International Journal of Primatology, Vol. 4, No. 4, 1983

Mandibular Ontogeny in the Miocene Great Ape *Dryopithecus*

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Received February 5, 1982; revised October 9, 1982

The type mandible of Dryopithecus fontani, *Lartet 1856, has been discovered to be not fully adult. Its development corresponds in dental age to that of a 6- to 8-year-old chimpanzee. Because of its immaturity, a number of seemingly distinctive features of this mandible (some of which resemble hominids) would have been lost with full adulthood. Closed tooth rows, a recurved canine, and a vertical ascending mandibular ramus are related to the age of the specimen. They therefore do not foreshadow hominid characteristics. It is stressed that consideration of individual age is an important factor in interpreting the dentitions of fossil and extant hominoids.*

KEY WORDS: Dentalage; juvenile type; *Dryopithecus.*

Eduard Lartet in 1856 described as *Dryopithecus fontani* a partial mandible of an ape from the Miocene locality of Saint-Gaudens (Haute-Garonne), in the lower foothills of the Pyrenees, southern France. Together with this find of three parts of one mandible, he also reported an ape humeral fragment that had been recovered at the same time. The humerus consists of a nearly complete diagphysis, lacking epiphyses. Lartet initially suggested that the loss of epiphysis might have been due to its being subadult and tentatively suggested that the upper limb bone might have

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belonged to the same individual as the type mandible (Lartet, 1856). Albert Gaudry (1890) subsequently described another and more complete mandible from Saint-Gaudens and discussed further the phyletic position of *Dryopithecus*. Finally, Harlé (1898) described and discussed a third mandible and some isolated but partly associated teeth from this same site. These half-dozen specimens constitute the entire sample from the type locality of the type species of *Dryopithecus*. Because of its possible importance to human phylogeny, *Dryopithecus fontani* has been extensively discussed (Harlé, 1899; Piveteau, 1957; Le Gros Clark and Leakey, 1951; Simons and Pilbeam, 1965).

Recently, one of us (ELS) had the opportunity to study the original French *Dryopithecus* mandibles in Paris and at Bordeaux. In the course of this study, a radiograph of the original type specimen of *Dryopithecus fontani* was made. This type (Specimen No. HGP 2a, b, and c, Muséum National d'Histoire Naturelle, Paris) has three parts, constituting a left horizontal mandibular ramus with P_3–M_2, an anterior symphyseal fragment with incisor roots or root sockets, and a right mandibular ramus with $\overline{C}$ through M_3 and part of the coronoid process of the ascending ramus.

The radiograph (Fig. 1) shows that neither root sockets nor roots had yet formed in the M_3 crypt of this individual. Relative immaturity explains why the only partially formed third molars of this individual were lost postmortem. In addition to incomplete M_3 development, this type specimen shows several other subadult features. The unerupted M_3 crowns had not yet produced an interstitial wear facet on either M_2. The right P_4 and the right $\overline{C}$ had not reached the occlusal level of the remainder of the dentition and the tip of the root of the right $\overline{C}$ had apparently not yet formed. The canine is also not fully erupted, the base of the enamel of the right $\overline{C}$ being 0.73 cm below the base of the other teeth. Relative youth is indicated by the lack of wear facets on the crowns of P_3, P_4, and M_2. In sum, the age of this fossil ape is at the stage when $\overline{C}$, P_4, and M_3 have not fully come into place, but M_2 has fully erupted. There are few, if any, other fossil apes of this particular dental age known. The subadult age at death in both the type mandible and the partial humerus from Saint-Gaudens tends to support Lartet's (1856) suggestion that both are remains of the same individual.

According to data presented by Schultz (1956) and Mann (1975), the age of the Saint-Gaudens *Dryopithecus* type appears to have been equivalent to that of a 6-year-old chimpanzee, *Pan troglodytes*. According to the data presented by Dean and Wood (1981), the type specimen would be of an age that is comparable to about an 8-year-old *P. troglodytes*.

Realization that the canine in this individual is not fully erupted also solves the problem of the placement of the anterior symphyseal portion which contains the incisor roots. On both sides of this fragment can be seen

Fig. 1. Positive print of the lateral view of the left and right mandibular horizontal rami of the type specimen (HGP-2) of *Dryopithecus fontani* from Saint-Gaudens, France, in the collections of the Musée National d'Histoire Naturelle, Paris. Size × 1.

parts of the mesial walls of the left and right canine root sockets, but previously no convincing solution of the placement of this piece of the jaw has been reached. Typically, the three separate parts of the find have been illustrated as not contacting each other, but spaced apart, with tooth rows parallel and the symphyseal fragment floating free between them (Lartet, 1856; Genet-Varcin, 1963). Moreover, the reconstruction of *Dryopithecus fontani* with parallel-sided tooth rows had seemed confirmed in the minds of some researchers by the second specimen from Saint-Gaudens, which includes the symphysis and exhibits seemingly parallel tooth rows. Inspection of this specimen (HGP 1) shows that the tooth rows actually converge posteriorly. There have been several breaks between component parts of the jaw. Cracks offsetting the arcade arrangement are obvious on both sides of the right canine and between left P_4 and M_1. As a result of these distortions, the dental arcade of HGP 1 is not in line and has been pushed together posteriorly (Fig. 2A). Since earlier writers have compared HGP 1 principally with modern great apes, which tend to have parallel-sided or even posteriorly convergent tooth rows, the distortion of this specimen has not been noted previously. Simons (1972) has pointed out that posteriorly divergent tooth rows typically characterize Miocene apes and monkeys; where the angle of arcade arrangements can be accurately determined, all are parabolic and none are U-shaped. With this in mind, it is clear that resetting the dislocation fractures of HGP 1 would give it such a posteriorly divergent arcade (Fig. 2B). In reconstructing the *Dryopithecus* type, one of us (ELS) discovered that the symphyseal fragment contacts the right $\bar{C}$ relatively high up in a location not recognized or reported in any previous reconstruction. With this placement serving as a basis for reconstruction, it is clear that the arcades do diverge posteriorly as expected for a Miocene ape and that the third molar crypts are still located in a laterally everted position as is typical in subadult hominoids (Fig. 2B).

Recognition of the type specimen of *Dryopithecus fontanti* as an immature individual clarifies the significance of several anomalous hominid-like features that have long puzzled students of hominoid evolution. These hominid-like characteristics include the following: (1) close crowding together of the tooth row; (2) verticality of the ascending mandibular ramus preserved on the right side (the leading edge of the coronoid process is at a right angle to the long axis of the tooth row); (3) shallowness of the mandibular ramus under M_3; (4) a vertically oriented and slightly backward-directed canine axis; (5) lapping of the lower P_3 outward and around the lower canine (with no trace of a diastema between them); and (6) unclear development of transverse tori on the internal aspect of the symphyses. Judging from the size of the canines and front premolar, the second Paris specimen, HGP 1, and the third Bordeaux mandible from the

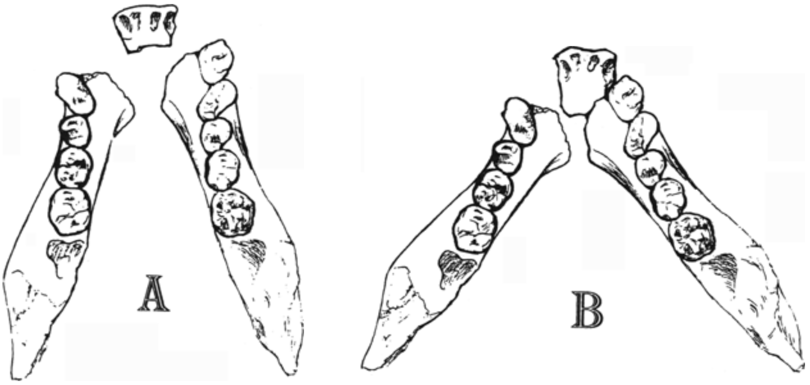

Fig. 2. Two views of the mandibular fragments of the type specimen of *Dryopithecus fontani*. One-half natural size.

Saint-Gaudens site apparently represent an adult female and an adult male, respectively. Neither of these two adult finds at Saint-Gaudens preserves as complete an ascending ramus as does the subadult type specimen, and so the angles of orientation of the long axis of the ascending ramus in relation to the horizontal axis of the tooth row cannot be determined as accurately as in the type. Nevertheless, the leading edge of the coronoid process in the Bordeaux mandible tilts posteriorly. In both adult mandibles the base of this leading edge on the left side has its anterior face arising behind the midline of M_3, whereas in the immature type specimen it arises alongside the back of M_2. Thus, with individual growth and aging, the ascending branch of the mandible in *D. fontani* moved further back in relation to the cheek teeth and sloped backward more obliquely. Such modifications are in line with other growth phenomena related to ontogenetic development in individuals of the modern great apes. This explains why, typically, diastemata occur in present-day apes on either side of the lower canine in full adults but are absent in subadult individuals. During ontogeny, the horizontal ramus deepens under the molars and becomes longer, while the cross-sectional area of the symphysis and associated tori grows thicker. All these phenomena distinguish the subadult type mandible of *Dryopithecus fontani* from the second and third (adult) finds of the species from the type locality. Of these two adult specimens, the female (Gaudry, 1890) is the more complete, retaining all lower teeth except M_3. The entire anterior mandibular body is also preserved but is broken off on each side about 1.5 cm behind the back end of M_2. As noted above, the mandibular rami have been crushed together posteriorly so that the posterior divergence typical of Miocene apes cannot be measured in this particular specimen. The P_3 of the second Paris specimen, HGP 1, and that of the third specimen in Bordeaux are quite different in absolute size, implying a sex difference, while their M_2–M_3 sizes are about the same. In spite of these differences, both mandibles, being adult, show a clear-cut diastema with a length of at least 0.5 cm between P_3 and $\bar{C}$. An even longer diastema separates lateral incisors from canines on both sides of the second Paris specimen, HGP 1. Because the left central and lateral incisors have drifted apart postmortem, they have been separated from each other and perhaps brought closer to the left canine. Consequently, the diastema lateral to the lower incisors may well have been even larger in life in HGP 1. Such an arrangement would resemble modern gorillas rather than chimpanzees.

In sum, we can now see in the *Dryopithecus fontani* type that the closed tooth row, the almost posteriorly recurved canine, and the vertical ascending ramus are age-related phenomena. They do not, as Gaudry (1890) first believed, mean that *Dryopithecus* shows dental and facial features that foreshadow hominid characters. In contrast to these conditions, early hominids such as *Australopithecus* and *Homo erectus* when ontogenetically young achieve closure between lower canine and P_3, exhibit corresponding contact facets, and retain into adulthood a shallow and thick mandible under the molars. As adults, these hominids show a forward-situated and vertically oriented ascending jaw ramus. These findings underscore the often restated but frequently overlooked necessity of considering the individual age at death in analyzing the dentitions of fossil and living hominoids. Changes in jaw and facial proportions related to chronological age necessarily affect conclusions concerning the relations that a particular fossil hominoid may have to modern hominids and pongids.

ACKNOWLEDGMENT

We acknowledge the award of an Alexander von Humbolt Foundation Senior Scientist's prize to Simons which enabled him to carry out the research reported here at the University of Kassel, West Germany.

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