

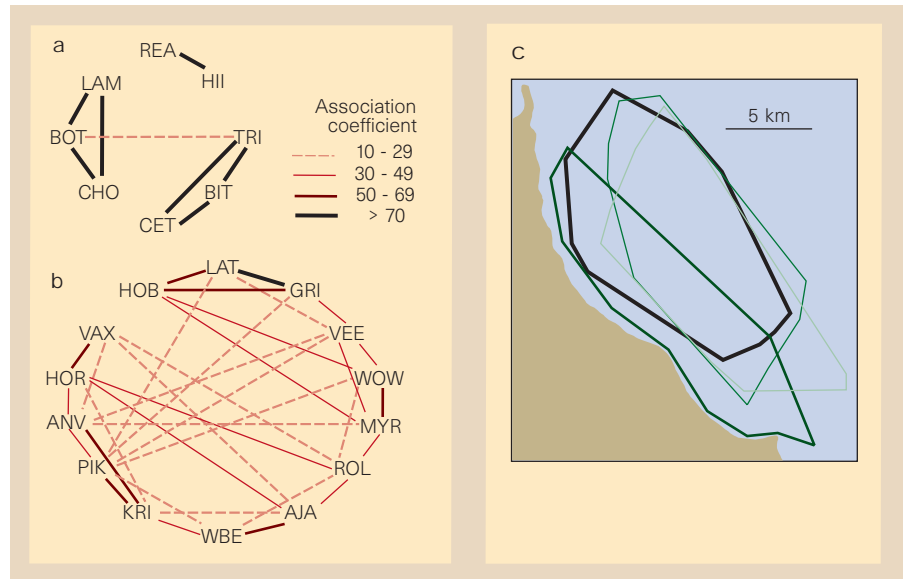
# Superalliance of bottlenose dolphins

It is quite common to find several levels of nested male alliances in human political organization<sup>1,2</sup> but these are extremely rare in other species<sup>3</sup>. Yet we found that male bottlenose dolphins (*Tursiops* sp.) at Shark Bay, Western Australia, form two levels of alliance within a social network of more than 400 individuals. Fourteen of the males formed highly labile alliances, rather than the more typical stable ones, and joined forces in a large 'superalliance' that competed directly with smaller teams of stable alliances.

Alliances of two or three male bottlenose dolphins have been reported in Shark Bay and Sarasota Bay, Florida<sup>3-7</sup>. Alliances in both populations are strong and stable over long periods, lasting up to 12 years in Shark Bay and 20 years in Sarasota<sup>7</sup>. As a measure of the strength of the association between individuals, we calculated association coefficients from observations of joint participation in consorting a female<sup>3</sup>. Values range from zero for two individuals who were never allies, to 100 for two individuals who were always in the same alliance. Males in the same alliance<sup>3-8</sup> typically had values of 80 to 100 (Fig. 1a), similar to those for mothers and their dependent offspring<sup>8</sup>.

Teams of two stable alliances were sometimes found to cooperate as 'second-order' alliances to attack other alliances or to defend against attacks. Stable alliances may maintain second-order alliance relationships with one or two other stable alliances, but only cooperate with one alliance at a time<sup>3,4</sup>. Second-order alliance relationships do not generally endure for more than a few years, and alliances that normally cooperate may oppose each other in some social contexts<sup>3</sup>.

There were no stable alliances in the superalliance (Fig. 1b). The composition of alliances in the superalliance was highly labile, as males often switched partners (Table 1). Over three years, we found evidence of 39 different alliances among the 14 superalliance males, including 35 trios and 4 pairs. Of the 14 males, 9 had eight or more alliance partners, none of which was with males from outside the superalliance.



**Figure 1** Contrasting patterns of alliance formation cannot be explained by habitat differences. a, b, 'Sociograms' showing the strength of association between: a, males in three stable alliances who formed second-order alliances together<sup>3</sup>; and b, males in the 14-member superalliance. The strength of the alliance is indicated by the association coefficient. c, The home range of the superalliance (black line) overlaps extensively with the ranges of three stable alliances. Each of the three stable-alliance ranges includes data from two stable alliances (5-6 individuals) that associated as a second-order alliance.

This lability was also evident within years: during June to October 1996, each of the 14 males was in 3-7 alliances and had 4-8 of the 14 males as alliance partners.

Analysis of association coefficients, group size (Table 1) and conflicts indicates that the superalliance is a very large second-order alliance. Association coefficients linking individuals in the superalliance (mean, 58; range, 34-97) were within the range linking stable male alliances that formed second-order alliances<sup>8</sup>.

We observed four conflicts involving between 6 and 14 members of the superalliance and teams of two stable alliances or a group of seven males who matured just before or early in the study. Superalliance males travelled up to 3 kilometres to join conflicts involving members of their group, and were victorious in each case.

The differences between the superalliance and stable alliances are not related

to age. Strong bonds are often evident before maturity in males who form stable alliances and may crystallize at maturity (age 10 to 12 years)<sup>6,7</sup>. Minimum ages of 14 to 19 years are known for ten of the members of the superalliance, judging from the first time they were photographed. The benefits of large group formation may increase in habitats with high predation risk and the costs may be reduced in habitats with more resources. However, these possibilities cannot explain the formation of superalliances because of the extensive overlap in home range between stable alliances and the superalliance (Fig. 1c).

This variation in alliance formation within one social group has not to our knowledge been described for any other species. The closest parallel is in male baboons (*Papio cynocephalus*), in which alliance formation is a conditional strategy used mostly by mid-ranking males against high-ranking males<sup>9</sup>. We cannot exclude the possibility that the large size of the dolphin superalliance allows individuals to compete with teams of stable alliances.

The extreme lability of alliances in the superalliance is puzzling, but may provide a mechanism by which males in the superalliance maintain affiliative bonds. Large brain size has been linked to complex social relationships, and alliance formation in particular<sup>10-12</sup>. Our findings suggest that the large brain size of bottlenose dolphins — only humans have larger brains relative to

	Stable alliances	Superalliance
Number of consortships	16-24	10-30
Number of alliances	1-2	5-11
Number of alliance partners	1-3	5-11
Alliance partners with primary alliance (%)	84-100	17-57
Mean male group size	3.6	6.1

The numbers of consortships, different alliances (pairs and trios) and alliance partners, and the percentage of consortships by each male's most common (primary) alliance, are compared for males in stable alliances (8 males, 62 consortships) and males in the superalliance (14 males, 100 consortships). The mean male group size was larger for members of the superalliance ( $n=57$ ) than for five stable alliances ( $n=115$ ; Mann-Whitney  $U$  test,  $P<0.001$ ). Stable alliances were never documented in male groups of 10 or more individuals, but 25% of groups with at least one member of the superalliance contained 10 or more of the 14 males.

body size — may be matched by the complexity of their social relationships.

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not significantly different ( $P > 0.05$ , Scheffé's  $F$ ) from those of archaic *Homo* (Gibraltar 1, 17.2 mm; Monte Circeo, 16.9 mm; Broken Hill, 17.2 mm). Figure 1a confirms that reduced MFP in anatomically modern humans is not associated with a shorter ASL.

To assess the spatial relationships of ASL and MFP in relative terms, we did a geometric morphometric analysis comparing Holocene modern human crania with the three archaic *Homo* fossils (Fig. 1b,c). The transformation grid indicates that, relative to the size of the landmark configuration, MFP is shortened and ASL is lengthened in Holocene *H. sapiens*. The factors underlying these changes may include facial reduction, increased basicranial flexion, and expansion of the temporal lobes in the middle cranial fossae. The comparison also suggests that the pharyngeal area between the palate and the foramen magnum is anteroposteriorly constricted in Holocene

modern humans, as was inferred by Lieberman<sup>1</sup>, but that this is unrelated to ASL.

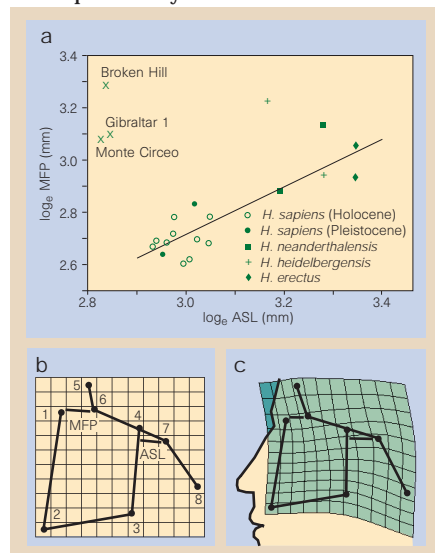
We conclude that, although ASL is intraspecifically correlated with MFP in modern humans and chimpanzees<sup>1</sup>, it does not account for the unique form of the modern human cranium. Our analysis highlights the need for research that integrates comparative morphometric analyses with developmental studies of cranial growth in human and non-human primates.

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**Figure 1** Analysis of measurements. a, Plot of ASL and MFP (after Fig. 3a of ref. 1), with new measurements of Broken Hill, Gibraltar 1 and Monte Circeo. MFP is the distance from nasion to foramen caecum perpendicular to the posterior maxillary plane. ASL is the minimum distance from sella to the posterior maxillary plane. b, c, Geometric morphometric comparison of eight facial, neurocranial and basicranial landmarks from 28 combined-sex Holocene *H. sapiens* skulls (Indian subcontinent), Monte Circeo, Gibraltar 1 and Broken Hill. Principal components analysis of tangent coordinates following generalized Procrustes analysis yields 12 non-zero eigenvectors<sup>4</sup>. Only principal component I (PC I; 37% total shape variance) separates fossil from extant specimens. The shapes represent means for the fossils (b) and Holocene *H. sapiens* (c), both on PC I and each rescaled to their respective mean size. A cartesian transformation grid (thin plate spline<sup>5</sup>) from fossil to extant means is superimposed. Numbers: 1, nasion; 2, prosthion; 3, maxillary tuberosity; 4, laterally projected average intersection between greater wings and planum sphenoidaleum; 5, anteriormost point of cranial cavity; 6, foramen caecum; 7, sella; 8, basion (estimated in Neanderthals); 3 to 4, posterior maxillary plane.

## Anterior sphenoid in modern humans

Lieberman has proposed<sup>1</sup> that reduced midfacial projection (MFP), in which most of the face lies beneath the neurocranium, is a major unique, derived character of anatomically modern *Homo sapiens*, and that this reduction is largely a consequence of reduced anterior sphenoid length (ASL). Lieberman's conclusions were based on comparisons of a small sample of archaic *Homo* crania with those of Holocene and Pleistocene anatomically modern *H. sapiens*. We have made new measurements of ASL and MFP, and find that ASL was incorrectly estimated in those archaic fossil crania in which these landmarks are unambiguously preserved. It turns out that the anterior sphenoid in modern humans is shorter than in archaic *Homo*.

The new measurements were taken from better-quality radiographs and computed tomography scans<sup>2,3</sup> and from the original specimens of Gibraltar 1 and Broken Hill (courtesy of C. Stringer, T. Molleson and F. Zonneveld). ASL values in Holocene and Pleistocene modern humans are 19.9 mm (s.d. 2.0) and 20.0 mm (s.d. 1.8), respectively<sup>1</sup>,

## Iodine oxide in the marine boundary layer

A striking example of the influence of halogen chemistry on tropospheric ozone levels is the episodic destruction of boundary-layer ozone during the Arctic sunrise by reactive halogen species<sup>1,2</sup>. We detected iodine oxide in the boundary layer at Mace Head, Ireland (53°20' N, 9°54' W) during May 1997, which indicates that iodine chemistry is occurring in the troposphere.

Reactive halogen species in the atmosphere act as catalysts in several photochemical reaction cycles that are closely linked with ozone<sup>3</sup>. Iodine atoms react preferentially with ozone, forming iodine oxide, IO. IO can react with itself or with the halogen oxides BrO and ClO to produce O<sub>2</sub> and halogen atoms. If these react with ozone, a catalytic mechanism destroys two ozone molecules per cycle. The reaction of IO with HO<sub>2</sub> forms HOI, which is rapidly photolysed into I and OH. This catalytic cycle also effectively destroys ozone.

The measurement of IO in the boundary layer has so far been unsuccessful. The upper limit of the mixing ratios, determined as 0.5–0.9 part per trillion (p.p.t.)<sup>3,4</sup>, agreed with model predictions<sup>5–9</sup>. We measured the concentrations of O<sub>3</sub>, NO<sub>2</sub>, SO<sub>2</sub>, HCHO, HONO, BrO, ClO and IO by using long-path differential optical absorption spectroscopy (LP-DOAS)<sup>10</sup> during the