would have to occur to explain the presence of denticles on the outer covering of sharks and other more basal vertebrates[5,6].

Both theories hinge on the idea that there is an inherent difference in the inductive power of ectoderm and endoderm, and that migration of one or the other is the crucial factor in tooth formation. Implicit in this is the notion that tooth and denticle anatomy reflects embryonic origins — that is, that actual tooth or denticle histology can reveal which embryonic tissue was the key source.

Soukoup *et al.*[1] now provide experimental grounds to debunk such ideas by testing the spatial distribution of ectoderm and endoderm in relation to erupting teeth. They took advantage of a line of transgenic axolotls[7] — a group of amphibians that have ample teeth in their mouth — in which cell lineages can be fluorescently labelled. By grafting ectoderm or endoderm labelled with a marker known as green fluorescent protein from transgenic into normal axolotls, and vice versa, the authors show that there is no relationship between ectodermal and endodermal origin and the shape or nature of the resulting teeth — at least at the point when such teeth become visible. The enamel of teeth can be of ectodermal, endodermal or mixed origin. This is a dramatic finding. It means that one cannot infer relative distributions of ectoderm and endoderm from tooth or denticle anatomy even in a living species, let alone in a fossil.

The caveat here is that a lack of relationship between the later position of these epithelia and teeth does not mean that these tissues do not influence tooth position. It may well be that, at some early critical moment, an ecto–endodermal boundary provides positional information or orientation for some teeth. Many early signalling centres in the body (such as the apical ectodermal ridge for limb development) are known to disassemble once they have done their job[8].

Nonetheless, Soukoup and colleagues' study removes the basis for theories depending on 'co-option' processes that would require migration of epithelial cells, and redirects future research. We need to study the molecular co-option of tooth or denticle genetic programs, a process that might have occurred several times independently in the history of jawed vertebrates. Which gene-regulatory regions are involved in switching on key regulators of tooth or denticle initiation in both epithelial and mesenchymal tissue? How, where and when did these genomic regions evolve? Are the same regions driving expression in ectoderm and endoderm? Are the regions involved in patterning denticle fields also used for organizing feathers and hair? And where are the 'atoms of information' that initiate, position and shape a tooth or denticle, and make its internal structure different from that of a dermal bone?

One can expect that there are combinations of transcription-factor proteins, bound to unique tooth or denticle genetic regulatory elements, that drive the earliest molecular inducers of teeth or denticles. Such combinations, and their phylogenetic distribution and history, will be the ultimate arbiters of palaeontological arguments over dental and denticle homology[9].

Discovery of the underlying tooth- or denticle-forming molecular programs will require transgenic analyses in paddlefish, catfish and sharks. Such analyses are not yet possible; nor are in-depth reconstructions of gene-regulatory sequences or bound transcription factors, necessitating the development of new experimental and bioinformatics approaches. Cracking such hard technical nuts will require strong intellectual teeth as well as robust body armour, given the vigour of opinion on this subject. ■

Georgy Koentges is at the Systems Biology Centre, University of Warwick, Coventry CV4 7AL, UK.
e-mail: g.koentges@warwick.ac.uk

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GEOMORPHOLOGY

How Tibet might keep its edge

Lewis A. Owen

The stability of the margins of the Himalayan–Tibetan mountain belt constitutes a puzzle. Repeated damming of major Tibetan rivers by glaciers, so controlling river erosion, is a possible explanation.

The collision of the Indian and Asian continental plates is the most dramatic tectonic event that Earth has experienced in the past 50 million years. It resulted in the formation of the Himalayan–Tibetan mountain belt, the growth of which initiated the south Asian monsoon, created some of the world's greatest rivers and gorges, and established the most highly glaciated realm outside polar regions. The combination of high topography, monsoon climate and great rivers and glaciers has produced intense erosion at the margins of these mountains, bringing deeply buried rocks quickly to the surface, most rapidly at the western and southeastern edges[1]. Defining landscape development in the Himalaya and Tibet, and the factors involved, is among the greatest challenges facing geoscientists, and it is one tackled

B. HALLET

Figure 1 | River deep, mountain high. At this site, which is just above where the Yarlung Tsangpo River (just off the photograph to the right) enters its gorge and slices its way through the Himalaya, impressive moraines extend from the flanks of the Namche Barwa massif and mark the limit of glaciation. The location corresponds to the place just upstream of the knick point shown in Figure 2.

by Korup and Montgomery on page 786 of this issue[2]. From their studies, centred on southeast Tibet, they propose that there are previously unrecognized links between glaciation, erosion and bedrock uplift.

There are various possible explanations of the interactions between climate, erosion and uplift in the Himalaya and Tibet, specifically for the western (Nanga Parbat) and southeastern (Namche Barwa) massifs. These include the 'tectonic aneurysm' model[1,3], according to which localized feedback between focused river erosion and rock uplift leads to dynamic interactions between topographic stresses, thermal weakening of the crust and uppermost mantle, and deformation. In another model, the 'glacial buzz-saw' model[4], glacial erosion controls the elevation of mountains regardless of uplift rates. These ideas have stimulated much research and debate, particularly over the relative importance of rivers and glaciers in driving landscape development.

Korup and Montgomery[2] add a new aspect to these debates. They argue that glaciation profoundly influences river erosion and sedimentation by damming water courses, which in turn controls the spatial distribution of erosion and the rate at which bedrock is brought to the Earth's surface. These interactions effectively help preserve the margin of Tibet, which would otherwise have retreated.

The authors' study focuses on the Yarlung Tsangpo River and its tributaries that drain Namche Barwa and form one of the deepest gorges on Earth (Fig. 1; see also the map on page 786 of this issue). These rivers, and others in similar high-mountain plateaux, should progressively erode towards their heads, resulting in steady degradation of a plateau's margins[5]. This is manifested in the headward migration of a river's 'knick point', an abrupt change in gradient in the longitudinal profile of a river. Such migration lowers the upstream elevation of the channel and basin; consequently, knick points should decline over time, and become less apparent as erosion progresses.

However, the margin of Tibet at Namche Barwa has apparently been stable over at least the past million years[6], essentially preserving the knick points along the Yarlung Tsangpo and its tributaries. As Korup and Montgomery point out, the stability of the entire Himalaya–Tibetan margin poses a conundrum. Previous explanations have invoked the existence of a dynamic equilibrium between tectonic uplift and erosion[7], or the role of landslides in protecting valley floors and in impeding channel incision[8].

Korup and Montgomery[2] used a combination of remote sensing and field investigation. They specifically looked for moraines — huge deposits of rocks and debris that pile up in front and at the sides of glaciers, and remain when a glacier retreats. They thereby identified 260 locations where glaciers have dammed the Yarlung Tsangpo and its tributaries above the heads of knick points. They also observed that broad river valleys with substantial terraces and thick sediments are present upstream of the moraines. In contrast, downstream of the moraines, stream channels are more confined and are usually entrenched in bedrock and sediments that were washed out from landforms produced by the glaciers. The overall result — protection of landforms from erosion upstream of a knick point, and increased erosion but uplift of bedrock downstream — is outlined in Figure 2.

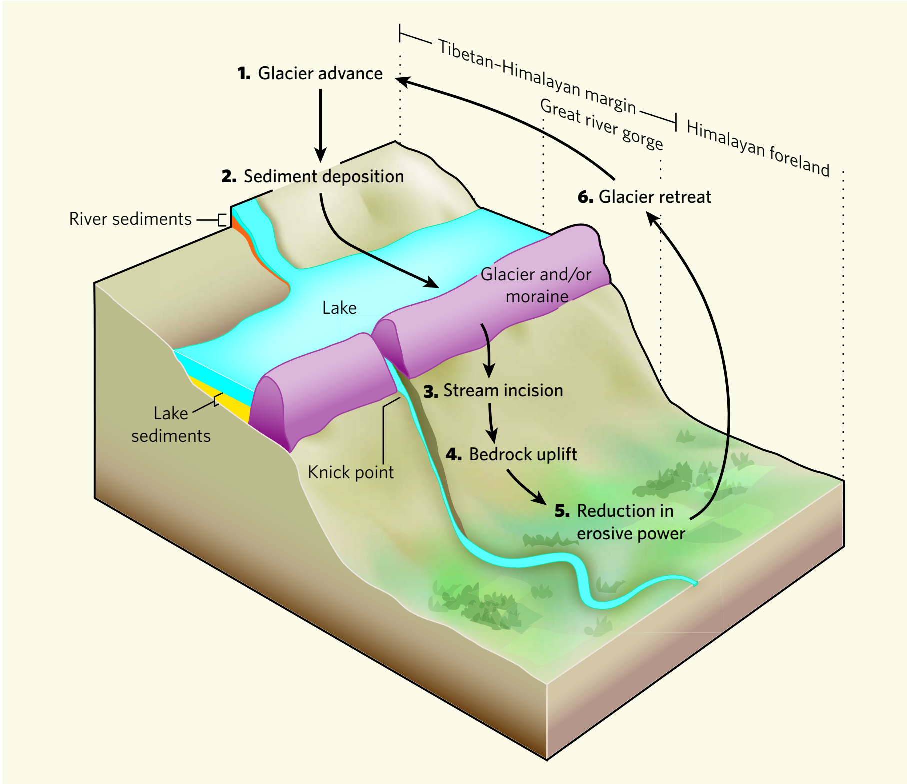

Figure 2 | Possible mechanism for the preservation of the edge of southeast Tibet. **The following is the sequence of events proposed by Korup and Montgomery[2] (diagram not to scale). 1, Glacier advance dams a river. 2, The deposition of sediments in the resulting upstream lake and stream both protects the valley floor from erosion and reduces the stream's erosive power. 3, Streams draining from the glacier and/or moraine are confined, so stream flow is strong and downstream erosion increases. 4, Stream incision into the bedrock essentially weakens the crust and enhances bedrock uplift to the surface. 5, As streams travel farther from the knick point, smaller gradients reduce their erosive power. 6, The glacier retreats, but the events are repeated numerous times as glaciers advance and retreat in response to climate change. The repetition of this mechanism maintains equilibrium between erosion and bedrock uplift, essentially preserving the topography of the margin of southeast Tibet.**

The geological evidence presented by Korup and Montgomery[2] shows that glaciers in the Namche Barwa region have advanced and retreated numerous times during the past 20,000 years or so, probably oscillating in a similar fashion since at least the beginning of the Quaternary ice age (some 2.5 million years ago). The authors quantified the degree of glaciation in the region by reconstructing the altitudes of former equilibrium lines for glaciers, a proxy for the extent of glaciation and hence climate. In this way also, they show that damming of the Yarlung Tsangpo and its tributaries has been a recurrent process, and has probably exercised strong control over the development of the landscape on million-year timescales. This repeated damming probably maintained rapid exhumation of bedrock at knick points, like that proposed in the tectonic-aneurysm model.

Korup and Montgomery's explanation of the interactions between glaciation, erosion and uplift in Namche Barwa is persuasive and will prompt fresh thinking among geoscientists. But how widely applicable might the explanation be? To answer this question, the generality and full significance of Korup and Montgomery's proposal will need to be assessed throughout the Himalaya and Tibet, and in other mountain belts. ■

Lewis A. Owen is in the Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221, USA.
e-mail: lewis.owen@uc.edu

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