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Global evolutionary relationships of Devonian proetide trilobites

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Abstract

The Proetida likely represent the only surviving trilobite clade past the Devonian mass extinction event(s). Although members of order Proetida have long been studied, the global phylogenetic relationships across this pivotal time are still unresolved. I used a Bayesian phylogenetic approach to construct a subordinal level tree for members within the superfamily Proetoidea. Two models, a relaxed and strict clock model, were compared and used to assess past reconstructions of clades within the order. The trees from both models highlight key relationships among proetides across the Devonian and show paraphyly in groups that have been considered monophyletic in the past. Trees from both models also suggest that major groups, e.g., the genus *Gerastos* Goldfuss, 1843 and the family Phillispidae (which represents the most diverse post-Devonian proetide group under current taxonomic schemes) are polyphyletic. This in turn suggests, in a paleobiological context, a more complex pattern of survivorship over the Late Devonian than previously suggested as well as pervasive parallelisms toward certain '*Gerastos*' or 'phillipsid' morphotypes.

Non-technical Summary

The Proetida likely represent the only surviving trilobite clade past the Devonian mass extinction event(s). Although members of order Proetida have long been studied, the global relationships of these trilobites across the Devonian are still not well known. I used a Bayesian phylogenetic approach to construct a subordinal-level tree for members within superfamily Proetoidea. Two models, a relaxed and strict clock model, were compared and used to assess past reconstructions of clades within the Proetoidea. The trees from both models highlight key relationships among proetides across the Devonian and show groups thought to be closely related that are not. Phylogenetic trees from both models also suggest that major groups, such as the genus *Gerastos* and the family Phillispidae (which represent the most diverse post-Devonian proetide group under current taxonomic schemes) most likely to do not represent one group but many groups. This in turn suggests, in a paleobiological context, a more complex pattern of survivorship over the Late Devonian than previously suggested as well as the convergent evolution of certain '*Gerastos*' or 'phillipsid' morphologies.

Introduction

The pinnacle of trilobite diversity occurs early in their evolutionary history: peak trilobite richness and diversity occurred in the end-Cambrian–early Ordovician (490–470 Ma), followed by an overall decline in the class for the remainder of the Paleozoic (Bault et al., 2022). The end-Ordovician and end-Devonian mass extinction (or mass depletion) events both accelerated this decline, and post-Devonian trilobites might be considered an example of a 'Dead Clade Walking' (Jablonski, 2001; Hopkins et al., 2023). Despite this overall decline in class Trilobita, only one order, Proetida, defied the odds: proetides are the last of the trilobites. All trilobite diversity for the remainder of the Paleozoic came from order Proetida (Brezinski, 1999; Lerosey-Aubril and Feist, 2012; Bault et al., 2022). Proetides achieved peak diversity in the Devonian, and although their diversity declined markedly over the Late Devonian depletion events, proetides rebounded after the Devonian and reachieved peak (or near peak) diversity in the early Carboniferous (Brezinski, 1999; Lerosey-Aubril and Feist, 2012; Bault et al., 2022). However, it must be noted that larger clade dynamics (e.g., at the ordinal level) often mask the dynamics of subclades (e.g., families or genera), e.g., origination/extinction dynamics within these subclades. Within the proetides, certain families continued to show declines in diversity while rebounding diversity might have been focused within one family; the composition of order Proetidea was fundamentally altered in the Tournaisian (358.9–346.7 Ma) with the rise and proliferation of the new family Phillipsiidae (Lerosey-Aubril and Feist, 2012; Bault et al., 2022). Although other families within Proetidea went extinct, thereby lowering overall diversity, the new family Phillipsiidae, and an

Articles

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older family Brachymetopidae, bolstered much of proetide diversity throughout the end-Paleozoic (Bault et al., 2022). This pattern is surprising especially when considering other prominent trilobite orders, e.g., Phacopida which, despite rebounding and holding high diversity along with proetides during the end-Devonian, ultimately went extinct while proetides persisted and experienced some diversification (Bault, 2023). Thus, a general description of trilobite diversification dynamics from the Devonian to the early Carboniferous might not adequately describe the diversification dynamics of the only post-Devonian surviving trilobite clade.

To begin to understand why proetides survived through the Devonian while other trilobites did not and continued to persist to the end of the Paleozoic, the relationships within Proetida during this interval need to be examined. I performed a phylogenetic analysis of members within the order Proetida, specifically the superfamily Proetoidea (Hawle and Corda, 1847). The proetides, often considered a 'disorderly' order (Bergström, 1977), have undergone much taxonomic revision, especially when it comes to the inclusion or exclusion of certain families (Fortey and Owens, 1975; Bergström, 1977; Lieberman, 1994; Fortey et al., 1997; Adrain, 2011; Lamsdell and Selden, 2015). Only recently, the order has been considered monophyletic (Lamsdell and Selden, 2015). My focus was to examine proetide relationships across the Devonian and into the early Carboniferous.

Proetidea taxonomic history and classification

Taxonomic history. In recent years, there has been a call to action to resolve some remaining gaps in higher-level trilobite systematics and phylogenetic relationships (Paterson, 2020). As is not uncommon with trilobite taxonomy at a higher classification level, proetide trilobites have suffered greatly from a lack of taxonomic clarity but more work is beginning to untangle proetide relationships (Adrain, 2011; Lamsdell and Selden, 2015). The relationships within the subclades of this order have been described (e.g., Fortey and Owens, 1975; Lieberman 1994; Adrain, 2011; Lamsdell and Selden, 2015). Figure 1 summarizes some of these classification schemes and the hypothesized relationships of and within superfamily Proetoidea. Membership within Proetidea has evolved based on more regional studies (e.g., Lieberman, 1994) and therefore more taxa can be incorporated into phylogenies (Fig. 1; Table 1). Additionally, Devonian-age regional proetides have been described from across the globe (e.g., Europe, China, Australia) and part of the aim of this study was to continue efforts to link these proetides to one another via phylogenetics. For the purposes of this study, I set out to build a proetide tree using the most up to data scheme presented by Lamsdell and Selden (2015).

Of interest in this study are members of Proetoidea. Clades within superfamily Proetoidea include the Proetideae, Rorringtoniidae, Scharyiidae, Tropidocorpyhidae, and the Phillipsidae (as general membership within Proetidea per Lamsdell and Selden, 2015). Some subgroups have been very contentious due to some 'unproetide-like' morphological characters (e.g., prominent eye ridges or up >10 thoracic segments in aulacopleuirds per Owens and Hammann, 1990). One such example is aulacopleurids, which were separated from superfamily Proetoidea into superfamily Aulacopleuroidea in the Treastise on Invertebrate Paleontology (Fortey et al., 1997) and into order Aulacopleurida by Adrian (2011) (Table 1). Other studies have examined aulacopleuirds specifically and have placed these trilobites closer to other subclades (e.g., Rorringtoniidae) with little mention of Proetidea (Adrain and

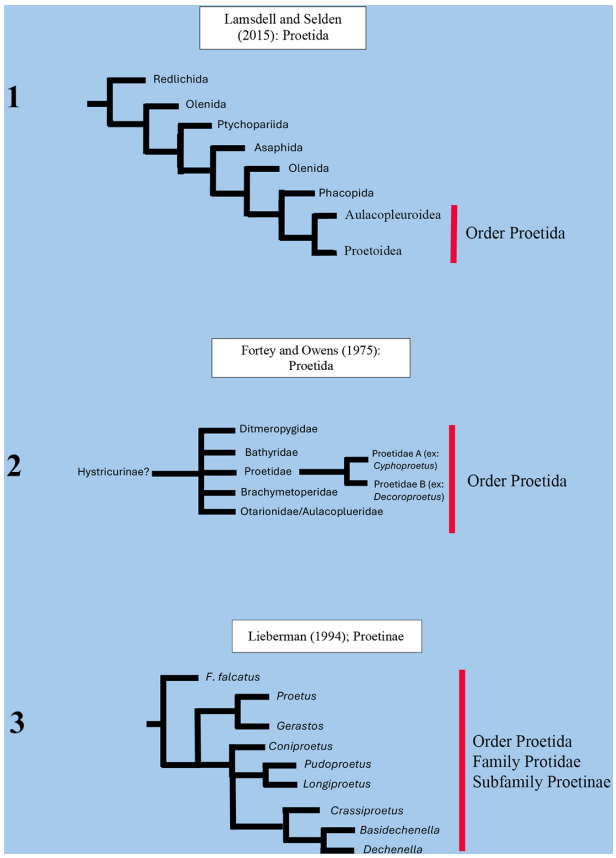


Figure 1. Example visualized classification schemes of proetide trilobites throughout the years. (**1**) The most recent classification scheme from Lamsdell and Selden (2015) established the monophyly of order Proetidea in the context of other major trilobite orders. Note: this cladogram is abbreviated with orders though genera used in this study. (**2**) Fortey and Owens (1975) proposed the order Proetidea and suggested that it might have arisen from Hystricurinae trilobites in the Ordovician. No clear sister relationships were reported, only the membership and characteristics of the order. (**3**) Lieberman (1994) described the relationships among Devonian members of the subfamily Proetinae (within order Proetida and family Proetidae) of eastern North America. Note: some genera were excluded from this cladogram.

Chatterton, 1993). In some cases, order Proetoidea was reduced to two families (Proetideae and Tropidocorpyhidae) with 15 families now grouped with the now-order Aulacopleurida (Adrain, 2011). This was updated later by Lamsdell and Selden (2015) in which families Aulacopleuridae, Bathyruidae, Brachmetopidae, Rorringtonidae, Dimeropygidae, Tropidocoryphidae, Scharyiidae, Otarionidae, and Hystericuridae were reincluded in Proetida (Table 1). Following Lamsdell and Selden (2015), some groups (i.e., aulacopleurids, bathyurids, and other contentious subgroups) were considered part of order Proetida but were not included because their membership within superfamily Proetoidea is still unclear.

Proetides (sensu Fortey and Owens, 1975) were placed just outside order Phacopida in Trilobita by Lamsdell and Selden (2015) (Fig. 1a). Before this, Fortey and Owens (1975) branched major families of proetides, including Proetideae, Bathyuridae, and Ditermeropygidae, from the Proetidea superfamily Hystricurinae, a group with its origins in the Ordovician (Fig. 1b). Lieberman (1994) further resolved large genera within the subfamily Proetinae, e.g., *Gerastos* Goldfuss, 1843; *Proetus* Steininger, 1831; *Basidechenella* Richter, 1912; and *Crassiproetus* Stumm, 1953 (Fig. 1c). In addition, five major divisions within Proetideae

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Table 1. Some examples of taxonomic assignments of proetide trilobites over time. Order Proetidea, established by Fortey and Owens (1975), has gone through much revision. Most of the revision includes subdividing the order based on a variety of morphological differences, e.g., Bergström (1977) highlighted issues with membership as described by Fortey and Owens (1975) based on enrollment and ontogeneic patterns of some groups

Source	Taxonomic Level of Study	Membership includes:
Fortey and Owens, 1975	Order (Proetidea)	Hystricurinae, Bathuridae, Glaphuirdae, Dimeopygidae, Otationidae, Brachymetopidae, Proetideae A, Proetideae B, Aulacopleuridae, Cornuproetinae (only some), Cyrtosymbolinae, Drevermannia 'group'
Bergström, 1977 (incorporating Bergström, 1973)	Divides Proetidea into three orders	Illaenida: Proetacea (e.g., Bathyuridae, Proetideae, Brachymetopidae); Ptychopariida: Solenpleuracea (e.g., Aulacopleuridae); Odontopleurida: Odontopleuracea, Cheiruracea (e.g., Glaphuridae, celmids, Odontolpleuridae)
Lieberman (1994)	Subfamily (Proetinae)	*Proetus* Steininger, 1831; *Falcatoproetus* Steininger, 1831; *Gerastos* Goldfuss, 1843; *Pudoprotetus* Hessler, 1963; *Longiproetus* Cavet and Pillet, 1958; *Coniproetus* Alberti, 1966; *Plesiowensus* Lieberman, 1994; *Arcticormistonia* Lieberman, 1994; *Crassiproetus* Stumm, 1953; *Basidechenella* Richter, 1912; *Ormistoniella* Cooper, 1982; *Aayemenaytcheia* Lieberman, 1994; *Dec{henella* Kayser, 1880; *Schizoproetus* Richter, 1912; *Schizoproetoides* Ormiston, 1967
Whittington et al., 1997 (Treatise)	Divided into three superfamilies	Proetoidea: Proetideae; Phillipsidae; Aulacopleuroidea: Aulacopleuridae, Brachymetopidae, Rorringtoniidae; Bathyuroidea: Bathyuridae, Dimeropygidae, Celmidae, Lecanopgidae, Glaphuridae, Holotrachelidae, Delphinidae
Adrain, 2011	Divides order Proetidea into two orders	Proetidea: Proetideae; Tropidocoryphidae; Aulacopleurida: Aulacopleuridae, Bathyuridae, Brachymetopidae, Crepicephalidae, Dimeropygidae, Ehmaniellidae, Holotrachelidae, Hystricuridae, Marjumiidae, Rorringtoniidae, Scharyiidae, Solenopleuridae, Telephinidae, Tricrepocephalidae
Lamsdell and Selden, 2015	Order Proetidea	Proetideae, Phillipsidae, Aulacopleuridae, Bathyuridae, Brachymetopidae, Rorringtoniidae, Dimeropygidae, Tropidocoryphidae, Scharyiidae, Otarionidae, Hystricuridae

were noted: Tropidocoryphinae, Cornuproetinae, Eremiproetinae, the '*Thebanaspis*' clade, and Proetinae (Lieberman, 1994; Lieberman and Karim, 2010). The resolution of these genera within Proetinae was strictly for eastern North America and demonstrated how some genera, e.g. *Proetus*, were monophyletic in this region (Lieberman, 1994).

Characteristics and ecology. Generally, members within Proetoidea have these features: crescent-shaped holochroal eyes, opisthoparian facial sutures, a well-developed occipital ring, 8–10 thoracic segments (to 22 at most), an isopygous pygidium, and < 127 mm (5 in) in length (Fig. 2; Fortey et al., 1997; Lamsdell and Selden, 2015). Across the order, there are other prominent features (e.g., well-developed

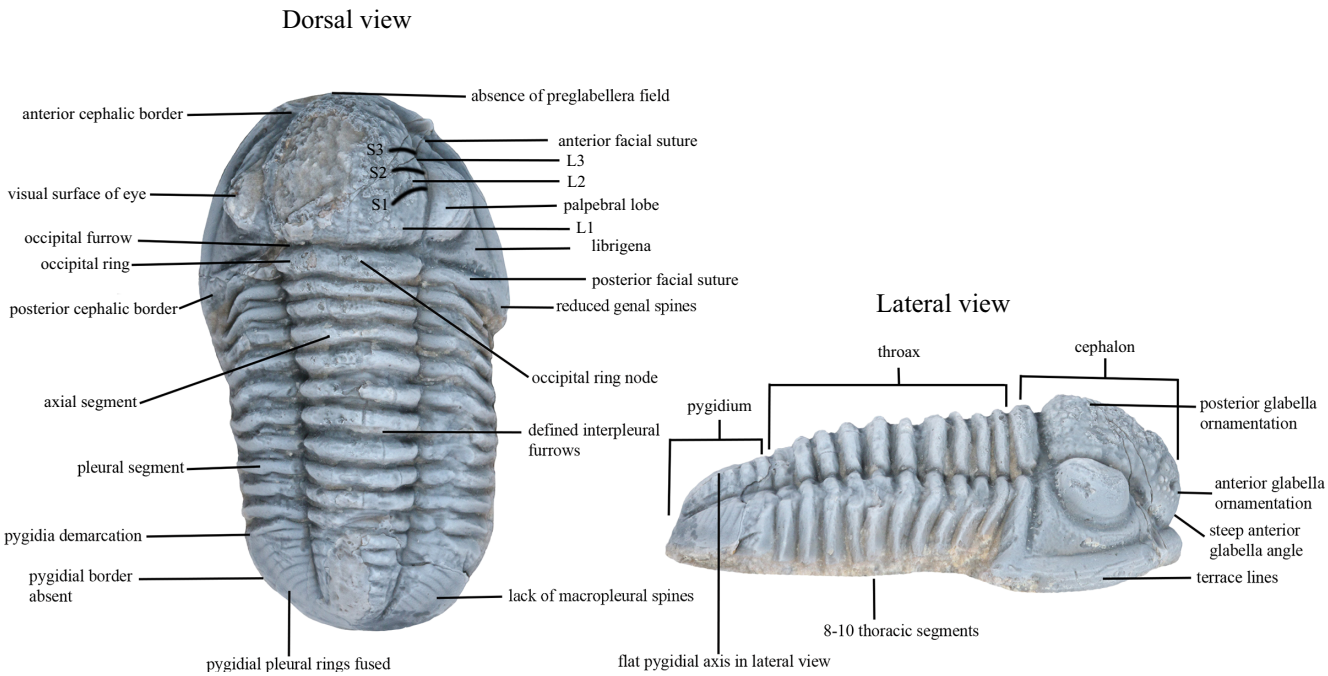


Figure 2. Morphology of the proetide exoskeleton in dorsal and lateral views.

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genal spines, presence of a small preglabellar field) although these features can vary widely across the clade and across time (early vs. late proetides). For example, early proetides (Silurian, e.g., *Decoroproetus* Přibyl, 1946) are more often rounded in dorsal view whereas later proetides (Carboniferous, e.g., *Phillipsia* Portlock, 1843) have more elongate bodies in dorsal view. This, of course, varies depending on the subclade in question.

In general, proetides are considered to have lived benthically in shallow water and potential reef environments (Fortey and Owens, 1975). Early proetides (Ordovician) are associated with midshelf carbonate environments and, throughout their history, proetides typically spread out across the continental shelf into both deeper and shallower waters (Fortey et al., 1997). Some proetides that transitioned to deeper parts of the continental shelf in the Devonian showed reduced eye size or became completely blind (Clarkson, 1967; Fortey and Owens, 1975).

Most early proetides (Cambrian–Ordovician) exhibited natant hypostomes (feeding structures not attached to the ventral side of the cephalon (doublure) and can be supported by a nonfossilized membrane), associated with particle feeding. In this case, soft tissue (labrum) would support the hypostome (hard mouthpart), which would lie under the beginning of the trilobite digestive system (see El Albani et al., 2024). It is thought that some proetides shifted to coterminant and/or impendent (hypostome firmly attached to the ventral side of the cephalon by a suture and not by soft tissue) later from the Devonian to the Permian (Fortey and Owens, 1999). This modification in hypostome morphology, specifically in the 'bracing' of the feeding structure, or the expansion of the glabella and preglabellar field (Fortey and Owens, 1999; Fortey, 2014) have been thought to demonstrate the shift in feeding ecology of proetides. Many late Paleozoic proetides developed an impendent hypostome often associated with predation, and this change has been hypothesized to show that proetides began occupying vacated trilobite niche space following the end-Devonian extinction events (Fortey and Owens, 1999). Proetides are thought to display multiple meraspid (juvenile) stages and differing developmental ontogenies (Speyer and Chatterton, 1990). For the purposes of this study, the ontogenetic development of proetides was not taken into consideration; only adult specimens were taken into account for morphological coding.

Materials and methods

Data acquisition. Specimens used in this study were documented through museum specimens and literature. A complete list of sources is found in Appendix 3.

Taxon sampling and data collection. This study encompasses proetides from the mid-Silurian (Wenlock, 433–427 Ma) to the early Carboniferous (Tournaisian, 358.9–346.7 Ma). Although this does not document the entirety of proetide history, I was more interested in examining proetide phylogenetics following the Devonian mass extinction and in the recovery interval during the early Carboniferous. I used 109 characters, a mixture of binary and multistate, to morphologically code 129 proetides from a global distribution.

In this study, there are more taxa than characters. This is primarily due to the fact that: (1) proetides are considered to have low morphological disparity (Hopkins et al., 2023); (2) proetides are implied to have few novelties over their clade's history (Lieberman and Karim, 2010); and (3) the dataset for this analysis was large. In approaching this study, another factor was considered: trilobites, in comparison to other groups, demonstrate high character exhaustion (Wagner, 2000). However, all of this does not imply that there are not enough characters to distinguish proetides from one another in a phylogenetic framework. To ensure reliable development of a phylogenetic hypothesis, the only characters that were used were clearly visible on specimens. If a character was not clearly visible, it was coded as '?'. This ensured as little 'coder-bias' as possible. Secondly, the combination of characters, not just the characters by themselves, was taken into consideration. This follows the principle that all character states are independent from one another (Sereno, 2007). Because there are infinitely more combinations of 109 characters (and far more character states) than 129 taxa that are allowed to evolve independently across the trees, there exists some degree of certainty in the hypotheses being produced. Lastly, the use of a Bayesian phylogenetic framework (see Phylogenetic analysis, below) allowed this study to produce a reliable phylogenetic hypothesis. Previous studies have demonstrated how analyses can proceed with fewer characters than taxa because additional data (e.g., temporal information) can also be included in a Bayesian analysis (Coiro et al., 2023). Therefore, the ratio of characters to taxa, although not typical, is acceptable because of character state independence and the nature of incorporating data into a Bayesian analysis.

Characters were mainly repurposed from Lieberman (1994) and Lamsdell and Selden (2015) (Appendix 1) whereas some characters were constructed to accommodate a higher taxonomic level (see those under 'Jordan-Burmeister (2025),' Appendix 1). All characters were for adult specimens; juvenile and instar characters were excluded from this study. The outgroup taxa were *Paraproetus brevifrons* Angelin, 1854 (Ordovidian proetide within family Proetideae), *Ogmocnemis irregularis* Kielan, 1960 (another Ordovician proetide within family Proetideae), and *Ascetopeltis barkingensis* Owens, 1973 (Ordovician proetide within family Tropidocoryphidae).

There are hundreds of proetides within order Proetida and superfamily Proetoidea. To ensure that the best representatives of global proetides were coded, I sampled the Paleobiology Database (PBDB, 2025) and noted the largest genera (>10 species within the genus) per each time stage of the late Silurian to the Middle Devonian. Well-known and more-globally cosmopolitan genera with more than ten species were initially coded (e.g., *Gerastos*, *Proetus*, *Basidechenella*). At least three species for these large (> 10 species) genera were coded. Following this, I coded species from smaller, more regional genera (< 10 species per genus or recorded from only one geographic basin, e.g., *Hollandiella lebruni* van Viersen and Larouge, 2020) to ensure that potential variations of proetides were represented. Taxa from modern-day North America, Europe, China, and Australia were coded and these locations were cross referenced in the literature to determine their approximate biogeographic region during the Devonian Period (Dowding and Ebach, 2018; Penn-Clarke and Harper, 2023). This served mainly for interpretation purposes and out of data exploration.

Taxon ages. Bayesian phylogenetic analyses (see below) incorporated the FBD (fossilized birth-death) tree, which required upper and lower bounds of first appearances of the analyzed taxa. These were based on the Paleobiology Database (PBDB, 2025) and were drawn from 513 occurrences from 376 localities representing 191 distinct rock units (formations and members) and assignments based on 354 taxonomic opinions. In support of this study, 134 localities and 226 occurrences were entered along with 324 taxonomic opinion records. An additional 75 localities and 47 occurrences were edited while vetting the data. I refined the ages of

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occurrences using an external database that redated collections based on conodont, graptolite, and ammonoid zonations for localities or relevant rock units (see Congreve et al., 2021). These dates reflect those given by Gradstein et al. (2020). This generated much more restricted ages for individual localities than the PBDB provides, and thus much more restricted lower and upper bounds on the ages of the first appearances than otherwise would be available from the PBDB.

Phylogenetic analysis. To examine the evolutionary dynamics within proetides across the Devonian and into the early Carboniferous, a Bayesian phylogenetic analysis was conducted in BEAST2 (v2.6.7) (Bouchaert et al., 2019). Although there are many options for performing phylogenetic analyses, a Bayesian analysis provides some unique features when building trees that include but are not limited to: (1) Bayesian analyses can outperform parsimony when discrete morphological data is used (Wright and Hills, 2014); (2) Bayesian analyses can incorporate multiple sources of evidence as priors, which includes stratigraphic ages of fossil taxa (Barido-Sottani et al., 2020); and (3) Bayesian models, e.g., the fossilized birth-death (FBD) process, can be incorporated for joint description of diversification and sampling across fossil lineages (Stadler, 2010; Heath et al., 2014) (see FBD description, below). Files for BEAST2 (.xml) were built using Beauti (v2.6.7) (Bouchaert et al., 2019). Character data were separated into four partitions (five, four, three, and two states), with separate Mk character substitution models (M2, M3, etc.) used for each (see Lewis, 2001). Note that the different Mk models assume the same rate of change rather than the same rates of state transition for each partition (see Wright et al., 2021). Among-character variation was modeled using a gamma distribution. The relevant scripts and commands are included as supplementary material to this paper.

Two separate analyses were run using two different clock models: a strict clock, in which rates are consistent over time, and an uncorrelated relaxed clock, in which rates vary among branches following a lognormal distribution (e.g., Drummond et al., 2006). These two clock models were compared to one another for this study (and are hereafter referred to as 'the clock models').

Prior probabilities for particular trees were generated using the FBD process (e.g., Heath et al., 2014). The FBD model has been used in previous studies employing Bayesian methods and provides prior probabilities for individual phylogenies given implicit divergence times (Stadler, 2010; Heath et al., 2014). The use of the FBD model in a Bayesian analysis for extinct clades with fossil taxa has also been demonstrated (Wright, 2017; Mulvey et al., 2025). The FBD model is a birth-death-sampling model that derives prior probabilities on particular phylogenetic topologies given rates of cladogenesis, extinction, and fossil recovery (sampling) (Heath et al., 2014). In the case of this study, starting values were set as follows: an origin time was set to a rescaled value of 130.0 Ma, diversification was set to 1.0, turnover was set to 0.5, sampling proportion was set to 0.5, and rho sampling was set to 0.0 (because rho is based on sampling in the modern and trilobites are completely extinct). The origin time was rescaled using the oldest trilobites in the analysis—*Paraproetus brevifrons* and *Ogmocnemis irregularis*, ~460 Ma—and the youngest in the analysis—*Eocyphinium seminiferum* (Phillips, 1836), ~340 Ma. The difference in ages between the oldest and youngest trilobites was ~115–120 Ma. Therefore, 115 Ma was used as the minimum origin time whereas I set the maximum origin time to 130 Ma to account for any margin of error. All rates were allowed to vary depending on the tree model. In the strict-clock model, these evolutionary processes varied equally across branches with one another. For the relaxed-clock model, however, these evolutionary processes were allowed to vary differently across the branches.

Origination rates were sampled from a gamma distribution, with the mean set using an exponential distribution and standard deviation set using another gamma distribution. Because extinction rates are not independent of origination rates, a turnover parameter following a log-normal distribution was used to establish extinction rates given the origination rate. Clade origin and sampling rates also were sampled from log-normal distributions. The total chain length for both clock models was set to 100,000,000 within a preburn-in of 1,000. Each clock model was run once and all parameters of each model reached convergence. A total of 10,000 trees was obtained for each clock model. Following this, maximum clade credibility trees for each clock model were built using the BEAST2 extension TreeAnnotator (v.2.6.7) (Bouchaert et al., 2019) (burn-in 30%, probabilities > 50% kept, mean height used). Additional model testing included running a stepping-stone-like test: nested sampling via the Nested Sampling Log Analyzer in the BEAST2 AppLauncher. From this, marginal likelihoods and standard deviations for each model could be obtained, which were in turn used to calculate a Bayes Factor (Table 2).

Repositories and institutional abbreviations. Types, figured, and other specimens examined in this study are deposited in the following institutions: American Museum of Natural History (AMNH), New York, USA; Field Museum of Natural History (FMNH), Chicago; and The Natural History Museum (NHM), London, UK.

Results

Overall, the posterior probabilities for the relaxed-clock trees were higher than those of the strict-clock trees (Table 2). This indicates that the observed data provide strong evidence to support this model and its hypothesis (evolutionary rates vary across branches) for proetide trilobites. Following the phylogenetic analysis detailed above, two maximum credibility trees for a relaxed-clock model and a strict-clock model were obtained. Although the relaxed clock

Table 2. Posterior probability and likelihood values of the relaxed-clock and strict-clock models. The posterior probability values indicate the probability of each model given the data and prior parameters. Likelihood values indicate the probability of the data given the parameters input initially. Both values are calculated from the output of BEAST2. Marginal likelihoods were calculated using the Nested Sampling Log Analyzer (NS) in BEAST2. Standard deviations (SD) are also included. Marginal likelihoods were used to calculate the Bayes Factor (Model A/Model B or relaxed-clock model/strict-clock model). The Bayes Factor of 1.51 indicates positive support for the relaxed-clock model per Kass and Raftery (1995)

Clock Model	Posterior probability value	Likelihood value	Marginal Likelihoods (via Nested Sampling)
Relaxed	−5518.410	−4565.635	−8075.94 (SD = 0.034)
Strict	−5756.207	−4650.830	−5351.51 (SD = 22.45)
Bayes Factor (relaxed clock)/ (strict clock marginal likelihoods)	-	-	1.51

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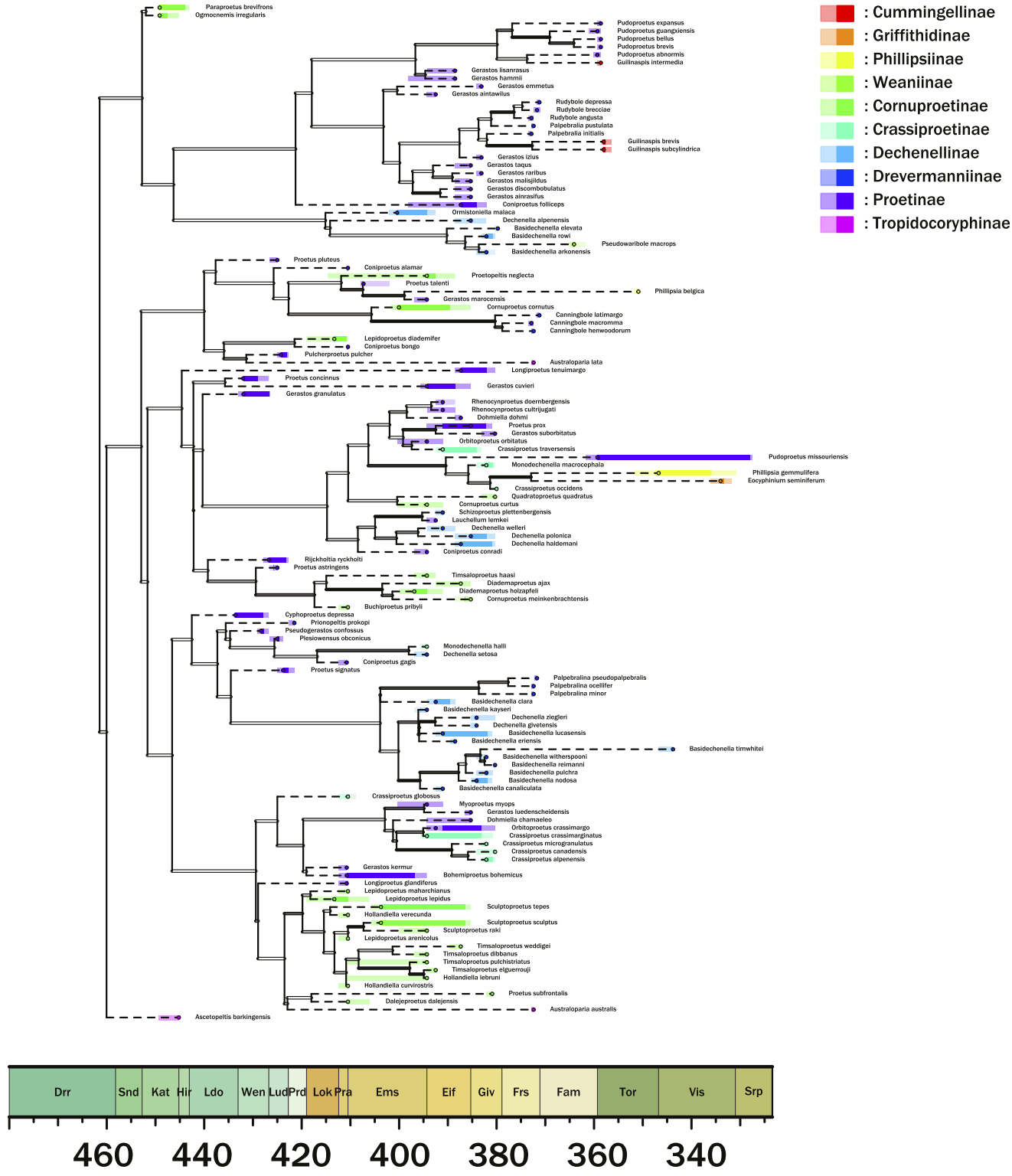


Figure 3. Relaxed-clock maximum clade credibility tree. Colors along branches represent historical subfamilies as seen in the figure key. Thicker, more solid lines indicate higher probability support (> 0.5) of branches; nonsolid lines represent lower probability support (< 0.5). Dashed lines represent the approximate age of each tip species in relation its nearest branching event. Species not otherwise mentioned in the text are: *Australoparia australis* (Feist and McNamara, 2013); *Australoparia lata* (Feist and McNamara, 2013); *Basidechenella canaliculata* (Hall, 1861); *Basidechenella elevata* (Cooper and Cloud, 1938); *Basidechenella eriensis* (Stumm, 1953); *Basidechenella kayseri* (Richter, 1909); *Basidechenella lucasensis* (Stumm, 1965); *Basidechenella nodosa* (Stumm, 1953); *Basidechenella pulchra* (Stumm, 1965); *Basidechenella reimanni* (Stumm, 1953); *Basidechenella timwhitei* Lieberman, 1994; *Basidechenella witherspooni* (Stumm, 1968); *Buchiproetus pribyli* (Alberti, 1969); *Canningbole henwoodorum* Feist and McNamara, 2013; *Canningbole latimargo* Feist and McNamara, 2013; *Canningbole macromma* Feist and McNamara, 2013; *Coniproetus alamar* Šnajdr, 1980; *Coniproetus bongo* Šnajdr, 1980; *Coniproetus conradi* (Hall, 1861); *Coniproetus folliceps* (Hall and Clarke, 1888); *Coniproetus gagis* (Šnajdr, 1980); *Cornuproetus cornutus* (Goldfuss, 1843); *Cornuproetus curtus* (Barrande, 1852); *Crassiproetus alpenensis* (Stumm, 1953); *Crassiproetus canadensis* (Stumm, 1953); *Crassiproetus crassimarginatus* Hall, 1843; *Crassiproetus globosus* (Maxomova, 1960); *Crassiproetus microgranulatus* (Stumm, 1953); *Crassiproetus occidens* (Hall, 1861); *Crassiproetus traversensis* (Stumm, 1953); *Cyphoproetus depressa* (Barrande, 1846);

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is the more likely model, I will discuss both phylogenetic hypotheses because both tree models demonstrate similar 'clade groupings,' which highlights the prevalence of these 'clade groupings' across both models and tree space. The results of both clock models (maximum clade credibility trees) can be seen in Table 2, Figures 3 and 4, and Appendix 2. Subfamilies are color-coded for interpretation in Figures 2 and 3.

Many pre-established clades from previous studies have high posterior probabilities (e.g., the *Pudoproetus* Hessler, 1963 branch, p.p. 0.8277). These clades are often more 'regional,' having been coded from samples in the same location (e.g., the Canning Basin, Australia) and around the same time (Late Devonian) (see Appendices 4a, b). Additionally, clades from potentially related bioregions in the Late Devonian, e.g., those from Australia and China, were more likely to be more closely related (Appendix 2). However, other clades, including pre-established ones, e.g., the *Pudoproetus* and *Palpebalina* Feist and McNamara, 2013 clades from the Late Devonian Canning Basin (Australia), were found to not be closely related, perhaps demonstrating that different lineages of proetides coexisted at least for a little while.

The maximum clade credibility tree makes subfamily dynamics apparent. The subfamily Proetinae holds much of the diversity throughout the Devonian globally (Fig. 4). This shifts slightly at the Devonian-Carboniferous boundary where, with the rise of Phillipsidae, much of the diversity is represented in Phillipsidae and holdover Proetinae members (e.g., *Basidechenella*). Polyphyly is present across both trees. This is most apparent within the genus *Gerastos* in which species fall out in different clades. Other large and 'classic' genera also display this pattern, including *Basidechenella*, *Proetus*, and *Phillipsia*.

The strict-clock results (Fig. 3) vary from the relaxed-clock results in some key ways. Firstly, the origin of the clade is different in the two clock models: the relaxed-clock model has a root much later (Darriwilian, Ordovician, 467–458 Ma) than the strict-clock model (Tremadocian, Ordovician, 485–477 Ma) (Figs. 3, 4). Consequently, this means that internal node ages are also later in the relaxed-clock model; many internal nodes for the relaxed-clock tree are in the Late Ordovician whereas internal nodes in the strict-clock tree sit in the Middle Ordovician (Figs. 3, 4). Secondly, the relatedness of many groups, e.g., the Ordovician outgroups *Paraproetus brevifrons* and *Ogmocnemis irregularis*, is now more distant and these taxa are not considered close sister taxa (Fig. 4). Thirdly, and in general, the posterior probabilities of the internal branches are larger for the relaxed-clock model than the strict-clock model. Lastly, the resolution of clades is very different: the relaxed-clock model produced larger clades with high probabilities (> 0.2) whereas the strict-clock model produced many smaller clades with high probabilities (> 0.2), often composed of two or three species (Appendix 3). Overall, the relationships among clades was relatively different from the relaxed-clock model, providing a very different tree topology. The strict-clock model, like the relaxed-clock, placed three main subclades close to one another in the tree topology: the '*Rudybole*' clade, a '*Gerastos*' clade, and a '*Pudoproetus*' clade, and separated the genus *Gerastos* across the tree (Appendix 3). The strict-clock model broke up major clades, e.g., the division of *Basidechenella* into three notable clades (Appendix 3). Additionally, the strict-clock model divided groups long considered to be related—e.g., *Timsaloproetus* Gibb and Chatterton, 2007; *Diademaproetus* Alberti, 1964; and *Cornuproetus* Richter and Richter, 1919—whereas the relaxed-clock model did not.

Discussion

Phylogenetic status of traditional taxonomic units. Traditional taxonomic units and phylogenetic studies are important building blocks for studies such as this one. This is partially due to the finer scale and detail (e.g., regional taxa, well-documented, multiple specimen representatives) on which previous studies built these taxonomies. When Devonian proetides were incorporated into a phylogeny with more global representation, some pre-established clades were maintained while others were fractured. Both the relaxed-clock and the strict-clock tree models highlighted polyphyletic relationships in some clades, e.g., the Phillipsidae, or within large genera, e.g., *Gerastos* (Fig. 5). The Phillipsidae clade, which is an important maintainer of proetide diversity for the remainder of the Paleozoic, fell along multiple branches and seemed to indicate the persistence of a 'phillipsid morphology' more than a phillipsid taxonomic unit (see Clade relationships and ecology, below). Evolutionarily, this could indicate that proetides that persisted through the end-Devonian might not have been closely related but could have shared some key morphological features. One prominent subfamily, Proetinae (which has classically encompassed the genera *Gerastos* and *Proetus*), is paraphyletic. Species within *Gerastos* and

Figure 3. (Continued)
Dalejeproetus dalejensis (Přibyl, 1971); *Dechenella haldemani* (Hall, 1861); *Dechenella polonica* Gürich, 1896; *Dechenella setosa* Whidborne, 1889; *Dechenella welleri* (Stauffer, 1909); *Diademaproetus ajax* Basse, 1997; *Diademaproetus holzapfeli* (Novák, 1890); *Dohmiella chamaeleo* (Richter and Richter, 1918); *Dohmiella dohmi* (Richter and Richter, 1918); *Gerastos ainrasifus* Gibb and Chatterton, 2010; *Gerastos aintawilus* Gibb and Chatterton, 2010; *Gerastos cuvieri* (Steininger, 1831); *Gerastos discombobulatus* Gibb and Chatterton, 2010; *Gerastos emmetus* Gibb and Chatterton, 2010; *Gerastos granulatus* (Lindström, 1885); *Gerastos hammii* Gibb and Chatterton, 2010; *Gerastos izius* Gibb and Chatterton, 2010; *Gerastos luedenscheidensis* (Basse, 1996); *Gerastos lisanrasus* Gibb and Chatterton, 2010; *Gerastos malisjildus* Gibb and Chatterton, 2010; *Gerastos marocensis* (Chatterton et al., 2006); *Gerastos raribus* Gibb and Chatterton, 2010; *Gerastos suborbitatus* (Holzapfel, 1895); *Gerastos taqus* Gibb and Chatterton, 2010; *Guilinaspis intermedia* Yuan and Xiang, 1998; *Hollandiella curvirostris* van Viersen and Larouge, 2020; *Hollandiella verecunda* van Viersen and Larouge, 2020; *Lauchellum lemkei* (Basse, 1997); *Lepidoproetus arenicolus* van Viersen and Larouge, 2020; *Lepidoproetus diademifer* (Chlupac and Vanek, 1965); *Lepidoproetus lepidus* (Barrande, 1846); *Lepidoproetus maharchianus* Johnson and Fortey, 2012; *Longiproetus glandiferus* (Novák, 1890); *Longiproetus tenuimargo* (Richter, 1909); *Monodechenella halli* (Stumm, 1953); *Monodechenella macrocephala* (Hall, 1861); *Myoproetus myops* (Barrande, 1846); *Orbitoproetus crassimargo* (Roemer, 1850); *Orbitoproetus orbitatus* (Barrande, 1846); *Ormistoniella malaca* (Lake, 1904); *Palpebralia initialis* Feist and McNamara, 2013; *Palpebralia pustulata* Feist and McNamara, 2013; *Palpebralina minor* Feist and McNamara, 2013; *Palpebralina ocellifer* Feist and McNamara, 2013; *Palpebralina pseudopalpebralis* Feist and McNamara, 2013; *Plesiowensus obconicus* (Lindström, 1885); *Prionopeltis prokopi* Šnajdr, 1976; *Proetopeltis neglecta* (Barrande, 1852); *Proetus astringens* Owens, 1973; *Proetus concinnus* (Dalman, 1827); *Proetus pluteus* Whittington and Campbell, 1967; *Proetus prox* (Richter and Richter, 1956); *Proetus signatus* Lindström, 1885; *Proetus subfrontalis* Whidborne, 1889; *Proetus talenti* (Chatterton, 1971); *Pseudogerastos confossus* (Owens, 1973); *Pudoproteus abnormis* Yuan and Xiang, 1998; *Pudoproteus bellus* (Yuan and Xiang, 1998); *Pudoproteus brevis* Yuan and Xiang, 1998; *Pudoproetus expansus* Yuan and Xiang, 1998; *Pudoproetus guangxiensis* (Zhai Ling, 1988); *Pudoproetus missouriensis* (Shumard, 1855); *Pulcherproetus pulcher* (Nieszkowski, 1857); *Quadratoproetus quadratus* (Maurer, 1885); *Rhenocynproetus cultrijugati* (Richter and Richter, 1918); *Rhenocynproetus doernbergensis* (Basse, 1996); *Rijckholtia ryckholti* (Barrande, 1846); *Rudybole angusta* Feist and McNamara, 2013; *Rudybole brecciae* (Richter, 1913); *Rudybole depressa* Feist and McNamara, 2013; *Schizoproetus plettenbergensis* Basse, 1997; *Sculptoproetus raki* van Viersen and Larouge, 2020; *Sculptoproetus sculptus* (Barrande, 1846); *Sculptoproetus tepes* Šnajdr, 1980; *Timsaloproetus dibbanus* Gibb and Chatterton, 2007; *Timsaloproetus elguerrouji* Gibb and Chatterton, 2007; *Timsaloproetus pulchristriatus* van Viersen and Larouge, 2020; *Timsaloproetus weddigei* van Viersen and Larouge, 2020.

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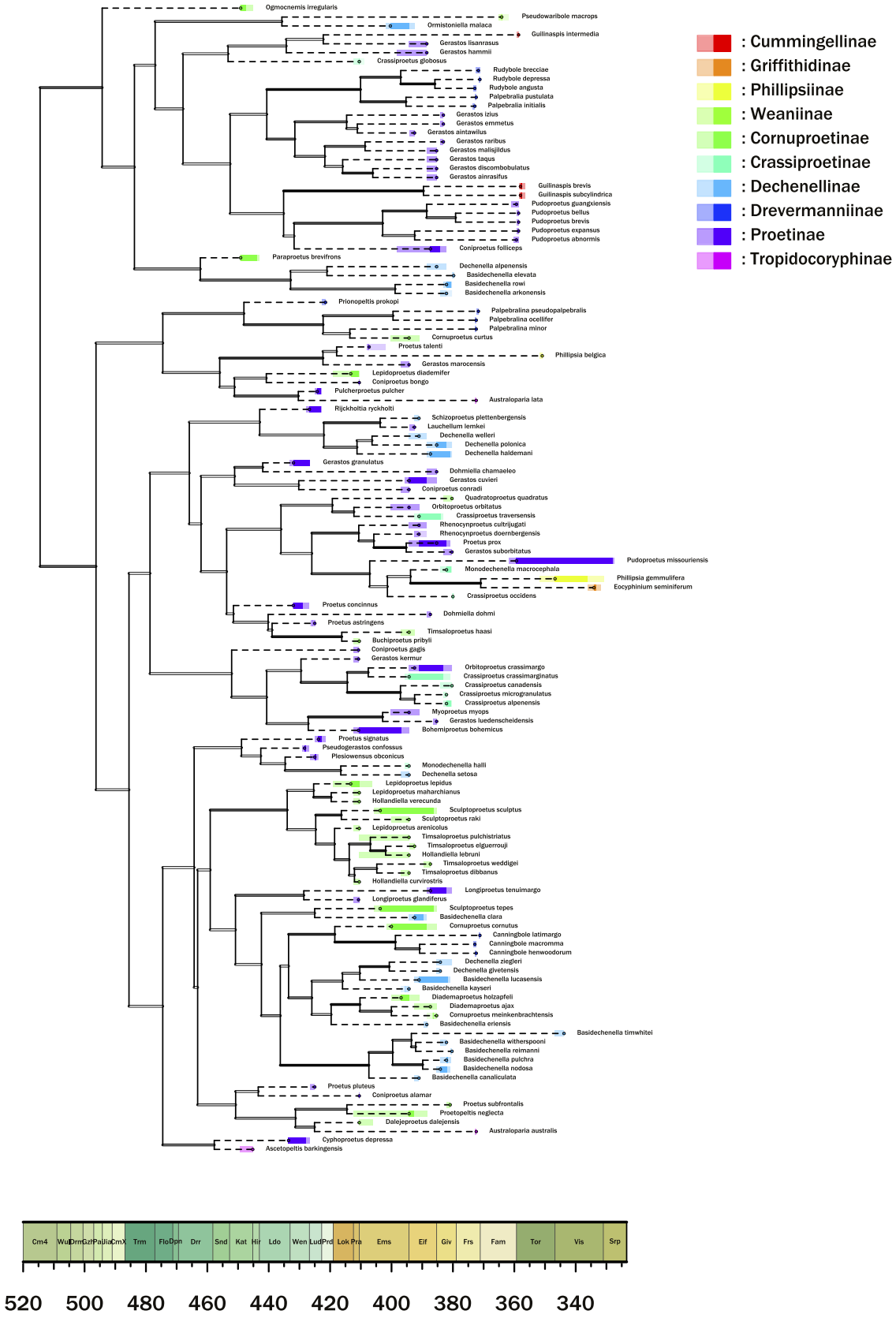
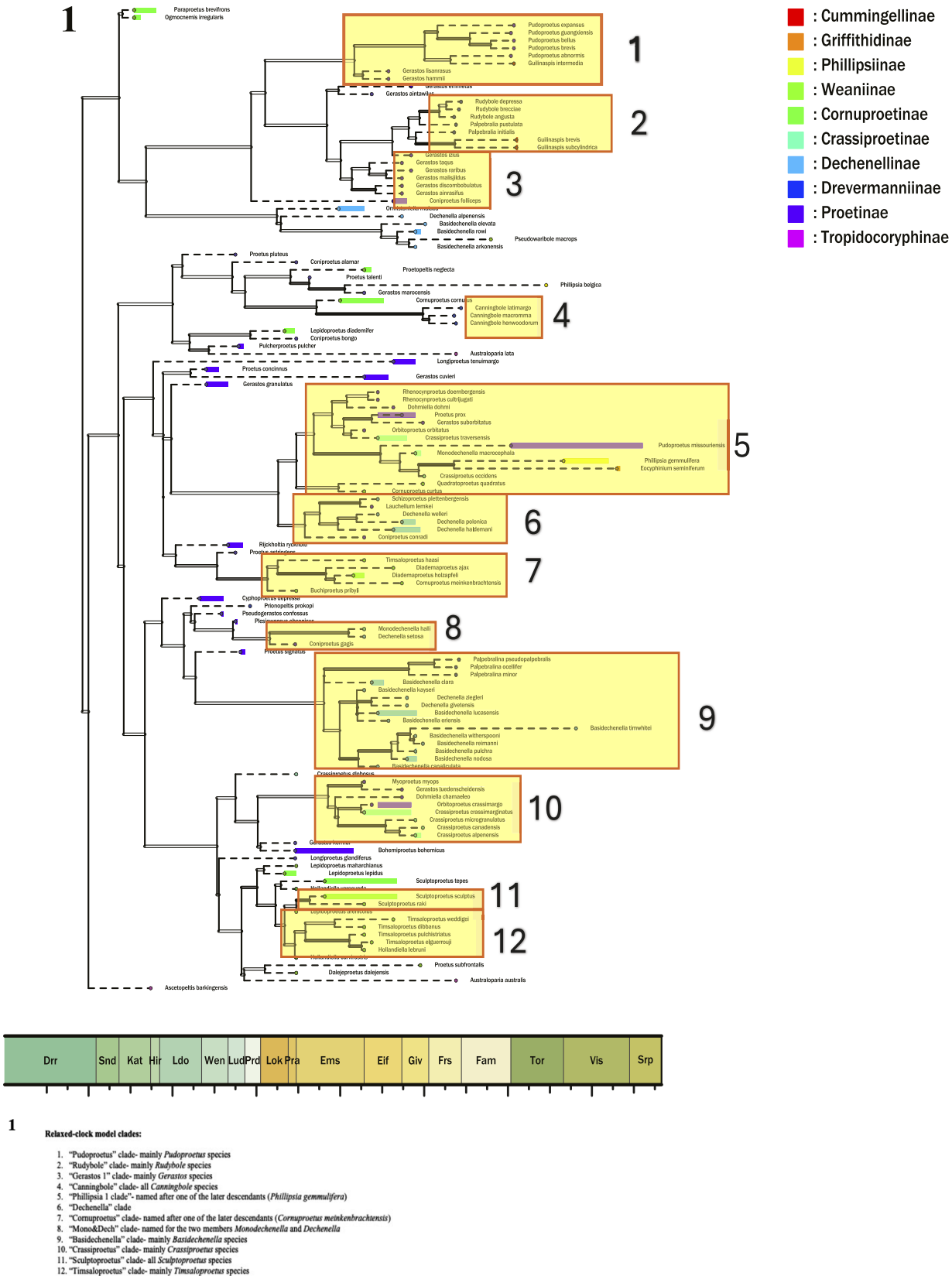


Figure 4. Strict-clock maximum clade credibility tree. Colors along branches represent historical subfamilies as seen in figure key. Thicker, more solid lines indicate higher probability support (> 0.5) of branches; thin or nonsolid lines represent lower probability support (< 0.5). Dashed lines represent the approximate age of each tip species in relation its nearest branching event. For species not otherwise mentioned in the text, see Figure 3.

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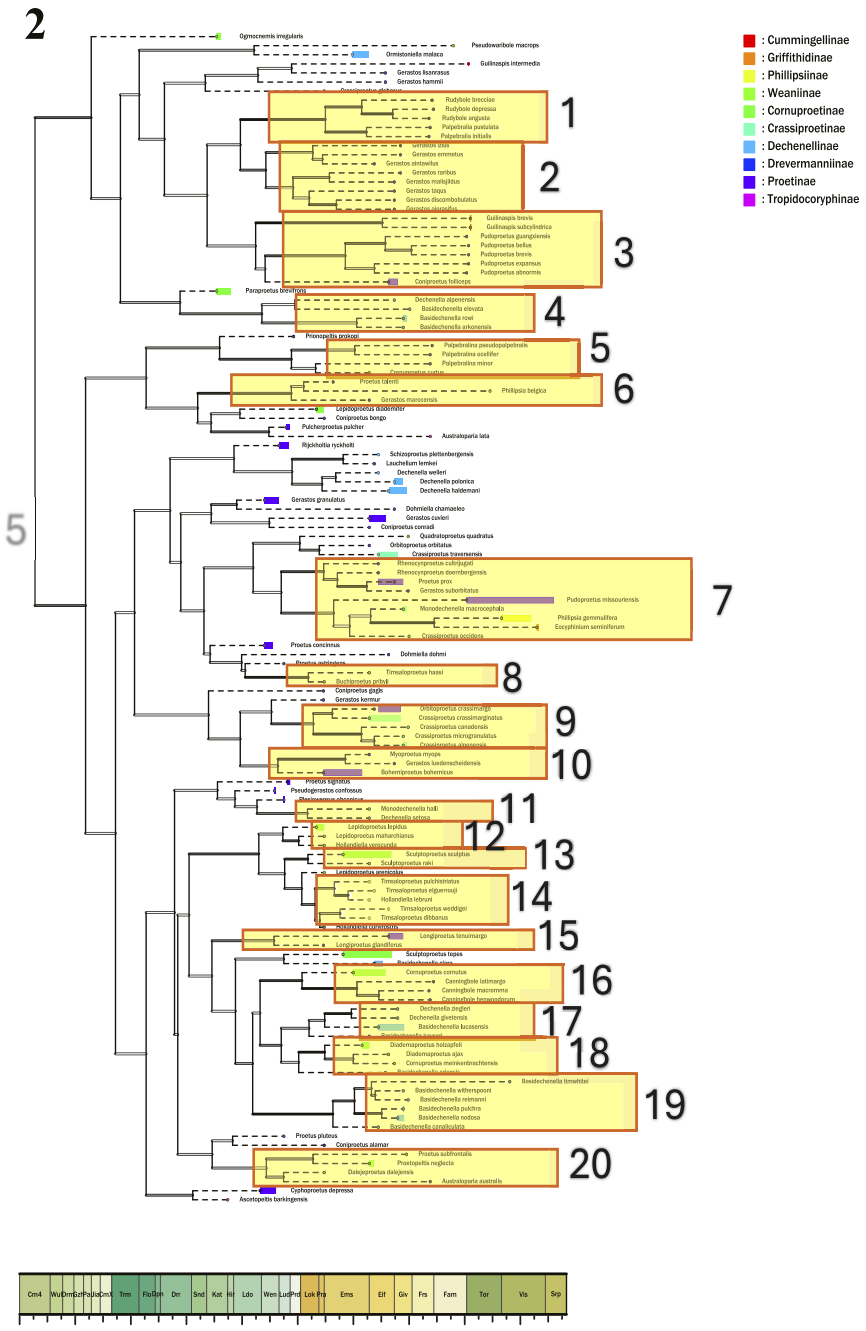
1

Relaxed-clock model clades:

1. "Pudoproetus" clade- mainly *Pudoproetus* species
2. "Rudybole" clade- mainly *Rudybole* species
3. "Gerastos 1" clade- mainly *Gerastos* species
4. "Canningbole" clade- all *Canningbole* species
5. "Phillipsia 1 clade"- named after one of the later descendants (*Phillipsia gemmulifera*)
6. "Dechenella" clade
7. "Cornuproetus" clade- named after one of the later descendants (*Cornuproetus meinkenbrachtensis*)
8. "Mono&Dech" clade- named for the two members *Monodechenella* and *Dechenella*
9. "Basidechenella" clade- mainly *Basidechenella* species
10. "Crassiproetus" clade- mainly *Crassiproetus* species
11. "Sculptoproetus" clade- all *Sculptoproetus* species
12. "Timsaloproetus" clade- mainly *Timsaloproetus* species

Figure 5. Clades shared across both tree hypotheses. (**1**) Relaxed-clock groups and (**2**) strict clock groups as identified and labelled for this study. Subclades were determined by the strength of the posterior probabilities (at least 0.4) of an internal node. Subclades were numbered and given a label (below) to help in visualizing the trees. Many subclades translate across both tree hypotheses and correspond to historical groupings. Subclades are more finely split for strict clock model (**2**). For species not otherwise mentioned in the text, see Figure 3.

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2 **Strict-clock model clades:**

1. "Rudybole" clade- mainly *Rudybole* species
2. "Gerastos 1" clade- mainly *Gerastos* species
3. "Pudoproetus" clade- mainly *Pudoproetus* species
4. "Basidechenella 1" clade- mainly *Basidechenella* species
5. "Palprebalina" clade- mainly *Palprebalina* species
6. "Phillipsia 1 clade"- named after one of the later descendants (*Phillipsia belgica*)
7. "Phillipsia 2 clade"- named after one of the later descendants (*Phillipsia gemmulifera*)
8. "Tim&Buch" clade- composed of *Timsaloproetus haasi* and *Buchiproetus pribyli*
9. "Crassiproetus" clade- mainly *Crassiproetus* species
10. "Gerastos II" clade- named after one of the later descendants (*Gerastos luedenscheidensis*)
11. "Mono&Dech" clade- named for the two members *Monodechenella* and *Dechenella*
12. "Lepidoproetus" clade- mainly *Lepidoproetus* species
13. "Sculptoproetus" clade- all *Sculptoproetus* species
14. "Timsaloproetus" clade- mainly *Timsaloproetus* species
15. "Longiproetus" clade- mainly *Longiproetus* species
16. "Canningbole" clade- all *Canningbole* species
17. "Basidechenella 2" clade- mainly *Basidechenella* species
18. "Diademaproetus" clade- mainly *Diademaproetus* species
19. "Basidechenella 3" clade- mainly *Basidechenella* species
20. "Australoparia" clade- named after one of the later descendants (*Australoparia australis*)

Figure 5. (Continued).

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Basidechenlla were scattered across both clock-model trees with varying degrees of posterior probabilities. Large clades exist that include or are sister to the outgroups *Ogmocnemis irregularis* and *Paraproetus brevifrons*, but with no sampled Silurian members. This could be because I included few Silurian members (in keeping within a strict Devonian time constraint) or because parallelisms between that clade and those two Ordovician species distorted the tree.

Other major subfamilies, e.g., Cornuproetinae and Dechenellinae, are also polyphyletic, but there are large clades composed mostly or entirely of species assigned to those subfamilies. Overall, survivorship of the major clades in the Devonian (i.e., those clades that have members into the Carboniferous) is polyphyletic, but both trees suggest some concentration of survivors in particular subclades. For example, '*Phillipsia* 1 Clade' (labelled 5 in Fig. 4a) have members that persist past the end-Devonian that do not belong in the same genus (e.g., *Phillipsia*; *Eocyphinium* Reed, 1942; and *Pudoproetus*).

Clade relationships and ecology. The way in which major, well-studied genera, e.g., *Gerastos* or *Basidechenella*, were resolved is one of the more significant results. The genus *Gerastos* has undergone much revision since its conception (Šnajdr, 1980; Lutke, 1980, 1990; Ellermann, 1992; Lieberman, 1994). *Gerastos* has been considered a monophyletic sister group to the genus *Proetus* in the past (Šnajdr, 1980; Kobayashi, 1985; Ellermann, 1992; Lieberman, 1994). Others, e.g., Lutke (1990), have considered *Gerastos* to be broken in two subgenera: one of which, *Devonoproetus* Lutke, 1990, gave rise to *Dohmiella* Lutke, 1990 and potentially *Longiproteus* Cavet and Pillet, 1958, and the other subgenus giving rise to other members, e.g., *Coniproetus* Alberti, 1966 and *Bohemiproetus* Pillet, 1969 (Lutke, 1990; van Viseran and Lerouge, 2021).

The relaxed-clock maximum clade-credibility tree result shows *Gerastos* spp. appearing in at least five different proetide subclades, typically with good support values. One species, *Gerastos kermur* Šnajdr, 1980, appeared closely related to *Bohemiproetus bohemicus* (Hawle and Corda, 1847), giving at least some credence to the Lutke (1990) theory of *Gerastos*' division into subgenera. Conversely, *Gerastos* spp. do not appear to be very closely related to *Dohimella* or *Longiproetus* spp., although there are very few representatives in this study. Results from this study indicate that *Gerastos* most likely constitutes multiple subgenera and/or is a large group linked by homoplasies. Other large proetide genera, e.g., *Phillipsia* or *Basidechenella*, also demonstrated this pattern (i.e., appearing multiple times on the tree, not closely related). Notably, *Basidechenella rowi* (Green, 1838) and *Basidechenella arkonensis* (Stumm, 1953) appeared more closely related to certain species, e.g., *Dechenella alpenensis* (Stumm, 1953) and *Pseudowaribole macrops* Yuan, 1988, whereas other *Basidechenella* spp. plotted distantly away from this subclade. All species (*Basidechenella rowi*, *Basidechenella arkonesis*, *Dechenella alpenesis*, and *Pseudowaribole macrops*) share distinct morphological features, e.g., long genal spines, a glabella indentation near S2, and large eyes. The other *Basidechenella* spp. correspond with other *Dechenella* spp. (e.g., *Dechenella ziegleri* Struve, 1992 and *Dechenella givetensis* Bignon and Crônier, 2011). These taxa, although having similar morphologies to the other *Basidechenella* spp. from which they are separated, seem to present a unique feature: heavy granulation on the cephalon. Although this is not universal, this might be partially responsible for both clock models parsing *Basidechenella* into two subclades. The character:taxa ratio might also have contributed to this. Adding more characters, especially instar characters, could alter this in the future.

Two species of *Phillipsia* were described as not closely related in the relaxed-clock and strict-clock models. These species, *Phillipsia belgica* (Osmólska, 1970) and *Phillipsia gemmulifera* (Phillips, 1836), often showed up in discourse together and have been considered related (Osmólska, 1970). In both clock models, the posterior probability of these taxa belonging with another sister group was at least 0.4.

Given the collection location (i.e., UK) and occurrence time (i.e., early Carboniferous) of *Phillipsia gemmulifera* and its sister *Eocyphinium seminiferum*, this relationship seems to be likely. All species—*Phillipsia gemmulifera*, its sister *Eocyphinium seminiferum, Phillipsia belgica*, and its sister *Gerastos tuberculatus marocensis* (Chatterton et al., 2006)—are all epifaunal deposit feeders so little can be determined from looking at environmental data. Lastly, it is hard not to notice morphological similarities between the *Phillipsia* spp. and their sister taxa. When looking at the *Phillipsia* spp. (Fig. 4a, b) with their respective sisters, the narrowness of the anterior glabella or its inflation seems to carry over as does eye size (small or large, respectively). This gives credence to the idea of a '*Phillipsia*-type morphology' persisting rather than the taxonomic unit. Additionally, if phillipsids are indeed divided, then there could be two '*Phillipsia*' clades: *Phillipsia* A (including *Phillipsia belgica*) with an earlier divergence time and *Phillipsia* B (including *Phillipsia gemmulifera*), which might have persisted slightly longer into the Carboniferous (Figs. 3, 4). This pattern, of morphological disparity and taxonomic disparity being decoupled and significant during a mass extinction event, has been observed in other invertebrate groups (Foote, 1993; Wan et al., 2021). Future work could include a systematic revision of both *Gerastos* and *Phillipsia* with these patterns in mind.

In terms of major morphological changes, many of the species in this study exhibit small eyes or eye reduction through time (e.g., many *Gerastos* spp.). As is observed in other trilobite orders, a number of proetides included in this study lost their eyes completely. Eye loss in trilobites is often associated with moving deeper along the continental shelf into aphotic waters (Richter, 1926; Clarkson, 1967; Feist and Clarkson, 1989). The blind trilobites in this study—species of *Rudybole* Feist and McNamara, 2013 and *Palpebralia* (Late Devonian, Australia; Feist and McNamara, 2013)—are not only closely related to some *Gerastos* spp. showing eye reduction but are also most closely related to two species of *Guilinaspis* Yuan and Xiang, 1998 (Carboniferous, China; Yuan and Xiang, 1998). Interestingly, one species of *Guilinaspis*, *Guilinaspis subcylindrica* Yuan and Xiang, 1998, has large eyes, larger than what is considered 'normal' (plesiomorphic) for a proetide. The other species of *Guilinaspis* did not have eyes that could be coded (missing a portion of the cephalon). The blind *Rudybole* and *Palpebralia* spp. were collected in fossil-rich Late Devonian forereef environments, found in association with cephalopods and crinoids, and given a red color by abundant hematite in the limestone (Feist and McNamara, 2013). Feist and McNamara (2013) noted that blindness might have an earlier (more ancestral) origin in the *Rudybole* lineage and does not seem to coincide with the movement of this group into deeper waters. In fact, many trilobites (including nonproetides) shifted to eyeless forms in the Famennian (Bault, 2023). Additionally, although proetide diversity is cut dramatically between stages in this basin (Canning Basin, Australia), the blind species not only persisted but rose during the aftermath of the Lower Kellwasser event (Feist and McNamara, 2013). Looking at the relationships between the blind Australian trilobites and the large-eyed Chinese trilobites, many members of the clade reduced or lost their eyes, and a later sister branch

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secondarily reobtained this feature, possibly due to changing environments from the end-Devonian through the early Carboniferous in the Southern Hemisphere (Girard et al., 2020). This, perhaps, adds credence to the idea that proetides were extremely plastic in their morphology, aiding in their survival through the extinction event(s) and recovery interval.

In terms of other major morphological changes, feeding structures and behavior potentially changed in one branch of the proetides. One species included in this study, *Timsaloproetus haasi* (Alberti, 1971), has been well described as having a forked hypostome (Gibb and Chatterton, 2007) that might have been used for processing large prey items (predation) or scavenging (Fortey and Owens, 1999; van Viersen and Lerouge, 2021). This is unusual for proetide trilobites, which were mainly detrital feeders with a natant hypostome (Fortey and Owens, 1975, 1999). *Timsaloproetus hassi* was separated from other members of its family and grouped with *Diademaproetus* and *Cornuproetus*. *Timsaloproetus* and *Diademaproetus* have long been considered related to *Cornuproetus* (Chatterton et al., 2006; Crônier et al., 2018; van Viersen and Lerouge, 2021), which was reflected in the relaxed-clock model tree for at least one species. All other species of *Timsaloproetus* were placed close to species of *Sculptoproetus* Erben, 1951 and *Hollandiella* van Viersen and Larouge, 2020 on the relaxed-clock tree. *Diademaproetus* spp. are morphologically odd proetides, having an extended, flat portion of their anterior cephalon that resembles a scoop or a spoon. A thickening or alteration of the anterior cephalic border can be seen as 'bracing' for the ventral doublure and hypostome, which is associated with predation/scavenging (Fortey and Owens, 1999) although *Diademaproetus* has yet to be described as such. It is difficult not to hypothesize that the group consisting of *Timsaloproetus hassi, Diademaproetus* spp., and *Cornuproetus meinkenbrachtensis* Basse, 1997 (which also has a thicker, lip-like anterior cephalic border) are an odd-ball or experimental group of proetides that incorporated predation into the order in the early Devonian.

More work in the future should be done to investigate the morphological changes (e.g., hypostome attachment, changing body shape, body-size calculations) of proetide trilobites across the latter half of the Paleozoic. Ecological niche space opened when other trilobites went extinct following the end-Devonian events. It has been hypothesized that proetides were able to move into some of this vacated niche space (Fortey and Owens, 1975), although not much has been done to test this idea. This query is especially interesting because proetides persisted for another 100 Myr, representing the bulk of trilobite existence on Earth. Additionally, the question of biogeographic changes and dispersal patterns of proetides across the end-Devonian are still in question. When looking at the biogeographic locations of taxa and their branches (based on the bioregions of Dowding and Ebach, 2018), there does not seem to be a clear pattern of clade survivorship other than that some of the longest living clades were from more northernly regions (e.g., eastern Americas or Cordellian) (Appendix 4). Additionally, many clades appear to be spread across two regions (e.g., Rhenish-Bohemian and eastern Americas) although this does not seem to have a bearing on clade survivorship (Appendix 4).

Contrasting clock models and future directions. The relaxed-clock results are the focus of the discussion here, although the strict-clock model results do have some strong groupings. For example, some of the *Guilinaspsis* spp.—specifically *Guilinaspsis brevis* (Yuan and Xiang, 1998) and *Guilinaspsis subcylindricus*—grouped with some of the *Pudoproetus* in the strict-clock tree rather than with *Palpebralia* Richter and Richter, 1927 in the relaxed-clock model, which seems likely because these *Guilinaspsis* and *Pudoproetus* species originated in the South China Sea (i.e., geographically and temporally closer). In this case, the strict-clock model identified a possible stratigraphic and temporal relationship between some of the species of *Guilinaspsis* and *Pudoproetus* whereas it seems the relaxed-clock model, with different rates among branches, determined that some *Guilinaspsis* spp. were closer to *Palpebralia* (and that stratigraphy and time were not the deciding factors in their relationship). The results of this study highlight the importance of global sampling when examining the relationships within a large group (e.g., ordinal-level analysis) rather than regional pools.

The results of this study help resolve part of the proetide tree but there are limitations that could be resolved with future work. For example, internal nodes and branches for the trees have lower posterior probabilities than the external tips and branches for both clock models. This is an artifact of sampling mainly Devonian taxa. To better understand order Proetida as a whole, older proetides (i.e., Silurian, or older in age) will be sampled in the future, which should help resolve some of the uncertainty within the tree(s). In general, more work needs to be done with earlier proetides (Ordovician–Silurian), which could help resolve their Cambrian ancestry. Among trilobites, there exists the 'cryptogenesis problem' (Stubblefield, 1959; Paterson, 2020). The cryptogenesis problem essentially states that the Cambrian origins of many post-Cambrian taxa are unknown or unresolved (Paterson, 2020). Currently, the Cambrian sister group to proetides is still unknown (Edgecombe, 1992; Fortey, 2001; Lamsdell and Selden, 2015; Paterson, 2020). Resolving the proetide part of the trilobite tree can only have a positive effect on resolving higher trilobite taxonomy.

In addition to increased sampling of older taxa, different and more complex character models can be incorporated to assess large groups like proetides. The evolution of large groups is, without a doubt, a complicated process to encapsulate. Although Bayesian models like the FBD model are an incredible tool to help unravel complexities of a group's macroevolution, these models can benefit from the addition of more priors and are versatile enough for users to do this. One possible way is create a multitype Bayesian analysis with morphological data and geographic data using an FBD-type model with a dispersal parameter (Vaughan and Stadler, 2025; Kühnert et al., 2016). Although this has been demonstrated on viral data to simulate the way in which viruses evolve across space, there is an exciting future in which this could be used for fossil data. As a final note, it always benefits a phylogenetic analysis to reexamine characters. This is especially true for characters used to initially describe smaller taxonomic units and then used to describe large taxonomic groups as seen in this study (and echoed by van Viersen and Lerouge, 2021). Trilobites are known to have unique issues when it comes to constructing their phylogenetic hypotheses based on character data; mainly, trilobites demonstrate more homoplasy and per-taxon decay rates in comparison with other clades and are therefore more prone to character exhaustion (Wagner, 2000). Future work will include reevaluating characters, especially as additional older taxa are incorporated.

Conclusions

Major subgroupings within the Proetoidea, e.g., Phillipsidae and other taxonomic groupings, appear to be very polyphyletic. This is most apparent in the genus *Gerastos*, which grouped with at least four other subclades across the tree. Some major groupings are composed

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largely of members of particular subfamilies, e.g., the '*Dechenella*' clade (Fig. 4a). Other genera, e.g., *Phillipsia*, which have been considered monophyletic in the past, were found to be polyphyletic. Their updated sister clades are not only plausible morphologically but also spatially. There is a possibility that differential survivorship at the end-Devonian of certain subclades based on morphology, e.g., '*Phillipsia* A' (labelled 5) and the '*Basidechenella*' (labelled 9) clades, might have occurred but future work needs to examine this more closely. Certain clades linked together by changes in their morphologies and ecologies including those having gone completely blind and those who demonstrated some alteration of feeding strategy. This study demonstrates the strength of morphological units over taxonomic units in the last of the Devonian trilobites.

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