

Three principal factors are important in understanding the origin of flight and its evolutionary history in each flying group:

1 Aerodynamic considerations define the physical requirements for flight and restrict the morphological and ecological possibilities for animals that fly. Aerodynamics of living vertebrates are well enough known to shed considerable light on parameters for fossil forms (Rayner *in* Hecht *et al.* 1985; Rayner 1988). Most important is the generation of sufficient thrust to create a vortex wake that propels the animal forward. Wing design, planform, and muscle physiology are instrumental in quantifying flight capabilities, and can to some extent be modelled in fossil forms by comparison with living ones.

2 Functional considerations are important in understanding the evolution of the flight apparatus and the generation of the flight stroke, the latter being the single property that defines powered flight (Padian 1985). All three groups of flying vertebrates use a vertical or down-and-forward stroke of the forelimbs to generate thrust. Each group, although built on the general tetrapod plan, has modified its basic equipment in different ways (Fig. 1). For example, the wing is functionally divided into three segments, of which the outermost is principally supported by the fourth finger in pterosaurs, the wrist and fused fingers in birds, and the unfused fingers in bats. But despite differences in the equipment, the flight strokes are essentially the same.

3 The evolution of flight is also influenced by phylogenetic factors. Organisms have to use what they inherit in order to solve evolutionary and ecological problems; their past history dictates in large measure what they are capable of doing in future. Therefore, understanding the phylogeny of organisms in detail helps us to understand the ecological milieu from which they evolved. As a result, complex adaptations may be dissected part by part simply by assembling the evolutionary sequence of forms that evolved the adaptation. Of course, this must be done by reference to other, functionally independent character sets (Gauthier & Padian *in* Hecht *et al.* 1985; Padian 1987).

In studying the evolution of flight, then, the aerodynamic factor provides us, in effect, with the laws that bound the possible solutions to the problem. The functional factor shows how the problem is solved. The phylogenetic factor shows much about why a given animal solved the problem in the particular way it did. With these three approaches in mind, the evolutionary histories of flight in pterosaurs, birds, and bats may be considered.

Pterosaurs

These first flying vertebrates were archosaurs very closely related to dinosaurs, and the common ancestor of the two groups seems to have been a small, lightly built, bipedal form of the Middle Triassic. Typically, pterosaurs have been pictured as bat-like lizards with poor terrestrial capability, but a large suite of features suggests that they were instead agile bipeds that moved much more like birds and other dinosaurs (Padian 1985). The wings were narrow and could not have been attached to the legs without spoiling vortex patterns over the wing.

Pterosaurs have been divided historically into two groups: the earlier, paraphyletic 'Rhamphorhynchoidea' and the later, monophyletic Pterodactyloidea (Wellnhofer 1978). The 'rhamphorhynchoids' retained the long tail of their archosaurian ancestors, hyperelongated the metacarpus and (especially) the fourth finger for flight, and stretched a wing of skin behind the forelimb running along the body wall to the tail. The wing membrane was invested with countless stiffening 'fibres', which were intercalated and oriented through the wing like the feather shafts of birds or the fingers of bats (Padian 1985). 'Rhamphorhynchoids' also hyperelongated the two phalanges of the fifth toe; adaptations for grasping or perching have been suggested without close argument, but the elongation was equally likely to have been merely a developmental consequence of elongating the outer digit of the hand.

It is often observed that in the history of any flying animals (including humans), early designs are highly stable aerodynamically. In more advanced forms, on the other hand, the designs become inherently unstable as the neurological control systems become more sophisticated. Pterodactyloid pterosaurs, like post-*Archaeopteryx* birds, lost the tail, a primary mechanism of dynamic stability. Pterodactyloids also shortened the humerus (the first functional segment of the wing), lengthened the metacarpus (much of the second section), and tended to shorten the wingfinger slightly (the third section). Aerodynamic reasons for this are not yet understood, but stability was probably involved. Large size and soaring habits characterized several lineages within Pterodactyloidea, including those of *Pteranodon* and *Quetzalcoatlus* (Late Cretaceous, North America), and these represented most of the latest known forms in the fossil record. No known pterosaurs show particular arboreal specializations, but it must be remembered that the terrestrial fossil record is biased toward aquatic environments and against forest and upland habitats.

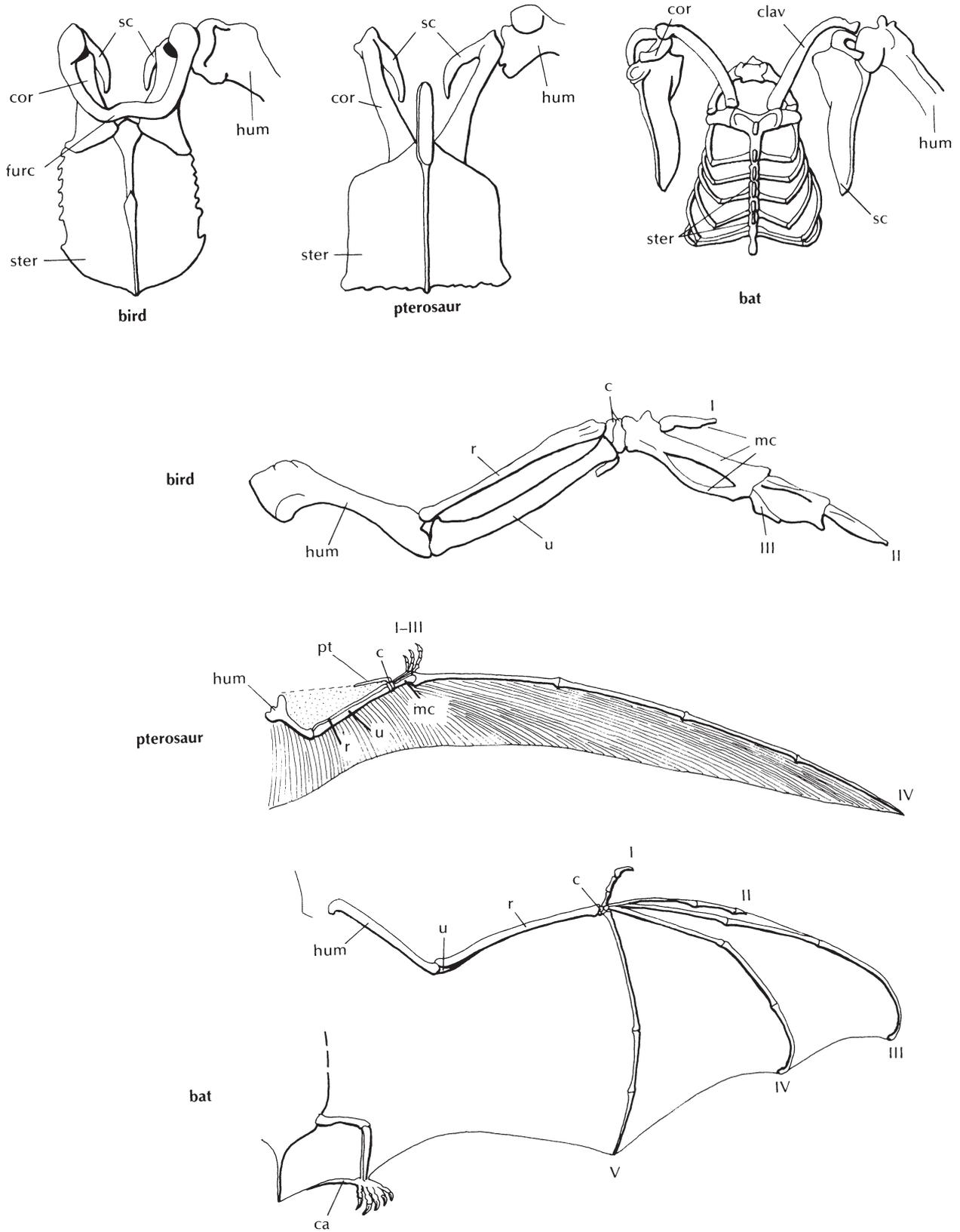


Fig. 1 Diagrammatic comparisons of the thoracic regions and forelimbs of the three groups of vertebrate flyers. Thoracic regions (above) are seen from the front; left forelimbs (below) in ventral view. Structurally, the coracoids of pterosaurs and birds seem to be functionally analogous to the clavicles of bats, as do the furcula of birds, the cristospine of pterosaurs, and the manubrium of bats. Abbreviations: *c*, carpus; *ca*, calcar; *clav*, clavicle; *cor*, coracoid; *furc*, furcula; *hum*, humerus; *mc*, metacarpus; *pt*, pteroid; *r*, radius; *sc*, scapula; *ster*, sternum; *u*, ulna; *I-V*, numbered digits. Not to scale. (From Padian 1985.)

Birds

Archaeopteryx, from the Late Jurassic Solnhofen Limestone of Bavaria (Section 3.11.7) is the first known bird, recognized by its flight feathers. In the nineteen-seventies J.H. Ostrom established its ancestry from among small carnivorous (coelurosaurian) dinosaurs, an idea first advanced a century ago by T.H. Huxley. Gauthier (1986) used over 200 nested synapomorphies to document the sequence of acquisition of characters that not only show how the major archosaurian groups are related to each other, but also how those characters relevant to flight evolved. Some features considered typically 'avian', such as the furcula (fused clavicles) and calcified sterna, appeared in carnivorous dinosaurs at a more general level than Aves. Other features, such as the perching foot, the reduced tail and teeth, and the fused carpometacarpus, appeared well after *Archaeopteryx*. Little is known of Cretaceous birds apart from a few open-water forms. The loon-like *Hesperornis* and the tern-like *Ichthyornis* (Late Cretaceous, Western Interior, North America) are not members of the orders of living birds; most of these have their first records in the Eocene or later. The refinement of flight adaptations in avian evolution is poorly known and must be reconstructed mainly with reference to living forms. Recent discoveries of Early Cretaceous birds from Spain show that by that time the dorsal vertebrae were reducing in number, the tail had been shortened to a pygostyle, the coracoids were strut-like and braced to the sternum, and the furcula (wishbone) had a prominent hypocleidium. A perching foot with trenchant recurved claws appears to have been well developed.

Archaeopteryx is perhaps the world's most famous fossil; it is the basis for a great diversity of approaches and viewpoints on the origin of birds and the early evolution of their flight (Hecht *et al.* 1985). The traditionally favoured view is that birds evolved in trees and passed through a fully gliding stage on the way to active flight (Bock *in* Hecht *et al.* 1985). It is easiest to evolve flight in this way (Rayner; Norberg; *in* Hecht *et al.* 1985), but this does not exclude other possibilities. The view that flight evolved from a small terrestrial animal that ran and leaped into the air, gaining flight gradually by the elaboration of 'proto-wings,' has recently been advocated (Ostrom; Gauthier & Padian; Caple *et al.*; *in* Hecht *et al.* 1985). The advantage of this view is that it is rooted in the evolution and ecology of avian ancestors, whereas the 'arboreal' theory is not; but

the disadvantage is the relative difficulty of evolving flight 'from the ground up'. Terrestrial speeds needed for take-off are uncomfortably high, judging from small living bipeds (Rayner *in* Hecht *et al.* 1985), whereas speed is easily gained by dropping out of a tree. It is difficult to see what evidence could resolve this question; most likely, some compromise between the two extremes will be most fruitful.

Bats

Little is known about the early evolution of bats; like pterosaurs, when they first appear in the fossil record (the Eocene *Icaronycteris*: Jepsen 1970) they are fully formed flyers, and the evolution of their flight can only be reconstructed from the skeletons of the earliest forms. Like gliding mammals, and unlike birds and pterosaurs, bats incorporate the hindlimbs in the wing membrane, which explains why their terrestrial ability is so poor: their fore- and hind limb locomotory systems are not independent, and stress has clearly been placed on the forelimb system. In all respects, bats seem to have followed the model for evolution from gliding forms (Rayner; Norberg; *in* Hecht *et al.* 1985). Based on analyses of the general distribution of their characters, bats appear to have evolved from a group of generally nocturnal, arboreal, insectivorous-omnivorous placentals. Some facility for echolocation and hanging upside down would seem to have appeared at an early stage in bat evolution. A nocturnal, arboreal form that could glide and hang upside down (thus freeing its forelimbs from most locomotory functions) would be a reasonable ancestor (Padian 1987).

For this reason, recent studies of the phylogenetic position of Chiroptera have generated considerable excitement and controversy. Although several workers have claimed that the Chiroptera are diphyletic (separate origins of megabats and microbats), cladistic studies by Novacek and his colleagues (e.g. Wible & Novacek 1988) have provided a consilience of skeletal and molecular evidence that appears to support chiropteran monophyly. Moreover, a suite of cranial and postcranial characters suggests that the closest sister-taxon to Chiroptera is Dermoptera, the so-called 'flying lemurs' now restricted to Southeast Asia. If Novacek and his co-workers are correct, some habits of the living dermopteran *Cynocephalus*, coincident with those discussed in the preceding paragraph, may shed light on the ecology of the common ancestor of the two groups.

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1.10 Angiosperms

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Introduction

The angiosperms or flowering plants are the most diverse living plant group with over 250 000 species. They dominate world vegetation, with the exception of moss-lichen tundra and high latitude northern hemisphere coniferous forest. They exhibit a wide range of life form and strategy, ranging from tiny free-floating aquatic duckweeds through epiphytes and lianas to tall forest trees. This diversity and dominance has, however, been attained relatively recently in terms of Earth history, apparently within the last 120 million years. The origin and subsequent diversification of the flowering plants has influenced community structure and the evolution of all other biotas.

Early fossil evidence

Several synapomorphies of the angiosperms (Crane 1985; Doyle & Donoghue in Friis *et al.* 1987) are features of reproductive biology not amenable to recognition in the fossil record. Characteristic pollen, wood, and leaves (Fig. 1) may, however, be easily detected. Like other plants, angiosperms are largely represented in the fossil record by organs (like pollen, leaves, seeds) which are dispersed or shed during life. The smallest and most widely

dispersed are most likely to be preserved. It is to be expected, then, that the earliest recognizable angiosperm fossils are pollen grains with the tectate/columellate wall (Fig. 1G). These monosulcate pollen, named *Clavatipollenites* (Fig. 2B), occur in the Early Cretaceous (Barremian) of England, West Africa, Argentina, and eastern North America (Muller; Walker & Walker; in Dilcher & Crepet 1985). *Clavatipollenites* pollen are very similar to grains produced by modern members of the magnoliid dicotyledon family Chloranthaceae, e.g. *Ascarina* (Walker & Walker in Dilcher & Crepet 1985). As pollen of other magnoliid plants lack the diagnostic wall structure and plant organs may evolve at different rates, there is no reason to assume that *Clavatipollenites* pollen represent either the earliest or the most primitive flowering plants.

Cladistic analyses

Recent cladistic analyses of fossil and modern seed-plant groups (Crane 1985; Doyle & Donoghue 1986; Doyle & Donoghue in Friis *et al.* 1987) imply a pre-Cretaceous origin of angiosperms, possibly as early as the Triassic. In these analyses an anthophyte clade can be defined (Fig. 3B), for which the sister group may be one of several Mesozoic seed plants

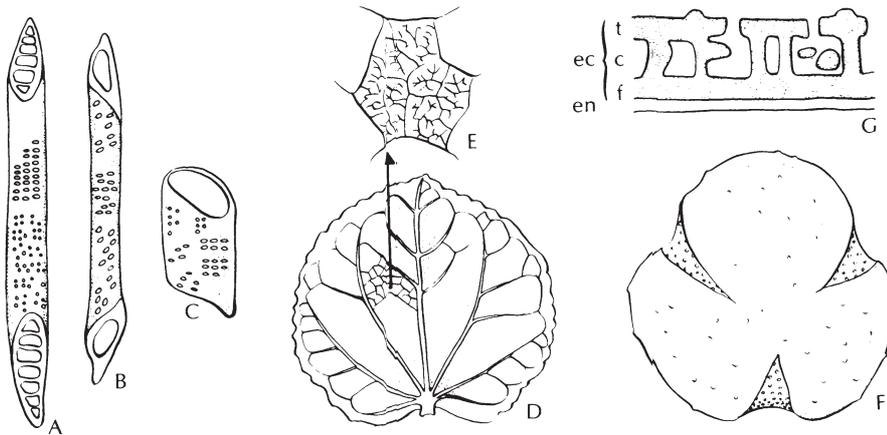


Fig. 1 Characteristic features of angiosperms detectable in the fossil record. A–C, vessel elements (lengths vary from about 200–1000 μm). D, E, dicotyledon leaf (length about 5 cm) with venation detail. F, tricolpate pollen grain (diameter about 30 μm). G, section of pollen wall (thickness about 1–3 μm) showing endexine (en) and ectexine (ec) divisible into footlayer (f), columnar layer (c), and tectum (t). (From Friis *et al.* 1987.)

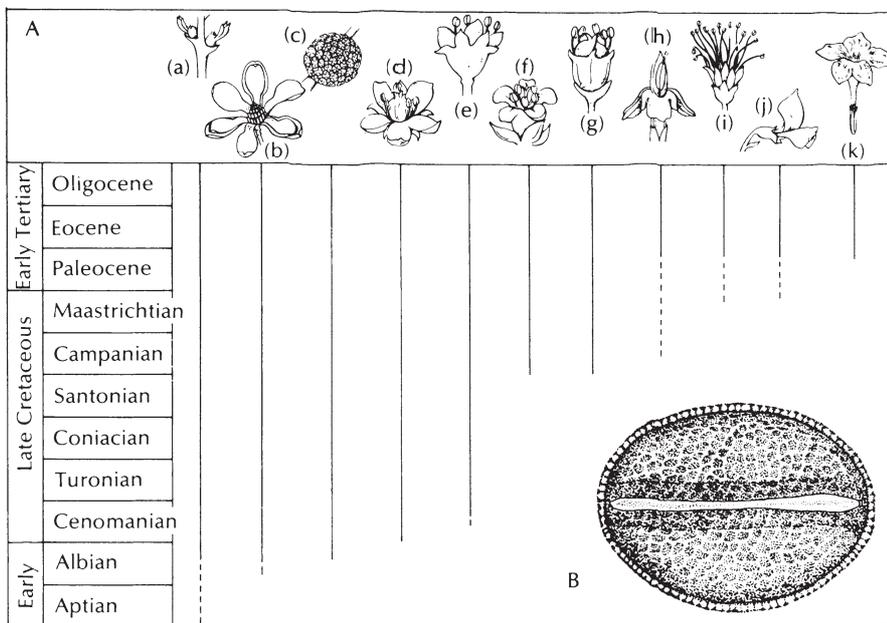


Fig. 2 A, Time of appearance of major floral types. Solid lines based on flower fossils, dashed lines on indirect evidence — mostly pollen. (From Friis & Crepet in Friis *et al.* 1987.) B, *Clavatipollenites*, monosulcate pollen (length 20 μm). (From Stewart 1983.)

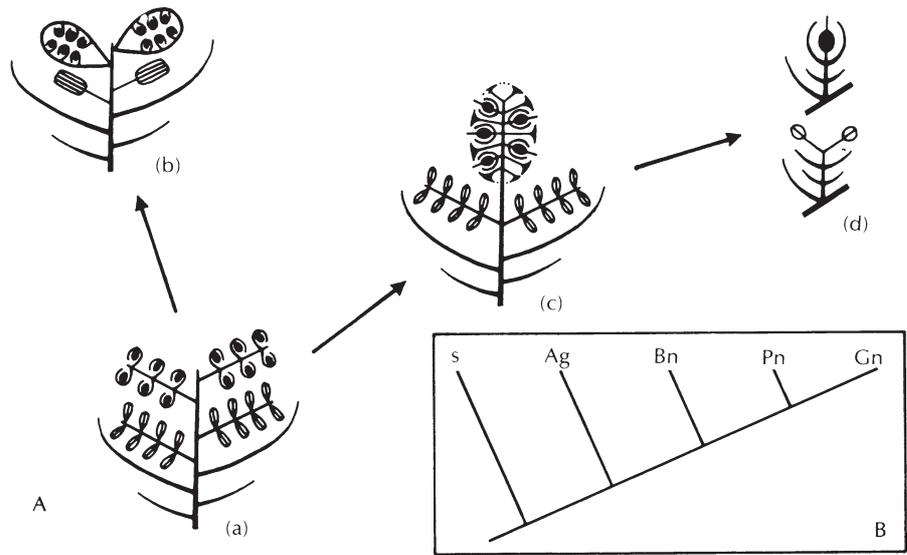
(*Caytonia*, glossopterids, corystosperms) that exhibit varying degrees of ovule protection, net leaf venation, fused pollen sacs, etc. (all later elaborated upon in members of the anthophyte clade). Flower-like organization of reproductive structures (Fig. 3A) typifies members of the clade, hence the proposed term anthophyte. This feature can no longer be seen as a uniquely angiosperm attribute. Fig. 3A represents the inferred character transformations in the reproductive structures of members of this clade. In angiosperms the microsporophyll (= stamen) is reduced but the megasporophyll (= carpel) remains complex. In Bennettitales the megasporophyll is reduced to a uniovulate unit but the microsporophyll remains complex. In Gnetales both micro- and megasporophyll are reduced.

According to these cladistic analyses the Gnetales are the closest living relatives of the angiosperms and these two groups share a common ancestry (along with Bennettitales and *Pentoxylon*) amongst Mesozoic seed plants. Careful study of these, especially Triassic representatives, and a clearer understanding of the fossil record of Gnetales, will clarify the phylogenetic history of the anthophyte clade.

Early radiation

Following the widespread appearance of *Clavatipollenites* pollen during the Barremian, other angiosperm pollen types occur in later Barremian and Aptian strata. These include probable

Fig. 3 A, Major character transformations in reproductive structures inferred from Fig. 3B and present in: (a) hypothetical ancestor; (b) angiosperm; (c) Bennettitales; (d) Gnetales. (From Friis *et al.* 1987.) B, The anthophyte clade: Ag = angiosperms, Bn = Bennettitales, Pn = *Pentoxylon*, Gn = Gnetales, s = sister group involving one or more of *Caytonia*, *Caytonia* according to author. (After Doyle & Donoghue *in* Friis *et al.* 1987.)



Chloranthaceae; forms similar to those of modern monocotyledons; and forms referable to the Winteraceae, another family of the magnoliid dicots. In the Aptian, tricolpate pollen (Fig. 1F) first indicate the presence of non-magnoliid ('higher') dicotyledons (Hamamelidae or Ranunculidae). In the Albian, pollen with endoapertures (tricolporate) signal the occurrence of probable Dilleniidae or Rosidae. Angiosperm pollen accounted for only up to 1% of palynofloras in the Barremian. By the late Albian they accounted for up to 70% in some low palaeolatitude areas, with lower proportions in middle palaeolatitudes. In the Turonian, angiosperms dominated palynofloras from many areas of the world (Muller; Walker & Walker; both *in* Dilcher & Crepet 1985).

Details of the early phase of angiosperm leaf diversification are largely based on material from eastern North America. Angiosperm leaves may be characterized by reticulate venation, in a hierarchical system often with free ending veinlets (Fig. 1D, E). Most Aptian angiosperm leaves are small, entire-margined and simple with pinnate venation, sometimes with a poorly developed hierarchy. Middle to Late Albian assemblages show an increase in diversity of leaf form, including pinnatifid and palmately lobed forms and cordate leaves. Forms similar to those of modern magnoliid (Chloranthaceae), hamamelid (Platanaceae), and rosid dicotyledons are recorded from the Albian (Upchurch *in* Dilcher & Crepet 1985; Upchurch & Wolfe *in* Friis *et al.* 1987).

A statistical assessment of the proportion of different plant groups in leaf floras (see Fig. 5) clearly

demonstrates the rapidity with which angiosperms became dominant elements, replacing cycadophytes and pteridophytes during the Early and earliest Late Cretaceous. The replacement generally took place later at higher palaeolatitudes. Angiosperm floral provinciality was well established by the Late Cretaceous.

Angiosperm herbs and small woody plants first entered early successional habitats such as stream sides, coastal plains, and other disturbed areas in a similar manner to the weeds of today (Retallack & Dilcher 1986; Crane *in* Friis *et al.* 1987). During the Late Albian they diversified into full aquatics, forest understory shrubs and riparian trees. Early in the Late Cretaceous angiosperms (probable shrubs and small trees) remained effective colonizers and expanded first into environments previously dominated by cycadophytes (including Bennettitales) and ferns.

The rise of angiosperms may have influenced certain dinosaur feeding strategies, reflected in the Late Cretaceous radiation of ornithischian herbivores (Coe *et al.* *in* Friis *et al.* 1987). Although angiosperms clearly dominated vegetation in many areas by the early Late Cretaceous, several significant advances took places later (see below).

Early floral biology

Recently, data on fossil flowers and, more rarely, on partially reconstructed whole plants has added to that from dispersed pollen and leaves (Friis & Crepet; Crepet & Friis; *in* Friis *et al.* 1987). Amongst the earliest known fossil flowers from the early

Late Albian of eastern North America are forms (Fig. 2A(a)) which are very similar to modern members of the Chloranthaceae, e.g. *Chloranthus*. The floral morphology suggests insect pollination, as does their similarity to modern insect pollinated *Chloranthus*. In contrast, the abundance of the early Cretaceous pollen *Clavatipollenites* suggests wind pollination, as in modern *Ascarina*. In the same fossil flora unisexual platanoid flowers also occur (Fig. 2A(c)).

These small, platanoid and chloranthoid flowers are usually considered derived by comparison with large showy bisexual flowers which also occur in the Albian (Fig. 2A(b)). The best known example is from the Albian/Cenomanian boundary of the Western Interior of North America (Fig. 4; Dilcher & Crane in Dilcher & Crepet 1985). This plant has been reconstructed using organic connection, attachment scars, and association evidence, from a suite of fossil organs occurring in one thin sedimentary unit. Its multifollicular fruit (named *Archaeanthus*) represents the primitive condition as predicted from, but not represented in, modern flowering plants. Other features of the flower (numerous free, spirally arranged parts) also conform to the traditional, hypothetical angiosperm archetype. However, certain aspects of the whole plant, e.g. the lobed leaf, are more advanced. The '*Archaeanthus* plant' shares most features with members of the Magnoliales, amongst living plants, but it cannot be assigned to a modern family. Strata of the same age have also yielded a more derived flower form (Fig. 2A(d)) with parts in whorls of five. Clearly all of these floral forms (Fig. 2A(a–d)) were represented very early in the evolution of flowering plants. They confirm the pattern of rapid diversification as inferred from pollen and leaves, and the early differentiation of 'higher' dicotyledons (Crane 1989). They also suggest the early existence of wind pollination and a range of insect pollination strategies.

Pollination biology and dispersal strategy

Insect pollination may characterize all members of the anthophyte clade and was therefore not a controlling factor in angiosperm origins. The enclosing carpel (megasporophyll enclosing ovules) and the receptive stigmatic surface on the carpel are, however, unique to the angiosperms. Together these permit control of pollen germination, hence fertilization, and allow for the exploitation of incompatibility mechanisms. Such mechanisms permit or

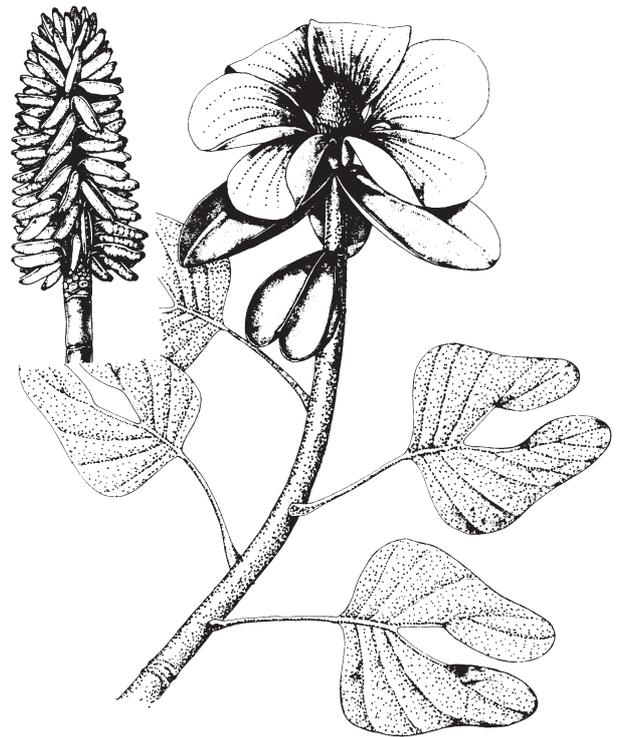


Fig. 4 Reconstruction of one of the best known Cretaceous angiosperms, '*Archaeanthus*' from the Dakota Formation, Albian/Cenomanian boundary, Kansas, U.S.A. External flower diameter about 130 mm. (From Dilcher & Crane in Dilcher & Crepet 1985.)

enforce cross fertilization with resultant enhanced variation. The carpel also provided for new means of seed dispersal through a range of fruit structures. Combined, these features increase speciation rates and reduce extinction rates, resulting in increased diversity and potential dominance in vegetation. Such features can be best exploited through controlled (biotic) transfer of pollen to the stigma rather than the more haphazard wind pollination.

The late Cretaceous and Early Tertiary evolution of floral form (Fig. 2A) reveals the continued elaboration associated with new pollination vectors. The earliest insect pollinated angiosperms probably possessed generalist flowers visited by a range of insects. Specialization for beetle pollination is indicated by the large robust magnolialean flowers with prolific pollen production (Fig. 2A(b)). Early Late Cretaceous flowers with reduction and fusion of whorled parts and nectar glands in discs (Fig. 2A(d–f)), along with inferior flowers with stout styles (stigmatic stalks) (Fig. 2A(g)), suggest increasing specialization for more specific insect pollinators, including those feeding on nectar as well as pollen. In the latest Cretaceous and Early

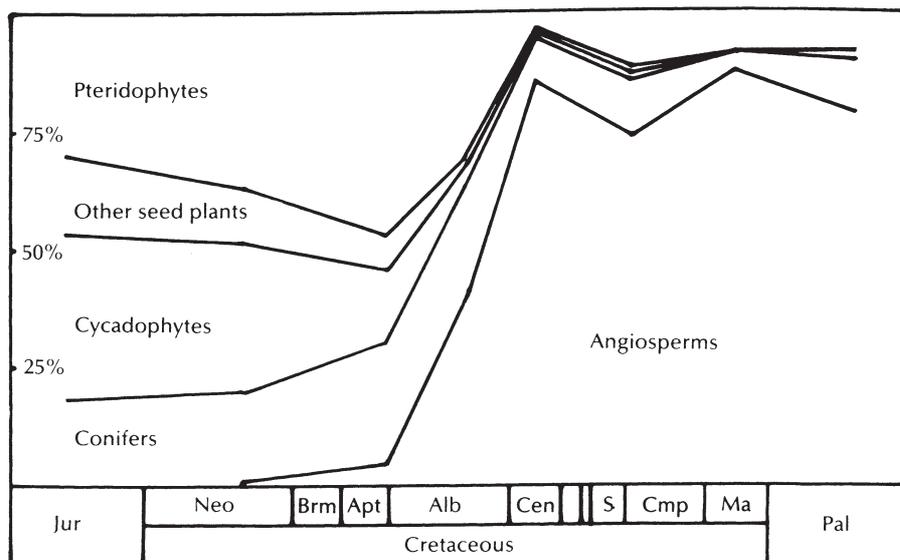


Fig. 5 Percentage contribution of major plant groups to ancient leaf floras from Jurassic to Palaeocene. (From Crane *in* Friis *et al.* 1987.)

Tertiary further elaborations such as zygomorphy (bilateral not radial floral symmetry, Fig. 2A(h, j)), brush flowers (Fig. 2A(i)), and long corolla tubes (Fig. 2A(k)) were developed. These are associated with advanced pollinators like bees and butterflies. Some of the more specialized 'faithful' plant-pollinator relationships were established by the Eocene (Crepet & Friis *in* Friis *et al.* 1987).

Fruiting structures also diversified to include fleshy fruits, along with a range of dry nuts and winged fruits (Tiffney *in* Dilcher & Crepet 1985; Friis & Crepet *in* Friis *et al.* 1987). The fruits not only indicate a range of dispersal types but also a range of establishment strategies. Large seeds, able to establish in shaded, canopy covered forest, became more widespread in contrast to the smaller seeds of the earliest angiosperms. This is consistent with an early Tertiary origination of angiosperm-dominated forests with angiosperms as the tall canopy trees, inferred from the fossil record of leaves and wood (Crane; Upchurch & Wolfe; *both in* Friis *et al.* 1987).

Later radiation

The fossil records of pollen, leaves, fruits, seeds, flowers, and wood all point to a major radiation and modernization of flowering plants in the latest Cretaceous and Early Tertiary (Fig. 5). This may in part have been in response to the Cretaceous/Tertiary event, followed by the diversification of mammals replacing dinosaurs as the main large vertebrates on land (Section 2.13.7). Extinction of the dinosaurs, whether gradual or sudden, resulted in the removal of large herbivores which were not

replaced by an equivalent diversity of large herbivorous mammals until the end of the Eocene (Coe *et al.*; Collinson & Hooker; Wing & Tiffney; *in* Friis *et al.* 1987). The later Tertiary saw a further radiation of angiosperms, particularly of the herbaceous groups which represent much of their modern diversity. Grasslands, for example, probably originated in the latest Oligocene or Miocene, perhaps in response to grazing mammals (Section 1.11).

Plant communities reconstructed from Early Tertiary floras are often said to be similar to those of the present day, although in reality none was identical in composition. Instead they combined elements whose nearest living relatives are widely separated ecologically and geographically (Collinson & Scott 1987; Crane *in* Friis *et al.* 1987). Some wetland herbaceous and wooded communities have a good fossil record which may eventually permit reconstruction of their evolution. In other cases, e.g. grasslands and montane forests, the record is far less promising.

Future studies should emphasize the sedimentological and taphonomic context of angiosperm fossils. This, together with more critical comparative studies of fossils and their living relatives, will lead to a fuller understanding of angiosperm evolution.

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1.11 Grasslands and Grazers

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Grasslands

Modern grasslands cover more than 30% of the Earth's land surface and contain more than 10 000 species of grasses that provide more than half the calories consumed by animals (including humans) every day. Yet, in spite of their obvious importance, the origin and evolution of grasslands has remained relatively obscure until recent decades when evidence from fossil grasses, vertebrates, and soils (palaeosols) has increased significantly.

A review by Thomasson (1987) of the history of palaeoagrostology indicates that undoubted fossil grasses are more widespread in the fossil record than previously thought, having been reported from most continents and many stratigraphic levels dating from the Oligocene; reports of probable fossil grasses may extend the age of the oldest grasses to the Eocene. The macromorphological remains of undoubted fossil grasses include anthoecia (husks) and caryopses, leaves, stems, roots, and rhizomes; many show external and internal micromorphological details (Fig. 1) that provide extensive information about phylogenetic relationships in several groups of grasses, the physiological pathways of photosynthesis in certain grasses, and diet in some herbivores. Macrofossils also ultimately constitute the most direct evidence for understanding the origin and evolution of grasslands. Microfossils, in the form of pollen and silica bodies (phytoliths), generally are less reliable for documenting the origin and spread of grasses and grasslands.

The most complete and remarkable record of fossil grasses comes from Late Oligocene–Miocene strata in central North America (Thomasson 1987). By the Late Miocene, all subfamilies of the Gramineae are present in these deposits (along with abundant remains of grazers), clearly indicating the widespread presence of grasslands in that region since at least the Middle Miocene.

The spread of grasslands in central North America during the Tertiary is evidenced by a dramatic increase in both numbers and varieties of fossil grasses (Thomasson 1987). From a comparatively limited Late Oligocene record of one genus (*Berriochloa*, including *Stipidium*) with only two or three species, a rich Late Miocene record comprises at least six genera (*Archaeoleersia*, *Berriochloa*, *Graminophyllum*, *Nassella*, *Paleoeriacoma*, and *Panicum*) with as many as 20–30 different species. Although living descendants of these Late Miocene grasses (e.g. *Nassella* and *Piptochaetium*) are especially common in open grasslands of Central and South America, some are found throughout the world (e.g. *Panicum* and *Stipa*). Tertiary grasslands undoubtedly disappeared under the harsh climate of the Pleistocene and were replaced by boreal forests and taiga; consequently modern grasslands are a post-Pleistocene development in central North America.

Fossil evidence for grasslands in other parts of the world is limited. Palmer (1976) provided conclusive evidence from grass cuticles for the presence

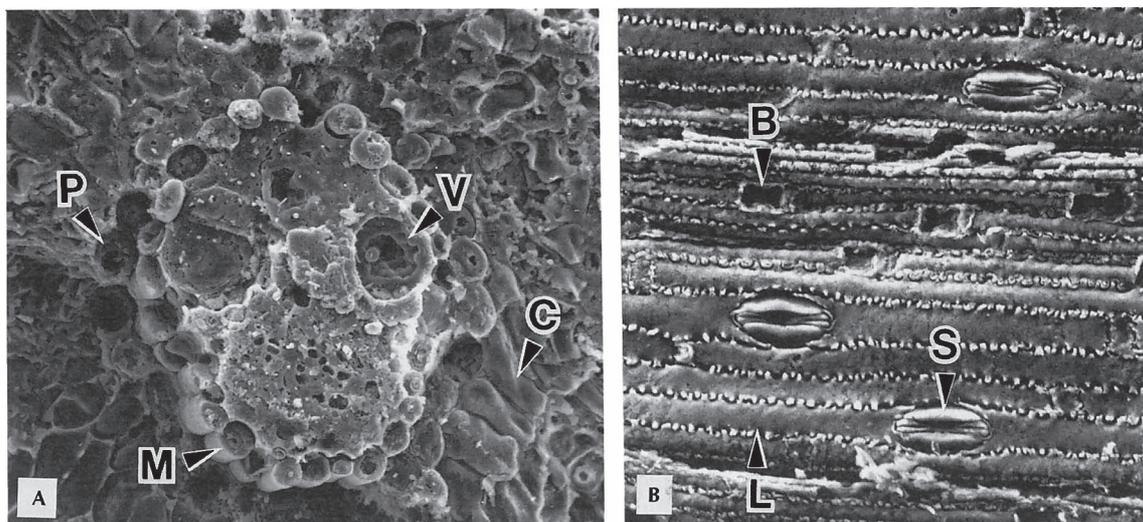


Fig. 1 A, Cross-section of vascular bundle in a grass leaf from Minium Quarry, Late Miocene, Northwest Kansas, $\times 500$. Note the double bundle sheaths. M = mestome, P = outer parenchyma, V = metaxylem vessel elements, and C = slightly radiate chlorenchyma. B, Surface of a grass leaf from locality KO45 in the Late Miocene Lukeino Formation, Kenya, $\times 620$. L = long cells with sinuous walls, S = stomata, and B = silica body cavities. (Photograph A by J. R. Thomasson, B by B. Jacobs.)

of open grasslands during the late Pleistocene in Africa; and B. Jacobs and G. J. Retallack independently (personal communication) have recently discovered fossil grasses in Miocene strata in Kenya that show great potential for elucidating the role of grasses during the Late Tertiary in Africa (Fig. 1B). Although well preserved grasses are known from Europe, they have not been studied sufficiently to suggest a specific habitat (e.g. grassland, woodland, etc.).

Next to fossil grasses themselves, the strongest indirect evidence for the origin and evolution of grasslands comes from studies of the dentition and skeletal structure of fossil vertebrates. Some studies of the vertebrate evidence suggest that grasslands first appeared in South America during the Eocene or Oligocene, in Africa during the Oligocene, in North America during the Late Eocene to Early Oligocene, in Central Asia, China, and Western Asia during the Miocene, and in Australia during the Pliocene (Webb 1977; Wright 1986). Other studies (see below) of large, mobile herbivores such as horses suggest that true grasslands (i.e. savannas, as opposed to woodlands with patches of grass) did not appear until the Middle Miocene.

Finally, palaeosols (fossil soils) provide clues to the emergence of grasslands. Fossil grassland soils can be recognized by the presence of calcic horizons, phytoliths (silica bodies), and grass-like root traces (the biological nature of the latter has only occasionally been documented by cellular details).

Palaeosols provide evidence for many features of ancient environments, including the nature of the plant community (i.e. grassland vs. forest) (Wright 1986). Contrary to most vertebrate evidence, palaeosols suggest that grasslands of a savanna or pampas type may have appeared during the Oligocene in North and South America; that small areas of relatively treeless prairie may have emerged in central North America (South Dakota) by the Late Oligocene; and that grasslands may have appeared in Northern Pakistan and India, and the Rift Valley in Kenya and Tanzania during the Miocene.

Grazers

One of the most striking features of the later Cenozoic (Neogene) terrestrial fossil record on all continents is the appearance of hooved mammals with limbs adapted for high speed running and dentitions adapted for dealing with a diet high in cellulose and/or grit. In the modern world these adaptations occur in such herbivorous animals as horses, bison, and certain antelopes and kangaroos that inhabit open grasslands and subsist exclusively or primarily on a diet of grasses. These 'grazers' contrast with the 'browsers' (e.g. moose, tapir) that consume primarily the leaves of dicotyledonous plants. Modern ecological studies have shown that many herbivores both graze and browse and are thus 'mixed feeders', but the end members are

none the less sufficiently distinct to be useful categories in discussing the evolution of the ungulates, or hooved mammals.

Structural features of the limbs and dentitions that distinguish modern grazers from browsers have been used to separate fossil ungulates into feeding categories, and to document the fact that the grazing habit has arisen independently in many families, primarily during and since the Miocene (a time of world-wide climatic deterioration; Janis 1984). Most published studies have identified as grazers those ungulates with hypsodont teeth (high crowned, where the height of the enamel-covered crown exceeds its length or width). Complex infoldings of the tooth crown and the presence of reinforcing cement on the occlusal surface are additional features characterizing the hypsodont teeth of nearly all living grazers. The postcranial skeletons of fossil ungulates with hypsodont teeth, where known, usually exhibit elongate limbs, especially in the distal segments (below the wrists and ankles). The correlation between grazing habit and hypsodont teeth and long limbs is good, but not perfect; an exception is the hippo, which does not have exceptionally high-crowned teeth and certainly lacks long limbs, but is clearly a grazer in the strictest sense, consuming only grass. (Would-be palaeoecologists can perhaps take some small comfort from the fact that the hippo feeds only on tender new growth — in contrast to the zebra, a more orthodox grazer, which consumes the older, tougher tops of plants).

With these qualifications in mind the most frequently cited example of a progressive adaptation to grazing — the evolution of the horse — may be examined. The accepted dogma among vertebrate palaeontologists has been that extensive grasslands appeared in the Miocene simultaneously with the first horses having high-crowned teeth and reduced lateral digits ('side toes') on the feet. Since it was first stated in the nineteenth century by R. Kowalevsky, the hypothesis of a coevolutionary relationship between the spread of siliceous grasses and the diversification of the horse family has received support from an increasingly well documented fossil record of the Equidae, especially in North America.

In the Eocene and Oligocene all horses had relatively short, strongly tridactyl feet and very low-crowned teeth, although a trend toward increased lophodonty ('ridginess') of the tooth crowns can be observed in the transition from Early Eocene *Hyracotherium* through Late Oligocene *Miohippus*.

Recent study of microwear facets on the cheek teeth show that these early horses ate relatively soft, low-fibre vegetation that required crushing and a limited amount of slicing, but little or no grinding (Rensberger *et al.* 1984). This interpretation is consistent with the palaeobotanical evidence for extensive forests and woodlands in western North America in the Early Tertiary.

The first hypsodont equids are included within *Merychippus* (*sensu lato*) from the Middle Miocene, some 17–18 Ma. Their habitat should probably be characterized as savanna woodland rather than open grassland, judging by the palaeobotanical evidence and by the fact that most contemporary ungulates (oreodonts, camels, protoceratids, dromomerycids, tapirs, rhinos, chalicotheres) had low-crowned dentitions. By 12 Ma, however, the *Merychippus* stock had diversified to such an extent that fossil beds in the central Great Plains frequently contain as many as five additional genera of 'grazing' horses [*Protohippus*, *Pliohippus*, *Calippus* (Fig. 2), *Pseudhipparion*, *Neohipparion*] as well as three 'browsing' genera (*Anchitherium*, *Hypohippus*, *Megahippus*), which are essentially much enlarged but otherwise little modified derivatives of the Oligocene *Miohippus*. *Parahippus*, morphologically intermediate between the 'browsing' and 'grazing' groups, is also found in the same death assemblages, making the Late Middle Miocene the time of greatest generic diversity within the Family Equidae. Stratigraphically higher deposits in the same area exhibit sedimentological and palaeobotanical evidence for a drier climate, fewer trees and more extensive grassland, facts that accord well with the extinction of the last genus of browsing horse 9 Ma, when eight well demarcated hypsodont genera were still thriving.

It is perhaps during this interval that the closest analogies can be drawn between North American savanna ecosystems and those of modern Africa (Webb 1983). Later Miocene deposits (5–8 Ma) record increasing aridity and further restriction of woodlands in the Great Plains. Selective extinctions of browsers occurred (all North American rhinos, dromomerycids, protoceratids, and gelocids) and hypsodont taxa also declined in diversity; all but two generic lineages of horses became extinct. By the Early Pliocene, surviving equids included only *Equus* (which remained abundant through the Pleistocene in North America and into the Recent of the Old World as zebras, asses, and horses) and *Nannippus* (a diminutive, extremely hypsodont form that probably still retained lateral digits) which became extinct at the end of the Pliocene.

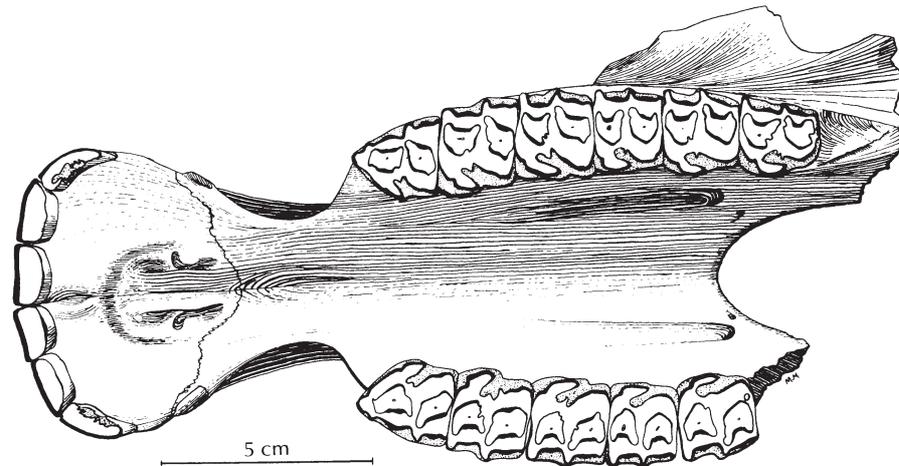


Fig. 2 Skull of extinct North American horse, *Calippus*, in palatal view showing laterally expanded muzzle and linear arrangement of incisors, presumably an adaptation for close cropping of siliceous grasses at ground level. Cheek teeth are prismatic, hypsodont, and heavily invested with cement in this genus, further indications of a grazing habit. *Calippus* was the first equid to evolve cheekteeth with a hypsodonty index (height/length of unworn teeth) exceeding 2.5, achieving this by the Middle Miocene, 14 Ma. It may not be coincidental that proboscideans (both mastodons and gomphotheres) reached North America at almost exactly the same time; like modern elephants, these early tuskers probably opened up areas of forest and woodland, thus encouraging the spread of grasslands and grazers.

The Late Tertiary decline of the Equidae has been much discussed. Some authors have pointed to parallel increases in diversity and abundance of contemporary ruminants (bovids, antilocaprids) and have suggested a causal relationship, attributing the differential evolutionary success of the cloven-hoofed ungulates to their remarkable ability to digest cellulose in the forestomach. Equids, in contrast, with their 'hindgut fermentation' were considered less efficient. Recent studies have complicated the picture, however. It appears that in some situations — namely an overabundance of high-fibre, low quality grass — horses may be more efficient than ruminants in utilizing grasslands (Janis 1984). Perhaps this accounts for the fact that horses, despite their decline in generic diversity, continued numerically to dominate Great Plains assemblages of large mammals from the Pliocene until well into the Late Pleistocene.

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1.12 Hominids

R. L. SUSMAN

Early hominids

Hominid evolution begins roughly 4 Ma with the first bipedal ape-men and ends with the origin of our own species (Fig. 1). The first stage is characterized by the appearance of *Australopithecus afarensis*, an ape-man that lived between 4 and 3 Ma in Eastern Africa. *A. afarensis* was highly sexually dimorphic, with males weighing as much as 80 kg and females as little as 30 kg. These earliest hominids had small brains (350 cm³), long upper limbs and short lower limbs compared with later hominids; their fingers and toes were long and curved by human standards. Many anatomical features suggest that at this stage of hominid evolution our ancestors still climbed trees while, at the same time, they were becoming bipedal (Stern & Susman 1983). There is no archaeological record at this time nor is there any anatomical evidence from the hand of *A. afarensis* that these early hominids used bone or stone tools.

Between 3 and 1.75 Ma there is a profusion of hominid species, including *Australopithecus africanus*, *Paranthropus robustus*, *P. boisei*, and *Homo habilis*. *A. africanus* had a brain size of 450–500 cm³ (measured in six individuals) and weighed, on average, around 50 kg (females c. 30 kg and males up to 65 kg). *A. africanus* was notable in having very large teeth, particularly the premolars and molars which are used to grind food; the surface area of premolars averaged 123 mm², compared to 107 mm² in the premolars of *A. afarensis*.

While some authors view *A. afarensis* and *A. africanus* as very similar (and perhaps even members of the same species), others maintain that *A. africanus* is the successor to *A. afarensis*. Morphologically, there are good reasons to conclude that *A. afarensis* was both specifically distinct from, and ancestral to, *A. africanus*. These include a progression in brain size, an increase in tooth surface area, and changes in the hip which may reflect an increasing (but not yet complete) reliance on bipedalism as a means of moving on the ground.

P. robustus occurs slightly later in the fossil record (> 2–1.2 Ma) than *A. africanus*. *Paranthropus* had huge teeth with premolars of 179 mm², and a brain averaging 500–550 cm³. Although these robust australopithecines are traditionally considered to have

been much larger than their gracile counterparts, the former may have been larger only with respect to their jaws and teeth; body weight in the two groups did not differ as much as their jaws and teeth might suggest. New palaeontological evidence uncovered at the Swartkrans, South Africa, suggests that *P. robustus* possessed a hand that was morphologically capable of human-like precision gripping, and may have used bone and stone tools to procure plant foods (Susman 1988). *P. robustus* was essentially a ground-dwelling, bipedal hominid — more adapted to life on the ground than either *A. afarensis* or *A. africanus*. The latest surviving members of this robust lineage became extinct 1.2 Ma.

Contemporary with *Paranthropus* were the first members of the genus *Homo*. The earliest was *Homo habilis*, a species that lived mostly on the wooded savannas, in the vicinity of large lakes or along rivers. Known principally from East Africa, *H. habilis* had a bigger brain than either *Australopithecus* or *Paranthropus*, with an average cranial capacity of 650–700 cm³. It had smaller teeth, with a premolar grinding surface of 109 mm², and correspondingly smaller jaws and chewing muscles. Its limbs (hands, feet, and leg) and limb proportions are decidedly human-like. In many details of the foot and hand *H. habilis* is similar to *P. robustus* as well as humans. *H. habilis* is found with stone artifacts, and its tool tradition is known as the Oldowan (Leakey 1971). The Oldowan consists primarily of flake-tools and tools made of quartzite and chert, trimmed on only one edge for the most part. There is no evidence from marks or indications of burning of animal bones at *H. habilis* sites to suggest that hunting was a major subsistence activity at this stage. At the same time plant remains (including pollen) at some sites indicate that plant food gathering was still a major occupation.

Homo erectus

At roughly 1.5 Ma *H. erectus* appears in the fossil record. *H. erectus*, thought to be the successor to *H. habilis*, represents a major adaptive shift. *H. erectus* is found throughout the Old World, from Africa to Europe and the Far East. There is a considerable

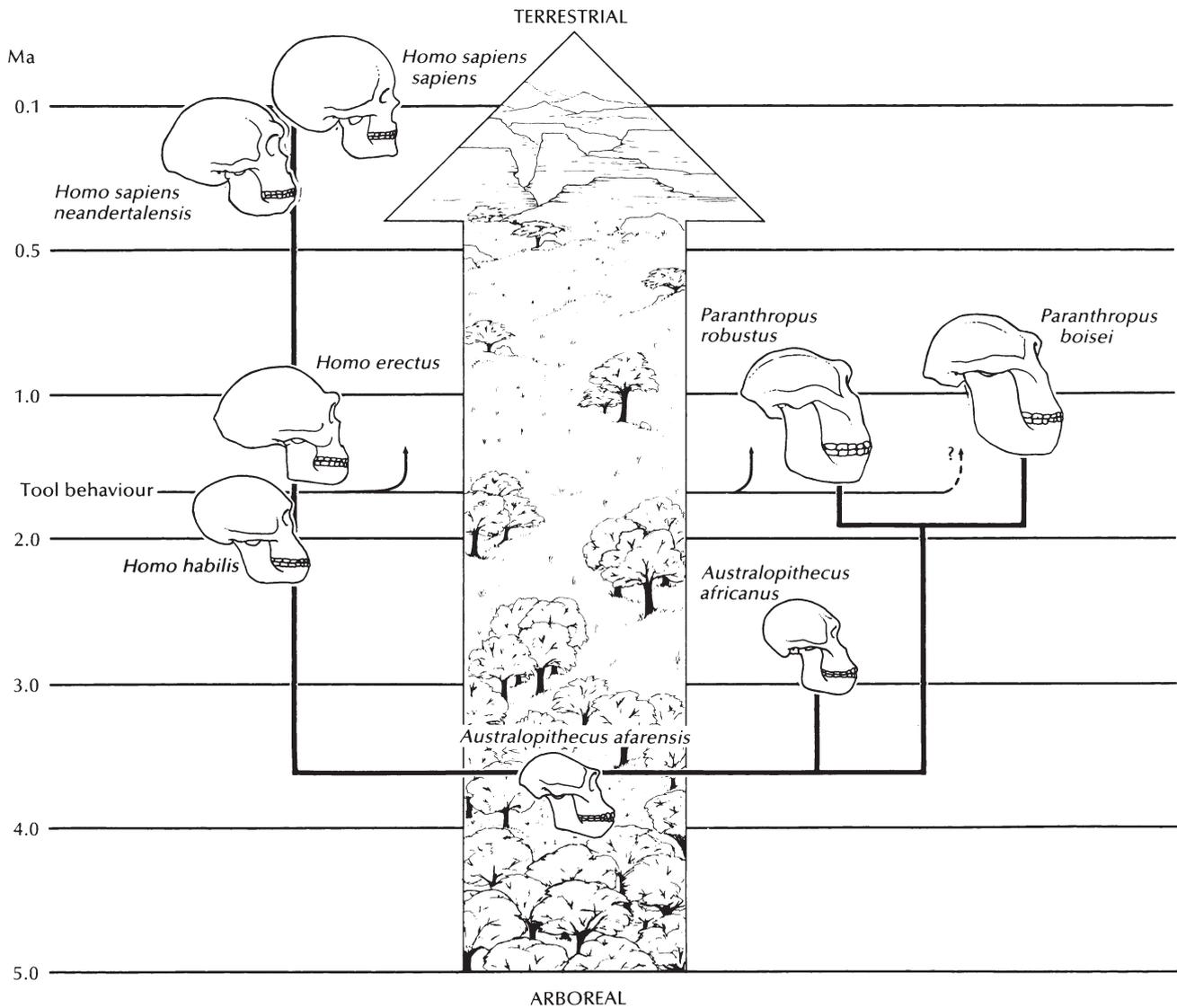


Fig. 1 Phylogeny of Plio-Pleistocene hominids from the earliest, *Australopithecus afarensis* (> 3 Ma) to the most recent, modern humans (*Homo sapiens sapiens*). Hominids continued to exhibit climbing adaptations until the appearance of *H. erectus*. Stone tools are firmly documented at c. 2 Ma (and may date back to 2.4 Ma) and were used by *Paranthropus*, as well as *H. habilis* and their descendants. The placement of *A. africanus* on the tree is equivocal.

increase in body size at this stage, a reduction in sexual dimorphism and in tooth size, and a considerable expansion of the brain. The skull of *H. erectus* is characterized by a very thick braincase with a volume of 1100 cm³, a long, low profile, very thick brow ridges, a well developed ridge on the occipital bone, a skull that has its widest diameter low down on the vault, and the absence of a chin.

With the advent of *H. erectus* there was a shift in subsistence from vegetarianism (and perhaps some scavenging) to hunting. Also at this time the first clear associations of hominids and charred animal

bones occur suggesting that *H. erectus* used fire to prepare, and possibly cook and/or preserve game. The stone artifacts recovered with *H. erectus* show technical improvement over the earlier Oldowan. This stage of cultural evolution has been called the Acheulean, and is characterized by large (35 cm long) hand axes. Although in Asia and Eastern Europe a modified Oldowan (pebble-chopper) industry persists into *H. erectus* times, in Africa and Western Europe hand axes characterize the Acheulean industry. Hand axes were made by flaking a stone core on two sides and creating a tool

that was sharp over most or all of its circumference. These tools not only indicate enhanced skills in perceiving a final form unlike the shape of the raw stone, but also greater selectivity in the choice of raw materials. As the Acheulean industry progressed, there is evidence of refined flaking techniques and the use of soft hammers including wood, horn, and bone. Use of soft hammers allowed the manufacture of finer edges on cutting and chopping tools. The remains of selected large mammals with cut marks, and indications of burning at *H. erectus* sites, suggest that hunting was a major subsistence activity at this stage. At the same time plant remains (including pollen) at Acheulean sites indicate that plant food gathering was still a major part of the subsistence activity of *H. erectus*.

Archaic *Homo sapiens*

The *H. erectus* grade existed for more than one million years. Their successors have been called archaic *H. sapiens*, and early representatives have been unearthed principally in Africa and Europe. Fossils indicate that by 300 000 years ago the earliest *H. sapiens* had spread throughout the Old World. There are conflicting views as to where *H. sapiens* originated from its geographically dispersed predecessor, *H. erectus*. Some suggest that local populations of *H. erectus* in different parts of the world evolved separately into the different races of *H. sapiens*. Another theory is that only a single population gave rise to *H. sapiens* and that this population eventually replaced the others. Confounding a better understanding of this phase in hominid evolution is a dearth of both firm radio-metric dates and good archaeological sites, and the fragmentary condition of hominid fossils.

Fossils from this time period include a distorted skull from Steinheim, West Germany, a partial braincase from Swanscombe, England, a skull from Kabwe, Zambia, and a partial skull from Bodo, Ethiopia. The cranial volume of archaic *H. sapiens* reached 1200–1300 cm³ (within the range of modern humans). The braincase is also thinner than that of *H. erectus*, with a somewhat higher forehead and a shorter face.

The stone tool industry associated with archaic *H. sapiens* indicates that as early as 500 000 years ago Acheulean tools became smaller and at 220 000 years ago a new technological innovation was introduced. The new method of tool making consisted of first preparing a cylindrical core, then striking long blades from it. This is known as the Levallois tech-

nique, and the new culture, called the Mousterian, first appears in Europe. The Mousterian is thought to have evolved from the advanced Acheulean. The transition from Acheulean to Mousterian was a gradual one, with considerable overlap between them.

The Neanderthals

Following the archaic *H. sapiens* of the Middle Pleistocene came the Neanderthals. One popular definition of Neanderthal is that group of hominids that occupied Europe and the Near East from 100 000 to 40 000 years ago. This stage is known from fragmentary skeletal remains of only 100 or so individuals. Neanderthals are distinguished from earlier archaic *H. sapiens* by their thin skull, rounded forehead, reduced brow ridges, prominent, broad nose, rounded orbits, flattened cheek bones, enlarged cranial volume (1500 cm³ and more), large pulp cavities in their small molar teeth, and a space between their last molar tooth and the vertical part of the jaw bone. Some Neanderthal skulls had a bun on the back where neck muscles attached, but others lacked this feature. Some Neanderthal jaws had a very weak chin, while others had a prominent mental eminence. Neanderthals were stockily built, with very thick-walled long bones even in the very young.

The Mousterian culture is closely associated with Neanderthals of the later Pleistocene, a period marked by increased cultural diversity. There were dozens of different types of stone implements in the Mousterian tool kit. Very specialized blade-tools were fashioned from pre-flaked cores, and pressure flaking was used to sharpen their edges. The Mousterians hunted large mammals and gathered plant foods. Our knowledge of their subsistence is aided by the fact that Mousterian artifacts and Neanderthal remains are found in cave sites (unlike earlier excavations of archaic *H. sapiens* that are found in fluvial deposits and in open-air sites).

Archaeological evidence reveals that Neanderthals buried their dead. Evidence of magico-religious beliefs comes from excavated grave goods. Hunting practices involved the exploitation of relatively few large species and the year round occupation of sites (rather than seasonal migration). Other cultural practices included the construction of shelters, the application of surgical procedures to the sick and injured, and the widespread use of fire. Around 40 000 years ago Neanderthals disappeared from the fossil record.

Modern humans

The remains of modern humans in the Upper Palaeolithic are far more common than those of Neanderthals, because of the increased practice of burying the dead. Hominid fossils in the 40 000 year time range are virtually indistinguishable from modern humans (some earlier remains dated *c.* 90 000 are also very modern looking). They had small, broad, non-projecting faces, high foreheads, protruding chins, and large (1500 cm³) cranial capacities. Their stature was similar to that of modern humans, in the 168–182 cm range. Jaws and teeth recovered from Europe suggest that they had widely varying diets. There are also Upper Palaeolithic fossil remains from Asia, Africa, and the Pacific.

Modern humans of the Upper Palaeolithic possessed a range of stone tool industries. The refined Upper Palaeolithic industries produced blade tools that were finished by soft hammers and pressure, rather than percussion flaking. Many of the stone tools were hafted onto arrow or spear shafts; other projectile points were made from bone and tusk. Scrapers, borers, and small cutting tools were fashioned for the preparation of shafts, skins, as well as food-stuffs.

Humans of the Upper Palaeolithic hunted, fished, and gathered plant foods in a wide range of environments from warm and humid to cold climates. In some areas, such as Northern Europe, there is evidence of seasonal exploitation of migrating game. Fossil evidence also reveals that rhinoceros, mam-

moth, and bear were hunted. In coastal areas there was heavy exploitation of marine resources. At two sites in Germany over 99% of the mammalian faunal remains consist of reindeer.

There is a considerable amount of cave art and plastic art beginning about 30 000 years ago in Europe. The functional significance of cave and chattel art has been debated but most subscribe either to the theory that art is related to hunting rituals occasioned by periodic (seasonal) shortages of food, or that the symbolism had sexual-reproductive connotations.

Humans in the Upper Palaeolithic survived injuries and disease to a greater extent than earlier hominids. The life expectancy of humans in the Upper Palaeolithic had improved over that of the earlier Neanderthals, although it was still low by modern day standards. Roughly half of European and Asian individuals reached the age of 21 years, and only 12% reached 40 years old.

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