The stem caecilian fossil record is restricted to two species: the well-known *Eocaecilia micropodia* (1, 2) from the Early Jurassic of Arizona and *Rubriceaella monbarroni* (3) from the Early Cretaceous of North Africa. Consequently, an ~70-Ma gap exists between *Eocaecilia* and early Permian tetrapods inferred previously to represent early stem caecilians (4–7). This prominent gap in the tetrapod fossil record hinders efforts to place caecilians into a broader phylogenetic context of tetrapod phylogeny and to identify patterns in the early derivation of the caecilian *Bauplan*. Although molecular (4–12) and morphological (4, 5) studies support that caecilians belong to a monophyletic Lissamphibia that descended from a tympanate ancestor (5), the early evolutionary history of the group remains a complete mystery. The fossils reported here from the Upper Triassic of Colorado substantially reduce this gap and allow caecilians to be placed with better confidence into tetrapod phylogeny.

**Results**

**Systematic Paleontology.** Tetrapoda Haworth, 1825; Temnospondyli Zittel, 1888; Stereospondyli Zittel, 1887; *Chinlestegophis jenkinsi* gen. et sp. nov.

**Etymology.** Jenkins’s amphibian-serpent from the Chinle. *“Chinle”* for the Chinle Triassic Formation; *“stego-”* (Greek) meaning cover or roof, but commonly applied to temnospondyl amphibians and other early tetrapods; *“ophis”* (Greek) meaning serpent. The species name honors paleontologist Farish Jenkins, whose work on the Jurassic *Eocaecilia* inspired the present study.

**Holotype.** Denver Museum of Nature & Science (DMNH) 56658, partial skull with lower jaw and disarticulated postcrania (Fig. 1 A–D). Discovered by B.J.S. in 1999 in the Upper Triassic Chinle Formation (“red siltstone” member), Main Elk Creek locality, Garfield County, Colorado (DMNH loc. 1306). The tetrapod assemblage is regarded as middle-late Norian in age (Revueltian land vertebrate faunachron) (13). More specific locality information is on file at DMNH and US Bureau of Land Management.

**Referred Material.** DMNH 39033, anterior skull, and partial lower jaw preserved in burrow fill (Fig. 1 E–G). Discovered, also by B.J.S., in 1997 in the Upper Triassic Chinle Formation (red siltstone member) of Eagle County, Colorado (DMNH loc. 692).

**Diagnosis.** Small stereospondyl with a combination of brachyopoid and caecilian characteristics. Unique features include the following: lateral line sulcus restricted to suborbital margins of jugal and postorbital; parietal–tabular narrowly contact [may be shared with *Compsoceros* (14)]; postfrontal anterior process long, forming the majority of the dorsomedical border of the orbit; finger-like process of prefrontal interlocks with notch on postfrontal. Shared features with stereospondyls include the following: paraprosphoid strongly surprised to pterygoid, supratemporal excluded from otic notch, secondary upper tooth row. A shared feature with stereospondyls and caecilians is opisthotic fused to exoccipital forming the majority of the dorsomedial border of the orbit; finger-like process of prefrontal interlocks with notch on postfrontal. Shared features with stereospondyls include the following: paraprosphoid strongly upturned to pterygoid, supra-temporal excluded from otic notch, secondary upper tooth row. A shared feature with stereospondyls and caecilians is opisthotic fused to exoccipital forming the majority of the dorsomedial border of the orbit; finger-like process of prefrontal interlocks with notch on postfrontal. Shared features with stereospondyls and caecilians are opisthotic fused to exoccipital forming the majority of the dorsomedial border of the orbit; finger-like process of prefrontal interlocks with notch on postfrontal. Shared features with stereospondyls and caecilians are opisthotic fused to exoccipital forming the majority of the dorsomedial border of the orbit; finger-like process of prefrontal interlocks with notch on postfrontal. Shared features with stereospondyls and caecilians include lachrymal fused to maxilla and two small posterior processes (“horns”) on the occipital exposure of the tabular, just

**Significance**

Research into modern amphibian origins is increasingly focusing on the limbless caecilians, a poorly studied group whose pre-Cenozoic fossils are limited to two species. We describe tiny fossils from the Triassic of Colorado with a mixture of traits found in caecilians and extinct Permian-Triassic temnospondyls: Stereospondyls. Computed 3D tomography shows how skull bones organized around internal structures, and we suggest how these may have become fused or simplified in caecilians. The fossils’ association with burrows highlights ecological diversity of Triassic amphibians as well as when and how burrowing evolved in the stereospondyl ancestors of caecilians. Our narrative for research on amphibian origins highlights the importance of stereospondyls, the most numerous and anatomically diverse amphibian group of the Triassic.

**Author contributions:** J.D.P., B.J.S., and A.K.H. designed research, performed research, contributed new reagents/analytic tools, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

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The origin of the limbless caecilians remains a lasting question in vertebrate evolution. Molecular phylogenies and morphology support that caecilians are the sister taxon of batrachians (frogs and salamanders), from which they diverged no later than the early Permian. Although recent efforts have discovered new, early members of the batrachian lineage, the record of pre-Cretaceous caecilians is limited to a single species, *Eocaecilia micropodia*. The position of *Eocaecilia* within tetrapod phylogeny is controversial, as it already acquired the specialized morphology that characterizes modern caecilians by the Jurassic. Here, we report on a small amphibian from the Upper Triassic of Colorado, United States, with a mélange of caecilian synapomorphies and general lissamphibian plesiomorphies. We evaluated its relationships by designing an inclusive phylogenetic analysis that broadly incorporates definitive members of the modern lissamphibian orders and a diversity of extinct temnospondyl amphibians, including stereospondyls. Our results place the taxon confidently within lissamphibians but demonstrate that the diversity of Permian and Triassic stereospondyls also falls within this group. This hypothesis of caecilian origins closes a substantial morphologic and temporal gap and explains the appeal of morphology-based polyphyly hypotheses for the origins of Lissamphibia while reconciling molecular support for the group’s monophyly. Stem caecilian morphology reveals a previously unrecognized stepwise acquisition of typical cranial apomorphies during the Triassic. A major implication is that many Palaeozoic total group lissamphibians (i.e., higher temnospondyls, including the stereospondyl subclade) fall within crown Lissamphibia, which must have originated before 315 million years ago.

Stem caecilian from the Triassic of Colorado sheds light on the origins of Lissamphibia

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posterior to otic notch (as in chigutisaurids). Shared features with Rileymillerus and some other small temnospondyls comprise palate exposed laterally in ventral margin of the orbit [LEP (lateral exposure of palatine)]. Shared features with Rileymillerus and caecilians include the following: orbits small and laterally directed. Shared features with caecilians include double tooth row on mandible; quadrate completely anterior to ear; broad, parallel-sided parasphenoid cultriform process >20% skull width; occipital condyles extend far beyond posterior edge of skull roof; and pterygoquadrate. Shared features with some other temnospondyls but not caecilians include large, laterally directed otic notch.

General Features. The holotype and attributed specimen of Chinlestegophis are both incomplete but preserve enough overlapping information to be attributed to the same species and to reconstruct most of the skull (Fig. 1). The skull of Chinlestegophis is less than 3 cm long, larger than most modern caecilians, but much smaller than other contemporary amphibians. Despite its small size, the orbits are small and laterally positioned, suggesting caecilian-like reduction in the size of the eye. A well-developed otic notch is present, indicating that Chinlestegophis had a fully tympanic ear, like many total group amphibians but unlike modern caecilians. The quadrate articulation is displaced far anterior to the ear, as in caecilians, possibly an adaptation for jaw opening in confined spaces.

The skull roof is generally conservative and compares well with the plesiomorphic total group amphibian condition. A few features are noteworthy, however. No separate lacrimal bone exists, and instead the nasolacrimal duct passes through the dorsal lamina of the maxilla (SI Appendix, Fig. S4). We interpret this as a fusion of the maxilla and lacrimal to form an incipient caecilian maxillopalatine. The topological associations of this feature vary between caecilians and batrachians, but the condition in Chinlestegophis is uniquely shared by caecilians and some brachyopoid temnospondyls (14–16), therefore making its expression phylogenetically important. Specifically, batrachians either do not enclose the nasolacrimal duct (frogs) (17) or incorporate the enclosing lacrimal into the prefrontal bone (salamanders) (18, 19), whereas caecilians incorporate the passage for the duct (which is modified into the tentacular foramen) into the maxillopalatine (20–22).

In the temporal region, there is a small, round supratemporal that is only loosely articulated to its surrounding calvarial elements. This bone is morphologically and topologically identical to an element identified as the "tabular" in Eocaecilia (2). In light of their position in the broader context of temnospondyl phylogeny, we suggest a reinterpretation of this element as a supratemporal, a possibility that was also acknowledged by Jenkins et al. (2). As in Eocaecilia, the element is not joined by interdigitating sutures to its neighboring bones but instead overlies ventral lappets of its surrounding calvarial bones [see p. 291 in Jenkins et al. (2)]. Its tentative attribution to the tabular in Eocaecilia was likely confounded by the formation of a fused os basale in this region, making the homologies of the calvariae difficult to interpret in the absence of separate tabular and occipital bones. The homologies are clarified by the holotype of Chinlestegophis, which preserves separate supratemporal, tabular, and occipital elements.

Palate and Suspensorium. The palate and suspensorium are well preserved in the type specimen and are atypical of other contemporaneous temnospondyl amphibians. The cultriform process is extremely broad and parallel-sided rather than narrow and tapering between large suborbital vacuities that typify most other temnospondyls. The opisthotic and exoccipitals are fused into an
Disarticulated postcranial elements are preserved in published online June 19, 2017 Eocaecilia, and Eocaecilia. Gerobatrachus is found to be the closest relative to the most among Paleozoic and early Mesozoic. We conducted a phylogenetic analysis and E5391 (4). Re- PNAS PLUS or the elongate lysorophian within late Paleozoic Image and the caecilian affinities of the Jurassic. Early members of the caecilian stem show steps toward the formation of a maxillopalatine (via fusion of the lacrima and maxilla) and os basale (via fusion of the exoccipitals and opisthotics). Chinlestegophis differs from more basal stem caecilians in exhibiting both an incipient os basale that incorpo- rates the posterocondral braincase and, perhaps, an incipient pterygoquadrate based on the structure of the suspension and apparent absence of the quadratejugal. This trend is further continued by Eocaecilia, which exhibits a complete os basale, pseudodentary, and pseudangular. A full maxillopalatine is seen only within the caecilian crown.

Discussion Lissamphibian Monophyly: Controversy and Consensus. Our study finds an unexpected phylogenetic position for caecilians within early tetrapods. This result is a major departure from current phylogenetic hypotheses of caecilian origins and demands further rigorous testing. However, we note that the phylogenetic relationships of caecilians have never before been tested within a larger sampling of total group lissamphibians and do not find strong support for any particular position of caecilians within early tetrapod diversity. Previous studies have placed caecilians (exemplified by Eocaecilia) in one of two disparate positions: within recumbirostran or lysorophian lepospondyls (6, 39) or within dissorophoid temnospondyls (4, 5). The former hypothesis, which proposes a polyphyletic Lissamphibia, is supported by general similarities in the gestalt of caecilians and the recumbirostran Rhynchonkos or the elongate lycosphoran Brachy- doctes (40, 41). However, recent studies of lepospondyl and caecilian braincases have found that much of this similarity has been overstated, and resemblances between the two groups may be due to miniaturization and shared fossorial lifestyle rather than common descent (36–38, 42). Prior placement of caecilians within dissorophoids is due to a combination of strong phylogenetic support for a dissorophoid origin of batrachians (6) in combination with soft tissue support for a monophyletic Lissamphibia (5). However, nondissorophoid members of the lissamphibian total group have been systematically excluded from studies of caecilian origins. As a result, the possibility that some Paleozoic or Triassic total group lissamphibians may be stem caecilians has never been formally tested in a phylogenetic framework until now. Our hy- pothesis shares some features with both hypotheses: A richly populated caecilian stem group is hypothesized as in the polyphyletic hypothesis, whereas reciprocal monophyly of lissamphibians and amniotes is preserved as in the dissorophid hypothesis and most molecular hypotheses. Our hypothesis differs, however, in the pattern, tempo, and chronology of morphological evolution in the caecilian stem during the Triassic.

In this light, our phylogenetic results are less surprising; prior analyses have been unequipped both to identify caecilian character-istics in nondissorophoid total group lissamphibians and,
Conversely, to identify characteristics of nondissorophoid total group lissamphibians in caecilians. Future studies must account for this by more comprehensive sampling of underrepresented Paleozoic tetrapod groups and their morphologic characters.

Evolution of Fossoriality in Caecilians. Stepwise change in sensory anatomy, possibly associated with a shift from semiaquatic to fossorial lifestyle, is also observed clearly along the caecilian stem. Chinlestegophis and its close relatives exhibit early signs of

Fig. 2. Time-calibrated phylogeny of temnospondyls illustrating the major divergences of Lissamphibia and its subgroups. (A) The traditional “dissorophoid hypothesis” for the origins of Lissamphibia implies a shallow divergence but with long ghost lineages spanning at least two mass extinctions. (B) Our hypothesis suggests a deep divergence with a caecilian total group that is well populated by fossil stem taxa, including the stereospondyls. (C) Detailed topology of the consensus Bayesian tree (see SI Appendix). Blue lineages represent the batrachian (frog and salamander) stem, whereas red lineages represent the caecilian stem. Numbered scale at top is in Ma. Light-blue interval to the left represents the minimum fossil calibration age for the divergence of crown Lissamphibia during the early–late Pennsylvanian (~315 Ma) (based on the Moscovian records of Platyrhinops and Amphibamus). Lavender circles are estimated molecular divergence dates for crown Lissamphibia from refs. 9–11, 24–33, which are curated on the Time Tree of Life database (www.timetree.org). Silhouettes of amphibians are from the open source PhyloPic.org. PTME, Permo-Triassic mass extinction; Tr-J, Triassic-Jurassic mass extinction.

Evolution of Fossoriality in Caecilians. Stepwise change in sensory anatomy, possibly associated with a shift from semiaquatic to fossorial lifestyle, is also observed clearly along the caecilian stem. Chinlestegophis and its close relatives exhibit early signs of
this process with the loss of most cranial sensory line canals as well as a shift in the position of the orbits from the dorsal to lateral surface of the skull. Eocaecilia approaches the crown condition, with a reduction in orbit size, loss of an external tympanic ear, and complete bony covering of the pineal organ. The timing of the integration of the nasolacrimal duct into the caecilian tentacle organ is uncertain; a sulcus associated with the opening of the nasolacrimal duct in the orbit is present in both Chinlestegophis and Eocaecilia in a similar position to the tentacular sulcus of the basal caecilian Epicrionops petersi [figure 10 in Jenkins et al. (2)]. Whether this sulcus in Chinlestegophis housed a tentacle organ or simply the primitive course of the nasolacrimal duct is uncertain, but its combination with the reduction of interpterygoid vacuities in Chinlestegophis may together indicate that the m. retractor bulbi had already lost its role in orbital retraction, unlike other temnospondyls (43), possibly freeing it for a caecilian-like function in tentacle retraction.

These stepwise changes in sensory structure morphology are consistent with stepwise acquisition of fossorial morphology and ichnology among amphiibious stereospondyls. The occurrence of one specimen of Chinlestegophis within a burrow is strongly suggestive that this taxon may have been at least facultatively fossorial, but whether Chinlestegophis was a secondary burrow occupant, like the Early Triassic stereospondyl Broomiestega (44), or was actively engaged in headfirst burrowing as in modern caecilians cannot be determined at this time. However, the consolidation of the skull, reduction of the orbits, and anteriorization of the jaw articulation suggests that Triassic stem group caecilians were increasingly specialized for life and feeding in confined spaces. Subsequent loss of a tympanic middle ear, reduction of the orbits, and closure of the pineal foramen in Eocaecilia (10) may indicate a shift from facultative to obligate burrowing in the latest Triassic or Early Jurassic. Notably, Chinlestegophis retains a circumorbital sulcus, which likely housed a cranial lateral line canal as is seen in some larval aquatic caecilians (45), suggesting that caecilian fossoriality does not preclude emergence of the behavior within a semiaquatic or aquatic environment.

Divergence Timing of Lissamphibia and Subgroups. By populating the Paleozoic caecilian and batrachian stem lineages, our phylogenetic results confidently move the minimum fossil calibration date of the caecilian–batrachian split from the late–early Permian (∼280 Ma) further back to the early–late Carboniferous (∼315–307 Ma). Late Carboniferous stem batrachians are represented by Amphibamus, Platyrhinops, and other taxa (46). Coeval stem caecilians might include Carboniferous eryopoids and earliest Permian stereospondylomorphs represented by Sclerocephalus and Archegosaurus (47). This is slightly younger than the median molecular clock estimate for the divergence of Gymnophiona and Batrachia, which is early–late Carboniferous (315–307 Ma). Late Carboniferous stem batrachians are represented by Amphibamus, Platyrhinops, and other taxa (46). Coeval stem caecilians might include Carboniferous eryopoids and earliest Permian stereospondylomorphs represented by Sclerocephalus and Archegosaurus (47). This is slightly younger than the median molecular clock estimate for the divergence of Gymnophiona and Batrachia, which is early–late Carboniferous (315–307 Ma). Late Carboniferous stem batrachians are represented by Amphibamus, Platyrhinops, and other taxa (46). Coeval stem caecilians might include Carboniferous eryopoids and earliest Permian stereospondylomorphs represented by Sclerocephalus and Archegosaurus (47). This is slightly younger than the median molecular clock estimate for the divergence of Gymnophiona and Batrachia, which is early–late Carboniferous (315–307 Ma).Late Carboniferous stem batrachians are represented by Amphibamus, Platyrhinops, and other taxa (46). Coeval stem caecilians might include Carboniferous eryopoids and earliest Permian stereospondylomorphs represented by Sclerocephalus and Archegosaurus (47). This is slightly younger than the median molecular clock estimate for the divergence of Gymnophiona and Batrachia, which is early–late Carboniferous (315–307 Ma). Late Carboniferous stem batrachians are represented by Amphibamus, Platyrhinops, and other taxa (46). Coeval stem caecilians might include Carboniferous eryopoids and earliest Permian stereospondylomorphs represented by Sclerocephalus and Archegosaurus (47). This is slightly younger than the median molecular clock estimate for the divergence of Gymnophiona and Batrachia, which is early–late Carboniferous (315–307 Ma). Late Carboniferous stem batrachians are represented by Amphibamus, Platyrhinops, and other taxa (46). Coeval stem caecilians might include Carboniferous eryopoids and earliest Permian stereospondylomorphs represented by Sclerocephalus and Archegosaurus (47). This is slightly younger than the median molecular clock estimate for the divergence of Gymnophiona and Batrachia, which is early–late Carboniferous (315–307 Ma). Late Carboniferous stem batrachians are represented by Amphibamus, Platyrhinops, and other taxa (46). Coeval stem caecilians might include Carboniferous eryopoids and earliest Permian stereospondylomorphs represented by Sclerocephalus and Archegosaurus (47). This is slightly younger than the median molecular clock estimate for the divergence of Gymnophiona and Batrachia, which is early–late Carboniferous (315–307 Ma).
Phylogenetic Methods. A combined data matrix using temnospondyl taxa sampled from Schoch (23) and Maddin et al. (4) was constructed and analyzed to test the position of Chilenolestes and caecilians in the larger context of tetrapod phylogeny. With the additions of Chilenolestes and Rileymillerus, we performed an initial pilot run on the Maddin et al. (4) data only, which showed no relation between these taxa and lepospondyls (SI Appendix, Fig. 5b). To evaluate effects of including stereospondyl taxa and characters, we combined the matrices but omitted most nontemnospondyl outgroups (except for Proterogyrinus and Greererpeton) to improve computing time. Thus, 76 taxa and 345 morphological characters were analyzed using Bayesian posterior probability in MrBayes v. 3.1.2 (50) and using parsimony in PAUP* 4.0a151 (51). The parsimony analysis was performed using the tree bisection–reconnection branch-swapping algorithm of PAUP*. All characters had equal weight, and none were ordered. For the Bayesian analysis, we used the default Mk model (52) in MrBayes with variable rates and running a Markov chain Monte Carlo for 10 million generations, sampling the posterior distribution every 100 generations. For the parsimony analysis, a heuristic search (random addition sequence with 10,000 replicates) was performed and recovered 882 most parsimonious trees (tree score, 1,514 steps; consistency index, 0.2642; retention index, 0.6858). The resulting consensus trees are presented in SI Appendix, Fig. 57.

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