

The results of this analysis indicate that the fossil taxon is nested between the genus *Petrosavia* and the family Triuridaceae, a completely achlorophyllous saprophytic clade. The clade formed by *Petrosavia*+fossil taxon+Triuridaceae is present in the all of the most parsimonious trees as well as in the consensus tree, and supports the possibility that the extinct plants were also saprophytic and achlorophyllous. We cannot be certain that the Turonian representatives of this clade were achlorophyllous, but an earlier origin of the clade, implied by the already modern aspect of the flowers and the diversity of species of Triuridaceae represented in these sediments, is consistent with this possibility. If so, this represents the earliest known fossil evidence of the saprophytic habit in angiosperms. Today, modern Triuridaceae are typically found in tropical forests, as saprophytes growing in leaf litter, or sometimes in more specialized habitats such as termite mounds.

The new fossils not only provide the oldest record of a monocotyledonous flower; they are also the most unequivocal and phylogenetically best understood of the putative early monocotyledonous fossils. The highly specialized nature of the presumed modern relatives of these monocotyledonous flowers presents a dilemma in our understanding of early monocotyledon and angiosperm diversification. Either the monocotyledonous clade is much older than its fossil representation indicates, or our interpretation of what constitutes a 'primitive' monocotyledon must be revised.

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Natural selection on human twinning

The frequency of twin deliveries varies among human populations¹. The highest twinning rates for caucasian populations have been recorded on the archipelago of Åland and Åboland, in south-west Finland^{2,3}, whereas multiple deliveries in adjacent mainland areas are historically rarer³. Using data from the pre-industrial era (1752–1850), we compare the lifetime reproductive success of mothers who produced twins with that of mothers of singletons in these archipelago and mainland sites. When we restrict our analysis to mothers with a genetic tendency to produce twins, we find that lifetime reproductive success is maximized by having twins on the archipelago, but by having singleton offspring on the mainland. This result is consistent with the difference in twinning rate being maintained by natural selection.

Our data are from Finnish church records of the pre-industrial period. During this era, twinning frequency was 21.3‰ on the archipelago and 14.9‰ on the mainland (comparison of twinning rates between 17 archipelago and 16 mainland parishes: $F_{1,25} = 35.32$, $P < 0.0001$). We collected data for eight random parishes on the mainland (Artjärvi, Ikaalinen, Haukipudas, Loimaa, Nurmijärvi, Paltamo, Sipoo and Tohmajärvi) and two on the archipelago (Rymättylä and Kustavi), and data for a further eight parishes on the mainland and fifteen on the archipelago (some small parishes were combined in the analysis) were collected by Mattila⁴ and Eriksson³, respectively.

We analysed the reproductive output of 81 mothers of twins from the archipelago (the parishes of Hiittinen, 60° N 22° 30' E, Kustavi, 60° 30' N 21°30' E, and Rymättylä, 60° 15' N 22° E, were used as area replicates within the archipelago) and 86 mothers of twins from the mainland (Ikaalinen, 61° 45' N 23° E, and Pulkkila, 64° 15' N 26° E). We paired each mother of twins with a control mother the same age (± 3 years) who had delivered only singleton children⁵. For each mother, we calculated realized lifetime reproductive output as the total number of children, including possible illegitimate children and those from earlier marriages, who had reached an age of 15 years.

Mothers of twins and singletons on the archipelago made the same contribution to the subsequent population, but on the

mainland, the reproductive output of mothers of twins was significantly lower than that of control mothers (Fig. 1a). As the figures refer to lifetime reproductive success, they include the effects of higher childbirth mortality ($G^2 = 9.93$, d.f. = 1, $P = 0.0002$) among mothers of twins.

Because we can safely assume that only dizygotic, but not monozygotic, twinning has a genetic component⁶, only the analysis of dizygotic twinning is relevant to evolution of the number of children produced at one time that is driven by natural selection. Given the demographic nature of our data, we can presume that the group of mothers who delivered twins of different sexes have a higher genetic tendency towards twinning than others: all twins of opposite sexes are dizygotic, whereas twins of the same sex may be either mono- or dizygotic. Our results from a smaller data set, using only mothers with twins of different sexes, confirm the evolutionary inference: the lifetime reproductive success of mothers of twins relative to that of singleton mothers differed significantly between the archipelago

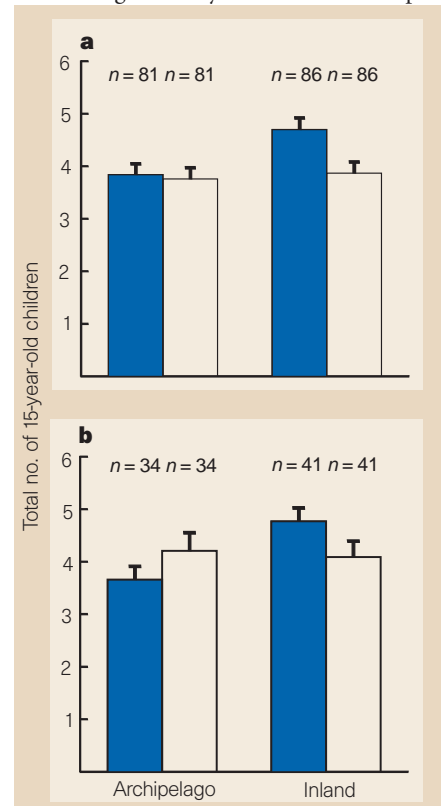


Figure 1 Total numbers of children (+ s.e.) raised successfully to adulthood by mothers of singletons (dark bars) and mothers of twins (pale bars) in archipelago and mainland areas of pre-industrial Finland. **a**, All mothers of twins included (ANOVA: difference between areas, $F_{1,3} = 2.46$, $P = 0.21$; difference between mothers of twins and singletons, $F_{1,165} = 6.11$, $P = 0.015$; interaction between area and mother type, $F_{1,165} = 4.47$, $P = 0.036$). **b**, Mothers with only different-sex twins included (area, $F_{1,3} = 1.73$, $P = 0.28$; mother type, $F_{1,73} = 0.08$, $P = 0.77$; area \times mother type, $F_{1,73} = 6.44$, $P = 0.013$).

ago and mainland areas (Fig. 1b).

Our study provides evidence for the hypothesis that differences in twinning frequencies in historically relatively isolated human populations may be maintained by natural selection, as the differences in the profitability of twinning between the areas are consistent with the predictions of life-history models. Such models suggest that predictable resource levels favour the evolution of increased reproductive output^{8,9}. In the archipelago, the amount of food available has traditionally been relatively high and constant, with total crop failures being rare and with survival ensured by fishing. In poor mainland areas, on the other hand, crop failures and subsequent famines have been common throughout the centuries¹⁰.

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A Roman “implant” reconsidered

A supposed “wrought iron” dental implant¹ was recently reported from a second century CE Gallo-Roman necropolis in Chantambre (Essonne, France), but in my view the data need to be re-evaluated in the light of what is known regarding ancient and modern dentistry^{2–4}. The item is described as “severely corroded”, for example, but an X-ray reveals a perfectly formed tooth with a smooth, intact surface free from the pitting expected on a small iron object interred for nearly 2,000 years under less than ideal conditions. The archaeological context and data on finds of iron in this and other tombs are not provided.

The production of a small, detailed replica of a human tooth in iron would test the skills of modern crafters. Less likely is that it would be accepted by a human body under questionably sterile conditions. This tooth appears to be a natural canine stained with oxides from proximity with an iron-rich

object. This explains the detailed shape, its appearance in the X-ray, and the analytical results reported¹. The principal types of known ancient dental appliances fall into two categories: decorative Etruscan examples of the seventh to first centuries BC^{2,5,6} and functional Near Eastern wire examples, developed in about 400 BC to stabilize loose teeth until they could regain natural anchorage⁷. Both types are known from the ancient literature and from unequivocal archaeological examples. Dental implants are unknown in the ancient medical texts or literature, and no archaeological examples have been verified.

Modern dental techniques developed late in the nineteenth century and are still evolving. The development of sophisticated implant materials that are accepted by the body is a very recent achievement^{8,9} related to parallel research done in bone joint replacement. Dental implantology is still emerging from experimental stages¹⁰, and requires sophisticated high-technology alloys and bonds of complex composition. With space-age technology and the most modern aseptic conditions, a five-year success rate of around 85% has now been achieved. Dental loss is commonly thought of as a normal factor of ageing, with replacements being limited to the well-to-do among the most industrialized countries. The likelihood that the ancient Romans would have been interested in attempting to fashion dental implants to replace lost teeth is remote.

I therefore suggest that the Chantambre specimen is a natural tooth stained with iron oxides, and not an iron implant. We have good reason to marvel at the massive construction projects of the Romans, and at their delicate carvings on impressively hard gemstones. The ability of ancient “surgeons” throughout the world to cut pieces from human skulls and to have many of their patients survive is equally amazing. But whether they were interested in or capable of creating true dental implants in my view requires more evidence.

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Crubézy et al. reply — We disagree with Becker’s view that the dental implant described in our earlier Scientific Correspondence¹ is a natural canine stained with iron oxides. The dental implant was located in a position normally taken by the upper second right premolar, a position in which a normal canine would not be found. Furthermore, the only goods associated with this burial were pottery, not iron or any metal objects². Even if there had been iron oxide contamination, it is unlikely that it would have affected only one tooth. Figure 1a in our earlier Scientific Correspondence shows that the piece of metal is corroded on its periphery; the “smooth, intact surface” observed on the X-ray is a common artefact of the technique. Finally, we have already noted that the implant was broken and that metallurgical analysis unambiguously identifies it as metal and not as a biological tissue.

The fabrication of a “detailed replica” of a human tooth is not as dubious as Becker maintains. Chemical analysis indicates that the metal was given its shape through hot-hammering and folding, a basic technique of ancient blacksmiths, including those of Gallo-Roman times. Concerning the successful retention of the implant, it is possible that the iron could have facilitated the osseointegration³; the absence of aseptic conditions does not systematically imply the rejection of the implant. The success of this procedure in an ancient population is no more amazing than the 70 per cent survival rate among patients who underwent trepanation⁴ or the successful performance of cataract surgery⁵.

Thus our anatomical, morphological, metallurgical and microscopic analyses of this specimen document, without question, the successful implantation of this dental prosthesis.

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