

4 Are *Papio baringensis* R. Leakey, 1969, and *P. quadratiostris* Iwamoto, 1982, species of *Papio* or *Theropithecus*?

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Summary

1. Eck & Jablonski (1984, 1987) have argued that the holotype crania of *Papio baringensis* (from the Chemeron Formation) and *Papio quadratiostris* (from the Omo Usno Formation) are actually specimens of *Theropithecus* which represent early stages of the *T. brumpti* lineage. These fossils are among the oldest members of the African Papionini which can be allocated to modern genera – the Usno Formation dates to about 3.4 Ma, while the Chemeron Formation is probably slightly younger, although its age is less definitely known.
2. Despite many morphological studies to the contrary, but in line with a variety of molecular analyses, we accept *Papio* (including *Mandrillus* as a subgenus) as the closest known relative of *Theropithecus* among the African Papionini. A mandrill-like cranial morphology (with relative lack of klinorhynchty even with a long face; only moderately deep midface; extended or ‘pointed’ rather than rounded external occipital protuberance; bulbous, not high-crowned, molars; large front teeth; and ovoid, closely-spaced orbits) is hypothesized to be close to the ancestral morphotype of the baboon–mandrill–gelada clade. Within *Theropithecus*, there are three major lineages: *T. gelada*, *T. oswaldi* (and almost surely *T. darti*) and *T. brumpti*. Based on previous research by others, we take as a working hypothesis the closer phyletic relationship of the first two contrasted with *T. brumpti*.
3. Eck & Jablonski discussed nine characters which were said to differentiate *Theropithecus* from *Papio* and which occurred in the two fossils on which this chapter focuses. We here review these features, showing that several of them in fact are

closely correlated as parts of functional complexes, rather than independent features; most of these, as is well known, relate to the feeding adaptations of *Theropithecus*, but the relatively small brain size of this genus is also important.

4. What Eck & Jablonski did not discuss, however, is the relative airorhynchy of *Theropithecus*, a radical departure from the ancestral moderately klinorhynch condition of African papionins (perhaps comparable to that seen in mandrills today). Although the two fossil skulls have small neurocrania, they are klinorhynch, like *Papio*. The teeth of *Papio quadratiostris* are basically not *gelada*-like, while those of the Chemeron skull are only possibly so.
5. Other features of *Theropithecus* which differentiate them from *Papio* and the two focal fossils include: the inferior buttressing of the mandible, laterally bowed zygomatics, inferiorly narrowed orbits (often short inferosuperiorly), increased midface height, extension of anterior temporalis origin (anterior temporal line) laterally on the posterior wall of the malar, production of a malar 'visor' and large maxillary tuberosity, a wide, short basiocciput with rounded rather than extended or 'pointed' external occipital protuberance, and a more anterior origin of the root of the zygomatic buttress (anterior to M³ rather than generally posterior to M²). Most of these features are directly linked to the great extent of

anterior temporalis and masseter in *Theropithecus* species.

6. Although the *baringensis* skull is not convincingly like *Theropithecus*, it may be tentatively referred to the *T. brumpti* lineage on the basis of dental similarities to another Chemeron mandible with less worn teeth (BC 1647) and in turn to definite *Theropithecus* jaws from early horizons in the Turkana Basin (see Leakey, chapter 3).
7. This allocation implies that early members of the *T. brumpti* lineage were conservative in the development of the *Theropithecus* dental pattern and reversed curve of Spee, as well as in retaining a more ancestral (relatively klinorhynch), *Papio*-like skull, compared to contemporaneous members of the *T. oswaldi* lineage. The latter, in turn, shared developing airorhynchy, orthognathy, reversed curve of Spee and greater molar complexity with *T. gelada*, suggesting that together they form the sister clade to the *T. brumpti* lineage. These two clades within *Theropithecus* evinced parallel development of the diagnostic molar pattern and the reversed curve of Spee.
8. Finally, fossils of *Papio* (*Dinopithecus*) from South Africa, Angola, and Ethiopia briefly described here are morphologically identical or closely similar to the *P. quadratiostris* skull and demonstrate that it (and the species) are best referred to that subgenus.

Introduction

In 1969, Richard Leakey reported the recovery of a partial cranium and associated mandible (KNM-BC 2) of a large papionin from the Chemeron Beds of the Baringo Basin, Kenya, which he named *Papio baringensis*. Leakey & Leakey (1976) reported a second specimen, KNM-BC 1647 (originally listed as BC 3, which is in fact the catalogue number of the holotype of *Paracolobus chemeroni* Leakey, 1969), from the same locality. This specimen, which was not illustrated, preserves only a partial lower dentition and some postcranial fragments. In 1982, Mitsuo Iwamoto described a nearly complete cranium without mandible from the Usno Formation of the Omo Group, Ethiopia, which he named *Papio quadratiostris*. This cranium is stored in the NME (see abbreviations at end of 'Introduction') collections but apparently has not yet received a formal catalogue number – it will be termed NME USNO here.

Eck & Jablonski (1984; also Eck, 1983) restudied these fossils in the context of an evaluation of the *Theropithecus* sample from the Omo Group and suggested that both crania were actually *Theropithecus* specimens, probably on the *T. brumpti* (Arambourg, 1947) clade. Delson (1984) rejected this view, combining the Usno skull with other Omo Group fossils previously termed *Papio* (Eck, 1977). Delson (1984) suggested that this species was morphologically closest to one from Swartkrans (South Africa) named *Dinopithecus ingens* Broom, 1937 and that *Dinopithecus* was best ranked as a subgenus of

Papio. Eck & Jablonski (1987) described the Omo *Theropithecus* sample in detail and reiterated their view of the *Theropithecus* status of the USNO and BC 2 crania. These two fossils (and more fragmentary remains allocated to the same species from East and West Turkana) are the earliest members of whichever genus they represent. Moreover, their generic allocation has important implications for the patterns of morphological transformation and phylogenetic geometry for these genera, which together dominate the fossil record of larger cercopithecines in the Pliocene and Pleistocene of eastern Africa. Here we assess their systematic position and their relationships to lineages of *Theropithecus* and *Papio*.

Abbreviations used in this paper for collections include: DGUNL: Departamento de Geologia, Universidade Nova de Lisboa, Portugal. KNM: Department of Palaeontology, National Museums of Kenya, Nairobi, Kenya. NME: National Museums of Ethiopia, Addis Ababa, Ethiopia. TMP: Transvaal Museum, Pretoria, South Africa.

Chronological position of specimens discussed

Although the basis for our study is morphology, the accurate determination of geological age for fossils is important in their overall evaluation. Eck & Jablonski (1984, pp. 127–8) carefully reviewed the available data bearing upon the ages of these specimens, concluding that the Chemeron fossils (from locality JM 90/91) were probably c. 4 Ma old, while the Usno skull (from the White Sands locality, probably Unit U8-U9) dated to c. 3.3–3.4 Ma.

Recent studies in the Turkana Basin (summarized by Feibel, Brown & McDougall, 1989) confirm the latter estimate, altering the probable range to between 3.35–3.50 Ma (Usno unit U-7 is equivalent to the Lokochot Tuff, with an estimated depositional age of 3.5 ± 0.1 Ma; unit U-10 is equivalent to Tuff B, with an estimated depositional age of 3.36 ± 0.04 Ma). On the other hand, new work in the Baringo Basin employing single-crystal laser fusion argon–argon dating and regional–faunal correlation suggests that locality JM 90/91 is somewhat younger, probably c. 3.2 Ma; although some questions remain about the relationship of this date to the fossils, unless the area of the locality lies within a fault-bounded block (for which there is no evidence), it is unlikely that it is older than 3.2 or younger than 2.5 Ma (A. Hill, pers. comm.). The age range of *Theropithecus brumpti*, by comparison, is c. 2.95–2.0 Ma (Eck & Jablonski, 1987; same estimates in Feibel *et al.* 1989).

M. Leakey (see chapter 3) discusses specimens allocated to all three taxa of the putative *T. brumpti* lineage from the Turkana Basin, including mainly fragmentary materials from as old as the USNO skull. The only described *Theropithecus* fossils older than the Omo *T. brumpti* are those of *T. darti* from the Hadar Formation, Ethiopia (see Eck, chapter 2), perhaps 3.35–2.90 Ma. Unpublished *Theropithecus* specimens from the Middle Awash Valley, Ethiopia, and a tooth from Lothagam-3 mentioned by Patterson, Behrensmeyer & Sill (1970; KNM-LT 417; see Delson, chapter 5) have an estimated age c. 4 Ma. According to T.D. White (pers. comm.), both of these assemblages could be as

young as the oldest Hadar material on faunal grounds but are likely to be somewhat older. No fossils undoubtedly identified as *Papio* are older than the Usno and Chemeron specimens. In the Omo sequence, material allocated to *Papio* (*Dinopithecus*) ranges precisely as does *T. brumpti*: submembers B11-G13, c. 2.95–2.0 Ma. Specimens from Sterkfontein (South Africa) and Leba (Angola) are probably younger than 2.7 Ma, and other occurrences younger still – e.g. Swartkrans c. 1.9–1.6 Ma (Delson, 1984, 1989).

Lineages of *Theropithecus* and its relationship to *Papio*

It is widely accepted that there are three major clades within the *Theropithecus* group: the living *T. gelada*, the widespread Plio-Pleistocene *T. oswardi*, and the geographically restricted *T. brumpti* (see Szalay & Delson, 1979; Eck & Jablonski, 1984, 1987; Eck, Leakey, and Jablonski – chapters 2, 3, and 7, respectively). The Pliocene *T. darti* (see Eck, chapter 2) is less well-known but generally accepted as closest to *T. oswardi*. The central question of this paper is the relationship of the two distinctive Pliocene fossils discussed above, but in order to approach that problem, not only the internal phyletic geometry of *Theropithecus*, but also the place of this genus within the Cercopithecinae must be briefly examined.

Jolly (1967), Maier (1970), and Szalay & Delson (1979), among others, recognized three subtribes within the cercopithecine tribe Papionini: Macacina, Papionina and Theropithecina (sometimes with differing

ranks or names). It was generally thought by these morphologists that the numerous distinctive, derived features of *Theropithecus* indicated an ancient origin for this genus. Cronin & Meikle (1979) presented new molecular data indicating a close relationship between *Papio* and *Theropithecus* among the Papionini. They argued that the derived features of *Theropithecus* might well have originated quickly from a *Papio*-like ancestry, perhaps in a punctuated equilibrium mode of evolutionary change. Delson (e.g. 1988; Strasser & Delson, 1987) recognized this argument and included *Theropithecus* within the subtribe Papionina, but continued to illustrate cladograms showing *Theropithecus* as the probable sister-taxon of all other papioninans. Few other workers have addressed this question recently. Fleagle (1988), for example, presented without discussion the cladogram of Strasser & Delson, the phylogram of Cronin & Sarich (1976, which agreed with Cronin & Meikle, 1979) and a third phylogram which placed three lineages of *Theropithecus* nearest to one for *Papio*.

Discussion during the Cambridge conference (summarized in Jablonski, chapter 7) and the results of our analysis here lead us to accept the probable sister-taxa relationship of *Papio* and *Theropithecus*. Disotell, Honeycutt & Ruvolo (1992) came to this conclusion from their new mtDNA studies of papionins as well. This grouping allows a better reconstruction of the ancestral morphotype (list of inferred character states) for *Theropithecus* and thus a better determination of the polarity of character transformation within the genus.

In terms of cranial and dental proportions, facial hafting and mandibular shape, we suggest that the most conservative living form, the one most similar to the last common ancestor of all baboons, may be *Papio* (*Mandrillus*) species (cf. Jolly, 1970). Holding aside the skeletal synapomorphies of this group (especially the swollen muzzle ridges), mandrills and drills present a suite of cranial character states which are similar to those seen in *T. brumpti*, the two focal fossils, and varieties of *P.* (*Papio*). These features, which will be discussed below in detail, include: a relative lack of cranial flexion, even with a long face; only moderately deep midface; extended or 'pointed' rather than rounded external occipital protuberance; bulbous, not high-crowned, molars; large front teeth; and ovoid, closely-spaced orbits. Some of these conditions (such as the low degree of flexion) are unusual for large African papionins but found elsewhere in the tribe.

Eck & Jablonski (1987, Table 42) produced a list of 51 cranial features which varied among the three well-known species of *Theropithecus*, in addition to the seven cranial (and two dental) shared-derived characters which for them diagnosed the genus. Of this set of 51, the three species all differed in 13 characters (their tabulation of Table 43 is incorrect in the 'Skull' or summation column, but accurate elsewhere). In 21 features, *T. oswaldi* is similar to *T. gelada*, in 11 *T. oswaldi* is similar to *T. brumpti* and in only five do *T. gelada* and *T. brumpti* share the same character state. Unfortunately, polarity was not assessed for these 51 characters, so it is not poss-

ible to tell whether the shared similarities are derived or plesiomorphic.

As a working hypothesis, to be examined and supported further below, we consider that *T. oswaldi* and *T. gelada* are sister-taxa, the pair being in turn the sister-taxon of *T. brumpti*. Following Eck and Leakey (see chapters 2 and 3, respectively) among other workers, *T. darti* from Makapansgat and Hadar appears to be closest to *T. oswaldi*, although less derived in certain dental and cranial characteristics. From this baseline, we now proceed to an evaluation of the systematic position of the Usno and Chemeron holotype crania. We first consider those points raised by Eck & Jablonski (1984, 1987), then examine other features of these two crania and finally evaluate relevant evidence obtained from other specimens.

Eck and Jablonski's arguments

In their 1984 paper, Eck & Jablonski (p. 111) listed seven features which were said to distinguish *Theropithecus* from *Papio* crania and dentitions: '(1) strong elevation of the temporomandibular joint above the occlusal plane and a tall, upright mandibular ramus; (2) anterior union of the temporal lines and sagittal crest long, if present; (3) great postorbital constriction; (4) inferiorly divergent lateral margins of the frontal processes of the zygomatic bones; (5) a long mandibular symphysis; (6) reduced incisors and a shallow maxillary incisive arc; and (7) molars with high, pinched cusps and well-developed longitudinal crests, M³s with large mesial and distal foveae, and M₃s with con-

sistently large hypoconulids.' All of these features were said to occur in BC 2, while all but number 5 were reported for NME USNO. In 1987, the same authors (p. 100) added two other features (here numbered): (8) a reversed curve of Spee (which had been briefly mentioned in 1984); and (9) large temporal fossae. We shall evaluate each of these in turn, with a special focus on the details of the relevant morphology in order to determine whether the suggested similarities are homologous or analogous (=convergent), as well as to ascertain their condition in the two early fossils.

Facial lengthening and klinorhynch

Character one relates the mandible to the cranium and (as is true for most of these characters) to the masticatory musculature, although there are some questions about the relative value of the different aspects combined here. The tendency for *Theropithecus* mandibles to have a relatively high, long, and vertically oriented ramus was briefly mentioned by Leakey & Whitworth (1958) and discussed at greater length by Jolly (1972). The height of the ramus is directly linked to the elevation of the temporomandibular joint, so that the pattern may be examined on either the cranium or the mandible. Eck & Jablonski (1984, p. 112) plotted three measurements of the cranium on a triangular graph to examine this feature, finding that *Papio* and *Theropithecus* did separate (with a narrow 'empty' zone between them), but that neither fossil specimen fell within the spread of extant (or clearly allocated extinct) species;

instead, both fossils clustered away from all others, apparently due to relatively high values of Eck & Jablonski's variable 1, the distance between the anterior base of the postglenoid process and the posterior root of M³.

The angulation of ramus to corpus is quite variable in papionins (see Plates 1–2 in Jolly, 1972, noting especially the verticality of the ramus in *Mandrillus*). Therefore, corporamal angulation is less important as a means of distinguishing between *Papio* and *Theropithecus*. This angle, often referred to as the gonial angle, is related to several areas of the masticatory apparatus which are part of somewhat autonomous (developmentally and functionally) regions. The appearance of verticality can be due to a vertical coronoid process, which is related to anterior temporalis development, or to the development of the gonial area, which is related functionally to the masseter-pterygoid 'sling', an area of great expansion in grazing ungulates. The final outcome in papionins is probably mostly the result of the mandible essentially 'tracking' the growing palate ontogenetically (Enlow, 1990, see p. 50) without much canalization of verticality.

Some aspects of the relationship between the corpus and ramus do distinguish between *Papio* and *Theropithecus* on average, but a simplistic analysis contrasting the two by analogy to a carnivore–herbivore distinction (cf. Maynard Smith & Savage, 1959; Eck & Jablonski, 1987; see Jablonski, chapter 11) is not sufficient. Perhaps the most telling problem with the grazing analogy is the concentration on the lateral view of the *Theropithe-*

cus skull. This projection does show a tall, often steeply angled mandible, but we must ask what has brought this about. In ungulates much of the great height of the ramus is contributed by the inferior extension of the gonial region. The expansion of gonion is linked to the anteroposterior elongation of the origin of the masseter onto the maxilla, but in most ungulates the zygoma rarely bows laterally.

The increase in the height of the midface in *Theropithecus* is also not seen in grazing ungulates. Ramal height increase in *Theropithecus* is due to midface height increase, not to elevation of the mandibular condyle as Eck & Jablonski claim. The thicker palate and nasomaxillary complex has probably developed to resist very high occlusal forces. *Theropithecus brumpti*, possibly less derived along these lines, does not show the same level of orthognathy or midface height increase seen in other members of the genus. However, its dentition and the anterior placement of the maxillary root of the zygoma (and thus the masseter) are perhaps a parallel solution to the adaptation presaged by its high-crowned, crenulated teeth.

The dorsal and frontal views of the cranium (Fig. 4.5 and 4.6) may be more telling than the lateral view of the mandible. The anterior approximation of the temporal lines (seen in the dorsal view) is the result of the medial enlargement of anterior temporalis and the relative orthognathy evidenced by the decreased importance of the anterior dentition in the apprehension of food. In order to maintain oblique leverage on the shearing crests of the teeth, the zygomatic arch

has bowed out laterally as seen from the frontal view (see Davis, 1964; Turner, 1970; Du Brul, 1974; Ward & Brown, 1986; also D. Dean, 1986, unpublished M.A. thesis, Temple Univ.). This great lateral expansion of the masseter muscle and anterior zygomatic arch is seen in *T. brumpti*. By analogy when the masseter has increased its anterior attachment area in an ungulate or rodent species it has most often taken root on the maxilla rather than producing the visor-like extensions seen in *T. brumpti* or the enlarged masseteric tubercle seen in other species of *Theropithecus* (see below). This 'reinforcement' can best be associated with high occlusal forces. It can reasonably be assumed that the bowing of the zygomatic, resulting in the lateral extension of the masseter's insertion, is an adaptation to putting high occlusal forces on obliquely angled surfaces.

Theropithecus dental morphology also belies the grazing ungulate model. While it is true that *Papio* and *T. brumpti* show elongate muzzles, no specimens of fossil or living *Theropithecus* show the incisor expansion or the canine loss and extensive premolar molarization associated with grazing in ungulates. It is likely that the long muzzle and relative lack of either klinorhynch or airorhynch seen in *T. brumpti* is a retention from a mandrill-like condition in these features predicted for the common ancestor of *Theropithecus* and *Papio*. There is no reason to assume that this conservative retention was a newly derived adaptation to large gape and large object feeding (see Jablonski, chapter 11).

Eck & Jablonski (1987; see Jablonski,

chapter 11) concentrated on the lateral cranial view of *Theropithecus* in making their analogy with grazing ungulates. However, this comparison invites a closer look. While most ungulates show superficially similar high-crowned teeth with ribbon-like crenulations and steeply angled power strokes (Hiemac & Crompton, 1985, p. 278), they do not tend toward airorhynch or increased midface height.

In *Papio*, as we shall discuss further below, the major distinction from other cercopithecines is increased klinorhynch (downward bending of the face on the neurocranium and base) in order to maintain the leverage needed by posterior temporalis to act on the anterior dentition. The klinorhynch modifications seen in large macaques or the extinct macacine *Paradolichopithecus* are different, in that the same result is attained by vertical height increases in the mid-face region.

To document this pattern of facial angulation, Fig. 4.1 presents histograms of the basal angle (between a line connecting basion and sella and the line of the [anterior] hard palate) in a number of extant baboon taxa of both sexes, based on data from Frick (1960). His small samples of drill and chacma baboon are grouped with mandrills and anubis baboons, respectively, and his specimens younger than subadult (without M³ erupting at all) are not included. It is clear that most *T. gelada* specimens have a very low basal angle, making them nearly airorhynch (with the face upwardly bent). Although a few *Papio* specimens overlap with them, the *Papio* show great variation while *Theropithecus* is restricted to the low end

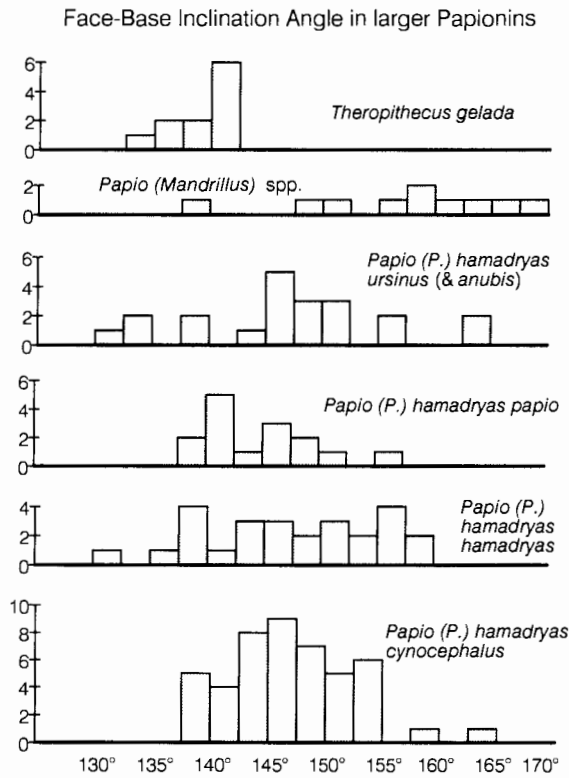


Fig. 4.1. Histograms of basal angle (see text) for six groups of baboons, data from Frick (1960), adults and subadults only, mixed sex, wild-shot and captive animals lumped. Note that *Theropithecus* is restricted to the low end of the range, while various *Papio* species are more variable but mainly in the center and high end.

of the range. It is likely that *Theropithecus* would have an even lower angle were it not for the increased height of the midface in this taxon. This height increase may be in part an adaptation to resist strain from powerful postcanine chewing, but perhaps even more important is the need to produce high occlusal pressure on high-crowned teeth which, even when extremely worn, maintain obliquely oriented shear edges and masticatory muscle lines of action. We suggest that the rela-

tionship of the face to the braincase is less variable in *T. gelada* than in other papionins due to selection for the application of high occlusal forces to the postcanine teeth at a consistent angle.

P. Dechow (unpublished 1980 Ph.D. dissertation, Univ. Chicago) also discussed the relative airorhynchy of geladas compared to other baboons, noting that it was due to the upturning of the face (especially seen at prosthion) relative to the neurocranium, combined with an extremely short face for its overall size. This places the masticatory muscles closer to the tooth row and allows the development of greater occlusal forces than in other baboons of comparable size (see also Jablonski, chapter 11). Dechow also found that *Papio (Mandrillus)* (both mandrills and drills) presented somewhat upturned anterior muzzles, but combined with long faces which are at least moderately klinorhynch.

It is not possible for us to duplicate Frick's measurements (based on X-rays) on the fossil casts available to us, but in order to demonstrate the relative airorhynchy of at least *T. oswaldi* and to place the two questioned fossils in context, we present lateral views of a number of extant and fossil crania (Fig. 4.2 and 4.3). The USNO skull is similar to *P. (Mandrillus)* in a number of features, such as the moderate angulation of the face and the apparent elevation of the TMJ. It is also interesting to note that the female *T. darti* from Hadar (see Fig. 4.3, bottom) appears less airorhynch than other specimens (including the Hadar male - see Eck, chapter 2), which may reflect variation in the development of this pattern in the earliest



Fig. 4.2. Left lateral views (in Frankfurt horizontal) of male crania of *Papio*, *Theropithecus* and other papionin species. Left page, top row, left to right: *T. gelada*, *T. oswaldi oswaldi* (Kanjera); bottom row: *Macaca thibetana* (one of the largest macaques), *Parapapio whitei* (Makapansgat). Right page, top row: *T. brumpti* (NME L. 345–287, Shungura, cast), *P. hamadryas kindae*; middle row: *?T. baringensis* (BC 2, cast), *P. hamadryas ursinus*; lower row: *P. (Dinopithecus) quadratiostris* (USNO), *Papio (Mandrillus) sphinx*. All brought to similar size, scale bars = 5 cm.

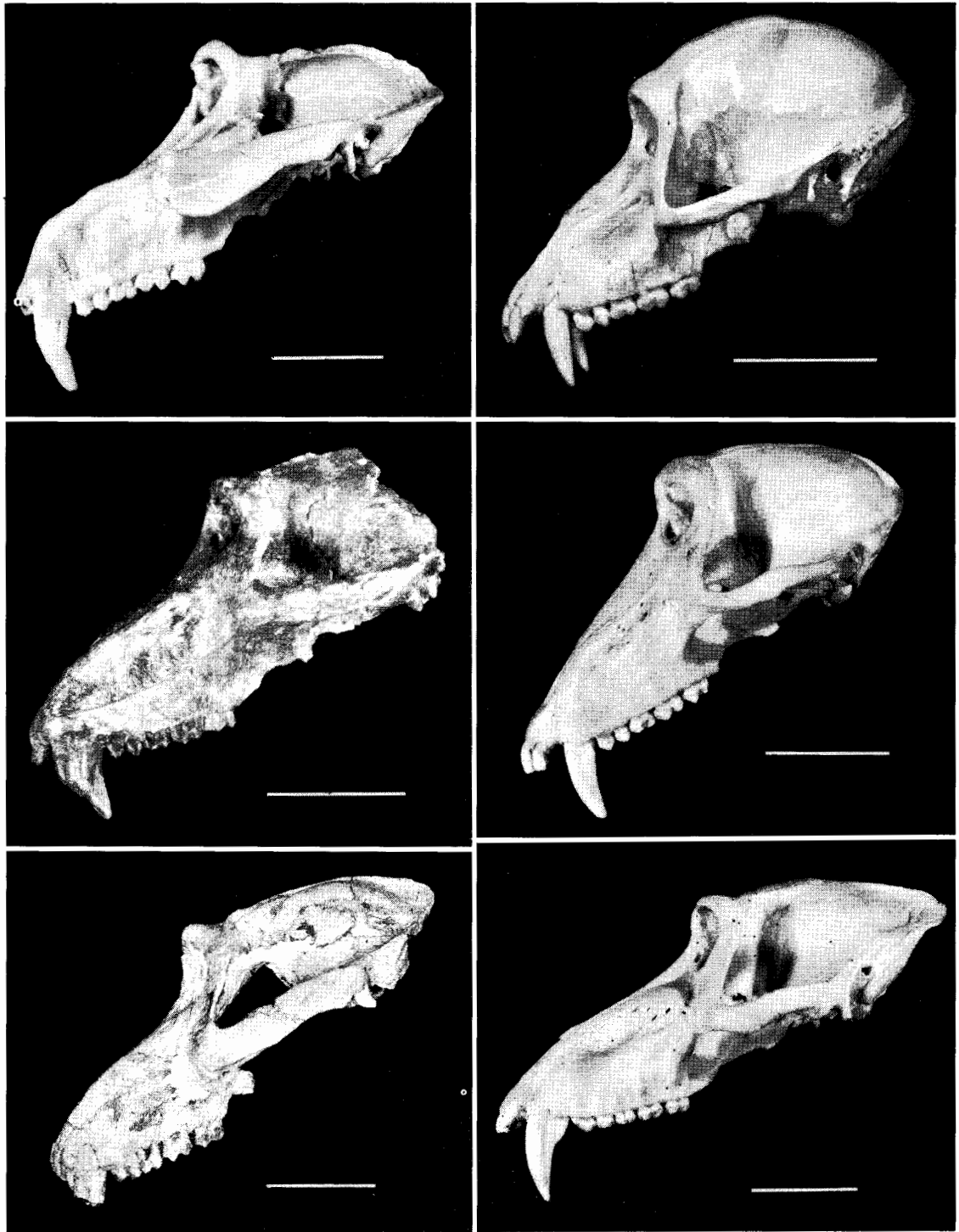


Fig. 4.2 - contd.

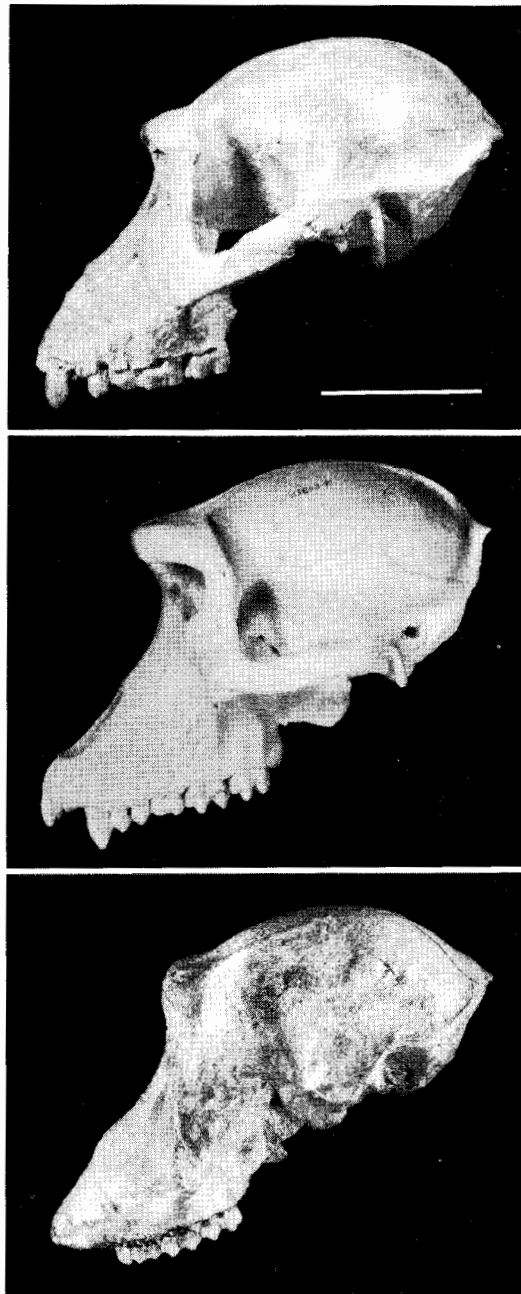


Fig. 4.3. Left lateral views (in Frankfurt horizontal) of female crania of *Theropithecus* species. Top to bottom: *T. oswaldi oswaldi*, Kanjera; *T. gelada*; *T. darti*, Hadar. Scale bar = 5 cm.

members of the genus. *T. brumpti* is also less klinorhynch than other members of the genus, appearing more like (*P.*) *Papio*, as does BC 2.

Relative brain size and chewing muscle orientation

In our opinion, characters 2, 3, and 9 are all part of a second functional complex which may be related to relative brain and masticatory muscle size irrespective of taxonomic differentiation. Given comparable development of the anterior temporalis, in a relatively small-brained individual (or species), this musculature would spread more widely over the vault than in a larger-brained relative; thus, the fusion of the temporal lines would lie anteriorly, the postorbital constriction would be tighter and the temporal fossae larger (the latter two are aspects of the same phenomenon).

It appears from inspection that both BC 2 and USNO have smaller braincases (and presumably brains) than extant baboons of comparable skull size. Moreover, Dechow (unpublished 1980 Ph.D. dissertation, Univ. Chicago) reported that *Theropithecus gelada* has a significantly smaller endocranial volume than does any living baboon, including the rather smaller *P. hamadryas kindae*. Martin (see chapter 10) confirms the relatively small brain size of *Theropithecus gelada* and finds the same result for *T. oswaldi*, evidence that *Theropithecus* is conservative for brain size. We propose that small brain size (and strong postorbital constriction) is symplesiomorphous for *Papio* and *Theropithe-*



Fig. 4.4. Inferior views, in occlusal plane orientation, of left temporal fossa in selected *Papio* and *Theropithecus* males. Left to right: *P. hamadryas kindae*, *P. h. ursinus*, *P. (D.) quadratiostris* (USNO, cast), ?*T. baringensis* (BC 2, cast), *T. gelada*. All brought to similar size, scale bars = 5 cm.

cus. Thus the presence of these two features in BC 2 and USNO is irrelevant in terms of discerning their phylogenetic relationships.

Although it is not one of their nine diagnostic features, Eck & Jablonski (1984, 1987) discussed in some detail the shape of the temporal fossa (especially its inferior outline) in living and extinct baboons. We have considered this question in the light of our analysis of the relationship between temporalis musculature and structures surrounding the temporal fossa. Eck & Jablonski (1984, p. 124) cited a nearly right-angle between the posterior margin of the temporal fossa and the sagittal plane in inferior view in *T. brumpti* and USNO, but not in BC 2. The last two specimens are compared to individuals of modern *Papio* and *Theropithecus* in Fig. 4.4, which reveals that only USNO is even vaguely 'squared-off' (like *T. brumpti*), while BC 2 is most like large, klinorhynch *Papio*. Smaller *Papio* also has a nearly squared posteromedial corner like USNO

(but cf. Fig. 4.7, in which a large *Papio* displays almost the same shape as USNO – the overlapping of the pterygoid plates also interferes with ready observation of this condition in undamaged specimens). The high degree of variation in this feature suggests that the similarity in this simplistic character is not necessarily homologous between USNO and *T. brumpti*.

Concentration on the shape of this posterointernal corner, moreover, misses the key fact of an expanded anterior temporalis above the fossa which encroaches into the posterior surface of the orbital cone and out onto the posterior surface of the malar. It is actually this bowing out of the zygomatic arch that distinguishes *Theropithecus* from *Papio*, not the quadrangular shape. The temporal fossa of *Papio* is like an oval from the inferior view. *Theropithecus* appears less ovoid because of the lateral bowing and anteroposterior shortening of the temporal fossae. Again, this shape is related to an increased development of the anterior

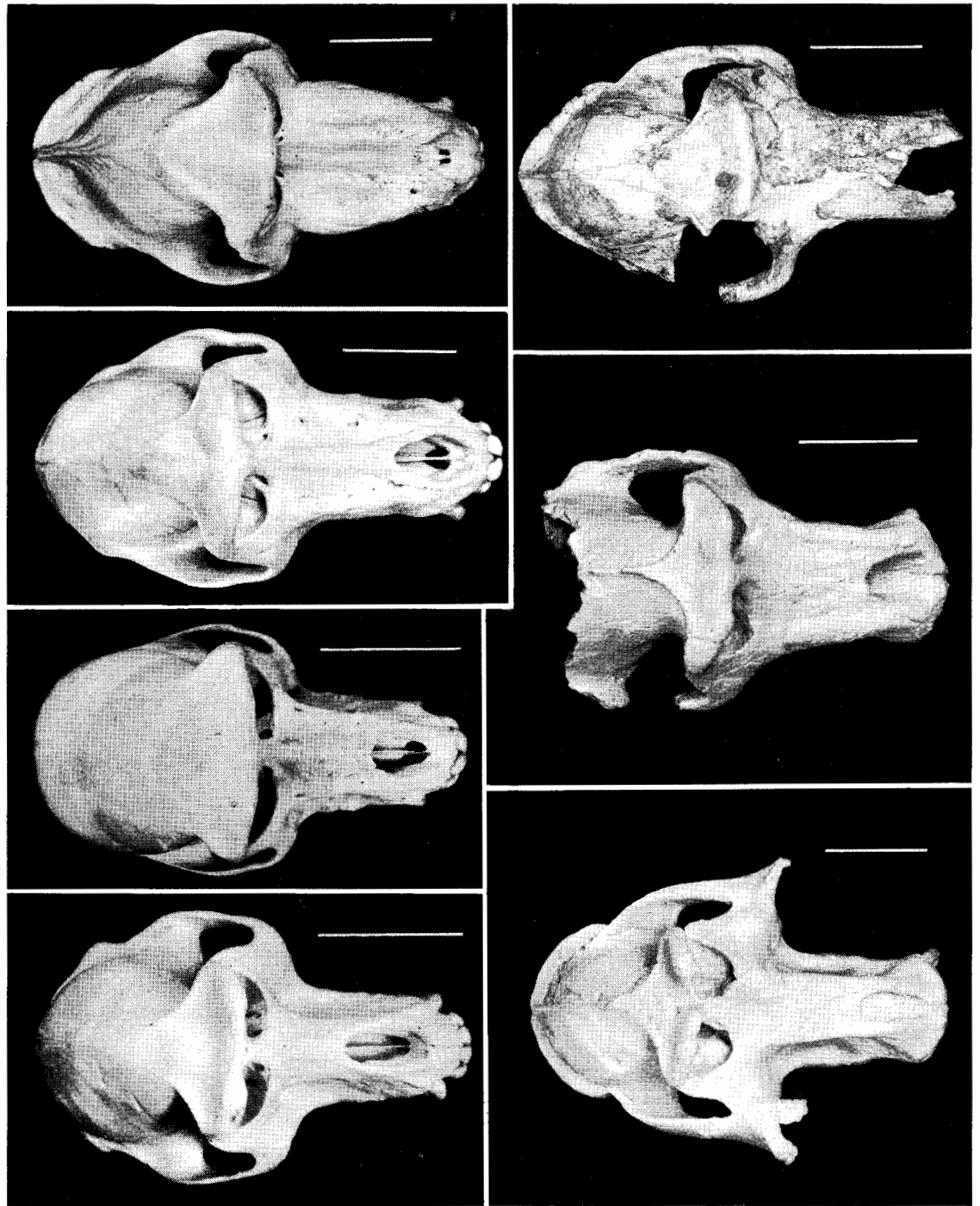


Fig. 4.5. Dorsal views (with occlusal plane horizontal) of male papionin crania. Left column, top to bottom: *Papio (Mandrillus) sphinx*, *P. (P.)*

temporalis and the masseter-pterygoid sling. In *Papio*, the fossa is extended anteroposteriorly to ensure that posterior temporalis can pull powerfully on the coronoid at an angle such that its line of action is directly in line with the incisive edges of the front teeth. The great anteroposterior length of the opening seen in *Papio* is cut off by the malar visor (see below) in *Theropithecus*. Neither BC 2 nor USNO have zygomatic arches that are bowed or extended out from the skull as far as they are in *Theropithecus*, nor are the arches as robust; by implication, their anterior temporalis (and masseter) muscles are less well developed also. Fig. 4.5 illustrates the two focal fossils and *T. brumpti* as well as a variety of modern baboon crania in dorsal (occlusal plane) view. The relative bowing of the zygomatic arches is obvious, and moreover the superior view of the posterior part of the temporal fossa shows the great similarity of BC 2 to larger *Papio*.

Malar and orbit shape

Character 4 may be more clearly stated as a tendency, in *Theropithecus* but not *Papio*, for the malar to widen inferolaterally. This forms a 'visor' (*sensu* Rak 1983; see pp. 99–102) that serves as a buttress for the laterally bowed zygomatic arch. Eck & Jablonski (1984, 1987) did not pursue their interpretation far enough

to include the three-dimensional angulation of this visor and its buttressing role. As noted above, the orbital cone is narrowed on the posterior surface of the malar because of the expanded anterior temporalis muscle. This bowing of the zygomatic is similar to the pattern seen in *Pongo*, where strong airorhynch has occurred (Ward & Brown, 1986). In airorhynch taxa (of which *Alouatta* is perhaps the most extreme) the premaxilla bends upward, as it does also in most *Theropithecus* *gelada* and *T. oswaldi*. Eck & Jablonski (1987, p. 54) described the orbits of *T. brumpti* as ovoid, but as in other *Theropithecus*, they are more accurately said to be elongate and narrower inferiorly than superiorly. By comparison, in *Papio*, the klinorhynch which is probably an ancestral feature for African papionins is taken to an extreme. The upper face projects forward, but the orbits are of roughly equal width superiorly and inferiorly, the zygomatic arch does not bow laterally and there is no 'visor' (see Fig. 4.6). Eck & Jablonski (1984, p. 124) noted that the zygomatic arch is not flared in either BC 2 or USNO; moreover, there is no 'visor' and the lower part of the orbit is about as wide as the upper.

This malar widening and zygomatic bowing in *Theropithecus* result in the anterior concentration of the origin of the masseter-temporalis muscle complex. Two other aspects of this complex are also

Caption to Fig. 4.5 – *contd.*

hamadryas ursinus, *P. (P.) hamadryas kindae*, *T. gelada*; right column: *P. (D.) quadratiostris* (USNO), ?*T. baringensis* (BC 2, cast), *T. brumpti* (NME L. 345–287, Shungura, cast). All brought to similar size, scale bars = 5 cm.

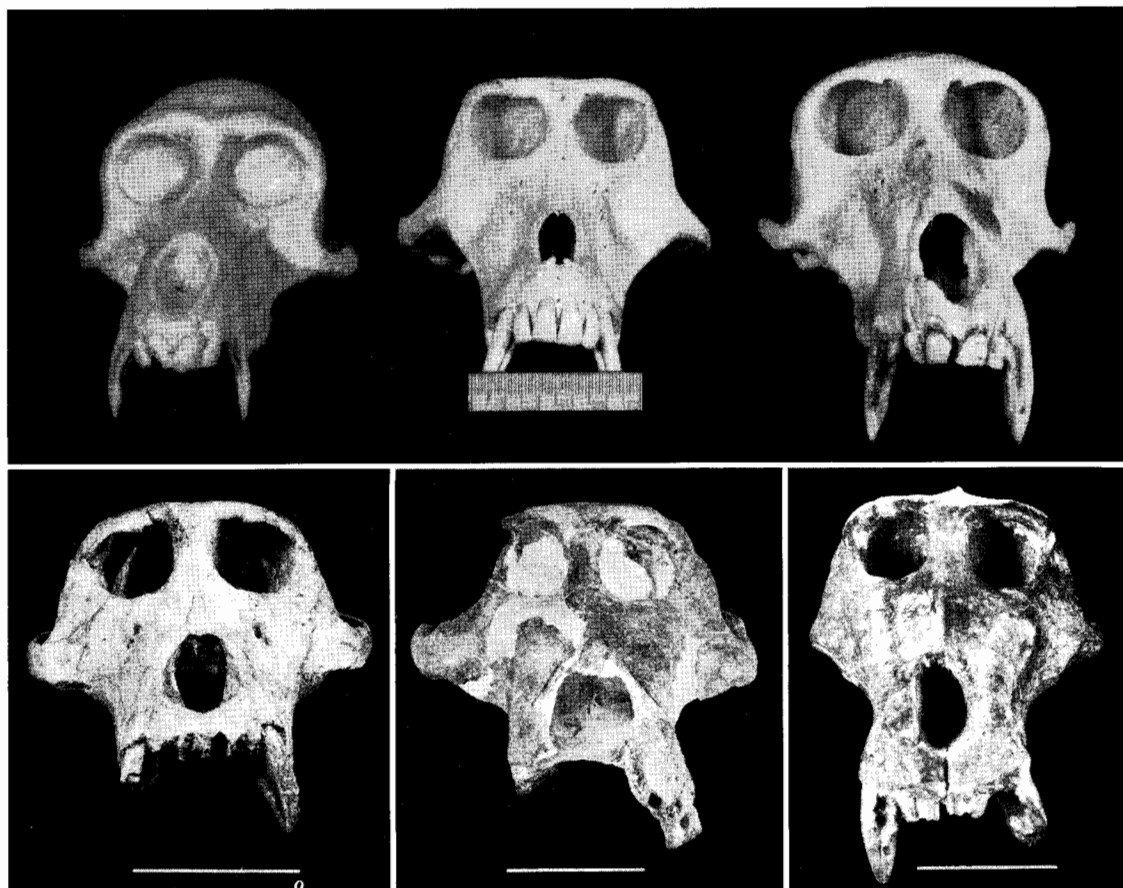


Fig. 4.6. Frontal views, mainly in Frankfurt horizontal, of male crania of *Papio* and *Theropithecus* species. Top row, left to right: *P. hamadryas kindae* (cast), *T. gelada*, *P. h. cynocephalus*; bottom row: *T. oswaldi* (Kanjera), *P. (D.) quadratiostris* (USNO), ?*T. baringensis* (BC 2, cast). Scale = 5 cm.

important in distinguishing *Theropithecus* from *Papio*. First, the area of origin of anterior temporalis expands medially and laterally; medially it encroaches upon the posterior surface of the orbital cone, while laterally it extends nearly to the lateral margin of the posterior surface of the malar. In *Papio*, there is far less lateral expansion, and the ridge marking the lateral extent is well medial to the malar edge.

Second, a maxillary tubercle (anterior-most attachment of superficial masseter) can be seen in all *Theropithecus* as a small eminence on the anteroinferior margin of the maxillary process of the malar. This tubercle essentially enlarges to form the extreme 'handle-bar' development seen in *T. brumpti*. The lateral bowing of the malar and zygomatic arch in *Theropithecus* moves the superficial masseter laterally, so that its line of action pulls

obliquely rather than vertically. In most other primates, including *Papio*, the zygomatic process of the maxilla and the frontal process of the zygomatic and the supporting mid- and upper-facial structures can resist the pull of the superficial masseter. However, the lateral position of the maxillary tubercle in *Theropithecus* requires the strengthening of the origin, as an 'anchor'. The lateral bowing and increased robusticity of the zygomatic arch produce a structure which can better resist such shearing forces than the relatively straight arch of *Papio*. Moreover, it permits the masseter to supply force at the necessary angle to the obliquely angled surfaces of the high-crowned, diagnostic *Theropithecus* dentition.

Mandibular buttressing

Eck & Jablonski's character 5 was reported as a long mandibular symphysis in *Theropithecus*, comparing the infradentale-menton distance to canine-molar tooththrow length. This ratio was generally higher in *Theropithecus* than in *Papio*, but with much overlap; the value for BC 2 fell within the overlap range, at the upper end of *Papio* values (the lack of a mandible with the USNO specimen precludes assessment of this feature). More important, however, is the apparent conflation, once again, of more than one functional feature in this 'character'. Examination of the morphology around the symphysis in most *Theropithecus* mandibles reveals three features: the planum alveolare is concave, leading into a weakly developed superior transverse torus; the inferior torus is more strongly developed, but the greatest but-

tressing is along the base of the corpus, which is thickened posteriorly well back toward gonion; and anteriorly, the mental ridges continue from this thickened base superiorly toward (but not reaching) infradentale, resulting in a high or tall superior half of the anterior symphysis. By comparison, in *Papio*, the planum is steeper and less hollowed, ending at a more sharply defined superior torus; the inferior torus is weaker, and there is no sign of thickening along the base of the corpus; and the superior part of the anterior symphysis is relatively less tall. The measurement taken by Eck & Jablonski combines the superior and inferior heights, which vary inversely in the two genera, but it does not reflect the toral and basal morphology (just the lengthening) which differ strongly between them. KNM-BC 2 clearly has no basal thickening, but does have a relatively long planum alveolare and stronger superior torus, all as in *Papio*.

Based on the work of Hylander and colleagues, Greaves (1988) and others, it is clear that the shape of the symphysis is controlled by stress-reduction adaptations. Unlike frugivorous cercopithecines and hominoids, the posterior temporalis muscle and the concomitant superior transverse torus are not enlarged in *Theropithecus*. However, it is likely that the posterior extension of the torus (almost comparable to a simian shelf) in *Theropithecus gelada* is most likely to be functionally related to the postcanine dentition. The posterior extension of the symphyseal shelf can resist 'wishboning' (simultaneous lateral pull on both sides) of the mandible due to the lateral placement

of the chewing muscles in *Theropithecus gelada* and the concomitant eversion of the lower border of the mandible at the beginning of the power stroke (Hylander, 1984). Hylander, Johnson & Crompton (1987) concluded that the wishboning of the symphysis is maintained or may actually increase after the powerful adductor force has been applied during phase I in anthropoid primates. It is therefore reasonable to speculate that, even though the masticatory muscle geometry in *Theropithecus* differs from that of *Macaca*, *Theropithecus* would have an increased wishboning of the mandible throughout the postcanine power stroke and the resultant posterior extension of the inferior torus (compared to *Papio*) would resist this.

Dental features

In terms of the dentition, characters 6 and 7 of Eck & Jablonski refer to the reduced incisors and high-crowned/high-relief molars of *Theropithecus*, respectively. These features of the teeth, as well as others noted below, are widely accepted as diagnostic of *Theropithecus* and at the origin of its adaptations. Moreover, character 8, the reversal of the curve of Spee, appears to be an adaptation to promote constancy of occlusal pressure along a toothrow in which the first molar is heavily worn while the third molar is still erupting; these two teeth are thus less elevated in the mandible than the intervening M_2 , resulting in the reversed curve, which is clearly related to this dental pattern.

However, the cheek teeth of both USNO

and BC 2 are worn to the point where differentiation between *Papio* and *Theropithecus* is nearly impossible, because similar molar wear occurs on aged individuals of both genera. On the other hand, the bases of the molar clefts (upper lingual and lower buccal) in *Theropithecus* are flattened, whereas those of *Papio* grade smoothly onto the sidewall of the crown (see illustrations in, for example, Szalay & Delson, 1979, and Delson & Hoffstetter, chapter 6). As far as can be discerned, the latter pattern occurs on USNO, while the situation for BC 2 is less clear.

Eck & Jablonski (1984, pp. 113 and 115) argued instead that the moderately worn third molars of both specimens allow the inference of high crowns and pinched cusps, as in *Theropithecus* but not *Papio*. However, neither the correlation between the observed features (acute angulation between buccal and lingual tooth walls and short but broad worn cusps) and the inferred characters, nor the correlation (or overlap) between those inferred features and generic distinction was demonstrated, rather merely stated.

The small incisors of *Theropithecus* are part of its adaptation for nibbling small hard objects brought to the mouth by hand. KNM-BC 2 clearly has small upper and lower incisors, as reported by all observers from Leakey (1969) onward. However, there are no incisors preserved in NME USNO, and there is some difference of opinion about its original condition. Iwamoto (1982) reported that the preserved alveolus for I^2 is smaller than in modern *Papio* of comparable cranial size, and this appears reasonable. But Iwamoto

went on to estimate the width of the incisor arc as 34–39 mm, within the range for the same modern *Papio*. Eck & Jablonski (1984) tentatively accepted this value, which they noted would be very large for *Theropithecus*, but indicated that one adult male *T. darti* from Hadar combines small alveoli and a large arc width due to a midline diastema. This is no more than a possibility for the Usno fossil, so that it was premature for Eck & Jablonski (1984) to assume that small incisors were present in this individual. Extrinsic evidence (see below) tends to contravene this suggestion.

Finally, in terms of their character 8, the curve of Spee shape, Eck & Jablonski (1984, p. 124) accepted a flat curve of Spee for KNM-BC 2 and 1647, but argued that there is a reversed curve typical of *Theropithecus* in the Usno specimen. We do not agree with that determination. This feature does characterize most *Theropithecus* (although not some of the earliest specimens, such as at Hadar), but we do not see it in NME USNO (compare lateral views in Figs 4.2 and 4.3).

Additional characters and their interpretation

As a result of the foregoing analysis, several of the features utilized by Eck & Jablonski (1984, 1987) both to diagnose *Theropithecus* as compared to *Papio* and especially to identify BC 2 and USNO as specimens of *Theropithecus* do not support their arguments. Their characters 1 and 5 combine mandibular conditions which are secondarily related to stress reduction and face size with elevation

above the occlusal plane of the temporomandibular joint and cranial base, of which only the mandibular conditions are truly diagnostic. Characters 2, 3, and 9 may be linked to relative brain as well as masticatory muscle size, especially in the two questionable fossils, and the details of temporal fossa shape have not been carefully analyzed. Feature 4 is poorly phrased, but is related to gelada airorhynch and the impact of temporalis musculature on the orbit, all of which will be discussed below. Finally, characters 6 and 7 (and 8) relate to the diagnostic dentition of *Theropithecus*, but some of the clearest features (e.g. flattened bases of the clefts and relative incision of the notches) are not mentioned, and we strongly question their application to USNO. KNM-BC 2 does have small incisors and perhaps a hint of the *Theropithecus* molar pattern, although it is so worn that certainty is not possible. In the following section, we consider several additional cranial features we have discerned which may help to distinguish these two genera.

Part of the generalized dolichocephalic profile of papioninans is due to their posterior neurocranium. A posteriorly extended posterior temporalis origin, often associated with a posteriorly pointed compound temporonuchal crest, is a corollary of the front tooth–posterior temporalis complex of all papionins (cf. Fig. 4.2 and 4.5 above). The superoinferior height of the temporalis origin forms an acute angle as it extends posteriorly. Finally, the distance between opisthion and the external occipital protuberance compared to posterior occipital breadth is also great in *Papio*. Figure 4.7 compares

(a)

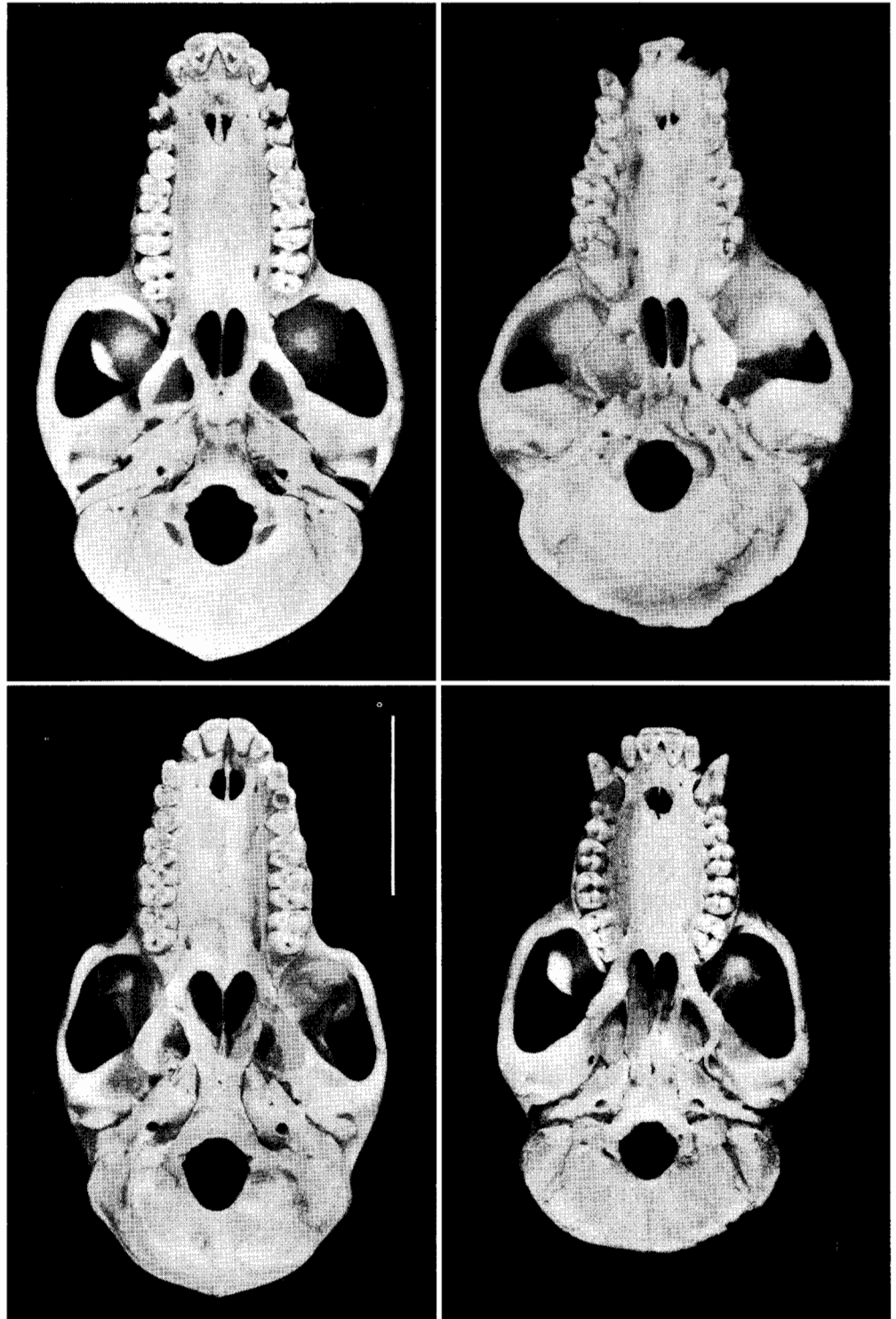
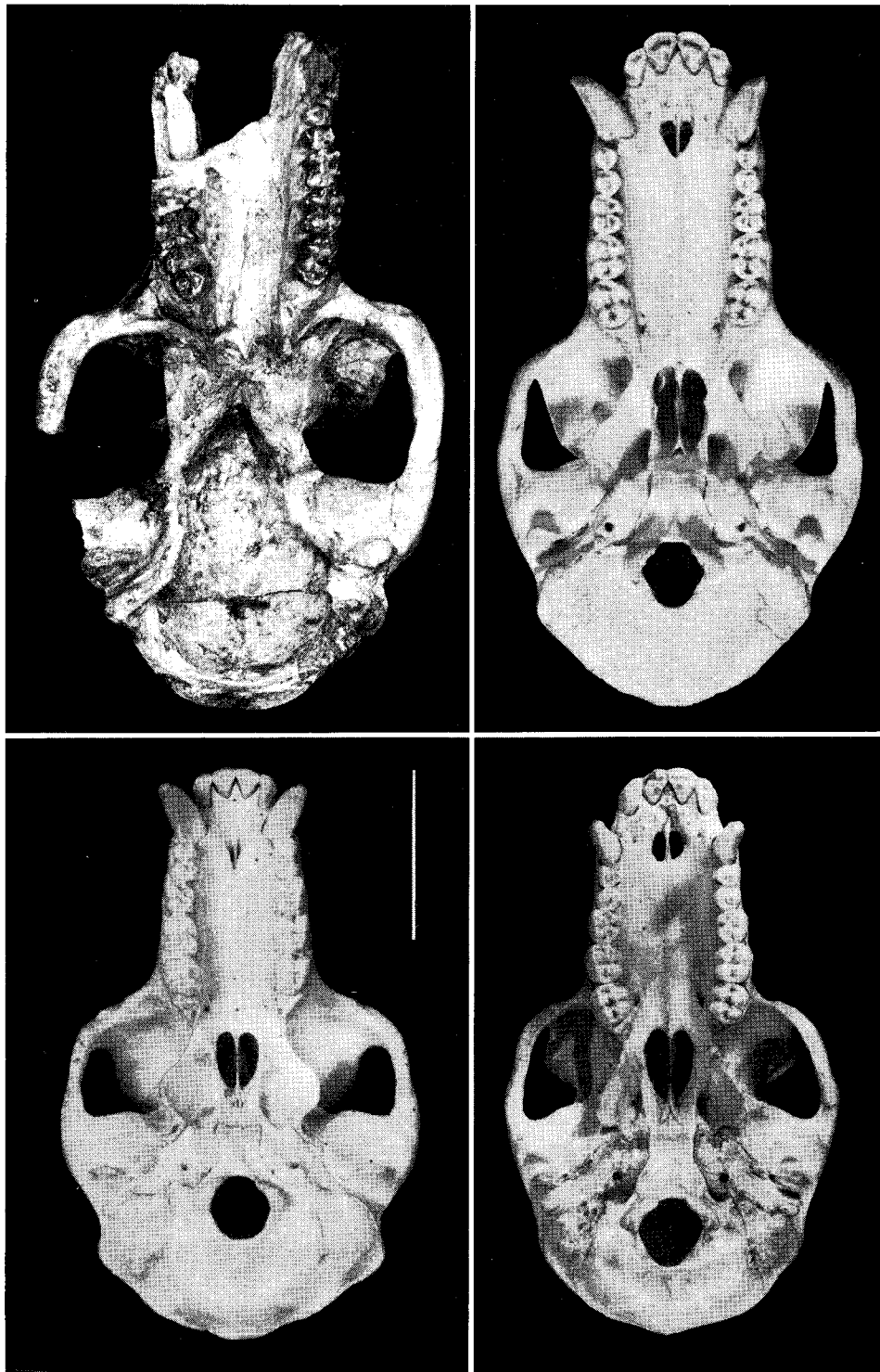


Fig. 4.7. Inferior views, in occlusal plane orientation, of selected papionin crania. (a) Top row, left to right: *Papio hamadryas ursinus*, female; *Theropithecus gelada*, female; bottom row: *Papio hamadryas kindae*,



(b)

female; *Macaca thibetana*, male. (b) Top row: *P. (D.) quadratiostris* (USNO), male; *P. h. ursinus*, male; bottom row: *T. gelada*, male; *P. h. kindae*, male. Scale bars = 5 cm.

this latter area in living and extinct *Macaca*, *Papio* and *Theropithecus*.

Extant and extinct *Theropithecus* are characterized by a more brachycephalic skull, including the neurocranium, which is more globular and rounded at the posterior end; *T. brumpti* is somewhat intermediate between other *Theropithecus* and *Papio*. In distinction to the typically elongate papioninan skull base, *Theropithecus* shows wide basioccipital and bimastoid breadth. This overall brachycephaly is a reversal which is convergent on *Macaca* and its large extinct relative *Paradolichopithecus*. Swindler, Sirianni & Tarrant (1973) found that *Papio hamadryas cynocephalus* and *Macaca nemestrina* have similar growth profiles, but that the differences between them primarily result from the narrower, more klinorhynch skull of the former species.

All extant and extinct *Theropithecus* show a derived suite of features related to expansion of the anterior temporalis and pterygoid-masseter sling. The expansion of the anterior temporalis muscle has resulted in an expanded and vertical coronoid, stronger post-orbital constriction and anteriorly convergent temporal lines; the anterior temporalis also expanded mediolaterally into the posterior cone of the orbit and far laterally onto the superoposterior surface of the malar. The expanded pterygoid-masseter sling has caused the zygomatic arch to bow laterally. The great bi-auricular breadth and the vertical height of the malar visor combine to cut off the posterior temporalis muscle from having a direct line of action on the front teeth (see Fig. 4.4); instead, posterior temporalis must act on the

incisors indirectly. This is to be expected, as it is well known that *Theropithecus* has smaller incisors and larger, more complex molars than do species of *Papio*.

Another indication of the greater emphasis on postcanine chewing in *Theropithecus* is the position of its maxillary zygomatic process root origin above or immediately posterior to M², whereas the root of the malar buttress is usually above or just posterior to M³ in other papionins. This position of the malar buttress supports the hypothesis that *Theropithecus* is secondarily orthognathous, as well as brachycephalic and airorhynch. Other factors confirming this condition are: the actual facial angle indicating airorhynch, the raised premaxillary segment of the palate and the bulbous, wide-based neurocranium.

Extrinsic evidence for systematic placement of both fossils

It thus appears that both of the focal fossil specimens are broadly conservative of character states which probably typified the common ancestor of *Papio* and *Theropithecus*. In such cases, even a few (perhaps just one) robust derived conditions may be enough to convincingly allocate a plesiomorphic fossil to one or the other clade. As yet, we do not find any such clear synapomorphy of either BC 2 or USNO with *Theropithecus*; the problem is that *Papio* is generally plesiomorphic with respect to its common ancestor with *Theropithecus*, so that potential derived features linking one of the fossils to *Papio* would be nearly impossible to identify. As argued elsewhere (Strasser & Delson,

1987, p. 93), the lack of derived characters by comparison to a sister taxon does not invalidate or make less distinct any diagnosable taxon, but it does render more difficult the identification of the earliest members of that clade as opposed to a common ancestor or 'stem' taxon. Additional material from other sites may help to better interpret both holotypes and their respective species.

?Theropithecus baringensis

Eck & Jablonski (1984, p. 113) and M.G. Leakey (pers. comm. to them) agreed that the teeth of a second Chemeron mandible fragment (KNM-BC 1647) are *Theropithecus*-like, although they are also moderately worn; Delson's notes indicate this as well. This resemblance is greatly strengthened by the presence at a comparable date of definite *Theropithecus*, albeit with relatively low-crowned and less complex teeth, in the Lokochot horizons of the Turkana Basin (see Leakey, chapter 3). If we accept the Eck–Jablonski–Leakey argument that it is unlikely that two papionin taxa of the same size would be represented in the few known specimens from locality JM 90/91, then in light of the new Turkana specimens, we are forced to accept hesitantly that BC 2 indeed represents an early member of the *Theropithecus brumpti* lineage. The implications of this view for *Theropithecus* phylogeny, if indeed correct, are far greater than indicated by the cited authors.

As noted above, Eck & Jablonski (1984, p. 124) accepted a flat curve of Spee for KNM-BC 2 and 1647, and because some

Hadar *Theropithecus* have a relatively flat curve, which is generally accepted as the ancestral condition, they were forced to infer that a reversed curve evolved independently three times in the three *Theropithecus* lineages. Moreover, even accepting that the dentition of ?*T. baringensis* is incipiently gelada-like, the contemporaneous forms from Hadar present fully developed *Theropithecus* molars (as do also the probably significantly older teeth from Lothagam [Delson, chapter 5, this volume] and perhaps the Awash). This would require the parallel development of the full molar pattern at least twice, depending upon the relationships of *T. gelada*. Finally, the same is true for the partial airorhynchus common at least to the *T. oswaldi* lineage and to *T. gelada*, but of uncertain development in the relatively long-faced *T. brumpti* group.

At the outset, we suggested that *T. brumpti* might be the sister taxon of the combined *T. gelada* and *T. oswaldi*–*T. darti* clades. The several derived characters seen in the first species (above and in Eck & Jablonski, 1987) are combined with a number of conservative features, including facial angulation (degree of klinorhynchus) and the height of the midface perhaps comparable to that expected for the common ancestor of *Papio* and *Theropithecus* and moderate-size incisors. On the other hand, *T. gelada* and *T. oswaldi* share the development of airorhynchus, compared to the ancestral African papionin condition, as well as a tendency toward orthognathus, a deeper midface and a shortened, rounded neurocranium. Although *T. oswaldi* itself shows progressive reduction in incisor size and an increase in molar

size and complexity through time, the early members of that sublineage (*T. darti* from Hadar and Makapansgat) share with *T. gelada* a moderate molar complexity and with *T. gelada* and *T. brumpti* moderate-size incisors (Eck & Jablonski, 1987; see Eck, chapter 2). The reversed curve of Spee and moderate molar complexity shared by *T. brumpti* and other species appear to have developed in parallel, as neither feature is present in early members of the *T. brumpti* lineage, such as BC 2 and BC 1647 from Chemeron or the various fragmentary remains from the Koobi Fora Formation (see Leakey, chapter 3). Thus, if KNM-BC 2 and 1647 are both early members of the *T. brumpti* lineage, the major division within *Theropithecus* must be between that clade and the remaining taxa. This view was tentatively supported on general character similarity by Eck & Jablonski (1984 and especially 1987), but Jablonski (see chapter 7) illustrates a split between the *T. brumpti*–*T. oswaldi* clades and the living *T. gelada*, which she considers the most conservative species of the genus. Our findings of shared airorhynchity in *T. gelada* and the *T. oswaldi* lineage rejects that interpretation. A further taxonomic evaluation of this finding is presented by Delson (see chapter 5).

Papio quadratirostris

It is less possible to be certain about the affinities of the USNO fossil. Leakey (see chapter 3) allocates several fragmentary specimens to the same taxon, but she then synonymizes it with parts of the *T. brumpti* lineage, and identification of

those fossils with Iwamoto's cranium is not clear. Delson (1984) referred *P. quadratirostris* to *Dinopithecus*, which was in turn argued to be a subgenus of *Papio*. Material allocated to *P.* (*Dinopithecus*) is known only from four other site groups: Schurweburg and Swartkrans (both South Africa), Leba (Angola) and the lower Shungura sequence (Omo Basin, Ethiopia). The fossils from the latter two samples are indistinguishable from each other, but significantly smaller than the Schurweburg and Swartkrans sample of *P.* (*D.*) *ingens* (see Figs 4.8–4.11).

The Shungura collection includes a male palate (NME L. 185-6), parts of three male mandibles, most of a female mandible (Omo 47-1970-2008) and parts of two fragmented female skulls (of which NME Omo 42-1972-1 is more complete) which have been tentatively reconstructed, as well as numerous smaller fragments and isolated teeth (E. Delson, unpub. data). The Leba sample (all numbered DGUNL LEBA02-19) includes a partial male maxilla (06), a partial frontal bone (probably male, 05), a female mandible (03) and a well-preserved female skull (lacking the superior region, 02) which are all nearly identical to their Shungura counterparts, along with other fragments (M.T. Antunes & E. Delson, unpub. data); other than a single mandible of *Cercopithecoides williamsi*, no other cercopithecoid species is represented among the 20 known specimens. The Swartkrans specimens (Freedman, 1957; Delson, unpub. data) include a partial female skull (TMP SK 553), a male neurocranium without face (SK 599, recently reconstructed by Dr. Ron Clarke), several

Table 4.1. Measurements (in mm) of male upper teeth of *Papio* (*Dinopithecus*) specimens.

Species: Site: Specimen Number	<i>P. (D.) quadratiostris</i>			<i>P. (D.) ingens</i>			
	Usno	Omo E	Leba	Schurw.	SK 1	SK 1	SK 1
	NME	NME	DGUNL	TMP	TMP	TMP	TMP
	USNO	L. 185-6	LEBA06	SB 7	SK 546	SK 578	SK 577
C ¹ W	12.0	<14	17.4		13.5	15.8	
C ¹ L	13.0	<17	17.8		21.0	20.1	
P ³ W	8.0	10.0	11.4		10.3	11.3	9.8
P ³ L	6.3	8.9			8.3	9.0	8.7
P ⁴ W	9.5	12.3	11.5		10.9	12.9	11.0
P ⁴ L	7.3	9.2	8.4		8.0	9.5	9.7
M ¹ AW	11.1				11.8	13.3	
M ¹ PW	11.5				11.8	12.5	
M ¹ L	11.7	13.0	11.9		13.5	14.1	
M ² AW	13.4	14.3	15.2	17.1			
M ² PW	13.1	13.2	14.2	16.4			
M ² L	14.3	15.1	15.8	17.9			
M ³ AW	13.8	15.0	16.0	16.6			
M ³ PW	12.1	12.5	12.7	13.7			
M ³ L	15.5	15.9	15.2	19.7			

Notes: NME, National Museum of Ethiopia, Addis Ababa; DGUNL, Departamento de Geologia, Universidade Nova de Lisboa, Portugal; TMP, Transvaal Museum, Pretoria, South Africa. Schurw., Schurweburg; SK 1, Swartkrans, 'Hanging Remnant' of member 1.

For canines and premolars, L(ength) is always maximum mesiodistal, W(idth) is maximum buccolingual, taken perpendicular to length. For molariform teeth, AW and PW, respectively, are taken across the mesial and distal loph(id)s usually at the cervix; L, however, is taken at interdental contact points, often estimated due to wear, and decreases significantly in worn teeth.

partial male maxillae and other fragments, while the Schurweburg holotype mandible (TMP SB 7) may be associated with a large damaged cranium bearing M²⁻³ (SB 3).

Table 4.1 presents measurements of C¹-M³ for the holotype of *P. (D.) quadratiostris* along with those for male specimens from the four mentioned sites. Dental metrics are quite similar for the two Omo specimens and the Leba maxilla

(and see Fig. 4.8), while the South African molars, at least, are rather larger. M.G. Leakey (pers. comm.) suggests that the premolars of NME USNO are relatively smaller compared to its molars than those of the other specimens, being similar to those of *T. brumpti* which are usually shorter than half the length of M². The situation observed for USNO may reflect its advanced state of wear, but without a

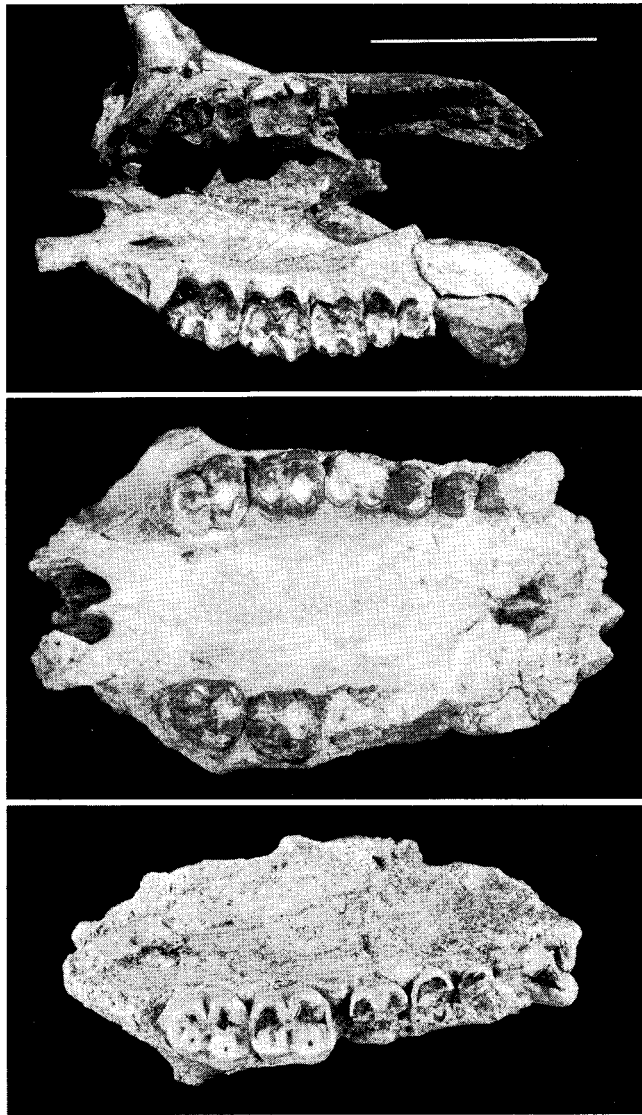


Fig. 4.8. Occlusal views of male maxillae referred to *Papio* (*Dinopithecus*) *quadratiostris*. Top to bottom: holotype (USNO), Shungura palate NME L. 185-6, Leba half palate DGUNL LEBA06. Scale bar = 5 cm.

sample of more individuals, such comparisons are difficult to evaluate; the purpose of these data is only to demonstrate overall similarity of size.

Table 4.2 lists several craniofacial measurements for the same material. The

Leba frontal (Fig. 4.9) is slightly smaller than the USNO cranium in nasion-bregma distance and biorbital width, but its temporal lines are fused farther anteriorly. The apparently adult Swartkrans skull (SK 599), which is unlikely to be *T. oswaldi*

Table 4.2. Measurements (in mm) of selected cranial dimensions of male Papio (Dinopithecus) specimens.

	<i>P. (D.) quadratiostris</i>			<i>P. (D.) ingens</i>
	Usno	Omo E	Leba	SK 1
Species:	USNO	L. 185-6	LEBA05/6*	SK 599
Site unit:	NME	NME	DGUNL	TMP
Specimen Number	USNO	L. 185-6	LEBA05/6*	SK 599
Nasion-Bregma	68.5		66.0	79.0
Nasion-Min. Temporal width pt.	85.0		50.0	72.0
Temporal Line width at level of postorbital constriction	32.5		13.0 (est.)	33.0 (est.)
Biorbital width	106.5		90.0	115.0+
Orbit width	29.0		28.0	30.0
Length M ³ -C ¹	72.5	82.0	77.0	
Length M ³ -P ³	53.0	63.0		
Length M ³ -M ¹	41.5	45.0	44.0	
Length P ⁴ -C ¹	32.0	36.5	34.0	
Length P ⁴ -P ³	13.0	18.0		
Alveolar process width at M ²	17.5	19.0	19.0	
Palate depth at M ²	10.0	12.0	11.0	

* Measurements on the frontal taken on LEBA05, dental values from LEBA06.

rather than *P. (Dinopithecus)* because of its short postglenoid processes (Fig. 4.10 and see Delson, chapter 5), is larger than either of the other two, and its relative point of temporal line fusion would appear to be intermediate. Moreover, the post-eromedial corner of its temporal fossa is rather squared in inferior view. As it is most unlikely that this specimen belongs to the *T. brumpti* lineage, the short post-glenoid and right-angled temporal fossa corner of that species are probably non-homologous with those described here.

The posterior neurocranium of each of the crania referred to *P. (Dinopithecus)*, both male and female (Fig. 4.10), has the narrowed and extended external occipital

protuberance typical of *Papio* (including USNO), as discussed above. In addition, the female mandibles from Leba and Shungura (Fig. 4.11) preserve large incisors, while all the mandibles have a typically *Papio* symphyseal morphology, as also discussed above. The Usno cranium occludes as well or better with the most complete male mandible from Shungura (unfortunately lacking incisors) than does the Shungura male palate. It appears to us highly unlikely that the holotype of *P. quadratiostris* had small incisors.

Taken together, the Leba and Shungura specimens document the presence in the 3–2 Ma range of a species of *P. (D.)* smaller

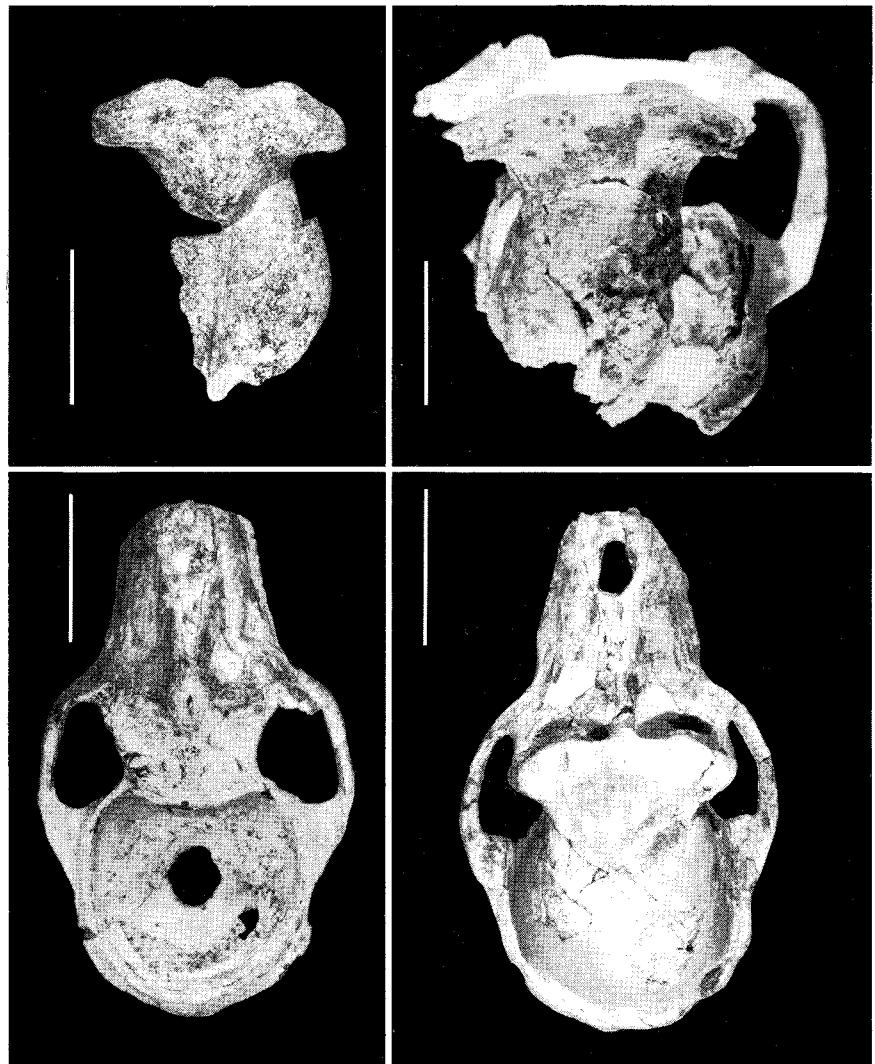


Fig. 4.9. Dorsal views (with oclusal plane horizontal) of crania referred to *Papio (Dinopithecus) quadratiostris*. Top row, left to right: Leba male? frontal DGUNL LEBA05, Swartkrans male cranium TMP SK 599 [*P. (D.) ingens*]; bottom row: Leba female cranium DGUNL LEBA02, Shungura female cranium NME Omo 42-1972-1. Cf. Fig. 4.5. Scale bar = 5 cm.

than the type species from Schurweburg and Swartkrans. The lack of any teeth with *Theropithecus* morphology at Leba suggests that the frontal does belong to the same species as the other cercopithecines,

using the same parsimony argument as was employed above for BC 2 and BC 1647. Since the frontal (LEBA 05) is too large for the female skull from Leba (02), it is probably male. Dentally, the species

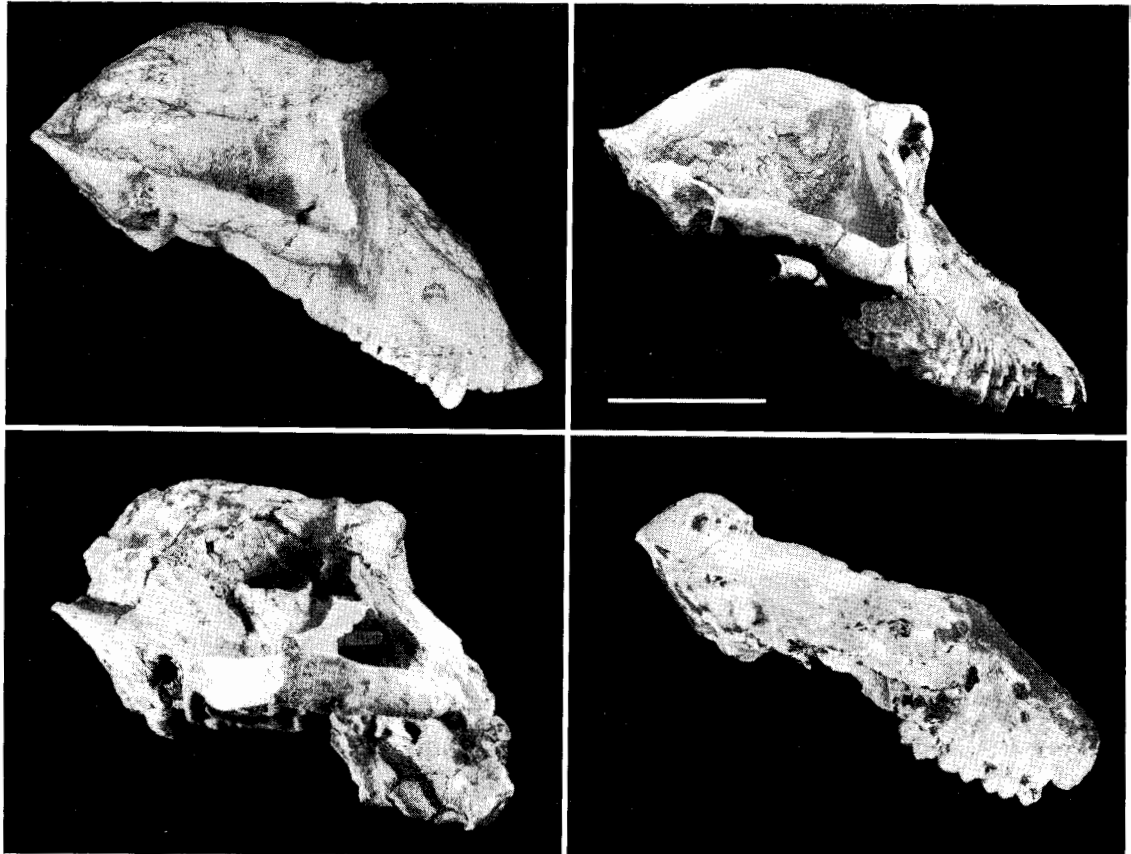


Fig. 4.10. Right lateral views, in Frankfurt horizontal, of crania referred to *Papio (Dinopithecus)* species. Left column, *P. (D.) ingens* from Swartkrans: female (TMP SK 553) above male (TMP SK 599). Right column, *P. (D.) quadratiostris*, Shungura female (NME Omo 42-1972-1) above Leba female (DGUNL LEBA02). Cf. Fig. 4.2. Scale bar = 5 cm.

known at Leba is comparable in size to NME USNO (and the Shungura fossils), and based on the Leba frontal, the temporal lines in males joined to form a sagittal crest quite far anteriorly, as was also probably the case for the Swartkrans population. In sum, the most likely conclusion is that the Usno fossil represents the same species as the specimens from the Shungura Formation and from Leba, a species which is best termed *P. (D.)*

quadratiostris Iwamoto, 1982. A relatively small brain size and strong postorbital constriction, as well as a flat muzzle dorsum and especially the lack of maxillary or mandibular corpus fossae, appear to be among the few diagnostic features of this basically conservative subgenus. The possibility that *P. (Dinopithecus)* is in some sense ancestral to *P. (Papio)* or to other extant baboons is intriguing but beyond the scope of this paper. Modern

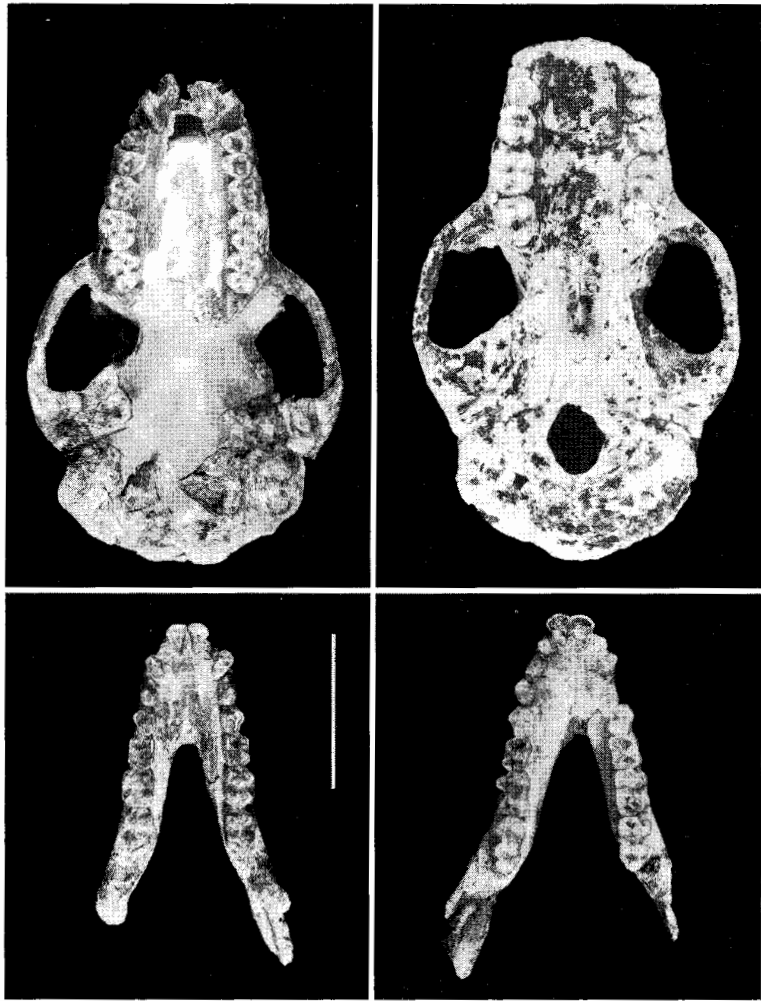


Fig. 4.11. Oclusal view of female specimens referred to *Papio* (*Dinopithecus*) *quadratiostris*. Left column Shungura cranium NME Omo 42-1972-1, mandible Omo 47-1970-2008; right column Leba cranium DGUNL LEBA02, mandible DGUNL LEBA03. Scale bar = 5 cm.

baboons (including mandrills), as well as all other Plio-Pleistocene species of *Papio*, have both larger brains and larger incisors than do species of *P. (Dinopithecus)* or *Theropithecus*, which is perhaps related to the exploitation of high-quality energy sources requiring preparation by the front

teeth but needing less grinding. It is possible that this distinction from *Theropithecus* lies at the root of the eventual replacement of that genus throughout its previous pan-African range by *Papio* in the later Pleistocene.

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