cannot be captured by conventional ways of measuring a treatment's effect on an individual[6,7]. Therefore, such outcomes should be considered, and hypotheses should be formed about them, in advance. For health interventions (as well as other types of intervention), such effects might depend on the variability of the individuals' connectivity in a community, their roles and patterns of spatial mobility, and the strength or cohesiveness of relationships. Effects might also depend on the extent of segregation into smaller groups on the basis of attributes such as gender, race or social standing[8].

Second, the populations in which such research takes place are often not involved in its design or evaluation. These studies are typically expensive, with ethical review having been conducted through institutional processes, often at elite universities in high-income countries. The opportunities for meaningful local participation, often by people and institutions from poorer countries, remain rare. Importantly, the impacts of these network-spillover effects might be particularly consequential in places where formal public services and institutional resources are limited, and where informal networks are key sources of information and support. Community cohesion and networks of solidarity and reciprocity can be crucial sources of resilience to external shocks such as crime, natural disasters and war[9]. Therefore, community participation and co-design serve a scientific purpose as well as an ethical one. Local knowledge will help researchers to identify relevant problems and outcomes, anticipate possible consequences and design studies to detect them, as well as increasing the adoption and long-term effectiveness of interventions[10,11].

Third, conventional procedures relating to informed consent focus mainly on people who receive the intervention. Because network structure shapes how people access resources and opportunities, RCTs such as the one examined in Papamichalis and colleagues' study raise a broader question: how should consent account for changes in relationships that affect people who were not treated and, therefore, were not given an opportunity to consider possible risks[12]?

Risk-free experiments are impossible, and the Honduran study does not establish that harm occurred or identify its mechanisms. However, it does illustrate why researchers and ethics committees should seriously consider consequences for the wider social environment. It also highlights why they should involve, both directly and indirectly, affected communities in weighing up who bears the hazards and who reaps the benefits. Future experiments that deliberately measure social networks can help to make some of these trade-offs visible and inform the development of ethical guidelines.

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Palaeontology

How early tetrapods got their neck

Tatsuya Hirasawa

As fish evolved into four-limbed creatures, their skull separated from their shoulders to form a neck. Now we learn that this early neck was surprisingly rigid. **See p.128**

In the *Ballad of a Thin Man*, Bob Dylan sang about a bewildered individual:

> You raise up your head
> And you ask, "Is this where it is?"
> ... something is happening here
> But you don't know what it is
> Do you, Mister Jones?

Were the first ancestors of terrestrial animals to drag themselves from water onto land acting much like Mister Jones? For the water-to-land transition that populated the planet with four-limbed animals called tetrapods, evolutionary biologists have long hypothesized that the separation of the skull from the shoulder bones was a change that enabled tetrapods to evolve a neck suitable for turning or raising their head to navigate a strange new world flourishing with plants and insects. On page 128, Korneisel *et al.*[1] present a counter-intuitive discovery about tetrapod neck evolution.

The conventional view of how tetrapod necks evolved arises from the stark contrast in body form between fishes and living tetrapod vertebrates (Fig. 1). In fishes, opercular bones support the gill covers and firmly link the skull to the shoulder bone called the girdle, leaving little room for independent head movement. During the transition to land, this bony connection was lost, freeing the skull from the girdle[2]. In organisms called amniotes, the lineage that includes mammals, reptiles and birds, this decoupling went a step further – during embryonic development, the internal organs shifted away from the neck into the chest cavity, freeing the neck region and enabling it to gain an unhindered capacity for elongation and flexibility[3]. Looking at highly specialized neck structures in modern species, it is easy to see why researchers intuitively linked head–shoulder separation directly to enhanced neck mobility.

Crucially, this potential for independent head movement was not built from scratch on land. The muscular machinery required to operate a neck had begun to evolve long before terrestrialization happened. Fossil evidence from the earliest known branch of jawed vertebrates, a group called placoderms, reveals that a distinct set of neck musculature had already evolved alongside the jaw joint, even at a time when the skull and shoulder girdle remained mechanically connected[4]. Evolutionary blueprints for head mobility therefore pre-existed in ancestral fishes, awaiting the subsequent skeletal and developmental changes that would later unlock neck freedom on land.

To answer whether these first limbed pioneers truly acted like Bob Dylan's Mister Jones, attention must focus on the fossil group called stem tetrapods, which were present around 390 million to 330 million years ago[5]. Although the deep-time fossil record is inherently fragmented, the ancient remains that do exist are indispensable for examining evolutionary history – much like how faint light from distant galaxies serves as the only direct evidence of the Universe's primordial past[6].

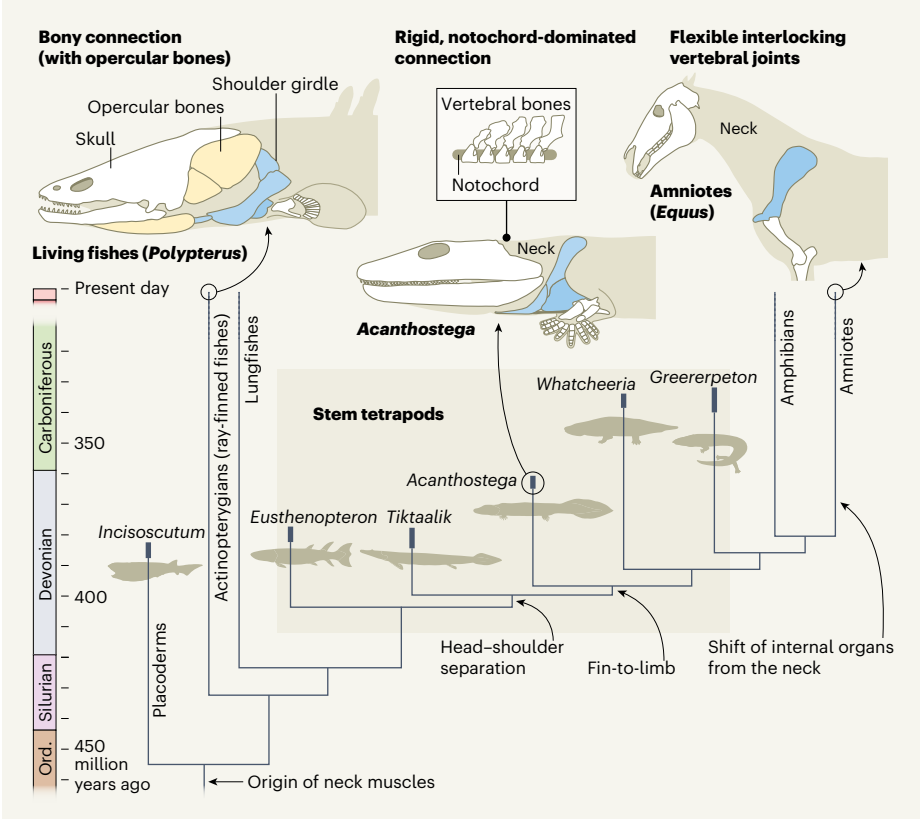


Figure 1 | Neck evolution. In living fishes, such as those of the genus *Polypterus*, the skull and shoulder girdle bones are mechanically connected by opercular bones. However, when some fish evolved into four-limbed creatures called tetrapods, those in the lineage called amniotes, which includes horses, developed a skull and shoulder girdle that are widely separated by a movable neck that is supported by vertebral joints. Korneisel *et al.*[1] sought to understand how necks evolved when head–shoulder separation occurred in early tetrapods called stem tetrapods, a group that includes *Acanthostega*. Such creatures had a neck region that contained a tissue called notochord and vertebral bones. The authors did physical tests on present-day lake sturgeon (*Acipenser fulvescens*; not shown), which has an anatomy that mirrors the notochord-dominated axial skeletons of early tetrapods. The findings indicate that stem tetrapods had limited neck mobility even after head–shoulder separation. (The timeline is based on references 5, 9 and 10 and the references therein; Ord, Ordovician.)

Indeed, previous studies[7] have successfully reconstructed early tetrapod movement by analysing 3D skeletal joint mobility for the limbs.

However, assessing head mobility in stem tetrapods introduces a profoundly different problem. Head–shoulder separation freed the skull from the shoulder girdle, and this leaves no direct bony connection joint between them. Instead of joint movement, any head movement relied entirely on the flexibility of the intervening neck region. In living tetrapods, such as humans, this mobility is precisely regulated by specialized, interlocking vertebral joints. In fact, well-developed, supportive vertebrae have evolved independently across several independent lineages[8]. However, such sophisticated joints were absent in stem tetrapods.

In the stem tetrapods, the neck region was mostly soft tissue organized around a structure termed an axial column, which was dominated by tissue called the notochord. In living land vertebrates such as humans, the notochord is present only transiently during embryonic development as a foundational support structure. Then, as development progresses, vertebral bones form around it, eventually taking over its supportive role. For stem tetrapods, however, this skeletal handover was far from complete. Their adult necks retained a primitive architecture lacking fully bony vertebral components, presenting a formidable challenge for conventional methods of skeletal modelling. This obstacle has, until now, left the true flexibility of the early tetrapod neck shrouded in mystery.

Enter Korneisel and colleagues, who sidestepped the long-standing technical challenges of modelling the anatomy by instead introducing a modern creature as a way to tackle the puzzle. Although most living fishes have evolved well-developed, bony vertebral columns, present-day lake sturgeons (*Acipenser fulvescens*) represent a rare exception, retaining a soft-tissue and notochord-dominated axial skeleton that mirrors the ancestral condition.

Recognizing this structural similarity, the authors performed physical tests on fresh sturgeon axial skeleton, which had not undergone chemical treatment, to simulate the biomechanical capacities of early tetrapod necks. Although notochords and other soft tissues are not preserved in fossils, the shape of a stem tetrapod skeleton enabled Korneisel and colleagues to narrow down the size and location of notochords and muscles. On the basis of data from their sturgeon tests, the authors could quantitatively determine the stiffness of fossil animals' necks, and thereby estimate how much bending their muscle force enabled.

The authors' results shatter the intuitive assumption of an inherently flexible neck region for stem tetrapods. Despite lacking bony vertebral components, this architecture was surprisingly rigid. The authors estimate that most stem tetrapods could move their heads less than 6° side-to-side and less than 3° backwards, and could not rotate their heads.

If mobility was not the driving force for skull detachment from the shoulder girdle in the first place, then what was? Crucially, Korneisel and colleagues demonstrate that head–shoulder separation did not shift in conjunction with neck flexibility. Instead, the answer probably lies beneath the body rather than at the top: forelimb-driven terrestrial motion, a pivotal innovation for early tetrapods conquering gravity on land[7] provides a far superior functional explanation. The neck therefore probably evolved not as an adaptation that arose to turn the head but rather as a mechanical consequence of stabilizing the body when walking evolved. In a grand twist of evolutionary irony, the first of our ancestors to drag themselves onto land were much more constrained than scientists ever imagined. They were, in a sense, like Mister Jones, stepping into a world where something monumental was happening, yet they were physically unable to turn their heads to see what it was.

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