# Visual kin recognition in chimpanzees

The ability to distinguish between members of one's own species has greatly assisted the evolution of sociality in mammals, leading to individualized relationships and cooperative networks. Because kin selection is important for the evolution of complex societies, other advantages must derive from the ability to distinguish kin from non-kin[1]. Taking advantage of the chimpanzee's face-recognition abilities and computer skills[2,3], we presented five subjects with the task of matching digitized portraits of unfamiliar females with their offspring. We find that chimpanzees can match the faces of mothers and sons, but not mothers and daughters, providing evidence for a mechanism of kin recognition in primates that is independent of previous experience with the individuals in question.

Two separate kin-recognition mechanisms have been proposed: early familiarity
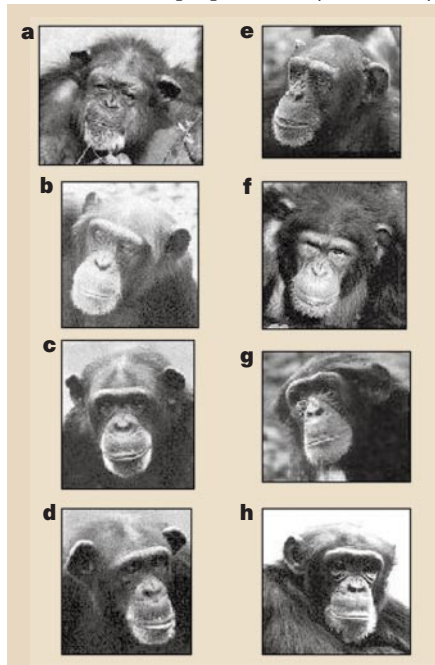
Figure 1 Mother–offspring pairs, showing two examples of each category: mother–daughter and mother–son. Left, mothers; right, offspring. The correct combinations here are **a** with **g** (daughter), **b** with **f** (son), **c** with **h** (son), and **d** with **e** (daughter). Stimuli were presented using a computerized testing model and a matching-to-sample format, which relied on the apes' skill to indicate their choice with a joystick-controlled cursor on the screen. In each trial, a single portrait of an adult female was presented as the sample, after which subjects were required to choose between two comparison portraits that matched the sample depending on whether it was a different portrait of the same female (IR trials), an offspring of this female (MD and MS trials), or an arbitrarily designated non-relative (UC trials). Further details of the test paradigm are available from the authors and in refs 2, 3.

and phenotypic matching[4,5]. Phenotypic matching by means of non-visual cues has been demonstrated in several non-primates, but not in primates[6–8]. Instead, kin recognition in primates seems to depend on previous experience, for example the ability of macaques to match photographs of familiar mothers and offspring[9]. But phenotypic matching would have the advantage of providing information about the kin status of individuals unknown to the observer, like the facial similarities that can be seen in human family albums.

Chimpanzees (*Pan troglodytes*) form loosely organized fission–fusion communities in the wild, in which even closely related individuals spend considerable time apart. Association is therefore not as reliable an index of kinship as in the best-studied monkey species, in which kin preferences seem to be socially learned[10].

We examined the chimpanzees' ability to recognize facial similarities in black-and-white portraits of unfamiliar conspecifics on a computer screen by using four types of discrimination. Individual recognition (IR) trials presented two different photographs of the same individual. Mother–offspring trials presented photographs of mothers and daughters (MD) or mothers and sons (MS) (Fig. 1). Finally, unrelated control (UC) trials presented photographs of individuals unrelated through maternal or paternal lines. We considered that subjects would perform best on the IR trials, and better on mother–offspring trials than on UC trials. Test subjects had never had any contact with the stimulus individuals, most of whom lived at distant locations. All offspring photographs depicted adults or subadults (more than seven years old).

Confirming earlier evidence of individual recognition[2], subjects did better on IR trials than on every other category (IR versus MS, $t(4) = 2.48$, $P < 0.05$; IR versus MD, $t(4) = 5.87$, $P < 0.005$; IR versus UC, $t(4) = 4.46$, $P < 0.01$). Subjects also did better on MS than on UC trials ($t(4) = 2.80$, $P < 0.025$), but unexpectedly no significant difference was found for performance on MD compared with UC trials. This means that subjects saw no more facial similarity between mothers and daughters than between unrelated individuals. Within the mother–offspring category, performance was significantly better for MS than for MD trials ($t(4) = 3.58$, $P < 0.05$). There was no overlap in performance on MD and MS pairs; the highest individual performance on MD trials (61.1%) was below the lowest performance on MS trials (64.5%). The mean performance on all stimulus categories, including the mean performance
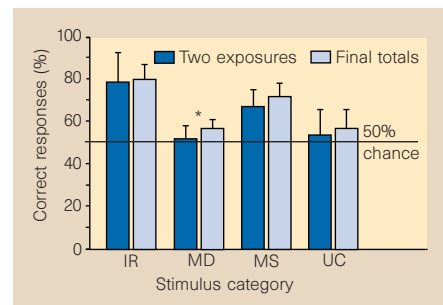
Figure 2 Mean performance for each stimulus category. Mean percentage (± s.d.) of correct responses is compared for each of the four discriminations (IR, individual recognition; MD, mother–daughter; MS, mother–son; UC, unrelated controls) with performance on the first day of testing. Whereas cumulative totals concerned between 604 and 648 trials per subject, the first two exposures to IR pairs totalled 24 trials, with 20 trials each of MD, MS and UC pairs. The asterisk marks the category in which performance was significantly better at the end of testing than on the first day ($P < 0.05$, two-tailed). This learning effect was evident only for mother–daughter pairs.

for the first testing session, is shown in Fig. 2. The superior performance on mother–son as opposed to mother–daughter pairs was evident from the onset of testing.

These findings indicate that chimpanzees perceive similarities in the faces of related but unfamiliar individuals, providing evidence of visual kin recognition at a purely phenotypic level. But this ability seems to be limited to recognizing mothers and sons. Perhaps facial similarities to do with sons, or males in general, are more noticeable to chimpanzees. Such an attentional bias would make sense from an evolutionary perspective in view of the chimpanzee's male philopatric society and the tendency towards 'political' alliances in which males incur great risk on behalf of other males[11]. Phenotypic matching might assist the recognition of subsets of related males who tend to support each other. The capacity might also have a role in inbreeding avoidance: a migrating young female should probably not settle in a community in which many males look like her mother, as these males might be related to her.

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The oldest fossil ascomycetes

Ascomycetes are the largest group of true fungi, and characteristically produce their sexual spores in a sac-like structure called the ascus. They include medicinal agents (such as ergot), plant pathogens (Dutch elm disease is caused by an ascomycete) and yeasts used in fermentation. We have found the oldest ascomycetous fungi with flask-shaped ascocarps in thin-section preparations of the Lower Devonian (400 million years old) Rhynie chert of Aberdeenshire, Scotland[1]. This discovery has implications for dating the origin of this group of fungi, and underscores the diversity of fungal–plant interactions early in the colonization of the land.

The fossils occur as closed fruiting bodies (perithecia) scattered just beneath the epidermis in the upright stems and rhizomes of the early land plant *Asteroxylon* (Fig. 1a); a few ascocarps have been identified on the scale leaves of this plant. Each globose perithecium (Fig. 1b) is approximately 400 μm in diameter and develops in the stomatal chamber beneath a pair of guard cells. At maturity, the perithecium has a slightly elongate neck through which the spores are released. The perithecium wall is constructed of two distinct layers of interwoven hyphae. Arising from the inner layer are numerous tightly packed, elongate asci (Fig. 1c), each up to 50 μm long. The ascus wall is thin and appears to consist of a single layer. Some asci have a slight invagination that encircles the tip of the ascus, suggesting the presence of some structural modification for spore release.

Arising from the same layer as the asci are delicate, thread-like structures. These may represent some form of sterile hairs (paraphyses) or be the remains of asci that have discharged their spores. Sterile hairs (periphyses) line the neck canal of each perithecium. Each ascus contains 16, and perhaps up to 32, elongate ascospores (Fig. 1c). Each ascospore is approximately 5 μm long, and many are bicelled (Fig. 1d). In other regions along the stems, tufts of hyphae extend through the cuticle of *Asteroxylon* and produce chains of conidiospores (non-sexual spores) at their tips.

The fossil history of the Ascomycota is poorly understood[2]. Although chains of asexual spores and perforate hyphae recovered from digested rock samples of Silurian age have been interpreted as ascomycetes[3], they may be modern contaminants or remains of some non-fungal group[4]. Molecular clock estimates have continued to push back in geological time the divergence of major fungal groups, with the most recent estimates suggesting that the basidiomycetes and ascomycetes diverged from one another about 500 million years ago[5].

Comparative gene sequence data have identified three groups of Ascomycota: Archiascomycetes (unicellular yeast-like forms), Hemiascomycetes (yeasts) and Euascomycetes (filamentous forms). Euascomycetes are a monophyletic group that includes the pyrenomycetes[6], which have elongate asci that arise as a single layer within a perithecium, and ascospores that are sometimes forcibly discharged at maturity. The most basal members of the Euascomycete group have not been resolved.

The Rhynie chert ascomycete fossils contain characters of the sexual stage of the fungus (such as perithecium, asci and ascospores) that are morphologically identical to those found in modern pyrenomycetes. They therefore provide the oldest evidence by approximately 250 million years of a major lineage of Euascomycetes with perithecial ascocarps. This is important because in some molecular trees the pyrenomycetes appear to be relatively recent compared with other ascomycetes. Because the characters in the Rhynie chert fossils are so well preserved, they can help to establish the sequence of phylogenetic events within this group. They therefore provide a means of calibrating the molecular clock data sets that are used to infer the phylogeny of fungal groups.

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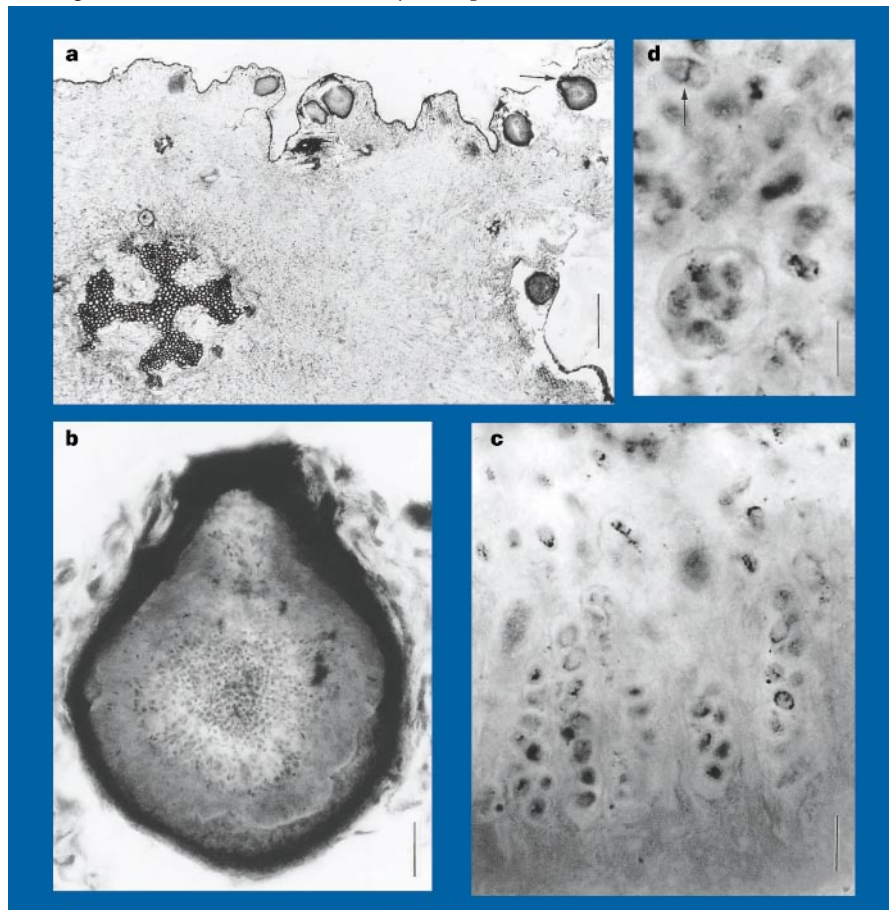
Figure 1 Lower Devonian ascomycete. **a,** Section of stem with ascocarps (arrow) in cortex. **b,** Perithecium in longitudinal section. **c,** Asci containing ascospores arising from inner wall of perithecium. **d,** Cross-section of ascus (lower left) with ascospores, some of which are bicelled (arrow). Scale bars: **a,** 500 μm; **b,** 50 μm; **c,** 10 μm; **d,** 20 μm.