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A new dissorophid temnospondyl from the Lower Permian of north-central Texas

*Un nouveau temnospondyle dissorophidé du Permien inférieur du Centre-Nord du Texas*Rainer R. Schoch^{a,*}, Hans-Dieter Sues^b^a Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany^b Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, MRC 121, PO Box 37012, Washington, DC 20013-7012, USA

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ABSTRACT

Dissorophidae form a clade of terrestrially adapted temnospondyls, which were widely distributed in Euramerica and Asia during the Permian. After a long phase of neglect, study of exquisitely preserved new material of the Early Permian *Cacops* from Oklahoma has prompted reconsideration of other dissorophids, such as the Early Permian *Conjunctio* from New Mexico. Here we report on a specimen previously referred to *Conjunctio* from the Nocona Formation of north-central Texas. It actually represents a distinct new taxon, for which the binomen *Scapanops neglecta* is proposed. It represents a small dissorophid with derived characters combining to give a unique skull configuration: extremely short skull table, jaw joint situated well anterior to occiput, large orbits with wide interorbital distance, and a preorbital region more than twice as long as the postorbital region. The external nares are elongate, and the outline of the skull is ovoid, widest at mid-level of the orbits. *S. neglecta* shares with eucacopines the presence of a rounded internarial fenestra and an anteroposteriorly short supratemporal. Phylogenetic analysis places *Scapanops* at the base of the clade Eucacopinae, more crownward than *Conjunctio* and as the sister-taxon to a grouping comprising *Cacops*, *Kamacops*, and *Zygosaurus*.

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R É S U M É

Les Dissorophidae forment un clade de temnospondyles adaptés à la vie terrestre, largement distribués en Euro-Amérique et en Asie pendant le Permien. Après une longue phase d'abandon, l'étude d'un nouveau matériel très bien conservé de *Cacops* du Permien inférieur d'Oklahoma a hâté le nouvel examen d'autres dissorophidés, tel *Conjunctio*, du Permien inférieur du Nouveau Mexique. Un spécimen d'abord rapporté à *Conjunctio* de la formation Nocona du Centre-Nord du Texas est décrit ici. Il se révèle actuellement comme un nouveau taxon distinct, pour lequel la dénomination de *Scapanops neglecta* est proposée. Il représente un petit dissorophidé aux caractères dérivés se combinant en une configuration de crâne unique: un plateau crânien étroit, une articulation de la mâchoire située nettement en avant de l'occiput, de grandes orbites avec une large distance inter-orbitale et une zone pré-orbitale deux fois plus longue que la zone post-orbitale. Les narines externes sont allongées et le contour du crâne est ovoïde, le plus large à mi-chemin des orbites.

Mots clés :

Tetrapoda

Temnospondyle

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S. neglecta partage avec les eucacopinés la présence d'une fenestra internasale arrondie et d'un supratemporal antéro-postérieurement court. Les analyses phylogénétiques placent *Scapanops* à la base du clade des Eucacopinae, plus vers le sommet que *Conjunctio* et en tant que taxon-frère d'un groupement comprenant *Cacops*, *Kamacops* et *Zygosaurus*.

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1. Introduction

The Permian red beds of Texas have yielded the highest known diversity of terrestrial temnospondyls, preserving an important component of Late Paleozoic tetrapod communities. One clade, Dissorophoidea, is distinguished by relatively small body size, disproportionately large heads, and short trunks. Among these, the small (5–10 cm long) amphibamids and the more heavily built, armored dissorophids (25–50 cm long) were the most taxonomically diverse and morphologically disparate groups. Amphibamidae have recently gained much attention because many authors viewed them as the stem-group of modern amphibians (Milner, 1993; Ruta et al., 2003; Sigurdson & Green, 2011) or at least Batrachia (frogs plus salamanders; Anderson et al., 2008), whereas Marjanović & Laurin (2008) regarded them as stem-tetrapods. In contrast, Dissorophidae have attracted little scientific interest since their comprehensive revision by Carroll (1964). DeMar (1966, 1968) published on the dorsal armor and the taxonomy of certain dissorophid taxa. Dilkes and Brown (2007) and Dilkes (2009) have examined the distinctive structure of the postcranial axial skeleton in *Cacops*. A recent review of dissorophid interrelationships has identified a range of problems affecting phylogenetic analyses of this group, often resulting from inadequate preparation of key specimens, especially from the Texan redbeds (Schoch, 2012).

The particular topic of our contribution closely relates to the research by the recipient of this Festschrift because he has, among many other topics, also done important work on dissorophid anatomy and diversity. His recent studies of new exquisitely preserved material referable to *Cacops* from the Early Permian fissure fillings in the Dolese Brothers limestone quarry at Fort Sill, Oklahoma (Fröbisch and Reisz, 2012; Reisz et al., 2009) have stimulated new interest in the anatomy and evolutionary history of Dissorophidae. Here we expand on the analysis of the clade including *Cacops* by examining a specimen that Carroll (1964) originally referred to *Conjunctio*. Our work has established that this specimen, in fact, represents a distinct and highly unusual taxon (Schoch, 2012). The objectives of the present study are:

- (1) to name and describe this new taxon;
- (2) differentiate it from *Conjunctio multidens*;
- (3) conduct a phylogenetic analysis to elucidate the position of the new taxon among Dissorophidae.

Institutional abbreviations: FMNH, Field Museum, Chicago, IL, USA; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; UCMP: Museum of Paleontology, University of California, Berkeley, CA, USA.

2. Systematic palaeontology

Temnospondyli Zittel, 1888

Dissorophoidea Bolt, 1969

Olsoniformes Anderson et al., 2008

Dissorophidae Boulenger, 1902

Eucacopinae new taxon

Definition (stem-based): The most inclusive clade that includes *Cacops apsidephorus* but not *Dissorophus multicinctus*.

Comment. Although the nomen *Cacopinae* would be the logical derivative from the name of the nominal genus *Cacops*, Noble (1931) already used *Cacopinae* for a group of frogs including *Cacopus* (now synonymized with *Uperodon*). We thus propose the replacement *Eucacopinae* for the dissorophid grouping including *Cacops*.

Scapanops new genus

Scapanops neglecta new species

Holotype. MCZ 2369, skull (midline length 7.9 cm) with a few associated appendicular elements (humerus, radius, clavicles) attached to the ventral side, and associated block with the right scapula and cleithrum, 14 vertebrae, ribs, and osteoderms (Fig. 1A–H). Collected by A.S. Romer on April 18, 1950.

Type horizon. Nocona Formation, Wichita Group; Lower Permian (Asselian).

Type locality. Halsell Hill, Clay County, North-central Texas, USA.

Etymology. Generic nomen derived from Greek *skapane*, spade, referring to the spade-like outline of the skull, and Greek *ops*, face, alluding to the general similarity to *Cacops*. Gender feminine. Specific epithet from Latin *neglectus*, overlooked, in allusion to its initial taxonomic fate.

Diagnosis. Autapomorphies:

- (1) broad interorbital region, combined with large orbits giving an ovoid skull outline;
- (2) very short posterior portion of skull roof;
- (3) preorbital region relatively longer than in any other known dissorophid, exceeding twice that of the postorbital portion of the skull roof;
- (4) quadrate condyles situated well anterior to occipital condyles;
- (5) dermal ornamentation on skull roof consisting of fine radial ridges but few pits.

Comment. Carroll (1964) originally referred MCZ 2369 to *Conjunctio* as *Conjunctio* sp. and first figured both sides of the skull and the associated string of vertebrae. However, the specimen clearly differs from *Conjunctio multidens* in the following features:

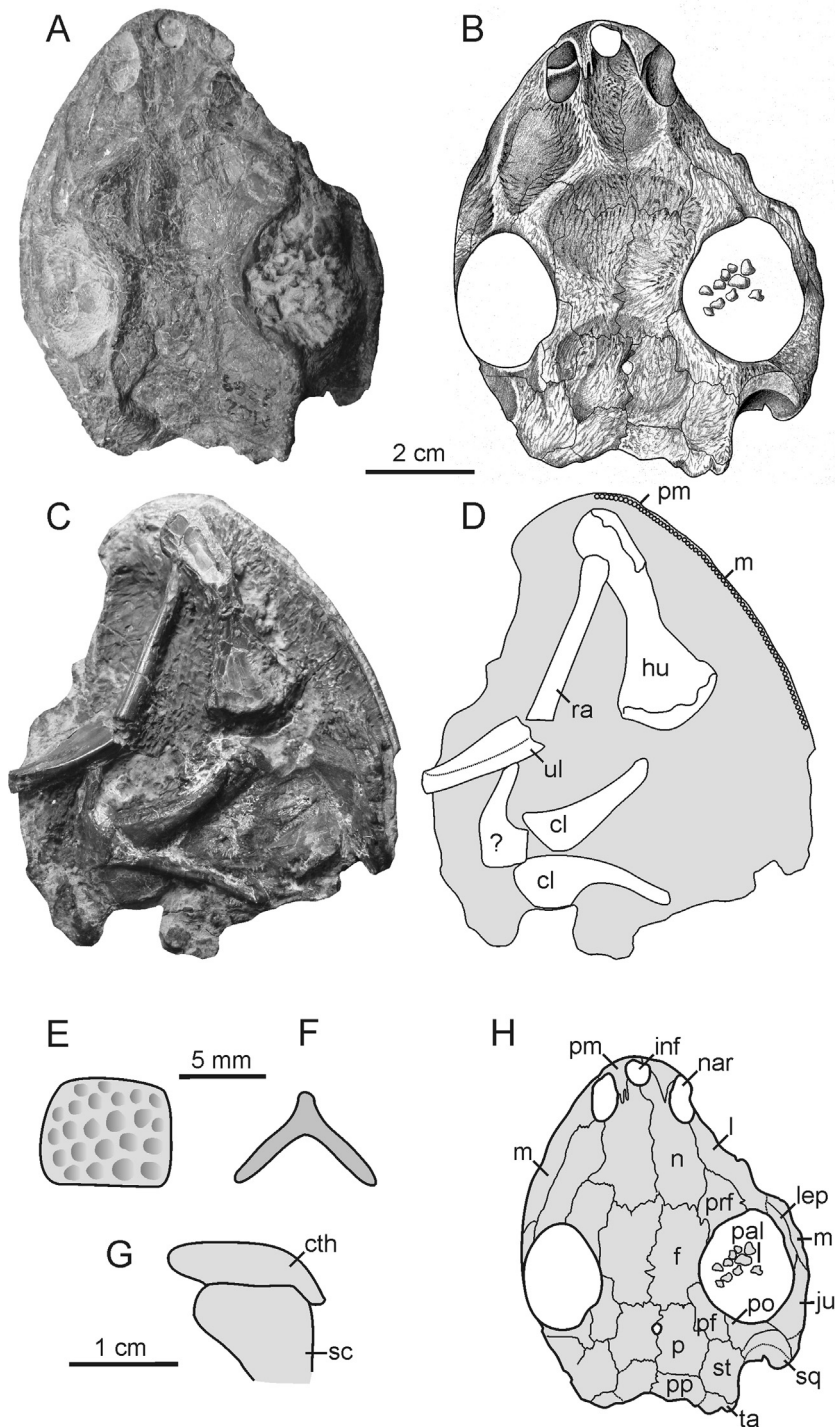


Fig. 1. Holotype of *Scapanops neglecta* (MCZ 2369). A–B. Skull in dorsal view. C–D. Skull with postcranial elements in ventral view. E. Osteoderm in dorsal view. F. Same in anterior view. G. Right scapula and cleithrum in lateral view. H. Skull roof with bones labelled. Abbreviations: cl, clavicle; cth, cleithrum; f, frontal; hu, humerus; inf, internarial; ju, jugal; l, lacrimal; lep, laterally exposed palatine; m, maxilla; n, nasal; nar, naris; p, parietal; pal, palatal ossicles; pf, postfrontal; prf, prefrontal; pm, premaxilla; po, postorbital; pp, postparietal; sc, scapula; sq, squamosal; st, supratemporal; ta, tabular; ul, ulna. The question mark denotes an unidentified postcranial element.

Fig. 1. Holotype de *Scapanops neglecta* (MCZ 2369). A–B. Crâne en vue dorsale. C–D. Crâne avec éléments post-crâniens en vue ventrale. E. Ostéoderme en vue dorsale. F. Le même en vue antérieure. G. Scapula et cleithrum droits en vue latérale. H. Boîte crânienne avec os marqués. Abréviations : cl : clavicule ; cth : cleithrum ; f : frontal ; hu : humérus ; inf : foramen internasal ; sc : scapula ; st : supratemporal ; ta : tabulaire ; ul : ulna. Le point d'interrogation correspond à un élément post-crânien non identifié.

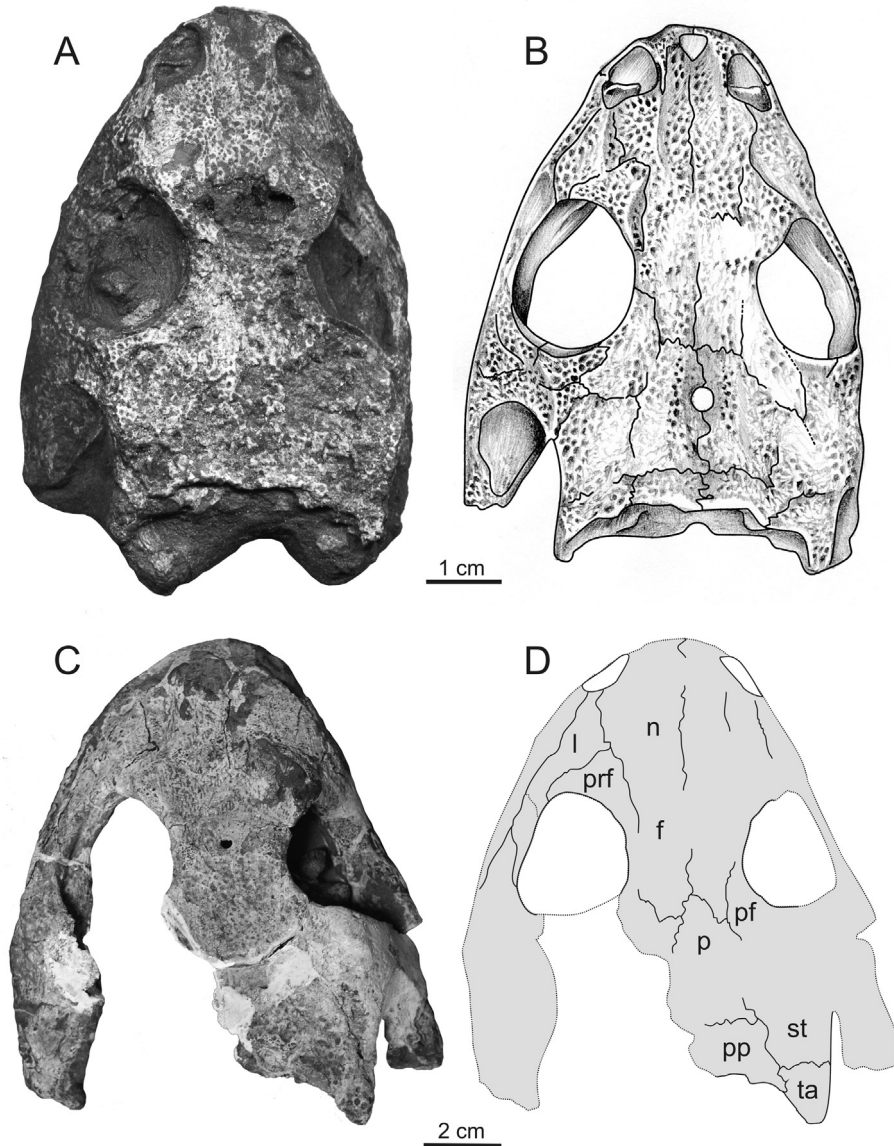


Fig. 2. Skulls referred to *Conjunctio multidens*, in dorsal view. A–B. UCMP 40103. C–D. FMNH 673 (holotype). Abbreviations: l: lacrimal; n: nasal; p: parietal; pf: postfrontal; pp: postparietal; st: supratemporal; ta: tabular.

Fig. 2. Crânes attribués à *Conjunctio multidens* en vue dorsale. A–B. UCMP 40103. C–D. FMNH 673 (holotype). Abréviations: st: supratemporal; ta: tabulaire.

- (a) orbits proportionally much larger (ratio of orbit length to skull length: 0.35 in *Scapanops*, 0.23 in *Conjunctio*);
- (b) outline of skull not ovoid, but widest at level of “cheek;”
- (c) external naris is substantially longer and aligned not parallel with maxilla but with midline suture;
- (d) postorbital portion of skull roof less than half length (0.4) of preorbital region.

Derived features shared by *Scapanops* and *Conjunctio* are the median fontanelle between the premaxillae, the smaller, more numerous teeth as compared to other disorophids, and osteoderms that are fused to the neural spines. However, all these features are not autapomorphies of the two taxa, but are shared with *Cacops*.

Below we provide an amended diagnosis of *Conjunctio multidens* (Fig. 2C–D).

Conjunctio Carroll, 1964

Conjunctio multidens Carroll, 1964

Holotype. FMNH 673, partial skull roof (midline length 11.3 cm; Fig. 2C–D).

Type horizon. Abo Formation, Lower Permian (Asselian–Sakmarian).

Type locality. West side of Puerco River, opposite Youngsville (in the earlier literature given as “El Rito,” which is now the official name of a larger town some 30 miles (48 km) to the north; Langston, 1953), Rio Arriba County, New Mexico, USA.

Referred specimen. UCMP 40103, a skull (length 6.1 cm), from the Cutler Formation (Lower Permian) of

Camp quarry (UCMP locality V-2814), one mile (1.6 km) southeast of Arroyo de Agua, Rio Arriba County, New Mexico, USA.

Revised diagnosis:

- (1) at least 70 tooth positions in the upper jaw (synapomorphy shared with *Cacops morrisoni* and *Scapanops neglecta*);
- (2) presence of internarial fenestra. Plesiomorphies (compared to *Cacops*);
- (3) interorbital distance wider, and skull at orbit mid-level broader;
- (4) posterior portion of skull roof moderately long with long supratemporal.

3. Description

3.1. Skull roof

The skull of MCZ 2369 has a unique shape among known temnospondyls, with a long, anteriorly tapered snout, large and round orbits, a wide interorbital distance, and a very short skull table (Fig. 3D). The ratio of interorbital distance to skull length (0.28) is greater than in *Dissorophus multicinctus* (0.25), *Conjunctio multidens* (0.25), and *Cacops morrisoni* (0.2). Even more distinctive is the size of the skull table, which reaches only 0.325 times the length of the preorbital region in *Scapanops*, contrasted by *Cacops morrisoni* (0.67), *Conjunctio* (0.9), *Dissorophus* (1.0), and *Broiliellus texensis* (1.45). The preorbital region is tapered anteriorly. The external nares are closely spaced, and the premaxillae and nasals bound a large rounded fenestra level with the anterior parts of the narial openings. The external nares are elongate and oval, anteriorly close to the jaw margin, but posteriorly far offset from the maxilla. The outline and relative size of the external naris are most similar to those in *Aspidosaurus* (Berman and Lucas, 2003; Broili, 1904). The nasal is only slightly longer than the frontal, whereas the lacrimal is greatly elongated compared to that of other dissorophoids, reaching about twice the length of the prefrontal. The prefrontal and postfrontal are separated, although the postfrontal has an anterior projection extending along the orbital margin. This feature is also found in *Conjunctio* and shared with more basal dissorophoids.

The skull table is not only much shorter, but also narrower than that in most other dissorophoids. The parietal is slightly narrower than the frontal, and the supratemporal is still slightly narrower than the parietal. The postparietal is relatively short but still longer than the tabular, which lacks a posterior horn. Both elements form a posterior flange. The postorbital consists of an elongate medial part and a slender lateral wing that contacts the jugal. The squamosal is extremely thin, restricted to the margin of the temporal notch. The “cheek” region is even shorter than the skull table, with the jaw joint situated well anterior to the occipital condyles. The temporal (“otic”) notch, which is wide and deep, resembles that of *Dissorophus*, especially in the very short distance between the notch and the posterior margin of the orbit. The squamosal makes only limited contact

with the supratemporal, which otherwise forms the medial margin of the temporal notch.

Similar to other dissorophids, the skull roof bears pronounced ridges that divide its dorsal surface into smaller depressions (Fig. 1B). As in *Cacops*, there is a large depression on the nasals and on the anterior portion of the frontals, bounded by a transverse ridge between the orbits. An additional depression is situated on the posterior portion of the frontals and on the parietals, and the pineal foramen is located within a transversely oval pit. The dermal ornamentation is not well preserved, but was much less pronounced and regionally differentiated than in *Cacops* or *Kamacops*. As in *Conjunctio*, *Dissorophus*, and *Broiliellus*, it was dominated by pits and the ridges were not as high as in the advanced eucacopines. It is also knobby in places.

The large orbits are filled with numerous small elements, probably palpebral ossicles and (or) scleral plates (Fig. 1B). Scleral plates are known from *Cacops morrisoni* (Reisz et al., 2009) and palpebral elements from *Broiliellus* sp. (RRS, personal examination).

3.2. Palate

The palatal surface is concealed by overlying postcranial bones, but the prepared regions expose only the internal side of the skull roof, indicating that palatal elements must have fallen off before final burial (Fig. 1C–D). The dentigerous shelves of the premaxilla and maxilla are exposed, revealing the approximate number of teeth in both elements (premaxilla: 16; maxilla: >75). The teeth are mostly subequal in size and have round bases. The teeth in the premaxilla and anterior part of maxilla are slightly larger (Carroll, 1964). The number and relative size of teeth led Carroll (1964) to refer MCZ 2369 to *Conjunctio*. However, similar tooth counts have also been reported for some amphibamid dissorophoids (Clack and Milner, 2010).

3.3. Postcranial skeleton

The ventral side of the skull is concealed by several postcranial elements, all of which are similar to the corresponding bones in other dissorophids and thus probably come from the same individual as the skull to which they are attached (Fig. 1C–D). An additional piece preserves about 14 vertebrae in articulation, five or six ribs, and the right scapula and cleithrum.

The largest limb bone is a left humerus exposed in ventral view. It is similar in its long and slender outline to that of *Cacops morrisoni* (Reisz et al., 2009). As in *C. morrisoni*, its distal end is weakly expanded and not fully ossified, unlike in the much larger humeri of *C. aspidephorus* and *Dissorophus multicinctus* (DeMar, 1968; Williston, 1910). Two additional elongate elements probably represent the radius and ulna, as suggested by Carroll (1964). Finally, both clavicles are also preserved, with small ventral blades typical of dissorophoids.

The few ribs, preserved in a series, are short with forked proximal portions, with spike-like uncinat processes that become shorter posteriorly. The right scapula is well

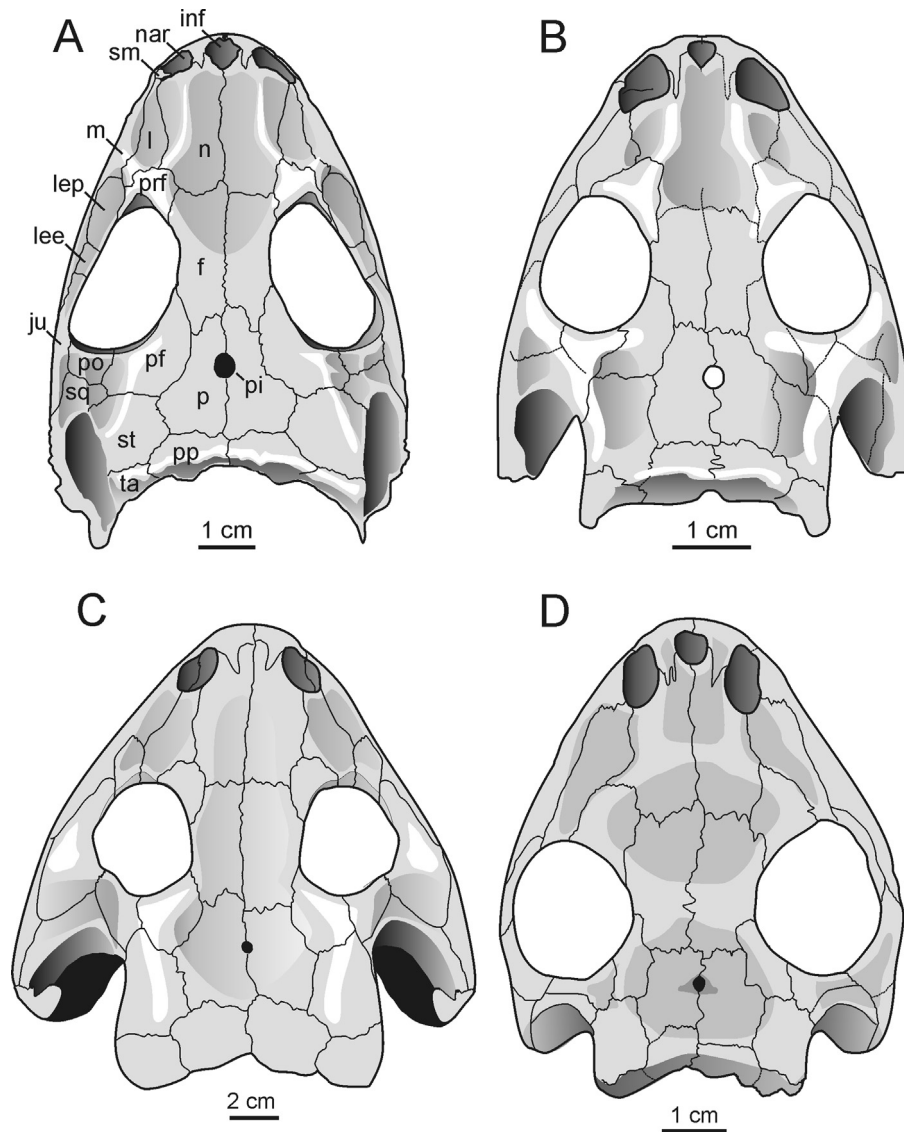


Fig. 3. Comparison of selected dissorophid skulls in dorsal view. A. *Cacops morrissi* (based on Reisz et al., 2009). B. *Coniunctio multidentis* (based on UCMP 40103). C. *Dissorophus multicinctus* (from Schoch, 2012). D. *Scapanops neglecta*. Abbreviations: lee: laterally exposed ectopterygoid; pi: pineal foramen; sm: septomaxilla.

Fig. 3. Comparaison de crânes sélectionnés de dissorophidés en vue dorsale. A. *Cacops morrissi* (d'après Reisz et al., 2009). B. *Coniunctio multidentis* (d'après UCMP 40103). C. *Dissorophus multicinctus* (d'après Schoch, 2012). D. *Scapanops neglecta*. Abréviations : lee : exposition latérale de l'ectoptérygoïde ; pi : foramen pinéal ; sm : septomaxilla.

ossified and with a complete, slightly expanded dorsal margin, to which the elongate cleithrum is attached as in *Cacops aspidephorus*. The cleithrum is more slender than in the latter taxon.

The osteoderms of *Scapanops* are small and square-shaped, with pitted ornamentation (Fig. 1E), and similar to those of *Cacops aspidephorus* and *Aspidosaurus chiton* (DeMar, 1966). They are slightly longer than the neural spine, and, as in *Aspidosaurus*, there was only a single layer of plates present. In end view, the osteoderms are shaped like an inverted V and lack a ventral projection (unlike in *Coniunctio multidentis*; Carroll, 1964).

4. Phylogenetic analysis

4.1. Objective

The description of new material of *Cacops* from the Early Permian fissure fillings in the Dolese Brothers limestone quarry at Fort Sill (Fröbisch and Reisz, 2012; Reisz et al., 2009) and modern cladistic analyses of related taxa (Polley and Reisz, 2011; Schoch, 2013) have triggered renewed interest in the interrelationships among Dissorophoidea. In the present study, we focus on:

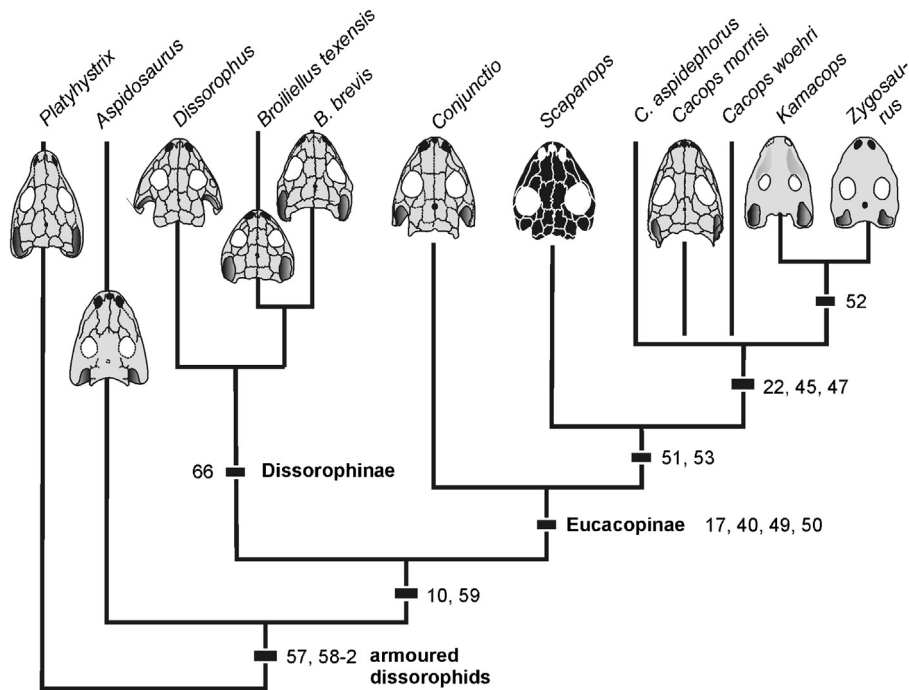


Fig. 4. Phylogeny of Dissorophidae, based on the strict consensus of the present TNT analysis. *Coniunctio* and *Scapanops* form successive basal nodes within Eucacopinae. Synapomorphies: 57: median unpaired osteoderms; 58-2: wide osteoderms; 66: pointed snout; 10: rectangular pterygoid flange; 59: pronounced ridges in the snout; 17: postparietal abbreviated; 40: internarial fenestra; 49: semilunar curvature (squamosal); 50: transverse ridge (postparietal); 51: postorbital skull longer than preorbital; 53: distance otic notch-orbit reduced; 22: interorbital width in the 0.2–0.24 range; 45: tabular fused to quadrate; 47: knobby exostoses; 52: height of suborbital bar less than 10% skull length.

Fig. 4. Phylogénie des Dissorophidae, sur la base du strict consensus de l'analyse TNT. *Coniunctio* et *Scapanops* forment des nœuds basaux successifs au sein des Eucacopinae. Synapomorphies : 57 : ostéodermes médians non appariés ; 58-2 : larges ostéodermes ; 66 : museau pointu ; 10 : rebord rectangulaire du ptéridoïde ; 59 : sillons prononcés sur le museau ; 17 : post-pariétal abrégé ; 40 : fenêtre internasale ; 49 : courbure en demi-lune (squamosal) ; 50 : sillon transverse (post-pariétal) ; 51 : crâne à zone postorbitale, plus longue que la zone préorbitale ; 53 : distance entre échancrure optique et orbite réduite ; 22 : largeur orbitale de 0,2 à 0,24 ; 45 : tabulaire fondu jusqu'au carré ; 47 : exostoses noueuses ; 52 : hauteur de la barre sub-orbitale de moins de 10% de la longueur du crâne.

- (1) assessing the phylogenetic position of *Scapanops*;
- (2) the relationship between *Scapanops* and *Coniunctio*.

Because only the skull roof is reasonably well preserved or exposed, we also include other dissorophoid taxa, notably Amphibamidae, to which *Scapanops* bears some resemblance in the morphology of the skull roof. Unfortunately, the palate, which differs considerably among dissorophoid clades, is not exposed in *Scapanops*.

4.2. Analysis

The software package TNT 1.1 (Goloboff et al., 2008) was employed for the phylogenetic analysis. All characters were treated as unordered. The parsimony analysis was performed in the heuristic search mode, both under the Traditional Search and New Technology Search options. Both searches yielded the same alternative topologies.

4.3. Data set

We employed a slightly modified version of Schoch's (2012) character-taxon matrix for Dissorophidae, excluding the "wild card" taxa *Brevadorsum profundum* and *Broiliellus texensis*, both of which are in urgent need of

restudy. *Coniunctio multidens* was coded from both the holotype and the referred specimen UCM 40103 ("Rio Arriba taxon" of Schoch, 2012). Hence, the matrix comprised 25 taxa and 70 characters, as listed in Schoch (2012).

4.4. Results

The analysis yielded three most parsimonious trees, each with a length of 126 steps, a Consistency Index (CI) of 0.611, and a Retention Index (RI) of 0.802. The general topology is very similar to that recovered by Schoch (2012), differing only in the more secure placement of *Coniunctio* among Eucacopinae. The three named species of *Cacops* (*C. aspidephorus*, *C. morrissi*, *C. woehri*) form an unresolved polytomy with the most derived eucacopines *Zygosaurus* and *Kamacops*. Fig. 4 lists the synapomorphies supporting each node.

4.5. Discussion

The present findings add to our knowledge of a diverse clade of the dissorophoid temnospondyls, Eucacopinae. These able terrestrial walkers (Dilkes, 2009) were more lightly built than the heavily armoured dissorophines, but had proportionately very large skulls with knobby

ornament, which tended to overprint the sutures in adult specimens of *Cacops aspidephorus*, *Kamacops*, and *Zygosaurus*. Eucacopines are known from Texas and New Mexico, France (R. Werneburg, personal communication 2012), European Russia, and China.

The present results show that, in addition to *Cacops* and the derived Russian forms *Kamacops* and *Zygosaurus*, there must have been a basal eucacopine radiation represented by forms such as *Conjunctio* and *Scapanops*. These basal taxa have osteoderms similar to those of *Aspidosaurus*, consisting of a single row of quadrangular plates. This lends support to the hypothesis that the double rows of osteoderms must have evolved independently in eucacopines and dissorophines (Schoch, 2012).

Conjunctio shares with *Cacops* the general skull proportions, the large pineal foramen, and the shape of the external naris. It differs by having slightly smaller orbits and a proportionately slightly longer skull table. The heart-shaped internarial fenestra is an additional feature shared by both taxa but is also present in *Scapanops*. In both taxa, the postparietal has a raised posterior margin, formed of hypertrophied dermal sculpturing. They also share with *Scapanops* the presence of a distinct occipital flange.

Considering their substantial morphological differences, it is interesting that *Conjunctio* and *Scapanops* also share an additional apomorphy, the high number of teeth in the upper jaw. This feature was originally noted by Carroll (1964) and led to his referral of the holotype of *Scapanops neglecta* to *Conjunctio*. If our hypothesis is valid, this apomorphy was shared by basal eucacopines and then reversed to fewer and larger teeth in the least inclusive clade that includes *Cacops* and *Kamacops*. This would suggest a shift in dietary preference from small (*Scapanops*, *Conjunctio*) to larger prey (*Cacops*, *Kamacops*, *Zygosaurus*).

Scapanops is distinguished by its short and narrow skull table, short “cheek” region, very short distance between temporal notch and orbits, and an elongated preorbital region exceeding that of most other dissorophoids, with the exception of *Kamacops* and *Zygosaurus*. The short skull table of *Cacops* differs strongly from that of *Scapanops* in that the supratemporal and parietal have very different outlines.

Scapanops resembles amphibamids in certain features such as the small postparietal and tabular, the disproportionately large temporal notch, and its close proximity to the orbit. However, the osteoderms, cranial sutures, and the presence of the system of ridges and depressions on the skull roof are clearly dissorophid characters that are not present in any known amphibamid. Schoch (2012) has discussed in detail the distinction between amphibamids and dissorophids, which is supported by numerous characters.

5. Conclusions

Recognition of the new taxon, *Scapanops neglecta*, and its comparison to *Conjunctio multidentis* adds significant data to our knowledge of dissorophid diversity, which apparently reached a peak during Early Permian (Asselian–Sakmarian) times. The following conclusions emerge from the present study:

Scapanops neglecta differs substantially from *Conjunctio*, the taxon to which it was originally referred by Carroll

(1964). It is characterized by an unusually broad skull at mid-orbit level, combined with a short skull table and pointed snout. In combination, these features result in a rounded, “spade-like” skull outline that is quite distinct among known temnospondyls. The external naris is relatively longer than in other dissorophids, but differs from the posteriorly extended naris of trematopids in its oval outline.

Despite their morphological differences, *Scapanops* and *Conjunctio* nest within the same clade of dissorophid temnospondyls, Eucacopinae. *Scapanops* shares a few homoplasies with (1) amphibamids (abbreviated skull table), (2) dissorophines (pointed snout), and (3) *Aspidosaurus* (elongated external naris). Notwithstanding, its position within a larger eucacopine clade is firmly supported when the two poorly known “wild card” taxa *Brevidorsum profundum* and *Broiliellus olsoni* are excluded.

Eucacopinae appear to have been the most diverse and disparate clade among the dissorophids, and also attained the widest geographical range, with diagnostic material known from many localities in North America, Europe, Russia, and China.

Acknowledgments

We take great pleasure in contributing to this Festschrift honoring our friend and colleague Robert Reisz, whose studies on Late Paleozoic tetrapods, including dissorophid temnospondyls, have established benchmarks for all future research on these animals.

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