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Euarthropod diversity in *Pokémon*: searching for the ancestral type

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Euarthropoda, including living (extant) groups like insects and arachnids, extinct groups like trilobites, and stem-group taxa (species diverging earlier on the evolutionary tree), is the most diverse animal group on the planet. Since the early Cambrian, Euarthropoda has been the most diverse and abundant group of animals ever to have lived (Giribet & Edgecombe, 2019). They have fundamentally impacted the evolution of Earth's environments and of other animal groups, and remain crucial for healthy ecosystem-functioning and to human societies. Given their importance, it is no surprise that euarthropod taxa are frequently represented in human culture. This extends to their representation in video games, and, in particular, their diversity of forms found within the *Pokémon* biosphere (The Pokémon Company, 1996–present).

Here, I present a taxonomic assessment of the euarthropod Pokémon up to the most recent generation (Gen. IX), place them in a cladistic framework based on real-world euarthropod phylogenetic analyses (that is, analyses about their evolutionary history and relationships), and reconstruct the ancestral primary type of euarthropod Pokémon. This allows for comparison to the biodiversity and morphological disparity of real-world Euarthropoda, and for demonstration of how we reconstruct ancestral characteristics using the fossil record.

METHODOLOGY

Taxonomic assignments were made to order-level based on observations of the morphological characteristics of the Pokémon using their official game models, the descriptions on Bulbapedia (https://bulbagarden.net/), and the taxonomic assignments presented in Prado & Almeida (2017). Some groups were not represented at the order-level; for trilobites (class Trilobita) and centipedes (class Chilopoda) the only representative Pokémon were not assignable to orders. Several assignments were changed from Prado & Almeida (2017), and new taxa were added from subsequent Pokémon generations. Additionally, Celebi and Pupitar were removed from the Euarthropoda – the former because only its wings suggest a euarthropod association (with wing structures being polyphyletic in animals) and it has an otherwise mythical 'fairy-like' appearance, and the latter because its pre- and post-evolutions are both reptilian, with Pupitar thus being apparently a reptilian animal irrespective of its arthropod-like exoskeleton.

The cladogram topology (that is, the diagram showing evolutionary relationships) was extracted from phylogenetic analyses of real-world euarthropods (Misof et al., 2014; Giribet & Edgecombe, 2019). Due to high levels of uncertainty around the broader evolutionary relationships of trilobites (e.g., Lieberman & Karim, 2010; Chip-

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man, 2015; Scholtz et al., 2019), the position of Trilobita reflects just one hypothetical placement. The tree was drawn using *iTOL: Interactive Tree of Life* (Letunic & Bork, 2024), with the tree topology defined in Newick format as:

> *((((Pedunculata, Decapoda), ((((((Diptera, Lepidoptera), (Coleoptera, Neuroptera)), Hymenoptera), Hemiptera), (((Blattodea, Mantodea), Phasmatodea), Orthoptera)), Odonata)), Chilopoda), ((Araneae, Scorpiones), Xiphosura)), Trilobita), Radiodonta);*

Ancestral state reconstructions were based on the primary type of each Pokémon. An assessment of ancestral state hypotheses was made using parsimony principles (i.e., based on the least number of evolutionary changes required given the cladogram's topology).

TAXONOMIC DIVERSITY AND MORPHOLOGICAL DISPARITY

107 euarthropod taxa are currently represented in the Pokémon global biodiversity, out of a total of 1025 taxa at writing (=10% of taxa). This is highly unrepresentative of Earth's extant animal biodiversity, with an estimated ~80% being arthropodan; there are 1,214,295 (Zhang, 2011) or 1,240,007 (IUCN, 2024) described arthropod species versus 1,565,919 described animal species in total (IUCN, 2024). Additionally, most arthropod species are undescribed, with estimates of living terrestrial arthropod biodiversity suggesting around 7 million taxa total (Stork, 2017). Although a Pokédex comparable to Earth's biosphere would lead to an 'insect Poké-world' with rather less morphological disparity, and this underrepresentation likely results from the low popularity of most euarthropodan Pokémon (see Le Vaillant, 2020). Within *Pokémon*, most euarthropod taxa are hexapods (more specifically, insects; Fig. 1), which corresponds with real-world diversity studies and estimates. Liria et al. (2020) found hexapods represent 92% of global terrestrial arthropod occurrences, while Zhang (2011) noted hexapods are 84% of described arthropod taxa total.

Amongst hexapod Pokémon, Lepidoptera (butterflies, moths) are overrepresented at 27% of taxa. Coleoptera (beetles)

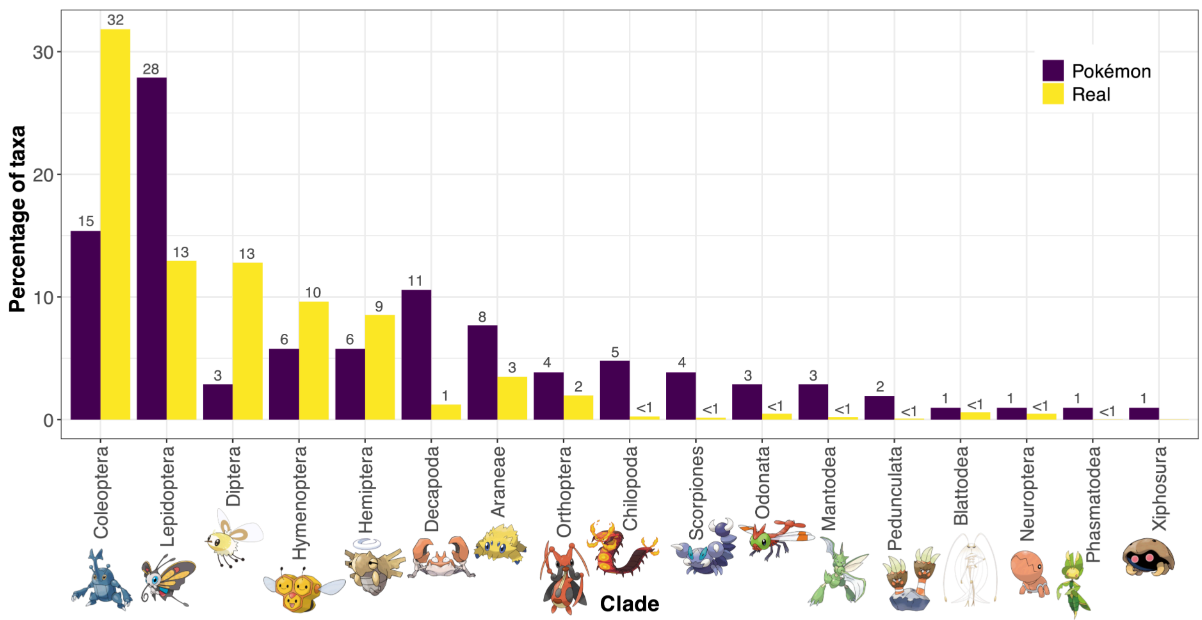

Figure 1. Comparison of the real-world (yellow) and Pokémon (purple) diversity for the different euarthropod groups represented amongst Pokémon taxa. Diversity is calculated as being the percentage of taxa the group represents out of the total of all Euarthropoda; rounded percentages are given above each bar. Images represent one Pokémon taxon for each group. The Pokémon images, extracted from Bulbapedia, are official artworks employed here under fair use.

are the second most diverse Pokémon group at 15% of taxa, with Decapoda (crabs, lobsters) third at 10% (Fig. 1). However, in terms of their real-world diversities, the numbers of lepidopteran and coleopteran Pokémon should be reversed, with Coleoptera being the most diverse real-world arthropodan group at 32% of taxa (386,500 species, Zhang, 2011) and lepidopterans at 13% (157,338, Zhang, 2011) (Fig. 1). This imbalance presumably reflects the greater appeal of butterflies and moths to beetles in the public eye. The Decapoda are also overrepresented in the Poké-world at 10% of taxa compared to ~1% of real-world species (14,898 species; Ahyong et al., 2011); this may result from the important role ascribed to decapod crustaceans in many cultures (e.g., as a food source), particularly in Japan. The other hexapod groups (Diptera, flies; Hymenoptera, bees, wasps, ants; Hemiptera, true bugs) are, like the Coleoptera, underrepresented in the Pokémon world (Fig. 1); all have >100,000 species (13%, 10%, 9% of euarthropod taxa respectively) in the real world (Zhang, 2011). In comparison, many non-hexapod groups are, like Decapoda, overrepresented amongst Pokémon; Araneae (spiders) are 8% of Pokémon euarthropods (42,473 species real-world; Zhang, 2011), Scorpiones 4% (1947 species; Zhang, 2011), and Chilopoda (centipedes) 5% (3100 species; Zhang, 2011). From the perspective of the fossil record, trilobites are massively underrepresented in the Pokémon world, having >20,000 described real species (Adrain, 2011), with many more still undescribed. Perhaps this is because their single representative, Kabutops, is intended to represent a fictional survival of trilobites hanging on to the modern day (a 'Dead Clade Walking'; Barnes et al., 2021).

Certain Pokémon taxa were more problematic in terms of their taxonomic assignments. Trapinch and Vibrava are clearly arthropods (Neuroptera, the antlions, and Odonata, dragonflies, respectively), though their final evolutionary form, Flygon, has an overwhelmingly reptilian morphology, with one pair of wings and four limbs in an overall dragon-like appearance. In comparison, the prior form Vibrava is classically dragonfly-like with two pairs of wings, paired antennae, insectoid limbs, and a segmented body. Pineco is a bagworm moth larva (Lepidoptera) in light of its morphology and behaviour of agglutinating bark and hanging from tree branches, mimicking the appearance of a pinecone, though its subsequent form Forestress has a less-euarthropodan appearance resulting from external plates and spines with a morphology unlike that of an exoskeleton. However, with no internal anatomical information available, we can assume Forestress is also a bagworm made of different agglutinated materials. Gligar and Gliscor are scorpion-like based on their limb morphology and stinger tails, though represent a novel life mode and adaptations for Scorpiones in being able to fly. This characteristic is presumably homoplasic, that is, evolved independently to flight in other euarthropodan groups. Fomantis and Lurantis are not considered euarthropodan based on their morphologies, descriptions, and names. 'Fomantis' seems to originate from the words 'faux' (false) and 'mantis', while Lurantis evokes either a 'lure' or 'fleur' (flower). Both appear to be comprised of plant material that mimics the look of mantids, are able to photosynthesise, and are single-type Grass Pokémon.

An interesting feature is the lack of morphological disparity within certain euarthropod Pokémon groups, particularly the Decapoda. Taking this representation to be a result of the way decapod crustaceans are viewed in the public eye, these Pokémon are all generically crab- or lobster-like, with a very limited colour palette – most decapod taxa are orange, with two being shades of blue. This strongly contrasts the real-world scenario, in which decapods are morphologically disparate and found in all manner of colour palettes. Similarly, Myriapoda is represented in the Pokémon universe by only centipede-like forms (Chilopoda) with a single pair of legs per body segment; no millipede (Diplopoda) forms seem to exist, despite being more diverse in the real-world (Zhang, 2011). The Pokémon chilopods also reflect only a sin-

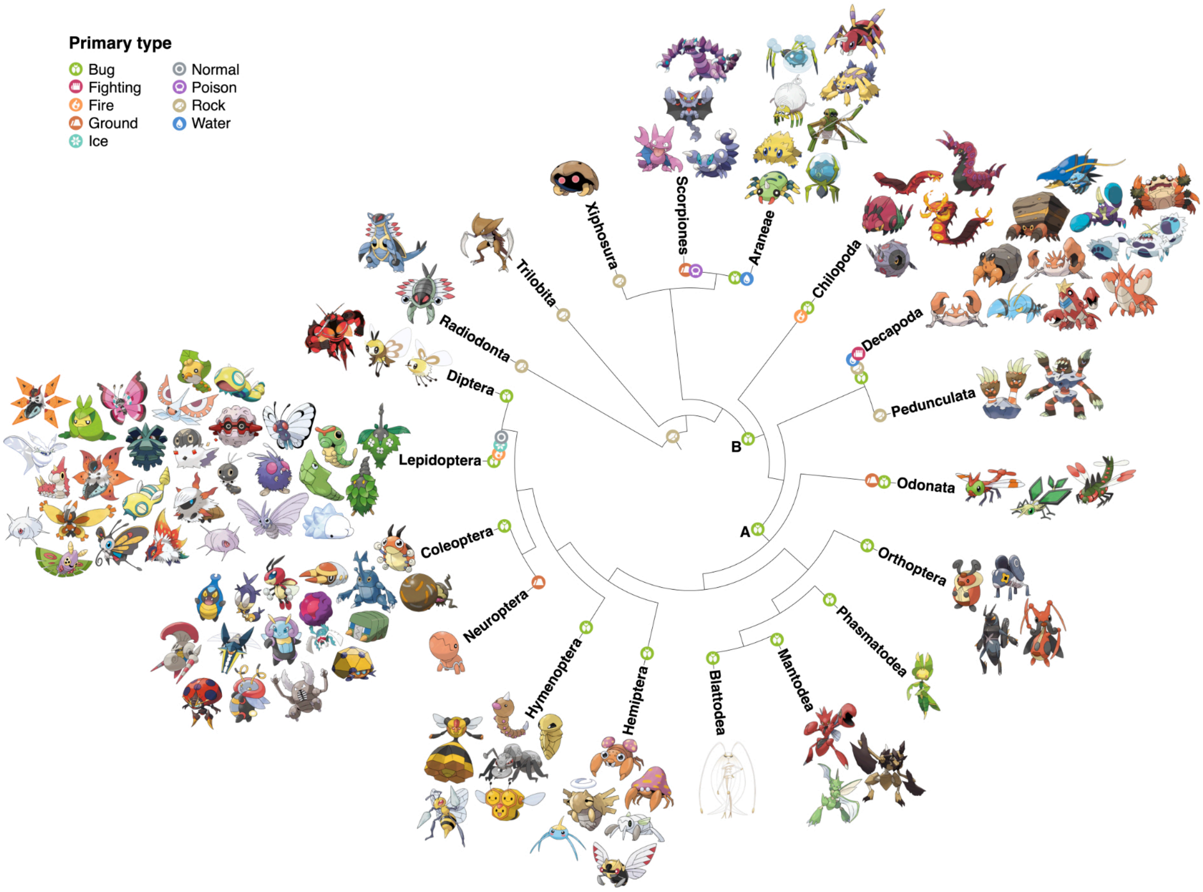

Figure 2. Cladogram of euarthropod Pokémon, with their evolutionary relationships derived from phylogenetic analyses of real-world taxa (see Misof et al., 2014; Giribet & Edgecombe, 2019). Images represent all Pokémon taxa present in each group. All group primary types are also displayed (see legend), and ancestral type state changes displayed at key nodes. A and B represent the two hypotheses for the shift to Bug-type, requiring an identical number of total step changes across the cladogram. The Pokémon images and Type symbols, extracted from Bulbapedia, are official artworks employed here under fair use.

gle colour palette, being predominantly red. Pokémon Scorpiones also reveal the public view of real-world scorpions, being purple-coloured and usually poison-type. We can thereby glean insights from cultural properties like Pokémon into the public perception of euarthropods in our living world (for a more detailed study of Pokémon perceptions and preferences, see Le Vaillant, 2020).

ANCESTRAL TYPE RECONSTRUCTION

Bug is by far the most common type for euarthropod, and particularly hexapod, Pokémon. This is somewhat circular, with the bug-type presumably originating in the Pokémon biosphere as a way of describing the morphologies and behaviours of the Gen. I hexapods (e.g., Caterpie). It is therefore likely that the earliest hexapod Pokémon were bugs, with Bug type being ancestral to the group and the occurrences of other types (Ground, Fire, Ice, and Normal) representing singular autapomorphies (Fig. 2). Based on it being the most common type, the decapods seem to be predominantly Water-types, though crustaceans may be ancestrally Rock-type as the Pedunculata are also Rock-type (Fig. 2). The Chelicerata (Xiphosura, Scorpiones and Araneae) are notably variable in their type designations (Fig. 2).

Of particular interest is the ancestral (original) type of Euarthropoda Pokémon. Owing to the inclusion of Radiodonta and Trilobita (both real-world extinct groups), the tree suggests the evolution of arthropod taxa from a Rock-type ancestry (Fig. 2), which is conducive with the next diverging group likely being Xiphosura, also Rock-type (horseshoe crabs, with their earliest real-world representatives roughly contemporaneous with trilobites and radiodonts; see Lamsdell, 2019). Given the type of Xiphosura and reasonably certain stem-euarthropod position of Radiodonta (Zheng et al., 2020), this result seems robust to whether Trilobita are in this position in the tree or closer to Mandibulata (i.e., Chilopoda to Hexapoda). However, this may also represent an instance of circularity ('circular evolution'?), as the 'fossil' Pokémon (i.e., trilobites and radiodonts) are presumably Rock-type owing to their original resurrection in-game from actual fossil specimens, *Jurassic Park*-style.

Importantly, this finding mirrors the importance of including extinct taxa in real-world studies of ancestral state reconstructions (e.g., Joy et al., 2016). Without the extinct Radiodonta and Trilobita, it would be more parsimonious to conclude that the ancestral type of euarthropod Pokémon was Bug, with one fewer type-change required on the resulting tree than for a Rock-type origin. With the inclusion of these fossil groups, the tree reveals that euarthropod Pokémon likely diverged from a Rock-type ancestor (Fig. 2).

Following their probable Rock-type origin, there are two hypotheses for the euarthropod Pokémon transition to predominantly Bug-type: (1) the ancestral Rock-type lingered until the split within Pancrustacea between Hexapoda and all other groups (Fig. 2: node A); and (2) Bug-type originated earlier at the divergence between Chelicerata (arachnids, etc.) and Mandibulata (Fig. 2: node B). Both hypotheses require 15 type changes along the tree presented in Figure 2, and so are equally plausible under a parsimony assessment.

SUMMARY

10% of Pokémon taxa clearly represent morphological and behavioural characteristics of real-world extant and fossil Euarthropoda. As such, these taxa can be taxonomically classified using our existing nomenclature and placed on a cladogram representing their hypothetical evolutionary relationships. In this way, we can reconstruct ancestral states of euarthropod Pokémon, such as their primary type, and better understand the evolutionary patterns inherent in the Pokémon world, understanding that the methods and problems involved mirror those for the biosphere of our natural world.

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