Returning to the roots: resolution, reproducibility, and robusticity in the phylogenetic inference of Dissorophidae (Amphibia: Temnospondyli) (#58550)

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Returning to the roots: resolution, reproducibility, and robusticity in the phylogenetic inference of Dissorophidae (Amphibia: Temnospondyli)

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Phylogenetic relationships of most extinct tetrapod clades remain poorly resolved, which may be variably attributed to a lack of study, the limitations of inference from phenotypic data, and constant revision of best practices. While methodological refinement continues to be essential, any phylogenetic analysis is inherently constrained by the underlying dataset that it analyzes. Therefore, it becomes equally important to assess the integrity of these datasets, especially when certain ones are repeatedly propagated, thus appearing to constitute a working consensus of sorts, in order to assess whether such a consensus is robust. Here I address the phylogeny of the Dissorophidae, a speciose clade of Paleozoic temnospondyl amphibians. This group is an ideal case study among temnospondyls for exploring phylogenetic methods and datasets because it has been extensively studied (eight phylogenetic studies to date) but with six studies using a single matrix that has been propagated with very little modification. In spite of the conserved nature of the matrix, dissorophid studies have produced anything but a conserved topology. Therefore, I analyzed an independently designed matrix, which tended to recover less resolution and some disparate nodes compared to previous studies. In order to reconcile these differences, I carefully examined previous matrices and analyses. While some differences are a matter of personal preference (e.g., analytical software), others relate to best practices (or a lack thereof). However, the most concerning discovery was the identification of pervasive dubious scorings that extend back to the origins of the previously propagated matrix. These include scores for skeletal features that are entirely unknown in a given taxon (e.g., postcrania in *Cacops woehri*) and characters for which there appear to be unstated working assumptions to scoring that are incompatible with the character definitions (e.g., scoring of taxa with incomplete skulls for characters based on skull length). Correction of these scores and other pervasive errors recovered a distinctly less resolved topology than previous studies, more in agreement with my own matrix. This suggests that previous analyses may have been compromised, and that the only real

consensus of dissorophid phylogeny is the lack of one.

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Abstract

Phylogenetic relationships of most extinct tetrapod clades remain poorly resolved, which may be variably attributed to a lack of study, the limitations of inference from phenotypic data, and constant revision of best practices. While methodological refinement continues to be essential, any phylogenetic analysis is inherently constrained by the underlying dataset that it analyzes. Therefore, it becomes equally important to assess the integrity of these datasets, especially when certain ones are repeatedly propagated, thus appearing to constitute a working consensus of sorts, in order to assess whether such a consensus is robust. Here I address the phylogeny of the Dissorophidae, a speciose clade of Paleozoic temnospondyl amphibians. This group is an ideal case study among temnospondyls for exploring phylogenetic methods and datasets because it has been extensively studied (eight phylogenetic studies to date) but with six studies using a single matrix that has been propagated with very little modification. In spite of the conserved nature of the matrix, dissorophid studies have produced anything but a conserved topology. Therefore, I analyzed an independently designed matrix, which tended to recover less resolution and some disparate nodes compared to previous studies. In order to reconcile these differences, I carefully examined previous matrices and analyses. While some differences are a matter of personal preference (e.g., analytical software), others relate to best practices (or a lack thereof). However, the most concerning discovery was the identification of pervasive dubious scorings that extend back to the origins of the previously propagated matrix. These include scores for skeletal features that are entirely unknown in a given taxon (e.g., postcrania in *Cacops woehri*) and characters for which there appear to be unstated working assumptions to scoring that are incompatible with the character definitions (e.g., scoring of taxa with incomplete skulls for characters based on skull length). Correction of these scores and other pervasive errors recovered a distinctly less resolved topology than previous studies, more in agreement with my own matrix. This suggests that previous analyses may have been compromised, and that the only real consensus of dissorophid phylogeny is the lack of one.

Introduction

Inferring phylogenetic relationships remains one of the most timeless pursuits within paleontology. The persistence of such studies owes to the essentiality of phylogeny as the macroevolutionary framework within which all other studies are situated and to the probable lability of any given topology when it relies entirely on morphological data and the discretization of continuous traits. Continual hypothesis testing thus remains an essential facet of contemporary research. While there is a broad interest in exploring clade-independent practices that are applicable to a broad range of studies (e.g., comparison of likelihood and parsimony methods, approaches to missing data and polymorphisms), it is equally important to critically examine the empirical datasets to be analyzed in order to assess their robusticity and reproducibility and to seek to improve them whenever possible.

One longstanding practice is the propagation of an existing matrix with modifications, at minimum by adding taxa of interest, and possibly more substantially by changing scores and character sampling. In this, there is an implicit goal of developing a semblance of a consensus matrix that the majority of workers have worked with (not necessarily within the confines of a single collaboration) and therein agree is well-designed to test the relationships of a given in-group. However, in propagating a matrix, each derivation is inherently a pseudoreplicate (non-independent), especially when changes beyond taxon addition are minimal. While propagation creates consistency between analyses, it also constrains the possible outcomes unless substantial changes are made. If a consensus emerges from such a matrix, it must be assessed whether this is a true defensible consensus. The easiest way to test this is with a novel (independent) matrix. Conversely if no consensus emerges from repeated propagation of a largely unchanged matrix, this is perhaps even more troubling, as this indicates that most topologies are labile and thus should not be relied upon heavily for qualitative discussion or for integration into other studies.

This study focuses on the phylogenetic relationships of Dissorophidae, a clade of dissorophoid temnospondyls (Fig. 1), as a case study in phylogenetic analyses of temnospondyls. Temnospondyli, often referred to as ‘amphibians’ in a broad sense, is best known for the clade’s longstanding role in the unresolved debate over lissamphibian origins, which has drawn extensive attention of phylogeneticists in recent decades (e.g., Laurin & Reisz, 1997; Anderson, 2001; McGowan, 2002; Ruta, Coates & Quicke, 2003; Vallin & Laurin, 2004; Lee & Anderson, 2006; Carroll, 2007; Ruta & Coates, 2007; Anderson et al., 2008a; Pyron, 2011; Sigurdsen & Green, 2011; Pardo, Small & Huttenlocker, 2017; Marjanović & Laurin, 2019; Schoch, Werneburg & Voigt, 2020). Workers interested in this topic have largely focused on Amphibamiformes, another dissorophoid clade, as the likely candidate within Temnospondyli. However, outside of this context, the phylogeny of most temnospondyl clades has received scant attention. Nonetheless, the intrarelationships of temnospondyls are of inherent import for this debate, especially with the recent proposal of a diphyletic origin of Lissamphibia from within Temnospondyli (Pardo, Small & Huttenlocker, 2017). Furthermore, with the increasing tractability of so-called “big data” studies with wide taxonomic breadth that are rooted in phylogenetic backbones, the phylogenetic relationships of these clades have acquired new import beyond the narrow scope of taxonomic specialists. Temnospondyls are both an excellent case study and an area in need of redress because they are not regarded as ‘charismatic taxa’ and thus suffer from a paucity of workers. As a result, certain workers or working groups may inadvertently exert disproportionate influence on the study of a given clade, which in phylogenetics, manifests as one worker’s matrix rapidly becoming the only utilized matrix.

Dissorophids, a clade of dissorophoids only peripherally related to the lissamphibian origins debate, are an ideal case study within Temnospondyli. Firstly, the clade is very speciose, with over 20 nominal taxa, and the anatomical foundation is well-established for many, with nearly 20 studies published in the 21st century alone. As a result, there is a more substantive history of phylogenetic inquiry into dissorophids than for less speciose Paleozoic clades, such as eryopoids or zatracheidids. To date, there have been eight studies that expressly addressed the phylogeny of Dissorophidae (Fröbisch & Reisz, 2012; Schoch, 2012; Holmes, Berman & Anderson, 2013; Maddin et al., 2013; Schoch & Sues, 2013; Liu, 2018; Dilkes, 2020; Gee et al., 2021). However, nearly all of them derive from the same source matrix (Schoch, 2012; Fig. 2) and are nearly identical in scoring, taxon sampling, and character sampling. Surprisingly, there is widespread disparity between their recovered topologies (Figs. 3–4). As remarked upon by Dilkes (2020:26), “results of recent attempts to unravel the phylogeny of dissorophids, even though they are using modified and hopefully updated versions of the same matrix, have consistently shown a lack of agreement on a broader pattern of dissorophid relationships with poor resolution and low support for most nodes that are present in a strict consensus tree.” The situation of dissorophids can be categorized as a largely consistent matrix producing largely inconsistent results. Finally, the study of dissorophids is relevant for other studies. Dissorophids are a common outgroup for amphibamiform studies, whether in comparative anatomical descriptions or in quantitative studies (e.g., Pérez-Ben, Schoch & Báez, 2018; Atkins, Reisz &

Maddin, 2019). Additionally, as ubiquitous components of early Permian terrestrial ecosystems, dissorophids (and their sister group, Trematopidae), are frequently sampled in broader studies of Paleozoic tetrapods at large (e.g., Brocklehurst et al., 2018; Dunne et al., 2018; Pardo et al., 2019).

I previously addressed the phylogeny of Trematopidae, the sister group to Dissorophidae (collectively Olsoniformes; Anderson et al., 2008b), which is less studied and for which there also remains no consensus (Gee, 2020b; Fig. 5). A key aspect of that study was demonstrating how taxon sampling (and more specifically, selective exclusion), can drastically improve or alter topological resolution. Previous olsoniform studies have either focused on dissorophids or trematopids – there has never been a matrix that evenly samples these clades as a collective in-group. The closest approximation is Atkins, Reisz & Maddin (2020), a derivation of Schoch (2018a) that samples six of the 10 trematopids (deficient in Carboniferous taxa as with other studies) and 11 dissorophids. Schoch's (2018a) matrix is also a derivation from Schoch (2012), though with an expanded and largely non-overlapping taxon sample, which is why I did not use either his matrix or the derivation of Atkins, Reisz & Maddin. In this study, I expand the taxon and character sampling of my previous trematopid-centric matrix to encompass dissorophids, thereby forming such a matrix. I opted to use my matrix, rather than the long-propagated dissorophid matrix of Schoch (2012) in order to approach these questions from as independent of a perspective as possible and in light of the markedly disparate topologies of different derivations of Schoch's matrix despite the matrix's conserved nature. Despite sampling Olsoniformes at large, this study is targeted primarily towards dissorophids simply because I have recently focused on trematopids, which are still a secondary focal group here. There are three primary objectives: (1) to test whether this independent matrix can produce either better resolution or stronger nodal support compared to previous studies and in turn to interpret that resolution; (2) to assess factors that might contribute to potentially spurious resolution in analyses that recover a high degree of resolution or that confound recovery of resolution in analyses that recover a low degree of resolution; and (3) to summarize the present state of the clade and to identify key areas in need of redress in order to work towards a consensus.

Materials & Methods

Taxon sampling. I sampled the vast majority of olsoniforms, with all ten of the undisputed trematopid species carried over from my previous analysis (Gee, 2020b). *Acheloma dunni* is regarded as a junior synonym of *Acheloma cumminsi*, and their scores are thus merged here. *Phonerpeton whitei* is excluded on the basis of a suspect differentiation from *Phonerpeton pricei*, which stems from the absence of detailed description or illustration. I expanded the sample to include most dissorophids, the recently described olsoniform *Palodromeus bairdi*, and the "stem dissorophoid" *Perryella olsoni* (Table 1).

In my previous study, I scored practically every published and figured trematopid specimen. I opted for a more selective approach in adding dissorophids, and the trematopid specimen-level OTUs are not carried over. The main reason is that many dissorophid specimens consist only of neural spines and osteoderms (e.g., DeMar, 1966b; May et al., 2011; Gee, Bevitt & Reisz, 2019) and can only be scored for a handful of characters (<10%). Dissorophid taxa that are excluded in their entirety are: *Aspidosaurus glascocki,* "*Aspidosaurus*" *apicalis,* "*Aspidosaurus*" *crucifer*, "*Aspidosaurus*" *peltatus*, and *Astreptorhachis ohioensis*. Very fragmentary cranial remains or those without sutures were excluded unless they were the holotype of a valid taxon (e.g., *Broiliellus arroyoensis*), as similar specimens were frequently problematic in my trematopid analysis. This exclusion includes the holotypes of "*Fayella chickashaensis*," "*Trematopsis seltini*," and two junior synonyms of *D. multicinctus*, "*Otocoelus mimeticus*" and "*Otocoelus testudineus*." The only holotype of a junior synonym that is sampled here is "*Longiscitula houghae*" because its cranial sutures are well-described and figured (DeMar, 1966a; Milner, 2003). Additionally, testing interspecific ontogenetic disparity in dissorophids was not a focus of this study (addressed in the Discussion), and therein assessing whether the matrix could detect intraspecific ontogenetic variation as a proof of concept was also not as essential. Almost two-thirds of dissorophids are represented only by the holotype in any event. I did run one permutation to assess this and thus *Anakamacops petrolicus*, *Cacops morrisi*, *Cacops woehri*, and *Conjunctio multidens* are scored at the specimen level.

Schoch & Milner (2014) listed several taxa as possible early diverging dissorophoids: *Macrerpeton huxleyi* from the late Carboniferous of Ohio; *Parioxys ferricolus* and *Parioxys bolli* from the early Permian of Texas; *Perryella olsoni* from the early Permian of Oklahoma; and *Stegops newberryi* from the late Carboniferous of Ohio. *Parioxys ferricolus* and *S. newberryi* are in need of redescription. *Parioxys bolli* (Carroll, 1964b) is included to test the performance of an exclusively postcranial skeleton (the holotype and only known specimen). *Perreylla olsoni* is included, but its position should only be interpreted in light of assumed dissorophoid affinities. Ruta & Bolt (2006) considered it to be a dvinosaur and recovered it as such in a broad analysis of Paleozoic temnospondyls, while Schoch (2018a) recovered it as the sister taxon to Dissorophoidea but in a dissorophoid-focused analysis with only one dvinosaur taxon. Schoch & Milner (2021) recently recovered *M. huxleyi* as a "stem dissorophoid," diverging before *P. olsoni*, so the former is not sampled here. '*Broiliellus hektotopos*' from the early Permian of Ohio was described as a dissorophid (Berman & Berman, 1975), but it has never been included in an analysis and is probably an amphibamiform (May et al., 2011), following Romer's (1952) initial interpretation of the holotype as a "branchiosaur." I included the holotype to test this in a phylogenetic framework.

The non-olsoniform outgroups were carried over from Gee (2020b): the amphibamiforms *Doleserpeton annectens, Eoscopus locklardi*, *Pasawioops mayi,* and *Tersomius texensis*, and the micromelerpetid *Micromelerpeton credneri*. The same non-dissorophids were included (*Dendrysekos helogenes, Eryops megacephalus*) but with *Chenoprosopus milleri* (Langston, 1953) replacing *Chenoprosopus lewisi* to better sample palatal characters. I replaced my previous functional outgroup, the anthracosaur *Proterogyrinus scheelei*, with the colosteid *Greererpeton burkemorani* (Smithson, 1982; Godrey, 1989a, 1989b; Bolt & Lombard, 2001) because the latter's preservation allows it to be confidently scored for more characters without relying on reconstructions (e.g., skull length-based characters), but scores for *P. scheelei* were still updated.

Character sampling. The character matrix was derived from that used in my trematopid analysis (Gee, 2020b), and characters are listed in Appendix 1. Additional characters were added to differentiate between dissorophids. I removed two characters (snout shape, palpebral ossifications; Appendix 2) and split one character (LEP) into two characters. There are a total of 112 characters; multi-state characters that can be hypothesized to be ordered in an evolutionary sense were ordered here. Of the 17 multistate characters, 14 were ordered (2, 4, 12, 19, 30, 33, 40, 53, 70, 72, 87, 102, 107, 110). Characters were equally weighted.

Character scoring. Scores were carried over at the species-level from Gee (2020b) unless noted in Appendix 2. Scoring was based strictly on the literature, and reconstructions were not utilized. Scoring of species-level operational taxonomic units (OTU) accounted for any polymorphisms that are not clearly attributable to ontogeny. Anatomical differences correlated with very slight size differences were treated more skeptically than those correlated with large size gaps in determining whether to code a condition as polymorphic or only for the inferred 'adult' condition. Comments on scoring approaches to specific characters and the treatment of taxa for which a character can only be scored from an immature specimen are provided in Appendix S2 of Gee (2020a) and in Appendix 3 here. The matrix as a NEXUS file is provided as Appendix 4.

I want to make particular mention of *Kamacops acervalis* here because it is difficult to reconcile its historical scoring with existing descriptions, figures of which are either reconstructions in palatal and lateral view or close-up illustrations of the occiput and braincase (Gubin, 1980; Schoch, 1999). The detailed discussion is relegated to Appendix 2, but I emphasize a few key points here because this taxon in particular (or more accurately, uncertainty over the taxon) influenced the design of the various permutations that I conducted here. The only published photograph of any specimen is a snout (Schoch & Milner, 2014:fig. 37E), which does not show any clear sutures. This taxon has also been reconstructed as a silhouette in dorsal view but without sutures by Schoch (2012:fig. 6), in contrast to most other dissorophids. Therefore, it is strange that there are cranial characters scored for this taxon (e.g., prefrontal-postfrontal suture). Additionally, none of the specimens of *K. acervalis* is even half-complete, and without photographs, it is unclear how much skeletal overlap exists between specimens, therein questioning the fidelity of the reconstructions. This is particularly important because the reconstruction appears to be the only means of scoring characters involving skull length that relate to proportions, including two of the three characters that differentiate *K. acervalis* from *Cacops*. At present, there is no way to reconcile some of the historic scores with the literature. Schoch indicated that he personally examined material of this taxon, so it is possible that he identified new features, but the data to support the scoring of many characters is not established in the literature. Therefore, I constructed two different species-level OTUs for this taxon. The first is termed the 'conservative' OTU and scores only based on the explicit descriptions and specimen illustrations (but not reconstructions) of Gubin (1980) and Schoch (1999). The second is termed the 'reconstructed' OTU and augments the previous one with data from reconstructions; this led to the scoring of an additional 20 characters. In neither are skull roof sutures scored except in the occipital region, so both OTUs are underscored compared to previous studies.

Phylogenetic analysis. I elected to perform only maximum parsimony analyses of the data matrix; the topologies recovered by a simple non-clock Bayesian analysis in my previous study (Gee, 2020b) did not differ substantially from those recovered by the parsimony analyses. Most discrepancies were related to additional resolution recovered in the Bayesian analysis only on account of the overestimation of support of posterior probabilities compared to bootstrap value.

The analyses were primarily performed in TNT v1.5 (Goloboff & Catalano, 2016). For permutations with more than 30 taxa, I used a heuristic search ("traditional search" in TNT) with the following parameters: 10,000 random addition sequence replicates, holding 10 trees at each step, and tree-bisection-and-reconnection (TBR). For permutations with 30 or fewer taxa, a branch-and-bound ("implicit enumeration" in TNT) search was used. Default settings of TNT (e.g., rule 1 for branch collapsing: min. length = 0) were otherwise maintained. I performed

10,000 bootstrap replicates with a heuristic search to assess nodal support for all permutations. Given the intensive computation time of branch-and-bound searches, I elected to use heuristic searches to calculate Bremer decay index after confirming that a heuristic search recovered the same set of MPTs as any branch-and-bound search. Topological interpretation is based primarily on the strict consensus trees, but majority-rule consensus trees were occasionally used to identify frequently occurring nodes. TNT was selected for its ability to rapidly process large datasets, which was a concern for permutations with species-level OTUs that have high proportions of missing data (as with some of the dissorophids here); no search (or resampling) exceeded nine hours. I used PAUP* 4.0a169 (Swofford, 2018) for several permutations that mirrored previous analyses conducted in PAUP*. The more taxonomically restricted TNT analyses can be run within PAUP* (no search exceeded 30 hours), although these analyses were consistently more costly, and bootstrapping could exceed 48 hours. All analyses were performed on a personal computer (MacBook Pro, 2015 model, 16 GB of RAM, macOSMojave 10.14.5).

As with my previous study, I performed a large number of permutations (Table 2). Almost all of the trematopid permutations were determined *a priori*, but because the focus of this study was different, most of these permutations were only determined after examining previous results. The first four permutations broadly sample Olsoniformes and have an eye towards testing topology, whereas the last five permutations relate more to assessing possible sources of disparity between previous studies.

1. **Permutation 1A (all olsoniforms)**: all presently valid species that I scored are sampled here at the species-level. Taxa: 47.
2. **Permutation 1B (wildcard removal)**: an Adams consensus was used to identify wildcard taxa in the previous permutation (method for identifying wildcards is listed in the Results). The analysis was subsequently rerun without these wildcards. Taxa: 39 / 40.
3. **Permutation 2 (best representatives)**: this permutation follows historic approaches by excluding poorly known taxa, which is arbitrarily defined as having either an overall low percentage of scoreable features or a low percentage specifically for cranial characters. The sampling thus omits any taxon for which cranial sutures are unknown: *Aspidosaurus chiton*, *Broiliellus arroyoensis, Iratusaurus vorax*, *Parioxys bolli*, and *Zygosaurus lucius*. Cranial material of *Aspidosaurus novomexicanus*, *Brevidorsum profundum*, *Diploseira angusta*, *Kamacops acervalis*, and *Nooxobeia gracilis* is relatively fragmentary, and these taxa are also excluded. Of the exclusions, *B. profundum*, *K. acervalis*, and *Z. lucius* were usually sampled in previous studies. All non-dissorophids are sufficiently characterized to be retained. Taxa: 37.
4. **Permutation 3 (dissorophid-focused)**: this permutation samples almost every nominal dissorophid but with a trimmed subset of trematopids, as would commonly be done for dissorophid-focused analyses. I excluded *Actiobates peabodyi*, *Mordex calliprepes*, and *Rotaryus gothae* as taxa probably represented only by markedly immature specimens. ‘*Broiliellus’ hektotopos* and *Parioxys bolli* were excluded since they were recovered well outside Dissorophidae in previous permutations. Taxa: 42.

I ran one permutation with specimen-level dissorophid OTUs to assessi whether the matrix can resolve intraspecific ontogeny in dissorophids.

5. **Permutation 4 (cacopine specimen-level OTU**): this permutation focuses on *Anakamacops petrolicus*, the three species of *Cacops*, and *Conjunctio multidens*, for which at least two individual specimens can be scored. Based on my trematopid analyses, poorly preserved or highly fragmentary specimens were clear confounds. Therefore, I omitted highly fragmentary referred material (like the two partial snouts referred to *Ca. woehri* by Gee, Bevitt & Reisz, 2019) and material without sutures (like the holotype and paratype of *Ca. aspidephorus*). *Iratusaurus vorax* and *Zygosaurus lucius* are excluded on the same grounds. Species-level dissorophid OTUs are restricted to *Broiliellus brevis*, *Dissorophus multicinctus* and *Kamacops acervalis*. OTUs: 32.

The third set of permutations relate to taxon sampling. As with my previous study, I ran so-called "mirror analyses" in which I took the taxon sample of a previous study and the character sample and scoring of my own study.

6. **Permutation 5 (taxon mirror of Dilkes, 2020)**: this permutation takes the taxon sample of Dilkes (2020) and the character sample and scoring of this study's matrix. Because not all equivalent taxa are found in my matrix, I replaced *Sclerocephalus haeuseri* with *Eryops megacephalus*, *Platyrhinops lyelli* with *Eoscopus locklardi*, and utilized *Dendrysekos helogenes* as the outgroup. I used the 'reconstructed' OTU of *Kamacops acervalis* to best approximate the historic scoring of this taxon. Although I intended to mirror all of Dilkes' parameters, the higher character count of my matrix (44% more characters) made a branch-and-bound search intractable in PAUP*; it bears noting that 29 taxa is well above the typical threshold for running this type of search. Therefore, I ran a heuristic search with 10,000 random addition sequence replicates, holding 10 trees per step; all other settings, including the bootstrapping, were mirrored where possible. I then removed the four wildcard taxa that Dilkes identified and reran the analysis; this trimmed sample was recognized to be tractable with a branch-and-bound search. Taxa: 29 (25 without wildcards).
7. **Permutation 6 (taxon mirror of Gee, 2020b)**: this permutation takes the taxon sample of Gee (2020) and the character sample and scoring of this study's matrix. *Acheloma* and *Phonerpeton* are treated as discussed above. I used *Proterogyrinus scheelei* as the outgroup (as with the original matrix and analysis) and excluded *Greererpeton burkemorani*. In order to account for the adjusted scoring of *A. cumminsi* and the exclusion of *Ph. whitei*, I also reanalyzed my original matrix with the revised treatments of these taxa but with the original scoring otherwise intact. Since only one OTU was changed, the revised string for *Acheloma cumminsi* (inclusive of data from *Acheloma dunni*) is provided in Appendix 2 rather than in a separate NEXUS file. Taxa: 23.

The next permutation is the result of a close examination of previous scores of the Schoch (2012) matrix and its derivations in which I identified a large number of cells that either were scored for features that are definitively unknown (e.g., postcrania of *Cacops woehri*) or that were unscored but that are definitely known (e.g., palatal features of *Fedexia striegeli*). Most of the cells that cannot be scored are scored identically to other members of a relatively exclusive in-group (e.g., all questionable scores of *C. woehri* are scored identical to at least one other species of *Cacops*).

This observation suggests that some scores have been "assumed," but not actually observed, based on inferred relatedness, a troubling prospect.

8. **Permutation 7 (updated version of Dilkes, 2020):** this permutation is a direct reanalysis of Dilkes' matrix with updated scores that focused on cells where the scoring or lack thereof seems unequivocally erroneous. I did not adjust scores unless there was strong evidence against the current score, so subjective decisions (e.g., is an atlas-axis sufficient postcranial representation to determine the absence of osteoderms in *Fedexia striegeli*) or scores that are neither confidently validated or invalidated from the literature and that could potentially be corroborated by personal observation (e.g., stapedial foramen in *Phonerpeton pricei*) were not changed. I only rescored cells for polymorphisms when this condition occurred within the same individual and was unequivocally non-taphonomic. I did factor in the datedness of literature sources as well. Therefore, some of the revised scores will differ from the equivalent score in my own matrix. These approaches minimize personal scoring philosophy and should provide an acceptable derivation of this matrix should other workers continue to use it. Any restored scores will have to be justified with appropriate data. All scoring changes are listed and justified in Appendix 5, and the revised matrix is provided as Appendix 6. The analysis was rerun in PAUP* following Dilkes' parameters.

Finally, when considering explanations for disparity in the degree of resolution and the placement of wildcard taxa, I observed that different programs have been used to examine the Schoch (2012) matrix and its derivations. Schoch (2012), Holmes, Berman & Anderson (2013), Maddin et al., (2013), and Dilkes (2020) used PAUP*, whereas Schoch & Sues (2013) and Liu (2018) used TNT. The analyses using TNT have recovered more resolution in the strict consensus and without any wildcards. It is known that these programs' algorithms and default settings differ, but studies rarely compare the results obtained by analyzing the same matrix. Therefore, I performed two permutations that analyze the same matrix with each program; I term these "parallel analyses." These analyses are not intended to test whether one program's results can be reproduced in the other but rather to test whether default parameters and algorithmic differences (usually default settings are employed by other workers) produce different results.

9. **Permutation 8 (parallel of trematopid mirror):** this permutation parallels permutation #6 (trematopid-focused sample, analyzed using TNT) in PAUP*; this permutation was chosen because it achieved a measurable degree of resolution in TNT and has a low taxon sample that would make it tractable for a branch-and-bound search in PAUP*.
10. **Permutation 9 (parallel of Dilkes, 2020):** this permutation parallels the original version of Dilkes (2020) matrix and the updated version that I analyzed in permutation #7, both using TNT (Dilkes' ran his analysis in PAUP*). Dilkes ran three permutations with a branch-and-bound search: a full taxon sample, a full taxon sample with osteoderm characters removed, and a reduced taxon sample without wildcards but with the full character sample. I paralleled the two with the full character sample. The iterations comparing different programs' analysis of Dilkes' original matrix are termed permutation 9A, and the iterations comparing the TNT

analysis of the original and updated versions of Dilkes' matrix are termed permutation 9B.

A nomenclatural note. The dissorophid subfamily defined by all taxa more closely related to *Cacops aspidephorus* than to *Dissorophus multicinctus* has usually been referred to as Eucacopinae following Schoch & Sues (2013), who noted that Cacopinae, the proper derivation from *Cacops*, was preoccupied for a group of microhylid frogs named for "*Cacopus*" (=*Uperodon*) per Noble (1931). The junior synonymy of the eponymous taxon and the synonymy of Cacopinae with Microhylinae do not affect the taxonomic priority of Cacopinae. However, as has been brought to my attention by David Marjanović, the proper derivation from *Cacopus* is Cacapodinae, and therefore, Cacopinae is both the correct and valid derivation from *Cacops*. Cacopinae was, in fact, erected with respect to dissorophids by Daly (1994:52), although I am not aware of any publication other than Berman et al. (2010) that identifies this as the authority. The name was rarely used ~~used~~ for over a decade, likely because *Cacops* was historically considered to be an aspidosaurine (e.g., Williston, 1914; DeMar, 1966b; Milner, 2003; Witzmann & Soler-Gijón, 2010). While Daly considered the eponymous aspidosaurine *Aspidosaurus* to be a dissorophine, making Aspidosaurinae a junior synonym of Dissorophinae, this aspect of her taxonomic framework has not been adopted by other workers (see Schoch & Milner, 2014). Cacopinae was then used as a terminal OTU (of *Cacops aspidephorus* + *Kamacops acervalis*) by Schoch & Rubidge (2005), which was followed by at least a dozen papers. Eucacopinae was widely adopted after 2013, but Schoch (2018a), Atkins, Reisz & Maddin (2019), Anderson, Scott & Reisz (2020), and Schoch & Milner (2021) recently employed Cacopinae, without comment, which I follow here.

Institutional abbreviations. AMNH FARB, American Museum of Natural History, Fossil Amphibians, Reptiles, and Birds, New York, NY; **BMRP**, Burpee Museum of Natural History, Rockford, IL; **CM**, Carnegie Museum, Pittsburgh, PA; **FMNH**, Field Museum of Natural History, Chicago, IL; **ICGAS**, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MCZ**, Museum of Comparative Zoology, Cambridge, MA; **OMNH**, Sam Noble Oklahoma Museum of Natural History, Norman, OK; **UCMP**, University of California Museum of Paleontology, Berkeley, CA; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, MH.

Results

My reporting practices are outlined here to reduce redundancy. Figured topologies are either strict consensus trees or Adams consensus trees (only permutation #1), and majority-rule consensus trees are used only to identify nodes that occur in an overwhelming majority of most parsimonious trees (MPTs). The associated MPTs of each permutation are included as .tre files in Appendix 7. All bootstrap values are reported, so any node without a listed bootstrap value was not recovered in more than 1% of the bootstrap replicates (common for TNT analyses). However, because bootstrap support below 50% and Bremer support below 3 is not considered strong, any values below these thresholds are colored in grey, whereas any values above these thresholds are colored in black.

The node-based definition of Dissorophoidea (the least inclusive grouping with *Dissorophus multicinctus* and *Micromelerpeton credneri*) and the stem-based definitions for

Trematopidae (most inclusive clade containing *Acheloma cumminsi* but not *D. multicinctus*), Dissorophidae (specifiers of Trematopidae inverted), Cacopinae (most inclusive clade containing *Cacops aspidephorus* but not *D. multicinctus*), and Dissorophinae (specifiers of Cacopinae inverted) are used here following Schoch & Milner (2014). Some specifiers for the node-based definitions of Xerodromes and Olsoniformes are not sampled in this analysis, but these names are used in the same sense as other workers (post-micromelerpetid dissorophoids and non-amphibamiform xerodromes, respectively). Nominal placement of taxa, specifically for dissorophids, is also from Schoch & Milner (2014). These definitions are employed in color swatches to visually facilitate the comparison of topologies and placement of taxa.

Permutation 1A (all olsoniforms). The iteration with the 'conservative' OTU of *Kamacops acervalis* recovered 1,180 MPTs with a length of 401 steps (CI = 0.319; RI = 0.594; Fig. 6A). The strict consensus is largely unresolved, although Dissorophidae (to the exclusion of *Parioxys bolli* and *Reiszerpeton renascentis*) is recovered. Within this clade, *Platyhystrix rugosus* is the earliest diverging taxon. Dissorophinae is the only other recovered clade and forms a single polytomy. All other dissorophids are single branches of a polytomy with Dissorophinae. Most nodes recovered only in the majority-rule consensus occur in only a slight majority of MPTs (e.g., Amphibamiformes inclusive of '*Broiliellus*' *hektotopos* in 59%). *Anconastes vesperus* and *Tambachia trogallas* are sister taxa in 96% of MPTs, and these form a clade with *Ecolsonia cutlerensis* in 77% of MPTs. *Acheloma cumminsi* + *Phonerpeton pricei*, the other typically well-supported relationship, is recovered in 76% of MPTs. Within Dissorophidae, all dissorophines to the exclusion of *B. reiszi* are recovered in 75% of MPTs. *Anakamacops petrolicus*, *Cacops aspidephorus*, *Cacops morrisi*, and *Zygosaurus lucius* form a clade in 66% of MPTs. Bremer and bootstrap support are consistently low, and most nodes found in the strict consensus are not recovered in the bootstrap consensus. The iteration with the 'reconstructed' OTU of *Kamacops acervalis* recovered 410 MPTs with the same length of 401 steps. The strict consensus differs only in the recovery of *A. vesperus* + *T. trogallas*, the recovery of *Ecolsonia cutlerensis* as the sister taxon to this pair, and the resolution of Dissorophinae (Fig. 6B). As with the previous iteration, most nodes recovered only in the majority-rule consensus are found only in a slight majority of MPTs (e.g., Olsoniformes, 64%). Amphibamiformes (92%), inclusive of '*B.*' *hektotopos*, is the exception.

Adams consensus trees were computed for both iterations in order to identify wildcard taxa (Fig. 7). The topologies are largely consistent with the main exception being Cacopinae as a result of the more informative OTU of *Kamacops acervalis* being employed. *Aspidosaurus binasser* and *Iratusaurus vorax* are recovered as cacopines in the Adams consensus from the 'reconstructed' OTU iteration (Fig. 7B) instead of as early diverging dissorophids. The configuration of the higher nested dissorophines has also shifted slightly, and Trematopidae is slightly more resolved. Wildcard identification was restricted to nominal olsoniforms, therein capturing *Palodromeus bairdi* as a wildcard, being recovered in a polytomy with the branch for Amphibamiformes and the branch for Olsoniformes (as formally defined). Within Dissorophidae, I removed any nominal dissorophid that was part of a polytomy outside of Cacopinae and Dissorophinae. Both iterations' trees identified poorly known dissorophids as wildcards: *Aspidosaurus chiton*, *Aspidosaurus novomexicanus*, *Nooxobeia gracilis*, and *Parioxys bolli*. In the iteration with the 'conservative' OTU of *K. acervalis,* this taxon, *A. binasser*, *Anakamacops petrolicus*, *I. vorax*, and *Zygosaurus lucius* were also identified as wildcards. For Trematopidae, I removed any taxon that was part of a basal polytomy; *Actiobates peabodyi*, *Mattauschia laticeps*, and *Mordex calliprepes* met this criterion in both iterations. These are the more fragmentary trematopids and have rarely been sampled in previous analyses.

Permutation 1B (wildcard removal). The iteration derived from with the previous permutation's analysis with the 'conservative' OTU of *Kamacops acervalis* (which excluded this OTU) recovered 66 MPTs with a length of 351 steps (CI = 0.362; RI = 0.597; Fig. 8A). Wildcard removal produced a weakly resolved topology that recovered Amphibamiformes, Olsoniformes, Trematopidae, Cacopinae, and Dissorophinae, but not Dissorophidae. Trematopidae is largely unresolved, with *Acheloma cumminsi* + *Phonerpeton pricei* as the only recovered relationship. Dissorophinae (*Broiliellus*, *Diploseira*, *Dissorophus*) is a single polytomy. Cacopinae consists only of the three species of *Cacops*, with *C. aspidephorus* and *C. morrisi* as sister taxa. All other dissorophids form a polytomy with Cacopinae, Dissorophinae, and Trematopidae. Two nodes occur in more than 80% of MPTs: all trematopids to the exclusion of *Ecolsonia cutlerensis* (81%) and *Anconastes vesperus* + *Tambachia trogallas* (84%). Bremer support is usually below 3, and most nodes were not even recovered in the bootstrapping, although the cacopine and trematopid were well-supported (the former likely because of the exclusion of all middle Permian dissorophids).

The iteration derived from the analysis with the 'reconstructed' OTU of *Kamacops acervalis* (which included this OTU) recovered 117 MPTs with a length of 368 steps (CI = 0.345; RI = 0.602; Fig. 8B). The strict consensus topology recovers major clades but mostly as large single polytomies. Trematopidae is configured the same as the previous iteration, as is Amphibamiformes. Both Cacopinae and Dissorophinae consist of one higher nested clade and one basal polytomy. In the former, the three species of *Cacops* and all middle Permian dissorophids are highly nested in a single polytomy, and *Aspidosaurus binasser*, *Conjunctio multidens*, and *Scapanops neglecta* lie at the base. In the latter, *Broiliellus arroyoensis* + *B. texensis* and *B. brevis* + *Dissorophus multicinctus* are highly nested with two sister pairs, with *B. olsoni*, *B. reiszi*, and *Diploseira angusta* at the base. Dissorophidae is now recovered, but to the exclusion of *Brevidorsum profundum*, *Platyhystrix rugosus*, and *Reiszerpeton renascentis*, which are recovered in a larger olsoniform polytomy with Dissorophidae and Trematopidae. Dissorophidae to the exclusion of *R. renascentis* is recovered in 97% of MPTs, and Olsoniformes, also to the exclusion of *R. renascentis*, is recovered in 84% of MPTs. Other identified nodes do not exceed 75% nodal occurrence (e.g., *Cacops* as a clade). Bremer and bootstrap support are consistently low.

Permutation 2 (Best representatives). The analysis recovered 19 MPTs with a length of 380 steps (CI = 0.334; RI = 0.588; Fig. 9). The strict consensus is moderately unresolved. Olsoniformes is not recovered, with all amphibamiforms (including '*Broiliellus*' *hektotopos*), *Reiszerpeton renascentis*, Trematopidae, and Dissorophidae to the exclusion of *R. renascentis* forming branches of a polytomy. Amphibamiformes inclusive of '*B.*' *hektotopos* and the four nominal amphibamiforms is recovered in 84% of MPTs. Olsoniformes is recovered in 84% of MPTs as well, as is a subset of all olsoniforms to the exclusion of *R. renascentis*. Trematopidae is poorly resolved, with only two historically recovered sister pairs, *Acheloma cumminsi* + *Phonerpeton pricei* and *Anconastes vesperus* + *Tambachia trogallas*, being recovered. In Dissorophidae, *Platyhystrix rugosus* diverges first, followed by *Aspidosaurus binasser* and *Conjunctio multidens* in a polytomy with Cacopinae and Dissorophinae. Cacopinae consists of the three species of *Cacops*, which form a grade, and *Anakamacops petrolicus*, which is the sister taxon of *C. aspidephorus*. Dissorophinae is a single polytomy and includes *Scapanops neglecta* in addition to *Broiliellus* and *Dissorophus multicinctus*. Bremer and bootstrap support are low.

Permutation 3. The iteration with the 'conservative' OTU of *Kamacops acervalis* recovered 387 MPTs with a length of 373 steps (CI = 0.340; RI = 0.591; Fig. 10). The strict consensus is largely unresolved with respect to Olsoniformes, which comprises a large polytomy. Trematopidae is recovered but to the exclusion of *Mattauschia laticeps*, although this taxon clusters with other trematopids in 88% of MPTs. The pair of *Eoscopus locklardi* + *Palodromeus bairdi* is recovered and is part of the olsoniform polytomy rather than the amphibamiform grade, but all other olsoniforms form a clade to the exclusion of this pair in 86% of MPTs. Dissorophidae (to the exclusion of *Reiszerpeton renascentis*) is recovered in 76% of MPTs. Dissorophinae (*Broiliellus*, *Diploseira*, *Dissorophus*) is not only recovered in the strict consensus but is also largely resolved, with *B. reiszi* as the earliest diverging taxon. Cacopinae (consisting not only of the traditional core of *Anakamacops* + *Cacops* + *Kamacops* + *Zygosaurus* but also of *Aspidosaurus binasser*, *Conjunctio multidens*, *Iratusaurus vorax*, *Nooxobeia gracilis*, and *Scapanops neglecta*) is recovered in 86% of MPTs. Both Bremer and bootstrap support are universally low.

The iteration with the 'reconstructed' OTU of *Kamacops acervalis* recovered 558 MPTs with the same length of 373 steps; the strict consensus topology remained unchanged, so it is not depicted separately. Dissorophid nodes identified only in the majority-rule consensus of the previous iteration have generally declined to less than 65%. One exception is a node not recovered in the previous iteration: the three species of *Cacops* form a clade in 90% of MPTs, with *C. aspidephorus* and *C. morrisi* recovered as sister taxa in 90% of MPTs. Bremer support did not change from the previous iteration, and bootstrap support changed only by 1–2%.

Permutation 4. The iteration with the 'conservative' OTU of *Kamacops acervalis* recovered 110 MPTs with a length of 278 steps (CI = 0.446; RI = 0.659; Fig. 11A). The strict consensus is poorly resolved. A noteworthy result is the recovery of the holotype of *Conjunctio multidens* (FMNH UC 673) at the base of Dissorophidae, whereas the two referred specimens are recovered as sister taxa at the base of Cacopinae (a similar configuration to that of Schoch, 2012). All other cacopines form a single polytomy with the exception of the pair of two specimens of *Cacops woehri*, the holotype (OMNH 73216) and a larger referred specimen (BMRP 2007.3.5). Bremer and bootstrap support are low for dissorophid nodes.

A few additional nodes are resolved in the majority-rule consensus (Fig. 11B). A second referred specimen of *C. woehri* (OMNH 79338) is recovered as the earliest diverging OTU within the polytomy of non-*Conjunctio* cacopines in 81% of MPTs. The three best-known specimens of *Cacops morrisi* (OMNH 53077, OMNH 73206a, OMNH 73206c) form a clade in 70% of MPTs. The other recovered nodes are for polytomies that are not monophyletic. One consists of both specimens of *Anakamacops petrolicus*, the species-level OTU of *K. acervalis*, and one referred specimen of *Cacops aspidephorus* (FMNH UC 900). The other consists of two specimens of *Cacops morrisi* and a second referred specimen of *Ca. aspidephorus* (UMMP 3417), which is the sister OTU to the holotype of *Ca. morrisi* (OMNH 53073).

The iteration with the 'reconstructed' OTU of *Kamacops acervalis* recovered 20 MPTs with a length of 279 steps (CI = 0.444; RI = 0.657). The strict consensus remains unchanged and is thus not depicted separately here. The majority-rule consensus is interestingly far less resolved than the previous iteration (only the cluster of three *Cacops* specimens is recovered in the majority-rule consensus). Bremer and bootstrap support are essentially unchanged.

Permutation 5 (taxon mirror of Dilkes, 2020). This permutation recovered 76 MPTs with a length of 295 steps (CI = 0.417; RI = 0.583; Fig. 12A). The strict consensus topology is discordant with that of Dilkes. Most nominal dissorophids form a single polytomy with a branch for Cacopinae, a branch for Trematopidae, the pair of *Broiliellus arroyoensis* + *B. texensis*, and *Eoscopus locklardi*. Trematopidae consists of two resolved clades: (1) *Fedexia striegeli* as the sister taxon to *Acheloma cumminsi* + *Phonerpeton pricei*, and (2) *Anconastes vesperus* + *Tambachia trogallas*. *Ecolsonia cutlerensis* forms a polytomy with these clades. In Dilkes' analysis, *E. cutlerensis* and *F. striegeli* were sister taxa and the earliest diverging branch of Trematopidae. As with Dilkes' analysis, Dissorophinae is not recovered. Cacopinae is recovered and consists of the same six taxa: three species of *Cacops*, *Anakamacops petrolicus*, *Kamacops acervalis*, and *Zygosaurus lucius*. Kamacopini is not recovered, and *Cacops aspidephorus* and *Cacops morrisi* are exclusive sister taxa, both contrary to Dilkes' analysis. A few historical nodes are identified in the majority-rule consensus, but only one (Olsoniformes, 89%) occurs in an overwhelming majority of MPTs; Dissorophidae (to the exclusion of *Reiszerpeton renascentis* here) and Dissorophinae are recovered in 68% of MPTs. Bootstrap and Bremer support were below meaningful thresholds except for Trematopidae. The Adams consensus (not presented here), does recover a more congruent dissorophid topology to that of Dilkes; *Anakamacops petrolicus* and *Kamacops acervalis* are sister taxa, and a Dissorophinae comprised of *Broiliellus*, *Diploseira*, and *Dissorophus* is recovered. Among dissorophids, *Conjunctio multidens*, *Platyhystrix rugosus*, *Reiszerpeton renascentis*, and *Scapanops neglecta* would be identified as wildcards following my approach in permutation #1.

The iteration with Dilkes' wildcards removed recovered 37 MPTs with a length of 270 steps (CI = 0.459; RI = 0.647; Fig. 12B). The strict consensus topology is more congruent with that of Dilkes, although with less resolution. *Platyhystrix rugosus* and *Aspidosaurus binasser* are the earliest diverging dissorophids, and Dissorophinae is recovered, albeit as a single polytomy. *Ecolsonia cutlerensis* is the sister taxon of *Anconastes vesperus* + *Tambachia trogallas*. The topology of Cacopinae is unchanged. Any nodes that are only resolved in the majority-rule consensus are barely above the 50% threshold (e.g., Kamacopini; 51%). Nodal support remained low.

Permutation 6. The rerun of my original trematopid matrix with the newly combined *Acheloma cumminsi* OTU and the exclusion of *Phonerpeton whitei* recovered 27 MPTs with a length of 209 steps (CI = 0.445; RI = 0.615; Fig. 13A). For comparison, the original analysis recovered 105 MPTs with a length of 210 steps (CI = 0.443, RI = 0.640). The strict consensus topology is nearly unchanged; Trematopidae, Dissorophidae, Olsoniformes, Amphibamiformes, and Dissorophoidea are all recovered, but Xerodromes is not. Within Trematopidae, the only resolved relationships are the pairing of *A. cumminsi* + *P. pricei* and *Rotaryus gothae* as the sister group to this pair. The resolution of *R. gothae* outside of the large polytomy is an intuitive result given the taxon sample modifications were made to long-snouted taxa. *Mattauschia laticeps* and *Mordex calliprepes* are sister taxa in 85% of MPTs, and all trematopids to the exclusion of these two taxa form a clade in 85% of MPTs. Nodal support is weak except for some non-trematopid nodes.

The mirror analysis with the same taxon treatment and the revised matrix's character sampling recovered 11 MPTs with a length of 283 steps (CI = 0.435; RI = 0.574; Fig. 13B). The strict consensus is slightly more resolved, although Amphibamiformes was not recovered as a clade. The only two resolved trematopid clades are *Acheloma cumminsi* + *Phonerpeton pricei* and the trio of *Anconastes vesperus*, *Ecolsonia cutlerensis*, and *Tambachia trogallas*; both are congruent with previous studies. *Rotaryus gothae* clusters with the other long-snouted taxa in 81% of MPTs, *Mattauschia laticeps* and *Mordex callipreples* are sister taxa in 81% of MPTs, and *Fedexia striegeli* forms a polytomy with the branches for the two resolved clades in 81% of MPTs. Nodal support has improved, including a change in Bremer support for Olsoniformes (from 2 to 4) and Trematopidae (from 2 to 3) that reaches the threshold for meaningful support.

Permutation 7. Analysis of the updated Dilkes' matrix recovered substantially more MPTs than the original analysis. With all 29 taxa, the analysis recovered 696 MPTs with a length of 169 steps (CI = 0.527; RI = 0.733; Fig. 14B), compared to 513 MPTs with a length of 163 steps (CI = 0.5460; RI = 0.7574; Fig. 14A). There is, however, an improvement in resolution in Dissorophidae in the new strict consensus. *Cacops aspidephorus* and *C. morrisi* are sister taxa to the exclusion of *C. woehri*, in contrast to the historic polytomy of these taxa, which form the entirety of Cacopinae here. Dissorophinae is largely a polytomy (not recovered as a clade in Dilkes' analysis), with *Scapanops neglecta* and *Diploseira angusta* as the earliest diverging taxa. Kamacopini is recovered in a polytomy with Cacopinae and Dissorophinae but is a subclade of Cacopinae in 75% of MPTs along with *Reiszerpeton renascentis*. Bremer and bootstrap support have generally slightly declined for nodes shared between the original and the reanalysis, and Bremer support is below the threshold of meaningful support for almost all nodes. From the majority-rule consensus, two other nodes recovered in earlier studies are identified: post-*Platyhystrix* dissorophids (77%) and that subset to the exclusion of *Aspidosaurus binasser* (77%). The resultant Adams consensus would identify a slightly different set of wildcards (*Aspidosaurus binasser* and *Platyhystrix rugosus* and not *Scapanops neglecta*) than in Dilkes' analysis, but I reran the search after removing the same four taxa that he identified as wildcards (*B. profundum*, *Conjunctio multidens*, *R. renascentis*, and *Scapanops neglecta*).

With removal of Dilkes' wildcards, the analysis recovered 40 MPTs with a length of 152 steps (CI = 0.553; RI = 0.748; Fig. 14D), in contrast to the original 27 MPTs with a length of 143 steps (CI = 0.5874; RI = 0.7839; Fig. 14C). The strict consensus is more resolved than the previous iteration but less resolved than Dilkes' equivalent topology. The relationships of *Cacops* are as with the previous iteration. Kamacopini is no longer recovered, but its nominal constituents are recovered as cacopines. In Dissorophinae, *Broiliellus olsoni* is now recovered as the earliest diverging taxon, followed by *B. reiszi* and then a polytomy of all other taxa, which differs from the original analysis (Fig. 13C). This configuration of Dissorophinae has not been previously recovered. *Acheloma cumminsi* and *Phonerpeton pricei* are now recovered as sister taxa in the strict consensus. Bremer and bootstrap support have again declined slightly for nodes shared with Dilkes' analysis. Most nodes have bootstrap support >50% except within Dissorophinae.

Permutation 8. The parallel analysis of the trematopid-focused sample in PAUP* recovered 15 MPTs with a length of 327 steps (CI = 0.511; RI = 0.574; Fig. 15A), compared to the 11 MPTs with a length of 283 steps (CI = 0.435; RI = 0.574; Fig. 15B) that I recovered in permutation #6 (reproduced from Fig. 13B). The topology is slightly less resolved, and there are noticeable differences in bootstrap support across the tree. Equivalent nodes were supported by higher bootstrap values in the PAUP* analysis; the difference from the same node in TNT ranged from 14% (Dissorophidae) to 50% (*Anconastes vesperus* + *Tambachia trogallas*). While a few nodes from the PAUP* analysis were supported by single-digit bootstrap support, most were not, and there are four nodes that rise above the 50% threshold from TNT to PAUP*. There were only a few nodes for which Bremer support changed and none crossed the threshold of 3 that is considered for "strong support." I note here that the PAUP* search took a particularly long time (27.5 hours) despite the eventual low number of MPTs and indicates the upper threshold of tractability for this matrix (23 taxa, 112 characters). A heuristic search with 10,000 random addition sequence replicates, holding 10 trees per step, recovered the same set of MPTs in just over a minute.

Permutation 9. The parallel analysis of Dilkes' (2020) original matrix with all 29 taxa and in TNT recovered 23 MPTs with a length of 157 steps (CI = 0.529; RI = 0.757; Fig. 16B), in contrast to the original study using PAUP* (513 MPTs of length 163 steps; CI = 0.5460; RI = 0.7574; Fig. 16A). The strict consensus is identical to that of Dilkes', as is the Bremer support, but bootstrap support is distinctly lower for all nodes, similar to the previous permutation. Here, the differences between the two analyses range from 4% (interestingly, this is the same *Anconastes vesperus* + *Tambachia trogallas* pair that saw an extreme difference in permutation #8) to 34% (*Kamacops acervalis* + *Zygosaurus lucius*). Five nodes dropped below the 50% threshold in the TNT analysis.

The TNT analysis of the matrix without Dilkes' wildcards recovered a single MPT with a length of 142 steps (CI = 0.585; RI = 0.780; Fig. 16D), in contrast to Dilkes' analysis in PAUP* (27 MPTs with a length of 143 steps; CI = 0.5874; RI = 0.7838; Fig. 16C). The differences relate only to resolution of polytomies recovered by Dilkes; there are no shifts in the general position of taxa. The same pattern of Bremer and bootstrap support was identified, with the latter ranging between 4% (*Anconastes vesperus* + *Tambachia trogallas*) and 38% (*Broiliellus brevis* + *B. olsoni* + *B. texensis*). Two nodes dropped below the 50% threshold in the TNT analysis.

The TNT analysis of my updated version of Dilkes' matrix with all taxa sampled recovered 44 MPTs with a length of 163 steps (CI = 0.509; RI = 0.733; Fig. 17A). Resolution has decreased across the tree with a large basal polytomy in Dissorophidae. *Aspidosaurus binasser*, *Brevidorsum profundum*, *Conjunctio multidens*, *Platyhystrix rugosus*, and *Reiszerpeton renascentis* form single branches in this polytomy. Cacopinae consists only of the three species of *Cacops*, with Kamacopini recovered as a separate clade. The one exception to the loss of resolution is that Dissorophinae is now recovered as a clade, with *Scapanops neglecta* as the earliest diverging taxon and all species of *Broiliellus*, *Diploseira*, and *Dissorophus*. Trematopidae has also lost resolution; only *Anconastes vesperus* + *Tambachia trogallas* is recovered. The Adams consensus (not depicted) would identify the same four wildcards as Dilkes (2020), as well as *P. rugosus*.

The TNT analysis without Dilkes' wildcards recovered 12 MPTs with a length of 150 steps (CI = 0.553; RI = 0.777; Fig. 17C). The tree is more resolved than in the previous iteration but does not recover Kamacopini, with the kamacopinines instead recovered as single branches of a polytomy with the clade of *Cacops*. The arrangement of Dissorophinae, with *Broiliellus olsoni* as the earliest diverging taxon, followed by *B. reiszi*, differs from both the previous iteration with all taxa sampled and from previous studies.

Discussion

The original goal of this study was to expand my previous trematopid matrix to encompass dissorophids as a means of independently testing the relationships of dissorophids and olsoniforms more broadly. This study "accomplished" that goal, but as may be apparent from a first-hand examination of the results and as I hope to make a case for here, the results of both this study and those of previous studies should be treated cautiously for a number of reasons. This discussion is therefore divided into three main sections: (1) a brief discussion of the first-hand results of the permutations performed here; (2) a broader discussion of topological disparity, identifiable sources of this disparity, and a critical examination of previous methodologies; and (3) a summary of the state of affairs in dissorophoid phylogenetics and taxonomy with some highlighted areas for future study.

Tallying topologies. This section summarizes the key findings from the various permutations that were performed in this study as they relate to the recovered topologies. It comes as little surprise that across the nine permutations that I ran here, there is little consensus; indeed, some standalone permutations recover little consensus. Trematopidae and Dissorophidae are usually recovered as clades with all of their nominal representatives. The main exception to this is in the full taxon sample (e.g., permutation #1, Figs. 6–8). *Parioxys bolli* is unsurprisingly not recovered as a definitive dissorophid, let alone as a dissorophoid (Fig. 7). The skew towards cranial characters in this matrix, a characteristic of other matrices as well, reflects the precedent of using cranial remains to differentiate taxa. Even with the expanded postcranial character sampling of this study's matrix, most characters can only be scored for a few taxa. If anything, the taxon may be the skeleton of a large trematopid; the majority-rule consensus of permutation #1A recovered *P. bolli* as a trematopid in 69% of MPTs.

A more surprising result is the consistent position of *Reiszerpeton renascentis* as an unplaced olsoniform (Figs. 6–7, 9), as it has always been recovered as a dissorophid in previous analyses (Figs. 3–4). One possibility is that this specimen is very immature and shares certain qualitative features with amphibamiforms; its original identification as a specimen of *Tersomius texensis* speaks to this. However, the consistent recovery of '*Broiliellus*' *hektotopos* outside of Olsoniformes as part of an amphibamiform grade or polytomy suggests that this is not the dominant factor. The lack of a monophyletic Amphibamiformes in most permutations likely reflects the character sampling being targeted as olsoniforms and being derived from olsoniform matrices. A different hypothesis is that full sampling of trematopids, including the rarely sampled Carboniferous taxa like *Mordex calliprepes*, draws the taxon down. Indeed, all previous analyses with *R. renascentis* have only sampled *Anconastes vesperus* and *Fedexia striegeli* for Carboniferous trematopids, and these are the youngest of the Carboniferous taxa. However, permutation #1B, which excludes these rarely sampled taxa, does not result in *R. renascentis* being recovered as a dissorophid.

The most likely scenario in my opinion is that the missing data for *Reiszerpeton renascentis* are more responsible for its peculiar position. The holotype is only a partial skull, incomplete posteriorly, and definitively lacks apomorphic ornamentation found in cacopines and dissorophines. Therefore, its combination of characters may approximate the "ancestral" olsoniform condition, even though there is no evidence of trematopid apomorphies or conditions contrary to the diagnosis of Dissorophidae. This conjecture could also account for why *Brevidorsum profundum* and *Platyhystrix rugosus* are not recovered within Dissorophidae in permutation #1B (Fig. 8). The holotype of the former is incomplete and badly preserved, relatively small, and lacks any cranial ornamentation apomorphies (Carroll, 1964a). The only semi-complete skull of the latter is badly crushed. While mostly complete longitudinally, the naris is not sufficiently preserved to be certain of its shape or the relationship of the elements that normally frame it (e.g., lacrimal; Berman, Reisz & Fracasso, 1981). It is not possible to characterize the presence or absence of osteoderms in either *B. profundum* or *R. renascentis*. I followed previous workers in scoring *P. rugosus* as explicitly lacking osteoderms (therein treating the condition of its spines as ornamentation of the spines, rather than a separate dermal ossification), a feature that sets it apart from all other dissorophids. Notably, however, Witzmann & Soler-Gijón (2010), the only published histological study of these spines, termed them as osteoderms. Dilkes' (2020) analysis of his matrix with and without osteoderm characters did result in a slightly change in topology, so the question has clear phylogenetic implications as well. Without these characters, *P. rugosus* formed a polytomy with *Aspidosaurus binasser* and a branch for all other dissorophids, rather than diverging before *A. binasser*.

There is usually poor resolution within Trematopidae except in trematopid-focused permutations, but all nominal trematopids are recovered as a clade in all permutations except in permutation #1A, with the full taxon sample and almost no resolution, and permutation #3, another poorly resolved permutation in which *Mattauschia laticeps* clusters with all other trematopids in only 88% of MPTs (Figs. 6, 10). The two permutations (#6, 8) that focused on trematopids recovered more resolution than in my previous study (Figs. 13, 15). The relationships are generally congruent with previous studies that recovered more resolution with more restricted taxon samples. *Anconastes vesperus* and *Tambachia trogallas* are frequently recovered as sister taxa, usually with *Ecolsonia cutlerensis* as the sister taxon to this pairing. *Acheloma cumminsi* and *Phonerpeton pricei* are also frequently recovered as sister taxa, usually with *Rotaryus gothae* as the sister taxon to this pairing. The relationships of the four remaining taxa, all Carboniferous in age, remains unresolved.

The resolution of Dissorophidae is quite variable, especially with respect to historical wildcard taxa or historically unsampled taxa, but Cacopinae and Dissorophinae are usually recovered in some form. The composition of Cacopinae (found in all permutations other than #1A and 3; Figs. 6, 10) is always at least the three species of *Cacops* (permutations #1B, 7; Figs. 8, 14B) but frequently includes *Anakamacops*, *Kamacops*, and *Zygosaurus* (Figs. 9, 14, 16). Kamacopini is sometimes not recovered, with its nominal constituents outside of Cacopinae (permutation #3; Fig. 10); not recovered, but with its nominal constituents within Cacopinae (permutations #1B, 5; Figs. 8, 12); or as a clade separate from Cacopinae (permutations #7, 9B; Fig. 14B, 17A). In no permutation do all three of *Anakamacops*, *Kamacops*, and *Zygosaurus* form a clade within Cacopinae (as with Dilkes, 2020, and contra Liu, 2018). Dissorophinae is a surprisingly resilient clade, being recovered in permutations that otherwise recovered very little resolution (e.g., permutations #1A, 1B, and 3; Figs. 6, 8, 10; although not in permutations #5 and 9A; Figs. 12, 16B). When recovered, it always consists of every species of *Broiliellus* (excepting '*B.*' *hektotopos*), *Diploseira angusta*, and *Dissorophus multicinctus*. This includes *B. arroyoensis*, which has never been previously sampled because the cranial sutures are entirely unknown; it is united with other nominal dissorophines here by its apomorphic ornamentation. The only instance in which another taxon is recovered as a dissorophine is permutation #7 (Fig. 14B) in which *Scapanops neglecta* is recovered as the earliest diverging taxon. This is consistent with most previous analyses other than Liu (2018), who recovered *Brevidorsum profundum*, *Conjunctio multidens*, *Reiszerpeton renascentis*, and *Scapanops neglecta* as the sister clade to the traditional dissorophines (Fig. 4B). It is also consistently very poorly resolved or only resolved with negligible nodal support, again mirroring the historical results other than Liu's.

Collectively, the results of the different permutations reflect a few influential factors. The first is taxon sampling; it is not surprising that including many poorly known taxa (permutations

#1A, 1B, 3) led to very poor resolution (Figs. 6–8, 10). This pattern was also apparent in my trematopid study in which restricting the taxon sample to that of previous studies recovered substantially more resolution than when all taxa were sampled (Gee, 2020b). Nonetheless, taxa like *Broiliellus arroyoensis* demonstrate that taxon sampling criteria must be nuanced and not rely on blanket characterizations such as "no cranial sutures known," as a handful of qualitative features may still be highly informative. The elongate trematopid nostril is another apomorphic feature that proved reliable in my previous study, even with isolated snouts (Gee, 2020b). The status of osteoderms also predictably exerts influence; as discussed above, nominal dissorophids that are recovered outside of Dissorophidae are either those for which the postcranial skeleton is not sufficient to score the presence/absence or where osteoderms are scored as being absent. Conversely, very fragmentary or uninformative taxa that clearly possessed osteoderms (e.g., *Aspidosaurus chiton*, *Nooxobeia gracilis*) were recovered within Dissorophidae. One surprise then in this regard is that the presence of tubercular ornamentation in *Iratusaurus vorax* and *N. gracilis*, a fairly distinctive cacopine apomorphy, was insufficient to draw them into Cacopinae in any permutation. The absence of this ornamentation in *Cacops woehri*, which still clusters with the other species of *Cacops*, might act as a confound, although both *I. vorax* and *N. gracilis* are some of the most fragmentary taxa sampled here (scored for <20% of characters; Table 1).

To summate, in spite of a few broadly conserved aspects (e.g., composition of Dissorophinae), there remain far more outstanding questions and uncertainties. Therefore, there is very little consensus in dissorophid intrarelationships, and as Dilkes (2020) remarked, it is somewhat surprising and perhaps concerning that there is so much disparity between previous studies that used a nearly identical character matrix. This questions whether any study, including this one, has produced a reasonably robust topology that is acceptable for use in other studies. The following sections present a more detailed discussion of my findings regarding potential methodological explanators for the persistent disparity, some of which are rather concerning and some of which may invalidate previous analyses.

The search for a consensus. Almost every living worker who has specialized in terrestrial dissorophoids in the last four decades (J. Anderson; D. Berman; D. Dilkes; N. Fröbisch; B. Gee; R. Holmes; A. Huttenlocker; H. Maddin; A.R. Milner; J. Pardo; R. Reisz; R. Schoch) has participated in dissorophid phylogenetic analysis, with only two (Fröbisch, Schoch) involved in more than one analysis. However, almost single previous analysis other than the present one directly derives from Schoch (2012), and almost every derivation is over 95% similar in character sampling, taxon sampling, and scoring to the original (Fig. 2). Two of the three direct derivations only added or subtracted taxa (Maddin et al., 2013; Schoch & Sues, 2013). The majority of cumulative changes present up through the Dilkes' derivation is the result of Dilkes adding seven new characters (cumulative changes summarized in Appendix 8). Gee et al.'s (2021) matrix is the most recent one to be published, although it is not a direct derivation, as it combined Holmes, Berman & Anderson's (2013) derivation with the amphibamiform-focused matrix of Maddin et al. (2013); accounting for elimination of redundancies, only 33 characters are carried over from the former. Fröbisch & Reisz (2012) used a slightly modified version of Polley & Reisz's (2011) trematopid matrix (Fig. 3A), although it only sampled five dissorophids. More importantly, all 53 characters of Polley & Reisz were incorporated into Schoch (2012), so Fröbisch & Reisz's matrix is very similar in character sampling, even if it is not a derivation of Schoch (2012). Schoch did not expressly state that he rescored characters but the absence of any polymorphisms in his matrix in comparison to nine in Polley & Reisz's matrix suggests as much.

The Gee (2020b) trematopid matrix and the derivation used here are also in part derived from Polley & Reisz and thus converge on the sampling of Schoch (2012), but my scoring was expressly novel for all characters.

In detailing this history, I want to emphasize that I am not advocating against the standard practice of propagating an existing matrix; there are many advantages to doing so. However, implicit in the use and propagation of a consensus matrix is the assumption that the underlying framework is largely sound. While there may be minor differences in scoring philosophy, such as whether reconstructions can be used, the matrix should obviously be as error-free as possible while maximizing the available data. If it is not, then widespread adoption of this matrix will result in widespread propagation of errors. As reflected in permutation #7 (Fig. 14, Appendices 5–6), I have concerns about the integrity of the widely propagated Schoch matrix. These findings therefore cast doubt on previous studies that used this matrix, which I outline in greater detail below.

Scoring issues. Examination of previous matrices for possible explanators of topological disparity led me to conduct a thorough survey of Dilkes' version of the Schoch (2012) matrix. I identified a large number of scores for features that are simply unknown in the given taxon (65 in total; Appendix 5). I also identified a smaller number of unscored cells that can definitively be scored from the literature (34 total) and scores that were scored for the wrong character state (30 total). I want to emphasize that the corrections I made are unequivocal errors in the sense that standard practices do not permit scoring of features that are unknown, and I did account for the datedness of some literature. While some typographical errors are to be expected in any matrix, the number (129 total erroneous scores) and pattern of these scores either suggest an intentionally non-standard coding philosophy that permits scoring of unknown features or an unusually large number of typographical errors. Most of these errors stem from either the original matrix or the first direct derivative (Holmes, Berman & Anderson, 2013), so they have been propagated through several analyses. Below I outline a few examples in detail.

Cacops provides the clearest example. For *Cacops woehri* (propagated score created by Holmes, Berman & Anderson), I identified 14 errors; in a matrix of 70–77 characters, this is a substantial amount. Ten of these relate to features that are simply not preserved (exoccipital, stapes, quadrate, postcrania). Having worked extensively on Richards Spur, from which *C. woehri* is known, I am not aware of any unpublished material of *C. woehri* that can reconcile these errors (but see Gee, Bevitt & Reisz, 2019:fig. 9.7-9.14 for an isolated jaw articulation that was assigned to Dissorophidae cf. *C. woehri*). At least the postcranial scores could not have been taken from the original scoring, Fröbisch & Reisz (2012), because that matrix has zero postcranial characters. One of the 14 errors is scored for the wrong state (tubercular ornamentation present); *C. woehri* lacks the tubercular ornamentation found in other historic cacopines (Fröbisch & Reisz, 2012; Fröbisch, Brar & Reisz, 2015; Gee, Bevitt & Reisz, 2019). Notably, of the 14 erroneous scores, 13 were scored identically to both of the other species of *Cacops*; the last score was only the same as *C. morrisi* (*C. aspidephorus* was left unscored). In fact, there were no characters for which the three species differed other than in the distribution of missing data. This false homogeneity certainly accounts for the unresolved relationships of the three species in all previous analyses (Figs. 4–5), despite the many features that separate them taxonomically (Fröbisch & Reisz, 2012; Gee & Reisz, 2018a) and the recent questioning of whether *C. woehri* is even properly placed in the genus (Anderson, Scott & Reisz, 2020). The most reasonable conclusion is that scores for *C. woehri* were "assumed" on the basis of the phenetic placement of the taxon within *Cacops*. This approach is problematic since a phylogenetic analysis should inform taxonomy, rather than vice versa, and the notable differences of *C. woehri* from the other two species suggests that it may have differed in other skeletal attributes that are not presently known for it.

Cacops aspidephorus also corroborates the hypothesis that scores have been "assumed." The taxon is famously known for the total absence of any knowledge of the cranial sutures (inclusive of the palate and braincase) due to poor preservation. Only in the past year has this gap been addressed (Anderson, Scott & Reisz, 2020). However, since Schoch's original matrix, there have been no fewer than 15 scores for which the sutures would have to be known in order to score the taxon. These scores have not been adjusted since the original scoring by Schoch, who did not personally examine the material (as indicated in his study). It is also telling that while Schoch reconstructed the cranial anatomy of almost every dissorophid with their respective known sutures, that of *C. aspidephorus* is only a silhouette (see figures 6 and 7 therein). While Anderson, Scott & Reisz's (2020) description corroborated many of these scorings, at least five original scores were shown to be errors (e.g., parasphenoid dentition, exoccipital-postparietal contact). One originally unscored character (postorbital-supratemporal) should have been scoreable if other cranial suture characters could have been scored. These erroneous scores are identical to those of *C. morrisi* and would have to have been "assumed" from this taxon (*C. woehri* was not sampled in the original matrix). This is further corroborated by the observation that *Cacops morrisi* does not show a strong pattern of erroneous scores, probably because it was the exemplar from which scores for the two other species were "assumed"; only one score is clearly erroneous: the iliac blade. No pelvis is known for the taxon, but this could have been "assumed" either based on the fact that the derived state is an olsoniform apomorphy or based on Williston's description of *C. aspidephorus*.

As discussed in the Methods and Appendix 2, the previous scoring for *Kamacops acervalis* cannot be fully corroborated by the literature. This taxon's cranial sutures have never been described or figured, but it is scored for many characters that require these sutures to be known and is specifically scored almost identically to the three species of *Cacops*. The only reconstruction of the skull roof of *K. acervalis* in dorsal view (Schoch, 2012:fig. 6) lacks sutures, like *C. aspidephorus*. If sutural characters could be scored for these taxa, it is unclear why they were not reconstructed with them. The scoring of my matrix is based on my assumption (justified, in my opinion) that the sutures are not actually known since the data to support their characterization have never been published. *Broiliellus*, with four commonly sampled species, does not clearly show evidence of widespread "assumed" scores. *Broiliellus olsoni* does have a few erroneous scores for elements that are not preserved, but no pattern is apparent for other species. *Broiliellus brevis* and *B. texensis* are difficult to assess from the literature given their datedness (Williston, 1914; Carroll, 1964a; DeMar, 1966b). These descriptions are not well-suited for scoring due to their brevity and limited figures. Schoch indicated that he personally examined material of both taxa, and therefore, it is likely that he was able to score features from personal examination that are not mentioned in the literature, contrary to *C. aspidephorus*.

Some of the errors that I identified are related to how characters are defined, something that Dilkes (2020:20-22) discussed at length. For example, the position of the jaw articulation is referenced by the position relative to the exoccipital facets, yet the character has been scored for some taxa in which the jaw articulation or the exoccipitals are unknown (e.g., *Cacops woehri*, *Scapanops neglecta*, *Tambachia trogallas*). It was probably assumed that the occiput was vertical (like in most temnospondyls), and therein that the occipital margin of the postparietals is an acceptable proxy for the exoccipitals' posterior extent. If this working assumption is widely used, the character should have been redefined (as I did here; Appendix 1), otherwise it could lead to asymmetric scoring where one worker operates with this unstated assumption and thus scores the character, but another worker operates strictly based on the character as defined and thus leaves it unscored. The other set of characters for which this applies are those related to the relative length or height of different regions of the skull (e.g., suborbital bar height, distance between otic notch and orbit). These are all defined by relation to the midline skull length, yet a number of taxa whose skulls are incomplete posteriorly were scored for these characters (e.g., *Broiliellus olsoni*, *Reiszerpeton renascentis*). These characters could be redefined based on a proxy to facilitate scoring of incomplete specimens (something that Liu, 2018, attempted, but that Dilkes, 2020, reversed). As defined, these characters cannot be scored from such specimens.

Certain characters also seem more susceptible to either "assumed" scoring, or in some instances, a peculiar lack of scoring. The best example of the latter is how exoccipital-tabular contact (only found in *Sclerocephalus* in the matrix) is often scored, but exoccipital-postparietal contact is not. This is in spite of frequent explicit description and figuring of the exoccipital-postparietal contact and the lack of an exoccipital-tabular contact. Some scores here also appear to have been "assumed" based on a taxon's broader affinity (e.g., to Dissorophidae). For example, a prefrontal-postfrontal contact is not found in any dissorophid and only in the earliest appearing trematopids (not sampled in Schoch's matrix or any derivation thereof). *Anconastes vesperus* is scored as lacking this contact, yet no specimen preserves the medial margins of the orbit (Berman, Reisz & Eberth, 1987). The dorsal quadrate process (a xerodrome feature as scored) is another example; several taxa without complete (or any) quadrates are scored as having this feature (e.g., *Cacops woehri*).

It is worth pointing out that many of the original erroneous scores, whether a typographic error, an assumption, or an inference, were not necessarily unjustified. It is reasonable to predict, for example, that *Cacops morrisi* would have an expanded iliac blade, an olsoniform synapomorphy. However, this feature has yet to be positively identified in *C. morrisi* and should not be scored as such. It is simply unknown. A phylogenetic analysis is a test of hypotheses that goes beyond the historical phenetic frameworks that were not only subject to, but predicated on, each worker's personal conceptions of relatedness. While a phylogenetic analysis may be a test of inferences, it is not a test that can be based on inferences – it is a test only properly based on strict observations. I am under no illusions that phylogenetic analyses are unbiased or completely objective – taxon sampling and character construction are just two ways in which workers' biases can be imposed upon the analysis. But there is an implicit aim for minimizing biases when conducting these analyses, and scores that are simply inferred based on phenetic taxonomic placement or previous phylogenetic placement are the opposite. Correcting for these as I have done has predictably reduced resolution and nodal support. While loss of resolution and nodal support is an unfavorable outcome, an analysis based only on what is properly observable is the only truly defensible topology. It is inherently a more accurate representation of both relationships and the confidence in which they are resolved. Relationships recovered from inferred "observations" are spurious. A lack of resolution does not necessarily indicate that the matrix is compromised or poorly constructed, and workers should not tinker with the matrix in a way that produces resolution at the cost of data integrity. The sampled characters could capture all of the historical characters that were incorporated into phenetic taxonomy yet be insufficient to recover statistical support for relationships. Such a possibility is inherently tied to the data available for each taxon, and therein, to the incomplete fossil record.

Slippery slope. The concerns I outlined in the matrix of Schoch (2012) and its derivations are not exclusive to this "family" of matrices. The 70 characters from Schoch's (2012) matrix were carried over to Schoch's (2018a) matrix, which broadly samples dissorophoids (Fig. 2). Presumably, the scores for the 10 taxa that are sampled in both matrices were also propagated; this appears to be the case based on a random assessment of cells that I corrected (i.e. the same erroneous scores are found in both matrices). The taxon sample of Schoch's (2018a) matrix was skewed towards amphibamiforms (only eight olsoniforms are sampled), but this matrix has been expanded in four studies (Atkins, Reisz & Maddin, 2019; Gee & Reisz, 2019; Schoch, Henrici & Hook, 2020; Schoch & Milner, 2021), three of which added olsoniforms. What appears to be the same matrix was also used by Schoch & Witzmann (2018) in their study of the micromelerpetid *Limnogyrinus*; this study preceded the online publication of Schoch (2018a) by a few weeks.

The densest taxon sampling with respect to olsoniforms is that of Atkins, Reisz & Maddin, but as far as I can discern, the scores for the first 70 characters for almost all newly added olsoniforms (*Anconastes, Aspidosaurus*, *Brevidorsum*, *Kamacops*, *Platyhystrix*, and the "Rio Arriba" and "Admiral" taxa) are taken directly from Schoch (2012). This would explain why the referred specimen of *Conjunctio multidens* is still treated as the "Rio Arriba Taxon," separate from the holotype, and why *Scapanops neglecta* is still termed the "Admiral Taxon"; both terms went into disuse following Schoch & Sues (2013). Therefore, the same erroneous scores present in Schoch (2012) would also be present in Atkins, Reisz & Maddin's matrix, which I again confirmed based on a random examination of equivalent cells that I corrected. Workers seeking to expand any version of Schoch's (2018a) matrix should carefully examine the matrix to assess the fidelity of scores in order to avoid the same issue of propagation of dubious scores. To end this section, I want to emphasize that my discussion of previous matrices' scores is not meant as overt criticism of other workers for the sake of being critical (it was not even part of my original study design), nor is it under any assumption that I or any other work produce entirely infallible work. It is instead meant to highlight that historic practices have produced a topology that is not reproducible under best practices (e.g., scoring only based on observed features), with the topology resulting from correction of errors being noticeably different.

The treatment of polymorphisms. The treatment of polymorphisms remains a contentious topic in phylogenetics (e.g., Wiens, 1999). Polymorphisms are generally rare in temnospondyl matrices; it was not until Liu (2018) that polymorphisms were introduced into a dissorophid matrix, and it was only for *Conjunctio multidens*. Dilkes (2020) subsequently introduced one polymorphic scoring for *Dissorophus multicinctus*. While some of this owes to the singleton representation of many taxa, there are also examples of incontrovertible biological variation within a single individual (e.g., postorbital-supratemporal contact in *Phonerpeton pricei*) that were not scored; this specific example is odd because Schoch (2012) explicitly called out this polymorphism (p. 128 therein) yet did not score it as such. A second example is his mention of the polymorphic state of the intertemporal in *Sclerocephalus*, another sampled taxon (p. 128 as well). In contrast to this propagated matrix, polymorphisms are widespread in my matrix; at the species-level, there are 52 polymorphisms.

It has historically been assumed that polymorphic characters are less reliable for inference (e.g., Wiens, 1995). Indeed, comparisons of matrices with polymorphisms with the same matrices without polymorphisms recover distinctly different topologies (e.g., Trinajstic & Dennis-Bryan, 2009; Watanabe, 2016; Garbin, Ascarrunz & Joyce, 2018). Nonetheless, representing intraspecific variation in some form is an oversimplification of the data - proper representation is essential, even if it comes at the expense of topological resolution. Furthermore, analysis of both simulated and empirical datasets has demonstrated that failing to score polymorphisms may in fact decrease accuracy (e.g., Wiens & Servedio, 1997, 1998; Wiens, 1998; Trinajstic & Dennis-Bryan, 2009). Therefore, there is no strong *a priori* standing for intentionally omitting polymorphisms. Numerous strategies for approaching polymorphisms have been discussed (e.g., Kornet & Turner, 1999; Wiens, 1999), but many are not well-suited for paleontological datasets. For example, scoring based on the frequency with which a certain state appears will require an appreciable sample size that is rarely met for most extinct tetrapods. The use of an alternative character state for polymorphisms (Wiens, 2000) is one option that does not rely on a large sample. However, no previous olsoniform study has utilized this approach in scoring (the use of 'a' for polymorphisms by Polley & Reisz seems to be only for visual alignment of the typeset matrix's columns). There is no consensus among any subset of workers as to the treatment of polymorphisms, but it should be emphasized that whatever approach is being employed should be explicitly stated, and ignoring polymorphisms should be discouraged.

Conjunctio multidens merits discussion here because it is scored for the most polymorphisms in derivations of the Schoch (2012) matrix. The holotype and the referred specimen historically known as the Rio Arriba Taxon (UCMP 40103) were historically separate OTUs and are superficially somewhat different, which may reflect that the holotype is nearly twice as large. Schoch & Sues (2013) did not report their new composite OTU of these two specimens, so the composite OTU currently in use is that of Liu (2018). There are five polymorphisms for *C. multidens*: interorbital width (23); tabular process (46); preorbital-postorbital ratio (52); tabular horn (64); and pointed snout (67). Two of these characters (23, 52) are related to skull proportions, which conceivably could be ontogenetically related. Another two (46, 64) relate to the same part of the tabular, and the first of these is explicitly known to be ontogenetically related in some dissorophids like *Cacops*. Any workers continuing to use this matrix should consider rescoring these with an eye towards ontogeny, as I did here, since polymorphisms are not scored for taxa represented by a much narrower size range of specimens that capture anatomical variation (e.g., the tabular horn of *Cacops morrisi*).

The last character (pointed snout) appears to be a typographic error introduced by Holmes, Berman & Anderson (2013). Per Schoch, a pointed (not parabolic or square-shaped) snout is only found in *Broiliellus, Dissorophus*, and *Scapanops* ("Admiral Taxon"); he scored it as absent in the holotype and the referred specimen of *Conjunctio multidens*. The change by Holmes, Berman & Anderson (2013) was only identified by examining their matrix; they did not list it in the text despite listing other scoring changes, further evidence that it is a typographic error. The final line of evidence is that the "Admiral Taxon" was scored as lacking a pointed snout in this derivation. The holotypes of *C. multidens* and *Scapanops neglecta* were scored as successive lines and could have been misread (Schoch's matrix was available only as a typeset figure). I hypothesized that this error could account for the shift of *C. multidens* from the base of Eucacopinae in Schoch & Sues (2013), who presumably scored the composite as lacking this feature (as in Schoch, 2018a), to the base of Dissorophinae in Liu (2018), which scored *C. multidens* as polymorphic. Since this was a simple test, I corrected the scoring of *C. multidens* from '0&1' to '0' and that of *Scapanops neglecta* from '0' to '1' and reanalyzed Liu's matrix. The MPT length increased by one step, but the same number of MPTs were recovered (six), and the strict consensus topology remained unchanged, indicating that at least this one possible propagated error is not the explanator of the unique topology recovered by Liu.

Software selection. One of the relatively understudied factors that may produce conflicting topologies between studies is the choice of software. While it is well-known that different programs often produce different topologies, the actual differences are rarely examined. As noted in the Methods, comparisons of previous studies suggest that the choice of PAUP* versus TNT is exerting a meaningful influence on dissorophid topology. Permutations #8 and 9A of this study identified a few topological differences between strict consensus trees recovered by the different programs (Figs. 15–16), but there is no clear pattern. PAUP* recovered more resolution in the trematopid parallel (Fig. 15), whereas TNT recovered more resolution in the parallel of Dilkes' (2020) original matrix (Fig. 16). In both instances, the increased resolution is compatible with the polytomies of the less resolved tree.

Because some of the inherent differences between programs (e.g., default branch collapsing rule, rounding rule for nodal frequency) do not correlate with biological principles that would clearly support using one parameter over another (compared to a parameter like character ordering), the topology of one program is not more "biologically accurate" or an "overestimate." These specific programs have recovered different topologies for the same matrix in other studies (e.g., Schoch, 2013, recovered less resolution using TNT), and this disparity will confound comparisons between studies that used different programs. In the future, it would be preferable if workers would use the same program as the previous iteration of the same foundational matrix to be properly comparative or to restrict any comparisons made with analyses that used a different program.

Support metrics. In theory, support metrics could be one means of comparing disparate topologies of the same matrix that were recovered from different programs. In permutation #8 (Fig. 15), all of the nodes that were recovered in PAUP* but not in TNT had Bremer support of 1 and bootstrap support below 40%. The same pattern (with much lower bootstrap) occurred in permutation #9A as well (Fig. 16). Unfortunately, reporting of support metrics for dissorophid studies is rather asymmetrical (Table 3). Holmes, Berman & Anderson (2013) and Schoch & Sues (2013) did not report any support metric. Maddin et al. (2013) reported bootstrap values, whereas Liu (2018) reported Bremer values. Schoch (2012) and Dilkes (2020) reported both metrics. There are thus two issues: (1) it is not possible to directly compare a node's Bremer support in one study to the equivalent node's bootstrap support in another study; and (2) even if the same metric is reported, if the analyses were conducted in different programs, the nodes are not necessarily properly equivalent (e.g., they may not contain the same subset of taxa). Therefore, the only proper comparison is between Dilkes' PAUP* analysis and Schoch's PAUP* analysis (Table 3), which shows that both Bremer and bootstrap have declined for dissorophid nodes, sometimes substantially so (e.g., *Kamacops* + *Zygosaurus*).

Reporting of at least one support metric is standard practice in contemporary phylogenetics, so in my opinion, studies without any support metrics should be regarded skeptically. As aptly put by Sanderson (1995:299), "without some assessment of reliability, a phylogeny has limited value. It may still function as an efficient summary of available information on character-state distributions among taxa…but it is effectively mute on the evolutionary history of those taxa…" Although expressed more in the context of standard parsimony bootstrapping, this stance is also valid for Bayesian analyses; not reporting posterior probabilities is concerning, especially because posteriors tend to overestimate support (Alfaro, Zoller & Lutzoni, 2003; Douady et al., 2003; Erixon et al., 2003; Simmons, Pickett & Mia, 2004; Zander, 2004) and especially with all-clades compatible trees, which force full resolution.

Aiming to achieve resolution regardless of support or interpreting topologies without consideration of support is problematic because it encourages "tinkering" with the matrix to produce either some semblance of resolution where none previously existed or to produce a topology consistent with previous analyses or with the authors' preconceived notions. The same is true of dismissing studies that recover poor resolution or that only emphasize well-supported nodes. It is always better to conservatively derive conclusions from only well-supported nodes rather than basing them on poorly supported, possibly spurious relationships. This point is salient here because nodes of the in-groups of this study's permutations tended to be poorly supported. Some of this is clearly associated with the sampling of poorly known taxa, reflected in the weakly resolved strict consensus topologies (e.g., Figs. 6, 8, 10). However, it bears noting that in previous studies of both dissorophids and trematopids, most dissorophid nodes fail to meet the threshold for meaningful support for at least one metric (Tables 3–4). My identification of widespread "assumed" scores also questions the robusticity of nodes (like *Cacops*).

One other point to emphasize is that bootstrap support in any TNT analysis is surprisingly low – usually below 50% – even for many nodes that have strong Bremer support, which is hardly unique to this study (see Schoch, 2013, and other studies cited below). Many nodes here have bootstrap support of <10%, and some nodes are not even recovered (<1% of bootstrap replicates); I have personally never run a PAUP* analysis in which a node recovered in the strict consensus was not recovered in the bootstrap tree. Conversely, some nodes were not recovered in the strict consensus topologies of this study were recovered in a small (<20%) of bootstrap replicates; these tended to be historical relationships (e.g., *Acheloma cumminsi* + *Phonerpeton pricei*). This may relate to limitations of TNT, which does not allow the user to define additional parameters of the heuristic search when bootstrapping (presumably TNT uses its default heuristic search parameters: 10 replicates, holding 10 trees per replication, and with TBR), in contrast to PAUP*. The weak support of these nodes underscores the essentiality of reporting support metrics alongside the topology. A cursory survey of recent temnospondyl studies that used TNT reveals three main clusters: (1) studies that do not report any support metrics (e.g., Liu, 2016; Schoch, 2018b, 2019; Schoch & Voigt, 2019; Schoch, Henrici & Hook, 2020; Schoch, Werneburg & Voigt, 2020; Schoch & Milner, 2021); (2) studies that only report Bremer support (e.g., Marsicano et al., 2017; Schoch, 2018a); and (3) studies that report the same pattern of weak bootstrap support within the in-group, even for nodes with very strong Bremer support (e.g., Eltink et al., 2016, 2017; Marzola et al., 2017; Pacheco et al., 2017; Chakravorti & Sengupta, 2018; Eltink, Schoch & Langer, 2019).

Phylogenetic relationships of olsoniforms.

A defensible consensus. The above discussion has cast substantial doubts on essentially all facets of olsoniform phylogenetics, ranging from topological differences between studies to substantial errors introduced in the character matrices to disparity between programs and in reporting of support metrics. Clearly there are many more unknowns than resolved quandaries that will require significant work to address. Given this, what can be confidently concluded regarding the phylogenetic relationships of Olsoniformes?

The monophyly of Olsoniformes, Trematopidae, and Dissorophidae is universally recovered and well-supported. The only previous study with appreciable olsoniform sampling that did not recover Olsoniformes was Fröbisch & Reisz (2012); the dissorophid sample (five species) is instead more closely related to the terrestrial amphibamiforms (historical 'amphibamids'). Limited sampling may also explain the paraphyletic Olsoniformes of Marjanović & Laurin's (2019) analysis of early tetrapods, which only sampled four taxa (*Acheloma cumminsi*, *Broiliellus brevis*, *Ecolsonia cutlerensis*, *Phonerpeton pricei*).

The relationships of trematopids remain poorly resolved regardless of the improved resolution in the new analyses (Figs. 13, 15). The only node that is almost always recovered and with good Bremer and bootstrap support is *Acheloma* + *Phonerpeton* (usually *A. cumminsi* and *P. pricei*). The pairing of *Anconastes vesperus* and *Tambachia trogallas* is also recovered in most studies, but it generally has low Bremer and bootstrap support (Table 4). Relationships of other taxa seem to be highly susceptible to sampling of other trematopids, as I previously noted (Gee, 2020b). For example, *Rotaryus gothae* is usually recovered as the sister taxon to *Acheloma* + *Phonerpeton* (Figs. 13, 15), but when *R. gothae* is excluded, *Fedexia striegeli* can shift up from the base of Trematopidae to become the sister taxon to the long-snouted taxa (Fig. 12). *Ecolsonia cutlerensis* remains a trematopid regardless of whether the sampling focuses on dissorophids, on trematopids, or on olsoniforms in general.

The classic concept of dissorophid relationships is a base of *Platyhystrix rugosus* and *Aspidosaurus binasser* and two higher nested subfamilies, Cacopinae and Dissorophinae. Although *P. rugosus* is usually recovered as diverging first, the nodal support for all post-*Platyhystrix* dissorophids is usually weakly supported, and it appears linked to the interpretation of osteoderms (or lack thereof) in *P. rugosus* (see Dilkes, 2020:fig. 12B). Cacopinae consists of at least *Cacops* and usually the three sampled middle Permian dissorophids (*Anakamacops, Kamacops, Zygosaurus*). However, the intrarelationships remain poorly resolved (e.g., Liu, 2018; Dilkes, 2020; Figs. 14, 16), and the erroneous scorings found in other matrices are not the only confound; the extremely fragmentary nature of *Zygosaurus* (historically scored the same as *Kamacops* for all overlapping characters) and the loss of its holotype are probably the more pressing matter. The closer relationship of *C. morrisi* to *C. aspidephorus* than to *C. woehri* that I recovered for the first time is in agreement with qualitative comparisons and diagnoses of these species. The composition of Kamacopini and whether it is even a clade (Figs. 13D, 16) remains unresolved. Dissorophinae always consists of at least *Broiliellus* and *Dissorophus*, and the newly named *Diploseira* also seems to be a stable component. However, the intrarelationships of these taxa remain poorly resolved; there are either large polytomies or very poorly supported resolution (Figs. 6–12, 14, 16–17). *Broiliellus arroyoensis*, historically not sampled, is recovered as a dissorophine based on its ornamentation, but it cannot improve the resolution of Dissorophinae since it lacks cranial sutures. The placement of *Brevidorsum profundum*, *Conjunctio multidens*, *Scapanops neglecta*, and *Reiszerpeton renascentis* is hardly resolved, and they should only be considered as unplaced dissorophids (contra Schoch & Milner, 2014, who consider all four as cacopines).

A summary of Dissorophidae. This section discusses the state of affairs with an eye towards future work. Having previously discussed the state and prospects of trematopid research (Gee, 2020b; see also, Milner, 2018), I now focus on dissorophids, summarizing the present state of knowledge for the four subclades (Aspidosaurinae, Cacopinae, Dissorophinae, and Platyhystricinae) and highlighting future areas in need of redress that will hopefully help to refine phylogenetic analyses.

The status of Cacops. *Cacops* comprises three species: *C. aspidephorus* (type species), *C. morrisi*, and *C. woehri* (Fig. 18). For over a century, the cranial morphology of *C. aspidephorus* was largely unknown, in stark contrast to the Richards Spur material of *C. morrisi* and *C. woehri* (Reisz, Schoch & Anderson, 2009; Fröbisch & Reisz, 2012; Fröbisch, Brar & Reisz, 2015; Gee & Reisz, 2018a; Gee, Bevitt & Reisz, 2019). Some previous analyses have surprisingly failed to recover a monophyletic *Cacops*, and all others could not resolve their intrarelationships (Fig. 18). In fact, Dilkes (2020) is the only study to recover a monophyletic *Cacops* with all three species sampled (Fig. 18J); while bootstrap support was strong (>70%), Bremer support was not (1).

The historic results are surprising given the stark dissimilarity of *Cacops woehri* to the other two species. Anderson, Scott & Reisz (2020) questioned whether *Cacops woehri* is properly placed in the genus, a suspicion that I agree with. My matrix is the first to resolve the interrelationships of the three species, with *C. woehri* as the sister taxon to the pair of *C. aspidephorus* and *C. morrisi* (Figs. 7–11), although this relationship is recovered with the updated version of Dilkes' matrix (Fig. 14), which substantially alters scores of this genus in particular. This topology cannot differentiate between a scenario in which *C. woehri* truly belongs in *Cacops* and one in which it is a different genus that is closely related to *Cacops*. The lack of postcrania hinders this discussion but also places an emphasis on the revision of *Parioxys ferricolus*, which Schoch & Milner (2014) note is similar to *Cacops*. The few photographs and early descriptions of *P. ferricolus* (Moustafa, 1955a, 1955b) do not indicate the presence of the tubercular ornamentation found in other cacopines, which could indicate that *C. woehri* is either closely related to, or synonymous with, *P. ferricolus*. The latter has long been marginalized in the literature, so it has not usually been compared to dissorophids, including by Fröbisch & Reisz (2012) in naming *C. woehri*.

The status of Broiliellus. *Broiliellus* is the most speciose dissorophid, with five valid species: *B. arroyoensis*, *B. brevis*, *B. olsoni*, *B. reiszi*, and *B. texensis* (Williston, 1914; Carroll, 1964a; DeMar, 1967; Holmes, Berman & Anderson, 2013). Even with the exclusion of "*B.*" *hektotopos*, the concept of *Broiliellus* remains convoluted (Fig. 19). In all previous analyses but one, the sampled species of *Broiliellus* do not form a clade. The one analysis that does recover a clade only sampled two species (Schoch & Sues, 2013; Fig. 19B).

Perhaps the most outstanding issue is that most species of *Broiliellus* have also not been (re)described in decades. The type species, *B. texensis*, has never been revised since Williston's (1914) original description (but see DeMar, 1966b:fig. 4). Material of *B. olsoni* is neither substantial nor well-preserved, and that of *B. arroyoensis* has no identifiable cranial sutures (DeMar, 1967). As I previously noted, descriptions of *B. brevis* and *B. texensis* are dated, short, and with limited figures (Williston, 1914; Carroll, 1964a). Isolated parts of the anatomy (e.g., LEP) are occasionally revised in comparative discussions (e.g., Bolt, 1974b; Dilkes, 2020), but at least the type species would benefit from a thorough redescription with contemporary photographic methods. There are no modern photographs of any of these species other than a cropped palatal view of *B. brevis* (Witzmann & Werneburg, 2017:fig. 13B), and as a result, some data exist only as scores in matrices that are probably based on personal observations that cannot be substantiated from the literature alone.

A detailed revision of the entire genus might recover a monophyletic *Broiliellus*, but this possibility seems unlikely at present. One possibility is that these taxa appear morphologically disparate in part because they are differently sized (i.e. this may be partially confounded by ontogenetic disparity). However, it seems more likely that some of the species will need to be placed in novel genera, perhaps all of them other than the type species. The present topological instability and lack of resolution does not allow for a confident determination of which taxa warrant reassignment or whether any subset of *Broiliellus* might form its own clade. Therefore, I refrain from erecting novel genera for the non-type species and recommend the use of quotation marks for these species.

The status of Aspidosaurus. This taxon has long been convoluted and likely represents a wastebasket taxon encompassing a semi-conserved osteoderm morphotype (Schoch & Milner, 2014). Most of the species are represented only by fragmentary isolated material that cannot even be determined to be valid without a good understanding of axial variation (if such variation exists). With the loss of all material of *Aspidosaurus chiton*, the functional representative is *Aspidosaurus binasser*, which preserves substantial axial variation, at least as interpreted. This discussion addresses this taxon and its peculiar mosaicism as part of this broader discussion of the state of affairs within Dissorophidae.

Aspidosaurus binasser is known only from the holotype, a partial skull (in several pieces) and numerous osteoderms and vertebral fragments (Berman & Lucas, 2003). Among the postcranial material are three types of osteoderms; the type 2 of Berman & Lucas is the stereotypical *Aspidosaurus* morphotype, while types 1 and 3 are hyperelongate but distinct from *Platyhystrix rugosus*. The material that I show in Figure 20, collected in the late 19th century from Wichita County, TX, consists of similar spines that lack the tubercles and the curvature of the spine (at least where preserved) that define *Platyhystrix.* The style of ornamentation and the transverse compression of the spines are thus very similar to what Berman & Lucas (2003) describe as type 1 and type 3 osteoderms in *A. binasser*. Notably, if previous workers' conjecture on the Wichita County sites is correct (see Romer, 1928:80; Romer 1935:1617; Milner & Schoch, 2013:116), the localities that the newly reported specimens were collected from are in the lower-middle part of the Wichita Group (Nocona-Petrolia Formations), much lower in section than the type locality of *A. binasser* (Arroyo Formation at the base of the Clear Fork Group). While stratigraphic occurrence is not diagnostic in a taxonomic sense, it is highly informative for dissorophid taxonomy. Despite a continuous record of the clade throughout the early Permian of Texas, no taxon is known to extend beyond one formation-level unit. At the time of the description of *Aspidosaurus binasser*, the type 1 and type 3 osteoderm morphotypes had never been reported from another locality, let alone from another formation. This implicitly augmented the cranial-postcranial association because it suggested that these types were not like the stereotypical *Aspidosaurus* morphotype or like *Platyhystrix* – almost always fragmentary, isolated postcrania with a relatively wide stratigraphic range. Material of these taxa is often found at the same sites as cranial material of other dissorophids or temnospondyls, but there is usually not an assumption that the postcrania pertain to an isolated skull simply because there are no duplicated skeletal regions. The new observation that the type 1 and type 3 morphotypes appear much lower in section suggests that these purportedly diagnostic morphotypes might in fact belong to a taxon (or taxa) that has a similarly skewed fossil record.

If there was direct articulation between the cranial and postcranial remains attributed to the holotype of *Aspidosaurus binasser*, the question could be settled quickly. However, there is no direct articulation between the preserved occiput and any of the postcrania. Berman & Lucas (2003) gave no indication as to the nature of the locality, such as the distribution or association of remains. Their mention of indeterminate synapsid material is taken to mean that no other distinct dissorophid was identified. Secondly, despite the preservation of the occiput and enough presacral vertebrae to estimate at least 20 positions, neither the atlas nor axis were identified. Thirdly, there is no direct articulation between any two of the three osteoderm morphotypes; they are either isolated fragments or short blocks with only one type. The same applies to the newly reported material. Lastly, no other dissorophid preserves the same stark variation along the axial column purported for *Aspidosaurus binasser* (Berman & Lucas, 2003 argued for some variation in *Aspidosaurus chiton* based on Broili, 1904), but numerous taxa preserve essentially no variation in either osteoderms or vertebrae throughout the presacral column (e.g., *Broiliellus*, *Cacops*, *Dissorophus*). Therefore, the cranial-postcranial association essentially hinges on the assumption that there is likely only one dissorophid at any given site.

Berman & Lucas (2003:244) indeed argued that "there is no reason to suspect more than one individual is represented." Prior to 2003, there were almost no localities with more than one named dissorophid (e.g., Coffee Creek / Romer's locality 34), which supported the assumption that dissorophid-bearing localities preserve only one dissorophid taxon (like the Cacops Bone Bed; Williston, 1910; or the Parioxys bone bed of Moustafa, 1952). Since however, the landscape has shifted drastically. Crucial among this is the recognition that multiple dissorophids co-occur at single localities, and that their skeletal representation can be highly asymmetrical. The Richards Spur locality is an excellent case study in this respect; *Cacops morrisi* is known from abundant cranial and postcranial material, and *Cacops woehri* is only known from semi-abundant cranial material. In contrast, an indeterminate dissorophine is represented only by a headless skeleton and isolated forelimb material, which I left unnamed and not associated with another taxon represented only by cranial material (*C. woehri* in this case; Gee & Reisz, 2018b; Gee, Bevitt & Reisz, 2019), and *Aspidosaurus* is represented by a single pair of articulated osteoderms (Gee, Bevitt & Reisz, 2019). Corn Hill in Archer County, TX; the type locality of *Brevidorsum profundum* and *Reiszerpeton renascentis* in Archer County; and the Archer City Bonebed are all additional examples of multi-dissorophid sites. Most dissorophid-bearing sites with only one documented dissorophid are type localities that have not produced much, if any, other tetrapod material. Collectively, these observations further the possibility that the holotype of *Aspidosaurus binasser* could really be a chimera of two taxa, one represented largely or exclusively by cranial fragments and one represented only by fragmentary postcrania.

I have not been able to examine the holotype of *Aspidosaurus binasser* myself given the present circumstances, but I doubt that I would be able to identify new evidence either definitively proving (e.g., cranial-postcranial articulation) or definitively disproving the association (e.g., identification of duplicated elements) and therein doubt that a redescription is warranted, which is why I raised these points here. Nonetheless, I believe that there is good reason to suspect that not all of the elements attributed to the holotype of *A. binasser* belong to either a single individual or to the same taxon and that the purportedly diagnostic type 1 and type 3 osteoderms are more like the stereotypical *Aspidosaurus* morphotype: one that persists for long time intervals and which is of dubious congenericity, let alone conspecificity, across its range. I do not rule out that some taxa could have been more stratigraphically extensive than others, but the appreciable fossil record of dissorophids indicates taxonomic brevity. The scoring of *A. binasser* is not greatly influenced by the cranial-postcranial association in either my matrix or that of other workers, but it would be preferable to restrict the characterization in the future if characters related to spine hyperelongation or axial variation are introduced. Chimerism of *A. binasser* would affect the validity of both *A. chiton* and *A. binasser* considering the latter's diagnosis is based only on the combination of osteoderm types. I make no ~~taxonomic~~ acts without having examined the type of *A. binasser* but highlight these issues since the interpretation has not been previously questioned.

The status of Platyhystrix. There has only ever been one species of *Platyhystrix*, so it may be surprising to see this taxon discussed. Here I focus on a matter related to the status of the holotype. AMNH FARB 4785 is a multi-taxic batch of material that was first designated as the holotype of "*Aspidosaurus apicalis*" (Cope, 1881). That taxon is of dubious validity, but the holotype of *P. rugosus*, extracted from this batch by Case in 1910 (as "*Ctenosaurus rugosus*") has retained the same number in the literature despite representing two taxa. Apparently, the *Platyhystrix* component was given a subletter designation (4785a) to differentiate them, per a collections tag with "*Ctenosaurus rugosus*" written on it, but this differentiated number never appeared in the original description or the subsequent literature. Since at least DeMar (1966b:76), the portion considered to be the holotype of "*A. apicalis*" (AMNH FARB 4785 proper) was considered lost (e.g., Bolt, 1974a; Berman & Lucas, 2003; Schoch & Milner, 2014).

During a collection visit in October 2017, I came across a specimen labeled as AMNH FARB 4785, without subletter designation (Fig. 21), and it matches the description of the holotype of "*Aspidosaurus apicalis*" instead of that for the holotype of *Platyhystrix rugosus.* The material assigned to *P. rugosus* is stated to be several neural spines, while that assigned to "*A. apicalis*" is specifically the apices ("summits") of the neural spines (Cope, 1881; Schoch & Milner, 2014), which we would now recognize as osteoderms associated with the spine. As far as I am aware, AMNH FARB 4785a has never been figured, probably because more complete specimens were figured and subsequently utilized as "proxy holotypes" for *P. rugosus* (Williston, 1911; Langston, 1953; Carroll, 1964a; Lewis & Vaughn, 1965). Williston described a spine that he compared favorably to Case's holotype, and his figure (pl. 26.1 therein) is of the stereotypical *Platyhystrix* morphology. This confirms that Case's (1911:fig. 15) illustrations of AMNH FARB 4785 represents the part that is properly "*A. apicalis*," the same subset that I examined. These are distinctly only osteoderms (and one intercentrum of questionable association), not neural spines, and they are much smaller than 11 cm in length (the listed size of one spine per Case). They are, however, in line with the size range given by Cope (less than 4 cm long and 3.5 cm wide). Therefore, as I mentioned previously (Gee, 2018), the holotype of "*A. apicalis*" (AMNH FARB 4785) is not lost. The novel revelation here is that this specimen has thus been mistaken for the holotype of *P. rugosus* (AMNH FARB 4785a), and this specimen is missing. There is no record of AMNH FARB 4785a in the museum database, nor was the specimen identified in the most recent inventory (C. Mehling, pers. comm., 2020). No personally examined specimen in the AMNH collection that was assigned to *Platyhystrix, Aspidosaurus,* or *Zatrachys* (these being frequently conflated in the early 20th century) matches the description of the holotype of *P. rugosus* save for one.

AMNH FARB 11544 is a collection of postcrania with a large number of neural spines (Fig. 22), first described, though mostly unfigured, by Berman, Reisz & Fracasso (1981). These purportedly belong to the same individual as AMNH FARB 11545, the only skull of *Platyhystrix*. The number of spines designated as the holotype of *P. rugosus* was never specified, but it is inferred that "several" is more than two, and the size of some spines of AMNH FARB 11544 is consistent with the measurements given by Case (1910). Some would certainly have been sufficient for proper comparison by Williston (1911). The collections tag indicates that AMNH FARB 4785(a) was collected by David Baldwin in 1881 from the Cutler Formation of Rio Arriba County, NM, the same formation, collector, and collection date as AMNH FARB

11544. Furthermore, Case (1910) mentioned "fragments of scapulae and limb bones associated with the holotype of *P. rugosus* are typically pelycosaurian in form," with the association deriving from his interpretation of the spines of "*Ctenosaurus*" *rugosus* as those of a pelycosaur. AMNH FARB 11544 includes three large fragments, one of which is a partial glenoid (Fig. 22D), and one of which is a limb end. These were not described by Berman, Reisz & Fracasso (1981), which implies that they also did not believe these fragments belonged to *P. rugosus*.

In my opinion, it seems quite likely that AMNH FARB 4785a was renumbered as AMNH FARB 11544, but that records of this were either not made or were subsequently lost. If the value of AMNH FARB 11545 as the only skull of *Platyhystrix rugosus* was not recognized for decades after its collection, that would explain why these two specimens were not described for a century. The postcranial material would have drawn little attention until it was identified that it articulated with the cranial material. However, there are no collection records indicating the transfer of the holotype of *P. rugosus* to a new number (C. Mehling, pers. comm., 2020). Without a record, their equivalency cannot be confirmed, as it remains possible that AMNH FARB 4785a was simply lost. Therefore, the type status designation remains with AMNH FARB 4785a, and I present the conundrum here in the hopes that perhaps other workers may be able to contribute new information to help resolve this matter.

Other dissorophids. Relevant points of the remaining taxa are collated here. *Dissorophus multicinctus*, while known from an extensive amount of material, would benefit from a systematic redescription. The osteoderms and vertebrae were described by Dilkes (2009) but were otherwise neglected since DeMar (1968). Similarly, the skull has not been redescribed since DeMar, who figured only one complete skull (MCZ 2122-1). While some studies cite Schoch (2012) for the cranial osteology, Schoch only presented a reconstruction, some of which Dilkes (2020) explicitly disagreed with (e.g., position of the jaw articulation). In addition to numerous specimens that were mentioned but not illustrated by DeMar, a number of specimens have been subsequently mentioned or photographed at a low resolution in a single profile. However, these brief references are never to a degree that permit detailed description, let alone scoring as a specimen-level OTU (e.g., MCZ 1468; Schoch & Milner, 2014:fig. 37C; MCZ 4170, MCZ 4186, and MCZ 4188; Dilkes, 2020:22).

Most of the wildcard taxa (or taxa not previously sampled) have poor prospects for resolving their relationships without new material (e.g., *Aspidosaurus novomexicanus*, *Brevidorsum profundum,* "*Broiliellus*" *arroyoensis*). A few taxa that are dissorophids only if they can be shown to be dissorophoids (*Iratusaurus vorax, Nooxobeia gracilis*) also likely have poor prospects. Neither preserves dissorophid synapomorphies (sensu Schoch & Milner, 2014), although the single series of median osteoderms in *N. gracilis* is suggestive of dissorophid affinities as Olson (1972) proposed. It seems doubtful that *N. gracilis* would represent a chroniosuchian, another clade with median osteoderms, as this group is only known in Eurasia. However, chroniosuchian material is rare and fragmentary. Recent studies have expanded their geographic range, including to the Upper Permian of Germany (Witzmann et al., 2019), where a single osteoderm-bearing vertebra ascribed to a dissorophid was reported from slightly older deposits (Witzmann, 2005). *Iratusaurus vorax* does not appear like any other temnospondyl with a closed otic notch (e.g., capitosaurs), but its description is extremely cursory, and the material is extremely fragmentary. Finally, *Parioxys bolli* may not belong to *Parioxys*, regardless of the relationship of *Parioxys ferricolus* to *Cacops*. The ilium of *P. bolli* indicates olsoniform affinities, but the remainder of the known skeleton is uninformative; the two sacral ribs that

Carroll (1964b) emphasized are not a dissorophid or an olsoniform synapomorphy. The limbs are relatively long, more like those of dissorophids, but ring-like intercentra are a feature found only in *Ecolsonia cutlerensis* and nearly so in *Acheloma cumminsi* (Olson, 1941; Berman, Reisz & Eberth, 1985; Dilkes & Reisz, 1987). Of note are lateral projections from each side of the base of the neural arch; these are otherwise found only in *E. cutlerensis* and in the type 1 vertebrae attributed to *Aspidosaurus binasser* (Berman, Reisz & Eberth, 1985; Berman & Lucas, 2003). This taxon may well prove to be a trematopid; it clustered with trematopids in 69% of MPTs in permutation #1A.

Ontogenetic disparity. Although I did not exhaustively test whether ontogenetic disparity might confound or bias the phylogenetic inference of dissorophids, this remains an open question in light of the size disparity across the clade, which is essentially an order of magnitude, greater than that observed for trematopids (Fig. 23). The temporal distribution of sizes is also non-random, as it was for trematopids. With the latter group, the earliest appearing taxon, *Mattauschia laticeps*, reached a skull length comparable to that of the much later appearing *Ecolsonia cutlerensis* (Milner, 2018), but there are other taxa between or concurrent with these occurrences of various smaller sizes. In dissorophids, all of the middle Permian taxa had skulls with a length of at least 18 cm (there are not even any individual specimens of an inferred smaller size), whereas most early Permian taxa did not exceed 12-13 cm (only three, *Aspidosaurus binasser*, *Cacops aspidephorus*, and *Platyhystrix rugosus*, exceed this). Therefore, it is possible that dissorophids did increase in size in the late stages of their evolution, perhaps correlated with the extirpation of trematopids and other large-bodied terrestrial temnospondyls (whether increased dissorophid size would be a driver or a product of other clades' extinction is unclear). While *A. binasser* and *P. rugosus* are traditionally recovered as the earliest diverging taxa (suggesting that large size could characterize most taxa, but that the majority are represented only by juveniles; Gee, 2020a), it is important to note the extremely poor Carboniferous record of dissorophids; quite possibly the earliest diverging dissorophids remain to be discovered. A third hypothesis is that only certain clades of dissorophids achieved large sizes. It is conspicuous that no dissorophine, including the well-sampled *Dissorophus multicinctus*, exceeded a skull length of 13 cm, while the other three subfamilies did. Size disparity among dissorophids could also relate to ecological differences from trematopids. In contrast to trematopids, for which there are only two localities in Europe (Nýřany, Bromacker) where two taxa co-occur, there are many localities where several dissorophids co-occur. Along with anatomical differences such as tooth count, skull proportions, and osteoderm morphology, size differences could also be predicted as a facet of niche partitioning.

The one permutation that I ran to assess this, focusing on cacopines for which numerous specimens can be individually scored, did not recover any clear signals of ontogenetic disparity. There is evidence that disparately sized specimens of the same species rarely form a clade, as seen for *Cacops morrisi* and *Conjunctio multidens*, but there is either no consensus on which size class diverges first (*Ca. morrisi*), or the larger specimen diverges first (*Co. multidens*), the inverse of the predicted outcome of ontogenetic disparity. A lack of skeletal overlap seems to produce the pattern of *Cacops woehri*, in which the holotype (partial skull) and one referred specimen (BMRP 2007.3.5, partial posterior skull) cluster even though they belonged to disparately sized individuals. Specimens of *Anakamacops petrolicus* have essentially no skeletal overlap, and an ontogenetic range was not sampled for *Cacops aspidephorus*.

In short, there remain many unknowns and confounds that limit the study of size patterns in dissorophids. In my dissertation (Gee, 2020a), I suggested that niche partitioning between life stages of a given taxon could result in a skewed sample that biases interpretations of "adult" size. For example, numerous skulls of *Cacops* between 10 and 12 cm in length are known and have thus been dubbed "adults" under a presumption of relative maturity. In fact, this size range does not come close to approximating the maximum size of *Cacops*, which could have been nearly double that size based on the single specimen of "*Trematopsis seltini*," estimated to 22 cm (=*Cacops* cf. *C. aspidephorus*; Milner, 1985). Isolated postcranial remains from Richards Spur suggest that at least one of *C. morrisi* and *C. woehri* also reached a larger size than is reflected by the cranial remains (Sullivan, Reisz & May, 2000; Gee, Bevitt & Reisz, 2019; Gee, 2020a). Intraspecific niche partitioning could have facilitated further taxic co-occurrence in addition to interspecific partitioning. As with trematopids, this remains a quandary that can likely only be resolved with additional collection, although a survey of existing collections might identify outlier datapoints (probably isolated postcrania or fragmentary cranial remains) that document larger body size than traditional proxies (e.g., complete skulls).

Considerations in backbone selection. With increasing computational abilities, paleontologists can sample broad taxonomic swaths while maintaining appreciable in-group sampling of any given clade. Technological advances have also expanded the range of analyses that can be conducted, leading to a proliferation of "big data" studies addressing macroevolutionary questions on scales that were previously untenable. Most of these studies are phylogenetically informed by an underlying backbone, the selection and design of which is obviously of great import but which is not always rationalized or explained in detail. This final section provides some preliminary comments on temnospondyl backbones in light of this study's findings.

The most widely utilized topology of Temnospondyli is the computer-assisted supertree of Ruta et al. (2007), which has been incorporated into numerous studies, usually in concert with other tetrapod (super)trees to form a larger informal supertree (e.g., Fortuny et al., 2011; Soul & Friedman, 2016; Dunne et al., 2018; Dickinson et al., 2021). It is noteworthy that this particular topology remains popular among non-taxonomic specialists, whereas temnospondyl workers tend to opt for a variety of alternative backbones. For example, Angielczyk & Ruta (2012) manually modified the topology of Ruta et al. (2007); Witzmann (2013) and Witzmann & Werneburg (2017) used the topology of Schoch's (2013) non-supertree analysis; Tarailo (2018) used Schoch (2013) as the large-scale backbone, with additions from Ruta et al. (2007) and Marsicano et al. (2017) for small-scale resolution; Witzmann & Ruta (2018) and Pérez-Ben, Báez & Schoch (2019) manually modified the topology of Schoch (2013); and Pardo et al. (2019) and Ruta et al. (2019) used the topology of Pardo, Small & Huttenlocker (2017).

Ruta et al.'s supertree may remain appealing in spite of its datedness because it is fully resolved and includes numerous wildcard taxa that are rarely sampled in other studies and that are highly unstable when they are sampled (e.g., *Bashkirosaurus*, *Capetus, Collidosuchus*, *Kashmirosaurus*, *Lapillopsis, Lysipterygium*, *Palatinerpeton, Parioxys*, *Peltobatrachus*, *Sassenisaurus*, *Stegops*). Of course, the fact that these taxa are excluded from analyses reflects the continued uncertainty over their placement, even in a phenetic framework, but this may only be well-known among taxonomic specialists. Some of these taxa are recovered in the proper clade in Ruta et al.'s supertree, but with uncertain relationships to other in-group taxa (e.g., *Collidosuchus*), while others remain of uncertain placement in general (e.g., *Lapillopsis*). The latter are of greater concern because there is a higher likelihood that their positions in the Ruta et al. topology are spurious. In general, this topology, while consistent in broad strokes with more recent non-supertree analyses (e.g., Schoch, 2013; Pardo, Small & Huttenlocker, 2017; Eltink, Schoch & Langer, 2019), differs markedly in some areas. Specifically for dissorophoids, branchiosaurids are accepted as nesting within the historical ‘Amphibamidae’ rather than as its sister group (e.g., Schoch & Milner, 2008; Fröbisch & Schoch, 2009); micromelerpetids are a clade at the base of Dissorophoidea rather than a grade of early diverging branchiosaurids (e.g., Schoch, 2018a); trematopids and dissorophids are sister taxa, not successively diverging branches within Dissorophoidea (e.g., Anderson et al., 2008b); *Ecolsonia* is a trematopid, not a dissorophid (Polley & Reisz, 2011; Schoch, 2018a; Gee, 2020b; this study); and *Parioxys* is probably a dissorophid, not an eryopoid (Schoch & Milner, 2014). The taxon sample is naturally outdated as well, but this manifests as what appears to be asymmetrical sampling based on the present body of recognized taxa; olsoniforms are among the undersampled clades.

These points are not meant as a criticism of the original study but rather evidence the predictable datedness of near two decades of anatomical and phylogenetic work. Nonetheless, it is clear that Ruta et al.’s supertree is no longer an accurate reflection of the consensus of temnospondyl relationships and should not be employed as such. Pardo et al. (2019) commented on potential issues of supertree construction and pseudoreplication, especially in light of newer non-supertree analyses performed by taxonomic specialists that challenge historical paradigms and that frequently contradict widely used, but more dated, supertrees. I endorse these authors’ approach to informal supertree construction (p. 11 of their supplemental file) in which they collate non-supertree topologies recovered by studies whose primary aim was to assess the phylogenetic relationships of a clade and in which they allow taxa with unresolved relationships (or that have never been included in an analysis) to be placed in a polytomy. Such an approach is preferable to enforcing resolution of dubious nature simply in order to achieve full resolution. I encourage non-specialists to consult with taxonomic experts with respect to the construction or selection of a backbone. Temnospondyli, like most other speciose clades, continues to be recovered with major areas of instability or weak support. This instability underscores the continued import not only of phylogenetic method refinement and analysis but also of the primary data collection (e.g., fieldwork, descriptive anatomy) that underpins the analysis.

Conclusions

Originally, I had intended to focus this study on expanding my character and taxon sample to broadly represent dissorophids, which I hoped would improve the resolution for trematopids as well. In the process of assessing explanators for topological differences, some of them substantial and often related more to differing degrees of resolution than to drastically different positions of taxa, this study shifted towards a focus on reproducibility and robusticity of previous ~~matric~~es. This endeavor admittedly became much more exhaustive than even I had anticipated, and like my trematopid analysis (Gee, 2020b), seems to have identified far more issues than it has resolved. In the end, this study has demonstrated that the phylogeny of Dissorophidae is not resolved, reproducible, or robust. Other key conclusions are outlined below:

1. The widely propagated matrix of Schoch (2012) contains substantial scoring errors that appear to represent “assumed” scores; these scores are for characters where the entire feature is not even preserved, let alone sufficient to be assessed (e.g., postcrania of *Cacops woehri*). These are ~~explicitly erroneous~~. Almost all of these originated early in the propagation of this matrix and have thus been carried forward into essentially every

dissorophid analysis. There are also numerous scores for taxa where complete element is required to score a character, but none is available for a given taxon (e.g., characters related to skull length for *Broiliellus olsoni*). Given the extensive number of unequivocal errors (Appendix 5), previous topologies should be treated skeptically, especially with respect to weakly supported nodes, as the corrected matrix recovers an overall less resolved topology.

2. The use of different programs and variable reporting of support metrics confounds proper comparisons between studies, but these are not the only factors that result in drastically different topologies from studies that are using largely identical character matrices. Persistent wildcards, character construction, and character scoring clearly exert strong influences as well, and a few changes to the matrix can result in drastic changes to the resultant topology. Workers should test for the effects of these phenomena (e.g., analyses with and without wildcard taxa) and clearly state and justify their preferred approaches.
3. The intrarelationships of both Dissorophidae and Trematopidae can be resolved through selective taxon sampling, but most in-group nodes fail to meet the thresholds to be considered as “well-supported” for at least one metric: Bremer decay index (> 2) or bootstrapping (> 50%). Support metrics are one means of comparing topologies produced by different studies, and resolved topologies that are reported without support metrics or with weak support should be treated skeptically.
4. The only “consensus” relationships within Dissorophidae are the early diverging position of *Aspidosaurus binasser* and *Platyhystrix rugosus*; a Cacopinae comprised of *Cacops* and probably *Anakamacops*, *Kamacops*, and *Zygosaurus*; and a Dissorophinae comprised of *Broiliellus*, *Diploseira*, and *Dissorophus*. Any worker seeking a topology for a backbone in a quantitative analysis should place all other taxa in a polytomy either above or with *As. binasser*, rather than selecting one of the many different resolved topologies that lack strong support for most nodes.

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Figure 1

Cranial reconstructions of select representatives of Olsoniformes.

(A) the cacopine dissorophid *Cacops morrisi* (after Reisz, Schoch & Anderson, 2009); (B) the dissorophine dissorophid *Dissorophus multicinctus* (after Schoch, 2012); (C) the long-snouted trematopid *Acheloma cumminsi* (after Dilkes & Reisz, 1987; Polley & Reisz, 2011); (D) the short-snouted trematopid *Ecolsonia cutlerensis* (after Berman, Reisz & Eberth, 1985). Not to scale.

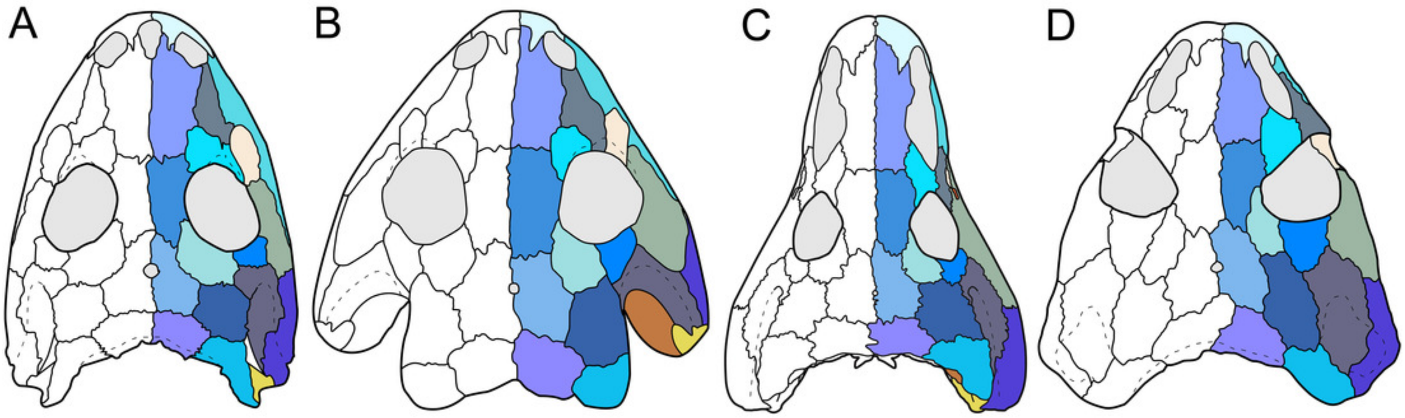
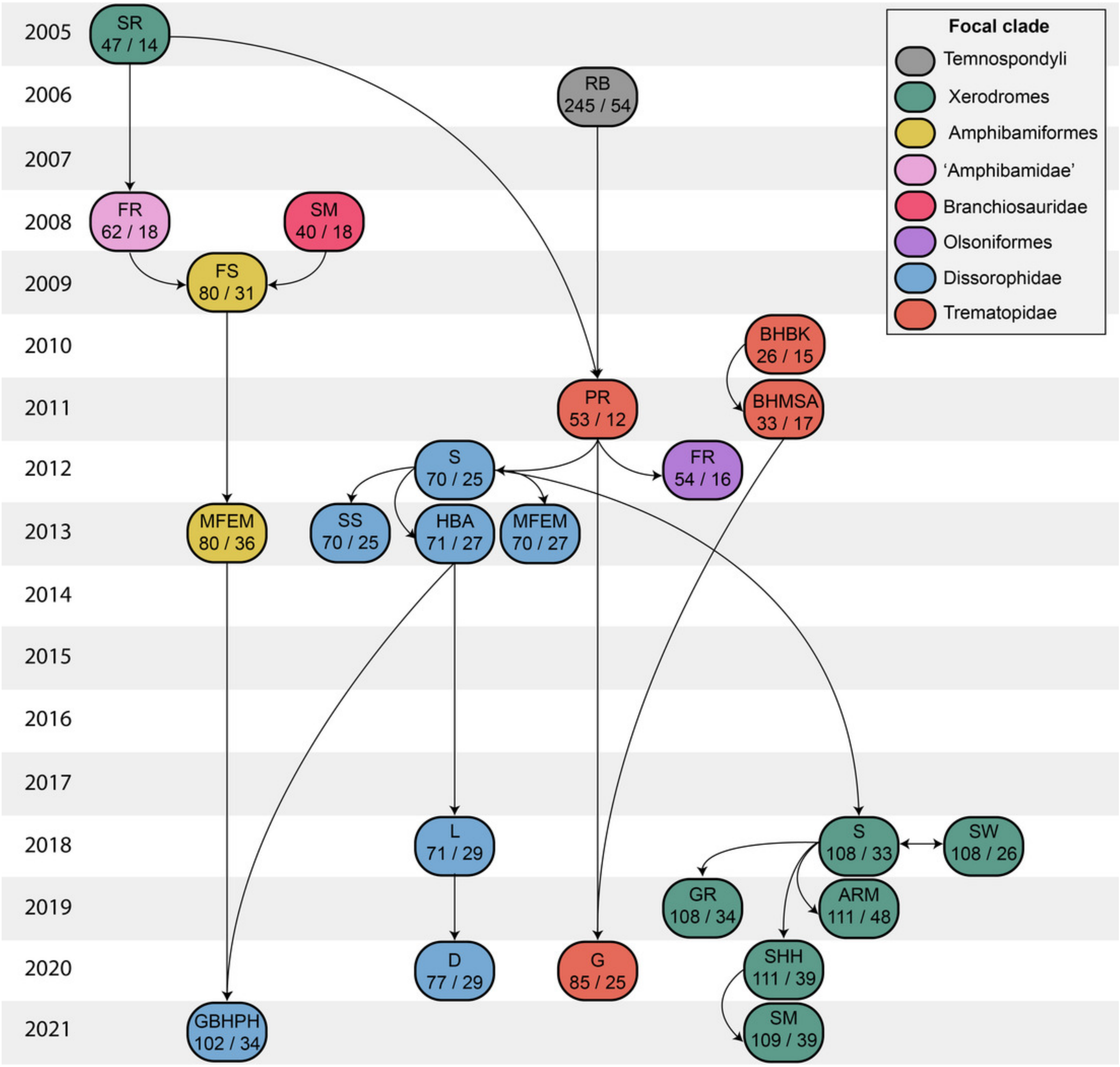


Figure 2

Genealogy of olsoniform-focused phylogenetic matrices.

Note that sources only reflect major contributions to character sampling. Number of characters is listed on the left, and number of all sampled taxa is listed on the right. ‘Focal clade’ refers to the most exclusive clade to which at least half of the sampled taxa belong. ‘Amphibamidae’ here refers to the historical concept of what is now Amphibamiformes (in part). Abbreviations: ARM, Atkins, Reisz & Maddin (2019); BHBK, Berman et al. (2010); BHMSA, Berman et al. (2011); D, Dilkes (2020); FR, Fröbisch & Reisz (2008, 2012); FS, Fröbisch & Schoch (2009); G, Gee (2020b); GBHPH, Gee et al. (2021); GR, Gee & Reisz (2019); HBA, Holmes, Berman & Anderson (2013); L, Liu (2018); MFEM, Maddin et al. (2013); PR, Polley & Reisz (2011); RB, Ruta & Bolt (2006); S, Schoch (2012, 2018a); SHH, Schoch, Henrici & Hook (2020); SM, Schoch & Milner (2008, 2021); SR, Schoch & Rubidge (2005); SS, Schoch & Sues (2013); SW, Schoch & Witzmann (2018).


2005
2006
2007
2008
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2011
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2016
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2020
2021
SR 47 / 14
RB 245 / 54
FR 62 / 18
SM 40 / 18
FS 80 / 31
BHBK 26 / 15
PR 53 / 12
BHMSA 33 / 17
S 70 / 25
FR 54 / 16
MFEM 80 / 36
SS 70 / 25
HBA 71 / 27
MFEM 70 / 27
L 71 / 29
S 108 / 33
SW 108 / 26
GR 108 / 34
ARM 111 / 48
D 77 / 29
G 85 / 25
SHH 111 / 39
GBHPH 102 / 34
SM 109 / 39
Focal clade
Temnospondyli
Xerodromes
Amphibamiformes
'Amphibamidae'
Branchiosauridae
Olsoniformes
Dissorophidae
Trematopidae

Figure 3

Comparison of tree topologies from early phylogenetic analyses of Dissorophidae.

Number of characters is listed on the left, and number of all sampled taxa is listed on the right. ‘Focal clade’ refers to the most exclusive clade to which at least half of the sampled taxa belong. ‘Amphibamidae’ here refers to the historical concept of what is now Amphibamiformes (in part). Abbreviations: BHBK, Berman et al. (2010); BHMSA, Berman et al. (2011); D, Dilkes (2020); FR, Fröbisch & Reisz (2008, 2012); FS, Fröbisch & Schoch (2009); G, Gee (2020b); GBHPH, Gee et al. (2021); HBA, Holmes, Berman & Anderson (2013); L, Liu (2018); MFEM, Maddin et al. (2013); PR, Polley & Reisz (2011); RB, Ruta & Bolt (2006); S, Schoch (2012); SM, Schoch & Milner (2008); SR, Schoch & Rubidge (2005); SS, Schoch & Sues (2013).

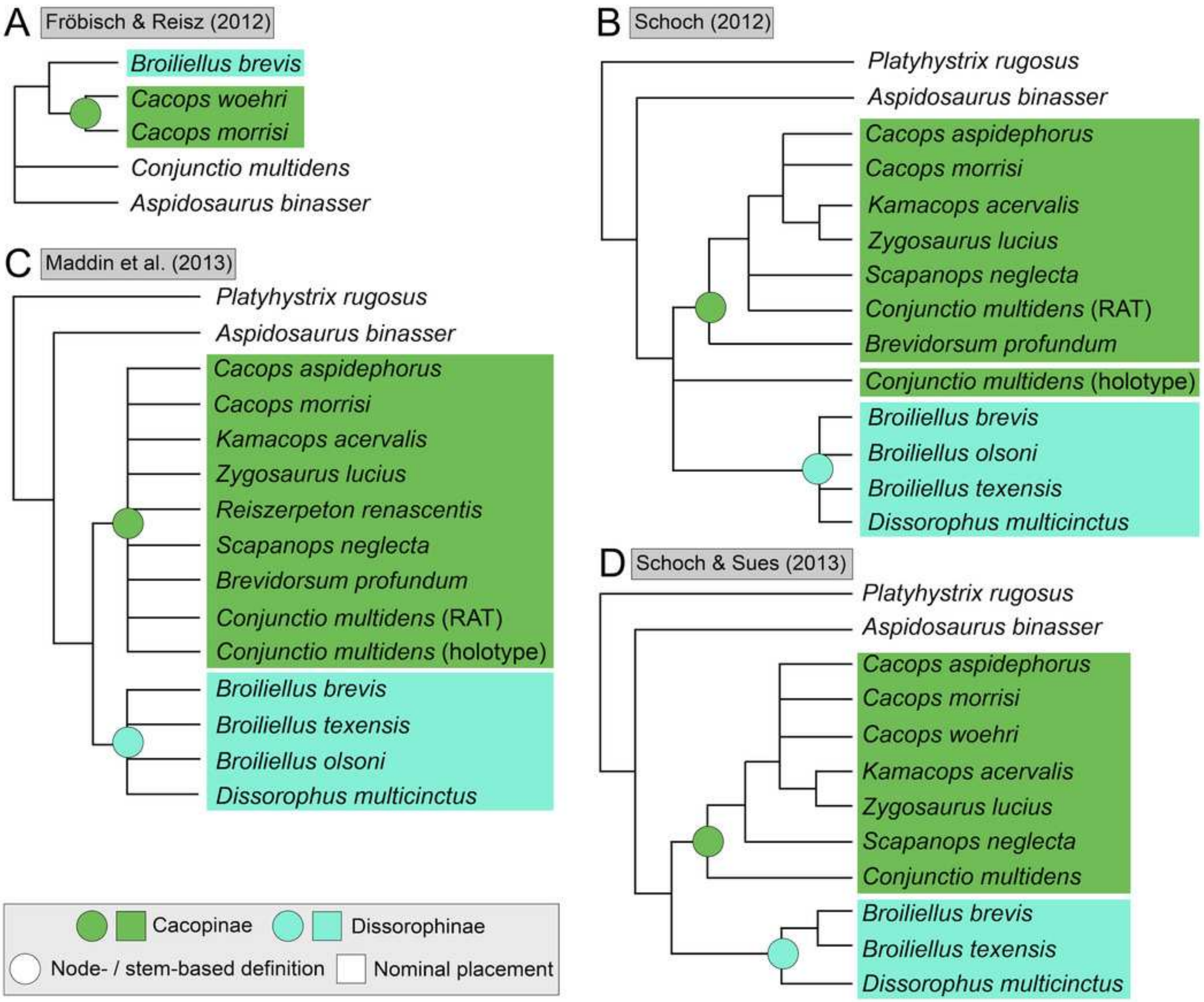
A
Fröbisch & Reisz (2012)
Broiliellus brevis
Cacops woehri
Cacops morrisi
Conjunctio multidens
Aspidosaurus binasser
B
Schoch (2012)
Platyhystrix rugosus
Aspidosaurus binasser
Cacops aspidephorus
Cacops morrisi
Kamacops acervalis
Zygosaurus lucius
Scapanops neglecta
Conjunctio multidens (RAT)
Brevidorsum profundum
Conjunctio multidens (holotype)
Broiliellus brevis
Broiliellus olsoni
Broiliellus texensis
Dissorophus multicinctus
C
Maddin et al. (2013)
Platyhystrix rugosus
Aspidosaurus binasser
Cacops aspidephorus
Cacops morrisi
Kamacops acervalis
Zygosaurus lucius
Reiszerpeton renascentis
Scapanops neglecta
Brevidorsum profundum
Conjunctio multidens (RAT)
Conjunctio multidens (holotype)
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
D
Schoch & Sues (2013)
Platyhystrix rugosus
Aspidosaurus binasser
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Scapanops neglecta
Conjunctio multidens
Broiliellus brevis
Broiliellus texensis
Dissorophus multicinctus
Cacopinae
Dissorophinae
Node- / stem-based definition
Nominal placement

Figure 4

Comparison of reported tree topologies from recent phylogenetic analyses of Dissorophidae.

All topologies represent strict consensus trees and are visually truncated to depict only dissorophids. Colors and symbols as with Figure 3. *Conjunctio multidens* represents a composite OTU unless otherwise indicated; Gee et al. (2021) recovered all three specimens as a clade, so they are collapsed to a single visual OTU here. For Holmes, Berman & Anderson (2013), the tree on the left represents the result of their analysis with scoring changes to the first referred specimen of *C. multidens* (UCMP 40103 [RAT]); the tree on the right represents the result with the original scorings from Schoch (2012). For Dilkes (2020), the tree on the left represents the result of his analysis with the full character and taxon sample; the tree on the right represents the result following the removal of wildcard taxa.

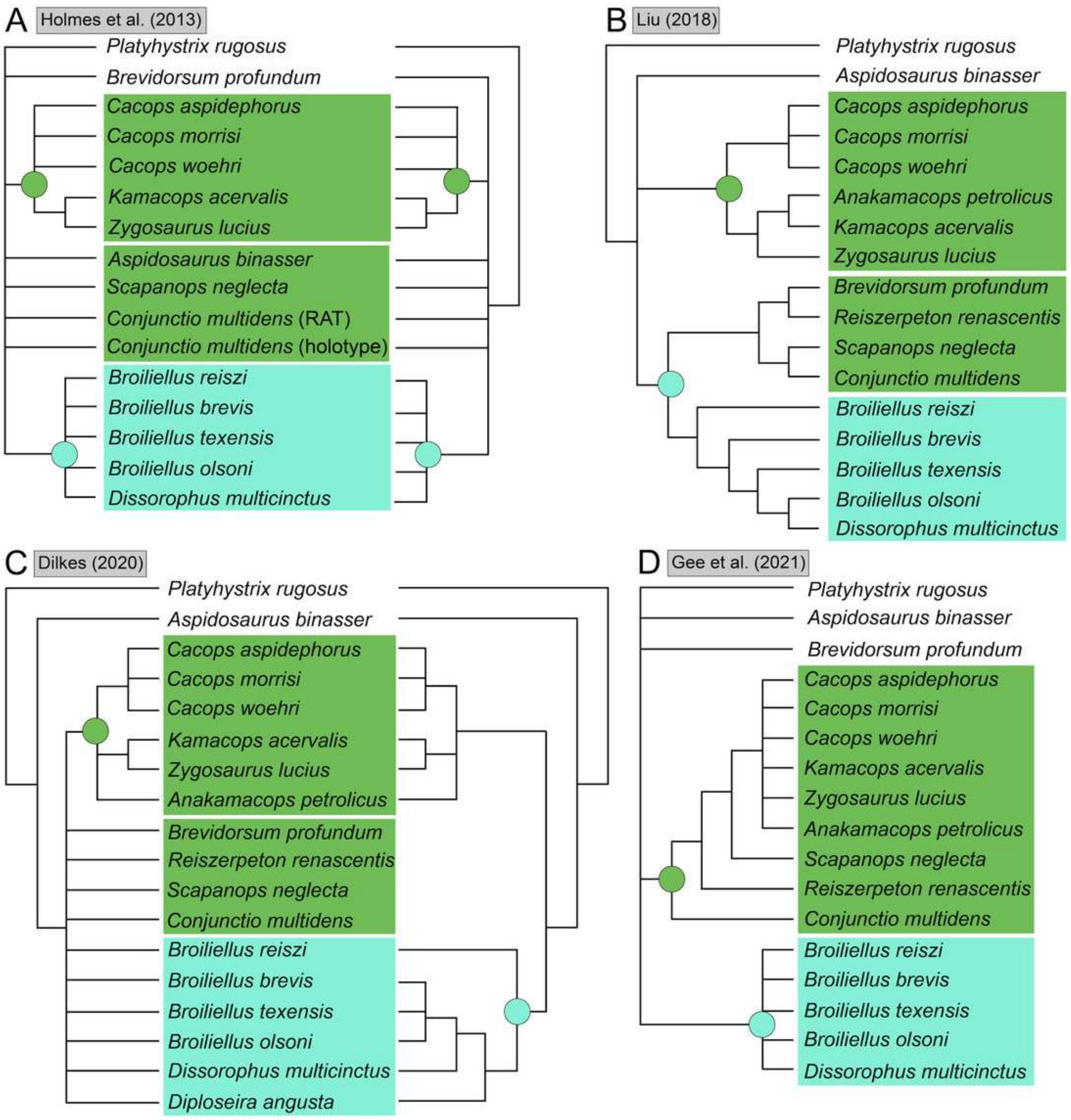
A
Holmes et al. (2013)
Platyhystrix rugosus
Brevidorsum profundum
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Aspidosaurus binasser
Scapanops neglecta
Conjunctio multidens (RAT)
Conjunctio multidens (holotype)
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
B
Liu (2018)
Platyhystrix rugosus
Aspidosaurus binasser
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Anakamacops petrolicus
Kamacops acervalis
Zygosaurus lucius
Brevidorsum profundum
Reiszerpeton renascentis
Scapanops neglecta
Conjunctio multidens
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
C
Dilkes (2020)
Platyhystrix rugosus
Aspidosaurus binasser
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus
Brevidorsum profundum
Reiszerpeton renascentis
Scapanops neglecta
Conjunctio multidens
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
Diploseira angusta
D
Gee et al. (2021)
Platyhystrix rugosus
Aspidosaurus binasser
Brevidorsum profundum
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus
Scapanops neglecta
Reiszerpeton renascentis
Conjunctio multidens
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus

Figure 5

Comparison of tree topologies from previous phylogenetic analyses of Trematopidae.

All topologies represent strict consensus trees and are visually truncated to depict only xerodromes. Nominal placement and nodal definitions from Schoch & Milner (2014).

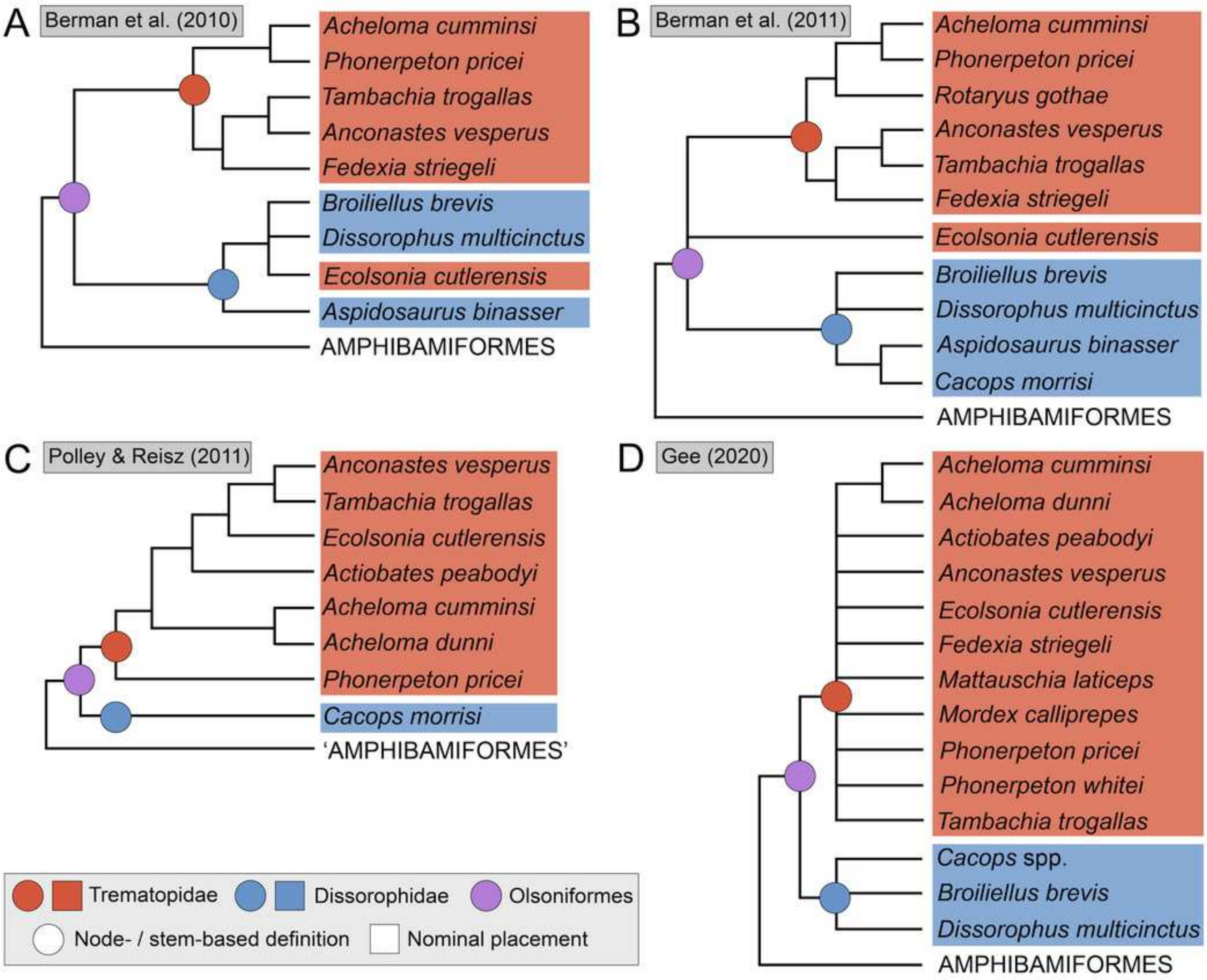

Figure 6

Strict consensus trees for permutation 1A (all scored olsoniforms).

(A) resultant tree from the iteration using the ‘conservative’ OTU of *Kamacops acervalis*; (B) resultant tree from the iteration using the ‘reconstructed’ OTU of *K. acervalis*. Bremer values are listed above the lines, and bootstrap values are listed below the lines. Gray text indicates a value falls below the conventional threshold of “strong support” (Bremer ≥ 3, bootstrap ≥ 50%). Nodes without bootstrap values were recovered in < 1% of bootstrap trees. Note that the part of the tree that is absent in part B (for space considerations) is configured the same as depicted in part A.

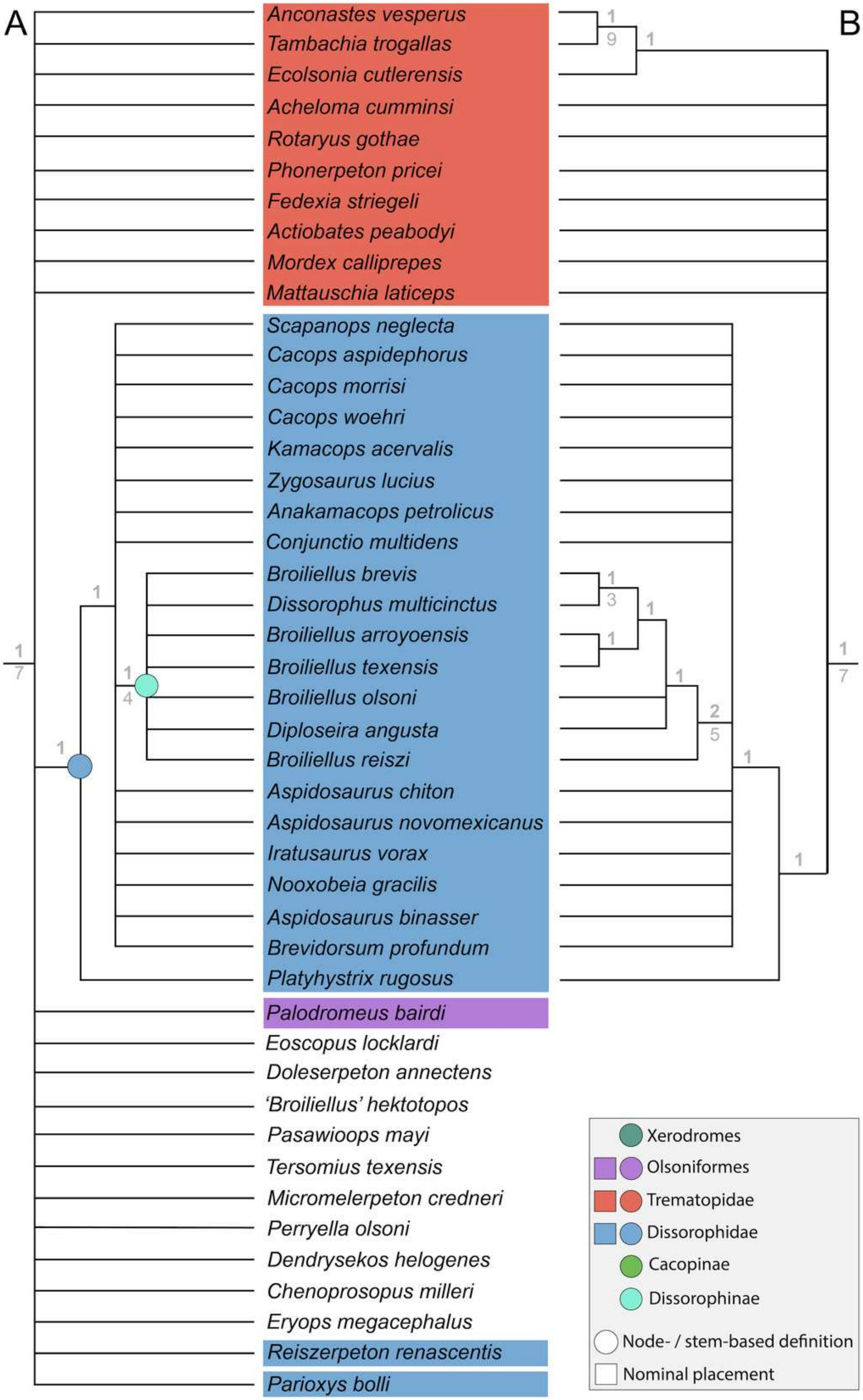
A
B
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Acheloma cumminsi
Rotaryus gothae
Phonerpeton pricei
Fedexia striegeli
Actiobates peabodyi
Mordex calliprepes
Mattauschia laticeps
Scapanops neglecta
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus
Conjunctio multidens
Broiliellus brevis
Dissorophus multicinctus
Broiliellus arroyoensis
Broiliellus texensis
Broiliellus olsoni
Diploseira angusta
Broiliellus reiszi
Aspidosaurus chiton
Aspidosaurus novomexicanus
Iratusaurus vorax
Nooxobeia gracilis
Aspidosaurus binasser
Brevidorsum profundum
Platyhystrix rugosus
Palodromeus bairdi
Eoscopus locklardi
Doleserpeton annectens
'Broiliellus' hektotopos
Pasawioops mayi
Tersomius texensis
Micromelerpeton credneri
Perryella olsoni
Dendrysekos helogenes
Chenoprosopus milleri
Eryops megacephalus
Reiszerpeton renascentis
Parioxys bolli
1
7
1
1
4
1
1
9
1
1
3
1
1
1
2
5
1
1
1
7
Xerodromes
Olsoniformes
Trematopidae
Dissorophidae
Cacopinae
Dissorophinae
Node- / stem-based definition
Nominal placement

Figure 7

Adams consensus trees for permutation 1A (all scored olsoniforms).

(A) resultant tree from the iteration using the ‘conservative’ OTU of *Kamacops acervalis*; (B) resultant tree from the iteration using the ‘reconstructed’ OTU of *K. acervalis*. Note that the latter tree recovered *Perryella olsoni* as diverging before *Micromelerpeton credneri*; this is not presented for space constraints and because these taxa are not olsoniforms and thus not subject to wildcard pruning. Colors and symbols as with Figure 6.

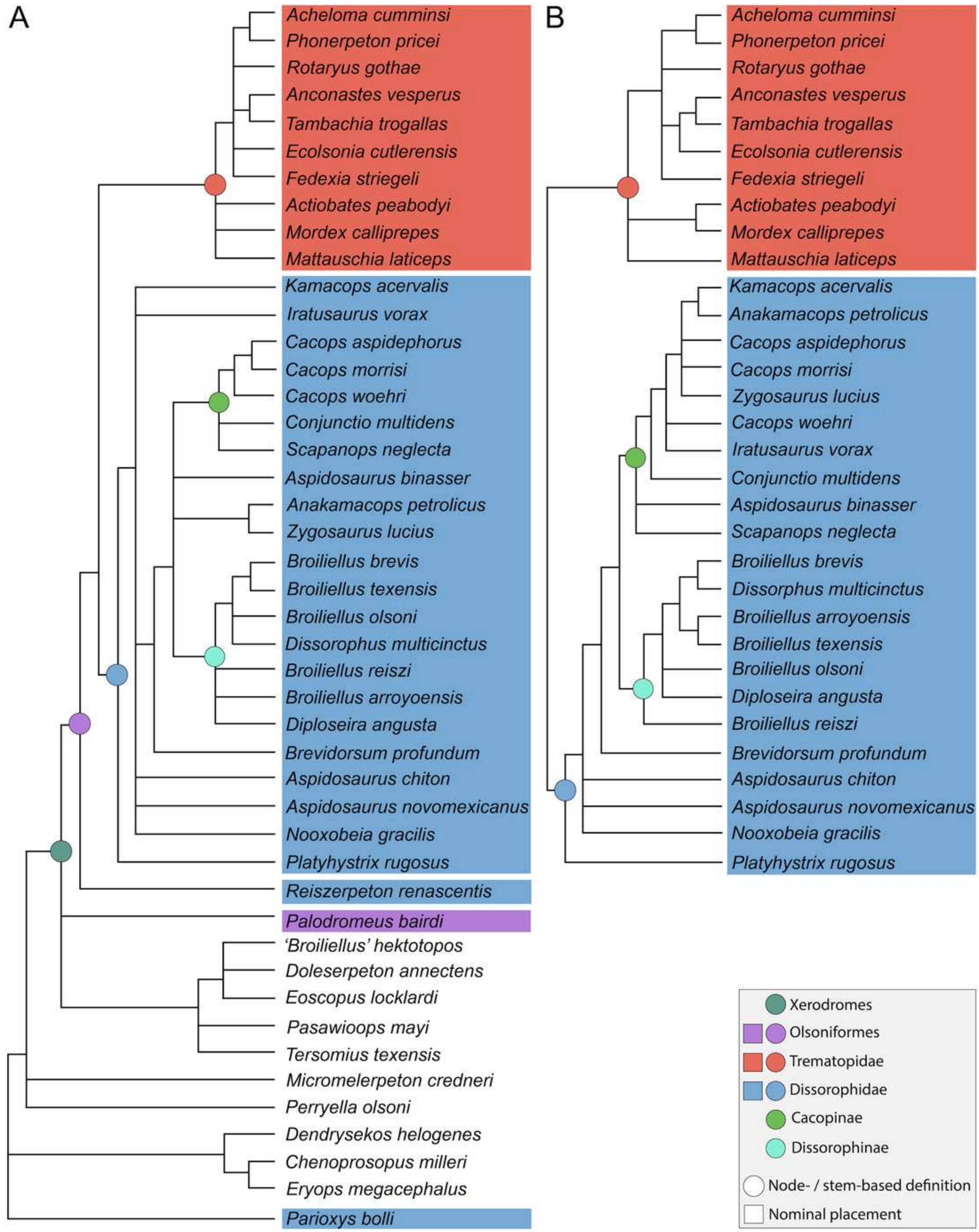
A
Acheloma cumminsi
Phonerpeton pricei
Rotaryus gothae
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Fedexia striegeli
Actiobates peabodyi
Mordex calliprepes
Mattauschia laticeps
Kamacops acervalis
Iratusaurus vorax
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Conjunctio multidens
Scapanops neglecta
Aspidosaurus binasser
Anakamacops petrolicus
Zygosaurus lucius
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
Broiliellus reiszi
Broiliellus arroyoensis
Diploseira angusta
Brevidorsum profundum
Aspidosaurus chiton
Aspidosaurus novomexicanus
Nooxobeia gracilis
Platyhystrix rugosus
Reiszerpeton renascentis
Palodromeus bairdi
'Broiliellus' hektotopos
Doleserpeton annectens
Eoscopus locklardi
Pasawioops mayi
Tersomius texensis
Micromelerpeton credneri
Perryella olsoni
Dendrysekos helogenes
Chenoprosopus milleri
Eryops megacephalus
Parioxys bolli
B
Acheloma cumminsi
Phonerpeton pricei
Rotaryus gothae
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Fedexia striegeli
Actiobates peabodyi
Mordex calliprepes
Mattauschia laticeps
Kamacops acervalis
Anakamacops petrolicus
Cacops aspidephorus
Cacops morrisi
Zygosaurus lucius
Cacops woehri
Iratusaurus vorax
Conjunctio multidens
Aspidosaurus binasser
Scapanops neglecta
Broiliellus brevis
Dissorphus multicinctus
Broiliellus arroyoensis
Broiliellus texensis
Broiliellus olsoni
Diploseira angusta
Broiliellus reiszi
Brevidorsum profundum
Aspidosaurus chiton
Aspidosaurus novomexicanus
Nooxobeia gracilis
Platyhystrix rugosus
● Xerodromes
■ ● Olsoniformes
■ ● Trematopidae
■ ● Dissorophidae
● Cacopinae
● Dissorophinae
○ Node- / stem-based definition
☐ Nominal placement

Figure 8

Strict consensus trees for permutation 1B (wildcard removal).

(A) resultant tree from the iteration using the ‘conservative’ OTU of *Kamacops acervalis*; (B) resultant tree from the iteration using the ‘reconstructed’ OTU of *K. acervalis*. Bremer values are listed above the lines, and bootstrap values are listed below the lines. Gray text indicates a value falls below the conventional threshold of “strong support” (Bremer ≥ 3, bootstrap ≥ 50%). Nodes without bootstrap values were recovered in < 1% of bootstrap trees. Colors and symbols as with Figure 6.

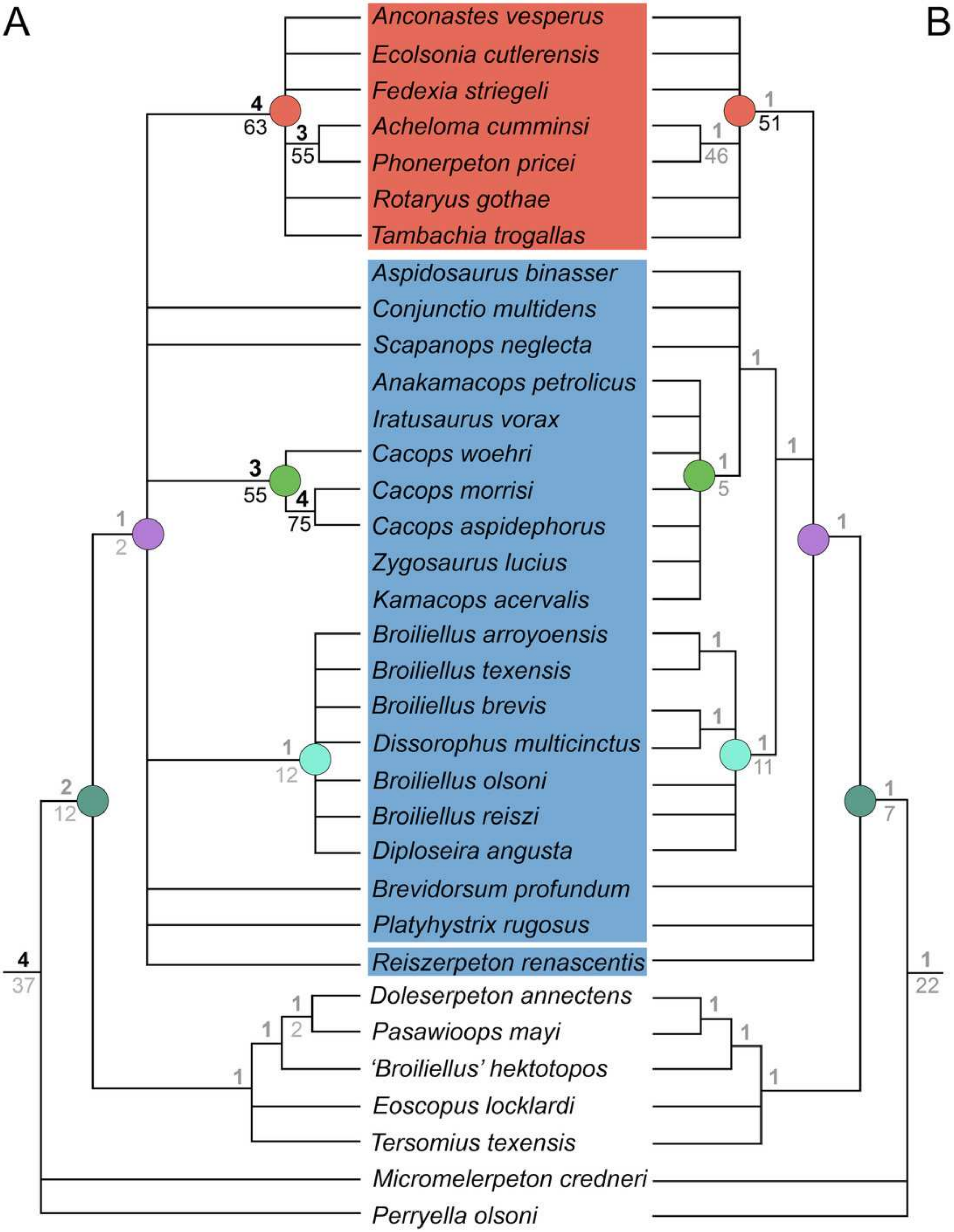
A
B
Anconastes vesperus
Ecolsonia cutlerensis
Fedexia striegeli
Acheloma cumminsi
Phonerpeton pricei
Rotaryus gothae
Tambachia trogallas
Aspidosaurus binasser
Conjunctio multidens
Scapanops neglecta
Anakamacops petrolicus
Iratusaurus vorax
Cacops woehri
Cacops morrisi
Cacops aspidephorus
Zygosaurus lucius
Kamacops acervalis
Broiliellus arroyoensis
Broiliellus texensis
Broiliellus brevis
Dissorophus multicinctus
Broiliellus olsoni
Broiliellus reiszi
Diploseira angusta
Brevidorsum profundum
Platyhystrix rugosus
Reiszerpeton renascentis
Doleserpeton annectens
Pasawioops mayi
'Broiliellus' hektotopos
Eoscopus locklardi
Tersomius texensis
Micromelerpeton credneri
Perryella olsoni
4
63
3
55
3
55
4
75
1
2
1
12
2
12
4
37
1
2
1
1
1
51
1
46
1
1
1
5
1
1
1
11
1
1
7
1
22
1
1
1

Figure 9

Strict consensus tree for permutation 2 (best representatives) from the iteration using the ‘conservative’ OTU of *Kamacops acervalis*.

The iteration with the ‘reconstructed’ OTU recovered the same topology with only minor deviations in bootstrap support and is not figured here. Colors and symbols as with Figure 6.

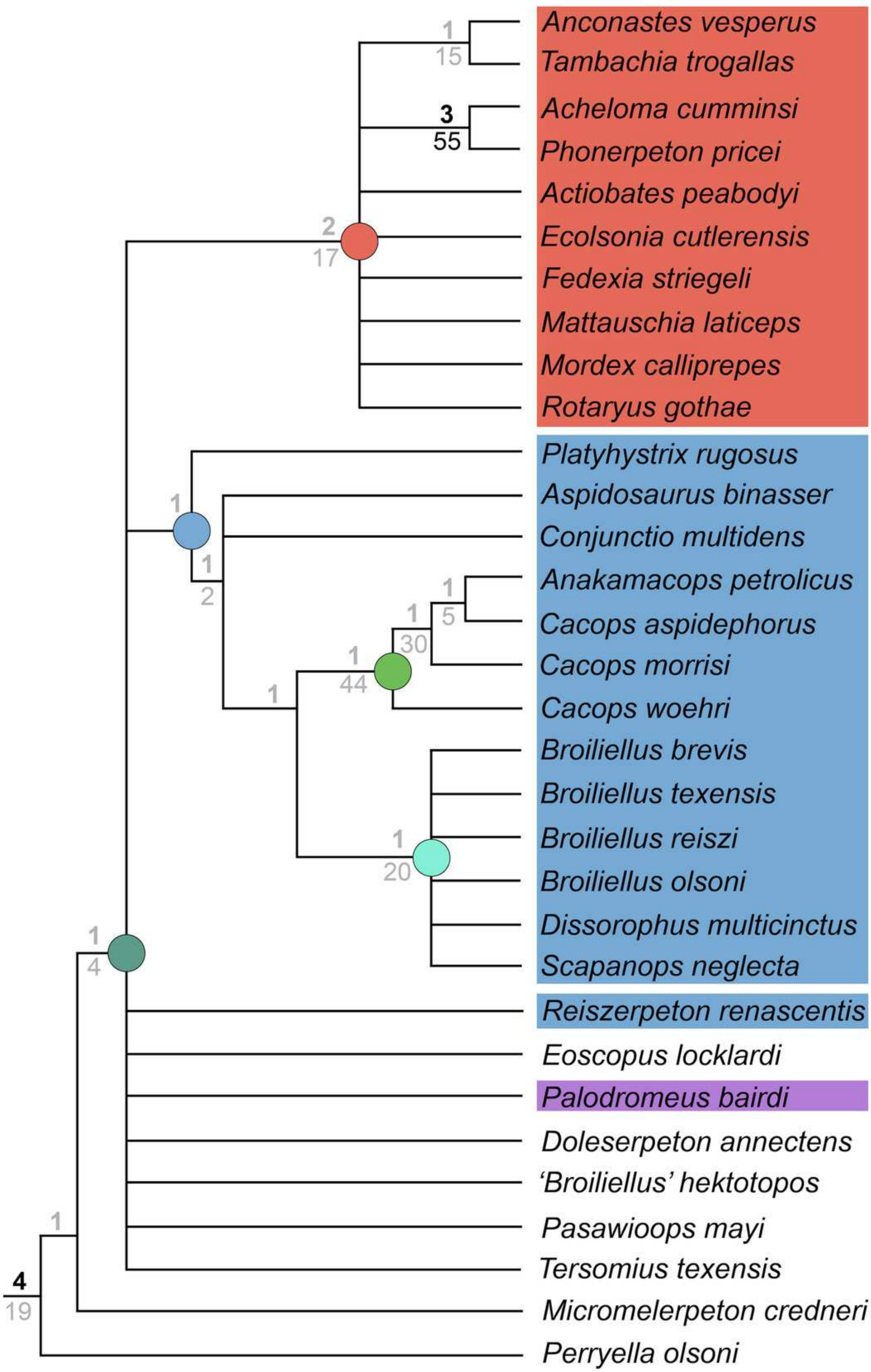
1
15
Anconastes vesperus
Tambachia trogallas
3
55
Acheloma cumminsi
Phonerpeton pricei
Actiobates peabodyi
2
17
Ecolsonia cutlerensis
Fedexia striegeli
Mattauschia laticeps
Mordex calliprepes
Rotaryus gothae
Platyhystrix rugosus
1
Aspidosaurus binasser
Conjunctio multidens
1
2
1
Anakamacops petrolicus
1
5
30
Cacops aspidephorus
Cacops morrisi
1
44
1
Cacops woehri
Broiliellus brevis
Broiliellus texensis
1
Broiliellus reiszi
20
Broiliellus olsoni
Dissorophus multicinctus
1
4
Scapanops neglecta
Reiszerpeton renascentis
Eoscopus locklardi
Palodromeus bairdi
Doleserpeton annectens
'Broiliellus' hektotopos
1
Pasawioops mayi
Tersomius texensis
4
19
Micromelerpeton credneri
Perryella olsoni

Figure 10

Strict consensus tree for permutation 3 (dissorophid-focused) from the iteration using the ‘conservative’ OTU of *Kamacops acervalis*.

1. The iteration with the ‘reconstructed’ OTU recovered the same topology with only minor deviations in bootstrap support and is not figured here. Colors and symbols as with Figure 6.

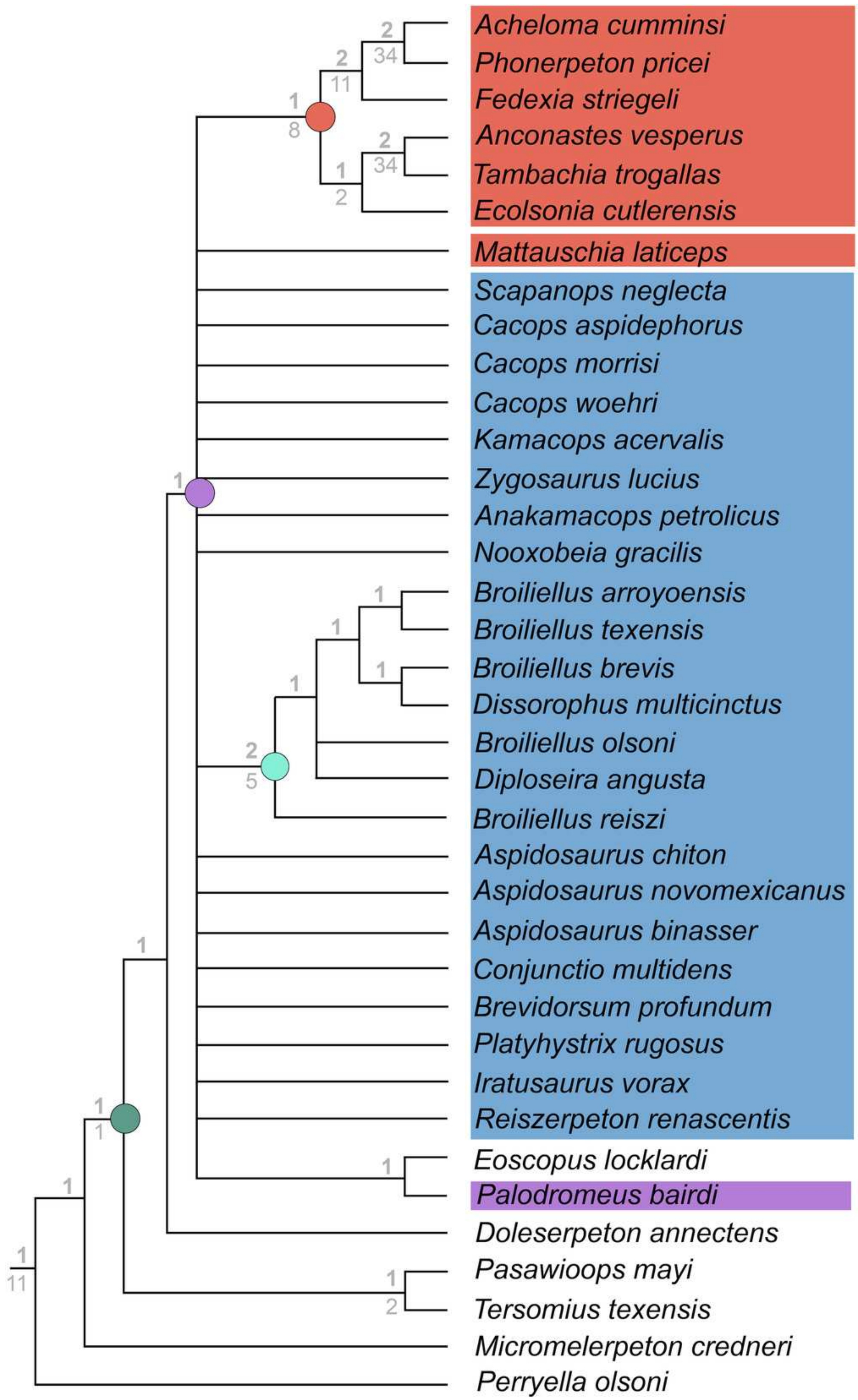
Acheloma cumminsi
Phonerpeton pricei
Fedexia striegeli
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Mattauschia laticeps
Scapanops neglecta
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus
Nooxobeia gracilis
Broiliellus arroyoensis
Broiliellus texensis
Broiliellus brevis
Dissorophus multicinctus
Broiliellus olsoni
Diploseira angusta
Broiliellus reiszi
Aspidosaurus chiton
Aspidosaurus novomexicanus
Aspidosaurus binasser
Conjunctio multidens
Brevidorsum profundum
Platyhystrix rugosus
Iratusaurus vorax
Reiszerpeton renascentis
Eoscopus locklardi
Palodromeus bairdi
Doleserpeton annectens
Pasawioops mayi
Tersomius texensis
Micromelerpeton credneri
Perryella olsoni
2
34
2
11
1
8
2
34
1
2
1
1
1
1
1
2
5
1
1
1
1
1
1
1
2
1
11

Figure 11

Consensus trees for permutation 4 (specimen-level OTUs).

(A) strict consensus tree; (B) 50%-majority rule consensus tree as calculated in TNT. Values above lines in part B represent nodal occurrence. Node labels, colors, and symbols as with Figures 6–7.

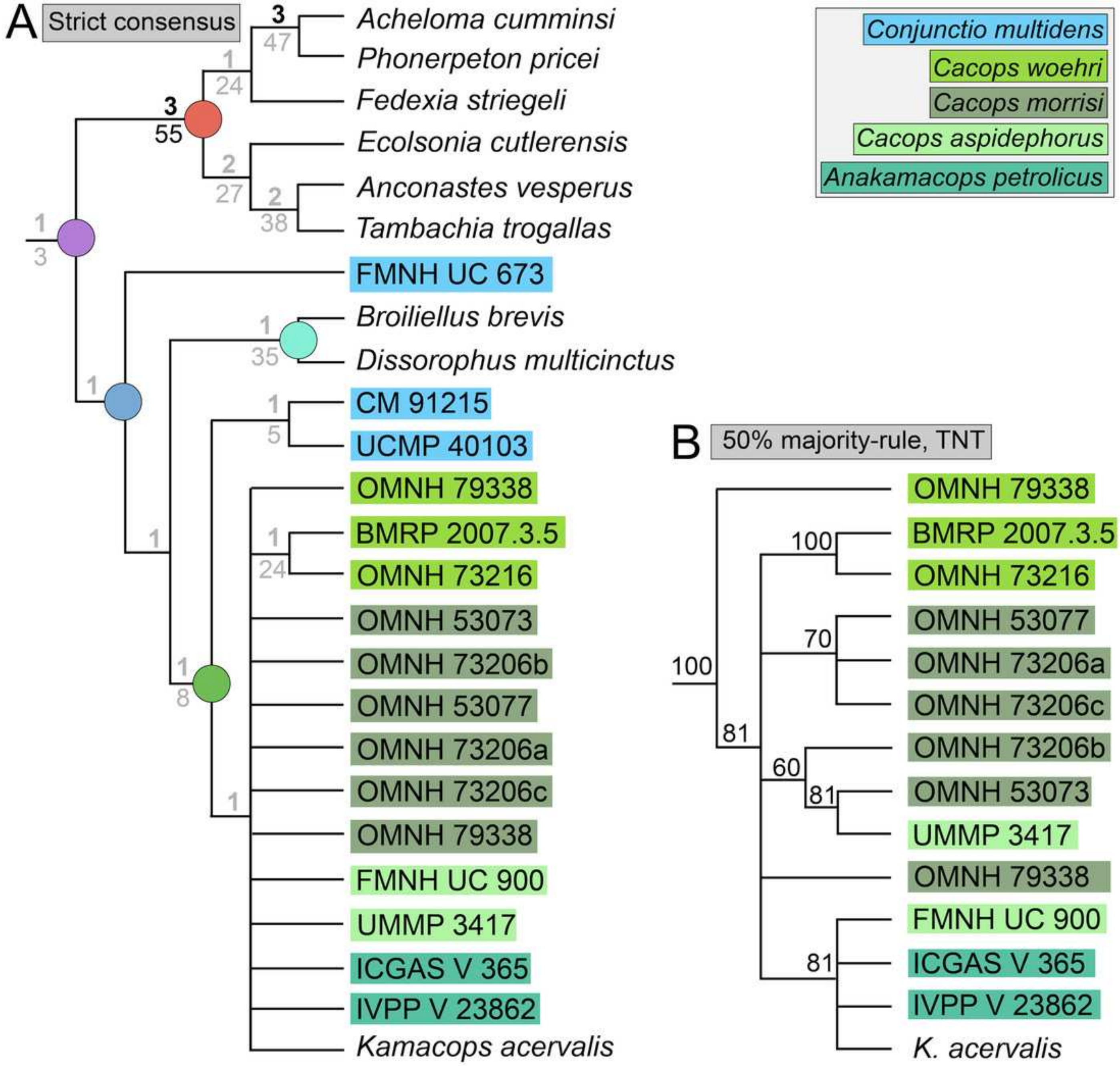
A
Strict consensus
Acheloma cumminsi
Phonerpeton pricei
Fedexia striegeli
Ecolsonia cutlerensis
Anconastes vesperus
Tambachia trogallas
FMNH UC 673
Broiliellus brevis
Dissorophus multicinctus
CM 91215
UCMP 40103
OMNH 79338
BMRP 2007.3.5
OMNH 73216
OMNH 53073
OMNH 73206b
OMNH 53077
OMNH 73206a
OMNH 73206c
OMNH 79338
FMNH UC 900
UMMP 3417
ICGAS V 365
IVPP V 23862
Kamacops acervalis
3 47
1 24
3 55
2 27
2 38
1 3
1 35
1
1 5
1
1 24
1 8
1
Conjunctio multidens
Cacops woehri
Cacops morrisi
Cacops aspidephorus
Anakamacops petrolicus
B
50% majority-rule, TNT
OMNH 79338
BMRP 2007.3.5
OMNH 73216
OMNH 53077
OMNH 73206a
OMNH 73206c
OMNH 73206b
OMNH 53073
UMMP 3417
OMNH 79338
FMNH UC 900
ICGAS V 365
IVPP V 23862
K. acervalis
100
100
70
81
60
81
81

Figure 12

Consensus trees for permutation 4 (specimen-level OTUs).

(A) strict consensus tree; (B) 50%-majority rule consensus tree as calculated in TNT; (C) 50%-majority rule consensus tree from the same set of MPTs but as calculated in PAUP*, demonstrating the effect of different default branch collapsing rules. Values above lines in parts B and C represent nodal occurrence; because PAUP* rounds up, whereas TNT does not, 1% differences are noted for some nodes that are recovered in the same number of MPTs. Colors and symbols as with Figure 6.

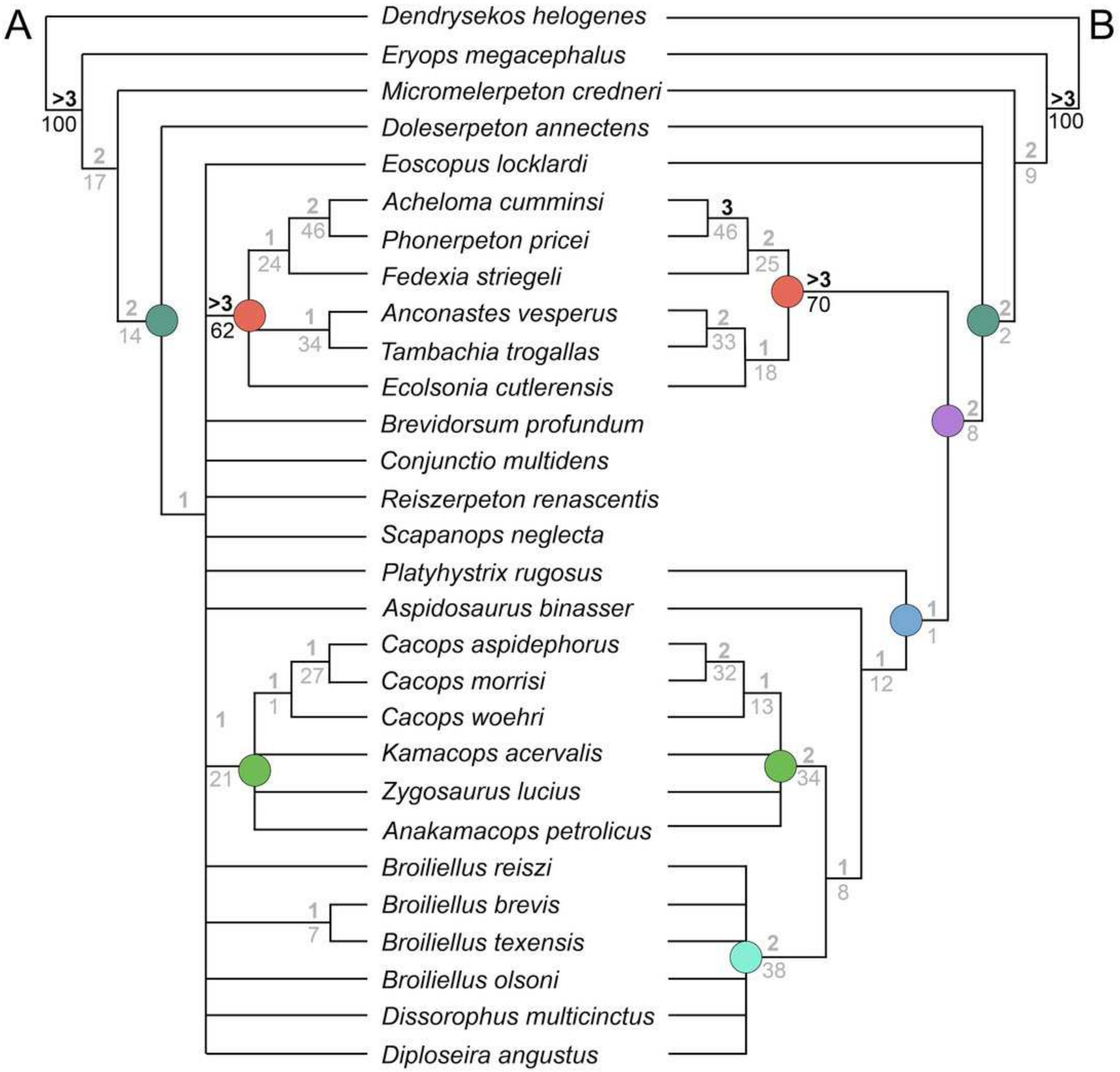
A
B
Dendrysekos helogenes
Eryops megacephalus
Micromelerpeton credneri
Doleserpeton annectens
Eoscopus locklardi
Acheloma cumminsi
Phonerpeton pricei
Fedexia striegeli
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Brevidorsum profundum
Conjunctio multidens
Reiszerpeton renascentis
Scapanops neglecta
Platyhystrix rugosus
Aspidosaurus binasser
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
Diploseira angustus
>3
100
2
17
2
14
>3
62
1
24
2
46
1
34
1
1
21
1
1
1
27
1
7
>3
100
2
9
2
2
3
46
2
25
>3
70
2
33
1
18
2
8
1
1
1
12
2
32
1
13
2
34
1
8
2
38

Figure 13

Comparison of strict consensus topologies for permutation 6 (taxon mirror of Gee, 2020b).

(A) resultant tree from the analysis of Gee’s (2020b) trematopid-focused matrix with a combined OTU of the previous scorings of *Acheloma cumminsi* and *Acheloma dunni* and with the exclusion of *Phonerpeton whitei*; (B) resultant tree from the same taxon sampling and the updated matrix of this study. Colors and symbols as with Figure 6.

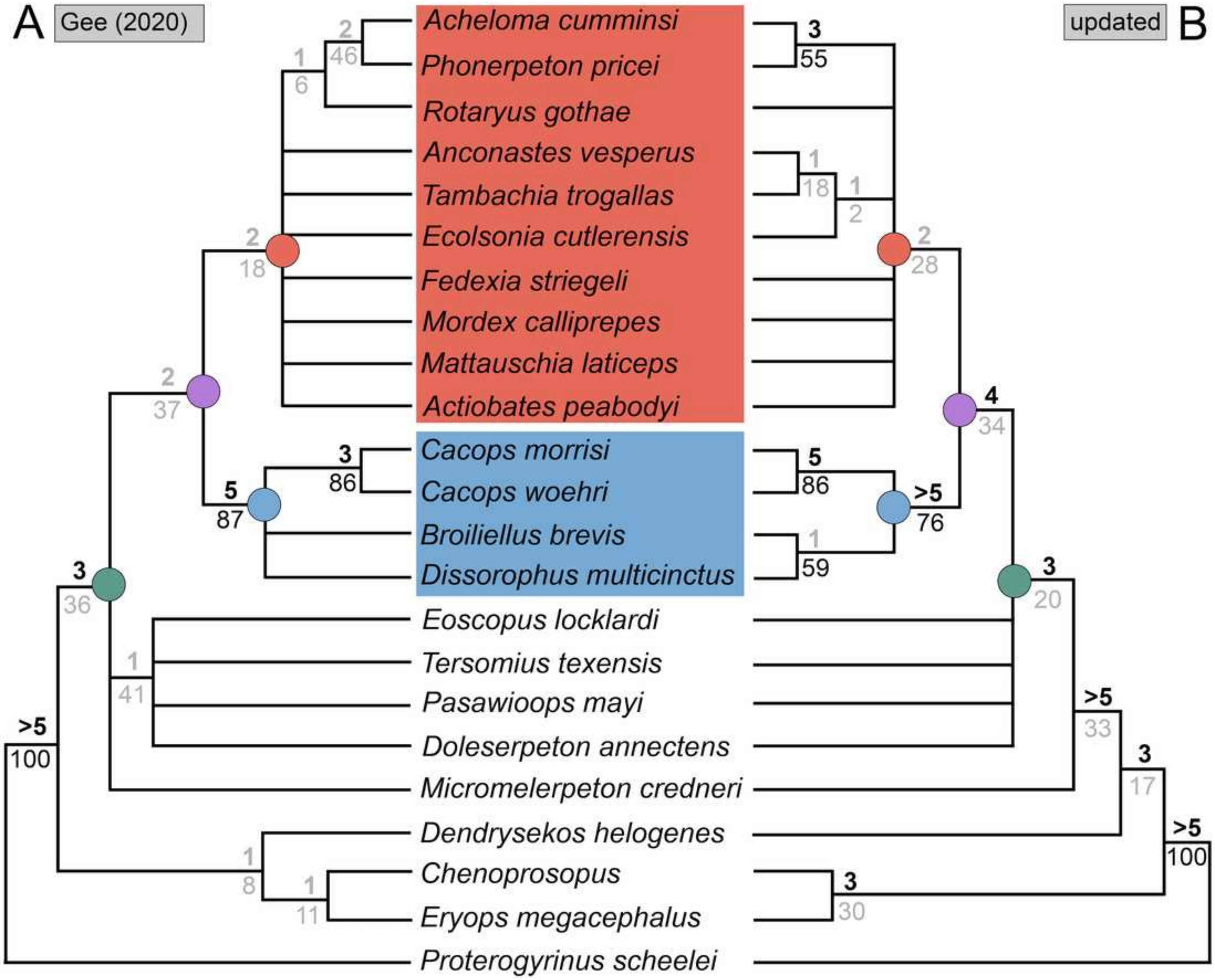

Figure 14

Comparison of strict consensus topologies for permutation 7 (updated matrix from Dilkes, 2020).

(A) resultant tree from Dilkes' (2020) original analysis with the full taxon sample; (B) resultant tree from the analysis of the updated matrix with the full taxon sample; (C) resultant tree from Dilkes' original analysis without the four wildcard taxa that he identified (*Brevidorsum*, *Conjunctio*, *Reiszerpeton*, *Scapanops*); (D) resultant tree from the reanalysis of the updated matrix without his wildcard taxa. Colors and symbols as with Figure 6.

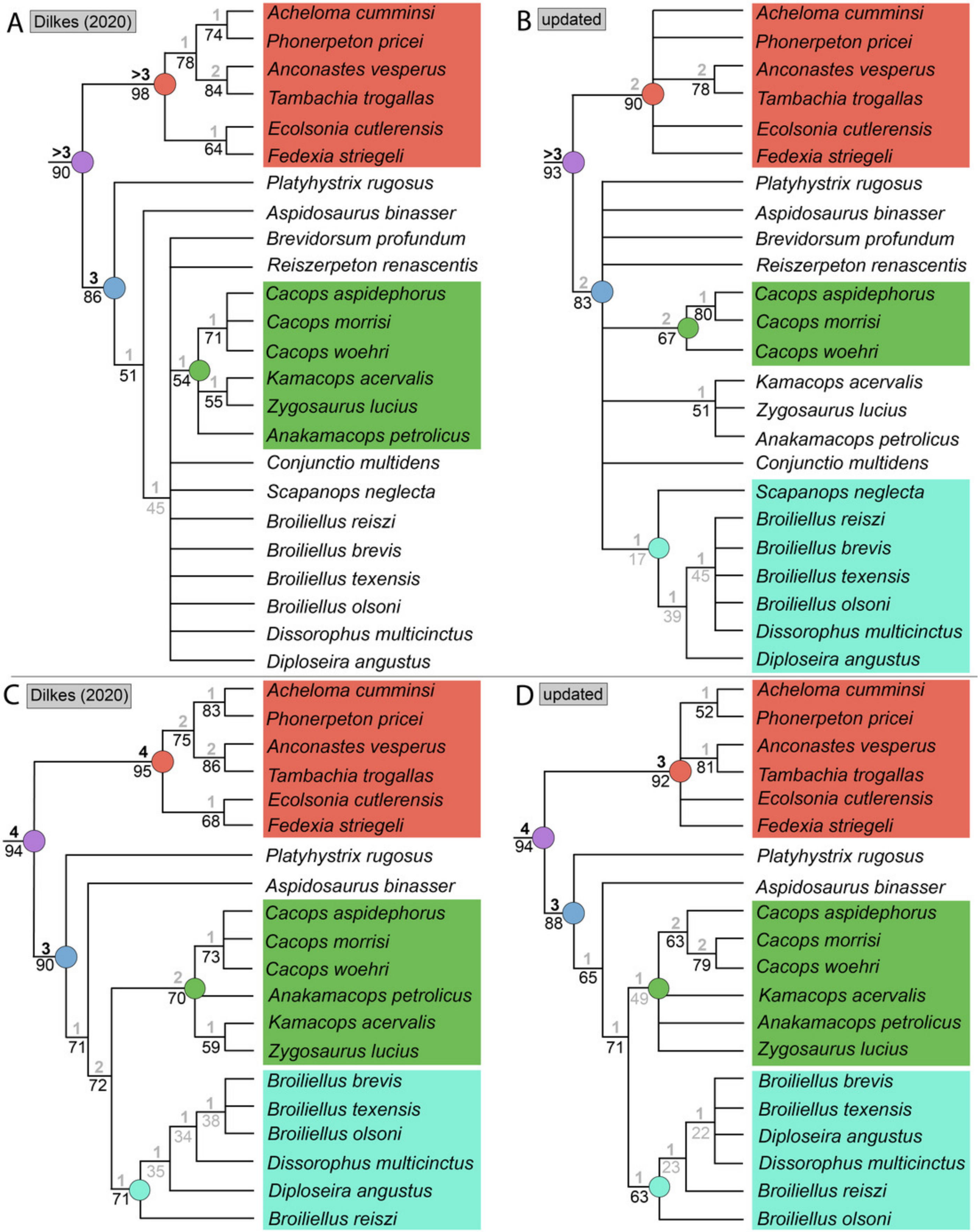
A
Dilkes (2020)
Acheloma cumminsi
Phonerpeton pricei
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Fedexia striegeli
Platyhystrix rugosus
Aspidosaurus binasser
Brevidorsum profundum
Reiszerpeton renascentis
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus
Conjunctio multidens
Scapanops neglecta
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
Diploseira angustus
1
74
1
78
>3
98
2
84
1
64
>3
90
3
86
1
51
1
71
1
54
1
55
1
45
B
updated
2
78
2
90
>3
93
2
83
1
80
2
67
1
51
1
17
1
45
1
39
C
Dilkes (2020)
1
83
2
75
4
95
2
86
1
68
4
94
3
90
1
73
2
70
1
59
1
71
2
72
1
38
1
34
1
35
1
71
Anakamacops petrolicus
Kamacops acervalis
Zygosaurus lucius
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
Diploseira angustus
Broiliellus reiszi
D
updated
1
52
3
92
1
81
4
94
3
88
2
63
2
79
1
65
1
49
1
71
1
22
1
23
1
63
Broiliellus brevis
Broiliellus texensis
Diploseira angustus
Dissorophus multicinctus
Broiliellus reiszi
Broiliellus olsoni

Figure 15

Comparison of strict consensus topologies for permutation 8 (comparison of TNT and PAUP* on a trematopid-focused sample using this study's revised matrix from Gee, 2020b)

(A) resultant tree from the analysis using TNT (repeated from Fig. 12B); (B) resultant tree from the analysis with PAUP*. Colors and symbols as with Figure 6.

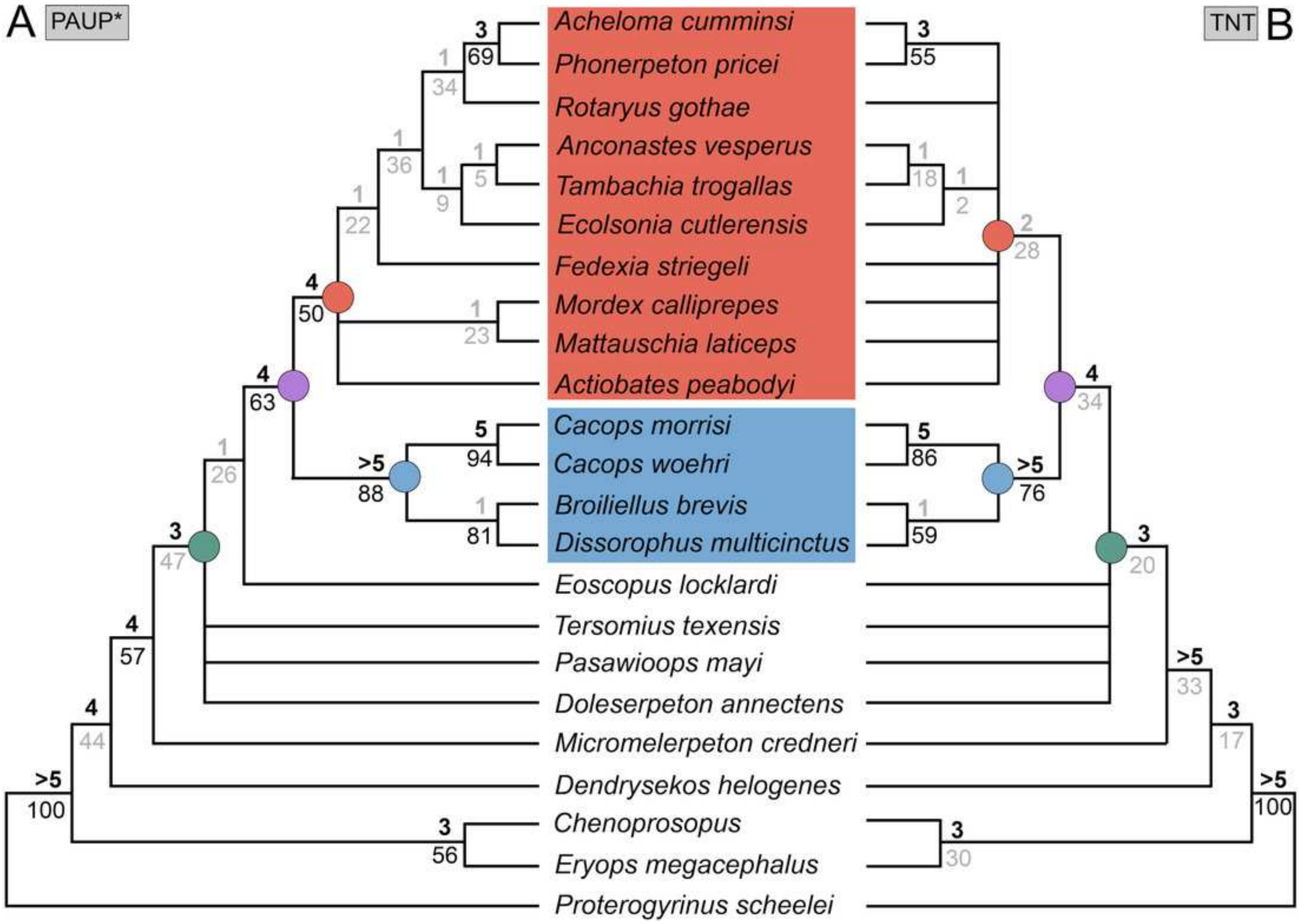

Figure 16

Comparison of strict consensus topologies for permutation 9A (comparison of TNT and PAUP* with the original matrix of Dilkes, 2020).

(A) resultant tree from Dilkes' (2020) original analysis in PAUP* with the full taxon sample; (B) resultant tree from the same matrix analyzed with TNT; (C) resultant tree from Dilkes' original analysis without the four wildcard taxa that he identified (*Brevidorsum*, *Conjunctio*, *Reiszerpeton*, *Scapanops*); (D) resultant tree from the same matrix analyzed with TNT. Colors and symbols as with Figure 6.

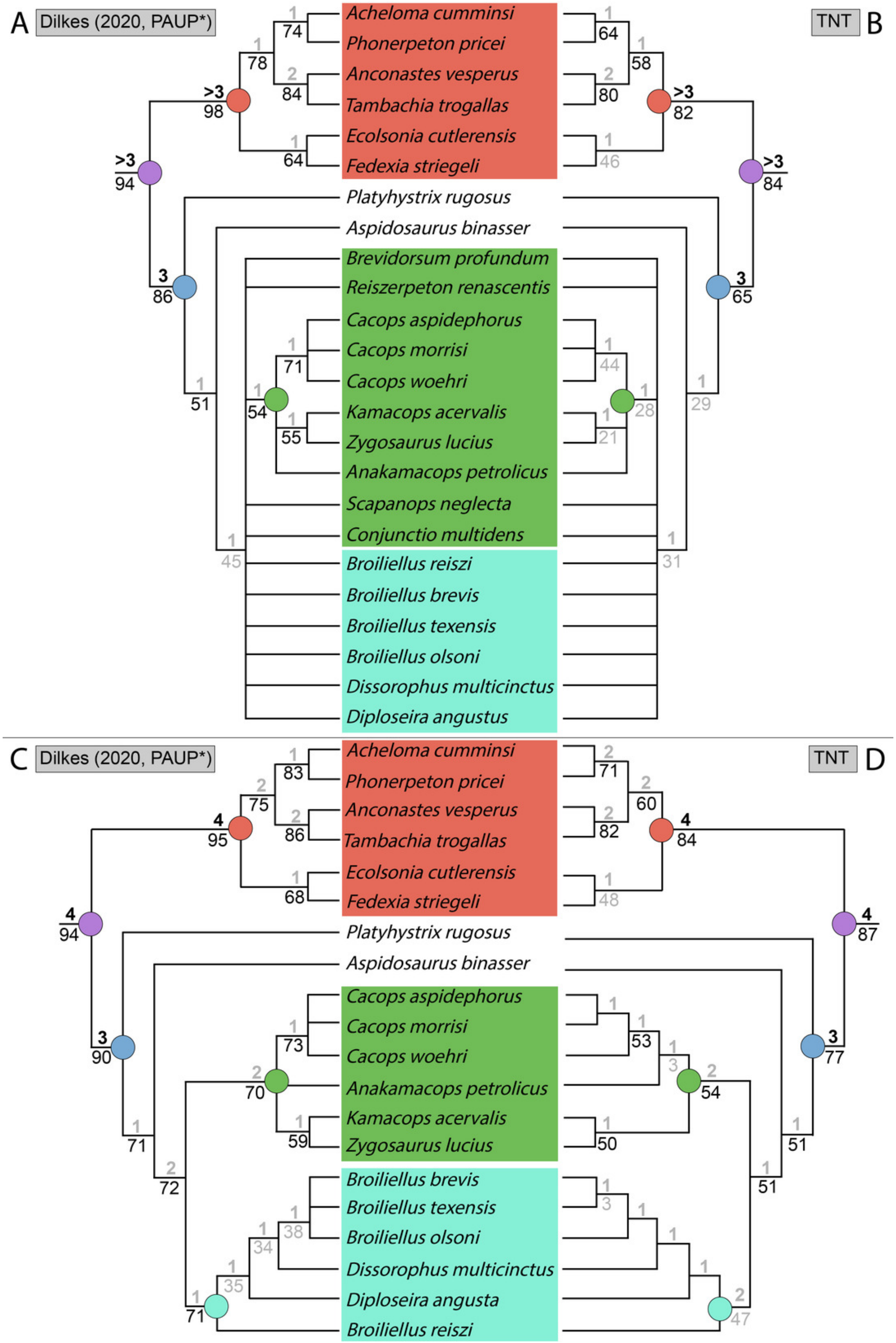
A
Dilkes (2020, PAUP*)
TNT
B
Acheloma cumminsi
Phonerpeton pricei
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Fedexia striegeli
Platyhystrix rugosus
Aspidosaurus binasser
Brevidorsum profundum
Reiszerpeton renascentis
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus
Scapanops neglecta
Conjunctio multidens
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
Diploseira angustus
C
Dilkes (2020, PAUP*)
TNT
D
Acheloma cumminsi
Phonerpeton pricei
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Fedexia striegeli
Platyhystrix rugosus
Aspidosaurus binasser
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Anakamacops petrolicus
Kamacops acervalis
Zygosaurus lucius
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
Diploseira angusta
Broiliellus reiszi

Figure 17

Comparison of strict consensus topologies for permutation 9B (comparison of the original and updated versions of the matrix of Dilkes, 2020, using TNT).

(A) resultant tree from the reanalysis of the updated version of Dilkes' (2020) matrix with the full taxon sample; (B) resultant tree from the analysis of the original version of Dilkes' matrix (repeated from Fig. 15B); (C) resultant tree from the reanalysis of the updated version of Dilkes' (2020) matrix without the four wildcard taxa that were identified by Dilkes (*Brevidorsum*, *Conjunctio*, *Reiszerpeton*, *Scapanops*); (D) resultant tree from the analysis of the original version of Dilkes' matrix (repeated from Fig. 15D). Colors and symbols as with Figure 6.

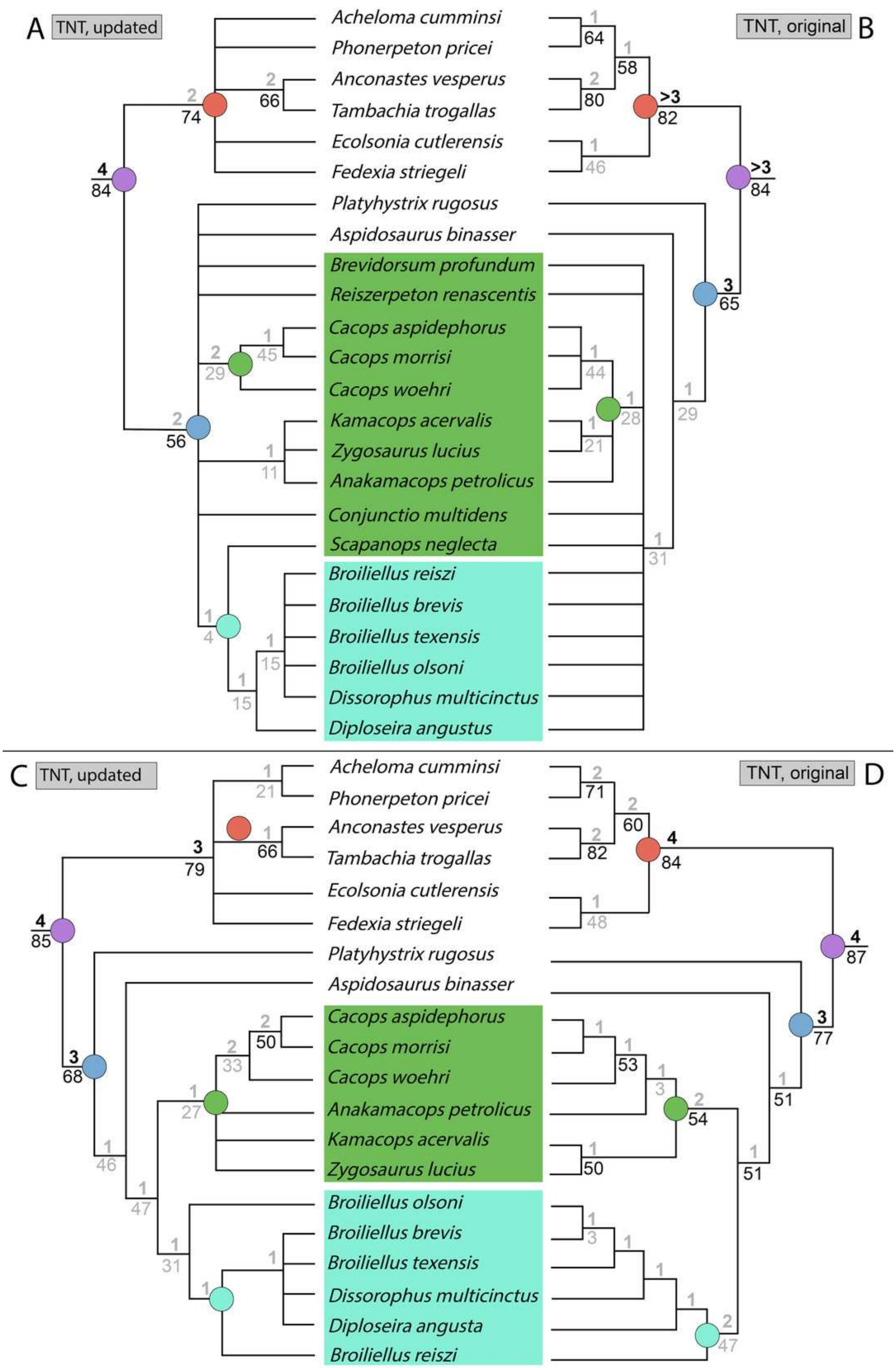
A
TNT, updated
TNT, original
B
Acheloma cumminsi
Phonerpeton pricei
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Fedexia striegeli
Platyhystrix rugosus
Aspidosaurus binasser
Brevidorsum profundum
Reiszerpeton renascentis
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus
Conjunctio multidens
Scapanops neglecta
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
Diploseira angustus
C
TNT, updated
TNT, original
D
Acheloma cumminsi
Phonerpeton pricei
Anconastes vesperus
Tambachia trogallas
Ecolsonia cutlerensis
Fedexia striegeli
Platyhystrix rugosus
Aspidosaurus binasser
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Anakamacops petrolicus
Kamacops acervalis
Zygosaurus lucius
Broiliellus olsoni
Broiliellus brevis
Broiliellus texensis
Dissorophus multicinctus
Diploseira angusta
Broiliellus reiszi

Figure 18

Morphological and phylogenetic concepts of *Cacops.*

(A-C) reconstruction of the skulls of the three species of *Cacops*; (D-K) pruned topologies from previous studies with the most exclusive clade that includes all sampled species of *Cacops* (shaded in green). (A) *Cacops aspidephorus* (from Anderson, Scott & Reisz, 2020); (B) *Cacops morrisi* (modified from Reisz, Schoch & Anderson, 2009); (C) *Cacops woehri* (new); (D) strict consensus of Fröbisch & Reisz (2012); (E) 50%-majority-rule consensus of Schoch (2012); (F) strict consensus of Schoch & Sues (2013); (G) strict consensus (left) and 50% majority-rule consensus (right) of Maddin et al. (2013); (H) strict consensus (left) and 50% majority-rule consensus (right) of Holmes, Berman & Anderson (2013); (I) strict consensus of Liu (2018); (J) strict consensus with wildcard dissorophids included (left) and excluded (right) of Dilkes (2020); (K) strict consensus of Gee et al. (2021). The two identical topologies figured for Holmes, Berman & Anderson represent their two permutations (with and without scoring changes for the "Rio Arriba Taxon"). The topology of Cacopinae is unchanged in their 50%-majority rule consensus trees. Scale bars equal to 1 cm for parts A-C.

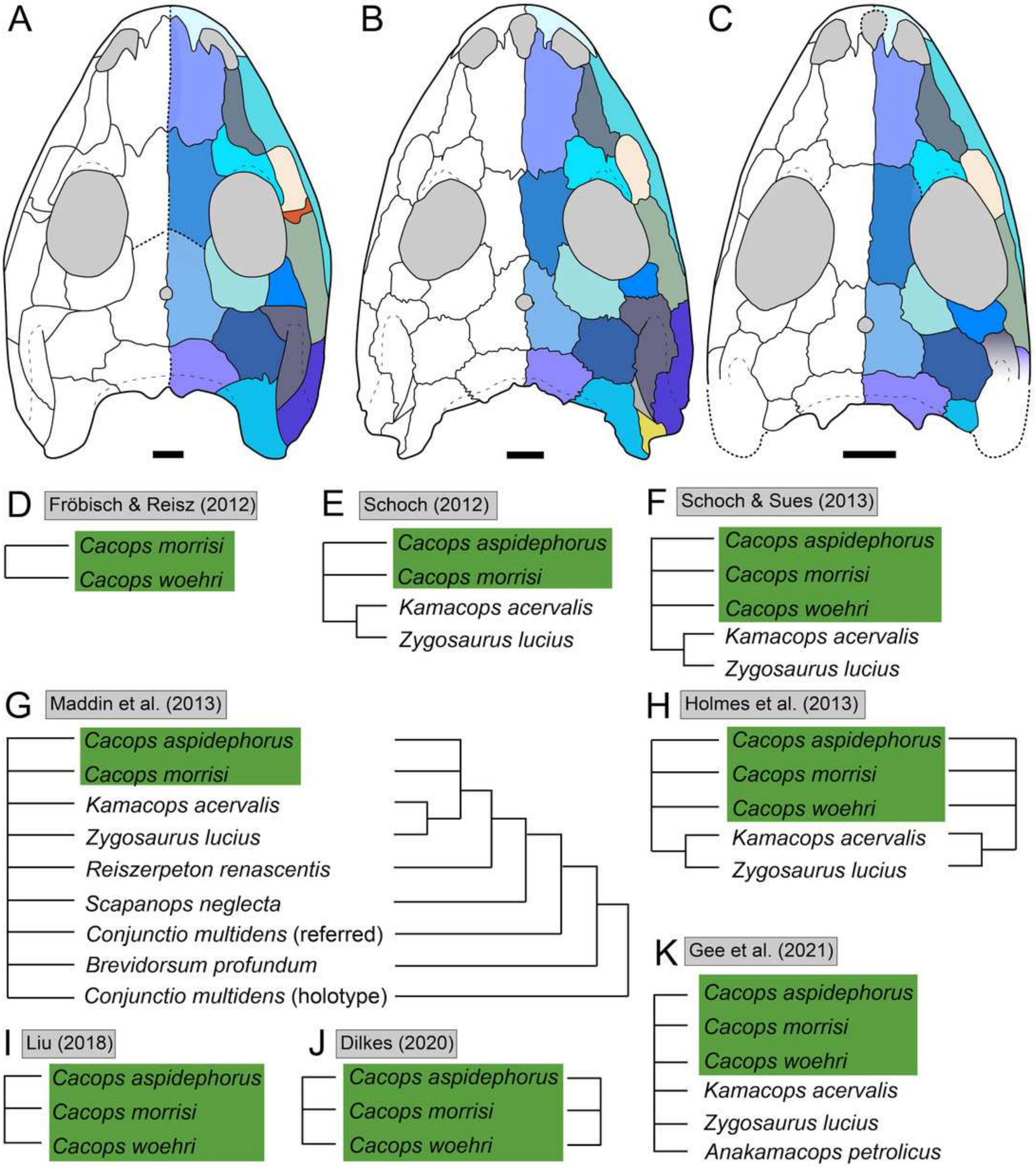
A
B
C
D
Fröbisch & Reisz (2012)
Cacops morrisi
Cacops woehri
E
Schoch (2012)
Cacops aspidephorus
Cacops morrisi
Kamacops acervalis
Zygosaurus lucius
F
Schoch & Sues (2013)
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
G
Maddin et al. (2013)
Cacops aspidephorus
Cacops morrisi
Kamacops acervalis
Zygosaurus lucius
Reiszerpeton renascentis
Scapanops neglecta
Conjunctio multidens (referred)
Brevidorsum profundum
Conjunctio multidens (holotype)
H
Holmes et al. (2013)
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
I
Liu (2018)
Cacops aspidephorus
Cacops morrisi
Cacops woehri
J
Dilkes (2020)
Cacops aspidephorus
Cacops morrisi
Cacops woehri
K
Gee et al. (2021)
Cacops aspidephorus
Cacops morrisi
Cacops woehri
Kamacops acervalis
Zygosaurus lucius
Anakamacops petrolicus

Figure 19

Morphological and phylogenetic concepts of *Broiliellus and Dissorophus.*

(A-H) pruned topologies from previous studies with the most exclusive clade that includes all sampled species of *Broiliellus* and *Dissorophus*; (I-M) reconstruction of the skulls of *Broiliellus* and *Dissorophus* with known sutures. (A) 50% majority-rule consensus tree of Schoch (2012); (B) strict consensus tree of Schoch & Sues (2013); (C) strict consensus (left) and 50% majority-rule consensus (right) of Maddin et al. (2013); (D) strict consensus (left) and 50% majority-rule consensus (right) of Holmes, Berman & Anderson (2013) with modified scorings for the “Rio Arriba Taxon” from Schoch (2012); (E) the same, but without modified scorings; (F) strict consensus of Liu (2018); (G) strict consensus with wildcard dissorophids included (left) and excluded (right) of Dilkes (2020); (H) strict consensus of Gee et al. (2021); (I) *Dissorophus multicinctus* (from Schoch, 2012); (J) *Broiliellus texensis* (from Schoch, 2012); (K) *B. brevis* (from Schoch, 2012); (L) *B. olsoni* (from Schoch, 2012); (M) *B. reiszi* (from Holmes, Berman & Anderson, 2013). Scale bars equal to 1 cm for parts I-M.

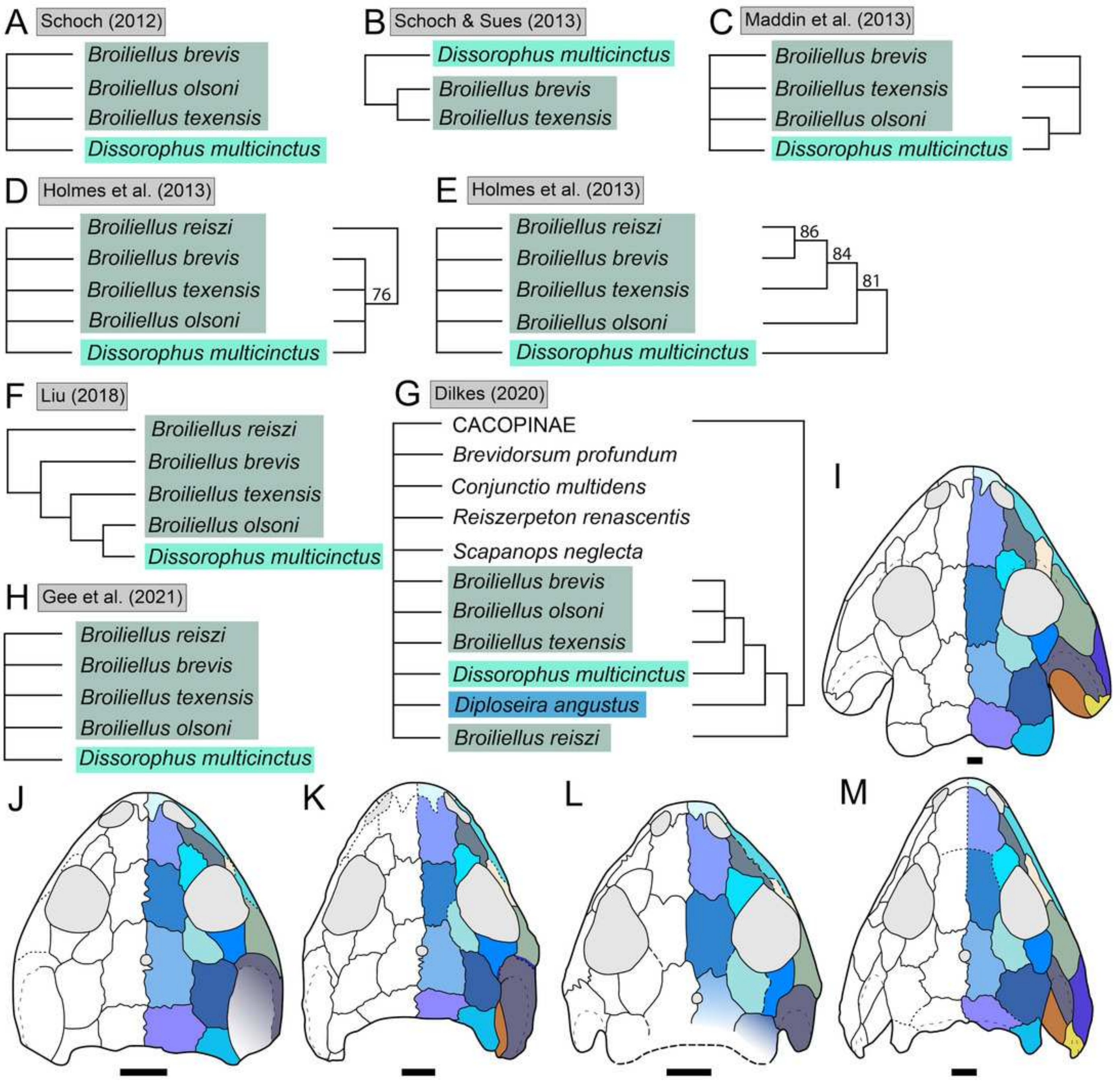
A
Schoch (2012)
Broiliellus brevis
Broiliellus olsoni
Broiliellus texensis
Dissorophus multicinctus
B
Schoch & Sues (2013)
Dissorophus multicinctus
Broiliellus brevis
Broiliellus texensis
C
Maddin et al. (2013)
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
D
Holmes et al. (2013)
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
76
E
Holmes et al. (2013)
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
86
84
81
F
Liu (2018)
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
G
Dilkes (2020)
CACOPINAE
Brevidorsum profundum
Conjunctio multidens
Reiszerpeton renascentis
Scapanops neglecta
Broiliellus brevis
Broiliellus olsoni
Broiliellus texensis
Dissorophus multicinctus
Diploseira angustus
Broiliellus reiszi
H
Gee et al. (2021)
Broiliellus reiszi
Broiliellus brevis
Broiliellus texensis
Broiliellus olsoni
Dissorophus multicinctus
I
J
K
L
M

Figure 20

Photographs of neural spines in the collections of the American Museum of Natural History resembling those attributed to *Aspidosaurus binasser*.

(A) AMNH FARB 23406 (identified as ?*Aspidosaurus*, collected from the north fork of the Little Wichita River, TX in 1880); (B) AMNH FARB 23407 (identified as ?*Aspidosaurus*, collected from unknown locality in the Wichita Basin of TX in 1878); (C) AMNH FARB 23408 in part (identified as *Aspidosaurus*, collected from unknown locality in the Wichita Basin of TX in 1878; only the piece clearly representing an ornamented spine is shown); (D) AMNH FARB 23409 (identified as *Aspidosaurus* sp., collected from unknown locality in the Wichita Basin of TX in 1878); (E) AMNH FARB 23410 (identified as *Aspidosaurus*, collected from Shell Point, Archer Co., TX; Nocona Formation in 1878); (F) AMNH FARB 23411 (not identified, collected from Wichita Co., TX in 1878); (G) AMNH FARB 23412 (identified as *Aspidosaurus* sp., collected from unknown locality in the Wichita Basin of TX). Identifiers are not named for any specimen. Scale bars equal to 1 cm.


A
AMNH 23406
B
C
AMNH 23408
D
E
AMNH 23410
F
AMNH 23411
G
AMNH 23412

Figure 21

Photographs of the holotype of “*Aspidosaurus apicalis*” (AMNH FARB 4785).

(A) presumed osteoderm in dorsal and ventral views; (B) the same in lateral view and in either anterior or posterior view (siding is indeterminate); (C) presumed osteoderm in dorsal and ventral profiles; (D) the same in either anterior or posterior view; (E) osteoderm fused to the tip of the neural spine in anterior and posterior views (siding is indeterminate); (F) the same in dorsal view. Scale bars equal to 1 cm.

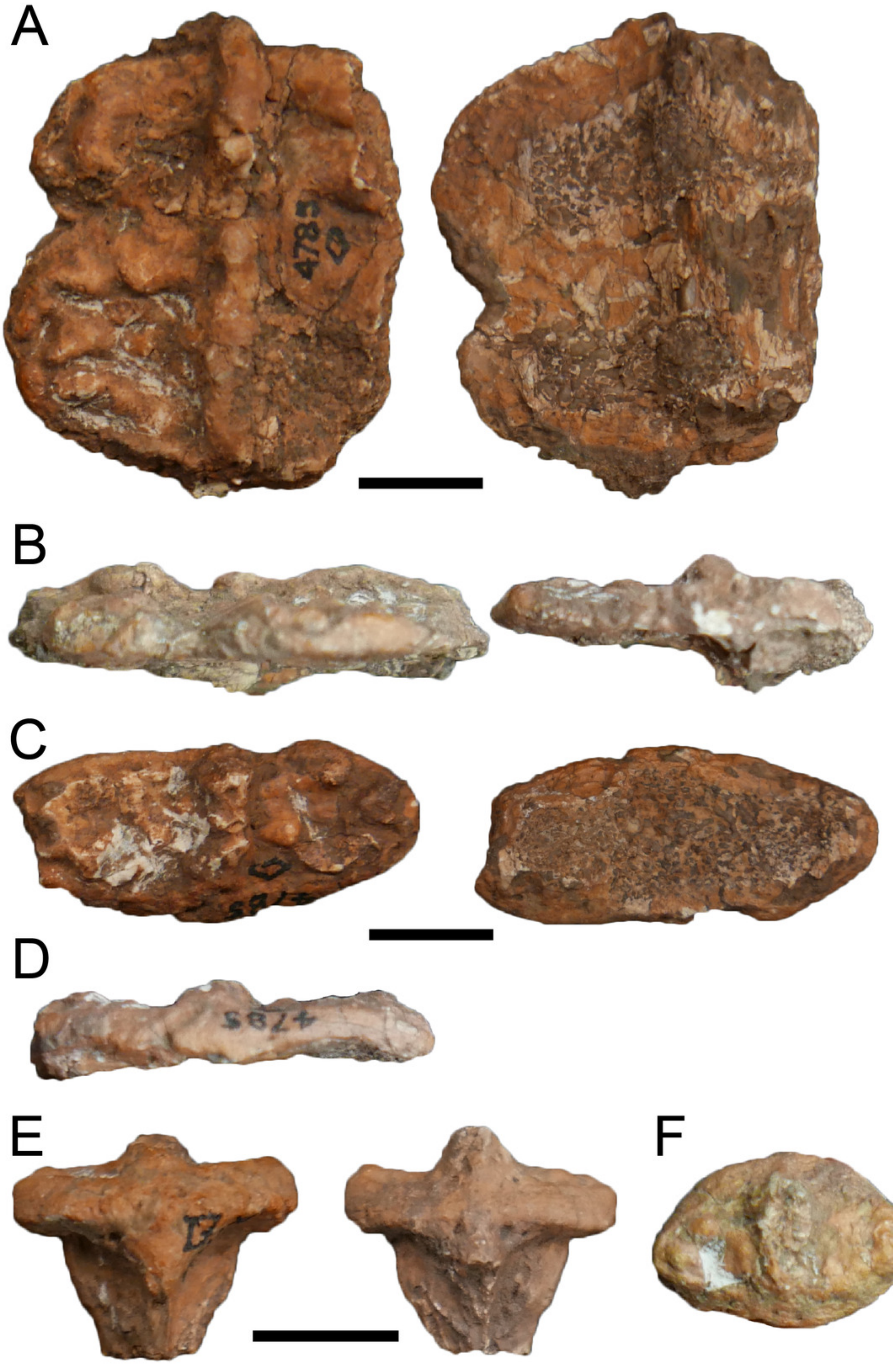
A
4785
B
C
D
4785
E
F

Figure 22

Photographs of postcranial material of *Platyhystrix rugosus* (AMNH FARB 11544).

(A) isolated neural spines associated with this individual of *P. rugosus*; (B) neural arches found in association with the other material figured here; (C) sacral ribs associated with this individual (see Berman, Reisz & Fracasso, 1981); (D) material catalogued under the same number but questionably associated with this taxon; the large fragment on the right may represent a synapsid scapula. Berman, Reisz & Fracasso (1981) conjectured that these postcrania of *P. rugosus* belonged to the skull that is catalogued as AMNH FARB 11545; the skull was not available at the time of my visit to assess the purported fit between one neural spine and a fragment on AMNH FARB 11545. Scale bars equal to 1 cm.


A
B
C
D

Figure 23

Comparative plot of known skull lengths and size ranges of olsoniforms.

Refer to Appendix 9 and Supplemental Table 3 for dataset and methods used to collect measurement data.

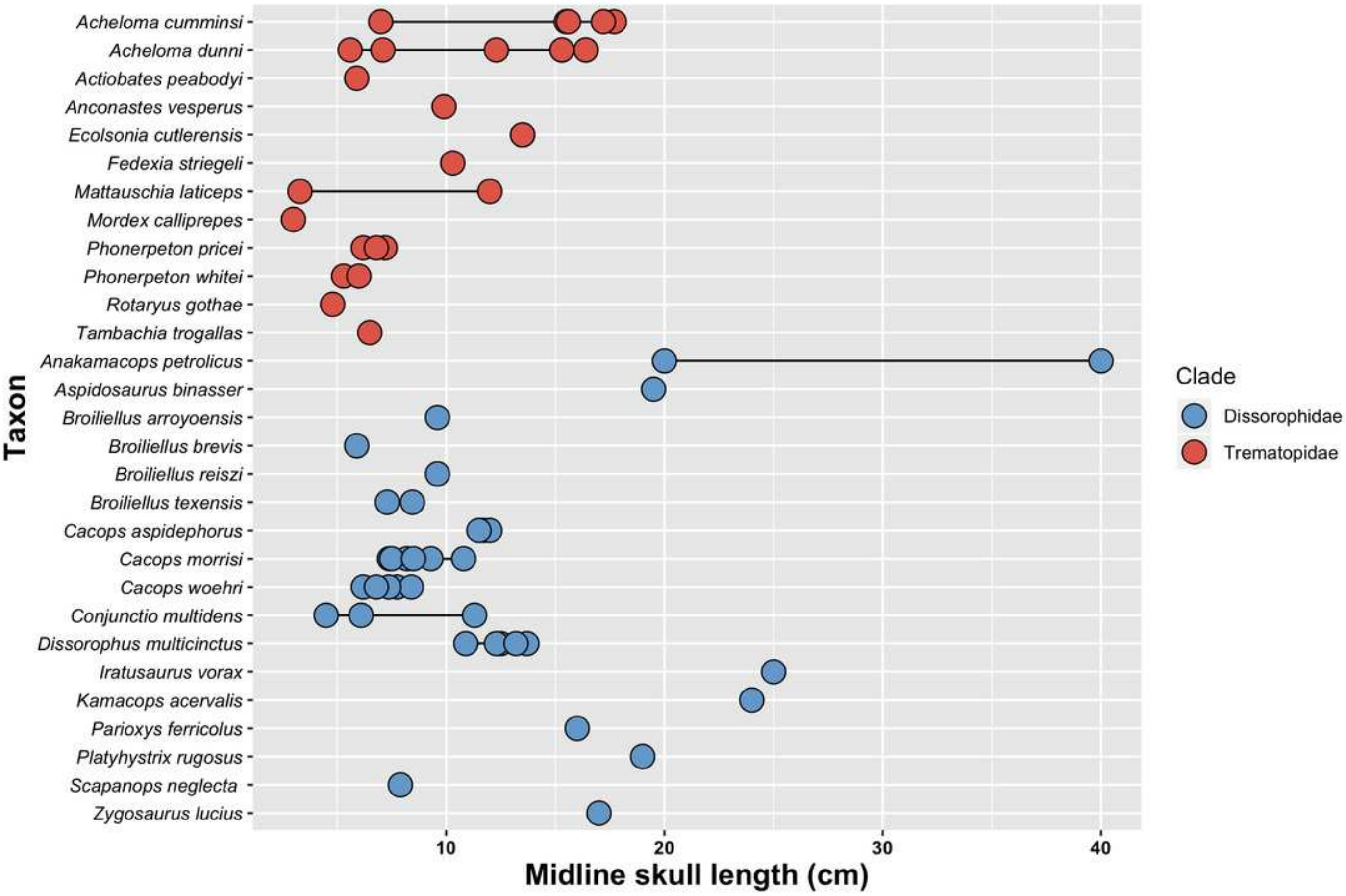

Table 1(on next page)

Summary of newly added olsoniform taxa.

Completeness refers to percent of characters that could be scored; note that this includes cells scored as inapplicable (-), even though most programs treat these as missing data (?).

Table 1. Summary of newly added olsoniform taxa. Completeness refers to percent of characters that could be scored; note that this includes cells scored as inapplicable (-), even though most programs treat these as missing data (?).

Taxon	**Time**	**Location**	**References**	**Completeness**
Anakamacops petrolicus	middle Permian	China	Li & Cheng (1999); Liu (2018)	70 (62.5%)
Aspidosaurus binasser	early Permian	USA (TX)	Berman & Lucas (2003)	54 (48.2%)
Aspidosaurus chiton	early Permian	USA (TX)	Broili (1904)	22 (19.6%)
Aspidosaurus novomexicanus	late Carboniferous	USA (NM)	Williston (1911); Carroll (1964a)	23 (20.5%)
Brevidorsum profundum	early Permian	USA (TX)	Carroll (1964a)	30 (26.7%)
Broiliellus arroyoensis	early Permian	USA (TX)	DeMar (1967)	24 (21.4%)
Broiliellus brevis	early Permian	USA (TX)	Carroll (1964a)	81 (72.3%)
'Broiliellus' hektotopos	early Permian	USA (OH)	Berman & Berman (1975)	42 (37.5%)
Broiliellus olsoni	early Permian	USA (TX)	DeMar (1967); Bolt (1974b)	39 (34.8%)
Broiliellus reiszi	early Permian	USA (NM)	Holmes, Berman & Anderson (2013)	91 (81.2%)
Broiliellus texensis	early Permian	USA (TX)	DeMar (1966); Bolt (1974b)	62 (55.3%)
Cacops aspidephorus	early Permian	USA (TX)	Williston (1910); Anderson (2005); Dilkes & Brown (2007); Dilkes (2009); Anderson, Scott & Reisz (2020)	106 (94.6%)
Cacops morrisi	early Permian	USA (OK)	Reisz, Anderson & Schoch (2009); Gee & Reisz (2018a); Gee, Bevitt & Reisz (2019)	101 (90.1%)
Cacops woehri	early Permian	USA (OK)	Fröbisch & Reisz (2012); Fröbisch, Brar & Reisz (2015); ; Gee, Bevitt & Reisz (2019)	75 (66.9%)
Conjunctio multidens	early Permian	USA (CO, NM)	Case & Williston (1913); Carroll (1964a); Schoch & Sues (2013); Gee et al. (2021)	60 (53.5%)
Diploseira angusta	early Permian	USA (TX)	Dilkes (2020)	49 (43.7%)
Dissorophus multicinctus	early Permian	USA (TX)	DeMar (1968); Milner (2003); Dilkes (2020)	104 (92.8%)
Iratusaurus vorax	middle Permian	Russia	Gubin (1980)	12 (10.7%)
Kamacops acervalis	middle Permian	Russia	Gubin (1980); Schoch (1999)	32 (28.5%); 52 (46.4%)
Nooxobeia gracilis	middle Permian	USA (OK)	Gee, Scott & Reisz (2018)	21 (18.7%)
Palodromeus bairdi	late Carboniferous	USA (OH)	Schoch, Henrici & Hook (2020)	70 (62.5%)
Parioxys bolli	early Permian	USA (TX)	Carroll (1964b)	11 (9.8%)
Platyhystrix rugosus	early Permian	USA (CO, NM)	Berman, Reisz & Fracasso (1981)	68 (60.0%)
Reiszerpton renascentis	early Permian	USA (TX)	Maddin et al. (2013)	57 (50.8%)
Scapanops neglecta	early Permian	USA (TX)	Carroll (1964a); Schoch & Sues (2013)	59 (52.6%)
Zygosaurus lucius	early Permian	Russia	Eichwald (1848); Efremov (1937)	19 (16.9%)

Table 2(on next page)

Summary of the permutations performed in this study, indicating software, search type, and general characterization of the analysis with respect to taxon and character sampling.

Note that the heuristic search in TNT is termed ‘traditional search,’ and the branch-and-bound search is termed ‘implicit enumeration.’

Table 2. Summary of the permutations performed in this study, indicating software, search type, and general characterization of the analysis with respect to taxon and character sampling.

Permutation	Software	Search	Analysis type
1A	TNT	Heuristic	Novel
1B	TNT	Heuristic	Novel
2	TNT	Heuristic	Novel
3	TNT	Heuristic	Novel
4	TNT	Heuristic	Novel
5	PAUP*	Both	Taxon mirror of Dilkes (2020)
6	TNT	Branch-and-bound	Taxon mirror of Gee (2020b)
7	PAUP*	Branch-and-bound	Matrix of Dilkes (2020), with scoring changes
8	PAUP*	Branch-and-bound	Parallel of permutation #6
9A	TNT	Branch-and-bound	Parallel of original Dilkes (2020) matrix
9B	TNT	Branch-and-bound	Parallel of permutation #7

Note that the heuristic search in TNT is termed ‘traditional search,’ and the branch-and-bound search is termed ‘implicit enumeration.’

Table 3(on next page)

Comparison of reported support metrics for focal nodes from dissorophid-focused analyses.

All nodes are from strict consensus trees except for Schoch (2012). Abbreviations refer to publications: S12, Schoch (2012); MFEM13, Maddin et al. (2013); L18, Liu (2018); D20, Dilkes (2020). 'A' and 'W' refer to the taxon samples employed by Dilkes: all taxa and without wildcards. The same sublettering is used for this study (permutation #7). An en-dash indicates that a node was not recovered, and 'NR' means that the value was not reported. Because the composition of Cacopinae and Dissorophinae sometimes includes certain wildcard taxa (e.g., *Conjunctio multidens*), these nodes are restricted to the same stable constituent taxa in this table. Cacopinae is comprised of *Cacops* + *Anakamacops* + *Kamacops* + *Zygosaurus*; and Dissorophinae is comprised of *Broiliellus* + *Diploseira* + *Dissorophus*.

Table 3. Comparison of reported support metrics for focal nodes from dissorophid-focused analyses.

All nodes are from strict consensus trees except for Schoch (2012). Abbreviations refer to publications: S12, Schoch (2012); MFEM13, Maddin et al. (2013); L18, Liu (2018); D20, Dilkes (2020). 'A' and 'W' refer to the taxon samples employed by Dilkes: all taxa and without wildcards. The same sublettering is used for this study (permutation #7). An en-dash indicates that a node was not recovered, and 'NR' means that the value was not reported. Because the composition of Cacopinae and Dissorophinae sometimes includes certain wildcard taxa (e.g., *Conjunctio multidens*), these nodes are restricted to the same stable constituent taxa in this table. Cacopinae is comprised of *Cacops* + *Anakamacops* + *Kamacops* + *Zygosaurus*; and Dissorophinae is comprised of *Broiliellus* + *Diploseira* + *Dissorophus*.

Clade	**S12**	**MFEM13**	**L18**	**D20 (A)**	**this study (A)**	**D20 (W)**	**this study (W)**
Olsoniformes	3 / 100	NR / 91	NR	>3 / 90	>3 / 93	4 / 94	4 / 94
Trematopidae	2 / 77	NR / 84	NR	>3 / 98	2 / 90	4 / 95	3 / 92
Dissorophidae	3 / 93	NR / 82	3 / NR	3 / 86	2 / 83	3 / 90	3 / 88
Cacopinae	3 / 98	–	3 / NR	1 / 54	–	2 / 70	1 / 49
Cacops	–	–	1 / NR	1 / 71	2 / 67	1 / 73	2 / 63
Dissorophinae	1 / 76	NR / 72	3 / NR	–	1 / 17	1 / 71	1 / 63
Post-*Platyhystrix*	1 / 60	NR / 69	1 / NR	1 / 51	–	1 / 71	1 / 65
Post-*Aspidosaurus*	1 / <50	NR	–	1 / 45	–	2 / 72	1 / 71

Table 4(on next page)

Comparison of reported support metrics for focal nodes from trematopid-focused analyses.

All nodes are from strict consensus trees. Abbreviations refer to publications: B10, Berman et al. (2010); B11, Berman et al. (2011); PR11, Polley & Reisz (2011); G20, Gee (2020b). Nodal support of Gee (2020b) refers to the permutation of that study that sampled all twelve trematopids at the species-level (figure 6 therein). This study's nodal support is derived from permutations 6 and 8 (Figs. 13B, 15). An en-dash indicates that a node was not recovered, and 'NR' means that the value was not reported.

Table 4. Comparison of reported support metrics for focal nodes from trematopid-focused analyses.

All nodes are from strict consensus trees. Abbreviations refer to publications: B10, Berman et al. (2010); B11, Berman et al. (2011); PR11, Polley & Reisz (2011); G20, Gee (2020b). Nodal support of Gee (2020b) refers to the permutation of that study that sampled all twelve trematopids at the species-level (figure 6 therein). This study's nodal support is derived from permutations 6 and 8 (Figs. 13B, 15). An en-dash indicates that a node was not recovered, and 'NR' means that the value was not reported.

Clade	**B10**	**B11**	**PR11**	**G20**	**this study (TNT)**	**this study (PAUP*)**
Olsoniformes	2 / NR	2 / NR	2 / 66	NR / 55	4 / 34	4 / 63
Dissorophidae	2 / NR	1 / NR	NR	NR / 97	>5 / 76	>5 / 92
Trematopidae	3 / NR	5 / NR	5 / 82	NR	2 / 28	4 / 52
Acheloma + Phonerpeton	4 / NR	7 / NR	–	NR / 92	3 / 55	3 / 78
Anconastes + Tambachia	1 / NR	1 / NR	6 / 77	–	1 / 18	1 / 52
Ecolsonia as trematopid?	No	No	Yes	Yes	Yes	Yes