Reprinted from Nature, Vol. 345, No. 6277, pp. 712–714, 21st June, 1990

-079.

New hominid skull material from the late Miocene of Macedonia in Northern Greece

L. de Bonis*, G. Bouvrain†, D. Geraads† & G. Koufos‡

* Laboratoire de Paléontologie des Vertébrés et Paléontologie humaine, UA CNRS 720, Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers Cedes, France
† Laboratoire de Paléontologie des Vertébrés et Paléontologie humaine, UA CNRS 49 et 720, Université de Paris VI, 4 place Jussieu, 75230 Paris Cedex, France
‡ Department of Geology and Physical Geography, Faculty of Sciences, University of Thessaloniki, Greece

MIOCENE hominoid material is very scarce[1–7] and has previously only been reported as cranial fragments in the Old World. Here we describe a new specimen of *Ouranopithecus macedoniensis*, which consists of the right part of the face of an adult male with a portion of the frontal bone, a portion of the left part of the face and the maxilla with complete dentition except the right third molar. The characters of this specimen are not congruent with those of *Sivapithecus* and the pongids, but are more primitive and plesiomorphic for the recent hominid clade (*Gorilla*, *Pan* and *Homo*). The dental characters differ morphologically and metrically from those of the recent great apes and fit better with *Australopithecus afarensis*[8]. *Ouranopithecus* now seems the best candidate forerunner of the Plio-pleistocene Homininae (*Australopithecus* and *Homo*). This specimen was discovered in September 1989, in the late Miocene deposits of central Macedonia (G.K., L. de B. and G.B.), and prepared by G.K. in Thessaloniki and G. Mouchelin in Poitiers. It comes from the new locality of Xirochori in the red sandstone of the Nea Messimbria formation[9]. The fossil is the property of the University of Thessaloniki, Greece (catalogue number XIR-1).

Mandibles and maxillae of bovids, giraffe and mastodonts were associated with the face of XIR-1 (see Fig. 1). This fauna is similar to other faunas from Macedonia found in two other localities of the same geological formation—Ravin de la Pluie (RPl) and Ravin des Zouaves no. 1 (RZ1). These faunas are assigned to the Vallesian Land Mammal Age on the basis of faunal correlation with other sites. It is impossible to date the Macedonian deposits directly by radiometric methods but some other localities which have yielded similar faunas have been dated to 9–10 Myr ago (the lower part of the late Miocene). These faunas contain many grazing mammals and can be considered as open environment (savanna) faunas.

The measurements of the dentition are given in Table 1. The right M^3 is missing but the other teeth are well preserved, except for the left M^1 which was partially broken and badly worn during life. The central incisors are larger than the lateral ones. There is a diastema between I^2 and the canine (C) and a very small space between the canine and P^3. The canine is relatively large, indicating that it belonged to a male specimen. The C/M^1 length ratio is 94%, in the range of female chimpanzees or gorillas. But there is a large sexual variation in *Ouranopithecus*[10]. The canine of XIR-1 is very similar to male specimens of Ravin de la Pluie. The size of the jugal teeth is also similar to male *Ouranopithecus* and we believe XIR-1 is a male (Fig. 2). The size of the canines is smaller than in any recent or Miocene great ape[10]. Compared with a male *Proconsul nyanzae*, these canines are half the size relative to the length of the jugal tooth rows.

The jugal teeth, premolars and molars are heavily enamelled, as are *Sivapithecus* or australopithecine teeth. P^3 and P^4 are small relative to the molars and only slightly dimorphic. There is a well characterized wear gradient on the molars; the dentine is largely exposed on M^1, a little on M^2 and not at all on M^3. They are moderately high crowned and the cusps are low. The general occlusal pattern is *Australopithecus*-like, but less cuspidated. *Proconsul* differs from XIR-1 by the larger canines, the thin enamel, the large cingulum of the molars and the higher external cusps of the premolars[1,2] (Table 2). *Sivapithecus* differs from XIR-1 by the larger canines but there are some similarities in the jugal teeth[7]. *Lufengpithecus* has long and narrow incisors and canines[11].

The face of the new fossil is well preserved and reasonably complete, but a little distorted by fossilization pressure on the right canine fossa area. It is female gorilla-sized but the prognathism is weaker. There is a brow ridge under the orbits and a glabella prominence. The brow ridge is large but not projecting like those of the gorilla or chimpanzee and it looks more like the brow ridges of some australopithecines. In this area, only the external table of the bone is preserved and it is difficult to know if there is a developed frontal sinus. The orbit is low and rectangular; the long axis is directed outwards and downwards. There is a large inter-orbital region. Large orbital foramina are visible on the edge of the orbits, but the bone is damaged on the two sides in the area of the infra-orbital foramina. The nasal bones are flattened and enlarged at their distal extremities. The nasal aperture is broad and the sides converge slightly towards

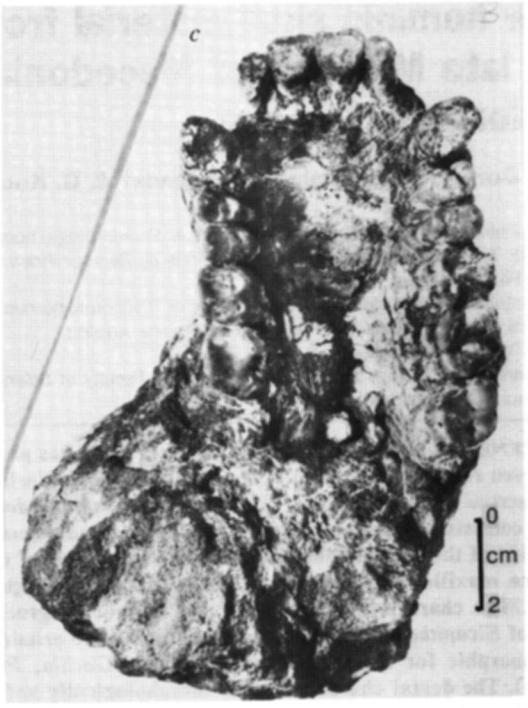
TABLE 1 Character measurements of XIR-1

Tooth no.	Definitions	Left	Right
Dental measurements (mm)			
I^1	MD	10.0	10.8
	La-Li	9.3	9.3
I^2	MD	6.4	6.5
	La-Li	8.0	7.8
C	max.MD	13.3	13.5
	Tr	13.2	14.3
P^3	MD	8.1	8.2
	Bu-Li	13.0	12.4
P^4	MD	9.0	8.1
	Bu-Li	13.5	13.2
M^1	MD	13.0	13.2
	Bu-Li	14.3	14.4
M^2	MD	14.8	15.0
	Bu-Li	15.5	14.9
M^3	MD	14.9	?
	Bu-Li	15.9	?
Facial measurements (mm)			
Glabella to nasion			9.9
Alveolar to nasion			95.0
Alveolar to naso-spinal			?
Nasal aperture height			?
Nasal aperture maximum breadth			35.0
Orbite height			30.0
Orbite breadth			33.0
Orbito-alveolar height			44.1
Minimum bi-orbital breadth			26.0
Bi-orbital breadth across lacrymal crests			24.0
External bi-orbital breadth			~129.0
Palatal length			96.0
Palatal breadth at M^2			~42.0

Bu-Li: buccal-lingual diameter; La-Li: labial-lingual diameter; MD: mesial-distal diameter; max., maximum.

TABLE 2 Character differences between *Proconsul* and *Ouranopithecus*

Proconsul	*Ouranopithecus*
Brow ridge absent	Brow ridge present
Large canines	Smaller canines
Honing facet present	Honing face absent
P_3 laterally compressed	P_3 lingually expanded
Upper premolar heteromorphic	Upper premolars more homeomorphic
Long premolars with regard to the molars	Shortened premolars with regard to the molars
No (or few) accessory cusps on M^3	Accessory cusps on M^3



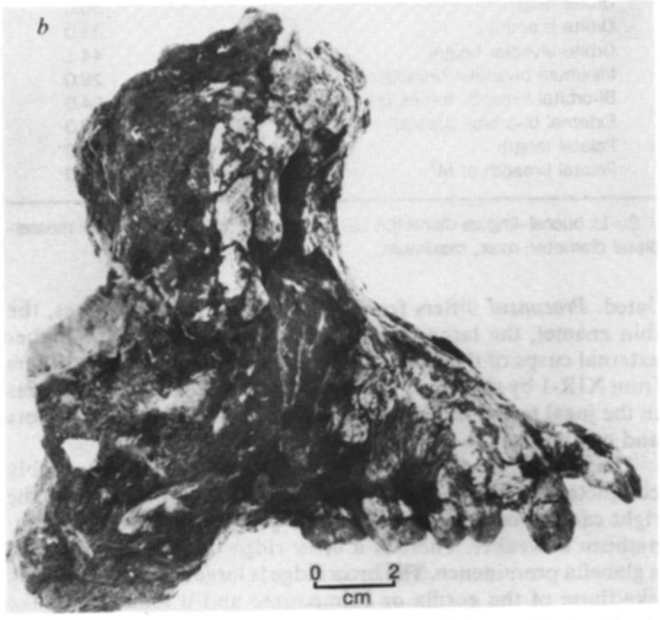


FIG. 1 *a*, Facial view of XIR-1. *b*, Lateral view of XIR-1. *c*, Palatal view of XIR-1.

the nasal bones. The canine fossa is present on the right maxilla. The naso-maxilla region is incomplete. Most of the upper part of the premaxilla has been destroyed, but on the left part the level of the premaxillary is much higher than the nasal floor, indicating that the posterior part of this bone was steeply inclined. The incisive canal is large, as it is on the specimen RPI 128 (ref. 12) and the whole area is similar to a primitive 'African' naso-maxillary pattern. The palate is deep (12.2 mm at the level of M^2), but the maxilla and palatine bones are largely dissolved.

The skull of *Proconsul* differs from XIR-1 by the lack of brow ridge; *Lufengpithecus* has an 'Asian' naso-maxillary pattern (orang pattern)[13]; *Sivapithecus* has the same 'Asian' pattern, high and oval orbits and small inter-orbital region and looks like *Pongo* (Pongidae). In the cranial structures *Ouranopithecus* shows most of the primitive characters of the great apes and Homininae but the brow ridge can be a derived character of African great apes and Homininae. The trend to reduced canines, the absence of the honing wear facet (for upper canine) on the anterior face of the lower third premolar and the round and swollen molar cusps of the molars[14], are shared by *Australopithecus* and *Homo* (Homininae) and all are interpreted as derived characters. The proportions of the lower dentition would demonstrate also that *Ouranopithecus* is linked with Plio-pleistocene Homininae[15]. If *Ouranopithecus* is a sister-group of all recent Hominidae, we must admit a reversion of these characters for gorillas and chimpanzees. It is more parsimonious to accept *Ouranopithecus* as the sister-group of only the Plio-pleistocene Homininae. The solution which considers *Ouranopithecus* as the sister-group of all great apes and man (Pongidae and Hominidae) would be even less parsimonious. In this case, the polarities of the characters, stated from out-group comparisons into other Catarrhini and from observations of the oldest known hominoids (that is *Proconsul*) are indicated in Table 2. We think it more probable that these features are shared derived features of both *Ouranopithecus* and *Australopithecus afarensis* than homoplasies.

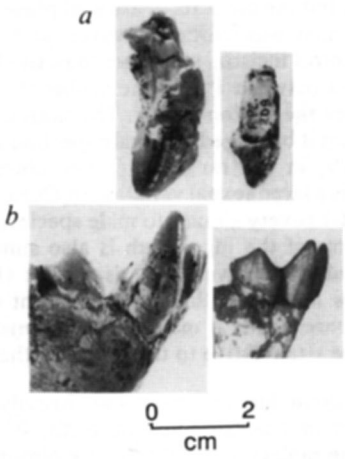


FIG. 2 *Ouranopithecus macedoniensis*. *a*, Upper canines; left, male (RPI 209); right, female (RPI 208). *b*, Lower canines; left, male (RPI 75); right, female (RPI 54).

Molecular data have recently provided information on the branching times of the different lineages of hominoids. The branching between man and African apes has been estimated to be 0.5–12 Myr ago[16,17], and between pongids and hominids, 10–19 Myr ago[18,19]. Recently some fossils which bear some characters of Catarrhini (Old World monkeys, apes and man) have been unearthed from marine and fluviatile deposits of North Africa which are considered late Eocene (40–45 Myr) on the basis of marine faunas[20]. This discovery indicates that the Catarrhini are older than previously thought and that the branching times of Primate lineages need to be reappraised. If *Ouranopithecus* is really a hominine, the branching with African great apes may be as old as 12 Myr. We believe that this genus can be considered a good Miocene ancestral morphotype for *Australopithecus* and man. □

Received 14 December 1989; accepted 26 April 1990.

1. Le Gros Clark, W. E. & Leakey, L. B. S. *The Miocene Hominoidea of East Africa* (British Museum (Natural History), 1–117 London, 1951).
2. Whybrow, P. J. & Andrews, P. *Folia Primatol.* **30,** 115–125 (1978).
3. Pilbeam, D. *Bull. Peabody Mus. nat. Hist.* **31,** 1–185 (1969).
4. Wu, R., Xu, Q. & Lu, Q. W. *Acta anthrop. sinica* **5,** 1–30 (1986).
5. Andrews, P. & Tekkaya, I. *Paleontology* **25,** 85–95 (1980).
6. de Bonis, L. & Melentis, J. *Anns. Paleont.* **64,** 185–202 (1978).
7. Pilbeam, D. *Nature* **295,** 232–234 (1982).
8. de Bonis, L., Johanson, D., Melentis, J. & White, T. *C. r. hebd. Séanc. Acad. Sci., Paris* **292,** 373–376 (1981).
9. de Bonis, L., Bouvrain, G. & Koufos, G. *Mod. Geol.* **13,** 141–147 (1988).
10. de Bonis, L. & Melentis, J. *Cour. Forsch. Inst. Senckenberg* **69,** 13–23 (1984).
11. Wu, R. *Acta anthrop. sinica* **6,** 169–174 (1987).
12. de Bonis, L. & Melentis, J. *C. r. hebd. Séanc. Acad. Sci., Paris* **304,** 767–769 (1987).
13. Kordos, L. *Anthrop. Hungarica* **20,** 9–22 (1988).
14. Johanson, D., White, T. & Coppens, Y. *Am. J. phys. Anthr.* **57,** 545–603 (1982).
15. Gelvin, B. *Am. J. phys. Anthrop.* **53,** 541–568 (1980).
16. Goodman, M. *Prog. Biophys. molec. Biol.* **38,** 105–164 (1981).
17. Benveniste, R. E. & Todaro, G. J. *Nature* **261,** 101–108 (1976).
18. Hasegawa, M., Kishino, H. & Yanno, T. *J. molec. Evol.* **22,** 160–174 (1985).
19. Hasegawa, M., Kishino, H. & Yanno, T. *Proc. Jap. Acad.* **60B,** 95–98 (1984).
20. de Bonis, L., Jaeger, J. J., Coiffait, B. & Coiffait, P. E. *C. r. hebd. Séanc. Acad. Sci., Paris* **306,** 929–934 (1988).

ACKNOWLEDGEMENTS. We thank P. Andrews and R. Defaye for help with the manuscript. The work was supported by the L. S. B. Leakey Foundation and the Fondation Singer-Polignac.