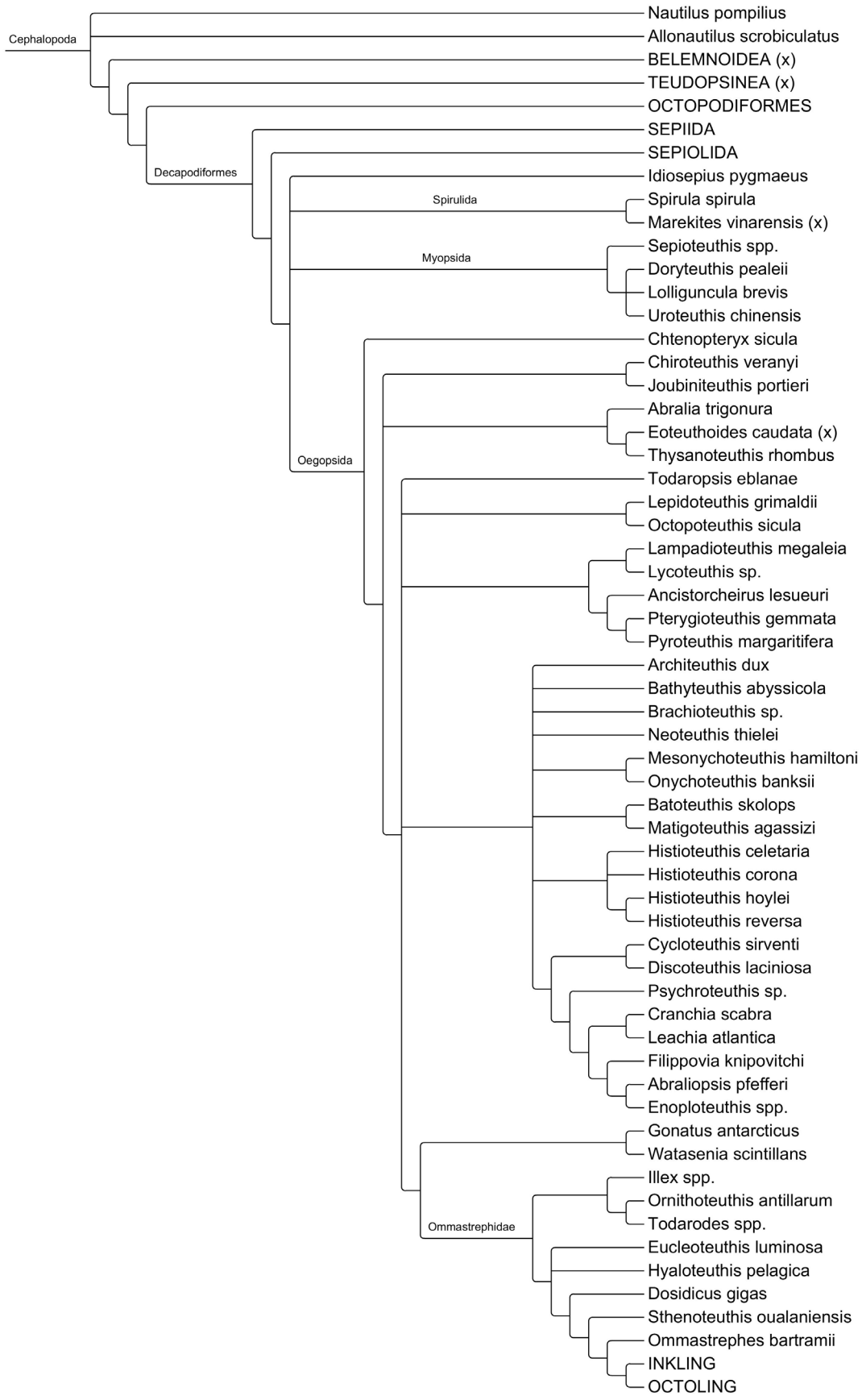

Figure 3. Strict consensus tree of the analysis with a molecular backbone constraint applied.

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Materials and data

Because the author lives approximately 10,000 years before the evolution of either Inklings or Octolings, he was unable to access any for study. However, he was able to access relevant game models and amiibos in private collections for the collection of morphological data. He also adopted a Sanei Inkling boy plush during the preparation of this manuscript.

Acknowledgements

Props to Nintendo for making this awesome franchise in the first place, and to an anonymous friend/reviewer for trying to dissuade me from doing this silly project.

About the author

Henry Thomas is a biology student at the University of California, Berkeley. He mostly studies pterosaurs, but also dabbles in the phylogeny of other creatures, regardless of whether or not they exist.