Innovations relating to the consumption of hard prey are implicated in ecological shifts in marine ecosystems as early as the mid-Paleozoic. Lungfishes represent the first and longest-ranging lineage of durophagous vertebrates, but how and when the various feeding specializations of this group arose remain unclear. Two exceptionally preserved fossils of the Early Devonian lobe-finned fish *Youngolepis* reveal the origin of the specialized lungfish feeding mechanism. *Youngolepis* has a radically restructured palate, reorienting jaw muscles for optimal force transition, coupled with radiating entopterygoid tooth rows like those of lungfish toothplates. This triturating surface occurs in conjunction with marginal dentition and blunt coronoid fangs, suggesting a role in crushing rather than piercing prey. Bayesian tip-dating analyses incorporating these morphological data indicate that the complete suite of lungfish feeding specializations may have arisen in as little as 7 million years, representing one of the most striking episodes of innovation during the initial evolutionary radiations of bony fishes.
Major changes in mid-Paleozoic aquatic ecosystems have been attributed to the expanded dietary breadth of jawed vertebrates\(^1,2\) following their first definitive appearance in the Silurian\(^3\). Paleobiological hypotheses implicate innovations in durophagy—the consumption of prey items protected by hard shells or exoskeletons—as drivers of ecological and evolutionary shifts in marine settings over the Phanerozoic\(^4-6\). Durophagy evolved many times in parallel among jawed vertebrates, including several groups of fishes\(^7-10\) and tetrapods\(^11-13\). Apart from ambiguous evidence from the Silurian\(^4\), the Early Devonian (late Lochkovian, ~415 Ma) sarcopterygian *Diabolepis* represents the first unambiguous vertebrate durophage\(^15\), predating the oldest examples in “placoderms”\(^9\), chondrichthysans\(^7\), actinopterygians\(^16\), and tetrapods\(^12\) by millions of years. This early lungfish shows functional hallmarks of the dipnoan body plan, including toothplates formed from non-shedding dentition—arranged teeth like the toothplates of *Diabolepis* and other crownward lungfishes. These represent biomechanical transformations consistent with durophagy, a hallmark of the feeding mode of dipnoans. *Youngolepis* therefore illustrates critical early stages in the development of a trophic strategy retained by a major vertebrate lineage for over 415 million years.

**Results**

**Description**

*Palate*. *Youngolepis* preserves the left ectopterygoid and a pair of palatoquadrates, dermopalatines, and entopterygoids (Figs. 1 and 2a–f). The left palatoquadrate, entopterygoid, ectopterygoid, and dermopalatine of *V28376* (Fig. 2f) are fully articulated. Together, the two specimens provide a complete picture of the palate of *Youngolepis*.

The palatoquadrate complex (comprising both dermal and endoskeletal components) has a short postorbital portion and long suborbital portion in lateral view, differing substantially from the proportions of other early bony fishes\(^36,37\). The postorbital region is anteroposteriorly narrow and dorsoventrally deep (Fig. 2a–f), and the adductor fossa (Fig. 2b, d) accounts for more than half of the overall length of the palate. Both the ascending process, which articulates with the braincase posteriorly to the orbit, and the autopalatine process, which articulates with the ehmoid region, are well preserved (Fig. 2b–e). The region of the palatoquadrate near the expected articulation with the basipterygoid process is unmineralized, forming a conspicuous notch.

The posteroventral margin of the palatoquadrate curves laterally, forming a thickened ridge that defines a broad surface for the origin of the adductor musculature in the adductor fossa (Fig. 2b–e). A well-developed, biconvex quadrate condyle at the posteroventral corner of the palate marks its articulation with the lower jaw. The inner side of the posterior blade of the palate bears a vertical trough representing the spiracular-hyomandibular recess (Fig. 2c, e). In buccal view, sigmoid sutures and gaps (Fig. 2a, f) in
patterns of dentition mark the boundaries between the three dermal bones that line the inner surface of the palate: entopterygoid, ectopterygoid, and dermopalatine. The dermopalatine bears a single stocky fang and associated replacement pit (Fig. 2f; Supplementary Fig. 1a) flanked laterally by numerous tiny teeth (Fig. 2e, f) along the outer edge of the bone. The ectopterygoid (Fig. 2a–f) is shorter than the dermopalatine, but also bears a stout fang (Fig. 2f). As the largest dermal bone of the palate, the entopterygoid comprises two laminae with different orientations and contrasting patterns of dentition (Fig. 2c, e, f). The more medial lamina (Fig. 2c, e, f) is thin in cross-section, vertically oriented, and bears a shagreen of small denticles similar to those of most early bony fishes. By contrast, the expanded horizontal lamina (Fig. 2f) is greatly thickened in cross-section, and bears well-developed, conical teeth that are deployed in a series of precisely patterned, radiating rows. Thirteen rows are present, each of which contains between 5 and 10 teeth (Fig. 2f). Within each row, teeth increase in size toward the lateral edge of the entopterygoid (Fig. 2f).

**Hyoid arch.** The hyoid arch consists of the hyomandibula, ceratohyal, and hypohyal (Figs. 2a–c, g, h; 3). Both hyomandibulae are preserved in V28375 (Fig. 2a–c) and the right one is preserved in V28376 (Fig. 2g, h); all share the same inverted triangular shape. The distal parts of hyomandibulae in V28375 are only shown vaguely in scans, possibly due to incomplete mineralization, and cannot be segmented. Previous studies permit restoration of the articulation between the hyomandibula and braincase. The hyomandibula has two swollen proximal heads, one dorsal and one ventral, corresponding to matching articulation areas on the otic region of the braincase. The dorsal head is stubby and located on the posterolateral side,
whereas the ventral head is slender and located on the anteromedial side (Fig. 2g, h). The hyomandibula tapers distally in V28376. Its inner face (Fig. 2h) is somewhat concave whereas the outer face (Fig. 2g) is slightly convex. The posterior margin of the hyomandibula bears a notch (Fig. 2g, h) possibly marking the path of the hyomandibular branch of the facial nerve. The presence of accessory bones (e.g., interhyal) linking the dorsal and ventral halves of the hyoid arch is unclear.

The ventral portion of the hyoid arch comprises the hypohyal and ceratohyal. The hypohyal is strongly curved (Fig. 3). Its narrow end articulates with the anterior face of basibranchial 1; a much broader facet meets the anterior end of the ceratohyal (Fig. 3). The ceratohyal is flat and broad, and bears a thickened ridge along its dorsolateral margin.

Gill skeleton. Specimen V28375 (Fig. 3a–e) preserves an articulated gill skeleton comprising the basibranchials, hypobranchials, ceratobranchials, and possible epibranchials. The basibranchial series includes three ossifications (Fig. 3a–c); the first two represent anterior and posterior halves of an incompletely mineralized basibranchial 1, while the last is basibranchial 2. Basibranchial 1 (Fig. 3a–c) forms an elongated hexagon, and its anterior margin bears an anterodorsally directed oval depression with two fossae (Fig. 3a, b, d–f) accommodating the hypohyals. A fossa (Fig. 3b, f) on the dorsal surface of basibranchial 1 accommodates an elliptical toothplate (Fig. 3a), and a shallow depression on the ventral surface marks the articulation with the urohyal (Fig. 3c, e). Basibranchial 1 bears three pairs of posterolaterally directed fossae (Fig. 3e). The first pair of fossae (Fig. 3e, f) are located immediately anterior to the unossified zone of basibranchial 1. These are deep, with well-defined edges, and accommodate the first pair of hypohyals (Fig. 3d–f). The second pair of fossae is located at the junction of the two ossified halves of basibranchial 1 and articulate with the second pair of hypobranchials (Fig. 3d, e). The third pair of fossae (Fig. 3d, e) are for the third pair of hypobranchials, and are located exclusively on the posterior ossification of basibranchial 1. The concave posterior margin of basibranchial 1 articulates with a much smaller, trapezoidal basibranchial 2 (Fig. 3a, b, e) that bears no hypobranchials. The slender urohyal (Fig. 3c, e, f) extends beneath the basibranchials. It is flattened anteriorly, has a rod-shaped middle portion, and tapers posteriorly before terminating with a rhombic expansion (Fig. 3c, e, f) that lies in a horizontal plane.

Youngolepis possesses four pairs of hypobranchials and ceratobranchials (Fig. 3a–e). The first two hypobranchials (Fig. 3a–d) have prominent proximal heads that articulate with basibranchial 1. The proximal ends of the third pair of hypobranchials are poorly mineralized (Fig. 2a–d). The fourth pair of hypobranchials (Fig. 2a–d) are different from the first three pairs: they are smaller and have an “L” shape. The fourth hypobranchials (Fig. 2a–e) articulate with the third hypobranchials, rather than directly with the basibranchial series. The ceratobranchials are much longer than the hypobranchials (Fig. 3a–e). The first two pairs of ceratobranchials (Fig. 3a–d) are similar in shape, with tapered distal ends and wide proximal ends that articulate with the hypobranchials. Each bears a vascular groove (Fig. 3c) on its ventral surface. The third and fourth pairs of ceratobranchials (Fig. 3a–e) are smaller and more rod-shaped. Some small ossifications might represent epibranchials (Fig. 3a–e), but they are too poorly preserved to determine their identity or association with specific branchial arches.

Inference of phylogenetic relationships and evolutionary timescale. Consistent with previous analyses, our parsimony analysis and Bayesian tip-dating analyses place Youngolepis as the sister taxon of the clade comprising Diabolepis plus all more crownward lungfishes (Fig. 4a; Supplementary Figs. 2–17). Support for this arrangement is high, with a Bremer support value of 4 and a Bayesian posterior probability of 1. All sampled portholepiforms are resolved as a clade in all analyses, and this group plus Powichthys represent the sister lineage of all other dipnomorphs. Tip-dating
analyses based on independent gamma rate (IGR) model (for details see the “Methods” section) estimate the divergence of porolepiforms and lungfishes at 422.28 Ma (95% credible interval: 426.34–418.88 Ma), Youngolepis and more crownward lungfishes at 419.53 Ma (95% credible interval: 423.53–416.99 Ma), and Diabolepis and more crownward lungfishes at 417.15 Ma (95% credible interval: 419.20–414.91 Ma) (Fig. 4a).

Discussion

Many characteristic features of lungfishes relate to their feeding apparatus.39,40. Our analysis of Youngolepis reveals the phylogenetically earliest evidence for some of these modifications, gives clues to their initial functional significance, and provides a timescale over which they likely evolved. This provides an enriched framework for understanding one of the most conspicuous aspects of ecomorphological innovation during the early evolutionary radiation of sarcopterygians: the processing of hard prey items.

Assembly of the lungfish feeding apparatus. Many structural peculiarities of dipnoan skulls relate to durophagy, and build upon features suggestive of strong bites in dipnomorphs more generally41. These include reorientation of the palatoquadrate and its fusion with the neurocranium, a shortened and non-suspensory hyomandibula, and a palatal bite formed by upper
Paleozoic, including ptyctodont placoderms, holocephalan other groups of durophagous fi... broad, well-de...

broad, well-developed pterygoid and prearticular toothplates with radial rows of teeth and a broad palatal bite (Fig. 4a; Supplementary Fig. 1b). The dentition of Diabolepis matches those of more crownward lungfishes in both structure and development, and thus provides few clues as to how this specialized arrangement arose from a more generalized osteichthyan pattern. Neither the hyomandibula nor palatoquadrate is known in Diabolepis, although it is apparent that the latter was unfused to the neurocranium. The complete skulls of Youngolepis reported here provide evidence for the initial modifications of the feeding apparatus near the base of the lungfish tree, and suggest a functional model for the origin of dipnoan durophagy.

The palate of Youngolepis diverges conspicuously from more general osteichthyan conditions (Fig. 4a). In sarcopterygians, and actinopterygians, the palatoquadrate primitively has a small suborbital ramus and a long postorbital portion from which the adductors mandibulae originate. The palatoquadrate complex and dermal cheek bones define an opening for these muscles that constitutes less than half of the length of the palate. A long, rod-like hyomandibula braces the posterior portion of the palatoquadrate, and roughly traces the dorsal margin of the palate. The suspensorium is therefore obliquely oriented, with the jaw joint often lying near the level of the rear of the skull roof. Youngolepis shows a very different arrangement. The hind region of the palatoquadrate has a near-vertical orientation. It is less distinctly separated from the suborbital portion, giving the palate a more triangular shape with a long opening for the jaw adductor muscles. These geometric changes have important consequences: they indicate a more vertical orientation of jaw muscles and a larger cross-section of those adductors, and also permit muscle attachments directly on the neurocranium as well as on the palatoquadrate. Collectively, these all point to a strong bite in Youngolepis. In association with a restructuring of the palate, the hyomandibula of Youngolepis is short and stout. This foreshadows the condition in lungfishes, and parallels other examples like tetrapods and holocephalans where the tight binding of the palate and the braincase relieves the hyomandibula of its suspensory role.

The palatal dentition of Youngolepis shows a striking combination of general traits with those resembling lungfish features (Fig. 4a). The entopterygoid of Youngolepis has an expanded horizontal lamina relative to that of outgroups, forming a broad, flat surface on the roof of the mouth. By contrast, porolepiforms and Powichthys bear numerous, small tooth plates that augment the entopterygoid in contributing to a flat buccal roof. In Youngolepis, the entopterygoid bears well-defined radial tooth rows, with individual cusps increasing in size toward the anterolateral margin of the entopterygoid. This resembles the pattern of dentition on the entopterygoid toothplates of Diabolepis and another unnamed lungfish from the Lochkovian of Vietnam. Some enlarged, dorsally directed cusps on the prearticular form a narrow shelf opposing the entopterygoid plate in Youngolepis, but these do not show the conspicuous radial patterning apparent on the palate. By contrast, Diabolepis has broad, well-defined prearticular toothplates. The internal structure of the entopterygoid teeth is indistinct in our scans, but the geometric correspondence to lungfish toothplates implies a similar developmental pattern in Youngolepis: the addition of non-shedding teeth at marginal loci as the bone grew. However, in contrast to Diabolepis and more crownward lungfishes, the toothplates of Youngolepis occur in conjunction with well-developed entopterygoids and dermopalatines that bear fangs and associated replacement pits, indicating periodic shedding. Similar coronoid fangs complement those of the palate (Fig. 4a). These blunt, squat fangs differ from the sharply pointed fangs of generalized rhipidistians, and suggest a role in crushing and fracturing—rather than piercing and ripping—prey. No such fangs are known in lungfishes, despite the presence of small marginal palatal bones sometimes interpreted as vomers, dermopalatines, or ectopopterygoids.

In contrast to the palate and dorsal hyoid arch, the ventral portion of the hyoid arch and gill skeleton of Youngolepis do not differ substantially from those of lungfish outgroups. The gill skeleton closely resembles that of porolepiforms, differing most conspicuously in retaining multiple basibranchials as in lungfishes and tetrapodomorphs. Broad, plate-like ceratohyalys suggest that suction—rather than ram—feeding was the principal mode of prey capture in porolepiforms and Youngolepis, matching what is known in living lungfishes.

Taken together, these features suggest distinctive food acquisition and processing in Youngolepis, providing a functional model for understanding the major trophic shift associated with the origin of lungfishes. Clues about ancestral feeding modes come from ecomorphological comparisons with living fishes, gut contents in articulated fossil sarcopterygians, and trace fossils from ecomorphological comparisons with living fishes. Gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians, gut contents in articulated fossil sarcopterygians.

Rapid trophic divergence in the lungfish lineage. The major lineages of crown sarcopterygians first appear in the Early Devonian fossil records, leading to inferences of rapid evolutionary change in the early history of several groups, including lungfishes. Our quantitative analyses reinforce this hypothesis. The distinctive features of the lungfish body plan—including autostyly and upper and lower toothplates—likely evolved in a short ~7 Ma window between the latest Silurian and the late Lochkovian. Both Youngolepis and Diabolepis are subtended by very short branches, suggesting that the overall anatomy of these two taxa might be reasonable models of ancestral stages along the lineage leading to lungfishes. We find that rates of change for characters most intimately associated with feeding (i.e., dentition plus mandibular, branchial, and hyoid arches) are accelerated at the same time as other traits, but to an even greater degree. This agrees with qualitative assessments of lungfish evolution noting the early and substantial modification of cranial structure relative to more conservative
postcranial, which closely resemble those of other early rhipidistians62. Lungfishes showing conspicuous modifications to median fin and body geometry first appear in the Middle Devonian1,7,2, with taxa approaching modern dipnoan anatomy in the latest Devonian3,3. This is consistent with theoretical4 and empirical23 studies suggesting that early stages of phenotypic divergence are concentrated in aspects of trophic morphology, including jaws and teeth.

Following their origin, lungfishes went on to inhabit a broad spectrum of aquatic habitats and became the most taxonomically diverse group of Devonian sarcopterygians31. This contrasts with the other principal lineage of dipnemorphs, Porolepiformes, which were characterized by morphological conservatism and remarkably low taxonomic diversity over their >50 Ma history64.

It seems probable that the distinctive lungfish feeding apparatus—-the first stages of which are apparent in Youngolepis—provided the group with major new ecological opportunities that promoted their celebrated early diversification62,65.

Methods

Fossil specimens. This research complies with all relevant ethical regulations. This study is based on two articulated specimens of Youngolepis praecursor (Fig. 1) (IVPP V28375 and V28376) housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, each of which consists of a nearly complete head and partial body. Both specimens are somewhat flattened, but individual bones are uncrushed. This material is collected by Min Zhu from the argillaceous limestone of the Xitun Formation (Early Devonian: late Lochkovian) in Qujing, Yunnan, China2.

Computed tomography. Specimens were prepared mechanically using pneumatic air scribes and needles under microscopes at IVPP. Both were scanned using a Nikon XT H 225ST industrial μCT scanner at the CTEES facility, Department of Earth and Environmental Sciences, University of Michigan. Both specimens were scanned using a tungsten target and the following parameters: IVPP V28375, voltage (kV) = 110 kV, current (mA) = 110 μA, effective pixel size = 11.55 μm, exposure time = 4.3 s, projections = 3141, images per projection = 2; filter = 0.35 mm Cu; IVPP V28376, voltage = 110 kV, current = 110 μA, effective pixel size = 12.15 μm, exposure time = 2.83 s, projections = 3141, images per projection = 2, filter = 0.23 mm Cu. Tomographic data were segmented using the software Mimics 22.0 (Materialise, Leuven, Belgium), with images of models rendered in Blender7.

Phylogenetic analysis. In order to assess the placement of Youngolepis and assess patterns of trait evolution in early dipnemorph phylogeny, we assembled a matrix based on morphological characters taken from four analyses: Challand et al.34 for lungfishes, Schultz76 for porolepiforms, Lu et al.34 for sarcopterygians more generally, and Giles et al.49 for actinopterygians. 10 new characters based on our own observations were added, and the states of the characters range from 2 to 6. The matrix (Supplementary Data 1) includes a total of 88 taxa (2 stem osteichthians, 3 actinopterygians, and 83 dipnemorphs). The character data entry and formation were performed in Mesquite 3.6180. All analyses were rooted on an offset exponential prior with a mean of 432.95 Ma and a minimum of 427.95 Ma, which were slightly older than the time range of the outgroup taxon (Guionia onerius)3.

To examine any differences in patterns of evolutionary rate through time for different anatomical regions (Supplementary Software), we performed analyses using two data partitions: the first included mandibular arch, hyoid arch, gill skeleton, and teeth (112 characters: 82–116, 123–187, 266–277) and the second contained all remaining characters (165 characters: 1–81, 117–122, 188–265), based on model settings mentioned above. Each analysis was run 200 million iterations, and the first 30% samples were discarded as burn-in.

Convergence of parameters was identified using Trace82 (ESS > 200). The results are given in Supplementary Table 1. Unpartitioned and partitioned analyses using the AR model failed to converge. Analyses using other models did converge with the exception of the partitioned analysis using IGR with no topological constraints. Because all analyses under the AR model failed to converge, and all converged analyses show comparable patterns of relationships, evolutionary timescale, and rates of character evolution over time, we did not perform the stepping-stone sampling to estimate marginal model likelihoods. On this basis, we regard our inferences about those patterns as robust to variation in assumptions of clock models. We presented the results of IGR model in the main text figure (Fig. 4), and all converged results in the supplement (Supplementary Figs. 4–17).

Data availability

The CT data and 3D models generated in this study have been deposited in the figshare database with the link: https://doi.org/10.6084/m9.figshare.15134253v1. The phylogenetic data generated in this study are provided in the Supplementary Data and Software files. The additional notes generated in this study are provided in the Supplementary Information file. The life reconstruction of Youngolepis praecursor and the associated biota is provided as the Supplementary Figure 18.

Code availability

The codes used for the study are provided in the Supplementary Software files.

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**Author contributions**
M.Z. and M.F. designed the project. M.F. and X.C. collected tomographic data. X.C. processed the tomographic data. X.C. and T.Q. assembled and analyzed the phylogenetic dataset. Y.Y. performed the tip-dating analyses. X.C. and M.F. interpreted the data and wrote the first draft of the manuscript. All authors discussed and commented on the final version of the manuscript.

**Competing interests**
The authors declare no competing interests.

**Additional information**

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