The Phylogeny of the order Pseudoscorpiones

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Abstract:

Pseudoscorpiones is an order of arachnids, members of which are commonly known as book scorpions or false scorpions. Since they first appeared in the Middle Devonian period, they have acted as important predators in microhabitats. The order's placement within Arachnida and its internal evolutionary relationships remains contentious. Furthermore, the fossil record of Pseudoscorpiones contains several extinct families as well as extinct genera within extant families, with a total of 49 fossil species across the Phanerozoic. The last morphological pseudoscorpion phylogeny was published by Harvey (1992), but this lacked the fossil record. I analysed the matrix with a different software and a range of extinct species. In this thesis, the literature review compares the foundations of Harvey (1992) alongside to more recent analyses of Psuedoscorpiones phylogeny to reflect upon the strengths, limitations, results, and the discussed hypotheses. I then update Harvey (1992) with the addition of fossils to the matrix. The addition of fossils does not significantly alter the relationships between extant families. There is evidence to both support the original placement of species (i.e. *Pseudocheirium insulae* etc.) and to contradict it (i.e. *Geogarypus gorskii* etc.). I also support hypotheses of Harvey (1992) (e.g. Dracochelidae is found within Chthonioidea, Epiocheirata and Iocheirata.) The addition of fossil taxa to a morphological analysis of Pseudoscorpiones is novel. This matrix provides an opportunity for newly discovered species (extant or fossil) to be placed within a cladistics framework. Future studies should focus on including more details to profiles of genera to reduce unknown or incorrect past interpretations, and thus to progress to a more reliable phylogenetic analysis.

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The Phylogeny of the order Pseudoscorpiones

1. Introduction:

  Despite being one of the first class of animals to be part of terrestrialisation, Arachnida still has a number of unanswered questions regarding the phylogeny across the number of clades it enveloped. One of these orders are known as Pseudoscorpiones, more commonly called book scorpions. They are set across the Phanerozoic eon with the first fossilized specimens being found in Gilboa (New York) that date back to the Givetian stage of the Middle Devonian by Schwarze et al. (2021) to extant genera being described in recent years, for example *Cystowithius ankeri* sp. found in Central Andes from Garcia & Romero-Ortiz (2021.)

  Due to this wide span of specimens, there have been numerous analyses done in order to develop a phylogenetic tree that can determine which clade is related to which within the Pseudoscorpiones order. The methods done in order to achieve this have varied; from the traditional analysis of every morphological character expressed by the order, in which Harvey (1992) had done to lay the foundation of the order's phylogenetic tree. This study has subsequently been referenced by later studies that utilize different methodologies, such as Benavides et al. (2019) with the use of genetic sampling from extant tissue samples. The results and discussions of how this history of studies had transgressed will be reviewed and discussed in relation to Pseudoscorpiones.

  Thus, this study proposes to not only conclude the strengths and limitations of each past research; but to also include modernized methods and missing fossil data to develop the latest iteration of the order's phylogenetic tree using morphological data. This is because pseudoscorpions have a wide variation of niches in each of the habitats due to the phoretic behaviour, which is when a pseudoscorpion is carried between places as it holds onto a limb of a larger animal (usually a flying insect.) Furthermore, in a more domestic sense pseudoscorpions have earned the name 'book scorpions' for their effectiveness in predating pests (i.e. insects such as book lice, various larvae, etc.) against irreplaceable artefacts belonging to archival and Academic institutions (such as libraries or museums.) With these uses that benefit both a healthy ecosystem and manmade procedures even to this day, a better understanding of pseudoscorpions through this study could then lead to clarifying conditions and distribution for their survival; as well as improving conditions to maximize their use to preserve valuable archives.

The aims for this study are as follows, with Harvey (1992) as the basis:
- To add fossil species in both extinct and the extant families originally studied.
- Update the methods in analysis techniques now available in later years.
- Reflect modernized practices by utilizing the phylogeny at a species level over the original family level. This also includes any changes to the characters to reflect later analyses to a more accurate manner.

In order to reach these aims, the following objectives are done in accordance:
- Make direct interpretations of phenotypical characters of each species from every relevant paper or treatise. These will all be added to the newly made matrix alongside the initial data from Harvey (1992.)
- Compare different studies by results and methodologies into a literature review to use the most relevant aspects for this analysis.
- Utilize these findings altogether into a production of a phylogenetic tree for the order, to then discuss and compare to the results of said previous studies.

The following chapter is the literature review of previous studies to Pseudoscorpiones; which will then lead to the methodology for this latest analysis after every idea is found from the predecessors. The results as well as the discussion will then follow, then the conclusion of what was effective and what needed improvements.

For the rest of this study, the following terms will be defined as such:
- Character – a number to describe a morphological part of a specimen. From Harvey (1992) for example, there were 125 characters in total.
- Trait – a version of a character that can differ between specimens as an autapomorphy (1, 2, etc.) or homoplasy (0.)
- Data – raw information about the characters that are yet to be analyzed into results.
- Study – a completed and published research procedure with analyzed data and discussion, which may or may not include raw data as supplementary material.

2. Literature review:

There were a wide variety of approaches to the Pseudoscorpiones order by different levels of scale. Each of them all share a common goal to understand the phylogenetic relationships of not just within the order itself, but in relation to the other orders in the Arachnida class. To focus on the relationships within the order itself, there are still numerous approaches and alternative priorities that involves the extant specimens and their living tissue.

As such, it is imperative to discuss and compare the types of methods to understand and thus improve from the initial framework of Harvey (1992) as it is one example among many.

The first method is the aforementioned framework that utilizes the oldest technique of palaeontology; to develop a matrix of morphological characters according to each specimen, to then create a phylogenetic tree based on autapomorphies. In Harvey (1992) definitions of anatomical characters are established (i.e. trichbothria, thin filaments each from a nodule of the pseudoscorpion's chitinous surface that usually is a sensory organ) before the total list of them are shown and described by observations to extant yet preserved specimens that each represent a taxonomic family. Each family are then given a binary score that depend if a character has a plesiomorphic (0) or autapomorphic (1, or 2 if the character differs further) trait. From these numbers, the discussion was then written as a treatise describing each family under sub-headings of each infraorder. The autapomorphic characters that define differences eventually developed a phylogenetic tree as shown in Figure 2a.

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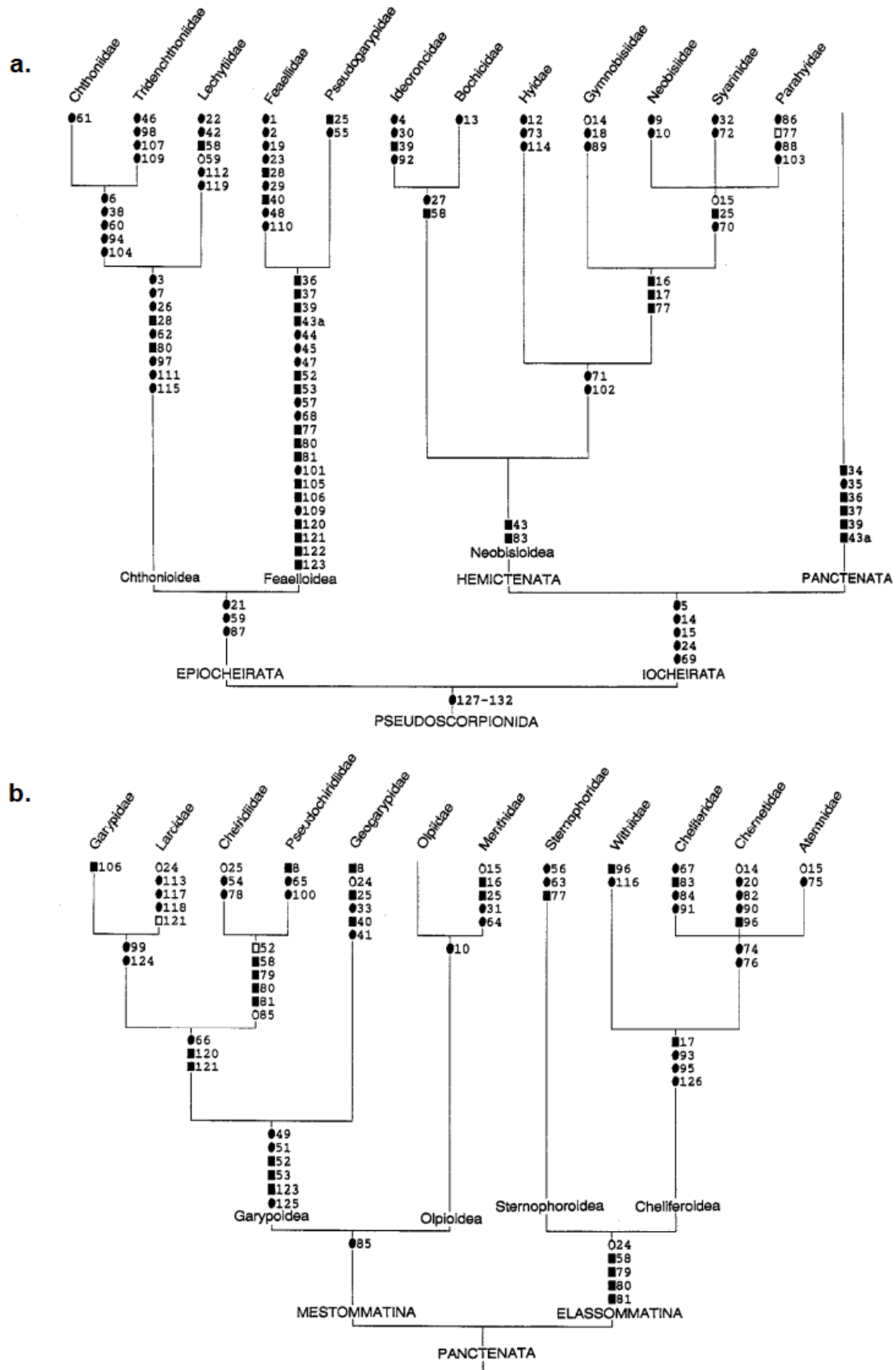
Figure 2a. *Phylogenetic tree generated from Harvey (1992.) a. Main tree. b. Details of Penctenata. Numbers correspond to morphological character of the original study only. Circle – autapomorphy. Square – homoplasy. White respective shape – evolutionary reversal.*

There are several weaknesses to this study, one of which has been acknowledged within the paper itself. This is the simplification of coding both an unknown (?) trait (i.e. can't observe and confirm a mating behaviour) and inapplicable trait (-) (i.e. if a median suture on a prosoma is absent, a character about lobes on said suture can't be possible) as the former only. Platnick et al. (1991) provides an explanation of how this could be problematic. The software used, Hennig86, can only include a single binary bit for each trait which includes both unknown and inapplicable, which results in computation errors of being unable to differentiate between these traits to the autapomorphy/homoplasy data and thus can render the resulting phylogenetic tree as unreliable with a higher count of 'unknown' data than it is in reality.

Furthermore, there are weaknesses within the character list itself. The main point includes the trichbothria on the pedipalps and each character that concerns them. It is explained in Harvey (1992) that each trichbothrium is labelled and observed in post-embryonic development of each pseudoscorpion's instars on where they will be upon the pedipalp's chelae. This is based on two theories that either each trichbothrium 'shifted' in its place on the pedipalp after molting in development, or it is replaced by a new strand in a different area. While it is noted to not pose a difference in the Harvey (1992) study, it is imperative to note that this reasoning can be flawed without a definite confirmation that each trichbothrium will be the same each time to be a character. This is evident in characters 48 to 50 in the original study as an example; from a logical question that if characters 49 and 50 specify a single trichbothrium from a pair, how can you tell which is which when it can't be directly traced through a molt? It seems it's impossible to do so and relies on the theory of shifting or replacing strands, which is seen as too uncertain to characterize as a morphological trait. Similarly to the trichbothria, there is character 2 (Figure 3b[1]) that refers to the shape of setae that has been addressed in Judson (2000) and will be readdressed here. Namely that setae can become kinked and/or bent during an animal's lifetime and may not be a viable morphological trait to discern phylogenetic relationships from.

In regard to the data, another flaw is the matter of phylogenetic relationships is limited to families rather than the more derived genera or species. While examples are listed in the descriptions of families as the discussion chapter, the study did not specify which species represented each family. Worse still, there have been numerous examples in the character list of species being exceptions that were

admittedly ignored (i.e. character 10 where *Syarinus* is the only genus in Syarinidae with rounded apexes of the pedipalps' coxae, yet the data is counted as homoplastic triangular apexes entirely.) These cases may be outliers, but it is believed for this modern study that the level of families is too imprecise and contradictory to the objectives centering on autapomorphies to discern relationships.

There are more minor flaws in the character list, such as multiple listed numbers for a single character (it is estimated the reason could be from the software's limitations) as well as outdated terms that have been less used in more recent years. Another weakness includes gaps of information in the study itself such as missing definitions or descriptions of certain characters or incorrect usage of terms for traits.

Despite the weaknesses, the results of Harvey (1992) included a phylogenetic tree (Figure 2a) that has been a framework to more recent studies about the order. This study will be no different, with updates and all to accommodate later findings.

The same phylogenetic tree from Harvey (1992) has also become a framework of the study of Harms & Dunlop (2017.) Instead of a direct approach in creating a new tree itself, the fossil specimens are the focus in being described and summarized in the distributions and age in the geological record. From these findings, the phylogenetic tree is then updated to include more recent changes or additions of families from the Harvey (1992) iteration, as well as relationships centered on chronological appearances. This is all shown in Figure 2b.

With the approach relying on the fossil record rather than descriptions of characters, it is only natural that this study will differ in structure than Harvey (1992) and similar reports. Nonetheless, there is a lack of descriptions to featured fossil species in each of the localities. Even a brief summary can suffice, as not all the referenced treatise and holotype descriptions are available as secondary reading.

Despite this, the study has been immensely helpful to create the list of all fossil species of pseudoscorpions into one compendium, with supplement histories for the locality of whence they are found.
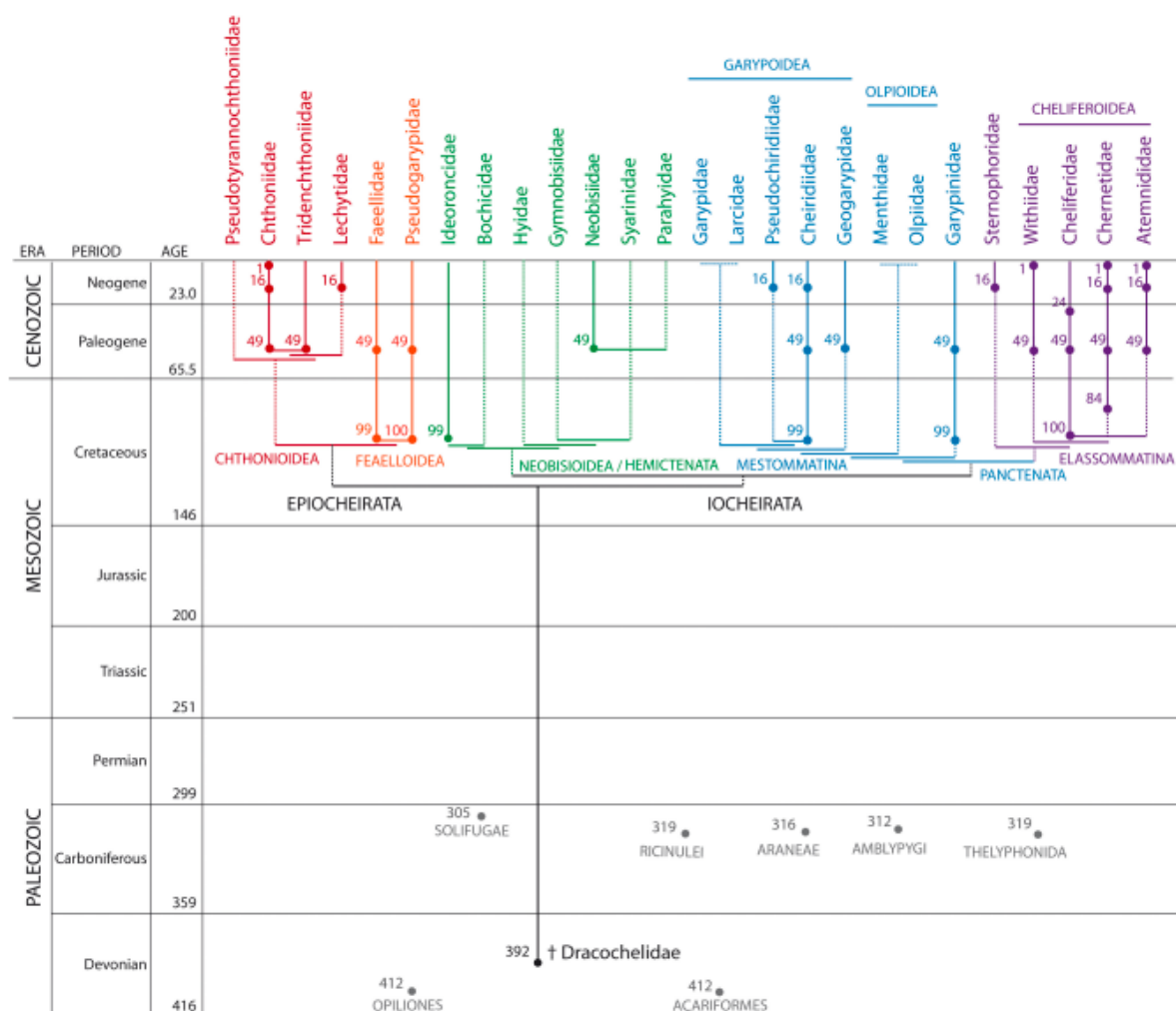
Figure 2b. *Phylogenetic tree developed from Harms & Dunlop (2017.) Noted in the study this was constructed from Harvey (1992) and included modifications based on Murienne et al. (2008.) Full lines – family has a fossil record. Dashed line – family is extant only. A circle indicates a family's minimum age in millions of years by fossil evidence if any. Other orders' minimum age by fossil record are listed as comparisons.*

Different matrices can be made not of morphological characters, but of genetic material of new specimens. In the case of Benavides et al. (2019) mRNA samples were prepared from multiple individuals to represent each family. Several software programs were named and utilized to construct matrices (and removed outlier data such as contaminations) and ergo phylogenetic trees were developed through simulations of the genetic libraries. Another objective in this analysis is also to apply dates in the fossil record of divergence in families to complete the generated phylogenetic trees if molecular data was not sufficient. In an interesting note, this analysis was done with Harvey as a co-author, and his (1992) paper was cited as a framework as well. The resulting phylogenetic tree generated from each of the objectives are shown as Figure 2c.

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Unlike the referenced Harvey (1992) a list of samples is made for each of several taxa to represent their respective family. Furthermore, a phylogenetic tree was created first-hand that utilizes genera and species before the summarized tree is made as Figure 2c. Effective too, as a species can differ by genomes at a larger rate than by phenotypical morphological traits, so this approach brings more accuracy to the phylogeny. Despite this, there still followed issues in receiving molecular data from specimens as specified in the study. Mainly of practical issues such as lost material from the small size of the specimens, or the inability to use important or rare specimens due to the destructive methods in receiving genetic material. This also links to how it is impossible to use fossil specimens in the molecular study; from either being unreachable within amber and with no genetic material surviving by the fossil's age. As such, Benavides et al. (2019) instead use the fossil specimens to time the diversification of Pseudoscorpiones with remarks to morphological traits in the discussion.

Thus, a molecular approach is not foolproof and doesn't necessarily make a morphological method obsolete. The latter does have benefits in preserving specimens for observations over rendering them into genetic data to avoid destruction. At least with recent technology. This however doesn't negate the use of Benavides et al. (2019) in updating the phylogenetic tree for Pseudoscorpiones in recent years. An objective not too different from this study.
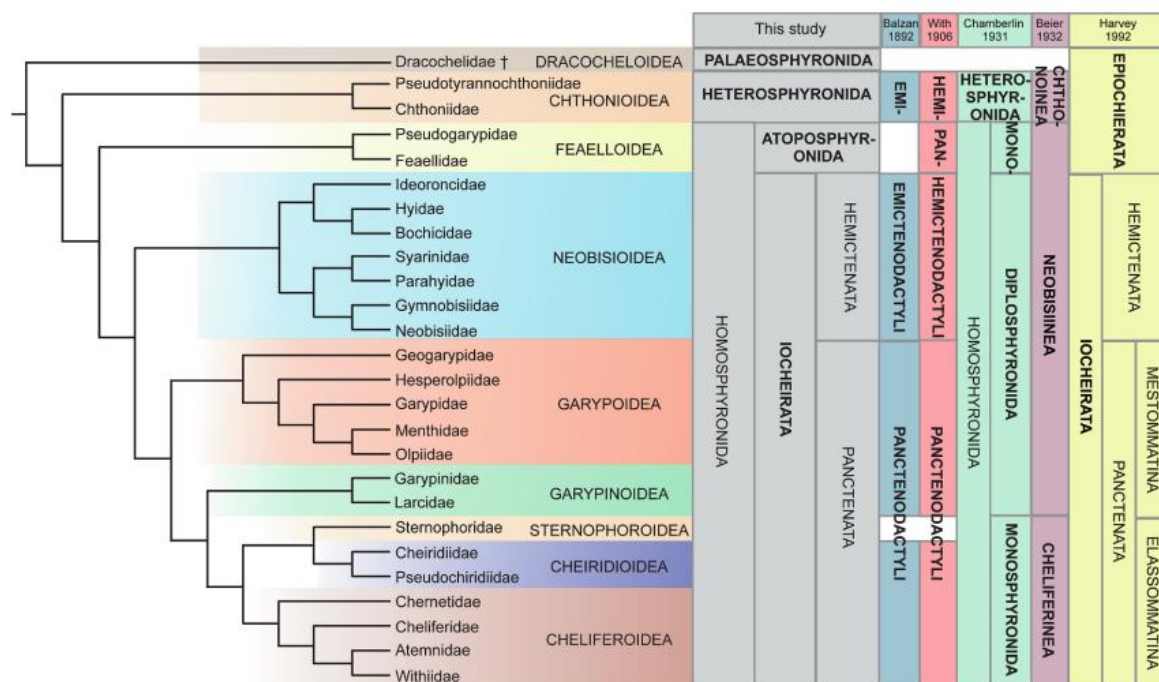
Figure 2c. Summarised phylogenetic tree developed from Benavides et al. (2019.) Harvey (1992) data was used for families with missing data (Menthidae and Pseudochiridiidae.) Previous studies featured here are in bold and referenced as follows: Balzan (1892) With (1906) Chamberlin (1931) and Beier (1932a & 1932b.)

Another unique method in interpreting relationships without the use of morphological characters is through observation of behaviour and niches of living pseudoscorpions. In Del-Claro & Tizi Pedroso (2009) this is covered by broad topics such as diet, reproduction, phoresy and more. The genus *Paratemnoides* in particular is the subject to a literature review concerning it, due to having species exhibiting social behaviour of colonies and 'pack hunting' to a single larger prey animal. Following a hypothesis that there is a connection between complex behaviour and derivation in evolutionary relationships, the notable genera (including the featured *Paratemnoides*) are noted into a phylogenetic tree adapted from Harvey (1992) shown as Figure 2d. It should be noted that no entirely new tree is created from this study's data. Discussion follows a hypothesized evolutionary 'story' of these behaviours through the appearance across extant pseudoscorpions.

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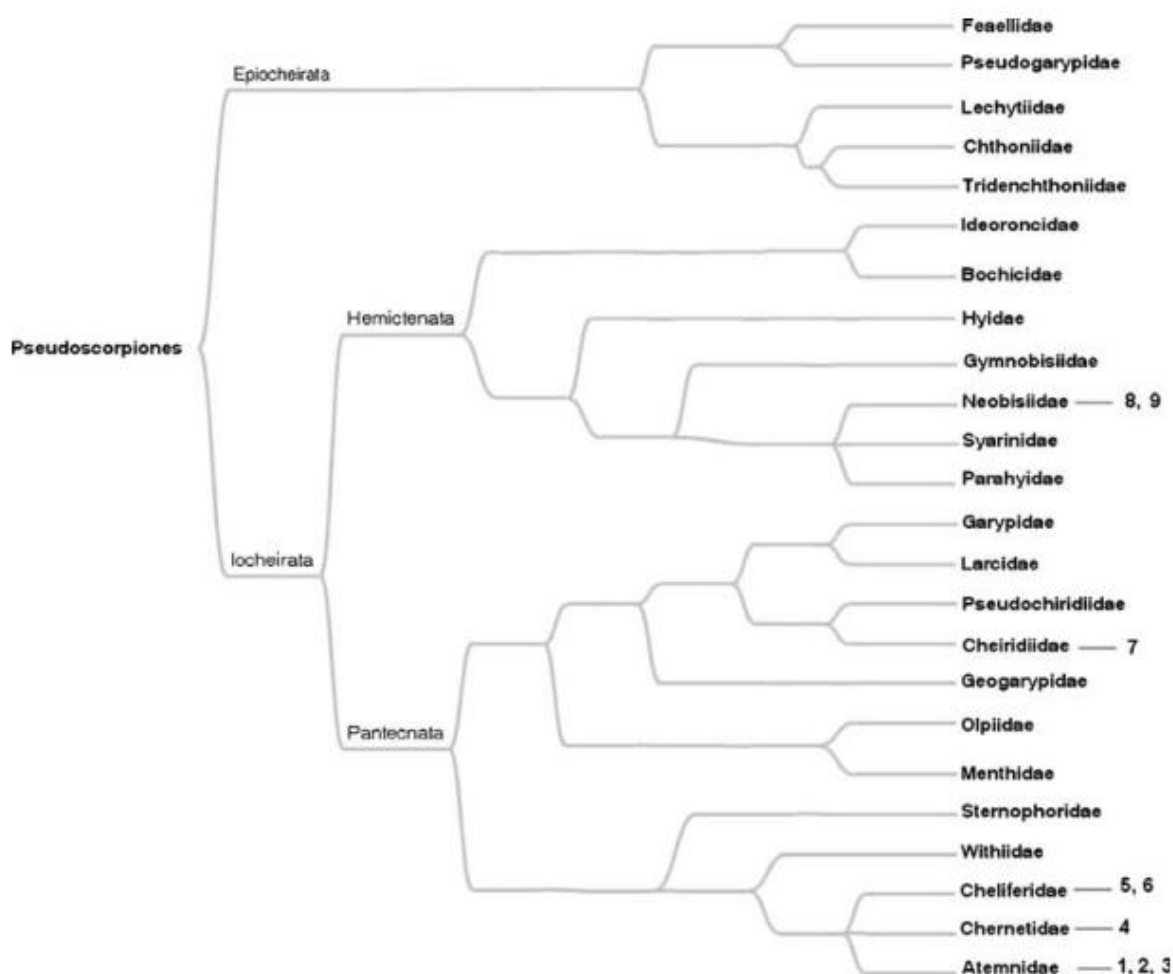
Figure 2d. *Summarised phylogenetic tree from Del-Claro & Tizi Pedroso (2009.) Adapted from Harvey (1992) the following numbers represent an extant species that exhibit social behaviour. Note the number 3. is how it is in the original study, as are the misspelling of Panctenata. 1.* Paratemnoides nidificator *(Atemnidae) 2.* Paratemnoides elongatus *(Atemnidae) 3.* Atemnus politus *(Atemnidae) 4.* Spernochernes schulzi *(Chernetidae) 5.* Hysterochelifer meridanus *(Cheliferidae) 6.* Chelifer cancroides *(Cheliferidae) 7.* Apocheiridium ferum *(Cheiridiidae) 8*. Neobisium maritimum *(Neobisiidae) 9.* Neobisium muscorum *(Neobisiidae)*

Due to referencing Harvey (1992) this study too focuses on families on its phylogenetic tree. It appears to be contradictory where certain genera are focused in the report and discussion; with a number system to the diagram being unclear to what taxa are represented unless the caption was read (and even then, the genera are initialized.) Additionally, there is a blatant logical flaw that most counts of social behaviour cannot be observed in fossil species. So far, only phoretic pseudoscorpions are observed in fossilized amber with other animals (Poinar et al. (1998) for examples) and while in theory there could be fossilized versions of other behaviours such as predation and reproduction; there have not been any such fossils discovered yet (mostly because of the pseudoscorpions' small and elusive size.) Ergo, this method can be limiting in discerning relationships if it can only

include extant taxa.

It should also be noted that through this study's methodology, the approach is not to create a phylogenetic tree from the prevalence of social behaviour but instead to create a 'timeline' of behaviour with an already established tree from another study. Even from this, the resulting discussion is admitted in being speculation. The lack of confidence in the results means this approach is not as reliable as morphological character observations nor is it as accurate as analyzing molecular genomes.

That said, it could be possible that in later years in the future; this method could gain more relevance if more information of both living specimens and of fossilized amber is discovered and described. There could be a proposed study to utilize all three main methods into one when more data can be acquired.

For now, with most of the issues realized it is easier to avoid similar pitfalls for this study in the present. Similarly, it is also clear to understand what strengths each of the previous studies had that can then be utilized as a framework for this current methodology. The concise method of writing a list of morphological characters and labelling each specimen for a matrix to compute a phylogenetic tree is the basic yet effective approach from Harvey (1992.) The list of available fossil specimens and where they currently taxonomically stand from Harms & Dunlop (2017) will also be useful to follow the aim of adding the fossil species to the mostly extant database of Harvey (1992.) And to prevent the issues of limiting computer software; similar methods of creating and comparing between theoretical phylogenetic trees can be made like how it was used in Benavides et al. (2019) (and to understand how to create phylogenetic trees to a genera/species level rather than by families.) Lastly, any future endeavors that can update the understanding to Pseudoscorpiones further from this own study can be found with newer and less orthodox methods like those found from Del-Claro & Tizi Pedroso (2009.)

Every research study reviewed thus far has been a hypothesis on what can improve the accuracy of the resultant phylogenetic trees. This study too follows the similar structure to determine not only a possible interpretation of phylogenetic relationships, but also which methods could prove the most effective. Furthermore, feedback to this study will be made in comparison to this review to understand what is effective and what would need improvement for any future research into this arachnid order.

3. Methodology:

From the literature review, the objective in utilizing the most relevant methods of older studies can follow onward to this study's remaining objectives of creating a new character matrix and then phylogenetic trees.

The process of collecting data should include existing specimens, both fossil and preserved extant paratypes; to log them into the matrix against characters. However, due to complications with current events this is limited to treatises, descriptions, and studies of specified taxa through online resources only. The families that are featured in Harvey (1992) first are also included in this study's matrix, including the data of the character traits. For each of these families that differ from Harvey (1992) a taxon is selected to represent the family that is stated to not include exceptions to the present data (for example, Bochicidae is noted for [0] for character 8 of this study in most of the family keeping four or more flagella on their chelicerae; yet *Mexobisium* spp. is specified to keep less flagella. *Antillobisium vachoni* is then selected to represent the family that has the plesiomorphic quantity of flagella.) For families that are not included in the original matrix of Harvey (1992) taxa are selected based on the availability of descriptions in online resources to create the most complete profile as possible.

In building from the framework of the previous study, inapplicable characters (i.e. this study's character 16 of where the anterior lobes on the prosoma cannot exist without the presence of character 15's said anterior lobes etc.) are marked as [-] and unconfirmed characters are marked as [?] The unconfirmed characters lack sufficient interpretations from a specimen to determine if a trait is more accurate without confidence. Future studies may be able to change this data with new evidence. Whereas inapplicable characters follow logic of existence or possibility in conjunction to previous, connected characters within the list, and thus will be impossible for it to differ from any possibly new data.

New data for both younger taxa and added/reinterpreted characters from the framework of Harvey (1992) are added through personal interpretations of provided photos of specimens, as well as supplemented with discussions and descriptions of relevant studies said photos belonged to. These studies are provided in Table 3a for each representative of the families.

It is advised to change the outgroup from the original choice of Solifugae (camel

spiders) to Scorpiones (true scorpions.) This is due to the prevailing difficulty of different rates of evolutionary changes, particularly with Pseudoscorpiones with a fast rate to the point that its placement in the Arachnida order is still without confidence. As such, Scorpiones is considered to either be a sister group to Pseudoscorpiones or more basal from it, so both options are more viable as an outgroup. From Solifugae, more recent studies have considered this order to be a sister clade to more distantly related orders than that of Pseudoscorpiones. This issue is summarized by Ontano et al. (2021) and applies here, with *Brotheas granulatus* representing the outgroup. Any characters unconfirmed from the source material are supplemented with Dunlop & Penney (2012.)

The software to analyze this study's data is TNT (Tree Analysis Using New Technology) Version 1.5 made available with the sponsorship of the Willi Hennig Society. The description about this program can be found at Goloboff & Catalano (2016.) In relevance to this study, several phylogenetic trees are made with both the equal and implied weighting options. The maximum RAM (random access memory) is 1 000, and was set as a command 'mxram 1000,' while the command 'hold 10000' provides space for 10 000 possible trees in memory during the traditional search tool upon the raw character matrix. With Wagner trees, 100 replies were used with 1 00 trees saved per replication to the tree bisection reconnection (TBR) algorithm.

Table 3a lists each of the taxa selected to represent the family (and in the case of the outgroup, order) with most of the data carried through from Harvey (1992.) Note that any specified differences of the species from the original data had been changed in the corresponding data matrix. The order of families is not taxonomic, but followed the order used in Harvey (1992) with new families added in the beginning. Taxa marked with a cross are extinct and are provided from the fossil taxa list in Harms & Dunlop (2017.) Families that are obsolete from Harvey (1992) (i.e. Lechytiidae etc.) have become part of the valid families (i.e. Chthoniidae) based on revisions of Benavides et al. (2019.) Garypinidae and Hesperolpiidae are unable to find suitable taxa with available resources, and this will be addressed further in the conclusion. Similarly, certain families are missing both an extant taxon and an extinct taxon for the same reasons. The references marked with ([2]) have information from the genus only and not the species. With the outgroup taxon, there are 37 taxa in total used for this study.

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Taxonomy:	Taxon:	Reference:
Scorpiones:	*Brotheas granulatus*	Ythier (2018)
Pseudoscorpiones:		
Dracochelidae:	*Dracochela deprehendor* †	Judson (2012)
Cheiridiidae:	*Apocheiridium lienhardi*	Mahnert (2011)[1]
Syarinidae:	*Ideoblothrus similis*	Muchmore (1982)
Pseudotyannochthoniidae:	*Allochthonius balticus* †	Schwarze et al. (2022)
Chthoniidae:	*Aphrastochthonius tenax*	Muchmore (1972)
	Pycnodithella harveyi	Harvey (1992)
	Lechytia novaezealandiae	Christophoryová & Krajčovičová (2020)[1]
	Paraliochthonius miomaya †	Judson (2016)[1]
Feaellidae:	*Feaella anderseni*	Harvey (1992)
	Protofeaella peetersae †	Henderickx & Boone (2016)[1]
Pseudogarypidae:	*Pseudogarypus orpheus*	Muchmore (1981)[1]
	Pseudogarypus synchrotron †	Henderickx et al. (2012)[1]
Ideoroncidae:	*Sironcus siamensis*	Harvey (2016)
Bochicidae:	*Antillobisium vachoni*	Harvey (1992)
Hyidae:	*Indohya damocles*	Harvey & Volschenk (2007)[1]
Gymnobisiidae:	*Gymnobisium inukshuk*	Harvey et al. (2016)[1]
Neobisiidae:	*Neobisium carcinoides*	Harvey (1992)
	Microcreagris koellnerorum †	Guo & Zhang (2016)[2]
Parahyidae:	*Parahya submersa*	Harvey (1992)
Garypidae:	*Garypus dissitus*	Harvey et al. (2020)[2]
Larcidae:	*Larca granulata*	Harvey (1992)

Pseudochiridiidae:	*Pseudochiridium insulae*	Díaz & Barroso (2013)
	Pseudochiridium lindae †	Judson (2007)
Geogarypidae:	*Geogarypus taylori*	Harvey (1992)
	Geogarypus gorskii †	Henderickx & Perkovsky (2012)
Olpiidae:	*Linnaeolpium linnaei*	Harvey & Leng (2008)[1]
Menthidae:	*Thenmus aigalites*	Harvey (1992)
Sternophoridae:	*Garyops sini*	Harvey (1985)
Withiidae:	*Nannowithius caecus*	Harvey (2015)
	Withius eucarpus †	Judson (2010)
Cheliferidae:	*Philomaoria pallipes*	Beier (1976)
	Heurtaultia rossiorum †	Judson (2009)
Chernetidae:	*Xenochernes caxinguba*	Harvey (1994)
	Oligochernes bachofeni †	Haug et al. (2020)[2]
Atemnidae:	*Diplotemnus balcanicus*	Novák & Harvey (2015)
	Progonatemnus succineus †	Harms & Dunlop (2017)[2]

Table 3a. List of selected taxa for the character matrix, with the study used in reference for this character matrix. † represents an extinct taxa. [1] The study in reference is also the original publication for the taxa. [2]Only information for the genus is available, not the species. In the case of Haug et al. (2020) only the photograph Fig. 1b was used as a reference.

The following Table 3b provides the character list that not only defines each character and the difference in traits; but will specify any changes from the framework of Harvey (1992.) Discussions that are made prior will also be noted as well as any refutes if relevant. Note that the characters 54 and 55 from the original study are omitted from this study entirely, due to the aforementioned issue of labelled trichbothria being uncertain to confirm through post-embryonic development.

#.	Name:	Traits

Character description

General:

1.	Pseudoderm:	absent (0), present (1)

Harvey (1992): A pseudoderm is an extra layer of cuticle across the exoskeleton made mostly of chitin, also known as an exocuticle. It was found in Garypidae and Larcidae
Now: This is a difficult character to determine for fossil taxa due to limitations in observing the layers of the exoskeletion without direct contact or damage to the amber or copal. So far, only the outgroup Scorpiones is confidently confirmed to have a present pseudoderm.

2.	Setae:	straight (0), kinked (1), bent (2)

Harvey (1992): The seta is a sensitive integument from the cuticle surface analogous to mammalian hair, which was described to either being straight, slightly curved, or completely curved without additional details. This character applied to only the dorsal surface of the entire body. The curved shape was found exclusively in Garypoidea with several genera (Synsphyronus, Paragarypus etc.) to have secondarily reversed to the straight setae. Cheliferoids were stated to have curved setae to a lesser extent to those found in Garypoidea, yet no example genera were given.
Now: The validation of this character is under debate with Judson (2000) refuting that truly straight setae are not possible in Pseudoscorpiones as a whole with many cheliferoids having a stronger curvature than it was previously implied. Yet Romero-Ortiz et al. (2021) have indicated visibly curved/bent setae on the pedipalps' trochanters of specimens from the Withiidae family. This character was then given a more detailed illustration with the description of Austinochernes andrewaustini *from Harvey (2021) after its placement in Chernetidae (from this study's Figures 8 and 27.) Thus, Figure 3b[1] is drawn to follow this definition to set the distinctions of each trait with the use of angles against the dorsal surface of the organism's exoskeleton.*

(0)   (1)   (2)
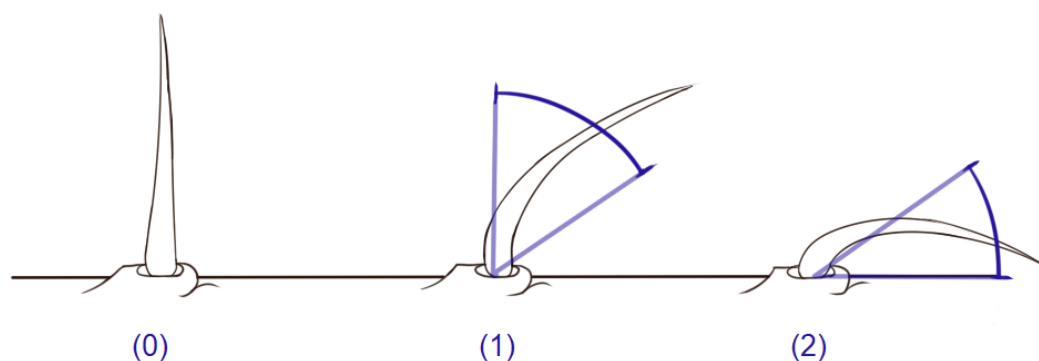
Figure 3b[1]. *Illustration demonstrating the traits of character 2. The angles that define each trait are shown in blue outlines. Straight (0) – the seta is perpendicular to the cuticle surface, kinked (1) – the seta is curved/kinked yet is closer to the perpendicular angle than to parallel (<45°); bent (2) – the seta is curved and is closer to the parallel angle against the cuticle surface (>45°.) Created in PaintTool SAI.*

Chelicerae:

3.	Membrane	absent (0), present (1)

Harvey (1992): Also known as a velum, the membrane was coded as autapomorphic to the infraorder Panctenata and was considered secondarily lost in some genera in Olpioidea (only one example was given, Amblyolpium.) It was said to be present in Garypoidea, Sternophoroidea, Cheliferoidea, and most notably in Olpioidea with given figures in that study (which were Figures 127, 177, 196, and 206.)

Now: The velum is defined as a soft palate typically covering a cavity at least in partial means, with this character applying only to the chelae of the chelicerae (not the pedipalps.) As Harvey (1992) lacked the definition of the membrane in text, it is interpreted from that study's figures that the velum is a bulge from the lateral margin of the chelicera's aperture to the carapace, which thus covers over said aperture. Figure 3b^2 illustrates this definition with notable taxa with absent velums or inapplicable shapes.
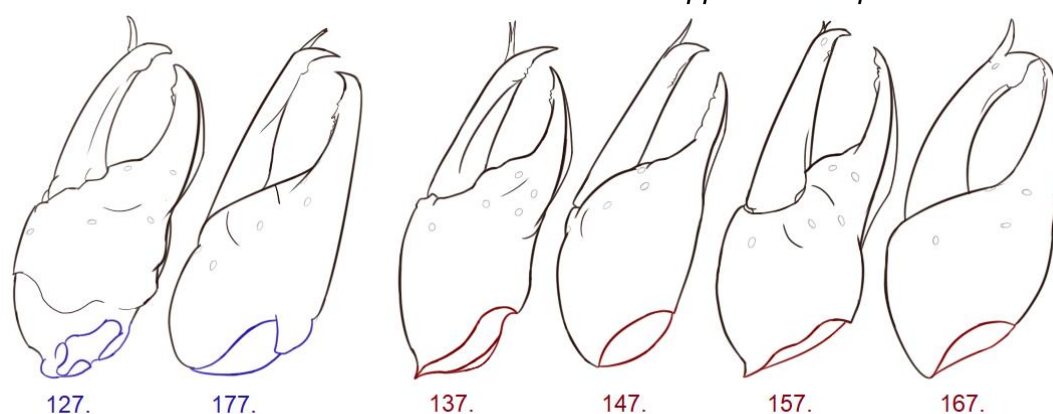
Figure 3b². *Illustration demonstrating the traits of character 3. What is considered the absent trait is outlined in red, and what is considered the present trait is outlined in blue. Each chelicera is referenced from Figures 127 to 177 in Harvey (1992) by their respective taxa from the study, with an angle unique to this study with the aperture to the carapace visible and perpendicular from the right lateral side. 127,* Garypus sini *from Garypidae. The membrane is present from the four nodes over the aperture. 177,* Beierolpium oceanicum *from Olpiidae. There is a membrane on the ventral margin over the aperture, even if said aperture is opened further from the average size across Pseudoscorpiones. 137,* Larca granulate *from Larcidae. There is no membrane as the aperture was opened further than the average size across Pseudoscorpiones instead. 147,* Cheiridium museorum *from Cheiridiidae. There are no modifications to the aperture including any membrane. 157,* Pseudochiridium clavigerum *from Pseudochiridiidae. There are only straight growths from the margin of the aperture, which does not cover over it. 167,* Geogarypus taylori *from Geogarypidae. The asymmetrical growth from the aperture's margin does not cover over it.*

| 4. | Lamina: | absent (0), present (1) |

Harvey (1992): The paper interpreted the lamina to be autapomorphic to the infraorder Panctenata and had independently appeared in an unnamed number of taxa in Ideoroncidae, the latter of which was considered as absent as a whole due to the limitations of applying the family level of taxonomy as discussed in the literature review.

Now: This character is an exterior layer around the entire chelicera, being made of chitin. Dhanus, Shravana, *and* Negroroncus *in the family Ideoroncidae are said to have present laminae in Harvey (2016) and this may not be exhaustive. This character is absent in solifugids (the previous outgroup,) cthonioids, fealloids, and neobisoids; it is present in garypoids, olpioids, sternophorids, and cheliferoids. Methods that are able to simulate the inside of specimens without damaging it or the matrix are necessary for these aforementioned three characters that rely on observing the chitinous layers of fossils. X-ray CT scanning is not accurate enough for this minute detail for such tiny specimens as noted in Racicot (2017) so this would be a matter for future research in improvements or inventions.*

| 5. | Serrations on mobile chelae: | numerous (0), reduced (1) |

Harvey (1992): This trait was given an unknown number of teeth on the internal margin of the chelicera, which was said to be found across Chelicerata including the former outgroup Solifugae (called Solifugida in the source material.) Chthonioidea and Neobisioidea were known to have enough serrations, with reductions to a lobe below the chelae's apex within Feaelloidea and Panctenata. These reductions are said to be autapomorphic.

Now: Serrations are a vertical line of small blades resembling 'teeth' down a ridge at the inferior centre of the mobile chela. It's considered that 'numerous' refers to more than two serrations or ridges from comparisons of the noted taxa from the figures in Harvey (1992) and how a singular lobe and a ridge combination was labelled a reduction. Thus, the label for the autapomorphic trait was renamed from 'few' to 'reduced' to avoid any incorrect assumptions that a larger number of serrations would apply here.

| 6. | Setae placement: | medial (0), distal (1) |

Harvey (1992): The medial placement is present in Chthonioidea and Neobisioidea only; and is considered plesiomorphic to outgroups and throughout albeit without confidence. This particular seta is known as gs, with notes that more than one may occur for taxa in Chernetidae and Cheliferidae. It is noted that there is a correlation between this character and character 11 of this study.

Now: For chelicerae they can appear as single or several strands of which can be medially on the mobile chela or distally to the serrula (fang's apex or tip.) This particular character is known as the galeal seta with Christophoryová et al. (2011) as an example. A suggested topic for future research can be if the number of setae in this lobe (singular, multiple) can be a viable new character before this current one. This was not added to this study as there is not yet enough evidence across morphological profiles to warrant it.

| 7. | Flagellar areole: | linear (0), elliptical (1) |

Harvey (1992): The shape of the areole itself as well as the placement of the flagella differ either it being linear in shape with a single row; or elliptical with two indistinct rows. The elliptical shape is considered autapomorphic and applies only to Chthoniidae and Tridenchthoniidae.

Now: An areole is a proportionally small bump upon the chitin that will contain flagella, analogous to areoles with spines of cacti. This character is directly connected to the following character 8 in this study. The outgroup Scorpiones would have no areoles at all for their flagella, which is why this character is inapplicable.

| 8. | Quantity of flagella: | > four (0), three/four (1), one/two (2) |

Harvey (1992): Mexobisium spp. in Bochicidae is found with a single flagellum, with the rest of the same family containing two or more. Feaelloids as well keep one or two flagella, whereas Ideoroncidae can contain four flagella and Panctenata having a maximum of four. Chthonioidea and Neobisioidea often have more than six flagella and is considered plesiomorphic. Any reduced numbers in other clades are thus considered synapomorphic and ergo autapomorphic in more derived clades.

Now: This character was originally split in Harvey (1992) that have been combined into one character here, as the quantities of flagella were supposedly on the previous character 7 of flagellar areole. With this, it will prevent long branching that can cause

errors between two characters of the same phylogenetic trait it defines. Parsimonious ways of combining characters can streamline the relationships to prevent errors. With a flagellum defined as a simple strand from the chitinous surface, it is considered similar to trichbothria exclusively on chelicerae. However, it must be noted that flagella are separate from trichbothria in definitions, in both this study and Harvey (1992.)

9.	Spinules on flagella:	present (0), absent (1)

Harvey (1992): Smaller branched spinules (small spines, analogous to a thorn) can be found on each flagellum in every genus in the Pseudoscorpiones order apart from geogarypids, whose flagella are a simple hair shape.
Now: This character may need to include microscopes in order to determine the traits in other specimens.

10.	Flagellum shape:	straight (0), curved (1), horizontal (2)

Harvey (1992): The shape of an individual flagellum can be straight and perpendicular to the chitinous surface; partially curved (in between the set angles,) or fully curved to be close to parallel with the surface and so considered horizontal. Harvey (1992) only notes of Lechytiidae flagella being curved or horizontal.
Now: This character can share a similar discussion of whether the curvature of the flagellum can be a viable morphological trait with this study's character 2 with setae. Figure 3b[1] can also represent this character through analogous means. Due to the size of the flagellum, a microscope may be necessary to clarify this character in more specimens to further complete their morphological profiles.

11.	Serrula exterior:	unfused (0), partially fused (1), fused (2)

Harvey (1992): The serrula is unfused from the areole in Chthonioidea, while it is partially fused (for a majority of its length) in Neobisioidea. In Feaelloidea, Garypoidea, Olpioidea, Sternophoroidea, and Cheliferoidea all have the serrulae completely fused to the areole, indicating a transition with the lack of fusion being basal.
Now: A serrula is the small point with in-built serrations in the chelicerae that aids in puncturing prey.

12.	Chelae surface texture:	smooth (0), sculptured (1)

Harvey (1992): The chelae surface texture was considered sculptured in Feaelloidea, which gives a rugged texture across the chitinous surface analogous to scales.
Now: Figure 3b[3] gives more detail to the character.
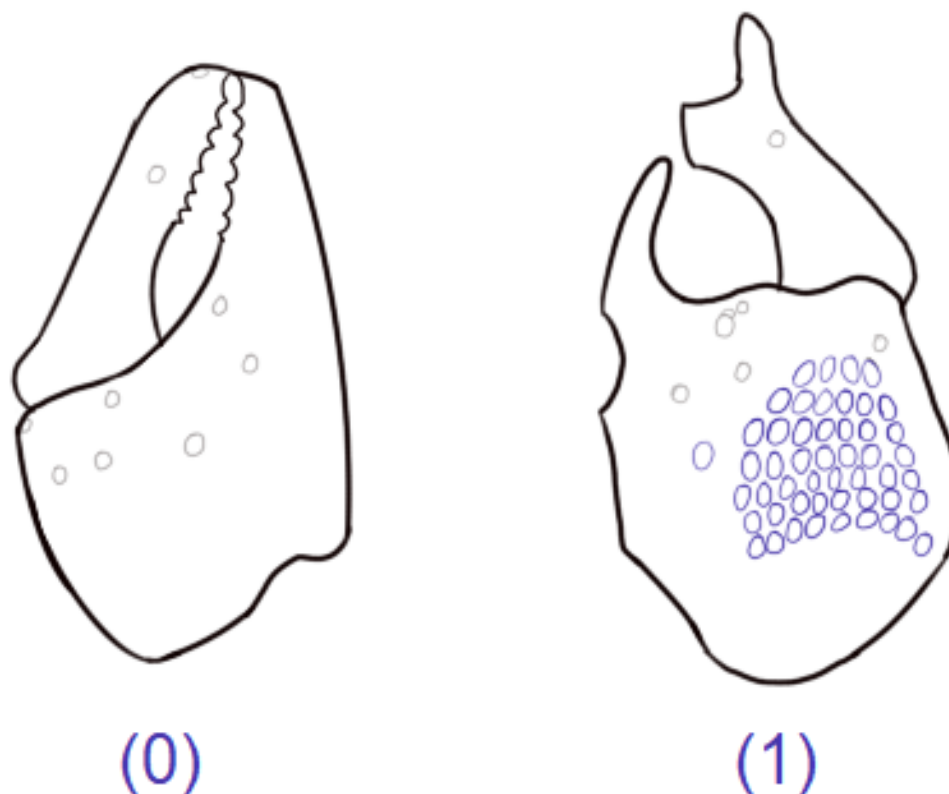
Figure 3b³. Illustration of two chelicerae from a dorsal view based on two genera referenced in Harvey (1992.) (0) Dhanus siamensis *from Ideoroncidae representing the smooth trait. (1)* Feaella anderseni *from Feaellidae representing the sculptured trait (in blue.) Trichbothria pits are shown as circles with low opacity with strands removed. Created in PaintTool SAI.*

13.	Serration fusion:	absent (0), present (1)

Harvey (1992): The interior centre of the immobile chelae of the chelicerae is often shaped with a vertical line of serrations. Feaelloidea is an exception where the more distal serrations had fused together into a single larger point.
Now: Note that a serration differs from a serrula here by not being at the chelicerae's distal tip.

14.	Galea lobes:	single (0), several (1)

Harvey (1992): The galea is defined as a helmet-like curved shape upon the mobile cheliceral finger, of which lobes of that description can be found on the mobile chelae in chelicerae on tridenchthoniids, supposedly in the nymphal life stages.
Now: The number of these lobes each are unspecified in Harvey (1992.) The 'several' trait may be referred to 'branched' or 'forked' in other studies i.e., Mahnert (1980) which may indicate the lobes are not separate from each other and an exact number may not be necessary for determination of this character.

<u>Prosoma:</u>

15.	Anterior lobes:	absent (0), present (1)

Harvey (1992): This character focuses on the presence of lobes (round, dense bumps) and are considered autapamorphic for feaelloids, despite a description is included for the anterior margin lacking such lobes (as straight, slightly convex, or in a waved shaped

unlike that of lobes.) These descriptions are described further in this study's characters 17 to 19.

Now: Observations from the figures of Harvey (1992) indicate that the lobes differentiate from the ridged lobe-less margin by the smaller angles between each lobe (by rule of thumb, less than 45° between the circumferences of each shape.)

16.	Median anterior lobes:	single (0), several (1)

Harvey (1992): These lobes differ by being found at the median centre of the carapace's anterior side, as well as being horizontal (lateral) in placement. Pseudogarypids have three anterior lobes while feaelloids vary between two to six across genera. Feaella krugeri *is a genus with a reduced number of lobes. Feaelloids in general are said to have a division between both sides of the median or centre of the anterior side, where pseudogarypids have two on both sides; and two species* Feaella mirabilis *and* Feaella mombasica *have a total of four.*

Now: By the definitions, the traits may refer to a lobe on each side of the median margin rather than the total. Further observations to the taxa Faella mirabilis *and* Feaella mombasica *would be needed to confirm this.*

17.	Anterior margin:	straight/curved (0), ridged (1)

Harvey (1992): In the centre of the anterior side of the prosoma is a margin that differs in shape, being either straight (or curved) or having a deeper ridge further into said prosoma. This ridge is present in garypoids yet it is less evident in pseudochiridiids. Every other pseudoscorpion family (excluding feaelloids) are said to have a straight or curved shape.
Now: In this case, 'curved' may refer to a convex shape of the carapace without a depressed margin at all, unlike that of the ridged shape or of lobes from characters 15 and 16. The convex margin doesn't convey as a separate trait from straight, seemingly from being unable to define the two in a consistent manner.

18.	Anterior margin texture:	smooth (0), serrate (1)

Harvey (1992): This is present in all chthonioids with the exception of the genus Lagyochthonius.
Now: Any overall shape of the anterior side of the prosoma that is curved or ridged may have smaller serrations or lobes lateral across said margin. The outgroup Scorpiones contain the latter within their anterior margin.

19.	Overall shape:	rectangular (0), triangular (1)

Harvey (1992): The entire carapace of the prosoma can be rectangular in shape which applies to most pseudoscorpions whereas the shape of garypoids is triangular, which is an autopamorphy of the group.
Now: With the addition of the outgroup Scorpiones to compare, the triangular trait remains autapomorphic.

20.	Eye protrusion:	absent (0), present (1)

Harvey (1992): The tubercles apply to garypoids and feaelloids in being autapomorphic and evolved convergently between the clades. For cheiridiids and pseudocheiridiids; the tubercles as well as the eyes may have been reduced.
Now: The eyes on the prosoma are either flat against the carapace or upon tubercles perpendicular to the surface.

21.	Eye position:	anterior margin (0), posterior margin (1)

Harvey (1992): The autapamorphic trait of the character is both present in both feaelloids and garypoids.
Now: The eyes can be found either at the anterior side of the prosoma, or proportionally more posterior by the third of the length of the carapace.

22.	Metazone:	flat (0), depressed (1)

Harvey (1992): A metazone in this context is the dorsal surface of chitin over the carapace. The depression to the interior of the prosoma can be found in cheiridiids only, with Pycnocheiridium mirum *unconfirmed whether it was found with the same trait or not.*
Now: As of this study this remains unconfirmed with the available resources. The metazone may be defined as being larger than and is dorsal over the anterior section of the carapace. With this, it can also be present for the outgroup representative Brotheas granulatus.

23.	Alae:	absent (0), present (1)

Harvey (1992): These are unique to pseudogarypids among the order.
Now: Alae are protrusions that point to the posterior (or perpendicular) from the lateral sides of the prosoma. Notably, this character was not described or defined in Harvey (1992.)

24.	Posterior margin:	straight (0), depressed (1)

Harvey (1992): The shape of the posterior margin of the prosoma is depressed into tergite I in sternophorids. Goniochernetinae would also keep the shape in convergence.
Now: According to figure 48 in Harvey (1992) the depression's apex faces to the anterior.

25.	Articulation to abdomen:	absent (0), present (1)

Harvey (1992): The articulation from the posterior side of the prosoma to the anterior side of the abdomen (including tergite I) differs in feaellids than other clades, how so is not specified.
Now: From Harvey (2018) the articulation was described as a posterior furrow connecting to the anterior side of the abdomen. The presence of this furrow is unique to feaellids. This may be larger in proportions in comparison to the posterior margin (of a smaller scaled ridge) in character 24. The outgroup representative Brotheas granulatus *have a lobed posterior margin that can have both articulation to the abdomen and have a depressed furrow from the previous character.*

26.	Quantity of eyes:	four (0), two (1), none (2)

Harvey (1992): The overall quantity of functional eyes or eyespots on a prosoma, where the plesiomorphic number are four (aka two pairs) positioned on the lateral sides of the carapace. Interestingly, this is the one of two characters in the list that have absence be the autapomorphic trait. The following is said to have the plesiomorphic quantity: Chthoniidae, Tridenchthoniidae, Feaellidae, Pseudogarypidae, Neobisiidae, Gymnobisiidae, Syarinidae, Parahyidae, Hyidae, Garypidae Larcidae, Geogarypidae, Olpiidae, and Menthidae. Some genera that display two eyes or one pair (or to no eyes at all as this is included as one variation) are within families Chthoniidae (those with no eyes are found in Tyrannochthonius, Lagynochthonius; Neochthonius, Paraliochthonius, Chthonius, Microchthonius, Mundochthonius, Mexichthonius, and Ephippiochthonius);*

Tridenchthoniidae, the entirety of Lechytiidae, Neobisiidae (eyes absent in nine species of Roncus*) and some in* Neobisium*,* Microcreagris*,* Acanthocreagris*,* Parobisium*, and* Bisetocreagris*,* Syarinidae (eyes absent in species of Ideoblothrus and Ideobisium*,* Pseudoblothrus, Lusoblothrus*, and* Chitrellina*) all of Ideoroncidae, Hyidae, all of Bochicidae, all of Cheiridiidae, all of Pseudochiridiidae, Olpiidae, Menthidae, all of Sternophoridae, and all of Cheliferoidea. Any genera not mentioned here are considered to have one or two pairs of eyes.*

Now: Following studies such as Harvey & Volschenk (2007) indicate more taxa to contribute to this character, such as several species of Idohya *with absent eyes and the review of Muchmore (1998) includes exclusion of* Bochica withi *from Bochicidae as it's described with only one pair of eyes. Eyespots are not regarded as complete eyes, for example* Pseudochiridium lindae *described in Judson (2007) is regarded as the autapomorphic none for this study with only one pair of eyespots present.*

Pedipalps:

| 27. | Overall shape: | angled (0), raptorial (1) |

Harvey (1992): The raptorial shape is unique in Feaellidae and so is considered autapomorphic.

Now: Raptorial means the femur is close to parallel alongside more distal segments. In contrast, angled will have the tarsi be closer to perpendicular against the proximal coxae and femurs.

| 28. | Median maxillary lyrifissure: | present (0), absent (1) |

Harvey (1992): This lyrifissure is absent only in Feaellidae and the chosen outgroup Solifugae, but with the former it is considered autapomorphic.

Now: A lyrifissure is a shallow pit or slit in the cuticle that can provide a sensory function. This lyrifissure, if present, will be the centre at the interior of the chelae in a slit-like shape. With the change in outgroup, Scorpiones are absent in lyrifissures as well.

| 29. | Lyrifissure shape: | circular (0), straight (1) |

Harvey (1992): This lyrifissure slit can be circular (or as an incomplete circle) or straight in shape. Only Chthonioidea have the straight lyrifissure which is autapomorphic to the group.

Now: It has been noted that Feaelloidea possess the median maxillary lyrifissure as the plesiomorphic circular shape, despite the previous character 28 stating the absence of said lyrifissure in Feaellidae. It is presumed that the family is an exception from the superfamily.

| 30. | Lyrifissure placement: | medial/distal (0), proximal (1) |

Harvey (1992): The proximal position closer to the tarsus is autapomorphic to Ideoroncidae that was noted as sub-basal.

Now: The position of the lyrifissure can be more medial (centre) or distal to the tip of the mobile chelae. The term was changed to be more consistent with terms medial and distal as 'basal' would be. How this placement is defined is illustrated in Figure 3b[4].

Figure 3b⁴. *Illustration of the pedipalp chelae of* Pycnodithella harvei *from a semi-dorsal view with the mobile chela finger open, referenced from Harvey (1992.) Trichbothria are shown as low-opacity circles with absent strands. The lyrifissure is represented as the blue crescent shape on the centre of the inner margin of the chela finger. t: nodus romosus. d: distal placement. m: medial placement. p: proximal placement. (0) is the medial or distal placement. (1) is the proximal placement. Both traits relate to the tarsus. Created in PaintTool SAI.*

31.	Posterior maxillary lyrifissure:	absent (0), present (1)

Harvey (1992): The trait is autapomorphic for Iocheirata while this character is absent in the outgroup solifugids, chthonoids, and feaelloids.
Now: A second lyrifissure is posterior of the tarsus, separate from the lyrifissure on the mobile chela. For the current outgroup Scorpiones, the lyrifissure is absent.

32.	Coxa jugum:	short and thick (0), long and sharp (1)

Harvey (1992): The shape of the jugum is short and thick enough to not overlap over the coxae themselves, but differs in families Cthoniidae and Tridenchthoniidae where it is longer and sharper (interpreted to overlap the coxae) and is thus considered autapomorphic.
Now: The jugum is a protrusion that can provide an anchoring point between a limb and a thorax from an arthropod. For pseudoscorpions, this jugum connects the coxae to the femurs with a slight overlapping protrusion.

33.	Pharyngeal pump keel:	short (0), enlarged (1)

Harvey (1992): The dorsal keel that anchors this structure is enlarged moreso in Cthoniidae than in other families, which is considered autapomorphic for the family.

Now: The pharyngeal pump is a structure within the prosoma that contracts in a rhythm to siphon liquidized foods from the mouth. With this character being an internal structure, this is difficult to observe in fossil species. For example, Paraliochthonius miomaya *is unknown in this character and the subsequent characters until 36 due to the coxae being obscured in the amber matrix, as noted in Judson (2016.)*

| 34. | Coxa shoulder: | absent (0), present (1) |

Harvey (1992): So-called as there is an indent to the pedipalps' coxae in which the overall shape is similar to a human scapula. This character is present in both Geogarypidae and Pseudochiridiidae possibly as unrelated derivations.

Now: The autapomorphic trait is also present in the outgroup Scorpiones, this could support the previous interpretation that this trait can be convergent. Through appearances found in several genera (i.e. Protofeaella peetersae *etc.) this could concur this trait has evolved convergently.*

| 35. | Coxa setae: | two (0), three or more (1) |

Harvey (1992): Setae in regard to the pedipalps' coxae can appear as a pair or more. Only some species within Neobisiidae have a higher quantity of setae, of which remain unnamed.

Now: Neobisium deltshevi, *described by Ćurčić et al. (2010) to have five setae; is an example of Neobisiidae with the autapomorphic trait.* Neobisium carcinoides *selected in this study's character matrix (Table 3a) is interpreted to have three setae from photographs of specimens, so the trait will differ from the character matrix in Harvey (1992) with an assumption a taxon with two setae was selected that keeps the previous matrix valid.*

| 36. | Coxa distal shape: | triangular (0), rounded (1) |

Harvey (1992): The character of rounded coxae (without a point) is said to be autapomorphic in Neobisiidae. The genus Syarinus *in Syarinidae also have rounded coxae according to Muchmore (1982) and was discounted from the family-based character matrix yet still noted.*

Now: The coxa may have a distal point that can either be round or triangular, at the margin to the femurs. Ideobisium similis *was selected for this study's character matrix and is said to have a triangular coxae from Muchmore (1982). Further research to include a species representative for* Syarinus *alongside* Ideobisium *could provide more confidence into Syarinidae for this character.*

| 37. | Femur trichbothria: | absent (0), present (1) |

Harvey (1992): One or two trichobothria are present on the femur in olpiids and menthids only. Unlike other characters concerning trichbothria, this character lacks labels to specific strands.

Now: Trichobothria are specialized setae that are sensitive to changes in the air including movement and electrical charge.

| 38. | Femur setae: | absent (0), present (1) |

Harvey (1992): Unspecified species in Hyidae only contain three or two setae across the femurs each. Why this character's traits apply to only presence of multiple setae or absent entirely instead of numbers of setae present remains unanswered.

Now: Setae differ from trichobothria by being comparatively shorter, lack the shallow pits, and are more generalized to physical touch sensitivity. In Harvey & Volschenk (2007) this

was then specified that the autapomorphic trait applies to all Hyidae species with variations in numbers (with the minimum of two from Hya chamberlini *etc. and species of* Indohya *having a maximum of four or five.) As evidenced in Judson (2012) what was determined as a pedipalpal femur of* Dracochela deprehendor *in that study's figure 7D still retains a seta, which can be assumed more were available during the specimen's lifetime before damage during taphonomy.*

39.	Femur proximal tubercle:	absent (0), present (1)

Harvey (1992): This character is only present in certain genera within Bochicidae, specifically the genera Vachonium*,* Antillobisium*, and* Troglobochia*. Within the same family it is absent in* Paravochonium *spp.,* Antillobisium mitchelli*,* Apohya *spp.,* Leucohya *spp.,* Mexobisium *spp.,* Troglobochica jamaicensis *and* Troglohya *spp.*
Now: A small blunt protrusion can be found on the proximal palpal femur, neighbouring the coxa margin.

40.	Immobile venom apparatus:	absent (0), present (1)

Harvey (1992): Venom apparatus in the pedipalps is one of the characters that defines the Pseudoscorpiones order. If this apparatus is present, it can be found in the immobile chelae of the pedipalps (known as the fixed chelae.) This is the case for Neobisiidae, Syarinidae, Parahyidae, Menthidae, and Atemnidae.
Now: The descriptions for this character and character 41 below are combined in Harvey (1992) which will be described separately for improved clarity.

41.	Mobile venom apparatus:	absent (0), present (1)

Harvey (1992): If this venom apparatus is present, it can be found on the mobile (segmented) chelae of the pedipalp. This can be found in Gymnobisiidae, Vachonium *and* Paravochonium *from Bochidae,* Indohya *in Hyidae, and Chernetidae. There is an absence of a venom apparatus entirely in Chthonoidea and Feaelloidea.*
Now: It is interesting to note that while the pedipalp venom apparatus in general defines Pseudoscorpiones, both this and character 40 is considered autapomorphic and not plesiomorphic from the most common ancestor of the order.

42.	Venom ducts:	proximal length (0), distal length (1)

Harvey (1992): A venom duct is considered long if it reaches past the most distal trichbothria across the tarsus. The trichbothria that defines the traits are labelled et *or* t*, the former applying to the immobile chelae and the latter to the mobile chelae. Neobisiidae, Syarinidae, Parahyidae, Gymnobisiidae, and Menthidae each have the autapomorphic short ducts. Olpiidae also contain short ducts between the types of pedipalpal chelae.*
Now: Venom ducts are channels between the glands and the nodus romosus, usually found at the distal point of each or one of the chelae of the pedipalps. The trichobothria referenced can be known as the most distal strands without individual labels being necessary. This is illustrated in Figure 3b[5]. For Olpiidae, the representative taxon Linnaeolpium linnaei *will be marked autapomorphic for the short venom duct noted in Harvey & Leng (2008.) More taxa to represent Olpiidae that have the longer venom ducts could be included in future research.*
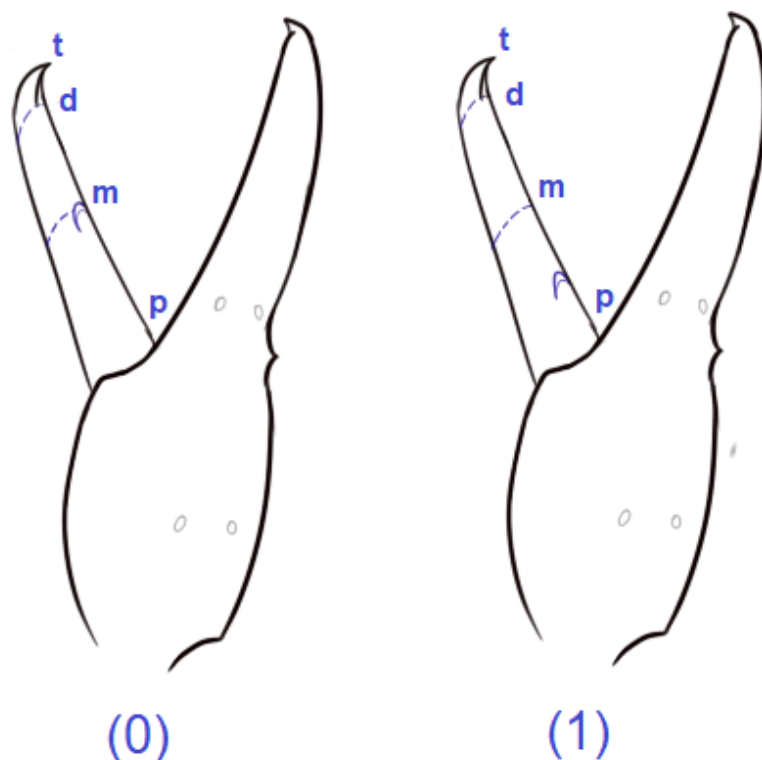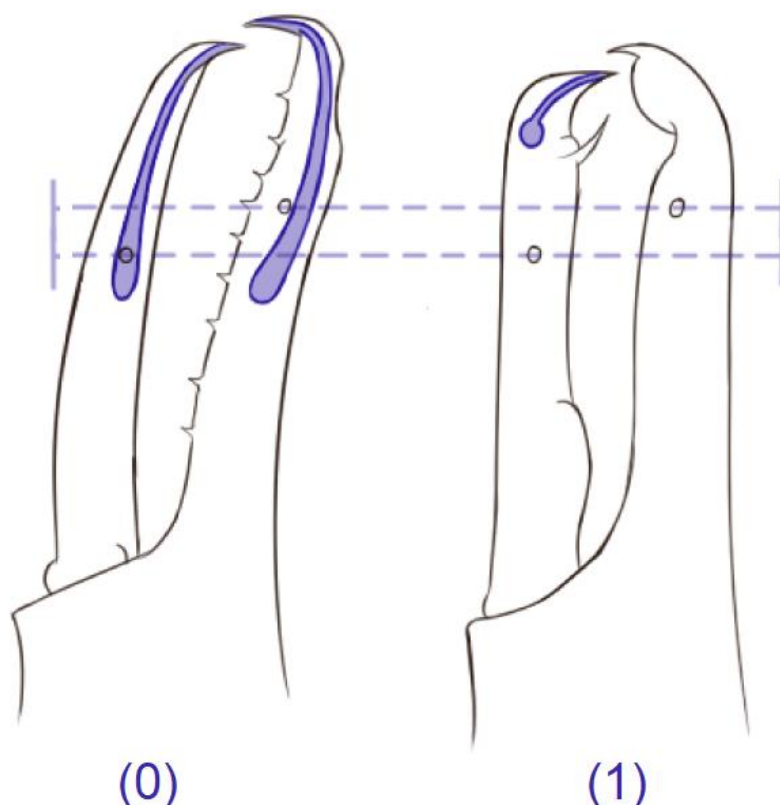
Figure 3b[5]. Illustration of the pedipalp chelae of two taxa seen from a semi-dorsal view with the mobile chela finger closed, referenced from Harvey (1992.) The internal venom ducts are highlighted in blue, with the blue dotted line representing the placement of the most distal trichobothria shown as black circles. The top line represents the immobile chela's trichobothrium (aka et) and the bottom line represents the mobile chela's trichobothrium (aka t.) (0) Hya minuta from Hyidae with the plesiomorphic long venom ducts. (1) Vachonobisium troglophilum from Gymnobisiidae with the autapomorphic short venom ducts.

| 43. | Nodus romosus: | ridged (0), flat (1) |

Harvey (1992): The enlarged size is considered autapomorphic to Neobisiidae, Syarinidae, Parahyidae, and Gymnobisiidae; as well as cheliferoids.
Now: A node is an opening at the tip of the chela to deliver venom. The node has a lateral ridge within the chela giving it a distinct ovalline shape at the distal tip. The 'enlarged' size would have the tip without a ridge and thus a 'flat' lateral margin of the chela in question. Both the definition of the character and description of each trait was given, so the traits are renamed from the vague 'normal' label to the more specific 'ridged' shape.

| 44. | Mobile chelae setae: | absent (0), present (1) |

Harvey (1992): Thickened straight setae can be found on the mobile chelae in Gymnobisiidae as an autapomorphic character.
Now: In comparisons of figures 90 to other pedipalps in Harvey (1992) this character could be defined as having higher quantities of setae than usual within Pseudoscorpiones.

| 45. | Medial serrated mobile chelae: | absent (0), present (1) |

Harvey (1992): The mobile chelae bear serrations that point posteriorly to the tarsus, all within the internal median margin. This is an autapomorphic trait in only Feaellidae.
Now: The autapomorphic trait was also found in fossil species such as Geogarypus gorskii, *which may instead be the cause of distortion in appearances through fossil*

matrices or through damage through taphonomy. It is regarded as an autapomorphic trait in this study's matrix to test what effects this may happen to the phylogenetic trees.

46.	Accessory chelae serration:	absent (0), present (1)

Harvey (1992): Both or either of the chelae can have a lone serration as an accessory. The presence is common in Chernetidae with the exception of taxon Myrmochernes africanus. Geogarypus *and* Indogarypus *from Geogarypidae also have accessory serrations present that is considered a convergent character.*
Now: The two representatives for Chernetidae include Xenochernes caxinguba*, which is described to have smooth chelae and thus no serrations in Harvey (1994.)* Oligochernes bachofeni *has not been confirmed for the chelal structure due to the only resource includes a specimen in amber discussed in Haug et al. (2020.) CT tomography may be necessary in the future to determine the chitinous texture to confirm this character.*

47.	Distal trichbothria:	absent (0), present (1)

Harvey (1992): On the distal margin of the immobile chelae there are a short pair of trichobothria close to the tip. These trichobothria are only present in chthonioids and feaelloids and was labelled collectively as xs.
Now: This trichbothria area is exclusive in this character, where it is only specified to be found on the external margin of the pedipalpal immobile chela within figures in Harvey (1992.)

48.	Trichobothria placement:	immobile chelae (0), tarsus (1)

Harvey (1992): Lechytiidae contain the trichobothria in the tarsus and are labelled eb *and* esb *respectively. The trichobothria labelled* ib *and* isb *are used as a reference in distance but are not involved in the character specifically for Lechytiidae.*
Now: Two trichbothria can either be found on the mobile chelae at the exterior proximal edge from the femur, or upon the exterior distal part of the chela tip. This character can be a confident example of how the area the trichobothria are found can be used over individual labels, for it is more parsimonious than the assertions trichobothria retain the label between an animal's growth and development through instars.

49.	Immobile chelae trichbothrium:	exterior proximal (0), interior distal (1)

Harvey (1992): This single trichbothrium featured in the previous character 48 (known as eb*) can be found at the exterior proximal section of the fixed chelae. This only applies to the protonymph instars, where this same trichbothrium is apparently found instead at the interior distal section of the same chelae in feaellids.*
Now: Future research may be necessary to determine if the trichbothrium does 'move' to the interior area in feaellids during an animal's growth, or if the trichbothrium (or the trichbothria in general) are redeveloped with the next instar alongside the chitinous body. If the latter is true, the label may be abundant if it applies to two trichbothria in two placements.

50.	Proximal immobile trichbothrium:	interior (0), posterior (1)

Harvey (1992): The specific trichbothrium is said to have a plesiomorphic position on the interior side of the immobile chelae which can be found in feaellids. This is a trichbothrium

separate from the pair featured in characters 48 and 49 so was given the label isb. *The placement differs to the posterior side in Iocheirata with multiple families having returned to the interior placement including* Syarinus *(in Syarinidae), Geogarypidae, Cheiridiidae (and Pseudocheiridiidae), Larcidae, Garypininae (in Olpiidae), and Sternophoroidea with Cheliferoidea.*

Now: Syarinus *could be included as another representative taxa for Syarinidae in a future review of this study's methodology, to determine if this autapomorphic character can affect the cladogram on a species level. Similarly,* Linnaeolpium linnaei *is in the subfamily Olpiinae so an additional taxa within Garypiniae can also be included as an additional representative.*

51.	Interior immobile trichbothrium:	proximal (0), distal (1)

Harvey (1992): A single trichbothrium can be situated either at the proximal area of the immobile chelae, or at a more distal area of the same chelae more in between its total length. This trichbothrium is labelled ist *and the former applies to Chthonioidea, Feaellidae, Gymnobisiidae, Hyidae, Ideoronicidae, some genera of Neobisiidae, some genera of Syarinidae, Garypoidea (excluding Geogarypidae), some genera in Olpiidae, Sternophoroidea, and most genera in Cheliferoidea. This position is considered plesiomorphic. The latter applies to Pseudogarypoidea, Bochicidae, some other genera in Neobisiidae and Syarinidae; Parahyidae, Geogarypidae, Menthidae, and some genera in Cheliferoidea. This altered position is considered autapomorphic, with a reversion to the proximal position in Microceagrinae in Neobisiidae as well as the genus* Syarinus *in Syranidae.*

Now: There is an implication that both positions are present on the chelae, and in that case is regarded as plesiomorphic. In which case, an argument could be made for future studies to possibly expand this character with a 'both' trait (possibly as (1) with the distal trait becoming (2)) when more information is available.

52.	Tarsus trichbothria:	lateral (0), dorsal (1)

Harvey (1992): Two more trichbothria can either be found in specific areas and were labelled as ib *and* isb. *For cththonoids, these trichbothria are set laterally across the tarsus on the dorsal margin. The proportion on placement with the length of the tarsus varies between being proximal, between proximal and medial, and distal (the last case is within Pseudotyrannochthonidae). In one genus* Mexichthonis *spp., the trichbothria are placed vertically across the tarsi's length.*

Now: This area can either be called a hand or, in this study, a pedipalpal tarsus.

53.	Margin trichbothria:	lateral (0), basally (1), distally (2)

Harvey (1992): Not applicable.

Now: A new character in tandem to the last character, in order to expand the observations of the different placements of the trichbothria upon the immobile chelae in regard to the dorsal chitinous surface. The plesiomorphic trait is lateral to connect it to character 52's plesiomorphic trait in Harvey (1992) with emphasis on the area rather than the trichbothria themselves. Because of the lateral trait being plesiomorphic, it may give an error if this character was given the inapplicable data (-) in the matrix instead. For reference, this character refers to the trichbothria labelled ib *and* isb *only.*

54.	Second margin trichbothrium:	On immobile (0), on mobile (1), on tarsus (2)

Harvey (1992): The previously mentioned trichbothrium (known as ib*) can either be found upon one of the unspecified chelae (immobile/fixed or mobile/movable) in Bochidae and Ideoronidae or upon the overall tarsus. Several genera from Syarinidae like* Nannobisium, Alocobisium, *as well as the clade within the subfamily Chitrellinae; also have the trichbothrium upon the chelae.*
Now: The two genera in Syarinidae as well as the subfamily can be additional representatives in Syarinidae for any future research using this study's methodology and database.

55.	Quantity of trichbothria:	fifteen or less (0), more than fifteen (1)

Harvey (1992): The total amount of trichbothria on both chelae and the tarsus from a single pedipalp. An average number is said to be twelve, from eight on the immobile chela and four on the mobile chela. Ideoroncids are shown to have a higher quantity than fifteen with an average between twenty to thirty-one on the immobile chela plus ten to fourteen on the mobile chela; despite the character stated to be a maximum of thirty trichbothria.
Now: The traits are renamed for a more concise range ('more than thirty' can still apply to the autapomorphic trait.)

56.	Quantity of trichbothria on chelae:	eight or less (0), nine or more (1)

Harvey (1992): Menthids are unique in containing only three trichbothria. Synsphyronus *in Garypidae has also been rectified to possess eight trichbothria. The study continued with a contention with specimens of* Maorigarypus *spp., where there is a refute on having not twelve trichbothria but eleven.*
Now: The total amount of trichbothria on the two chelae of each pedipalp, excluding the tarsus itself, vary between the clades. To prevent this in the future, the traits are renamed in this study to remove a 'maximum' amount in case of future discoveries being found with more after all.

57.	Trichbothria shape:	triangular (0), ovalline (1)

Harvey (1992): The specific trichbothria upon all genera of Syanidae are said to be ovalline instead of triangular (like human hair strands at a microscopic level.)
Now: The plesiomorphic trait is renamed from lanceolate, for further clarity of the overall shape.

58.	Pits on tarsus:	absent (0), present (1)

Harvey (1992): There are shallow pits in the chitin of the exterior side of the tarsus in Geogarypids.
Now: The function of these pits is unspecified and couldn't be found from the available resources of this study.

<u>Limbs:</u>

59.	Coxal spines:	absent (0), present (1)

Harvey (1992): Small spines that differ in structure to setae can be found on the coxae of both the pedipalps and legs (excluding legs IV) of chthonioids and feaelloids. It is said that

they appear as granulations to certain chthoniod families such as Lechytidae or the genus Sathrochthonius *spp. which suggests the spines are part of the chitin instead of being a separate material like setae.*

Now: That said, it could be argued that this character could be expanded to count the granulation as an autapomorphic trait. A lack of resources available to determine granulations from different spines prevented this.

60.	Coxal tubercle:	absent (0), present (1)

Harvey (1992): This character is considered autapomorphic for Chthoniidae and Tridenchthoniidae and have been lost independently across the genera of both families. It is noted that Pseudoscorpiones lack any sclerotized regions between coxae that are present in other Arachnida orders such as Solifugida. The genera that retain tubercles in Chthoniidae are as follows: Allocthonius, Aphrastoctonius, Chthoniella, Chthonius, Mundochthonius, Pseudotyrannocthonius, Sathrochthonius, *and* Selachthonius. *For Tridenchthoniidae the genera that retain the tubercles are* Compsaditha, Ditha, Dithella, Neoditha, Neoditha, Paraditha, *and* Tridenchthonius.

Now: These are tubercles between each pair of coxae of which they are small round protrusions directly from the chitinous surface, but whether this applies to all coxae of each limb remains unspecified. It is also known as the intercoxal tubercle and may refer to coxae III and IV in regard to Benedict (1978.) For Scorpiones, the tubercles are absent as well with Volschenk & Prendini (2008) being an example with Aops oncodactylus.

61.	Setae on tubercle:	absent (0), single (1), multiple (2)

Harvey (1992): If the tubercle upon the coxae is present, it may either have a single seta or two setae upon it. It is noted that a single seta can be found on tubercles within Tridenchthoniidae; while in Chthoniidae it's more common to have two. There are exceptions to the latter family, where the taxa Aphrastochthonius tenax *(interestingly, it is noted that this is only present in the male holotype) and* Mundochthonius holsingeri *have one seta on their tubercle. Having two setae is considered autapomorphic, and can also be known as bisetose (a single seta is known as monosetose in comparison.)*

Now: The absent plesiomorphic trait is added to prevent contradictions with this study's character 60 with an absent tubercle entirely, as the plesiomorphic trait are shared between the characters without using the inapplicable mark that could cause false negatives during phylogenetic analyses.

62.	Coxa I shoulder:	absent (0), present (1)

Harvey (1992): On the coxae of the first pair of legs known as coxa I, in chthonioids a protrusion can be found facing in an anterior direction; with a shape in analogy to the human scapula bone. This is considered autapomorphic for the aforementioned family.

Now: With the additional taxa in this study's matrix, this autapmorphic trait remains within Chthoniidae.

63.	Pseudosternum:	absent (0), present (1)

Harvey (1992): Sternophorids have desclerotised the medial (centre) part of their coxae to form a 'pseudosternum' that are directly from said coxae. This differs from sternums of other arachnids as being separate pieces in between whole coxae (or no sternums at all regarding other pseudoscorpions.)

Now: Considering the previous discussion of the lack of a sternum between coxae within the Pseudoscorpiones, as evident in characters 60 and 61 in this study; the outgroup Scorpiones would have this character absent.

| 64. | Coxal articulation: | absent (0), present (1) |

Harvey (1992): This character is only found in Menthidae and is considered unusual.
Now: The shapes of coxae II and III are rounder and articulate between each other that joints of a human tibia can be analogies to.

| 65. | Coxa IV size: | medium (0), less than double size (1), over double size (2) |

Harvey (1992): The posterior side of coxae IV in pseudochiridiids are considered to be comparatively larger than coxae IV of other families, and thus autapomorphic.
Now: To what extent is unclear, as swellings were identified in some cheliferoids such as Megachernes *spp. and* Protochelifer *spp. but are vaguely considered insignificant. These swellings are regarded as the autapomorphic trait 'less than double size' in this study to expand this character and accommodate the two genera for any future research that implements them.*

| 66. | Coxal width: | consistent (0), exponential (1) |

Harvey (1992): The overall size of each pair of coxae can increase from coxae I to coxae IV, with the latter being the largest in comparison; of which the posterior end is wider. This is considered autapomorphic for all pseudogarypids and garypids (excluding geogarypids). This trait is also present in some taxa of cheliferids such as Chelifer cancroides. *For other families, the width of the posterior end of the coxae remains consistent across each pair of them.*
Now: The autapomorphic trait is also present in both taxa within Pseudochiridiidae represented in this study's matrix.

| 67. | Coxal sac (male only): | absent (0), present (1) |

Harvey (1992): Male pseudoscorpions have a sac in the medial centre of each of coxae IV shown as a pore. This is considered plesiomorphic and certain genera of cheliferids (such as Philomaoria *sp. and* Ellingsenius indicus *etc.) have considered to have secondarily lost this sac.*
Now: Due to the appearance of a pore from an outside perspective, as well as the difficulty in determining sex from incomplete or obscured specimens; this character is near impossible to observe for this study with the resources at hand. Despite this, CT tomography in future research may make this possible. The outgroup Scorpiones instead have pectines for the same function, and so for this character it is inapplicable.

| 68. | Femur I & II sensillum: | present (0), absent (1) |

Harvey (1992): In the case of pseudoscorpions, the sensilla (excluding setae) appear as slits as well. They can be a single slit or multiple upon the dorsal chitinous surface of femurs I and II. Feaelloids have secondarily lost these traits.
Now: Sensilla are known as a group of sensory neurons formed together into a varied shape as a sensory organ above, across, or below the chitin. In other studies for Arachnida they can also be known as lyriform organs, and can be regarded as single if several slits are conjoint to a single organ as shown in Barth & Stagl (1976.) It may be considered that the number of slits could be a new character afterwards to quantify them as traits, yet this was not done in this study due to the lack of resources to find exact numbers of sensilla for each taxon. Any taxa that have autapomorphically lost the sensilla, including the outgroup Scorpiones, will be inapplicable to the following characters 69 to 74.

69.	Femur I & II sensillum placement:	proximal (0), distal (1)

Harvey (1992): The placement of the sensilla slits on femurs I and II can either be more proximal (closer to the coxae) or more distal (closer to the patellae). The former applies to Chthonioidea and the latter to Iocheirata. With a lack of homology to the outgroup (Solifugids) it was considered the distal position to be autapomorphic.
Now: With the change of outgroup of this study to Scorpiones, it is confirmed that the distal position is autapomorphic. More information is in the Discussion chapter.

70.	Femur I & II sensillum angle:	perpendicular (0), parallel (1)

Harvey (1992): The parallel position is present in Chthonioidea, Garypoidea, Olpioidea, Sternophoroidea, and Cheliferoidea. Neobisioidea also applies but with three exceptions, Neobisiidae, Syarinidae, and Parahyidae of which the sensilla are perpendicular.
Now: Compared to the chitinous surface of the femur, the sensilla can have a parallel position between its own dorsal side and the femur's chitin; or the sensilla will be angled perpendicular between the surface and the previous parallel position. Geogarypus taylori *was reinterpreted in Harvey & Volschenk (2007) to have the autapomorphic parallel angle.*

71.	Femur I & II three sensilla:	absent (0), present (1)

Harvey (1992): Next to the aforementioned sensillum/sensilla in the aforementioned characters 68 to 69, it is said that three sensilla slits (that are comparatively smaller) are also present on femurs I and II. These sensilla were found in Neobisiidae, Syarinidae, Parahyidae, and Hyidae and thus is unique within Neobisioidea. In certain genera such as Ideoblothrus, Chitrella, *etc. these slits have considered to be secondarily lost. Interestingly, it is unknown if this trait is present in gymnobisiids or bochicids.*
Now: In Harvey & Volschenk (2007) further observations show the representative for Gymnobisiidae in this study (Mirobisium sp.) to have the parallel autapomorphic trait from character 70 here. However, it has been contradicted where a note was made of the absence of examining gymnobisiids for the three secondary sensilla (character 70) in Harvey (1992) that was rectified in Harvey & Volschenk (2007) yet no such rectification was found involving the secondary sensilla; only the angle of the main sensilla of the previous characters. From this, the status of both Mirobisium *sp. (to represent Gymnobisiidae) and* Antillobisium vachboni *(to represent Bochicidae) for this specific character remains unknown until direct observation can be done in the future.*

72.	Femur I & II three sensilla placement:	proximal (0), distal (1)

Harvey (1992): If these three smaller sensilla are present, they either appear more proximal (closer to the coxae) or more distal (closer to the patellae), that are supposedly (but not confirmed outright) on the dorsal surface of the femur. The former applies to Neobisiidae, Parahyidae, Hyidae and the latter applies to Syarinidae. It was considered that the distal position is autapomorphic despite the aforementioned absence of sensilla in the Solifugae outgroup.
Now: Similar to the previous characters in regard to sensilla, this is confirmed to be the case for the Scorpiones outgroup in this study. So too would the issues around

Gymnobisiidae and Bochicidae include this character including future observations to appropriate specimens.

73.	Femur I & II sensilla mound:	absent (0), present (1)

Harvey (1992): There is an anterior mound over the chitinous surface where the three sensilla can be found ventrally upon. This is only found in genera within Hyidae.
Now: The autapmorphic trait remains within Hyidae only, but with the uncertainty in determining this character in fossil species it is yet to be a confident interpretation.

74.	Femur I & II sensilla shape:	straight (0), curved (1), semi-circular (2), circular (3)

Harvey (1992): The overall shape of each sensillum on femur I and II can be either straight or curved. The straight shape is said to be more common, where the curved shape can be found in Cheliferidae, Chernetidae, and Atemnidae. It is the curved shape that is subsequently considered autapomorphic.
Now: The character in this study is the result in combining characters 74 and 75 from Harvey (1992) as they both refer to the same sensilla and the shapes be the traits. It is assumed the characters were separate to accommodate the limitations of the software of the time; and that each trait after curved would be autapomorphic, to prevent possible errors that may arise if the autapomorphic 'curved' trait in character 74 from Harvey (1992) is regarded as the plesiomorphic 'otherwise' trait the character afterwards.

75.	Femur to patella I & II:	slanted (0), perpendicular (1)

Harvey (1992): For Cheliferidae, Atemnidae, and Chernetidae; the slanted joint applies while the rest of most of the Pseudoscorpiones order apply to the perpendicular angle.
Now: While this was named a junction in Harvey (1992) the indented joint between the distal edge of the femur to the proximal side of the patella in limbs I and II can either be slanted in comparison to these sides, or perpendicular against them. There is no determination that the slanted joint (also known as oblique, a synonym) is plesiomorphic however. These traits are given more evidence with Harvey (1998) in retrospect to describe the genus Anysrius.

76.	Femur to patella III & IV:	slanted (0), perpendicular (1)

Harvey (1992): This character applies to limb IV but not to limb III within the description. In contrast to the previous character with limbs I and II, it is the slanted angle that is more common among the Pseudoscorpiones order. The exceptions with the perpendicular angle are independent taxa across Feaelloidea, Gymnobisiidae, Neobisiidae, Syarinidae, and Sternophoridae; of which this trait could be autapomorphic. In Syarinidae and Parahyidae, it was considered the perpendicular position has been secondarily lost to the plesiomorphic slanted angle, which includes the genus Syarinus. *However, Parahyidae was considered perpendicular as a whole despite the slanted position found in the genera* Nannobisium, Ideobisium, *and* Ideoblothrus.
Now: Similar to the previous character 75 of this study, the indented joint between the distal side of the femur attached to the proximal side of the patella can either be slanted in comparison to the latter's side or perpendicular against it. As Ideoblothrus *is the genus that represents Syarinidae in this study, this family is regarded to have the perpendicular junction. Future research to include more species (possibly* Syarinus*) could determine if this character can affect phylogenetic relationships within the family and beyond it.*

| 77. | Femurs to patellae: | segmented (0), fused (1) |

Harvey (1992): The overall segments of the femurs and patellae could be fused into a single segment, with no indented joint or possibility of movement between the two. This character applies to limbs I and II of cheiridiids and are also known as a podomere. Vestigial sutures are said to also been found, but it is unknown if this is on an individual specimen scale or across taxa as a whole.
Now: As of this study, this remains unconfirmed.

| 78. | Femur to patella I & II proportions: | femur longer (0), patella longer (1) |

Harvey (1992): In regard to length between the proximal and distal sides, either the femur is longer, or the patella is, at least in regard to limbs I and II. The femur being longer is the more common trait among the taxa of the Pseudoscorpiones order, where the opposite applies (or of which the patella is equal in length to the femur) to selected families. In Cheiridiidae, Pseudochiridiidae, Sternophoroidea, Cheliferoidea, Garypidae (excluding genus Garypus*) and Olpiidae (including genus* Xenolpium.*) The enlengthened patellae has evolved independently between families, of which had limited movement between the joints. A reason for this isn't considered, however. Garypidae and Olpiidae were placed in the longer femur category by the presence of the trait among the genera.*
Now: With Garypus *representing Garypidae for this study, an additional representative may also be necessary to represent a taxa in the family with the autapomorphic trait. For Olpiidae, the representative taxon* Linnaeolpium linnaei *is of equal proportions between the femur and patella as described in Harvey & Leng (2008) which currently is regarded as plesiomorphic in Harvey (1992.) In this case, an additional trait or character for equal proportions could be considered in future research.*

| 79. | Metatarsus to tarsus I & II: | segmented (0), fused (1) |

Harvey (1992): To the most anterior limbs of I and II, the connection between the metatarsus to the tarsus may either be separated from each other by a segmented joint (and thus seen as distinct parts) or are fused without a joint to resemble one segment. It has been interpreted as convergent evolution with feaelloids, cheiridiids, pseudochiridiids, sternophoroids, cheliferoids, unnamed species of Synsphyronus*, and* Geogarypus conatus *having the fused tarsi to these limbs. Chthonioids are also said to have fusions in the anterior limbs; where it is stated that other genera may have tarsi fusions in the posterior pair of limbs instead. This clade is the reason the pairs of limbs are separated to differentiate between families.*
Now: The fusion has also been found in Pseudotyrannochthoniidae, Atemnidae, and Pseudogarypidae. With the former including a fossil species, future research could be done to determine if the trait could be convergent.

| 80. | Metatarsus to tarsus III & IV: | segmented (0), fused (1) |

Harvey (1992): Similar to the previous character, the more posterior limbs III and IV may have the metatarsi to the tarsi segmented with a joint between them or as a fused part altogether.
Now: These characters stayed separate due to the reason given in character 79.

| 81. | Tarsi slit sensillum: | flat (0), raised (1) |

Harvey (1992): The raised shape of the slit is considered autapomorphic to Chernetidae, whereas in every other family the slits are flat against the chitin.
Now: The sensillum is a proximal slit seen on the tarsi within each limb, with an analogy to a straight keloid scar on mammalian skin. As the outgroup Scorpiones instead use carinae and setae for similar functions, they are inapplicable to this character.

| 82. | Tarsal setae: | triangular (0), serrated (1) |

Harvey (1992): The setae found on the tarsi can be triangular in shape (known as acuminate,) or have finer serrations (or dentate) as found in neobisioids and most cheliferids. It is considered autapomorphic for the latter clade.
Now: Serrated setae generally on the limbs were found and described as pinnate for Pseudochiridium insulae *from Hoff (1964.)*

| 83. | Tarsus I claws (male only): | consistent (0), asymmetrical (1) |

Harvey (1992): Found exclusively in male pseudoscorpions, these tarsi claws are only found on the most anterior limb I, and in life were used for mating. The consistent shapes of these claws are said to be secondary reductions in certain genera, which are Aperittochelifer, Australochelifer, Nannochelifer, Philomaoria, *and* Protochelifer.
Now: For fossil species, this character could be used to determine the sex of specimens if possible (through the difficulties of obscurity with the matrix or an incomplete specimen, as examples). This isn't attempted in this study due to the unavailability of multiple specimens to compare.

| 84. | Arolia proportion to claws: | shorter (0), longer (1) |

Harvey (1992): The proportions between the arolium and the claws between it may have the former be shorter or equal in length from the tarsus's edge. With the arolia being longer than the claws, it is considered autapomorphic in the Mestommatina clade, including a secondary loss to an equal/short length in Garypus, Paramenthus, Cheiridiidae, and Pseudochiridiidae. *Peculiarly, the genera* Ideoroncus, Shravana, Nhatrangia, Typhloroncus, Afroroncus, Nannoroncus, Negroroncus, *and species of* Albiorix *are also said to have lengthened arolia but were excluded from the character matrix in Harvey (1992) for simplicity due to presumption of a convergently evolved trait that are secondarily lost in* Dhanus *and other species of* Albiorix.
Now: The arolium is a lobe on the proximal end on the tarsus between the two claws. It is concurred to add the aforementioned taxa to future research to further improve the character matrix.

| 85. | Arolia protrusions: | absent (0), present (1) |

Harvey (1992): The arolia found from the proximal edge of each of the tarsi appear to have two distal extensions in the family Parahyidae only.
Now: These extensions are proportionally shorter than the claws, so would not be a contradiction to this study's character 84.

Abdomen:

| 86. | Tergite shape: | straight (0), pointed (1) |

Harvey (1992): For the autapomorphic pointed shape, it is specified this is present on pseudochiridiids' anterior tergites.

Now: The tergites across the abdomen, as the segments that connect the posterior margin of the carapace to the anus; either have a straight triangular shape, or a pointed chevron-like shape.

87.	Tergite XI and sternite XI:	segmented (0), fused (1)

Harvey (1992): The fusion is found in feaelloids, as well as a possible convergently evolved trait in unspecified genera in Pseudogarypidae and Ideoroncidae. A different version of the fusion is noted but was not specified further.

Now: Counting from the most anterior tergite labelled I, the following tergite XI and sternite XI are either separate movable segments or fused together into a single segment. Thus, pseudoscorpions can either have eleven or ten tergites/sternites in total. Judson (2000) provides an argument that the traits to this character should be reversed (fusion being plesiomorphic, segmented being autapomorphic) due to the parsimonious reason from the minority of families being found with segmentation. Future research could be done to find evidence in phylogenetic analyses with the inclusion of more basal and fossil taxa to a more complete profile of specimens. This character is inapplicable for the outgroup as Brotheas granulatus *only have 8 segments in total.*

88.	Pleural membrane:	ridged (0), granulated (1)

Harvey (1992): The pleural membrane is ventral from the abdomen to assist in the respiratory system. The plesiomorphic shape of the membrane is described to have vertical ridges across the membrane, from anterior to posterior. Examples of the ridged shape can be found in Ideoroncide, Bochicidae, Olpiidae, Menthidae, Syarinus, *and* Ideoblothrus *(the latter two genera from Syarinidae.) The granulated shape of the membrane would give a sandpaper-like texture and is considered an autapomorphic trait for genera in Gymnobisiidae, Hyidae, Neobisiidae, Parahyidae, and* Ideobisium *in Syarinidae. Syarinidae in particular is noted to have secondarily lost the granulated trait.*
Now: With the granulated trait found in the selected taxa in Chthoniidae, it could be considered the family may have secondarily lost the trait with Lechytia novaezealandiae *similarly to Syarinidae.*

89.	Pleural membrane	ridged (0), minutely pointed (1),
	margin:	pointed (2)

Harvey (1992): The pleural membrane may have small sized points/protrusions across it, and these are autapomorphic to Parahyidae only.
Now: The two characters originally from Harvey (1992) in relation to the pleural membrane have been combined by the traits for the same reasons as character 74 of this study. The pointed autapomorphic trait can be considered double in proportion to minutely pointed.

90.	Pleural sclerites:	absent (0), present (1)

Harvey (1992): The pleural membrane in feaelloids can be seen with segmented sclerites similar to the dorsal tergites of the abdomen. It is noted that there are reduced sclerites found on unspecific genera of Pseydogarypidae, Garypidae (with a specified genus of Anagarypus *spp.) and Geogarypidae.*
Now: It may be suggested to expand this character to include a range of sizes of the pleural sclerites with direct observation to specimens.

91.	Helix mark of spiracle:	absent (0), present (1)

Harvey (1992): The spiracles forming a complex helix shape is considered autapomorphic among most of Pseudoscorpiones, that have since been secondarily lost both times in Feaelloidea and Garypidae.

Now: Due to being an interior organ, this is difficult to determine for fossil specimens. The outgroup Scorpiones have simpler spiracle shapes according to Kamenz et al. (2005.)

92.	Sclerites over spiracles:	absent (0), present (1)

Harvey (1992): A sclerite can be found as a guard over a respective spiracle, which is found only in Tridenchthoniidae.

Now: Unlike the previous character 91, this character can be observed with the aid of microscopy (or CT tomography) on specimens (living or fossilised)

93.	Spiracle shape:	crossed (0), slanted (1)

Harvey (1992): The overall shape of each spiracle can be slanting against the surface of the chitin yet not perpendicular to it either, which are present in Tridenchthoniidae and are also labelled transverse. Whereas the plesiomorphic trait can have the spiracle be crossed in shape instead that is seen in Epiocheirata. It is stated that both traits are present across Iocheirata through unspecified genera.

Now: Similar to character 91, the internal shape can't be observed by fossil specimens encased in matrix without destruction. This character would require further revisions in future research to provide clearer definitions of the traits. The shapes of spiracles provided by Kamenz et al. (2005) for the outgroup order all share the autapomorphic slanted trait.

94.	Spiracles near sclerites IV & V:	absent (0), separate (1), fused (2)

Harvey (1992): Feaelloids have spiracles present not in sclerites III and IV but instead the more posterior IV & V sternites.

Now: This character is combined from the original character matrix to refer to the 'disassociation' described as the autapomorphic 'separate' trait upon the sternites, for similar reasons with characters 74 and 89 of this study. With the structure of book lungs, the character is considered fused for the outgroup Scorpiones.

95.	Anterior tracheae:	thick (0), narrow (1)

Harvey (1992): Within the abdomen, the tracheae are two separate pairs that lead to the spiracles of the III and IV sternites, from branching tracheoles. This system is found in the outgroup Solifugids, while Pseudoscorpiones can vary with the tracheae by ways of thickness in the vessels. The tracheae can either be thickened that branch into tracheoles from the connected posterior coxae at the prosoma (with a distinct note of feaelloids being shorter and branch more posterior from said coxae.) In the tracheae that lead to the spiracles in the sternites, they branch almost immediately into the abdomen. In Chthonioidea by contrast, the tracheae are narrow and do not branch into the anterior section from the coxae. The latter condition is said to be autapomorphic.

Now: It can be argued that the traits can instead be labelled by 'single' or 'branched' instead, yet the original traits remain to prevent confusion with shapes of other characters like setae or genitalia. With this being an internal character, this is difficult to determine for fossil species. Unlike the previous character of this study, the outgroup Scorpiones have the book lung system that lacks the tracheae Pseudoscorpiones have altogether; and so are inapplicable.

| 96. | Genital covering setae (male only): | narrow (0), branched (1) |

Harvey (1992): Male individuals in the family Lechytiidae possess singular branched setae (a Y-shape.)
Now: In male pseudoscorpions, the setae on the edge of the posterior genital operculum (a plate over an aperture) are mostly narrow and straight. It could be argued that this character could belong to the Male Genitalia subsection of the list, yet since it confers to the operculum only it remains in the Abdomen subsection.

| 97. | Setae on genital sclerites: | anterior (0), posterior (1) |

Harvey (1992): Setae can be found in the posterior edge of sternites III and IV in larcids, which can be found in both sexes and earlier instars.
Now: This character also remains in the Abdomen subsection and remains separate from the previous character 97 as it includes both sexes.

| 98. | Genital covering setae proportions (female only): | consistent (0), minute (1) |

Harvey (1992): The setae on the genital operculae of female pseudoscorpions can be of visible lengths along the edge, or in Hyidae the setae may be microscopic (specified to be less than 0.003 mm in length.)
Now: Similar to character 96, this character remains in the Abdomen subsection due to regarding the operculae only over the female genitalia.

| 99. | Posterior genital covering (male only): | not cleft (0), cleft (1) |

Harvey (1992): The genital operculum of male pseudoscorpions in Chthonoidea have a cleft shape within the cover, which is considered autapomorphic.
Now: This character alongside this study's characters 96 and 98 will be difficult to determine on fossil specimens due to uncertainties around sexual dimorphism if any that can differentiate them. The general limitations of obscuring matrix and impossibility of destructive methods also apply, especially to sex determinatism even if individuals have been found and confirmed for a fossil taxon.

| 100. | Sensory setae on sclerites: | absent (0), present (1) |

Harvey (1992): Areas of sensitive setae on the dorsal sternites on withiids of all sexes (and instars) were found. These setae are said to be secondarily lost from male Protowithius *and* Termitowithius *or a basal absence.*
Now: The two genera could be added in future research to represent the family Withiidae alongside this study's representatives Nannowithius *and* Withius.

| 101. | Sternite XI sclerotization: | present (0), absent (1) |

Harvey (1992): The ventral anal plates in sternite XI are sclerotized around it (in which to harden in thickness and/or darken in colour,) which is absent in larcids as it's considered an autapomorphic trait for the clade.
Now: Similar to character 87, the outgroup representative Brotheas granulatus *only contains 8 segments and would then be inapplicable to the consequent characters 102 to 104, as well as character 106 all of this study.* Protofeaella peetersae *in Feaellidae was*

considered to have sclerotized sternites as well, which could indicate a derivation of the fossil species from the extant sister genera.

102.	Sternite XI:	present (0), absent (1)

Harvey (1992): The sternite itself is absent in Lechytiidae and is autapomorphic in the family.

Now: Due to the absence of this character (from fusion according to character 87,) the characters 100, 101, 103, and 104 would in practice refer to sternite X. This character and character 103 have also switched placements in the character list from what was listed in Harvey (1992) for the overall sternite be introduced then to include features referencing it.

103.	Sternite XI lyrifissure:	absent (0), few (1), many (2)

Harvey (1992): Most pseudoscorpions keep longer lyrifissures as well as smaller sized slits. In larcids, the longer lyrifissures are absent in what is considered an autapomorphic trait.

Now: The specific sternite XI keeps lyrifissures for sensing stimulation.

104.	Sternite XI anus closure:	absent (0), present (1)

Harvey (1992): The anus can be found in the joint between tergite XI and sternite XI, at the most posterior end of the entire abdomen. The anus is in an operculum for Garypidae, Larcidae, Cheiridiidae, and Pseudochiridiidae with sternite XI in a subventral covering.

Now: Feaelloidea includes both tergite XI and sternite XI fused together as a cover (in reference to this study's character 87) and could be argued to create a new trait to refer to this. However, for parsimonious reasons with the condition being identical according to Harvey (1992) it is instead 'unofficially' regarded as a 'sternite X anus closure' for this clade in particular.

105.	Anal rim:	flat (0), raised (1)

Harvey (1992): The anal rim may appear as a raised ridge in garypids, cheiridiids, and pseudochiridiids as a possible autapomorphic trait. The raised ridge has also been said to be convergently evolved in Feaelloidea. Larcidae was considered to be 'raised' despite the secondary loss of the trait, of which had been estimated to be linked to the lack of sclerotization.

Now: To keep consistency where the examples of secondary loss had retained these traits from other characters, Larca granulata *will have the plesiomorphic trait in this study.*

106.	Anal plates:	desclerotized (0), sclerotized (1)

Harvey (1992): Tergite XII and sternite XII are considered to be anal plates. These tergites and sternites are heavy sclerotized with them being considered autapomorphic in feaelloids.

Now: For pseudoscorpions with tergite and sternite XI fused (in regard to this study's character 87,) this character can also be referred as tergite XI and sternite XI unofficially.

107.	Overall shape:	subrectangular (0), ovaline (1)

Harvey (1992): The abdomen in feaelloids and garypoids is ovaline in shape with the peak curvature wider than the cephalothorax. It is theorized the ovaline shape is autapomorphic for both families and are evolved convergently.

Now: The overall shape of the abdomen, including all of the tergites and sternites together, for most pseudoscorpions is subrectangular with the abdomen being of similar width to the cephalothorax (at the median length.)

Physiology:

<u>Male genitalia:</u>

| 108. | Setae across in atrium: | absent (0), present (1) |

Harvey (1992): Setae can be found patterned as vertical columns in the genital atrium from anterior to posterior. It is found in chthonioids and feaelloids and is considered autapomorphic, while in hyids it was estimated to be a convergent trait.
Now: For this character and the following characters in this subsection, it should be noted it is difficult to determine for fossil taxa due to limitations described before. This could be rectified in further research and any updated methods that prevent fossil destruction.

| 109. | Quantity of setae: | few (0), many (1) |

Harvey (1992): The setae within the aforementioned atrium are set in unspecified numerous numbers on oval-shaped platelets in the single species Parahya submersa, more than the average quantity of setae other male pseudoscorpions possess.
Now: The figure from Harvey (1991) featuring Parahya includes 8 setae on each margin of the atrium, with 16 in total. An exact number of the average number of setae for other taxa could not be found but can be presumed to be 15 or less.

| 110. | Genitalia size: | consistent (0), enlarged (1) |

Harvey (1992): Gymnobisiids have enlarged genitalia in mass according to indirect communication. The proportion of scale to other male pseudoscorpions outside the clade are unspecified.
Now: Direct observation to specimens belonging to this family will be necessary in future research to determine the differences and provide clearer proportional definitions.

| 111. | Genitalia shape: | (0) absent, (1) Barrois organ |

Harvey (1992): This character is said to be autapomorphic to chernetids. It is implied but not outright stated that the male genitalia have rod-like shapes that are largely absent for this particular order. In remarks for Atemnidae, it was further specified in being called Barrois' organ. It is then described as the male genitalia extending to the anterior point without articulation there, along with two furrows in the carapace. It is considered an uncertain character for Atemnidae due to the Barrois' organ found in only one studied specimen.
Now: The autapomorphic trait is renamed to give clarity over the more vague 'lateral rods' is not specified in the original character list.

| 112. | 'Ram's horn' organs: | absent (0), present (1) |

Harvey (1992): 'Ram's horn' organs refer to the lateral protrusions at the diverticulum (the passage connecting the genital organs) found in the posterior ventral section in the system. The term refers to how the protrusions resemble the ridges of a ram's horns as an analogy. It is noted that the organs turn inside out during mating and are considered autapomorphic to cheliferids only. The suggestion from previous studies that these organs had directly descended from the genital sacs had been denied. Certain genera (Australochelifer, species of Ellingsenius spp., Philomaoria, and Protochelifer) are noted to have secondarily lost this trait.
Now: Similarly with other internal characters, this will be difficult to observe within fossil specimens without limitations of matrix obscurity or specimen destruction.

| 113. | Median genital sac: | one (0), two (1) |

Harvey (1992): The median genital sacs are connected to the ventral diverticulum through a duct, of which the quantity of the sacs can vary among taxa. Ideoroncidae contain two sacs and are considered autapomorphic for the family (incorrectly noted as an order.)
Now: Syarinidae are noted to have either two sacs or one sac across each of the genus, with no note on whether this could be a secondary loss or convergent evolution. More on this matter will be in the Discussion chapter.

114.	Spermatophore shape:	simple (0), complex (1)

Harvey (1992): The overall shape of produced spermatophores can vary, specifically that Chthonioidea, Feaelloidea, Neobisioidea, and Garypoidea would produce an 'i' shape of a thin stalk with a spherical top. Cheliferoidea differs with a more complex yet unspecified shape, of which is considered autapomorphic. Sternophoroidea are considered to have an unknown shape as well as notable other clades.
Now: The spermatophore is the collection of sperm and protein that can be carried by the male pseudoscorpions outside of their bodies during mating. The autapomorphic 'i' shape is explained by Legg (2008) with the 'dot' above the stalk containing pheromones for the receiving female. It is also discussed in Legg (2008) that the shape of spermatophores correlate to both habitat environments and the shape of the female counterpart's spermathecae. In which case, new characters could be made from this one to correspond any new descriptions made in the future to see if this can be evidence for speciation and thus more phylogenetic derivations.

115.	Spermatophore stalk	simple (0), complex (1)
	shape:	

Harvey (1992): Chthoniidae and Tridenchthoniidae are said to have a 'collar' of protrusions from the anterior section just below the spherical top, analogous to a water lily's thorns; and are considered autapomorphic. It is estimated yet not confirmed that Lechytiidae may also have complexities to the spermatophore stalk.
Now: This character could be combined with the aforementioned character, of which the stalk section of the spermatophore can appear plain. This character is left specified from character 114 due to a lack of detail of other possible shapes to utilize as traits or new characters.

Female genitalia:

116.	Spermathecae:	absent (0), present (1), reduced (2)

Harvey (1992): In pseudoscorpions, the presence of spermathecae in most cheliferoids are a possible autapomorphic trait.
Now: Spermathecae are organs that can store collected sperm for later fertilization within the female individual. The reduced trait is added due to the differences in size between Epichernes *and* Dinocheirus *as stated in Muchmore & Hentschel (1982.) There may also be a connection between this character and characters 114 and 115 if the interpretation from Legg (2008) discussed there can be proven. Further research will be needed. Similar with the Male Genitilia subsection, internal structures are difficult to determine for fossil specimens and require further research into non-destructive methods.*

117.	Lateral ingrowths:	absent (0), present (1)

Harvey (1992): Lateral apodemes are found in female withiids and chernetids exclusively that is suggested to be evidence for a sister relationship between the families. If this is

correct, Withiidae is said to have secondarily lost the earlier femur to patella junction (this study's character 76) from Cheliferidae, Atemnidae, and Chernetidae.
Now: Apodemes are known as ridges grown within the internal sides of the exoskeleton as anchor points for musculature, named ingrowths for this study.

118.	Lateral ingrowth frames:	absent (0), present (1)

Harvey (1992): This is only present in female chthonioids and is considered an autapomorphic character.
Now: A frame may imply that the apodeme (featured in character 117) is connected to the internal side of the exoskeleton in incomplete rungs rather as a full ridge.

119.	Lateral ingrowth sclerotization:	weak (0), strong (1)

Harvey (1992): From the aforementioned framed apodeme of character 117, tridenchthoniids' are thicker in frame width as an autapomorphic trait.
Now: The scope of this thicker frame remains unspecified, so it can be assumed that the proportion can be doubled in width to define the 'strong' trait.

120.	Median inserted plate:	single (0), multiple (1)

Harvey (1992): This can be interpreted as a plesiomorphic trait in female pseudoscorpions from Harvey (1985) and subsequently Harvey (1992.) This plate can also be known as a cribriform plate. Multiple plates can be considered as autapomorphic and have been convergently developed across families but are specified as only two or more. Examples include Garypidae, Larcidae, genera of Sternophoridae, Withiidae, Chernetidae, Cheliferidae, Atemnidae, Cheiridiidae, and Neobisiidae. This character had since been simplified this character to only single or two plates for Garypidae and Larcidae.
Now: This character refers to a single centre plate that is sieve-like in texture (with pores).

121.	Mating behaviour:	simple (0), complex dancing (1)

Harvey (1992): It is described that the male holds the female between their pedipalps. However, this character remains enigmatic with unknown data from Lechytiidae, Feaellidae, Pseudochiridiidae, Menthidae, Sternophoridae, and Neobisioidea excluding Neobisiidae.
Now: During life, cheliferoid pseudoscorpions can be observed with complex dancing behaviour during mating and passing the spermatophore deposited by the male to the female. Further research will be needed with living, collected specimens.

Figure 3b. *Morphological character list*

To combine the previous tables, the last Table 3c now lists each taxon to a corresponding trait for all 121 morphological characters. The structure uses Table 4 from Harvey (1992) as a framework. The list is split into two (Tables 3c[1] and 3c[2]) for all of the taxa. As specified before, the cross (†) represents an extinct taxon; a dash is an inapplicable character (-) and a question mark is an unconfirmed trait (?)

The Phylogeny of the order Pseudoscorpiones

	Brotheas g.	*Dracochela d.* †	*Apocheiridium l.*	*Ideoblothrus s.*	*Allochthonius b.* †	*Aphrastochthonius t.*	*Pycnodithella h.*	*Lechytia n.*	*Paraliochthonius m.* †	*Feaella a.*	*Protofeaella p.* †	*Pseudogarypus o.*	*Pseudogarypus s.* †	*Sironcus s.*	*Antillobisium v.*	*Indohya d.*	*Gymnobisium i.*	*Neobisium c.*	*Microcreagris k.* †
General																			
1. Pseudoderm: (0) absent, (1) present	1	0	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
2. Setae: (0) straight, (1) kinked, (2) bent	0	1	2	0	0	0	0	0	1	0	?	0	?	1	0	0	1	0	0
Chelicerae:																			
3. Membrane: (0) absent, (1) present	0	0	1	0	0	0	0	0	0	0	?	0	?	0	0	0	0	0	?
4. Lamina: (0) absent (1) present	0	?	1	0	0	0	0	0	0	0	?	0	?	0	0	0	0	0	?
5. Serrations on mobile chelae: (0) numerous, (1) reduced	0	0	1	0	?	0	0	0	1	1	?	1	?	0	0	0	1	0	?
6. Setae placement: (0) medial, (1) distal	0	0	1	0	0	0	0	0	0	1	?	1	?	0	0	0	0	0	?
7. Flagellar areole: (0) linear (1) elliptical	-	0	0	0	?	1	1	0	0	0	?	0	?	0	0	0	0	0	?
8. Quantity of flagella: (0) > four (1) three/four (2) one/two	0	1	1	0	?	0	0	1	0	2	?	2	?	1	1	0	0	0	?
9. Spinules on flagella: (0) present, (1) absent	0	0	0	1	?	1	0	0	0	0	?	0	?	0	0	0	0	0	?
10. Flagellum shape: (0) straight, (1) curved, (2) horizontal	0	0	0	0	?	0	0	1	0	0	?	0	?	0	0	0	0	0	?
11. Serrula exterior: (0) unfused, (1) partially fused, (2) fused	0	0	2	1	0	0	0	0	0	2	?	2	?	1	1	1	1	1	?

12. Chelae surface texture: (0) smooth, (1) sculptured	1	0	0	0	0	0	0	0	0	1	?	1	?	0	0	0	0	0	?
13. Serration fusion: (0) absent, (1) present	0	0	0	0	0	0	0	1	0	1	?	1	?	0	0	0	0	0	?
14. Galea lobes: (0) single, (1) several	-	1	0	0	0	0	1	0	0	0	?	0	?	0	1	0	1	0	?
Prosoma: 15. Anterior lobes: (0) absent, (1) present	0	?	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
16. Median anterior lobes: (0) single, (1) several	-	?	-	-	-	-	-	-	-	1	0	0	0	-	-	-	-	-	-
17. Anterior margin: (0) straight/curved, (1) ridged	1	?	1	1	-	0	0	0	0	-	-	-	-	0	0	0	0	0	0
18. Anterior margin's texture: (0) smooth, (1) serrate	1	?	0	0	-	1	1	1	0	0	0	0	0	0	0	0	0	0	0
19. Overall shape: (0) rectangular, (1) triangular	0	?	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
20. Eye protrusion: (0) absent, (1) present	1	?	0	-	0	-	0	0	0	1	-	1	1	1	-	0	-	0	0
21. Eye position: (0) anterior margin, (1) posterior margin	0	?	1	-	0	-	0	0	0	1	-	1	0	0	-	0	-	0	0
22. Metazone: (0) flat, (1) depressed	1	?	1	0	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0
23. Alae: (0) absent, (1) present	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
24. Posterior margin: (0) straight, (1) depressed	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?
25. Articulation to abdomen: (0) absent, (1) present	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	?

26. Quantity of eyes: (0) four, (1) two, (2) none	0	?	1	2	1	2	0	1	1	0	2	0	0	1	2	0	2	0	0
Pedipalps: 27. Overall shape: (0) angled, (1) raptorial	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
28. Median maxillary lyrifissure: (0) present, (1) absent	1	?	0	0	?	0	0	0	1	1	?	0	?	0	0	0	0	0	?
29. Lyrifissure shape: (0) circular, (1) straight	-	?	0	0	?	1	1	1	1	-	?	0	?	0	0	0	0	0	?
30. Lyrifissure placement: (0) medial/distal (1) proximal	-	?	0	0	?	0	0	1	0	-	?	0	?	1	0	0	0	0	?
31. Posterior maxillary lyrifissure: (0) absent, (1) present	-	?	1	1	?	0	0	0	0	0	?	0	?	1	1	1	1	1	?
32. Coxa jugum: (0) short & thick, (1) long & sharp	-	0	0	0	?	1	1	0	?	0	1	0	?	0	0	0	0	0	?
33. Pharyngeal pump keel: (0) short, (1) enlarged	0	0	0	0	?	1	1	1	?	0	?	0	?	0	0	0	0	0	?
34. Coxa shoulder: (0) absent, (1) present	1	?	0	0	?	1	0	0	?	0	1	0	0	0	0	0	0	0	?
35. Coxa setae: (0) two, (1) three or more	1	1	1	0	?	1	0	1	?	0	?	0	?	0	0	0	0	1	?
36. Coxa distal shape: (0) triangular (1) rounded	0	?	0	0	?	0	0	0	?	0	0	0	0	0	0	0	0	1	?
37. Femur trichbothria: (0) absent, (1) present	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?
38. Femur setae: (0) absent, (1) present	1	1	0	0	1	0	0	0	1	0	?	0	?	0	0	1	0	0	?
39. Femur proximal tubercle:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?

(0) absent, (1) present																		
40. Immobile venom apparatus: (0) absent, (1) present	0	0	1	1	0	0	0	0	?	0	?	0	?	1	1	0	0	1	?
41. Mobile venom apparatus: (0) absent, (1) present	0	0	1	0	0	0	0	0	?	0	?	0	?	1	1	1	1	0	?
42. Venom ducts: (0) proximal length. (1) distal length.	-	-	0	1	-	-	-	-	?	-	?	-	?	0	0	0	1	1	?
43. Nodus romosus: (0) ridged (1) flat	-	-	1	1	-	-	-	-	?	-	?	-	?	0	0	0	1	1	?
44. Mobile chelae setae: (0) absent, (1) present	1	1	0	0	0	0	0	0	1	0	?	0	?	0	0	0	1	0	?
45. Medial serrated mobile chelae: (0) absent, (1) present	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	?
46. Accessory chelae serration: (0) absent, (1) present	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	?
47. Distal trichobothria: (0) absent, (1) present	0	1	0	0	0	0	1	1	0	1	?	1	0	0	0	0	0	0	?
48. Trichbothria placement: (0) immobile chelae, (1) tarsus	1	0	0	0	1	1	0	1	0	0	?	0	0	0	1	0	0	0	?
49. Immobile chelae trichbothrium: (0) exterior proximal, (1) interior distal	0	0	0	0	0	0	0	0	0	1	?	0	0	0	0	0	0	0	?
50. Proximal immobile trichbothrium: (0) interior, (1) posterior	0	0	0	1	1	1	0	0	1	0	?	0	1	1	1	1	1	1	?
51. Interior immobile trichbothrium: (0) proximal, (1) distal	1	0	0	1	0	0	0	0	0	0	?	1	1	0	1	0	0	1	?

Character																			
52. Tarsus trichbothria: (0) lateral, (1) dorsal	0	1	0	0	1	1	1	1	0	0	?	0	0	0	0	0	0	0	?
53. Margin trichbothria: (0) lateral, (1) basally, (2) distally	0	1	0	0	1	2	0	1	0	0	?	0	0	1	1	0	0	0	?
54. Second margin trichbothrium: (0) on immobile chelae, (1) on mobile chelae, (2) on tarsus	0	2	0	0	0	2	0	2	2	1	?	0	0	0	0	0	0	0	?
55. Quantity of trichbothria: (0) fifteen or less, (1) more than fifteen	1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	0	?
56. Quantity of trichbothria on chelae: (0) eight or less (1) nine or more	1	0	0	0	1	0	0	0	1	0	?	0	0	1	0	0	1	0	?
57. Trichbothria shape: (0) triangular (1) ovaline	0	0	0	1	0	0	0	0	0	0	?	0	?	0	0	0	0	0	?
58. Pits on tarsus: (0) absent, (1) present	1	1	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?
Limbs: 59. Coxal spines: (0) absent, (1) present	0	1	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	?
60. Coxal tubercle: (0) absent, (1) present	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	?
61. Setae on tubercle: (0) absent, (1) single, (2) multiple	0	1	0	0	?	1	1	0	0	0	0	0	?	0	0	0	0	0	?
62. Coxa I shoulder: (0) absent, (1) present	0	?	0	0	?	1	1	1	1	0	0	0	0	0	0	0	0	0	?
63. Pseudosternum: (0) absent, (1) present	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?

Character																			
64. Coxal articulation: (0) absent, (1) present	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
65. Coxal IV size: (0) medium, (1) less than double size, (2) over double size	0	?	0	0	?	0	0	0	?	0	0	0	0	0	0	0	0	0	?
66. Coxal width: (0) consistent, (1) exponential	0	?	1	0	?	0	0	0	?	0	0	1	1	0	0	0	0	0	?
67. Coxal sac (male only): (0) absent, (1) present	-	?	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
68. Femur I & II sensillum: (0) present, (1) absent	1	0	0	0	?	0	0	0	?	1	?	1	?	0	?	0	0	0	?
69. Femur I & II sensillum placement: (0) proximal, (1) distal,	-	0	1	1	?	0	0	0	?	-	?	-	?	1	?	1	0	1	?
70. Femur I & II sensillum angle: (0) perpendicular, (1) parallel	-	0	0	1	?	0	0	0	?	-	?	-	?	0	?	0	1	1	?
71. Femur I & II three sensilla: (0) absent, (1) present	-	0	0	1	?	0	0	0	?	-	?	-	?	0	?	1	0	0	?
72. Femur I & II three sensilla placement: (0) proximal, (1) distal	-	0	0	1	?	0	0	0	?	-	?	-	?	0	?	0	-	0	?
73. Femur I & II sensilla mound: (0) absent, (1) present	-	0	0	0	?	0	0	0	?	-	?	-	?	0	?	1	0	0	?
74. Femur I & II sensilla shape: (0) straight, (1) curved, (2) semi-circular, (3) circular	-	0	2	0	?	0	0	0	?	-	?	-	?	0	?	0	-	0	?
75. Femur to patella I & II: (0) slanted, (1) perpendicular	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
76. Femur to patella III & IV: (0) slanted,	0	1	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0	1	0

(1) perpendicular																			
77. Femurs to patellae: (0) segmented, (1) fused	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78. Femur to patella I & II proportions: (0) femur longer, (1) patella longer	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
79. Metatarsus to tarsus I & II: (0) segmented, (1) fused	0	0	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0
80. Metatarsus to tarsus III & IV: (0) segmented, (1) fused	0	?	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
81. Tarsi slit sensillum: (0) flat (1) raised	-	?	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
82. Tarsal setae: (0) triangular, (1) serrated	0	0	0	1	?	0	0	0	0	0	?	0	?	1	-	1	1	1	?
83. Tarsus I claws (male only): (0) consistent, (1) asymmetrical	-	?	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
84. Arolia proportion to claws: (0) shorter, (1) longer	-	1	0	1	?	0	0	0	0	0	?	0	0	0	1	0	0	0	0
85. Arolia protrusions: (0) absent, (1) present	-	1	0	0	?	0	0	0	1	0	?	0	0	1	0	0	0	0	?
Abdomen: 86. Tergite shape: (0) straight, (1) pointed	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
87. Tergite XI and sternite XI: (0) segmented, (1) fused	-	?	0	0	1	1	0	1	0	0	1	1	1	1	0	0	1	0	0
88. Pleural membrane: (0) ridged, (1) granulated	1	1	0	0	?	1	1	0	1	0	0	1	0	0	0	1	1	1	0

89. Pleural membrane margin: (0) ridged, (1) minutely pointed, (2) pointed	1	1	0	0	?	1	2	0	0	0	0	2	0	0	0	1	1	1	0
90. Pleural sclerites: (0) absent, (1) present	0	0	0	0	?	0	0	0	0	1	1	0	?	0	0	0	0	0	0
91. Helix mark of spiracle: (0) absent, (1) present	0	?	0	0	?	0	0	0	?	1	?	1	?	1	0	0	0	0	?
92. Sclerites over spiracles: (0) absent, (1) present	1	?	0	0	?	0	1	0	?	0	?	0	?	0	0	0	0	0	?
93. Spiracle shape: (0) crossed, (1) slanted	1	?	1	1	?	0	1	0	?	0	?	0	?	1	0	1	-	0	?
94. Spiracles near sclerites IV & V: (0) absent, (1) separate, (2) fused	2	?	0	0	?	0	0	0	?	1	?	1	?	0	0	0	0	0	?
95. Anterior tracheae: (0) thick, (1) narrow	-	?	0	0	?	1	1	1	?	0	?	0	?	0	0	0	0	0	?
96. Genital covering setae (male only): (0) narrow, (1) branched	0	?	0	0	?	0	0	1	?	0	?	0	?	0	0	0	0	0	?
97. Setae on genital sclerites: (0) anterior, (1) posterior	1	?	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
98. Genital covering setae proportions (female only): (0) consistent, (1) minute	0	?	0	0	?	0	0	0	?	0	?	0	?	0	0	1	0	0	?
99. Posterior genital covering (male only): (0) not cleft, (1) cleft	1	?	0	0	0	1	1	1	1	0	?	0	?	0	0	0	0	0	?
100. Sensory setae on sclerites: (0) absent, (1) present	1	1	0	0	?	0	0	0	?	0	?	1	?	0	0	0	0	0	?
101. Sternite XI sclerotization:	-	?	0	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0

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Character																			
(0) present, (1) absent																			
102. Sternite XI: (0) present, (1) absent	-	?	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
103. Sternite XI lyrifissure: (0) absent, (1) few, (2) many	-	?	0	0	0	0	0	-	-	0	0	0	?	0	0	0	0	0	0
104. Sternite XI anus closure: (0) absent, (1) present	-	?	1	0	?	0	0	0	?	1	1	1	1	1	0	0	0	0	0
105. Anal rim: (0) flat, (1) raised	1	?	1	0	?	0	0	0	?	1	1	1	0	0	0	0	0	0	1
106. Anal plates: (0) desclerotized, (1) sclerotized	-	?	0	0	?	0	0	0	?	1	1	1	?	0	0	0	0	0	1
107. Overall shape: (0) subrectangular, (1) ovaline	0	0	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	1
Male genitalia: 108. Setae across in atrium: (0) absent, (1) present	0	?	0	1	?	1	1	1	1	1	?	1	?	0	0	0	0	0	?
109. Quantity of setae: (0) few, (1), many	-	?	0	1	?	0	0	0	?	0	?	1	?	0	0	0	0	0	?
110. Genitalia size: (0) consistent, (1) enlarged	-	?	0	0	?	0	0	0	?	0	?	0	?	0	0	0	1	0	?
111. Genitalia shape: (0) absent, (1) Barrois organ	1	?	0	0	?	0	0	0	?	0	?	0	?	0	0	1	0	0	?
112. 'Ram's horn' organs: (0) absent, (1) present	0	?	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
113. Median genital sac: (0) one, (1) two	-	?	0	0	?	0	0	0	?	0	?	0	?	1	0	0	0	0	?
114. Spermatophore shape: (0) simple, (1) complex	0	?	1	?	?	0	0	?	?	?	?	0	?	?	?	?	?	0	?

Character																			
115. Spermatophore stalk shape: (0) simple, (1) complex	0	?	0	?	?	1	1	?	?	?	?	0	?	?	?	?	?	0	?
Female genitalia: 116. Spermathecae: (0) absent, (1) present, (2) reduced	1	?	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
117. Lateral ingrowths: (0) absent, (1) present	0	?	1	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
118. Lateral ingrowth frames: (0) absent, (1) present	0	?	0	0	?	1	1	1	?	0	?	0	?	0	0	0	0	0	?
119. Lateral ingrowth sclerotization: (0) weak, (1) strong	0	?	-	-	?	0	0	0	?	-	?	-	?	-	-	-	-	-	?
120. Median inserted plate: (0) single, (1) multiple	0	?	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	?
121. Mating behaviour: (0) simple, (1) complex dancing	1	-	1	?	-	0	0	?	-	?	-	0	-	?	?	0	0	0	-

Figure 3c¹. *First half of the character matrix, with data of both tables 3a. and 3b. (?) trait is unknown and/or unconfirmed. (-) is an inapplicable trait. All species are initialised.* Brotheas granulatus *to* Microcreagris koellnerorum *are covered.*

Character	*Parahya s.*	*Garypus d.*	*Larca g.*	*Pseudochiridium i.*	*Pseudochiridium l.* †	*Geogarypus t.*	*Geogarypus g.* †	*Linnaeolpium l.*	*Thenmus a.*	*Garyops s.*	*Nannowithius c.*	*Withius e.* †	*Philomaoria p.*	*Heurtaultia r.* †	*Xenochernes c.*	*Oligochernes b.* †	*Diplotemnus b.*	*Progonatemnus s.* †
General 1. Pseudoderm: (0) absent, (1) present	0	1	1	0	0	0	?	0	0	0	0	?	0	?	0	?	0	?
2. Setae: (0) straight, (1) kinked, (2) bent	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Chelicerae:																		

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Character																		
3. Membrane: (0) absent, (1) present	0	1	1	0	?	1	?	1	1	1	1	?	1	?	1	?	1	?
4. Lamina: (0) absent (1) present	0	1	1	1	?	1	?	1	1	1	1	?	1	?	1	?	1	?
5. Serrations on mobile chelae: (0) numerous, (1) reduced	0	1	1	1	1	1	?	1	1	1	1	?	1	1	1	?	1	?
6. Setae placement: (0) medial, (1) distal	0	1	1	1	1	1	?	1	1	1	1	?	1	1	1	?	1	1
7. Flagellar areole: (0) linear (1) elliptical	0	0	0	0	0	0	?	0	0	0	0	?	0	0	1	?	0	1
8. Quantity of flagella: (0) > four (1) three/four (2) one/two	0	1	1	1	1	1	?	2	1	1	1	?	1	2	1	?	1	1
9. Spinules on flagella: (0) present, (1) absent	0	1	0	0	0	0	?	0	0	1	0	?	0	0	0	?	0	1
10. Flagellum shape: (0) straight, (1) curved, (2) horizontal	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	?	0	0
11. Serrula exterior: (0) unfused, (1) partially fused, (2) fused	1	2	2	1	0	2	?	1	2	2	2	2	2	1	2	?	2	0
12. Chelae surface texture: (0) smooth, (1) sculptured	0	0	0	0	0	0	?	0	0	0	0	?	0	1	0	?	0	0
13. Serration fusion: (0) absent, (1) present	0	0	0	0	0	0	?	0	0	0	1	1	0	0	0	?	0	1
14. Galea lobes: (0) single, (1) several	0	0	0	1	0	0	?	1	0	0	0	1	0	0	0	?	0	1
Prosoma: 15. Anterior lobes: (0) absent, (1) present	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?
16. Median anterior lobes: (0) single, (1) several	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	?

Character																		
17. Anterior margin: (0) straight/curved, (1) ridged	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	?	1	?
18. Anterior margin's texture: (0) smooth, (1) serrate	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	1	?
19. Overall shape: (0) rectangular, (1) triangular	0	1	1	1	1	1	1	0	0	0	0	1	0	0	1	1	0	?
20. Eye protrusion: (0) absent, (1) present	0	1	1	-	-	1	1	0	0	-	-	?	0	0	-	?	0	?
21. Eye position: (0) anterior margin, (1) posterior margin	0	0	1	-	-	1	1	0	0	-	-	?	0	0	-	?	0	?
22. Metazone: (0) flat, (1) depressed	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	?	0	?
23. Alae: (0) absent, (1) present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?
24. Posterior margin: (0) straight, (1) depressed	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0
25. Articulation to abdomen: (0) absent, (1) present	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	0
26. Quantity of eyes: (0) four, (1) two, (2) none	0	0	0	2	2	0	0	1	0	2	2	?	1	1	2	?	1	?
Pedipalps: 27. Overall shape: (0) angled, (1) raptorial	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28. Median maxillary lyrifissure: (0) present, (1) absent	0	0	0	0	1	0	?	0	0	0	1	0	0	0	0	?	0	?
29. Lyrifissure shape: (0) circular, (1) straight	0	0	0	0	-	0	?	0	0	0	-	0	0	0	0	?	0	?
30. Lyrifissure placement: (0) medial/distal (1) proximal	0	0	0	0	-	0	?	0	0	0	-	1	0	0	0	?	0	?

Character																		
31. Posterior maxillary lyrifissure: (0) absent, (1) present	1	1	1	1	0	1	?	1	1	1	1	?	1	?	1	?	1	?
32. Coxa jugum: (0) short & thick, (1) long & sharp	0	0	0	0	1	0	?	0	0	0	0	?	0	?	0	?	0	0
33. Pharyngeal pump keel: (0) short, (1) enlarged	0	0	0	0	?	0	?	0	0	0	0	?	0	?	0	?	0	?
34. Coxa shoulder: (0) absent, (1) present	0	0	0	1	1	1	?	0	0	0	0	?	0	0	0	?	1	?
35. Coxa setae: (0) two, (1) three or more	0	0	0	1	1	0	?	0	0	0	0	?	0	1	0	?	0	?
36. Coxa distal shape: (0) triangular (1) rounded	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	?	0	?
37. Femur trichbothria: (0) absent, (1) present	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
38. Femur setae: (0) absent, (1) present	0	0	0	1	1	0	1	0	0	1	0	1	0	1	0	1	0	1
39. Femur proximal tubercle: (0) absent, (1) present	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	1	?
40. Immobile venom apparatus: (0) absent, (1) present	1	1	1	1	?	1	?	1	1	1	1	1	1	1	0	?	1	?
41. Mobile venom apparatus: (0) absent, (1) present	0	1	1	1	?	1	?	1	0	1	1	1	1	1	1	?	0	?
42. Venom ducts: (0) proximal length. (1) distal length.	1	0	0	0	?	0	?	0	1	0	0	0	0	0	0	?	0	?
43. Nodus romosus: (0) ridged (1) flat	1	0	0	0	?	0	?	0	0	0	1	0	1	?	1	?	1	?
44. Mobile chelae setae: (0) absent, (1) present	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1

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Character																		
45. Medial serrated mobile chelae: (0) absent, (1) present	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	?	0	?
46. Accessory chelae serration: (0) absent, (1) present	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	?	0	?
47. Distal trichbothria: (0) absent, (1) present	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	?	0	1
48. Trichbothria placement: (0) immobile chelae, (1) tarsus	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	0	?
49. Immobile chelae trichbothrium: (0) exterior proximal, (1) interior distal	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	?
50. Proximal immobile trichbothrium: (0) interior, (1) posterior	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	?	0	?
51. Interior immobile trichbothrium: (0) proximal, (1) distal	1	0	0	0	1	1	0	0	1	0	0	0	1	1	0	?	0	?
52. Tarsus trichbothria: (0) lateral, (1) dorsal	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	?	0	?
53. Margin trichbothria: (0) lateral, (1) basally, (2) distally	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	?	0	?
54. Second margin trichbothrium: (0) on immobile chelae, (1) on mobile chelae, (2) on tarsus	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	?
55. Quantity of trichbothria: (0) fifteen or less, (1) more than fifteen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?
56. Quantity of trichbothria on chelae:	0	1	0	0	0	0	1	1	1	1	1	1	0	1	1	?	0	?

(0) eight or less (1) nine or more																		
57. Trichbothria shape: (0) triangular (1) ovaline	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?
58. Pits on tarsus: (0) absent, (1) present	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	?	0	?
Limbs: 59. Coxal spines: (0) absent, (1) present	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	?	0	1
60. Coxal tubercle: (0) absent, (1) present	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	?	0	?
61. Setae on tubercle: (0) absent, (1) single, (2) multiple	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	?	0	?
62. Coxa I shoulder: (0) absent, (1) present	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	?	0	?
63. Pseudosternum: (0) absent, (1) present	0	0	0	0	0	0	?	0	0	1	0	?	0	0	0	?	0	?
64. Coxal articulation: (0) absent, (1) present	0	0	0	0	0	0	?	0	1	0	0	?	0	0	0	?	0	?
65. Coxal IV size: (0) medium, (1) less than double size, (2) over double size	0	0	0	1	2	0	?	0	0	0	0	?	0	0	0	?	0	?
66. Coxal width: (0) consistent, (1) exponential	0	1	1	1	1	0	?	0	0	0	0	?	0	0	0	?	0	?
67. Coxal sac (male only): (0) absent, (1) present	0	0	0	0	0	0	?	0	0	0	1	?	0	0	0	?	0	?
68. Femur I & II sensillum: (0) present, (1) absent	0	0	0	0	?	0	?	0	0	0	0	?	0	?	0	?	0	?
69. Femur I & II sensillum placement: (0) proximal, (1) distal,	1	1	1	1	?	1	?	1	1	1	1	?	1	?	0	?	1	?

Character																		
70. Femur I & II sensillum angle: (0) perpendicular, (1) parallel	1	0	0	0	?	1	?	0	0	0	0	?	0	?	0	?	0	?
71. Femur I & II three sensilla: (0) absent, (1) present	1	0	0	0	?	0	?	0	0	0	0	?	0	?	0	?	0	?
72. Femur I & II three sensilla placement: (0) proximal, (1) distal	0	0	0	0	?	0	?	0	0	0	0	?	0	?	0	?	0	?
73. Femur I & II sensilla mound: (0) absent, (1) present	0	0	0	0	?	0	?	0	0	0	0	?	0	?	0	?	0	?
74. Femur I & II sensilla shape: (0) straight, (1) curved, (2) semi-circular, (3) circular	0	0	0	0	?	0	?	0	0	0	0	?	1	?	0	?	2	?
75. Femur to patella I & II: (0) slanted, (1) perpendicular	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	?	1	0
76. Femur to patella III & IV: (0) slanted, (1) perpendicular	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0
77. Femurs to patellae: (0) segmented, (1) fused	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0
78. Femur to patella I & II proportions: (0) femur longer, (1) patella longer	0	0	0	1	1	0	1	0	0	1	1	1	1	1	0	?	1	1
79. Metatarsus to tarsus I & II: (0) segmented, (1) fused	0	0	0	1	1	0	1	0	0	1	1	0	1	?	0	?	1	0
80. Metatarsus to tarsus III & IV: (0) segmented, (1) fused	0	0	0	1	1	0	1	0	0	1	1	0	1	?	0	?	1	0
81. Tarsi slit sensillum: (0) flat (1) raised	0	0	0	0	?	0	?	0	0	0	0	?	0	?	1	?	0	?
82. Tarsal setae:	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	?	0	?

The Phylogeny of the order Pseudoscorpiones

Character																		
(0) triangular, (1) serrated																		
83. Tarsus I claws (male only): (0) consistent, (1) asymmetrical	0	0	0	0	?	0	?	0	0	0	0	?	1	1	0	?	0	?
84. Arolia proportion to claws: (0) shorter, (1) longer	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	?	0	0
85. Arolia protrusions: (0) absent, (1) present	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0
Abdomen: 86. Tergite shape: (0) straight, (1) pointed	0	0	0	1	1	0	0	0	0	0	0	?	0	?	0	0	0	0
87. Tergite XI and sternite XI: (0) segmented, (1) fused	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	?	0	0
88. Pleural membrane: (0) ridged, (1) granulated	1	0	0	0	0	0	?	0	0	0	0	?	0	?	0	?	0	?
89. Pleural membrane margin: (0) ridged, (1) minutely pointed, (2) pointed	1	0	0	0	0	0	?	0	0	0	0	?	0	?	0	?	0	?
90. Pleural sclerites: (0) absent, (1) present	0	0	0	0	0	0	?	0	0	0	0	?	0	?	0	?	0	?
91. Helix mark of spiracle: (0) absent, (1) present	0	1	0	0	?	0	?	1	0	0	1	?	0	?	0	?	0	?
92. Sclerites over spiracles: (0) absent, (1) present	0	0	0	0	?	0	?	0	0	0	0	1	0	?	1	?	0	?
93. Spiracle shape: (0) crossed, (1) slanted	0	0	1	0	?	1	?	1	1	0	1	?	1	?	0	?	1	?
94. Spiracles near sclerites IV & V: (0) absent, (1) separate, (2) fused	0	0	0	0	?	0	?	0	0	0	0	?	0	?	0	?	0	?

Character																		
95. Anterior tracheae: (0) thick, (1) narrow	0	0	0	0	1	0	?	0	0	0	0	?	0	?	0	?	0	?
96. Genital covering setae (male only): (0) narrow, (1) branched	0	0	0	0	1	0	?	0	0	0	1	?	0	?	0	?	1	?
97. Setae on genital sclerites: (0) anterior, (1) posterior	0	0	1	0	0	0	?	0	0	0	1	?	0	?	0	?	0	?
98. Genital covering setae proportions (female only): (0) consistent, (1) minute	0	0	0	0	0	0	?	0	0	0	1	?	0	?	0	?	0	?
99. Posterior genital covering (male only): (0) not cleft, (1) cleft	0	0	0	0	0	0	?	0	0	0	0	?	0	?	0	?	0	?
100. Sensory setae on sclerites: (0) absent, (1) present	0	0	0	0	0	0	?	0	0	0	1	?	0	?	0	1	0	?
101. Sternite XI sclerotization: (0) present, (1) absent	0	0	1	0	0	0	?	0	0	0	0	?	0	?	0	?	0	?
102. Sternite XI: (0) present, (1) absent	0	0	0	0	1	0	?	0	0	0	0	0	0	?	0	?	0	?
103. Sternite XI lyrifissure: (0) absent, (1) few, (2) many	0	0	1	0	?	0	?	0	0	0	0	?	0	?	0	?	0	?
104. Sternite XI anus closure: (0) absent, (1) present	0	1	1	1	0	0	?	0	0	0	0	?	0	?	0	?	0	?
105. Anal rim: (0) flat, (1) raised	0	1	0	1	1	0	?	0	0	0	0	?	1	?	0	?	0	?
106. Anal plates: (0) desclerotized, (1) sclerotized	0	0	0	0	0	0	?	0	0	1	0	?	0	?	0	?	0	?
107. Overall shape: (0) subrectangular, (1) ovaline	0	1	1	1	1	1	0	0	0	0	0	0	0	?	0	1	0	0
Male genitalia:																		

Character																		
108. Setae across in atrium: (0) absent, (1) present	1	0	0	0	1	0	?	1	0	0	0	?	0	?	1	?	0	?
109. Quantity of setae: (0) few, (1), many	1	0	0	1	0	0	?	0	0	0	0	?	0	?	1	?	0	?
110. Genitalia size: (0) consistent, (1) enlarged	0	0	0	0	0	0	?	0	0	0	0	?	0	?	0	?	0	?
111. Genitalia shape: (0) absent, (1) Barrois organ	0	0	0	0	0	0	?	0	0	0	1	?	0	?	1	?	0	?
112. 'Ram's horn' organs: (0) absent, (1) present	0	0	0	0	1	0	?	0	0	0	0	?	1	?	0	?	0	?
113. Median genital sac: (0) one, (1) two	0	0	0	0	0	0	?	0	0	0	0	?	0	?	0	?	0	?
114. Spermatophore shape: (0) simple, (1) complex	?	0	0	?	?	0	?	0	?	?	1	?	0	?	1	?	1	?
115. Spermatophore stalk shape: (0) simple, (1) complex	?	0	0	?	?	0	?	0	?	?	0	?	0	?	0	?	0	?
Female genitalia: 116. Spermathecae: (0) absent, (1) present, (2) reduced	0	0	0	0	?	0	?	0	0	0	1	?	1	?	1	?	1	?
117. Lateral ingrowths: (0) absent, (1) present	0	1	0	0	?	0	?	0	0	1	1	?	0	?	1	?	0	?
118. Lateral ingrowth frames: (0) absent, (1) present	0	0	0	0	?	0	?	0	0	1	0	?	0	?	0	?	-	?
119. Lateral ingrowth sclerotization: (0) weak, (1) strong	-	-	-	-	?	-	?	-	-	0	-	?	-	?	-	?	0	?
120. Median inserted plate: (0) single, (1) multiple	0	1	1	0	?	0	?	0	0	0	0	?	0	?	0	?	1	?

121. Mating behaviour: (0) simple, (1) complex dancing	?	0	0	?	-	0	-	0	?	?	1	-	1	-	1	-	0	-

Figure 3c². *Second half of the character matrix, with data of both tables 3a. and 3b. (?) trait is unknown and/or unconfirmed. (-) is an inapplicable trait. All species are initialised.* Parahya submersa *to* Progonatemnus succineus *are covered.*
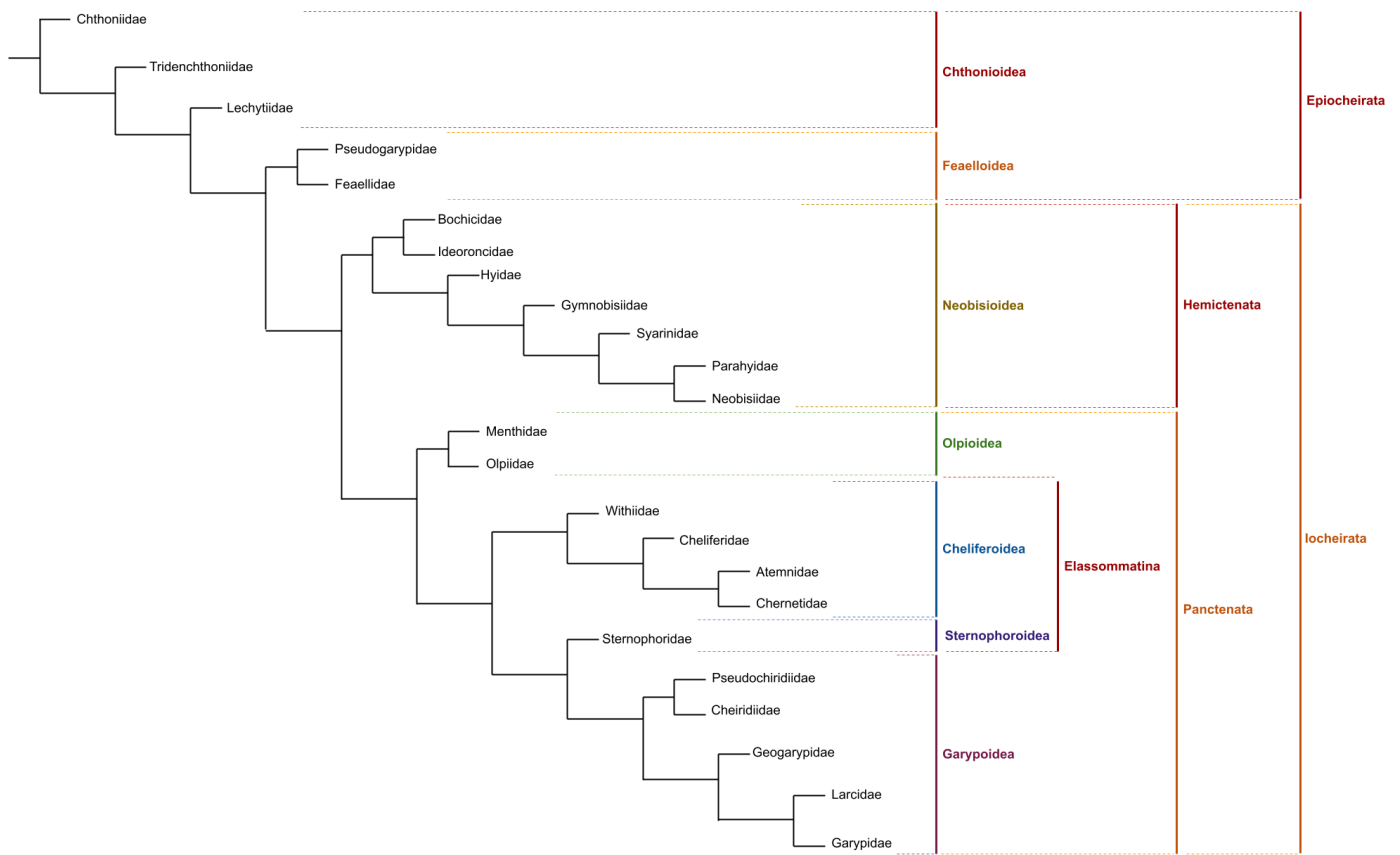
Results:

Figure 4a[1]. *Phylogenetic tree using the character matrix and taxa directly from Harvey (1992) to TNT. Clades labelled as is from the original study's results. Used the Implied weighting settings with* k=4.0. *Colours used only to correspond and distinguish clades. Made from Google Drawings.*

    The first two cladograms include the original character matrix from Harvey (1992) without any additional or updated information from this study's methods and reviews. This is to revisit the original matrix and determine if the updated cladistical software could affect the topology. Figure 4a[1] uses the same settings as the following cladograms (the collective Figure 4b[2]) for consistency in comparisons.

    From the original phylogenetic tree, the Epiocheirata clade is mostly similar with a single difference that Chthoniidae is no longer a sister family to Tridenchthoniidae. Similarly Syarinidae is reinterpreted to be a basal family from Parahyidae and Neobisiidae within Hemictenata. The largest difference is the placement of Elassommatina as an earlier branch from Garypoidea yet more derived than Olpoidea; whereas in the original study the former had a sister relationship to the collective Mestommatina.

The Phylogeny of the order Pseudoscorpiones
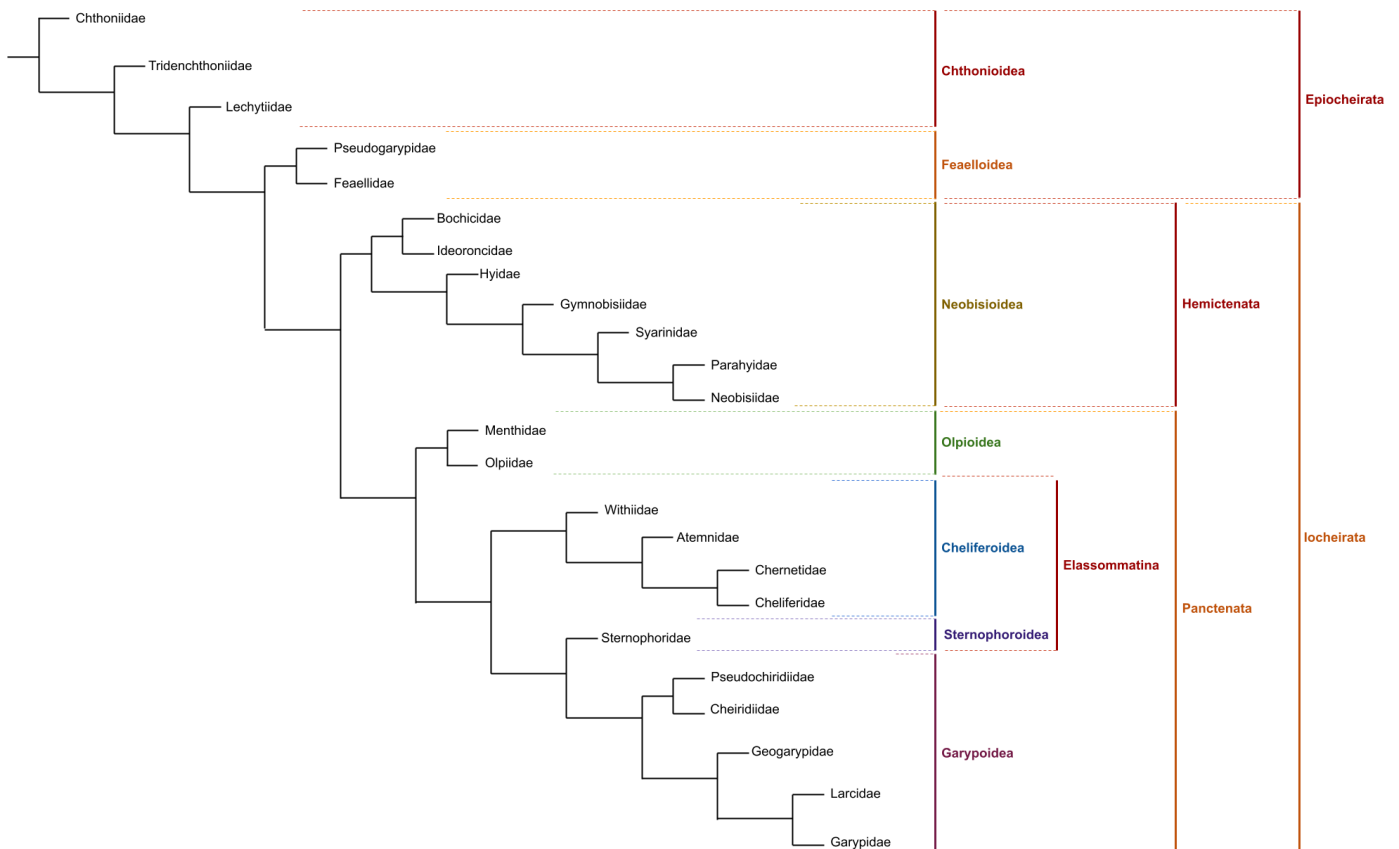
Figure 4a². *Phylogenetic tree using the character matrix and taxa directly from Harvey (1992) to TNT. Clades labelled as is from the original study's results. Implied weighting options were switched off. Colours used only to correspond and distinguish clades. Made from Google Drawings.*

Figure 4a² was made with the same analysis technique with the only distinctive change being the lack of the implied weighting, from then be known as equal weighting. The method of adding 'weight' or consistency priority to characters more likely to be homoplasies between each other had been deactivated in the software for this tree. This was done for two reasons; this cladogram is the subject of trial-and-error to determine the suitable concavity constant (k) for this study's own matrix. This constant is thus named in Goloboff (2013). Lower numbers of the constant caused the clades to be shown as equally homoplastic as each other. Higher quantities had shown no changes to the resulting cladograms that mirror collective Figures 4a. Kitching et al. (1998) provides more insight into this matter.

For the cladogram itself, the only difference found from Figure 4a¹ is the placement of families Atemnidae and Cheliferidae and which of them would be the basal clade from Chernetidae. It is unknown why this is the case, and all the differences in the topology from the original cladogram from Harvey (1998) also applies to Figure 4a².

The Phylogeny of the order Pseudoscorpiones

What follows is an equal weighting version of the tree where a basal polytomy is formed with a majority being fossil taxa, the other fossil taxa shown in sister 'relationships' between each other. More derived taxa (i.e. *Pseudogarypus synchrotron* etc.) appear 'basal' to extant taxa instead. This illustrates the flaws of this methodology through incomplete characters.
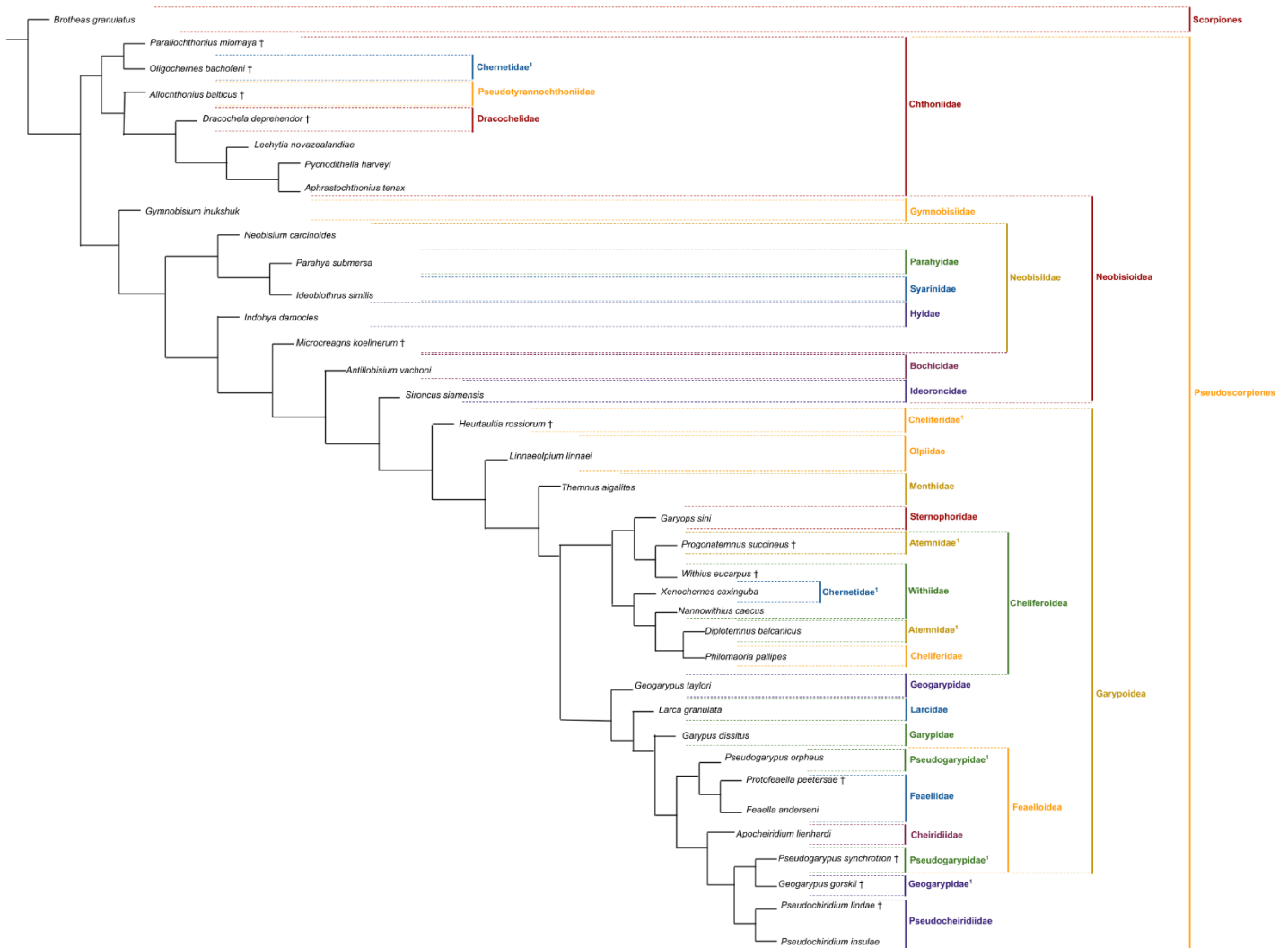
Figure 4b[1]. *Phylogenetic tree generated from TNT Ver. 1.5. with equal weighting (implied weighting switched off.) Orders, superfamilies, and families included based on data from Harvey (1992) and Benavides et al. (2019.) [1] indicates taxa found 'outside' their designated family based on previous studies. † represents an extinct taxon. Coloured clades correspond to Figure 4b[2] for clearer comparisons between cladograms. Retraced on Google Drawings.*

Therefore, to mitigate the issues of incomplete characters implied weighting is used in relation to the consistency from the character matrix to avoid excessive homoplastic relationships being regarded by the software (which are more likely to

occur with equal weighting.) With these selected settings, Figure 4b[2] is generated and deemed the main phylogenetic tree of this study that will be compared to the previous studies featured in the literature review.
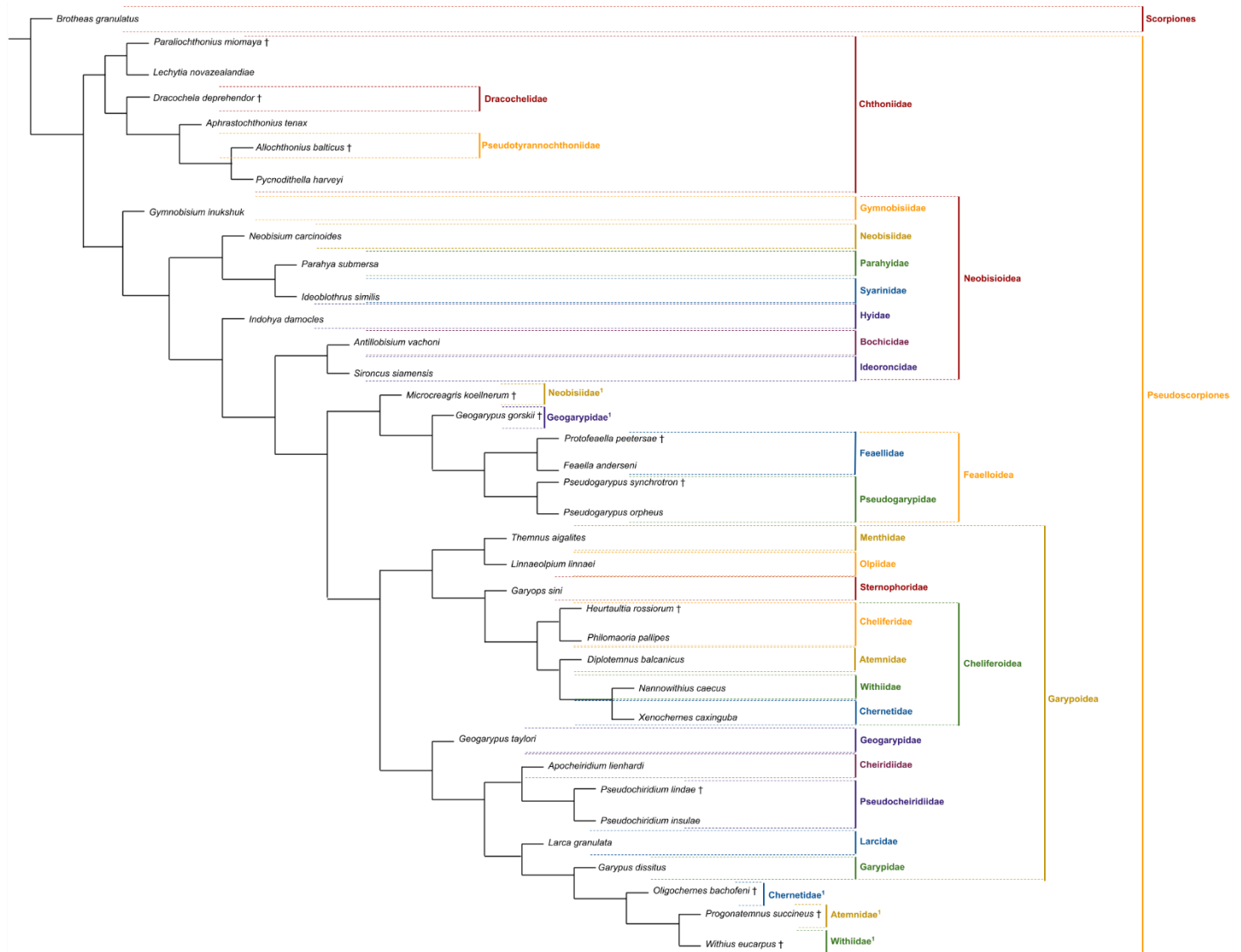
Figure 4b[2]. *Phylogenetic tree generated from TNT Ver. 1.5. with implied weighting (K = 4.0.) Orders, superfamilies, and families included based on data from Harvey (1992) and Benavides et al. (2019.)* [1] *indicates taxa found 'outside' their designated family based on previous studies.* † *represents an extinct taxon. Retraced on Google Drawings.*

A third analysis is then made to discern if the fossil taxa have had an impact to the overall phylogenetic tree. To do this, extinct taxa are deactivated within the software itself to retain data as reference to the active extant data points as argued in Goloboff et al (2016.) The resulting tree is shown as collective Figures 4c. Similar to the previous cladograms, two versions with implied and equal weighting are

generated for comparison. The most interesting note in the topology includes Garypoidea being shown as paraphyletic in regard to Cheliferoidea.
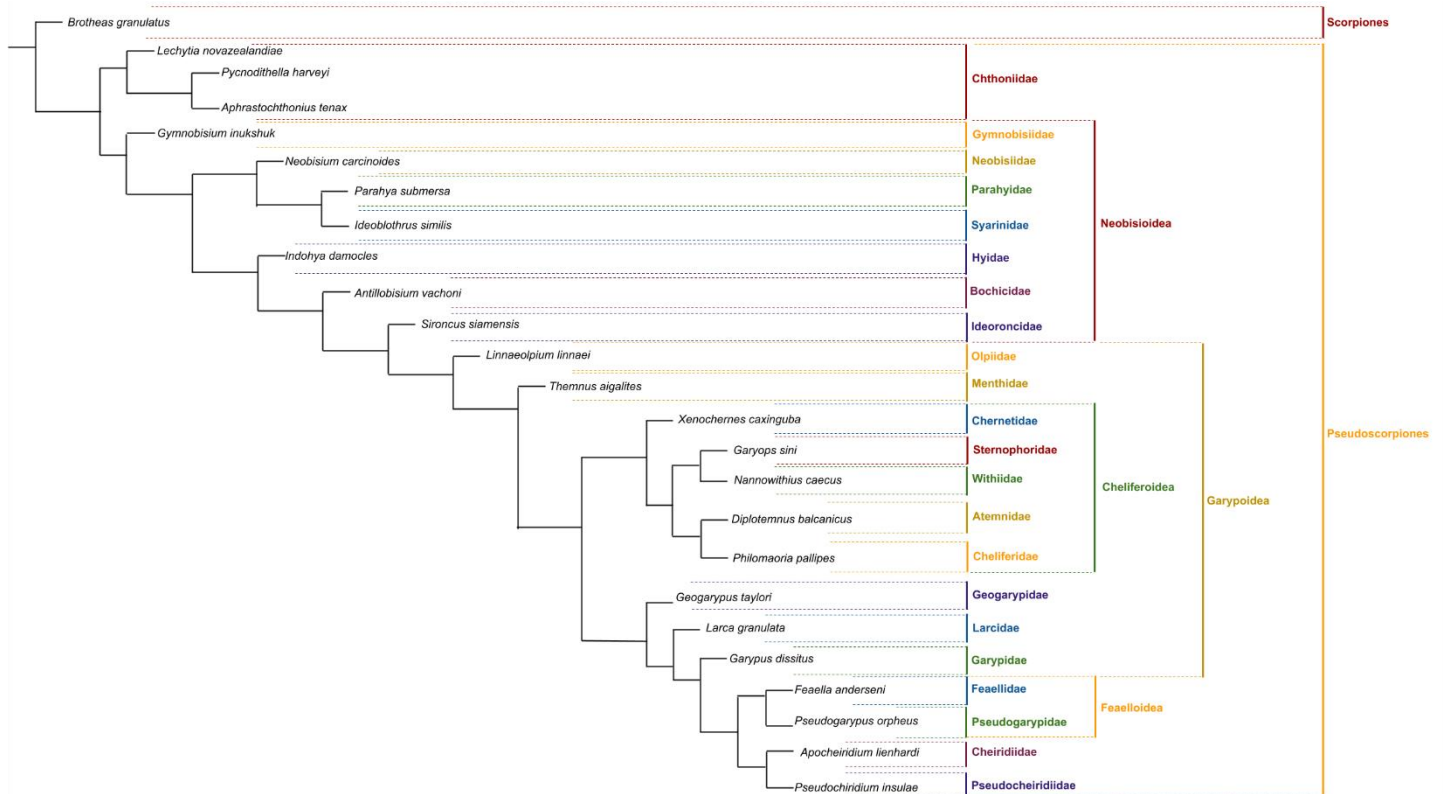
Figure 4c[1]. Phylogenetic tree generated from TNT Ver. 1.5. with equal weighting (implied weighting switched off.) Extinct taxa remain in the matrix yet were deactivated before analysis. Orders, superfamilies, and families included based on data from Harvey (1992) and Benavides et al. (2019.) Coloured clades correspond to Figure 4b[2] for clearer comparisons between cladograms. Retraced on Google Drawings.

In comparing the Figures of 4b and 4c, there have been insignificant differences beyond the deactivation of the fossil taxa. For the respective cladograms with equal weighting, the phylogenetic relationships regarding *Xenochernes* is contested on whether it is basal to Sternophoridae or to Withiidae and Cheliferidae. Another distinction includes the interpretation that Garypoidea may be paraphyletic with the inclusion of Feaelloidea through derivations from the former superfamily. Otherwise, it can be interpreted that the extant taxa may have given a greater impact to the cladistical analysis of the fossil taxa than the reverse. More details will be in the Discussion chapter.

With the respective phylogenetic trees of 4b and 4c to implied weighting, the inclusion of the fossil taxa representatives in Feaelloidea gives an interpretation that it is distinct and a sister clade to the basal families within Garypoidea; rather than as a paraphyletic inclusion if the fossil taxa are deactivated. This is of particular note

when the fossil taxa involved have comparatively more complete profiles than others. This too is explored further in the Discussion chapter in the relevant taxonomic reviews.
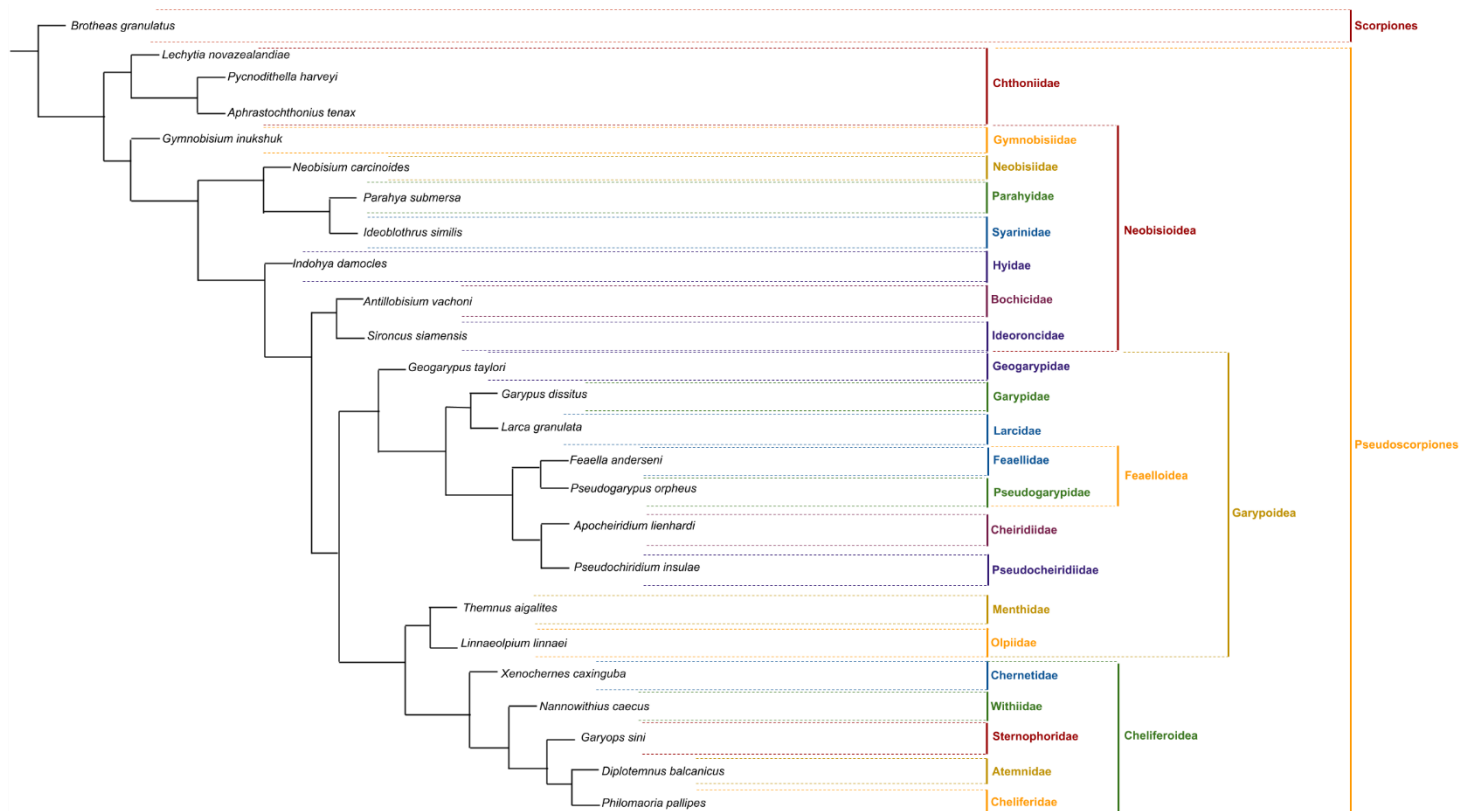

Figure 4c². Phylogenetic tree generated from TNT Ver. 1.5. with implied weighting (K = 4.0.) Extinct taxa remain in the matrix yet were deactivated before analysis. Orders, superfamilies, and families included based on data from Harvey (1992) and Benavides et al. (2019.) Coloured clades correspond to Figure 4b² for clearer comparisons between cladograms. Retraced on Google Drawings.

The revisited cladograms from Harvey (1992) (Figures 4a) can be difficult to compare to Figures 4b and especially 4c due to the changes in the focused taxonomic level, the additional taxa, and any outdated clades disregarded over the years. Yet, certain differences can be found between the topologies particularly the placement of Feaelloidea and its level of derivation across the order's cladistical history. Harvey (1992) determined the superfamily to be basal from Neobisioidea, while the cladogram with active fossil taxa interpret it to be more derived than the same clade.

The following comparisons and what remains constant can create more topics of research and discussion on how fossil taxa in phylogenetic analyses can change resulting trees, depending on its completed profile within the character matrix. The Conclusion will summarise this.

Discussion:

First, it is important to compare this study's phylogenetic tree with those from the previous studies to understand the strengths and weaknesses of this methodology inspired by them all.

Harvey (1992):

There are several similarities that make up the 'core' or more basal taxonomic levels between the two trees. Epiocheirata, for example, is said to be comprised by two branching superfamilies Chthonioidea and Feaelloidea. In both superfamilies across both studies, each of the featured families are sister taxa between selections of two. In Harvey (1992) it is theorized that *Dracochela* is also part of Epiocherata, with this study giving credence to this on being shown as a sister family to Chthoniidae. This family also shows affirmations that *Lechytia novazealandiae* corresponds to the now unused family 'Lechytiidae' in splitting from the other taxa. Neobisioidea in Iocheirata also show similar relationships with Ideoroncidae and Bochicidae being the most basal split in both trees in conjunction to the other families. So too do the trees show similar relationships with Olpioidea being a basal split from Garypoidea and Cheliferoidea; with Geogarypidae and Withidae being the most basal families respectively.

However, there are notable differences between the trees that don't refer to outdated or more recent clades. In Epiocheirata, while Pseudotyrannochthoniidae is considered a sister family to Feaellidae in Harvey (1992) in this study it is seen as a sister family to Chthoniidae instead. With Pseudotyrannochthoniidae being a family that only have fossil taxa to represent it in this study, that may have an impact on its placement between Feaelloidea or Chthonioidea. A future study that can include a possible extant taxon for this family could potentially refute one of these placements. The largest difference concerns the Panctenata clade, where from Harvey (1992) to this study; Olpioidea had not only be seen from being a sister clade to Garypoidea to Cheliferoidea, but also Withidae and Cheliferidae swapping the basal level for the rest of Cheliferoidea. Such significant changes may not be excused by the inclusion of fossil taxa as Figures 4c show the same differences with the fossil taxa inactive. It could refer to minor changes of the character matrix to correspond to the genus rather than the family as originally noted from Harvey (1992.)

Harms & Dunlop (2017):

   Even through different approaches between morphological traits and chromosomal timeframes, similarities can still be found between the trees. The Epiocheirata clade shows similar relationships in both trees, including how Pseudotyrannochthoniidae being seen as a sister group to the collective Chthoniidae. Feaelloidea as well show a similar branch between the trees. In regard to Mestommatina, both of these studies show the collective Garypidae and Larcidae sister families are themselves a sister group to the pair Pseudochiridiidae and Cheiridiidae. This is also shared by Harvey (1992.)

   In reference, because this is missing data from the phylogenetic tree of Harms & Dunlop (2017) the minimum age of the Scorpiones (this study's outgroup) in the fossil record is 439 Mya according to Howard et al. (2019.) An interesting note is this predates the instance of *Dracochela* in the Devonian. With that said, an important distinction to note is the difference in taxonomic levels in Cheliferoidea between Harms & Dunlop (2017) and this study. In the former, Withiidae is the most basal in this superfamily. In the latter, it is Cheliferidae. With both how the tree in Harvey 1992 supports the tree in Harms & Dunlop (2017) as well as the second 'Withiidae' specimen *Withius eucarpus* being found instead in Mestommatina in Figures 4b, so far this section of this study's phylogenetic tree is found to be lacking in reliable results.

Benavides et al. (2019):

   Similar from before, with the approaches in generating the results being opposite in priorities between these two studies; between molecular and morphological characters, it is important to understand the contexts and how they can differ more than any similarities. It is noted that both the phylogenetic trees in question have developed similar superfamilies and most of the families belonging to the clade.

   However, the differences far outnumber the similarities. To start with, Dracochelidae is considered its own superfamily Dracocheloidea in Benavides et al. (2019) whereas in this study it is found in Chthonioidea. This could have a logical reason that there isn't any genetic material from *Dracochela* to analyse to begin with. From there, the question of which of the two superfamilies in Epiocheirata (in reference to Harvey (1992)) is more basal to the other is also contradictory. For this study it is seen as Feaelloidea, for the Benavides et al. (2019) study it is

Chthonioidea. Furthermore, in this study Bochicidae is a sister family to Ideoroncidae when in the previous study the former is with Hyidae. The most notable difference is the status of the sister families Menthidae and Olpiidae; where in the previous study they are the most derived pair in Garypoidea, yet in this study they are a basal sister group from the superfamily altogether. Altogether, these differences may attribute to the main flaw of molecular analysis of missing extinct taxa that could affect relationships. This type of comparison is also made in Garwood & Dunlop (2014.)

Del Claro et al. (2009):

   With this cladistic tree in question, the approaches between morphological characters and behaviour evolution should be into consideration. Interestingly, the first notable similarity is the Neobisioidea collective being similar by the phylogenetic order of the families, from the family sister group of Ideoroncidae and Bochicidae, to Gymnobisiidae then the derived group of Syarinidae, Neobisiidae, and Parahyidae. The Panctenata clade as well show similar cladistic relationships between the two studies in question; most notably how Sternophoridae could be a basal branch from Cheliferoidea.

   There are minor differences in matters of scale, such as the placement of Withiidae being a more basal level than it is seen in this study of being a sister family to Chernetidae. Although it should be noted that the sample size for Del Claro et al. (2009) only included five families out of the potential twenty-three featured in the tree, where Harvey (1992) is the main framework for most of the relationships that would require quantitative data. As such, this method in determining social behaviour as characters could be a potential perspective to complement a phylogenetic tree based on morphological characters; with Harvey (1992) and this study's results as examples.

   If the objectives in updating the general phylogeny of Pseudoscorpiones can be done through focusing to the genera and species rather than the families; then there should be new interpretations and remarks for each of the selected taxa. The following will be listed in taxonomy according to Figures 4c and Benavides et al. (2019) for supplementary clade names. The relationships from the analysis in this study will be provided.

Order **SCORPIONES** Koch, 1837

Brotheas granulatus Simon 1877

Despite this being the outgroup, this is still present as a profile to emphasize the impact the change has made to the phylogenetic analysis from the former outgroup Solifugae. It has been regarded in Harvey (1992) that Solifugae had lacked the femur sensilla which in consequence left the status of the autapomorphic trait without confidence. In this study, Scorpiones are shown with sensilla according to Barth & Stagl (1976) and in reference to these traits; more confidence can be given to the characters concerning limb sensilla for Pseudoscorpiones. In matters of a phylogenetic relationship to the order, molecular evidence has been found in Garwood & Dunlop (2014.)

Order **PSEUDOSCORPIONES** De Geer 1778

Discharge through mobile chelae upon pedipalps. Pedipalpal tibia and tarsus form pedipalpal chelae. Mobile chelicera with 1 (or more) seta(e) at subdistal distance. Absent medial eyes. Present branched chelicerae flagellum. Egg sac attached to female operculum.

Suborder **EPIOCHEIRATA** Harvey 1992

Venom apparatus absent. Mobile chelae have a distal trichbothrium. Commonly occurring coxal spines. Male genital atrium has 2 rows of setae.

Superfamily **CHTHONIOIDEA** Daday 1888

Dorsal trichbothria on pedipalpal tarsus. Straight medium maxillary lyrifissure. Present female lateral apodeme frame. Coxa I has anterior protuberance.

Family **CHTHONIIDAE** Daday 1888

Coxae tubercles are branched in shape, sometimes secondarily lost.

Paraliochthonius miomaya † Judson 2016

As found in Judson (2016) it remains within Chthonidae. Furthermore, it is shown as the earliest branch within the family. With this taxon lacking (or have obscured) branched setae on the coxal tubercle (that diagnoses Chthoniidae,) this could indicate this character is more derived than previously thought.

Lechytia novaezealandiae Christophoryová & Krajčovičová 2020

In representing the outdated 'Lechytiidae' family, this genus being calculated on a basal level from the other Chthoniidae genera can give credence (from a morphological perspective) to Benavides et al. (2019) to consider the family paraphyletic and thus reduced to a subfamily. This is further supported in having it be a sister taxon to the extinct *Paraliochthonius miomaya.*

Aphrastochthonius tenax Chamberlin 1962

The one of the two genera in this family that stayed consistent in regard to family validation. And yet, it appears to be more derived than *Dracochela* yet more basal from *Allochthonius,* suggesting that their respective families may be paraphyletic.

Pycnodithella harveyi Kennedy 1989

Initially representing 'Tridenchthoniidae,' in a similar manner to *Lechytia* this family is seen as redundant and paraphyletic from sequence analysis according to Benavides et al. (2019.) This study seems to support this change with this genus appearing as the latest branch within alongside a lack of significant consistency to warrant a family separate from Chthoniidae*.*

Family **DRACOCHELIDAE** Schawaller et al. 1991
Smooth serrula on chelicerae. Linear flagella.

Dracochela deprehendor † Schawaller, Shear *& Bonamo 1991*

This is the only taxonomic family in Pseudoscorpiones to (as of this study) retain no extant genera. *Dracochela* is the only genus and has been under contention since its discovery about its relationships with other genera. Due to being the oldest discovered fossil pseudoscorpion, this ties into the prevailing issue of the fast evolutionary rates the order is observed to have. With this, the many uncertain factors tying around the genus suggests why there has not been an agreed cladistical level. Through this study's methods, it is suggested that *Dracochela* is an earlier branch from the Pseudotyrannochthoniidae and is either related to or within Chthoniidae. More new discoveries can confirm or refute this in the future.

Family **PSEUDOTYRANNOCHTHONIIDAE** Beier 1932

Dorsal trichbothria distal on tarsus. Mobile pedipalpal chela's trichbothrium more distal. Coxa I have coxal blades. Rounded coxa I.

Allochthonius balticus † Schwarze et al 2022

Similar to Dracochelidae, the cladistic tree suggests it could be paraphyletic within Chthoniidae. It may be more likely it is a sister family to it within Chthonioidea from evidence of the related research studies against this study, such as Benavides et al. (2019.)

Suborder **IOCHEIRATA** Harvey 1992

Present venom apparatus in either or both chelae. Present posterior maxillary lyrifissure.

Microcreagris koellnerorum † Schawaller *1978*

This taxon is originally from the Neobisiidae family yet is placed as an earlier branch to the Feaelloidea superfamily. With no diagnostic traits in this matrix it can be said in confidence that the reason for the 'basal' level is in fact due to the lack of confirmed characters in total. More information will be needed to complete the matrix for this taxon further through this study's methods.

Geogarypus gorskii † Henderickx 2005

This is another fossil taxon that appeared in the phylogenetic tree outside of its originally described family. In this case however, this taxon is found within the Feaelloidea branch. It can be said this taxon could be placed within the family if it had a more detailed character profile or not.

Superfamily **NEOBISIOIDEA** J.C. Chamberlin 1930

Serrated subterminal tarsal setae (plesiomorphic with Hemictenata.)

Family **GYMNOBISIIDAE** Beier 1947

Chelicerae mobile chelae have distal thickened setae. Enlarged male genitalia. Absent venom apparatus from immobile chelae.

Gymnobisium inukshuk Harvey & Giribet 2016

An interesting taxon to have the immobile venom apparatus absent, which is one of the diagnostic characters for this family. With the character consistency

in the matrix, this taxon's placement to Neobisoidea given more confidence over a potential placement in the venom-less Epiocheirata suborder. From its basal branching within the superfamily, it could be considered the trait to be present later in the evolutionary lineage.

Family **NEOBISIIDAE** Chamberlin 1930

3 or more setae on apex of pedipalpal coxae. Round pedipalpal coxae. Absent venom apparatus from mobile chelae.

Neobisium carcinoides Hermann 1804

This taxon has more autapomorphies than *Ideobisium similis* and *Parahya submersa,* namely the pedipalp coxae's shape and number of setae as examples; of which could be included as new diagnostic traits to further distinguish these families.

Family **PARAHYIDAE** Bristowe 1931

Extended arolia. Femur and patella IV fused. Absent venom apparatus from mobile chelae.

Parahya submersa Bristowe 1931

Arolia protrusions from the limbs could be another possible new diagnosis to further separate these families and determine if they do share a sister relationship. Future research specializing into these families or Neobisioidea as a whole can bring more insight into this matter.

Family **SYARINIDAE** Chamberlin 1930

Absent venom apparatus from mobile chelae. Mobile chelae trichbothrium tapered basally.

Ideobisium similis Balzan 1892

It has been difficult to determine a significant diagnosis to separate this family from other derived Neobisioidea families, particularly with Neobisiidae. Across the reviewed phylogenetic trees, including this study's, there is no same answer. The femur I & II three sensilla (particularly their distal placement) could be a possible new diagnostic trait for this genus (and perhaps the family.)

Family **HYIDAE** Chamberlin 1930

Femurs I and II have sub-basal mounds. Female anterior genital opercula have minute setae. Pedipalpal femur have 2 or 3 short setae on posterior-basal margin.

Indohya damocles Harvey & Volschenk 2007

The matter of cladistic levels across the studies' phylogenetic trees varying between a basal branch, a sister relationship, or even a part of the Bochicidae and Ideoroncidae pair brings this taxon on less certain grounds of its placement. It is believed that this tree can give evidence for the sister relation to the aforementioned families, and thus branching off from Gymnobisiidae and to the resulting derived families.

Family **BOCHICIDAE** Chamberlin 1930

Pedipalpal femur have sub-basal tubercle from posterior margin, unless secondarily lost.

Antillobisium vachoni Dumitresco & Orghidan 1977

This genus is considered a basal sister taxon next to *Sironcus siamensis* for Neobisioidea, and with having the diagnostic serrated setae on the limbs' tarsi this is easy to understand why. There are enough different traits of characters (i.e. less fused serrula on chelicerae etc.) to warrant different families for each of these taxa, in contrast to the Chthoniidae merge.

Family **IDEORONCIDAE** Chamberlin 1930

20 to 31 trichbothria on immobile chelae. 10 to 14 trichbothria on mobile chelae.

Sironcus siamensis With 1906

Similar to *Antillobisium vachoni* in Bochicidae which is the sister taxon, this taxon in particular represents the family that may have an uncertain placement in the cladistical levels. With the difference highlighted from Benavides et al. (2019) there could be a matter of differences in genetic genomes that may not be expressed in exterior (and some interior) phenotypes for this morphological study. Further research may be needed to give confidence to either placement, if both approaches for data could be utilized in an accurate manner.

Superfamily **FEAELLOIDEA** Ellingsen

Carapace has 3-6 anterior lobes. Spiracles closer to sternites IV and V. Fused tergite XI and sternite XI. Sclerotised anal plates (tergite and sternite XII.) Commonly occurring platelets on pleural membrane.

Family **FEAELLIDAE** Ellingsen

Raptorial pedipalps. Absent median maxillary lyrifissure. Pointed cheliceral flagellum. Anterior of carapace have 2 or more medial lobes. Articulation joint between carapace and tergite I. Spiracles fused to sternites IV and V.

Protofeaella peetersae † Henderickx & Boone 2016

A genus not featured in the original Harvey (1992) remarks; this genus displays diagnostic traits (i.e. raptorial pedipalps etc.) that diagnoses the family, as well as having traits differing from *Feaella* such as secondarily losing both pairs of eyes as one example. This gives credence that the loss of eyes by various genera across the families may be more common in the order than first thought.

Feaella anderseni Harvey 1989b

In having a few unique traits from sister taxa *Protofeaella* such as protruded eyes and anterior lobes etc., this genus has a lot of character consistency that gives confidence of the taxonomic family being basal in the overall order even with near complete character matrices.

Family **PSEUDOGARYPIDAE** J.C. Chamberlin 1923

Present carapacal alae.

Pseudogarypus synchrotron † *Henderickx 2012*

This study's cladistical tree gives confidence to the original description of Henderickx et al. (2012) of being another species to the *Pseudogarypus* genus. Of interesting note are the 'misplaced' fossil taxa *Microcreagris kollnerum* and *Geogarypus gorskii* appear as an earlier branch between its family and Feaellidae. This could support the notion that the former two fossil genera may need more detailed character profiles if the weighting compared the amount of unknown characters between the four fossils.

Pseudogarypus orpheus Nelson 1975

> It is confident that its family is a sister clade to the Feaellidae family and thus it can be considered monophyletic. Similarly it shares a sister branch with its fossilised species counterpart.

Superfamily **GARYPOIDEA** Chamberlin 1930

Triangular carapace. Eyes (if any) set on tubercles and at posterior margin. Anterior margin of carapace lobed. Oval abdomens. General setae are curved (excluding Garypidae.)

> The most significant impact found in Figure 4b[2] is the inclusion of the superfamily Cheliferoidea within the evolutionary branches between the collective Menthidae, Olpiidae, and Sternophoridae; and earlier than the rest of the original families in Garypoidea. If more confidence is given in this placement with future analyses, it could be suggested to remove the former three families from Garypoidea.

Family **MENTHIDAE** Chamberlin 1930

Round articulated joint between coxae II and III. Absent venom apparatus from mobile chelae. Three accessory trichbothria on tarsus and immobile chelae (at adult instar.)

Themnus aigalites Harvey 1990

> At a similar cladistic branching to Feaelloidea, yet in this study this taxon is placed outside of Neobisioidea and also the Cheliferoidea. For the latter, it remains a sister taxon with *Linnaeolpium linnaei* from Olpiidae.

Family **OLPIIDAE** Banks 1895

Round articulated joint between coxae II and III. Absent venom apparatus from mobile chelae. Three accessory trichbothria on tarsus and immobile chelae (at adult instar.)
(Plesiomorphic with Menthidae.)

Linnaeolpium linnaei Harvey & Leng 2008

> In conjunction with *Themnus aigalites,* they are originally interpreted to be sister taxa to Garypoidea which is not the case in this study. This may not display an accurate relationship due a lack of evidence of other studies, and further research is needed with similar methods to give confirmation or refutation on this placement.

Family **STERNOPHORIDAE** Chamberlin 1923

Present pseudosternum. Chevron-shaped posterior margin of carapace.

Garyops sini Chamberlin 1923

With a diagnostic character of a pseudosternum, this is the only taxon in the matrix to have it as an autapomorphic trait. Harvey (1992) suggested for research into the genitalia characters to complete this family's matrix profile. This can be concurred as well as suggesting to include more genera for a larger sample size.

Family **GEOGARYPIDAE** Chamberlin 1930

Pits in external margin of immobile chelae. Single pointed cheliceral flagellum. Absent spinules on flagellum.

Geogarypus taylori Harvey 1986

In both of the phylogenetic trees of this study, the main tree of Figure 4b[2]. and the inactive fossil tree of Figure 4c[2]; this taxon is considered a branch from the superfamily Cheliferoidea and the subsequent derived families after. With a lack of change between the trees and subsequent similar relationships in the reviewed studies, this placement could be considered confident.

Family **CHEIRIDIIDAE** Risso 1827

Metazone present on carapace. Femora and patellae are fused on each leg.

Apocheiridium lienhardi Mahnert 2011

This taxon shares a number of autapomorphic traits with *Pseudogarypus synchrotron,* for example the prosoma shape and the anterior margin. The diagnostic characters for this family as well include a depressed metazone and fused metatarsi to tarsi in all four pairs of limbs; of which are all also autapomorphic for *Pseudogarypus synchrotron.* In regard to this taxon however, it is confident in its relationships to Pseudochiridiidae and within the superfamily in character consistency across the featured phylogenetic trees.

Family **PSEUDOCHIRIDIIDAE** Chamberlin 1923

Expanded coxae at posterior. Chervon-shaped tergites.

Pseudochiridium lindae *Judson 2007*

Considered the most derived sampled taxa in Cheiridioidea and subsequently Garypoidea, it is found as a sister taxon to the fossil species *Pseudochiridium insulae.*

Pseudochiridium insulae † *Hoff 1964*

It is noted that this taxon also exists as extant as well as found in Dominician amber; this character matrix refers only to the fossil specimens. This can provide credence to not only the family as a whole for a possibly accurate fossil species within it but can also provide new insights to the *Pseudochiridium* genus as a whole, particularly with the addition of the extant version in any future analyses.

Family **LARCIDAE** Harvey 1992

Desclerotised area around anal plate. Sternites III and IV have row of setae at posterior margin. Small lyrifissures at sternite XI.

Larca granulata *Harvey 1986*

Similar to *Garypus dissitus* in the circumstances of the pair's cladistical level in the superfamily. However, the sister relationship between the two families seems to have strong prevalence across phylogenetic trees both in this study and in the reviewed trees.

Family **GARYPIDAE** Daday 1888

Absent stigmatic helix. Curved setae sometimes lost.

Garypus dissitus *Harvey 2020*

With a sister taxa relationship to *Larca granulata,* both of them are somewhat derived from the Garypoidea superfamily. This may have a correlation in having (as of yet) no fossil taxa within either family. This may change with future discoveries.

Superfamily **CHELIFEROIDEA** Risso 1826

Present spermathecae. Complex spermatophore. Performs mating dance.

As mentioned with Garypoidea, this superfamily's inclusion could make either family paraphyletic. This is yet to be given much confidence particularly as it contradicts other cladograms such as that found at Benavides et al. (2012.)

Family **CHELIFERIDAE** Risso 1826

Ram's horn organs present. Male coxae IV have coxal sacs. Asymmetrical claws in male leg pair I.

Heurtaultia rossiorum † Judson 2009

This may be another case of despite a lack of detail in the taxon's character profile, it is found as a sister genus within the originally placed family. Cheliferidae itself however is found to be an earlier branch instead of Chernetidae.

Philomaoria pallipes White 1849

Curiously, while this taxon is shown a basal branch in Chelierfoidea in Figure 4b[2], in Figure 4c[2] with the fossil taxa inactive it is instead the most derived family and vice versa with Withiidae and Chernetidae. This is further evidence of the impact the additional fossil taxa can do to the phylogenetic relationships, with more data available (through adequate weighting) to analyze between autapomorphies. In the case of this taxon, it can be estimated that the inclusion *Heurtaultia rossiorum* provided this difference in relationships in this very study.

Family **ATEMNIDAE** Kishida 1929

Absent venom apparatus from mobile chelae.

Diplotemnus insolitus Chamberlin 1933

With the aforementioned uncertain relationship with Cheliferidae, and indirectly with the more derived Cheliferoidea clades Withiidae and Chernetidae; it is proposed that the character 111 from this study (male genitalia shape) to be a focus as a further research topic and whether if this can apply as a diagnostic or at least autapomorphic trait for Atemnidae. This taxon in particular is confirmed to have the Barroi's organ in Muchmore (1975)

the same study that suggests this character can determine more genera within this family. To concur, this character could also provide a new possible diagnosis to potentially separate it further from other families within Cheliferoidea.

Progonatemnus succineus † Beier 1955

While this taxon is originally interpreted in being in Atemnidae, it is instead found as one of the most 'derived' species in the cladogram. It is carefully concluded that a more detailed character profile to its morphology may mitigate this issue. It is unlikely to have been misplaced in its original taxonomy.

Family **WITHIIDAE** Chamberlin 1931
Sensory setae on posterior sternites (all males, some females.)

Nannowithius caecus Simon 1900

In Figure 4c^2, the placement of this taxa remains unchanged with the omission of its fossil taxon counterpart within this particular family. This is given credence to a similar derived cladistic level found in Benavides et al. (2019).

Withius eucarpus † Dalman 1826

Despite this taxon being originally placed in Withiidae, this fossil taxon is instead placed as a sister 'clade' to Garypoidea. This is considered an error in the implied weighting, which may had been caused by an inadequate number of characters for this taxon. More direct observations to complete the matrix further can amend this.

Family **CHERNETIDAE** Menge 1855
Tarsi have proximal raised slit sensillum. Absent/reduced venom apparatus in immobile chelae. Chelae have more than 1 accessory tooth. Differently shaped male genitalia.

Xenochernes caxinguba Feio 1945

Similar to the Withiidae counterpart taxon, this taxon is considered more derived than Atemnidae and is also the most derived in Cheliferioidea.

Oligochernes bachofeni † <small>Beier 1937</small>

This taxon is made a 'sister' genus to *Withius eucarpus* and is also considered an unreliable placement in the phylogenetic tree. A more complete character matrix should be able to amend this too, which should be noted have been listed under their respective families in this list instead for clarity.

Conclusion:

Overall, this research project has indeed proceeded to review previous projects that all share the aim to understand the ancient and diverse order Pseudoscorpiones. So too has the methods of the reviewed studies provide a framework for not only a streamlined character list to pertain to every pseudoscorpion, but also finding new perspective and insights that are yet to be found. Now that they are, they can be reconsidered for more research projects with even further development in technology and experience to improve the processes further.

The aims of this study have been reached with interesting results. With the updated software analysing the original dataset from Harvey (1992) there have been different topologies that are compared between the past and present, which have given confidence to later reinterpretations of families from subsequent studies with this dataset as a framework.

Upon adding fossils to this study's matrix, it is considered curious that instead the expected results of the fossil taxa influencing the phylogenetic relationships of the extant taxa; it appears to be the opposite. This is a new observation that have yet to be done within the history of studying Pseudoscorpiones and should open up possibilities of yet to be discovered fossil taxa if this influence of phylogenetic relationships to extant species remains or changes.

The main flaws of this study include inexperience in implementing changes to the methods or implementing new ideas have led to unconfident interpretations. The limitations of resources available to input the sampling of taxa (and respective traits) have also caused the consequences of likely errors in the phylogenetic tree.

Yet for the more reliable findings from this study that have been found, future research can be created to refute or strengthen them through repeated (or updated) methods. The discovery of new specimens, either as living extant animals or fossils; will inevitably test this method and the matrix itself even further.

The implementation of more than one approach to understanding Pseudoscorpiones, such as morphological comparisons or molecular phylogeny, into one large-scale research project could mitigate limitations caused by a single approach. Garwood & Dunlop (2014) provides an example for this generalized

method for Chelicerata. The reviews and comparisons made in this study can be the start to projects that can center orders within the subphylum in the near future and is one step closer to understanding the enigmatic full stop-sized pseudoscorpions and their biological history.

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