Current Biology
Magazine

Primer

The Triassic

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The Triassic, lasting from 252 to 201 million years (Myr) ago, was crucial in the origin of modern ecosystems. It is the seventh of the 11 geological systems or periods into which the Phanerozoic, the fossiliferous last 540 million years, of Earth history is divided. It might seem strange to select just one of these divisions of time as somehow more significant than the others. However, this was the span of time during which all of the key modern vertebrate groups originated — the neoselachian sharks, neopterygian bony fishes, lissamphibians, turtles, lepidosaurs, crocodilomorphs, and mammals. If birds are theropod dinosaurs, which they are, then this clade also arose in the Triassic.

Further, in the seas there was a major remodelling of ecosystems and acceleration in evolution — the Mesozoic Marine Revolution. This was the time when new, voracious predators, such as neogastropods, malacostracan arthropods, neoselachians, and marine reptiles, became involved in arms races with their prey, the corals, bivalves, echinoids, and bony fishes.

In this primer, I explore a division of geological time that is seemingly remote, yet which documents a unique phase in the history of life. In doing so, some key methodological issues will be highlighted; improvements in rock dating and the fossil record, the use of large phylogenetic trees in the study of macroevolution, and how new methods allow palaeontologists to identify not only patterns, but also processes in the deep-time history of life.

Rock dating and the fossil record of the Triassic

In textbooks, the history of life is often painted against a backdrop of a rather vaguely dated rock record. However, in the past 20 years there has been a massive improvement in the quality of rock dating, and so geological time scales are much richer and more precisely dated than might have been thought possible a few years ago. This is thanks to improvements in radioisotopic dating, other methods of geochronometry, and international coordination in defining key time boundaries.

When Friedrich von Alberti named the Triassic (Figure 1A) in 1834, geologists had no inkling of the age of the Earth, other than that it was ancient. He applied the term ‘Triassic’ in recognition of the three obvious rock divisions visible in Germany, namely the Buntsandstein (terrestrial sandstones), Muschelkalk (marine limestones), and Keuper (terrestrial sandstones). After the discovery of radioactivity in 1896, Ernest Rutherford suggested in 1904 that radioactive decay might provide a metronome to estimate deep time, and the first rock dates were published by Arthur Holmes in 1913. Despite the technical difficulties, these early dates were actually close to modern values, but error bars were large. Until 1990, error bars on radioisotopic dates remained at the ±5% level, meaning that a date of, say, 200 Myr might be anything from 190–210 Myr. This is far from satisfactory for the study of evolutionary rates.

However, in the past 20 years, error bars on ancient dates have shrunk to fractions of 1%, so geologists now debate whether the Permian-Triassic mass extinction (detailed below) lasted for 60,000 or 180,000 years. The improvements in precision are a result of increasing care in rock sampling, technical improvements to mass spectrometers, and intensive cross matching of dates from the same rocks using different isotope series.

The quality of the fossil record is subject to constant debate and enquiry. In the past twenty years, extensive new information on the Triassic fossil record has come from China, Russia and South America, confirming known patterns and adding new information. In some cases, changes in fossil faunas and floras can be studied in increments of centimetres, representing time spans of tens or hundreds of thousands of years.

Triassic environments

In the Triassic, all continents were fused as the supercontinent Pangaea (Figure 1B). In the constant dance of the Earth’s tectonic plates, this phase of maximum fusion began in the Carboniferous, some 300 Myr ago, when Gondwana (modern South America, Africa, India, Antarctica, and Australia) moved north to join with Laurasia (modern North America, Europe, and Asia) and smaller plates comprising Siberia and parts of China to the east.

Triassic climates were warm and equable, with no polar icecaps. There was a broad arid belt extending over most of North and South America, Europe, and Africa. Towards the poles, warm temperate bands extended across Asiatic Russia in the north, and India, Australia and Antarctica in the south (Figure 1B). Marine organisms are represented by fossils from the Panthalassa and Tethys oceans, whereas terrestrial organisms are best known from the northern and southern temperate belts.

Pangaea began to break up near the end of the Triassic when massive volcanic eruptions in the Atlantic region — known as the Central Atlantic Magmatic Province — spewed massive volumes of basalt onto what is now the east coast of North America, parts of southwest Europe and northeast Africa. This magmatic activity was associated with the rifting of the North Atlantic Ocean, as North America rotated westward and Europe eastward. Later, in the Cretaceous some 100 Myr ago, the South Atlantic opened, South America and Africa drifted apart, and India, Australia and Antarctica began their stately progressions to their present locations.

The Permian-Triassic mass extinction (PTME)

The Triassic began with similarly massive basalt eruptions, this time in the Siberian Traps in eastern Russia. Volcanism in both the Siberian Traps and the Central Atlantic Magmatic Province produced millions of cubic kilometres of lava. Although the lava bubbled up through vents, just like with Icelandic volcanoes today, and did not erupt from pointed Plinian-type volcanoes, the impacts on life were no less devastating.

In volcanic eruptions, the lava flows are, of course, terrifying and kill all life in their path. Further, in explosive eruptions, the associated volcaniclastic flows — masses of ash and molten-rock bombs — can kill instantly. More significant, however, are the gases ejected from the volcanic vent during an eruption — primarily sulphur dioxide,

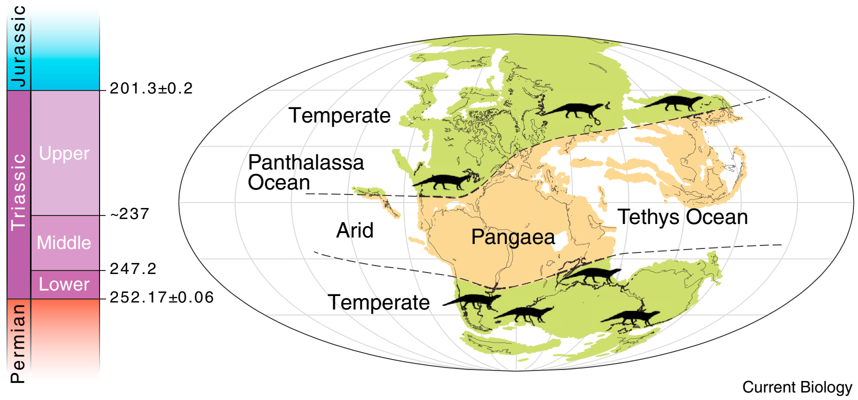

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Figure 1. Triassic time and place.
Left: The Triassic time scale spans some 50 Myr, separated by mass extinctions at the beginning and end. Right: Palaeogeographic map of the world in the Triassic, showing the major climatic belts, and especially the extent of the arid-climate 'dead zone' (beige) of the Early Triassic. Most organisms are found in the temperate zones (green). Map generated with the online palaeogeographic map generator at http://fossilworks.org/cgi-bin/bridge.pl?action=mapForm; image drafted by Simon Powell, ©University of Bristol.

carbon dioxide, and methane. The latter two are key greenhouse-warming gases, and isotopic evidence from rock sections spanning the Permian-Triassic boundary show that there was a flash heating episode when temperatures rose by some 15°C.

This global warming had numerous consequences. On land and in the sea, organisms either died or moved poleward, and the temperature increase raised tropical-sea temperatures to over 40°C. On land, the cocktail of volcanic gases not only caused warming, but also acid rain upon mixing with rainwater. The acid rain killed trees, and the loss of plant cover, in turn, released massive amounts of soil; comprehensive erosion over the land surface washed debris into the shallow seas. Further, the global warming pushed thermoclines down and disrupted ocean circulation. There is abundant evidence of worldwide oceanic anoxia.

The soil stripping on land, seabed anoxia, and sharp warming proved too much for life, and an estimated 90–95% of all species died out within years, or tens of years. This level of extinction, in which fewer than one in ten species survived, was unprecedented — no other mass extinction, even those that came later at the end of the Triassic and at the end of the Cretaceous, when the dinosaurs succumbed, was of such a magnitude.

Recovery

The significance of the Triassic in the history of life resides in the magnitude of the PTME. The event was so profound that ecosystems were entirely destroyed. In the case of other mass extinctions, it seems that at least some key taxa within many ecosystems survived; thus, empty niches were defined and could be filled, preserving in some cases the overall shape of the pre-extinction food web. Not so after the PTME.

There is no theory for recovery after mass extinction. Based on observations of ecological succession following local-scale destruction of ecosystems, it is expected that fast-breeding taxa will radiate fast and opportunistically. These in turn are overtaken by the core plants and animals that form the basis of the long-term ecosystem, which typically reconstructs itself from the bottom up — smaller plants, then larger plants, then herbivores, then carnivores.

The recovery from the PTME was perhaps slowed by the profundity of the extinction, but also by the fact that physical environments did not bounce back to normal. In fact, there were three additional global-warming shocks through the initial 6 Myr of the Triassic. These were of the same magnitude as the killing events at the Permian-Triassic boundary, and there is much debate about the geological driver. Nonetheless, this meant that fast-evolving species, such as foraminifera and ammonites in the oceans, which had bounced back to some extent, were further devastated, several times, until ocean-atmosphere systems settled back to normal 6 Myr after the PTME.

Punctuation of the history of life

Victorian palaeontologists observed a sharp change in the kinds of fossils between Permian and Triassic rocks. Indeed, this was the basis for the demarcation of the Palaeozoic ('ancient life') and Mesozoic ('middle life') eras. Much later, following the first substantial database compilations of the known fossil record, Jack Sepkoski famously distinguished a major shift in the global diversification of life across the Permian-Triassic boundary. In 1984, he noted this as a crisis point in which evolution was reset, and this was identified independently by Leigh Van Valen, also in 1984.

Both authors picked out the Permian-Triassic boundary as the single point over the past 540 Myr when the evolution of marine life had shifted from one state to another. Sepkoski discriminated the Palaeozoic Fauna from the Modern Fauna using the term 'Evolutionary Fauna' as a global, macroevolutionary term spanning hundreds of millions of years (Figure 2A). The Palaeozoic Fauna comprises brachiopods, rugose and tabulate corals, cephalopods, crinoids, starfish, ostracods, and graptolites, whereas the Modern Fauna comprises bivalves, gastropods, malacostracans, echinoids, bony fishes, sharks, and marine tetrapods.

The same analysis has not been done for terrestrial life, but the PTME was as much a marker of massive change in dominant plants and animals as well (Figure 2B). Among tetrapods, the temnospondyls, parareptiles, and synapsids of the late Palaeozoic gave way to lissamphibians, turtles, lepidosaurs (lizards and relatives), archosaurs (crocodiles, dinosaurs, birds, and relatives), and mammals. Among fishes, the hybodont sharks and others of the late Palaeozoic began to be replaced by neoselachians in the Triassic, and the thick-scaled basal bony fishes by neopterygians and later teleosts. Among insects, key modern groups, such as Diptera (flies), Trichoptera (caddisflies), Lepidoptera (butterflies and moths), and

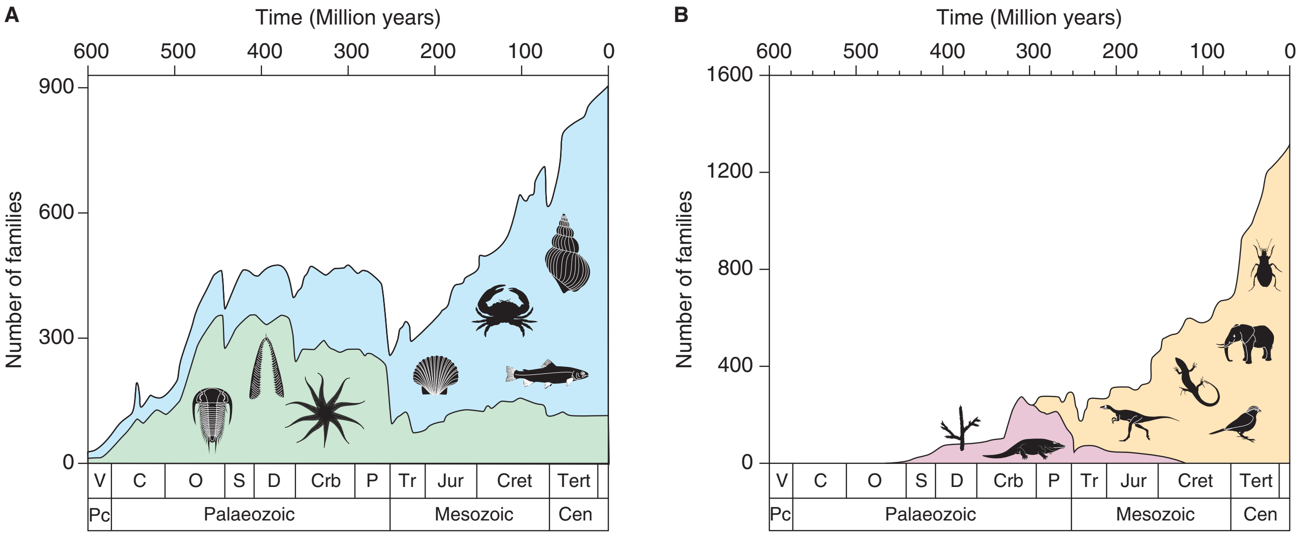

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Figure 2. Palaeozoic life was replaced by Modern evolutionary faunas during the Triassic.
The plots show time series of diversity counts for families of marine (A) and terrestrial (B) life. Green and pink areas represent Palaeozoic fauna that were decimated by the PTME. So-called 'modern' plants and animals (blue and beige) appeared in the Palaeozoic, but remained at low diversity until the PTME largely wiped them out. The modern groups, such as bivalves, gastropods, crustaceans, and bony fishes in the sea (A) and dinosaurs, lepidosaurs, beetles, mammals and birds on land (B) built new ecosystems that persist to the present. V, Vendian; C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; Crb, Carboniferous; P, Permian; Tr, Triassic; Jur, Jurassic; Cret, Cretaceous; Tert, Tertiary; Pc, Precambrian; Cen, Cenozoic. (Graphs from Sepkoski, 1984 and Benton, 1995; silhouettes of organisms based on various sources; image drafted by Simon Powell, ©University of Bristol.)

Hymenoptera (bees, wasps, and ants) all arose in the Late Triassic; Coleoptera (beetles) and Neuroptera (lacewings) showed substantial expansions at this time. These key insect clades now comprise the bulk of modern biodiversity, and all can be tracked back to Triassic origins.

The differentiation of plants through this time is less clear, as it appears that most major groups survived through the PTME; however, key new seed ferns and conifers expanded in the Triassic. In fact, for plants, arguably the main transition to modern floras happened in the Cretaceous with the rise of the flowering plants — the angiosperms. These served as a key driver of the Cretaceous Terrestrial Revolution, when insects that ate and pollinated the new plants massively expanded in diversity, as too did their predators, the spiders, lizards, birds, and mammals.

In Triassic seas

Many of the seabed invertebrates of the Palaeozoic survived into the Triassic, but the brachiopods, cephalopods, crinoids, starfish, and ostracods had been massively depleted, and the rugose and tabulate corals, trilobites, and graptolites entirely wiped out. Importantly, other survivors, such as bivalves and gastropods, recovered and diversified substantially. These shelled organisms were more versatile than the brachiopods, as they were capable of burrowing (bivalves, echinoids), attaching to rocks (oysters), moving freely over the seabed (gastropods), or even swimming (scallops).

Most devastating of all was the loss of corals; without them, there were no reefs, and the so-called 'coral gap' persisted for some 10 Myr of the Early and Middle Triassic until the first of the modern scleractinian corals emerged.

The other main seabed animals to expand after the PTME included new groups of rather voracious hunters: the predatory gastropods, with their ability to drill holes in the shells of their prey; the malacostracans, such as lobsters and crabs that could snip through hard skeletons; shell-crushing bony fishes and placodonts; and fast-swimming predatory neoselachian sharks and marine reptiles. These new predators stimulated an array of avoidance behaviours among prey animals, such as burrowing or fast swimming, or thickened shells to resist attack.

This is a classic evolutionary arms race, in which predator and prey evolve their feeding and defensive strategies in lockstep, and was termed the Mesozoic Marine Revolution by Geerat Vermeij in 1977. The Mesozoic Marine Revolution was once posited to have begun in the Jurassic or Cretaceous, but it seems it began in the Middle Triassic, when exceptional faunas, such as those from Luoping in southwest China (Figure 3), show many of the new predators already in existence and building their grip on shallow marine ecosystems.

On land — the coming of the dinosaurs

On land, many plant groups, insects, and some tetrapods (such as the crocodile-like temnospondyl amphibians and the small procolophonid reptiles) survived the PTME. However, the landscape of the earliest Triassic had been devastated by massive loss of plants and erosion of soil. Indeed, there was a 'coal gap' on land, a time of some 10 Myr when no coals were deposited worldwide, indicating the absence of forests. The loss of forests on land, like the loss of coral reefs in shallow seas, must have massively affected the potential for biodiversity to recover.

After 6 Myr, new groups emerged. Notably, some of the previously

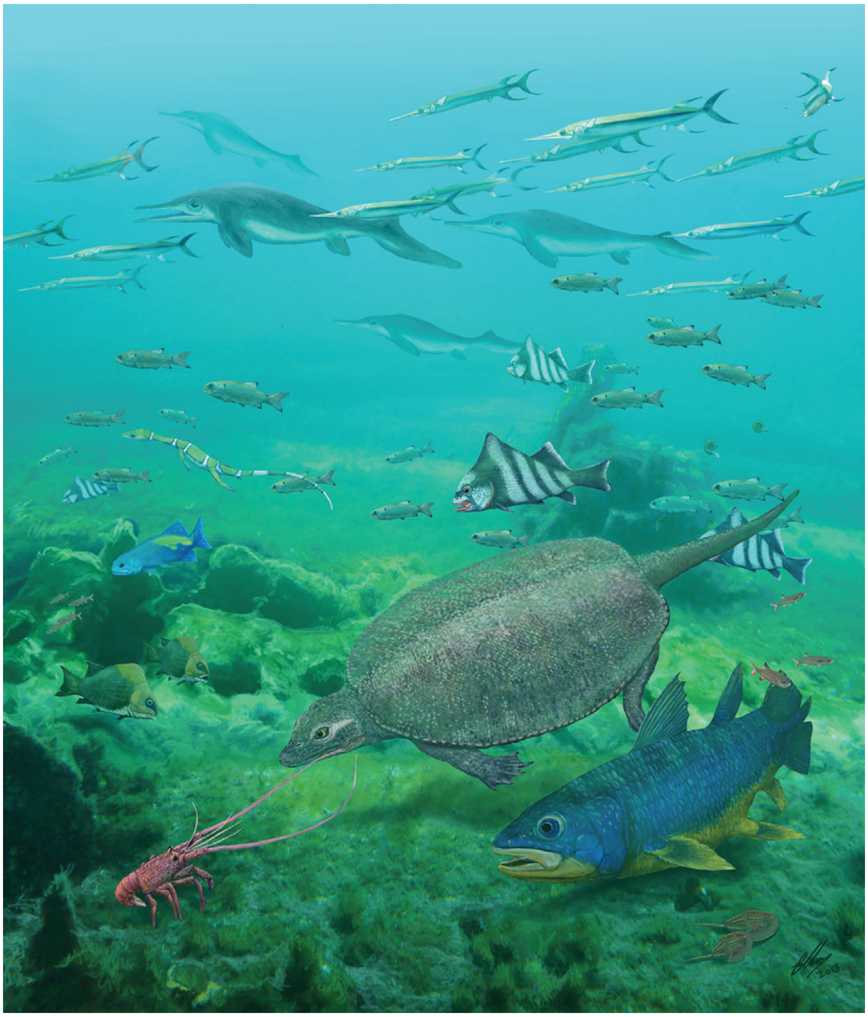

Figure 3. Lobster lunch of Luoping.
The ‘modern’ animals of a muddy seabed during the Middle Triassic at Luoping in southwest China. In the foreground, an early rock lobster (*Yunnanopalinura schrami*) attracts the unwanted attention of the coelacanth *Luopingcoelacanthus eurylacrimalis* and the armoured reptile *Sinosaurosphargis yunguiensis*, allowing a pair of horseshoe crabs (*Yunnanolimulus luopingensis*) to scuttle away unnoticed. Behind them cruise other aquatic reptiles: the ichthyosaurs *Mixosaurus* cf. *panxianensis* and the little pachypleurosaur *Dianopachysaurus dingi*. Swarming around is a diverse community of actinopterygians: ubiquitous *Sangiorgioichthys sui* (numerous fish with black-tipped fins), sleek *Sinosaurichthys longimedialis* (thin with long snout), tiny *Marcopoloichthys ani* (very small with red-spotted fins), scaleless *Gymnoichthys inopinatus* (blue with yellow back) and the deep-bodied *Kyphosichthys grandei* (brown and yellow) and *Luoxiongichthys hyperdorsalis* (black and white). Painting by Brian Choo © 2013.

dominant tetrapod groups, such as dicynodonts, rebounded and became abundant. Most importantly, the archosaurs diversified; these today include crocodiles and birds, and they arose at the very end of the Permian. Archosaurs benefitted from the emptied Early Triassic world, diversifying first as fish and flesh-eaters, and then adding herbivorous groups during the Triassic.

Until recently, the earliest, relatively abundant, skeletons of dinosaurs were known from South American rocks dating to about 230 Myr ago. New fossil evidence, however, extends the earliest dinosaur records back to the beginning of the Middle Triassic, within 7–8 Myr of the mass extinction, and so the origin of dinosaurs can be tied to the trigger of a great mass extinction event, just as can their eventual demise 66 Myr ago.

On land too, the first frogs, turtles, rhynchocephalians (ancestors of the living tuatara, and close relatives of lizards), crocodilomorphs, and mammals all appeared around the middle of the Triassic.

Models of macroevolution

These narratives of the recovery of life say little about the processes involved. Now, new methods of ecosystem analysis, morphometrics, and phylogenetic comparative methods have allowed hypotheses of pattern and process to be assessed.

Peter Roopnarine and Ken Angielczyk have analysed terrestrial ecosystems through the PTME, and they find that Late Permian and Middle Triassic ecosystems were relatively stable, whereas the earliest Triassic communities were not. Their method involves analysis of reconstructed food webs with relative biomass information, and iterated many times to account for uncertainties. Stability is assessed by randomly removing taxa and exploring the consequences. The method allows forensic analysis of the nature of ecosystem collapse and rebuilding in deep-time examples.

Morphometric studies have been deployed widely in exploring recovery from the PTME. For example, Marcello Ruta and colleagues showed that the herbivorous dicynodonts passed through a macroevolutionary bottleneck. They had been diverse in species numbers and in morphology before the event, and then were reduced to only three or four surviving lineages. After 6 Myr, dicynodont species richness recovered, but their disparity (that is, morphological diversity) never recovered to pre-extinction levels. In other such studies, diversity and disparity are nearly always decoupled, with disparity usually leading diversity, except in the case of ammonoids, for which species richness rose rapidly in the Early Triassic, but disparity flat-lined.

Phylogenetic comparative methods are being ever more widely applied to deep-time questions in macroevolution; for example, to detect times of unusually fast or slow evolution, or to fit models of evolution. In the case of the origin of dinosaurs, a number of these studies have been reported, some showing, for example, that most of the key steps in dinosaurian evolution happened early in their history, in the Late Triassic and Early Jurassic.

After that, they were coasting, or even slowing down, in terms of the turnover of species origins and extinctions.

There was a long-held assumption that dinosaurs rose to prominence through a process of large-scale competition, in which they actively expanded their ecospace at the expense of other Triassic tetrapods, such as the synapsids (mammal-like reptiles including dicynodonts) and crurotarsan archosaurs. In a macroevolutionary exploration of dinosaurian origins, Steve Brusatte and colleagues found that dinosaurs expanded in diversity and disparity through the Late Triassic. However, the diversity and disparity of their supposedly inferior competitors, the crurotarsans, were increasing at about the same rate. After the Crurotarsi largely died out during the mass extinction at the end of the Triassic, the dinosaurs diversified a little, but did not expand their morphospace substantially.

The conclusion that dinosaurs emerged without making a major impact on their supposed competitors was confirmed in a phylogenetic comparative study by Roland Sookias and colleagues, who explored changing body size through time. In a phylogenetic context, the shrinking mean size of the synapsids and the increasing mean size of the archosaurs and relatives both followed Brownian-Motion models. This means the rates of change cannot be distinguished from random walks, and hence evolution is described as 'passive' rather than 'active'. Dinosaurs likely originated opportunistically, following extinction events, rather than by active replacement of competitors.

Conclusion

Of all the geological periods, the Triassic stands out as unusual in that it serves to document recovery from the largest of all mass extinctions. This massive punctuation in the history of life marked the origin of modern ecosystems. Documentation of the fossil record of the Triassic has improved tremendously thanks to astonishing new discoveries from China. Further, the accuracy and precision of dating and correlation worldwide have improved enormously. Geologists are also able to reconstruct ancient continental distributions, climates, and atmosphere–ocean biogeochemical cycles with confidence. Future work will concentrate on filling gaps and extending fossil ranges. Methods of discovering and dating phylogenetic trees will continue to improve, and computational methods of exploring these patterns to derive models in macroevolution mark a rich opportunity for new research.

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Unsupervised statistical learning in newly hatched chicks

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The ability to extract probabilistic information from visual inputs has been reported in human adults and infants (reviewed in [1,2]), and in adults of non-human species, though only under supervised (conditioning) procedures [3]. Here, we report spontaneous sensitivity to the probabilistic structure underlying sequences of visual stimuli in newly hatched domestic chicks using filial imprinting, suggesting that statistical learning may be fully operating at the onset of life in precocial avian species.

We exposed visually naive, newly hatched chicks to a stream of four shapes for 2 hours. Shapes were presented one at a time in the centre of a computer screen. The order was defined by transitional probabilities (TPs) within/between shape-pairs. Each shape was presented for two seconds and loomed from 2 to 10 cm in height in a continuous loop (see Supplemental Information for details). The familiar sequence consisted of two shape-pairs defined by statistical dependencies within and between pairs' elements. For instance (Figure 1A left), Pair 1 consisted of a *square* always followed by an *X-shape* (TP within-pair = 1.0) and Pair 2 consisted of a *circle* always followed by a *triangle* (TP within-pair = 1.0). Because there were no pauses between pairs, the only cue available to segment the stream was the statistical structure of the sequence (TP between pairs = 0.5).

The apparatus consisted of two identical computer screens placed at the opposite ends of a runway, simultaneously playing the two test sequences (Figure 1B; see Supplemental Information for details). The chicks' behaviour was recorded for six consecutive minutes by a camera placed above the apparatus.

In Experiment 1, the test stimuli consisted of the familiar stream and an unfamiliar stream: a semi-random