CHAPTER 8
JACOVEC CAVERN PRIMATES

8.a. Taxonomy

The Order Primates is represented by Australopithecus, Parapapio jonesi, Parapapio broomi, colobine, Papio izodi and taxonomically indeterminate cercopithecoid. Measurements are provided in Table 8.1.

Systematic palaeontology

Family: CERCOPITHECIDAЕ

Subfamily: Cercopithecinae

• Parapapio jonesi (Broom, 1940)

Extinct papionini

Material

BP/3/22786, left mandible fragment (Plate. 8.1)

Description

The specimen is a fragment of the horizontal ramus with the lower canine, P₃ and P₄ in place. The buccal surface of the specimen is exposed while the lingual surface is encased in orange breccia. The identification of this specimen to species was provided by Dr. R. J. Clarke, based on the relatively large canine and premolars. The basal border below the teeth is broken. The break is fresh indicating this probably occurred during the excavation. This resulted in the exposure and partial breaking of the lower canine root.
Family: CERCOPITHECIDAE

Subfamily: Cercopithecinae

♣ *Parapapio broomi* (Jones 1937)

Extinct papionini

Material

BP/3/22780, left mandible fragment (Plate. 8.2)

Description

The specimen is preserved from the anterior alveolar border of the first incisor to the posterior alveolar border of the most anterior root of P₄. The lingual incisal alveolar region is damaged. Compared with the modern *Papio* and *P. jonesi*, the mental foramen is more pronounced and closer to the alveoli than in the modern *Papio*. The depth of the mandible from the alveoli to the basal border is also shallower in the extinct species than in the modern *Papio*. Species identification was provided by Dr. R. J. Clarke based on the above characters.

Family: CERCOPITHECIDAE

Subfamily: Colobinae

♣ Colobine indet.

Indeterminate colobus monkey

Material

BP/3/22787, left supraorbital fragment (Plate 8.3)

Description

The specimen is a well preserved supraorbital fragment. There is a distinct torus with a deep supratoral sulcus characteristic of colobine species.
Twelve hominid specimens have been recovered from the Jacovec Cavern (Partridge et al. 2003: Table 1), all of which derive from the orange breccia. Four adult individuals were identified from isolated teeth and portions of maxilla with embedded teeth (Partridge et al. 2003). Only four hominid postcranial elements had been recovered in the time of the current study. A total of three hundred and thirteen specimens belonging to non-hominid primates were recovered. These non-hominid primates represented in the Jacovec Cavern infill have been divided into three size classes: large, medium and small. The large primates are the least represented with only seven specimens assigned to this category. The seven specimens derive from the crania and postcranial (Appendix II). Medium size primates comprise the highest representation among the non-hominid primates, with a total of a hundred and ninety (61%) of the total non-hominid primate specimens. Juveniles in this size class are represented by twenty specimens deriving almost entirely from the crania, especially teeth (Appendix II). The adults are represented by a majority of specimens deriving from postcrania. Postcranial part representation from the medium size adults indicates that the ulna has the highest representation both in terms of NISP, MAU and %MAU (Table 8.2, Figure 8.1).

Small size class primates comprise 37% of the total non-hominid primate NISP, with an aggregate of a hundred and sixteen specimens. Twenty of the specimens belong to juvenile individuals while the rest derive from adult individuals. Small size class adult postcranial skeletal element representation indicates a high representation of femur and radius (Table 8.3, Figure 8.2). Craniodental representation from the three classes indicates a majority of elements deriving from medium size class adults, with only one P4 representing large size class (Table 8.4).
Minimum Number of Individuals

The primate MNI in the Jacovec Cavern assemblage is 19. This accounts for 28% of the total macrofauna assemblage represented in the infill. Of these 19 individuals, six are hominids while the rest are non-hominid primates. All of the Jacovec Cavern hominid fossils were recognized only as belonging to *Australopithecus* species (Partridge *et al.* 2003). Three of the thirteen non-hominid primates were identified to species as detailed above, while the other ten individuals could not be placed into taxa. The large size primates are represented by one adult; medium size primates by four adults and three juveniles; and small primates by three adults and two juveniles.

8.b. Taphonomy

Bone Modification

Two hominid and nine non-hominid primate specimens display definite evidence of carnivore modification. The greater trochanter of hominid femur (StW 598) has been gnawed away as well as the lateral extremity of hominid clavicle (StW 606) (Partridge *et al.* 2003). Definite carnivore gnaw marks are visible at both ends of this clavicle (Partridge *et al.* 2003). Of the nine non-hominid primate modified bones, seven derive from the small size primates. These include two femora shafts; both bearing carnivore tooth scores and tooth pits; also identified were three fibula shafts displaying carnivore tooth pits; and a tibia and a rib both with carnivore tooth pits were also recovered. From medium size primate, a metapodial, bearing carnivore tooth marks and a right proximal ulna, bearing carnivore tooth punctures and tooth scores were identified.
Assemblage formation

There are various scenarios that could result in primate skeletal elements being accumulated in cave sites. The three most prominent are: where the primates are preyed upon by predator(s) in their sleeping quarters; where the primates die naturally in their place of abode; and where a specialized predator brings in and accumulates primate remains, either as refuse or scat assemblage (Brain 1981; Pickering 1999). In instances of natural death within the cave, complete or partially complete and, in some cases, articulated or articulating skeletal elements are expected. These possess no predepositional biotically derived modifications but may display both abiotic and biotic postdepositional modification. Biotically derived postdepositional modification would in this case be from boring insects, while abiotic modification would result from corrosion by debris, soil leaching and subaerial weathering. These categories of modification may be absent in instances of mummification e.g., as with the Stw 573 Australopithecus skeleton from Sterkfontein Member 2 (Clarke 1999). However, even in cases where natural death and perfect or near perfect preservation has occurred, recovery of such fossils may be, and usually is, compromised by postdepositional vertical and horizontal disturbances. These disturbances, in the case of dolomitic caves, are in the form of breccia collapse, and/or gravitational slump. The result is bone disintegration and fragmentation leading to loss of bones especially the less dense such as vertebrae, ribs and scapula.

Death trap and/or natural death within the cave is not envisaged in the accumulation of both the hominid and non-hominid primate assemblage within the Jacovec Cavern. The low representation of craniodental elements, especially teeth, which have a longer survival span, compared to other skeletal elements, even in cases of intense postdepositional destruction; the low representation of compact bones,
which owing to their high structural density also survive better than other postcrani al elements; and the absence of antimeric pairs argue against both death trap and natural death within the cave.

Primates are at risk of predation by raptor birds (e.g. Oates 1977; Izawa 1978; Gautier-Hion & Tutin 1988; Shultz 2001), snakes (Struhsaker 1967), carnivores (e.g., Allen & Loveridge 1933; Nishida 1972) and other primates (Goodall 1968; Wrangham 1975; Boesch-Achermann 2000). Of these, the carnivores have been most studied as they usually accumulate the remains of their victims where they rest or den. The leopards are the key predators of primates through stalking them in their sleeping places at night or resting places during the day (e.g., Boesch 1991; Bailey 1993; Zuberbühler et al., 1999). In their research, Zuberbühler and Jenny (2002) documented that large body size primates are more prone to predation than their smaller counterparts. They equated this to more agility of the smaller primates in the forest canopy making them more difficult to capture. The two researchers also documented higher rates of predation among larger groups of primates than smaller ones. This they attributed to the ease of leopards locating larger groups, “thereby outweighing the benefits of increased vigilance and dilution” (Zuberbühler & Jenny 2002: 882), and/or “that leopards preferred preying on large groups because there is a greater possibility of monkeys being on the ground” (Zuberbühler & Jenny 2002: 882). This situation was however reversed in the case of chimpanzee predation, where “relative to their body size, chimpanzees suffered from low predation pressure” (Zuberbühler & Jenny 2002: 882). The chimpanzees were envisioned to “have reached a critical threshold level and grown out of the main prey range of leopards” (Zuberbühler & Jenny 2002: 882). Stemming from this research therefore, it can be expected that primates equivalent and bigger in size to the chimpanzees should be
represented less often in leopard-accumulated assemblages in comparison to other smaller primates. In their investigation of leopard consumption of primate individuals, Pickering (2001a,b) and Pickering and Carlson (2004) documented a higher representation of all limb bones, axes, scapulae,ossa coxae and atlases in the refuse assemblage relative to the scat assemblage, while on the other hand, there was a higher presentation of patella, carpal, metapodial, tarsal, thoracic and lumbar vertebra, clavicle and phalanx specimens in the scat assemblage than in the refuse assemblage. This disparity, they concluded was based on sequence of consumption and locations of skeletal elements “in regions of focused consumption” (Pickering and Carlson 2004: 40).

Primates exploit deep cave recesses, cliff overhangs and edges of surface holes as resting and sleeping ground (Brain 1981; Gow 1973; Simons 1966). Leopards also exploit these grounds as hunting zones, where they catch their prey and drag it into deeper recesses of the cave for consumption (Brain 1993). In unfortunate cases, either or both the predator and the prey fall to their deaths, to the ground below where they get incorporated with other debris (Simons 1966).

An attempt to interpret the taphonomic aspects of the primate assemblage from the Jacovec Cavern was conducted with the results of the above studies in mind. The main indication that carnivores were, at least in part, responsible for the accumulation of the primate assemblage is the presence of carnivore-modified primate bones. However, the percentage of modified bones is much lower than that which has been observed from some of the carnivore-accumulated primate assemblages. Two examples are 71% of postcranial NISP of Mount Suswa baboons (Simons 1966) and 40% of postcranial NISP of baboon carcasses fed experimentally to leopards (Pickering 2001a,b). A critical issue that must be taken into consideration while
comparing the Jacovec Cavern fossil primate assemblage to modern experimental assemblages is the time averaged postdepositional destruction. Whereas the modern experimental assemblages were not subjected to any postdepositional destruction, the Jacovec cavern assemblage has had to endure various mechanical (e.g., tumbling and compaction) and chemical (e.g., leaching) processes, which compromised the quality of bone and bone surface leading to possible deletion of entire bones or original surfaces of the bones. This would have lowered the frequencies of observable carnivore-related modifications.

Various carnivores which today are (leopard, lion and hyaena) and/or may have been (sabertooth cats and *Chasmaporthetes*) predators of both hominid and non-hominid primates are represented within the Jacovec Cavern fossil assemblage. Any of the large and medium carnivores represented could have been responsible for the accumulation of the primate bone assemblage either within the vicinity of the cave and/or inside. Skeletal part representation is in part consistent with observed frequencies of refuse assemblages after leopard ravaging on primate carcasses (Carlson & Pickering 2003). The resemblance to the refuse assemblage is in the high representation of limb bones and less representation of carpals, tarsals and phalanges. However, it differs in the low representation and near absence of craniodental elements. High frequencies of craniodental elements are expected if the refuse assemblage has not been transported after leopard feeding cessation. From the skeletal part representation, it is thus highly likely that consumption of the primate individuals took place outside the cave, and the remains washed in from the grounds above.
8.c. Conclusions

The collapse within the Jacovec Cavern apparently caused fragmentation of some of the bones which can be recognized from fresh breaks. This may have rendered some of the bones unidentifiable through breakage into unidentifiable fragments. This could also have reduced the frequency of identifiable biotic and abiotic modifications. However, the skeletal part representation and the available modified bones assisted in drawing conclusions into the possible modes of accumulation responsible for the accumulation of the Jacovec Cavern primate assemblage. The low representation of compact bones which survive better than other skeletal elements due to their higher structural density, and low representation of cranial elements argues against death trap situation. The skeletal part representation and presence of carnivore modified bones strongly support the notion that the primate assemblage from the Jacovec Cavern was accumulated by carnivores. Voiding is however not inferred, and remains were most probably washed in from the vicinity of the cave.

In my earlier analysis (Kibii 2000) I had pointed out that the Jacovec Cavern assemblage (formerly referred to as Combined Breccia Primate assemblage) highly resembled a scat assemblage accumulated by voiding carnivores. This conclusion had been arrived at from observations of the absence of cranial parts and high representation of digital elements. I had however indicated that the interpretation must be regarded with caution due to the small sample size that was available at the time. With the newly expanded primate sample from this infill, this conclusion has demanded a review. The new data lead to an inference that the primate remains form a refuse assemblage, which implicates the actions of carnivores which preyed on the primate individuals and accumulated the remains within the vicinity of the cave.
Current evidence does not support voiding, where the assemblage would approximate a scat assemblage.