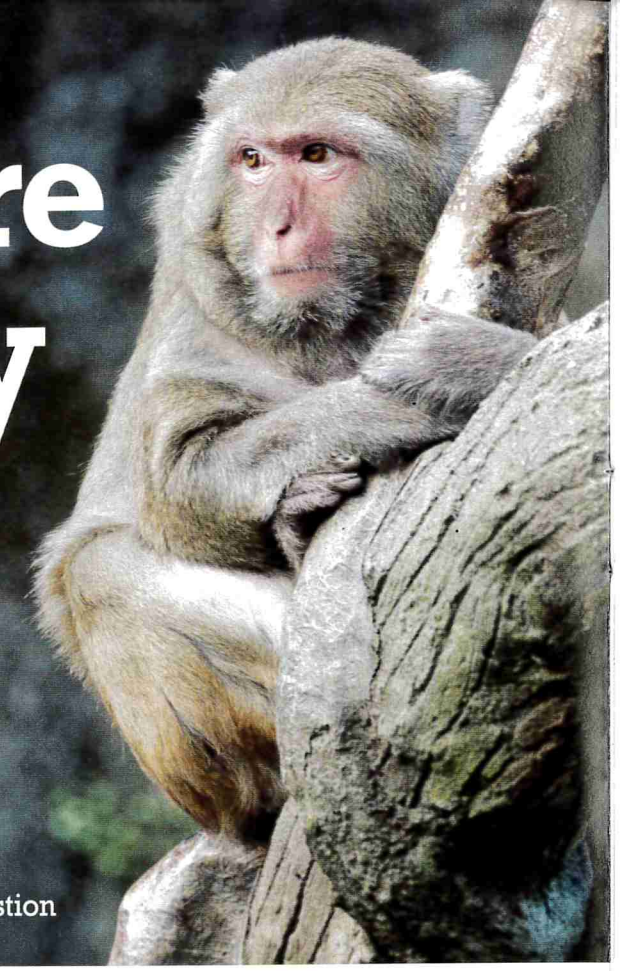
The measure of a monkey

Speciation and hybrids



Duncan Wright

What can the evolution of two macaque species tell us about speciation? Science writer Duncan Wright examines this question

AQA: 3.4.4 Genetic diversity and adaptation; 3.4.5 Species and taxonomy; 3.7.3 Evolution may lead to speciation

Edexcel A: 4.4 Natural selection can lead to adaptation; 4.6(i) Species concept; 5.19 Allopatric and sympatric speciation

Edexcel B: 3.1 Classification; 3.2 Natural selection

OCR A: 4.2.2 Classification and evolution; 6.1.2(g) Allopatric and sympatric speciation

OCR B: 3.1.3 The development of species; 5.1.2(e) Geographical and reproductive isolation

WJEC Eduqas: 2.2.1(f) The concept of species; 2.2.6(i) Isolation and speciation

Key words

Speciation
Vicariance
Hybridisation
Reproductive isolation

At last! After an hour's hike up the Tianmu Historic Trail in the unforgiving Taiwanese heat, I'd found them. To the left of the trail, on a raised patch of earth overlooking a sheer drop down the mountain, was a group of infant Formosan rock macaques. I crept forward to try to get a better shot with my camera, when suddenly — whump! The space between me and the infants was now occupied by an imposing male macaque, and the quiet mountain was suddenly filled with the sound of monkey chatter. Outmanoeuvred and out of my natural habitat, I began to think perhaps I had made a mistake. Eager to avoid a face full of macaque teeth, I broke eye contact and started to step slowly away, backwards. I didn't get my photo, but at least my face was still intact.

The Formosan rock macaque (*Macaca cyclopis*) is one of two primate species native to Taiwan, the other species being humans. Rock macaques primarily inhabit mountainous regions, where they forage for plant matter, insects and small vertebrates. Much like a hamster, the macaques store food in cheek pouches for later consumption. They are closely related to both rhesus macaques (*Macaca mulatta*), after which the Rhesus blood group is named, and Japanese macaques (*Macaca fuscata*).

Allopatric speciation

While rhesus macaques are broadly distributed across the Asian mainland, both Formosan rock macaques and Japanese macaques are **insular species**, restricted to Taiwan and the Japanese islands, respectively. How did these non-seafaring animals find themselves confined to these islands? The answer lies in their DNA and the Earth's history.

Taiwan and Japan have not always been islands: lower sea levels during **glacial periods** meant that Taiwan and Japan were connected to the mainland by **land bridges**. Comparison of **mitochondrial DNA** implies that an ancestral rhesus macaque population split between 380 000 and 440 000 years ago, and suggests that rhesus macaques migrated to Taiwan and Japan. A subsequent rise in sea levels cut off these islands from the mainland, causing the resident macaques to become isolated from the rest of the gene pool.

These island macaques evolved to become separate species with distinct physical characteristics. Japanese macaques have stumpy tails and distinctive red faces, while Formosan rock macaques have long tails and less colourful faces.

Terms explained

Allele A variant of a given gene.

Allopatric speciation The process whereby new species evolve from geographically isolated populations of a single species.

Courtship Behaviour and rituals used to attract a mate.

Gene flow The transfer of genes from one population to another.

Glacial period A time period associated with glacial advance.

Insular species A species with an island distribution.

Land bridge A connecting strip of land between two larger land areas.

Mitochondrial DNA The 16 569 bp of circular DNA found in mitochondria, encoding 37 genes.

Japanese macaques, famous for their enjoyment of hot springs, relaxing in Onsen Jigokudan Park, 130 km northwest of Tokyo

The emergence of these species is an example of **allopatric speciation**. The first step in this process is the geographical isolation (also known as vicariance) of populations of the same species. In our example, the macaques were isolated by rising sea levels. The isolated populations are unable to breed with one another, and there is thus no exchange of genetic material between them (i.e. there is no **gene flow**). The populations then slowly undergo genetic divergence, through various mechanisms (see Box 1). The gradual accumulation of genetic changes may ultimately result in reproductive isolation, meaning that, were the two populations to encounter one another again, they would be unable to exchange genes (see Figure 1). Reproductive isolation can be caused by several factors, as shown in Box 2.

Box 1 Genetic divergence

The gene pools of isolated populations can diverge through the following processes.

- Mutation: random genetic mutations occur in each population, resulting in distinct gene pools. Some of these mutations do not affect an organism's ability to survive and reproduce (they are 'neutral') but may still be passed on by chance (see 'genetic drift' below).
- Natural selection: other mutations may enhance an organism's ability to reproduce in a particular environment. Organisms with such mutations are thus more likely to pass their favourable **alleles** of genes to more offspring. For example, mutations that increase the chance of survival in Taiwan's subtropical heat would be more likely to be retained in Formosan rock macaques.
- Genetic drift: it is not always the fittest organisms that survive and pass on their genes — there is also an element of chance involved. If organisms fail to mate through bad luck (say, an encounter with a human hunter), their alleles may be lost from the gene pool. Such a random change in the frequencies of alleles is called genetic drift.

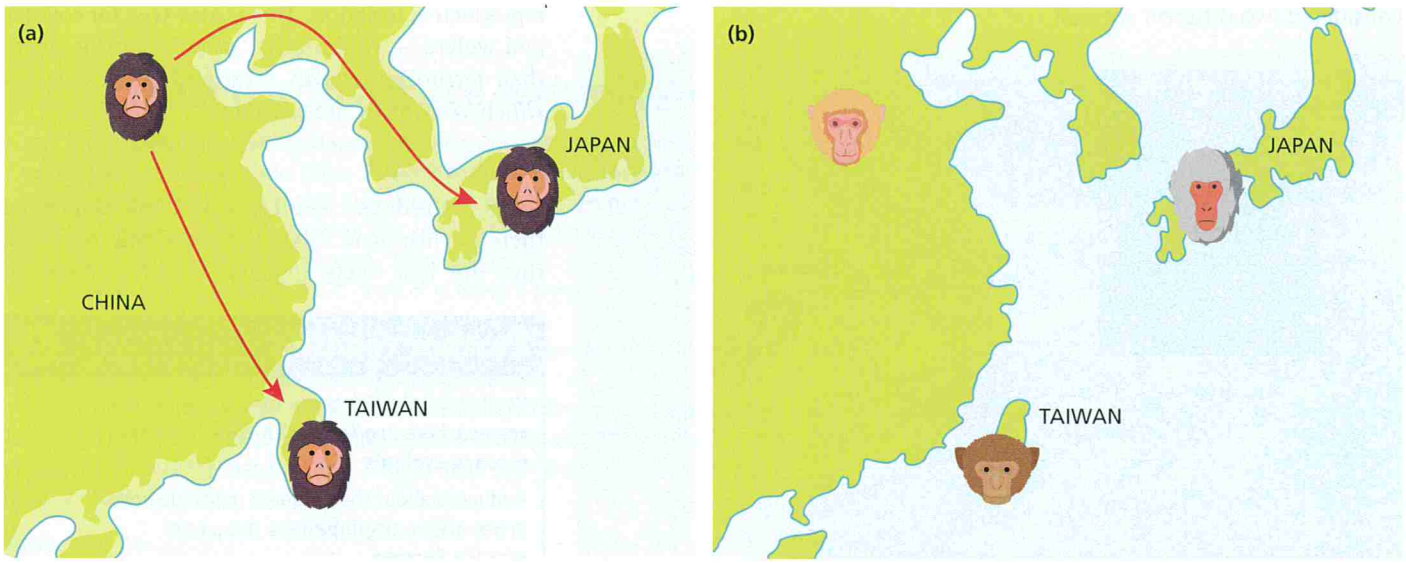


Figure 1 Speciation in macaques. **(a)** During earlier glacial periods, rhesus macaques migrated from the Asian mainland to Taiwan and Japan via land bridges. **(b)** Taiwan and Japan later became islands, isolating their resident macaque populations from the wider population. Subsequent genetic divergence caused distinct species to form in Taiwan, Japan and continental Asia

Formosan rock macaque in Taipei, Taiwan. Formosan rock macaques have long tails and less colourful faces than Japanese macaques, which have stumpy tails and distinctive red faces (see page 11)

Hybridisation

Although Formosan rock macaques can swim, it is unlikely they would have the stamina to swim over 1000 kilometres from Taiwan to Japan. Even if a macaque clung on to a piece of wood that was washed out to sea, and that wood just happened to float all the way to Japan, the macaque would be unlikely to find enough food to survive in the open ocean. The bottom line is that Formosan rock macaques and Japanese macaques would probably not have encountered one another had it not been for human intervention.

Formosan rock macaques were taken to zoos and research centres in Japan and some of them managed to escape. Indeed, enough macaques escaped from a private zoo in Wakayama City to set up their own breeding population (see Figure 2). This particular group has been known to mate with Japanese macaques, producing fertile hybrids between the two species.

But wait. We tend to think that different species cannot interbreed and even if they can, the offspring tend to be sterile. Matings between donkeys and horses produce (usually) sterile mules or hinnies. If Japanese macaques and Formosan rock macaques can produce fertile offspring, can they really be considered two different species?

Figure 2 Sites of *Macaca cyclopis* breeding populations in Japan

Box 2 Reproductive isolation

Reproductive isolation can occur at two main levels — pre-zygotic (before fertilisation or mating) and post-zygotic (after fertilisation).

Pre-zygotic barriers

- Behavioural isolation: two populations will not interbreed because of differences in **courtship** behaviour.
- Mechanical isolation: differences in the size, shape, and/or location of genitals prevent mating.
- Gametic isolation: the sperm and egg (or pollen and ovule) are incompatible for fertilisation.

Post-zygotic barriers

- Non-viable hybrid: the egg is fertilised but the embryo fails to develop normally.
- Hybrid sterility: the hybrid develops normally but has low fertility or is completely sterile.

Definition of species

This brings us to 'the species problem' — how does one define species? The biologist Ernst Mayr defined a species as:

> groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups

In other words, organisms can interbreed with members of the same species, but not with members of other species. However, there are several problems with this definition (see Box 3). One problem is that it does not account for hybridisation between closely related species, such as our macaques. Although Formosan rock macaques and Japanese macaques exhibit distinctive physical and genetic properties, they have not yet undergone complete reproductive isolation. This is also true for coyotes and wolves — canines that meet and mate where their territories overlap, creating hybrid zones in which 'coywolves' are common.

Hybrid success

Often, hybrids are less fertile and less adapted to their environment than their parents, meaning they are less likely to pass on their genes. In

Further reading

Read about the Formosan rock macaque here: **www.arkive.org/formosan-rock-macaque/macaca-cyclopis**

And more about the Japanese macaque here: **www.arkive.org/japanese-macaque/macaca-fuscata**

Read Richard Dawkins' book on evolution — *The Blind Watchmaker.*

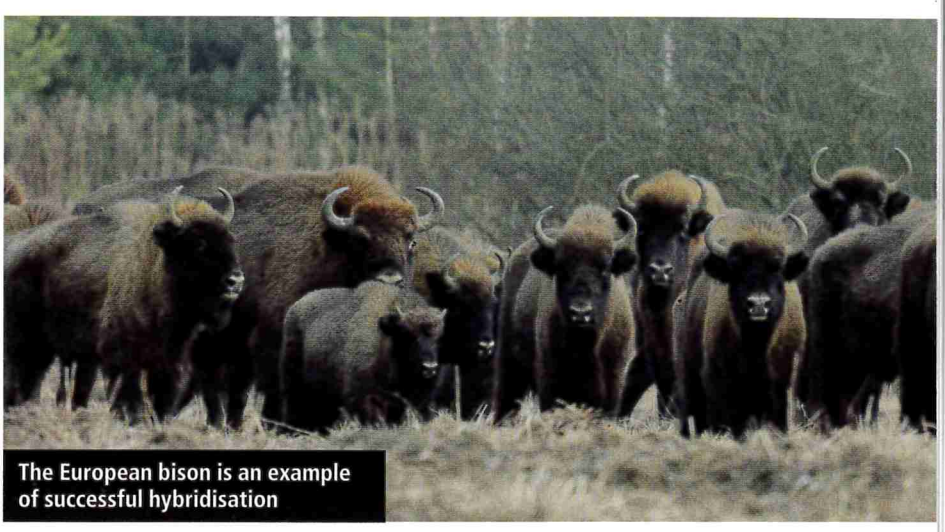
Box 3 Defining species

The Mayr definition of species is challenged by the following situations.

- Asexual reproduction: members of asexually reproducing species (such as bacteria) cannot be defined based on their ability to interbreed.
- Ring species: sometimes it is not clear where one species ends and another begins. Ring species (such as the *Larus* gull, see p. 25, this issue) consist of a long chain of populations (say, 'ABCDEFGH') — neighbouring populations can interbreed (for example, members of A can breed with members of B), but the two ends are reproductively isolated from one another (members of A do not breed with H).
- Hybridisation: sometimes reproductive isolation between two related species is not complete, and members of distinct populations can interbreed to produce hybrids (e.g. macaques).

such cases, natural selection will favour organisms that mate with members of their own species, effectively reinforcing separation between the two species. Over time, complete reproductive isolation may develop, even in the absence of geographical isolation. Sometimes, however, hybrids may be so well adapted to their environment that they become a new species. One notable example is the European bison, which is believed to have arisen as a hybrid of two extinct species: the steppe bison and the aurochs (the former is also the ancestor of the American bison, and the latter is the ancestor of domesticated European cattle).

Which of these two fates awaits hybrids of Formosan rock macaques and Japanese macaques? We may never know, as natural selection is being supplanted by artificial selection. In 2003, the



The European bison is an example of successful hybridisation

Wakayama Prefectural Government launched a campaign to exterminate hybrids of these two species, as part of a wider movement to limit damage to ecosystems caused by invasive alien species. Sadly, the greatest threat facing macaques is not hybridisation, but rather destruction of their environment by human encroachment. While a group of macaques may be able to scare off one human, they are defenceless against the destructive force that is human society.

Dr Duncan Wright completed a PhD in molecular genetics at The University of Warwick and subsequently worked as a postdoctoral researcher in Taiwan. He currently works in scientific publishing.

Key points

- Rising sea levels caused the ancestors of Japanese macaques and Formosan rock macaques to become separated from each other.
- Geographical separation prevented interbreeding between the two groups, causing them to slowly undergo genetic divergence.
- Genetic divergence may eventually result in reproductive isolation, preventing organisms of two species from producing fertile offspring.
- Formosan rock macaques and Japanese macaques can still mate and produce fertile offspring, and so do not exhibit complete reproductive isolation.

Francis Crick Institute exhibition

Craft & Graft: Making Science Happen, Francis Crick Institute, 1 Midland Rd, London NW1 1ST (near Kings Cross Station) until 30 November 2019

A new exhibition from the Francis Crick Institute offers visitors the chance to go behind the scenes and see the work of five specialist departments which support the institute's ground-breaking research. They include:

- Glass Wash, which cleans 750 000 items of glassware a year
- Fly Facility, which nurtures over 1.5 million flies
- Cell Services (or 'Librarians of life-forms'), which grows around 100 billion cells a month

Biological Sciences Review has a link with the institute: its director Sir Paul Nurse is on our advisory panel and articles from Sir Paul and other authors from the institute regularly appear in the magazine (e.g. 'Cancer stem cells: the seeds of a tumour', Vol. 30, No. 4).

Opening hours:

Wednesday 10 a.m.–8 p.m.
Thursday, Friday, Saturday 10 a.m.–4 p.m
Admission is free

The Fly Facility