logical system operating over thousands of years or longer (*1*). This system transfers subglacial water from areas of basal melting to areas of basal freezing. The resulting internal mass and heat redistribution is currently not accounted for by ice sheet models.

The lowermost part of the Antarctic ice sheet is of particular importance to ice core scientists searching for new drill sites with climate records beyond the recently achieved ~800,000 years ago (*7*). Simulations predict that meteoric ice that originated as surface snow ~1 million years ago is now in the lowermost tens of meters of the ice sheet (*4*). Prior to the work of Bell *et al*., their study area, the Gamburtsev Mountains, represented one of the prime targets for finding the oldest ice on Earth. However, the search for ancient climate records in ice will be complicated wherever the accreted basal ice is tens of meters thick.

The Antarctic accreted ice layers are an attractive target for scientific exploration—as illustrated by the scientific insights into biology, hydrology, and geochemistry of subglacial Lake Vostok gained from the analyses of accreted lake ice found in the Vostok ice core (*8*). Even though subglacial Lake Vostok has yet to be penetrated and explored, its potential as a microbial habitat is supported by the fact that accreted lake ice samples have bacterial concentrations up to seven times as high as the overlying meteoric ice (*8*). This evidence provides also the key underpinning for the conjecture that Antarctic subglacial aquatic environments hold a large pool of bacterial carbon in diverse microbial environs (*5*, *9*). Whereas Lake Vostok appears to contain relatively fresh water, solute exclusion during freeze-on of accreted ice may generate more saline water bodies and drive geochemical heterogeneity of subglacial microbial habitats (*10*, *11*).

Basal ice represents a key mechanical boundary layer controlling the rate of ice sheet motion over geologic substrata. Most ice deformation happens just above the base of a polar ice sheet, either as a result of laminar shear or in association with basal ice sliding. Much research is currently focused on improving ice sheet models to refine predictions of future sea level changes (*6*). These models typically use only rheological parameters of meteoric ice. However, basal accreted ice may be considerably weaker than meteoric ice due to its higher content of water, sediments, and ionic impurities (*12*). Softer ice deforms faster and will yield greater changes in ice velocity than stiffer ice in response to the same stress change. Hence, the widespread presence of thick, accreted basal ice layers may make the Antarctic ice sheet more susceptible to rapid changes in geometry than previously thought.

The discovery of thick, widespread accreted ice layers changes in fundamental ways our understanding of the Antarctic ice sheet. Further mapping and modeling of these ice bodies is necessary to aid the ongoing search for the oldest ice on Earth. New models of subglacial water generation, flow, and freezing will have to be developed to account for this large internal mass and heat redistribution within the ice sheet. Future coring and sampling of Antarctica's deep, frozen "lakes" will unlock a new archive of spatial and temporal changes in deep Antarctic microbial habitats and water drainage systems. Ice sheet models will explore the potential impact of soft basal ice on the sensitivity of ice sheet mass balance to climate changes.

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10.1126/science.1202888

PALEONTOLOGY

On Dental Occlusion and Saber Teeth

An early mammal relative from Brazil offers insight into the early evolution of herbivory.

Jörg Fröbisch

Studies of fossil vertebrates belonging to the group Synapsida are central to understanding mammalian origins. Synapsida includes mammals and is one of the two major clades of amniotes (all fully terrestrial vertebrates). The other is Reptilia, which includes modern turtles, snakes, lizards, crocodiles, and birds. The therapsids, one major group of nonmammalian synapsids (historically but erroneously known as "mammal-like reptiles") have been particularly important to understanding the acquisition of mammalian characteristics. One of the key features within the evolutionary history of synapsids is the morphological differentiation of their dentition (teeth) over time (*1*). On page 1603 of this issue, Cisneros *et al.* (*2*) describe a new therapsid fossil from South America, *Tiarajudens eccentricus,* which displays a unique dentition, including broad chewing teeth on the palate and a pair of extremely long saber canines. The discovery provides novel insights into early tooth differentiation in synapsids and into the evolution of herbivory (plant eating) and its accompanying complex social interactions.

Nonmammalian synapsids are important to our understanding of the evolution of terrestrial ecosystems. Numerous clades of now-extinct synapsids dominated life on land during most of the late Paleozoic and early Mesozoic eras. Although several synapsid clades (Anomodontia, Therocephalia, and Cynodontia) survived the most severe extinction event in Earth's history at the end of the Permian, only nonmammalian cynodonts flourished until the Cretaceous. This group gave rise to mammals near the Triassic-Jurassic boundary (*3*). In the Late Paleozoic, a drastic faunal shift occurred in the terrestrial realm. A Late Carboniferous and Early Permian fauna dominated by "pelycosaurs," a basal group of synapsids, gave way to therapsid-dominated faunas in the Middle and Late Permian. This

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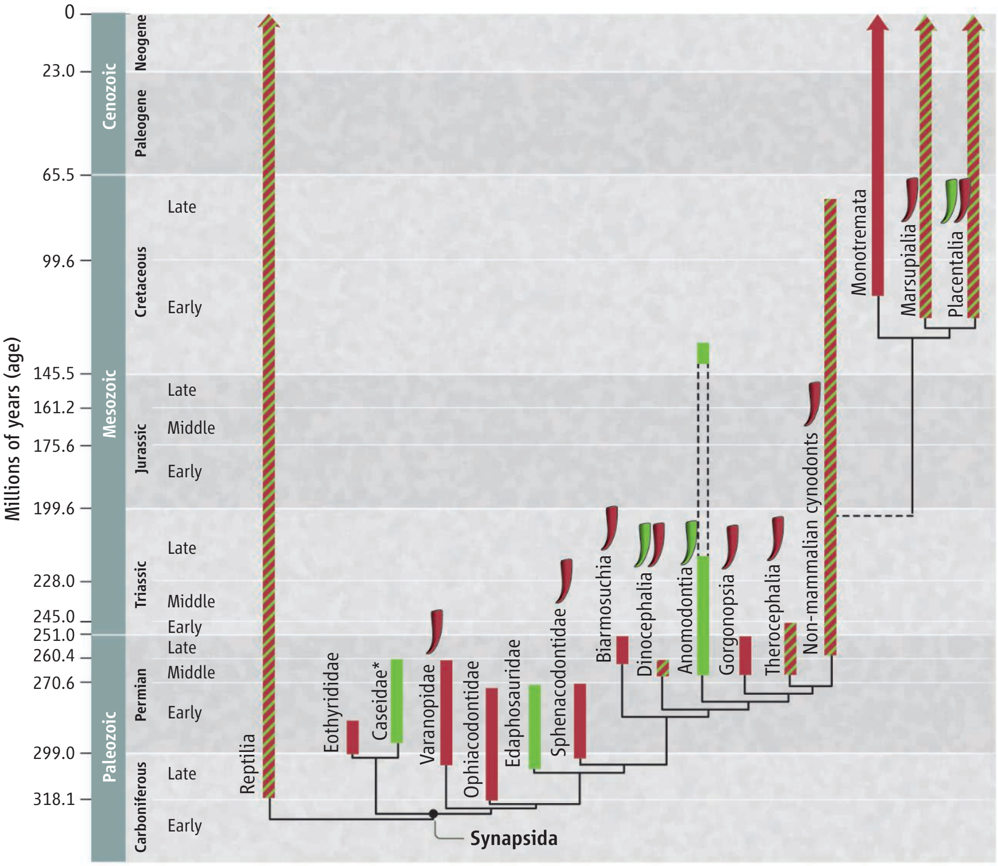

Dental occlusion and saber teeth in synapsids. Green and red boxes indicate temporal ranges of major subgroups within Synapsida, and connecting lines describe their evolutionary relationships. Carnivorous forms in red; herbivorous forms in green. Subgroups in red and green include both herbivorous and carnivorous forms. Herbivory is generally associated with dental occlusion, except in caseids (asterisk). Saber teeth depict the presence of enlarged canines (including saber teeth, tusks, and simply enlarged canines). *Tiarajudens eccentricus* (from Brazil) is the only herbivore with saber teeth in the Paleozoic era.

shift was accompanied by a major change in ecosystem structure. Early terrestrial vertebrate ecosystems primarily consisted of insectivorous and carnivorous forms with few herbivores. In contrast, Late Permian ecosystems display the earliest evidence for a modern pattern of trophic interactions, with large numbers of herbivores supporting a relatively small number of top predators (*4*).

Over time, therapsids show an increasing development of mammalian characters. These include the evolution of the mammalian middle ear, a bony secondary palate, and a mammalian "phalangeal formula" (the number of phalangeal bones in each digit). They also develop a more upright posture in the fore and hind limbs and begin to explore new habitats (*5*–*7*). Various clades of synapsids, such as anomodonts during most of the Late Permian and Early Triassic, independently evolved a herbivorous mode of life and often represented the major primary consumers among vertebrates of their times (*8*).

Tiarajudens eccentricus belongs to Anomodontia, the most abundant and speciose clade among nonmammalian synapsids. Anomodonts were the major herbivores of the Late Permian and Early Triassic. They achieved a cosmopolitan distribution, with specimens known from every present-day continent, reflecting their great taxonomic diversity (*9*, *10*). This is mirrored by an enormous morphological disparity; anomodonts included small fossorial (mole-like burrowing) forms, large browsing and "grazing" forms, and semiaquatic (amphibious) and arboreal (tree-climbing) body plans (*11*–*13*). This diversity is unparalleled by any other clade of Permian-Triassic terrestrial tetrapods. In addition, anomodonts were among the first synapsids to display an increasing development of mammalian characters. Indeed, "mammalian characters" could instead be termed "anomodontian characters."

The discovery of *Tiarajudens,* in Middle Permian deposits in Brazil, sheds new light on the early diversification of therapsids and particularly anomodonts. *Tiarajudens* is of particular importance because of its unique, specialized dentition. Also, it seems to belong to a new aberrant clade of basal anomodonts, called Anomocephaloidea, that lived on the southern supercontinent of Gondwana. Anomocephaloidea stands in contrast to the venyukovioids, a well-known clade of basal anomodonts that lived on the northern supercontinent of Laurasia.

The early evolution of dental occlusion (the contact between upper and lower teeth) and saber canines in *Tiarajudens* is of special interest. The evolution of herbivory is often accompanied by dental occlusion (*14*) (see the figure). In fact, the evolution of high-fiber herbivory and dental occlusion in basal anomodonts has previously been documented in the slightly younger and specialized climber *Suminia* (*15*). However, this close relative of *Tiarajudens* lacks any enlarged canines and shows dental occlusion between its marginal dentition in the upper and lower jaws. Therefore, the degree of heterodonty (tooth differentiation) in *Tiarajudens* is remarkable. In particular, the transversely expanded palatal teeth on the pterygoid and ectopterygoid are unique among synapsids. Together with other recently discovered basal anomodonts, such as *Suminia* (from Russia) and *Biseridens* (from China), as well as the highly successful beaked dicynodonts, *Tiarajudens* shows that anomodonts displayed by far the most disparate feeding strategies of any group of Paleozoic herbivores.

The evolution of saber teeth is comparably rare among tetrapods and exceedingly uncommon in herbivorous forms (see the figure). The presence and extent of the saber teeth in the Brazilian anomodont is extraordinary, in particular when considering its parallel evolution to the continuously growing tusk displayed by a group of derived anomodonts, the dicynodonts (*16*). In fact, the tusks of the similarly herbivorous dicynodonts evolved even before the saber teeth of the Brazilian form, and their behavioral implications have been discussed in detail for the sexually dimorphic *Diictodon* (*17*).

These findings raise a question: When is a saber tooth a saber tooth, and when is it a tusk or simply an enlarged canine? The existing literature is quite imprecise, but saber teeth tend to be laterally compressed, whereas tusks tend to be rather round in cross section and continuously growing, such as in modern elephants, wild boars, and walruses. Finally, the distinction of saber teeth and tusks from ordinary large canines appears to be vague and primarily based on length. *Tiarajudens* seems to further blur this distinction, since anomodonts evolved both approaches (saber teeth and tusks) to enlarge their canines, even though they might have had similar functions, such as deterring predators and intraspecific display or combat (*2*, *17*).

The discovery of extraordinary fossils such as *Tiarajudens eccentricus* provides new insights into the dental diversification and early evolution of herbivory in tetropods and the complex evolutionary history of synapsids. Nonetheless, future research applying integrative and quantitative approaches to the study of herbivory will be needed to further investigate its significance for the evolution of terrestrial vertebrate ecosystems.

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MATERIALS SCIENCE

Electronic Bonding Revealed by Electron Diffraction

A new electron diffraction method reveals a tetrahedral bond network in aluminum that can account for the directional nature of its mechanical properties.

Paul A. Midgley

When atoms come together to form a crystal, a redistribution of electron charge creates bonds that govern almost all of the crystal's physical and chemical properties. Ab initio calculations can provide theoretical determination of the bonding charge density, but experimental verification can be fraught with difficulty because the change in the total charge density, as measured via diffraction experiments, is very small. For example, in aluminum (Al), most of the electrons are highly delocalized and form a free electron gas, but some of the electron density forms highly directional bonds. On page 1583 of this issue, Nakashima *et al.* (*1*) demonstrate the use of ultrasensitive convergent-beam electron diffraction (CBED) to map the bonding charge density of Al to an unrivaled accuracy. These results lead to a greater understanding of this metal's mechanical properties.

For many decades, efforts have been made to determine bonding charge density with both x-ray and electron diffraction. Crystallographic studies measure the pattern of different intensities of the scattered reflections. These patterns are modeled by determining structure factors, which sum up the individual scattering contributions of each atom that is positioned in the unit cell, the repeating block within the crystal. For x-rays, the structure factors are associated with the electron charge density; for electrons, they are associated with the electrostatic potential, which can yield the charge density via Poisson's equation.

The charged nature of the electron ensures that the interaction between the electron and the crystal is far stronger than the equivalent x-ray interaction (by a factor of 100 to 1000), and that charge-density effects are more likely to be observed. The stronger interaction means that electrons scatter many times before exiting the crystal. Unlike most x-ray diffraction data, electron diffraction patterns

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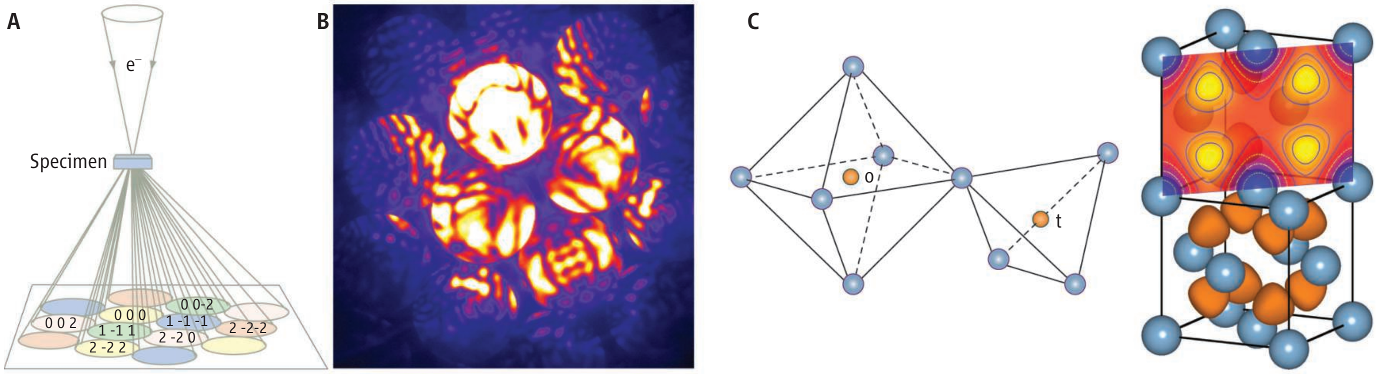

Making a difference with diffraction. (**A**) Schematic representation of convergent-beam electron diffraction (CBED) showing the formation of pattern-containing disks of different diffraction beams (the beam order is given by the three-digit Miller indices). (**B**) An experimental CBED pattern from aluminum determined by Nakashima *et al.* (**C**) The corresponding bonding charge density they determined using a differential form of the CBED pattern, along with an illustration of the octahedral (o) and tetrahedral (t) sites in the lattice (the latter is the bond position that matches the pattern of excess charge density).

On Dental Occlusion and Saber Teeth

Jörg Fröbisch

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