PARADOLICHOPITHECUS, A LARGE TERRESTRIAL MONKEY (CERCOPITHECIDAE, PRIMATES) FROM THE PLIO-PLEISTOCENE OF SOUTHERN EUROPE AND ITS IMPORTANCE FOR MAMMALIAN BIOCHRONOLOGY

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Summary

Paradolichopithecus is a large terrestrial cercopithecine monkey probably derived from an early Pliocene Macaca stock. P. sp. is known from fragmentary remains in France, Spain and Romania in the early Villafranchian (mid Pliocene, ca 3.5-4 m.y. ago). The slightly larger P. arvernensis is known by a single female cranium (holotype) from Senèze, France and by many excellent specimens' from Graunceanu, Romania (possibly distinguishable as P. a. geticus). Both of the latter sites are of late Villafranchian age, probably 1.8-2 m.y. old (earliest Pleistocene). The genus thus ranges from early to fate (but not final) Villafranchian and may be useful as an approximate age indicator.

Résumé

Paradolichopithecus est un grand single cynomorphe terrestriel cercopitheciné. Son origine était probablement d'une groupe-souche de Macaca d'âge Pliocêne ancien. P. sp. est connu des restes fragmentaires provenant de France, Espagne et Roumanie d'âge Villafranchien ancien (Pliocène moyen, il y a ca. 3,4-5 m. a.). L'espèce un peu plus grande P. arvemensis est connue par un crâne unique femelle (l'holotype) provenante de Senèze, France, et par plusieurs spécimens excellents provenants de Graunceanu, Roumanic (peutêtre separable comme P. a. geticus). Les deux dernières gisements sont d'âge Villafranchien récent, probablement 1,8-2 m. a. (Pléistocène tout ancien). Donc, cette genre s'étend du Villafranchien ancien a récent (mais pas rerminal), on peut l'employer éventuellement comme indicateur d'âge approximatif.

Numerous species of cercopithecid monkeys have been described from the Neogene (Miocene through Pleistocene) of Europe, all currently under study by one of us (E.D.). New materials of the largest of these have recently been recovered by researches under the direction of the second author (D. N-P.) and will be described in detail by us elsewhere (DELSON, PLOPSOR, and BOLOMEY, in preparation), followed by a revision of the genus (by E.D.). The purpose of this note is to present distributional data and the outlines of the planned revision, especially as it may affect biostratigraphical considerations and mammalian biochronology.

The first known specimen referable to Paradolichopithecus was described in 1929 by Ch. DEPÉRET, in one of his last publications. A nearly complete female cranium from Senèze, France, was made the holotype of Dolichopithecus arrennensis. Unfortunately, the type species of Dolichopithecus was D. ruscinensis DE-PERET, 1889, a member of the monkey subfamily. Colobinae, while the new skull proved to be cercopithecine. This error of DEPÉRET's long confused students of fossil monkeys (see DELSON, 1973). In 1964, NECRASOV, SAMSON and RADU-LESCO described a female palate and mandible of a similar-sized cercopithecine from Grăunceanu, Romania, as the then new genus and species Paradolichopithecus geticus. They recognized the affinity of this form with the Senèze species, but erroneously considered both animals to be colobines. DELSON (1971) reported a partial male mandible and an isolated P4 of a somewhat smaller animal from Cova Bonica, Spain, but refrained from making any taxonomic changes before study of these specimens had been completed.

At the last CMNS meeting, DELSON (1974a) presented an overwiew of corcopithecid distribution in Europe, grouping these three finds and two others as "Dolichopithecus" arremensis. The other specimens are an isolated upper molar (M²) from Vialette, France, reported by SCHAUB (1943) and some deciduous teeth in a partial mandible from Măluşteni, Romania, discussed as Dolichopitheens ruscinensis by SIMIONESCU (1930; see Fig. 7). Additional specimens of "P. getiens" from Grăunceanu were briefly reported by BOLOMEY (1965) and have now been further cleaned and are under study. They include: four partial adult male skulls with teeth; a nearly complete adult male mandible; two partial subadult male mandibles; a partial subadult female maxilla and cranial fragments; some additional isolated teeth; and a number of partial long bones, including humerus, ulna, radius and femur. It is not yet possible to make definitive statements, but it appears likely that the Senèze and Graunceanu populations represented a single species best termed Paradolichopithecus arvemensis. The Romanian specimens could be designated by the subspecific nomen geticus, but the lack of an adult female skull for comparison with the Senèze holotype renders distinction difficult. On the other, hand, the three more fragmentary finds are all smaller (and apparently older) and may now be termed Paradolichopithecus sp., potentially representing an earlier stage in the evolution of this genus.

The relationships of *Paradolichopithecus* have been shown by DELSON (1973) to lie clearly with the macaques (*Macaca*) on the basis of facial form, rather than with the African baboons (*Papio s.l.*) of similar size. JOLLY (1967) suggested that "D." arvernensis might be congeneric with *Procynocephalus wimani* SCHLOS-SER, 1924 of the Chinese "Villafranchian", and SIMONS (1970) formalized this view. In fact, *Procynocephalus* is known from very limited material (most of which has been studied by E.D.), and it seems most prudent to retain the two genera as

separate until clear evidence of morphological features in common can be presented. The two genera (at least two Asian species are known) admittedly are of quite similar size and apparently equivalent terrestriality of limb bones, but they may represent parallel-trending lineages from a common ancestral stock of Macaca. The latter genus first occurs (outside Africa) in the early Ruscinian of France and the Tatrot (mid-Villafranchian equivalent) of India; known Procynocephalus is somewhat younger. Further comparisons must also be made with the South African early Pleistocene forms Dinopithecus and Gorgopithecus, Papio-like genera with rather larger teeth but unknown postcrania (see FREEDMAN, 1957). In terms of size, Paradolichopithecus arvemensis is about as large as the largest living and fossil species of Papio, but the female skull appears relatively larger by comparison to the male (see DELSON, 1974b for a general review of cercopithecid evolution).

Five southern European localities have thus yielded remains of Paradolichopit-becus, with the most complete and numerous material coming from Grăunceanu, Romania. The five sites appear to range in age from earliest to late Villafranchian i. e. mid Pliocene to earliest Pleistocene (see below). Senèze, the type locality, is widely accepted as late Villafranchian, but placed at different levels within this sub-age. HEINTZ (1968, 1970) has considered it to typify his "Villafranchian supérieur A", falling at the end of this interval, while AZZAROLI (1970) has argued for its placement in zone B of his upper Villafranchian. In part, this may be due to differing definitions of zones A and B. DELSON (1974c) has divided the Villafranchian into early, middle, late and final, the latter corresponding to zone B of HEINTZ, with Senèze central in the late Villafranchian. DELSON (1973) also suggested that an approximate chronometric age of 1.8-2.0 M.Y. could be extrapolated for the Senèze mammals from studies of diatomites and paleomagnetism.¹

¹The mammalian fossils from Senèze come from the top levels of a long section representing the filling of a crater lake (BOUT, 1969, 1970). Cores taken in this maar have allowed the study of diatomite layers and paleomagnetism. EHRLICH (1968) estimated that the diatoms represented a time span of 0.2-0.3 m.y. PREVOT and DALRYMPLE (1970) reported a basalt flow at the base of the maar date to 2.3 m.y. and a 132 m sediment core sequence which is all of reversed polarity except for a 5-10 m zone some 25 m below the top. If the total sequence does indeed represent about 0.25 m.y., this normal interval must be much shorter than the Olduvai normal event of about 150,000 yr duration and may equate to the Réunion event(s) of GROMME and HAY (1971) at about 2.0-2.1 m, y. This would indicate an age of somewhat less than 2.0 m.y. for the still younger Senèze mammals. The slightly older nearby local fauna of Le Coupet is overlain by a reverse-polarity flow dated at 1.92 m.y., while another nearby flow (at Vazeilles) is dated at 1.8 m.y., with normal polarity as expected (Olduvai event age; see BOUT, 1969). BOUT (1970) suggested that the Senèze fauna was 1.6 m.y. old, but he did not then have the definitive date on the underlying basalt, which suggests greater antiquity. Unfortunately, more precision in dating the important Senèze fossils may not be forthcoming unless the mammals can be precisely linked to the paleomagnetic stratigraphy or fission track dating can be attempted (BOUT, 1969). At present, it may be suggested that the mammals of Le Coupet lived about 2.0 m.y. ago, at the start of the late Villafranchian, while the Senèze forms lived somewhat later, probably before 1.8 m.y.

At the other end of the Villafranchian, the problem of its separation from the preceding Ruscinian is still far from being resolved. This question becomes important when considering the age of Vialette, a site clearly younger than the type Ruscinian of Perpignan, which is already late in the age. Vialette may also be slightly older than Fornace RDB at Villafranca d'Asti (type Villafranchian), where some specimens of Dicerorhinus etruscus may occur alongside D. jeanvireti (GUE-RIN, 1972) and where Ursus cf. minimus is present (SAVAGE and CURTIS, 1970; see also SAMSON and RADULESCO, 1973). If the Villafranchian is considered to begin with those local faunas equal in age or younger than Villafranca, then Vialette (as well as Hajnáčka, Măluşteni, Baraolt, etc.) would be latest Ruscinian by definition. GUERIN (1972) has suggested an "early early" Villafranchian, essentially pre-Villafranca in age, for these sites, and this view may be accepted until more formal definitions are made (perhaps at this meeting). Vialette has been found to underlie a basalt flow dated to 3.8 m.y. (SAVAGE and CURTIS, 1970; SAVAGE, in litt.), suggesting roughly 4 m.y. for the Villafranchian Ruscinian boundary2 and ca 3.9 m.y. for Vialette.

The site of Cova Bonica is unfortunately difficult to date, as it is a cave filling containing both later Pleistocene and "early Villafranchian" elements (J. MICHAUX, personal communication). Because no primate like *Paradolichopithecus* is known later in Europe, it seems safe to consider that the monkey fossils were associated with the *Trilophomys* of mid Pliocene age from the cave.

SAMSON and RADULESCO (1973) have recently evaluated the Plio-Pleistocene mammal faunas of Romania, enabling both Măluşteni and Grăunceanu to be placed in the continental biochronologic framework. They have not included primate distributions in their revision (in fact lamenting the lack of recent studies of primates and camivores on a continental scale), but DELSON (1974a) has reported that Dolichopithecus ruscinensis is present at Mălușteni, Berești and Baraolt-Căpeni, ?Mesopithecus monspessulanus at all but Bereşti (which yields an "impoverished" fauna) and Paradolichopithecus only at the first of these. All three localities were assigned to the early Villafranchian, roughly coeval with Vialette. The several local faunas of the Tetoiu (previously Bugiulesti) region have been divided into at least three zones, of which Graunceanu was placed in the oldest, intermediate in age between Le Coupet and Senèze (late Villafranchian). These authors have noted that while several "stages" can be discerned within the late Villafranchian, all are much older than the Italian sites of Farneta and Imola, on which AZZAROLI (1970) based his "Upper Villafranchian B". They are thus basically in agreement with DELSON (1974a) in separating the late Villafranchian from the final part of this age. It is clear that Grăunceanu is similar in age to Senèze on faunal grounds

²AMBROSETTI et al. (1972) give a date of 4.2 m.y. for a level heteropic with an "early Villafranchian" local fauna from Poggio Mirteto, Italy. This is most interesting, but the faunal list comprises only Anancus arvernensis and Tapirus arvernensis, two species known from Ruscinian as well as early Villafranchian localities. Thus the precise biochronological age of this local fauna (and of the date) is as yet undertermined.

(as evidenced further by the joint presence of *Paradolichopithecus arvemensis*), and the suggestion of a somewhat greater age for the Romanian locality must be investigated in more detail.

In conclusion, Paradolichopithecus species as now known span most of the Villafranchian mammal age. Small early representatives may be among the relatively few large-mammal species which first appear at the very beginning of this age. The earliest Villafranchian is the time of greatest diversity of cercopithecids in Europe, with four species known: D. ruscinensis, ?M. monspessulanus, P. sp. and a macage (e.g., at Villafranca and Balaruc-2). Analysis of the distribution pattern of these monkeys will be of interest but must await greater understanding of the local paleoenvironments determined from other taxa. No specimens of Paradolichopithecus are yet known from the middle (or "late early") Villafranchian, but they are to be expected. Most previous mammalian biostratigraphers have correlated the Pliocene Pleistocene (=Piacenzian-Calabrian) boundary with the transition from early to middle Villafranchian. In our opinion, the former boundary must be defined in the marine paleontologic realm (as with all epoch divisions) and thence correlated to the continents. The generally accepted age of ca 1.9 m.y. for the boundary as thus defined correlates closely with the start of the late Villafranchian mammal age in Europe, although the earliest localities of this age (e.g., Le Coupet) might possibly be Pliocene. On this basis, the first appearance of Paradolichopithecus arvernensis is earliest Pleistocene and may eventually serve as a marker for this horizon. Apparently the genus did not survive into the final Villafranchian, perhaps due to the onset of colder climate and changed paleoenvironmental conditions in the Eburonian. Unfortunately, Paradolichopithecus is still so rare that precise biochronological conclusions cannot yet be drawn from its presence in a local fauna, but additional discoveries should improve this situation in the future.

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