

of the cranium and provides the upper jaw with a remarkable range of mobility. Mobility of the upper jaw is severely restricted in palaeognaths, in which the pterygoid instead forms rigid, immobile joints with the palatine and the base of the skull. Other dinosaurs, including the earliest non-modern birds, had immobile palates similar to those of palaeognaths, and so it has long been assumed that the ancestor of all living birds must also have had an immobile palate. In that scenario, palaeognaths would indeed live up to their name of ‘old jaw’.

Benito *et al.* used 3D imaging and quantitative shape analyses to demonstrate that the pterygoid of *Janavis* is decidedly more like those of neognaths (especially ducks and chickens) than those of palaeognaths, and show that it is complete with mobile joints with the palatine and skull base. The presence of a neognath-like palate in a close relative of modern birds supports a revised sequence of evolutionary events, in which neognaths are the true inheritors of the ancestral avian condition, and palaeognaths represent a surprising reversion to the characteristics of a pre-modern-bird state.

This report of *Janavis* is auspiciously timed. Some studies have described nearly complete bony palates from other close relatives of living birds, including *Ichthyornis*, that are more consistent with a neognath-like palate than a palaeognath-like one^{4,6}, calling into question the historical reputation of neognaths as palatal innovators. Unfortunately, those bony palates did not preserve the most telling element, the pterygoid. *Janavis* finally fills that gap, and in so doing, poses some surprising new questions and reframes some old ones.

What evolutionary pressures drove the ancestors of palaeognaths to evolve back along a pathway to having an immobile palate? That transition seems to have been a bad move – popular hypotheses implicate the palate in helping to drive the staggering diversification in Neognathae (comprising more than 11,000 living species) when compared with Palaeognathae (less than 100 living species)⁷. A mobile palate provides neognaths with a range of advantages over palaeognaths, including wider gapes, stronger bite forces and the ability to handle food more dexterously^{8,9}. Although the link between palate type and species diversification bears further testing, discoveries such as *Janavis* provide an intriguing new context for consideration.

Janavis and other near relatives of living birds have a lot more to tell us, not only about which beak type came first, but also how those beak types evolved in the first place. Adult ichthyornithines have a bone in the palate called the hemipterygoid that is known only in hatchling neognaths and is lost in adults^{4,6}. What effect, if any, does that extra bone have on the potential mobility of the beak in early

birds? Why was it lost in adult neognaths? What happened to it in palaeognaths? Some of those stories might come from the beaks of birds such as *Janavis* – but only if we keep looking for them.

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Climate science

Rapid warming linked to leap in tropical seasonality

Alyssa R. Atwood

Seasonal variation in tropical sea surface temperatures doubled during an abrupt warming event 11,700 years ago. This shows that seasonal changes must be considered when inferring past climatic events, and predicting those to come. **See p.88**

Since the peak of the last glacial state 21,000 years ago, Earth’s climate system has warmed to the present interglacial state, known as the Holocene. But this trend was not smooth – temperatures jumped by up to 10° C over a period of years to decades during two warming events around 14,700 and 11,700 years ago^{1–3}. No modern analogue exists for these abrupt climate events. This makes such events crucial for grasping the erratic way in which the climate system can respond to external changes, with relevance to understanding current anthropogenic warming trends. Although these deglacial changes are generally well characterized on decadal and longer timescales, little is known about them on shorter timescales. On page 88, Wörmer *et al.*⁴ report that data on these shorter timescales reveal that surface temperatures in the tropical Atlantic Ocean showed a large increase in seasonal variation at the start of the Holocene.

The warming of the past 21,000 years was caused by gradual changes in Earth’s orbit. These changes led to an increase in the amount of sunlight received during summers in the Northern Hemisphere, which melted the large ice sheets there, allowing more sunlight to be absorbed at Earth’s surface and triggering further warming. In contrast to the gradual pace of the orbital changes, however, the climate system warmed in fits and starts, highlighting the existence of tipping points, or thresholds, at which small changes can induce new states.

Around 14,700 years ago, an event known as the Bölling–Allerød warm period brought the climate system abruptly out of the last ice age, with temperatures rising rapidly from glacial

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to interglacial conditions in just a few decades. Temperatures eventually dropped back into glacial conditions, culminating in a period known as the Younger Dryas cold event around 12,900 years ago^{1–3,5}. This event was probably driven by a large injection of meltwater from the ice sheets into the North Atlantic Ocean that disrupted ocean circulation patterns^{6,7}. The cooling terminated abruptly around 11,700 years ago, marking the onset of the Holocene, and involved a second period of rapid warming of up to 10° C over several decades or less^{1,2}.

These events are well characterized for the polar regions, but high-resolution data detailing how tropical temperatures varied during this time are sparse. This is especially true in the tropical oceans, because these data typically come from the chemical composition of marine sediments, which accumulate slowly and get mixed by organisms living on the sea floor. The Cariaco Basin is an exception – a source of palaeoclimate information of high temporal resolution in the tropics. The basin lies off the northern shelf of Venezuela, so it accumulates material from both the land and ocean, and an absence of oxygen in its deep waters leads to conditions that prevent marine organisms from mixing the sediment.

At 10° N latitude, the Cariaco Basin is situated at the northernmost boundary of the Atlantic Intertropical Convergence Zone, which is a region characterized by heavy rainfall from converging moist, low-level winds. Seasonal changes in sea surface temperatures in this region produce a strong annual cycle of rainfall, winds and upwelling (the wind-driven upward

motion of deep water towards the ocean surface). This cycle creates clear seasonal layers in the sediment, which differ in colour and in elemental composition. Sediments from this region therefore offer a continuous annual record of past climate conditions from the last deglaciation to the present⁸.

Wörmer *et al.* reconstructed sea surface temperatures in the Cariaco Basin during the deglaciation by performing mass-spectrometry imaging on long-chain biomolecules known as alkenones. These molecules are produced by certain marine algae that respond to changes in water temperature by altering the molecular composition of their cell membranes. When the algae die, their remains settle on the sea floor, and the relative abundances of two types of alkenone in the sediment provide a record of past ocean temperatures over time⁹.

Alkenones are usually extracted chemically from centimetre-thick sections of sediment¹⁰, but the authors' imaging technique allowed them to measure alkenone abundances in submillimetre-sized spots on thin vertical slices of samples that remained intact. This method was previously used¹¹ by members of the same research group to reconstruct the annual cycle of sea surface temperatures in the Santa Barbara Basin over a period spanning 1984 to 2009.

In the present study, the authors measured around 20,000 spots for every 5-cm sample of sediment, enabling them to reconstruct annual average temperatures, as well as the temperature difference between seasons that are characterized by upwelling and those that are not. The reconstructions span the period from 11,900 to 11,200 years ago, capturing the transition from the end of the Younger Dryas cold event to the onset of the Holocene.

Wörmer *et al.* found that average annual temperatures in the Cariaco Basin did not change substantially during the rapid warming event between the late Younger Dryas period and the early Holocene. However, the seasonality – calculated as the difference between the average sea surface temperature in the non-upwelling and upwelling seasons – increased from 0.8 to 1.8 °C (Fig. 1). The authors showed that this seasonality increase coincided with a pronounced decrease in the reflectance of the sediment, which indicates a reduced average upwelling intensity.

The authors infer that the coincident changes in temperature seasonality and in sediment reflectance are consistent with a northward shift in the mean position of the Atlantic Intertropical Convergence Zone, or to a northward expansion of its seasonal range during the Holocene, relative to the late Younger Dryas period. They argue that these conditions would lead to reduced upwelling and the subsequent development of warm surface layers during summer and autumn, establishing a seasonal temperature variation

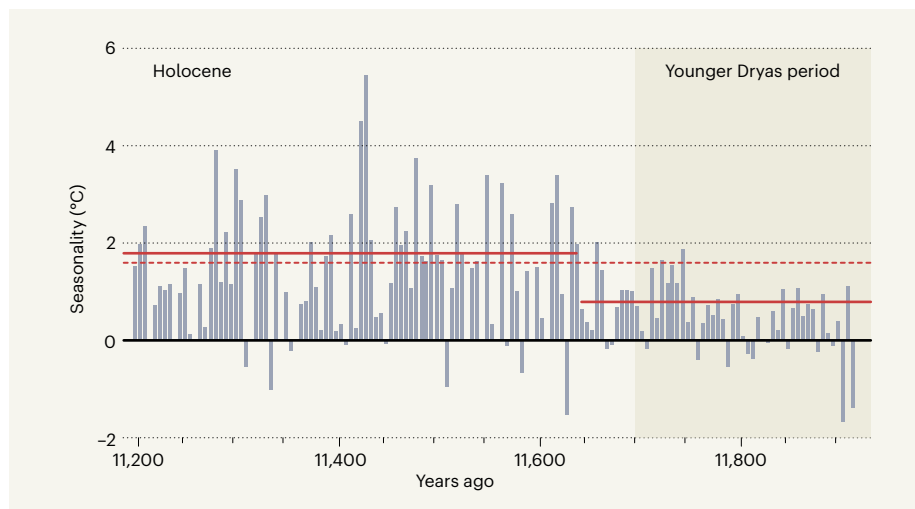


Figure 1 | Increased seasonal variation at the start of the Holocene. Wörmer *et al.*⁴ analysed sediment from the Cariaco Basin off the coast of Venezuela to infer sea surface temperatures during the abrupt transition between a period of cooling (the Younger Dryas cold event) and the current interglacial state (the Holocene). The high temporal resolution of the authors' imaging technique revealed an increase in seasonality, calculated as the difference between the average sea surface temperature in seasons that are characterized by upwelling (the wind-driven upward motion of deep water towards the ocean surface) and those that are not. The seasonality increased from 0.8 to 1.8 °C (solid red lines), which is close to the present-day seasonality of 1.6 °C (dashed red line). (Adapted from Fig. 3a of ref. 4.)

that mimics the modern climate.

The study also showed that interannual (year-to-year) temperature variability was higher in the early Holocene than during the late Younger Dryas period, which the authors suggest might be related to enhancement of the El Niño–Southern Oscillation (the periodic variation in sea surface temperatures, winds and sea-level pressure in the tropical Pacific Ocean) during the early Holocene compared with the late Younger Dryas period.

On the basis of these findings, the authors conclude that the climate variability on seasonal to interannual timescales was more sensitive to global climate changes than was the variability on longer timescales during this period. They suggest that the substantial differences between their temperature trends and previous low-resolution reconstructions from the Cariaco Basin could be due to changes in seasonality. In a complementary study published last year, accounting for seasonality also reconciled discrepancies between model simulations and global temperature reconstructions for the Holocene and the last interglacial period¹². Both sets of findings underscore the need to account for seasonality when developing robust climate reconstructions.

The study provides tantalizing evidence for marked changes in seasonal and interannual climate variability in the tropical North Atlantic during the most recent period of abrupt climate change, substantially expanding our view of the global adjustments to climate change. However, climate reconstructions are not without uncertainties. One potential source of uncertainty is the fact that temperature

reconstructions derived from alkenones can be sensitive to changes in nutrient concentration. For instance, in the study from the Santa Barbara Basin¹¹, reconstructed seasonal temperature variations were slightly lower than observed variations, and this discrepancy was attributed to nutrient changes driven by upwelling. Given the inferred seasonal changes in upwelling in the Cariaco Basin during the transition from the Younger Dryas period to the early Holocene, it is possible that Wörmer and colleagues' temperature reconstructions also contain an imprint of a nutrient effect.

Although the current study is focused on the temperature differences between seasons, extending the authors' reconstructions to examine temperature changes during the upwelling and non-upwelling seasons independently could increase our understanding of the seasonality changes even further. Looking at other parts of the deglaciation and Holocene would also build on these findings.

High-resolution palaeoclimate records, such as those in Wörmer and colleagues' study, provide an increasingly detailed view of how the climate system operates. These records help to refine our knowledge of the global interconnections associated with climate change.

Such high-resolution reconstructions also open the door to myriad testable hypotheses. Wörmer and co-workers' study provides crucial data for investigations into the tropical Atlantic variations using climate-model simulations, and will provide inspiration for the development of other palaeoclimate records that could identify changes in seasonality during this pivotal time in climate history.

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Cell biology

Uncoordinated protein coordinates cell migration

Alain Chédotal

Mounting evidence suggests that developing neurons and metastatic cancer cells migrate through similar mechanisms. Characterization of a previously unknown complex involved in cell migration confirms this idea.

During development, many cell types – including neurons – migrate in and across organs to reach the position they will occupy for the remainder of their lives. Similarly, in cancers, metastatic cells escape tumours and disperse around the body. Three decades of research have shown that cell migration is not random. Instead, the cell’s motility, its orientation and whether it leaves or settles in a specific location are influenced and guided by molecular signals from neighbouring and, sometimes, distant cells¹. Several families of cell-guidance molecules have been identified², but how they interact to coordinate cell movements is not well defined. Writing in *Cell*, Akkermans *et al.*³ add to this picture through the characterization of a molecular complex that controls neuronal and metastatic cell migration.

In 1974, the biologist Sydney Brenner treated nematode worms (*Caenorhabditis elegans*) with a chemical that induces genetic mutations, and isolated more than 50 mutants that displayed uncoordinated body movements⁴. This included one mutant, carrying alterations in a gene dubbed *unc-5*, that had an abnormal nervous system. It was later found that *unc-5* encodes a membrane-spanning protein of the immunoglobulin family, expressed by both migrating cells and developing neurons. It is a receptor for the secreted protein *unc-6* (ref. 5).

Parallel studies^{6,7} identified four *unc-5* proteins (Unc5A, Unc5B, Unc5C and Unc5D) in vertebrates, all of which bind to Netrin-1, the vertebrate *unc-6*. However, Unc5 receptors can also interact with other proteins either in the

same cell (in *cis*) or in adjacent cells (in *trans*)^{2,8}. In most settings, binding between Unc5 and Netrin-1 inhibits cell motility, but Unc5 receptors that are bound to either Netrin-1 or other partners can influence a large range of developmental processes, including brain wiring, blood-vessel growth and cancer^{2,9}.

Akkermans *et al.* used an array of methods to show that Unc5 receptors interact with a protein called Glypican 3 (GPC3) in humans and

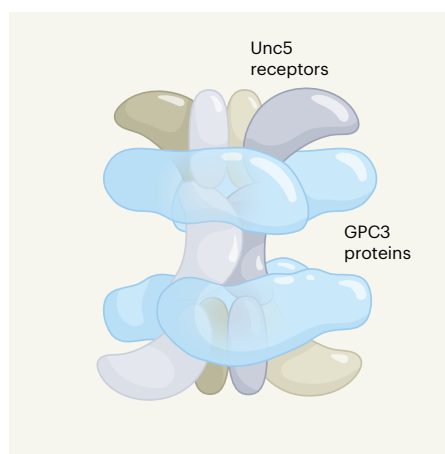


Figure 1 | The core of the GPC3–Unc5 protein complex. Akkermans *et al.*³ resolved crystal structures for mouse and human GPC3–Unc5 protein complexes. They found that the core of each complex contains the extracellular domains of four Unc5 receptors, arranged in two antiparallel pairs. The receptors are encased by pairs of GPC3 proteins at either end.

mice. GPC3 belongs to a small group of extracellular proteins that are covalently linked to the cell surface by a glycosylphosphatidylinositol anchor.

The authors resolved the crystal structure of mouse and human GPC3–Unc5 complexes using X-ray crystallography. Surprisingly, rather than simple dimers, GPC3 and Unc5 proteins assemble into a large octameric complex that contains a core tetramer of four Unc5 proteins, bracketed at either end by pairs of GPC3 proteins (Fig. 1). The researchers found that GPC3 and Unc5 can interact both in *cis* and in *trans*; however, in *cis* interactions inhibit in *trans* interactions. All four members of the Unc5 receptor family seem to bind equally to GPC3, but previous work¹⁰ suggests that the five other Glypican family members do not interact with any Unc5 protein.

What is the function of the GPC3–Unc5 complex? Akkermans *et al.* first focused on the brain’s cerebral cortex, where GPC3 is expressed by apical progenitor cells. These cells have long processes that act as a scaffold along which neurons expressing Unc5 migrate. To avoid the fact that the large palette of Unc5 and GPC3 binding partners could complicate their analysis, the authors developed an approach to selectively modify the GPC3–Unc5 complex. They identified small antibodies called llama nanobodies that could enhance (in the case of a nanobody called Nano^{elue}) or inhibit (in the case of Nano^{break}) GPC3–Unc5 interactions.

The researchers placed Unc5-expressing neurons on a surface that contained stripes of GPC3 *in vitro*. The found that the neurons were repelled from the GPC3 stripes, and showed that adding Nano^{break} can overcome this repulsion. Interfering with GPC3–Unc5 interaction *in vivo* – by using nanobodies, by blocking GPC3 production or by overexpressing the extracellular portion of Unc5 – significantly delayed cortical neuron migration (Fig. 2a). Thus, interactions between these binding partners promote or facilitate migration, perhaps to ensure that Unc5-expressing neurons reach the correct final position in the brain at the correct time. Given that Unc5 proteins are involved in neuronal migration in many brain regions outside the cortex, the GPC3–Unc5 complex could have other neurodevelopmental functions, too.

Unc5 proteins and GPC3 have been linked to the development of various types of cancer, and are expressed in some cultured tumour cells⁹. This prompted Akkermans and colleagues to investigate the role of GPC3–Unc5 complexes in tumour-cell migration. They found that, when very aggressive cancer cells that expressed both Unc5 and GPC3 were transplanted into a chick embryo, they migrated extensively along nerves and settled in neuronal masses called peripheral ganglia. Reducing the levels of Unc5 or GPC3 in these transplanted cells, or unbalancing GPC3–Unc5 interactions using nanobodies or mutated receptors, impeded