PALEONTOLOGY

A Silurian maxillate placoderm illuminates jaw evolution

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The discovery of *Entelognathus* revealed the presence of maxilla, premaxilla, and dentary, supposedly diagnostic osteichthyan bones, in a Silurian placoderm. However, the relationship between these marginal jaw bones and the gnathal plates of conventional placoderms, thought to represent the inner dental arcade, remains uncertain. Here we report a second Silurian maxillate placoderm, which bridges the gnathal and maxillate conditions. We propose that the maxilla, premaxilla, and dentary are homologous to the gnathal plates of placoderms and that all belong to the same dental arcade. The gnathal-maxillate transformation occurred concurrently in upper and lower jaws, predating the addition of infradentary bones to the lower jaw.

Macromeric dermal skeletons incorporating jaw bones are found in the clade Osteichthyes (bony fishes and tetrapods) and the paraphyletic group Placodermi (jawed stem gnathostomes). Osteichthyans have a maxilla, premaxilla, and dentary, all with facial laminae, whereas placoderms have supposedly nonhomologous gnathal plates that lack facial laminae. *Entelognathus* from the Late Silurian (Ludlow) Xiaoxiang vertebrate fauna (*1*, *2*) of Yunnan, China, revealed the presence of maxilla, premaxilla, dentary, and infradentaries (*3–7*) in a vertebrate with a dermal skeleton otherwise typical of placoderms (*2*, *8*). Phylogenetic analyses place *Entelognathus* near the top of the gnathostome stem group, but it is uncertain whether the apparent homology of the jaw bones in *Entelognathus* and osteichthyans is supported by phylogenetic congruence (*2*, *8–11*). Here we describe a second maxillate placoderm from the Xiaoxiang fauna (Figs. 1 and 2; figs. S1 to S7; and fig. S8, A and B), which illuminates the evolution of the dermal jaw (*12–15*), resolves the phylogenetic uncertainty around *Entelognathus*, and provides a comparative context for the bizarre facial morphology of the latter genus.

The holotype of *Qilinyu rostrata* (gen. et sp. nov.) (*16*) (Fig. 1 and figs. S2 to S4) represents a three-dimensionally preserved fish. It is 126 mm in length as preserved, with an estimated total body length of more than 20 cm. In general terms, *Qilinyu* combines arthrodire-like and antiarch-like characteristics (*17–24*).

The most conspicuous feature of *Qilinyu* is its moderately developed rostrum in front of the domed cranial vault, which is suggestive

of a dolphin-like head profile. Apart from this rostrum and the presence of two pairs of postorbital plates and paired central plates, the skull roof is similar to that of *Entelognathus* (*2*). The mouth and nostrils are located on the flattened ventral surface of the head. The eyes of *Qilinyu* are small and laterally positioned. Unlike in *Entelognathus*, the sclerotic ring is not fused with the skull roof and dermal cheek.

The maxilla and premaxilla (Figs. 1 and 2A and figs. S1 to S5) bear both facial and palatal laminae, as in *Entelognathus* (*2*). There are no dermal bones internal to them in the oral cavity. Immediately behind the upper jaw in the holotype, the perichondrally ossified Meckelian cartilage (Fig. 1, B and D and figs. S2B and S4A) is preserved in articulation with the mouth closed. No dermal lower jaw bones are preserved in the holotype. However, in specimen V20733.1 (Fig. 2A and figs. S5, D and E, and S6G), an L-shaped dentary bone in internal aspect is preserved, slightly displaced. A further four dentaries preserved in external aspect (Fig. 2, B and C, and fig. S6, C to F) show a tuberculate area with three divisions (palatal lamina, facial lamina, and a depressed posterior division bearing smaller tubercles) and a posterolateral unornamented process. Left and right dentaries do not meet in the midline; a "step" in the anterior margin of the Meckelian cartilage marks the position of the mesial extremity of the dentary. Infradentaries are absent.

The dermal cheek, opercular region, and trunk armor show a combination of characteristics shared with *Entelognathus* (for example, the presence of a jugal) (*2*) and antiarchs (the absence of an opercular cartilage) (*22*, *25*), as well as distinct features (three median dorsal plates) (Fig. 1, A and C and figs. S1; S2; S5, D and E; and S6B). For a full description, see the supplementary text. The long trunk armor and flattened ventral surface create a somewhat antiarch-like appearance.

Qilinyu provides the first detailed evidence of paired appendages in maxillate placoderms. The pectoral fin is covered by minute scales resembling the trunk scales of some early antiarchs (*26*). The anterolateral margin of the scale cover appears to be the true leading edge of the
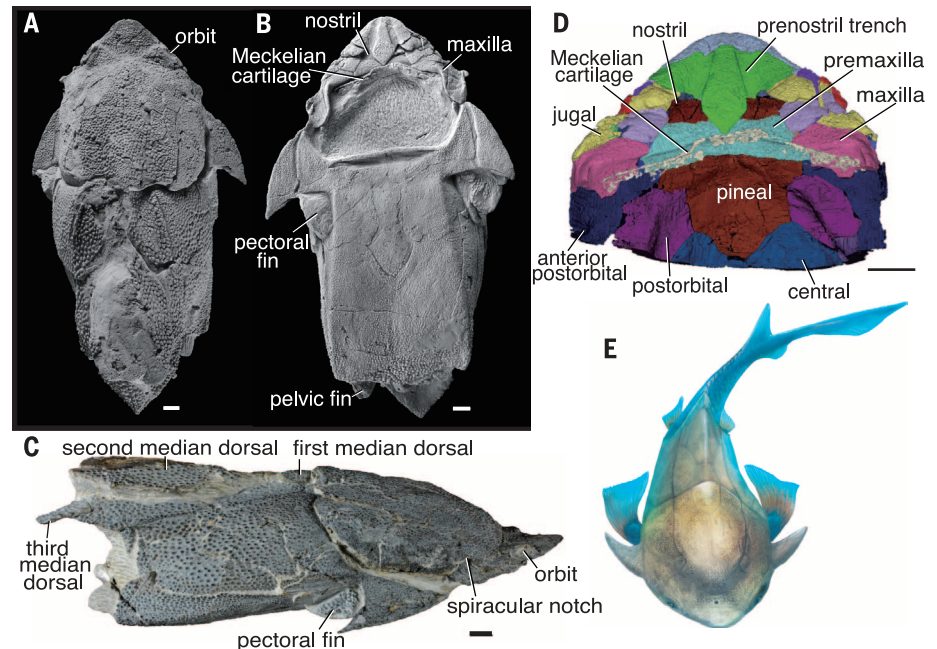
Fig. 1. *Qilinyu rostrata* (gen. et sp. nov.), a 423-million-year-old fish from the Kuanti Formation (late Ludlow, Silurian) of Qujing, Yunnan. (**A** to **C**) Holotype V20732, a three-dimensionally preserved specimen with skull and trunk armor, shown in dorsal (A), ventral (B), and lateral (C) views. (**D**) Skull in ventral view, as revealed by the computed microtomography restoration of the holotype. (**E**) Life restoration. Scale bars, 5 mm.

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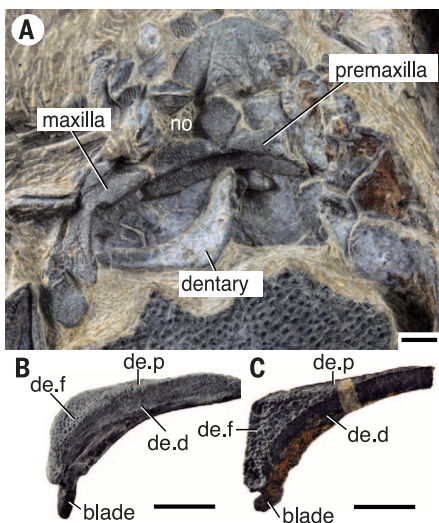
Fig. 2. Dentary specimens of *Qilinyu rostrata* (gen. et sp. nov). (**A**) Part of an articulated specimen (V20733.2) in ventral view, showing the slightly displaced dentary. (**B** and **C**) Ventral view of dentaries of specimens V20735.2 (B) and V20735.1 (C). de.d, depressed area of dentary; de.f, facial lamina of dentary; de.p, palatal lamina of dentary; no, nostril. Scale bars, 10 mm.

Fig. 3. Summary phylogeny showing the transformation of the dermal jaw bones from a gnathal to a maxillate condition. This phylogeny is simplified from the strict consensus tree of the 1248 most parsimonious trees (fig. S10). co, coronoid series; de, dentary; dp, dermopalatine series; id, infradentary; lg, infragnathal; ju, jugal; mc, Meckelian cartilage; md1 to md3, first to third median dorsal plate; mx, maxilla; op, opercular; pmx, premaxilla; pq, palatoquadrate; Sg, supragnathal; s.s., sensu stricto. Brown body color, jawless stem gnathostome (ostracoderm); green body color, jawed stem gnathostome (placoderm); blue body color, crown gnathostome. Red arrows, mouth position; purple arrowheads, division between head and trunk armor.

fin, but considering the hydrodynamic balance of the fish, we assume that the fin must have had a broad posterodistal brim without scale cover (Fig. 1E and fig. S1). The pelvic fin (Fig. 1B and fig. S2B) is also covered by minute scales and located immediately behind the ventral wall of the trunk armor. A large plate medial to the pelvic fin is interpreted as the dermal pelvic plate (fig. S2B).

Maximum parsimony and Bayesian inference analyses, using a data set with 372 characters and 104 taxa, place *Qilinyu* consistently as the sister group of *Entelognathus*, *Janusiscus*, and crown gnathostomes (Fig. 3, figs. S9 to S11, and data S1 and S2). According to the Bayesian analysis (fig. S11), the antiarchs, with which *Qilinyu* shares many similarities, are positioned at the base of jawed vertebrates, successively followed by *Brindabellaspis* (27), *Romundina* (9), and the *Jagorina*-*Gemuendina* clade (18), all of which bear dorsal nasal openings positioned near the eyes. However, this phylogenetic resolution at the base of jawed vertebrates is lost in the maximum parsimony analysis (figs. S9 and S10).

Qilinyu expands our understanding of maxillate placoderms, previously represented only by *Entelognathus* (2). *Qilinyu* has a different body shape, with a ventrally positioned mouth and nostrils that are suggestive of a benthic feeder. The immobile eyes of *Entelognathus* are absent in *Qilinyu*, which has small and apparently mobile eyes of conventional placoderm type. Most importantly, the character combination of *Qilinyu* and its phylogenetic position as the most basal maxillate vertebrate illuminate the relationship between the marginal jaw bones of osteichthyans and the gnathal plates of placoderms (17–19, 22).
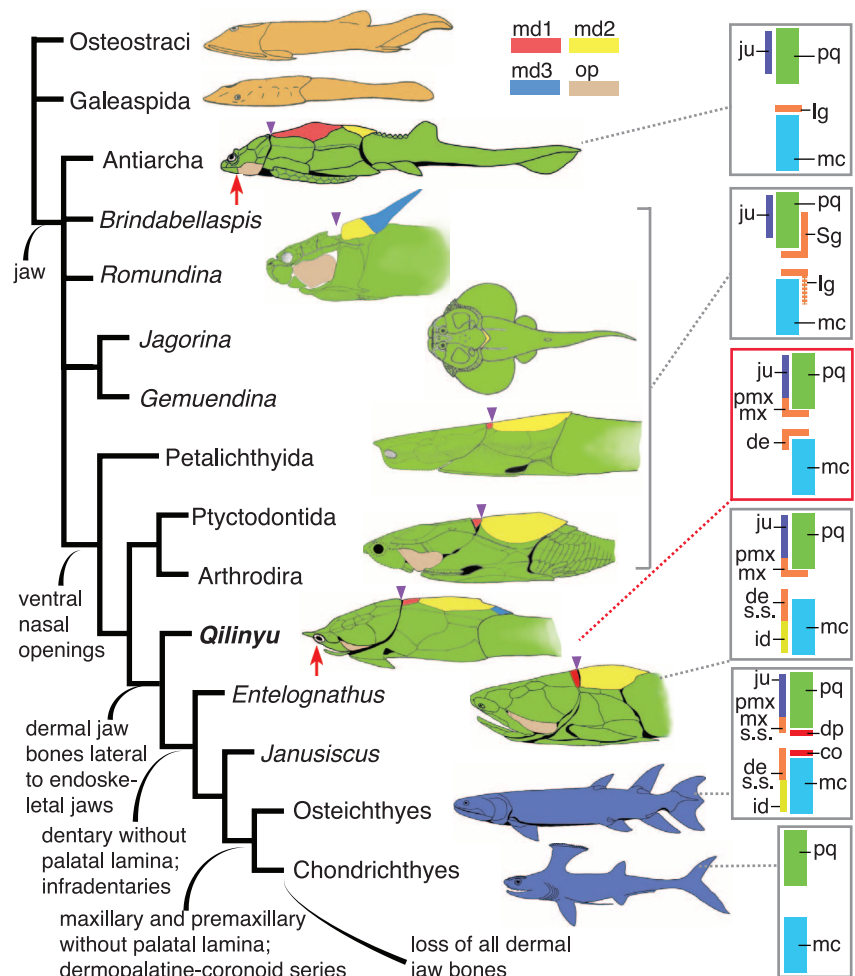
Entelognathus and *Qilinyu* have maxillae and premaxillae that carry broad palatal laminae. This contrasts with the crown-group osteichthyan condition, where these bones essentially lack palatal laminae (6, 19). The dentary of *Entelognathus* has only a narrow biting edge, whereas that of *Qilinyu* has a narrow palatal lamina. Again, the crown osteichthyan condition is a biting edge. We infer that the maxilla, premaxilla, and dentary all originally had laminae that extended into the oral cavity and were lost prior to the osteichthyan crown group node.

Neither *Entelognathus* nor *Qilinyu* has any dermal jaw bones internal to the marginal arcade. Both holotypes have the mouth wholly or partly closed, showing that this is a genuine absence and not a taphonomic loss. Placoderms typically carry one dermal bone on the Meckelian cartilage (infragnathal), one on the palatoquadrate (posterior supragnathal), and one on the

ethmoid (anterior supragnathal) (17–24, 28). These bones lack facial laminae and have been homologized with the inner dental arcade (coronoids, ectopterygoids, dermopalatines, and vomers) of osteichthyans (2, 17, 18, 22). However, in number and anteroposterior position relative to the mandibular arch, they actually resemble the dentary, maxilla, and premaxilla; the osteichthyan inner arcade always contains a greater number of bones. In *Entelognathus* and *Qilinyu*, the inner arcade is absent and the marginal bones carry oral laminae that—especially in the upper jaw—correspond precisely in position to the gnathal plates of placoderms. The only major difference is that the marginal jaw bones of *Entelognathus* and *Qilinyu* have facial laminae, whereas placoderm gnathal plates do not.

We are thus faced with two alternative homology hypotheses. The traditional identification of the placoderm gnathals with the inner

dental arcade (*2, 17, 18, 22*) implies that the three gnathals were lost at the internode between arthrodires and *Qilinyu* and replaced with three new bones that occupied essentially the same positions but were slightly more external. Alternatively, if the gnathals are identified with the outer dental arcade, these bones remained in place and acquired facial laminae. Given the overall pattern stability of the dermal skeleton, the second hypothesis seems more probable. It also does not require the inner dental arcade to be acquired in placoderms, lost in *Qilinyu* and *Entelognathus*, and then reevolved in osteichthyans. In any case, the boundary between inner and outer arcades is not completely rigid: For example, in the early tetrapod *Discosauriscus*, the posterior coronoid (a bone of the inner arcade) contributes to the external face of the lower jaw (*29*).

Under our new hypothesis, the dermal jaw bones form part of the overall pattern conservation of the dermal skeleton from placoderms to osteichthyans (*2, 4*). In their earliest form, the gnathal plates seen, for example, in antiarchs and arthrodires were entirely oral and lacked facial laminae. Facial laminae were acquired at the internode below *Qilinyu*. Between *Qilinyu* and *Entelognathus*, the dentary lost its oral lamina, and the lower jaw acquired an external covering of infradentary bones. Between *Entelognathus* and crown osteichthyans, the maxilla and premaxilla lost their palatal (i.e., oral) laminae, and a new inner arcade of coronoids, ectopterygoids, dermopalatines, and vomers evolved.

This picture of gradual transformation underscores the emerging view of osteichthyans as the more conservative clade of crown gnathostomes (*2, 9–11, 30*), contrasting with the historically dominant perception of chondrichthyans as primitive and informative about ancestral gnathostome conditions (*17, 18*). We predict that future discoveries from the Xiaoxiang fauna will continue to fuel the debate about jawed vertebrate origins and challenge long-held beliefs about their evolution.

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EVOLUTION

Predictable convergence in hemoglobin function has unpredictable molecular underpinnings

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To investigate the predictability of genetic adaptation, we examined the molecular basis of convergence in hemoglobin function in comparisons involving 56 avian taxa that have contrasting altitudinal range limits. Convergent increases in hemoglobin-oxygen affinity were pervasive among high-altitude taxa, but few such changes were attributable to parallel amino acid substitutions at key residues. Thus, predictable changes in biochemical phenotype do not have a predictable molecular basis. Experiments involving resurrected ancestral proteins revealed that historical substitutions have context-dependent effects, indicating that possible adaptive solutions are contingent on prior history. Mutations that produce an adaptive change in one species may represent precluded possibilities in other species because of differences in genetic background.

A fundamental question in evolutionary genetics concerns the extent to which adaptive convergence in phenotype is caused by convergent or parallel changes at the molecular sequence level. This question has important implications for understanding the inherent repeatability (and, hence, predictability) of molecular adaptation. One especially powerful approach for addressing this question involves the examination of phylogenetically replicated changes in protein function that can be traced to specific amino acid replacements. If adaptive changes in protein function can only be produced by a small number of possible mutations at a small number of key sites—representing "forced moves" in genotype space—then evolutionary outcomes may be highly predictable. Alternatively, if adaptive changes can be produced by numerous possible mutations—involving different structural or functional mechanisms, but achieving equally serviceable results—then evolutionary outcomes may be more idiosyncratic and unpredictable (*1–4*). The probability of replicated substitution at the same site in different species may be further reduced by context-dependent mutational effects (epistasis), because a given mutation will only contribute to adaptive convergence if it retains a beneficial effect across divergent genetic backgrounds (*4*).

To assess the pervasiveness of parallel molecular evolution and to investigate its causes, we examined replicated changes in the oxygenation properties of hemoglobin (Hb) in multiple bird

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Science

A Silurian maxillate placoderm illuminates jaw evolution

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Jaws from the jawless
Until a fossil called Entelognathus was found to contain a tripartite jaw a few years ago, it was believed that the skeletons of early osteichthyans (bony fish), the ancestors of all vertebrates, were derived independently of those of the earlier placoderms (so-called jawless fish). Zhu *et al.* now describe a second Silurian placoderm that more securely bridges the jawless toothlike plates of placoderms to the development of the jawed condition that ultimately led to the three-boned jaw in ancestors of modern vertebrates (see the Perspective by Long). This finding upends the traditional belief that the two types of jaw were nonhomologous and sheds light on the evolution of the complex maxilla, a key component of diversification across many modern taxa, including humans.
Science, this issue p. 334; see also p. 280

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