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*Scorpions: Fossil Record, Biome Diversity, Cuticle Traits, Phylogeny, and Terrestrialisation*

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## **Scorpions: Fossil Record, Biome Diversity, Cuticle Traits, Phylogeny, and Terrestrialisation**

### **Summary**

Poor fossilisation hinders our understanding of arthropod terrestrialisation. However, scorpions, with chemically resistant cuticular material dating to the Silurian (~444 Mya), uniquely enable study of arthropod terrestrialisation through analysis of anatomical change over time. Unlike other arthropods, scorpions have not returned to water, potentially due to aquaporin presence/absence. Additionally, Palaeozoic scorpions are unusually diverse, possibly due to a genuine radiation, though biases like moult/carcass identification errors and phylogenetic uncertainties exist. Recognising bias is crucial for understanding early terrestrial fauna, as arthropods, including scorpions, contributed significantly to Palaeozoic animal diversity. Therefore, Howard's (2021) total-evidence phylogeny, which most accurately places scorpion species in Buthida or Iurida clades, should be used in future diversity studies. Surprisingly, Legg *et al.*, (2012) suggested Palaeozoic scorpions were not diverse at all considering biome distribution. Here, I globally map scorpion fossils to accept this hypothesis. Consistently high Margalef diversity values in Palaeozoic (1.28) and Mesozoic/Cenozoic (1.26) arid biomes are suggestive of *in situ* desert scorpion evolution, and previous biased Palaeozoic diversity measures. Palaeozoic (1.07) and Mesozoic/Cenozoic (0.145) tropical scorpions have lower diversity, possibly due to vegetation survival. Confirming this requires future research combining tropical palaeobotanical and scorpion fossils.

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## 1 Introduction

Early arthropods were crucial to past ecological networks, with Devonian and Carboniferous scorpions being significant terrestrial predators (Aria, 2022). Extant scorpions still significantly predate insects, particularly in warm terrestrial deserts and tropical rainforests (Wood, 2019). However, debates surround Palaeozoic scorpion distribution, with chemically unique, well-preserved, Silurian cuticular fossils suggesting potential aquatic ancestry (Jeram, 1989). Hence, the scorpion fossil record may be vital for understanding terrestrialisation, often hindered by large evolutionary barriers between water and land (Kazlev, 2002). Nevertheless, Palaeozoic arthropod groups independently terrestrialised multiple times, significantly increasing faunal diversity (Shear and Kukalova-Peck, 1990).

Even so, Palaeozoic scorpions were unusually diverse compared to Mesozoic/Cenozoic scorpions (Jeram, 1989). Validating these diversity measures is critical for comprehending past and present scorpion ecological impacts (Coelho *et al.*, 2022), despite challenges linked to potential bias. Species misidentification within scorpion phylogenies may inflate diversity measures, distorting interpretations of shared evolutionary histories and adaptations for terrestrialisation among supposedly related species (Kjellesvig-Waering, 1986). Additionally, Palaeozoic scorpion diversity might be limited when considering biome distribution (Legg *et al.*, 2012). This hypothesis remains unexplored.

This dissertation explores scorpion fossil finds, cuticle composition, phylogeny, and terrestrialisation. It globally maps scorpion distribution over time to quantitatively analyse the palaeobiome hypothesis. Key points are: (1) Palaeozoic scorpion fossils spark debate on true diversity versus fossil record bias; (2) Chemically resistant scorpion cuticle fossilises exceptionally; (3) Howard's (2021) total-evidence phylogeny most accurately places scorpions into Buthida or Iurida clades; (4) Scorpion ancestral aquatic habits are debated, and; (5) Scorpion diversity peaks in arid biomes, likely due to allopatric speciation.

## **2 The scorpion fossil record**

Despite being listed since the Palaeozoic, fossil scorpions are rare (Lourenco and Gall, 2004). While numerous fossil scorpions are fragmentary (see 3.1), most scorpion palaeodiversity is linked to exceptionally preserved complete fossils discovered in Konservat-Lagerstätten (Howard, 2021). Silurian scorpions from the volcanoclastic Scottish Midlothian Pentland Hills (Lamsdell, 2012) and Triassic scorpions in temporary pools of the French Grès à Voltzia Formation (Briggs and Gall, 1990) are notable examples. Here I provide a general overview of scorpion fossil finds by geological period.

### **2.1 Palaeozoic**

#### **2.1.1 Silurian**

*Dolichophonus loudonesis* from the Scottish Pentland Hills is likely the oldest scorpion (Telychian) (Laurie, 1899). However, identifying the earliest fossil scorpion is contentious due to the potential existence of undiscovered earlier group members. To address this, flexible dating methods called soft maxima that use confidence intervals in the focal clade can be used. These imply scorpions potentially existed in the Early Silurian/Ordovician (Dunlop *et al.*, 2016; Howard *et al.*, 2019). Future research should combine soft maxima with fossil hard minimum age constraints to more accurately estimate the first appearance of scorpions (Howard., 2021).

#### **2.1.2 Devonian**

Early Devonian *Palaeohelcura* trackways in Antarctica may have been created by large terrestrial scorpions like *Brontoscorpio* or *Praearcturus*. The deposition environment—subaqueous or in temporary emergent settings—is unclear (Rolfe and Lawson, 1985). To determine deposition, experiments akin to Brady (1947) comparing *Palaeohelcura* trackways to modern scorpion trails are needed (Bradshaw, 1981). A notable Late Devonian discovery is *Gondwanascorpio*, the first Gondwanan terrestrial animal (Gess, 2013). *Gondwanascorpio* strongly resembles Laurasian taxa, suggesting increased global homogenisation during the Late Devonian, possibly due to Gondwana's increased proximity to Laurasia (Gess, 2013).

#### **2.1.3 Carboniferous**

The Carboniferous Coal Measures contain a remarkable diversity of 3D-preserved scorpions, with over sixty species found (Legg *et al.*, 2012; Dunlop *et al.*, 2016). Questions persist about whether this diversity reflects a true period of radiation or if it is an artefact of the fossil record

(Dunlop, 2008b). Despite uncertainties, the Carboniferous appears pivotal for scorpions, hosting all three major lineages—palaeo-, meso-, and neoscorpions. Thus, higher Carboniferous diversity could truly reflect a wider range of scorpion body plans (Jeram, 1993). The stronger hypothesis is elusive as the relative impact of poor taxonomic practices versus biases in the fossil record (see 2.3) cannot be quantified. Future models recognising progressively more derived clades with higher resolution (e.g., Legg *et al.*, 2012), should be built upon to resolve this issue (Dunlop *et al.*, 2016).

#### **2.1.4 Permian**

Limited material obscures aspects of Permian scorpion evolution, ecology and habitat. However, a complete scorpion fossil from Germany indicates that certain lineages extended from the Carboniferous into the Permian, with basal and derived forms coexisting from the Late Carboniferous to at least the mid-Triassic (Martine *et al.*, 2020; Dunlop *et al.*, 2016).

### **2.2 Mesozoic and Cenozoic**

#### **2.2.1 Triassic, Jurassic and Cretaceous**

Triassic, Jurassic, and Cretaceous scorpion fossils preserved in amber are rare. Triassic fossils suggest recovery of terrestrial forms after the Late-Permian mass extinction (Lourenco and Gall, 2004; Magnani *et al.*, 2022). Jurassic scorpions hinder accurate taxonomic assignment due to frequent misidentification (Dunlop *et al.*, 2016). Cretaceous fossils, like Chactidae from the Crato Formation, Brazil, and Palaeoburmesebuthidae from Burmese amber, provide evidence for modern and extinct scorpion families (Menon, 2007; Xuan *et al.*, 2022).

#### **2.2.2 Palaeogene, Neogene and Quaternary**

Palaeogene fossil scorpions have been found in Baltic amber, although they may be older due to potential redeposition (Lourenco, 2023). Neogene amber deposits in Mexico and the Caribbean preserve Buthid scorpions (Riquelme *et al.*, 2015). Quaternary fossils from Madagascar and Columbia are found in copal (Lourenco, 2009; Lourenco and Weitschat, 2005).

### **2.3 Scorpion distribution and diversity by palaeobiome**

While the fossil record of most extant arthropods is skewed towards the Cenozoic (Dunlop *et al.*, 2008b), scorpions exhibit greater diversity in the Palaeozoic, with 81 species compared to 39 Mesozoic and 27 Cenozoic species (Viaretti *et al.*, 2023). It remains unknown whether these observations reflect true diversity levels. Bias may stem from the differing preservation

potentials of cuticles from different arthropod groups (see 3.1), taxonomic over-splitting due to questionable species descriptions made in Kjellesvig-Waering's (1986) influential work, or increased sampling bias from numerous scorpion-rich Palaeozoic localities (Jeram, 1989).

Legg *et al.*, (2012) postulated that Palaeozoic scorpions were not diverse at all if you control for scorpion distribution across palaeobiomes. Today scorpions are more diverse in desert (arid) than tropical biomes (Poilis, 1990), a pattern qualitatively described in some Palaeozoic deposits restricted by geography and age, like the Mazon Creek Lagerstatten (Legg *et al.*, 2012). However, further investigation is needed to ascertain whether this pattern holds true on a global scale, across a diverse range of geological ages.

Here I aim to conduct a database search to map scorpion biogeographical distribution, from the Silurian (~ 444 Mya) to the Holocene (~ 11,700 years ago - present day), and use this data to assess how scorpion diversity changes in different palaeobiomes over geological time.

I hypothesise that in both the Palaeozoic, and the rest of geological time (Mesozoic and Cenozoic), scorpion diversity will be the highest in arid biomes.

### **2.3.1 Methods**

#### **2.3.1.1 Systematic review**

I downloaded scorpion fossil distribution data using literature records from The Palaeobiology Database (2023) (<https://paleobiodb.org/#/>).

Search terms included:

- Scorpiones taxa, collected using accepted species names only to avoid naming confusion, and collected with only regular taxa (not form taxa or ichnotaxa) to increase confidence in linking a single scorpion fossil to a single species.

Output data included:

- Accepted Species Name
- Abundance Value
- Geological Period (early\_interval, late\_interval)
- Age (Max\_Ma, Min\_Ma).
- Palaeogeography (Palaeolong, Palaeolat coordinates)
- A reference for each fossil entry

I then carried out a PRISMA screening process to ensure that records analysed were appropriate for my specific hypothesis (figure 1):

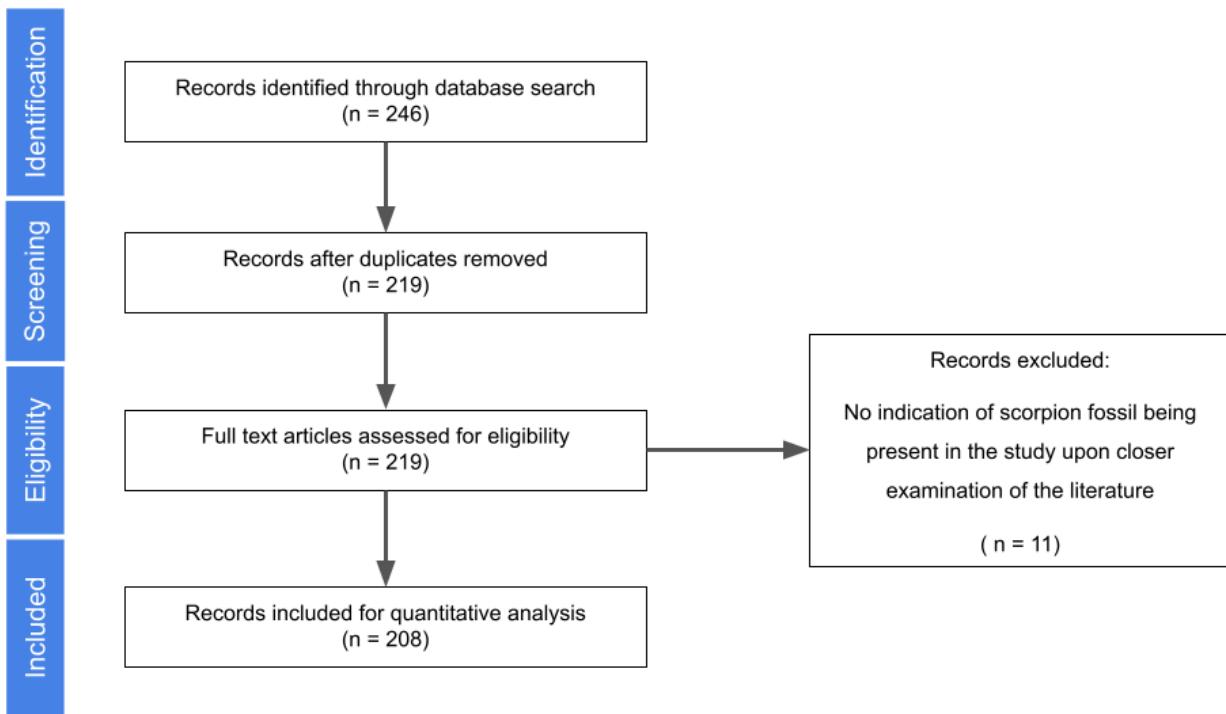


Figure 1: PRISMA flow chart detailing scorpion fossil specimen search strategy for quantitative analysis.

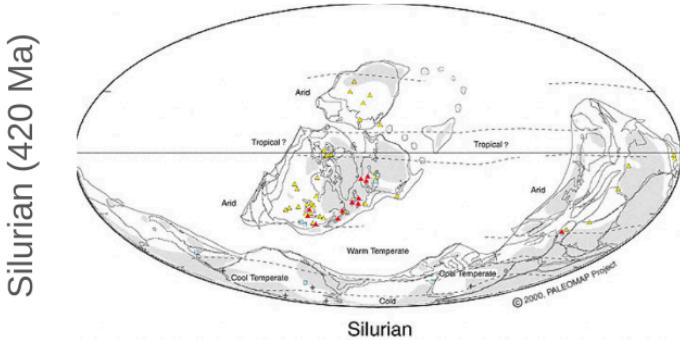
I also scored record quality based on robustness and data uncertainty, following Lim *et al.*, (2021). High quality records had references with micrographs of specimens for taxonomic validation. Medium quality records were present in the literature but lacked micrographs. Low quality records were solely found in the Palaeobiology Database and not in the literature.

Appendix 1 contains the literature sources used to compile the scorpion fossil dataset.

### **2.3.1.2 Mapping and palaeobiome allocation**

Using my dataset and R (v.4.3.2), I mapped global scorpion fossil distribution across all geological periods (fig.2) (example code in Appendix 2) (Moon, 2021). I then assigned all scorpion fossils (red) to a palaeobiome (Arid, Cool temperate, Warm temperate, or Tropical) using the Scotese reference maps (fig.2).

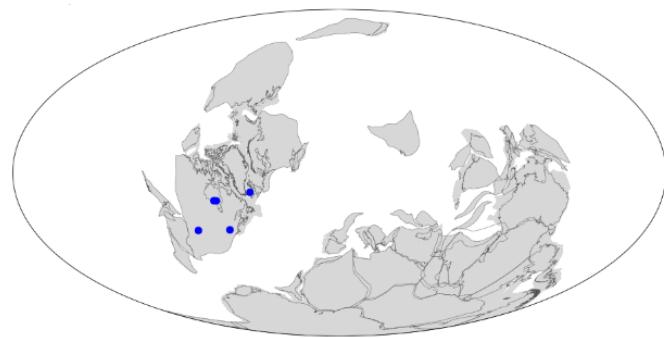
Reference climate map  
(Scotese, 2000; 2021)



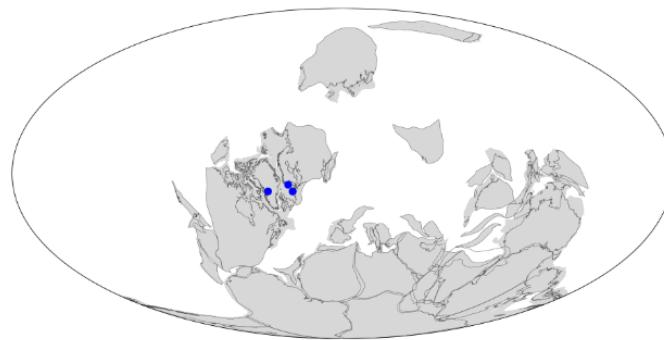
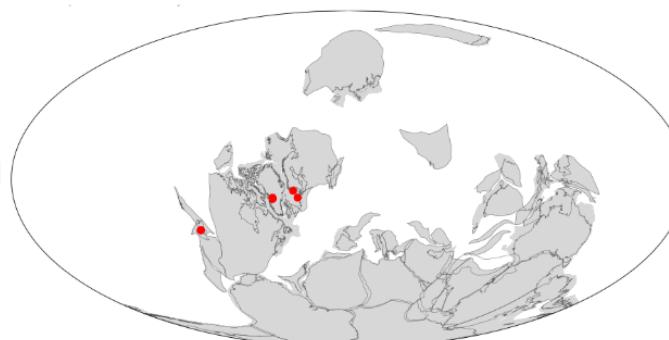
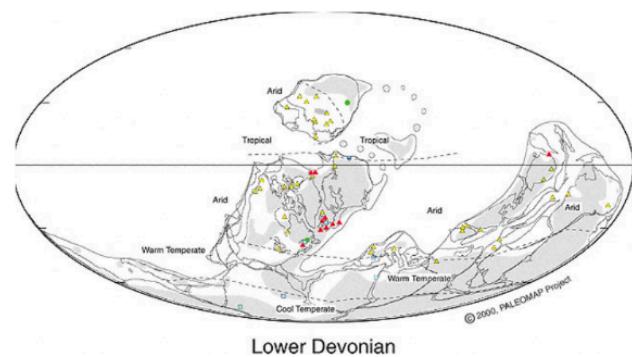
Scorpion biogeographical distribution  
(all records)



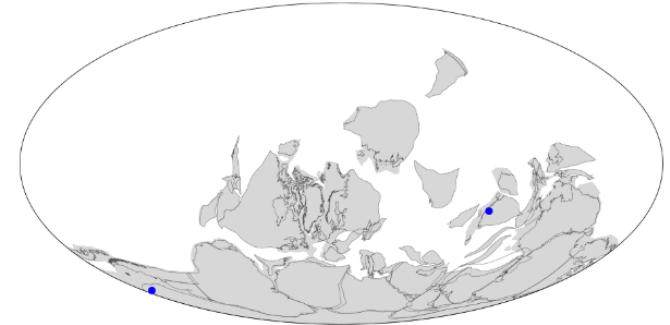
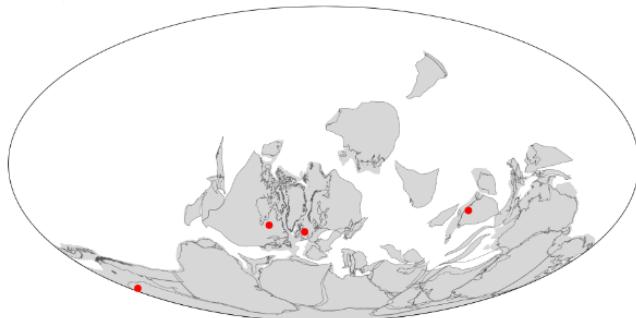
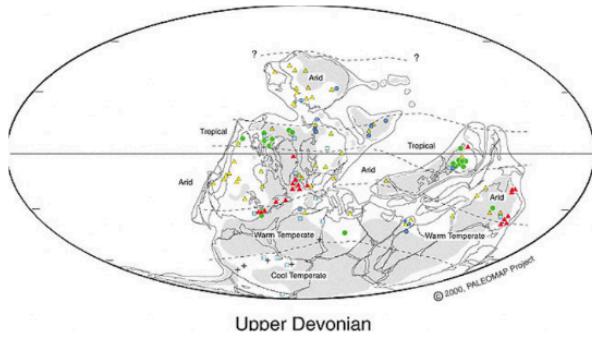
Scorpion Biogeographical distribution  
(High-quality records only)



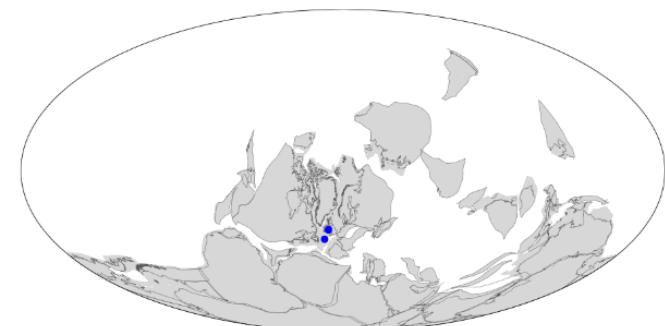
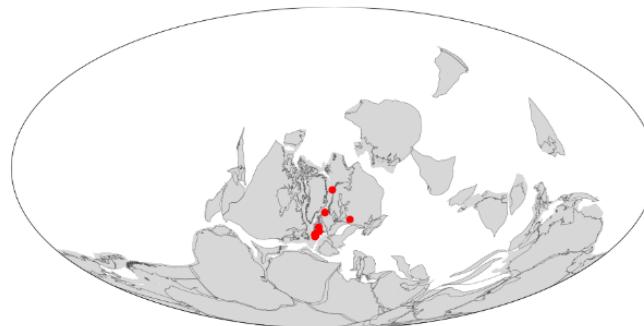
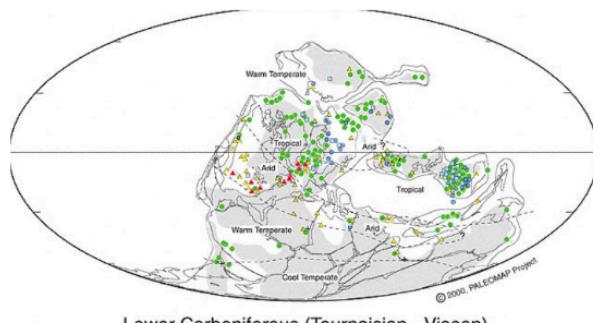
Early Devonian (400 Ma)



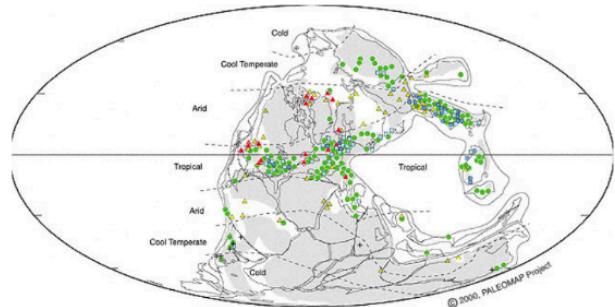
Late Devonian (360 Ma)



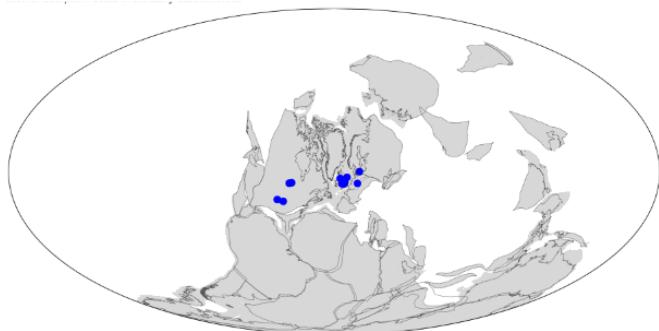
Early Carboniferous (~335 Ma)



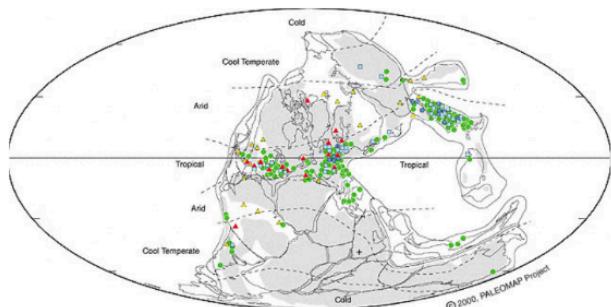
Late Carboniferous (~315 Ma)



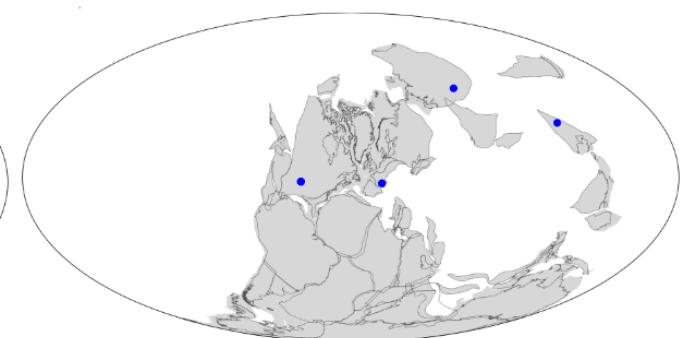
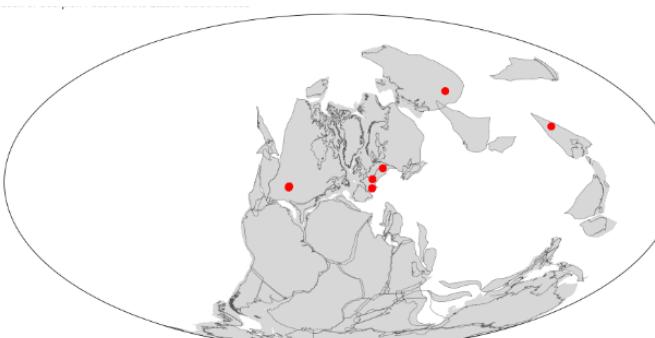
Upper Carboniferous (Bashkirian - Moscovian)



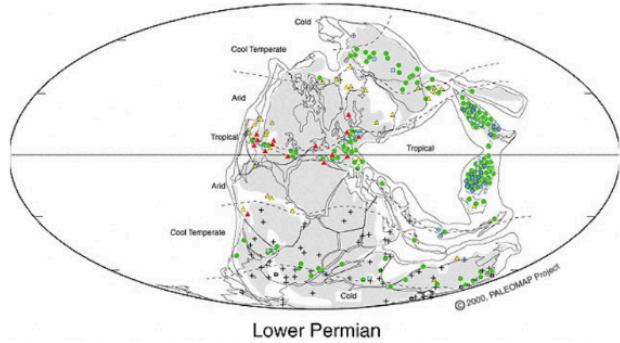
Latest Carboniferous (~303 Ma)



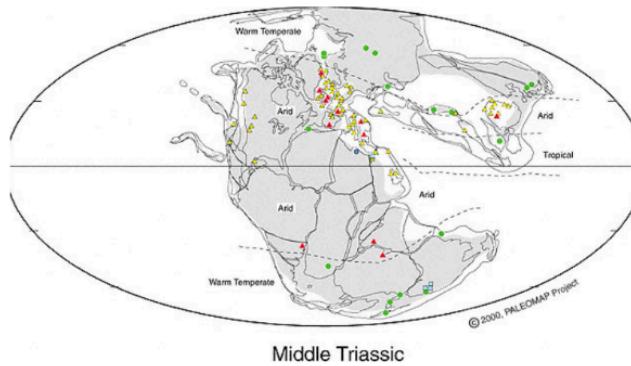
Upper Carboniferous (Gzelian)



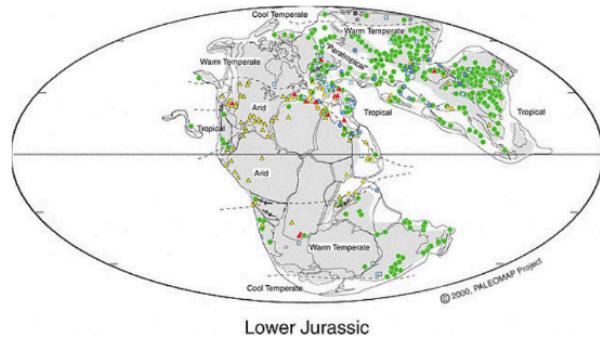
Early Permian (280 Ma)



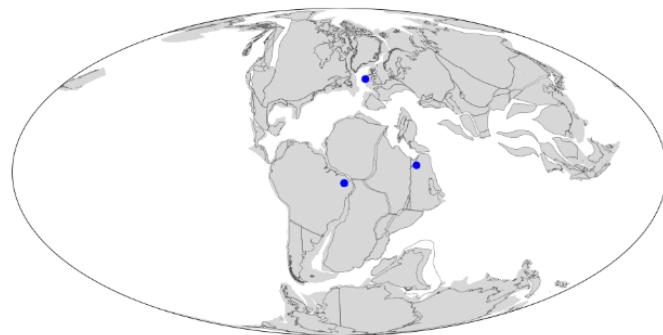
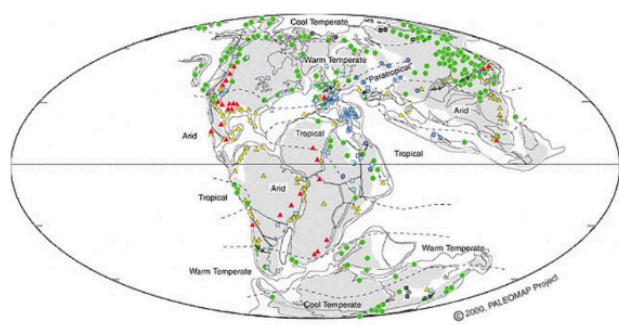
Middle Triassic (~ 240 Ma)



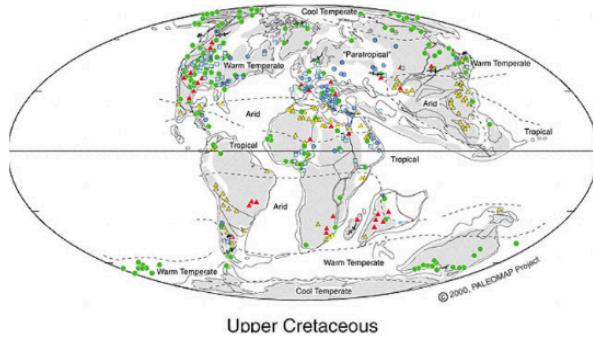
Early Jurassic (~ 200 Ma)



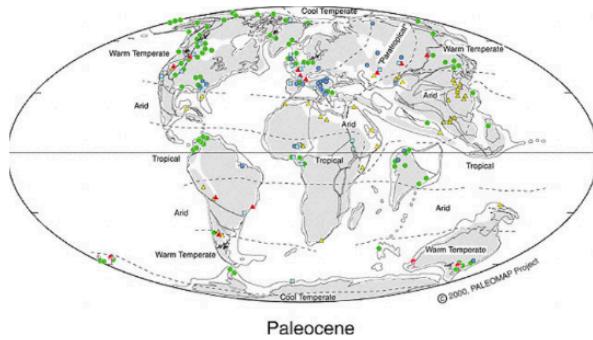
Early Cretaceous (~ 120 Ma)



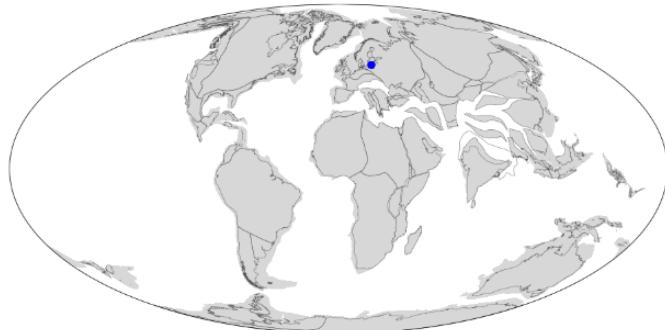
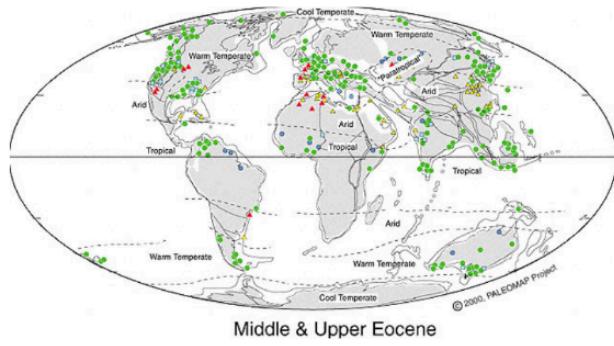
Late Cretaceous (~ 80 Ma)



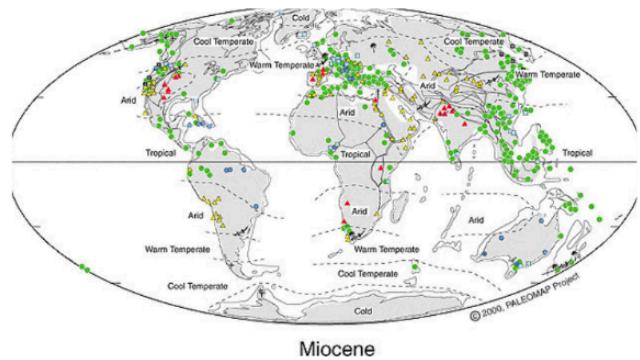
Palaeocene (~ 60 Ma)



Late Eocene (~ 45 Ma)



Miocene (~ 14 Ma)



Holocene (~ 11,700 - 0 years)

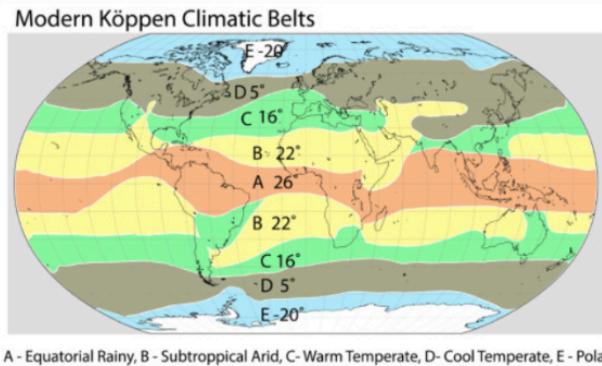


Figure 2: Scorpion fossil distribution through time. Reference palaeobiome maps (left) from Scotese (2000;2021). All fossil occurrences are mapped in red (middle), and only high-quality records are in blue (right). Continental plates were mapped at the midpoint of each period using GPlates (<https://www.gplates.org/>).

### **2.3.1.3 Quantifying scorpion diversity by palaeobiome**

In R, scorpion diversity (red, fig.2) by palaeobiome was calculated for each geological period in which scorpion fossils were identified, using the Margalef Index ( $d$ ),  $d = (S-1)/\ln(n)$ , an indicator of species richness count (S) that accounts for effect size and higher species richness expected with a greater number of individuals (n) (Araia *et al.*, 2019). Margalef Diversity Indices were temporally standardised ( $(d')$ ) = Margalef Index ( $d$ ) \* (Period duration/Era duration)) (Lim *et al.*, 2021). Standardised Margalef Indices were grouped by Palaeozoic or Other (Mesozoic/Cenozoic) Era and Biome. The cumulative sum of the Standardised Margalef Index was calculated for each group (Table 1; Table 2, 3.s.f).

## **2.4 Results**

Tables 1 and 2 summarise the results of the analysis:

Table 1: Palaeozoic scorpion diversity by biome

Biome	Standardised Margalef Index ( $d'$ )
Arid	1.28
Tropical	1.07
Cool Temperate	0.00

Table 2: Other (Mesozoic/Cenozoic) scorpion diversity by biome

Biome	Standardised Margalef Index ( $d'$ )
Arid	1.26
Tropical	0.145
Warm Temperate	0.0835

## **2.5 Discussion**

My hypothesis that scorpion diversity would be higher in arid biomes in both the Palaeozoic and Mesozoic/Cenozoic (Other) eras is correct (Table 1; Table 2). Arid biomes have the highest Standardized Margalef Index ( $d'$ ) in both Palaeozoic (1.28) and Other (1.26) geological eras. These similar values align with Legg *et al.*'s (2012) suggestion that when controlling for

palaeobiome distribution, Palaeozoic scorpions were not diverse at all. The consistently high diversity in arid desert biomes can be explained by two main factors.

Firstly, the harsh desert environment likely imposed strong evolutionary pressure on scorpions over time in terms of foraging and food stress (Polis, 1988). Unpredictable desert food availability directly impacts scorpion growth and reproduction (Bradley, 1988). Optimality theory suggests that scorpions maximise energy acquisition in both high and low desert food availability conditions (Polis, 1998). During low food availability, scorpions consume a broader range of smaller prey less frequently, sometimes predating other noxious scorpions (Polis, 1980). This shift in feeding behaviour directly influences life history characteristics, potentially providing scorpions with adaptations for long-term desert survival. When comparing multiple desert regions with varying food availability, different species adapt to different food regimes, contributing to increased species richness and diversity across all desert biomes as a whole (Polis, 1998). However, some Silurian scorpions (fig.2) in semi-arid regions lived in water-inundated environments. Here the stresses of a harsh desert terrestrial environment may not apply, making optimality theory less relevant in explaining higher scorpion diversity (Waddington *et al.*, 2015).

A stronger explanation for high diversity is that specialised desert scorpions evolved *in situ* from more generalist species, leading to the independent evolution of Bothriridae (South American), Vaejovidae (North America), and Scorpionidae (originally tropical Gondwanan) families (Nenlin and Fet, 1992; Fet *et al.*, 1998). This *in situ* evolution, often in isolated coastal dunes and riverbanks, facilitated rapid evolution through allopatric speciation, increasing overall desert scorpion diversity (Kryzhanovsky, 1965). The initial generalist ecology of scorpions may explain their consistent survival as 'living fossils' across various biomes over geological time, albeit with lower diversities (Table 1: Tropical,  $d' = 1.07$ , Cool Temperate,  $d' = 0.00$ ; Table 2: Tropical,  $d' = 0.145$ , Warm Temperate,  $d' = 0.0835$ ). The reason for lower diversity in non-arid biomes remains unclear. During large-scale environmental events/mass extinctions, burrowing scorpions have a better chance of survival underground (Feng *et al.*, 2022; Cowles, 2018). However, large tropical vegetation changes, such as the complete destruction of equatorial tropical forests after the Permian–Triassic ecologic crisis (fig.2, Early Permian, Middle Triassic) (Looy *et al.*, 1999; Pfefferkorn, 1999), or rapid shifts in vegetation structure after strong tropical summer monsoons of the Early-Middle Holocene (fig.2, Holocene) (Ye *et al.*, 2018), may have hindered tropical scorpion survival, due to habitat destruction and low scorpion dispersal ability after destructive events (Foerster *et al.*, 2020). The connection between vegetation structure and scorpion

diversity remains unexplored. Future studies should investigate both palaeobotanical/palynological and scorpion fossil records to understand this interaction over geological time.

Estimating scorpion biodiversity changes is limited by significant sampling effort variations between Palaeozoic and Other aged localities (see 2.3). Rarefaction is commonly used to standardise diversity measures to achieve equal subsample coverage, but can be misleading as it compresses richness ratios (Close *et al.*, 2018). The Margalef Index ( $d$ ) is a stronger diversity measure, being advantageous over rarefaction by correcting for sampling effort variation whilst being independent of sample size (Fernandez *et al.*, 2021). However, recent work by Kunakh *et al.*, (2023) suggests a high level of dependence of  $d$  on sample size, impacting its ability to reflect meaningful diversity differences. Margalef's (1973) original formula has not been adjusted to overcome this issue. Addressing this concern is crucial for future studies to accurately calculate diversity changes.

### **3 The scorpion cuticle**

#### **3.1 Structure and chemistry**

Scorpion cuticles boast the highest preservation rate among arthropods, attributed to their structurally unique and chemically inert hyaline exocuticle layer (Table 3) (Jeram, 1989).

Table 3: Comparison of arthropod, Recent scorpion, and fossil scorpion cuticle structure and chemistry

	Structure	Chemistry
Arthropod	Can be divided into two regions, the epicuticle (~2µm, lacks chitin) and procuticle (~ 50% chitin)	Cuticle fossilised in mineralised and non-mineralised forms  Middle Devonian arthropod cuticles show chemical preservation similar to the scorpion hyaline exocuticle, suggesting potential hyaline exocuticle loss in Recent forms
Recent Scorpion	Shares general arthropod cuticle structure with an additional hyaline exocuticle layer  Hyaline exocuticle is composed of a laminate and a non-laminate region. Thickness varies in extant taxa, forming 10-20% of cuticle thickness	Histochemical and x-ray analyses suggest the hyaline exocuticle is composed of chitin in a lipoprotein complex  Transmission Electron Microscopy reveals that electron-dense microfibrils contribute to the inert nature of the cuticle
Fossil Scorpion	Hyaline exocuticle layer is akin to Recent scorpions  However the inner cuticle layer, laminate in Recent scorpions, is fibrous in fossils  Despite incongruent features, Recent and fossil hyaline exocuticles are likely homologous	Energy Dispersive Electron Microprobe analysis shows high fossil chitin content, suggesting preservation of the original chitinous cuticle. Permineralization by calcite, silica, or phosphate is ruled out, as fossil cuticles are unreactive with acids. Fossil internal microstructure resembles the Recent hyaline exocuticle, suggesting a composition of microfibrils in a lipoprotein-chitin complex

Despite excellent chemical preservation, cuticle fossils are frequently fragmented due to necrosis, transportation, disarticulation, and insufficient long-term chemical alterations needed for complete fossilisation (Jeram, 1989; Gupta *et al.*, 2006).

### **3.2 Distinguishing between carcasses and moults**

Moults uniquely provide direct evidence of animal behaviour in the fossil record, and are especially important in understanding faunal life history strategies, constraining morphology during the evolution of modern animal groups. Scorpion moults offer valuable information on development and growth through comparative studies (Daley and Dradge, 2016). During a lifetime, Recent scorpions moult approximately eight times. Additionally, moults show greater resistance to scavenging damage than carcasses, meaning moults are more commonly preserved than carcasses in the fossil record (Waddington *et al.*, 2015; Clarke and Ruedemann, 1912). Consequently, it is challenging to determine the relative abundance, and therefore importance, of extinct scorpions in ancient ecosystems (McCoy and Brandt, 2009), especially when fragmentary material complicates fossil moult and carcass identification (Jeram, 1989). Nonetheless, key indicators exist for each origin.

#### **3.2.1 Carcasses**

Taphonomic features, like retracted chelicerae, straight body lines, and folded legs, also seen in resting modern scorpions, allow for confident identification of complete fossil carcasses (Viaretti *et al.*, 2023). A rare, but strong, indicator of a scorpion carcass is ‘New skin in old’ where a new hyaline exocuticle forms underneath the old cuticle prior to moulting (Jeram, 1989). Broken cuticles fossilised in coal likely come from predated scorpion carcasses. However, careful consideration of fossil morphology, depositional environment, and taphonomic factors is needed for accurate carcass identification (Daley and Dradge, 2016). Arthropod studies on brachiopods and trilobites have identified decayed carcasses through CT scans. These studies measure density differences between carcasses and the surrounding sediment, considering cuticle susceptibility to microbial degradation, fragmentation, and disarticulation (Waskom *et al.*, 2023; Jeram, 1989). Future CT scans on scorpions would aid in accurate carcass identification.

#### **3.2.2 Moults**

Scorpions moult through a front-facing horizontal gape suture, producing exoskeletons that could be mistaken for carcasses after the suture closes (Daley and Dradge, 2016). Moults can be confidently identified through podomere ‘telescoping’ where posterior sclerites move forward beneath anterior sclerites during ecdysis (Jeram, 1989). Moults taphonomically differ from carcasses (see 3.2.1), displaying extended chelicerae, curved body lines, extended pedipalps, and splayed legs (Viaretti *et al.*, 2023).

A debated method of moult identification involves studying three cheliceral articles in Recent scorpions (fig.4a): the protomerite, deuteromerite, and tritomerite (Shultz, 2007). However, Kjellsvig-Waering (1986) identified four cheliceral articles. The ‘fourth’ cheliceral article might be an internal tendon only seen in fossil moults (Selden *et al.*, 1984). Whether the fourth cheliceral article is a genuine part or a tendon, and in turn whether the tendon can be used in moult identification, will remain unknown until more specimens are thoroughly re-examined (Dunlop *et al.*, 2008a).

## **4 The scorpion phylogeny**

### **4.1 Morphology-based phylogenies**

Earlier phylogenetic hypotheses were based only on discrete morphological characters (Howard, 2021). Jeram (1998) produced the most comprehensive discrete character matrix to date for 20 Palaeozoic scorpions, representative of 26 morphological characters (absence = 0, presence = 1, indeterminate = ?) including macrosetae presence/absence and abdominal plate ornamentation. Computational analysis of this matrix generated a phylogeny that separated the basal Proscorpidae and Palaeophonidae families from the derived Mesoscorpionina suborder + 'palaeosterns' + crown group. However, this study is limited in many ways. Firstly, a poor database with few specimens and a lack of knowledge about their morphology makes it difficult to group scorpions, especially when many show a mosaic of characters which hinder the natural grouping of taxa. Secondly, indeterminate characters in the matrix make tree topology highly sensitive to the specific characters analysed, or how characters were coded to produce the phylogeny. Finally, if scorpions from two or more lineages independently terrestrialised, convergence is expected due to similar selection pressures, which may mask true evolutionary relationships.

These limitations are common in many morphological-based studies, which generally propose a basal split between the Buthidae family and non-buthid scorpions. The positions of the Pseudochactidae and Chaerilidae families are debated for their resemblance to both groups (fig. 3a).

### **4.2 Genomic-based phylogenies**

Sharma *et al.*, (2015) conducted the most comprehensive phylogenomic study on scorpions, analysing 5025 genes from all superfamilies. 25 species transcriptomes were generated through tissue preservation techniques and RNA sequencing, and stored in sequence libraries. Outgroup data was obtained from Genbank. Reads were filtered and trimmed for sequence assembly. A range of supermatrices were used to construct a phylogeny, which challenged previous morphology-based hypotheses, by grouping Pseudochactidae, Chaerilidae, and Buthidae into a clade (Buthida), that is the sister group to all other extant scorpions (Iurida) (fig. 3b).

Notably, all analyses consistently support a singular origin for katoikogenic parental investment in non-bothriurid scorpions, where embryos are sustained by connections to the maternal

digestive system (Sharma *et al.*, 2015). Katoikogenic development is linked to changes in the timing of appearance of embryonic morphological structures for digesting maternal nutrients, suggesting that embryonic development, beyond terrestrialisation, played a role in shaping scorpion morphology. The relative significance of katoikogenic development versus terrestrialisation in determining morphology remains unclear and should be explored in future studies by studying the elongate metasoma (fig.4a) in fossil embryos, a morphological character which is known to form well before adaptations for terrestrialisation appear (Farley, 2008; Farley, 1998).

### **4.3 Total-evidence phylogenies**

Recently, Howard (2021) constructed a phylogenomic matrix using 18 scorpion and 5 outgroup transcriptomes downloaded from NCBI. They reconstructed mRNA transcripts and computationally translated them into proteins to make a total-evidence phylogenetic tree with 53,634 aligned amino acid sites, using relaxed molecular clock and maximum likelihood models. Fossils were integrated into the ‘time tree’/phylogram using node-calibration methodologies that do not take into account previous phylogenetic positioning, but do account for uncertainty in fossil placement within the phylogeny (May *et al.*, 2021; Klopfstein and Spasojevic, 2019). This currently makes the phylogeny the strongest to use in wider scorpion diversity studies.

The phylogram produced (fig.3c) confers with Sharma *et al.*'s (2015, 2018) classification of scorpions into Buthida or Iurida clades. Contrary to earlier beliefs of a Silurian-Carboniferous split, dating now indicates the scorpion crown group diverged in the Carboniferous-Permian. This revision is likely due to the increased use of scorpion calibration fossils in Howard's (2021) study.

Despite recent improvements, total-evidence methods often show demonstratively incorrect ages due to a lack of realistic models to describe morphological evolution, and uncertainties in fossil dating methods (Barido-Sottani *et al.*, 2020; May *et al.*, 2021). The fossilised birth-death process, that uses a Bayesian approach to account for biases relating to sampling processes and fossilisation, will be important in future studies to robustly address these issues, unifying extant and extinct species in a single evolutionary model (Heath *et al.*, 2014; Stadler *et al.*, 2018).

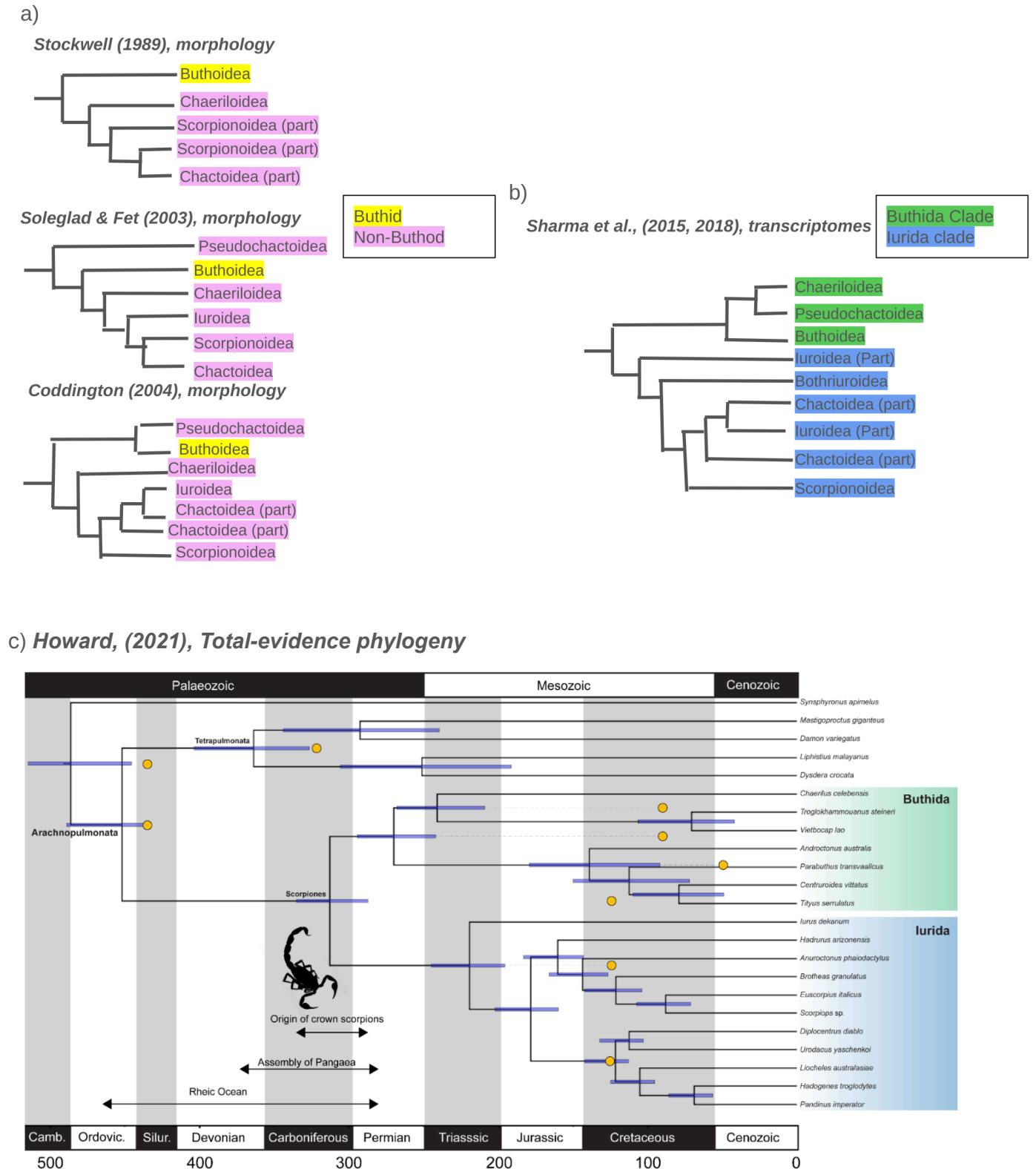


Figure 3: Scorpion Phylogeny Comparison. a) Morphology-based hypotheses (Stockwell, 1989; Soleglad & Fet, 2003; Coddington, 2004) - Buthid (yellow) and Non-Buthid (pink) taxa. b)

Genetic-based hypotheses (Sharma *et al.*, 2015, 2018) - Buthida Clade (green) and Iurida Clade (blue) taxa. c) Total-evidence phylogeny (Howard, 2021) - Buthida Clade (green) and Iurida Clade (blue) taxa, showing Carboniferous-Permian crown group divergence.

## **5 Marine-subaerial transition**

Aquatic Silurian scorpions were likely ancestral to Recent terrestrial scorpions. Such antecedents are absent from other chelicerate groups, highlighting the significance of the scorpion fossil record in elucidating when and how arthropods terrestrialised (Jeram, 1989). Arthropod terrestrialisation would have been challenging due to the different densities, viscosities, and refractive indices of water and air (Chou *et al.*, 2020). Adaptations for land involved significant changes in reproductive, locomotory, and sensory systems, addressing higher desiccation rates in drier environments, and modifying physiological functions optimised for seawater rather than air (Benoit *et al.*, 2023).

### **5.1 Morphological adaptations**

Morphological adaptations required to terrestrialise can be seen in the fossil record through changes in scorpion anatomy (see fig.4) over time (e.g., Scholtz and Kamenz, 2006). Although convergent evolution is seen in some characters, such as the book lungs, it is usually easy to identify and disregard as evidence (e.g., scorpion malpighian tubules as evidence for arachnid monophyly; Dunlop and Webster, 1999).

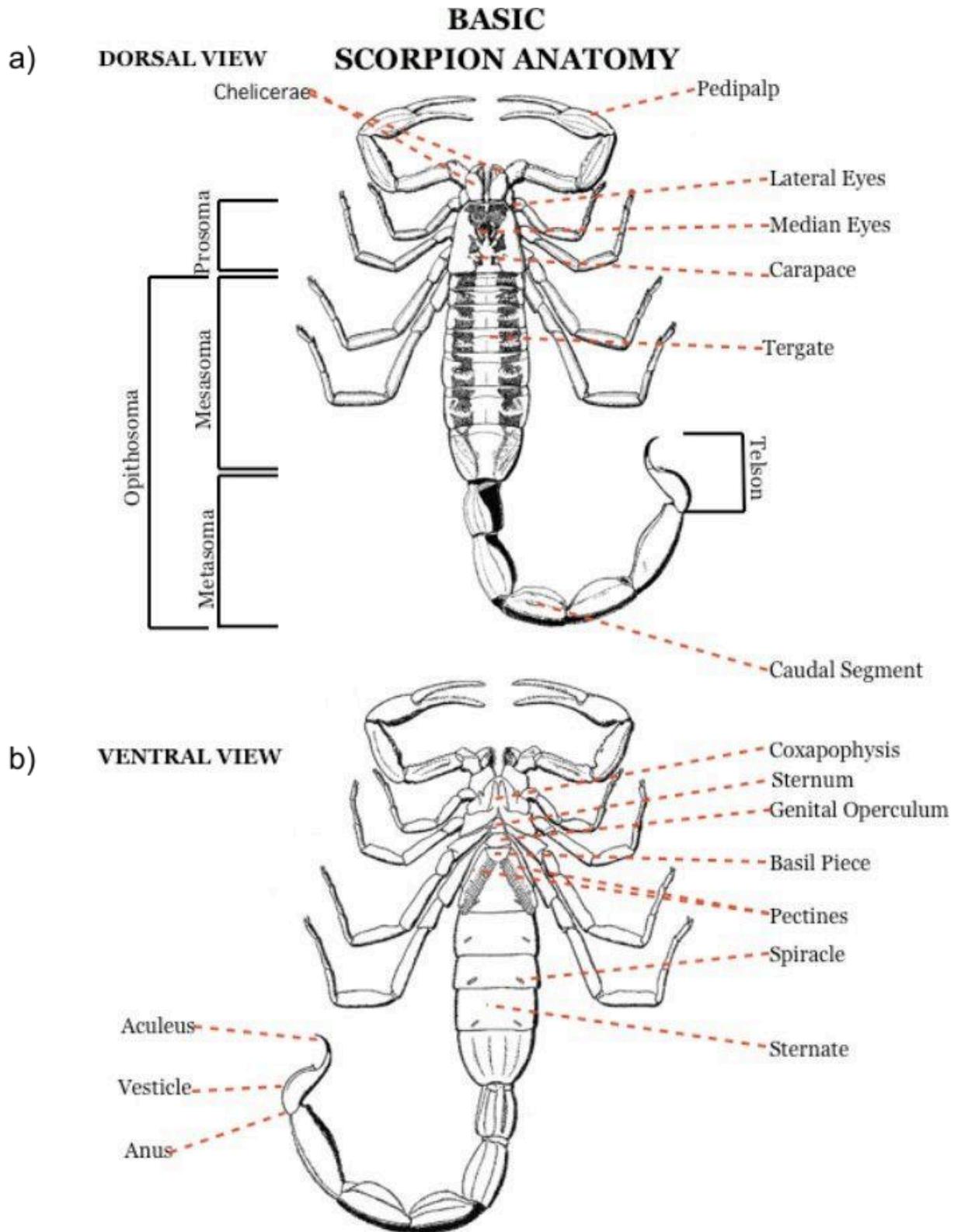


Figure 4: Dorsal (a) and ventral (b) scorpion anatomy (The Scorpion Hobby, 2023).

### **5.1.1 Vision**

Aquatic Silurian scorpions had raised anteriorly positioned median eyes for a broad field of vision, suited to a benthic predatory lifestyle (Dunlop and Selden, 2013; Fritsch *et al.*, 2017). As only the hyaline exocuticle eye layer has been preserved, it is futile to speculate how terrestrialisation changed scorpion eyes (Neville, 2012). However, the fossil record shows median eyes becoming caudally displaced over time, so they are positioned far behind the carapace margin (Jeram, 1989). In most Recent scorpions, median eyes (fig.4a) are central to the carapace and are superio-lateral, whilst in burrowing taxa, they lie on the posterior half of the carapace (Jeram, 1993). This suggests the main function of the median eyes is no longer predation. Further investigation shows the median and lateral eyes (fig.4a) are poor at resolving images or detecting light intensity changes (Fleissner, 1977), even in diurnal scorpions (Jeram, 1989). The evolutionary driver for these changes may be linked to the central nervous system and circadian rhythm, although deducing this solely from the scorpion fossil record is challenging (Williams, 1987; Legg *et al.*, 2012).

### **5.1.2 Sensing air movements**

Trichobothria are arachnid cuticular filiform hairs found on adult scorpion pedipalps (fig.4a) that have characteristically long setae (Messlinger, 1987). They help scorpions sense the terrestrial environment and locate prey relative to wind direction (Barth and Holler, 1999). Trichobothria do not work in water (Garwood and Edgecombe, 2011), and in scorpions date back to at least the Lower Carboniferous (Jeram, 1989). Stockwell, (1989) argues that trichobothria were absent in aquatic scorpions. A stronger argument is that they evolved from putative pre-carboniferous setae of aquatic scorpions, given that such structures have been identified through electron microscopy (Jeram, 1989).

### **5.1.3 Locomotion**

Changes in morphology of the walking legs are potential indicators of locomotion on land. A Silurian scorpion from the Eramosa Formation (430 Ma), Ontario, Canada, provides surprising insights into the aquatic vs. terrestrial debate (Waddington *et al.*, 2015). Despite being discovered in a marine environment, its leg morphology, featuring a short tarsus like all Recent scorpions, suggests occasional moulting on land before returning to water. The accuracy of this interpretation is debated, as it is challenging to determine whether the fossil was a carcass or moult (see 3.2). If the latter is true, the short tarsus may result from leg flexibility limitations produced as an artefact of telescoping (see 3.2.2).

### **5.1.4 Feeding**

Silurian scorpions likely used their chelicerae (fig.4a) and mesal gnathobases on the first pair of walking legs to feed, similar to modern horseshoe crabs and extinct eurypterids (Dunlop *et al.*, 2008a). Contrastingly, modern scorpions liquid-feed through a pre-oral cavity, formed by anterior projections of the coxae in the first two pairs of legs called the coxal apophyses (fig.4b; coxapophysis) (Simone *et al.*, 2022). The Middle Devonian *Branchioscorpio* shows the earliest evidence of an oral tube (Rolle and Lawson, 1985). Liquid feeding is likely unique to terrestrial environments, being less effective in water where digestive fluids can be diluted or dispersed (Jeram, 1989). Kjellesvig-Waering (1986) noted a decrease in chelicerae size since the Silurian, possibly linked to changes in feeding behaviour, though cheliceral size is also influenced by burrowing as seen in *Opisthophthalmus* (Jeram, 1998).

### **5.1.5 Respiration**

Gills are a source of disagreement in scorpion evolution. Supposed "gills" have been described in *Waeringoscorpio* (Devonian) (Poschmann *et al.*, 2008), as have external filamentous structures from book lungs, similar to the tracheal gills of secondarily aquatic freshwater insects (Stormer, 1972). Poschmann *et al.*, (2008) consequently hypothesised that scorpions were also secondarily aquatic, interpreting gills to be autapomorphic, rather than evidence of a gill-lung/water-land transition (Howard., 2021). Some "gills" found are not homologous with the book lungs of modern scorpions (Stormer, 1972). If this is used to dispute an aquatic origin, it is challenging to explain why scorpions are the only terrestrial arthropods fossilised in near-shore environments often alongside other aquatic taxa (Clarke and Rudemann, 1912), especially without knowing if fossils have been transported post-mortem (Howard., 2021).

The origin of scorpion opisthosomal (fig.4a) appendages adds complexity to the gill-lung transition (Di *et al.*, 2018). Mutant scorpions with appendicular extensions of book lungs exhibit shortened walking legs across opisthosomal appendages, indicating homology with walking legs, not derivation from gills. This challenges the idea of a shared transformation series between book lungs and gills (Howard, 2021).

## **5.2 Behavioural adaptations**

### **5.2.1 Nocturnal activity**

The eyes of Silurian scorpions suggest they were diurnal (Jeram, 1989). Contrastingly, Recent scorpions are mostly nocturnal to prevent desiccation and reduce competition with daytime

predators (Cloudsley-Thompson, 2012; Adams *et al.*, 2016). This diurnal-nocturnal shift is reflected in changes in the sensory system, including a reduction in the number of lateral eye ocelli, indicating a diminished role of visual sensilla in prey capture (Jeram, 1989). The appearance and development of different sensilla, especially trichobothria, suggests scorpions became nocturnal during the Late Carboniferous (Stockwell, 1989; Jeram, 1998).

### **5.2.2 Reproduction**

Faster growth of male, compared to female, scorpion pectines (fig. 4b) suggest they were a Palaeozoic secondary sexual trait that played a key role in reproduction (Polis and Farley, 1979). Maximum pectine complexity occurred in Lower Carboniferous scorpions like *Pulmonoscorpius* and *Centromachus*, followed by a reduction in relative size and tooth number (Jeram, 1989). Recent scorpions possess pectines with chemosensitive and hygroreceptor capabilities, though their functions remain unclear (Trabalon and Bagnères, 2010).

Spermatophore development is considered a terrestrial adaptation, although it is not visible in scorpion fossils (Jeram, 1989). Diverse sperm transfer methods in marine ancestors imply the possibility of indirect transfer among aquatic interstitial forms. Consequently, complex sperm transfer systems do not exclusively signify a terrestrial lifestyle (Selden and Jeram, 1989).

### **5.3 The timing and routes for scorpion terrestrialisation**

The earliest evidence of an unambiguous scorpion terrestrial character (coxal apophyses) dates back to the Early Devonian (Jeram, 1989). By the Lower Carboniferous, multiple lineages exhibit terrestrial traits, suggesting a terrestrialisation period between the Early Devonian-Lower Carboniferous (Legg *et al.*, 2012). However, without direct evidence for the two definite indicators of terrestrial habit, book lungs or trichobothria, estimating the timing of scorpion terrestrialisation remains uncertain. Thus, it is possible scorpions terrestrialised as early as the Silurian (Jeram, 1989).

During the Middle Silurian, scorpions may have terrestrialised via two possible routes. The first involves direct movement onto land through the intertidal zone, akin to Recent amphibious crabs (Rolfe and Lawson, 1985). The second involves scorpions moving onto land through freshwater (Jeram and Selden, 1989). The hyaline exocuticle of scorpions, with low water permeability, may have facilitated easy entry into freshwater compared to other marine arthropods (Selden and Edwards, 1989). To enter freshwater, scorpions would have needed to develop new osmoregulatory mechanisms to tolerate small, short-term changes in salinity

(Lozano-Fernandez *et al.*, 2016). Yet, Recent scorpions have hemolymph solute concentrations similar to seawater and show poor osmoregulation abilities, suggesting the intertidal route is strongest in explaining how scorpions terrestrialised (Bjerke *et al.*, 1989). Terrestrialisation via freshwater remains plausible as different scorpion lineages underwent multiple terrestrialisation events. Conflicting perspectives arise from divergent approaches. Some rely only on the scorpion fossil record, favouring a freshwater origin (Howard *et al.*, 2019). Others compare scorpions to close terrestrial relatives, noting intertidal terrestrialisation in arachnids and myriapods (Lozano-Fernandez *et al.*, 2016).

#### **5.4 Did scorpions terrestrialise more than once?**

Scorpions likely underwent mosaic evolution characterised by diverse terrestrial adaptations emerging in various scorpion lineages at distinct times (Jeram, 1989), leading to the simultaneous terrestrialisation of multiple scorpion groups (Howard *et al.*, 2019). It remains unclear why scorpions never reverted to aquatic life unlike some arthropod counterparts, for example crabs (Newcomb, 2023). Molecular phylogenetic research by Wang *et al.*, (2023) suggests that initial arthropod terrestrialisation was associated with the presence/absence of an aquaporin subfamily that controls water fluxes across arthropod membranes. Whether aquaporin presence/absence prevented scorpions from returning to water remains unknown due to limited genomic data available for study (Newcomb, 2023).

### **6 Conclusions**

- Palaeozoic fossils, especially from the Carboniferous, prompt debate on whether high scorpion diversity was reflective of a genuine radiation or fossil record bias.
- By mapping scorpion distribution over time I found that scorpion diversity peaks in arid biomes, possibly due to *in situ* allopatric speciation or evolutionary pressures related to desert food availability. The latter does not explain aquatic Silurian scorpion diversity.
- Chemically resistant scorpion hyaline exocuticle fossilises well. Moults can be confidently identified by telescoping, and carcasses by ‘New skin in old’. Future use of CT scans could help identify damaged carcasses within sediment.
- Howard’s (2021) phylogeny most accurately positions scorpion species in Buthida or Iurida clades, estimating a Carboniferous-Permian crown group divergence.
- Debates surround the ancestral aquatic habits of scorpions. The reason for scorpions not returning to water remains unknown, but recent studies propose a link to aquaporin presence/absence.

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**Appendix 2: Example scorpion biogeography code**

```
#install.packages  
  
install.packages("./RCourse/rgdal_1.6-7.tar.gz", type = "source", repos = NULL)  
  
  
# Load the library  
  
library(rgdal)  
  
  
# Silurian scorpion biogeography ----  
  
  
# Load in data ----  
  
# all records  
  
fossil_data <- read.csv("./dissertation/Silurian.csv")  
  
# high quality records  
  
high_data <- read.csv("./dissertation/SilurianHigh.csv")  
  
  
# obtain Silurian map from gplates -----  
  
# Replace 'silurian_coastline_url' and 'silurian_polygons_url' with the actual URLs  
  
silurian_coastline_url <-  
"http://gws.gplates.org/reconstruct/coastlines/?time=420&model=GOLONKA"  
  
silurian_polygons_url <-  
"http://gws.gplates.org/reconstruct/static_polygons/?time=420&model=GOLONKA"  
  
  
silurian_coastlines <- rgdal::readOGR(silurian_coastline_url)  
silurian_polygons <- rgdal::readOGR(silurian_polygons_url)
```

```
# Prepare data for plotting ----  
  
# Tidy up the spatial data  
  
silurian_coastlines <- broom::tidy(silurian_coastlines)  
  
silurian_polygons <- broom::tidy(silurian_polygons)  
  
  
# create the map ----  
  
silurian_map <-  
  
  ggplot() +  
  
  geom_map(  
  
    data = silurian_polygons, map = silurian_polygons,  
  
    aes(x = long, y = lat, map_id = id),  
  
    size = 0.15, fill = "#d8d8d8"  
  
) +  
  
  geom_map(  
  
    data = silurian_coastlines, map = silurian_coastlines,  
  
    aes(x = long, y = lat, map_id = id),  
  
    size = 0.15, fill = NA, colour = "grey30"  
  
) +  
  
  geom_rect(  
  
    data = data.frame(xmin = -180, xmax = 180, ymin = -90, ymax = 90),  
  
    aes(xmin = xmin, xmax = xmax, ymin = ymin, ymax = ymax),  
  
    color = 1, fill = NA, size = 0.3  
  
) +
```

```
coord_map("mollweide") +  
ggthemes::theme_map()  
  
silurian_map +  
labs(  
  title = "Palaeogeographical map of continental plate (grey) arrangement\nin the Silurian (420  
Ma) with modern coastlines outlined above."  
)  
  
# plot fossil scorpion points (all records) ----  
silurian_map +  
geom_point(  
  data = fossil_data,  
  aes(x = paleolng, y = paleolat),  
  color = "red", size = 3  
) +  
labs(  
  title = "Distribution of Scorpion Fossils in the Silurian"  
)  
  
# plot fossil scorpion ponints (high quality records) ----  
silurian_map +  
geom_point(  
  data = high_data,
```

```
aes(x = paleolng, y = paleolat),  
color = "blue", size = 3  
) +  
labs(  
title = "Distribution of Scorpion Fossils in the Silurian"
```

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