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Eagle involvement in accumulation of the Taung child fauna

Of the major South African hominid fossil sites, Taung is unique in that it has yielded only a single hominid specimen—that of the infant Type skull of *Australopithecus africanus*. Furthermore, the associated fauna is of exceptional composition, being comprised mainly of small-sized animals, many of which display unusual damage to the bones and skulls. Most early accounts interpreted these characteristics of the Taung assemblage as being due to the carnivorous activities of australopithecines. Recent excavations have failed to reveal either further ape-man remains or fossils of large animals. We present data demonstrating the similarity of the Taung hominid assemblage to those accumulated by extant large birds of prey and suggest that such a bird of prey was the taphonomic agent responsible for the accumulation of most of the Taung fossils, including the *Australopithecus* infant skull.

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Introduction

The 3–4 year old juvenile Taung Skull found at the Buxton Limeworks near Taung, South Africa in 1924, was not only the first ape-man fossil to be discovered but was also the first fossil hominid to be recovered from a limestone cavern in South Africa (Dart, 1925). Subsequent discoveries from 1936 onward of several ape-men and associated fossils in dolomitic limestone caverns at Sterkfontein, Kromdraai, Makapansgat and Swartkrans concentrated attention on those sites. Much of these latter bone deposits were still in existence and could be systematically excavated and studied, unlike the Taung skull locality, most of which had been blasted away. Thus the question of the mode of accumulation of the Taung fossils has often been overshadowed by interpretations of the agencies of collection of the more "intact" sites. That was not, however, always the case. A perusal of the earlier literature reveals that Raymond Dart, Robert Broom and Aleš Hrdlička not only devoted attention to the fauna which accompanied the Taung child but also addressed the possible mode of its accumulation. In 1981 Brain (pp. 263–264) concluded that at least some of the Taung baboon and antelope fossils "represent food remains of a carnivore, very probably a leopard". Recent detailed excavations of the Taung deposits have failed to reveal any further ape-man remains (McKee & Tobias, 1994). These latter authors have suggested carnivores and water action as modes of accumulation of the Taung fossil material. Here we examine both the early and the recent theories, add new observations, and present the hypothesis that the primary collecting agent of the Taung child and much of the fauna was neither a mammalian carnivore nor water but a large bird of prey.

To evaluate the bird of prey hypothesis, we shall first present an historical overview that examines the peculiarities of the Taung assemblage. This is followed by observations on the hunting behaviour of three extant African eagles for use as modern homologues of the theoretical Taung bird of prey. It should be emphasized that these examples are given only to illustrate the collecting capabilities of modern African raptors and are not intended to be a comprehensive review of the behaviour of extant birds of prey. The discussion of the extant raptor behaviour is followed by a brief examination of modern African mammalian bone collectors. After further examination of the taphonomic peculiarities of the Taung assemblage, along with comparison of the modern and fossil data, we will conclude that numerous fossil specimens from Taung were accumulated by large birds of prey.

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An historical review of the peculiarities of the Taung fossil assemblage

Following the discovery of the Taung child at the Buxton limeworks quarry in 1924, both Dart (1926, 1929, 1934, 1949*a*,*b*, 1953; Dart & Craig, 1959) and Broom (1934, 1946) made observations (discussed below) on the small size of the accompanying fauna, the damage to the bones and the situation of the cave in which the skull was found. On the basis of these observations they ruled out carnivores as collecting agents but proposed instead that ape-men had accumulated the bones in the cavern and had inflicted the damage on the skulls. Such conclusions were to form the basis for Dart's osteodontokeratic hypothesis (Dart, 1957).

The composition and small body size of the Taung fossil fauna

As early as 1926, Dart noted the absence of large bones in the Taung hominid deposits. Three years later he wrote:

> Examination of the bone deposit at Taungs shows that it contains the remains of thousands of bone fragments. It is a cavern lair or kitchen-midden heap of a carnivorous beast. It is not a water-borne deposit and the Taungs remains could not have been washed into the cavern from the surface. The bones are chiefly those of small animals like baboons, bok, tortoises, rodents, bats and birds. Eggshells and crabshells have also been found. This fauna is one which is not characteristic of the lair of a leopard, hyena or other large carnivore, but is comparable with the cave deposits formed by primitive man. (Dart, 1929).

In his description of the fauna associated with the Taung skull, Broom (1934) noted that there was "a considerable number of different small animals". There were many skulls of small baboons and "large numbers of Hyrax skulls all of which have been broken", including the remains of six broken hyrax skulls within one block of breccia "smaller than a closed fist". He named the hyrax *Procavia antiqua* and observed (1946) that it was the second most common animal in the collection.

Certainly the Taung fossil assemblage is unique amongst South African early hominid-bearing fossil sites in its small size distribution of animals and paucity of fauna commonly found at the other ape-man sites of Sterkfontein, Kromdraai, Swartkrans, Makapansgat and Gladysvale [Table 1 and Figure 1, to be compared later to Figures 2–4; for faunal lists, see Broom (1946) and Brain (1981, 1985)]. Broom (1946) noted that there was a striking absence of medium and large-size carnivores and that there were no large broken bones such as one would find in the lair of a carnivore. Further animals that Broom (1934) identified from Taung were a small species of spring hare, *Pedetes gracilis*, a giant sand mole or bathyergid, *Gypsorhychus darti*, as well as two new species of small antelope that were represented only by maxilla fragments.

Broom (1934, p. 479) believed these traits in the assemblage could only be due to hominid predation:

> If as seems moderately certain, the animals of the bone breccia were all killed by *Australopithecus*, we get a good deal of light on the habits and mentality of this man-ape. He must have been powerful, and he must have used sticks or stones to have killed baboons, and I think he probably hunted in packs.
>
> His giant moles could only have been obtained by digging, and it seems certain that he must have used stones or sticks for digging them out. He probably caught his spring hares in a similar manner.
>
> The antelopes were probably got through a pack surrounding waterholes and killing the bucks with sticks or stones. The dassies would be difficult for him to obtain except by well aimed stones. It would be practically impossible for any man of to-day to capture single handed without weapons

Table 1 **List of the Taung fauna by size**

Species	MNI*
Large-sized mammals (>20·0 kg)	
Panthera cf pardus	1
Gazella sp.	1
Palaeotragiscus longiceps	1
Notochoerus cf. *capensis*	1
Syncerus cf. *acoelotus*	1
Tragelaphus cf. *angasi*	1
Medium-sized mammals (2·0–20·0 kg)	
Australopithecus africanus†	1
Cercopithecoides williamsi	>1
Papio izodi	>5
Parapapio broomi	<5
Parapapio antiquus	>5
Canis mesomelas	1
Cephalophus parvus	
Oreotragus major	
Hystrix africaeaustralis	
Small-sized mammals (0·01–2·0 kg)	
Procavia antiqua	
Procavia transvaalensis	
Herpestes sp.	
Cryptomys robertsi	
Gypsorhychus darti	
Gypsorhychus minor	
Mystromys antiquus	
Proodontomys cookei	
Desmodillus auriculatus	
Acomys cf. *cahirinus*	
Dasymys sp. nov.	
Dendromus sp.	
Malacothrix cf. *typica*	
Mastomys cf. *natalensis*	
Otomys gracilis	
Prototomys campbelli	
Rhabdomys sp.	
Tatera cf. *brantsii*	
Thallomys debruyni	
Pedetes gracilis	
Petromus minor	
Rhinolophus cf. *darlingi*	
Crocidura taungensis	
Crocidura cf. *bicolor*	
Suncus varilla	
Elephantulus sp.	
Elephantulus antiquus	
Macroscelides proboscideus	
Chelonia	
Pelomedusa sp.	
Aves	
cf. *Athena noctua*	
Aves unident. (eggshells)	

*MNI = minimum number of individuals where estimable. In the case of non-human primates where a > or < sign is used, the exact MNI is not known. Specimens included in the category "large-sized mammals" are done so based on adult body weights. As all of these animals except *P. pardus* and *N.* cf. *capensis* have been identified as juveniles, it is not known whether the application of a >20 kg body weight estimate is correct. Furthermore, in no case is a "Large-sized mammal" represented by more than isolated fragments, thus presenting the possibility that the specimens were brought to the cave dismembered (see text).

†As opposed to the adult body weight, since the Taung child cranium is definitively that of an infant, *Australopithecus africanus* is included in the category "medium-sized mammals".

"Taung fauna" refers to all fauna from the Dart and Hrdlička areas as reported by Cooke (1990) and McKee (1993*b*).

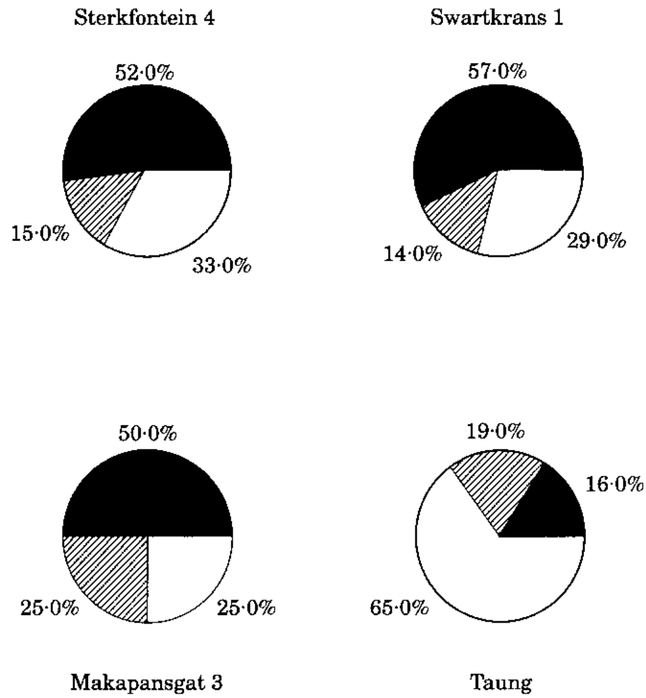

Figure 1. Representation of mammal species by size at selected South African fossil hominid-bearing cave deposits. Small=0·01–2·0 kg average adult body weight; medium=2–20 kg average adult body weight; large= >20 kg average adult body weight. Average adult body weight for extant species is based on Smithers (1983). Extinct species adult body weights were estimated by the authors based on bone sizes and/or the average adult body weight of the closest living species or genera, where applicable. The sites chosen are only intended to represent general trends in South African cave deposits. Swartkrans 2, Sterkfontein 5, Kromdraai A and B and Gladysvale all show similar species size representation to Swartkrans 1, Sterkfontein 4 and Makapansgat 3. All data derived from Brain (1981), Cooke (1990) and McKee (1993*b*). (□), Small; (▨), medium; (■), large.

> or tools a baboon, a buck, a spring-hare, a mole or a dassie; though he might occasionally kill any one of them, except perhaps the mole, by the throw of a stone.

It is worth noting that the Taung *Australopithecus* skull was also that of a small creature, a 3–4 year old child (Bromage, 1985), probably weighing no more than 10–12 kg (approximately the maximum weight of a juvenile chimpanzee with a similar-sized skull). Furthermore, the non-human primate fossils that have been recovered from Taung are those of extremely small baboons being, on average, smaller in size than those of extant female baboons.

Finally, both Broom (1934) and Dart (1929) noted the presence of bird eggshells, parts of crabs, lizards and tortoise shells. It is important to emphasize that, according to Dart & Craig (1959, p. 5), eggshells and pieces of tortoise carapace were in the blocks of breccia associated with the Hrdlička-Taung skull when they were delivered to him. Hrdlička (1925) also mentioned "turtle and an egg the size of a goose egg". Cooke (1990) illustrated a nearly complete tortoise carapace and the skull of a small bird recovered by the 1947–1948 University of California Expedition.

Recent excavations at Taung have resulted in the recovery of many more fossils of small baboons, crab parts, tortoise carapaces, large eggshells, a partial hyrax cranium, and some remains of small antelopes from the area of the "Dart" and "Hrdlička" pinnacles (McKee, 1993*a*,*b*; McKee & Tobias, 1994). The eggshells have been identified as those of a bird (McKee, pers. comm.). The most recently published mammalian faunal list (Table 1) adds only three new species to previous reports (*Gazella* sp., *Parapapio broomi* and *Panthera* cf. *pardus*) (McKee, 1993*b*). Although McKee (1993*b*, p. 368) mentions "postcranial bones of *Panthera* cf. *pardus*" he has informed us that this species is only represented by a single crescent-shaped sesamoid bone that he has subsequently assigned to cf. *Panthera* sp. McKee & Tobias (1994) have recently discussed the recovery of "some postcranial bones . . . of a large class III bovid" from deposits on the face of the Dart pinnacle. The larger Taung bovid material that McKee (1993*b*) has shown us is still embedded in breccia but appears to comprise a single shaft of a femur and a vertebra that are, in our estimates, of a small to medium-sized class III bovid according to Brain's (1974) classification system. On the whole, therefore, the recently excavated material does not contradict the historically described pattern of the fossil assemblage.

Damage to the Taung fossils

Soon after the discovery of the Taung skull, Dart (1926) began to speculate on the damage to baboon bones from the deposits, noting that many of the skulls show signs of fracture prior to fossilization. Such damage consists of the removal of the base of the brain case, small puncture marks in the vault, and v-shaped marks on the broken edges of the braincase. He also commented (1926, p. 321), "Recently I have been successful in isolating, from the breccia, part of the innominate bone of a baboon which was broken, splintered, and probably chewed before fossilisation." He attributed this damage to the activity of *Australopithecus*. Based on the above observations, Dart had concluded by 1929 that the Taung child belonged to a form of predaceous and cave-dwelling anthropoid that he described as "an animal-hunting, flesh-eating, shell-cracking and bone-breaking ape". Five years later, Dart (1934) added "stream-searching" and "bird-nest rifling" to the behaviour of *Australopithecus*, "a practised and skilful wielder of lethal weapons of the chase". In that publication, he described and illustrated the observations he had made on damage to baboon skulls from Taung: "The skulls are not only broken, but they show radiating fractures due to the impact of sharp objects, probably stones, in the right parieto–temporal region of the skull."

Dart wrote further on this theme in two papers entitled "The bone-bludgeon hunting technique of *Australopithecus*" (1949*a*) and "The predatory implemental technique of *Australopithecus*" (1949*b*). In the latter paper, he published detailed descriptions and photographs of damage which he categorized as "double-depressional fractures", "distorted muzzles and fractured mandibles", "punctured depressions", and "openings of skulls and crushing by hand". He further noted that skulls displayed sharply localized damage and that in many of them the direction of the blow could be inferred. In his description of skull openings, he discussed missing areas of the skull above, behind or below, and the finding of isolated calvarial fragments, all of which suggested to him the deliberate opening of the skull to extract the cerebral contents. He referred to one cranium from Taung (No. 992 in the Department of Anatomy and Human Biology, University of the Witwatersrand) which displayed shearing off of the calvarial outer table. He argued "that after the bone had been elevated by means of finger and thumb, it had been torn away from within outwards".

All of these categories of damage which Dart attributed to the predatory habits of *Australopithecus* can now be documented in assemblages produced by large birds of prey. We summarize these categories of damage as follows:

1. depression fractures and puncture marks in crania resulting from talon damage;
2. the opening of skulls and removal of basicranium as a result of a bird of prey feeding on the brain;
3. the crushing of skulls and fractured and distorted maxillae and mandibles from feeding activities;
4. v-shaped nicks in areas of damage caused by the beak during feeding.

Observations on the habits of extant birds of prey and their potential as collecting agents of medium and large-sized animals

Ornithologists have documented extensively extant raptors killing and collecting small and medium-sized animals (e.g. Seyfarth *et al.*, 1980; Struhsaker, 1982; Steyn, 1982; Ginn *et al.*, 1989; Gargett, 1990; Maclean, 1993 etc.). However, the recognition of the potential importance of large birds of prey as agents responsible for the collection of medium-sized animals has been largely overlooked by Plio-Pleistocene palaeontologists. The detailed studies of the taphonomy of Plio-Pleistocene fossil sites by Brain (1981, 1985) and Andrews (1990) have primarily considered large raptors as collecting agents of microvertebrates and small mammals, although both studies acknowledge that large birds of prey at times collect medium-sized animals.

Studies of the behaviour of African raptors have led to the realization that many of the larger birds of prey occupy trophic positions similar to those of medium-sized carnivores. The largest of the extant eagles on the continent are the martial eagle (*Polemaetus bellicosus*), the crowned eagle (*Stephanoaetus coronatus*), and the black eagle (*Aquila verreauxii*), and it is the behaviour of these species that will be discussed here. While there are many other species of large raptor in Africa as well as in Europe, Asia, North and South America, we have chosen only three African eagles to discuss. Their capabilities and behaviour are adequate for the evaluation of the present hypothesis and, singly or in combination, they present likely homologous candidate species for the avian collecting agent(s) of some of the Taung fauna. In particular, we consider the crowned eagle to be the best modern homologue of our hypothetical Taung Plio-Pleistocene bird of prey.

The crowned eagle

The crowned eagle is a large eagle with a wingspan often exceeding 1·9 m (Maclean, 1993). Its range extends in suitable habitats across the continent from Ethiopia to West Africa, and southward to the eastern part of southern Africa. It is considered primarily as a forest eagle, although its habitats include open woodland, thickly wooded rocky country, riverine woodlands and relic forest patches (Steyn, 1982; Tarboton & Allan, 1984; Ginn *et al.*, 1989; Maclean, 1993). It is a voracious predator of mammals and the prey list of the crowned eagle is extensive; antelope prey commonly include bushbuck, grysbok, common and blue duiker, steenbok and klipspringer with the heaviest prey regularly taken being bushbuck that weigh up to 30 kg (Steyn, 1982; Tarboton & Allan, 1984; Ginn *et al.*, 1989). Primates are a favoured prey of this eagle, with vervet, samango and colobus monkeys, bushbabies and young chacma baboons being frequently taken (Seyfarth *et al.*, 1980; Struhsaker, 1982; Steyn, 1982; Tarboton & Allan, 1984; Ginn *et al.*, 1989). Debris below some nests has been reported to contain almost solely primate remains, namely mangabeys, black and white colobus and blue monkeys (Steyn, 1982; Maclean, 1993). In Zambia, crowned eagles have even been recorded attacking, and nearly killing, a 7-year-old human child of approximately 20 kg (Steyn, 1982), and there are

Table 2 **Species lists from crowned eagle nests in South Africa derived from Tarboton & Allan (1984)**

	Sites				
Prey	1	2	3	4	5
Reptiles					1
Veranus sp.					
Mammals					
Papio ursinus			2		
Cercopithecus aethiops	2		9	11	1
Cercopithecus albogularis		1	3	1	
Thryonomys swinderianus	1	1	1	2	3
Viverra civetta					1
Genetta sp.			1		2
subfam. Herpestinae				3	1
domestic cat?				1	
fam. Procaviidae	12	1	6	22	23
fam. Bovidae (adult)		1			5
fam. Bovidae (juvenile)	2		16	36	27

Site 1, Levubu River, Kruger National Park (one nest); 2, Soutpansberg (one nest); 3, Mariepskop (three nests); 4, Sabie area (seven nests); 5, Barberton area (two nests). Numbers indicate total number of bone pieces.

numerous reported cases of adult humans being attacked while near nests (Steyn, 1982; Ginn *et al.*, 1989). In Zimbabwe, part of a juvenile human skull was recovered from the nest of a crowned eagle, the child having presumably been attacked and killed by the nesting birds (D. M. Henry quoted by Steyn, 1982). Smaller prey of the crowned eagle includes hyraxes, hares, squirrels, monitor lizards and birds, including young ostriches (Struhsaker & Leland, 1979; Steyn, 1982; Tarboton & Allan, 1984; Ginn *et al.*, 1989; Maclean, 1993). Crowned eagles are capable of lifting prey greater than their own body weight (Steyn, 1982; Ginn *et al.*, 1989). If prey is found to be too heavy for flight, it is dismembered and its parts are usually cached in trees (Steyn, 1982).

The crowned eagle usually nests in leafy living trees at a height of 12–30 m, but nests have been reported on sheer cliff faces (Steyn, 1982; Ginn *et al.*, 1989). Nest sites are recorded to have considerable litter of monkey and antelope skulls and bones beneath them (Steyn, 1982; Tarboton & Allan, 1984; Ginn *et al.*, 1989; G. Avery, pers. comm.). We were kindly permitted to examine a very large collection of bones from beneath a crowned eagle's nest in Nature's Valley in the Cape which is currently under study by Dr Graham Avery of the South African Museum. The collection includes large numbers of monkeys and other skulls including the partial cranium of a bushbuck which also show damage similar to that observed on the fossil baboon skulls from Taung (discussed below). Most striking are the puncture marks, fractures on the tops of the crania, the removal of large areas of the calvaria and v-shaped nicks along broken margins (Figures 5 and 11). Table 2 contains lists of prey reported by Tarboton & Allan (1984) to have been collected from beneath crowned eagle nests in the Kruger National Park, South Africa. The prey lists in this table illustrate fairly typical crowned eagle assemblages. The numbers listed with each species indicate the number of bones recovered and not the minimum number of individuals, which was not recorded. In three of the samples (sites 3, 4 and 5), juvenile antelope parts dominate the list of larger mammals, but monkey bones represent the next most common medium or large-sized animal preserved. In two of the sites

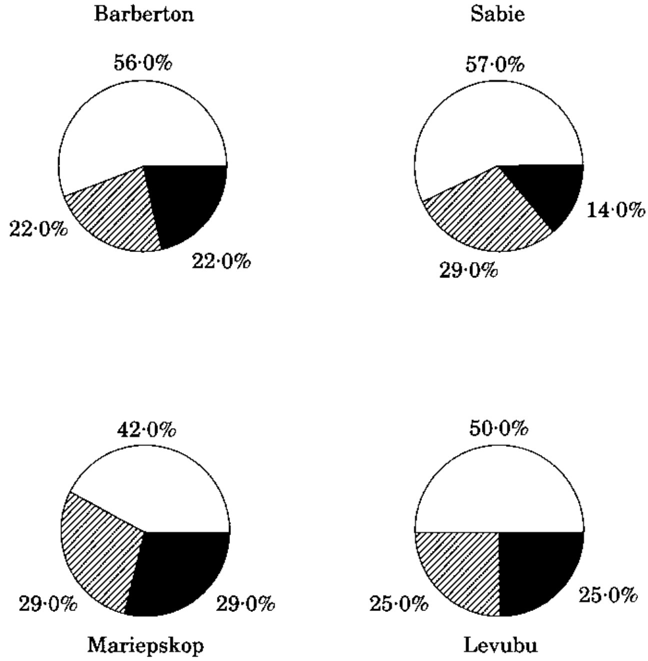

Figure 2. Representation of mammal species by size at selected South African crowned eagle nests. Small = 0·01–2·0 kg average adult body weight; medium = 2–20 kg average adult body weight; large = >20 kg average adult body weight. Average adult body weight for extant species is based on Smithers (1983). The sites chosen are only intended to represent general trends observed in bone collections found at South African crowned eagle nests. Nest data derived from Tarboton & Allan (1984). (□), Small; (▨), medium; (■), large.

(sites 1 and 2) monkeys are recovered in equal numbers to those of bovids. Hyrax bones are the most common small animal parts found beneath nests, and they are the most common animal recovered from two of the nest sites. In all four of the crowned eagle sites, small mammal species (<2 kg adult body weight) represent over 40% of all mammal species found beneath nests and over 50% at three of the sites (Figure 2). Tarboton & Allan (1984) report that of the antelopes (which are included in the large mammal category >20 kg), 91% of 87 bones were juvenile, although few could be identified to species due to the fragmentary nature of the sample.

The method by which the crowned eagle catches and kills its prey has not been extensively documented, but it is most likely to use methods similar to the better studied black eagle. Since the method of killing has direct bearing on the taphonomic features discussed, this issue is explored in detail in the black eagle section.

The martial eagle

The martial eagle is the largest bird of prey in Africa with recorded wingspans of over 2·5 m (Maclean, 1993). It is distributed throughout southern Africa and northwards to the Sahara. However, the martial eagle prefers bushveld country to forested areas and it is found also in arid regions such as the Namib Desert (Steyn, 1982; Ginn *et al.*, 1989). It is reported to be not as frequent a hunter of primates (Maclean, 1993). Its prey consists of monitor lizards, game birds, hares, mongeese, warthog, grey duiker and aardwolf (Tarboton & Allan, 1984). We have found no records of attacks on humans by this eagle. The martial eagle prefers to nest in trees but, with significance to our Taung hypothesis, it has been recorded nesting in potholes in cliffs in Angola (Steyn, 1982).

The black eagle

The black eagle, with a wingspan up to ca. 2 m, is the smallest eagle selected for discussion. Its behaviour is the best documented of any large African raptor and specific habits of this species have a bearing on the discussion.

The black eagle is widespread throughout Africa southward from the Sinai Desert. It frequents rocky hills and mountainous areas. Its favoured prey is often reported to be the rock hyrax and yellow spotted hyrax, with prey preference for these species recorded as high as 98% (Gargett, 1990). However, in some cases the black eagle has been recorded to take a wide spectrum of prey including monkeys and small antelopes (Steyn, 1982; Ginn *et al.*, 1989). It has been recorded to take antelope up to the size of juvenile bushbuck (around 15 kg) (Gargett, 1990). Vervet monkeys are a common prey of the black eagle (Gargett, 1990; L.R.B., pers. obs. at Gladysvale), and in Zimbabwe, vervets and bushbabies are the preferred prey after hyraxes (Gargett, 1990). Black eagles are reported to take young chacma baboons (Steyn, 1982; Gargett, 1990). The cranium of a juvenile chacma baboon was recovered at Gladysvale by Mr M. Weiner for the authors. It lay beneath a black eagle nest among other bone debris and had undoubtedly been taken by the nesting pair.

Black eagles have also been frequently observed to scavenge carnivore kills of large animals (Gargett, 1990). One such incident was observed in 1992 at Gladysvale by L.R.B. and approximately 50 scientists during a field excursion of the Congress of the Palaeontological Society of Southern Africa. In this instance, a pair of black eagles was observed feeding on an adult blesbok (*Damaliscus dorcus*) ram carcass that had, by all indications, been killed recently by a leopard. Blesbok rams are large class II antelope according to Brain's (1974) bovid size classification system. Such scavenging behaviour can thus be responsible for introducing occasional large adult bovid remains to eagle-accumulated bone assemblages.

Of particular relevance to the interpretation of the Taung faunal assemblage is the fact that black eagles have been reported to take land tortoises (Gargett, 1990; C. J. Vernon pers. comm. to Gargett). The only remains usually left after feeding are the carapaces and a few bones. Leshem (1979–1980) reports that a single pair of the closely allied golden eagles has been observed to take as many as 84 land tortoises over a 119 day period. The tortoises were reportedly killed by being dropped from a height of 30–60 m before being consumed. As previously mentioned, fossilized tortoise carapaces have frequently been found in the Buxton bone breccias (Dart, 1925; Cooke, 1990; McKee, 1993; McKee & Tobias, 1994), whilst one segment of carapace is in a chunk of breccia associated with the hominid child cranium (Dart & Craig, 1959).

Gargett (1990, p. 102) reports that, with few exceptions, the black eagle "nests on rock ledges, in small caves or recesses in rock faces, or on isolated rock pillars". Most nests are reported to be situated low in relation to the height of surrounding hills (Gargett, 1990). Nest sites may be used intermittently over generations with time spans of over 30 years' occupation being recorded (Gargett, 1990).

Gargett (1990, p. 76) reports the following feeding behaviour as typical for the black eagle:

> When a complete animal is brought the eagle removes the caeca first, which are not eaten, and then usually eats from the head. The eyes are eaten and the tongue; the jaw is forced open so that the

Table 3 **Species lists from hyaena lairs in South Africa**

Prey	Sites 1	2	3	4
Mammals				
Felis caracal		5 (6)		
Canis mesomelas	1 (1)	14 (14)		
Otocyon megalotis		13 (13)	1 (1)	
Proteles cristatus		1 (1)	1 (3)	
Mellivora capensis		2 (2)		
small carnivore ?mongoose	1 (1)			
Carnivore indet.		(24)	(7)	
Orycteropus afer		1 (2)	1 (1)	
Ovis/Capra		1 (1)		
Bos taurus	4 (21)	1 (7)		
Raphicerus campestris		11 (15)	2 (2)	
Sylvicapra grimmia	(1)	2 (3)		
Antidorcas marsupialis		10 (41)		1 (1)
Aepyceros melampus	3 (8)			
Tragelaphus strepsiceros	2 (3)			
Alcelaphus buselaphus		1 (2)		
Connochaetes taurinus		2 (3)		
Oryx gazella		5 (7)	1 (1)	4 (5)
Antelope class I		(18)	(8)	
Antelope class II		(14)	(13)	(2)
Antelope class III		(24)	(7)	(1)
Phacochoerus aethiopicus	3 (4)			
Hystrix africaeaustralis		1 (2)		
Struthio camelus		2 (3) (5)*	1 (1)	
Indeterminate fragments		21	(12)	(62)

Data for sites 1 and 2 derived from Brain (1981); data for sites 3 and 4 derived from Mills & Mills (1977). Sites 1, Tweeputkoppies (*H. brunnea*); 2, Kalahari (*H. brunnea*); 3, Kasperdraai (*Crocuta crocuta*); 4, Urikaruus (*Crocuta crocuta* and *Hystrix africaeaustralis*).

*Eggshell fragment.

Numbers indicate minimum number of individuals attributed to a species and numbers in parentheses indicate number of pieces.

eagle can penetrate through the palate to the brain, which is also eaten. The scalp is removed from the cranium; the skin is removed from the face, chin and neck and eaten, together with the ears. The head is then broken off the neck by twisting the neck vertebrae and eating the disks between them. Long strings of the spinal cord and bone marrow are pulled out and eaten, so are small thin shreds of the stomach and intestines. The heart, lungs and liver are eaten, together with the ribs, legs, feet and most of the vertebrae.

Gargett (1990) reports that for large hyraxes usually only the skull (sometimes undamaged), a few vertebrae and the pelvic girdle are all that remain of the skeleton. For medium-sized animals, only part of the cranium and lower jaw and parts of the pelvis typically remain. Below the Gladysvale black eagle nest we recovered remains that include hare and hyrax skulls and their limb bones, chewed and punctured pelvic bones, punctured and chewed bird bones (Figures 6 and 8), as well as the skull of a juvenile chacma baboon with characteristic puncture marks (Figure 12). (For a list of prey and characteristic damage to skulls, see also Brain, 1981 pp. 106–108, Figure 109.)

Table 4 **Species lists from leopard lairs in South Africa**

Prey	Sites			
	1	2	3	4
Reptiles				
Chelonia indet.	1 (11)	1 (6)		
Mammals				
Papio ursinus	1 (20)	1 (1)	1 (3)	
Panthera pardus	1 (50)	2 (26)		
Lycaon pictus	1 (39)			
Felis caracal				1
Ovis/Capra		1 (4)		
Bos sp.		1 (7)		
Oreotragus oreotragus	2 (26)	1 (4)	4 (38)	
Raphicerus campestris			1 (3)	1
Damaliscus dorcus				4
Redunca fulvorufula				2
Taurotragus oryx				1
Tragelaphus strepsiceros		2 (8)		
Oryx gazella		1 (1)	1 (3)	
Antelope class II	2 (10)	1 (7)		
Antelope class III	1 (2)	3 (96)		
Equus zebra	2 (13)	2 (6)		
Procavia capensis	4 (13)	2 (4)	6 (79)	
Hystrix africaeaustralis				2 (2)
Indeterminate fragments	(45)	(117)		

All data for sites 1, 2 and 3 derived from Brain (1981), data for site 4 derived from Berger & McKee (1995). Site 1, Portsmut; 2, Hakos; 3, Quartzburg; 4, John Nash Nature Reserve.

Numbers indicate minimum number of individuals attributed to a species and numbers in parentheses indicate number of pieces.

A brief review of the bone-accumulating habits of extant African cave-frequenting mammals

The collecting habits of African mammalian carnivores are well known and have been extensively documented by Brain (1981), amongst many others. It is not the purpose of this paper to review this extensive literature. However, for comparative purposes with the bird of prey assemblages described above, the collections of two known cave-frequenting mammalian carnivores are listed in Tables 3 and 4. These lists clearly demonstrate the differences between the bone collections of these two extant mammalian carnivores and those of birds of prey (Table 2). In general, when a hyaena or a leopard is the primary collecting agent of a bone sample, the sample tends to show a greater variety of medium and large-sized species along with a greater number of large mammalian species than would be expected in the bone collections of a bird of prey (Pienaar, 1969).

Hyaenas

Mammalian carnivores such as hyaenas tend to break and crunch bones, leaving characteristic scars and puncture marks from their premolar cracking and incisor/canine gnawing of pieces (Maguire *et al.*, 1980; Brain 1981). Many of the bone collections from hyaena dens in Africa contain large numbers of unidentifiable bone fragments (Mills & Mills, 1977; Hill, 1978; Brain,

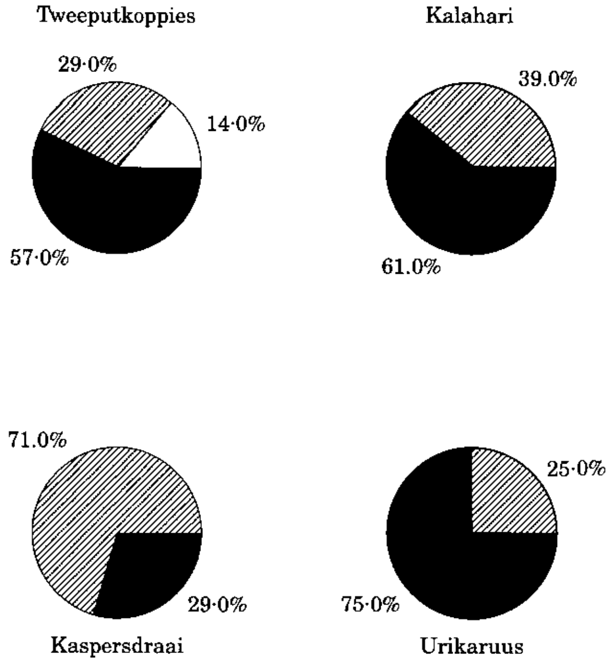

Figure 3. Representation of mammal species by size at selected South African hyaena lairs. Small=0·01–2·0 kg average adult body weight; medium=2–20 kg average adult body weight; large=>20 kg average adult body weight. Average adult body weight for extant species is based on Smithers (1983). Data for Tweeputkoppies (*Hyaena brunnea*) and Kalahari (*Hyaena brunnea*) derived from Brain (1981); data for Kasperdraai (*Crocuta crocuta*) with (*Hystrix africaeaustralis*) from Mills & Mills (1977). The sites chosen are only intended to represent general trends observed in bone collections found at South African hyaena lairs. (□), Small; (▨), medium; (■), large.

1981) (Table 3). The remains of small mammal species are exceptionally rare in hyaena accumulations (Figure 3), but of the two hyaenas in southern Africa, the brown hyaena (*Hyaena brunnea*) and the spotted hyaena (*Crocuta crocuta*), the brown hyaena more commonly takes small mammals. However, these small mammals are usually other carnivores. Thus a high carnivore:ungulate ratio is considered to be a characteristic of brown hyaena accumulations (Mills & Mills, 1977; Brain, 1981). The Taung accumulation does not correspond in damage and composition to those of hyaenas (Figures 1 and 3).

Leopards

Simons (1966) made a detailed study of bones from leopard lairs in the Mount Suswa Caves of Kenya and listed the characteristic damage inflicted by leopards on skulls and limb bones of baboons. He found that ends of long bones and blades of scapulae were chewed and that brow ridges, zygomatic arches, and lateral pterygoid plates were chewed. Tooth-holes occurred in the orbits and muzzle, as well as sometimes in the bones of the braincase. All but one of the 14 mandibles examined had one or both ascending rami chewed (Simons 1966, Table IV). Brain (1981) confirms that leopard accumulations are easily identifiable by the preservation of parts and by unique damage to bones. Further confirmation of such characteristic damage is given by Berger & McKee (1995). Depressed fractures and v-shaped nicks such as those found on the Taung fossils are not characteristic of leopard

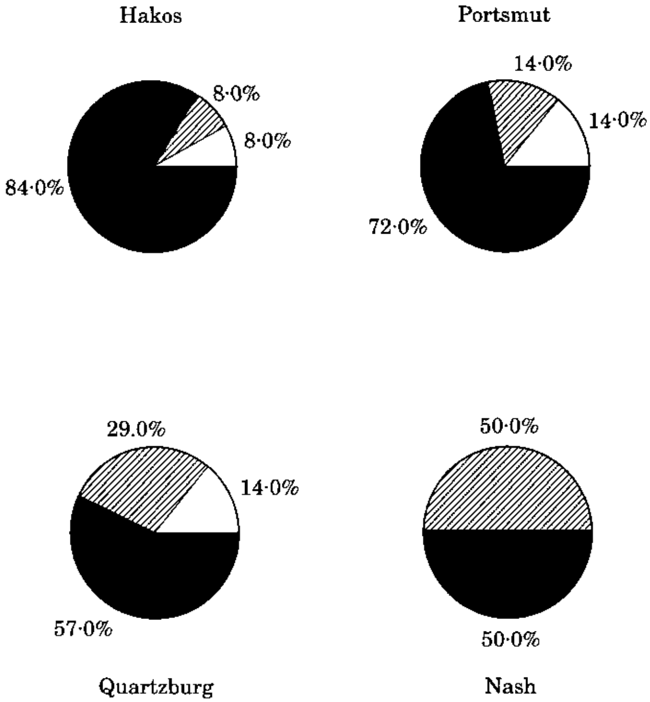

Figure 4. Representation of mammal species by size at selected South African leopard lairs. Small=0·01–2·0 kg average adult body weight; medium=2–20 kg average adult body weight; large=>20 kg average adult body weight. Average adult body weight for extant species based on Smithers (1983). Data for Portsmut, Hakos, and Quartzburg derived from Brain (1981); data for Nash derived from Berger & McKee (in press). The sites chosen are only intended to represent general trends observed in bone collections found at South African leopard lairs. (□), Small; (▨), medium; (■), large.

damage. Antelope found in leopard lairs tend to have what Brain (1981) has described as an "eaten out" appearance, where only the head and lower limb segments survive the feeding.

Because leopards are extremely opportunistic in their hunting practices, the species diversity found in their lairs tends to be high (Table 4). As with the bone accumulations of hyaenas and unlike the Taung assemblage, large mammal species tend to be better represented than medium or small-sized mammal species (Figures 1 and 4).

Porcupines

Porcupines are another common and important African bone collector. However, their bone assemblages, or assemblages to which they have contributed, are easily recognizable since porcupines leave characteristic gnaw marks from their chisel-like incisors (Hughes, 1958; Maguire 1976; Maguire *et al.*, 1980; Brain 1981). Furthermore, porcupines accumulate bones of a great and random variety of species, many of which can be of large size.

Features of the Taung fauna consistent with eagle behaviour

To illustrate the bird of prey hypothesis, we here discuss six points about the Taung fauna that are relevant to the recognition of a bird of prey as the main agent responsible for the assemblage.

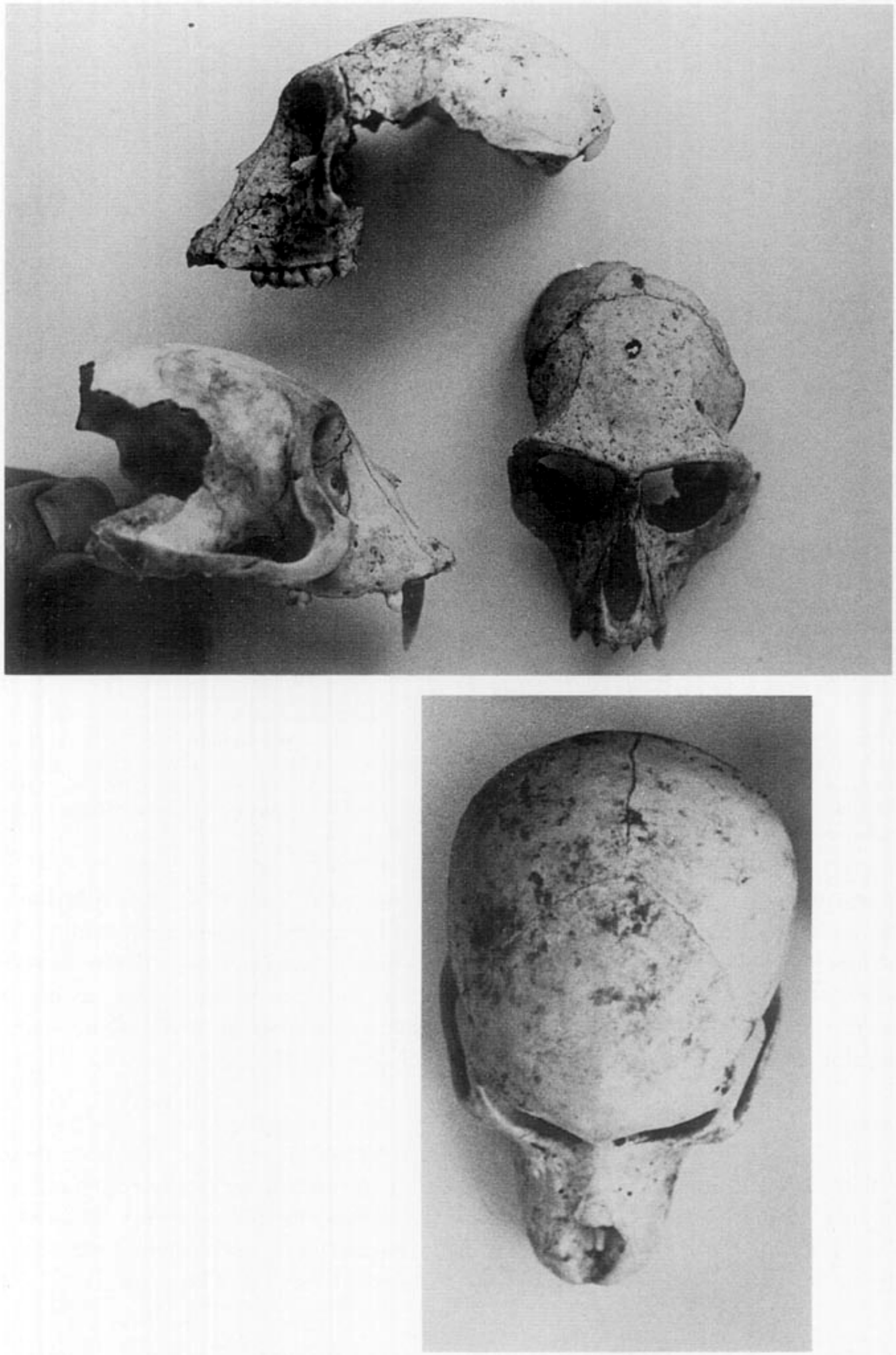

Figure 5. Monkey skulls from beneath a crowned eagle nest at Natures Valley, South Africa. The three vervet monkey skulls at the top show broken-away braincases. Below is a complete, undamaged young baboon cranium.

1. The body sizes of the animals in the Taung assemblage are remarkably homogeneous, in contrast to the character of mammalian carnivore and porcupine assemblages. Table 1 lists by species and adult body weight the total known mammalian faunal assemblage from the Dart and Hrdlička pinnacles at Taung. The Dart pinnacle, adjacent to the Hrdlička pinnacle, is believed to be the most likely source area of the Taung child (McKee & Tobias, 1994). What is readily apparent is that the Taung fauna is dominated by mammal species whose estimated adult body weights are <20 kg. In each case where a mammal has been identified as weighing >20 kg, the identification has been made from isolated fragments. This leaves open the possibility that the larger mammals were brought to the cave as dismembered parts, as is the case with most large animals found in modern crowned eagle accumulations. If dismemberment had occurred, then the fossils recovered from Taung are well within the prey size range of several extant large African birds of prey.

The uniqueness of the Taung faunal collection is emphasized when the same body-size criteria are used for analysis of other well-known hominid sites in southern Africa (Figure 1). Sterkfontein Member 4, Makapansgat Member 3 and Swartkrans Member 1 are all believed to be predominantly accumulated by mammalian bone collectors, although some contribution by owls has added to the small mammal collection (Brain, 1981, 1985). Each of these sites, therefore, presents a dominant percentage of mammal species in the >20 kg, or large mammal category. These percentages also compare well with the modern accumulations made by known mammalian carnivores from sites in South Africa (Figures 3 and 4). In contrast, as discussed above, the Taung fauna is dominated by small animal species <2 kg of adult body weight (Figure 1), a pattern which compares more closely with the bone collections made by extant African crowned eagles (Figure 2).

Brain (1981, p. 262) originally suggested that a cave-dwelling owl, such as the Cape eagle owl *Bubo capensis*, was responsible for the accumulation of small animal remains at Taung, whilst the medium and large-sized prey could have been collected by a mammalian predator such as a leopard. However, the absence of typical leopard damage on the baboon crania, and indeed the absence of any carnivore tooth marks and the minimal representation of large fauna, seems to argue against carnivore involvement. By contrast, no bones from Taung, including those of the few larger mammals, are outside the collecting capabilities of a large bird of prey. Indeed, Brain (pers. comm.) has expressed support for our theory of eagle involvement in the Taung accumulation.

2. The skulls from the Taung fossil assemblage are reasonably complete (allowing for blast damage). In fact some of the specimens, including the *Australopithecus* skull, still have mandibles attached. Mammalian carnivores such as hyaenas tend to break and crunch skulls and limb bones, leaving characteristic scars and puncture marks. Leopards usually chew parts of the skull and ends of long bones, whilst also leaving characteristic scars and puncture marks (Simons, 1966; Brain, 1981, 1985). Although leopards may leave baboon skulls relatively intact, there is in almost every case some chewing damage to the specimen [see Simons (1966) and Brain (1981 pp. 296–297) for detailed lists of specimens from the Mount Suswa, Portsmut, Hakos and Quartzburg leopard lairs]. The same pattern holds true for antelope skulls found in leopard accumulations. In addition, not a single "eaten out" carcass of an antelope has been discovered in the Taung assemblage. The easily identified gnaw marks of porcupines, another possible collecting agent, are absent in the Taung collection. Porcupines are furthermore unlikely to leave whole baboon skulls.

Many of the baboon skulls from Taung are in good condition, showing no indications of chewing damage, although some postcranial bones do exhibit damage. Of these specimens,

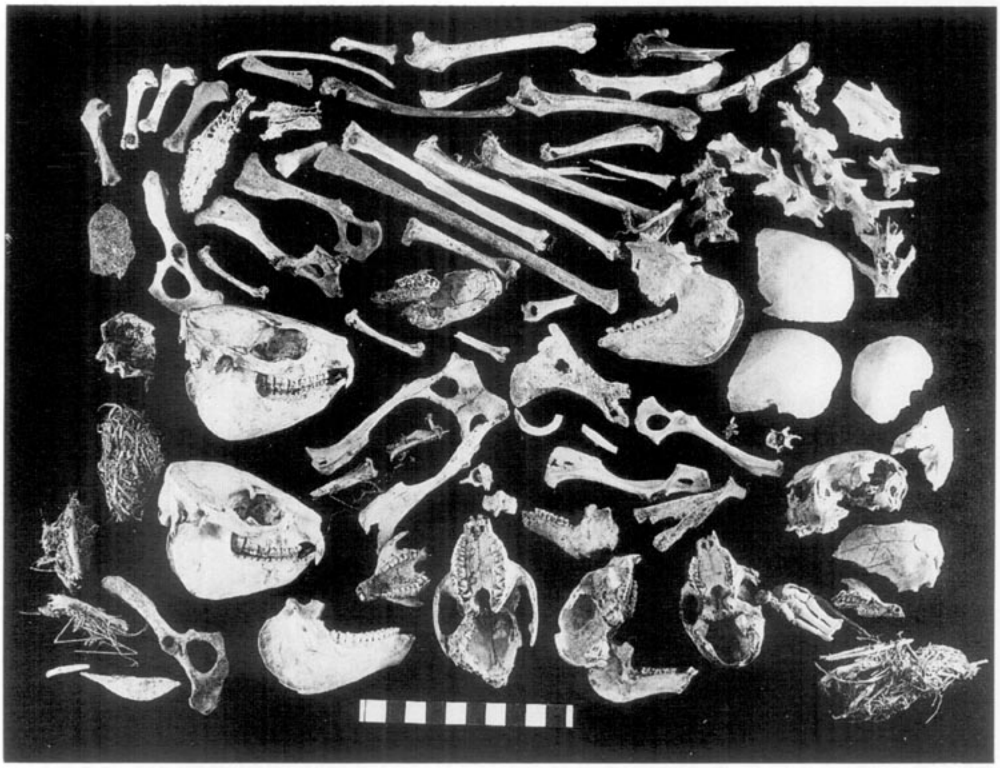

Figure 6. Bones collected from beneath a black eagle nest near Gladysvale. The collection includes the remains of hyrax, hare, birds and baboon. Note the three hyrax skulls at bottom centre with cranial bases removed.

none could be excluded from typical eagle damage. Birds of prey not only chew the meat-bearing bones, leaving punctures and tears similar to those made by leopards (Figure 7), but they are also known to leave some postcranial and cranial bones intact, including undamaged skulls (Figure 5).

Nevertheless, in some of the fossil baboon specimens from Taung, there are holes punched through the skull, removal of cranial bases, and v-shaped nicks in the lower broken margins of the calvaria (Figures 8–12). In baboon cranium South African Museum No. (SAM) 5356 (not illustrated), the base is missing and could not have been removed by blasting as there is neither a natural endocast of the base nor has the base been sheared across. Instead the breccia in that region has been chipped by developing tools, indicating that the base was most probably removed prior to fossilization. There is cracking and depression of the parietals due to pre-fossilization crushing of the skull. On the right side of the vault there is a perforation that was clearly made prior to breccia infilling, i.e. prior to fossilization. Such removal of the basicranium and a small hole in the braincase are common features of eagle-damaged skulls (Figures 5 and 8; G. Avery, pers. comm.).

The Taung bones were deposited in caverns within tufa rather than within dolomite. Thus there were no dolomite roof falls or rocky talus slopes that could break, crush and distort bones within the cavern. So, apart from obvious blast damage, any other noticeable modification

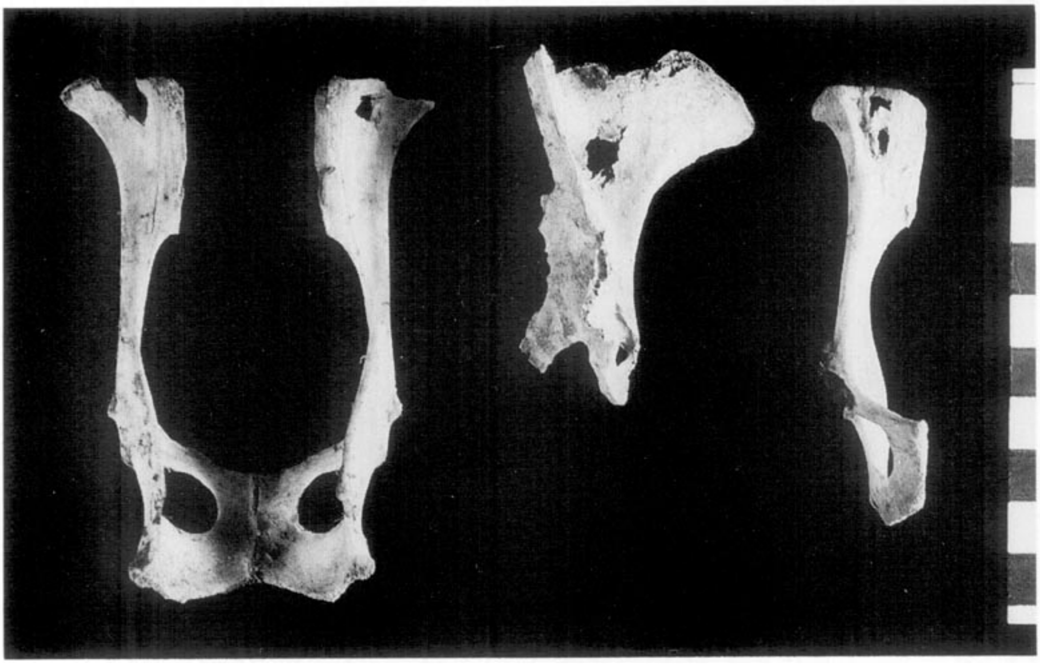

Figure 7. Hyrax pelvic bones (left and right) and a bird breastbone (centre) with perforations made by eagles. Collected from beneath a black eagle nest near Gladysvale.

such as depressions, fractures and holes in the bones could not have resulted from rockfall and therefore may reasonably be considered a result of pre-fossilization modification by animal agency.

3. The presence of tortoise carapaces with no apparent carnivore damage, in significant numbers, seems incompatible with known mammalian predator feeding habits but is consistent with the behaviour of some birds of prey. Although the crowned eagle has not been documented collecting tortoises, the black and martial eagles, as well as many other African birds of prey, have been recorded killing, collecting and feeding on large numbers of tortoises.

4. The presence of several large bird eggshells implies that, at times, large birds were nesting in the vicinity of the Taung hominid deposit. Hrdlička's (1925) statement that the eggs he recovered were as large as goose eggs indicates a bird of substantial size.

5. Despite much searching of the breccias of Taung by various expeditions since 1924, including nearly 6 years of intensive work by J. K. McKee (McKee, 1993*a*; McKee & Tobias, 1994), not a single other specimen of hominid has been recovered. In this respect the Taung site differs markedly from other South African ape-man sites such as Swartkrans, Sterkfontein, Makapansgat and Kromdraai, from which numbers of adult and juvenile hominids have been found. At each of these sites, there are indications that bones were collected by carnivores and porcupines (see Brain, 1981, 1985). This leads us to infer that the taphonomic conditions which must have led to the accumulation of adult and sub-adult remains at the Transvaal hominid-bearing sites did not occur in the hominid site at Taung. The occurrence at Taung of only a single infant hominid cranium with mandible still attached would be consistent with the predatory attack of an eagle on an australopithecine infant that in size would most probably not have differed substantially from that of the larger Taung baboons.

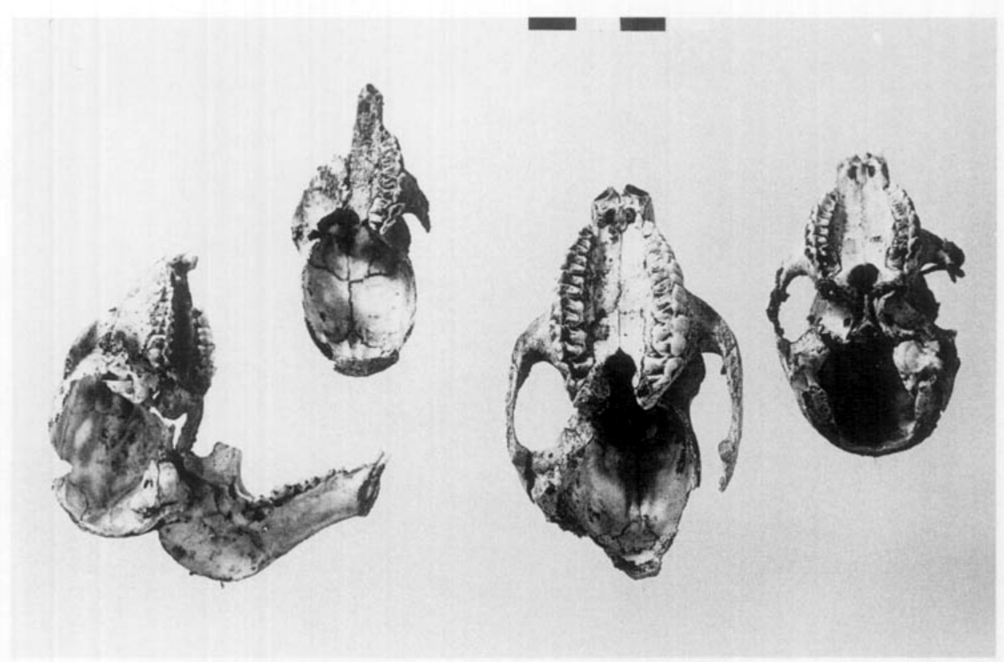

Figure 8. Hyrax skulls with basicrania removed by eagles. Collected from beneath a black eagle nest near Gladysvale.

6. The site of the Taung fossil assemblage in a cave within tufa, presumably on or near a high cliff face of the escarpment, would not be inconsistent with the nest-positioning behaviour of several extant birds of prey. Tobias (1985), Partridge *et al.* (1991) and Tobias *et al.* (1993), have attempted to reconstruct the geology of the area around the Dart and Hrdlička pinnacles from where the Taung child is believed to have derived. Even more recently McKee (1993) and McKee & Tobias (1994) have attempted to reconstruct the geology of the area near the middle of the Dart pinnacle which McKee believes is very close to the exact location from where the Taung child was originally recovered (McKee, 1993*a*; McKee & Tobias, 1994). McKee holds that the cave from which the Taung child was recovered was most probably a composite of primary caves and secondary solution cavities that were part of the "dry" portion of a carapace cave—i.e. a cave formed between concentric layers of calcium carbonate within a tufa flow (see Brain, 1985; McKee, 1993*a*; McKee & Tobias, 1994). According to McKee (1993*a*; McKee & Tobias, 1994), fossils, including the child's skull, were presumably washed into this cave. However, we feel that two main points reduce the likelihood that the fossils were washed very far, if at all, into a carapace cave situation. Firstly, the relatively pristine condition of the bone surfaces of most of the fossils recovered from this area seems to preclude the possibility that the bones were transported for any great distance by the action of water and left to weather in a "dry" area of a cave. Secondly, the absence of large or small rounded stream cobbles (a feature of carapace caves noted by McKee, 1993*a*) in this area of the deposit, seems to reduce the likelihood that watercourses of any substantial size were present at the time of deposition of the fossils.

Nevertheless, we suggest that a number of other geological situations would allow fossil material from a bird of prey nest to collect in situations similar to those observed at Taung.

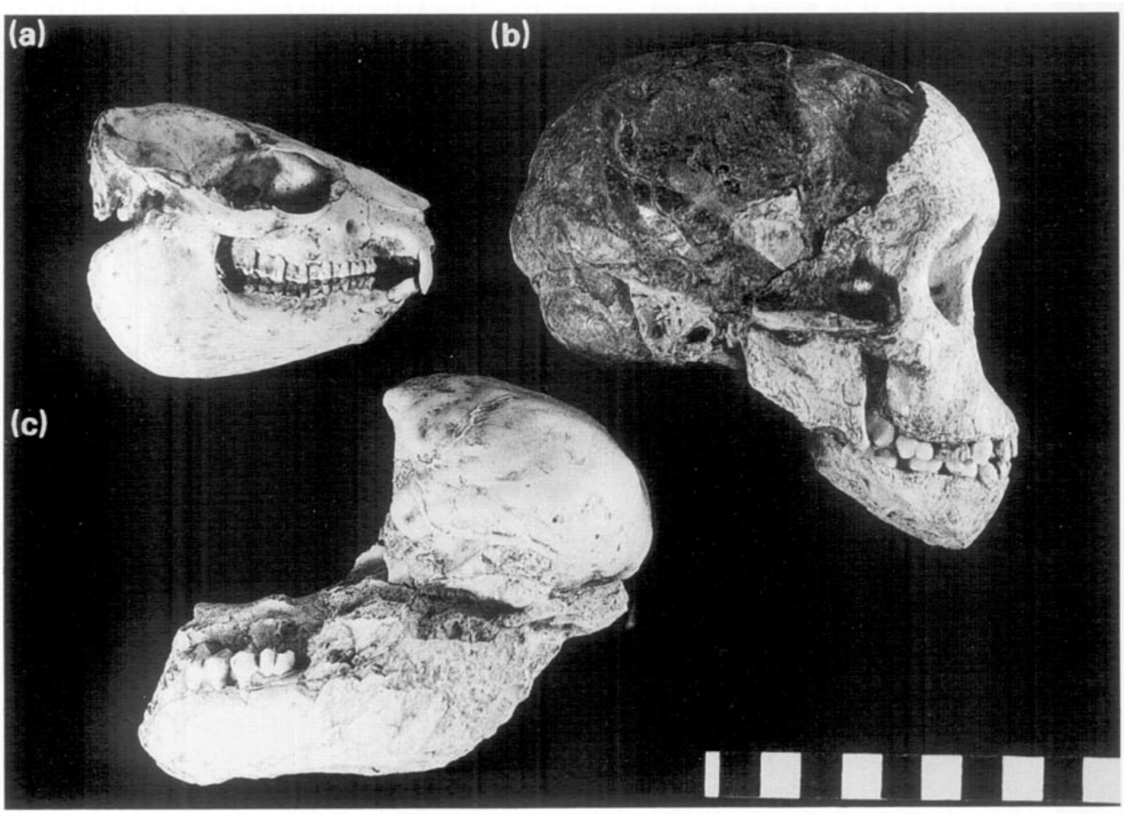

Figure 9. (a) Hyrax skull with mandible attached. Collected from beneath a black eagle nest near Gladysvale. (b) Taung hominid infant skull with mandible attached. This skull was fossilized with its mandible in occlusion. It was seemingly complete prior to blast damage and was undistorted. In these respects, it is unique by comparison with all other australopithecine fossils. (c) Fossil baboon skull (SAM 5357) from Taung, with mandible attached. Except for small areas of blast damage, this is a complete articulated baboon cranium and mandible with no damage to the ascending rami. This is not what is normally expected from specimens recovered from leopard lairs or other carnivore-damaged monkey skulls (see Simons, 1966; Brain, 1981). In such cases, the mandibles are usually found separated from the cranium and the skull and mandible normally show signs of having been chewed. On the other hand, articulated crania and mandibles of primates and other animals are frequently found beneath eagles' nests. It is noteworthy that the Taung *Australopithecus* skull is the only early hominid fossil yet recovered that retains the mandible in occlusion.

Solution cavities or potholes situated below a nest, either on a cliff face or in a tree on a tufa flow, could collect the fossil material. A shelter or cave on a ledge below the nest might give access to bones that either tumbled in or were washed a short distance into the subterranean system. Alternatively, a large bird of prey could have utilized a cave or rock shelter directly as a nesting site, much as black eagles or golden eagles frequently do today (Steyn, 1982; Ginn *et al.*, 1989; Gargett, 1990), or the bird might have lived in a pothole as has been observed for martial eagles (Steyn, 1982).

Conclusions

In total, the Taung fauna is relatively small in size compared to that collected by extant mammalian carnivores or porcupines and the damage to the Taung fossils is consistent with

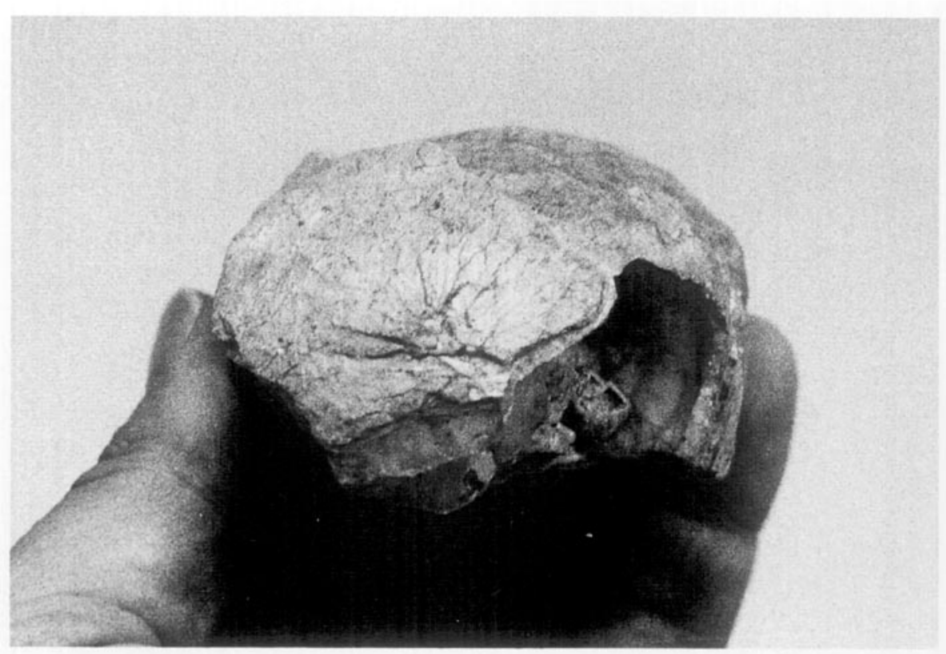

Figure 10. Left side of Taung fossil baboon braincase (SAM 5358) showing perforation with radiating fracture. The posterior portion of the braincase of this baboon cranium has a small perforation through the left parietal bone. The perforation is filled with breccia (i.e. prior to fossilization), with slightly elevated bone on one side of the perforation and short cracks radiating from it. This area of damage resembles closely the perforation of monkey skulls caused by eagle talons (Figure 11).

that produced by birds of prey when they dismember or feed on a carcass. It is not consistent with that made by mammalian bone collectors. Given the above data, it seems unlikely that the collection of the Taung fossil fauna could be attributed to any known mammalian bone collector. We therefore suggest that most of the Taung fauna was collected by a non-mammalian agent and that the collecting agent which produced the unusual Taung faunal assemblage is a species of large eagle.

We would not presume to guess at the exact species of eagle responsible for the collection of the Taung assemblage, although the crowned eagle is a likely candidate. The presence of *Tragelaphus* cf. *angasi* (nyala) in the Taung assemblage indicates that at times the environment of Taung was considerably wetter and more tropical than it is presently. If as a result of a wetter and more tropical climate in the Taung area there were larger trees and more extensive forests along the watercourses, this may have provided enough cover in the area for a primarily forest hunting bird of prey such as the crowned eagle. There is, of course, always the possibility that an extinct bird of prey was present in the Taung area during the Plio-Pleistocene. Future studies of recently recovered large birds eggs from Taung might resolve the question of which eagle species was present at Taung.

We stress again that we do not suggest that *all* of the fossils at Taung necessarily result from the predatory actions of eagles. Elements of the assemblage may have been contributed by other animal agents. We recognize that in fossilization situations, the taphonomic processes are often multi-faceted. However, we are inferring from the data cited and reviewed here, that a

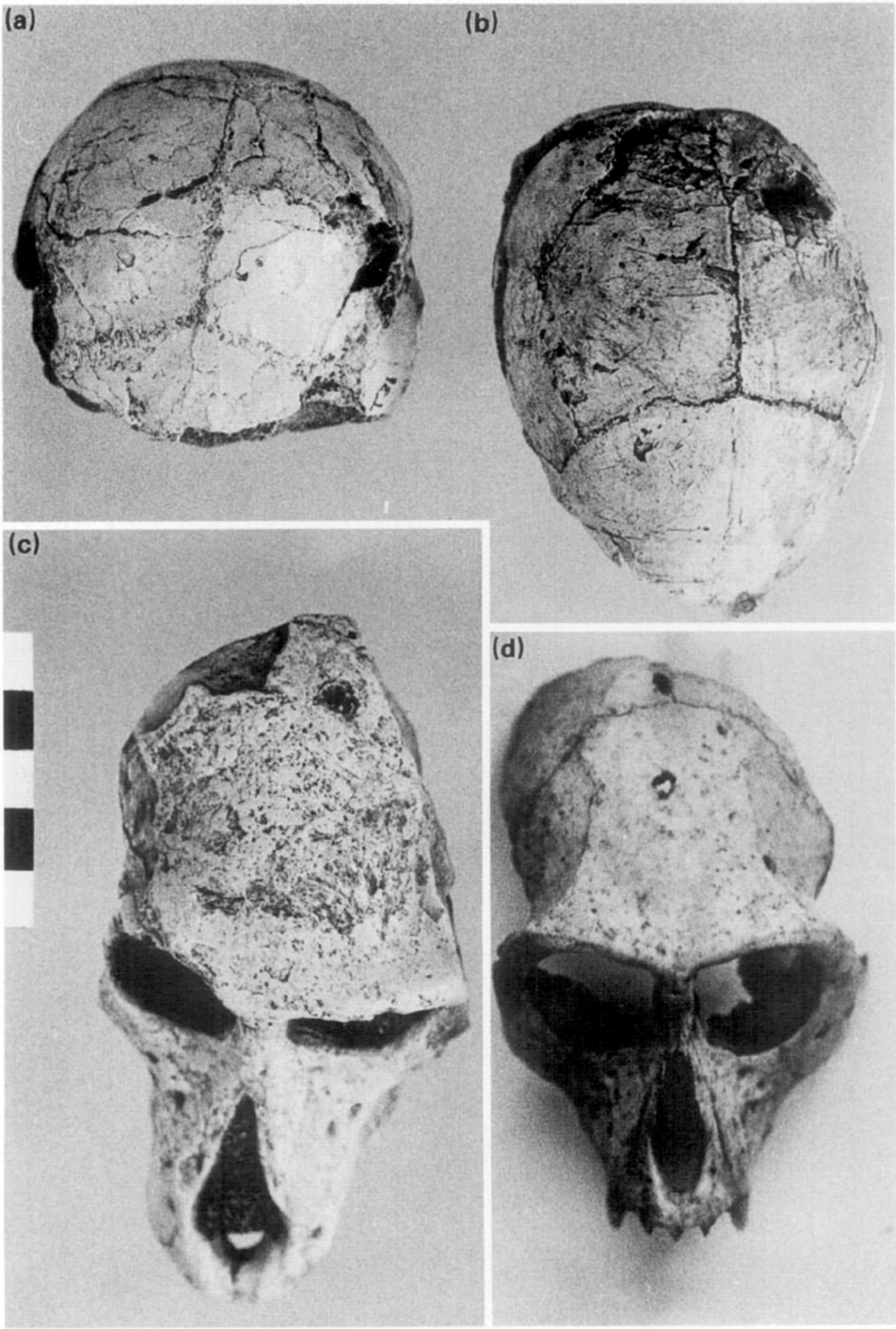

Figure 11. (a) Taung fossil baboon (T31) with depressed hole in left parietal. (b) Taung fossil baboon (T33) with depressed hole in left parietal. Both of these baboon skulls have cracked and pushed in flaps of bone about 1 cm wide in their left parietals. This is similar to damage on modern baboon skulls that is apparently inflicted by an eagle's beak (Figure 12). T31 is also cracked and distorted across the parietals like skull SAM 5356 while T33 has slight depressions in both parietals as though squeezed or crushed. (c) Taung fossil baboon (SAM 5364) with perforation in parietal that was clearly produced prior to endocast formation. (d) Vervet monkey skull from beneath a crowned eagles nest at Natures Valley, South Africa, showing perforation in frontal.

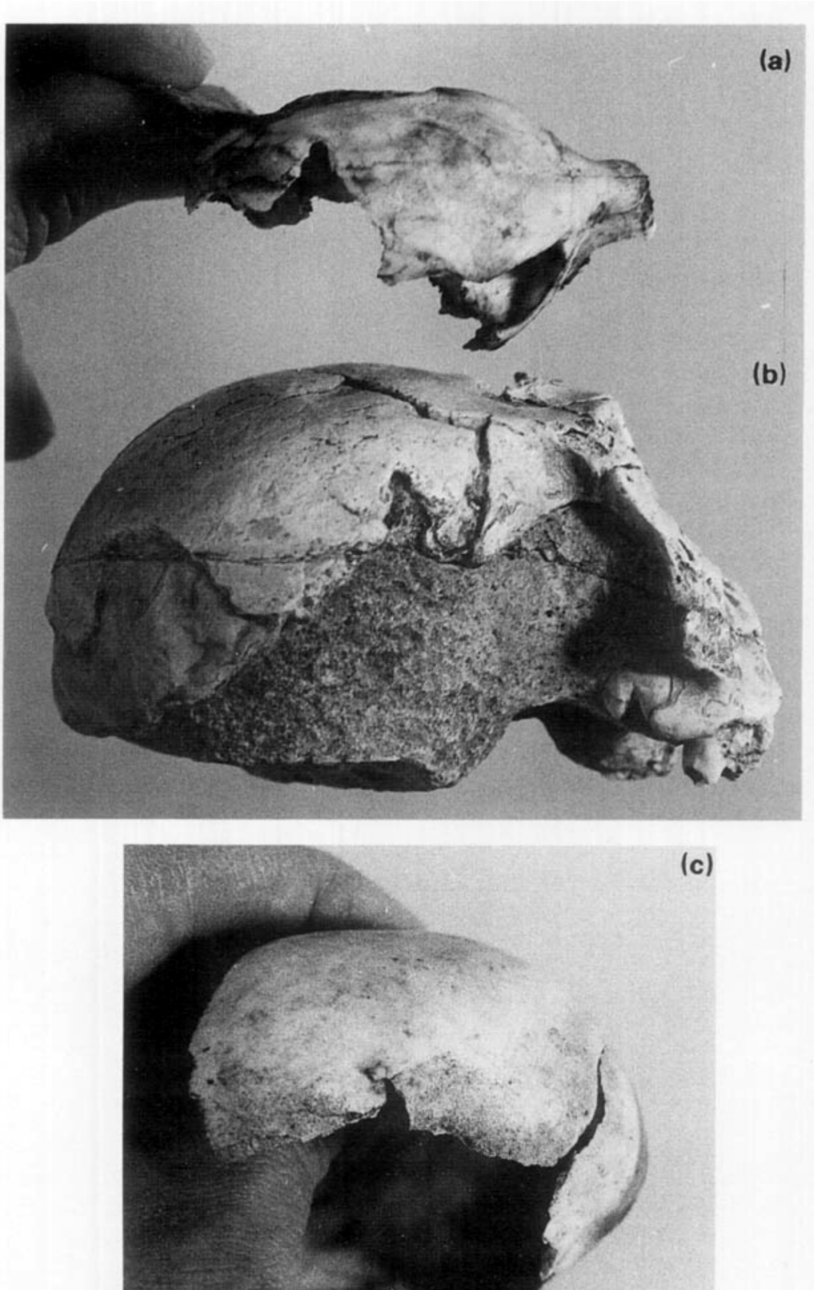

Figure 12.

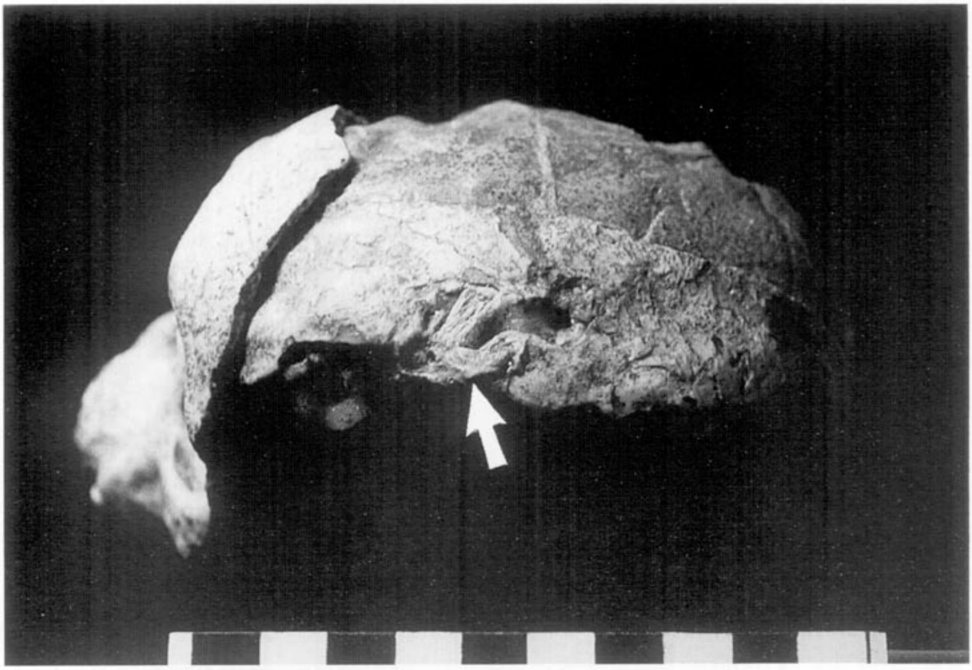

Figure 13. Superior view of the Taung child skull showing apparent vault fragments (arrowed) embedded in the endocast that probably result from pushed in holes in the braincase. P. V. Tobias pointed out to us this depressed area of bone on the superior part of the endocast and we have noted a similar depression in the skull T33 of a fossil baboon from Taung (Figure 11). These areas of damage resemble the depression of bone made by eagles in monkey and hyrax skulls collected by ourselves and G. Avery (Figures 11 and 12).

substantial portion of the Taung fauna, including the fauna reputedly associated with, and inclusive of, the Taung child, was collected by a large raptor.

As early as 1926 Dart noted the very points which led us to the hypothesis that a bird of prey had collected much of the Taung fossil fauna.

> It has been suggested by some that the Australopithecus child was itself the prey of some larger carnivorous creature of which this deposit indicates the den. The absence of any bones of larger animals in that recess and the completeness of the Taungs remains is against such an hypothesis. On the other hand the material, which looks like the comminuted bones of turtles, birds, small insectivores, rodents, baboons, and perhaps small bok, as well as birds' eggshells, indicates by its nature, its sparsity, and its searched over and exhausted character, the careful and thorough picking

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Figure 12. (a) V-shaped nicks in broken margin of a hyrax skull from the Gladysvale black eagle nest. (b) Taung fossil baboon (SAM 5366) and a young baboon cranium from the Gladysvale black eagle nest (c) also showing v-shaped nicks accompanied by a depressed flap of bone. The SAM 5366 baboon cranium very obviously had its base removed prior to fossilization, as demonstrated by the irregularly broken margins of the base of the calotte and endocast. The adjacent breccia has been chipped by a developing tool. In the centre of this breccia base is a large, smooth, natural surface that is not an endocast and was never covered by bone. On the right lower margin of the broken calotte the v-shaped nick perfectly matches similarly shaped beak marks in the modern hyrax and baboon specimens from a black eagle nest. On the left side of the cranium, where the bone is missing due to blasting, there is one small, smooth, shallow perforation and one small depression in the endocast that are not artefactual and are most probably due to punctures in the bone prior to endocast formation.

of an animal, which did not live to kill large animals, but killed small animals in order to live. (Dart, 1926, p. 319)

We thus conclude with the proposition that the Taung child and much of the associated fauna was killed and collected by a large bird of prey. We recognize that our conclusion most likely indicates that no adult australopithecine will ever be recovered from the deposits associated with the Taung child skull and that there is a high probability that the collection of the Taung child itself was a singular occurrence.

Acknowledgements

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