by the Press would make higher donations to charity when observed than when not observed. In contrast, in this experiment, autistic people did not show hypocrisy; they did not vary their donations in relation to whether an observer was present or not. This is as would be predicted from if they lacked mentalizing.

While mentalising was initially tested solely in terms of explicit tests, such as the 'Sally-Anne' task [9], which children can pass from about age five, it is now known that the spontaneous and automatic ability to mentalize is present even in infants under one year old [10]. Furthermore, in its automatic form, as assessed by involuntary eye gaze, it is absent even in able autistic adults [11]. Interestingly, this absence does not preclude the acquisition of an explicit 'Theory of Mind'. Many able autistic adults can pass explicit tests, but their ability to use mentalizing in an implicit form has rarely been tested. Given this updated account of mindblindness in autism as a lack of implicit mentalizing, we would like to suggest that the hypocrisy revealed by Izuma *et al.* [1] in ordinary participants was implicit. However, it remains to be seen whether this is the case.

In a second task, Izuma *et al.* [1] investigated whether autistic people would be subject to the audience effect when this did not involve mentalizing. The audience effect is associated with facilitation of performance on a moderately easy task by the mere presence of others, via an increase in arousal [12]. The authors chose the Continuous Performance Task: this task is attention demanding, but easy to perform. Here, there was an audience effect, an increase in performance when an observer was present, not only in the control group, but also in the autistic group. This is an important finding, as it rules out that the autistic participants were simply not affected by the presence of others. This is consistent with anecdotal observations that people with autism spectrum disorder (ASD) enjoy the attention they get from others when displaying their special talents.

Our desire for a good reputation is not only seen in admirable and apparently altruistic behaviour when observed, but also in selfish behaviour when not observed. It would therefore be predicted that in situations where a benefit can be obtained by cheating when unobserved, autistic people would not cheat. Thus the present study reinforces the belief that people with ASD are transparently trustworthy. This reminds us of the possibility that before autism was recognised some affected individuals were probably venerated as saints and as blessed fools [13].

What would autistic people do under more explicit conditions? Might this rob them of their sainthood? The updated version of the mindblindness account is that there is a deficit only in spontaneous mentalizing. We would predict that people who have acquired an explicit Theory of Mind and can use mental states to explain and justify behaviour would be amenable to being taught about reputation management. They might be induced to donate more generously in the presence of an observer if told in advance about possible benefits in terms of applause and attention. This is not a very subtle strategy and the increased donation would be an instrumental act rather than a clever form of reputation management. However, if this sort of explicit teaching worked and was widely applied, then perhaps the novel test provided by Izuma and colleagues would no longer be able to differentiate autistic and neurotypical groups.

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Plant Evolution: Pulses of Extinction and Speciation in Gymnosperm Diversity

Living gymnosperms represent the survivors of ancient seed plant lineages whose fossil record reaches back 270 million years. Two recent studies find that recent pulses of extinction and speciation have shaped today's gymnosperm diversity, contradicting the widespread assumption that gymnosperms have remained largely unchanged for tens of millions of years.

Charles C. Davis*
and Hanno Schaefer

Gymnosperms are a group of woody seed plants that includes conifers, cycads, ginkgos, and the lesser-known gnetophytes (Figure 1). These plants are of huge economic importance, especially for their timber and horticultural value. Their name means

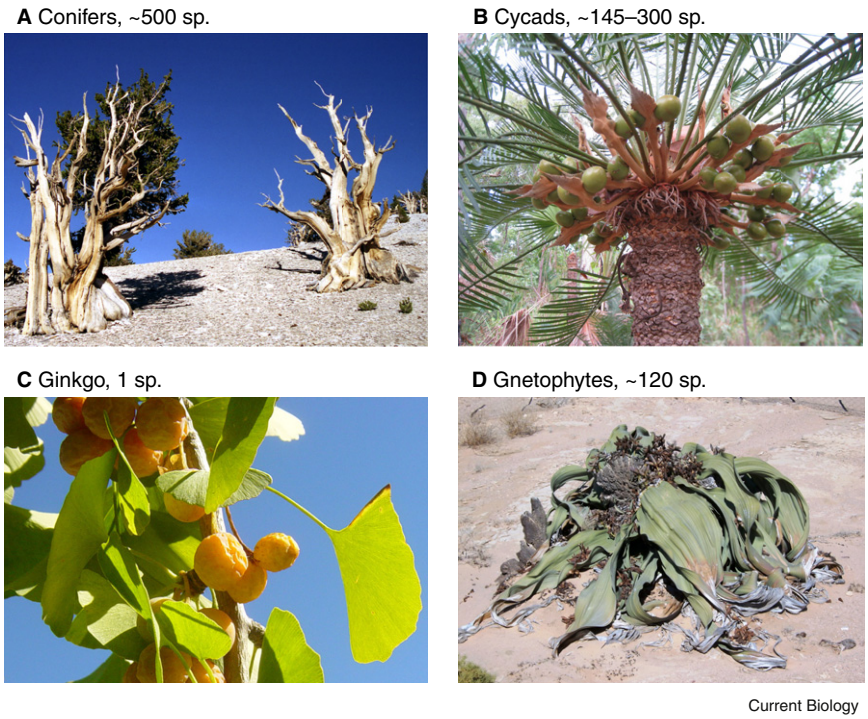

Figure 1. Living representatives of the major gymnosperm lineages with extant species.
(A) Conifers (bristlecone pine, *Pinus longaeva*), (B) cycads (Armstrong's cycad, *Cycas armstrongii*), (C) ginkgo (*Ginkgo biloba*), and (D) gnetophytes (*Welwitschia mirabilis*). Images copyright J. Gordon, J. Tann, M. LaBar, and P. Kosina, respectively.

'naked seed', and refers to one of their defining features — the seed is not borne in a carpel, the protective structure that is a hallmark of their close relatives, the flowering plants (angiosperms). The evolutionary history of gymnosperms traces back tens of millions of years, and these plants reached their dominance when non-avian dinosaurs roamed the Earth. Today's gymnosperms, however, are but a shadow of their former glory — only 850 to 1,000 species presently inhabit our planet. Scientists have long assumed that much of the living gymnosperm diversity is relictual, representing the last remnants of their formidable past. This assumption is due in part to the fact that the overall morphology of numerous living species, including the charismatic ginkgo, dawn redwood, and *Wollemia* pine, has remained similar for millions of years. Two recent phylogenetic studies [1,2], published in *New Phytologist* and *Science,* challenge this view, however, and instead paint a very different picture of the tempo and mode of gymnosperm diversification. What emerges is a history of gymnosperms characterized by pulses of recent extinction and surprisingly recent bursts of speciation of today's living descendants.

The two studies used very different, but complementary, approaches to shed light on the evolutionary history of the gymnosperms. Crisp and Cook [1] sampled species broadly to include representatives of all living gymnosperm lineages. In contrast, Nagalingum *et al.* [2] sampled maximally within a single lineage, the cycads (Figure 1), which include 145–300 species [3,4] distributed in tropical and subtropical regions around the world. Both studies assembled DNA sequence data and estimated divergence times using fossil-calibrated phylogenies. Crisp and Cook [1] additionally assessed speciation and extinction patterns during the Cenozoic (65 million years ago (Ma) to the present). Estimating extinction rates from living diversity alone is controversial [5]. To alleviate these concerns, Crisp and Cook [1] integrated the fossil record to assess the relative roles of extinction and speciation for gymnosperms versus angiosperms. This integration then allowed them to determine whether the great disparity between living gymnosperm and angiosperm species diversity can be explained primarily by extinction in gymnosperms or whether lower speciation rates are also implicated in this pattern. Nagalingum *et al.* [2], in contrast, avoided estimating extinction rates, arguing that the more recent cycad fossil record is too imperfectly known.

Both studies demonstrate that the living gymnosperms are not relicts, so-called 'living fossils', but are instead recent. In their global analysis, Crisp and Cook [1] found that most Cenozoic crown group gymnosperms are significantly younger than their angiosperm counterparts (median age ~32 Ma (Oligocene) versus ~50 Ma (Eocene)). The more taxonomically focused study by Nagalingum *et al.* [2] corroborates these findings. They found that crown group diversifications in all five major cycad clades occurred between around 5 and 10 Ma (Figure 2). Their cycad phylogeny is characterized by very long internal branches juxtaposed against very short tips. Thus, the phylogeny resembles a coppiced sycamore — a tree with long stems and shallow, bushy crowns. These findings, combined with numerous recent molecular divergence time studies for gymnosperms, including *Agathis* [6], *Cedrus* [7], *Ephedra* [8], *Gnetum* [9], *Juniperus* [10], *Phyllocladus* [11], *Pinus* [12], Podocarpaceae [13], and *Pseudotsuga* [14], paint a new picture of living gymnosperms that is characterized by their origin on a more recent landscape. What distinguishes the study by Crisp and Cook [1] is their global analysis of extinction and its influence on gymnosperm diversity. What distinguishes the study by Nagalingum *et al.* [2] is not that they found recent origins of crown group cycads — similar divergence time estimates for cycads had been reported previously [15] — but rather that all major cycad subclades are found to exhibit nearly simultaneous diversification on separate continents.

These studies point toward a pattern of major extinction and speciation pulses in gymnosperms beginning around the end of the Eocene (~35 Ma). One major factor that may have triggered these phenomena is global climate change. Gymnosperms probably occupied warmer, wetter, aseasonal environments for much of their early evolution [16]. The end of the Eocene, however, marked a major shift

in the terrestrial environment that left the world much cooler, drier, and more seasonal [17]. Crisp and Cook [1] identified that living gymnosperm diversity can be best explained by the exceptionally high rates of extinction, perhaps due to this cooling, and not by lower speciation rates. Angiosperms, it appears, were more resistant to extinction during this time [18]. Crisp and Cook [1] did not assess earlier pulses of extinction, but a comprehensive assessment of the Southern Hemisphere gymnosperm fossil record points toward climate change during the recent Neogene (23–2.5 Ma), especially drying and cooling at mid latitudes, as the driving factor leading to the more restricted present-day distribution and diversity of cycads [16]. All of these data suggest that the declines in cycad diversity may have also been strongest during the Cenozoic, and not during earlier time periods.

At the same time, these climatic changes may have triggered pulses of diversification among the lucky survivors. The available divergence time estimates across multiple clades, however, are not as conclusive about the contemporaneous nature of their diversification. Nagalingum *et al.* [2] suggest that the diversification of major crown group cycads occurred between around 5 and 10 Ma. These age estimates have wide confidence intervals (around 10 million years), and furthermore, their diversification rate plots suggest multiple pulses of diversification within this window (Figure 2). For example, the large genus *Encephalartos* peaks in diversification around 10 Ma whereas *Ceratozamia* peaks at around 5 Ma. Given the nearly 300 million year history of cycads, these radiations might still be considered contemporaneous, but on closer inspection they may be the result of different triggers, perhaps continent-specific climate change or coevolution with weevil or thrips pollinators [19]. Additionally, the crown group age estimates for cycads in the Crisp and Cook study [1] are much older and range from 10 to 50 million years. Although their cycad taxon sampling is not nearly as rich, increasing this sampling is bound to push the crown group ages even further into the distant past. The major difference between these two analyses is in the interpretation and placement of the fossils used to constrain their molecular divergence time estimates. Nagalingum *et al.* [2] placed the oldest known cycad fossil, *Crossozamia* (~270 million years old), at the stem node of the cycad lineage, whereas Crisp and Cook [1] followed earlier recommendations by Hermsen *et al.* [20] and placed it at the crown node. Similarly, Nagalingum *et al.* [2] assigned two Eocene-aged cycad fossils to the respective stem group nodes of the genera *Lepidozamia* and *Bowenia*, while Crisp and Cook [1] placed these fossils in the crown nodes. The approach of Nagalingum *et al.* [2] biases the estimated cycad crown ages to be younger, while the approach of Crisp and Cook [1] biases the estimated ages to be older. The truth is likely to be somewhere in between, and these differences demonstrate the need for a better integration of the fossil record to improve our understanding of the tempo and mode of diversification in the gymnosperm tree of life. Such analyses will also depend on a profound understanding of the morphology of both extant and fossil gymnosperms. Only then will we be able to assess phylogenetic and biogeographical affinities, evolutionary transitions, and diversification patterns in this charismatic and important group of plants.

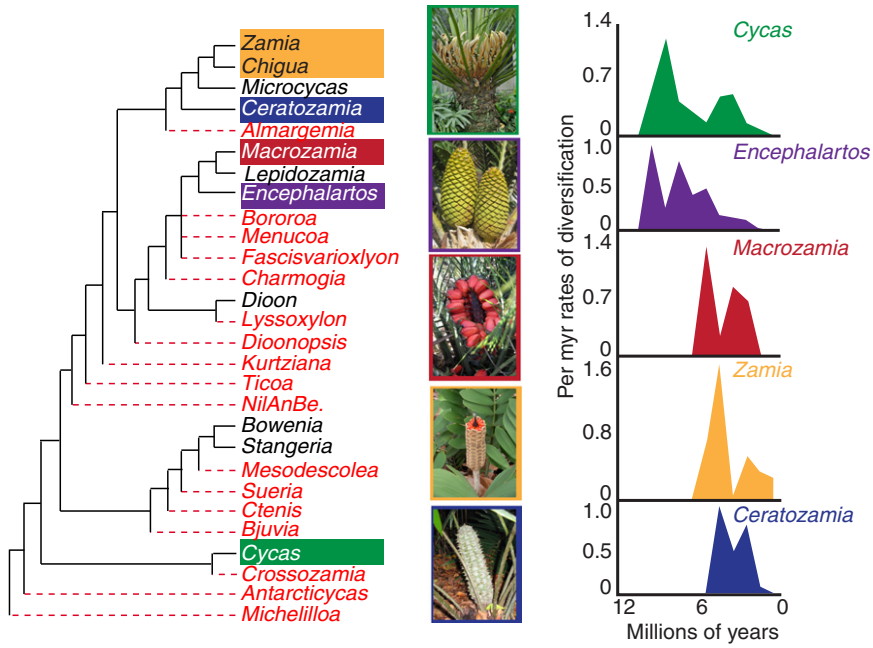

Figure 2. Phylogeny of cycads.

Living (black) and extinct (red) lineages are shown. Diversification rates through time plots of main cycad lineages are redrawn from [2] and color-coded. Pictures representing all major genera shown. Images copyright from top to bottom, G. Shepherd, T. Rulkens, D. Fletcher, M. Lundy and W. Atkinson. Phylogeny adapted from [20].

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Chemoreception: Identifying Friends and Foes

The vomeronasal organ detects chemical cues that trigger sexual, aggressive and defensive behaviors. An *in situ* hybridization analysis has identified the specificities of nearly a hundred VNO receptors and elucidated the logic by which they encode these cues.

Tong-Wey Koh and John R. Carlson

In his seminal essay 'The Hedgehog and the Fox', Sir Isaiah Berlin divided thinkers into two categories. Plato, Pascal, and Dostoevsky are like hedgehogs, which 'know one big thing', whereas Aristotle, Montaigne, and Goethe are like foxes, which 'know many things'. While Berlin later revealed that he had intended this celebrated distinction as a kind of game, the ability to distinguish hedgehogs and foxes is not a game for mice. It can mean the difference between life and death. A remarkable new study by Catherine Dulac and colleagues [1] has provided new insight into the molecular mechanisms by which mice make such distinctions.

How do mice identify the presence of animals that pose a threat, and of those that present opportunities for food or reproduction? Animals can be identified on the basis of pheromones (conspecific cues) or kairomones (heterospecific cues that benefit the recipient) [2]. The vomeronasal organ (VNO) is exquisitely sensitive to pheromones, containing neurons that are narrowly tuned to specific ligands [3]. Genetic or surgical disruption of VNO function in mice leads to profound but specific alterations of social behaviors [4]. The VNO acts in the sensing of individual differences, sex and the physiological status of conspecifics, in addition to the detection of kairomones from predators [5–7].

The VNO expresses more than 250 putative chemoreceptors. Most of these receptors belong to two families of heterotrimeric G-protein-coupled receptors, the V1Rs and the V2Rs [8–12]. V1Rs and V2Rs are thought to be expressed in a one receptor–one neuron pattern, with the exception of the broadly -expressed V2R2 clade [13,14]. Expression of V1R and V2R members are spatially segregated, with V1Rs expressed in the apical layer of the VNO neuroepithelium and V2Rs in the basal layer.

For only a very few of these receptors have ligands been previously identified. Efforts to map ligands to VNO receptors have focused on a single receptor or a single ligand [15,16]. Isogai *et al.* [1], in a *tour de force*, systematically characterized the functional specificities of nearly a hundred VNO receptors [1]. To accomplish this, they first improved an existing method of detecting VNO responses. Immediate early genes are induced in vomeronasal neurons by chemical cues. Isogai *et al.* [1] screened a panel of immediate early genes in the VNO of female mice that had been exposed to bedding used by male mice. One gene, *Egr1,* was found to be induced particularly strongly. *Egr1* induction was confirmed to reflect neuronal activation, as determined by calcium imaging and patch-clamp electrophysiology. Thus, by performing double labeling with *Egr1* and VNO receptor probes, it was possible to detect the activation of neurons expressing particular receptors by particular chemical cues.

Mice were exposed to a panel of ~30 chemical cues, including conspecific scents derived from the same or opposite sex, and heterospecific scents representing predators, prey, or neutral species. The heterospecific cues were derived from: mammalian predators, including foxes, ferrets, and bobcats; avian predators, including hawks and owls; reptilian predators, including snakes and alligators; potential prey, represented by insect larvae; related rodents that are sympatric with the wild ancestors of laboratory mice; and presumably neutral species such as woodchucks. Using probes that target 139 VNO receptors, Isogai *et al.* [1] were able to identify 88 receptors (56 V1Rs and 32 V2Rs) that responded to subsets of this panel of animal scents.

Isogai *et al.* [1] found that 28 receptors responded to mouse cues, and 26 of these responded to sex-specific cues. Some receptors were activated by female-specific cues in both males and females, while other receptors were activated by female-specific cues only in males. Some receptors responded to