The Hyaenidae: taxonomy, systematics and evolution

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LARS WERDELIN and NIKOS SOLOUNIAS

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Today the Hyaenidae is a small carnivore family. In the fossil record, however, hyaenids are both diverse and abundant, and nearly 100 species have been named. Hyaenids have an expanded ectotympanic and semi-recumbent to recumbent septum bullae, and all fossil taxa likely to display this morphology are reviewed herein. Taxonomic and nomenclatural problems have hampered the study of this group. The taxa are treated in two groups: the core taxa, including the 18 (3 Recent and 15 fossil) best known taxa, and the remaining taxa, which for the most part are poorly known. In the phylogenetic analysis of the extant taxa it is found that *Proteles cristatus* is sister group to the other three species, which form an unresolved trichotomy. Next, *P. cristatus* is removed and the fossil core taxa added. The resulting cladogram topology is (Ancestor (*P. orbignyi*, (*T. spocki* (*I. viverrinum* (*H. wongii* (*H. hyaenoides* (((*L. dubia* (*C. borissiaki*, *C. lunensis*)) (*P. reperta* (*I. abronia* (*B. beaumonti* (*L. lycyaenoides* (*H. hyaena* (*P. brunnea* (*P. perrieri* (*P. brevirostris* (*A. eximia* (*C. crocuta*)))))))))))))))))). The remaining taxa are placed with reference to this cladogram, and a cladistic classification of the Hyaenidae is presented on this basis. The interrelationships of Feloidea are discussed on the basis of several recent publications. The fossil record of hyaenids negates many current ideas, and the feloid cladogram is at present unresolved. The key taxon *Herpestides antiquus* is reviewed and found to share no synapomorphies with hyaenids. The age of the Hyaenidae is suggested to be some 25 million years. This is compatible with biochemical dates. Macroevolutionary patterns in the Hyaenidae are examined on the basis of the established cladogram and are found to be overwhelmingly gradual. Taxic patterns show that the Hyaenidae were most diverse in the late Miocene (Turolian). The family is divided into 'hyaenid' and 'non-hyaenid' forms. The diversity patterns of these two groups differ. The 'non-hyaenid' forms show a decrease in diversity which is strongly correlated with the invasion of Eurasia by dogs (family Canidae) in the late Miocene–early Pliocene. Biogeographic patterns within the Hyaenidae are generally uninformative. ☐ *Carnivora, Feloidea, Hyaenidae, Neogene, Recent, taxonomy, systematics, evolution.*

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Contents

Introduction

This monograph concerns the family Hyaenidae. The word 'hyaena' bears with it a number of negative connotations due to our cultural biases and our consequent conception of these animals as cowardly scavengers. When we think of hyaenas we usually think of large, dog-like, scavenging animals inhabiting the savannahs of Africa. If we go a little further, we often equate 'hyaena' with 'spotted hyaena' (*Crocuta crocuta*). In actual fact, our conceptions are, as so often is the case in natural history, a little skewed. The spotted hyaena is only one of four living species in the family Hyaenidae. It is quite large as mammals go, with a body size approximately that of a large dog (average body weight 50–60 kg). It is the largest of the hyaenas, and also the commonest. However, our equating of 'hyaena' with 'spotted hyaena' is above all due to the fact that this species is by far the easiest to observe of the hyaenas, as it lives in fairly large clans, which are more conspicuous than one or a few animals only. The spotted hyaena has been the subject of one of the most famous studies in wildlife ecology ever conducted, the one by Kruuk (1972). This study has done much to change the traditional view of the spotted hyaena as a cowardly scavenger leading a secondhand life. Instead, Kruuk shows that the spotted hyaena is an active predator which is as likely to be chased off from its kill by lions (the 'king of beasts'), as to chase lions away. Some 60% of the food consumed by spotted hyaenas in the Serengeti was killed by them (Kruuk 1972, pp. 107–116). In the Ngorongoro Crater, this percentage fluctuated widely between clans (Kruuk 1972, p. 117), but the conclusion that the spotted hyaena is mainly an active hunter is inescapable. What differentiates this species from other carnivores in East Africa (except *Hyaena hyaena*) is its striking adaptations for cracking and consuming bones, not the mythical condition of pure scavenging.

The next hyaenid species in order of size is the brown hyaena, *Parahyaena brunnea*. This is a somewhat smaller animal than the spotted hyaena (average body weight about 40 kg), and is mostly nocturnal, which means that it is poorly known. In recent years it has been intensively studied in the Kalahari, however (Mills 1982a, 1983a, 1983b, 1984, 1987, 1989 and other studies), bringing to light a number of very interesting ecological differences between it and the sympatric spotted hyaena. The brown hyaena is almost exclusively restricted to southern and south-western Africa, and is considered endangered.

The third extant hyaenid species is the striped hyaena, *Hyaena hyaena*. It is smaller than the two species already mentioned, with an average body weight of about 30 kg. *H. hyaena* is the only hyaenid species with a present distribution outside Africa, being found in a large part of western and northeastern Africa, the Middle East, the southern USSR, Pakistan, and India. It has been less well studied than the spotted and brown hyaenas. A useful summary of information about the ecology and behavior of this species was given by Rieger (1979).

The fourth and final hyaenid species is quite different from the other three. It is the aardwolf, *Proteles cristatus*, a small (average body weight about 10 kg), termite-eating animal, sparsely distributed throughout a large part of eastern and southern Africa. In external appearance the aardwolf is similar to the striped hyaena, only much smaller, and this similarity has been suggested to be due to mimicry (Gingerich 1975). It seems likely, however, that the similarity is to a large extent due to primitive retention of an ancestral trait (e.g., Kingdon 1977).

These are the extant hyaenas; what of fossils? Here the story is quite different and forms the hub around which this review turns. As we shall see, hyaenas were much more diverse in the past than they are at present, and the bulk of the species had adaptations that differed markedly from those of the extant forms. Seen as a whole, the family Hyaenidae may arguably be considered to be the most abundant carnivore family in the fossil record outside the Americas and Australia, both in terms of the number of specimens, and of the number of species. This diversity and abundance makes it possible to describe the phylogeny and evolution of hyaenids in some detail; renders this essay possible, in fact.

Despite their superficial resemblance to dogs, the hyaenas are members of the Feloidea, a group which also includes the cats, family Felidae, viverrids (civets and their allies), family Viverridae, and herpestids (mongooses and their allies), family Herpestidae. The exact relationships of these families to each other are debated and will be discussed in detail later. The superficial resemblance of the extant bone-cracking (bone-cracking is here defined as the point-to-point cracking open of bones to obtain the nutritious marrow inside) hyaenas to dogs alluded to above was more than superficial in the past. This was particularly so in the Miocene, when morphological convergence between hyaenids and small to medium-sized canids was remarkable. This is another aspect of hyaenid evolution that will be discussed below.

The monograph is organized as follows: first we define the problem, i.e., what a hyaena actually is in the context of our work, then we discuss individual species of hyaenid, with particular emphasis on the four extant species and the 15 best known fossil species. Then we discuss the morphological characters used in the phylogenetic analyses. The next section is the phylogenetic analysis of the 19 taxa previously discussed. This eventually results in a cladogram, which we call the core cladogram. In the following section we discuss the interrelationships of Feloidea in detail and consider the position of some fossils in relation to this group. We also consider the possible limits of the extant feloid families with reference to the fossil record of hyaenids, and finally discuss the age of the family Hyaenidae as suggested by paleontological and biochemical data. In the final section we discuss the morphological and ecological evolution of hyaenids in the light of the core cladogram, and also some macroevolutionary patterns within the family as a whole. The monograph ends with a brief discussion of biogeography.

Acknowledgements. – It is of course impossible to thank all those people who have helped or supported us during the course of such a work as this. However, some people and institutions must be thanked. First and foremost is our friend, teacher and colleague Björn Kurtén. Björn was always supportive of our research, always willing to share his knowledge of fossil carnivores. It is our hope that he would have liked this paper, had he lived to see its completion.

We would like to thank Björn Lindsten, who drew the hyaena skulls figured herein and also cooperated in making the life restorations of fossil hyaenas which are so important in bringing this research to life. Many people have read and commented on the manuscript in various forms and stages of completion or assisted in various other ways. We would like to thank Harley Armstrong, John van Couvering, Jeremy D. Hooker, F. Clark Howell, Michael J. Novacek, David Pilbeam, Uno Samuelson, Yu. A. Semenov, Solweig Stuenes, Richard H. Tedford, Alan Turner, Alan Walker, Qiu Zhanxiang, The Department of Cell Biology and Anatomy, Johns Hopkins University, School of Medicine, the Department of Palaeozoology, Swedish Museum of Natural History, and all those people, too numerous to mention by name, who have provided access to collections in their care.

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Delimiting the family

Before commencing our review of extant and fossil hyaenas, we must consider what actually constitutes the family Hyaenidae, so that the reasons for our selection of fossil taxa to include in our discussions are clear.

What is a hyaena?

Present day Hyaenidae, including *Proteles*, are readily distinguished from other Feloidea – Felidae, Herpestidae and Viverridae – on the basis of morphological (Flynn *et al.* 1988; Hunt 1974, 1987, 1989; Winge 1895) and chromosomal (Wurster & Benirschke 1968) characters. Due to the fragmentary nature of the material, this is not always the case with fossil forms. Early in the study of fossil hyaenids, species of *'Thalassictis'* and *'Ictitherium'* were placed in the Viverridae on the basis of the plesiomorphic characters of their dentition. Winge (1895) was the first to show that these forms were hyaenids, and his work has been expanded by, e.g., De Beaumont (1964) and Hunt (1974). Similarly, forms such as *Tungurictis* and *Plioviverrops* have most often been referred to the Viverridae, but have been suggested to be hyaenids by others (De Beaumont 1969b; De Beaumont & Mein 1972; Solounias 1981; Hunt 1989), largely on the basis of their bulla structure, which approaches the derived hyaenid condition in many respects. Specifically, these forms have a posteriorly expanded ectotympanic and reduced caudal entotympanic. This character can be found in certain extant viverrids and in the felid *Uncia uncia*, the snow leopard, (Hunt 1987), but is in general a characteristic of hyaenids, although developed to a much greater degree in extant derived forms (*Crocuta, Parahyaena,* and *Hyaena*). Thus, although the bulla structure of forms such as *Plioviverrops* and *Tungurictis* does not *necessarily* place them in the Hyaenidae, the weight of the evidence clearly points in this direction, and they are therefore included here.

The *Percrocuta* problem

There is one group of species for which familial status is still equivocal, although they have nearly always been referred to the Hyaenidae on the basis of derived dental features such as loss of $M^2/_2$ and enlarged premolars (chiefly $P^3/_3$). These forms are generally called 'percrocutoid', and referred to the genera *Percrocuta* Kretzoi, *Dinocrocuta* Schmidt-Kittler, and perhaps *Allohyaena* Kretzoi (Howell & Petter 1985). These taxa share derived features, such as a reduced P^4 protocone, loss of M_1 metaconid, and reduction of M_1 talonid. Taken individually these features are paralleled in derived hyaenids *sensu stricto* (taxa that show the typical derived hyaenid bulla morphology), but as a whole they form a unique combination of characters. The percrocutoids are also exceptional in two other regards: they appear earlier in the fossil record than advanced hyaenids *sensu stricto*, and their remains are few compared with those of hyaenas *sensu stricto* and are often poorly preserved.

Recently, however, Schmidt-Kittler (1976; Chen & Schmidt-Kittler 1983) has demonstrated, on the basis of the structure of the deciduous dentition, that percrocutoids are likely to be phylogenetically quite distant from hyaenids *sensu stricto*, and instead share a common ancestry with 'stenoplesictines' (Chen & Schmidt-Kittler 1983, p. 168). Since the relevant features of the dP_4 in percrocutoids appear to be derived, this feature allies them cladistically with taxa outside the monophyletic Hyaenidae, and excludes all possibility of their being members of this family. Schmidt-Kittler (1976) also pointed out that *Adcrocuta eximia* differs from other percrocutoids in these features and is undoubtedly a true hyaenid.

This radical view has recently received strong support with the find of a skull of *Dinocrocuta gigantea* with preserved basicranium (Qiu *et al.* 1988a). The basicranial and bullar features of this specimen as described by Qiu *et al.* (1988a) and seen in their illustrations seem, as far as we can determine, quite different from those of hyaenids *sensu stricto.* A further relevant feature, of less significance but more commonly preserved, is the more anteriorly positioned orbit relative to the tooth row in percrocutoids than in hyaenids. This feature is constant in all undistorted percrocutoid specimens, and is important in that it is present in *'Hyaena' salonicae*, a species the allocation of which has been in doubt (Andrews 1916; De Beaumont 1979), but which must now definitely be referred to the percrocutoids.

The upshot of these recent developments is that the percrocutoids must be excluded from the Hyaenidae, and should, on the basis of their deciduous dentition and basicranial structure, be referred to a family of their own, the Percrocutidae, so named herein. The analysis of this group is beyond the scope of this paper and will be pursued elsewhere.

There is, however, one taxon which has recently (Qiu *et al.* 1988b) been referred to *Percrocuta,* but does not share the characters of this group either in dentition or in basicranial structure. This species, *'P.' primordialis*, was referred to the genus by Qiu *et al.* (1988b, p. 126) on the basis of 'the loss of $M^2/_2$, the strong reduction of M_1, the robustness of the premolars etc.' However, these characters are all present in derived hyaenids *sensu stricto* as well and thus do not form a basis for allocation to *Percrocuta.* We can only presume that the relatively great age of the specimen (MN Zone 6) has influenced the taxonomic decision, since derived hyaenas of this age are not known, while percrocutoids are well known from this time period. However, geological age is not a taxonomic character, and we must look elsewhere for characters that unite this specimen with one or the other group: hyaenids *sensu stricto* or percrocutoids. The most commonly cited derived character uniting percrocutoids is the reduced P^4 protocone. In *'P.' primordialis* the protocone is large and unreduced as in normal hyaenids. Qiu *et al.* (1988b) write in comparing their species with *P. abessalomi* (Gabunia 1958, 1973): 'The P^4 in *P. abessalomi* has a much reduced protocone, but rather large parastyle, while in the Tongxin species the protocone is large, but parastyle is poorly developed.' Thus, *'P.' primordialis* does not share these important derived features of percrocutoids. Further, P^1 is present bilaterally in *'P.' primordialis* but is otherwise unknown in percrocutoids. The above are all features in which *'P.' primordialis* is primitive relative to percrocutoids, and they are therefore not proof of non-relatedness. However, the bulla structure of *'P.' primordialis* is undoubtedly derived relative to that of percrocutoids as exemplified by *Dinocrocuta gigantea* (Qiu *et al.* 1988a). In *'P.' primordialis* the bulla is inflated, which it is apparently not in *D. gigantea* ; in *'P.' primordialis*, the posterior (caudal entotympanic) chamber is small relative to the anterior (tympanic) chamber, whereas in *D. gigantea* this is, as far as can be determined, not the case. These features are derived features characterizing hyaenids *sensu stricto*, and it is with this group that *'P.' primordialis* has its affinities. Finally, we believe, from what can be seen in the illustrations of the bulla of *'P.' primordialis*, that Qiu *et al.* (1988b) have somewhat exaggerated its differences from derived hyaenids, particularly regarding the position of the crista tympanica, and that the bulla of this species belongs to bulla type 4 of Hunt (1987). In general, we feel that the bulla of this form is very similar to that of *Tungurictis* as reconstructed by Hunt (1989).

Material

It is, of course, not possible to examine and evaluate personally all material covered in a work such as this. The bulk of our analysis is based on our previous extensive work on Miocene–Pliocene hyaenids (Kurtén & Werdelin 1988; Solounias 1981; Solounias & De Beaumont 1981; Werdelin 1988a, 1988b; Werdelin & Solounias 1990; Werdelin, Turner & Solounias, MS). In particular, work on Chinese fossil hyaenids has given us a firm overall grasp of the variability of hyaenid species, which has been a mainstay in our taxonomic work on the group. The Chinese material is in the collections of the American Museum of Natural History, New York, USA, and the Palaeontological Museum, University of Uppsala, Sweden. In addition, we have studied collections of fossil hyaenids in many museums in Europe. Collections in Africa, China, and India we have not seen. This is particularly problematic with regard to the Sivalik hyaenids, and our uncertainty regarding these forms is consequently greater than for other taxa. Although we have not seen the collections of hyaenids from Langebaanweg, South Africa, in the South African Museum, we have had at our disposal the notes on these specimens made by Dr. Alan Turner, University of Liverpool, and these notes have been invaluable (see also Werdelin, Turner & Solounias, MS). In the light of our analyses of material we have seen, our comments on material we have not seen appear only moderately more uncertain.

The following abbreviations for museum collections have been used: RM, Swedish Museum of Natural History; PIU, Palaeontological Institute, University of Uppsala;

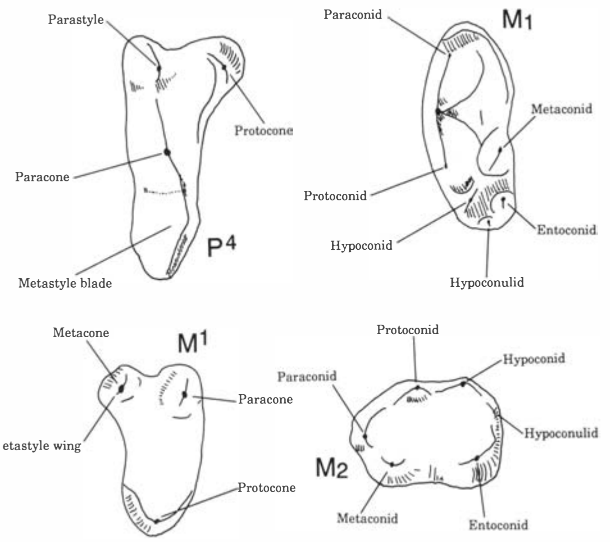


Fig. 1. Schematic diagram of hyaenid P^4, M^1, and M_{1-2}, showing dental terminology used in this paper.

AMNH, American Museum of Natural History; NHMW, Natural History Museum, Vienna; BM, The Natural History Museum, London; SMNL, Natural History Museum, Ludwigsburg.

Methods

Each facet of a paper such as this requires its own methods. Dental terminology is illustrated in Fig. 1. Aside from these morphological features we have used the following measurements in the taxonomic work (Fig. 2):

LC_i: anteroposterior length of lower canine at base of enamel
WC_i: transverse width of lower canine at base of enamel
LP_1, LP_2, LP_3, LP_4, LM_1, LM_2: anteroposterior length of respective tooth
LpP_4: length of major cusp of P_4
LtM_1: Length of trigonid of M_1
WP_2, WP_3, WP_4, WM_1, WM_2: transverse width of respective tooth
LC^s: anteroposterior length of upper canine at base of enamel
WC^s: transverse width of upper canine at base of enamel
LI^3: anteroposterior length of third upper incisor
LP^1, LP^2, LP^3, LM^1, LM^2: anteroposterior length of respective tooth
WP^2, WP^3, WM^1, WM^2: transverse width of respective tooth
LP^4: anteroposterior length of P^4
WaP^4: width of P^4 at protocone
$WblP^4$: width of P^4 between paracone and metastyle
LpP^4: length of paracone of P^4
LmP^4: length of metastyle of P^4
C–cond: length of mandible from anterior end of canine to posterior extremity of condyle
HPC: height of coronoid process
Cond–ang: distance from dorsal margin of condyle to ventral margin of angular process
P_2–M_1: inclusive distance between P_2 and M_1
Hdia: dorsoventral depth of mandible at diastema
$HbehM_1$: dorsoventral depth of mandible behind M_1
PL: length of palate
C–C: width of skull between buccal margins of canines
P–P: width of skull between buccal margins of P_4
IOB: least width between orbits
POP: width of skull between post-orbital processes
POC: least width of skull at post-orbital constriction
ZB: greatest width of skull at zygomatic arches
CB: greatest width of occipital condyles.

Dental measurements were taken with vernier calipers to the nearest 0.1 mm. Skull measurements were taken to the nearest 1 mm. In the statistical analyses the raw data were transformed into $\log_{10}$. Metric work has been based mainly on the ratio diagram method of Simpson (1941). In cases where bivariate statistical methods have been used, these are standard and follow procedures in Sokal & Rohlf (1981).

In the phylogenetic analyses, parsimony analysis has been used. We have used the PAUP 3.0i program for the Apple Macintosh™, written by David Swofford. ACCTRAN optimization has been used throughout. MAXTREES has been limited only by internal memory and was never approached.

Other information on these analyses and other methods used herein is provided in the appropriate sections.

In nomenclature we have throughout this work adopted the convention of using generic names without quotation marks, e.g., *Ictitherium viverrinum*, to mean that this species belongs to a monophyletic taxon with the generic name *Ictitherium.* Generic names in quotation marks, e.g., *'Protictitherium' cingulatum*, means that this species belongs to a grade group generally referred to as *Protictitherium.* To take the latter example further, there are a number of species referred to *'Protictitherium'*, and these are all placed at the same node in the overall cladogram. However, there are no characters available that would serve as synapomorphies to unite them as a monophyletic taxon *Protictitherium*, and therefore only the genotypic species can be so designated, leaving the remainder as a grade-group and possibly paraphyletic taxon.

Parsimony

The methodology of cladistic analysis has been expounded on numerous times over the past decade and a half, and in general need not be belabored here. However, there is one aspect of cladistic analyses that still seems to be poorly understood and the subject of some conceptual confusion. This is the concept of parsimony and its use in phylogenetic studies. This concept has been objected to by many non-cladists (some randomly selected recent references include Bartsch 1988 and Carroll 1988; also Krishtalka, oral presentation at 5th International Theriological Congress, Rome, 1989) on the grounds that evolution itself is not parsimonious. Carroll (1988) puts it as follows (p. 7): 'In general this principle [parsimony] is logical and to some degree underlies all scientific thinking. However we may question the degree to which it is applicable to establishing phylogenies. In the case of phylogenetic analysis, the use of parsimony is based on the assumption that most characters evolved only once and that convergence is rare. Surprisingly, supporters of this doctrine have never tested this assumption.'

This quotation is clearly pulled out of context, but, we believe, not unfairly so, and it is instructive to dissect it to see what it is that Carroll (and many others, as noted) objects to and why. The concept of parsimony is one of the

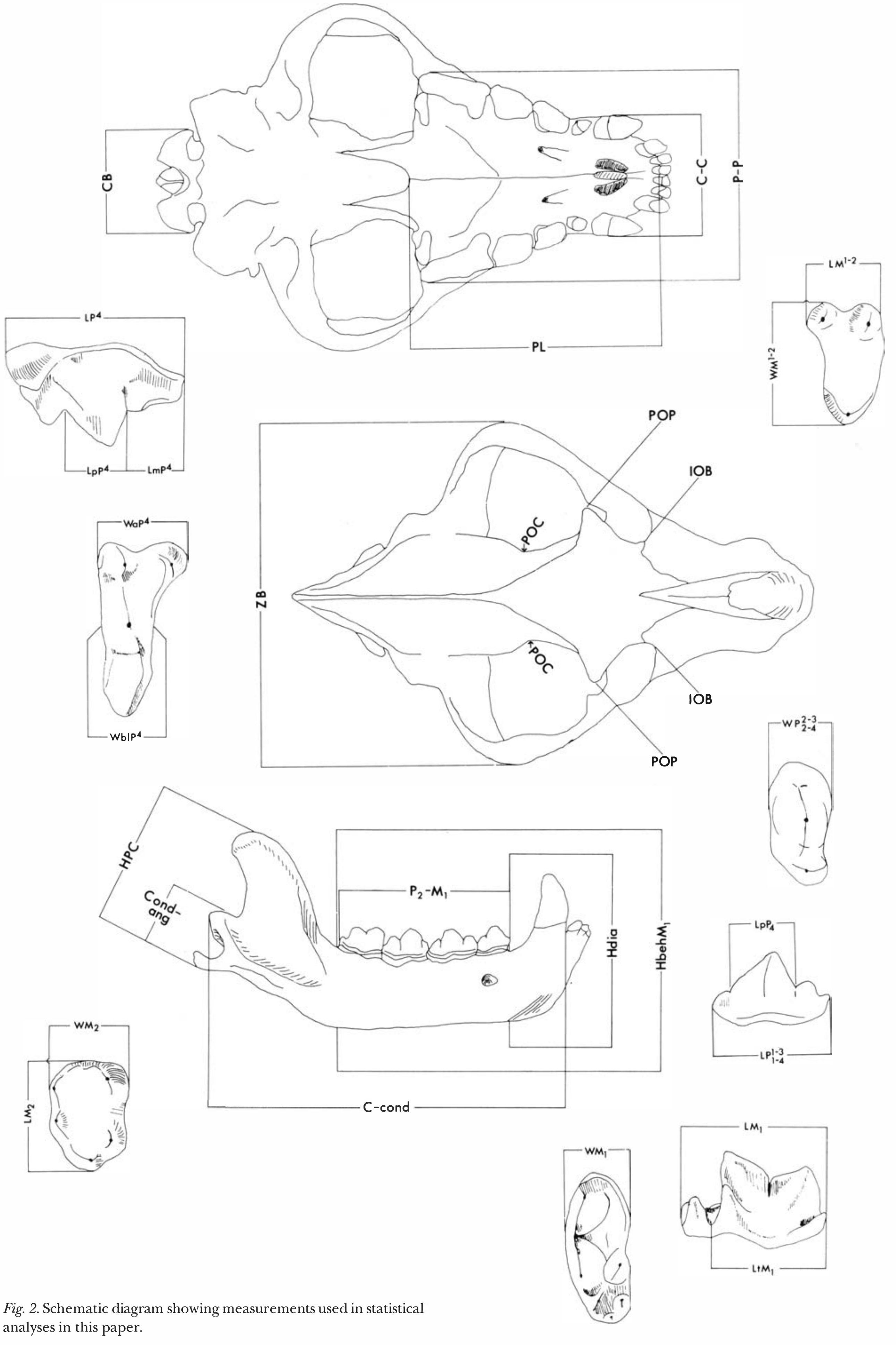


Fig. 2. Schematic diagram showing measurements used in statistical analyses in this paper.

cornerstones of modern scientific thought, and one of the few ways that have been devised of understanding the world around us, in particular the world of the intellect. This is particularly evident in the philosophic movements of the past decades, as neither structuralist philosophy nor the more recent post-structuralist developments would have been possible without the concept of parsimony in its classic sense. To suggest that it 'to some degree' underlies scientific thinking is to denigrate the past 600 years' work in the philosophy of science.

The principle of parsimony has by many been incorrectly called 'Ockham's razor'. In fact, the principle goes back to Aristotle, and was used by several philosophers between him and William of Ockham, notably by Duns Scotus. However, William of Ockham was undoubtedly the first to use the principle extensively and consistently in his logical writings. He phrased it as follows (one of several variants): *'Quia fit per plura quod potest equaliter fieri per pauciora'* [It is vain to do by more what can equally be done by fewer] (*Reportatio, 254, O,* quoted from Leff 1975). Thus, in science no hypotheses to explain a phenomenon should be posited beyond those necessary. Ockham had this concept perfectly clear as a methodological principle in the early parts of the 14th century, and it is somewhat strange to find that it is still not understood some 650 years later. Ockham used the principle to excise unnecessary, mainly metaphysical hypotheses, and indeed his work spelled an end to metaphysical scholasticism. Cladists now use the concept to excise evolutionary metaphysics from phylogeny reconstruction. Ockham was excommunicated for his pains, but we have grown a little wiser since then.

In the second part of the quotation, Carroll goes on to state that the use of parsimony is based on an assumption about character evolution. This is patently untrue. Evolution may be entirely unparsimonious – this, if it could be established, would then be a fact of nature. However, in order to study the world, we still require operational principles, and in particular we require the principle of parsimony. This is it then: parsimony is an operational principle as to how we can study and understand the world, and choose between otherwise equally acceptable hypotheses, and its use does not imply any assumptions about the nature of that world. This has been elegantly shown by Farris (1983), who demonstrated that parsimony is still the best principle, even in a strongly non-parsimonious world. The last part of Carroll's comment falls of its own weight, as in fact no cladist has claimed either that evolution is parsimonious or that convergence is rare. This type of assertion has only been made by commentators who wished to criticize cladistic principles by setting up a straw man concept.

The final word on parsimony, and truly a death knell to those who believe that evolution must be parsimonious in order for the concept to apply, can be given to Popper (1972, p. 301), who states, paraphrasing Quine: '... only if Plato's beard is sufficiently tough, and tangled by many entities, can it be worth our while to use Ockham's razor.' What beard can be tougher and tangled by more entities than that of evolution?

Taxa

In the following, each species is treated separately, in order of naming. Partial synonymies are provided, incorporating essential or confusing references. The locality distributions are as complete as it has been possible to make them, incorporating all material seen by us, as well as specimens that we have been able to refer taxonomically on other grounds. Doubtful presences are also noted. Age determinations, in terms of MN zones, are made on the basis of the locality distributions. In addition, a commentary on the state of our knowledge of each species is provided. This commentary also includes data that are of interest but for various reasons have not been used in the systematic analyses to follow.

Taxa denoted by an asterisk before the species name are here considered the 'core taxa'. These are the four extant species, and the 15 best known fossil ones. These 19 species will form the basis for the phylogenetic analysis that follows in the following section.

**Hyaena hyaena* (Linnaeus, 1758)

Fig. 3

Synonymy. – ☐1758 *Canis hyaena* sp. nov. – Linnaeus, p. 40. ☐1771 *Hyaena hyaena* gen. nov. – Brünnich, p. 34. ☐1777 *Hyaena striata* sp. nov. – Zimmermann, p. 366. ☐1820 *Hyaena fasciata* sp. nov. – Thunberg, p. 59. ☐1938 *Hyaena striata* Zimmermann – Kretzoi, p. 116. ☐1952 *Hyaena makapani* sp. nov. – Toerien, pp. 293–296, Figs. 1–3.

Localities (fossil). – Ethiopia: Usno, Shungura B; Kenya: West Turkana; South Africa: Kromdraai, Makapansgat 3, Swartkrans 1; Tanzania: Olduvai 2. (Fig. 7.)

Age. – Villafranchian–Recent

Discussion. – We here consider *Hyaena prisca*, by a number of authors thought to be a synonym of *H. hyaena* (e.g., Howell & Petter 1980), to be synonymous with *Pliocrocuta perrieri*, which means that there is no known record of *H. hyaena* from Europe.

This species is much less well known than either of the other extant hyaenids, although some minor studies have been carried out (Kruuk 1976; Bouskila 1984). Work on this species up to the end of the 1970's is usefully summarized by Rieger (1979). These studies show that its social system is basically similar to those of the spotted and brown hyaenas, and that, like the brown hyaena, it is a catholic feeder, emphasizing carrion, but also eating small mammals, vegetables and fruit.

Most studies of this species have assumed that it is the most primitive of the three extant scavenging species. As we shall see, our study provides no basis for this belief. The absence of a fossil record of the species outside Africa is an indication that its invasion of extra-African areas may be quite recent.

**Crocuta crocuta* (Erxleben, 1777)

Fig. 4

Synonymy. – □1777 *Canis crocuta* sp. nov. – Erxleben, p. 578. □1811 *Hyaena maculata* sp. nov. – Thunberg, p. 302. □1817 *Hyaena capensis* sp. nov. – Desmarest, p. 499. □1823 *Hyaena spelaea* sp. nov – Goldfuss, pp. 456–462, Pls. 15, 16:1–3; 17:3. □1828 *Crocuta crocuta* gen. nov. – Kaup, col. 1145. □1828 *Crocotta crocuta* gen. nov. – Kaup, p. 78. □1868 *Hyaena sivalensis* sp. nov. – Falconer & Cautley *in* Falconer, p. 548. □*pars* 1884 *Hyaena felina* sp. nov. – Lydekker, pp. 281–285, Fig. 13, Pls. 33:1; 39:1. □*pars* 1884 *Hyaena colvini* sp. nov. – Lydekker, p. 294, Pl. 35:5. □1915 *Hyaena ultima* sp. nov. – Matsumoto, pp. 2–3, Pl.1:1–3 □1927 *Hyaena ultima* Matsumoto – Zdansky, pp. 20–22, Pl. 2:5–6. □1932 *Crocuta sivalensis* (Falconer & Cautley) – Pilgrim, pp. 134–137. □1934 *Hyaena ultima* Matsumoto – Pei, pp. 116–118, Fig. 36, Pl. 12:5. □1938 *Crocuta crocuta* (Erxleben) – Kretzoi, p. 119. □1954 *Crocuta spelaea* (Goldfuss) – Ewer, pp. 566–570, Figs. 1–2, Pl. 1:1. □1954 *Crocuta ultra* sp. nov. – Ewer, pp. 570–579, Figs. 3–8, Pls. 1:2–3, 2:1–3. □1954 *Crocuta venustula* sp. nov. – Ewer, pp. 828–830, Figs. 7–9. □1954 *Crocuta* cf. *spelaea* (Goldfuss) – Ewer, pp. 835–836. □1984 *Crocuta crocuta* (Erxleben) – Turner, pp. 399–418. □1989 *Crocuta ultima* (Matsumoto) – Huang, pp. 197–204.

Localities (fossil). – Ethiopia: Awash Matabaietu, ?Hadar, Shungura G; Kenya: Olorgesailie. South Africa: Elandsfontein, Kromdraai A, Swartkrans 1, Sterkfontein 4; Tanzania: Olduvai 1, 2. In addition, the species is found in hundreds of Pleistocene cave sites throughout Europe and Asia. (Fig. 8.) (See also *C. sivalensis* and *C. dietrichi.*)

Age. – Villafranchian–Recent

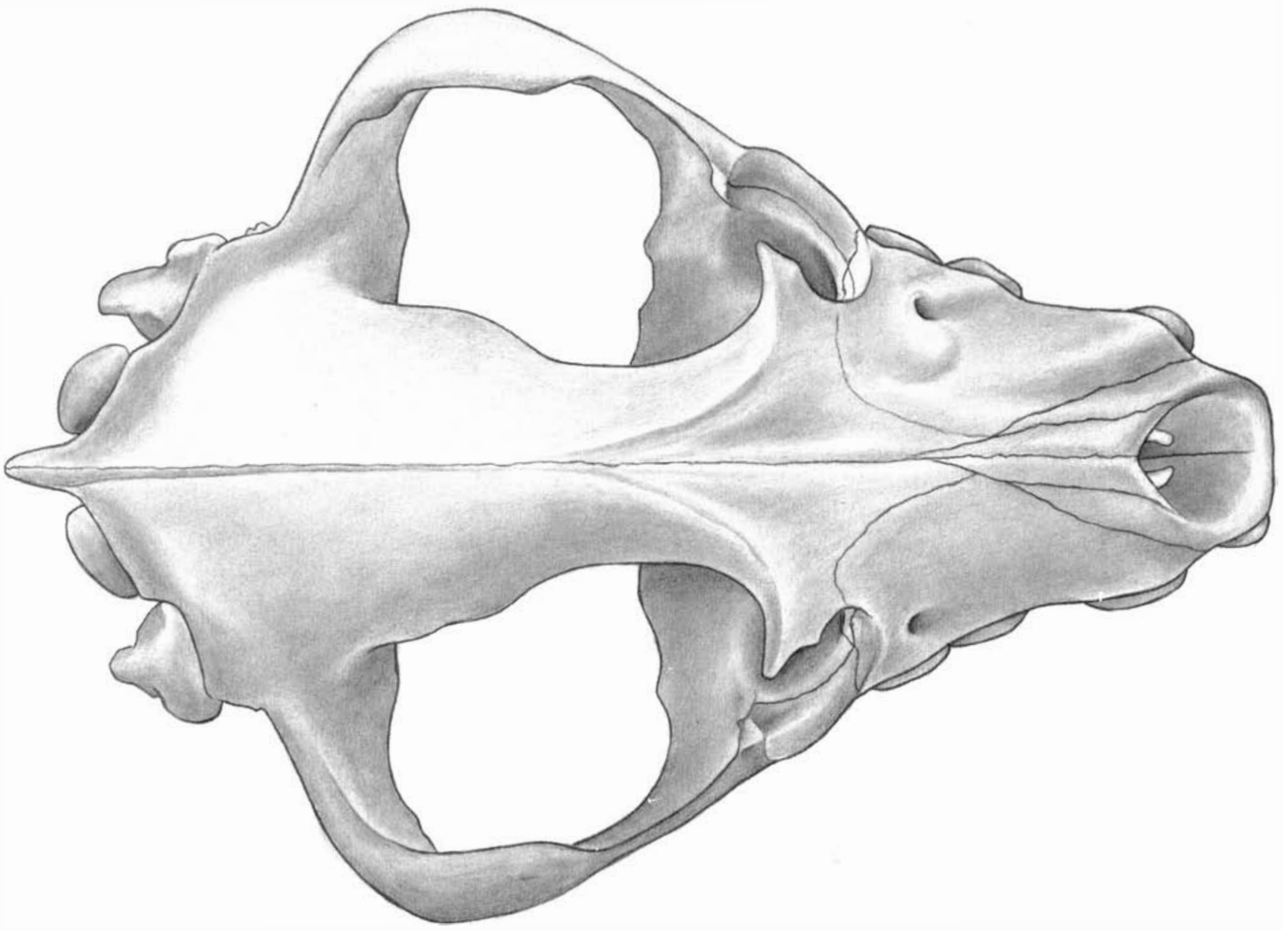
Discussion. – The spotted hyaena, currently exclusively African, had an extremely large geographic range in the past, encompassing most of Asia and Europe, as well as Africa (Fig. 8). As can be seen from the synonymy above, a great many species, recent as well as fossil, have been named within this range. Other authors have, however, conclusively shown that these species are simply geographic variants of a single, morphologically plastic species (e.g., Kurtén 1957c; Turner 1984). Kurtén (1957c) showed that a great deal of the size variation seen in *C. crocuta* can be accounted for by a strong correlation between body size and temperature.

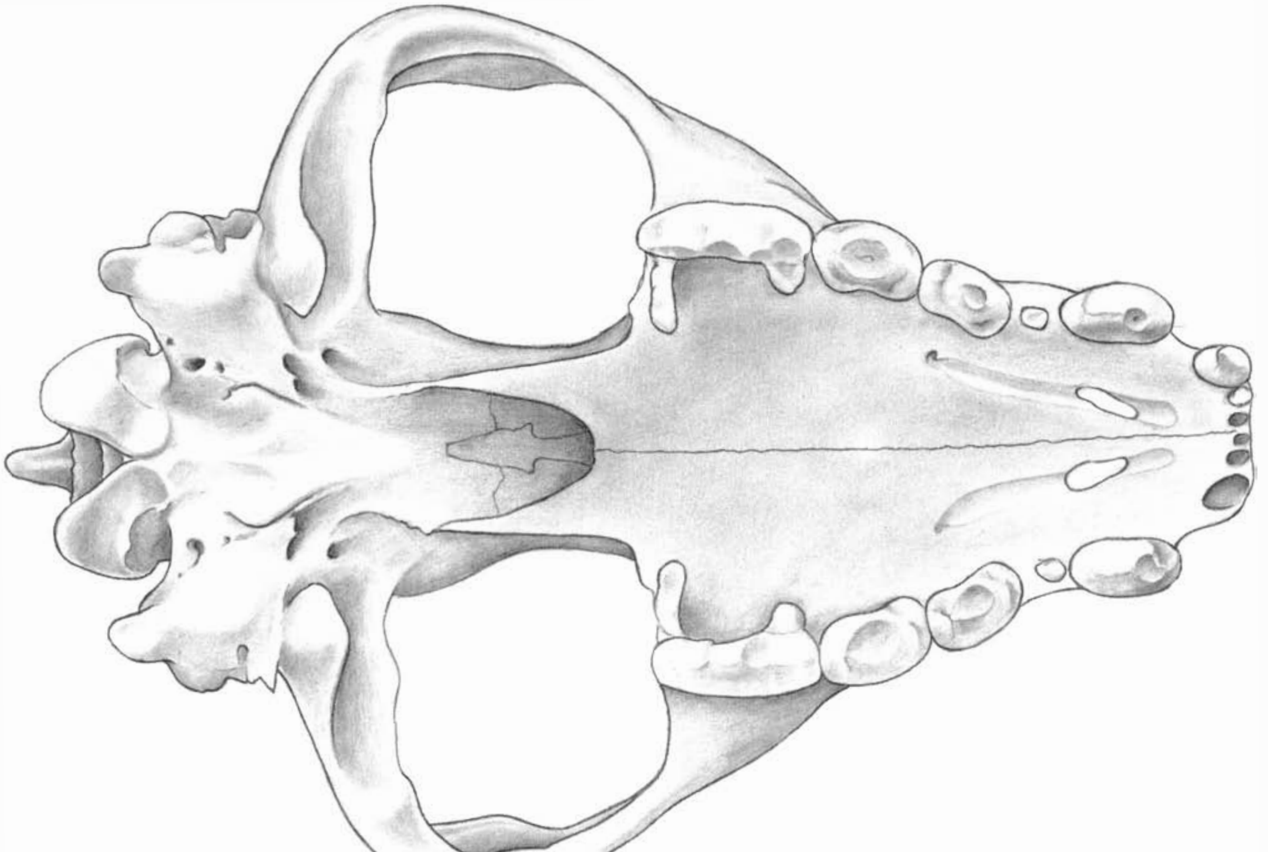
In Europe the cave hyaena, *C. crocuta spelaea*, is a very common member of Pleistocene faunas, and in some cases has been found in immense numbers in caves. The caves are in some cases thought to have been used as denning sites, while other sites are natural trap caves. Several such caves are found in England, typical examples being Kent's Cavern, near Torquay, and Tornewton Cave in South Devon, where tens of thousands of specimens have been found. A similar occurrence on the continent is Teufelslucken in Austria. Like most carnivores, the cave hyaena is poorly represented in Ice Age art, but a beautiful ivory sculpture of a cave hyaena was found in the cave of La Madeleine in Dordogne, France (Kurtén 1968).

As will be seen throughout this text, *C. crocuta* is highly autapomorphic in its morphology. It exhibits adaptations for both bone-cracking and meat-slicing, and represents an extreme of development of such a dual-purpose dentition (Werdelin 1989). However, the most autapomorphic trait exhibited by spotted hyaenas, and probably the most debated (Racey & Skinner 1979; Neaves *et al.* 1980; Gould 1981; Lindeque & Skinner 1982; Frank *et al.* 1985; Hamilton *et al.* 1986) is the sexual monomorphism and the strongly masculinized genitalia of female spotted hyaenas. Frank (1986b) presents a compelling case for selection favoring increased aggressiveness in females. Aggressive females would be able to outcompete other individuals for food in the highly competitive situation surrounding a spotted hyaena kill. Increased competitive ability at kills should result in greater success at rearing cubs, both due to the nutritional status of the female, and to her being able to ensure adequate food for young cubs. Support for this hypothesis comes, i.a., from the fact that cub starvation is rare in spotted hyaenas (Kruuk 1972; Frank 1986a, b), while in other social carnivores, e.g., wolves (Van Ballenberghe & Mech 1975) it is common, especially when food is scarce. If this scenario is correct, it would suggest that the sexual monomorphism seen in *C. crocuta* is due mainly to an incidental effect of increased androgen levels, but that it may also be accentuated by selection for masculinized external genitalia in females. In other hyaenid species, where competition for highly clumped patches of food may be less, these factors have not come into play.

The autapomorphism of *C. crocuta* extends to its ecology and behavior. Indeed, this species exhibits many behavioral traits which are highly peculiar among carnivores, and for which analogies must be sought within other mammalian orders (Kruuk, 1972; Frank 1986a, b). The hyaena group, or clan, is composed of a number of matrilines, with inheritance of maternal rank, along similar lines to Japanese macaques (Kawai 1958), bonnet macaques (Silk *et al.* 1981), or vervet monkeys (Horrocks & Hunte 1983). Frank (1986b) suggests that the hypothesis presented by Wragham (1980) to account for female-bonded groups in primates may be applicable to spotted hyaenas as well.

An idea with great intrinsic merit and important evolutionary implications is the hypothesis presented by Frank (1986b; cf. Trivers & Willard 1973) that reproductive success of dominant females in spotted hyaenas can be measured in terms of the number of male offspring. This is based on the observation that sons of the alpha female have different behavior patterns than other males, being less submissive towards the normally dominant females, and leaving the clan at a later date than other males. Furthermore, since individual characteristics seem to be very important in determining male dominance (Frank 1986b), the implication is that these males can achieve dominance in their new clans and therefore sire many offspring. The value of such 'supermales' is evident and the hypothesis needs to be followed up. From an evolutionary point of view, the possibility that dominant females of spotted hyaenas may influence the sex of their offspring is important, since male offspring can produce many more cubs than females, thus raising the possibility of great evolutionary





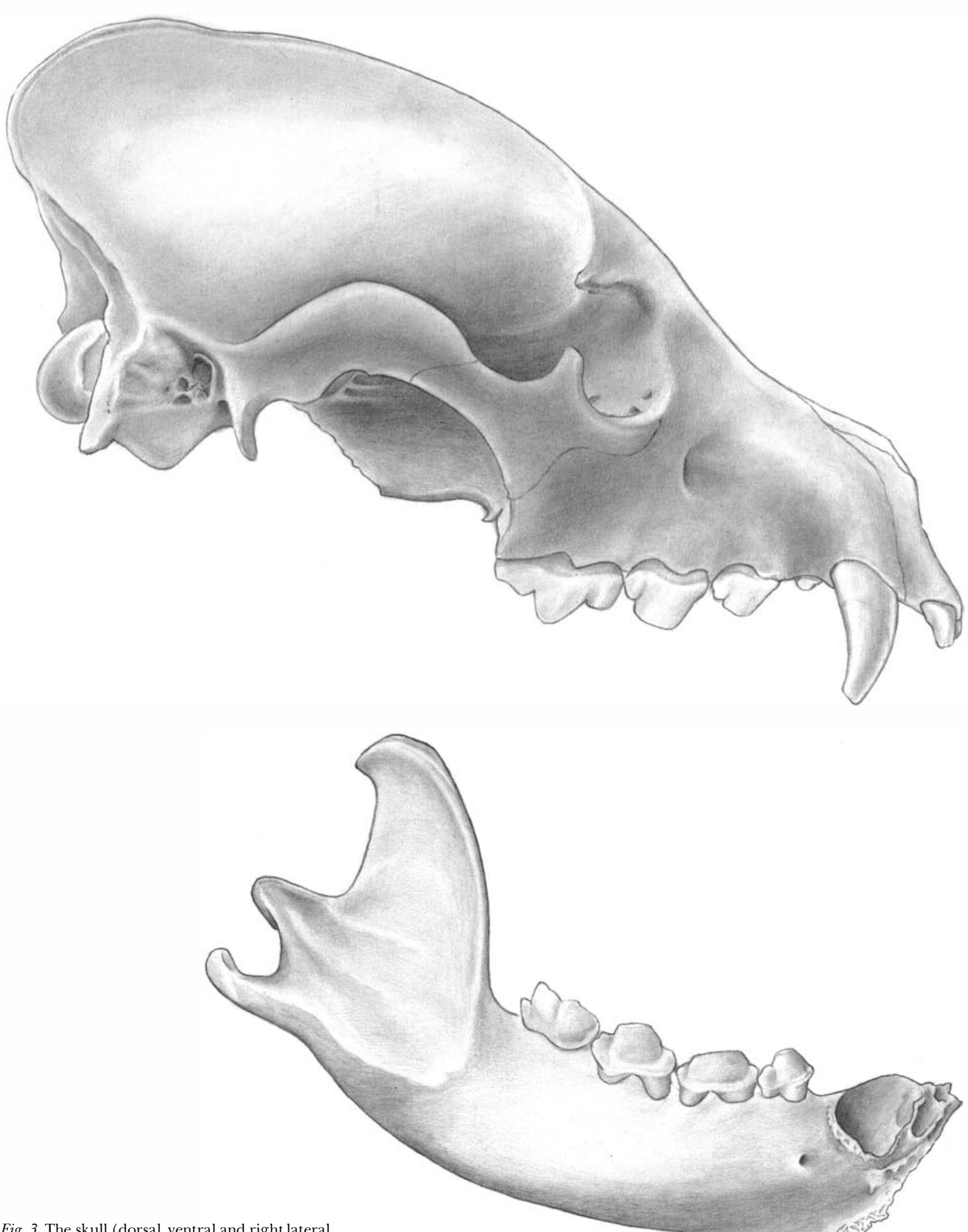
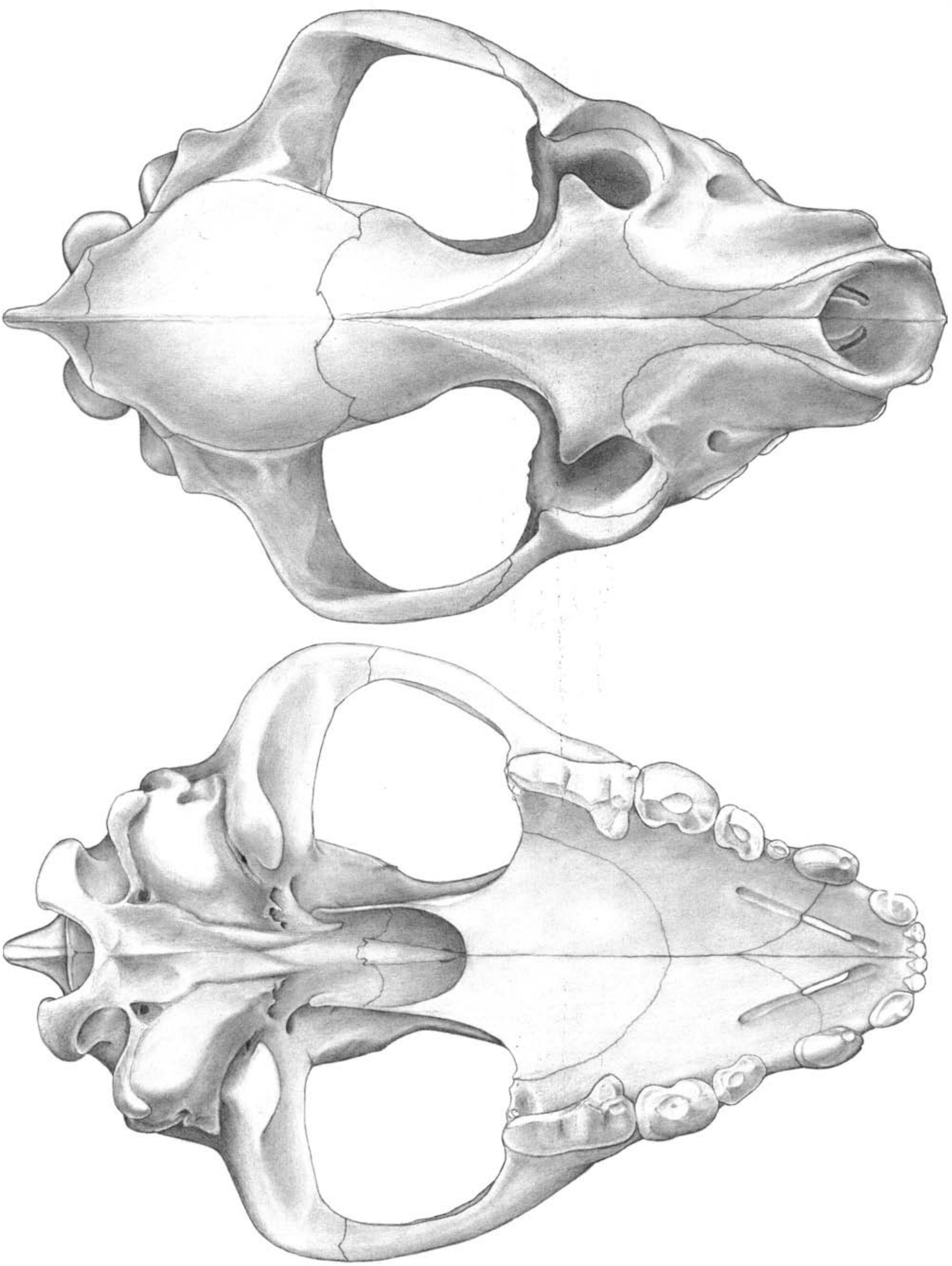


Fig. 3. The skull (dorsal, ventral and right lateral view) and right ramus (right lateral view) of *Hyaena hyaena* (RM A580401, Teheran).

flexibility within this species. Such flexibility is indeed seen in the geographic and temporal patterns of variability of the species.

Recently (Frank & Glickman 1989) another unusual (for a mammal) behavior has been reported in the spotted hyaena. Observations both in the wild and in captivity indicate that in same-sex litters, severe fighting from birth results in the death of one of the siblings. This fighting is mediated by the fact that spotted hyaenas are born with deciduous incisors and canines fully erupted. Such siblic-



ide is common in large raptors (termed the 'Cain and Abel syndrome'), but is otherwise unknown in mammals. The selective function of this behavior in spotted hyaenas is unknown, analogies with birds apparently not being applicable to this case.

Thus, when it is remarked below that *C. crocuta* is highly autapomorphic in its morphology, it may also be remembered that it is equally autapomorphic in its ecological and ethological characteristics. This argues for either very rapid divergence, and/or a long time lapse since the divergence

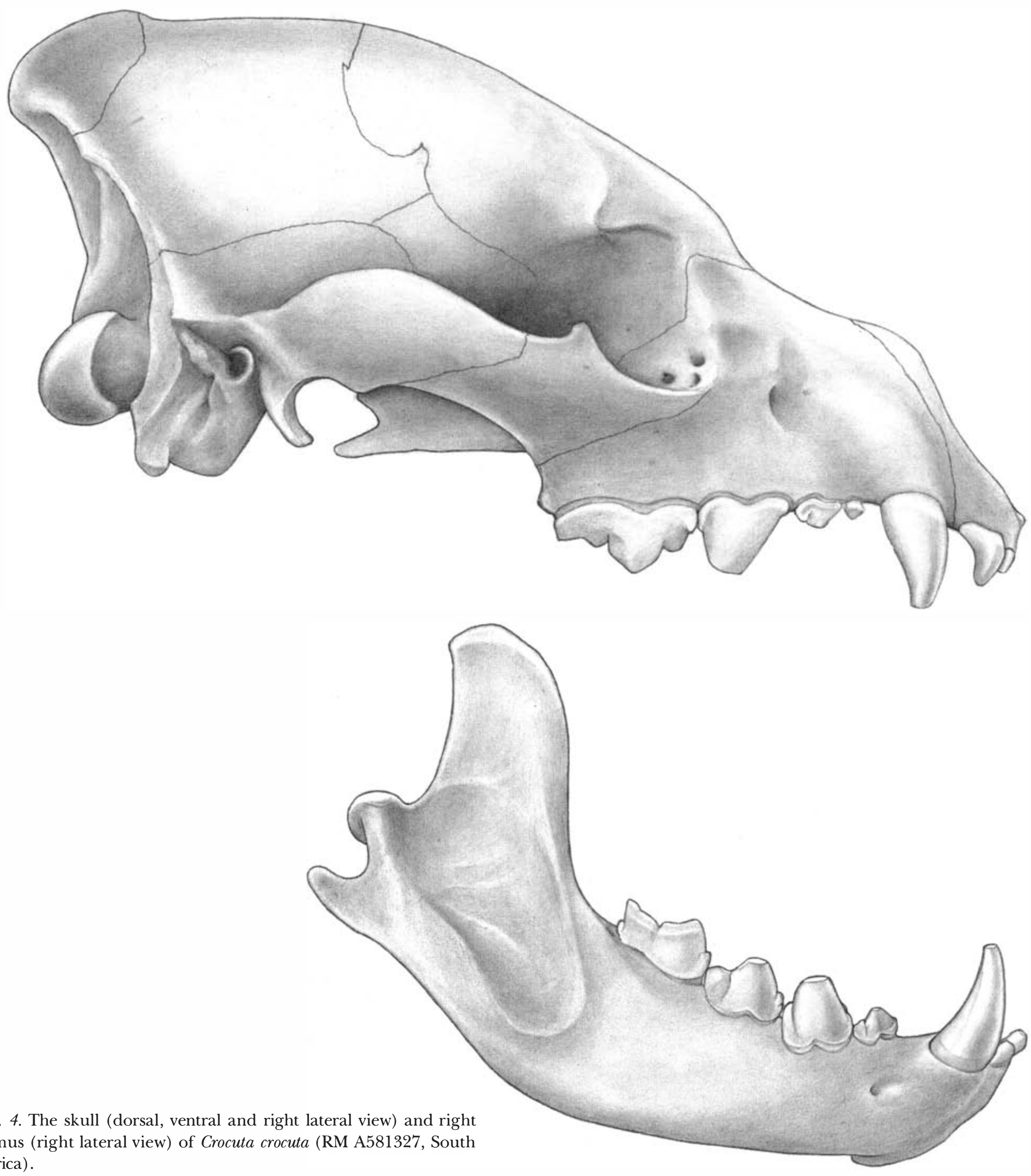


Fig. 4. The skull (dorsal, ventral and right lateral view) and right ramus (right lateral view) of *Crocuta crocuta* (RM A581327, South Africa).

of the extant hyaenid species from each other. Both seem to be true (Wayne *et al.* 1989; and below).

**Proteles cristatus* (Sparrman, 1783)

Fig. 5

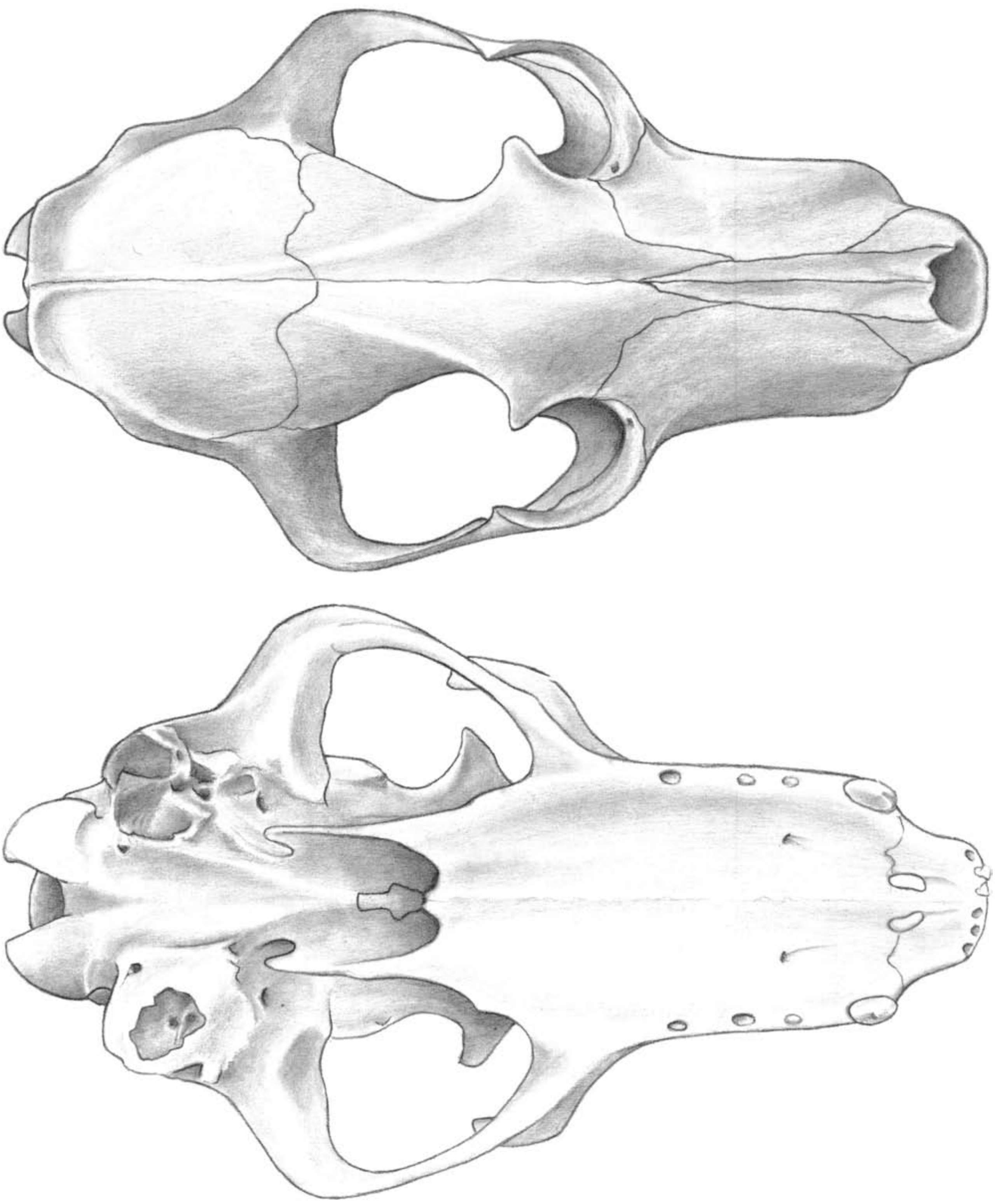
Synonymy. – □1783 *Viverra cristata* sp. nov. – Sparrman, p. 581. □1822 *Viverra hyaenoides* sp. nov. – Desmarest, p. 538. □1824 *Proteles lalandi* gen. et sp. nov. – I. Geoffroyi, p. 371.

Localities (fossil). – South Africa: Swartkrans 1, 2. (Fig. 9.)

Age. – Pleistocene–Recent

Discussion. – That the aardwolf is a hyaena is amply confirmed by chromosomal characters (Wurster & Benirschke 1968). On the other hand, it is an exceedingly primitive hyaena with regard to those morphological features in which it can be compared with other hyaenids, fossil and extant. This is true, e.g., of the auditory bulla and the basicranial region. In other characters, such as the dentition, it is highly autapomorphic due to its adaptation for termite eating. This creates special problems in attempting to assess the phylogenetic position of the species, as will be seen below.

In its ecological adaptation to eating termites, *P. cristatus* differs from other similarly adapted taxa, such as aardvarks and anteaters, in its inability to penetrate the termite



mounds with strong claws. This means that *P. cristatus* is limited to eating termites that appear on the surface. Studies by Richardson (Richardson 1987a, 1987b, 1987c; Richardson & Coetzee 1988; summarized in Richardson 1990) have shown that the aardwolf almost exclusively feeds on one species of termite, *Trinervitermes trinervoides*, a species that forages in the open. During winter, when *T. trinervoides* retreats to its mounds and is scarce on the surface, *Hodotermes* sp. is utilized. However, the latter cannot exist in areas where winter temperatures fall below a certain level, and the geographic range of *P. cristatus* is fragmented accordingly (Fig. 9).

P. cristatus is a monogamous species, with an adult pair occupying a defended territory (Kruuk & Sands 1972). This is almost certainly a result of its feeding ecology, and there is here no basis for judging whether this social structure is primitive for hyaenids or autapomorphic for *P. cristatus*.

Cladistically, the branch leading to this species split from other hyaenids very early in the evolution of the group. A

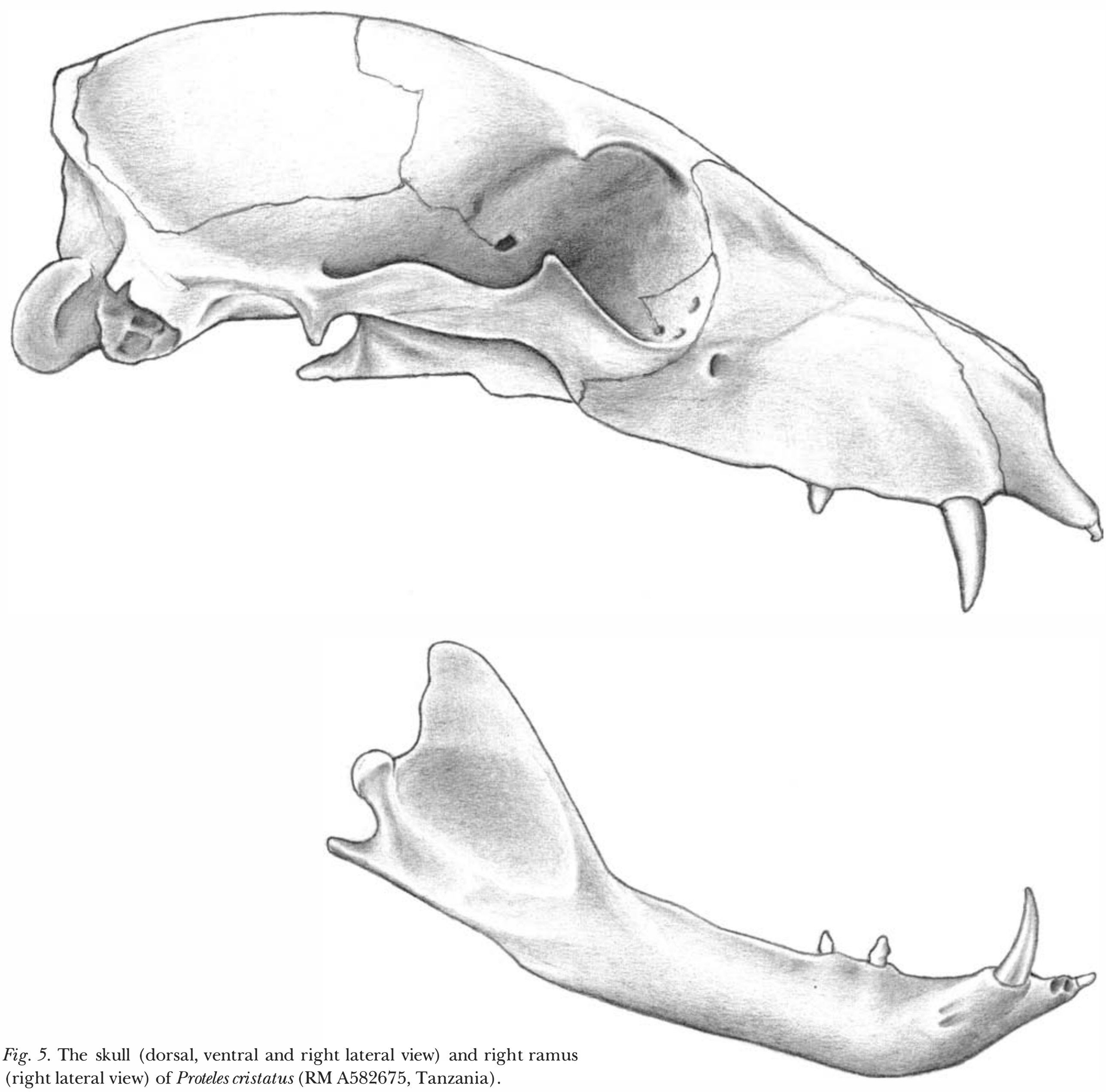


Fig. 5. The skull (dorsal, ventral and right lateral view) and right ramus (right lateral view) of *Proteles cristatus* (RM A582675, Tanzania).

splitting date of 20 Ma or more is indicated. However, the inability to dig into termite mounds and the apparent absence of fossil *Proteles* older than 1.5–2 Ma argues for a recent date for the evolution of the ecological adaptations of the species. We have no explanation to offer for this discrepancy at the present time. We merely point out the conflict between the cladistic age of *Proteles* and the age of the oldest fossils of the genus. (See *P. amplidenta*, below.)

**Parahyaena brunnea* (Thunberg, 1820)

Fig. 6

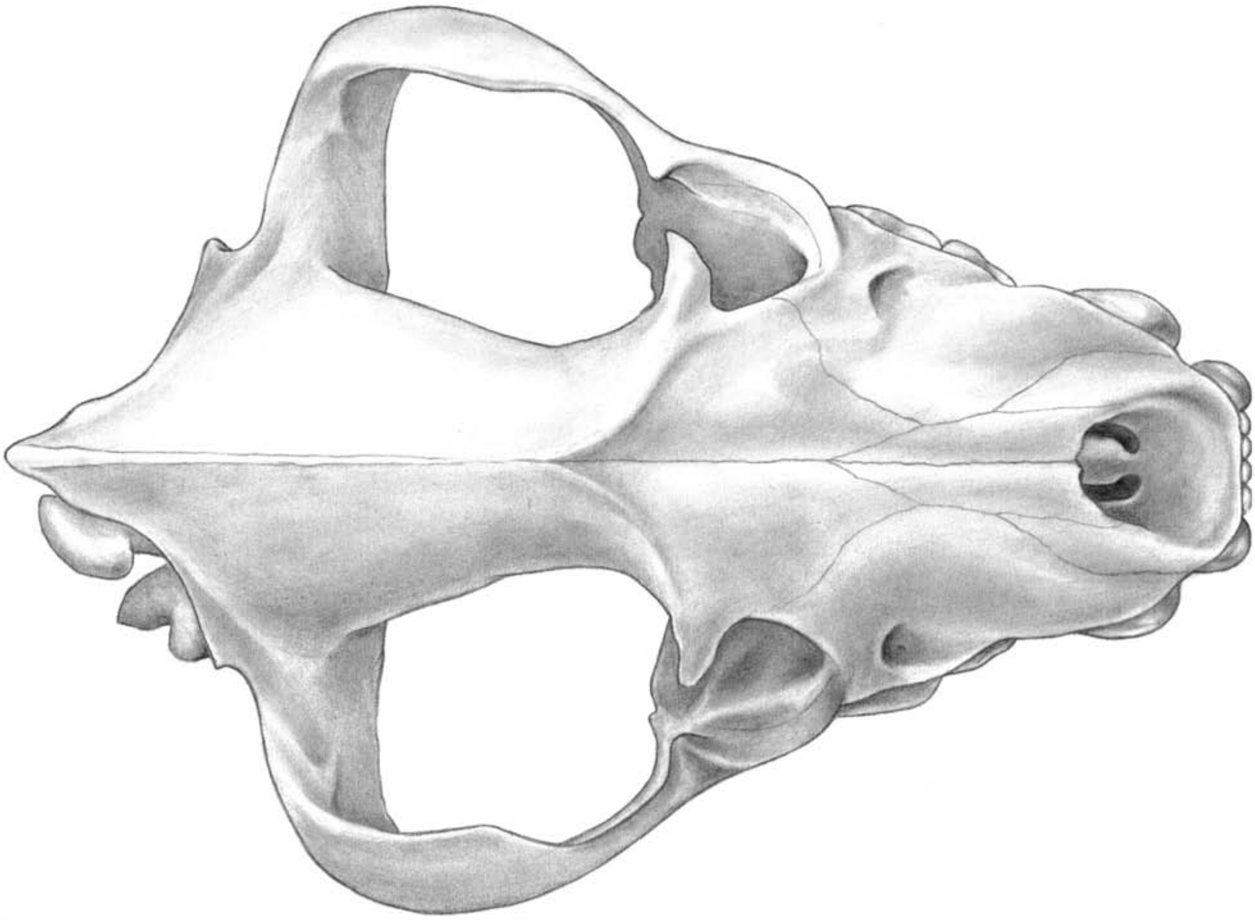
Synonymy. – □1820 *Hyaena brunnea* sp. nov. – Thunberg, p. 59. □1827 *Hyaena villosa* sp. nov. – Smith, p. 461. □1974a *Hyaena (Parahyaena) brunnea* subgen. nov. – Hendey, p. 149.

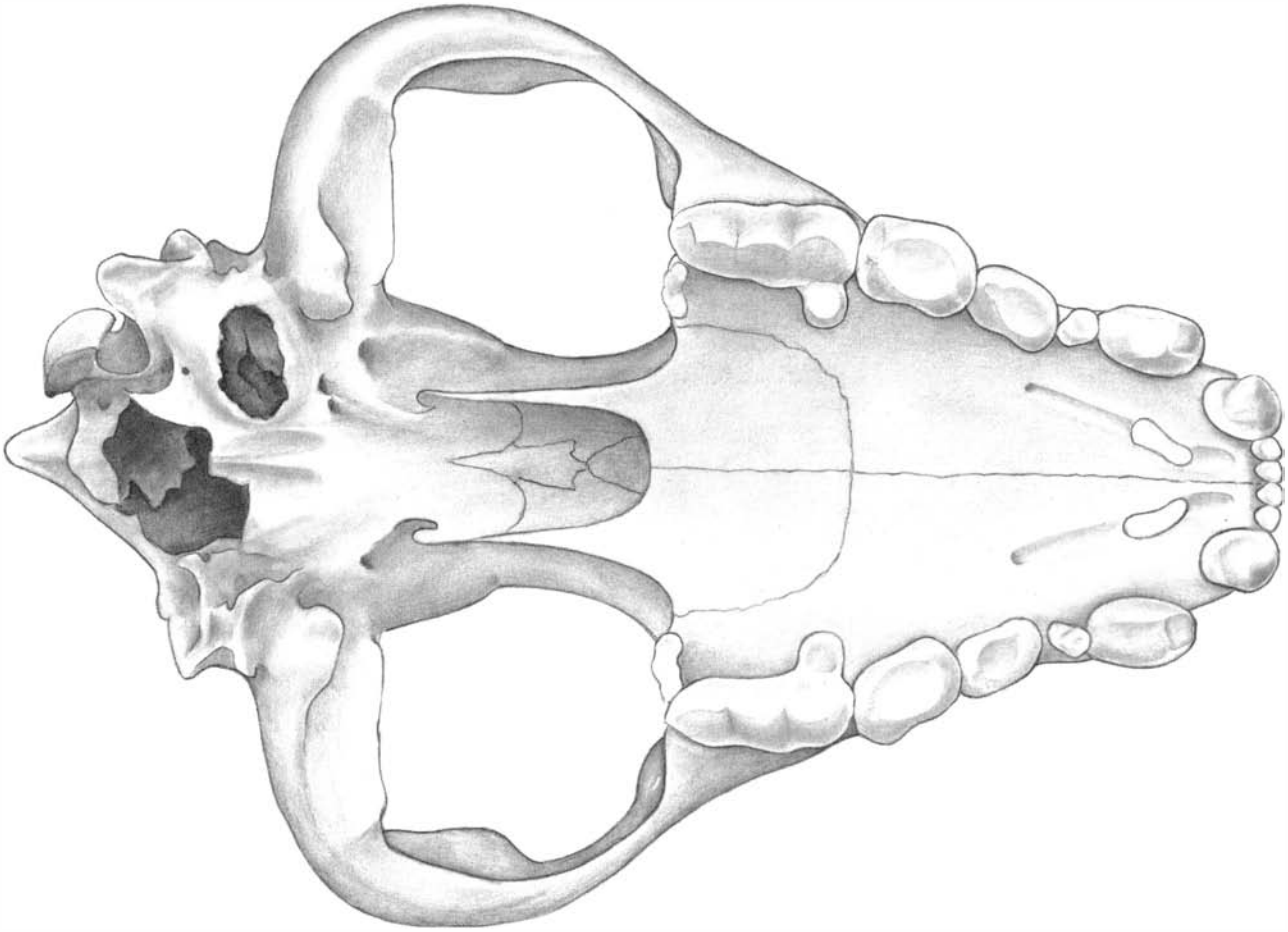
Localities (fossil). – Ethiopia: ?Hadar, ?Omo Usno, ?Shungura C, E, F, G; South Africa: Elandsfontein, Kromdraai A, Sterkfontein 4, Swartkrans 1, 2. (Fig. 10.)

Age. – ?Villafranchian–Recent

Discussion. – As can be seen from the localities given above, the brown hyaena may previously have had a much greater range than at present, when it is confined to parts of southern and southwestern Africa (Fig. 10). The Ethiopian finds are not well defined, however, and could possibly pertain to some other taxon.

The extant brown hyaena is less well studied than the spotted hyaena, but has nevertheless been the focus of intense interest over the past decade and a half (e.g., Owens & Owens 1979a, b; Mills 1982a, 1983a, b, 1984, 1987, 1989 and others), so that compared to many other carnivores, the brown hyaena is well studied. Unlike spotted hyaenas, brown hyaenas are solitary foragers. Most of their food is carrion, but they also engage in opportunistic hunting of small mammals and birds. Their diet is further supplemented by a certain amount of vegetables and, particularly, fruit.





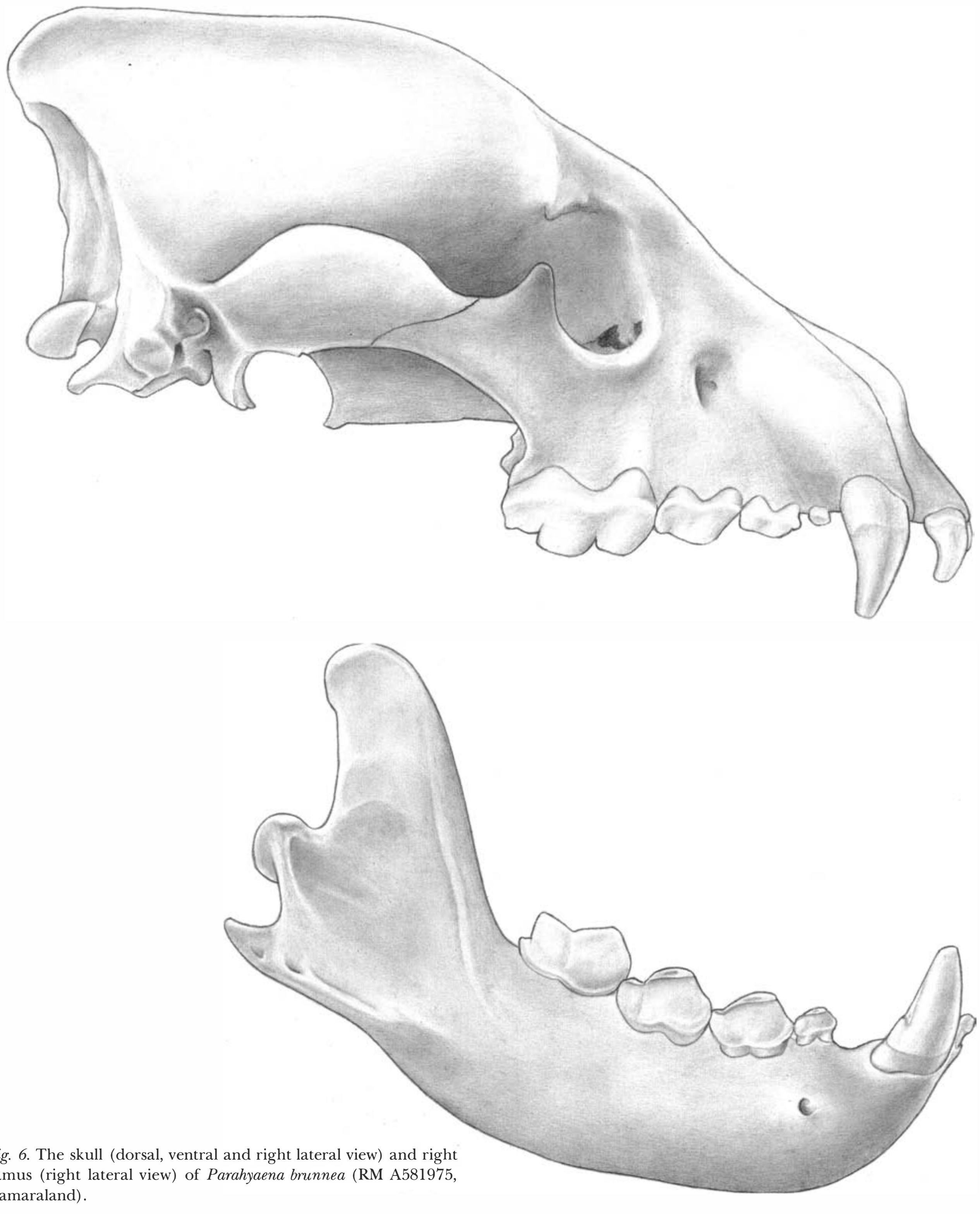


Fig. 6. The skull (dorsal, ventral and right lateral view) and right ramus (right lateral view) of *Parahyaena brunnea* (RM A581975, Damaraland).

Despite their solitary foraging, brown hyaenas, like their spotted relatives, live in clans that share a common territory and feed together on large clumps of food (large carcasses). The density of brown hyaenas in a territory is dependent on the quality of food it contains (Mills 1982a). The social organization within the clans is basically the same as for spotted hyaenas, but fluctuations in group size were greater than for the latter species (Frank 1986a; Mills 1989), possibly due to the differences in feeding habits between the two species. The most noticeable difference in denning behavior between the two species is that brown hyaenas carry parts of carcasses back to the den, which is not the case in spotted hyaenas (Mills 1982b). The result is that meat forms a substantial part of the diet of young brown hyaenas much sooner than is the case in spotted hyaenas.

In broad terms, the social systems of brown and spotted hyaenas are similar, an observation that extends to striped

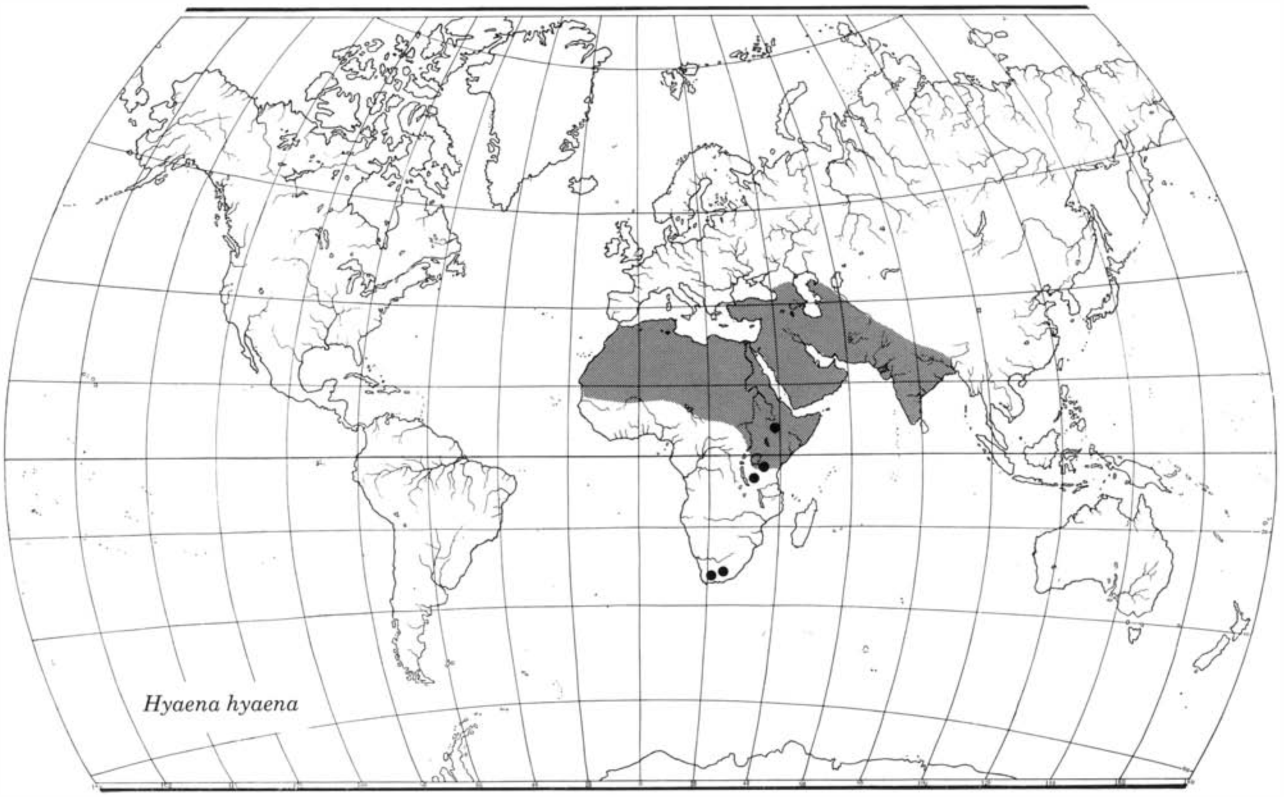


Fig. 7. Map showing (stippled) current range of *H. hyaena*. Dots mark fossil localities outside current range.

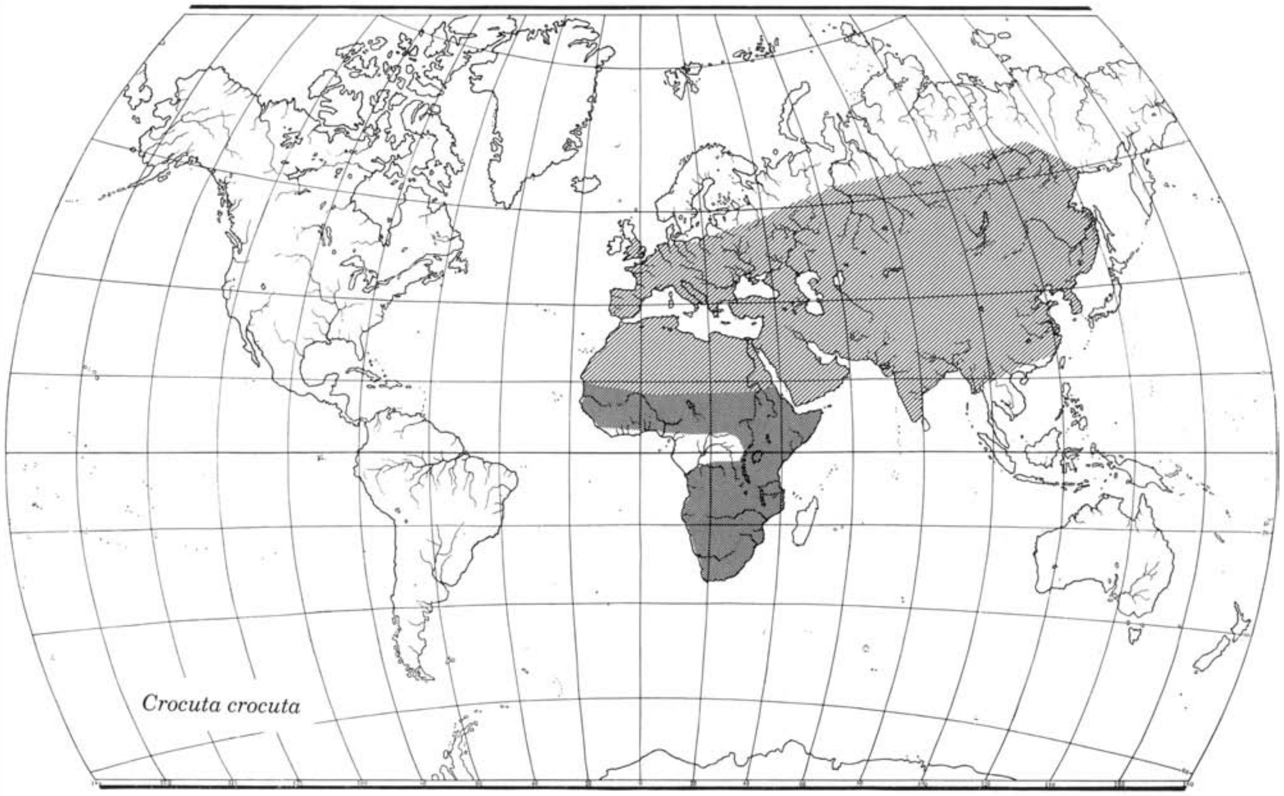


Fig. 8. Map showing (stippled) current range of *C. crocuta* and (shaded) maximum range in the Pleistocene.

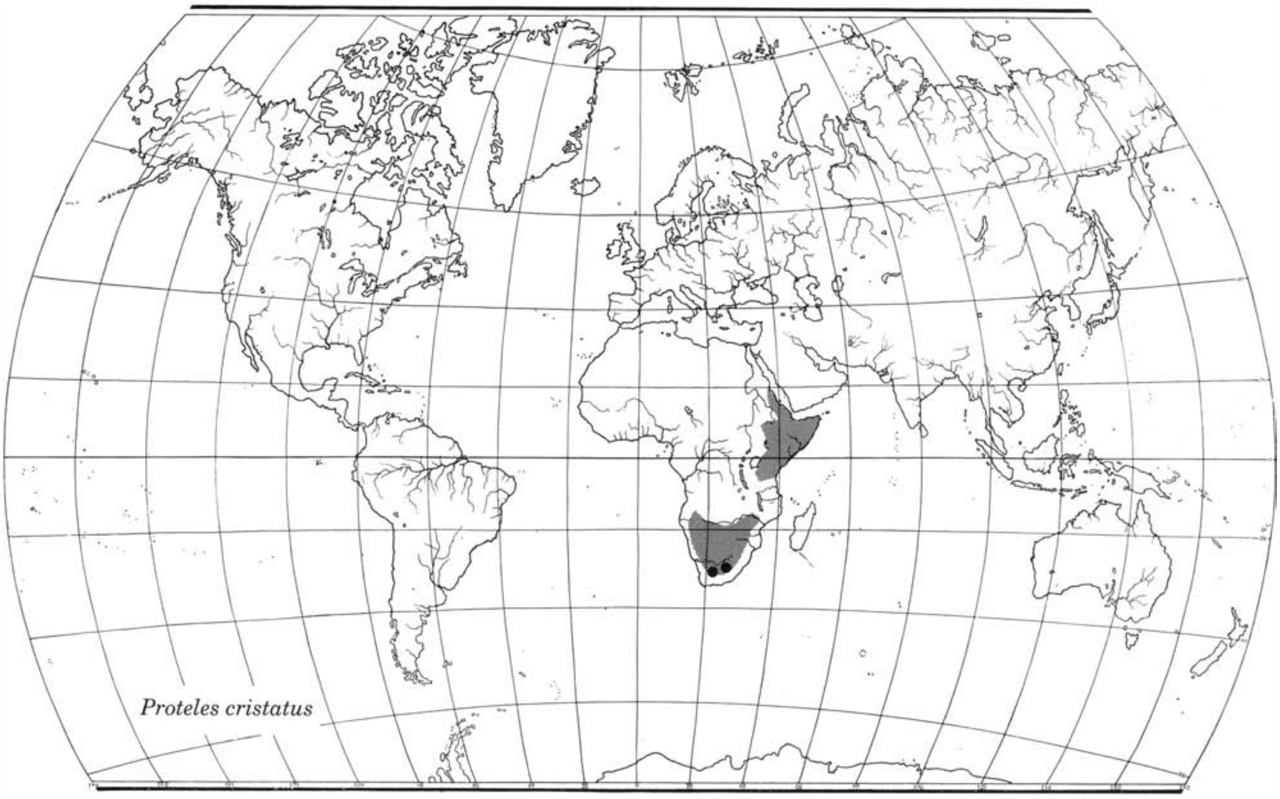


Fig. 9. Map showing (stippled) current range of *P. cristatus*. Dots represent fossil finds.

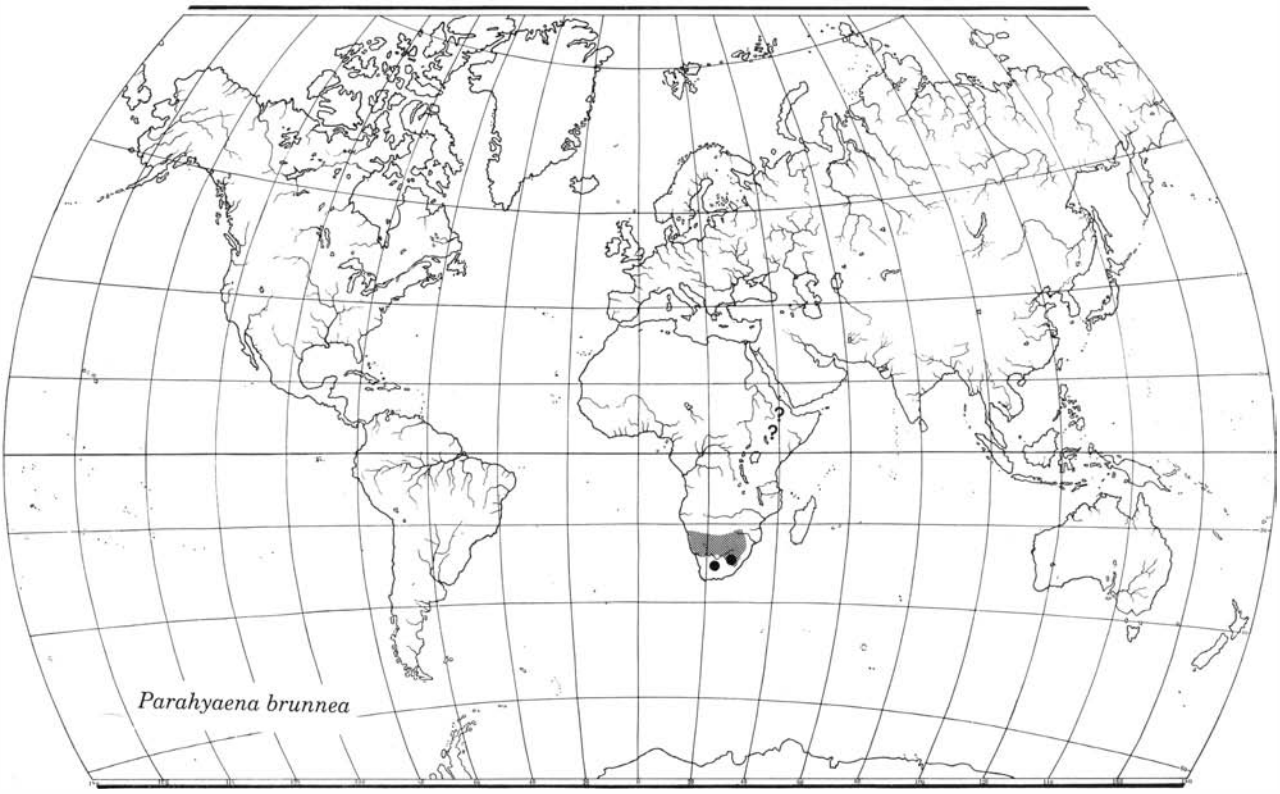


Fig. 10. Map showing (stippled) current range of *P. brunnea*. Dots represent fossil finds and question marks indicate doubtful fossil occurrences.

hyaenas as well (Kruuk 1976; Bouskila 1984; see that species). In view of the inferred dates for the cladogenetic events leading to these species (see below), these similarities, which must be interpreted as being inherited from a common ancestor in the middle Miocene at the latest, are remarkably ancient.

*_Pliocrocuta perrieri_ (Croizet & Jobert, 1828)

Synonymy. – □1828 *Hyaena perrieri* sp. nov. – Croizet & Jobert, p. 178, Pls. 1:5; 2:2, 3, 5; 4:3, 5, 6. □1828 *Hyaena arvernensis* sp. nov. – Croizet & Jobert, p. 180, Pls. 1:4; 2:1; 3:2; 4:1–3. □1828 *Hyaena monspessulana* sp. nov. – Christol & Bravard, p. 368 (*nomen nudum*). □1828 *Hyaena prisca* sp. nov. – Serres, Dubreuil & Jeanjean, p. 269. □1883 *Hyaena topariensis* sp. nov. – Forsyth Major, p. 2. □1889 *Hyaena topariensis* Major – Weithofer, p. 342, Pls. 1:1–4; 2:1–2; 3:3; 4:3–4. □1890 *Hyaena arvernensis* var. *pyrenaica* subsp. nov. – Depéret, p. 112, Pl. 10:3–4. □1910 *Hyaena striata* Zimmermann – Harlé, p. 41. □1938 *Hyaena (Pliohyaena) arvernensis* Croizet & Jobert – Kretzoi, p. 116. □1938 *Pliocrocuta perrieri* gen. nov. – Kretzoi, p. 118. □*pars* 1952 *Hyaena marini* sp. nov. – Villalta Comella, pp. 65–75, Pls. 9:1; 11:1. □1954 *Crocuta (Plesiocrocuta) perrieri* subgen. nov. – Viret, pp. 46–52, Pls. 5:1–2; 6:1–8; 7:1–5; 8:1–2. □1954 *Hyaena donnezani* sp. nov. – Viret, p. 52, Figs. 4–5. □1956 *Crocuta sivalensis* (Falconer & Cautley) – Yatsko, p. 335. □1956 *Hyaena hyaena monspessulana* Christol – Kurtén, p. 36. □1965 *Hyaena arambourgi* sp. nov. – Ozansoy, pp. 40–41, Pl. 4:2–3. □1970 *Pachycrocuta perrieri* Croizet & Jobert – Ficcarelli & Torre, p. 18. □1970 *Hyaena donnezani* Viret – Ficcarelli & Torre, p. 15. □1971 *Hyaena donnezani* Viret – Crusafont Pairó & Aguirre, p. 2476. □1971 *Hyaena prisca* Serres – Bonifay, pp. 155–178, Figs. 28–30, Pls. 9–13. □1974a *Hyaena (Parahyaena) perrieri* Croizet & Jobert – Hendey, p. 149. □1974 *Hyaena (Parahyaena) pyrenaica* Depéret – Hendey, p. 149. □1974 *Hyaena (Hyaena) prisca* Serres – Hendey, pp. 147–149. □1976 *Hyaena donnezani* Viret – Adrover, Morales & Soria, p. 190, Figs. 1–4, 5:6. □1980 *Pachycrocuta perrieri* (Croizet & Jobert) – Howell & Petter, pp. 598–602. □1980 *Pachycrocuta pyrenaica* (Depéret) – Howell & Petter pp. 591–598. □1980 *Hyaena prisca* Serres – Howell & Petter, pp. 612–613. □1987 *Pliohyaena pyrenaica* (Depéret) – Qiu, pp. 43–50, Figs. 8–10, Pls. 6:2; 7:1–2; 8:1–2; 9:1–3. □1987 *Pliohyaena perrieri* (Croizet & Jobert) – Qiu, pp. 50–52, Pls. 10:1–2; 11:1.

Localities. – Austria: Hollabrunn; China: Haiyan, Hsia Chwang, Hsingyangcun, Ichuangtsun, Malancun, Nihowan, Niu Wa Kou, Wangjianggou, Yinjiao, Zhangwagou (Chang Wa Kou); Czechoslovakia: Hajnačka; France: Ardé, Etouaires, Es-Taliens, L'Escale, Lunel-Viel, Montmaurin, Montsaunes, Senèze, Serrat d'En Vacquer, St-Vallier, Vallonet; Germany: Erpfinger Höhle, Greusnach, Gundersheim, Mauer, Mosbach; Great Britain: Red Crag; Greece: Petralona; Italy: Montipoli, Olivola, Tasso; Netherlands: Tegelen; Spain: La Calera II, La Puebla de Valverde, Layna, Villaroya; Tunisia: Aïn Brimba; Turkey: Gülyazi, Yassiören; USSR: Kuruksai, Navorukho, Odessa Catacombs.

Age. – Ruscinian–Post-Villafranchian (Cromerian).

Discussion. – It will be noted from the synonymy above that we are here considering *Pliocrocuta perrieri* and *Pliocrocuta pyrenaica* synonymous. Since this runs contrary to current opinion (Howell & Petter 1980; Qiu 1987), the case for synonymy will be argued in some detail. Howell & Petter (1980) mainly utilize metric data in their comparisons between various samples of *Pachycrocuta* and *Pliocrocuta*. In their analyses, they compare samples and individual specimens of *Pliocrocuta pyrenaica* with a combined Villafranchian sample of *Pliocrocuta perrieri* (Howell & Petter 1980, Figs. 4–5). This approach is altogether reasonable, but has had the unfortunate consequence that variation within *Pliocrocuta perrieri* has been ignored. Since the difference in metrics between the two taxa is slight in any case, this intra-specific variation becomes very important. We have here reanalyzed the data of Howell & Petter (1980, Tables 2–4). Instead of using *H. hyaena* as standard and combining all Villafranchian *P. perrieri* into one sample, we have used the sample of *P. perrieri* from Villaroya as a standard, comparing it with other samples of *P. perrieri* and with *P. pyrenaica*. In addition we have included a sample of *P. brevirostris* from Europe for comparative purposes. The results of this analysis are shown in Fig. 11. The numbered samples in the figure are samples of *P. perrieri* from Etouaires (type locality), Val d'Arno, St-Vallier, Senèze, and La Puebla de Valverde. It is especially important to note the considerable variation between these samples. Some, such as St-Vallier, are robust and have broad premolars, whereas others, such as La Puebla de Valverde, are small, with relatively slender premolars. As a matter of fact, there appears to be some indication of geographic variation between the samples, as the two Spanish samples (Villaroya and La Puebla de Valverde), are very similar to each other, and differ from the French samples (Etouaires, St-Vallier, Senèze), which in turn are quite similar to each other. In addition, all samples have metric characteristics that are unique to them, a pattern which is also seen in similar analyses of other hyaenid species (Werdelin 1988b). The type specimen of *Pliocrocuta pyrenaica* is the one from Serrat d'En Vacquer (*A* in Fig. 11). Howell & Petter (1980, p. 594) state that in comparison with *P. perrieri* this specimen has narrower $P^2/_2$ and $P^3/_3$, and that P^4 and the trigonid of M_1 are relatively short. Inspection of Fig. 11 herein shows that this is only partly correct. P_2 and P^3 are, indeed, narrow relative to all samples of *P. perrieri*, but P_3 and P^2 are of quite normal width for *P. perrieri*, and are, in fact, wider than the same teeth in the Villaroya sample. The trigonid of M_1 of the Serrat d'En Vacquer specimen is relatively shorter than in all samples of *P. perrieri*, whereas the shortness of P^4 is seemingly spurious, this tooth having the same length/width proportions as the Val d'Arno sample of *P. perrieri*. With this noted, it should also be remembered that these comparisons have been between a single specimen on the one hand, and samples of specimens on the other. There is nothing to say that individual specimens from Villaroya may not have had the same proportions as the specimen from Serrat d'En Vacquer. Thus, taken on its own merits, the Serrat d'En Vacquer specimen may or may not belong to a species distinct from *P. perrieri*. With this single specimen as the sole basis of comparison, Depéret (1890) was

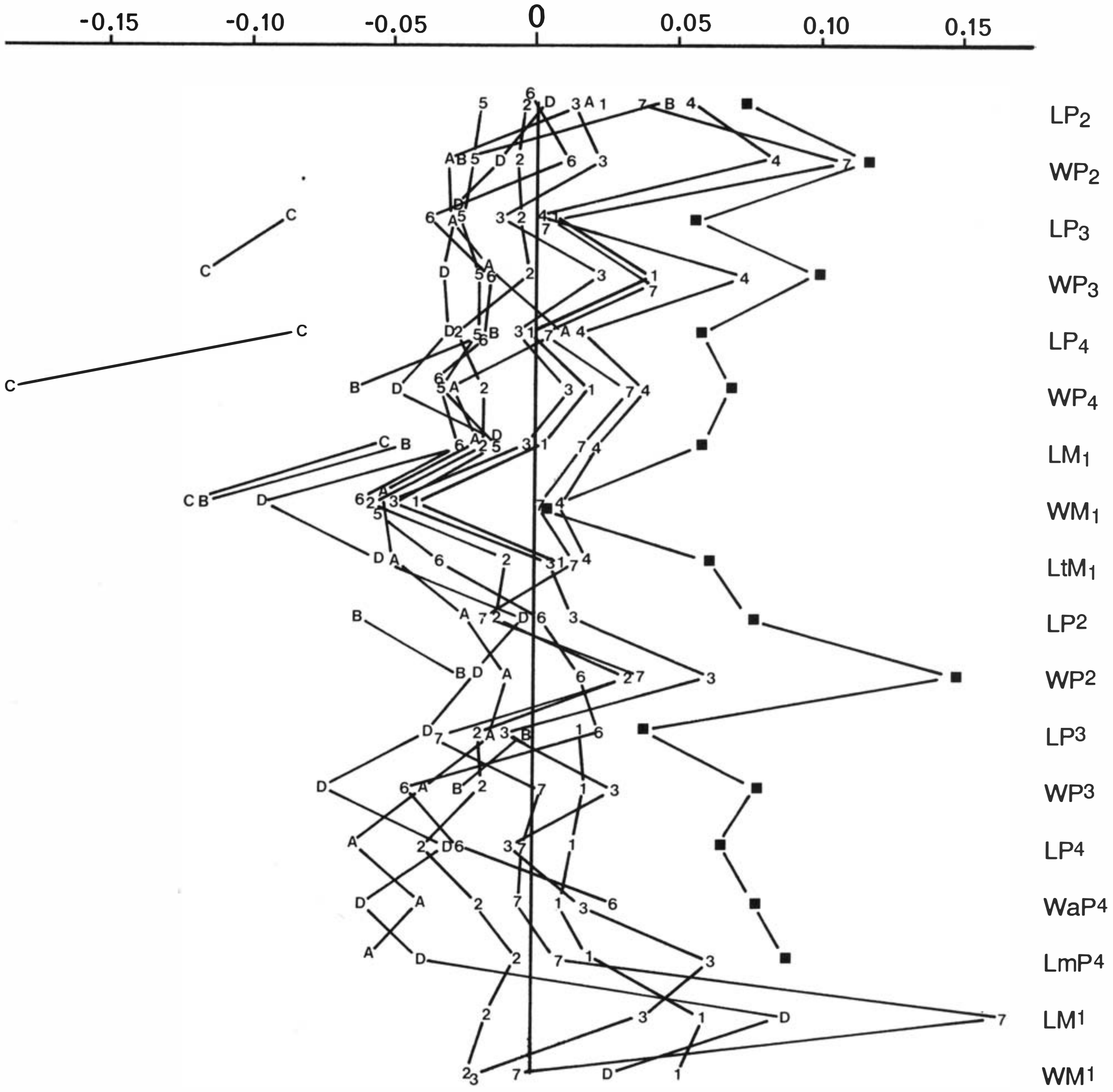


Fig. 11. Ratio diagram of various samples of hyaenids referred to *P. pyrenaica* and *P. perrieri.* Standard = Villaroya sample. A = Serrat d'en Vacquer specimen; B = La Calera specimens; C = Layna specimens (see also Fig. 19); D = Odessa sample; 1 = Etouaires sample; 2 = Val d'Arno sample; 3 = St. Vallier sample; 4 = Senèze sample; La Puebla de Valverde sample; 6 = Chang Wa Kou sample; 7 = Hsia Chwang sample; ■ = *P. brevirostris*, European sample. All data are taken from Howell & Petter (1980).

undoubtedly correct in not making this specific distinction, and Viret (1954) and others were wrong to make it. It thus becomes necessary to examine other material attributed to *P. pyrenaica* in order to resolve this issue.

The first specimens to be considered are the ones from La Calera, attributed to *H. donnezani* (=*P. pyrenaica*) by Adrover *et al.* (1976) and further discussed by Howell & Petter (1980) (*B* in Fig. 11). The P_2 of this sample shows the same relative width as the specimen from Serrat d'En Vacquer, as does the P_4. However, the M_1 is exceptional for its narrowness, a characteristic that is not present in *P. pyrenaica* from Serrat d'En Vacquer. Of the upper teeth, P^2 is relatively wider than in most *P. perrieri*, while the proportions of P^3 approach those of the Serrat d'En Vacquer specimen. Thus, these specimens have features in which they resemble the Serrat d'En Vacquer specimen and one feature (P^2 width) in which they more resemble *P. perrieri.* However, the most notable feature of the La Calera hyaenid is the narrow M_1, which is not a feature of the Serrat d'En Vacquer specimen at all. It may be, however, that the M_1 from La Calera does not belong with the other specimens, as we shall see.

The specimens from Layna are considered next (*C* in Fig. 11). These were attributed to *Hyaena donnezani* (=*P. pyrenaica*) by Crusafont Pairó & Aguirre (1971), and further discussed by Howell & Petter (1980). As is evident from Fig. 11, the metric features of these specimens renders attribution of them to either *P. pyrenaica* or *P. perrieri* out of the question. It should be noted, however, that the proportions of M_1 from Layna are the same as those of the M_1 from La Calera, suggesting that these teeth may belong to the same taxon, a taxon distinct from the other La Calera teeth.

The largest sample attributed by Howell & Petter (1980) to *P. pyrenaica* is that from the Odessa Catacombs, originally referred to *Crocuta sivalensis* by Yatsko (1956) (*D* in Fig. 11). In this sample, P_2 is only slightly narrower than in *P. perrieri* from Villaroya. The same is true of P_4. M_1 in the Odessa Catacombs sample has the same narrow shape as those from La Calera and Layna, but is larger. P^3 in the Odessa sample is narrow, as is P^4. The former characteristic is also seen in the Serrat d'En Vacquer specimen, the latter is not. Finally, M^1 in the Odessa sample is relatively long and narrow compared with most samples of *P. perrieri*.

To sum up the data on these samples, there are differences between them and 'typical' *P. perrieri*. However, except for the relative widths of P_2, P_4, and P^3, these differences are not consistent between samples. Indeed, some of the most outstanding features of certain samples are not seen in other samples at all. That there should be some differences between these samples and *P. perrieri* from Villafranchian deposits is not unexpected in view of their greater age. Together, the variation in these samples of *Pliocrocuta* is only slightly greater than in samples of single species of *'Thalassictis'* and *Palinhyaena* from China, and considerably less than between species of *'Thalassictis'* (Werdelin 1988b).

This discussion must, however, also take into account specimens of *Pliocrocuta* from China. There are two sets of such specimens: a collection in the American Museum of Natural History, attributed by Howell & Petter (1980) to *P. perrieri* and by Qiu (1987) to *P. pyrenaica*, and specimens described by Qiu (1987) as *P. pyrenaica* and *P. perrieri*. The former sample is included in Fig. 11. It can be readily seen from the figure that the attribution by Howell & Petter (1980) is fully justified, and that of Qiu (1987) wholly untenable. These specimens cannot be distinguished from *P. perrieri* either in metrics (Fig. 11) or, as our personal observations have shown, in morphological features.

Besides these metric characteristics, Qiu (1987) discusses only a few features in his referral of the majority of his specimens to *P. pyrenaica*. Most of these are characters that are primitive within the group comprised of the Recent hyaenas, *Adcrocuta*, *Pliocrocuta*, and *Pachycrocuta* (see below, and also Werdelin & Solounias 1990), characters such as the relative enlargment of I^3 and the loss of $M\frac{2}{2}$. However, he does point to some interesting characters of the deciduous dentition, e.g., their relatively great width, and, in comparison with a specimen of *P. perrieri* from Villaroya (Qiu 1987, Fig. 9), the larger lingual cusp and more closely appressed anterior cusps of a Chinese specimen of dP^3. These comparisons are based on very small samples, however, and the true variability in these characters is not known. This means that the widths of the deciduous teeth, which are only just outside the range of *P. perrieri* from Europe anyway, are of little value in this connection. The condition of dP^3 is also variable – a specimen figured by Viret (1954, Pl. 7:7) appears to show the anterior cusps more appressed and less in line than the Villaroya specimen, which are characters more like those of Qiu's specimen of *P. pyrenaica* than of his *P. perrieri*. There thus remains the larger lingual cusp of the Chinese specimen. We have no doubt that this character is real and that this represents a more primitive condition than in *P. perrieri* from Europe. However, it is merely one character in one specimen, and as such can hardly form the basis for specific distinction.

In summary, we conclude that, while Ruscinian specimens of *Pliocrocuta* on the whole tend to show slightly more primitive features than Villafranchian ones, the differences found are small – less than between species of *'Thalassictis'* from China (Werdelin 1988b) – and it seems to us reasonable to include them all within a single species; a species that changed slightly during its evolution, to be sure, becoming larger and more robust: trending, in fact, towards the condition seen in *Pachycrocuta brevirostris*.

The synonymy between *P. perrieri* and *H. prisca* proposed here is briefly discussed under the latter species. Another synonymy, between *P. perrieri* and *P. brunnea* was recently proposed by Turner (1990). His points regarding the distinguishing features of the dentitions of these two forms being of doubtful taxonomic significance are well taken. If the dentition were the only feature available, his proposed synonymy would be quite accurate, as would his comment that if specimens of *P. perrieri* had been found in Africa they would likely have been referred to *P. brunnea*. However, there are features, especially the shape of the basioccipital, that distinguish these taxa to the degree that synonymy is highly unlikely. The features uniting them are primitive retentions.

Hyaena prisca Serres, Dubreuil & Jeanjean, 1828

Discussion. – This form was considered a separate species by Bonifay (1971), and (with reservations) by Howell & Petter (1980). Other authors, e.g. Kurtén (1956), have considered it conspecific with the extant *H. hyaena*. Metrically, it is very similar to this species, the main difference being its larger size (Kurtén 1956; Howell & Petter 1980). However, *H. prisca* also shows similarities in metric characters with *P. perrieri* (Howell & Petter 1980), and Turner (1990) has suggested synonymy between these two species. This suggestion is further corroborated by the presence in *H. prisca* from Lunel-Viel (Bonifay 1971) of characters of *P. perrieri*, such as the posteriorly located premaxillary–maxillary contact on the palate, and the shape of the basioccipitals (see below). We conclude that *H. prisca* is a synonym of *P. perrieri*. We have included this separate section on *H. prisca* for ease of reference.

Palhyaena hipparionum (Gervais, 1846)

Synonymy. – □1846 *Hyaena hipparionum* sp. nov. – Gervais, p. 261. □1850 *Hyaena hipparionum* Gervais – Gervais, p. 121, Pl. 12:1. □1859 *Hyaena (Palhyaena) hipparionum* Gervais –

Gervais, p. 242, Pl. 12:1. □1873 *Ictitherium hipparionum* (Gervais) – Gaudry, pp. 18–21, Pl. 2:8–9.

Localities. – France: Mt Leberon.

Age. – Turolian (MN Zone 12).

Discussion. – Reasons why this form is at present indeterminate are given elsewhere (Solounias 1981; Werdelin 1988b). Until the type specimen has been found and restudied, we consider this name a *nomen dubium* (for a useful discussion of this term, we refer to Mones 1989).

**Pachycrocuta brevirostris* (Aymard, 1846)

Synonymy. – □1846 *Hyaena brevirostris,* sp. nov. – Aymard, p. 153. □1870 *Hyaena sinensis* sp. nov. – Owen, pp. 422–424, Pl. 28:5–7. □1884 *Hyaena felina* Bose – Lydekker, p. 285, Pls. 38:1; 39:1. □1889 *Hyaena robusta* sp. nov. – Weithofer, p. 46, Pls. 2:3–5; 3:1–2; 4:1–2. □1893 *Hyaena brevirostris* Aymard – Boule, pp. 85–97, Pl.1:1–3. □1908 *Hyaena bathygnatha* sp. nov. – Dubois, p. 1265. □1925 *Hyaena sinensis* Owen – Zdansky, pp. 22–23, Pls. 3:3–3; 4:1–2. □1928 *Hyaena sinensis* Owen – Zdansky, pp. 42–47, Fig. 3, Pl. 3:10–21. □1930 *Hyaena sinensis* Owen – Teilhard de Chardin & Piveteau, pp. 101–104, Pl. 20:1–2. □*pars* 1932 *Crocuta sivalensis* Falconer & Cautley – Pilgrim, pp. 134–137. □1934 *Hyaena sinensis* Owen – Pei, pp. 91–110, Figs. 25–32, Pls. 14:1; 15:3–5; 16:2–4; 17:1; 18:1; 19:1.3, 20:1–6, 21:1–8. □1934 *Hyaena zdanskyi* sp. nov. – Pei, pp. 110–116, Figs. 33–34, Pls. 13:1; 15:1; 16:1; 18:2–3; 20:7. □1934 *Hyaena licenti* sp. nov. – Pei, pp. 120–121. □1938 *Pachycrocuta brevirostris* gen. nov. – Kretzoi, p. 118. □1956 *Hyaena brevirostris* Aymard – Kurtén, pp. 38–39, Fig. 11A–B. □1970 *Pachycrocuta brevirostris* (Aymard) – Ficcarelli & Torre, p. 18. □1970 *Pachycrocuta felina* (Bose) – Ficcarelli & Torre, p. 18. □1974a *Hyaena (Parahyaena) brevirostris* Aymard – Hendey, p. 149. □1980 *Pachycrocuta brevirostris* (Aymard) – Howell & Petter, pp. 605–607. □1989 *Pachycrocuta licenti* (Pei) – Huang, pp. 197–204. □1989 *Pachycrocuta sinensis* (Owen) – Huang, pp. 197–204.

Localities. – China: Chang Chih Hsien, Choukoutien Loc. 1, Fu Min Hsien, Haiyan, Nihowan. Czechoslovakia: Stránska Skála; GDR: Meiningen; France: Sainzelles; Germany: Süssenborn, Würzburg–Schalksberg; Great Britain: Cromer Forest Bed; Greece: Petralona; Hungary: Gombaszög; India: ?Haro River; Indonesia: Sangiran; Italy: Foggia, Olivola, Tasso; Pakistan: Jamu District, Sivaliks; Yugoslavia: Manastirec.

Age. – Villafranchian–Post-Villafranchian (Cromerian).

Discussion. – This widespread and distinctive species is not as well known as one would expect. However, due to its extreme features, it is easy to distinguish from other hyaenids (Howell & Petter 1980; Kurtén 1956). It is the largest known hyaena, with a skull size approximately that of a lion.

Thalassictis robusta Gervais, 1850, *ex* Von Nordmann, MS

Synonymy. – □1850 *Thalassictis robusta* Nordmann – Gervais, p. 120. □1858 *Thalassictis robusta* Nordmann – Von Nordmann, pp. 150–156, Pl. 5:1–8, 10. □1859 *Thalassictis robusta* Nordmann – Gervais, p. 222. □1938 *Ictitherium robustum* (Nordmann) – Kretzoi, p. 113. □1954 *Ictitherium robustum* (Nordmann) – Kurtén, pp. 4–13, Figs. 1–5. □1981 *Thalassictis robusta* Nordmann – Solounias, pp. 67–68. □1982 *Thalassictis robusta* Gervais ex Nordmann – Kurtén, pp. 1009–1018, Fig. 1 (upper), 2 (upper). □?1986 *Thalassictis robusta* Nordmann – De Beaumont, pp. 36–37, Figs. 4–5. □1988b *Thalassictis robusta* Gervais ex Nordmann – Werdelin, p. 251.

Localities. – Germany: ?Höwenegg; USSR: Kishinev, Moldavian SSR.

Age. – ?Vallesian (MN Zone ?9).

Discussion. – Most of the taxonomic story of this species will be described under *Ictitherium viverrinum* below. Most references to *'I. robustum'* in the literature are to *I. viverrinum*, the true *T. robusta* only being discussed by a very few authors (Kurtén 1954, 1957b, 1982; De Beaumont 1986). Part of the problem was the designation by Pilgrim (1931) of *T. incerta* as type species of *Thalassictis,* thereby invalidating the use of the name for hyaenids, as *T. incerta* is a synonym of *Amphicyon major* (Kurtén 1982). However, Pilgrim was not aware that Palmer (1904) had already made *T. robusta* the type species of the genus. Thus, both *Thalassictis* and *T. robusta* are valid hyaenid taxa.

The identification of *T. robusta* at Höwenegg by De Beaumont (1986) is highly doubtful. It is based chiefly on M_1 of the Höwenegg specimen being smaller than that of *H. wongii* from China and Europe. However, these populations are separated temporally from the Höwenegg one, and this may have influenced the results. The Höwenegg *T. robusta* lacks the characteristic broad premolars of *T. robusta* from Kishinev (see Werdelin 1988b), which weakens the case for the referral of these specimens to that species. However, the question is difficult to resolve on the basis of the available data, and we leave the Höwenegg specimen as a doubtful occurrence of *T. robusta.*

Kurtén (1982) suggested a synonymy between *Thalassictis* and Kretzoi's (1938) genus *Miohyaena.* This seems to be a valid suggestion, as the type species of these genera share the same derived features of the upper and lower molars, but are more primitive than, e.g., *Hyaenotherium* (see below) in the structure of the lower carnassial, with its short and low paraconid and high protoconid (cf. Von Nordmann 1850: Pl. 5:7; Depéret 1892: Pl. 1:19).

Approximate phylogenetic position. – More derived than *Ictitherium* in the reduction of the posterior molars, less derived than *Hyaenotherium* in the morphology of M_1. A position between nodes 2 and 3 on the core cladogram is indicated.

**Ictitherium viverrinum* Roth & Wagner, 1854

Synonymy. – □1840 *Galeotherium* gen. nov. – Wagner, p. 165, Pl. 1:4–6 (*genus caelebs*). □1848 *Ictitherium* gen. nov. – Wagner, p. 375 (*nomen nudum*). □1854 *Ictitherium viverrinum* sp. nov. – Roth & Wagner, pp. 392–396, Pl. 2:3–5. □1862–1867 *Ictitherium robustum* (Nadmann) – Gaudry, p. 52, Pls. 7–10. □1862 *Thalassictis gracilis* sp. nov. – Hensel, pp. 566–567, Fig. 5. □1862 *Thalassictis viverrina* (Roth & Wagner) – Hensel, p. 566, Fig. 4. □1924 *Ictitherium gaudryi* sp. nov. – Zdansky, pp. 67–72, Fig. 3, Pls. 12:5–6; 13:1–6. □1924 *Ictitherium sinense* sp. nov. – Zdansky, pp. 72–73, Pl. 14:1–2. □1929 *Ictitherium robustum* Gaudry – Arambourg & Piveteau, pp. 65–66, Pl. 10:1. □1938 *Ictitherium viverrinum* Roth & Wagner – Kretzoi, p. 113. □1938 *Palhyaena ?gaudryi* Zdansky – Kretzoi, p. 113. □1938 *Sinictitherium sinense* gen. nov. – Kretzoi, p. 114. □1981 *Ictitherium viverrinum* Roth & Wagner – Solounias, pp. 61–66, Fig. 15. □1982 *Ictitherium viverrinum* Roth & Wagner – Kurtén, pp. 1009–1016, Figs. 1 (lower), 2 (lower). □1988a *Ictitherium viverrinum* Roth & Wagner – Werdelin, p. 101, Fig. 7. □1988 *Ictitherium viverrinum* Roth & Wagner – De Beaumont, pp. 28–29, Pl. 2:7.

Localities. – China: Loc. 12, Loc. 31, Chen Chia Mao Kou (Zdansky's Loc. 108), Chen Kou, Chin Kou, Chou Chia Kou, Huan Lou Kou (Zdansky's Loc. 109), Liao Wan Kou, Nan Ho, Ta Tung Kou, Yan Mu Kou (Zdansky's Loc. 49); France: Montredon; Germany: Vösendorf; Greece: Pikermi, Ravin des Zouaves 5, Samos, Vathylakkos 2 and 3; USSR: Belka, Chobruchi, Grebeniki, Novoelisavetovka. Yugoslavia: Titov Veles.

Age. – Turolian (MN Zone 11–12).

Discussion. – The complex taxonomic history of this species has been discussed extensively elsewhere (Kurtén 1982; Solounias 1981; Werdelin 1988a), but is worth repeating. The species *I. viverrinum*, which is the type species of *Ictitherium*, was erected by Roth & Wagner (1854) on the basis of material from Pikermi, Greece. Some years later, Gaudry (1862–1867) synonymizes the Pikermi material with *Thalassictis robusta*, a species described by Von Nordmann (1858), but originally published by Gervais (1850) on the basis of casts and Von Nordmann's manuscript. *Thalassictis robusta* is the type species of *Thalassictis*, as designated by Palmer (1904) (see above).

Over the years, most authors have unquestioningly accepted Gaudry's opinion and synonymized these species, wherefore '*Ictitherium robustum*' has been in general use, and most references to *I. viverrinum* bear that name. Recent work by Solounias (1981) and Kurtén (1982) has shown that Gaudry was incorrect, and that *I. viverrinum* and *T. robusta* are quite distinct, both morphologically and phylogenetically. This work has been augmented by Werdelin (1988a, 1988b) on the basis of large data samples from China. These studies have shown that most of the references to '*I. robustum*' are actually specimens of *Hyaenotherium wongii*, and that *I. viverrinum* proper is a much rarer member of Eurasian Turolian faunas.

Several authors (e.g., Kretzoi 1938; Solounias 1981; and Semenov 1989) have suggested that *Ictitherium sinense* Zdansky should be maintained as a distinct species. However, Abu Bakr (1959) and Werdelin (1988a) proposed, on the basis of metric data, that *I. sinense* was an aberrant specimen of *I. gaudryi* (=*I. viverrinum*). In the absence of further data, we maintain that viewpoint here, whilst realizing that the matter may still be reopened if new material is found that resembles the type specimen of this species.

Specimens referred by Qi (1989) to this taxon can be referred (with some doubt) to *Ictitherium* sp. nov. (Qi, Fig. 2:1) and '*Thalassictis*' sp. (Fig. 2:2–3), and an extension of the temporal range is not necessary on these grounds (see also below for a discussion of these specimens).

**Adcrocuta eximia* (Roth & Wagner, 1854)

Synonymy. – □1854 *Hyaena eximia* sp. nov. – Roth & Wagner, pp. 396–398, Pl. 2:6. □1857 *Hyaena eximia* Roth & Wagner – Wagner, p. 120, Pl. 5:9–10. □*pars* 1859 *Hyaena hipparionum* Gervais – Gervais, p. 242, Pl. 24:2–3. □1887 *Hyaena eximia* Roth & Wagner – Kittl, p. 332, Pl. 17:1–2, 18:1. □1903 *Hyaena* sp. – Schlosser, p. 33, Pls. 2:4, 5, 13; 3:1–5. □1924 *Hyaena variabilis* sp. nov. – Zdansky, pp. 93–103, Figs. 11–13, Pls. 18:3–4; 19:3–4; 20:1–4; 21:1–4; 22:1–4. □*pars* 1924 *Hyaena honanensis* sp. nov. – Zdansky, pp. 103–107, Pls. 23:1–4; 24:1–3. □1931 *Crocuta eximia* (Roth & Wagner) – Pilgrim, pp. 116–124, Pls. 1:1–3; 2:1. □*pars* 1932 *Crocuta gigantea latro* ssp. nov. – Pilgrim, pp. 146–149. □1932 *Crocuta mordax* sp. nov. – Pilgrim, pp. 150–153, Pls. 6:1, 3, 4; 7:10. □1938 *Adcrocuta eximia* gen. nov. – Kretzoi, p. 118. □1938 *Adcrocuta praecursor* sp. nov. – Kretzoi, p. 118. □1938 *Adcrocuta variabilis* (Zdansky) – Kretzoi, p. 118. □1957a *Crocuta (Percrocuta) eximia* (Roth & Wagner) – Kurtén, pp. 397–400. □1967 *Crocuta miriani* sp. nov. – Meladze, pp. 31–34, Pls. 3:1–2; 4:1–3. □1970 *Adcrocuta eximia* (Roth & Wagner) – Ficcarelli & Torre, p. 25. □1976 *Adcrocuta eximia* (Roth & Wagner) – Schmidt-Kittler, pp. 59–63, Figs. 54–55, Pl. 3:4–6. □1980 *Adcrocuta eximia* (Roth & Wagner) – Koufos, pp. 83–92, Figs. 29–30, Pl. 9:7, 10:1. □1981 *Adcrocuta eximia* Roth & Wagner – De Bonis & Koufos, pp. 79–86, Fig. 1, Pl. 1–4. □1985 *Adcrocuta eximia* Roth & Wagner – Howell & Petter, pp. 460–472. □1987 *Chasmaporthetes bonisi* sp. nov. – Koufos, pp. 913–920, Pl. 1:1–2, 3C.

Localities. – Bulgaria: Kalimantsi; China: Loc. 12, Tie Chia Kou (Zdansky's Loc. 30), Loc. 31, San Chia Liang Kou (Zdansky's Loc. 43[1]), Loc. 44, Yan Mu Kou (Zdansky's Loc. 49), Chen Chia Mao Kou (Zdansky's Loc. 108), Huan Lou Kou (Zdansky's Loc. 109), Loc. 110, Loc. 114n, Ma Hua Tan (Zdansky's Loc. 114s), Loc. 115, Chao Tsu Kou (Zdansky's Loc. 116v), Chang Chia Chuang, Chin Kou, Chou Chia Kou, Chou Fen Ta, Hsiao Kou Shan, Hsin Yao, Kou Chia Ta, Liao Wan Kou, Ma Chi Liang Kou, Nan Hao Hsia, Nan Ho, Pai Tao Tsun, Ta Tung Kou, Tung Ta Ling, Ta Tsun, Wang Lou Kou; France: Mt Leberon; Greece: Dytiko, Halmyropotamos, Pikermi, Prokoma, Ravin de la Pluie, Ravin des Zouaves 1 and 5, Samos; Hungary: Baltavar, Polgárdi; Iran: Maragheh; Libya: Sahabi; Pakistan: Hasnot; Rumania: Çimislia; Spain: Arquillo de la Fontana,

?Concud, Los Aljezares, Los Mansuetos, Masia del Barbo, Pena del Macho, Piera; Turkey: ?Amasya, Çoban Pinar, Karain, Kavak Dere, Kinik, ?Kuyutarla, Mahmutgazi, ?Mugla; USSR: Bazalethi, Belka, Cherevichnoe, Grebeniki, Novaja Emetovka, Novoelisavetovka, Novoukrainka, Pavlodar, Starokondakovo, Chobruchi, Taraklia; Yugoslavia: Titov Veles.

Age. – Vallesian–Turolian (MN Zones 10–13).

Discussion. – The specific identity of this form has been clear to nearly all writers since it was first described by Roth & Wagner (1854). With its large size, powerful premolars, reduced P^4 protocone, and short, broad skull it is readily separated from other hyaenids in Turolian deposits. Thus, it can be easily identified on the basis of quite fragmentary remains, which forms part of the reason why it is known from so many countries and localities.

On the other hand, the systematic position of this species has been a much more complex topic. The early writers all referred the form to the genus *Hyaena*, chiefly because all large hyaenas, including the spotted hyaena, *C. crocuta*, were then referred to this genus. The first to remove the species from *Hyaena* was Pilgrim (1931, 1932), who placed it in *Crocuta*, a genus that he expanded greatly to encompass the early 'percrocutoid' hyaenas (see above). In 1938, Kretzoi radically rearranged hyaenid taxonomy, creating many new genera, among which were *Percrocuta* for some 'percrocutoids' and *Adcrocuta* for others, including (as genotype) *A. eximia*. Kretzoi's work was generally ignored until Kurtén (1957a) resurrected *Percrocuta* (including *Adcrocuta*) as a subgenus of *Crocuta*. Some years later, Ficcarelli & Torre (1970) revived the use of both these generic names.

A turning point in the study of *A. eximia* came with the work of Schmidt-Kittler (1976). In this paper, and in a subsequent work (Chen & Schmidt-Kittler 1983), the deciduous dentition of percrocutoids is discussed, with the result that *A. eximia* is made the sole representative of the genus *Adcrocuta*. These arguments have been followed by most subsequent authors (Howell & Petter 1985; Qiu 1987; Werdelin & Solounias 1990).

At the same time as the generic allocation of *A. eximia* has been stabilized, its phylogenetic position has remained in limbo. Most authors, following Schmidt-Kittler (1976), have considered this genus a precociously advanced Miocene sideline in hyaenid evolution (Galiano & Frailey 1977; Howell & Petter 1985; Qiu 1987), and no serious attempts have been made to address the question of its relationships. Recently, however, Werdelin & Solounias (1990) have studied this question in a cladistic analysis. Their analysis shows clearly that *A. eximia* is the sister-taxon of *Crocuta*, thus essentially confirming the views of, i.a. Kurtén (1957), Pilgrim (1931), and Şenyürek (1958). This result will be further expanded on below. It should be noted, however, that since *A. eximia* has at least one autapomorphy not seen in *Crocuta* (reduced P^4 protocone), it is probably not directly ancestral to that genus.

As has been argued by previous authors (Howell & Petter 1985), there is no evidence for more than one species in *Adcrocuta*. The species *Adcrocuta australis* from Langebaanweg, South Africa (Hendey 1974a, 1978) has been shown by Qiu (1987) and Werdelin & Solounias (1990) to belong to the genus *Chasmaporthetes* (see below).

A detailed justification for synonymizing *C. bonisi* (see synonymy above) with *A. eximia* is given below, under the heading of the former taxon.

**Plioviverrops orbignyi* (Gaudry & Lartet, 1856)

Synonymy. – ☐1856 *Viverra orbignyi* – Gaudry & Lartet, p. 273. ☐1861 *Thalassictis orbignyi* (Gaudry & Lartet) – Gaudry, p. 533, Pl. 10:3. ☐1862–1867 *Ictitherium orbignyi* (Gaudry & Lartet) – Gaudry, p. 74, Pl. 11. ☐1938 *Plioviverrops orbignyi* (Gaudry) – Kretzoi, p. 114. ☐1969b *Plioviverrops orbignyi* (Gaudry & Lartet) – De Beaumont, pp. 1–6, Fig. 1, Pl. 1:1–3. ☐1969 *Plioviverrops orbignyi* (Gaudry) – Crusafont Pairó & Petter, p. 23, Pl. 4:3–4. ☐1972 *Plioviverrops orbignyi* (Gaudry) – De Beaumont & Mein, pp. 383–393, Figs. 2–4, Pl. 1:1. ☐1980 *Plioviverrops orbignyi* (Gaudry & Lartet) – Koufos, pp. 67–76, Figs. 20–21, Pl. 9:1–2. ☐1981 *Plioviverrops orbignyi* (Gaudry & Lartet) – Solounias, pp. 58–61, Fig. 14.

Localities. – Greece: Pikermi, Ravin de Pluie, Samos, Vathylakkos 2.

Age. – Vallesian–Turolian (MN Zone 10–12).

Discussion. – The morphology and evolution of this genus and species has been extensively discussed by others (De Beaumont 1969b; De Beaumont & Mein 1972). These authors comment on the primitiveness of *Plioviverrops*, particularly as regards the auditory bulla, which is comparable to that of *Proteles*, and represents stage 4 of Hunt (1987). However, unlike in *Proteles*, the alisphenoid canal is present (De Beaumont 1969b, Pl. 1:1C), a primitive character state (Wozencraft 1989). Within the genus *Plioviverrops*, *P. orbignyi* is the most derived in its dental characters, having gone far in its development towards a hypocarnivorous morphology (Crusafont Pairó & Truyols Santonja 1956, 1957). Thenius (1966) has suggested that *Proteles cristatus* may be derived from *P. orbignyi*. As we comment below, this is the most plausible suggestion regarding the ancestry of the aardwolf, albeit still a highly speculative one.

Lycyaena chaeretis (Gaudry, 1861)

Synonymy. – ☐1861 *Hyaena chaeretis* sp. nov. – Gaudry, p. 534, Pl. 9:3–6. ☐1862 *Lycyaena chaeretis* gen. nov. – Hensel, p. 567. ☐1931 *Lycyaena chaeretis* (Gaudry) – Pilgrim, pp. 104–113, Figs. 28–29. ☐1938 *Lycyaena chaeretis* (Gaudry & Lartet) – Kretzoi, p. 115. ☐1981 *Thalassictis chaeretis* (Gaudry) – Solounias, pp. 74–75, Fig. 18D–F. ☐1981 *Thalassictis* sp. nov. – Solounias, pp. 76–78, Fig. 19. ☐1981 *Thalassictis (Lycyaena) chaeretis* (Gaudry) – Solounias & De Beaumont, p. 299. ☐1981 *Thalassictis (Lycyaena)* sp. nov. – Solounias & De Beaumont, p. 299. ☐1988b *Thalassictis (Lycyaena) chaeretis* (Gaudry) – Werdelin, pp. 246–251.

Localities. – Greece: Pikermi, Samos.

Age. – Turolian (MN Zone 12).

Discussion. – The conception of *L. chaeretis* has varied somewhat between different authors. In particular, Solounias (1981; Solounias & De Beaumont 1981), has wished to subdivide the specimens from Samos into two species of *Thalassictis.* This was based on the idea that the specimens here referred to *Belbus beaumonti* are similar in nature to the type specimen of *T. chaeretis* from Pikermi. However, comparison of Pl. 11:3–4 of Gaudry (1861) with Fig. 19E of Solounias (1981) makes it quite clear that these are the same taxon and that therefore *Thalassictis* sp. nov. of Solounias (1981) is actually *T. chaeretis,* whereas the skull in Fig. 18A–C of Solounias (1981) is *B. beaumonti.* It should be noted that the partial mandible in Fig. 18D–F of Solounias (1981) is another specimen of *T. chaeretis.*

The hyaenid faunas of Pikermi and Samos on the one hand, and Baode (Pao Te), China, on the other, are in general quite similar, with several species previously thought distinct having lately been shown to be conspecific (Werdelin 1988a, 1988b). *L. chaeretis* from Pikermi and Samos is very similar to the Chinese *L. dubia* (see below), and it is highly likely that these forms are also conspecific. The available material from Greece is too small to establish conspecificity in the way that was done for *H. wongii, I. viverrinum* and *A. eximia* in the same faunas. Nevertheless, this is probably the case, although *L. dubia* appears slightly more progressive, in that M^1 is somewhat more reduced in this form.

Solounias (1981) synonymizes *L. chaeretis* with *L. crusafonti* from Tunisia (Kurtén 1976). However, this does not seem to be correct. Data published by Werdelin (1988b) show that the proportions of M_1 are quite different in the two taxa. Relative to *L. chaeretis,* the Tunisian form has a broader carnassial with a longer talonid. Both of these traits are primitive and neither supports synonymy.

The specimens ascribed to *L.* aff. *chaeretis* by Ginsburg *et al.* (1981) do not display the characters of this genus (such as the loss of M_2). Morphologically and metrically they are similar to *H. namaquensis,* but the material available is not sufficient to firmly ascribe them to that taxon in view of the temporal and geographic separation.

In view of the probable synonymy between *L. chaeretis* and *L. dubia,* only the better known of the two (*L. dubia*) has been used in the core data for phylogenetic analysis.

Approximate phylogenetic position. – As noted, this form is very close to *L. dubia,* and whether conspecific with the Chinese form or not, must be placed very near it in the cladogram.

Hyaenictis graeca Gaudry, 1861

Synonymy. – □1861 *Hyaenictis graeca* gen. et sp. nov. – Gaudry, p. 527, Pl. 11:1–2. □1862–1867 *Hyaenictis graeca* Gaudry – Gaudry, p. 95, Pl. 15:6–8. □1938 *Hyaenictis graeca* Gaudry – Kretzoi, p. 116. □1981 *Hyaenictis graeca* Gaudry – Solounias, pp. 90–91. □1985 *Hyaenictis graeca* Gaudry – Howell & Petter, pp. 467–469, Pl. 2:4–5.

Localities. – Greece: Pikermi.

Age. – Turolian (MN Zone 12).

Discussion. – This is a taxon that, not least due to the lack of material, has been the subject of a number of proposals regarding affinities. The most radical such proposal was that of Solounias (1981): that it is a senior synonym of *Adcrocuta eximia.* However, this position is not tenable, as clarified by Howell & Petter (1985) and Qiu (1987). These authors added no ideas of their own regarding the affinities of *H. graeca,* but, as is discussed in detail elsewhere (Werdelin, Turner & Solounias, MS), it is unquestionable that the genus and species are valid as proposed. This being so, it is curious that no more material has been found, although perhaps specimens are lying unrecognized in museum collections. However, the specimens referred to this species by Ginsburg (1977) are unfortunately not sufficient to allow distinction between this species and *'Hyaenictitherium' namaquensis.*

Approximate phylogenetic position. – Arguments for a position between nodes 5 and 6 on the core cladogram for this taxon are presented by Werdelin, Turner & Solounias (MS).

Crocuta sivalensis (Falconer & Cautley, 1868)

Synonymy. – □1835 *Hyaena* – Baker, p. 569, Pl. 46:22–23. □1868 *Hyaena sivalensis* sp. nov. – Falconer & Cautley *in* Falconer, p. 548. □*pars* 1884 *Hyaena felina* sp. nov. – Lydekker, pp. 281–285, Fig. 13, Pls. 38:1; 39:1. □*pars* 1884 *Hyaena colvini* sp. nov. – Lydekker, p. 294, Pl. 35:5. □1932 *Crocuta sivalensis* (Falconer & Cautley) – Pilgrim, pp. 134–137. □1968 *Crocuta taliyangari* sp. nov. – Prasad, pp. 24–26, Pl. 3:1–2. □1968 *Crocuta pinjorensis* sp. nov. – Prasad, pp. 27–28, Pl. 5:1. □1987 *Crocuta sivalensis* (Falconer) – De Vos, Leinders & Hussain, pp. 350, 366–367, Pl. 1–2. □1987 *Crocuta felina* (Bose) – De Vos, Leinders & Hussain, p. 351. □1987 *Crocuta colvini* (Lydekker) – De Vos, Leinders & Hussain, pp. 352–353.

Localities. – Sivaliks: Haritalyangar, Loc. H-GSP 8460, 14 km SE of New Mirpur, Upper Sivaliks 'Sivalik Hills, between Markanda Pass and Pinjor' (upper Sivaliks).

Age. – Upper Sivaliks (?Villafranchian).

Discussion. – This taxon is very close to the Recent *C. crocuta,* and, indeed, A. Turner (personal communication to LW, July, 1989) considers the two synonymous. Whether this is correct or not need not concern us in this context: we will merely note the strong likelihood that the geographic range of *C. crocuta* should be extended to the Indian subcontinent. For a thorough discussion of specimens and species history, we refer to De Vos *et al.* (1987).

The specimens of *C. taliyangari* described by Prasad (1968) undoubtedly belong here. The teeth he interpreted as P_{3-4} are in reality P_{2-3}, and match the measurements of *C. sivalensis* closely. The latter observation also applies to *C. pinjorensis.*

Approximate phylogenetic position. – As noted, this form may be conspecific with the Recent *C. crocuta* and should be placed as sister taxon to that form in the cladogram.

Lepthyaena sivalensis (Lydekker, 1877)

Synonymy. – □1877 *Ictitherium sivalense* sp. nov. – Lydekker, p. 32. □1884 *Lepthyaena sivalensis* gen. nov. – Lydekker, p. 312, Pl. 45:8–9. □1932 *Ictitherium sivalense* Lydekker – Pilgrim, pp. 114–119, Pls. 5:3, 4, 7; 9:4. □1935 *Ictitherium sivalense* Lydekker – Colbert, pp. 104–107. □1938 *Ictitherium sivalense* Lydekker – Kretzoi, p. 113. □1987 *Ictitherium sivalense* Lydekker – De Vos, Leinders & Hussain, pp. 359–360. □1988b *Lepthyaena sivalensis* (Lydekker) – Werdelin, p. 255.

Localities. – Sivaliks: Dhurnal, Haritalyangar, Hasnot, Khaur.

Age. – Nagri–?lower Dhok Pathan (Vallesian–Turolian).

Discussion. – This taxon is the most difficult of the Sivalik taxa to place correctly. The upper molars are reduced as in *'Thalassictis'*, whereas the upper carnassial retains all the characteristics of *Ictitherium.* In a previous paper (Werdelin 1988b), one of us suggested possible affinities between this taxon and *Palinhyaena* from China. While maintaining that there are a number of suggestive similarities, such as the shape and size of P^4 and M^{1-2}, and the relative width of the lower premolars (cf Werdelin 1988b, Fig. 25), comparison of the two forms with regard to the diagnostic morphological features of *P. reperta* suggests that there is no basis for referring these two taxa to the same genus: *Palinhyaena* is clearly more derived than the Sivalik form. However, neither can *L. sivalensis* be referred to any other genus, and we conclude that the genus *Lepthyaena* is valid as proposed.

Approximate phylogenetic position. – The exact position of this taxon is indeterminable, and we place it *incertae sedis.* However, we also note that it has reached the thalassictine level of reduction of the upper molars (i.e. above node 2 in the core cladogram).

Lycyaena macrostoma (Lydekker, 1884)

Synonymy. – □1884 *Hyaena macrostoma* sp. nov. – Lydekker, pp. 298–303, Pls. 36:2; 37:1–2; 38:4, 39:6. □1897 *Lycyaena macrostoma* (Lydekker) – Trouessart, p. 320. 1929 *Hyaena macrostoma* Lydekker – Matthew, pp. 492–493. □1932 *Lycyaena macrostoma* (Lydekker) – Pilgrim, pp. 125–130, Pl. 5:9–10. □1935 *Lycyaena macrostoma* (Lydekker) – Colbert pp. 108–109. □1938 *Lycyaena ?macrostoma* (Lydekker) – Kretzoi, 1938, p. 115. □?1968 *Lycyaena macrostoma* (Lydekker) – Prasad, pp. 23–24, Pl. 4:1. □1987 *Thalassictis macrostoma* (Lydekker) – De Vos, Leinders & Hussain, pp. 361–362.

Localities. – Sivaliks: ?Haritalyangar, Hasnot, Jabi, Wadia.

Age. – Dhok Pathan (Turolian).

Discussion. – This is perhaps the least problematic of the Sivalik hyaenids. It is in most respects closely comparable to *L. chaeretis* and *L. dubia*, but is somewhat larger, and has a broader M_1 (Werdelin 1988b). Pilgrim (1932) expressed some uncertainty regarding whether *L. macrostoma* was really distinct from *L. chaeretis.* We agree that they are very close but, in the absence of additional data on the Sivalik species, prefer to keep it distinct and use the broad M_1 as a distinguishing character.

The description and figures given by Prasad (1968) are indeterminate, and there is no reason to extend the stratigraphic range of the species on this account.

Approximate phylogenetic position. – As noted, this form is very close to *L. chaeretis* and *L. dubia*, and may be placed with them in the cladogram.

Pliocrocuta pyrenaica (Depéret, 1890)

Discussion. – This form, previously considered a valid species (Howell & Petter 1980; Qiu 1987; Viret 1954), is here considered a synonym of *P. perrieri.* The justification for this procedure is elaborated under the heading of the latter species above. We retain this separate listing of *'P. pyrenaica'* for ease of reference only.

Protictitherium crassum (Depéret, 1892)

Synonymy. – □1892 *Herpestes crassus* sp. nov. – Depéret, p. 91, Pl. 1:4–17. □1903 *Progenetta crassa* (Depéret) – Forsyth Major, p. 535. □1938 *Protictitherium crassum* gen. nov. – Kretzoi, p. 113. □1951 *Progenetta crassa* (Depéret) – Viret, p. 83, Pl. 3:4–5. □1964 *Progenetta crassa* (Depéret) – Crusafont Pairó, p. 177. □1965 *Ictitherium arambourgi* sp. nov. – Ozansoy, p. 27, Pl. 2:2. □1969 *Progenetta crassa* form A – Crusafont Pairó & Petter, pp. 12–17, Figs. 2–5, Pl. 3:1–9. □1969 *Progenetta crassa* form B – Crusafont Pairó & Petter, pp. 17–18, Pl. 3:10–13. □1976 *Protictitherium crassum* (Depéret) – Schmidt-Kittler, pp. 78–80, Pl. 2:2–3. □?1980 *Protictitherium crassum* (Depéret) – Koufos, pp. 35–40, Fig. 13, Pls. 3:2; 4:1.

Localities. – France: La Grive Saint-Alban, Montredon; Greece: ?Dytiko; Spain: Can Llobateres I and II, Los Valles de Fuentedueña; Turkey: Akçaköy, Mahmutgazi, Sofça, Yassiören; USSR: Kalfa, Sevastopol.

Age. – Astaracian–?Turolian (MN Zones 7–?13).

Discussion. – As is also noted below, we have here accepted Schmidt-Kittler's (1976) synonymization of *P. crassum* and *I. arambourgi.* However, the content of this species and inclusion of other specimens still requires consideration. The material described as *Progenetta crassa* forms A and B by Crusafont Pairó & Petter (1969) is closely similar to the type material from La Grive, described by Depéret (1892), which in turn is very close to the material from Turkey (Fig. 12). This material clearly all belongs to one taxon. However, the material from Can Bayona described by Crusafont Pairó & Petter (1969) as *P. crassa llopisi* ssp. nov. shows clear differences from all the other material in the very narrow P_3 and in the proportions of P^4. Further, the M_1, (although worn, as noted by Crusafont Pairó & Petter 1969) seems lower in the Can Bayona mandible, and has a higher metaconid and longer talonid. In general shape, the M_1 of this specimen is more reminiscent of M_1 of *Plioviverrops* than is M_1 of any other Spanish specimen of *P. crassum.* Lastly, the assumed greater age of other specimens of *P. crassum* may

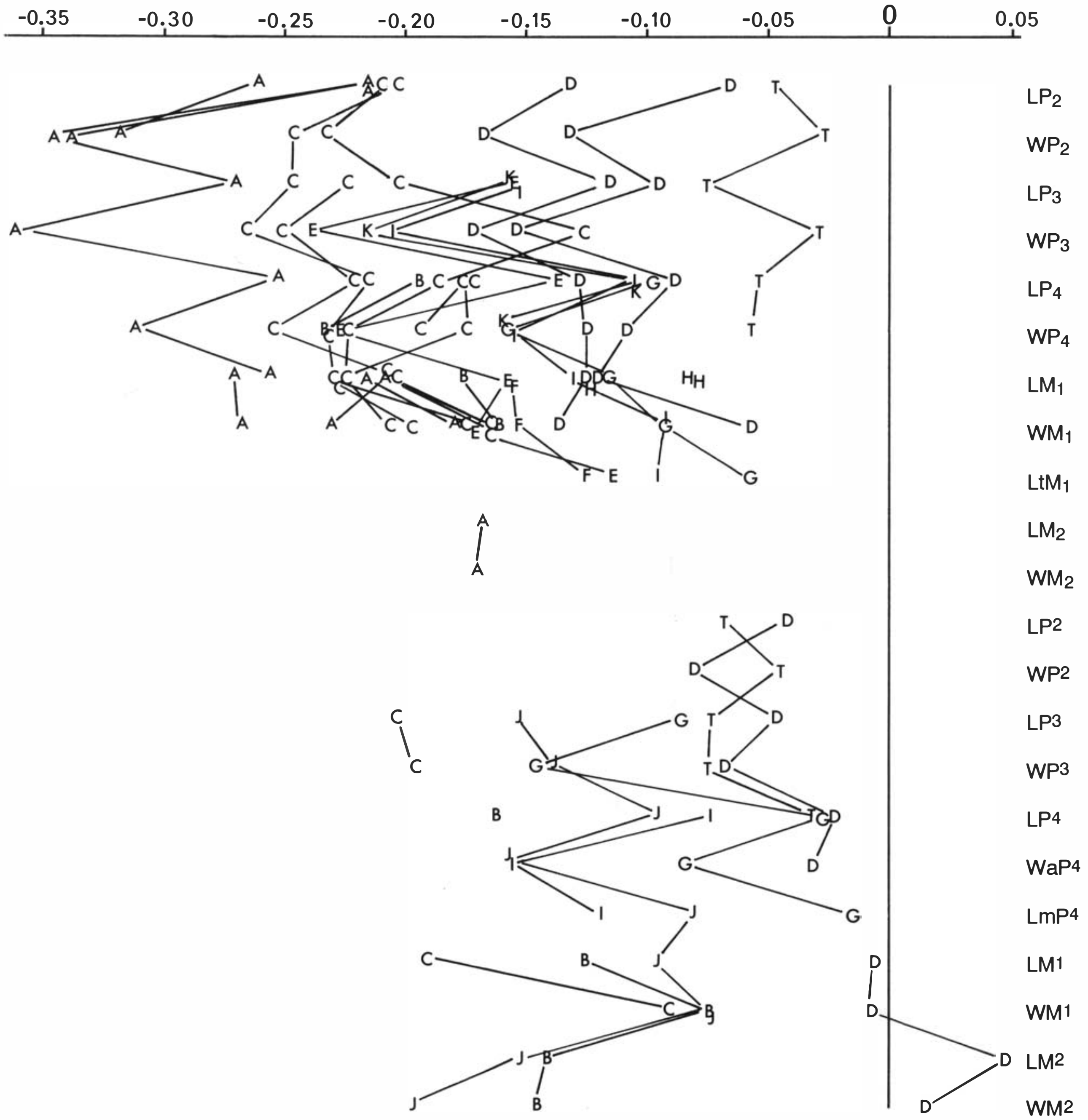


Fig. 12. Ratio diagram of samples of *'Protictitherium'* spp. Standard = *Ictitherium viverrinum* (Chinese sample); A = *'P.' intermedium*; B = *P.* aff. *gaillardi*; C = *'P.' cingulatum*; D = *'P.' crassum* (data on A–D from Schmidt-Kittler 1976); E = *'P.' gaillardi*, form A; F = *'P.' gaillardi*, form B; G = *'P.' crassum*, form A; H = *'P.' crassum*, form B; I = *'P.' llopisi* (data on E–I from Crusafont Pairó & Petter 1969); J = *'P.' punicum*; K = *P. arambourgi* (data from Ozansoy 1965); T = *I. tauricum* (data from Borissiak 1915).

also argue against ascribing the Can Bayona material to this species. In the absence of additional data, we would prefer to keep *'Protictitherium' llopisi* distinct from *P. crassum.*

The temporal gap between the accepted hypodigm of *P. crassum* and the material from Dytiko referred to this species by Koufos (1980) is considerable, as noted by De Bonis *et al.* (1986), and different species may in fact be involved. The available material is insufficient for a revision, however, and we prefer to leave matters as they are.

Approximate phylogenetic position. – This species and the others referred to *'Protictitherium'* are very primitive indeed, and may be placed below node 1 in the core cladogram.

'Protictitherium' gaillardi (Forsyth Major, 1903)

Synonymy. – □1899 *Herpestes crassus* – Gaillard, p. 60, Pl. 2:1–3. □1903 *Progenetta gaillardi* sp. nov. – Forsyth Major, p. 535. □1925 *Herpestes dissimilis* sp. nov. – Stehlin & Helbing, p. 56. □1951 *Progenetta gaillardi* F. Major – Viret, p. 83. □1958 *Progenetta gaillardi* Major – Mein, p. 53, Fig. 72. □1969 *Progenetta gaillardi* Forsyth Major form A – Crusafont Pairó & Petter, pp. 9–11, Pls. 2:1, 5, 6; 3:14. □1969 *Progenetta gaillardi* Forsyth Major form B – Crusafont Pairó & Petter, pp. 11–12, Pl. 3:15. □1976 *Progenetta gaillardi* Forsyth Major – Petter, pp. 148–149, Fig. 10, Pl. 1:28–35.

Localities. – France: La Grive Saint-Alban, Pontlevoy; Spain: Arroyo del Val IV, Can Llobateres, Can Ponsich, Castell de Barbera, Hostalets de Pierola, Paracuellos de Jarama. Turkey: ?Paşalar.

Age. – Astaracian–Vallesian (MN Zones 5–9).

Discussion. – Another of the still poorly known La Grive species, *'P.' gaillardi* is similar in most of its characters to *P. crassum*, but appears significantly smaller. It is very likely that the *P.* aff. *gaillardi* from Paşalar described by Schmidt-Kittler (1976) actually belongs to this species, although the differences between this material and the type material from La Grive indicate that the caution exhibited by Schmidt-Kittler is justified (Fig. 12). If new material is found during the ongoing excavations at Paşalar, this problem may be resolved.

Approximate phylogenetic position. – Like other species of *'Protictitherium'*, this one can be placed below node 1 in the core cladogram.

'Thalassictis' certa (Forsyth Major, 1903)

Synonymy. – □*pars* 1892 *Progenetta incerta* gen. et sp. nov. – Depéret, pp. 34–36, Pl. 1:18–19. □1903 *Progenetta certa* sp. nov. – Forsyth Major, p. 534. 1938 *Miohyaena certa* gen. nov. – Kretzoi, pp. 114–115. □1951 *Progenetta certa* Forsyth Major – Viret, pp. 82–83, Pls. 1:12–15; 2:1.

Localities. – France: La Grive Saint-Alban.

Age. – Astaracian (MN Zones 7–8).

Discussion. – The status of *Progenetta* has been discussed in detail by others (e.g., Abu Bakr, 1959; Kurtén 1982). The specimens from La Grive attributed to this species (Depéret 1892; Viret 1951) have a combination of primitive and derived features not seen in other taxa. Primitive features are the short and low M_1 paraconid, the high, narrow P^3, and the forwardly extending, long and narrow P^4 protocone. Derived features are the reduced upper molars, the long P^4 metastyle, and the short M_1 talonid. Kurtén (1982) suggested that *Miohyaena* may be synonymous with *Thalassictis*. As noted under *T. robusta* we regard this conclusion as probably correct, since after *Hyaenotherium wongii* is removed from *Thalassictis*, the two genera share the same characteristics. The two species are not synonymous, however, and *T. robusta* appears somewhat more derived than *'T.' certa* in having broader premolars.

Approximate phylogenetic position. – The reduced molars indicate a position above node 2, and the primitive M_1 a position below node 3.

'Thalassictis' sarmatica (Pavlow, 1908)

Synonymy. – □1908 *Ictitherium sarmaticum* sp. nov. – Pavlow, pp. 29–41, Pls. 1:1; 2:1. □1931 *Ictitherium sarmaticum* Pavlow – Pilgrim, pp. 100–101.

Localities. – USSR: Kishinev, Moldavian SSR.

Age. – ?Vallesian (?MN Zone ?9–?10).

Discussion. – This is yet another species that is clearly distinct from others of the same age and shows a mixture of primitive and derived characters. The P^4, with its anteriorly positioned protocone, is primitive, resembling the same tooth in *Ictitherium adroveri*. The upper molars, however, are very much reduced compared to those of *Ictitherium*, and approach *H. wongii* in this respect. A feature of interest is the small P^2. The only species approaching *'T.' sarmatica* in the relative lengths of the premolars is *Ictitherium kurteni*, which species is, however, much more primitive in the size and morphology of M^{1-2}.

Semenov (1989) synonymizes this species with *T. robusta*. The reasons for this are not entirely clear. We feel that the broad premolars of the latter species and the narrow ones of *'T.' sarmatica* preclude such synonymy. It is difficult to make any other comparisons between these taxa, since the available materials do not overlap, with the exception of P^4 which serves to distinguish both species from *Ictitherium* spp. but is otherwise not diagnostic at this level.

Approximate phylogenetic position. – As noted, this species can be distinguished from *Ictitherium* spp. on the basis of the morphology of P^4 and M^{1-2}. However, the available material does not allow definite allocation to either *Thalassictis* or *Hyaenotherium*. We believe that an allocation to *Hyaenotherium* is unlikely, and accordingly refer this species to *Thalassictis*, with a position between nodes 2 and 3 in the core cladogram.

'Hyaenictitherium' indicum (Pilgrim, 1910)

Synonymy. – □*pars* 1910 *Palhyaena indica* sp. nov. – Pilgrim, p. 64. □*pars* 1913 *Palhyaena* cf. *hipparionum* Gervais – Pilgrim, pp. 282, 289. □*pars* 1929 *Palhyaena indica* Pilgrim – Matthew, p. 493. □*pars* 1935 *Ictitherium indicum* (Pilgrim) – Colbert, pp. 107–108.

Localities. – Sivaliks: Hasnot.

Age. – Dhok Pathan (Turolian).

Discussion. – This taxon presents some nomenclatural difficulties. The original discussion of this species by Pilgrim (1910) is as follows (in its entirety):

> This species is established on a maxilla, found at Asnot, which is somewhat inferior in size to *Palhyaena hipparionum* Gerv. and has rather broader molars. It is almost certain that the mandible, described by Lydekker under the name of *Hyaena sivalensis* Bose, also belongs to this species. In it the last premolar is more nearly equal in size to the carnassial than is the case in *P.* aff. *hipparionum* described by Schlosser from China. The fragmentary tooth, described and figured by Lydekker as the lower carnassial of *Hyaenodon* is, as Schlosser has pointed out, an upper carnassial. It is probably a species of *Palhyaena*, to which I shall provisionally refer it.

Thus, the holotype of the species is clearly stated to be a maxilla from Hasnot. However, in his later discussion of the species, Pilgrim (1932) creates a remarkable state of confusion by the following statement (p. 120): 'Matthew (1929, p. 493) and I myself (Pilgrim, 1910, p. 64) are mistaken in quoting a maxilla as the holotype of the species. The only upper teeth of the species known are the two specimens of

P^4 mentioned below, one of which is figured in Pl. V, fig. 8 of the present work.' This may be interpreted as suggesting that Pilgrim's rationale for changing the holotype designation is that the maxilla referred to previously was not figured. However, the International Code of Zoological Nomenclature makes no such provisions, and the maxilla was, and is, the holotype of *'H.' indicum*. This was also clearly and correctly noted by Colbert (1935). Subsequent authors, e.g., De Vos *et al.* (1987), are incorrect in referring to GSI-D53 as the holotype of this taxon. Pilgrim's statement goes further, however, in that he specifically excludes the maxilla from what he then discusses as *'H.' indicum*, i.e., in his opinion the two were distinct taxa. This means that, since the species name follows the original holotype, the remaining sample would require another name. The holotype maxilla is unnumbered and of unknown present location, and *H. indicum* must therefore be considered a *nomen dubium*. We thus propose that *H. indicum* be restricted to the currently unlocated maxilla, and that the remainder of the sample be referred to a new species *'H.' pilgrimi*, for which the holotype is the mandible, Geological Survey of India specimen no. D53, figured by Lydekker (1884: Pls. 38:2; 39:5)

'Hyaenictitherium' pilgrimi sp. nov.

Synonymy. – □*pars* 1884 *Hyaena sivalensis* – Lydekker, p. 306, Pls. 38:2; 39:5. □*pars* 1910 *Palhyaena indica* sp. nov. – Pilgrim, p. 64. □*pars* 1913 *Palhyaena* cf. *hipparionum* Gervais – Pilgrim, pp. 282, 289. □*pars* 1929 *Palhyaena indica* Pilgrim – Matthew, p. 493. □1932 *Ictitherium indicum* (Pilgrim) – Pilgrim, pp. 119–122, Pls. 4:11–12; 5:8. □*pars* 1935 *Ictitherium indicum* (Pilgrim) – Colbert, pp. 107–108. □1938 *Hyaenictitherium indicum* (Pilgrim) – Kretzoi, p. 114. □1987 *Thalassictis indicum* (Pilgrim) – De Vos, Leinders & Hussain, p. 361. □1988b *'Ictitherium' indicum* (Pilgrim) – Werdelin, pp. 255–256.

Localities. – Sivaliks: Bhandar, Hasnot, Nila.

Age. – Dhok Pathan (Turolian).

Discussion. – The reason for erecting a new species has been stated above. This taxon thus comprises all specimens previously referred to *'H.' indicum* except the original holotype maxilla of Pilgrim (1910).

There is little to add here to the discussion of this taxon given in Werdelin (1988b). It clearly belongs to the thalassictine grade of development, but differs from all *'Thalassictis'* in the posteriorly placed protocone on P^4. In metric characters it is close to *L. macrostoma* (Werdelin 1988b), and a close connection between these taxa may be found upon restudy of the available material.

Approximate phylogenetic position. – A position near node 4 of the core tree is indicated.

'Thalassictis' proava (Pilgrim, 1910)

Synonymy. – □1910 *Palhyaena proava* sp. nov. – Pilgrim, p. 65. □1913 *Progenetta proava* (Pilgrim) – Pilgrim, pp. 282, 312. □1929 *Progenetta proava* (Pilgrim) – Matthew, pp. 488–489. □1932 *Lycyaena? proava* (Pilgrim) – Pilgrim, pp. 130–133, Pl. 5:1, 6. □1932 *Lycyaena? chinjiensis* sp. nov. – Pilgrim, pp. 133–134, Pl. 6:6. □1935 *Lycyaena? chinjiensis* Pilgrim – Colbert, p. 109. □1935 *Progenetta proava* (Pilgrim) – Colbert, pp. 109–110. □1938 *Hyaenictitherium proavum* (Pilgrim) – Kretzoi, p. 114. □1938 *Miohyaena chinjiensis* (Pilgrim) – Kretzoi, p. 115. □1987 *Miohyaena proava* (Pilgrim) – De Vos, Leinders & Hussain, pp. 363–364. □1988 *Thalassictis proava* (Pilgrim) – Werdelin, pp. 247–248. □1988 *Thalassictis chinjiensis* (Pilgrim) – Werdelin, p. 250.

Localities. – Pakistan: Chinji.

Age. – Chinji Formation (Upper Astaracian–Vallesian, MN Zones 8–10)

Discussion. – It has previously been suggested (Colbert 1935; De Vos *et al.* 1987; Werdelin 1988b) that this species is synonymous with *'T.' chinjiensis*. We here formally place the latter taxon in synonymy with the former. *'T.' proava* represents a small *'Thalassictis'*-grade taxon, probably close to *T. robusta* (see Werdelin 1988b).

Approximate phylogenetic position. – Like *T. robusta*, this taxon may be placed between nodes 2 and 3 in the core cladogram.

**Chasmaporthetes lunensis* (Del Campana, 1914)

Synonymy. – □1914 *Lycyaena lunensis* sp. nov. – Del Campana, pp. 87–104, Pl. 11. □*pars* 1924 *Hyaena honanensis* sp. nov. – Zdansky, pp. 103–107, Pl. 23:5–6. □1935 *Hyaena honanensis* Zdansky – Zdansky, p. 7. □1938 *Lycyaenops lunensis* (Del Campana) – Kretzoi, p. 115. □1941 *Euryboas bielawskyi* sp. nov. – Schaub, pp. 279–285, Pls. 18:1–7, 9; 19:1–3; 20:1–3. □*pars* 1952 *Hyaena marini* sp. nov. – Villalta Comella, pp. 65–75, Pls. 8:1; 10:1–2. □1954 *Euryboas lunensis* – Viret, pp. 53–59, Figs. 5–6, Pls. 8:3–5; 9:1. □1967 *Euryboas lunensis* (Del Campana) – De Beaumont, p. 104. □1967 *Euryboas lunensis* (Del Campana) – Ficcarelli & Torre, pp. 193–198, Fig. 1. □1977 *Chasmaporthetes kani* sp. nov. – Galiano & Frailey, pp. 1–7, Figs. 1–2. □1977 *Euryboas bielawskyi* Schaub – Galiano & Frailey, p. 8. □1987 *Chasmaporthetes kani* Galiano & Frailey – Qiu, pp. 25–37, Fig. 6, Pls. 1:1–2; 2:1–2; 3:1–3; 4:1 □1988 *Chasmaporthetes lunensis* (Del Campana) – Kurtén & Werdelin, pp. 48–48, Fig. 1.

Localities. – China: Loc A, Dongancun, Hsia-Chuang, Malancun, Ma Tzu Kou, Niu Wa Kou, Ouniwa, Zhaohuangcun; France: Etouaires, Pardines, Roccaneyra, Senèze, St-Vallier; Germany: Erpfinger Höhle, Neulingen, Schernfeld; Italy: Inferno, Olivola, Triversa; People's Republic of Mongolia: Shamar; Spain: La Puebla de Valverde, Layna, Villaroya; Turkey: Gülyazi; USSR: Beregovaia, ?Odessa Catacombs.

Age. – Ruscinian–Villafranchian.

Discussion. – This species has recently been the subject of extensive treatment (Kurtén & Werdelin 1988; Qiu 1987). These authors are in agreement regarding the synonymy of *Chasmaporthetes* and *Euryboas*, but differ in many details of their conception of the species involved. These differences mainly center around the narrower conception of the species involved utilized by Qiu (1987) compared with that of Kurtén & Werdelin (1988). The new material of *Chasmaporthetes* described by Qiu (1987; not available to Kurtén & Werdelin 1988) has not caused any modification in the views of one of us (LW) regarding the species involved. Here we shall briefly comment on Qiu's (1987, pp. 40–41) analysis of these specimens and species.

The status of *Chasmaporthetes bielawskyi* is the most important difference between the treatments of the genus. It is considered a valid species by Qiu (1987), as well as by Galiano & Frailey (1977) and Berta (1981) (as *Euryboas*). Kurtén & Werdelin (1988), however, consider *C. bielawskyi* to be a synonym of *C. lunensis.* Study of Qiu's (1987) reasoning explains this difference. Finding that the distance between the tooth rows in the type specimen (lower jaws) of *C. bielawskyi* (Schaub 1941) is relatively great compared with other *Chasmaporthetes,* Qiu has selected the broadest of the skulls of *Chasmaporthetes* from St-Vallier (Viret 1954), Lyon Museum QSV 53, as a match for the lower jaw. The metric analysis may well be correct: these are the broadest specimens of *C. lunensis.* The differences are slight, however. The type specimen of *C. kani* (Galiano & Frailey 1977) is only slightly narrower than QSV 53, as is true of the type specimen of *C. lunensis* (Del Campana 1914). This latter feature is noted by Qiu, who states: *'aber er ist insgesamt viel größer als Schaub's Unterkiefer'.* If this is true, then it is also true of QSV 53, which is only slightly smaller than the type specimen of *C. lunensis.* The dental features assigned to *C. bielawskyi,* i.e. relatively smaller $P^2/_2$ and $P^3/_3$, are not tenable, as can be seen by inspection of Figs. 3–7 and Appendix, Tables 4–7 in Kurtén & Werdelin (1988).

In essence, the procedure used by Qiu in validating *C. bielawskyi* amounts to selecting the extremes of variation in a population and designating these as separate species, without taking into account the intermediates. This is not acceptable taxonomic practice, and we conclude that *C. bielawskyi* is a synonym of *C. lunensis.*

In their analysis, Kurtén & Werdelin (1988) found that Asiatic specimens of *C. lunensis* differed significantly from European ones in the length of P_4. They based a subspecies, *C. l. honanensis,* partly on this difference. In his conception of *C. kani* [=*C. honanensis*] Qiu has overlooked the designation by Zdansky (1935) of a lectotype for his *'Hyaena' honanensis.* This lectotype belongs to *Chasmaporthetes* (Kurtén & Werdelin 1988), rather than to *Crocuta,* the crocutoid features of the species as originally described pertaining to the lower dentition specimens, which were subsequently referred to *Adcrocuta eximia.* Qiu also includes specimens from Serrat d'En Vacquer (tentatively referred to *C. borissiaki* by Kurtén & Werdelin 1988) and Layna, thus in effect creating a temporal rather than a geographic subspecies. Unfortunately, this referral obliterates the difference in P_4 length found by Kurtén & Werdelin (1988), since the Layna specimens all have a relatively long P_4. Since Qiu himself does not discuss differences between *C. kani* and *C. lunensis,* and since the main difference found by Kurtén & Werdelin (1988) is not relevant to his conception of these species, we conclude that they should be considered synonymous.

One further important comment is made by Qiu (1987, p. 41). This concerns the hyaenid remains from Schernfeld, near Eichstätt, described by Dehm (1962) as *Hyaena perrieri.* Qiu refers these specimens to *C. lunensis* on morphological and metric grounds. We are in full agreement with his results, although the specimens are larger than any *C. lunensis* previously known. The morphology of P^2 in particular, is characteristic, and quite different from that of *Pliocrocuta.* This lower Pleistocene record therefore represents the youngest occurrence of *C. lunensis* hitherto known.

'Hyaenictitherium' parvum (Khomenko, 1914)

Synonymy. – □1914 *Lycyaena parva* sp. nov. – Khomenko, pp. 5–7, Pl. 1:1. □1915 ?*Lycyaena parva* Khomenko – Alekseev, p. 380, Pl. 10:14. □1988b *Lycyaena parva* Khomenko – Werdelin, p. 250. □1989 *Hyaenictitherium venator* sp. nov. – Semenov, pp. 126–129, Fig. 37–39.

Localities. – USSR: Belka, Grossulovo, Novaja Emetovka-2, ?Novoelisavetovka, Taraklia, Tudorovo.

Age. – Turolian (MN Zone ?11–12).

Discussion. – In a previous report, one of us (Werdelin, 1988a) referred to this taxon as one of a number of species that may be allocated to *Lycyaena.* This was admittedly done without having seen the original figures of Khomenko (1914), only the text, which is in Russian, but does provide approximate measurements. In so doing, Werdelin (1988b) inexcusably overlooked the mention of M_2 in the text. This tooth is readily seen in Khomenko's figure (1914, Pl. 1:1). Thus, *'Lycyaena' parva* can be removed from this genus. Instead, the type mandible of *'L.' parva* almost certainly belongs to the same taxon as the palate illustrated next to it (Khomenko 1914, Pl. 1:2), which was described by Khomenko as *Ictitherium hipparionum.* In addition, Khomenko (1914) describes an isolated P_4, which he ascribes to *L. chaeretis,* chiefly because it is larger than *'L.' parva.* However, this tooth is a good deal smaller than P_4 of *L. chaeretis* from Pikermi and may represent the same taxon as the other specimens.

The question to be answered is what taxon these specimens belong to. Unfortunately, this depends somewhat on the hypodigm one selects. If all these specimens are considered conspecific, then they cannot be distinguished from *H. hyaenoides,* and should be referred to that species. However, from a nomenclatural point of view the key specimen is, of course, the type of *'L.' parva.* This specimen is almost exactly intermediate between the Chinese samples of *H. wongii* and *H. hyaenoides* in size, and a specific allocation is impossible. Thus, the status of *'L.' parva* is unclear and can only be solved by renewed study of the original material. Such study is urgently required, as *'L.' parva* is almost certainly a senior synonym of either of the two Chinese taxa. Until such a study is undertaken, we prefer to leave the taxonomy of these forms at status quo.

The specimen from Novoelisavetovka, ascribed by Alekseev (1915) to *Lycyaena parva* is an entirely different proposition from the type material. This mandible (Alekseev 1915, Pl. 10:14) apparently lacks an M_2, and may thus very well belong to *Lycyaena*. However, the structure of the M_1 talonid and the posterolingual cingulum of P_4 are more primitive than in any *Lycyaena*. This specimen may represent a new taxon or may, alternatively, be an aberrant individual of a known taxon retaining M_2. This question cannot be resolved without restudy of the original specimen from Novoelisavetovka. As it stands, this specimen is in any case irrelevant to the status of *'Lycyaena' parva*.

Semenov (1989) took a similar stand in erecting the new species *Hyaenictitherium venator* for a taxon encompassing these specimens. We agree with him that they should probably be placed in the genus *Hyaenictitherium* and that they may represent a new taxon within that genus. However, Semenov apparently overlooked the fact that his type series includes the type specimen of *'Lycyaena' parva. H. venator* is thus a junior synonym of *'L.' parva.*

Approximate phylogenetic position. – A position somewhere near node 4 on the cladogram is indicated.

Ictitherium tauricum Borissiak, 1915

Synonymy. – □1915 *Ictitherium tauricum* sp. nov. – Borissiak, pp. 17–20, Pl. 3:3–4. □1931 *Ictitherium tauricum* Borissiak – Pilgrim, p. 101. □1938 *Protictitherium? tauricum* (Borissiak) – Kretzoi, p. 113. □*pars* 1976 *Protictitherium crassum* Depéret – Schmidt-Kittler, p. 78.

Localities. – USSR: Sevastopol, Ukrainian SSR.

Age. – ?Upper Vallesian (?MN Zone 10)

Discussion. – Schmidt-Kittler (1976) synonymizes this species with *Protictitherium crassum*. However, the premolars of *I. tauricum* are, on the basis of measurements given, significantly broader (Fig. 12) and, more importantly, the anteriorly placed P^4 of *P. crassum* (to which Schmidt-Kittler 1976 calls particular attention, as it is a feature that distinguishes *Ictitherium* from *'Protictitherium'*) is not present in *I. tauricum*. Instead, the protocone is situated more or less as in *I. viverrinum*, but appears reduced relative to that taxon. We thus prefer to maintain *I. tauricum* within *Ictitherium*, and distinct from *P. crassum*, while acknowledging that the similarities pointed out by Schmidt-Kittler (1976) are real.

Approximate phylogenetic position. – The morphology of P^4 indicates a position near *I. viverrinum*, i.e. at node 2 in the core tree.

Chasmaporthetes ossifragus Hay, 1921

Synonymy. – □1921 *Chasmaporthetes ossifragus* gen. et sp. nov. – Hay, pp. 634–637, Pl. 124:5–6. □1940 *Ailuraena johnstoni* gen. et sp. nov. – Stirton & Christian, pp. 445–448. □1941 *Chasmaporthetes johnstoni* (Stirton & Christian) – Stirton & Christian, p. 198. □*pars* 1988 *Chasmaporthetes ossifragus* Hay – Kurtén & Werdelin, p. 50.

Localities. – USA: Anita, Benson, Cita Canyon, Comosi, Dry Mountain, Duncan; Mexico: El Golfo de Santa Clara, Goleta, Miñaca Mesa.

Age. – Blancan (Upper Pliocene).

Discussion. – The remarkable achievement of Hay (1921) in referring the type specimen of *C. ossifragus* to the Hyaenidae has been commented on elsewhere (Kurtén & Werdelin 1988). It may, however, have been sufficient if he had limited himself to referring it to family, rather than creating a new genus and species for it. Although *C. ossifragus* and *C. johnstoni* are most probably synonymous (Kurtén & Anderson 1980; Kurtén & Werdelin 1988; but see Berta 1981 and Galiano & Frailey 1977 for a contrary opinion), the nature of the holotype, an edentulous, fragmentary ramus, has made it very difficult to establish the range of variation acceptable within the species, and, for that matter, the genus. This lies at the heart of the discussion regarding the status and affinities of *Chasmaporthetes* (Berta 1981; Galiano & Frailey 1977; Kurtén & Werdelin 1988; Qiu 1987).

Berta (1981) referred material from several localities in Florida (Santa Fe River IB, XV, Inglis IA) to *C. ossifragus*. However, Kurtén & Werdelin (1988) questioned this assignment on the basis of the relative lengths of P_4 and M_1; these two teeth are approximately equal in length in *C. ossifragus* (including the type specimen, as measured from the alveoli), but in the mandible from Inglis (UF 18088), M_1 is approximately 20% longer than P_4. Qiu (1987) mistakenly used the latter character state as a characteristic of *C. ossifragus*, and referred several specimens from China to *C.* cf. *ossifragus* on this basis. These Chinese specimens, therefore do not show similarities to *C. ossifragus* in general, but to the Florida *Chasmaporthetes* in particular. The question thus arises whether there is any particular connection between these forms or whether the strongest distinguishing characteristic, the M_1 length, has evolved in parallel. Synonymy between *C. lunensis* and *C. johnstoni* (as distinct from *C. ossifragus*) has already been suggested by others (Berta 1981; Galiano & Frailey 1977).

It would seem to be stretching the species concept of *C. lunensis* relative to other well established hyaenid species, such as, e.g., *H. wongii* among fossil taxa, to include the North American material within this species. As shown by Kurtén & Werdelin (1988, Figs. 4–7), *C. ossifragus* differs from *C. lunensis* in several characters, such as P^3 width, and P^4 metastyle length. Within North America, the Florida material differs from other *Chasmaporthetes* specimens in a number of features, as discussed by Berta (1981) and Kurtén & Werdelin (1988). The latter authors suggested subspecific status for the Florida form. Subsequent work by those authors has led to the conclusion that specific status is probably warranted, and this is also our present conclusion.

On the assumption that Qiu (1987) is correct in referring all specimens with long M_1 to the same species, the situation in China is the same as in North America. Qiu's interpretation is reasonable, although difficult to establish for certain due to the poor preservation of the Uppsala specimens (of which the skull was referred to *C. lunensis* *honanensis* by Kurtén & Werdelin 1988, and the mandible not seen by those authors). Although more or less identical to *C. lunensis* in metrics, with the exception of the long M_1, the new form differs substantially from that species in morphology. The M_1 talonid is even more reduced and appressed to the protoconid than in *C. lunensis*, the anterior faces of the main cusps of the lower premolars more concave, and the anterior accessory cusp of P_3 remarkably large, in the Beijing specimen, V7280, even larger than the posterior accessory cusp, a feature unique among hyaenids. Of the upper dentition, little can be said, although the P^4 metastyle appears very long and the blade narrow relative to the condition in *C. lunensis*. Unfortunately, the specimen is too poorly preserved for accurate measurement. Thus, we conclude that these Chinese specimens represent a valid new taxon.

The final question is whether these two new taxa are, in fact, identical, or not. To judge by the available data, they are not. These two forms really only resemble each other in the lengths of M_1 and the P^4 metastyle, which are clearly correlated characters and should be counted as one. In other respects, the Chinese form differs from the Florida one in the same morphological features and metric characteristics as distinguish it from Chinese *C. lunensis*. In conclusion: neither the Florida material described by Berta (1981) as *C. ossifragus*, nor the Chinese material described by Qiu (1987) as *C.* cf. *ossifragus* actually belongs to this species. These materials represent two distinct new species, neither of which will be named here.

Approximate phylogenetic position. – This taxon should be placed near *C. lunensis* in the cladogram.

**Hyaenotherium wongii* (Zdansky, 1924)

Synonymy. – □1862–1867 *Ictitherium hipparionum* (Gervais) – Gaudry p. 68, Pl. 12:1–2. □1887 *Palhyaena hipparionum* (Gervais) – Kittl, pp. 333–335, Pl. 18:2–7. □1924 *Ictitherium wongii* sp. nov. – Zdansky, pp. 73–84, Figs. 4–6, Pls. 14:3–6; 15:1–4; 16:1–2. □1925 *Ictitherium hipparionum* (Gervais) – De Mecquenem, p. 50, Pl. 9:3. □1938 *Ictitherium ?wongii* Zdansky – Kretzoi, p. 113. □*pars* 1938 *Palhyaena hipparionum* (Gervais) – Kretzoi, p. 113. □1939 *Ictitherium hipparionum* (Gervais) – Krokos, p. 160. □1952 *Hyaenalopex atticus* gen. et sp. nov. – Kretzoi, p. 21. □1980 *Palhyaena wongii* (Zdansky) – Howell & Petter, pp. 584, 588. □1980 *Ictitherium hipparionum* (Gervais) – Koufos, pp. 56–65, Figs. 18–19, Pls. 7:2–3; 8:1. □1981 *Thalassictis wongii* (Zdansky) – Solounias pp. 71–74, Fig. 17. □1985 *Thalassictis mesotes* sp. nov. – Kurtén pp. 81–82, Figs. 1–2. □1988b *Thalassictis wongii* (Zdansky) – Werdelin, pp. 223–230, Fig. 9. □1989 *Hyaenotherium magnum* gen. et sp. nov. – Semenov, pp. 94–105, Figs. 28–31. □1989 *Hyaenotherium wongii* (Zdansky) – Semenov, pp. 105–118.

Localities. – China: Tie Chia Kou (Zdansky's Loc. 30), Loc. 35, Loc. 43, Yan Mu Kou (Zdansky's Loc. 49), Chen Chia Mao Kou (Zdansky's Loc. 108), Huan Lou Kou (Zdansky's Loc. 109), Loc. 110, Nan Liang Kou (Zdansky's Loc. 111), Loc. 115, Loc. 116, Chao Tsu Kou (Zdansky's Loc. 116v), Chin Kou, Chou Chia Kou, Fu Ku Hsien, He Tsui Chu, Hsi Mao Kou, Hsiao Kou Chan, Hsin Yao, Jen Tse Kou, Kou Chia Ta, Kuer Shan, Lao Yeh Mao Kou, Liao Wan Kou, Lou Wan Kou, Lu Kao Ling, Ma Chi Liang Kou, Nan Hao Hsia, Nan Ho, Pai Tao Tsun, Tu Kou; Germany: Höwenegg; Greece: Pikermi, Ravin des Zouaves, Samos, Vathylakkos 2 and 3; Iran: Maragheh; USSR: Akin, Bota-Mojnak, Cherevichnoe, ?Grebeniki.

Age. – Vallesian–Turolian (MN Zones 9–12).

Discussion. – European specimens of this species were for a long time considered to belong to *Palhyaena hipparionum*, a species that is indeterminate (see above). It is the most abundant hyaenid of the classic Pontian faunas of Eurasia and is represented by over 100 specimens from China alone. It is quite variable in metrics (see discussion in Werdelin 1988b), but, due to the large number of specimens, it has been possible to determine that this variation is gradual in nature, and that only one species is represented, despite suggestions to the contrary (Kurtén 1985; Qiu 1985).

Despite the relatively young age of *H. wongii* from China, Samos and Pikermi, the species is primitive in many of its features, such as the narrow premolars, the relatively low-crowned M_1, and the relatively long M_1 talonid (Crusafont Pairó & Petter 1969; Werdelin 1988b). Although recognizing that *Ictitherium* and *'Thalassictis'* (as used by them) were distinct genera, Crusafont Pairó & Petter (1969) aligned *H. wongii* with *Ictitherium* on the basis of the long M_1 talonid. However, as shown by Kurtén (1982) and Werdelin (1988a, 1988b), *H. wongii* displays all those characters of M_1 and P^4 that distinguish *T. robusta* from *I. viverrinum*. In general terms, *T. robusta* and *H. wongii* are quite close in morphology, but the latter is in many respects decidedly more primitive, despite its greater overall size. On the other hand, *H. wongii* is more derived than *'Thalassictis'* spp. in the structure of M_1, which has a paraconid and protoconid of equal height. The structure of the lower carnassial of *H. wongii* is thus like that of *Hyaenictitherium* and more advanced hyaenas, and this species is accordingly considered more derived than *'Thalassictis'* spp. Relative to taxa such as *P. orbignyi*, *H. wongii* is more derived not only in its dental morphology, but also in the morphology of the auditory bulla, which is essentially like *Hyaena* in its general characteristics (De Beaumont 1964). The alisphenoid canal is lost, a derived feature that distinguishes *H. wongii* from *T. spocki* and *P. orbignyi*.

Recently, Semenov (1989) erected the new genus and species *Hyaenotherium magnum* for some specimens from Cherevichnoe and Maragheh, distinguishing them from *H. wongii* (also included by him in *Hyaenotherium*) on the basis of some slight differences in size and proportions. However, as noted by him (p. 104), the samples he had available for study were relatively small, and in particular, the comparative material of *H. wongii* described by Zdansky (1924) is difficult to use due to inaccuracies in the published measurements. Studies of the Chinese material (Werdelin, 1988b) show that Semenov was correct in expressing some reservations in this regard. The expanded samples and corrected measurements establish a much greater range of variability within *H. wongii* than previously realized. A comparison of the appended tables in Werdelin (1988b) with Tables 6 and 8 of Semenov (1989) show that the sample of *Hyaenotherium magnum* from Cherevichnoe fits well into the range of variation exhibited by the different samples of *H. wongii* from China and Europe. We conclude that these two taxa are synonymous. At the same time, the present cladistic analysis shows that Semenov (1989) was amply justified in erecting the new genus *Hyaenotherium* for these specimens.

**Hyaenictitherium hyaenoides* (Zdansky, 1924)

Synonymy. – □1887 *Palhyaena hipparionum* (Gervais) – Kittl, pp. 333–335, Pl. 15:3. □1900 *Ictitherium hipparionum* Sintsov, p. 347. □1924 *Ictitherium hyaenoides* sp. nov. – Zdansky, pp. 84–91, Fig. 7, Pls. 16:3–4; 17:1–4. □1925 *Ictitherium hipparionum* (Gervais) – De Mecquenem, p. 50, Pl. 9:6 □1938 *Hyaenictitherium hyaenoides* gen. nov. – Kretzoi, p. 114. □1941 *Ictitherium hipparionum* (Gervais) – Orlov, pp. 61–78, Figs. 1–4. □1979 *Lycyaena spathulata* sp. nov. – Qiu, Huang & Guo, p. 200. □1980 *Hyaenictitherium hyaenoides* (Zdansky) – Howell & Petter, pp. 584, 588–589. □1981 *Thalassictis (Hyaenictitherium) hyaenoides* (Zdansky) – Solounias & De Beaumont, p. 295, Fig. 1A. □*pars* 1985 *Thalassictis hyaenoides* (Zdansky) – Qiu, pp. 97–98, Pls. 2:3; 3:2–3; 4:1. □*pars* 1985 *Thalassictis wongii* (Zdansky) – Qiu, pp. 98–99, Pl. 4:2. □1988b *Thalassictis hyaenoides* (Zdansky) – Werdelin, pp. 229–234, Fig. 11. □1989 *Hyaenictitherium hyaenoides* (Zdansky) – Semenov, pp. 122–126, Figs. 34–36.

Localities. – China: San Chia Liang Kou (Zdansky's Loc. 43(1), Loc. 44, Yan Mu Kou (Zdansky's Loc. 49), Chen Chia Mao Kou (Zdansky's Loc. 108), Huan Lou Kou (Zdansky's Loc. 109), Loc. 116, Chin Kou, Hsiao Kou Shan, Liao Wan Kou, Lu Kao Ling, Nan Ho, Pai Tao Tsun, Ta Tung Kou; Iran: Maragheh; USSR: Grossulovo, Kalmakpaj, Novo-Emetovka.

Age. – Turolian (MN Zones 11–12).

Discussion. – The content and morphological features of this species were in doubt for a long time. It was not until the recognition of *Palinhyaena reperta* by Qiu *et al.* (1979) that it proved possible to distinguish the two taxa conflated in Zdansky's (1924) conception of *H. hyaenoides* from each other. This topic has been dealt with extensively elsewhere (Qiu 1985; Werdelin 1988b), and will not be considered further herein.

With the elimination of specimens belonging to *P. reperta*, *H. hyaenoides* has been shown to be a large *'Thalassictis'*-like form, exhibiting character states more primitive than *P. reperta*, such as a longer M_1 talonid (the analysis of talonid length of *H. hyaenoides* in Crusafont Pairó & Petter 1969 is based on *P. reperta*), but more derived than *H. wongii* (e.g., broader premolars). It is clear from the renewed analysis of this species that Kretzoi (1938) was justified in erecting the new genus *Hyaenictitherium* for it.

**Lycyaena dubia* Zdansky, 1924

Synonymy. – □1924 ?*Lycyaena dubia* sp. nov. – Zdansky, pp. 91–93, Fig. 10, Pl. 33:2–3. □1981 *Thalassictis (Lycyaena)* sp. nov. – Solounias & De Beaumont, p. 295, Fig. 1B. □1985 *Thalassictis (Lycyaena) dubia* (Zdansky) – Qiu, p. 100, Pl. 4:3. □1988b *Thalassictis (Lycyaena) dubia* (Zdansky) – Werdelin, pp. 246–251, Fig. 20.

Localities. – China: Yan Mu Kou (Zdansky's Loc. 49), Chen Chia Mao Kou (Zdansky's Loc. 108), Chou Chia Kou, Hsiao Kou Shan, Liao Wan Kou, Nan Ho, Pai Ma Kou, Pai Tao Tsun, Tu Kou.

Age. – Turolian (MN Zone 12).

Discussion. – Perhaps because Zdansky himself was unsure of its affiliations, the *Lycyaena* he described (Zdansky 1924), *L. dubia,* has been ignored by most subsequent writers. When Solounias & De Beaumont (1981), wrote about *Lycyaena* from the Frick collection of Chinese fossil hyaenids in the American Museum of Natural History, they referred to this material as a new species rather than resurrecting Zdansky's species. Recently, however, *L. dubia* has been revived (Qiu 1985; Werdelin 1988b), and has been clearly shown to be a well defined species of *Lycyaena*. Werdelin (1988b) has, as noted above, shown that *L. dubia* is close to *L. chaeretis* from Samos and Pikermi, so close that they may be conspecific. However, until sufficient material has been recovered of the latter species, it is better to consider *L. dubia* a distinct species of *Lycyaena*. Furthermore, since *L. dubia* is the better known of these species, it has been used in the core data set as representative of *Lycyaena*.

'Leecyaena' bosei (Matthew, 1929)

Synonymy. – □1868 *Felis cristata* (*errore*) – Falconer, p. 548, Pl. 25:1–4. □*pars* 1880 *Hyaena sivalensis* Falconer & Cautley – Bose, p. 128. □1884 *Hyaena sivalensis* Bose – Lydekker, p. 303, Pl. 34. □1929 *Hyaena bosei* sp. nov. – Matthew, p. 493, Fig. 28. □1932 *Hyaenictis bosei* (Matthew) – Pilgrim, pp. 122–125. □1935 *Hyaenictis bosei* (Matthew) – Colbert, p 108. □*pars* 1970 *Leecyaena bosei* (Matthew) – Ficcarelli & Torre, p. 27. □1987 *Hyaenictis bosei* (Matthew) – De Vos, Leinders & Hussain, pp. 364–365.

Localities. – Sivaliks: Exact locality not known.

Age. – Not known. Pilgrim (1932) suggests that it comes from the Pinjor Stage of the Upper Sivaliks. The species may thus be Ruscinian/Villafranchian.

Discussion. – As noted elsewhere (Werdelin, Turner & Solounias, MS), this species cannot be referred to *Hyaenictis*. However, *'H.' bosei* bears considerable resemblances to *Leecyaena lycyaenoides*, as comparison of Fig. 13 with Pl. 1:1 of Young & Liu (1948) will show. Young & Liu (1948) discounted affinity between these two taxa on the basis of the shape of the snout and upper carnassial, and the position of M^1. However, their comparison was based on Matthew's (1929) figure of *'H.' bosei*, an illustration that differs from the actual specimen in some respects, notably in the shape and position of the protocone of P^4. The same

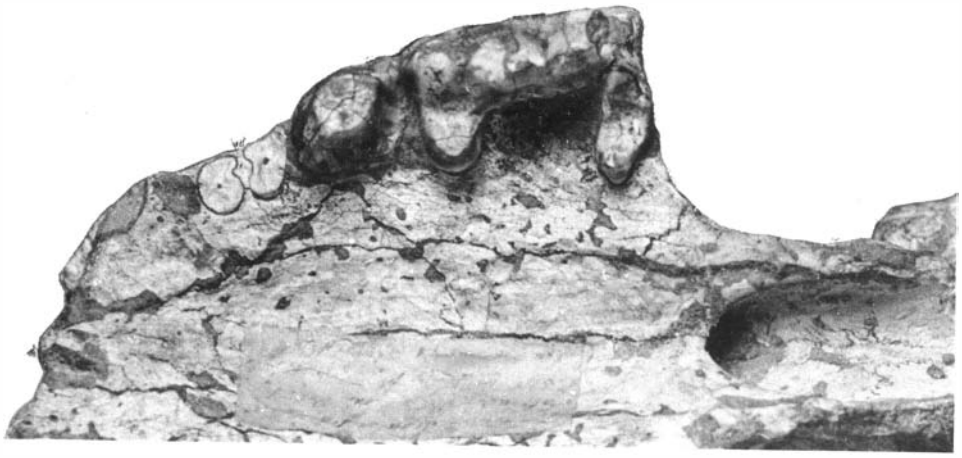


Fig. 13. Dentition of holotype of *'L.' bosei* (BM M37133). Natural size.

is true of the relationship between the drawing of *L. lycyaenoides* and the actual specimen. In Fig. 1B of Young & Liu (1948), M^1 is drawn as if it where placed some distance away from P^4, and at right angles to it, whereas in reality this tooth is placed adjacent to P^4 as in all other hyaenids (except *C. crocuta*), which can be clearly seen in Pl. 1:1 of the same paper. The angle of M^1 against P^4 is more obtuse in *L. lycyaenoides* than in *'H.' bosei*, and in this respect, and its greater size, the Chinese form is derived relative to the Sivalik species. Nevertheless, these forms are close, and Young & Liu (1948) were correct in comparing them.

'H.' bosei also shows general similarities to *I. abronia* (Hendey 1974a, Fig. 19), particularly in the relative sizes of P^{3-4} and in the size and position of M^1. However, *I. abronia* is more primitive in retaining M^2 (in most specimens).

Approximate phylogenetic position. – The discussion above suggests that this taxon should be placed somewhere between nodes 9 and 11 in the cladogram. We tentatively suggest that it may be close to *Leecyaena lycyaenoides* (node 10).

'Hyaenictitherium' namaquensis (Stromer, 1931)

Synonymy. – □1931 *Hyaena namaquensis* sp. nov. – Stromer, pp. 26–31, Pls. 1:1–2; 2:1–2. □1974a *Hyaena* sp. B – Hendey, pp. 118–125, Figs. 22–23. □1978 *Hyaenictitherium namaquensis* (Stromer) – Hendey, p. 282. □1980 *Hyaenictitherium* cf. *namaquensis* (Stromer) – Howell & Petter, pp. 583–584. □1980 *Ictitherium arkesilai* sp. nov. – Esu & Kotsakis, pp. 243–245, Pl. 21.

Localities. – Libya: Sahabi; Namibia: Kleinzee; South Africa: Langebaanweg.

Age. – Ruscinian.

Discussion. – A discussion of this species and its probable affinities is presented elsewhere (Werdelin, Turner & Solounias, MS). Hendey (1978) was undoubtedly correct in referring his *Hyaena* sp. B from Langebaanweg to *'H.' namaquensis.* As can be seen from the data presented by Esu & Kotsakis (1980) and Howell & Petter (1980), *I. arkesilai* matches this species in nearly every particular, and there is no reason to keep them distinct. This taxon may also be present in the Omo Group (Howell & Petter 1976).

Approximate phylogenetic position. – Near *Hyaenictitherium hyaenoides* at node 4 in the core cladogram.

**Chasmaporthetes borissiaki* (Khomenko, 1932)

Synonymy. – □1932 *Hyaena borissiaki* sp. nov. – Khomenko, pp. 129, Pl. 1–9. □1955b *Hyaena borissiaki* Khomenko – Ewer, pp. 852–853. □1967 *'Hyaena' borissiaki* Khomenko – De Beaumont, p. 105. □1970 *Lycyaena borissiaki* (Khomenko) – Ficcarelli & Torre, p. 28. □1977 *Chasmaporthetes borissiaki* (Khomenko) – Galiano & Frailey, p. 9. □1981 *Chasmaporthetes borissiaki* (Khomenko) – Berta, pp. 352–353. □1987 *Chasmaporthetes borissiaki* (Khomenko) – Qiu, p. 40. □1988 *Chasmaporthetes borissiaki* (Khomenko) – Kurtén & Werdelin, p. 48.

Localities. – France: Perpignan; USSR: 'Roussillon fauna', Moldavian SSR.

Age. – Ruscinian.

Discussion. – This taxon is discussed by Werdelin, Turner & Solounias (MS), who note that it is similar in most respects to taxa referred there to *Hyaenictis sensu lato.* However, in the reduced P^4 protocone and loss of M_2, it does display derived characters of *Chasmaporthetes,* and thus, while almost intermediate between typical members of these genera, can confidently be placed with the latter on the basis of these synapomorphies.

'Thalassictis' chinjiensis (Pilgrim, 1932)

Discussion. – We are here synonymizing this taxon with *'T.' proava,* as suggested by several authors (Colbert 1935; De Vos *et al.* 1987; Schütt 1971). This separate listing of *'T.' chinjiensis* is retained for ease of reference only.

Lycyaenops rhomboidea Kretzoi, 1938

Synonymy. – □1938 *Lycyaenops rhomboidea* gen. et sp. nov. – Kretzoi, p. 115, Fig. 3.

Localities. – Hungary: Pestszentlörinc.

Age. – Turolian (?MN Zone 12)

Discussion. – When he described this new genus and species, Kretzoi (1938) also included *Chasmaporthetes lunensis* in the genus. However, this is surely not correct: the premolars of *L. rhomboideae* as illustrated by Kretzoi (1938, Fig. 3) bear no similarity whatsoever to those of *Chasmaporthetes* in their general characteristics. In fact, the characters of *L. rhomboideae* as seen in this illustration: robust, low premolars with low, but large accessory cusps, and an M_1 with a low, long blade and strongly reduced uni- or bicuspid talonid (it should be remarked that Kretzoi was not entirely incorrect: the M_1 is strongly reminiscent of *Chasmaporthetes*), make it impossible to relate this species to any other known hyaenid species, or even lineage. The combination of characters is so bizarre that one wonders whether the specimen as illustrated is a composite. In any case, we consider *L. rhomboideae* a *nomen dubium* pending restudy of the Pestszentlörinc material.

Approximate phylogenetic position. – Indeterminate.

**Tunguricitis spocki* Colbert, 1939

Synonymy. – □1939 *Tunguricitis spocki* gen. et sp. nov. – Colbert, pp. 67–71, Figs. 12–13.

Localities. – China: Tung Gur.

Age. – Astaracian (MN Zone 8).

Discussion. – The dental morphology of *T. spocki* is treated in some detail below, under *'Protictitherium' punicum.* It shows several autapomorphic characters and is of little use in determining the relationships of the taxon. The auditory bulla seems generally comparable to that of *H. wongii* (Hunt 1989), and more advanced than that of *Plioviverrops.* The alisphenoid canal is retained in *T. spocki* (Colbert 1939, Fig. 13), as it is in *Plioviverrops.*

'Thalassictis' montadai (Villalta Comella & Crusafont Pairó, 1943)

Synonymy. – □1943 *Ictitherium montadai* sp. nov. – Villalta Comella & Crusafont Pairó, p. 103, Figs. 26–28, Pls. 7, 8, 9, 10:1. □1951 *Progenetta* aff. *montadai* Villalta & Crusafont – Viret, p. 85, Pl. 1:16. □1969 *Progenetta montadai* Villalta & Crusafont Pairó – Crusafont Pairó & Petter, pp. 19–22, Pls. 1:1–2; 2:2–4, 7–8. □1973 *Progenetta montadai* Villalta & Crusafont Pairó – Crusafont Pairó & Golpe Posse, pp. 106–113, Pl. 1–5. □1976 *Miohyaena montadai* Villalta & Crusafont – Schmidt-Kittler, pp. 88–90, Pl. 2:4.

Localities. – Spain: Ballestar, Can Barra, Can Mata, Hostalets de Pierola. Turkey: Yeni Eskisihar.

Age. – Upper Astaracian – lower Vallesian (MN Zones 8–9).

Discussion. – There is little to add here to the discussions of this taxon given by Crusafont Pairó & Petter (1969) and Schmidt-Kittler (1976). It is considerably more derived in its morphology than *'T.' certa,* especially in the upper dentition (Crusafont Pairó & Petter 1969: Pl. 2:8), but shows the same primitive M_1 paraconid as that taxon. We conclude that referral to *'Thalassictis'* rather than *Hyaenotherium* is justified, at least for the Astaracian material. The Vallesian material seems to show some more derived features of the M_1 (e.g., higher paraconid), and referral to *'Thalassictis'* then becomes more questionable. This also implies doubt as to the homogeneity of the material ascribed to this species by various authors. However, since we have not been able to study all the material personally, we prefer to keep the taxonomy at status quo.

Approximate phylogenetic position. – *'T.' montadai* may be placed between nodes 2 and 3 of the core cladogram.

Plioviverrops guerini (Villalta Comella & Crusafont Pairó, 1945)

Synonymy. – □1945 *Herpestes guerini* sp. nov. – Villalta Comella & Crusafont Pairó, pp. 94–99, Figs. 4–5, Pl. 2:2–3. □1969 *Plioviverrops? guerini* Villalta & Crusafont Pairó – Crusafont Pairó & Petter, pp. 24–26, Pl. 4:7–8. □1972 *Plioviverrops guerini* Villalta & Crusafont – De Beaumont & Mein, pp. 390–391.

Localities. – Spain: Concud, Los Mansuetos, Piera.

Age. – Turolian (MN Zone 12).

Discussion. – The few available specimens of this species indicate an animal similar to, but slightly larger than, *Plioviverrops gaudryi.* The proportions of the M_1 cusps clearly indicate affinities with *Plioviverrops,* but at the same time this form is less derived than the approximately contemporaneous *P. orbignyi* in having a lower metaconid and higher protoconid than that species.

Approximate phylogenetic position. – Its close relationship with *P. orbignyi* makes it possible to place this taxon in a group with the other species of *Plioviverrops* at node 1 in the core cladogram.

Hyaenictis almerai Villalta Comella & Crusafont Pairó, 1945

Synonymy. – □1945 *Hyaenictis almerai* sp. nov. – Villalta Comella & Crusafont Pairó, pp. 114–117, Fig. 18, Pl. 6:1.

Localities. – Spain: Sant Miquell del Taudell.

Age. – Turolian (?MN Zone 12).

Discussion. – The type and only specimen of this species shows a remarkable combination of characters, which makes it very difficult indeed to establish its generic status. We shall attempt here to narrow the possibilities down by considering its characters one by one.

M_2: The specimen preserves the alveolus for a small M_2. The size of this alveolus excludes taxa such as *Ictitherium* and more primitive genera from consideration.

M_1: In general outline, this tooth strongly resembles M_1 of *C. borissiaki* (Khomenko 1932, Pl. 5:3–4). The metaconid is absent. In taxa in which the metaconid is regularly absent, it may sometimes appear as an atavism (e.g., *A. eximia*). In taxa in which the metaconid is regularly present, however, it is apparently much more rarely lost as an individual variation (in the many specimens of *T. wongii*, there is not one which does not have the metaconid present). Thus, the absence of the metaconid leads us to exclude taxa such as *'Thalassictis'* and *Lycyaena*, as well as genera placed cladistically between these two.

P_4: This tooth is very similar to P_4 in *B. beaumonti*, and presumably this was the basis for the referral of the latter species to *Hyaenictis* by Qiu (1987). At the same time, it is also morphologically close to P_4 in *C. borissiaki*. These resemblances are probably due to primitive retentions, and have little value in the present context.

P_3: Is again similar to *B. beaumonti*, although it has a straighter profile and a much larger anterior accessory cusp. Again, the closest comparison is with *C. borissiaki*.

P_2: Has a distinctly 'ictithere' look, with its low profile and straight, sloping anterior face. This is very different from P_2 in *B. beaumonti*, in which the anterior face of P_2 is nearly vertical, and the entire tooth strongly asymmetrical (De Beaumont 1968). In fact, none of the species that may in other respects be compared with *H. almerai* has a P_2 that looks anything like this.

Ramus: Has two mental foramina. This character is variable in several taxa, and is of little value in establishing the affinities of an isolated specimen. The ramus has a flat ventral profile, similar to that seen in *H. hyaenoides* and *L. dubia* (Werdelin 1988b) and quite different from that of, e.g., *P. reperta*.

In conclusion, there are only a few taxa that have characters, such as loss of the M_1 metaconid, which relate them to *H. almerai*. Of these, *Crocuta* and *Pachycrocuta* are out of the question, due to other characteristics, as is *Adcrocuta*. There remain *Chasmaporthetes* and *Hyaenictis*. As we have hinted at above, the closest comparison of *H. almerai* is with *C. borissiaki*; these taxa share features such as the shortened M_1 talonid (relative to, among others, *H. graeca*) and the convex anterior faces of the major cusps of P_{3-4}, which indicate some form of relationship. At the same time, *H. almerai* is more primitive than *C. borissiaki* in its retention of M_2, and has evolved away from *Chasmaporthetes* in its broader and more imbricated premolars. *H. almerai* thus does not fit comfortably into either *Chasmaporthetes* or *Hyaenictis* as those taxa are conceived by Werdelin, Turner & Solounias (MS). However, it is at the general *Hyaenictis* grade of development, and we here provisionally keep it in that genus, while recognizing that it may eventually require a genus of its own.

Approximate phylogenetic position. – The discussion above, and in the paper by Werdelin, Turner & Solounias (MS), suggests a position between nodes 5 and 6 in the core tree.

Hyaenictis? silberbergi (Broom *in* Broom & Schepers, 1946)

Synonymy. – □1945 *Lycyaena silberbergi* sp. nov. (*nomen nudum*) – Broom, p. 389, Fig. 1. □1946 *Lycyaena silberbergi* sp. nov. – Broom *in* Broom & Schepers, p. 83, Fig. 8. □1948 *Lycyaena silberbergi* Broom – Broom, pp. 17–19, Fig. 11. □1955b *Lycyaena silberbergi* Broom – Ewer, pp. 839–842, Figs. 1–2, Pl. 1:1. □*pars* 1967 *Lycyaena silberbergi* Broom – Ewer, p. 116. □*pars* 1987 *Chasmaporthetes silberbergi* (Broom) – Qiu, p. 41.

Localities. – South Africa: Sterkfontein, Swartkrans; Tanzania: Laetoli.

Age. – Lower Pleistocene.

Discussion. – Article 13 of the *International Code of Zoological Nomenclature* (ICZN) (Ride *et al.* 1985) states that in order to be available, every scientific name published after 1930 must be 'accompanied by a description or definition that states in words characters that are purported to differentiate the taxon'. The first publication of the name *Lycyaena silberbergi* is by Broom (1945). Broom's comments on the species in this paper read in full (1945, p. 389):

> I have just had given me a few days ago by the Abbé Breuil the snout of a primitive hyaena. This was found by Dr. H.K. Silberberg at Sterkfontein three years ago. I have seen Dr. Silberberg and find that he picked up the specimen in the lower part of the Sterkfontein cave. The spot is almost directly below that in which the *Plesianthropus* type skull was found; but at about 60 ft. lower level. The fossils which I have collected at this lower level appear to be similar to those above.
>
> We already knew a species of *Crocuta* from Kromdraai very closely allied to the European *Crocuta spelaea*, and from some part of Sterkfontein a jaw of *Hyaena hyaena*, and from the main Sterkfontein cave portions of a hyaena with the crowns of the teeth hopelessly broken. The hyaena discovered by Dr. Silberberg is a Pliocene type which must, I think, be placed in the genus *Lycyaena*. *Lycyaena* is a primitive genus found in the Lower and Middle Pliocene of Europe and India. While there is a possibility of the Pliocene *Hyaena* surviving into Pleistocene with the sabre-tooth cats, it now seems more likely that the Sterkfontein cave is Pliocene; and if so we must put the other caves to an earlier date also.

The species name is given in the figure caption. It is evident that none of this can be construed as 'characters that are purported to differentiate the taxon', since there is no mention of any characters whatsoever. We thus conclude that *L. silberbergi* of Broom, 1945, is a *nomen nudum*.

The situation with regard to Broom & Schepers (1946) is different, however. Aside from a discussion of the origin of the specimen, and comments on its stratigraphical significance, as in the earlier paper, Broom has this to say about *L. silberbergi* (1946, p. 83):

> A few teeth of both jaws are preserved and these show that while the animal is a hyaena it differs markedly from both the living Hyaenas and from Crocuta, and that the species belongs to or is near to the Pliocene genus Lycyaena. I at once visited Dr. Silberberg, and found that he had personally picked up the specimen in the lower workings at the Sterkfontein cave. The spot where it was found is about directly below the spot where the type skull of Plesianthropus was found, but at about 60 feet lower level. Though this working is so much lower, the other specimens I found here did not seem to indicate any difference in age. *As will be seen from the figure the premolars are larger than in modern hyaenas and the anterior and posterior cusps better developed.* [Italics added].

While in no way constituting an exhaustive or even sufficient description of the species, these comments on characters differentiating the type from modern hyaenas are undoubtedly sufficient to make the name valid within the meaning of Article 13 of the code, cited above. We thus conclude that the valid authorship reference for this species is Broom *in* Broom & Schepers, 1946, not Broom, 1948, as per other writers (Ewer 1955b; Kurtén & Werdelin 1988).

Most commentators have suggested synonymy between this species and *C. nitidula* (Ewer 1967; Qiu 1987). Detailed arguments why this is probably not the case are presented elsewhere (Werdelin, Turner & Solounias, MS). On the other hand, it is clear that this species must belong to either *Chasmaporthetes* or its sister-genus *Hyaenictis.* Which of these genera is the proper home for the species is still unclear. On the one hand, it is quite different from its contemporary *C. nitidula,* but on the other it displays several characteristics which differentiate it from other *Hyaenictis.* These problems are discussed by Turner (1987) and Werdelin, Turner & Solounias (MS). For purposes of this monograph, we refer the species questionably to *Hyaenictis.*

Approximate phylogenetic position. – As in the case of the previous taxon, a position between nodes 5 and 6 of the core tree is indicated.

**Leecyaena lycyaenoides* Young & Liu, 1948

Synonymy. – □1948 *Leecyaena lycyaenoides* gen. et sp. nov. – Young & Liu, pp. 274–280, Fig. 1, Pl. 1:1–2. □1987 *Leecyaena lycyaenoides* Young & Liu – Qiu, pp. 71–72, Pl. 9:4.

Localities. – China: Yûshe (exact locality not known).

Age. – ??Ruscinian.

Discussion. – With its combination of primitive (narrow premolars, large M^1, presence of M_2) and derived (large I^3, reduced premolar accessory cusps) characters, this form has long been a problem taxon in hyaenid phylogeny. Qiu (1987) has recently suggested it as a stem group to his *Pliohyaena* (=*Pliocrocuta*). Whilst generally agreeing with this assessment, we find it somewhat too restrictive, as it does not take into account all modern hyaenas. Indications are (see also below) that *L. lycyaenoides* is structurally close to the ancestor of the group including all Recent hyaenas (crown group of authors).

Ictitherium pannonicum Kretzoi, 1952

Synonymy. – □1938 *Palhyaena hungarica* – Kretzoi, p. 113 (*nomen nudum*). □1952 *Ictitherium* cf. *robustum* Nordmann – Kretzoi, p. 18, Pl. 2:6. □1952 *Ictitherium pannonicum* sp. nov. – Kretzoi, pp. 18–19, Pl. 2:3, 5. □1952 *Palhyaena hungarica* sp. nov. – Kretzoi, pp. 19–22, Fig. 2, Pl. 2:1, 2, 7. □?1985 *Ictitherium pannonicum* Kretzoi – Semenov, pp. 23–27, Fig. 1. □?1986 *Thalassictis* aff. *hipparionum* (Gervais) – Adrover *et al.*, pp. 504–506, Fig. 1d. □1989 *Ictitherium pannonicum* Kretzoi – Semenov, pp. 70–73, Figs. 23–24.

Localities. – Hungary: Polgárdi; Spain: ?Valdecebro; USSR: ?Chobruchi, ?Cherevichnoe, ?Novaja Emetovka.

Age. – Turolian (MN Zones ?12–13).

Discussion. – The Polgárdi 'ictithere' has long been thought simply to be another sample of one of the common Turolian species, either *H. wongii* or *I. viverrinum,* and the discriminating features pointed out by Kretzoi (1952) have been discounted. The recent renewed discussion of this species by Semenov (1985) forces reconsideration of this issue, upon which it is evident that Kretzoi (1952) was amply justified in erecting a new species for the Polgárdi material.

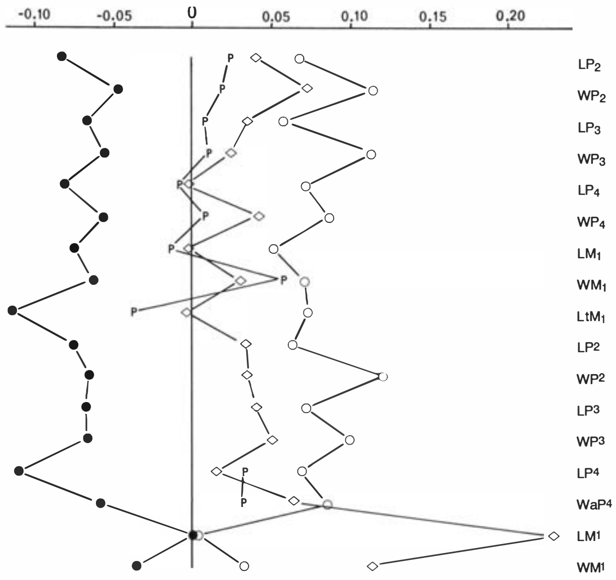


Fig. 14. Ratio diagram of some hyaenid taxa. Standard = *H. wongii* (Chinese sample); ○ = *H. hyaenoides* (Chinese sample); ● = *I. viverrinum* (Chinese sample); ◇ = *I.* cf. *pannonicum* (Black Sea sample, data from Semenov 1985); P = *I. pannonicum* (Polgárdi, data from Semenov 1985).

In his original discussion of *I. pannonicum* [including *P. hungarica* – this synonymy can hardly be doubted – and Kretzoi's *I.* cf. *robustum,* as Semenov (1985) is clearly correct in identifying this tooth as an M^2, rather than M^1, as suggested by Kretzoi], Kretzoi (1952) notes the particularly large M_2 as a distinguishing characteristic. However, several inconsistencies and errors in Kretzoi's (1952) treatment of this species have rendered his work of doubtful value. First of all, Kretzoi (1952) selected as holotype of his *I. pannonicum* a specimen, Ob/2653, that he does not figure, which casts some small doubt on the scope of the species. This does not, however, invalidate the species, as Semenov (1985) seems to suggest, since the ICZN does not make any provisions regarding illustration of types. Second, Kretzoi (1952) has illustrated one specimen (Pl. 2:3) that does not match the descriptions of the material given in the text. Third, the characteristic M_2 is nowhere illustrated, it is only described in the text, and specimens with this tooth missing are illustrated instead (Kretzoi 1952, Fig. 2, Pl.2:1). In view of these uncertainties, it is understandable that most writers have viewed *I. pannonicum* with circumspection.

However, the description of material from the southern USSR by Semenov (1985) has shed entirely new light on this issue. This author describes further material showing the extremely large M_2 stated by Kretzoi to be characteristic of *I. pannonicum.* The M_2 of Semenov's (1985) material can be clearly seen in his illustration and is accompanied by a correspondingly large M^{1-2}.

Having thus established the validity of Kretzoi's (1952) *I. pannonicum,* as distinct from *'Thalassictis'* spp. of the same

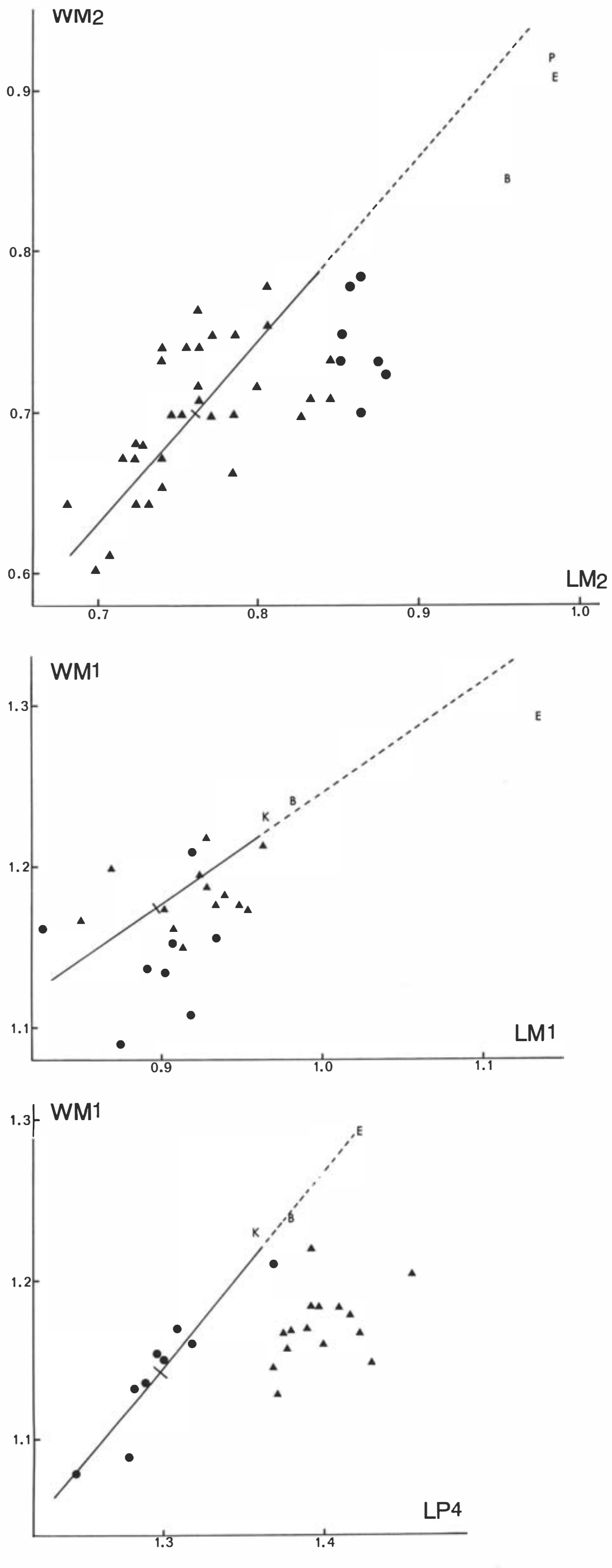


Fig. 15. Bivariate diagrams showing allometric relationship of molars of some species of *Ictitherium.* ▲ = *H. wongii* (Chinese specimens); ● = *I. viverrinum* (Chinese specimens); B = *I. intuberculatum* (data from Ozansoy 1965); E = *I.* cf. *pannonicum* (Black Sea, data from Semenov 1989); K = *I. kurteni*; P = *I. pannonicum* (Polgárdi, data from Semenov 1985). In the top two diagrams the reduced major axis is for *H. wongii* as no line for *I. viverrinum* is defined. In the bottom diagram the axis is for *I. viverrinum.* The solid line represents two standard deviations around the mean, the dotted line represents extrapolation.

size range, two questions arise. (1) Does the Polgárdi material belong to the same species as the Black Sea material? (2) What are the affinities of these materials?. Despite the similarities in such features as the shape and size of M_1 and, particularly, the size of M_2 and M^{1-2}, the answer to the first question must probably be no. The features mentioned are all primitive characters, which distinguish these forms from more derived hyaenids, such as *T. wongii*, cf. reduction in size of M^1 at node 3 in the core cladogram (Fig. 37). In other features, such as the shape of P^4 (compare Kretzoi 1952, Pl. 2:7, with Semenov 1985, Fig. 1B) and the metrics of the premolars (Fig. 14), as well as (so far as can be judged from the figures; Kretzoi, Fig. 2, Pl. 2:1–3, 5; Semenov, Fig. 1C–D) the shape and proportions of the cusps of P_4, these two forms are at least sufficiently different that their synonymy must be strongly questioned. However, since we have not seen the material personally, we prefer to here retain the synonymy employed by Semenov (1985, 1989).

As regards the affinities of *I. pannonicum* from Polgárdi and the Black Sea region, it is clear that this material, as explicitly noted by Kretzoi (1952) belongs to the *Ictitherium sensu lato* grade group of taxa, i.e., should be placed below node 3 in the core cladogram (Fig. 37). Among all hyaenid species that have unreduced posterior molars, these taxa are the largest. In the proportions of the teeth they show a marked similarity to *I. viverrinum* (Fig. 14), and thus differ clearly from another large ictithere, *I. kurteni*, in which the P^3 is greatly enlarged (Werdelin 1988a). In the ratio diagram (Fig. 14), it appears that the posterior molars of these forms are relatively larger than, and differently proportioned from, those of *I. viverrinum*. More detailed analysis reveals, however, that this is a simple allometric effect (Fig. 15). Thus, there is on present evidence nothing, aside from their markedly greater size, to differentiate these forms from *I. viverrinum*. This size difference is so great, however, as to preclude synonymy, and we conclude that *I. pannonicum* from Polgárdi is a valid taxon, and that it is either closely related to, or may be conspecific with, the material described under that name by Semenov (1985).

Although somewhat larger than the Polgárdi specimens of *I. pannonicum*, the specimen referred to *Thalassictis* aff. *hipparionum* by Adrover *et al.* (1986) shows the characters of *Ictitherium* in the carnassial (low blade, long talonid). The alveolus for M_2 in this specimen is quite large, and the specimen may belong to *I. pannonicum* or some closely related taxon.

Schmidt-Kittler (1976) considered *I. pannonicum* synonymous with his *I. hipparionum hipparionum*. This is clearly incorrect: the alveolus for M_2 in the figured specimen (Schmidt-Kittler 1976, Pl.4:2) is small, which is also noted in the text (p. 84: *Die M_2-alveole ist sehr klein...*). In this diagnostic character, Schmidt-Kittler's material is very different from (far more derived than) *I. pannonicum*, and synonymy is out of the question. Schmidt-Kittler (1976) in his discussion further relates his *I. hipparionum hipparionum* to the 'ictithere' from Maragheh (Schmidt-Kittler 1976, Fig. 85), which in reality is two taxa, both more derived than *Ictitherium* (Werdelin 1988b).

Approximate phylogenetic position. – This taxon, along with some few others, represents a previously unrecognized radiation of *Ictitherium*. It can be placed near *I. viverrinum* on the core tree.

'Pachycrocuta' bellax (Ewer, 1954)

Synonymy. – ☐1952 *Crocuta* cf. *brevirostris* – Toerien, p. 295. ☐1954 *Hyaena bellax* sp. nov. – Ewer, p. 579, Figs. 9, 11, Pl. 3:1–3. ☐1970 *Pachycrocuta bellax* (Ewer) – Ficcarelli & Torre, p. 18. ☐1974a *Hyaena (Parahyaena) bellax* Ewer – Hendey, p. 149. ☐1980 *Pachycrocuta bellax* (Ewer) – Howell & Petter, pp. 607–610. ☐1986 ?*Pachycrocuta bellax* (Ewer) – Turner, pp. 207–208.

Localities. – South Africa: Kromdraai A, Makapansgat 3, Sterkfontein 4, 5..

Age. – Villafranchian–Pleistocene.

Discussion. – This hyaenid is represented by scanty remains from the two above-mentioned localities. It is highly likely that it is synonymous with *P. brevirostris* (Turner 1990), but appears in several respects (position of infra-orbital foramen, shape and size of accessory cusps on premolars, shape and size of P^2, presence of metaconid on M_1) to be more primitive than the Eurasian form. However, these characteristics could also be accounted for by individual variation. The available material is insufficient to settle this question without renewed study of the entire material of *P. brevirostris.* We therefore provisionally retain the species *'P.' bellax.*

Approximate phylogenetic position. – Probably close to *P. brevirostris.*

'Hyaenictis' forfex (Ewer, 1955a)

Discussion. – Turner (1988) has convincingly shown that this species is based on a composite specimen: a mandible from *P. brunnea* mistakenly associated with a skull of *H. hyaena.* Thus, *H. forfex* need not concern us further here.

Chasmaporthetes nitidula (Ewer, 1955b)

Synonymy. – ☐1955b *Lycyaena nitidula* sp. nov. – Ewer, pp. 842–847, Figs. 3–6, Pl. 1:2. ☐*pars* 1967 *Lycyaena silberbergi* Broom – Ewer, p. 116. ☐1967 *Euryboas nitidula* (Ewer) – De Beaumont, p. 105. ☐1977 *Chasmaporthetes nitidula* (Ewer) – Galiano & Frailey, p. 9. ☐*pars* 1987 *Chasmaporthetes silberbergi* (Broom) – Qiu, p. 41. ☐1988 *Chasmaporthetes nitidula* (Ewer) – Kurtén & Werdelin, p. 50.

Localities. – South Africa: Swartkrans.

Age. – Lower Pleistocene.

Discussion. – The affinities of this taxon with *Chasmaporthetes* are not in doubt (Kurtén & Werdelin 1988). It represents an extreme within this genus with its very high premolars exhibiting greatly enlarged accessory cusps. Despite suggestions to the contrary (Ewer 1967; Qiu 1987) it is probably not conspecific with *H.? silberbergi* (see above, and Werdelin, Turner & Solounias, MS).

Approximate phylogenetic position. – This taxon should be placed, as one of several *Chasmaporthetes*, near *C. lunensis* on the core tree.

'Hyaenictis' piveteaui Ozansoy, 1965

Discussion. – Both Schmidt-Kittler (1976) and Howell & Petter (1985) have suggested that *H. piveteaui* was based on juvenile specimens of *Dinocrocuta senyureki.* We concur with this assessment, and this species will not be considered further here.

'Protictitherium' arambourgi (Ozansoy, 1965)

Discussion. – Schmidt-Kittler (1976) synonymizes this species with *Protictitherium crassum.* In view of the close resemblance in both morphology and measurements between the Yassiören mandible and those described by Schmidt-Kittler (1976), this assessment can hardly be questioned. However, the composition of *P. crassum* must be viewed with circumspection, a theme that is dealt with under the heading of that species (see above). The separate listing of *'P.' arambourgi* is presented here for convenience.

The specimens referred to this species by Ginsburg (1977), in particular the M^1, are more derived, and probably pertain to a small species of *'Thalassictis'* or *Hyaenotherium.*

Ictitherium intuberculatum Ozansoy, 1965

Synonymy. – ☐1965 *Ictitherium intuberculatum* sp. nov. – Ozansoy, pp. 27–30, Pl. 2:3, 4, 8.

Localities. – Turkey: Yassiören.

Age. – Vallesian (MN Zones 9–10).

Discussion. – Ozansoy (1965) did not designate a holotype for this species, and we hereby designate the mandible figured by him (Ozansoy 1965, Pl. 2:3) as the lectotype. To judge by its size and metric characteristics, this species is very close to *I. pannonicum* from Polgárdi (Figs. 14–15). It could well be conspecific with the Hungarian form, but there are some differences in the relative proportions of M_2 and M^1 (Figs. 14–15), and this, combined with the lack of diagnostic features in the figures, causes us to take a conservative approach and not synonymize the two. We emphasize this possibility, however.

Approximate phylogenetic position. – Whether or not it is conspecific with *I. pannonicum,* this species belongs to *Ictitherium sensu stricto,* and should be placed near *I. viverrinum* in the core cladogram.

'Ictitherium' prius Ozansoy, 1965

Synonymy. – ☐1965 *Ictitherium prius* sp. nov. – Ozansoy, pp. 25–26.

Localities. – Turkey: Sarilar.

Age. – ?Turolian (found on surface).

Discussion. – The description of this species, which is inadequate, suggests an animal of the size of a small *'Protictitherium'*. Until a more exhaustive description is published, we consider this species a *nomen dubium*.

Approximate phylogenetic position. – Indeterminate.

Pliocrocuta arambourgi (Ozansoy, 1965)

Discussion. – This species was considered conspecific with *Pachycrocuta* by Ficcarelli & Torre (1970) and Schütt (1971), and with *P. perrieri* by Howell & Petter (1985) We concur with the latter assessment.

Ictitherium ibericum Meladze, 1967

Synonymy. – ☐1967 *Ictitherium ibericum* sp. nov. – Meladze, p. 25–31, Pls. 1:5–6; 2:1–5. ☐1967 Melinae gen. – Meladze, p. 21, Pl. 1:2. ☐1989 *Ictitherium ibericum* Meladze – Semenov, p. 51, Fig. 20.

Localities. – USSR: Bazalethi.

Age. – Turolian (?MN Zone 13)

Discussion. – This poorly known species can be identified as a member of the genus *Ictitherium* on the basis of its large M_2 and M^{1-2} (Fig. 18). It is similar in size to *I. viverrinum*, but has shorter and broader premolars. Semenov (1989) also notes the less forwardly inclined protocone of P^4 as a distinguishing characteristic of *I. ibericum* relative to. *I. viverrinum*.

Approximate phylogenetic position. – With other *Ictitherium* at node 2 of the core cladogram.

'Ictitherium' nagrii Prasad, 1968

Synonymy. – ☐1968 *Ictitherium nagrii* sp. nov. – Prasad, pp. 22–23, Pls. 3:6; 23:2.

Localities. – India: Haritalyangar.

Age. – Nagri Formation (?Upper Vallesian – ?Lower Turolian).

Discussion. – Neither the descriptions nor the illustrations of this species given by Prasad (1968), nor in fact the material itself, which consists of a single fragmentary left mandible with P_{2-3}, are adequate for the identification of a new species of hyaenid. The teeth are of the general size of *L. sivalensis*. *I. nagrii* should be considered a *nomen vanum* (cf. Mones 1989).

'Protictitherium' llopisi (Crusafont Pairó & Petter, 1969)

Synonymy. – *Progenetta crassa llopisi* ssp. nov. – Crusafont Pairó & Petter, pp. 104–105, Pl. 4:2, 5.

Localities. – Spain: Can Bayona.

Age. – Vallesian–Turolian (MN Zones 10–12).

Discussion. – The reasons for our recognizing this form as a separate species are given under *P. crassum*, above.

Approximate phylogenetic position. – Below node 1 in the core tree, together with other species of *'Protictitherium'*.

'Ictitherium' adroveri Crusafont Pairó & Petter, 1969

Synonymy. – ☐1969 *Ictitherium adroveri* sp. nov. – Crusafont Pairó & Petter, pp. 22–23, Pl. 4:1, 6.

Localities. – Spain: Arquillo, Los Mansuetos.

Age. – Turolian (MN Zones 12–13).

Discussion. – This species is based on two isolated teeth: an M_1 from Los Mansuetos and a P^4 from Arquillo, both Turolian localities (Crusafont Pairó & Petter 1969). Neither of these teeth shows any particular distinguishing characteristics, except perhaps the P^4, in which the protocone extends slightly in front of the parastyle. This character is a primitive trait, however, and does not distinguish the tooth from such taxa as *'T.' sarmatica*. In their text, Crusafont Pairó & Petter (1969) note that they associate these two teeth by size and morphology. However, there is nothing particular in the morphology to suggest affinity, and size is at best a dubious taxonomic character in hyaenids (see, e.g., Turner 1984 and Werdelin 1988a, 1988b). Thus, we conclude that there is nothing in particular to say that these specimens in fact belong to the same species, and further, that no characters distinguishing either of these specimens from other contemporaneous hyaenids have been placed in evidence. We consider *I. adroveri* a *nomen dubium*.

Plioviverrops gervaisi De Beaumont & Mein, 1972

Synonymy. – ☐*pars* 1958 *Progenetta*? cf. *praecurrens* Dehm – Mein, p. 53. ☐1972 *Plioviverrops gervaisi* sp. nov. – De Beaumont & Mein, pp. 384–386, Pl. 1:3–7. ☐?1976 *Plioviverrops gervaisi* De Beaumont & Mein – Petter, p. 147, Pl. 1:39.

Localities. – France: Vieux–Collonges. Spain: ?Catalayud.

Age. – Orléanian (Upper Burdigalian) (MN Zone 4b).

Discussion. – De Beaumont & Mein (1972) described some few teeth from Vieux-Collonges under this name. However, in view of the small number of specimens of this species and of *P. gaudryi*, there must remain some doubt concerning the distinction between these two species. It is not unthinkable, in view of the morphological variability of other hyaenid species, that all these specimens pertain to the same species, despite their disparate ages. However, with this said, we have nothing to add to the descriptions and discussion of the specimens given by De Beaumont & Mein (1972).

As noted by Schmidt-Kittler (1976), this species and *'P.' intermedium* show marked similarities in the general structure of M_1. Most of these similarities are primitive characteristics, such as the height of the protoconid and structure of the talonid. Schmidt-Kittler (1976) concludes that *'P.' intermedium* is slightly but distinctly more derived in the direction of species such as *'P.' gaillardi* and *'P.' cingulatum.*

P. gervaisi is the oldest known hyaenid.

Approximate phylogenetic position. – This species can be placed together with other species of *Plioviverrops*, at node 1 in the core tree.

Plioviverrops gaudryi De Beaumont & Mein, 1972

Synonymy. – □*pars* 1951 *Jourdanictis grivensis* gen. et sp. nov. – Viret, pp. 75–76, Fig. 18, Pl. 2:8. □1972 *Plioviverrops gaudryi* sp. nov. – De Beaumont & Mein, p. 386, Fig. 2 (center), Pl. 1:2.

Localities. – France: La Grive Saint-Alban.

Age. – Astaracian (MN Zones 7–8).

Discussion. – This species, like *P. gervaisi*, is based on only a few teeth, and for this reason there must remain some doubt regarding the distinction between these two taxa. Other than that, there is little we can add to the descriptions of De Beaumont & Mein (1972) and Viret (1951), and we agree with the conclusion that these taxa point (in an evolutionary sense) towards *P. orbignyi.*

Approximate phylogenetic position. – Together with other species of *Plioviverrops* at node 1 in the core tree.

Proteles amplidenta nom. nov.

Synonymy. – □1974b *Proteles transvaalensis* sp. nov. – Hendey, pp. 35–38, Pl. 3.

Localities. – South Africa: Kromdraai Site B, Swartkrans.

Age. – Pleistocene.

Discussion. – Hendey (1974b) named the fossil *Proteles* from Kromdraai and Swartkrans *P. transvaalensis.* Unfortunately, this name is preoccupied by *P. cristatus transvaalensis* Roberts, 1932, a subspecies of the Recent species. The fossil material, for which the specific distinction from the extant form is not here questioned, requires a new name. We propose *Proteles amplidenta*, in reference to the somewhat larger dentition of the fossil form. *P. amplidenta* is morphologically similar to the extant *P. cristatus*, but is larger in overall size, has a larger canine, smaller and more anteriorly placed P_2, and more anteriorly placed P_3 (Gingerich 1974a; Hendey 1973; Hendey 1974b). This species does not aid in identifying the ancestors of *Proteles.* Presumably the termite-eating adaptation of this genus goes back in time well beyond this splitting event.

Approximate phylogenetic position. – Sister taxon to *Proteles cristatus.*

**Ikelohyaena abronia* (Hendey, 1974a)

Synonymy. – □1974a *Hyaena abronia* sp. nov. – Hendey, pp. 103–118, Figs. 19–21. □1974a *Hyaenictis preforfex* sp. nov. – Hendey, pp. 125–133, Fig. 24. □1978 *Hyaena abronia* Hendey – Hendey, pp. 270–279, Fig. 1B. □1978 *Ictitherium preforfex* (Hendey) – Hendey, p. 280, Figs. 1A, 2A. □1980 *Hyaena abronia* Hendey – Howell & Petter, pp. 585–590. □?1987 Hyaenidae *incertae sedis* – Barry, pp. 243–244, Fig. 7.10.

Localities. – Kenya: Lothagam; South Africa: Langebaanweg; Tanzania: ?Laetoli.

Age. – Langebaanian (MN Zone 14) – Villafranchian (equivalent).

Discussion. – Arguments for the synonymy of this species and *Ictitherium preforfex* are given in detail elsewhere (Werdelin, Turner & Solounias, MS). We here select *I. abronia* as the valid name for the taxon. The two mandibles illustrated by Hendey (1978, Figs. 1–2) represent extremes of variation within this taxon. *I. abronia* is derived in several features, such as the shape of the anterior end of the zygomatic arch. There is, however, no evidence of a special relationship between *I. abronia* and *H. hyaena* such as that suggested by Hendey (1978). The features uniting these taxa are simply plesiomorphic relative to those seen in *Crocuta.*

Barry (1987) suggests that his hyaenid *incertae sedis* (specimens LAET 3338 and LAET 1849) may be conspecific with *Hyaenictis preforfex*, which we here synonymize with *I. abronia.* We concur with this assessment and very tentatively refer these specimens to *I. abronia.*

Ictitherium preforfex (Hendey, 1974a)

Discussion. – Arguments for synonymizing this species with *Ikelohyaena abronia* are presented elsewhere (Werdelin, Turner & Solounias, MS). Suffice it to say that the main character distinguishing these species in Hendey's (1974a, 1978) formulation was simply size, and that the two mandibles shown in Hendey (1978, Figs. 1–2) represent extremes of variation within this taxon. This range of variation is comparable to that shown by *H. wongii* from China, where extremes have also upon occasion been split off (Kurtén 1985; Qiu 1985). Access to larger samples has enabled demonstration that these proposed taxa are simply at one end of the range of variation of *H. wongii* (Werdelin 1988b), and the same is true in the present case.

Chasmaporthetes australis (Hendey, 1974a)

Synonymy. – □1974a *Percrocuta australis* sp. nov. – Hendey, pp. 91–103, Figs. 14–15. □1978 *Adcrocuta australis* (Hendey) – Hendey, pp. 271, Fig. 6B. □1987 *Chasmaporthetes australis* (Hendey) – Qiu, p. 27.

Localities. – South Africa: Langebaanweg.

Age. – Langebaanian (MN Zone 14).

Discussion. – The affinities of this form have recently been independently investigated by Qiu (1987) and Werdelin & Solounias (1990), who have arrived at the same conclusion: that the form described by Hendey (1978) as *Adcrocuta australis* in reality belongs to *Chasmaporthetes.* It differs from the other (and younger) South African *Chasmaporthetes*, *C. nitidula*, particularly in the relative lengths of P_{3-4}. The latter tooth is much shorter in *C. australis* (see Werdelin, Turner & Solounias, MS).

Approximate phylogenetic position. – Together with other species of *Chasmaporthetes*, near *C. lunensis* in the core tree.

Hyaenidae 'species E' from Langebaanweg

Synonymy. – ☐1974a Hyaenidae, 'species E' Hendey, pp. 138–142, Fig. 26. ☐1988b hyaenid 'species E' – Werdelin, pp. 254–255.

Localities. – South Africa: Langebaanweg.

Age. – Langebaanian (MN Zone 14).

Discussion. – The similarity between the only available specimen of this form and *B. beaumonti* has been noted previously (Werdelin 1988b). Unfortunately, no more material of the species has been found, and although it is undoubtedly distinct from other known Hyaenidae, we refrain from naming it.

Approximate phylogenetic position. – Near *B. beaumonti* on the core cladogram. The available material does not allow for any closer positioning.

'Protictitherium' punicum (Kurtén, 1976)

Synonymy. – ☐1976 *Tunguricits punica* sp. nov. – Kurtén, pp. 179–182, Figs. 1–2.

Localities. – Tunisia: Bled Douarah Loc. 18.

Age. – Vallesian (MN Zone 9).

Discussion. – There are strong reasons for doubting the allocation of this species to *Tunguricits*. This necessitates a brief review of the comparative morphology of *'P.' punicum*, relative to *T. spocki*, *Herpestides antiquus*, (*Viverra antiqua* of Kurtén 1976) and *'Protictitherium'* spp.

M^2: This tooth is somewhat reduced in width, but not in length, relative to M^2 in *T. spocki*. This is clearly seen in the illustrations (Kurtén 1976, Fig. 2; Colbert 1939, Fig. 14), which show M^2 of *'P.' punicum* to be squarish in occlusal view, compared with the more oblong M^2 of *T. spocki*. The occlusal morphology of M^2 in the two taxa is also quite different. If the M^2 of *'P.' punicum* is held with its longest dimension vertical, the metastyle wing lies clearly below the level of the paracone. In *T. spocki* the metastyle nearly reaches the level of the paracone. In both these features, *'P.' punicum* is more like *H. antiquus* and *'Protictitherium'*; correspondence with the latter genus is particularly close (cf. Kurtén 1976, Fig. 2; Schmidt-Kittler 1976, Fig. 69). The condition in *T. spocki* is probably due to a reduction in size of the paracone of M^2. By outgroup comparison we suggest that this condition is derived.

M^1: As pointed out by Kurtén (1976), the metacone of *'P.' punicum* has shifted mediad relative to its position in *T. spocki*. This leads to the same condition as in M^2: the metastyle wing lies much further below the level of the paracone in *'P.' punicum* than in *T. spocki*. The anterior side of M^1 in *'P.' punicum* is clearly and fairly smoothly convex, whereas in *T. spocki* this side is formed of two nearly straight edges, with a marked angle between them. It should also be noted that even though the relative positions of M^1 and P^4 are incorrectly figured by Colbert (1939, Fig. 14; M^1 should be placed further anteromedially and more closely applied to P^4) nevertheless the angle between these two teeth is quite different in the two taxa, being substantially more acute in *'P.' punicum* than in *T. spocki*. In the morphology of M^1, *'P.' punicum* is, again, closer to *H. antiquus* and *'Protictitherium'*. We conclude that the morphological features of M^1 in *T. spocki* are, again, derived. As regards the position of M^1 relative to P^4, however, the situation is different. While *'Protictitherium'* and *'P.' punicum* are again similar in having M^1 and P^4 semiparallel for some distance, *T. spocki* and *H. antiquus* (cf. De Beaumont 1967, Pl. 2:2) both show a relatively obtuse angle between these teeth. We suggest that this is the primitive state, and that *'P.' punicum* shares the derived state as a synapomorphy with *'Protictitherium'*.

P^4: The upper carnassial of *'P.' punicum* is long and slender, even more so than it is in *T. spocki*, and has a short and plump protocone that ends a short distance anterior to the parastyle. In *T. spocki*, however, the protocone is notably long and slender, and ends further anteriorly than the protocone in *'P.' punicum* (although this feature is somewhat exaggerated in Colbert 1939, Fig. 14). The anteriorly positioned protocone is primitive (Wozencraft 1989), and in this feature *'P.' punicum* seems more derived than *T. spocki*. The same is true as regards the shape of the protocone. Although not as forwardly directed as in *T. spocki*, the protocone of *Protictitherium crassum* is also long and slender (Crusafont Pairó & Petter 1969, Pl. 3:10), as is the case in *H. antiquus*, although the condition is not as clear in this taxon. The short and broad protocone of *'P.' punicum* is thus derived. In all, the P^4 of *'P.' punicum* bears a remarkable morphological similarity to the (much larger) P^4 of *'Ictitherium adroveri'* (Crusafont Pairó & Petter 1969, Pl. 4:1).

P^3: This tooth is damaged in *T. spocki*, and not much can be said, beyond the fact that it is much more slender in that taxon than in *'P.' punicum*. The P^3 of the latter taxon is also quite different from that of *H. antiquus*, which bears a small but distinct lingual cusp. It is, however, quite similar in general characteristics, including the cingulum and large posterior accessory cusp, to P^3 in *'Protictitherium' cingulatum* (Schmidt-Kittler 1976, Fig. 82), although the latter species is slightly smaller.

In summary, *T. spocki* has a number of apparent autapomorphies, not shared with *'P.' punicum*, and the latter species shares several derived (relative to *T. spocki*) characters with species assigned to *'Protictitherium'*. We conclude that it is with the latter taxon, rather than *Tunguricits*, that the Tunisian form has its affinities. Within *'Protictitherium'*, *'P'. punicum* seems closest to *'P.' cingulatum*, but the comparative material is insufficient for a more extensive consideration of possible relationships.

Approximate phylogenetic position. – Since its affiliations lie with *'Protictitherium'*, it should be placed together with other species in that genus, below node 1 in the core tree.

Lycyaena crusafonti Kurtén, 1976

Synonymy. – ☐1976 *Lycyaena crusafonti* sp. nov. – Kurtén, pp. 183–187, Figs. 5–7. ☐1981 *Lycyaena chaeretis* (Gaudry) – Solounias, pp. 74–75.

Localities. – Tunisia: Bled Douarah, Loc. 17.

Age. – Vallesian (MN Zone 9).

Discussion. – The material of this species is entirely unsatisfactory, being just sufficient to establish its difference from other, similar, hyaenids, and to place it with some confidence in *Lycyaena.* It is the largest known *Lycyaena.*

Approximate phylogenetic position. – This species is similar to other species of *Lycyaena* as far as can be determined from the available material, and should be placed near *L. dubia* in the core tree.

'Protictitherium' intermedium Schmidt-Kittler, 1976

Synonymy. – ☐1976 *Protictitherium intermedium* sp. nov. – Schmidt-Kittler, pp. 66–70, Figs. 60–65, Pl. 3:1.

Localities. – Turkey: Çandir, Paşalar.

Age. – Astaracian (MN Zones 6–7).

Discussion. – This is the oldest *'Protictitherium'* known, the smallest in overall size, and dentally perhaps the most primitive known hyaenid. One markedly primitive feature is that the protoconid of M_1 is very tall relative to the paraconid, as can be clearly seen in the illustration given by Schmidt-Kittler (1976, Pl. 3:1B). These proportions give the tooth a very herpestid-like aspect, reminiscent of the Recent *Herpestes ichneumon* or even the Astaracian *'Herpestes' aurelianensis* (Viret 1951, Fig. 19).

Approximate phylogenetic position. – Like the other species of *'Protictitherium'*, this one should be placed below node 1 in the core cladogram.

'Protictitherium' cingulatum Schmidt-Kittler, 1976

Synonymy. – ☐1976 *Protictitherium cingulatum* sp. nov. – Schmidt-Kittler, pp. 74–78, Figs. 76–82, Pl. 2:1.

Localities. – Turkey: Yeni Eskisihar.

Age. – Astaracian (?MN Zone 8).

Discussion. – There is little to add to the exhaustive description of this species given by Schmidt-Kittler (1976). *'P.' cingulatum* resembles *P. crassum* in general morphology but is significantly smaller. Its possible affinities with *'P.' punicum* have already been noted. It appears more derived than *'P.' intermedium* in the proportions of M_1, but otherwise these two Turkish species are very similar.

Approximate phylogenetic position. – Below node 1 in the core cladogram, like other species of *'Protictitherium'.*

**Palinhyaena reperta* Qiu, Huang & Guo, 1979

Synonymy. – ☐*pars* 1924 *Ictitherium hyaenoides* sp. nov. – Zdansky, pp. 84–91, Figs. 8–9, Pl. 18:1–2. ☐*pars* 1938 *Hyaenictitherium hyaenoides* (Zdansky) – Kretzoi, p. 114. ☐1979 *Palinhyaena reperta* gen. et sp. nov. – Qiu, Huang & Guo, p. 208, Fig. 1, Pl. 3. ☐1979 *Palinhyaena imbricata* sp. nov. – Qiu, Huang & Guo, pp. 207–215, Figs. 1 (middle pair), 2 (middle), 6 (lower), Pls. 2:3; 3; 4:1–2; 5:1–3; 6:1. ☐1985 *Palinhyaena reperta* Qiu, Huang & Guo – Qiu, pp. 92–97, Pls. 1:1–3, 2:1–4, 3:1. ☐1988b *Palinhyaena reperta* Qiu, Huang & Guo – Werdelin, pp. 233–236, Fig. 12.

Localities. – China: Tie Chia Kou (Zdansky's Loc. 30), Yan Mu Kou (Zdansky's Loc. 49), Chen Chia Mao Kou (Zdansky's Loc. 108), Loc. 115, Loc. 116, Chien Liao Kou, Chin Kou, Die Chia Kou, Nan Ho, Qingyang, Teh Chia Kou, Tu Kou.

Age. – Turolian (MN Zone 12).

Discussion. – One of the pivotal points in the understanding of the Chinese Turolian hyaenids was the description of *P. reperta* by Qiu *et al.* (1979). This allowed the later (Qiu 1985; Werdelin 1988a) recognition that *Hyaenictitherium hyaenoides* of Zdansky (1924) was composed of two taxa.

P. reperta shows a number of derived features relative to *'Thalassictis'* and *Hyaenotherium*, especially in its broader (more 'hyaenid') premolars, and the shorter M_1 talonid. *P. reperta* is not present in the Turolian faunas of Greece, where it would seem to be replaced by *Belbus beaumonti*, a still more derived taxon (see below).

Chasmaporthetes sp. from Florida

Synonymy. – ☐1981 *Chasmaporthetes ossifragus* Hay – Berta, pp. 343–350, Figs. 2–10. ☐1988 *Chasmaporthetes ossifragus* Hay – Kurtén & Werdelin, pp. 50–51.

Age. – Late Blancan – early Irvingtonian.

Localities. – USA: Inglis 1A, Santa Fe River IB, Santa Fe River XV.

Discussion. – A discussion of this form is presented under *Chasmaporthetes ossifragus*, above. It is undoubtedly distinct from other North American *Chasmaporthetes*, but we refrain from naming this taxon here.

Approximate phylogenetic position. – Probably sister taxon to *C. ossifragus.*

'Protictitherium' sumegense Kretzoi, 1984

Synonymy. – ☐1984 *Protictitherium sumegense* sp. nov. – Kretzoi, p. 218.

Localities. – Hungary: Sümeg.

Age. – Turolian (MN Zone 11–12).

Fig. 16. Photograph of right ramus of *B. beaumonti* (cast of SMNL 13118) in (top) buccal and (bottom) lingual view. This specimen can be favorably compared with that illustrated by De Beaumont (1968). Natural size.

Discussion. – This is another species that has not been figured. Given this, and uncertainties regarding the actual characters of the species, we suggest that this form is at present best considered a *nomen dubium.*

**Belbus beaumonti* (Qiu, 1987)

Synonymy. – □1968 *Hyaena* sp. – De Beaumont, pp. 21–26, Pl. 1:1–2. □1969a *Hyaena dubia* (Zdansky) – De Beaumont, pp. 49–54, Pl. 1:1–2. □1980 *Hyaenictitherium* cf. *hyaenoides* (Zdansky) – Howell & Petter, pp. 583, 588. □1981 *Thalassictis hyaenoides* (Zdansky) – Solounias pp. 69–71, Fig. 16. □*pars* 1981 *Lycyaena chaeretis* (Gaudry) – Solounias, pp. 74–76, Fig. 18A–C. □*pars* 1981 *Thalassictis (Hyaenictitherium) hyaenoides* (Zdansky) – Solounias & De Beaumont, pp. 293–304. □1981 *Pachycrocuta* sp. – Solounias & De Beaumont, pp. 293–304. □1987 *Hyaenictis beaumonti* sp. nov. – Qiu, pp. 72–73. □1988b cf. *Palinhyaena* sp. – Werdelin, pp. 253–255.

Localities. – Greece: Samos.

Age. – Turolian (MN Zone 12).

Discussion. – Suggestions regarding the affinities of these specimens have been many. In his description of a lower jaw (Basel SAM 33), De Beaumont (1968) rightly noted the derived features of the premolars and carnassial, and suggested that this Turolian form had affinities with post-Miocene *Hyaena.* He also correctly noted its similarity to *'Ictitherium hyaenoides'* (those specimens that actually belong to *P. reperta*). Given the impossibility of finding any contemporaneous species to ally it with, and given its generally derived features, he quite properly referred the mandible to *Hyaena* sp. Later, Solounias (1981; Solounias & De Beaumont 1981) found another mandible from Samos, this time in the collections of the museum in Ludwigsburg (SMNL 13118), which is identical with SAM 33 in its characters (Fig. 16).

In 1969, De Beaumont described another Samos specimen, this time a skull in the Natural History Museum, Vienna (De Beaumont 1969a). In his description he noted similarities between this skull (NHMW A4752) and the mandible previously described. He again tried to ascertain the affinities of these specimens, with little success, suggesting that they may have affinities with *Lycyaena dubia* from China. This opinion, however, is based on a faulty conception of Zdansky's species and can be discounted. Solounias (1981) suggested that the type specimen of *L. chaeretis* from Pikermi was similar to the specimens here discussed, and referred them accordingly. As noted under *L. chaeretis*, this position is not tenable, and indeed Solounias later (Solounias & De Beaumont 1981) abandoned this position, suggesting, as had Howell & Petter earlier (1980), affinities with *H. hyaenoides*. As an alternative hypothesis, Solounias & De Beaumont (1981) suggested affinities with *Pachycrocuta* for the skull, but not for the mandibles, which were suggested to be at a more primitive stage of evolution.

This latter suggestion was discounted by Qiu (1987), who again united the specimens into a single species, which he recognized as different from all named species of hyaenid. He named this species *Hyaenictis beaumonti*. However, this generic attribution is clearly faulty, since *B. beaumonti* shows none of the characteristics of *Hyaenictis graeca*, and vice versa. This topic is considered in detail elsewhere (Werdelin, Turner & Solounias, MS). We will here only briefly consider Qiu's (1987, p. 73) reasons for the generic allocation of this form.

Qiu suggests as common characters the tooth formula and that certain characters have evolved in the direction of *Crocuta*. However, the first character is plesiomorphic at this level and is shared with numerous other hyaenid taxa. The 'crocutine' adaptations of *B. beaumonti* are in clear evidence, but there are no such indications in *Hyaenictis graeca*, with its relatively narrow premolars, large accessory cusps on premolars, and straight, as opposed to convex anterior margin of P$_3$. Thus, allocation to *Hyaenictis* is out of the question. However, Qiu (1987) also noted the similarities with *P. reperta*, as did Werdelin (1988b), who suggested that these forms and 'hyaenid sp. E' from Langebaanweg were closely related.

'Chasmaporthetes bonisi' (Koufos 1987)

Synonymy. – □1980 *Adcrocuta eximia* Roth & Wagner – Koufos, p. 86, Pl. 10:1. □1987 *Chasmaporthetes bonisi* sp. nov. – Koufos, pp. 913–920, Pl. 1:1–2, 3C.

Localities. – Greece: Dytiko.

Age. – Turolian (MN Zone 13).

Discussion. – A good deal of special pleading enabled Koufos (1987) to distinguish this species from *A. eximia* and place it in *Chasmaporthetes*. We shall consider his characters in turn.

Ramus: shallow in *C. bonisi* vs. deep (or high) in *A. eximia*. This is a function of age. Since both specimens referred to *C. bonisi* are from young individuals (premolars hardly worn), the comparison is meaningless. The mental foramen is most often single in *A. eximia*, but when it is double its position is variable. There are even specimens with three mental foramina (Fig. 20). In *Chasmaporthetes* the mental foramen is invariably single.

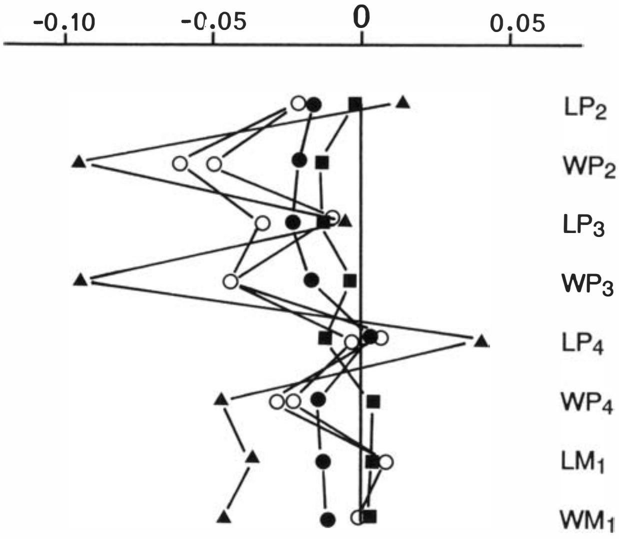


Fig. 17. Ratio diagram comparing the specimens of *'C. bonisi'* with samples of *Adcrocuta* and *Chasmaporthetes*. Standard = *A. eximia* (China); ○ = *'C. bonisi'* (data from Koufos 1987); ● = *A. eximia* (Samos); ■ = *A. eximia* (Pikermi); ▲= *C. lunensis* (European sample).

P$_1$: This tooth is present in both taxa. Koufos (1987) states that it is large in *A. eximia*, which may be the case, but is irrelevant, since only the alveolus of the tooth is known in *C. bonisi*, and the comparison therefore cannot be made.

P$_2$: This tooth is stated by Koufos (1987) to be less robust than P$_2$ in *A. eximia*. Whilst not questioning the slenderness of this tooth, we note (Fig. 17) that the tooth is no slenderer than a P$_2$ of *A. eximia* of the same size as the Dytiko specimens, which are just below the size range of Chinese *A. eximia*, which in turn are very slightly larger than *A. eximia* from Samos and Pikermi (Werdelin & Solounias 1990). The shape of this tooth in *A. eximia* is highly variable, as can be seen even in the restricted sample illustrated by Koufos (1987, Pl. 1:3). We do not see any possibility of using the occlusal shape or extent of the cingula as distinguishing characters between the Dytiko specimens and *A. eximia*. The P$_2$ of *Chasmaporthetes* can be seen in Fig. 17 to be much narrower than the same tooth in either of the other materials.

P$_3$: The same comments apply to this tooth as to P$_2$. The development of an anterior accessory cusp in *A. eximia* is variable, but generally it is rudimentary or absent. Koufos is confused on this point, stating in the text that it is present and large in *A. eximia*, but correctly noting its rudimentary nature in his Table 1. The P$_3$ of *Chasmaporthetes* is markedly narrower than the P$_3$ of either the Dytiko material or *A. eximia* (Fig. 17). In *Chasmaporthetes*, moreover, the anterior accessory cusp of P$_3$ is large, not rudimentary or absent as in the Dytiko hyaenid.

P$_4$: This is the tooth that differs the most from typical *A. eximia*. Points of difference noted by Koufos are the larger anterior accessory cusp of the Dytiko specimens (although this may be influenced by the lack of wear on the premolars), and the placement of the anterior accessory cusp in line with the other cusps, rather than mesiolingually, as in *A. eximia*. However, the statement that this tooth is less robust than P_4 of *A. eximia* is clearly incorrect (Fig. 17). The P_4 of *Chasmaporthetes* can be seen to be slightly more slender than in *A. eximia*.

M_1: The metaconid is absent in all taxa concerned (it is present in so few specimens of *A. eximia* as to make comparison impossible). Despite comments by Koufos, the M_1 talonid as described and figured presents no differences from *A. eximia*, except in the slightly greater reduction of the entoconid. The taxonomic usefulness of such a character is questionable, however, especially as the talonid of the Dytiko specimen bears no similarity at all to the unicuspid, trenchant talonid of typical *Chasmaporthetes*.

The inescapable conclusion from the above, and from viewing Koufos' (1987) illustrations, is that *'C.' bonisi* is very different indeed from *Chasmaporthetes* as that genus has been defined by other authors (Berta 1981; Galiano & Frailey 1977; Kurtén & Werdelin 1988; Qiu 1987; Werdelin, Turner & Solounias, MS) and certainly cannot be referred to it. On the other hand, the similarities between the Dytiko specimens and *A. eximia* are evident. Despite the slight differences between the Dytiko specimens and typical *A. eximia* (differences that may perhaps be due to the young age of the former specimens and suggest some minor evolutionary changes), we suggest that *'C.' bonisi* is a synonym of *A. eximia*. This is the first assessment made by Koufos (1980) of these specimens, and in our opinion clearly the correct one.

Ictitherium kurteni Werdelin, 1988a

Synonymy. – □1988a *Ictitherium kurteni* sp. nov. – Werdelin, pp. 101–102, Fig. 6.

Localities. – China: Chang Chia Chuang.

Age. – Turolian (MN Zone 12).

Discussion. – There is nothing to add to the discussion of this species given in Werdelin (1988a). It differs from all other species in the *'Ictitherium'* grade group, including the large forms from Polgárdi and the Black Sea, in its markedly enlarged P^3.

Approximate phylogenetic position. – This species should be placed together with other *Ictitherium*, near *I. viverrinum* in the core tree.

Chasmaporthetes exitelus Kurtén & Werdelin, 1988

Synonymy. – □1988 *Chasmaporthetes exitelus* sp. nov. – Kurtén & Werdelin, p. 51, Fig. 2.

Localities. – China: Loc. 116v.

Age. – Turolian (MN Zone 12).

Discussion. – This taxon was referred to *Chasmaporthetes* on the basis of the elongated metastyle of P^4. Elsewhere (Werdelin, Turner & Solounias, MS) arguments are given why this is, despite the slender evidence on which it is based, still the most likely genus for this taxon.

Approximate phylogenetic position. – This species should probably be placed between nodes 5 and 6 of the core tree.

Tongxinictis primordialis (Qiu, Ye & Cao, 1988)

Synonymy. – □1988 *Percrocuta primordialis* sp. nov. – Qiu, Ye & Cao, pp. 116–127, Fig. 1, Pls. 1–2.

Localities. – China: Maerzuizigou, Yinziling.

Age. – Lower Tungurian (Astaracian; MN Zone 6).

Discussion. – This species was discussed briefly in the introduction, regarding the delimitation of the family Hyaenidae. As noted there, it differs in all respects from other species assigned to the Percrocutidae, and is clearly a hyaenid *sensu stricto*. The characters of this species indicate that it cannot be referred to any known genus, and we therefore propose the name *Tongxinictis* gen. nov., type species *Tongxinictis primordialis*, for this form; named after the county where it was found (Qiu *et al.* 1988b).

The great age of this species may be somewhat surprising in view of its advanced dental characters. However, in most other features, *T. primordialis* is quite primitive, and more in line with its geological age (the age of the Hyaenidae and other matters will be considered below). This is particularly true of the basicranium and auditory bulla. The latter is clearly at stage 4 of Hunt (1987), and is in general comparable to that of *Plioviverrops*, although, since the basicranium is relatively shortened in *T. primordialis*, the bulla is placed more obliquely in that taxon. The foramina of the basicranium are located as in other primitive hyaenids (Colbert 1939; De Beaumont 1969b) and there appears to be an alisphenoid canal present, although this is hard to tell from the photographs. That all these features are primitive is indicated by their presence in *H. antiquus* (De Beaumont 1967).

Thus, the discovery of a dentally derived hyaenid in MN Zone 6 is interesting, but not, after all, surprising. More material, particularly the lower carnassial, is eagerly awaited.

Approximate phylogenetic position. – This species is difficult to place, due to its combination of primitive auditory bulla and derived dentition. However, the primitive stage 4 bulla argues for a position between nodes 1 and 2 in the cladogram.

'Thalassictis' spelaea (Semenov, 1988)

Synonymy. – □1988 *Ictitherium spelaeum* sp. nov. – Semenov, pp. 46–47, Figs. 1–4. □1989 *Ictitherium spelaeum* Semenov – Semenov, pp. 66–67, Fig. 21.

Localities. – USSR: Gritsev.

Age. – Vallesian (MN Zone 9)

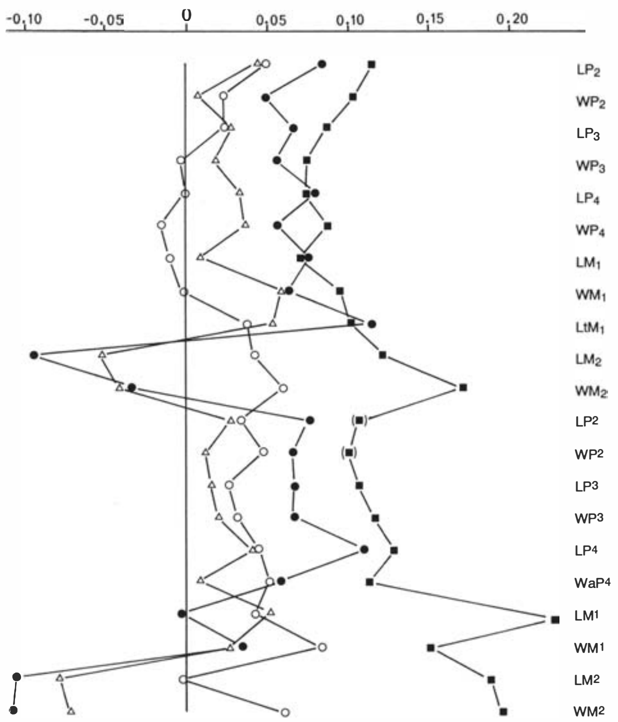


Fig. 18. Ratio diagram of some hyaenid taxa. Standard = *Ictitherium viverrinum* (Chinese sample); ●= *Hyaenotherium wongii* (Chinese sample); ■= *I.* cf. *pannonicum* (Black Sea sample, data from Semenov 1985); ○ = *I. ibericum* (data from Semenov 1989); △= *'Thalassictis' spelaea* (data from Semenov 1989).

Discussion. – Semenov (1988, 1989) refers this taxon to *Ictitherium*, but several characters suggest that this referral is incorrect. Both M^1 and M^2 are considerably smaller than in other *Ictitherium* (Fig. 18; cf. Semenov 1989, Fig. 19). This is accompanied by a reduction in size of the metastyle wing of M^1, which is also characteristic of the genera *'Thalassictis'* and *Hyaenotherium*. Furthermore, the internal angle between P^4 and M^{1-2} is reduced in the Gritsev material compared to typical *Ictitherium*. This angular relationship (albeit the external angle in his formulation) is correctly singled out by Semenov (1989, Fig. 14) as a character distinguishing *'Thalassictis'* from *Ictitherium*. (Semenov's figure caption refers to *T. robusta*, but the material on which he bases this comparison pertains to *'T.' sarmatica* as conceived herein. The comparison is still valid, however.) This angular relationship clearly places the Gritsev material with *'Thalassictis'* or *Hyaenotherium*.

The upper carnassial of the Gritsev species is unfortunately too poorly preserved to allow for detailed comparisons with other taxa. The lower carnassial, however, is well preserved and illustrated (Semenov 1988, Figs. 3–4; 1989, Figs. 19, 21). It can be clearly distinguished from the lower carnassial of *Ictitherium* on the basis of its relatively short talonid and the relatively high protoconid, again features that are singled out by Semenov as useful in distinguishing between *'Thalassictis'* and *Ictitherium*.

In sum, this species cannot be retained within *Ictitherium*, but must be referred to *'Thalassictis'* (it is less derived than *Hyaenotherium* in the structure of M_1), as *'T.' spelaea*.

This species may eventually prove to be conspecific with *T. robusta*, but pending restudy of this question, we retain *'T.' spelaea* as a separate species in this text.

Approximate phylogenetic position. – With other species of *'Thalassictis'*, between nodes 2 and 3 of the core cladogram.

Crocuta dietrichi Petter & Howell, 1989

Synonymy. – □1987 *Crocuta* sp. – Barry, p. 241, Figs. 7, 9:a–c. □1989 *Crocuta dietrichi* sp. nov. – Petter & Howell, pp. 1031–1038, Fig. 1.

Localities. – Tanzania: Laetoli.

Age. – Ruscinian/Villafranchian (3.76–2.41 M.y.)

Discussion. – This newly described taxon is stated by Petter & Howell (1989) to represent a link between *P. reperta* and *C. crocuta*. Phylogenetically, this is no help, however, as there are a number of taxa already in this position (see Figs. 37–38). Morphologically, the specimens illustrated are very close to the Recent *C. crocuta*. Turner (1990) suggests that they are conspecific, which may well be the case, whereas Barry (1987) believes that they may turn out to be conspecific with *C. sivalensis*. Be that as it may, any further work on *Crocuta* will require a thorough study of geographic variation within the Recent species, both at present and in the Pleistocene (*C. c. spelaea*), reanalysis of *C. sivalensis*, restudy of *'C. honanensis'* from China (the specimens referred to this taxon by Qiu 1987 are, in our view, almost certainly synonymous with *C. crocuta*), and a consideration of all *Crocuta* material from Laetoli (Barry 1987) and West Turkana (Harris *et al.* 1988). Until such a study has been carried out, there is little sense in trying to discuss the interrelationships of various taxa proposed within this genus.

Approximate phylogenetic position. – This species, no matter what its taxonomic status, should be placed near *C. crocuta* in the core tree.

Miohyaenotherium bessarabicum Semenov, 1989

Synonymy. – □1938 *Ictitherium hipparionum* var. *bessarabica* – Simionescu, pp. 2–5, Figs. 1–7, Pls. 2:1; 3:1–3. □1938 *Lycyaena parva* Khomenko – Simionescu, pp. 12–13, Figs. 19–20, Pls. 2:6; 3:4. □1973 *Ictitherium hipparionum* var. *garedziensis* (Gervais) – Gabashvili, pp. 7–11, Pls. 2–3. □1989 *Miohyaenotherium bessarabicum* gen. et sp. nov. – Semenov, pp. 130–132, Fig. 40.

Localities. – USSR: Belka, Cimislia, Udabno.

Age. – Turolian (MN Zone 11–12).

Discussion. – Semenov (1989) erected the new genus and species *Miohyaenotherium bessarabicum* on the basis of some remains from Belka, and a few scattered specimens previously referred to *'I. hipparionum'*. He cites four characters to distinguish this genus from *Hyaenotherium* and *Hyaenictitherium* (Semenov, 1989, Fig. 27): the lateral profile of the auditory bulla and paroccipital process, the development

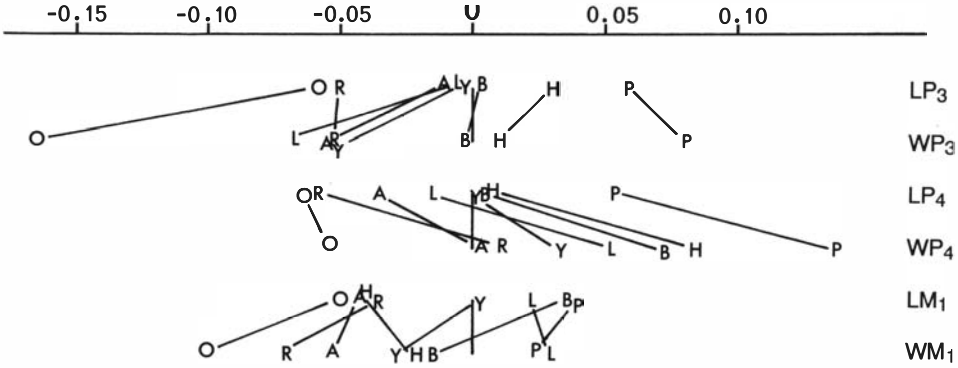


Fig. 19. Ratio diagram comparing Layna specimens (see *P. perrieri*, above) with various hyaenid taxa. Standard = Layna specimens, data from Howell & Petter 1980); A = *I. abronia*; B = *B. beaumonti*; H = *H. hyaena* (African sample); L = *C. lunensis* (Layna specimens); O = *H. wongii* (Chinese sample); P = *P. perrieri* (Odessa sample; data from Howell & Petter (1980); R = *P. reperta* (China); Y = *H. hyaenoides* (China).

of the rim of the external auditory meatus, the shape of the lower border of the mandible, and the relative sizes of the talonid cusps of M_1. Of these, the auditory bulla and paroccipital process, as well as the mandibular border, are characters that are too variable between specimens and during ontogeny (the shape of the mandible in the specimens illustrated by Gabashvili 1973, Pl. 2:1–2, is clearly due to the fact that both these mandibles belong to juvenile individuals in which the cheek teeth are erupting or just barely erupted) to be of use in diagnosing a genus. The other two characters, especially the external auditory meatus, are very interesting in view of the documented differences between extant hyaenids in this region (Buckland-Wright, 1969; cf. below). The intra-specific variability of these characters is poorly known, however, and should be investigated with care. The published illustrations of specimens referred to *M. bessarabicum* are not adequate for assessing the utility of these characters. We suspect that this taxon may be synonymous with *'Hyaenictitherium' parvum* (see above), but until we can examine the specimens at first hand, this cannot be demonstrated, and we prefer to keep these taxa separate at the present time.

Approximate phylogenetic position. – A position somewhere between nodes 3 and 4 on the core cladogram is likely, but, as noted under *'Hyaenictitherium' parvum*, the taxonomic difficulties render an accurate assessment difficult.

Hyaenictis sp. from Langebaanweg

Synonymy. – ☐1978 *Euryboas* sp. – Hendey, p. 271, Fig. 6A. ☐*pars* 1988 *Chasmaporthetes* sp. – Kurtén & Werdelin, p. 51.

Localities. – South Africa: Langebaanweg.

Age. – Langebaanian (MN Zone 14).

Discussion. – This and the other Langebaanweg species are fully discussed by Werdelin, Turner & Solounias (MS). It is intermediate between *'Hyaenictitherium' namaquensis* and *Chasmaporthetes australis.*

Approximate phylogenetic position. – With other species of *Hyaenictis* between nodes 5 and 6 of the core cladogram.

Some additional material

Qi (1989) describes and illustrates as *I.* cf. *gaudryi* some specimens from the 'middle Miocene' of the Altai region, Xinjiang. In fact, none of these very interesting specimens can be referred to *I. gaudryi* (=*I. viverrinum*). The partial mandible (Qi's Fig. 2:1) bears some resemblance to that of *I. pannonicum* and *I. intuberculatum*, particularly in the structure of M_2. However, the specimen is much smaller than either of these species, and probably represents a new species of *Ictitherium*. The isolated carnassial (Qi's Fig. 2:3) shows entirely different features, demonstrating that at least two taxa are represented in this material. The short talonid and low paraconid of this specimen testify to its probable affinities with *'Thalassictis'.* In fact, it bears considerable resemblance to the M_1 of *'T'. certa* (see above). The presence of *'Thalassictis'* accords well with the middle Miocene age quoted for this faunule. The remaining specimens are not diagnostic, though we would tentatively suggest that the mandible fragment (Qi's Fig. 2:2) may belong with the *'Thalassictis'* carnassial and the isolated P_4 with *Ictitherium.*

As noted above, the material from Layna referred to *P. pyrenaica* (= *P. perrieri*) cannot in reality be referred *in toto* to this taxon. In Fig. 19, we compare the proportions of these teeth with other hyaenids. We may note that the P_3 in its proportions is very similar to that of *B. beaumonti*, which we feel to be significant, due to the characteristic nature of P_3 in that taxon. The P_4 , however, is narrower than in any taxon with which it is compared here, even than *H. wongii*, which has very narrow premolars. This suggests either that the measurement is incorrect as given, or that the identification is wrong (no illustration of the specimens has been given). In any case, this specimen cannot confidently be referred to any known hyaenid taxon. The carnassial is fairly large and robust, on the other hand, and may in fact pertain to *P. perrieri.* All together, it would appear (1) that these specimens do not represent a single species, (2) that *P. perrieri* may be present in the collection, and (3) that a taxon similar to *B. beaumonti* may be present at Layna. The latter possibility especially requires further study.

Characters

In this section we present a master list of characters that will later be used in the systematic analyses. The characters are identified by a sequential numbering system. These numbers will be used throughout the remainder of this paper, even though not all characters are used in all aspects of the analyses. Since some characters, e.g. breadth of premolars, may sustain changes in their coding depending on the context in which they are used, not all characters are coded in this section. Such characters will be referred to in the systematic section to follow and elsewhere, as required.

Characters of the skull and dentition

Since the fossil material of hyaenids almost exclusively consists of skulls and jaws, we have concentrated our search for characters to this anatomical region, incorporating studies of both extant and extinct species in the analyses.

Character 1 – Presence or absence of M_2

Coding. – 0 (present); 1 (absent).

Comments. – The loss of M_2 is clearly a derived character in advanced hyaenids. However, it is likely that this loss may have occurred more than once among hyaenids. Furthermore, the loss of M_2 is in nearly all cases coupled with the loss of M^2, and often P_1 as well. In order not to excessively weight this character complex, none of these characters have been used in the general phylogenetic analyses in this paper. (See also comments under character no. 6.)

Character 2 – Presence or absence of P_1

Coding. – 0 (present); 1 (absent).

Comments. – Again, the loss of this tooth is derived, but the character has not been used in the general phylogenetic analyses.

Character 3 – Presence or absence of P^1

Coding. – 0 (present); 1 (absent).

Comments. – This tooth is present in all hyaenids with the exception of *C. crocuta* and *Chasmaporthetes* spp. (Kurtén & Werdelin 1988), where it is sometimes absent. This polymorphic condition is interpreted as independently derived within these taxa by comparison with other character distributions.

Character 4 – Presence or absence of M^2

Coding. – 0 (present); 1 (absent).

Comments. – As with M_2, it is likely that this tooth has been lost more than once in hyaenid evolution. Moreover, its loss is coupled to a reduction in size of M^1. Again, this character is not used in the general phylogenetic analyses.

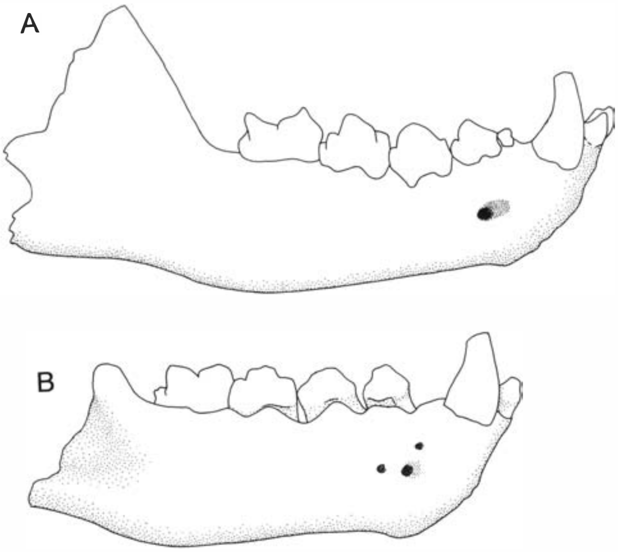


Fig. 20. Two specimens of *Adcrocuta eximia* showing (A) one mental foramen (PIU M57/58) and (B) three mental foramina (PIU M3860). Not to scale.

Character 5 – Number of mental foramina

Coding. – 0 (more than one mental foramen); 1 (one mental foramen).

Comments. – Primitively, hyaenids have more than one mental foramen. Some early forms have two, some as many as three. The derived character state occurs in most post-Miocene hyaenids. In many taxa, this character is polymorphic (Fig. 20), and even in extant hyaenids, a double or even triple mental foramen can occur as an individual variation. In order to use this potentially very important character, we have decided to code as 1 (derived state) all taxa in which specimens with only a single mental foramen are known, and as 0 (primitive) taxa in which only specimens with two or more mental foramina are known. This means that a taxon such as *H. wongii*, in which many specimens have two mental foramina and others only one, will be coded 1, while *L. dubia*, in which all known specimens have two mental foramina, will be coded 0.

Character 6 – Stage of reduction in size of M^1 relative to P^4

Coding. – In steps from 0 (not reduced relative to primitive condition) to 6 (most reduced).

Comments. – This character was coded by plotting length of P^4 against width of M^1, and deriving character states from that plot, using the basal relationship as 0. Nearly all taxa fall neatly into the steps defined by this plot (in which allometry is taken into account), as shown in Fig. 21. However, some taxa straddle two steps and have consequently been coded as polymorphic for this character. As this character is strongly correlated with the loss of M^2 and M_2, it has been used in the general phylogenetic analyses in lieu of the loss characters (nos. 1–4), which as noted above may (a) exhibit parallelism and (b) be overly weighted if introduced into the analyses.

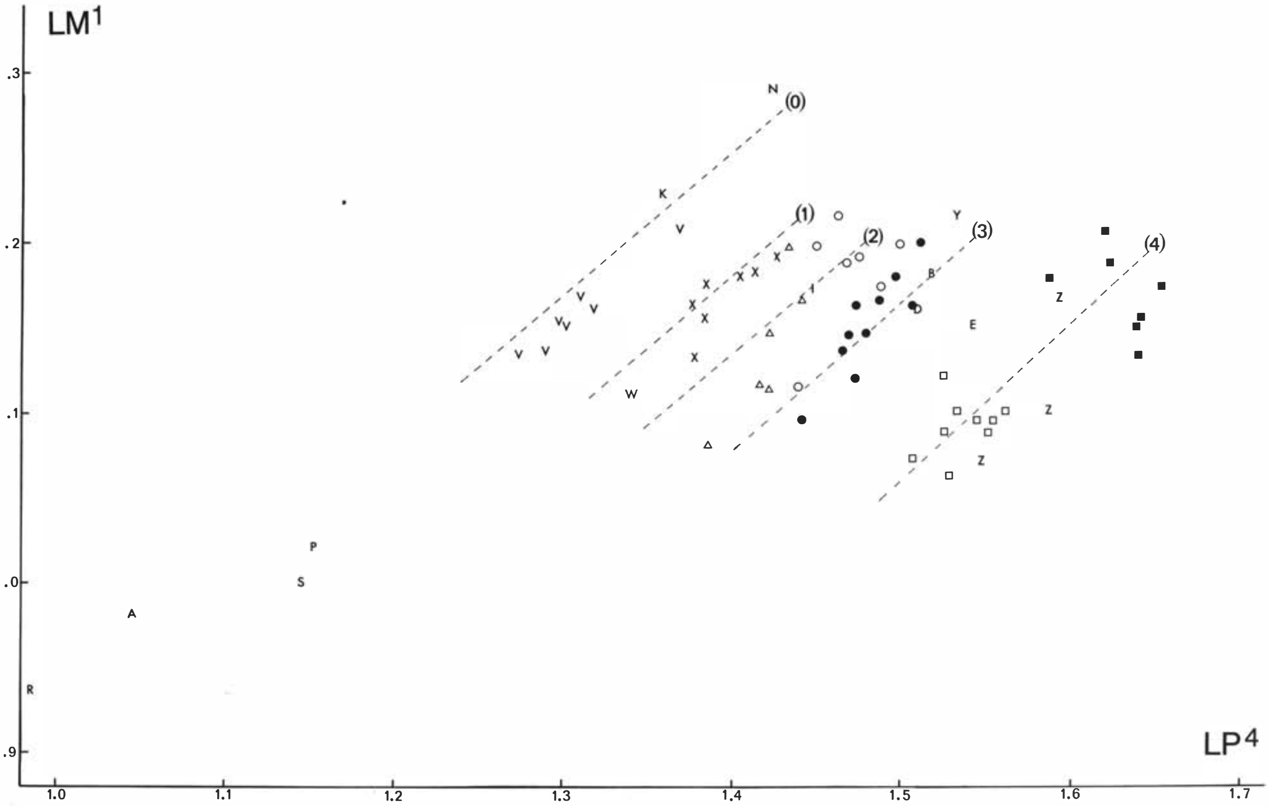


Fig. 21. Bivariate diagram showing basis for coding of relative size of M^1. ● = *H. hyaena*; ■ = *P. brevirostris;* ○ = *H. hyaenoides*; □ = *P. brunnea;* A = *Herpestides antiquus*; B = *C. borissiaki*; D = *L. dubia*; E = *P. perrieri*; I = *I. abronia*; K = *I. kurteni*; N = *I.* cf. *pannonicum* (data from Semenov 1985); P = *'P.' punicum*; R = *P. orbignyi* (data from De Beaumont 1969b); S = *T. spocki*; V = *I. viverrinum*; W = *Lepthyaena sivalensis*; X = *H. wongii*; Z = *A. eximia*. *C. crocuta* lies off the graph to the lower right. The codings are noted as numbers in parentheses. The lines are intended as lures for the unwary.

Character 7 – Number of talonid cusps on M_1

Coding. – 0 (three talonid cusps present); 1 (only two talonid cusps in evidence); 2 (talonid unicuspid).

Comments. – The work of Schmidt-Kittler (1976; also Semenov 1989) has shown the importance of the development of the talonid cusps in the early evolution of hyaenids. However, in the broader view taken here, a much rougher coding has had to be made, a coding that does not take into account the relative sizes of these cusps. The state coded 0, which is the primitive condition, is so coded in species that do not show any reduction in the number of talonid cusps. This means that, e.g., *H. wongii* and *I. viverrinum* are coded identically for this character, despite the disparate sizes and morphologies of their M_1 talonids (Crusafont Pairó & Petter 1969; Kurtén 1982; Schmidt-Kittler 1976; Werdelin 1988a, b). Species in which the hypoconulid is lost or vestigial, while the hypoconid and entoconid are present, are coded 1. Finally, forms with only a single large talonid cusp (*Crocuta*, *Chasmaporthetes*) are coded 2.

Character 8 – Presence or absence of metaconid on M_1

Coding. – 1 (present); 0 (absent).

Comments. – The absence of the metaconid is clearly derived. In some few taxa, the presence/absence of the metaconid is polymorphic (e.g., *Adcrocuta eximia*). In these cases the modal state is coded. In the case of *A. eximia*, for example, the metaconid is only present in one out of 20 specimens in the PIU and AMNH collections. The reverse situation, i.e. the metaconid being absent in a small percentage of a specific sample, has not been seen to occur.

Character 9 – Position of protocone of P^4

Coding. – 0 (protocone extending anteriorly of parastyle); 1 (anterior face of protocone approximately level with anterior face of parastyle); 2 (anterior face of protocone not extending anteriorly to anterior face of parastyle).

Comments. – The primitive condition of the protocone extending far anteriorly is only seen in the small early hyaenids, such as *'Protictitherium'* (Schmidt-Kittler 1976), *Tungurictis* (Fig. 22A; Colbert 1939) and *Plioviverrops* (De Beaumont 1969b; De Beaumont & Mein 1972). The derived condition of a posteriorly positioned protocone (character state 2) is seen only in a very few hyaenid taxa, such *A. eximia* and *L. lycyaenoides* (Fig. 22C), but is characteristic of the Percrocutidae, as discussed in the introduction.

Character 10 – Shape of tooth row

Coding. – 0 (tooth row straight); 1 (tooth row curved, or convex).

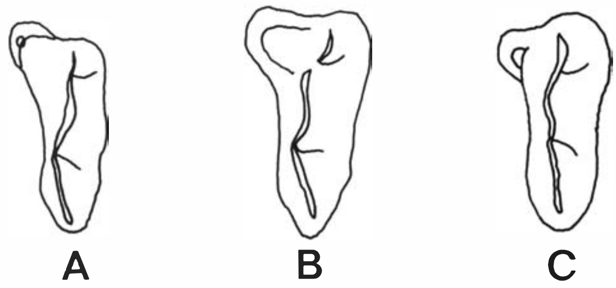


Fig. 22. The upper carnassial of (A) *T. spocki*, protocone anterior to parastyle; (B) *H. hyaenoides*, protocone level with parastyle; (C) *L. lycyaenoides* (after Young & Liu 1948), protocone posterior to parastyle. Not to scale.

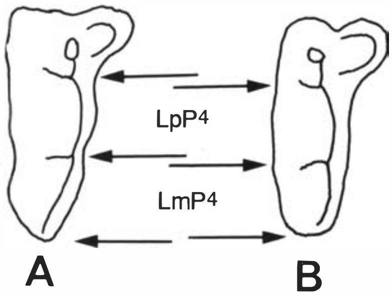


Fig. 23. Upper carnassials of (A) *Hyaenotherium* and (B) *Ictitherium*, showing the shorter metastyle blade of the latter taxon. Not to scale.

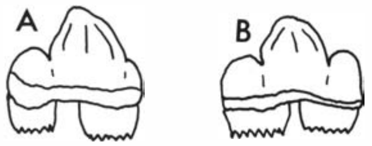


Fig. 24. P_4 of (A) *B. beaumonti* showing small and appressed anterior accessory cusp (anterior to the right), and (B) *C. nitidula* (after Ewer 1955b) showing large and free anterior accessory cusp. Not to scale.

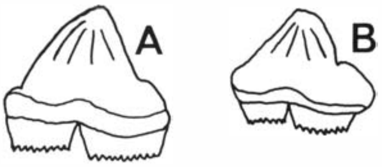


Fig. 25. P_3 of (A) *B. beaumonti* showing convex anterior face (anterior to the left), and (B) *I. viverrinum* showing straight anterior face. Not to scale.

Comments. – In the very early, small forms the tooth rows are straight, becoming curved as the body size of the taxa increases. This is presumably related to the ecological–functional requirements of the animals. In some *Chasmaporthetes* the tooth rows are secondarily straight, at least in immature specimens (e.g., *C. borissiaki*, *C. lunensis*; Khomenko 1932; Schaub 1941]. In some taxa (e.g., *Pachycrocuta brevirostris*) the tooth rows are extremely curved. The latter character state has not been coded separately, however, since this would require an elaborate measure of the curvature of the tooth row relative to its length. This was not feasible with the data at hand.

Character 11 – Relative length of paracone and metastyle of P^4

Coding. – 0 (metastyle equal in length to, or shorter than, paracone); 1 (metastyle longer than paracone).

Comments. – This character has seen most use in distinguishing the Turolian taxa from each other (Kurtén 1982; Werdelin 1988a, 1988b). However, this length relation is variable also in other taxa and is a useful systematic character (Fig. 23).

Character 12 – Placement of carnassials in tooth row

Coding. – 0 (carnassials in line with tooth row, i.e. at an angle relative to the sagittal plane); 1 (carnassials parallel to sagittal plane).

Comments. – Kurtén & Werdelin (1988) discussed this feature, finding that a placement of the carnassials parallel to the sagittal plane moves the shearing element out of the way of the bone-cracking element of the dentition. The derived condition here is therefore an indication of advanced adaptations to bone-cracking.

Character 13 – Size of anterior accessory cusp of P_4

Coding. – 0 (large); 1 (small).

Comments. – Judging the size of an accessory cusp is always a subjective exercise (see Fig. 24). Where possible, this feature has been related to the size of the main cusp, but data to allow this comparison were not available for many species. Thus, we admit to an element of subjectivity in this character, although we do not feel that this impairs its usefulness. Certainly, the difference in size of the anterior accessory cusps of taxa such as *A. eximia* and *Chasmaporthetes* spp. is indisputable.

Character 14 – Placement of anterior accessory cusp of P_4

Coding. – 0 (free of main cusp); 1 (appressed to main cusp).

Comments. – The coding of this character is less subjective than the former (see Fig. 24). The most important criterion here is if there is a clear cleft between the main cusp of P_4 and the anterior accessory cusp, or whether they are separated by a closed notch.

Character 15 – Shape of anterior face of P_3

Coding. – 0 (concave/straight); 1 (convex).

Comments. – This is an important character (Fig. 25), that may be correlated with the preceding one. The coding has not presented any difficulty, except for the extremely derived *C. crocuta*, in which the anterior face of P_3 is straight, but may in all likelihood have become so secondarily. However, it is coded as observed (i.e. 0).

Character 16 – Relative width of P_3

Coding. – Not coded here.

Comments. – This character and the following four were coded in relation to subgroups of hyaenids, and not in relation to the family as a whole. It is of little value to say that the P_3 of *C. crocuta* is wider than that of *T. spocki*, and such comparisons have been deleted from the phylogenetic work. However, it is of interest to say that *L. dubia* has a narrower P_3 than *L. macrostoma*. Such comparisons have been made, and are used in analyses of selected groups of taxa, as specified below. Codings are given in the text when required.

Character 17 – Relative length of P_2

Coding. – Not coded here.

Comments. – See comments under character no. 16.

Character 18 – Relative length of M_1

Coding. – Not coded here.

Comments. – See comments under character no. 16.

Character 19 – Relative length of P^2

Coding. – Not coded here.

Comments. – See comments under character no. 16.

Character 20 – Relative length of P^4

Coding. – Not coded here.

Comments. – See comments under character no. 16.

Character 21 – Length of palate

Coding. – 0 (ends at level of last upper molar); 1 (continues beyond last upper molar).

Comments. – This character is also difficult to deal with when considering the family Hyaenidae as a whole. This is due to the variable presence of M^2 within members of the family. There is a problem of coding due to the question whether a palate ending at the level of M^2 in a species retaining this tooth should be considered the same character state as a palate that ends just behind M^1 in a species lacking M^2, or whether it should be coded the same as a palate ending at the level of M^1 in this second species. We have chosen to use this character only within groups whose members have the same number of upper molars.

Character 22 – Position of infra-orbital foramen

Coding. – 0 (placed above posterior end of P^3 or junction between P^3 and P^4); 1 (positioned above middle of P^3); 2 (positioned anterior to middle of P^3).

Comments. – This character has been commented on by others (Qiu 1987). The functional significance of the most derived character state has been considered by one of us in another context (Werdelin 1989). It should be noted that we have coded this character relative to a horisontal palatal plane, whereas Qiu (1987) appears to have held the basicranial axis horisontal instead. Our approach makes it easier to code isolated maxillary fragments, but also means that the codings are not equivalent.

Character 23 – Position of anterior margin of orbit

Coding. – 0 (above the anterior end of P^4); 1 (above P^3).

Comments. – All hyaenids with the exception of *Plioviverrops orbignyi* show the primitive character state. This character was introduced in order to distinguish Hyaenidae proper from Percrocutidae. The derived condition in *P. orbignyi* is not homologous with the condition in Percrocutidae, but instead derives from an enlargment of the orbit in this form, as can be seen in De Beaumont's (1969b) Pl. 1:1a. See also the previous discussion of the Percrocutidae.

Character 24 – Suture between premaxillary and frontal on snout

Coding. – 0 (absent); 1 (present).

Comments. – The polarity of this character is somewhat difficult to ascertain, as the condition in Viverridae and Herpestidae is quite variable. However, most appear to have a premaxillary–frontal contact, as does *Herpestides*, which has been suggested to be a structural (if not genealogical, see below) ancestor of the Hyaenidae (De Beaumont 1967). The internal polarity within the Hyaenidae, based on the distribution of other characters, seems also to favor the interpretation of this state as primitive for Hyaenidae as a whole, as the suture is present in the structurally primitive *Tungurictis* and *Plioviverrops*, and is lost in more advanced taxa such as *Thalassictis* and *Hyaenictitherium*.

In their analysis of hyaenid interrelationships, Galiano & Frailey (1977) mention this feature in a footnote, as an autapomorphy of *Percrocuta*. However, the suture is modally present in *C. crocuta*, *A. eximia*, and *H. hyaena*, based in skulls we have seen (Figs. 3, 4, 5). In *P. brunnea*, however, the distance between the frontal and maxillary is invariably great (Fig. 6). The presence of a fronto-maxillary suture in the taxa mentioned clearly represents a secondarily derived condition.

Character 25 – Size of inferior oblique muscle fossa at maxillary–lacrimal suture postero-dorsal to infra-orbital foramen

Coding. – 0 (small); 1 (large).

Comments. – Within the orbital mosaic, all hyaenids investigated have an inferior oblique muscle fossa at the suture between the maxillary and lacrimal (Fig. 26). This fossa displays a deeper invasion of the maxillary bone in *P. brunnea* than in the other Recent taxa (Fig. 26). Outgroup comparison indicates that this is a derived condition (see, e.g., De Beaumont 1967, Fig. 2), although in *Herpestides*, what is presumed to be the homologous fossa (*'faible lacune circulaire'* of De Beaumont, 1967, p. 83) is located on the palatine–maxillary suture, somewhat dorso-ventrally to its position in Recent hyaenids. *Proteles* takes an intermediate position, with the fenestra (very small in this taxon) being located at the juncture between maxillary, palatine, and lacrimal (Fig. 26).

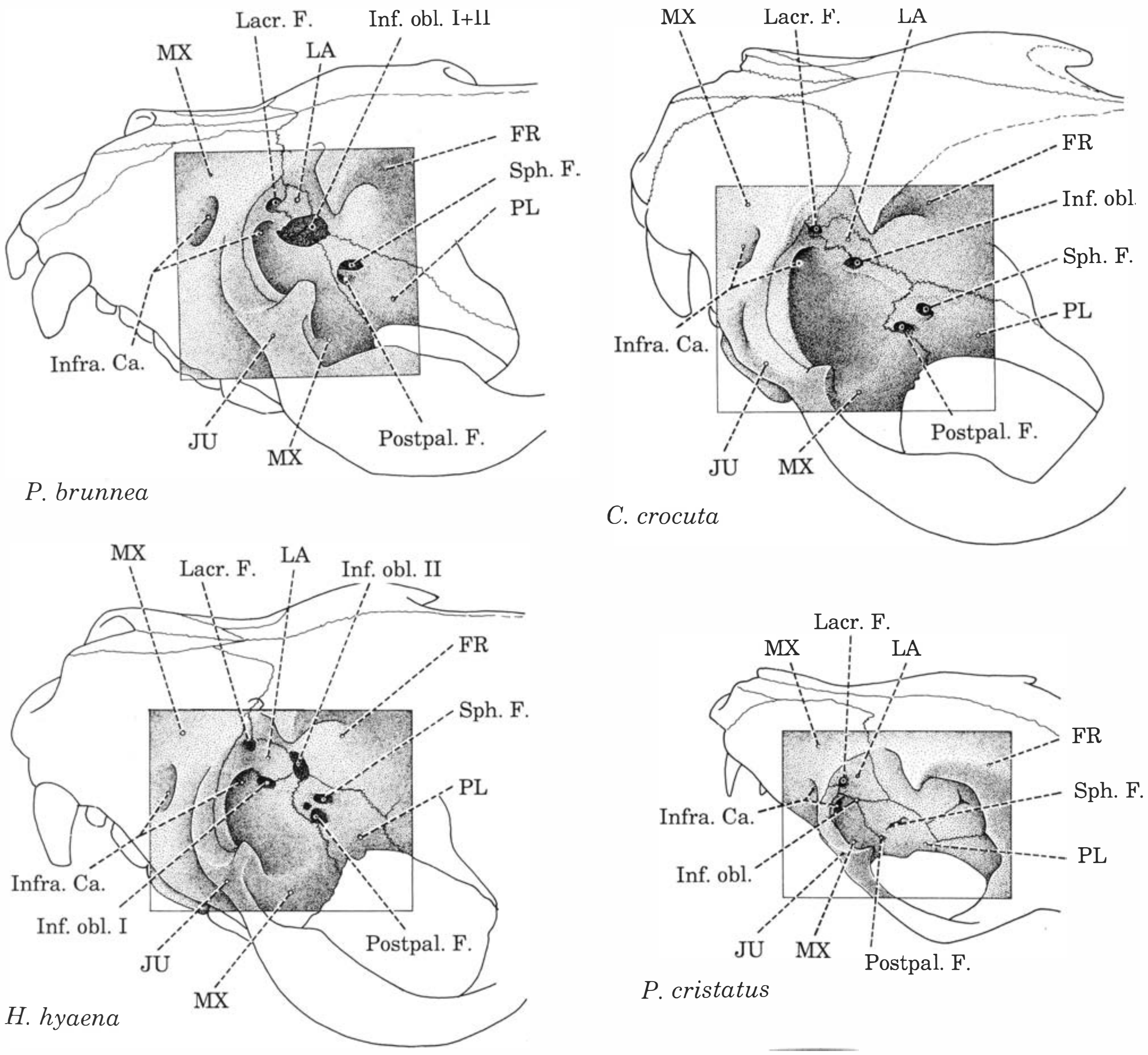


Fig. 26. Illustrations of orbital region of extant hyaenids, showing characteristic features. Abbreviations: FR: Frontal; JU: Jugal; LA: Lacrimal; MX: Maxillary; PL: Palatine; Inf.obl. I: fossa for inferior oblique muscle; Inf.obl. II: second fossa for inferior oblique muscle; Infra.Ca.: infraorbital canal; Lacr.F.: lacrimal foramen; Postpal. F.: postpalatine foramen; Sph.F.: sphenoid foramen. Same specimens as in Figs. 3–6. Not to scale.

Character 26 – Inferior oblique muscle fossa II at juncture between maxillary, lacrimal, and frontal

Coding. – 0 (absent); 1 (present).

Comments. – In both *H. hyaena* and *P. brunnea*, there is a fossa at the juncture between maxillary, lacrimal and frontal. We interpret it as a second fossa for the inferior oblique muscle responsible for lateral movements of the eye. In Fig. 26, the orbit of *P. brunnea* shows only one large fossa, but this is because the bony bar separating the fossae is broken in this specimen (condition verified by inspection of other specimens). A second fossa is also sometimes encountered in young *C. crocuta*, but this second fossa generally becomes grown over with bone in mature individuals (Fig. 26). There is no evidence of such a fossa in *P. cristatus* or any of the outgroups. We interpret it as a derived condition and have coded it as present in *H. hyaena* and *P. brunnea*. As we shall see, it is the only synapomorphy uniting these taxa in a cladistic phylogeny.

Character 27 – Sphenoid foramen and postpalatine foramen position

Coding. – 0 (well separated, distinct foramina); 1 (foramina located close together in a single depression).

Comments. – As De Beaumont (1967) noted for *Herpestides*, these foramina are superposed, one lying just dorsally to the other. However, in *P. cristatus*, *C. crocuta*, and *H. hyaena*, these foramina, while lying adjacent to each other, are well separated, each within its own depression (Fig. 26). In *P. brunnea*, the two foramina lie closer together, and emanate into a common depression (Fig. 26), a condition that we interpret as derived.

Character 28 – The contribution of the maxillary to the antero-internal rim of the zygomatic arch

Coding. – 0 (small to none); 1 (maxillary makes up a substantial portion of the antero-dorsal margin of the zygomatic arch).

Comments. – In primitive forms, as well as in the outgroups, the antero-internal jugo-maxillary suture is located well down on the orbital (inner) side of the zygomatic arch (Fig. 5). In derived hyaenids, however, the maxillary contribution to the zygomatic arch is greater, and the jugo-maxillary suture is located on the dorsal side of the zygomatic arch (ventro-lateral margin of the orbit), which is here formed into a shelf (Figs. 3, 4, 6).

Character 29 – Lacrimal–palatine suture in orbital mosaic

Coding. – 0 (present); 1 (absent).

Comments. – This character is used by Wozencraft (1989) in his work on carnivore phylogeny. In primitive hyaenids (e.g., *Proteles*), there is a broad lacrimal–palatine contact, just as in the outgroups (Fig. 26). In the other extant hyaenids, however, a corner of the maxillary intervenes between the lacrimal and the orbital wing of the palatine, with (*H. hyaena*, *P. brunnea*) or without (*C. crocuta*) a fossa (character 26) in this position (Fig. 26). The derived condition of these forms parallels that of Otariidae, Odobenidae, and Phocidae (Wozencraft 1989).

Character 30 – Nasal wings of premaxilla

Coding. – 0 (divergent); 1 (vertical).

Comments. – In *H. hyaena* the nasal wings of the premaxilla are vertically placed and parallel (Fig. 27). In all other taxa in which this character could be investigated they diverge dorsad (Fig. 27). We take this to represent an autapomorphy of *H. hyaena*.

Character 31 – Processes for the nuchal ligaments

Coding. – 0 (small); 1 (large).

Comments. – The processes for the attachment of the nuchal ligaments on the occipital just beneath the terminus of the sagittal crest are generally much larger in *P. brunnea* than in other hyaenids, including *C. crocuta*.

Character 32 – Shape of basioccipital in ventral view

Coding. – 0 (flat); 1 (low lateral ridges and central groove).

Comments. – This character was discussed by Qiu (1987). In most hyaenids, the anterior end of the basioccipital–basisphenoid–pterygoid complex is flat. In some derived forms, such as *C. crocuta* (Fig. 4) and *A. eximia*, this region forms two low ridges, with a central groove. The condition in the outgroups is somewhat variable. However, *Herpestides* clearly has a flat area here, which, together with the character distribution within the Hyaenidae, has enabled us to select this as the primitive character state.

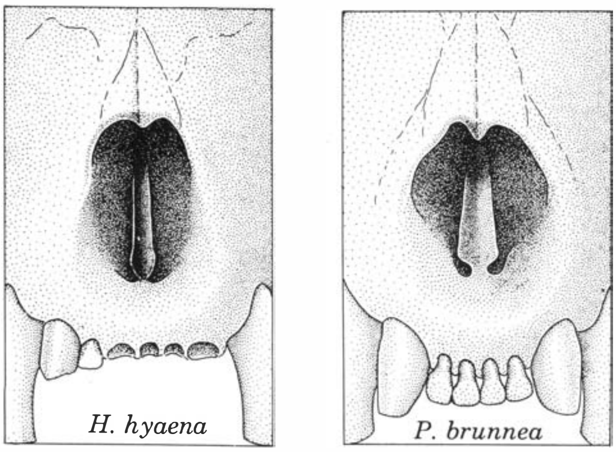


Fig. 27. Nasal region of *H. hyaena* and *P. brunnea*, showing parallel position of the nasal wings of the premaxilla in the former taxon. Same specimens as in Figs. 3 and 6. Not to scale.

Character 33 – Position of premaxillary–maxillary suture on palate

Coding. – 0 (near the middle of the incisive fossa); 1 (at the postero-lateral margin of the incisive fossa).

Comments. – This character is also discussed by Qiu (1987). Polarity is again very difficult to establish, as the condition in the outgroups is variable. We have again relied on *Herpestides*, in which the suture ends near the middle of the incisive fossa. (We may anticipate the phylogenetic analysis here, and note that these questions of polarity in a few characters do not have any influence on the topology of the cladograms constructed by PAUP. Changing the polarity merely results in some additional reversals in the middle of the cladogram.)

Character 34 – Shape of incisive fossa

Coding. – 0 (broad); 1 (narrow).

Comments. – In most hyaenids, as well as in the outgroups, the incisive fossa is broad, i.e. oval or rounded. In *C. crocuta*, however, it is closed off and slit-like (Fig. 4). The latter condition is clearly derived.

Character 35 – Position of major palatine foramen

Coding. – 0 (at palatine–maxillary suture); 1 (far forwards on palate).

Comments. – This character is one that was used by Wozencraft (1989) in his phylogenetic analysis of the order Carnivora. The condition in the outgroups is variable, with felids having the foramen at the palatine–maxillary suture, and herpestids having it anteriorly, which is also the case in hyaenids. We have used this character merely to establish a synapomorphy uniting hyaenids relative to the 'hypothetical ancestor' of the phylogenetic analysis. Qiu (1987) has used the exact position of the major palatine foramen relative to the tooth row in his phylogenetic investigations. However, we found that this approach did not give consistent results, and have not used it here. In this context, it is extremely interesting that *Herpestides* has the major palatine foramen located slightly anterior to the palatine–maxillary suture, but clearly on the maxillary itself (De Beaumont 1967:Pl 1:1C). This intermediate condition is not seen in any Recent feliform carnivore we have studied (see further below).

Character 36 – Shape of jugal–maxillary suture in external view

Coding. – 0 (angled downwards posteriorly); 1 (straight).

Comments. – This is another character discussed by Qiu (1987). He suggested that the straight suture was primitive. However, indications are that the reverse is the case. In respect of Qiu's taxa, the angled downward character state is clearly primitive, as it is seen in taxa such as *Hyaenotherium* and *Ictitherium*, which form part of the outgroup complex of his work. With regard to the Hyaenidae as a whole, the situation is more difficult, as the outgroups again vary among themselves. However, *Herpestides* (De Beaumont 1967, Pl. 1:1A) has an angled jugo-maxillary suture, as do felids, and we take this to be the primitive condition.

Character 37 – Dorsal exposure of nuchal bone

Coding. – 0 (strong); 1 (weak).

Comments. – This character is discussed by Buckland-Wright (1969) and Qiu (1987). *C. crocuta* has a much smaller and weaker dorsal exposure of the nuchal than either *H. hyaena* or *P. brunnea.* We take the former condition to be derived within this group of taxa. The character state distribution in the Hyaenidae as a whole is difficult to evaluate, due to insufficient material to use for the allometric analysis that would be required.

Character 38 – Size of supramastoid crest

Coding. – 0 (weak); 1 (strong).

Comments. – Yet another character discussed by Buckland-Wright (1969) and Qiu (1987). The former author compared only *H. hyaena* with *C. crocuta,* finding that they differed in this character, with the former having a weak supramastoid crest, the latter a strong one. This arrangement was accepted by Qiu (1987) in his phylogenetic discussion. However, examination has shown the supramastoid crest of *P. brunnea* to be as robust as that of *C. crocuta,* and much more so than that of *H. hyaena.* This would seem to be the derived condition.

Character 39 – Size of mastoid crest

Coding. – 0 (short); 1 (long).

Comments. – The same comments as for the previous character apply here. Buckland-Wright (1969) originally described the character states in *H. hyaena* and *C. crocuta,* and these were uncritically accepted by Qiu (1987), without reference to *P. brunnea.* In *H. hyaena,* as well as in the outgroups, the mastoid crest ends at the postero-dorsal end of the external auditory meatus. In *P. brunnea* and *C. crocuta,* on the other hand, the mastoid crest continues beyond this point well towards the ventral end of the external auditory meatus, a condition that is probably derived.

Character 40 – Placement of septum bullae

Coding. – 0 (vertical); 1 (semihorisontal to horisontal).

Comments. – The morphology of the bulla of hyaenids has been thoroughly discussed in Hunt (1974, 1987). In this context we will merely note that the septum bullae of *Proteles* and of most herpestids, as well as *Herpestides* (De Beaumont 1967, Fig. 3) is horizontally positioned, dividing off an anterior, tympanic, chamber from the posterior, caudal entotympanic chamber. In derived hyaenids, such as *Crocuta,* the septum is semi-horisontal to horisontal (recumbent). This derived character state is seen in most fossil hyaenids in which the bulla is preserved.

Character 41 – Shape of caudal entotympanic

Coding. – 0 (uniform); 1 (local ventral expansion).

Comments. – The local ventral expansion of the caudal entotympanic is an autapomorphy of *Proteles,* and is not seen in any other taxon in the outgroup or the ingroup.

Character 42 – Size of tympanic

Coding. – 0 (small); 1 (medium); 2 (large).

Comments. – This is another character of the unique 'hyaenid' bulla type (see Hunt 1974, 1987, for a discussion). In the outgroups and in *Proteles,* the tympanic chamber of the bulla is small relative to the caudal entotympanic chamber. In derived forms, however, the tympanic has grown caudad and ventrad to cover the caudal entotympanic, to form a bulla with a lower (ventral) tympanic chamber and an upper (dorsal) caudal entotympanic chamber, cf. Qiu (1987, Fig. 13).

Character 43 – Position of external auditory meatus

Coding. – 0 (far forwards of nuchal crest); 1 (level with nuchal crest).

Comments. – In the outgroups, and in primitive hyaenids such as *Proteles* (Fig. 5) and *Ictitherium,* the external auditory meatus is located some distance anterior to the juncture between supramastoid crest and nuchal crest. In more derived hyaenids, this distance is considerably reduced (Figs. 3, 4, 6).

Character 44 – Shape of nuchal crest

Coding. – 0 (antero-posteriorly inclined); 1 (nearly vertical or vertical).

Comments. – In primitive forms, as well as in most outgroups, the nuchal crest is straight, but inclined from the vertical. In derived hyaenids the nuchal crest is vertical in its ventral portion, then turns postero-dorsad to meet the expanded nuchal. This character and the previous one are probably strongly interdependent, and we have only used one of them in any single phylogenetic analysis, generally the present one, as it is more often codable on fossil material.

Characters of the postcranial skeleton

As noted, postcranial remains of fossil hyaenas are scarce, and furthermore, identifications of many taxa, especially Turolian ones, are dubious. Therefore we have restricted our search for characters of the postcranial skeleton to the extant hyaenids. Useful characters are extraordinarily difficult to find. Most features that show differences between the four taxa are either shared by *C. crocuta, P. brunnea*, and *H. hyaena* as probable synapomorphies uniting these taxa relative to *P. cristatus*, or are clear autapomorphies of *C. crocuta*. Examples of the latter are the size of the attachment areas for the omohyoid and rhomboideus on the scapula and the shape of the iliac blade. However, probable autapomorphies of *H. hyaena* (e.g., origin of the rectus femoris) and *P. brunnea* (shape of attachment area of subscapularis) are also in evidence. There are only two characters that we feel reasonably certain represent synapomorphies uniting two of the extant derived hyaenas to the exclusion of the third species. These are presented below. The third character of the postcranial skeleton, the size of metacarpal I, is often used in the literature.

Character 45 – Size of metacarpal I

Coding. – 0 (large); 1 (reduced).

Comments. – This bone is vestigial in *H. hyaena, P. brunnea*, and *C. crocuta*. This is a derived state uniting these species relative to *Proteles*, where the MC I is much larger. A large MC I is also seen in most fossil taxa for which this element is known (see, e.g., Hendey 1974a). The suggestion that advanced hyaenids *sensu stricto* can be distinguished from *Percrocuta* on this basis (Galiano & Frailey 1977) is without foundation, as the specimens on which this belief was based actually pertain to *Chasmaporthetes* (Qiu 1987; Werdelin & Solounias 1990; this paper).

Character 46 – Overlap between articulated atlas and axis

Coding. – 0 (short); 1 (long).

Comments. – In *P. cristatus* and *H. hyaena*, the atlas and axis have a relatively short overlap. Compared to this, the overlap in *P. brunnea* and *C. crocuta* is relatively long. This probably has to do with the angle of the articular facets relative to the sagittal plane, but this feature is difficult to measure. We consider the condition in *P. brunnea* and *C. crocuta* derived.

Character 47 – Angle of scapular spine in posterior view

Coding. – 0 (angled); 1 (straight).

Comments. – In *P. brunnea, P. cristatus* and most viverrids and herpestids, the dorsal end of the scapular spine when seen in posterior view sticks out at an angle from the scapula. In *C. crocuta* and *H. hyaena*, however, the transition is smooth (Fig. 28). We consider this a synapomorphy uniting the latter two species.

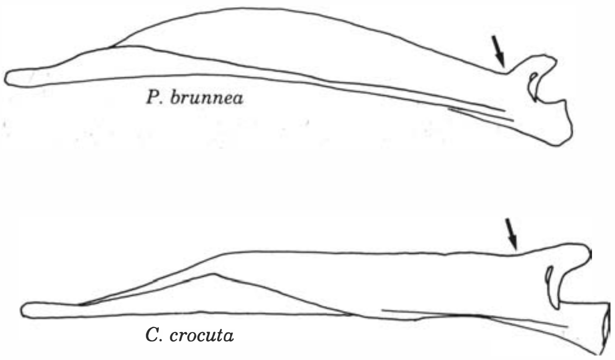


Fig. 28. Posterior view of scapula of *P. brunnea* (AMNH 83590) and *C. crocuta* (AMNH 147880) showing derived condition of scapular spine in the latter (and in *H. hyaena*). Not to scale.

Phylogenetic analysis

Historical background

Despite the many descriptive and taxonomic works on fossil hyaenas published over the past 200 years, surprisingly few authors have discussed the interrelationships of the various hyaenid taxa. In part this is due to confusion regarding the limits of the family Hyaenidae itself. The early authors, such as Roth & Wagner (1854), Von Nordmann (1858), and Gaudry (1862–1867) regarded what we now consider as primitive hyaenid genera, such as *Ictitherium* and *'Thalassictis'*, to be viverrids of a hyaenoid type. All other, more derived forms were included in the genus *Hyaena*, including *'H. hipparionum'* (Gervais 1846, 1850), although this form was subsequently transferred to the subgenus *H. (Palhyaena)* by Gervais himself (1859), and still later to *Ictitherium* by Gaudry (1862–1867).

The first authors to describe new fossil genera within what they themselves considered to be the family Hyaenidae were Gaudry (1861), who described *Hyaenictis graeca* as a form spanning the gap between hyaenoid viverrids and hyaenas proper, and Hensel (1862), who coined the name *Lycyaena* for Gaudry's (1861) species *Hyaena chaeretis*. This latter form was considered by Hensel (1862) to be closer to modern hyaenas than was *Hyaenictis*.

Within the genus *Hyaena* as then conceived, the spotted hyaena (now *Crocuta crocuta)* was early on understood to be considerably different from the other forms, and was consigned to a separate subgenus by Gervais (1859). *Hyaena prisca* (Serres *et al.* 1828), was unanimously considered to be closely related to the modern striped hyaena *Hyaena hyaena* (then commonly *Hyaena striata*), an opinion which has remained valid to this day, but is reconsidered by Turner (1990) and herein. Regarding the affinities of the other fossil forms known at that time, such as *Hyaena perrieri* (Croizet & Jobert 1828), and *Hyaena brevirostris* (Aymard 1846), there was considerable confusion, however. To a great extent this was due to the limited knowledge of the structure and affinities of the brown hyaena, *Parahyaena brunnea* (then commonly *Hyaena fusca*), a situation which has not changed significantly in the past 150 years.

In 1862–1867, Gaudry became the first to truly discuss the phylogeny of hyaenids. He does this in the form of a key

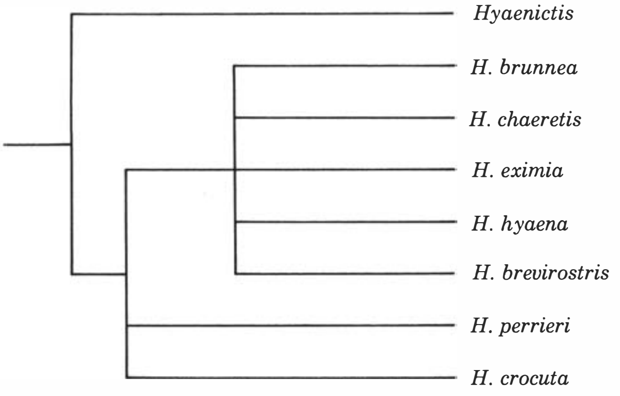


Fig. 29. Cladogram representation of Gaudry's (1862–1867) view of hyaenid interrelationships. Note that all species except *Hyaenictis* are referred to *Hyaena.*

to the relevant taxa (illustrated in diagram form in Fig. 29), and suggests that *P. brunnea, H. hyaena, P. brevirostris, A. eximia,* and *L. chaeretis* form one stem, with *Crocuta* representing a second and *P. perrieri* standing in between these, and with *Hyaenictis* as primitive ancestor. If one moves *Lycyaena* closer to *Hyaenictis* and places *Crocuta* as sister taxon to *Adcrocuta,* Gaudry's ideas resemble the topology of our final cladogram (see below) surprisingly closely.

In 1873, Gaudry redescribed *Palhyaena hipparionum,* which he had earlier transferred to the genus *Ictitherium* (Gaudry 1862–1867). In the course of his discussion he notes that the loss of M^2 may be considered a synapomorphy of hyaenids, distinguishing them from viverrids. This is the first clear statement to this effect.

In his monograph on Sivalik and Narbada Carnivora, Lydekker (1884) describes a new genus, *Lepthyaena,* while at the same time collapsing *Hyaenictis* into *Hyaena,* together with *Hyaena chaeretis* (Lydekker was apparently not aware of Hensel's 1862 *Lycyaena*). Lydekker rightly notes the relationship between *Hyaena* and viverrids through *Ictitherium,* and also correctly notes the paraphyletic nature of the family Viverridae as then conceived. Later (p. 133) Lydekker is the first (excepting the brief remarks by Gaudry 1862–1867) to directly address the question of the interrelationships of hyaenids. He does not, however, make much headway, for the most part because his conceptions of the species involved were faulty. However, he does come at least close to suggesting that *Ictitherium* should be grouped with the Hyaenidae, and that his new species *'Hyaena' macrostoma* (now *Lycyaena*) is closely related to *Lycyaena chaeretis.*

Another step forward is represented by Schlosser (1890), who presents a diagram of hyaenid interrelationships (reproduced in cladogram form in Fig. 30 herein). He has allied *Lycyaena chaeretis* (but not *L. macrostoma*) with the *Ictitherium* group of viverrids. In the *Hyaena* group his conception of relationships is largely unresolved, but we may note that he allies *H. hyaena* with *H. prisca,* as had all previous authors. Furthermore, he has *P. brunnea* nearer to *Crocuta* than to *H. hyaena,* a position also taken by more recent paleontologists (Galiano & Frailey 1977) in opposition to most neontologists.

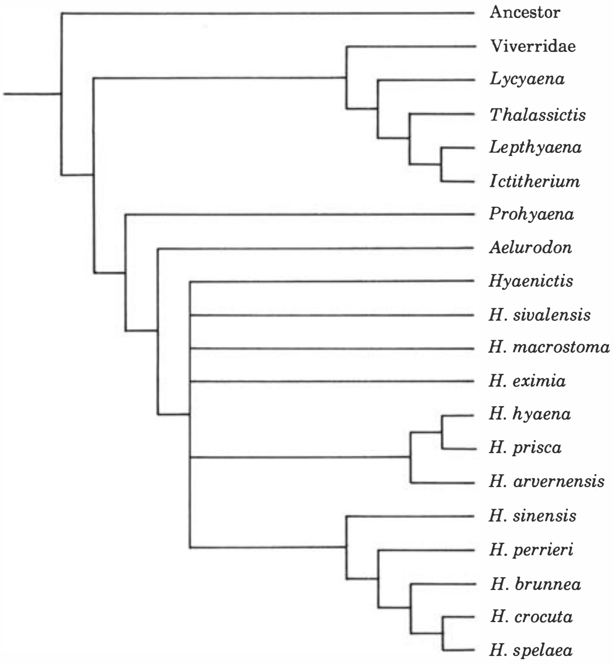


Fig. 30. Cladogram representation of Schlosser's (1890) view of hyaenid interrelationships. *Prohyaena* and *Aelurodon* are borophagine canids, at that time thought to be hyaenas. Note phylogenetic separation of *H. hyaena* and *P. brunnea.*

After Schlosser's exposition there is a long hiatus during which the emphasis is on pure description. Even in the most extensive work of the following 40 years (Zdansky 1924), there is almost no consideration at all of hyaenid interrelationships. The sole exception during this period is Winge's (1895) important contribution to hyaenid phylogeny. He is the first to present an essentially modern diagnosis of the Hyaenidae, using characteristics of the bulla. By this means he is the first to transfer *Ictitherium* and allied forms to the Hyaenidae.

In 1929, Arambourg & Piveteau present a brief discussion of hyaenid interrelationships, the first since Schlosser (1890). They unite *H. hyaena* and *P. brunnea* on the basis of the symplesiomorphic structure (relative to *C. crocuta*) of the M_1 talonid. Their subsequent discussion mainly concerns the line leading from *Hyaena eximia* (now *Adcrocuta*) to *C. crocuta* by way, they suggest, of *Hyaena perrieri* and *Hyaena brevirostris.* In this reasoning they are close to Schlosser, as can be seen from Fig. 30.

Pilgrim (1931) is the first paleontological writer to accept Winge's (1895) definition of the Hyaenidae. In this work, Pilgrim includes a lengthy discussion of his ideas concerning hyaenid phylogeny, but it is not until 1932 that he publishes a diagram depicting his views. This diagram is reproduced in cladogram form in Fig. 31 herein. The main differences from Schlosser's diagram, apart from the inclusion of *Ictitherium* and its allies in the Hyaenidae, are the addition of many more taxa (especially those belonging to what will be referred to below as the 'percrocutoid' group), the suggested close relationship between *H. hyaena* and *P. brunnea,* and the inclusion of *H. perrieri* and *H. brevirostris* in *Crocuta* (although this last point is implicit in Schlosser's

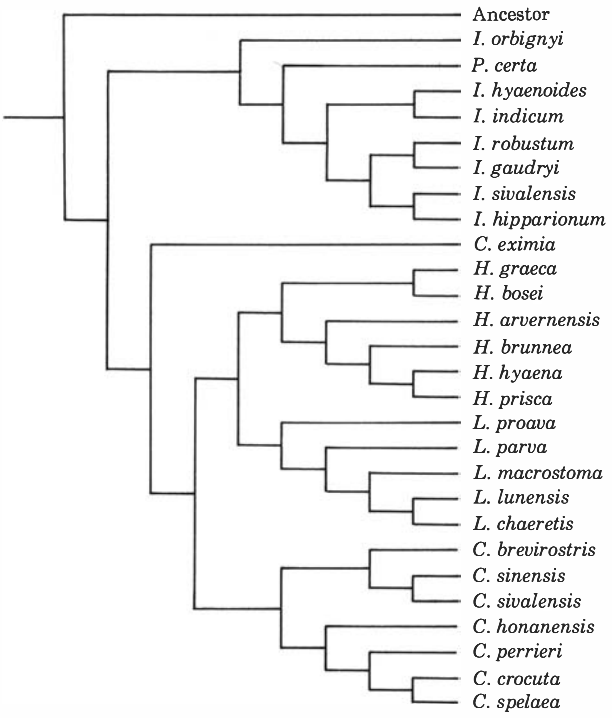


Fig. 31. Cladogram representation of Pilgrim's (1932) view of hyaenid interrelationships. Note referral of *P. brevirostris* and *P. perrieri* to *Crocuta*.

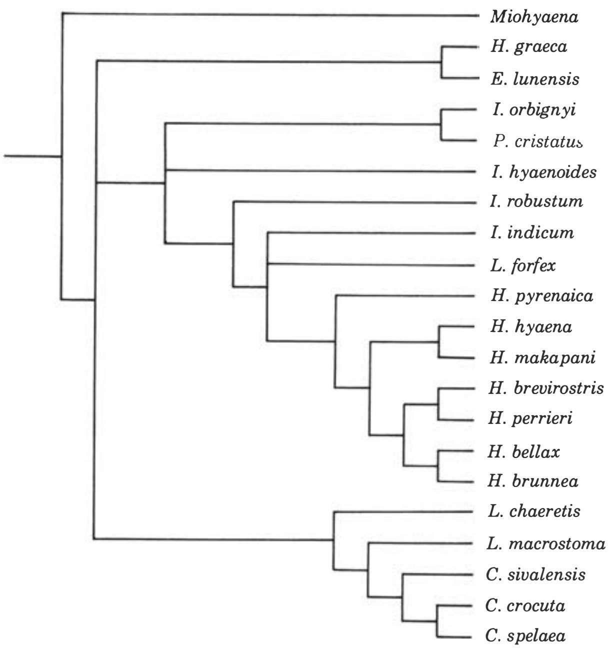


Fig. 32. Cladogram representation of Thenius' (1966) view of hyaenid interrelationships. Note inferred relationships between *Hyaenictis* and *Chasmaporthetes* (as *Euryboas lunensis*) and *Plioviverrops* (as *I. orbignyi*) and *Proteles*.

diagram). In all, Pilgrim's (1932) diagram is essentially modern in many respects.

The next major attempt to assess hyaenid phylogeny and evolution was made by Kretzoi (1938). He tried to produce a consistent classification of the family, separating it into two subfamilies, Ictitheriinae and Hyaeninae (originally proposed by Schlosser). The first incorporates *Ictitherium* and *Palhyaena*, and the new genera *Protictitherium*, *Sinictitherium* and *Hyaenictitherium*. The second subfamily includes all other hyaenids, for which Kretzoi creates some eight new genera apart from those already recognized at the time. It can be noted that Kretzoi used his names to depict his views of the relationships of the various forms, and sometimes also their structure or hypothesized ecology. Thus, *Hyaenictitherium* is a hyaena-like ictithere. This great mass of new names created enormous problems for subsequent workers on the group, and many chose to disregard Kretzoi's work. In hindsight, however, we would like to clearly state that Kretzoi was correct in most of his taxonomic decisions, including the separation of such genera as *Adcrocuta*, *Percrocuta*, *Pliocrocuta*, and *Pachycrocuta*. Thus, our views on hyaenid taxonomy, if not phylogeny, are closer to Kretzoi's (1938) views today than they have been at any time in the past fifty years.

As regards the Hyaenidae as a whole, Kretzoi (1938) considered the family to be diphyletic, with the Ictitheriinae and Hyaeninae having evolved independently from separate viverrid ancestors.

The same separation into the subfamilies Ictitheriinae and Hyaeninae is used by Simpson (1945), although this writer did not recognize (or was not aware of – Simpson's work being completed several years before it was published) Kretzoi's new genera.

After the 1940's there has been a long period of systematic revision of hyaenids, interspersed with occasional phylogenetic suggestions. This revisionary work still continues (e.g., Howell & Petter 1980; Werdelin 1988a, 1988b; Semenov 1989), but has now reached a point where phylogenetic analysis is no longer hampered by taxonomic confusion to the degree it has been in the past.

The first worker after Pilgrim (1932) to present diagrams depicting the suggested interrelationships of hyaenids is Ewer (1955b). Her studies were mainly concerned with the ancestry of the Recent species, and only briefly touch upon other matters. Like Pilgrim she considers *H. hyaena* and *P. brunnea* closely related.

Arambourg (1959) discusses the phylogeny of hyaenids, in particular the modern forms, and arrives at the for the time reasonable, if perhaps unduly pessimistic, conclusion that the then current state of knowledge did not allow for any statements at all concerning this question. This conclusion is, once again, to a great extent due to the taxonomic confusion prevalent at that time regarding many forms.

Abu Bakr (1959), in an unpublished thesis, discusses the phylogeny of hyaenids on the basis of the material from Samos. His conclusions are general, but among other things he suggests a main stem leading from Viverrinae through *Ictitherium*, *Lycyaena*, and *Leecyaena* to derived hyaenids. Abu Bakr's thoughts on the subject are, however, hard to follow, as he tends to lump all manner of disparate taxa into *Ictitherium*.

The next major contribution to hyaenid phylogeny was made by Thenius (1966). His diagram of hyaenid interrelationships is reproduced in cladogram form in Fig. 32 herein. Innovative aspects include the association of *Lycyaena* with *Crocuta*, and of *Hyaenictis* with *Euryboas*. Thenius also recognizes that the percrocutoid forms (to which he adds *Adcrocuta eximia*) form a group of separate ancestry from other hyaenids. Lastly, Thenius does away with the Ictitheriinae as a separate subfamily. With some exceptions, this view of hyaenid phylogeny is still the commonly accepted one. For further details we refer to Thenius' (1966) valuable discussion.

In a series of articles De Beaumont (1967, 1968, 1969a) discusses selected aspects of hyaenid interrelationships, modifying Thenius' results in several ways, but concentrating (De Beaumont 1967) on the basal history of the family, which he derives from *Herpestides*. Here De Beaumont is the first to suggest the inclusion of *Tunguricits* in the Hyaenidae, and to suggest a relationship between *Hyaena borissiaki* and *Chasmaporthetes* spp., ideas that have subsequently proved to be of great importance.

Crusafont Pairó & Petter (1969) present a diagram in which they suggest (as had most authors prior to Thenius) that the Hyaenidae should be separated into two monophyletic groups, the Ictitheriinae, including *Progenetta*, *Plioviverrops*, *Ictitherium*, *Hyaenictis*, *Euryboas*, and *Lycyaena*, and the Hyaeninae, including *Hyaena*, *Crocuta*, and *Percrocuta*. This latter suggestion is based on the observed strong resemblances between the Miocene *Percrocuta* species and modern hyaenas, resemblances that are now considered to be convergent.

During the 1970's a spate of ideas concerning the interrelationships of hyaenids appeared, beginning with Ficcarelli & Torre (1970). These authors present a number of novel ideas, the most important of which is the validation of *Adcrocuta* as a genus separate from *Percrocuta*. Ficcarelli & Torre suggest a derivation of *Hyaena* from *Ictitherium* and of *Euryboas* from *Lycyaena*. They do not attempt to connect the various lineages in the Miocene, however.

The next attempt to address the question of hyaenid interrelationships was made by Hendey (1974a). He sets *Percrocuta* well off from other hyaenids, and presents novel ideas regarding the inclusion of several African taxa (notably *Ikelohyaena abronia* and *'P.' bellax*) into the ancestry of the modern species. The most important point raised by Hendey concerns the relationship between *H. hyaena* and *P. brunnea*. He suggests that these species are only distantly related, with a common ancestor in the Miocene, and that *P. brunnea* is more closely related to *Pachycrocuta* spp. than to *H. hyaena*. In consequence of this he separates the two modern forms at the subgeneric level, suggesting the name *Parahyaena* for *P. brunnea* and its relatives. As we shall see below, Hendey's suggestions are well justified.

The next person to study this subject was Schmidt-Kittler (1976). In this work a major step forward was taken with the recognition that the percrocutas (with the exception of *Adcrocuta eximia*) are distinct from hyaenids and show derived characters in common with stenoplesictines. The remaining aspects of Schmidt-Kittler's hypothesis are quite close to the ideas of Thenius (1966).

The first explicitly cladistic hypothesis of hyaenid interrelationships was presented by Galiano & Frailey (1977). Like several authors before them they find that *H. hyaena* and *P. brunnea* are not sister groups. However, they do conclude that the extant forms, together with the Plio-Pleistocene genus *Pachycrocuta* form a monophyletic group. This is in opposition to most earlier workers, who have derived *Hyaena* and *Crocuta* from separate Miocene ancestors.

The continuing research on the Langebaanweg fossil fauna of South Africa led Hendey (1978) to a further discussion of hyaenid interrelationships, wherein he modified his views from 1974 somewhat, but retained the opinion the *H. hyaena* and *P. brunnea* were only distantly related. The most important points in Hendey's (1978) paper center around his discussion of *Chasmaporthetes*, which stems from an earlier paper (Hendey 1975). We shall have cause to return to these questions later in this paper.

The bulk of work on hyaenids during the 1980's has dealt with taxonomic issues, and it is this work that has led hyaenid taxonomy to the stage where a monograph such as the present one is even possible. However, during the 1980's there have also been some important papers discussing hyaenid interrelationships. Among these are Howell & Petter (1980), Solounias (1981), and Solounias & De Beaumont (1981). Qiu (1987) has made a fundamental contribution with his extensive discussion of the interrelationships of Plio-Pleistocene hyaenids. Especially important is his analysis showing *Crocuta* and *Pachycrocuta* (=*Pliohyaena* of Qiu) to be sister taxa. Unfortunately, his analysis is marred by several factors, including the incorrect lumping of *H. hyaena* and *P. brunnea*, incorrect polarity determinations, and errors of procedure. These problems are addressed in part by Werdelin & Solounias (1990) and will be further considered below.

Recently, a major contribution to hyaenid taxonomy and systematics has been published by Semenov (1989). In several ways his approach resembles the one taken here, including the distinction between genera such as *Ictitherium*, *Thalassictis*, *Hyaenotherium* and *Hyaenictitherium*, and in the understanding of the ecological roles of many of these taxa. However, Semenov's analysis also differs in several respects from ours. The most important difference is that Semenov, contrary to most current opinion (see, e.g., above) considers the ictitheres (*Protictitherium*, *Ictitherium*, *Thalassictis* and *Plioviverrops*) to be specialized members of the Viverridae, and that their resemblance to primitive hyaenids (Hyaenotheriini in his taxonomic scheme; *Hyaenotherium*, *Hyaenictitherium* and allies) is due to convergence. Semenov states in his summary (1989, p. 167) that 'Peculiarities in the skull morphology of ictitheres serve as proof that these carnivores could not initiate the family Hyaenidae, and therefore, they are rather remote in phylogenetic respect from representatives of the tribe Hyaenotheriini'. Unfortunately, Semenov's (1989, p. 40) diagnosis of the Viverridae (n.b., including Herpestidae) is composed entirely of characters (alisphenoid canal present, ossified auditory bulla, bony external auditory meatus, tooth formula, etc.) that are either uninformative for phylogeny at this level or plesiomorphic relative to the condition in Hyaenidae. The same comments apply to his diagnosis of Ictitheriinae (1989, p. 41). No other characters are in evidence in the figures, and we must conclude that, while the possibility of convergence in characters related to ecological specializations must always be kept in mind, Semenov has not established the monophyly of either his Viverridae or Ictitheriinae. Until such a time as synapomorphies uniting Ictitheriinae with some family other than Hyaenidae can be found, we will stand by the evidence presented here that they should be considered hyaenids.

Another difference between the present work and that of Semenov (1989) is that he unites *Hyaenotherium*, *Hyaenictitherium*, and *Miohyaenotherium* into the tribe Hyaenotheriini. This an attractive hypothesis which has been entertained by many authors (e.g., Werdelin, 1988b, wherein material of these three genera were all discussed as *Thalassictis*). However, our current analysis indicates that this group is not monophyletic, but part of the paraphyletic stem lineage leading up to the split between the modern hyaenid group and the *Chasmaporthetes* group (see below). Again, Semenov in his diagnosis (1989, p. 91) unites Hyaenotheriini by characters that are plesiomorphic relative to those of Hyaenini (the remaining hyaenids).

We conclude that although Semenov (1989) presents some interesting hypotheses (as well as highly interesting and insightful character analyses at the generic level), the validity of these hypotheses has yet to be established

The Recent taxa

The phylogenetic analysis of the Recent Hyaenidae presents special problems due, for the most part, to the curious mixture of plesiomorphic and autapomorphic character states exhibited by *Proteles cristatus*. We have therefore analysed data matrices incorporating only *C. crocuta*, *H. hyaena*, and *P. brunnea*, with a hypothetical ancestor, as well as a data set which in addition to these taxa also includes *P. cristatus*.

Interrelationships of extant bone-cracking hyaenids. – The first analysis is of all informative characters in the entire data set (Table 1). Out of the 47 characters in the master character list, 18 varied among the Recent derived hyaenids. Only 7 of those characters were informative in this context, however. The analysis of this data matrix using the exhaustive search option of PAUP resulted in a single most parsimonious tree (out of three possible trees, see below) of 28 steps and consistency index (c.i.) 0.812. This tree, which is shown in Fig. 33A, has *C. crocuta* and *P. brunnea* as sister taxa, and *H. hyaena* as the sister taxon of these two. The character states uniting *C. crocuta* and *P. brunnea* are: M^1 reduced (6:4), P^4 metastyle long (11:1), supramastoid crest strong (38:1), and overlap between atlas and axis long (46:1).

Table 1. Data matrix used in the PAUP analysis of the three extant bone-cracking hyaenids. The character numbers refer to the character list given in the text.

Character	6	8	11	21	22	24	25	26	27	31	32	33	34	36	38	39	46	47
Taxon																		
P. brunnea	4	0	1	1	1	1	1	1	1	2	0	0	0	0	1	0	1	0
H. hyaena	3	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	1
C. crocuta	6	1	1	0	2	0	0	0	0	0	1	1	1	1	1	1	1	1
Hypanc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

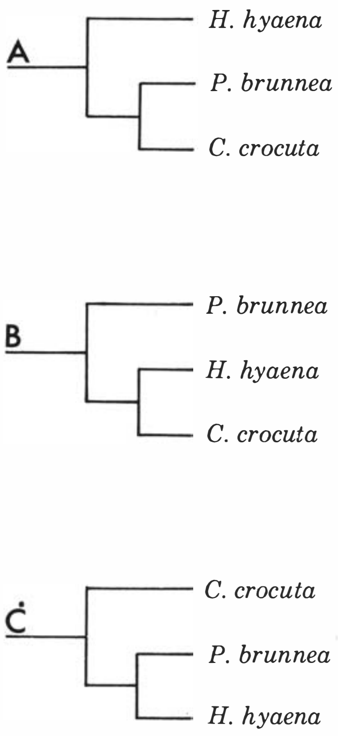


Fig. 33. The three possible rooted trees for the three larger extant hyaenas. □A. Best supported tree (l=28, c.i.=0.81). □B. Second best tree (l=30, c.i.=0.72). □C. Poorest tree (l=31, c.i.=0.68).

The second tree (Fig. 33B), which at 30 steps is two steps longer than the shortest tree for this data set, and has a c.i. of 0.722, unites *H. hyaena* and *C. crocuta* as sister taxa, with *P. brunnea* as the sister taxon to these. Two characters unite *C. crocuta* and *H. hyaena* here: the anterior position of the infra-orbital foramen (character 22:2), and the shape of the scapular spine (47:1). The third tree (Fig. 33C), finally, has a length of 31 steps and c.i. of 0.684. It has *H. hyaena* and *P. brunnea* as sister taxa, united by the presence of a second inferior oblique muscle fossa at the maxillary–lacrimal–frontal juncture (26:1).

In summary, these analyses show that support is strongest for a topology with *C. crocuta* and *P. brunnea* as sister taxa, a conclusion also arrived at by Galiano & Frailey (1977; but see Werdelin & Solounias, 1990). The topology with the weakest support of the three is the traditional one, with a monophyletic genus *Hyaena*. The latter result is of fundamental importance in showing that the genus *Hyaena* as traditionally conceived is in all probability based on primitive retentions (symplesiomorphies), or, which is probably a more correct interpretation, that *Hyaena* has been based on the many and obvious autapomorphies of *C. crocuta*.

Introducing PROTELES CRISTATUS. – This much said, it is time to enter *P. cristatus* into the analyses. When analyzing *P. cristatus*, however, nearly all dental characters had to be deleted since, due to the strongly autapomorphic character of the dentition in this species, most of the characters are not applicable to it. The result of this analysis is shown in Fig. 34 and Table 2. A total of 26 variable characters were analysed, of which 14 were informative. Using the exhaustive search option of PAUP, two equally parsimonious trees (Fig. 34A, B) of 32 steps and c.i. 0.762 were found. A third tree (Fig. 34C) is just one step longer than these two. The next available topology, on the other hand, is another six steps away. The first of the two shortest trees has *C. crocuta*

Table 2. Data matrix used in the PAUP analysis of the four extant hyaenid taxa. The character numbers refer to the character list given in the text.

Character	5	10	21	22	23	24	25	26	27	28	31	32	33	34	35	36	38	39	45	40	41	42	43	44	46	47
Taxon																										
P. brunnea	1	1	1	1	0	1	1	1	1	1	2	0	0	0	1	0	1	0	1	1	0	1	1	1	1	0
H. hyaena	1	1	0	2	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	1	0	1	1	1	0	1
C. crocuta	1	1	0	2	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
P. cristatus	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0
Hypanc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

and *P. brunnea* as sister taxa, united by the strong supramastoid crest (38:1) and the long overlap between atlas and axis (46:1). The second of the two shortest trees has *C. crocuta* and *H. hyaena* as sister taxa. They are united by the anterior position of the infra-orbital foramen (22:2), the presence of a premaxillary–frontal suture (24:1), and the shape of the scapular spine (47:1).

The third tree extracted, which is one step shorter than the two most parsimonious trees, has *P. brunnea* and *H. hyaena* as sister taxa, united by the position of the premaxillary–maxillary suture on the palate (33:0), and the presence of a second inferior oblique muscle fossa at the maxillary–lacrimal–frontal juncture (26:1)

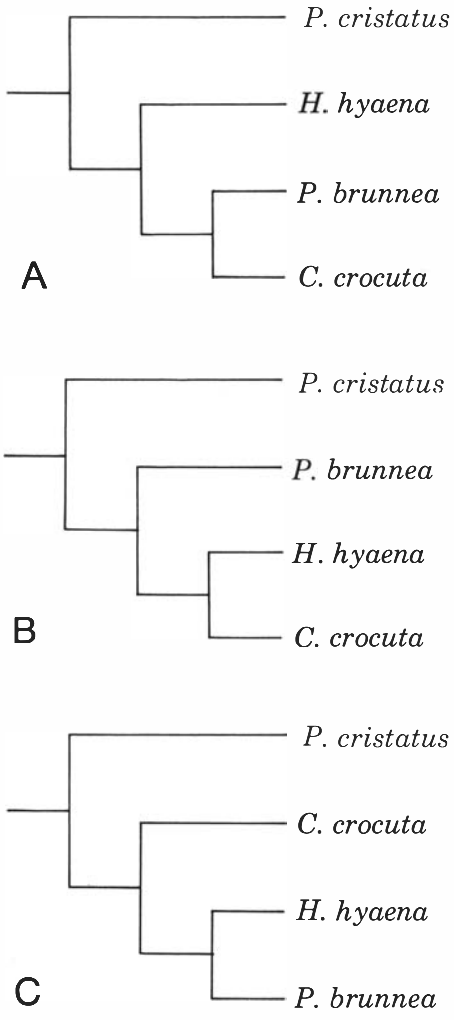


Fig. 34. Three of the nine possible rooted trees for all extant hyaenids. □A, B. Equally parsimonious trees (*l*=32, c.i.=0.76). □C. Poorer tree (*l*=33, c.i.=0.72). The shortest tree which does not have *P. cristatus* as the primitive sister taxon to the other taxa is 39 steps long.

The differences in synapomorphy schemes between this analysis and the one not including *P. cristatus* shows the importance of how many taxa are analysed, the levels of analysis, and the incorporation of fossils in the analyses. For Hyaenidae as a whole, e.g., the presence of a premaxillary–frontal contact is primitive, as seen both by its presence in primitive fossil hyaenids, and in several of the outgroups, including *Herpestides*. It is just as clearly the derived state in extant hyaenids, since to make this state primitive would unite *P. cristatus* and *P. brunnea* into a monophyletic group, a topology requiring a large number of character reversals. However, excluding *P. cristatus* from the analysis causes the absence of such a contact to be most parsimoniously interpreted as an autapomorphy of *P. brunnea*, while inclusion of *P. cristatus* makes the outgroup to *C. crocuta* + *H. hyaena* paraphyletic, and therefore the presence of the contact apomorphic to them. The same result would have been obtained with the inclusion of any of the better known fossil taxa; in the absence of *P. cristatus*, inclusion of fossils would therefore have been necessary. This line of reasoning is no different from that used in outgroup analysis (Maddison *et al.* 1984; Watrous & Wheeler 1981). The same approach must be applied to the ingroup, since the ingroup in its turn consists of outgroup and ingroup, at a different level. The same line of reasoning applies to the position of the premaxillary–maxillary suture on the palate. In the present scheme it may appear as a synapomorphy uniting *H. hyaena* and *P. brunnea* (see above), but with the inclusion of fossils it is clearly shown to exhibit the primitive condition in these taxa, and secondarily derived in *C. crocuta.*

It is not really possible to make a choice between the three trees, although perhaps the second is best supported, as there are three synapomorphies uniting *C. crocuta* and *H. hyaena* versus only two at this node in the other two trees. Whilst noting this very weak support of a *C. crocuta* + *H. hyaena* clade as opposed to any other arrangement, we conclude that the Recent Hyaenidae offer no firm data in support of a resolved scheme of interrelationships. Another indication of the difficulty involved is the very low number of informative characters we found, most characters investigated being either invariant for *C. crocuta*, *P. brunnea*, and *H. hyaena*, or autapomorphic for one of these taxa, or for *P. cristatus*. The best we can do at this stage is to place *P. cristatus* as sister group to an unresolved trichotomy of *C. crocuta* + *H. hyaena* + *P. brunnea*.

Fossil taxa

The position of PROTELES CRISTATUS relative to fossil taxa. – As noted above, *P. cristatus* is highly autapomorphic in its dental characters, and many of the characters that will be used in the analysis of fossil and Recent hyaenids together are not applicable to it. Therefore, before introducing fossils into the study of the interrelationships of Hyaenidae we must establish as accurately as possible the phylogenetic position of this species, so that it can be left out of the analyses to follow.

The first character complex to consider with regard to *P. cristatus* is the auditory bulla. Characters such as the position of the septum, the relative sizes of the bullar chambers, etc., firmly place the aardwolf below the genus *Ictitherium.* The latter has a bulla that is more derived in the direction of the advanced hyaenids in the cladogram (see below, Fig. 38). This allows us to establish the minimum age for this branching as mid-Miocene (the oldest occurrence of the analyzed fossil taxa included in the analysis being MN Zone 9 for *H. wongii*). The lineage leading to the Recent *P. cristatus* has thus been distinct from other Hyaenidae since at least the mid-Miocene. This conclusion, which has been reached by most other authors (e.g., Thenius 1966), is in stark contrast to the meager fossil record of the lineage, which is limited to some few finds in southern Africa (Gingerich 1974a; Hendey 1973, 1974a, 1974b). The oldest of these are the specimens from Swartkrans and Kromdraai, which are referred to a distinct species (herein named *P. amplidentus*) by Hendey (1974b). This species is more primitive than the extant *P. cristatus* in certain details of the skull and dentition (Hendey 1973, 1974b), but overall is a typical aardwolf, providing no additional information regarding the affinities of the genus.

The position of *Proteles* relative to the genera *Plioviverrops*, *Protictitherium*, *Tongxinictis* and *Tunguricits* is more problematical. The bulla morphology suggests that *Proteles* is more primitive than, e.g., *Tunguricits* and *Tongxinictis*, but the presence of the alisphenoid canal in these taxa and its absence in *Proteles* suggests the opposite, as does the loss of posterior molars in *Proteles.* The latter character could, however, in view of the reduced dentition of *Proteles,* easily be a convergence between this taxon and genera such as *Hyaena* and *Crocuta.*

A number of suggestions regarding the ancestry of *P. cristatus* have been advanced. One theme in these has been suggestions that this species is derived from *Lycyaena* or *Lycyaena*-like ancestors (e.g., Ewer & Cooke 1964). This seems implausible, in view of the many derived features of *Lycyaena* spp. relative to *P. cristatus* in, e.g., the basicranial region as well as the dentition. Another, more plausible suggestion is that *P. cristatus* is derived from *Plioviverrops*-like ancestors (Thenius 1966). This suggestion is to some extent underscored by the subsequent description by De Beaumont & Mein (1972) of additional taxa of *Plioviverrops*, suggesting a trend toward dental reduction in this genus. Although possibly somewhat more derived in bulla structure than *Proteles*, *Plioviverrops* is much more primitive in this regard than *Lycyaena* (De Beaumont 1969b; De Beaumont & Mein 1972). Thus, the most plausible suggestion is still that *Proteles* and *Plioviverrops* share a common ancestry, probably some time in the early Miocene, although with the material at hand such suggestions, in De Beaumont's words (1969b, p. 6) *'paraissent terriblement hypothétiques'.*

Analysis of the core taxa. – With the position if *Proteles* thus settled as best possible, we turn to the phylogenetic analysis of the remaining core taxa, which we may term hyaenids with unreduced dentition. The data set consisting of 18 taxa and a hypothetical ancestor, coded for 20 characters (18 informative), is shown in Table 3. This data set was analysed using the branch-and-bound algorithm of PAUP. A total of 16 most parsimonious trees were found, each with a length of 51 steps and c.i. of 0.532. The 16 trees are shown in Fig. 35, and their strict consensus tree in Fig. 36.

Table 3. The core data matrix used in the PAUP analysis. The character numbers refer to the character list given in the text.

Character	5	6	7	8	9	10	11	12	13	14	15	22	23	24	28	32	33	35	36	44
Taxon																				
H. hyaenoides	1	2	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0
L. dubia	0	3	0	0	1	1	1	0	0	0	0	0	0	1	0	?	0	1	?	0
I. viverrinum	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0
L. lycyaenoides	1	2	1	0	2	1	1	0	0	1	0	1	0	?	?	0	?	1	?	?
C. lunensis	1	3	2	1	1	1	1	0	0	0	1	0	0	1	?	0	0	1	?	1
C. borissiaki	1	3	1	1	1	0	1	0	0	0	1	0	0	1	0	0	?	1	?	0
P. reperta	1	2	0	0	1	1	0	0	1	0	1	0	0	1	1	0	?	1	0	?
I. abronia	1	2	0	0	1	1	0	0	1	0	0	1	0	1	1	0	0	1	?	0
A. eximia	1	4	1	1	2	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1
P. perrieri	1	4	1	0	1	1	1	1	0	1	0	2	0	1	1	1	1	1	1	1
P. brevirostris	1	4	1	1	1	1	1	1	0	1	0	2	0	1	1	1	1	1	1	1
T. spocki	?	0	?	?	0	0	0	0	0	0	0	0	0	0	0	?	0	1	?	0
B. beaumonti	1	2	0	0	1	1	0	0	1	1	1	1	0	1	1	?	?	1	?	0
P. orbignyi	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	?	?	1	?	0
P. brunnea	1	4	1	0	1	1	1	1	1	1	0	1	0	1	1	0	0	1	0	1
H. hyaena	1	3	1	0	1	1	0	1	1	1	0	2	0	0	1	0	0	1	0	1
C. crocuta	1	6	2	1	1	1	1	1	1	1	0	2	0	0	1	1	1	1	1	1
H. wongii	1	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0
Hypanc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

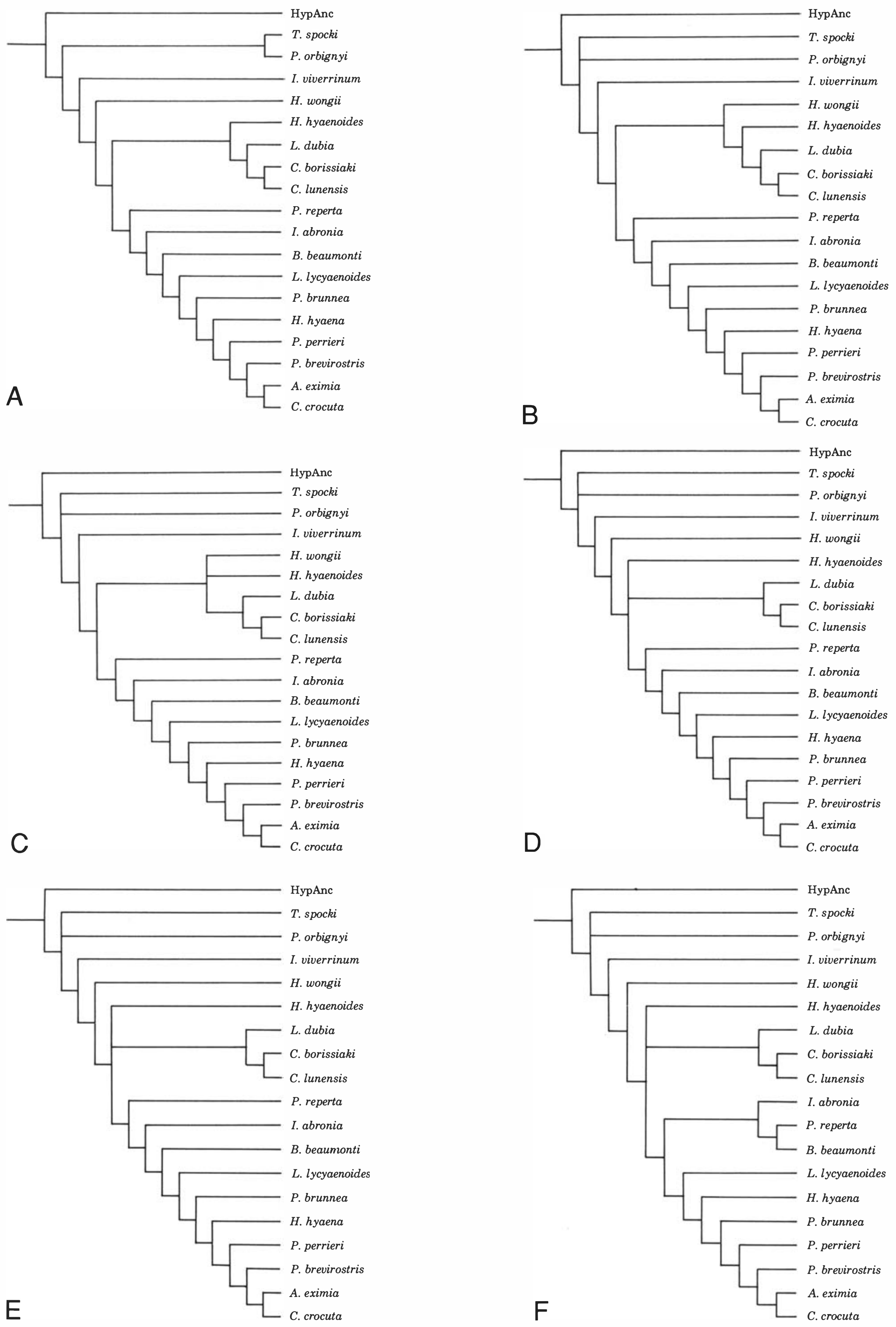


Fig. 35. The 16 equally parsimonious trees obtained from the analysis of the core data matrix (Table 3). All trees have l=51, c.i.=0.53.

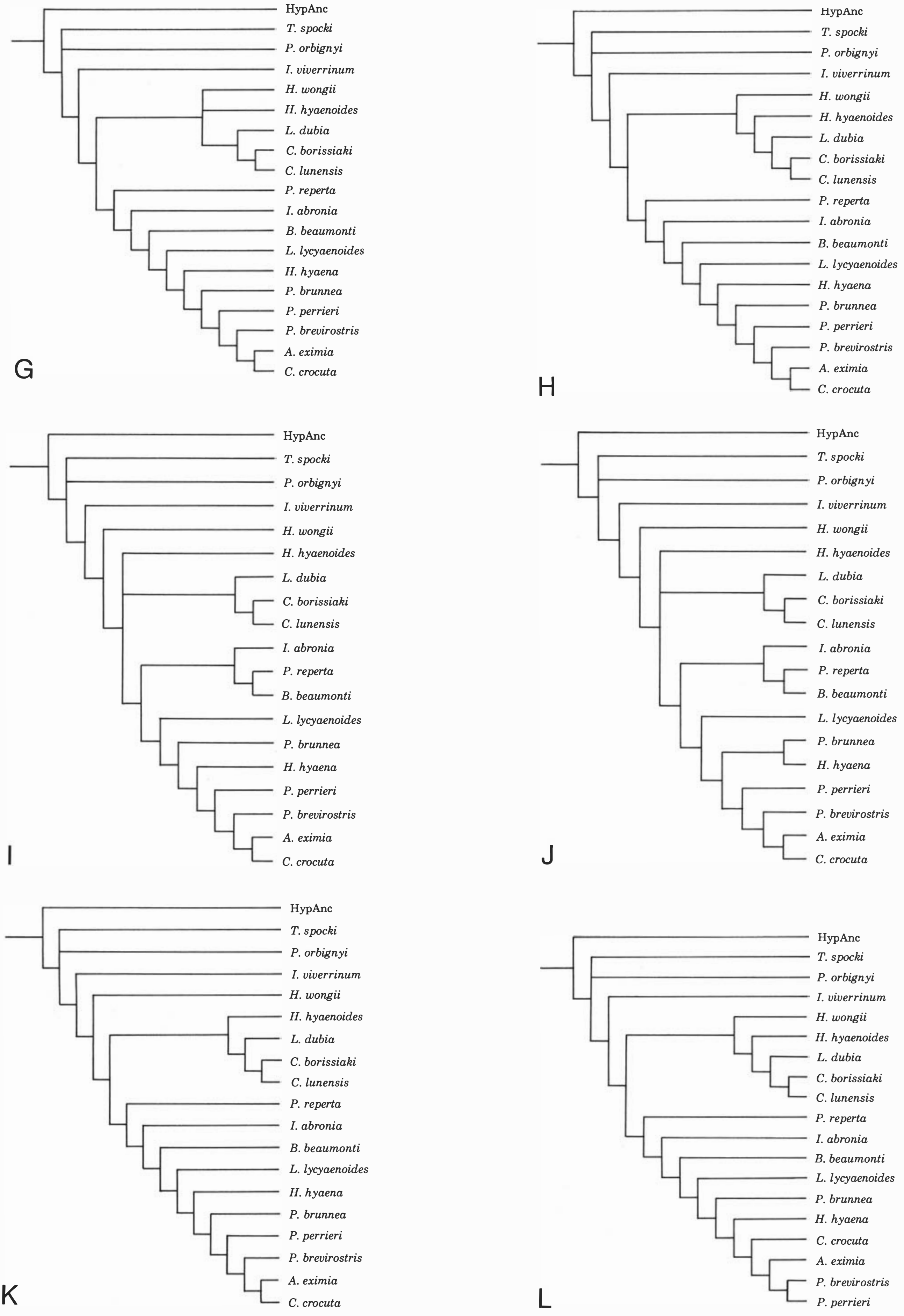


Fig. 35 (continued).

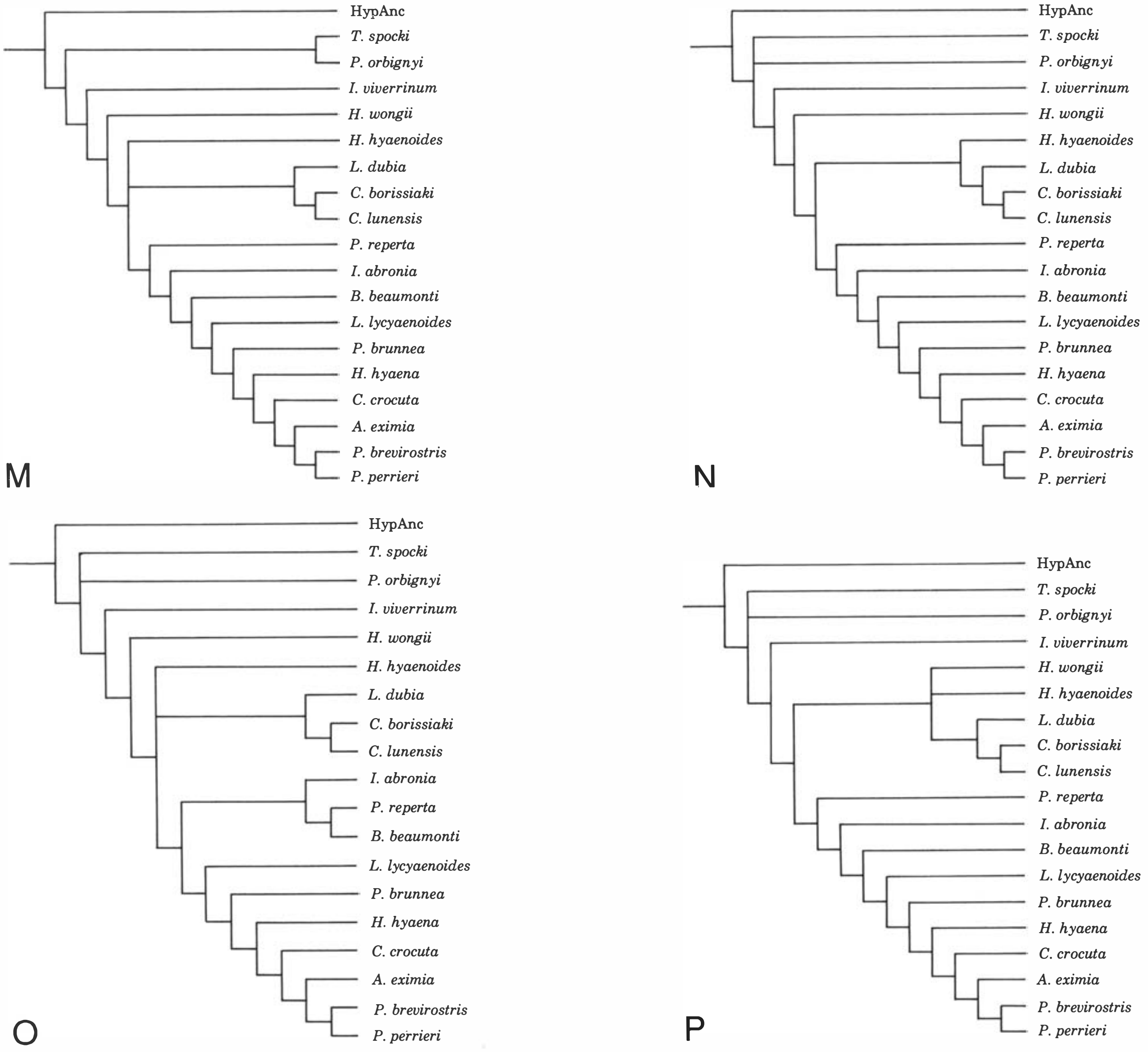


Fig. 35 (continued).

Although the resolution leaves something to be desired, several points are worth noting in this figure. Starting from the top of the tree, we may note that *P. brevirostris* and *P. perrieri* are not placed as sister taxa in the consensus; they are so placed in only 5 of the 16 trees. The lack of resolution in the relationships of *H. hyaena* and *P. brunnea*, confirming the results outlined previously, is also noteworthy. Of the 16 trees, 10 have *H. hyaena* as sister group to the clade including *C. crocuta*, 5 have *P. brunnea* in this position, while one has *H. hyaena* and *P. brunnea* as sister taxa.

Of particular interest is the position of *L. lycyaenoides* as sister group to extant hyaenas and their closest relatives (crown group of authors). The position of *L. lycyaenoides* is supported by the following character states: talonid of M_1 reduced (7:1) (parallelism with *Chasmaporthetes*), P^4 metastyle longer than paracone (11:1) (this character was reversed in the node below *L. lycyaenoides* and is re-reversed here), anterior accessory cusp of P_4 appressed to main cusp (14:1), and nuchal crest ventrally vertical (44:1). The position of *P. reperta*, *B. beaumonti*, and *I. abronia* is also of great interest, in view of the suggestions regarding their affinities put forward by De Beaumont (1968, 1969a), Hendey (1974a, 1978), Qiu (1985, 1987; Qiu *et al.* 1979), and Solounias & De Beaumont (1981). The paraphyletic nature of what has previously been called *'Thalassictis'* is shown by the fact that the two species included, *H. wongii* and *H. hyaenoides*, are not united as sister taxa in the consensus, nor in any one of the 16 component trees. The presence of a clade uniting *L. dubia* with the two species of *Chasmaporthetes* represents corroboration of the relationship between these taxa envisaged by Galiano & Frailey (1977). This clade is, however, only supported by the reduction of M^1 (6:3), which is paralleled by taxa from *H. hyaena* upwards. Thus, support for a *Lycyaena+Chasmaporthetes* clade is present, but not strong. Finally, all taxa from *'Thalassictis'* upwards are separated from *I. viverrinum* by: generally single

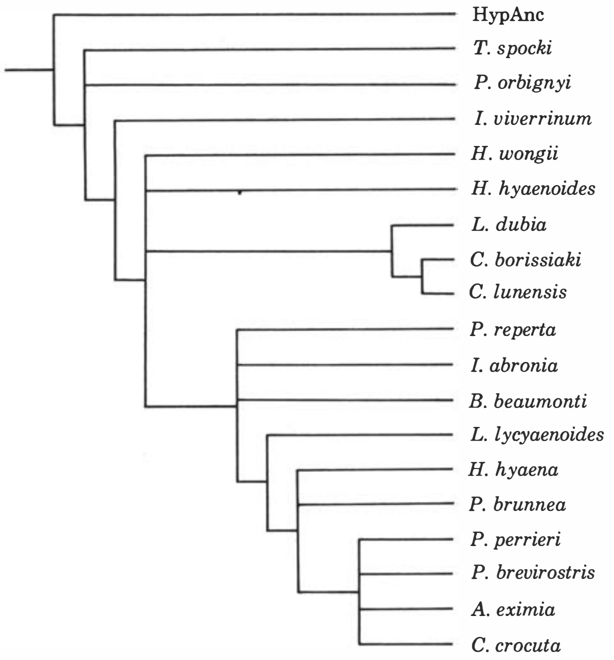


Fig. 36. Strict (Nelson) consensus tree of the 16 trees shown in Fig. 35.

mental foramen present (5:1) (reversed in *L. dubia*), M^1 reduced (6:2), and the long metastyle of P^4 (11:1) (reversed in several taxa).

In order to obtain the maximum possible information from the data available, and, hopefully, to obtain a better resolved tree, we employed a successive weighting approach, by weighting each character as a linear function of its consistency index with the original result (Farris 1969; Carpenter 1988). The additive binary coded character matrix is given in Table 4. The weights stabilized after two iterations (Table 5). This approach resulted in 2 equally parsimonious trees with a c.i. of 0.661 (several other weighting algorithms were tried, but all yielded the same result). Thus, the number of trees was reduced and their consistency with the input data was improved – both desirable results. Furthermore, it is evident upon inspection of the two trees that they differ only in the placement of *H. hyaenoides*, and this difference in placement is due entirely to a lack of data. This taxon can be placed in an unresolved trichotomy, as in the tree in Fig. 37, or it can be placed as sister taxon to *Lycyaena*+*Chasmaporthetes*. The latter placement does not have any characters to support it, but neither does it make the tree any longer, and it is therefore acceptable in a parsimony analysis. This alternative will henceforth be ignored.

The following comments on the tree in Fig. 37, which we will term the core tree, will begin from the top (node 15) and move downwards, towards node 1. At node 15 we now have a *C. crocuta* + *A. eximia* clade (see also Werdelin & Solounias 1990), which is supported by the presence of a premaxillary–frontal contact on the snout (24:1). *P. brevirostris* is joined to these two taxa at node 14 by the absence of the metaconid on M_1 (8:1) (also at node 7).

At the next node, node 13, we have *P. perrieri*. This node is one of the strongest in the tree, being supported by: the reduced anterior accessory cusp on P_4 (13:0) (weak character), the grooved basioccipital (32:1) (very strong character), the position of the premaxillary–maxillary suture on the palate (33:1), and the shape of the jugo-maxillary suture (36:1). The successive weighting approach has resolved the interrelationships of *H. hyaena* and *P. brunnea*, placing the latter one node above the former in the tree. This node, node 12, is not strong, being supported only by the more reduced M^1 of the taxa placed above this node (6:4). However, this is a condition unique to these taxa, and cannot be discounted easily.

The node uniting *H. hyaena* with the other Recent taxa into a monophyletic group, node 11, is a strong one, being supported by a reduction in size of M^1 (6:3), the sagittally

Table 4. The core data matrix transformed by additive binary coding. The character numbers here are sequential, and do not refer back to the text.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Taxon																												
H. hyaenoides	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0
L. dubia	0	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	?	0	1	?	0	0	0
I. viverrinum	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0
L. lycyaenoides	1	1	1	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0	0	?	?	0	?	1	?	?	0	1
C. lunensis	1	1	1	1	0	0	0	1	1	1	1	0	1	1	0	1	0	0	0	1	?	0	0	1	?	1	0	0
C. borissiaki	1	1	1	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1	0	0	?	1	?	0	0	0
P. reperta	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	?	1	0	?	1	0
I. abronia	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	0	0	1	?	0	1	0
A. eximia	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1
P. perrieri	1	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1
P. brevirostris	1	1	1	1	1	0	0	1	0	1	1	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1
T. spocki	?	0	0	0	0	0	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	?	?	1	?	0	0	0
B. beaumonti	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	1	?	?	1	?	0	1	1
P. orbignyi	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	?	?	1	?	0	0	0
P. brunnea	1	1	1	1	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	1	0	1	1	1
H. hyaena	1	1	1	1	0	0	0	1	0	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1	0	1	1	1
C. crocuta	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	1	1	1	1	1
H. wongii	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Hypanc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5. Weights obtained during successive weightings analysis of the data matrix in Table 4.

Character	Weights at first iteration	Final weights
1	0.500	0.500
2	1.000	1.000
3	0.500	1.000
4	0.500	0.500
5	0.500	1.000
6	0	0
7	0	0
8	0.500	0.500
9	0.500	0.500
10	0.333	0.500
11	1.000	1.000
12	0.500	0.500
13	0.500	0.500
14	0.250	0.250
15	1.000	1.000
16	0.250	0.250
17	0.333	0.500
18	0.333	0.333
19	0	0
20	0.250	0.333
21	1.000	1.000
22	1.000	1.000
23	1.000	1.000
24	0	0
25	1.000	1.000
26	0.500	0.500
27	0.200	0.200
28	0.500	1.000

oriented carnassial (12:1), and an anteriorly placed infra-orbital foramen (22:2) (reversed in *P. brunnea*). It may thus be noted that the minimum age of separation of the Recent 'derived' hyaenids is Vallesian (MN Zone 10), which is the earliest occurrence of *A. eximia* (De Bonis & Koufos 1981). This minimum age is supported by, and supports, the DNA hybridization age of 10 Ma for this split (Wayne *et al.* 1989).

The next taxon down is *L. lycyaenoides*, at node 10. This node is supported by the same characters as in the previous analysis (see above).

The most important difference between the successive weighting consensus tree and the previous one is that the former has resolved the polychotomy involving *I. abronia*, *B. beaumonti*, and *P. reperta*. *B. beaumonti* is placed at node 9, which is supported by the anterior accessory cusps of P_4 being appressed to the main cusp (14:1). *I. abronia* is placed one step further down, its node (node 8) being supported by the anterior position of the infra-orbital foramen (22:1). At node 7, *P. reperta* is placed as the sister taxon to all the above taxa. This node is supported by two relatively weak characters, the short P^4 metastyle (11:0) and the reduced anterior accessory cusps on P_4 (13:0), and by one very strong one, the large contribution of the maxillary to the antero-internal end of the zygomatic arch (28:1).

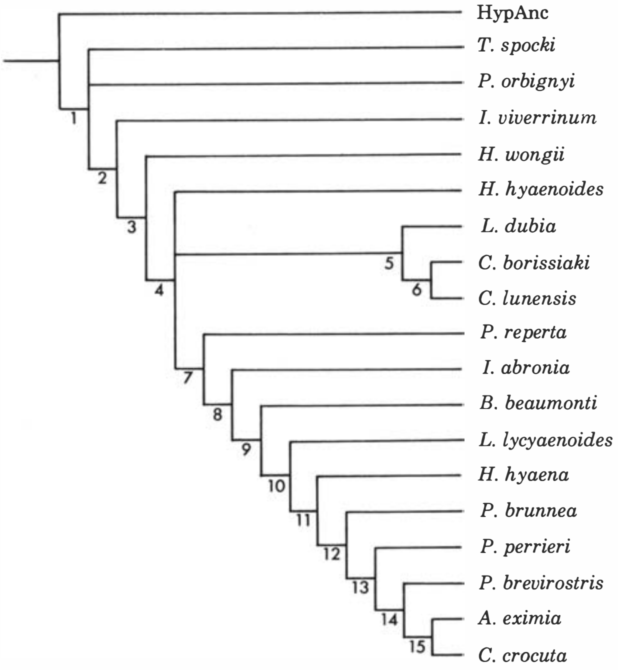


Fig. 37. Core tree, obtained from two iterations of successive weighting (c.i.=0.661). The second tree is identical to this one, except that *H. hyaenoides* is placed as sister taxon to *Lycyaena*+*Chasmaporthetes*.

Nodes 6 and 5 of the present tree were also present above, and define a *Chasmaporthetes* clade and a *Lycyaena*+*Chasmaporthetes* clade, respectively. Node 6, the *Chasmaporthetes* node, is supported by: reduced number of talonid cusps (7:1), metaconid on M_1 lost (8:1) (also at node 15), and anterior face of P_3 concave. Node 6, which unites *Lycyaena* with *Chasmaporthetes*, is supported by a reduction in size of M^1 (6:3) (paralleled at node 11).

Node 4 is the unresolved trichotomy involving *H. hyaenoides*. This node is supported by the reduction in size of M^1 (6:2).

At node 3 we have *H. wongii*. It is noteworthy that, despite the uncertainty regarding the position of *H. hyaenoides*, this taxon is clearly separated from *H. wongii*. Node 3 is supported by: generally single mental foramen (5:1), reduction of M^1 (6:1), and long P^4 metastyle (11:1). The next sister taxon down is *I. viverrinum* at node 2, a node that is supported by a posteriorly placed P^4 protocone (9:1), a curved tooth row (10:1) (reversed in *C. borissiaki*), and the loss of the premaxillary–frontal contact on the snout (24:0) (reversed at node 14).

At the base of the tree we have another unresolved trichotomy, this time involving *P. orbignyi* and *T. spocki*.

This tree (Fig. 37), for all its uncertainties and lack of resolution, is the best result we have been able to obtain, using as near an optimal combination of taxa and characters as we were able to find. In the following section we will use this tree as a baseline, and try to position less well known taxa with reference to it.

The position of the remaining taxa. – Fig. 38 shows a cladogram of all species within the Hyaenidae that we consider possible to place phylogenetically with some degree of accuracy. Excluded are some taxa *incertae sedis*, as well as the *nomina dubia* previously discussed. The numbered nodes are the same as in the analysis presented above, with the exceptions noted below. Nodes identified alphabetically are such that have not been incorporated in the previous analyses.

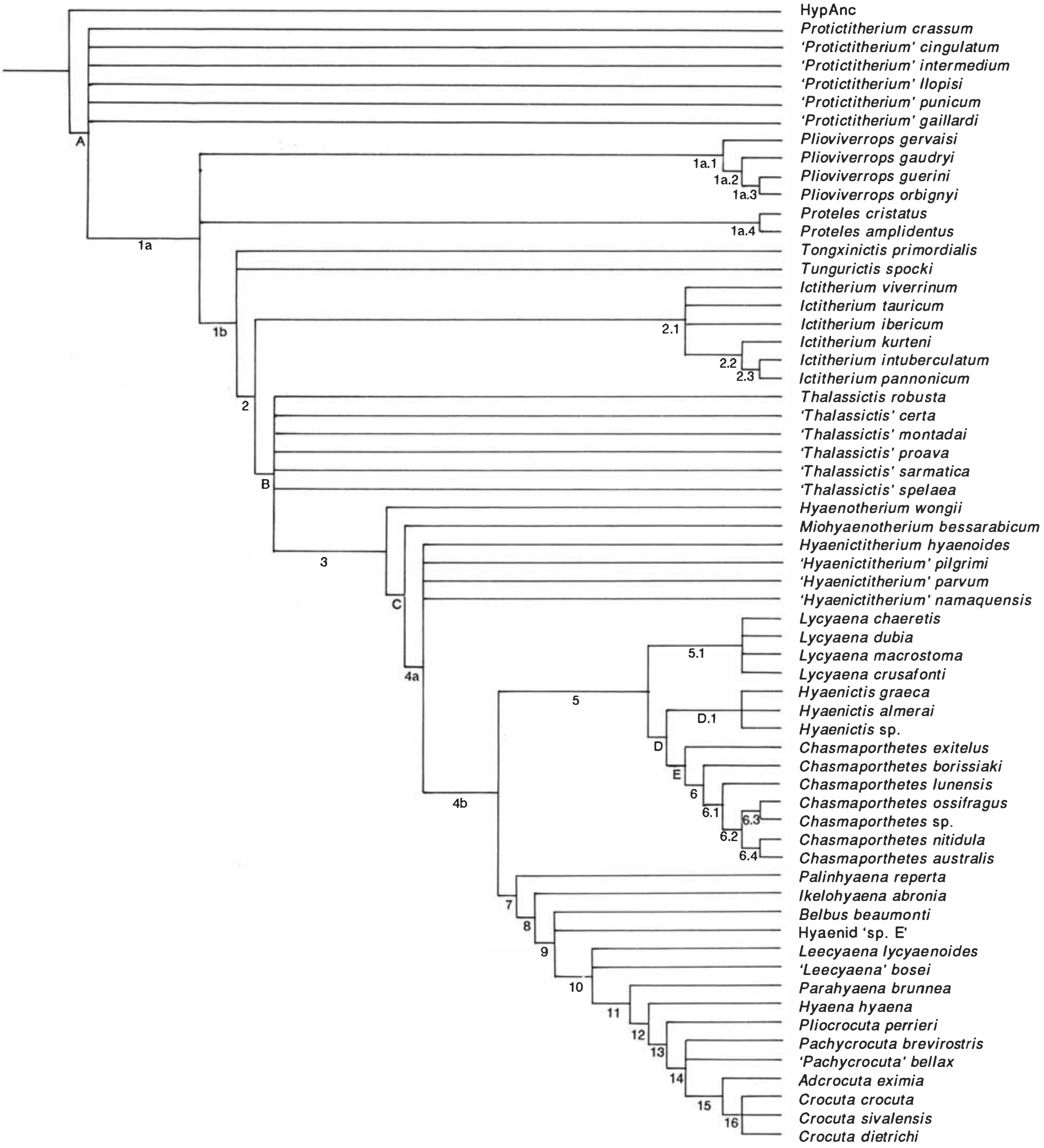


Fig. 38. Cladogram of all reasonably well known hyaenid taxa. The numbered nodes in this figure correspond to the numbered nodes in Fig. 37. Lettered nodes are new.

Finally, nodes given with decimal notation are subordinate nodes.

The most difficult part of the hyaenid tree to resolve is clearly the base, incorporating the most primitive taxa. In the previous analysis, there was no resolution obtained between *P. orbignyi* and *T. spocki*. However, analysis of the bulla structure of these taxa (characters not included in the computer analysis) indicates that the latter species is somewhat more derived, and in Fig. 38 we have consequently split node 1 into two: nodes 1(a) and 1(b). Other taxa placed near the base of the cladogram are *Proteles*, the problems in the placing of which are noted above, and *'Protictitherium'*. This latter genus presents special problems in this context, as it is only known from fragmentary remains, mostly of jaws and teeth. There is no bulla known. The structure of M_1 is extremely primitive in the species assigned to *'Protictitherium'*, more so in our estimation than in any of the other hyaenid taxa. This causes us to place *'Protictitherium'* at the base of our cladogram, at node *A*. We emphasize that this might change if a specimen with a well-preserved auditory bulla is discovered. All species of *'Protictitherium'* are highly plesiomorphic in their charac-

Table 6. A cladistic classification of the Hyaenidae. This classification employs a combination of indentation and sequencing, and is directly derived from the cladogram in Fig. 38.

- *Protictitherium* Kretzoi, 1938
    - *Protictitherium crassum* (Depéret, 1892)
    - *'Protictitherium' gaillardi* (Forsyth Major, 1903)
    - *'Protictitherium' cingulatum* Schmidt-Kittler, 1976
    - *'Protictitherium' intermedium* Schmidt-Kittler, 1976
    - *'Protictitherium' llopisi* (Crusafont Pairó & Petter, 1969)
    - *'Protictitherium' punicum* (Kurtén, 1976)
- *Plioviverrops* Kretzoi, 1938
    - *Plioviverrops gaudryi* De Beaumont & Mein, 1972
    - *Plioviverrops gervaisi* De Beaumont & Mein, 1972
    - *Plioviverrops guerini* (Villalta & Crusafont Pairó, 1945)
    - *Plioviverrops orbignyi* (Gaudry & Lartet, 1856)
- *Proteles* I. Geoffroyi, 1824
    - *Proteles cristatus* (Sparrman, 1783)
    - *Proteles amplidentus* nom. nov.
- *Tongxinictis* gen. nov.
    - *Tongxinictis primordialis* (Qiu, Ye & Cao, 1988)
- *Tunguricits* Colbert, 1939
    - *Tunguricits spocki* Colbert, 1939
- *Ictitherium* Wagner, 1848
    - *Ictitherium viverrinum* Roth & Wagner, 1854
    - *Ictitherium tauricum* Borissiak, 1915
    - *Ictitherium ibericum* Meladze, 1967
        - *Ictitherium kurteni* Werdelin, 1988
        - *Ictitherium intuberculatum* Ozansoy, 1965
        - *Ictitherium pannonicum* Kretzoi, 1952
- *Thalassictis* Gervais *ex* Nordmann, 1850
    - *Thalassictis robusta* Gervais *ex* Nordmann, 1850
    - *'Thalassictis' certa* (Forsyth Major, 1903)
    - *'Thalassictis' montadai* (Villalta & Crusafont Pairó, 1943)
    - *'Thalassictis' proava* (Pilgrim, 1932)
    - *'Thalassictis' sarmatica* (Pavlow, 1908)
    - *'Thalassictis' spelaea* (Semenov, 1988)
- *Hyaenotherium* Semenov, 1989
    - *Hyaenotherium wongii* (Zdansky, 1924)
- *Miohyaenotherium* Semenov, 1989
    - *Miohyaenotherium bessarabicum* Semenov, 1989
- *Hyaenictitherium* Kretzoi, 1938
    - *Hyaenictitherium hyaenoides* (Zdansky, 1924)
    - *'Hyaenictitherium' parvum* (Khomenko, 1914)
    - *'Hyaenictitherium' pilgrimi* sp. nov.
    - *'Hyaenictitherium' namaquensis* (Stromer, 1931)
- *Lycyaena* Hensel, 1862
    - *Lycyaena chaeretis* (Gaudry, 1861)
    - *Lycyaena dubia* Zdansky, 1924
    - *Lycyaena macrostoma* (Lydekker, 1884)
    - *Lycyaena crusafonti* Kurtén, 1976
- *Hyaenictis* Gaudry, 1861
    - *Hyaenictis graeca* Gaudry, 1861
    - *Hyaenictis almerai* Villalta & Crusafont Pairó, 1945
    - *Hyaenictis* sp. (Langebaanweg)
- *Chasmaporthetes* Hay, 1921
    - *Chasmaporthetes exitelus* Kurtén & Werdelin, 1988
    - *Chasmaporthetes borissiaki* (Khomenko, 1932)
    - *Chasmaporthetes lunensis* (Del Campana, 1914)
        - *Chasmaporthetes ossifragus* Hay, 1921
        - *Chasmaporthetes* sp. (Florida)
            - *Chasmaporthetes nitidula* (Ewer, 1955)
            - *Chasmaporthetes australis* (Hendey, 1974)
- *Palinhyaena* Qiu, Huang & Guo, 1979
    - *Palinhyaena reperta* Qiu, Huang & Guo, 1979
- *Ikelohyaena* gen. nov.
    - *I. abronia* (Hendey, 1974)
- *Belbus* gen. nov.
    - *B. beaumonti* (Qiu, 1987)
- Hyaenid 'sp. E' (Langebaanweg)
- *Leecyaena* Young & Liu, 1948
    - *Leecyaena lycyaenoides* Young & Liu, 1948
    - *'Leecyaena' bosei* (Matthew, 1929)
- *Parahyaena* Hendey, 1974
    - *Parahyaena brunnea* (Thunberg, 1820)
- *Hyaena* Zimmermann, 1777
    - *Hyaena hyaena* (Linnaeus, 1758)
- *Pliocrocuta* Kretzoi, 1938
    - *Pliocrocuta perrieri* (Croizet & Jobert, 1828)
- *Pachycrocuta* Kretzoi, 1938
    - *Pachycrocuta brevirostris* (Aymard, 1846)
    - *'Pachycrocuta' bellax* (Ewer, 1954)
- *Adcrocuta* Kretzoi, 1938
    - *Adcrocuta eximia* (Roth & Wagner, 1854)
- *Crocuta* Kaup, 1829
    - *Crocuta crocuta* (Erxleben, 1777)
    - *Crocuta sivalensis* (Falconer & Cautley, 1868)
    - *Crocuta dietrichi* Petter & Howell, 1989

Hyaenidae *incertae sedis*:

- *Lepthyaena* Lydekker, 1884
    - *Lepthyaena sivalensis* (Lydekker, 1877)
- *Lycyaenops* Kretzoi, 1938
    - *Lycyaenops rhomboideae* Kretzoi, 1938

ters, and no synapomorphies uniting the genus have been identified. Indeed, we consider it highly likely that *'Protictitherium'* is a paraphyletic assemblage.

The next node up from *'Protictitherium'* is the aforementioned 1(a). Here we have *Plioviverrops*, for which we feel that there is good evidence for monophyly in the characters of dental change outlined by De Beaumont & Mein (1972). Of the species of *Plioviverrops*, *P. orbignyi* is the most derived, with *P. guerini* as its sister taxon. The distinction between *P. gervaisi* and *P. gaudryi* is not entirely certain, as noted above (nodes 1a.1, 1a.2, and 1a.3). At node 1(a) we have also placed *Proteles*, chiefly on the basis of bulla structure. However, this position of *Proteles* requires that the alisphenoid canal has been lost independently in this taxon and in taxa above node 2 (Fig. 38), a point that should be kept in mind in future analyses.

At the next node, node 1(b), we have *T. spocki*, as noted above. Here we have also somewhat subjectively placed *Tongxinictis primordialis*, mainly on the basis of our assessment, from the figures in Qiu *et al.* (1988b), that the bulla structure of this species approaches *T. spocki.* The dental characters of *Tongxinictis* would also seem to preclude a position lower in the cladogram, while the bulla structure and the presence of an alisphenoid canal seem to rule out a position higher up.

The next node is node 2, at which we have *Ictitherium.* We consider this genus to be monophyletic (node 2.1) on the basis of the structure of M_1, which has a reduced protoconid compared to taxa below and above *Ictitherium* in the cladogram. The character of paraconid and protoconid equal or subequal in height appears in the cladogram from node 3 and upwards, but is there associated with reduced posterior molars, and appears to be due as much to an increase in height of the paraconid as a reduction of the protoconid. In *Ictitherium,* on the other hand, the paraconid is still low. Within *Ictitherium,* there seems to be a clade comprised of taxa with increased size and stronger 'hyaenoid' adaptations, i.e. enlarged premolars (node 2.2). The two species *I. intuberculatum* and *I. pannonicum* (node 2.3) are very similar and still larger than *I. kurteni.*

The next node, node *B,* is defined by a reduction in the length of the M_1 talonid and the posterior molars. The first taxa we find here are species of *'Thalassictis'.* They are more plesiomorphic than all other taxa with reduced posterior molars in their M_1 structure, which retains the primitively low paraconid and high protoconid. However, we have found no characters to identify *'Thalassictis'* as a monophyletic genus, and, indeed, we consider it probably paraphyletic.

The next node up is node 3 from the computer analysis. An important character here is, as noted, that the M_1 paraconid and protoconid are equal or subequal in height. At this node we find *H. wongii.* The next node, node *C,* is not well defined, but the arguments made by Semenov (1989) for placing *Miohyaenotherium* between *Hyaenotherium* and *'Hyaenictitherium'* cannot be ignored, and we elect to follow his analysis.

Node 4 was not resolved in the computer analysis, but recourse to other characters, especially the narrower premolars and, of course, the absence of M^2 and M_2, enables us to place *Lycyaena* in a clade with *Hyaenictis* and *Chasmaporthetes* [node 4(b) and 5], while retaining *'Hyaenictitherium'* one node below this [node 4(a)]. *'Hyaenictitherium'* is yet another taxon that cannot be identified as monophyletic.

Node 5 is the same as in the previous analysis, and is defined, i.a., by the loss of M^2 and M_2. Node 5.1 identifies *Lycyaena* on the basis of the presence of more than one mental foramen (a reversal) and the narrow premolars (relatively narrower than in any hyaenid above node 3). Node D.2, which unites *Hyaenictis* and *Chasmaporthetes,* is defined on the basis of, i.a., their similarly derived premolar morphology.

We feel that *Hyaenictis* (node D.1) is probably monophyletic, although this is difficult to establish. In any case, the presence of M_2 is derived within the clade from node 5 and upwards, although, of course, it is a reversal. The reappearance of this tooth may be an allometric effect of the longer M_1 of *Hyaenictis* relative to *Lycyaena.* At node D.2 we have united *H.? silberbergi* and *H.* sp. from Langebaanweg on the basis of their geographic provenance (a subjective assessment at best).

At node E we have *Chasmaporthetes,* chiefly defined on the basis of the elongated P^4 metastyle. *C. exitelus* is clearly very primitive, as is *C. borissiaki* (node 6). *C. lunensis* (node 6.1) is more derived, both dentally and cranially. Higher up (nodes 6.2, 6.3, and 6.4) we have united species of *Chasmaporthetes* chiefly on the basis of geographic provenance.

The remainder of the nodes are identical to those of the previous analysis. We have placed hyaenid species 'E' from Langebaanweg together with *B. beaumonti,* and *'Leecyaena' bosei* together with *L. lycyaenoides.* Finally, at node 16, we have some further species of *Crocuta.* As noted previously, this node cannot be resolved without further detailed work on the taxonomy of *Crocuta* spp.

This review leads to the classification of the Hyaenidae given in Table 6.

Systematic paleontology

Some new generic-level taxa are created due to the topology of the cladogram presented above. These new names have been used earlier in the text, but are formally characterized here.

Genus *Tongxinictis* gen. nov.

Etymology. – After the Tongxin district where it was found, and the Latin suffix *-ictis,* weasel, a common suffix in the Hyaenidae. Feminine.

Type and only species. – *Tongxinictis primordialis* (Qiu, Ye & Cao, 1988).

Diagnosis. – Small genus; type 4 bulla, median lacerate foramen not covered by bulla wall; M^2 lost; premolars with convex anterior margins.

Comments. – The diagnosis of this taxon given by Qiu *et al.* (1988b) is intended to distinguish it from species of *Percrocuta* and is not useful in this context.

Ikelohyaena gen. nov.

Etomology. – After Greek ικελοζ, like, and Latin *hyaena.* In reference to the (plesiomorphic) similarity of the type species to *Hyaena hyaena.* Feminine.

Type and only species. – *Ikelohyaena abronia* (Hendey, 1974).

Diagnosis. – A genus slightly smaller than *Hyaena* in size; maxillary contribution to zygomatic arch large, premolars, especially $P^3\!/_3$, enlarged, but not strongly conical and anterior edge only slightly convex; anterior accessory cusps not appressed to main cusp of premolars; infra-orbital foramen positioned above midline of P^3; P^4 metastyle short; $M^2\!/_2$ present.

Comments. – A description of the type species was given by Hendey (1974a).

Belbus gen. nov.

Etymology. – After latin *belbus*, hyaena. Masculine.

Type and only species. – *Belbus beaumonti* (Qiu, 1987).

Diagnosis. – Size as in *Hyaena*; premolars markedly bulbous; $P\frac{3}{3}$ enlarged in size and conical in shape, with strongly convex anterior edge; anterior accessory cusps of premolars reduced and appressed to main cusp; M_1 talonid not reduced; P^4 metastyle short; M^2 lost; M_2 retained.

Comments. – All specimens referred to this taxon are young individuals, and its adult size is not known. Descriptions of the material was given by De Beaumont (1968, 1969a).

Interrelationships of Feloidea

Several important papers dealing with the interrelationships of carnivores have been published in recent years (Flynn & Galiano 1982; Flynn *et al.* 1988; Hunt 1987, 1989; Wozencraft 1989). This spate of new information and interpretation demonstrates the renewed interest in this question, and in systematics in general, with the advent of cladistic methodology. Unfortunately, however, there remains a good deal of uncertainty, even regarding the interrelationships of the Recent families of Carnivores, let alone the extinct groups.

Flynn & Galiano (1982) define the superfamily Feloidea as a monophyletic taxon within the infraorder Aeluroida, comprising all the living and fossil members of the families Hyaenidae, Viverridae, and Felidae of Simpson (1945). To these families we must add the Herpestidae, which Simpson included in the Viverridae, but which all primary systematic studies have shown to be distinct from that family (Gregory & Hellman 1939; Winge 1895; Wozencraft 1984; Wurster & Benirschke 1968). As noted by Flynn *et al.* (1988), several conflicting hypotheses of relationships within the Feloidea have been proposed. In particular, the hypotheses of Hunt (1987, 1989) and Wozencraft (1989) conflict (Fig. 39), the former suggesting a sister-group relationship between Hyaenidae and Herpestidae, the latter one between Hyaenidae and Felidae. In the following, we shall attempt to contribute to this general question by considering systematic hypotheses regarding the interrelationships of aeluroids in the light of the hypothesis of hyaenid interrelationships discussed above, and the primitive hyaenid morphology derived therefrom.

In order to do this, however, it is necessary to consider the morphology and systematic relationships of *Herpestides antiquus* in some detail. This species was suggested by De Beaumont (1967; De Beaumont & Mein 1972) and Hunt (1987, 1989) to be structurally ancestral to hyaenids, and was explicitly used by Hunt (1987, p. 63) as evidence for a chronocline of taxa leading from ancestral forms with a herpestid-like auditory bulla to the modern hyaenids with their derived bulla type. Thus, the systematic position of *Herpestides vis-à-vis* Hyaenidae (and other feloid families) becomes a vital issue to the discussion of the interrelationships of Feloidea.

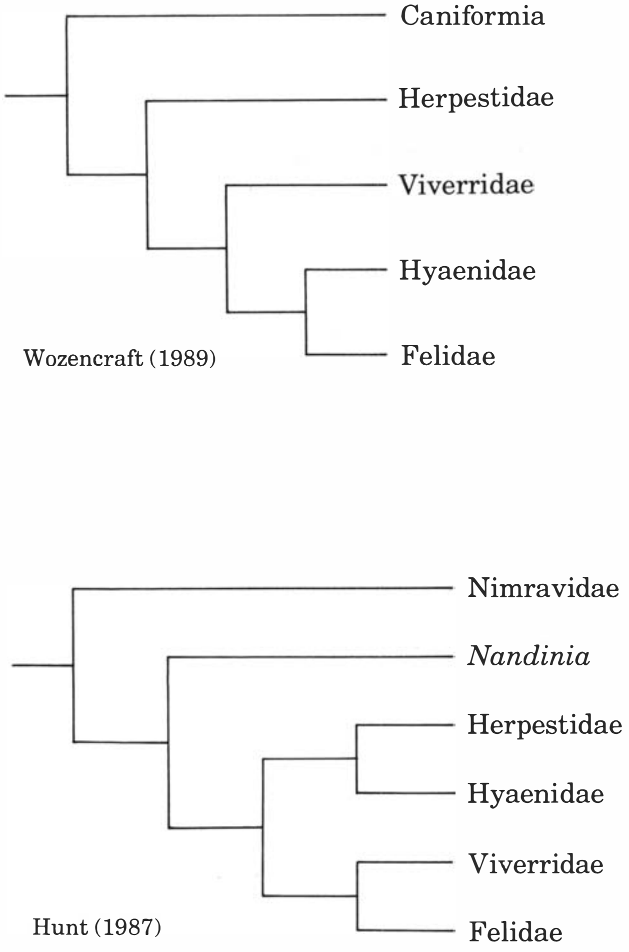


Fig. 39. Two competing hypotheses of feloid interrelationships, as labeled.

Character analysis and morphology of *Herpestides antiquus*

Herpestides antiquus has been most fully discussed by De Beaumont (1967), who illustrates and describes the auditory bulla and other key features. There is little new information we can add to his description, augmented by the comments made by Petter (1974) in her work on the Madagascar viverrids. What new information may be found in the following will be entirely due to a consistent consideration of the probable primitive morphologies of the families of Feloidea in the light of character transformations within the Hyaenidae. In order not to expend inordinately much space on redescribing *H. antiquus*, we shall take as our starting point the list of characters used by Wozencraft (1989) in his study of carnivore phylogeny, discussing only those that are stated to vary between feloid families or that are of special significance to *H. antiquus*. We shall then add features used by others (e.g., Flynn *et al.* 1988; Hunt 1987), as well as characters of interest to the phylogeny of Hyaenidae.

Location of major palatine foramen. – This is character 35 of our list above. The major palatine foramina are located at the suture between the maxillary and palatine in Felidae, but far forwards on the maxillary in Hyaenidae, Viverridae, and Herpestidae. Outgroup comparison with Caniformia and Viverravidae indicates that the condition seen in Felidae represents the primitive state. However, if a position of Nimravidae as sister group to Feloidea should be substantiated (Hunt 1987), this polarity determination would be reversed, for in this family the major palatine foramina are located well anteriorly on the maxillary, as is also evidently the case in Barbourofelinae (Schultz *et al.* 1970). However, we can also approach this from another viewpoint, that of ontogeny. During ontogeny, the major palatine foramina migrate forward from the palatine–maxillary suture in those taxa in which it takes an anterior position. Viewed by the criterion of generality (Nelson 1978) (see also De Queiroz 1985), the posterior position of the major palatine foramina must then be viewed as primitive.

As noted previously, the major palatine foramina of *H. antiquus* take up a position a few millimeters in front of the palatine–maxillary suture; a position intermediate between that observed for the major palatine foramina of modern carnivores. Since the posterior position seen in Felidae is primitive (or a secondary reversal), *H. antiquus* is apparently somewhat more derived than that family in this respect. However, it is at the same time clearly more primitive than any of the modern Hyaenidae, Viverridae, and Herpestidae, and we will consider *H. antiquus* to be primitive relative to this group with regard to the position of the major palatine foramina.

Relative length of palatine and maxillary. – In Herpestidae, the midline length of the palatine is much greater than the midline length of the maxillary. Outgroup comparison indicates that this is a derived condition within Feloidea and a synapomorphy uniting members of this family. In *H. antiquus*, the palatine and maxillary are approximately equal in length, and the palatine does not show the great posterior extension of the palatine over the pterygoids characteristic of Herpestidae. *H. antiquus* illustrates the primitive condition for this character.

Relative position of infra-orbital foramen and lacrimal canal. – In Felidae, the anterior opening of the infra-orbital foramen lies ventral to the lacrimal canal. In other Feloidea the lacrimal canal lies clearly posterior to the infra-orbital foramen. The condition in Nimravidae is not entirely clear, but the infra-orbital foramen appears to lie slightly anterior to the lacrimal canal. The condition seen in Felidae is almost certainly derived and is related to the shortening of the rostrum in this family. In *H. antiquus*, the relationship between the infra-orbital foramen and lacrimal canal is the primitive one. *H. antiquus* thus once again exhibits the primitive feloid condition.

Presence or absence of alisphenoid canal. – This canal is present in Herpestidae and Viverridae, but absent in Felidae and Hyaenidae, and has been used as one of the synapomorphies uniting the latter two families (Wozencraft 1989). Judging from outgroup comparisons, the absence of the alisphenoid canal is clearly derived (it is present in primitive Caniformia and in Nimravidae; Hunt 1987), and the situation would seem to be as above. However, the alisphenoid canal is present in primitive hyaenids such as *Tungurictis* (Colbert 1939, Fig. 13), *Plioviverrops* (De Beaumont 1969b, Pl. 1:1C) and probably *Tongxinictis* (Qiu *et al.* 1988b, Pl. 2:1). Because of its loss within the Hyaenidae as defined here (we shall return to the question of the definition of the Hyaenidae below), the absence of the alisphenoid canal can therefore not be used as a synapomorphy uniting Felidae and Hyaenidae, except for the unlikely event that the Felidae originated *within* the Hyaenidae as defined here. The latter suggestion does not appear very plausible.

In *H. antiquus* the alisphenoid canal is clearly present, as can be seen in De Beaumont's (1967) Pl. 1:1C. The condition represented in *H. antiquus* is the primitive one for feloids.

Presence or absence of carotid canal. – In Felidae, the carotid canal is absent, which is a derived condition unique to this family (Davis & Story 1943; Hunt 1974). It is present (primitive condition) in all hyaenids examined, as well as in *H. antiquus.*

The formation of a bony external auditory meatus. – In both Herpestidae and Hyaenidae, the ectotympanic forms a bony external auditory meatus. By outgroup comparison, this is a derived condition within the Feloidea, and one that has been used as a synapomorphy linking these two families (Hunt 1987). However, Wozencraft (1989) notes that there are strong morphological grounds for doubting the homology of this trait between Herpestidae and Hyaenidae, and this doubt is confirmed by the absence of a bony external auditory meatus in primitive hyaenids (*Plioviverrops, Tungurictis, Tongxinictis*). This feature is particularly clearly seen in the illustrations by Qiu *et al.* (1988b). Thus, the external auditory meatal tubes of herpestids and hyaenids evolved independently. There is no bony external auditory meatus in *H. antiquus*, and again this species shows the primitive feloid condition.

Medial portion of caudal entotympanic. – This part of the caudal entotympanic is strongly inflated in Felidae and Viverridae, a condition suggested by outgroup comparison to be derived relative to the less inflated medial portion of the caudal entotympanic of Herpestidae and Hyaenidae. The latter condition is true of all fossil and living hyaenids, and is the condition seen in *H. antiquus* as well.

Size of paroccipital process. – The paroccipital process abuts the bulla in all Feloidea except *Nandinia binotata* (Hunt 1987). It is short in Herpestidae and Felidae, and long in Hyaenidae and Viverridae. Wozencraft (1989) suggests that the latter condition is derived on the basis of outgroup analysis, and ontogenetic study suggests the same. In primitive hyaenids (especially *Plioviverrops*), the paroccipital process is still short, suggesting independent derivation of the derived condition within Hyaenidae and Viverridae. *H. antiquus* has a relatively short paroccipital process and thus displays the primitive condition for feloids.

Cruciate sulcus in brain. – The cruciate sulcus is present in all feloids except Viverridae. This loss has been suggested to be the derived condition (Wozencraft 1989), but the polarity is exceedingly difficult to determine. The cruciate sulcus is present in extant arctoids, which would suggest that this state is primitive. However, the sulcus is absent in Nimravidae, and this state could then be seen as primitive for Feloidea, if Hunt's (1987) placement of nimravids is correct. No ontogenetic data on the brain is available to shed light on this issue, and for the time being we can merely note that, while no studies of endocranial casts of primitive hyaenids have been published, Radinsky (1971) mentions unpublished data on an endocast of *Ictitherium* spp., in which the cruciate sulcus is present. In *H. antiquus* the cruciate sulcus is absent, however, a condition it shares with Viverridae.

Lingual cusp on P^3. – The presence of a lingual cusp on P^3 is said to be a derived character state of the Herpestidae. This is a moot point, as a lingual cusp is also present in some viverrids (*Genetta*). There is no lingual cusp on P^3 in any fossil hyaenid. Kretzoi (1938) mentions a third, lingual root and 'rudimentary deuterocone' on P^3 in *Allohyaena kadici*. However, we do not consider this form a hyaenid, regardless of whether it has affinities with the Percrocutidae, as suggested by Howell & Petter (1985). In *H. antiquus* there is a small but distinct lingual cusp in at least some specimens (De Beaumont 1967), a feature that would constitute a synapomorphy between *H. antiquus* and Herpestidae. However, *Kichechia zamanae*, a putative Miocene herpestid from Rusinga Island, Kenya (Savage 1965), does not have a lingual cusp on P^3, wherefore the value of this character is debatable. The character requires further analysis.

Presence or absence of P_1. – This is character 2 of our list. Wozencraft (1989) notes the absence of P_1 as a synapomorphy uniting Felidae and Hyaenidae (this trait is obviously derived). However, this is not acceptable, as the loss of P_1 is a relatively late feature of hyaenid evolution. It is present as far up as node 10 in our core cladogram (Fig. 37), and is also present in *A. eximia*, at node 15. It is present in well known, undoubted Hyaenidae such as *H. wongii*. P_1 was thus lost independently in Felidae and Hyaenidae. In *H. antiquus*, P_1 is present: the primitive condition.

Size of M^1. – The same comments apply to this character as to the former one. M^1 is large in most fossil hyaenids; it is not until fairly recently in hyaenid evolution that M^1 has been reduced beyond the condition seen in many viverrids. In *H. antiquus* M^1 is present and large.

Presence of M^2. – This is character 4 of our list. Again, this is a character which has been used to unite Felidae and Hyaenidae, but which can be shown to have been independently lost in these families, since it is present in many fossil hyaenid taxa. In *H. antiquus* M^2 is present.

Presence of M_2. This is character 1 of our list. The same comments apply to this character: it is present in many fossil hyaenids and has been independently lost in Felidae and Hyaenidae. M_2 is present in *H. antiquus.*

Recumbent septum bullae and allied features. – Hunt (1987) uses the transverse or recumbent septum bullae as a character uniting Herpestidae with Hyaenidae (advanced Hyaenidae subsequently carry this much further, and the recumbent septum bullae becomes more and more horizontal). Hunt discusses this feature in conjunction with the restriction of the caudal entotympanic to the posterior auditory region, which he also apparently considers derived. However, Hunt also considers the condition seen in Felidae and Viverridae (anterior migration of caudal entotympanic chamber to a position ventral to the ectotympanic; septum bullae diagonally placed) derived. Unfortunately, it is not clear from Hunt's discussion of bulla ontogeny how he derives the polarities for these features.

In Hunt's (1987, p. 40) discussion of these features, he first briefly discusses what he considers to be the primitive type of bulla: that of *Nandinia binotata*, in which there is little or no change in the bulla configuration during ontogeny, and, of course, no septum bullae formed by apposition of bulla elements. However, all this really states is that ontogenetic change in bulla configuration is a derived condition, and thus in that sense all other Feloidea are derived. The presence of a true septum bullae is also a derived feature of all Feloidea except *N. binotata* (this presumes that Hunt is correct is considering the bulla of *N. binotata* primitive in the first place, which we do not here question). In Hyaenidae the septum bullae is considered secondarily lost, although this has yet to be demonstrated, either in ontogeny or on fossil material.

The bulla morphology of *N. binotata* gives no indication of how many times the bulla morphologies of other feloid families have been derived from this primitive condition. Hunt (1987, Fig. 21) suggests that this has occurred twice, once in Viverridae–Felidae and once in Herpestidae–Hyaenidae. While these transformations are plausible, we would suggest that it is equally plausible to assume that the herpestid bulla is primitive for Feloidea excluding *N. binotata*, and that the other bulla types all evolved from this intermediate stage. That the bulla of herpestids (bulla type 3 of Hunt 1987) is intermediate is indicated by its placement at the center of the morphological spectrum of bulla types in Feloidea (Hunt, 1987, Fig. 14). Regarding the ontogenetic growth of the bulla elements, Hunt (1987, p. 41) states that 'the anterior chamber of the bulla either remains directly in front of the posterior chamber, or secondarily tends to grow backward under the posterior chamber'. This comment suggests that Hunt has grouped these forms (Herpestidae and Hyaenidae) together by their common *tendency* to backward growth of the anterior chamber, rather than that it actually *is* posteriorly enlarged in all taxa. If it were not for the fact that backward growth of the anterior chamber is almost certainly independently derived in these two families, being present in some, but not all members of both groups, and most especially absent in *P. cristatus,* this state could be accepted as a synapomorphy. As it is, however, it is more parsimonious to suggest that the basic herpestid condition is primitive, and that the other bulla configurations have derived from it. The *tendency* to backward growth of the anterior chamber may also be a relatively primitive trait, as it is seen in the felid *Uncia uncia* (the snow leopard), and also, though less clearly, in *Otocolobus manul* (Pallas' cat).

H. antiquus has a typically herpestid bulla, and if the arguments above for the primitiveness of this bulla type relative to other Feloidea (except *N. binotata*) can be accepted, then *H. antiquus* has a primitive bulla morphology.

Claw type. – Hunt (1987) and Flynn *et al.* (1988) considered the non-retractile claws of Herpestidae and Hyaenidae to be a derived feature uniting these two groups. However, on the basis of outgroup comparison Wozencraft (1989) suggested that non-retractile claws are primitive within Feloidea. There has been little information available from the fossil record relevant to this matter, but recently Semenov (1989) suggested that taxa such as *Ictitherium* and (especially) *Protictitherium* had retractile or partly retractile claws. If this can be substantiated, then clearly non-retractile claws are derived for hyaenids, but are independently acquired from those of herpestids, contrary to the suggestion by Hunt (1987) and Flynn *et al.* (1988).

Position of internal carotid artery. – The perbullar state, in which the internal carotid artery runs within a bony tube in the medial bulla wall, is derived in comparison with the transpromontorial course, in which the internal carotid artery runs on the ventral surface of the petrosal promontorium. Within Feloidea, only Herpestidae exhibit the derived perbullar state. All fossil hyaenids for which the state is known with some confidence have a transpromontorial course of the internal carotid artery. The same is true of *H. antiquus*, which thus exhibits the primitive feloid condition.

In addition to these characters, Flynn *et al.* (1988) mention a number of other osteological features that are shared between various groupings of feloid families. However, these authors make no attempt to evaluate the polarity of these characters, being content to note that there is conflicting character evidence within the group. Some characters are also difficult to define from their list. Thus, features such as entotympanic elongated and ectotympanic enlarged are difficult to evaluate on the basis of such a simple, non-relational statement. However, bullar ontogeny has been discussed above. Other characters mentioned by Flynn *et al.* (1988) are as follows.

P^4 larger than M^1. – Since no precise definition of how the term larger is to be understood is in evidence, this character is somewhat difficult to evaluate. However, it is clear that P^4 is substantially larger than M^1 in Felidae, Hyaenidae, and Viverridae, whereas in most Herpestidae it is smaller. Unfortunately, it is almost impossible to evaluate the polarity of this character, as it is variable within the most significant outgroups, except Nimravidae, in which M^1 is considerably reduced. The latter condition is almost certainly derived, but it is at present not possible to make a choice between viewing P^4 and M^1 equal in size (seen in *Viverravus*; Matthew 1909, Pl. 43) or M^1 larger as the primitive condition. In *H. antiquus*, M^1 is quite small relative to P^4, and this taxon is unlike Herpestidae in this respect.

Hallux and pollex reduced or lost. – This is our character 40 in part. A reduction or loss of these elements is probably a derived feature of Herpestidae, Felidae, and Hyaenidae. However, it is not clear to what degree this reduction has proceeded independently in the three families. For example, MC I is a vestigial element in modern hyaenas (except *P. cristatus*), but was a substantial element, similar in morphology to the MC I of *P. cristatus*, until quite late in hyaenid phylogeny. In *I. abronia*, MC I has a distal articular facet (Hendey 1974a) and was therefore probably associated with at least one phalanx. The hallux and pollex of *H. antiquus* are not known.

Digitigrade stance with compressed metapodials. – It is not clear that this feature can be adequately distinguished from the preceding one, especially since both have a strong ecological component in their association with cursorial adaptations.

Postglenoid foramen lost. – Here there is a difference of opinion regarding coding. Wozencraft (1989) codes this character as present (primitive) versus vestigial/lost (Feloidea, 'pinnipeds'), and thus as uninformative in this context. Flynn *et al.* (1988), on the other hand, have postglenoid foramen lost as a character shared by Felidae and Hyaenidae. That the loss of the postglenoid foramen is a derived trait is not in question. Regarding the coding, we lean towards the first interpretation, as we have seen several herpestids in which there is no trace of a postglenoid foramen, and in at least one specimen of *P. cristatus* (in the collections of the Swedish Museum of Natural History) there is a small foramen on the postglenoid process just anterolaterally to the auditory bulla which may represent a vestigial postglenoid foramen. (This foramen is not seen in the specimen illustrated by Hunt 1974, Pl. 12). In *H. antiquus*, there is a small but distinct postglenoid foramen (De Beaumont 1967), and, again, this taxon illustrates a relatively primitive condition.

Of the characters used by the aforementioned authors in their analyses of feloid interrelationships, these are all that were informative and can be evaluated on fossil material. A number of characters dealing with soft anatomy and external appearance have also been used in this context. These can naturally not be studied on fossil material. While noting that several of these features appear to be very strong synapomorphies, e.g., the major arterial shunts in Felidae and Hyaenidae (Bugge 1978), the extensive parallelism between feloid families that can be demonstrated from the fossil record (see, e.g., alisphenoid canal and other features, above) should lead to a healthy skepticism regarding the validity of synapomorphies for which the primitive state in the families is only inferred from extant taxa. We do not by this mean to suggest that none of these features are valid synapomorphies, only that there is no reason to treat non-fossilizable characters differently from fossilizable ones, for which the evidence shows numerous character state changes within families. This is thus a strong *prima facie* case for the importance of including fossils, where available, in phylogenetic analyses.

After this character analysis, we are left with the character state matrix shown in Table 7. An analysis of this matrix, rooted at the best estimate of primitive states, as per above, leads to one most parsimonious tree, This tree has Felidae and Viverridae as sister groups, on the basis of the inflated medial portion of the ectotympanic. Sister group to these

Table 7. Data matrix obtained from character analysis of feloids, as discussed in the text. Zeros indicate that the group exhibits the state interpreted as primitive. All characters are unordered

Taxon	Hyaenidae	Felidae	Herpestidae	Viverridae
Character				
Major palatine foramen	1	0	1	1
Palatine length	0	0	1	0
IOF/lacrimal canal	0	1	0	0
Alisphenoid canal	0	1	0	0
Carotid canal	0	1	0	0
External auditory meatus	1	0	2	0
Caudal entotympanic	0	1	0	1
Paroccipital process	0	0	0	1
Cruciate sulcus	0	0	0	1
Lingual cusp of P^3	0	0	1	0
Absence of P_1	0	1	0	0
Size of M^1	0	1	0	0
Presence of M^2	0	1	0	0
Presence of M_2	0	1	0	0
Claws	0	0	1	0
Internal carotid artery	0	0	1	0
P^4/M^1	0	0	1	0
Hallux and pollex	1	1	1	0

taxa is the Hyaenidae, on the basis of the primitively retractile claws of this group (Semenov 1989). The one contradictory character is the position of the major palatine foramen, in which the derived state would unite Herpestidae, Hyaenidae, and Viverridae, to the exclusion of Felidae. This result is clearly unsatisfactory. After reviewing the fossil record, 15 out of 18 characters were found to be autapomorphic to one of the families, and only three were phylogenetically informative. Even these three can be considered questionable, since the only paleontological data used were of Hyaenidae, and because the polarity determination at least in the case of retractile claws is open to interpretation. If the fossil record for Viverridae were more complete, they might also be found to have primitively had a herpestid-like bulla and perhaps non-retractile claws (considered derived by Flynn *et al.* 1988).

Before proceeding to a discussion of the reasons for the unsatisfactory result of this phylogenetic study, the position of *H. antiquus* must be briefly considered. It is clear from Table 6 and from the character analysis above that this species is generally plesiomorphic. Out of the 18 characters investigated, *H. antiquus* exhibits the plesiomorphic state in 16. It shares one possible synapomorphy with Viverridae (absence of the cruciate sulcus), and one with the Herpestidae (the presence of a lingual cusp on P^3). Both are only weakly corroborated. In other relevant features, such as dental characters, *H. antiquus* has been considered a plausible model for the ancestral hyaenid. However, this form of 'ancestral type' reasoning is clearly reminiscent of Goldilocks and the Three Bears – not too hot and not too cold, but just right – and is a strong indication of plesiomorphy. This is generally confirmed by study of the dentition of *H. antiquus* (De Beaumont 1967): with the possible exception of the lingual cusp on P^3, we have been able to identify no clearly derived dental feature that *H. antiquus* shares with any of the extant families of feloid. In summary, *H. antiquus* shares no derived features with Hyaenidae, and Hunt (1987, 1989) is incorrect in using this species as a model of a primitive hyaenid, for example in his statement that the cruciate sulcus is absent in primitive hyaenids (Hunt 1987, p. 48).

Prospects for phylogenetic analysis of Feloidea

The picture of feloid interrelationships painted above is a bleak one, with an essentially unresolved tree and characters that upon recourse to the fossil record turn out to be either plesiomorphic or autapomorphic. In the case of unfossilizable characters, there must, in addition, remain some doubt regarding the primitive state within each of the families. Is there any way out of this dilemma? Is morphological data useless for resolving these relationships? What is the status of paleontological data in this matter?

First we must identify the reason for the dilemma. The extant feloids form four distinct and stable families. With the addition of fossil taxa, the boundaries between the families become less and less distinct, since it must be our goal to maintain these four families as monophyletic sister taxa. Unless we ascribe to some die-hard school of macromutational evolution, we must accept that the characters exhibited by end members of the families must have been assembled piecemeal (Levinton 1988; Radinsky 1982). The rate of assemblage may have varied between families, but the general pattern is the same, and is strongly corroborated by the phylogeny of Hyaenidae presented herein. This being so, we must expect the evidence for monophyly to get gradually weaker as more and more plesiomorphic taxa are added, and, in the end, the monophyly of the family as a whole may rest on a single, seemingly insignificant character (Fig. 40). In the case of hyaenids, the problem is compounded by the fact that the living members of the family form two distinct groups, one composed of three very advanced forms, and the other of a single form, *P. cristatus*, which is a mixture of a few very primitive (for a hyaenid) traits and many extremely derived autapomorphic ones. This means that in many cases *P. cristatus* is a hindrance rather than a help in determining character polarity within the Hyaenidae.

Thus, the first part of the dilemma is that the difference between the families at the time of the original radiation may have been very slight indeed, and may in fact lie beyond the limits of resolution of paleontological material. It is thus a matter of missing data. The second part of the problem has been argued cogently by Gauthier *et al.* (1988; Donoghue *et al.* 1989). They note that the transformations within a clade leading up to the extant forms are also, in the absence of fossils, a form of missing data. For example, the presence of M_2 in hyaenids cannot be determined on the basis of the extant taxa. Recourse to fossils shows that this indeterminacy is due to a form of missing data. The possibility of fossils falsifying a phylogeny based on extant taxa is therefore also a result of data missing from the extant taxa. This then, is the inner nature of the conun-

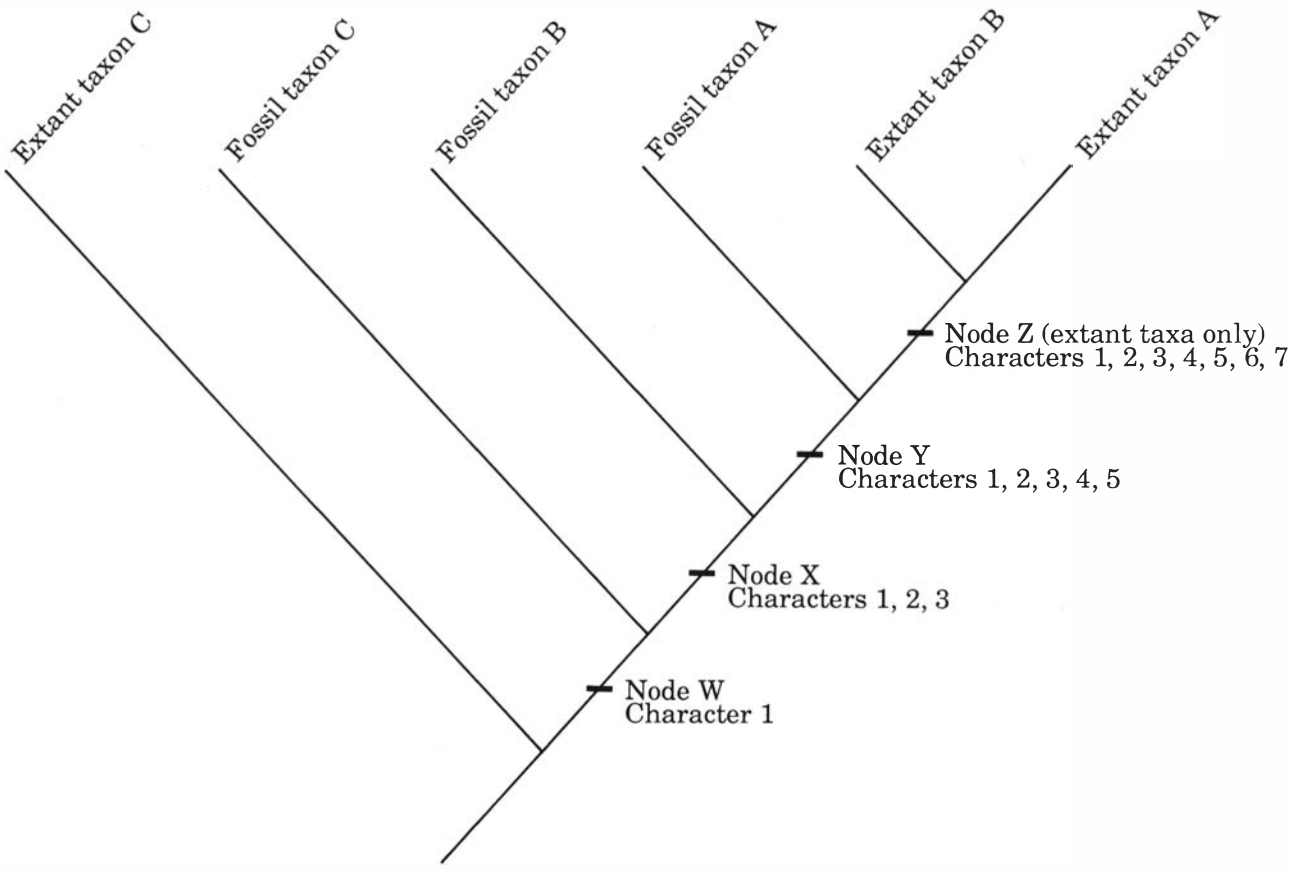


Fig. 40. Hypothetical cladogram to illustrate problems encountered in phylogenetic analyses with and without fossils. Let us suppose that node Z characterizes a family. If no fossils are included, this family as shown here can be distinguished from its living sister taxon by a suite of seven characters (1–7). This is a simple and ideal situation. However, then we find fossil taxa A–C, which have progressively fewer synapomorphies with the extant taxa. Since our goal must reasonably be to incorporate these fossils into the same family as defined by node Z (otherwise we will have an unnecessary number of monotypic fossil families to deal with), the family is correspondingly distinguished by fewer characters (at node W by only one character). This might be seen as an argument for avoiding the incorporation of fossil and extant taxa in the same analysis. However, if we suppose that we have some extraneous extant taxon, say taxon D, which has characters 6 and 7, we might be inclined, in the absence of the fossil information, to place this as sister taxon to node Z. If we made use of the fossils, however, we could have seen that the extant morphotype at node Z is built up starting with character 1, and that the presence of characters 6 and 7 alone in taxon D thus must be a parallel development. This more or less describes the situation encountered in the Hyaenidae, and shows the importance of fossils to the study of feloid interrelationships.

drum: fossils are less informative than living organisms with regard to potential evidence for phylogenetic studies (Gauthier *et al.* 1988; Donoghue *et al.* 1989); therefore phylogenetic studies based on fossils will have less resolving power than those based on extant taxa; however, a phylogeny based purely on extant taxa can also be spurious due to missing data on character transformations within the groups involved; additional evidence on these character transformations can be provided by the fossil record; thus, fossils provide essential additional information which, when available, is necessary to phylogenetic analyses.

Thus far, we have discussed the situation in terms of an operational dilemma. But does it in reality constitute a problem? For those who view such lack of resolution as that seen here as a failure of comparative anatomy (Bergström 1986, 1989) it may well be so. Others take lack of resolution at face value, to indicate rampant polyphyly (Bjerring 1984). We prefer to view this lack of resolution as an indication that more work is needed, and therefore as an opportunity for the future. Because it is based on additional data, we view our unresolved phylogeny as an improvement on that obtained by Wozencraft (1989) (which we, incidentally, have not falsified – adding characters of the soft anatomy to our data matrix will still yield his result, with Hyaenidae and Felidae as sister taxa), which in its turn is an improvement on previous results, as it also is based on more data. We have confidence that additional finds, more detailed morphological study, and more rigorous application of cladistic principles will enable us to obtain greater and greater resolution, although at the same time we recognize that that one feature that distinguished the first hyaenid from the common ancestor of hyaenids and their sister-taxon, whichever it may turn out to be, may not be a feature that can be detected in the fossil record, and that, therefore, there truly is a limit on phylogenetic resolution.

With this said, we may note that there may also be an evolutionary explanation, beyond the quality of the data, for the difficulty in resolving the interrelationships of the feloid families. This reason suggests itself both from the fossil record and from molecular data (Wayne *et al.* 1989), and is that the original feloid radiation may have proceeded very rapidly (see also discussion below). If this was so, there may not have been sufficient time for morphological changes to assemble before the next split. This also means that what we find in the fossil record will most likely either be members of one of the four extant families, or forms belonging to taxa that existed before the feloid radiation began. Sister taxa to supra-familial groupings within the Feloidea will be difficult to find and identify.

What is a hyaena revisited

Early in this study we briefly considered the definition of a hyaena. There we noted that, in the vernacular, a hyaena is a fairly large, dog-like carnivore with adaptations to cracking bones. The inclusion of *P. cristatus* in the Hyaenidae means that this definition certainly will not do. In the light of what has been said above regarding Feloidea, how do we decide what a hyaena is? Unfortunately, there is no simple answer to this question, even given the data and analysis presented in this paper. The extant taxa can be readily grouped as Hyaenidae on the basis of their derived karyotype (Wurster & Benirschke 1968), but this is not applicable to fossils. When these are introduced, we find that there is no single character that can serve as a synapomorphy for all taxa that we have included in the family. Stage 5 bullae (Hunt 1987) are only known in hyaenids, and all taxa with this bulla type are clearly hyaenid (taxa from *Tungurictis* upwards in the cladograms). The more primitive taxa constitute a bigger problem. However, while stage 4 bullae are present in some herpestid and felid species, they are clearly in the direction of the derived hyaenid bulla type, and therefore we have taken taxa with this bulla type to be hyaenids. This makes *P. orbignyi*, and *T. primordialis* hyaenids. This decision is strengthened by the fact that the last mentioned taxon has a dentition that is more derived (in the hyaenid direction) than any known herpestid or viverrid. In the matter of *'Protictitherium'* spp., we have to rely to some degree on faith, since the bulla is not known in any of these taxa. However, the continuum of dental morphology from primitive *'Protictitherium'* to advanced *Ictitherium* is so smooth, that the inclusion of the former genus in the Hyaenidae must be seen as justified.

The age of the Hyaenidae and the feloid families

The oldest known hyaenid, as the group has been defined here, is *Plioviverrops gervaisi*, which comes from Vieux-Collonges, MN Zone 4b (Mein 1979; Savage & Russell 1983). Thus, a minimum age for the family of approximately 17 Ma can be established. However, the presence of a more derived hyaenid (*Tongxinictis primordialis*) from MN Zone 6 suggests that the minimum age should be pushed back somewhat, although probably not much, since *Plioviverrops* spp. are placed close to the root of the hyaenid tree. A minimum age for the group of 20 Ma, perhaps down into the Agenian, would seem reasonable on the basis of the known fossil record. It is perhaps not coincidental that this is the approximate age of the first certain members of the other feloid families as well. We have already noted the difficulty in assigning the Agenian species *Herpestides antiquus* to any of the extant families, despite the abundant and well preserved material available, and we consider earlier records of extant families to be doubtful (*pace* Hunt 1989). A more extensive discussion of this topic is, however, beyond the scope of the present paper.

Several molecular datings of the splitting of the feloid families have also been published. Unfortunately, these dates are mutually strongly contradictory. Reciprocal average microcomplement fixation suggested a date for the felid–hyaenid split of approximately 25 Ma (Collier & O'Brien 1985). Isozyme genetic distance data, however (O'Brien *et al.* 1987), have suggested a figure of some 18 Ma. Both of these figures are fairly close to the 20 Ma minimum age obtained from the fossil record. Thermal stability of DNA hybrids, on the other hand, has suggested a date for the feloid split of approximately 40 Ma (Wayne *et al.* 1989). However, it is clear from the discussion by these authors that the 40 million year age cited by them is a calibration date derived from the fossil record, and that the age of the split of the feloid families in this analysis is not an independent variable. They cite several authors for the date of the feloid split in the fossil record, but none of these authors have dealt specifically with this question. At the most, they have considered the division between Caniformia and Feliformia (e.g., Flynn & Galiano 1982), which is not the same thing as a split between the extant feloid families. For the most part, discussions of feloids in the paleontological literature have used old dates for the origins of the feloid families, dates based on phenetic criteria and not on cladistic analysis. Thus, it is believed that 'stenoplesictines' have a special relationship with viverrids, which would thus place the origin of this family well down in the Oligocene. This hypothesis of relationship is based on plesiomorphy, rather than shared derived characters, and is of little value to the present issue. It seems equally plausible that 'stenoplesictines' represent a primitive stem group of feloids that preceded the split of the extant families (but see Hunt 1989). The most useful approach would seem to be to take as many calibration dates as possible and obtain some form of consensus from the entire set. With the current explosive interest in phylogeny, these calibration dates can subsequently be corrected, and with them the molecular dates, up to such a time as this line of investigation leads to a mutually acceptable result.

At present, we feel that the original molecular dates suggested by Collier & O'Brien (1985) may be very close to the truth. The same is true for the suggested 10 Ma age of the *Hyaena–Crocuta* split. This date is, upon comparison with the fossil record and the cladogram of Hyaenidae presented here, seen to be surprisingly accurate. It may be a few million years on the low side, however, since the oldest *A. eximia* is uppermost Vallesian, and this sets the minimum age for the split at somewhere around 11 Ma. In view of the importance of establishing the age of the basal radiation of hyaenids, molecular study of *Proteles* would be of great interest.

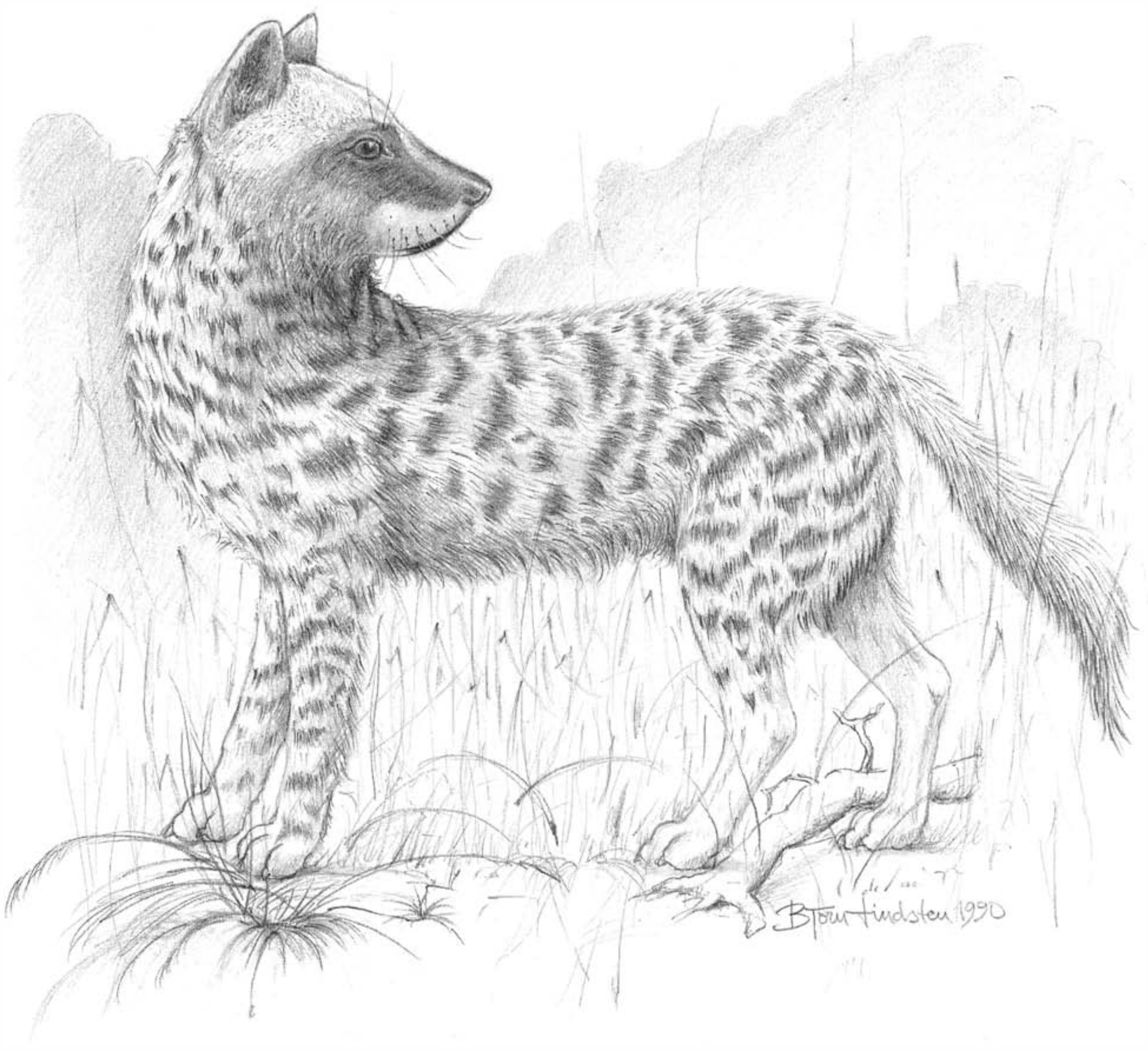


Fig. 41. Life restoration of *Ictitherium viverrinum.* See Appendix for further details.

Evolution of Hyaenidae: structure and function

In this chapter we will analyze the fossil record of hyaenas in search of patterns of evolution. As has been pointed out by a number of commentators (Cracraft 1981; Donoghue 1989; Lauder 1981; Levinton 1988), investigating the phylogenetic pattern of a group, i.e., developing an historical hypothesis of descent, is primary to any study of evolutionary patterns within that group. Thus, we will first study morphological patterns on the basis of the cladograms we have presented. In this section we will try to answer questions regarding the rate and timing of evolutionary trends within Hyaenidae: is their evolution spasmodic or gradual, coordinated or mosaic, divergent or convergent. We will discuss the evolution of the first 'typical' hyaenids, the thalassictines, from their viverrid-like antecedents, and their subsequent evolution toward the structurally specialized meat/bone eating hyaenas of today.

In the following section, we will discuss taxic patterns of evolution. One of the most interesting aspects of hyaenid evolution concerns the increased taxonomic turnover in the terminal Miocene. On the basis of the greatly expanded data base assembled in this paper, we shall analyze this aspect in greater detail in order to try to reach an understanding of the magnitude of the change, its structural, functional and ecological significance, and the underlying reasons behind it.

Morphological and functional evolution

General patterns. – The functional evolution of early hyaenids is poorly known, due to a great extent to the scarcity and fragmentary nature of the material. *Plioviverrops* spp. are united in having evolved adaptations away from the general

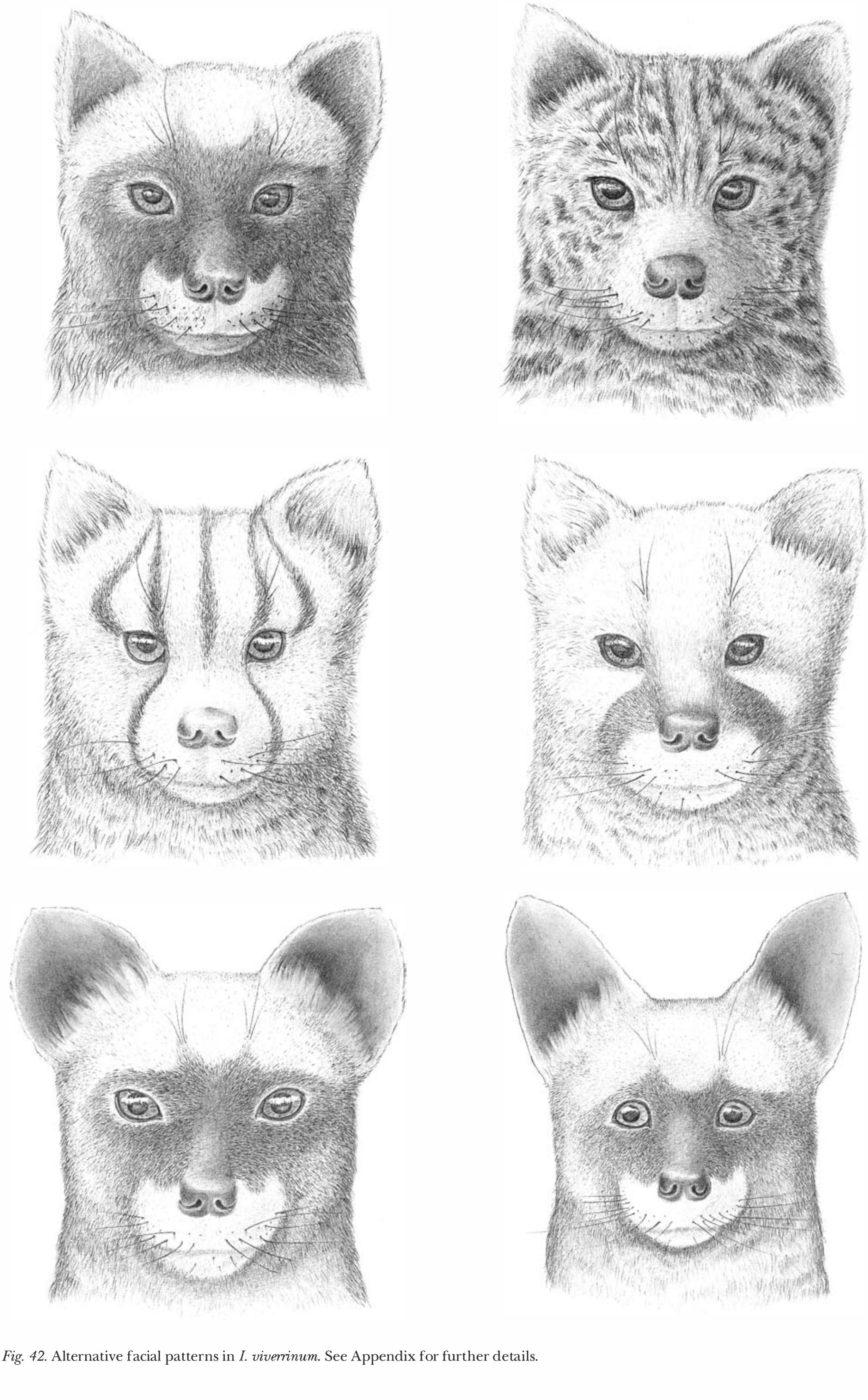
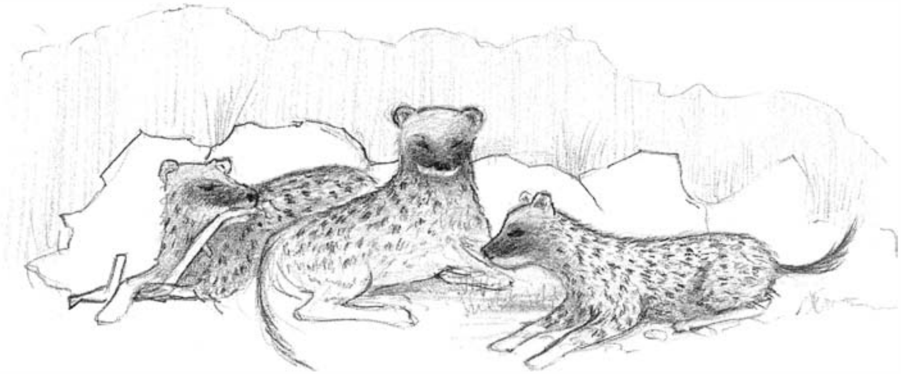
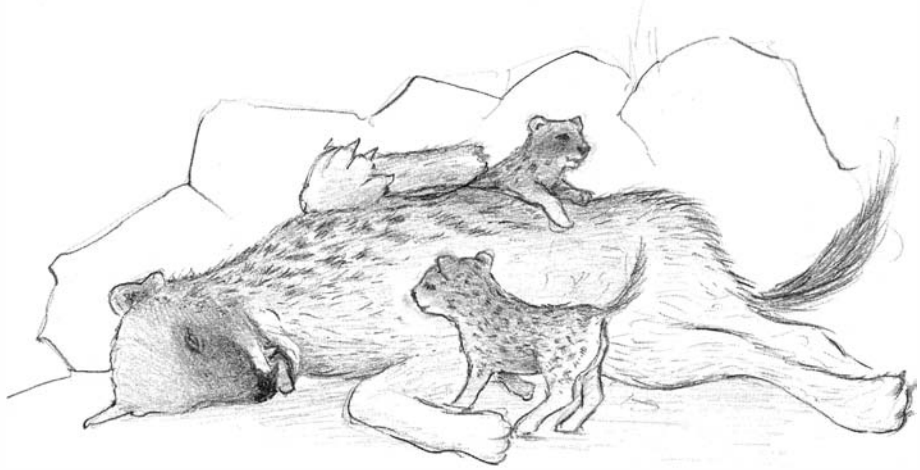


Fig. 42. Alternative facial patterns in *I. viverrinum.* See Appendix for further details.





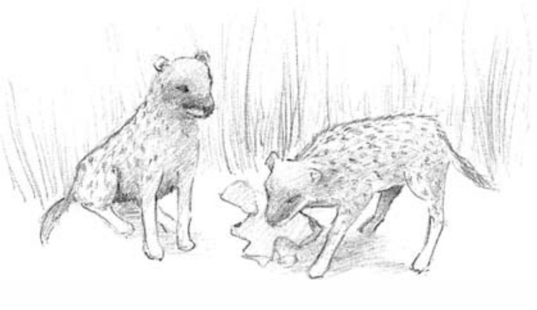


Fig. 43. Impressions of *I. viverrinum.*

trend of hyaenid evolution, and towards a small omnivore–insectivore niche. In the fossil record this trend culminates in the late Miocene with *P. orbignyi*, with its small premolars and long M_1 with very low trigonid and high metaconid. It is this trend that made Thenius (1966) suggest that *P. cristatus* may have evolved from *Plioviverrops*, and if so, then the general trend towards dental reduction and simplification must have continued to the present day, without leaving a hitherto known fossil record.

Species of *'Protictitherium'* are unfortunately only known from dental material. They have been differentiated mainly on the basis of differing patterns of cusp development on the M_1 talonid (Crusafont Pairó & Petter 1969; Schmidt-Kittler 1976), and it is difficult to establish any clear patterns or trends from these characters alone. One apparent trend within these species is, however, that geologically older species tend to be smaller than geologically younger ones. Since it cannot on present evidence be resolved

Fig. 44. Life restoration of *Hyaenictitherium hyaenoides*. See Appendix for further details.

whether *'Protictitherium'* is a natural (monophyletic) group or not, it can also not be stated whether this trend is a trend within this genus, or whether it is a part of a general trend in hyaenid evolution.

Be that as it may, if we ignore *Tongxinictis* and *Tungurictis*, which are taxa of uncertain status and functional adaptation (both seemingly highly autapomorphic in their dental characters), the next grade, *Ictitherium*, does consist of larger species, and this is also the main character in which they are derived beyond *'Protictitherium'*. With the exception of *I. viverrinum* (Figs. 41–43), the species of *Ictitherium* are poorly known. Present knowledge indicates that these taxa have relatively broader premolars than *'Protictitherium'*, and at the same time a relative lowering of the M_1 trigonid. This group of species has generally been slated as 'civet-like' in the literature, but this is far from correct. Instead,

Fig. 45. Life restoration of *Palinhyaena reperta.* See Appendix for further details.

the long, slender skull and snout, generalized premolars, relatively large M_1 talonid and relatively unreduced M_2 and M^{1-2} make them very similar phenetically to small or medium-sized canids, such as the jackals (Fig. 49), and it seems not unlikely that they had a similar mode of life as modern day jackals, although it should be noted that they had shorter limbs than these extant canids, and were likely not as cursorial.

The next grade, *'Thalassictis'*, establishes the general trend toward hypercarnivory which hyaenid evolution will follow. At this node, the M_1 talonid is considerably reduced, M_2 reduced, and P^4 lengthened. At the same time, M_1 in *'Thalassictis'* retains the primitive aspect of *'Protictitherium'*, with a low paraconid and high protoconid. At the next node, the species *Hyaenotherium wongii* has lost this primitive appearance of the M_1, but has not evolved any other clearly distinguishing characters. At the following nodes we have first *Miohyaenotherium*, then *'Hyaenictitherium'*. These species are considerably larger than those belonging to *'Hyaenotherium'* and *'Thalassictis'*. *'Hyaenictitherium'* is almost certainly a paraphyletic group. However, as a whole these taxa have evolved beyond *Hyaenotherium*, particularly in having broader premolars. This is the first major step towards broader premolars, a trend that will be discussed in detail below.

All members of the 'thalassictine' group (taxa from *'Thalassictis'* to *Hyaenictitherium*) are basically canid-like, just like *Ictitherium.* The postcranial skeleton of these forms is not well known, but preliminary investigations (Orlov 1939; personal observations by LW) indicate that there was a development towards a more cursorial adaptation than in *Ictitherium.* This, together with general abundance, suggests that at least some forms, e.g., *H. wongii*, may have been pack-hunting. In general, species in the 'thalassictine' group are more abundant in the fossil record than species in the 'ictithere' group (taxa from *'Protictitherium'* to *Ictitherium*), which suggests a general shift in ecological adaptations. Within this shift, *'Hyaenictitherium'* spp. (Fig. 44) represent the 'wolves' or 'hunting dogs' among hyaenas, and the skull of *Hyaenictitherium hyaenoides* (Fig. 48) bears strong phenetic resemblances to the skull of the African hunting dog, *Lycaon pictus*, or the skull of the dire wolf, *Canis dirus.* (Fig. 49). The last of these 'wolf-hyaenas' was *'Hyaenictitherium' namaquensis*, which is Langebaanian (early Ruscinian, MN Zone 14) in age.

After the 'thalassictines', hyaenid evolution splits into two major clades. One includes hypercarnivorous, cursorial forms, belonging to the genera *Lycyaena*, *Hyaenictis*, and *Chasmaporthetes.* Trends within this group include a general, if moderate, increase in size, development of the shearing component of the dentition at the expense of the bone-cracking component, and the evolution of a highly cursorial skeleton. General discussions of this group have been published by Berta (1981), Galiano & Frailey (1977), Kurtén & Werdelin (1988), and Werdelin, Turner & Solounias (MS).

The second group is that commencing with *P. reperta* (Fig. 45) and leading ultimately to the extant genera *Hyaena, Parahyaena*, and *Crocuta.* This group also shows a clear trend towards size increase. In most, but not all, taxa the bone-cracking component of the dentition is emphasized at the expense of the shearing component. In general, this group comprises what we in the vernacular today call 'hyaenas.' Trends within this group will be considered in more detail below.

Size trends. – We have discussed the trends towards greater size seen in hyaenids in general. Here we will consider size in relation to the phylogeny depicted in the core cladogram. Since complete skeletons are nearly non-existent, and only a few species are represented by complete and undistorted skulls, we have used the length of the upper carnassial as a measure of species size. Carnassial length is strongly correlated with size and shows minimal variability (Gingerich 1974b), and is therefore a useful measure in this context. As data, we have used the best available, geographically restricted samples of the taxa included. In some cases, of course, there is only one specimen of a species available. *C. crocuta* is highly variable in size (Turner 1984), and we have used a sample of *C. c. spelaea* from Kent's Cavern, Great Britain, for this species. This sample represents a size maximum for the species, which should be noted when studying Fig. 46.

Fig. 46 is a diagram showing the relationship between phylogenetic position, coded as taxon number from the bottom of the core cladogram, and length of the upper carnassial. We have here excluded *C. borissiaki* and *C. lunensis* from consideration, as these two taxa are part of a side radiation of hyaenids, away from the stem leading to the extant hyaenas (see Figs. 37–38). The figure shows that there has been a general and fairly gradual, though not entirely continuous, increase in size. There is no indication of a sudden leap in size anywhere in this phylogenetic lineage. We interpret the gradual increase in size to be correlated with the gradual assembly of characters leading up to the bone-cracking terminal forms. Bone-cracking has appeared in a number of lineages of carnivorous mammals (carnivorans, creodonts, dasyurids, borhyaenids), and in almost all cases bone-crackers have been among the largest forms within their taxon, the exception being the borophagine canids, where the bone-cracking forms *Osteoborus* and *Borophagus* are quite small (Munthe 1989; Werdelin 1989). It is thus reasonable to expect, in a lineage leading towards powerful bone-cracking forms, to find a trend towards size increase.

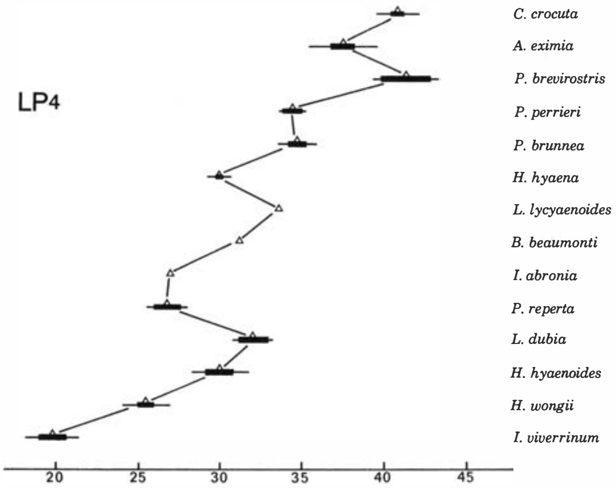


Fig. 46. Diagram showing length of upper carnassial plotted against position on core cladogram. (It should be kept in mind for this and subsequent similar diagrams that the points do not represent hypothetical common ancestors, but are the taxa themselves, and therefore each point may incorporate an autapomorphic component. The discussions in the text of these diagrams should not, however, be affected by this fact.)

It should be noted that if the taxa were plotted according to geological age, the pattern would be quite different, since there have been large bone-cracking forms (e.g., *A. eximia*) since the Miocene. Taking the average size of the hyaenids in each interval would also show a size increase towards the Recent, but we fail to see the relevance of such data. Morphological trends can be analyzed stratigraphically only to the extent that stratigraphy and phylogeny are congruent, and if they are not, then recourse to stratigraphy is futile (see also Cracraft 1981). This should not be construed to mean that we consider carefully documented stratigraphic–morphological ('stratophenetic') studies (Bown & Rose 1987; Rose & Bown 1984, 1986) to be of no value in studies of evolution. On the contrary, we have in our work on hyaenid taxonomy (Kurtén & Werdelin 1988; Werdelin 1988a, 1988b; Werdelin & Solounias 1990; Werdelin, Turner & Solounias, MS) emphasized the variability and morphological intergrading of species, a fact reflected in the sometimes arbitrary nature of referrals of single specimens to one species or another. Further, in a temporally and geographically restricted basin such as the Bighorn Basin studied by Bown and Rose, and within a limited set of taxa, it is to be expected that stratigraphy will, in fact, be congruent with phylogeny (whether the taxa have evolved *in situ* or not), and in such a case there need be no conflict between cladistically based analyses of phylogenetic trends and stratophenetic ones, except for the fact that the latter strive for a finer resolution; a resolution that is not obtainable with fossil hyaenids.

We do disagree with the stratophenetic approach as expressed by Bown & Rose (1987) in one sense, and that is that we do not consider species in any way arbitrary units. In paleontological studies, no matter how finely resolved, there is a certain arbitrary element added to identification of species, which is that there is no guarantee that the features we see on the fossils are in any way related to the species identifying characters of the actual animal (specific mate recognition system, SMRS, see Paterson 1981, 1985; Turner 1985; Turner & Chamberlain 1989). Instead, there is strong evidence, as suggested by Turner & Chamberlain (1989) among others, that such characters as those used here in identifying hyaenid species, or by Bown and Rose in their work on omomyid primates, are epiphenomena of the speciation process. As we understand it, the controversy surrounding the hypothesis of punctuated equilibria (Eldredge & Gould 1972; Gould & Eldredge 1977; Stanley 1979) concerns whether this epiphenomenon is closely linked temporally to the speciation event itself, or whether it may appear later and at a relatively gradual pace. Current evidence, part of it assembled by stratophenetic means, strongly favors the latter alternative (Bown & Rose 1987; Levinton 1988), despite some suggestions to the contrary, e.g., Fortey (1985). A more thorough discussion of the expected evolutionary patterns of different types of characters is presented by Eldredge (1989).

Relative width of P^3*.* – The relative width of $P^3/_3$ is an important variable in the evolution of hyaenids, as it is these teeth that are the principal bone-cracking teeth. In order to crack bones efficiently, and without risk of breakage, a tooth should have a pyramidal shape and, especially, a broad base. This widening of the tooth base will be reflected in the width of P^3 (this tooth is used because it is available in all species discussed) relative to the length of the same tooth.

Fig. 47 is a diagram plotting relative width of P^3 against position on the core cladogram, as above. This diagram can be interpreted to mean a number of things. The most obvious pattern is, however, that there is a marked trend towards species with a broader P^3. This change appears gradual throughout. The one major step in the trend is between *H. hyaena* and *P. brunnea*. Other than this, the deviations from the trend (linear regression gives the following equation: y=57.565x–27.996, r=0.945) are due to deviations of individual taxa. Nowhere does the trend accelerate or decelerate appreciably.

Thus, the evidence shows that the evolution of P^3 into a pyramidal, broad-based bone-cracking tooth was something that occurred gradually within the Hyaenidae. Naturally, some species may have invaded more strongly scavenging niches (with concomitant bone-cracking), but these have been individual excursions from the general trend, and not a sudden burst of evolution within a new niche. There is on this evidence no basis for separating hyaenas into bone-crackers and non-bone-crackers. Instead, we suggest that hyaenid phylogeny argues for a gradual adaptation to fuller utilization of prey, whether killed by the hyaenas themselves, or scavenged.

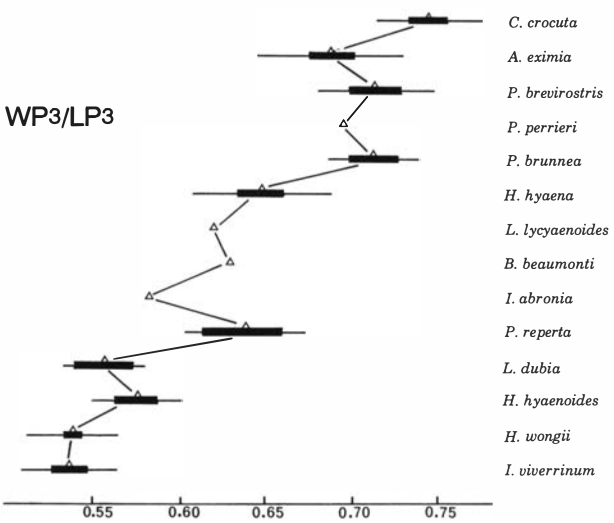


Fig. 47. Diagram plotting relationship between length and width of P^3 to position on core cladogram.

Skull shape. – The vaulted forehead of extant hyaenas was pinpointed by Werdelin (1989) as a functionally significant characteristic of bone-cracking carnivores. A vaulted forehead will allow a smooth transition of stresses at the top of the skull. In forms with a straight forehead, these forces are instead compounded at the top of the skull. The importance of this feature is shown by its presence in several distinct lineages of bone-cracking carnivores: in hyaenids, in borophagine canids, and in percrocutids (although distorted, the strongly vaulted forehead of *D. gigantea* is clearly seen in the illustrations of Qiu *et al.* (1988a).

Well preserved undistorted skulls, although rare, are available for nearly all species included in the core cladogram, with the exception of *B. beaumonti* and *L. lycyaenoides.* In addition, material of *I. abronia* and *L. dubia* was not available for comparison. Skulls of the remaining species are illustrated in Fig. 48. These illustrations show that the configuration seen in *H. hyaena* and *P. brunnea* is basically present already in *P. reperta*, whereas in the more primitive forms, such as *H. wongii*, the skull is much more canid-like, with a straight forehead. In lateral view the skulls of these primitive forms resemble small to medium sized canids such as jackals (Fig. 49), whereas the skull of *H. hyaenoides* is, as noted, very similar to *Canis dirus* in lateral gestalt (Fig. 48). In ventral view, however, the skull of *H. hyaenoides* is seen to be relatively shorter, and also broader across the zygomatic arches (Fig. 53).

The shortness of the snout of *P. reperta* (Figs. 49, 53, 54) should be viewed somewhat circumspectly, as this specimen is a juvenile, in which the permanent canines are not yet fully erupted. That the skull shape of this species is quite different from that of *H. wongii* is clear, however. Unfortunately, the following two phylogenetic steps are not represented by any skulls, and we next turn to *H. hyaena*, which can be seen to be somewhat advanced over *P. reperta* (advanced in the sense of closeness to the condition at the topmost node of the cladogram) in that the snout is higher, as are the nares. This leads to a deceptively straight profile, but the arc drawn in the diagram shows the vaulting to be there. The condition in *P. brunnea*, *P. perrieri*, and *P. brevirostris* represents only minor advance over that of *H. hyaena.* In *A. eximia.* however, we can see an approach to the condition in *C. crocuta*, in which the arc nearly coincides with the sagittal crest at the top of the skull.

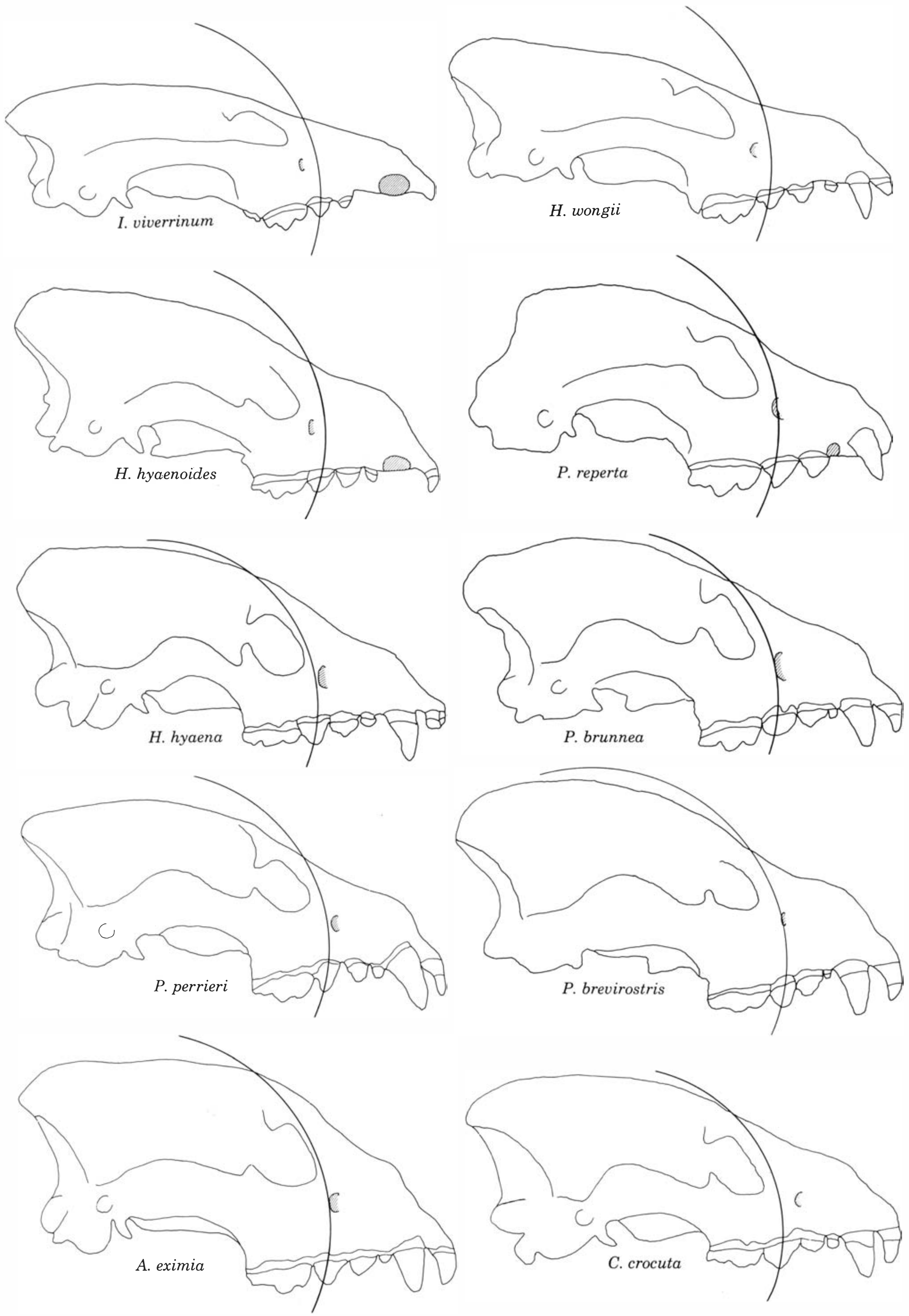


Fig. 48. Schematic drawings of skulls of ten hyaenid species in lateral view. Note the relationship between P^3, the infraorbital foramen, the forehead, and the arc drawn. See discussion in text. All drawn to the same basal length.

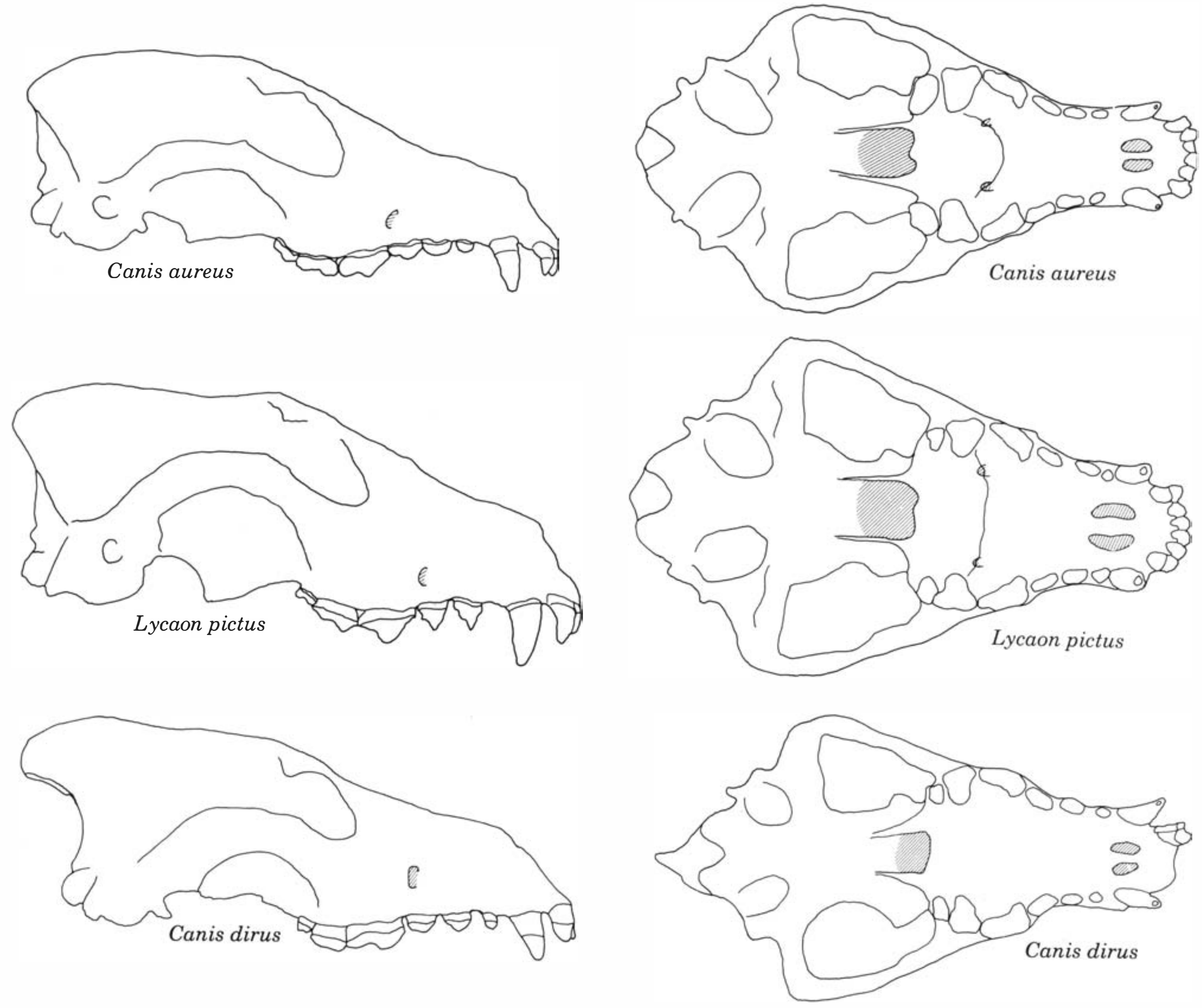


Fig. 49. Schematic drawings of skulls of three canid species in lateral and ventral view. For comparison with Figs. 49 and 53. See discussion in text. All drawn to the same basal length.

To summarize this section, we may note that, once again, the feature investigated shows no great leaps in morphology in the course of hyaenid phylogeny. The greatest steps would seem to have been from *H. wongii* to *H. hyaenoides*, where the dorsal skull profile evolves from straight to somewhat vaulted, and from *H. hyaenoides* to *P. reperta*, where the position of the arc is shifted relative to the infra-orbital foramen (Fig. 48). However, even these steps are nearly obliterated when individual variation is taken into account. There are specimens of *H. wongii* with somewhat vaulted skull profiles, just as there are specimens of *H. hyaenoides* in which the vaulting is less distinct than in others. The development of vaulting in any case preceded the development of advanced adaptations to bone-cracking. Again, morphological evolution in hyaenids points to gradual adaptation to a better utilization of the available prey.

Loss of teeth. – In a discussion of bone-cracking in borophagine canids, Werdelin (1989) noted that: 'given the evolution of premolar bone-cracking in a carnivore retaining its posterior molars, P_4 will always be selected for that function, rather than P_3.' If we turn this argument on its head, we may state that a prerequisite for the evolution of bone-cracking at $P^3/_3$ is that the posterior molars are lost (or at least greatly reduced). Thus, the reduction of M^1 and loss of $M^2/_2$ are important features of hyaenid evolution.

The reduction of M^1 was used as a character in our phylogenetic analysis, and any discussion here of its evolutionary importance based on the core cladogram would raise a problem of tautology. We merely present a figure (Fig. 50) mapping this character on the cladogram. Both M^2 and M_2 have been lost several times in hyaenid evolution: at least once in the *Lycyaena–Chasmaporthetes* lineage, and once in the *Palinhyaena–Crocuta* lineage. However, although closely correlated, the loss of these teeth is not entirely congruent. M_2 is absent in all taxa from *H. hyaena* and upwards in the tree, whereas M^2 is lost already in *B. beaumonti*. There are thus some 'threshold' taxa in which M_2 is present, but M^2 is not. This is true also in the *Lycyaena–Chasmaporthetes* lineage, where M_2 is present, but M^2 lost in some or all species of the genus *Hyaenictis*. Even though these losses can be considered important on functional

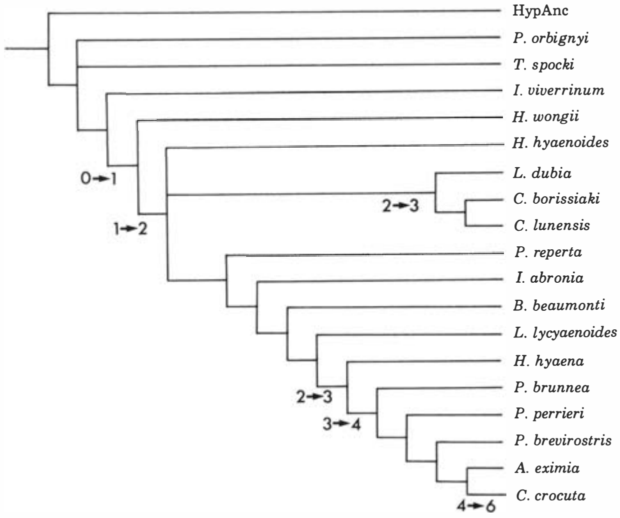


Fig. 50. Diagram mapping changes in character states of character 6 (relative size of M^1) on the core cladogram.

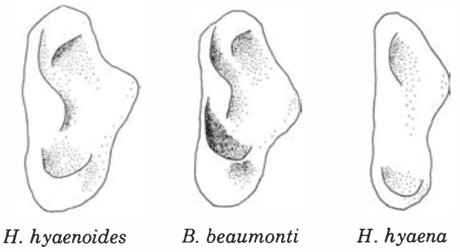


Fig. 51. First upper molars of *H. hyaenoides*, *B. beaumonti*, and *H. hyaena*. Note the relatively primitive character of M^1 in *B. beaumonti*. Not to scale.

grounds for an animal adapted to cracking bones with $P^3/_3$, they evidently appeared only gradually, and even then not concurrently. It might be argued that M_2 may have been lost later in phylogeny as it is no longer functional (it is, after all, occasionally present as an anomaly in, e.g., *H. hyaena*; Turner 1988). This seems not to be the case, however. Although non-functional in *H. hyaena*, there are strong reasons for believing that M_2 articulated with the metastyle wing of M^1 in at least *B. beaumonti* (personal observations from manipulating casts), in which M^1, and particularly the metastyle wing, is less reduced than in the Recent species (Fig. 51). Thus, M_2 was functional in at least some of these taxa, and remained as an obstacle in the functional adaptation to $P^3/_3$ bone-cracking (see analysis in Werdelin 1989).

Sagittally oriented carnassials. – This was suggested by Kurtén & Werdelin (1988) to be a valuable character in extant hyaenas, as a sagittally oriented carnassial would swing this tooth, and the shearing component of the dentition, away from the bone-cracking component, and thus reduce wear on the shearing blades. Since this character was used in the phylogenetic analysis, comments on its distribution would be tautologous here. We illustrate its distribution in Fig. 52, and note that it is absent in *L. lycyaenoides*, but present in *H. hyaena* and all subsequent forms.

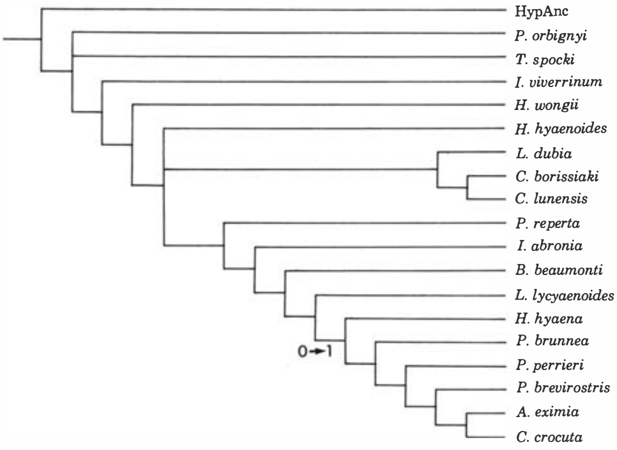


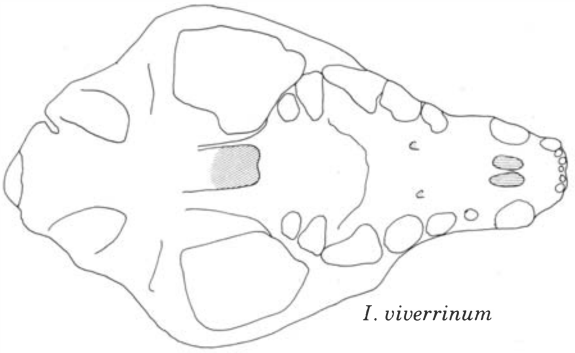
Fig. 52. Diagram mapping changes in character states of character 12 (placement of carnassials in tooth row) on the core cladogram.

Width of rostrum. – Finally, we analyze the width of the rostrum, measured as the distance between the lateral margins of the upper canine alveoli relative to the length of the palate (Figs. 53, 54). Here at last we have a character that shows stasis and then a sudden burst of evolution. In species from *H. hyaenoides* to *P. brunnea*, rostrum width is 44–46% of palate length. Given the measurement error and other factors, this represents essentially no difference at all. However, in *P. perrieri* this value is approximately 50%, and in *P. brevirostris* and *A. eximia* 54%. In *C. crocuta*, it is slightly less, 53%. Thus, the most derived hyaenids are substantially broader across the rostrum than less derived forms. The same is true of the posterior width of the palate, although data for this measurement were not sufficient to produce a similar diagram. Such a broadening pushes the jaw width of hyaenids from the canid range towards the felid range (Greaves 1985). At present we have no functional explanation to offer for this pattern. We simply present it in order to show that not all morphological features show a gradual development throughout hyaenid phylogeny, although we believe that the evolution of hyaenids in general has been governed by gradual, rather than episodic, change.

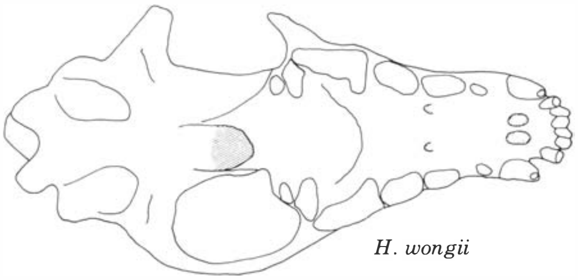
Taxic evolutionary patterns

Here we shall attempt to depict the diversity of hyaenids through time, in terms of absolute diversity and in terms of the number of first and last appearances in each time period. To be stringently conceived, such an analysis should, apart from the taxa actually known from the fossil record, also take into account those 'ghost' taxa that are not known but must have been there (Norell 1988). That is, time periods should be added to the count in order to make sister taxa of the same age. However, the following analysis will be based on known taxa only, for two reasons.

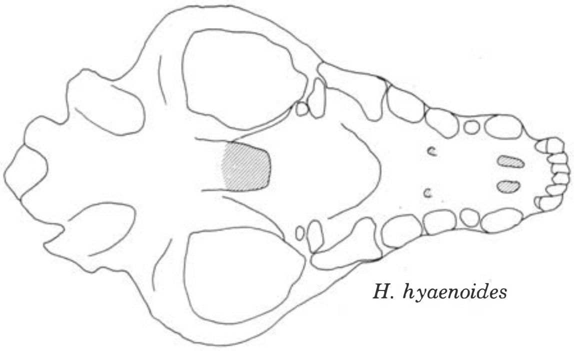
Fig. 53. Schematic drawings of skulls of ten hyaenid taxa in ventral view. Note widening of intra-canine distance in *P. perrieri* and subsequent taxa (cf. Fig. 54). All drawn to the same basal length.



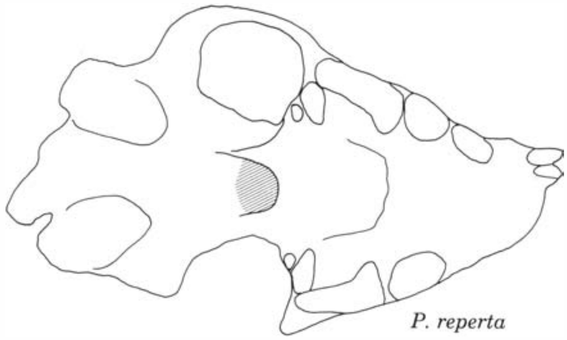
I. viverrinum



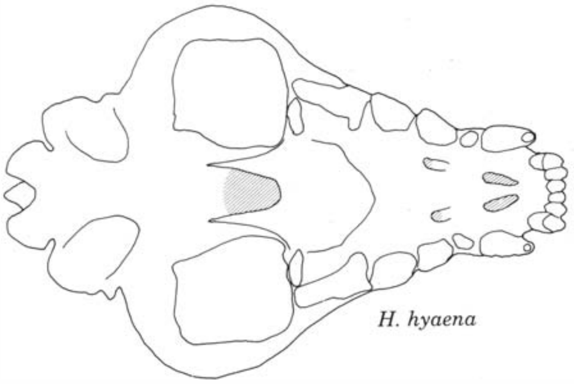
H. wongii



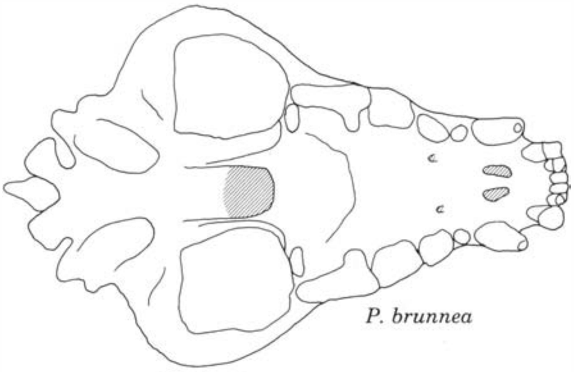
H. hyaenoides



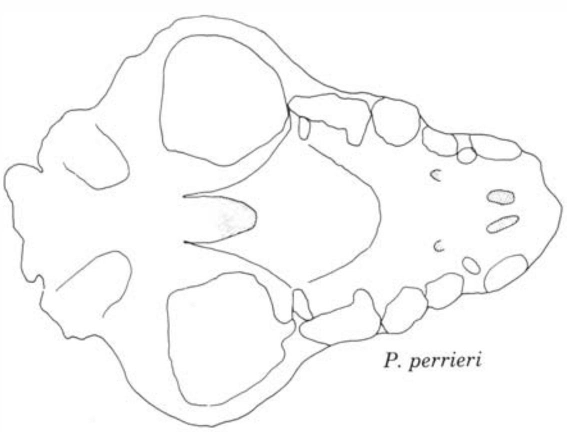
P. reperta



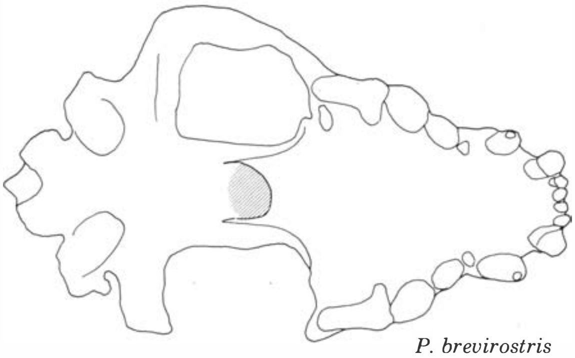
H. hyaena



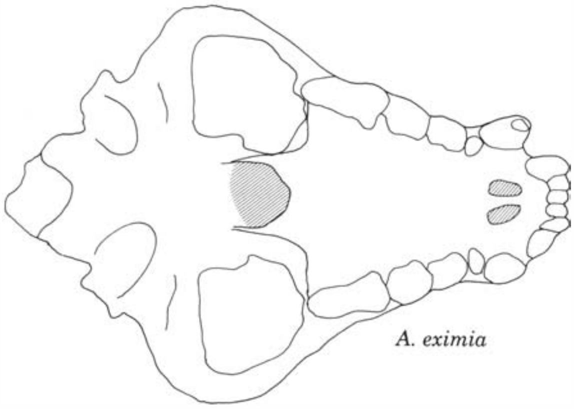
P. brunnea



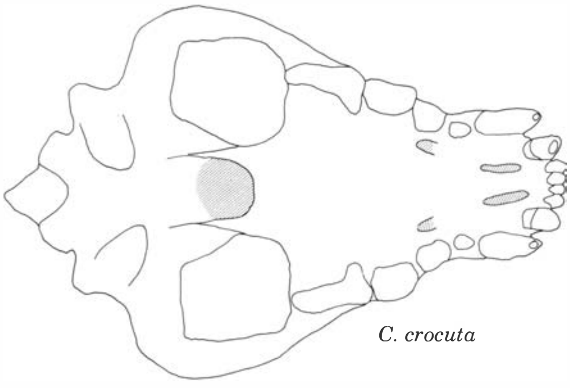
P. perrieri



P. brevirostris



A. eximia



C. crocuta

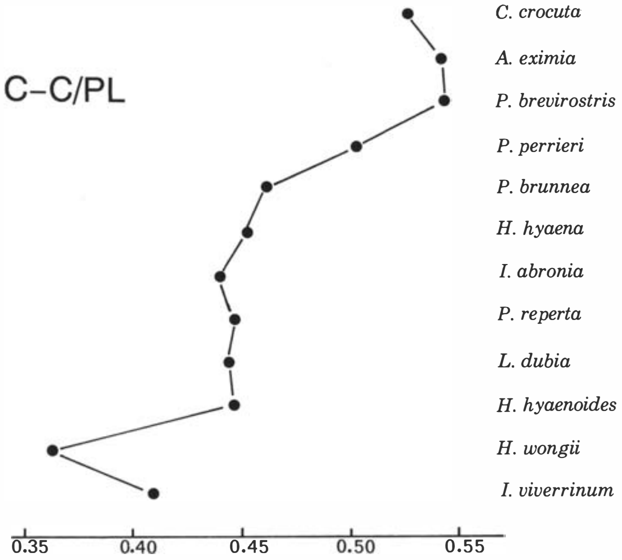


Fig. 54. Diagram plotting width between canines relative to palatine length against position on core cladogram. See discussion in text.

The first is that our stratigraphic control is in many cases insufficient. If ghosts are added, earlier time periods will tend to be heavily favoured if the stratigraphic scheme is rough. If this analysis could have used MN Zones rather than land mammal ages, the bias would have been considerably less. The second reason why we have not included ghosts in our analysis is that, as noted here and by Werdelin & Solounias (1990), *A. eximia* is sister taxon to *C. crocuta.* The earliest record of *A. eximia* species is Vallesian, and since this species is placed very high up in the cladogram, this will tend to add a large number of Vallesian ghosts to the total taxon count. However, the Vallesian record of *A. eximia* is limited to a single specimen from the Ravin de la Pluie, Greece (De Bonis & Koufos 1981). This single specimen thus affects the analysis greatly, and we feel that to base our conclusions on the stratigraphic and taxonomic assessment of a single specimen (which we ourselves have not seen) would not be sound practice at the present time. Instead, we present in Fig. 55 an comparison of total species abundance with and without ghosts, and invite the reader to keep in mind the possible presence of ghosts, particularly in the consideration of the abundance and first appearances of species in the 'hyaenid' clade below. We also look forward to the future conversion of some of these ghost taxa into fossils.

In Fig. 55 we can see the total number of hyaenid species plotted against land mammal age. Although the intervals are not strictly equivalent, it is clear that there is a sharp rise in diversity from the first appearance of hyaenids in the Orléanian, to the Turolian, where the diversity peaks, with 24 species known from this period. After the Turolian, the diversity of hyaenids drops sharply, to a mere 11 species known in the Ruscinian, and then to the four extant species. A 'pull of the Recent' effect is conspicuously absent from these data.

What is clear from this diagram is that hyaenid diversity peaked sharply at the end of the Miocene, and has since suffered a slow but steady decline. We shall try to seek an explanation for this in the morphology of the species, after we have considered the pattern of first and last appearances.

Since most species do not range over more than one land mammal age, the patterns of first and last appearances follow each other closely (Fig. 56). The figures also closely match those for total diversity (Fig. 55). It is interesting to note that there are generally more first appearances than last appearances in each interval, with the exception of the Turolian (preceding a sharp drop in diversity) and the Pleistocene (low figures for both first and last appearances).

The analysis of the Hyaenidae as a whole is interesting, but is not detailed enough to answer questions regarding the causal basis of the changes in diversity seen within the family. In order to address this side of the issue, we have separated the taxa into what we somewhat arbitrarily term 'hyaenid-like' taxa (i.e., taxa that show adaptations towards the mode of life represented by the extant genera *Hyaena*, *Parahyaena*, and *Crocuta*), which specifically are all taxa from *P. reperta* upwards in the total cladogram, and taxa with other adaptations, many of them 'canid-like.' Dia-

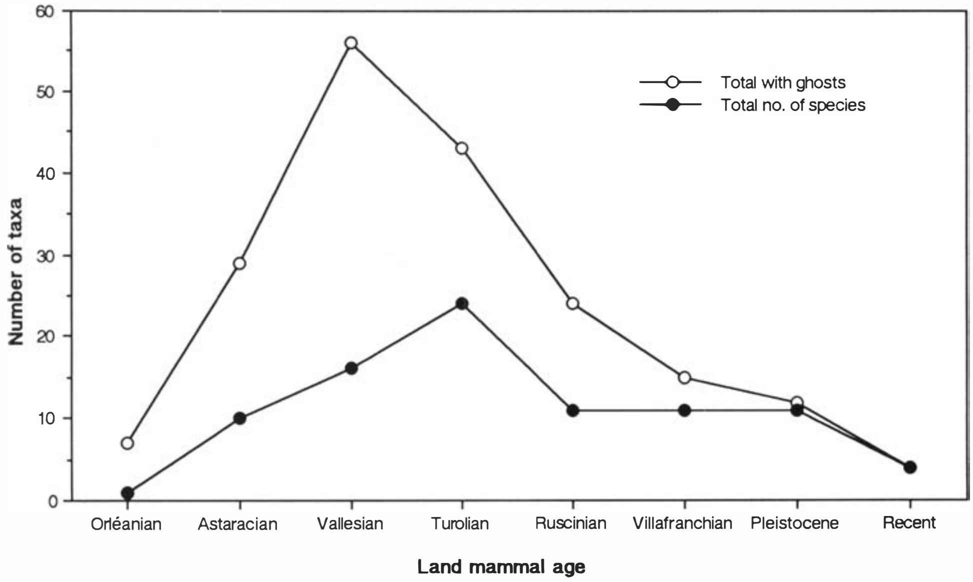


Fig. 55. Plot of number of taxa against land mammal age for all hyaenids, with and without ghosts. Note maximum at end of Miocene and subsequent decrease in diversity.

Fig. 56. Plot of first and last appearances of hyaenids against land mammal age. Note that the number of first appearances is generally higher than the number of last appearances, except at critical extinction episodes.

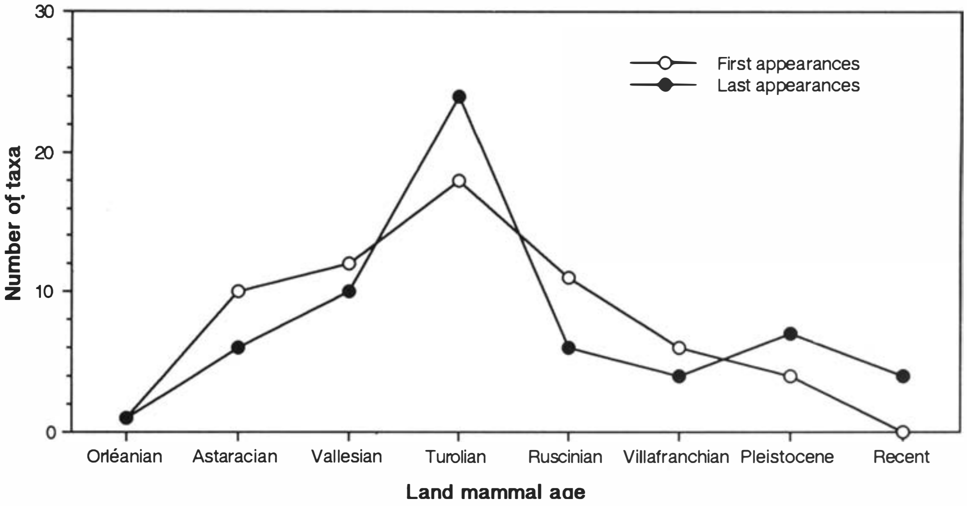


Fig. 57. Plot of number of taxa of selected groups of hyaenids. 'Hyaenid' and 'non-hyaenid' taxa are discussed in the text. 'Chasmaporthetines' are defined by node 5 in Fig. 38. Note increase in 'hyaenid' taxa even after the end of the Miocene.

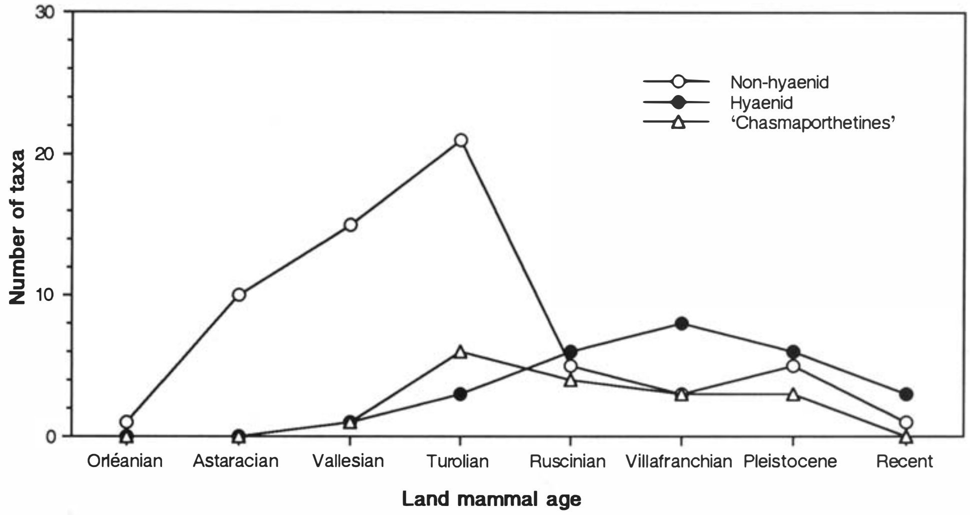
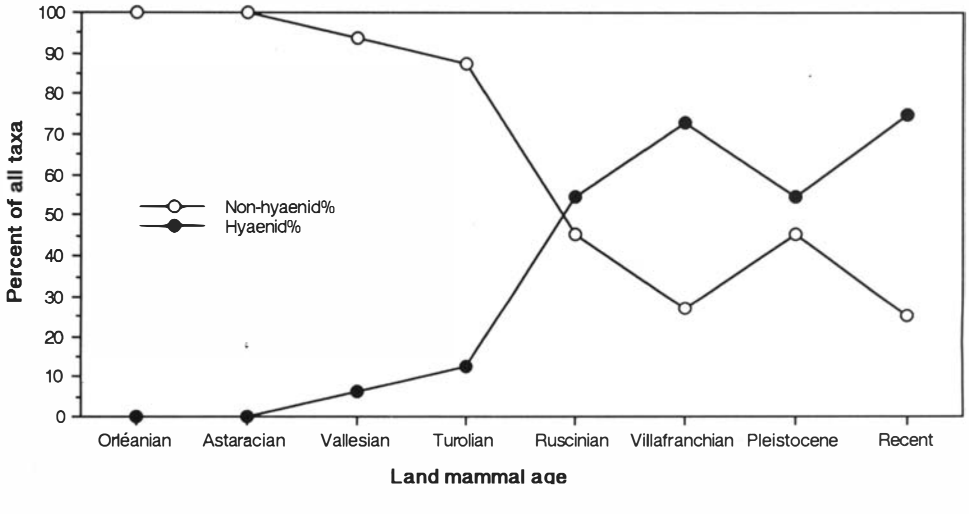


Fig. 58. Same diagram as Fig. 57 (without 'Chasmaporthetines'), but data expressed as percentage of all taxa.



grams of abundance of these categories against land mammal age are shown in Figs. 57–58. In Fig. 57, absolute abundances are shown. This diagram shows that the diversification of hyaenids (of a 'non-hyaenid' type) began in the Orléanian and proceeded rapidly, with 10 species known in the Astaracian, 15 in the Vallesian, and 21 in the Turolian. This figure illustrates well the dramatic decline in abundance of 'non-hyaenid' taxa after the Turolian. The diversification of 'hyaenid-like' taxa proceeded much more slowly, as is expected, since the two groups are not sister taxa, and hence not of the same age, with a beginning in the Vallesian, and steady increase until the Pleistocene. Fig. 58 shows the same data expressed as the percentage of all hyaenid taxa in each land mammal age, showing the replacement within the family of one type with another. Figs. 59–60 show the diversity patterns for the two types of taxa separated into first and last appearances.

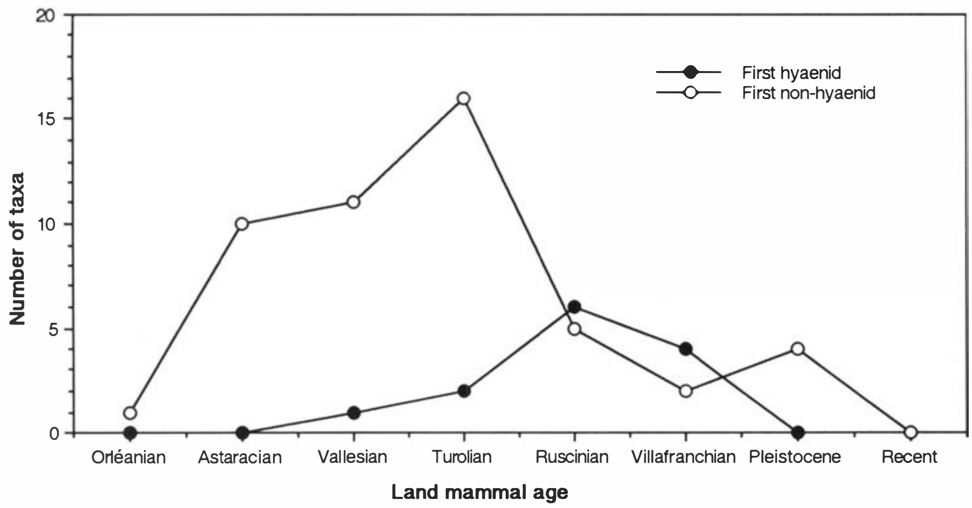


Fig. 59. Plot of first appearances of 'hyaenid' and 'non-hyaenid' taxa against land mammal age.

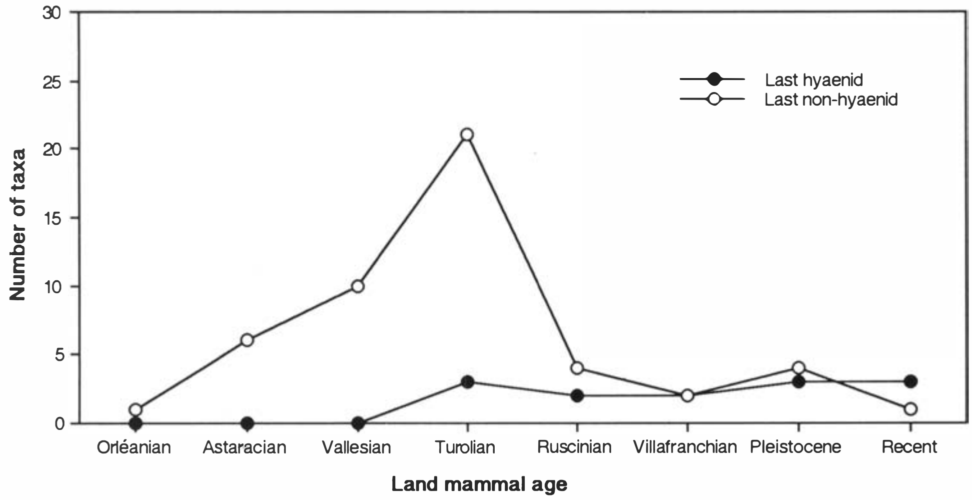


Fig. 60. Plot of last appearances of 'hyaenid' and 'non-hyaenid' taxa against land mammal age.

The reasons for the observed diversity patterns are still at the speculative stage, but we can offer some reasonable suggestions. It has been proposed (Ewer 1967) that the drop in diversity of hyaenids towards the Recent was related to the decline and extinction of machairodont (sabertoothed) felids. However, the analysis of 'hyaenid' versus 'non-hyaenid' taxa shows that the completely dominant feature of hyaenid evolution is the dramatic decline in diversity at the Miocene–Pliocene boundary (Figs. 57–58). It is quite evident that this has nothing to do with sabertooths, as the 'hyaenid' taxa were not affected to anything like the degree seen in the other taxa. Further, the number of 'hyaenid' taxa continued to increase until the Pleistocene, and it appears likely that the decline in diversity seen subsequently is due to the general extinction of megafauna, correlated with, but not causally connected to, the extinction of sabertooths.

There are two features that we see as requiring explanation. One is the lag in appearance between 'hyaenid' and 'non-hyaenid' taxa. There are three factors that should be taken into account in an explanation of this feature. One is, as mentioned above, that the two clades being compared are not of the same age. However, part of the question posed here is why they are not of the same age, so the cladogram topology is part of the question, rather than part of the answer. Another factor of importance is simply the lag time in evolution which suggests that if a group evolves from generalized ancestors, it will take at least some time before more specialized forms appear. The third factor is that the bone-cracking niches by definition occupied by the 'hyaenid-like' taxa were already occupied by the morphologically extremely similar and presumably ecologically equivalent Percrocutidae when true hyaenids first appeared. Whether true hyaenids outcompeted percrocutids in the large niches or whether this is a case of passive replacement is unknown, although the range compilations of Howell & Petter (1985) suggest that the first alternative may be more plausible. However, little headway will be made in this area until the relationships of Percrocutidae are analyzed in detail and we know what type of animal they were.

The second feature of hyaenid diversity requiring explanation is the dramatic decrease in diversity of 'non-hyaenid' taxa at the end of the Turolian. A key feature here is that this drop in diversity is correlated with the appearance of canids in Eurasia, first in the Turolian, then more species in the Ruscinian and Villafranchian (data in Savage & Russell 1983). The morphological similarity between many hyaenids and canids is notable, and this similarity may probably be extended to their ecological niches.

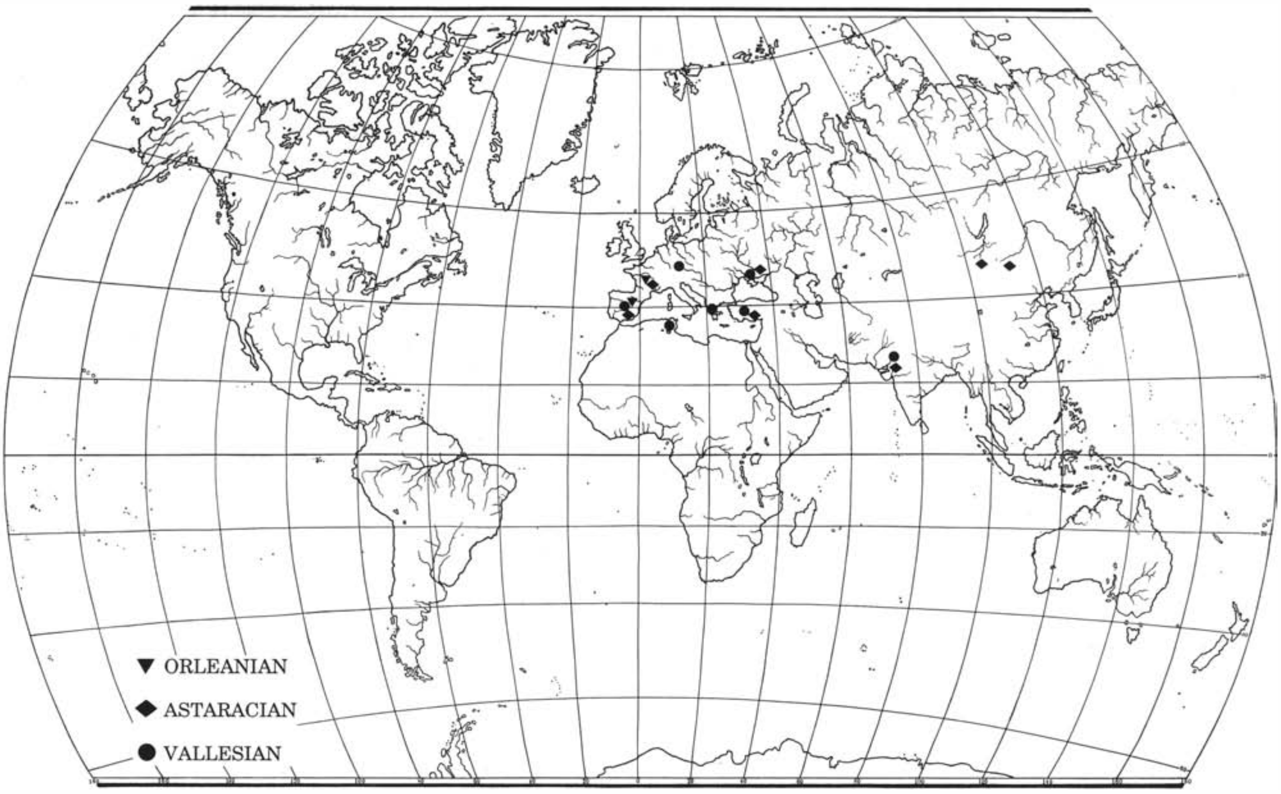


Fig. 61. Geographic occurrence of fossil hyaenids in the Orléanian, Astaracian, and Vallesian, as labeled. On this and the subsequent maps we have made no attempt to distinguish individual localities. The dots are placed by country or region only. Also, no indeterminate finds ('hyaenid, sp.') are recorded here. The maps thus represent minimal distributions.

Again, it is not possible to state whether canids outcompeted hyaenids (active replacement), or passively replaced small hyaenids after these had become extinct due to other, possibly climatic, causes. The continuous presence of canids in North America during the origin and diversification of hyaenids in Eurasia and Africa might perhaps speak more for passive than active replacement. The final observation we can make in this regard, which may be symptomatic of the situation as a whole, is that the diversity of hyaenids in the Langebaanweg fauna, South Africa (lowermost Ruscinian; Hendey 1981), where the sympatric canids are extremely rare elements of the fauna, is twice that of the entire Ruscinian of Europe, where there are a number of relatively common sympatric canids.

Biogeographic evolution

Hyaenids today have large geographic ranges, and fossil hyaenids are no exception to this rule. Even small hyaenas such as *I. viverrinum* were widespread (Werdelin 1988a, 1988b; Werdelin & Solounias 1990). This makes it very difficult to get any real information out of the geographic distribution of fossil hyaenas (Figs. 61–65).

The very oldest hyaenids are European (Fig. 61), but this may well be an artefact, as hyaenids only slightly younger are found in China. In Africa, the earliest hyaenids do not appear until the Vallesian (Fig. 61; *P. punicum*, *L. crusafonti*). However, this may also be an artefact of the lack of appropriate faunas. It is well to remember that the only known ursid from sub-Saharan Africa is from Langebaanweg, South Africa (Hendey 1980), implying that surely bears must have been present elsewhere in Africa, and that their apparent absence is due to the paucity of faunas and fossils.

The late appearance of hyaenids in North America, on the other hand, cannot be ascribed to a lack of suitable faunas. If there were any hyaenids present in the Clarendonian or Hemphillian, they would surely have been found. As it is, the scavenging niches occupied by some hyaenas in Eurasia and Africa were taken up by borophagine canids (*Osteoborus* and *Borophagus*) in North America (Munthe 1989; Werdelin 1989), and the first hyaenids, which appear in the early Blancan (Fig. 64), are members of the cursorially adapted, non bone-cracking (relatively speaking) genus *Chasmaporthetes* (Kurtén & Werdelin 1988).

Apart from these remarks, there are no discernible patterns in the biogeography of hyaenids, a fact that may be due to their great dispersal ability.

Summary

The family Hyaenidae is the smallest extant family in the Feloidea, but one with an abundant and diverse fossil record. We have assessed the status of all described and named taxa, and created new synonymies, e.g., between *P. perrieri* and *P. pyrenaica*, while raising other taxa to valid

Fig. 62. Geographic occurrence of fossil hyaenids in the Turolian.

Fig. 63. Geographic occurrence of fossil hyaenids in the Ruscinian.

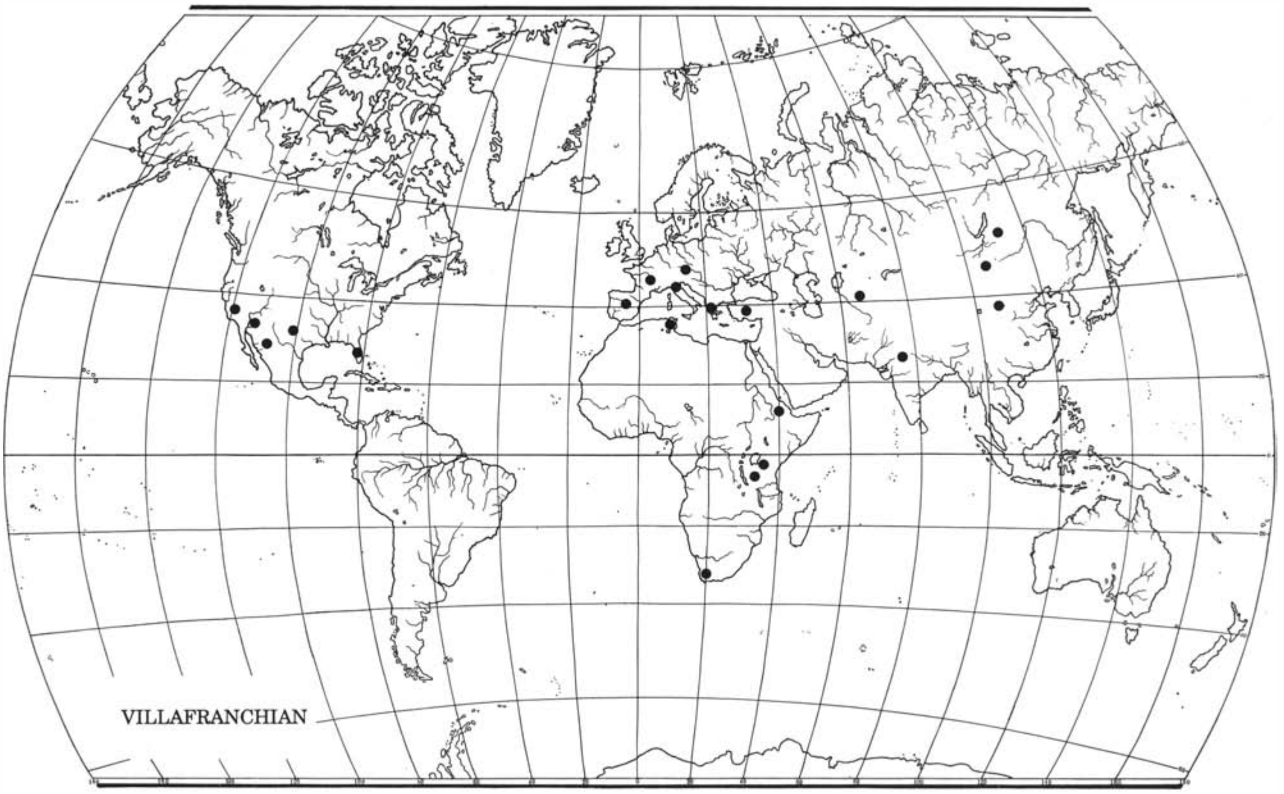


Fig. 64. Geographic occurrence of fossil hyaenids in the Villafranchian. Note that this period and the next represent the acme of geographic range (but not taxonomic diversity) of hyaenids.

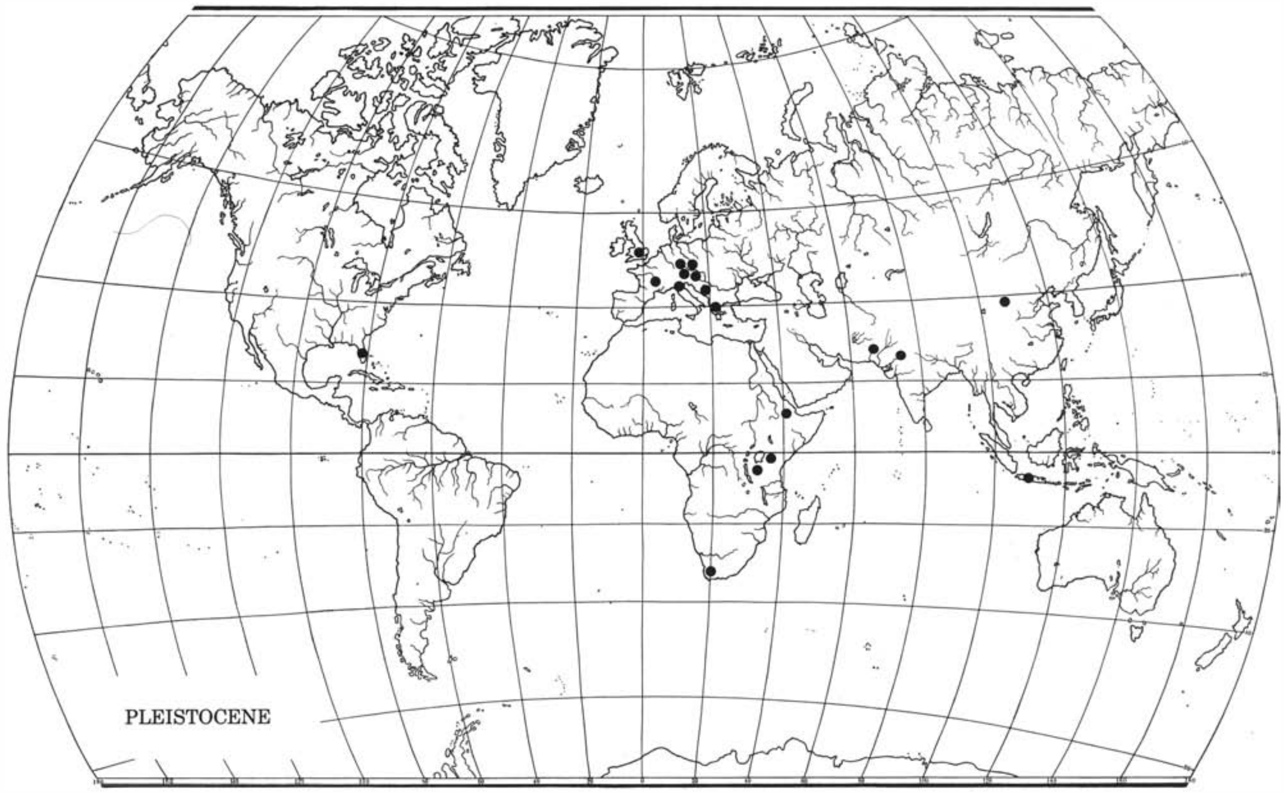


Fig. 65. Geographic occurrence of fossil hyaenids in the Pleistocene.

species, e.g., *'Protictitherium' llopisi.* We have also reviewed a number of nomenclatural problems. One unresolved taxonomic question is the status of *'Thalassictis' parva.* This species is likely to be synonymous with either *Hyaenotherium wongii* or *Hyaenictitherium hyaenoides*, in either case being the senior synonym, which may create future confusion. We have identified a previously unrecognized radiation of *Ictitherium*, including such large forms as *I. pannonicum* and *I. intuberculatum.*

We present two levels of phylogenetic hypothesis. In the first we have analyzed the 19 best known taxa in detail, producing a most parsimonious cladogram (Fig. 37). With this as core data, we have provisionally placed other, less well known taxa with reference to this topology (Fig. 38). This has led to the recognition of some monophyletic taxa, and of some unresolved grade groups.

The early hyaenids form a main stem of generally small to medium sized, dog-like forms, showing a general trend towards increase in size, culminating in *Hyaenictitherium hyaenoides*, which is approximately equal to the extant striped hyaena in size.

Hyaenid taxa above *'Hyaenictitherium'* in the cladogram belong to two distinct monophyletic groups. One of these includes the genera *Lycyaena*, *Hyaenictis*, and *Chasmaporthetes.* Within this group, which includes forms with adaptations to a cursorial, active hunting niche and away from scavenging, there is a general trend towards size increase and reduction of the anteriormost and posteriormost teeth. The other monophyletic group is the one that includes the extant derived hyaenids. Within this group there is also a general trend towards increase in size, and a concomitant assembly of skull and dental features representing adaptations to bone-cracking.

We view the evolution of hyaenids as overwhelmingly gradual. The species, when studied with regard to their total variability, often grade insensibly into each other, as do the genera. Large specimens of *Hyaenotherium wongii* are, for example, difficult to distinguish from small specimens of *Hyaenictitherium hyaenoides*, a distinct genus (see also Werdelin 1988b). Viewed over the entire family, the evolution of hyaenids from small, fox-like forms to large, scavenging 'typical' hyaenas can be followed step by step, and the assembly of features defining the most derived forms has taken place piecemeal since the Miocene. Nowhere is there any indication of major breaks identifying macroevolutionary leaps.

When we analyzed the pattern of diversity, first appearances, and last appearances of hyaenid taxa through the Neogene, we found that the taxa could conveniently be separated into 'non-hyaenid' and 'hyaenid' forms on the basis of their inferred ecological niches, and that these two groups have separate taxic evolutionary histories. 'Non-hyaenid' taxa have a maximal diversity in the late Miocene, followed by a dramatic decline in diversity. With the exception of the aardwolf, this group is now extinct. 'Hyaenid-like' taxa have their maximal diversity somewhat later in time, and their subsequent decrease in diversity is not as severe as for the small hyaenids. We suggest that this difference in pattern may be due to differential extinction caused by sorting processes at lower levels (Vrba 1980; Vrba & Eldredge 1984; Vrba & Gould 1986).

Taken as a whole, the Hyaenidae have their maximum diversity in the late Miocene (Turolian Land Mammal Age). The subsequent decrease in diversity within the family is correlated with an increase in diversity of dogs, family Canidae, invaders to Eurasia from North America in the late Miocene. Whether this correlation is due to active or passive replacement cannot be determined on the basis of the present data.

We have also considered the relationships of hyaenids to other families of Feloidea. Several recent papers have proposed phylogenetic hypotheses for this group (Flynn *et al.* 1988; Hunt 1987; Wozencraft 1989). With the addition of information from the fossil record of hyaenids we find that none of these hypotheses is tenable, and that the relationships of Feloidea are unresolved, mainly due to the great degree of parallelism seen between the lineages. On the basis of both paleontological and biochemical data, the age of the Hyaenidae, and of the feloid radiation as a whole, is suggested to be no more than 25 Ma. Fossil feloids older than this may belong to a previously unrecognized stem group of feloids that preceded the radiation of the extant families.

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Appendix

Reconstructing fossil hyaenas

Lars Werdelin and Björn Lindsten

Even before publication we have been asked questions regarding the reconstructions of fossil hyaenas here published as Figs. 41–45. We therefore feel an obligation not only to show fossil hyaenas as living, breathing animals, which we have done, but also to 'reconstruct the reconstruction', as it were. This section explains our procedure in making these reconstructions. The senior author would like to mention that much of the inspiration for this section came from the pleasure and stimulus received from the drawings of extinct animals by the late Hubert Pepper. The unsurpassed reconstruction of *Chasmaporthetes* by Henry Galiano (in Berta 1981) was also a major source of inspiration.

In any reconstruction of a fossil animal it is necessary to understand the fundamental building blocks that produce the living animal. These are of three different types. Most fundamental are the restrictions imposed by the materials of which a living animal is composed. Materials such as bone, muscle, blood, etc., have physical limitations that cannot be exceeded. This aspect is of minor concern in this context, as the animals to be reconstructed belong to a well known group with several living members. It is unlikely that there are any surprising limitations of this nature that would cause us to revise our image of the external appearance of fossil hyaenids.

The second type of building block is adaptation to the environment. Of course, at some level, all characteristics are adaptations to some environment, but we here mean the more obvious such characteristics, i.e., adaptations to the animal's immediate environment. An example of such a characteristic in the present context would be the intensity of the spotting of the fur. This is because it is a general rule that animals living in, e.g., arid or semi-arid environments will have less distinct coat color patterns than animals living in a forested environment. This holds true both between closely related species (e.g., lion and tiger) and within species (e.g., the coat pattern of bobcats in North America).

The third building block of the living animal is its phylogenetic history. This aspect is clearly closely related to the former, because all characters have an adaptational basis at some level. However, we here have in mind characters that are not adaptations to the immediate environment. Examples of such characters in Carnivora are, e.g., that M_1 and P^4 form the carnassial pair rather than any other pair of teeth (inherited from the carnivoran ancestor). It is this type of character which makes a hyaena a hyaena rather than a dog, even though it may live like a dog does today. It is this type of character which makes systematics at all possible.

The net result of these building blocks is a sort of palimpsest of characters overlying other characters, created as new adaptations have partially erased older ones or redirected them towards other functions. This palimpsest effect is one that we have striven to make particularly clear in our reconstructions. The effect we hope for is that the reader (or viewer) will say (or at least think) 'this animal looks familiar', or 'but this is just a', and then find that it isn't what he thought it was.

The first species reconstructed is *Ictitherium viverrinum.* This species is primitive in the sense that it lies far down on the hyaenid phylogenetic tree. It is relatively common in late Miocene Eurasian faunas, although it is much less common than some other species, such as *Hyaenotherium wongii.* Both anatomy and inferred ecology suggest that this animal may have held a niche similar to that of present day jackals (*Canis* spp.) in present-day Africa. It is small and of gracile build, shows no particular emphasis on any dental adaptation, and probably lived in small groups (though not packs) in both open and closed terrain.

Our reconstruction of this animal began with an illustration of black-backed jackal (*Canis mesomelas*). A beautiful drawing of this animal was published by Kingdon (1977). However, the fossils tell us that *I. viverrinum* had relatively shorter legs than this animal. This is natural, since very long legs are typical of *Canis* but not of hyaenids. Thus, our first step was to shorten the legs, and especially the distal elements. On the other hand, *I. viverrinum,* like nearly all hyaenids, had a relatively massive head and neck region, which contrasts sharply with the particularly gracile head and forequarters of the jackal. This is really the entire basis for the body proportions of this reconstruction. It was made much easier by the fact that bones of the skeleton of this species are well known, which is not true of the other two species reconstructed. The coat pattern is based on the idea that a pattern of broken stripes is primitive for hyaenas. The intensity of the pattern indicates that this is an animal from a fairly closed environment.

The facial pattern of *I. viverrinum* was studied in detail (Fig. 42). The first drawing in this figure shows the same pattern as Fig. 41. This pattern is based on the facial pattern of *Civettictis civetta,* a viverrid that lives in forested environments. Note how this facial pattern makes the shape of the face indistinct and tends to shorten it dramatically (compared with some of the other variants). The second alternative is based on the facial pattern of a felid, *Uncia uncia,* the snow leopard. In this case it is the contour of the head that becomes indistinct, the whole face tends to blur, and the position of the eyes becomes less determinate. The third alternative is modelled on the viverrid *Hemigale derbyanus,* and shows an effect opposite that of alternative two, with the eyes strongly emphasized through the position of the longitudinal stripes. The fourth alternative, finally, is based on the viverrid *Genetta genetta,* which has a facial pattern that flattens the muzzle and, indeed the whole face, noticeably.

Besides the coat pattern, there are other features that are beyond the limits of paleontology to reconstruct precisely. Such features are the position and size of the ears and eyes, although the latter can be determined to some extent by studying the skull of the animal in question. We provide two alternatives here, both employing the facial coat pattern of alternative one, that based on *C. civetta.* In the first case we have made the ears larger and rounder and set the eyes further apart. This has served to increase the width of the face. In the second case we have made the ears very large, similar to the ears of *Proteles cristatus,* while at the same time placing the eyes closer together and turning the outer corners of the eyes down rather than up. The resultant effect is very close to the appearance of *Proteles cristatus.*

With this analysis we hope to have served two purposes, one scientific, and one cautionary. We hope to have shown the importance of facial patterns to the appearance of animals, demonstrating that differences in facial pattern change the impression of the head of an animal dramatically. Secondly, we hope to have introduced a cautionary note into the reconstruction of fossil mammals in general. Since differences in coat pattern influence the viewer's impressions of an animal dramatically, those engaged in reconstructions of this type must guard against introducing too many unconscious biases into their analyses. Otherwise, reconstructions tend to become too much of self-fulfilling prophecies.

The final figure of *I. viverrinum* (Fig. 43) was included because we wished to point out in an accessible form that these were living and breathing animals, rather than the stylized shop-window mannequins or dramatically posing beasts of most reconstructions. Nothing could be less

Fig. 66. Wolf, *Canis lupus.* Preliminary sketch for the reconstruction of *Hyaenictitherium hyaenoides* (Fig. 44).

Fig. 67. First step towards the reconstruction of *Hyaenictitherium hyaenoides* (Fig. 44).

dramatic (or dignified) than an animal about to fall on its rump through scratching itself too enthusiastically!

The second fossil hyaenid we reconstructed was *Hyaenictitherium hyaenoides* (Fig. 44), which was repeatedly referred to as wolf-like in the main text of this monograph. Acting upon this belief, we began this reconstruction with a sketch of a wolf (Fig. 66). As in the previous case, the main alterations were to the length of the limbs and the shape of the skull. The former, especially the distal elements were shortened relative to body size. The snout was shortened and broadened, while at the same time retaining the forehead curve characteristic of these animals (see main text). The forequarters were emphasized relative to the hindquarters. This resulted in a preliminary sketch of *H. hyaenoides* (Fig. 67). After viewing this sketch, we decided to further reduce the length of the limbs. This was done with less justification than in the case of *I. viverrinum* since in this case very few post-cranial limb bones are known. However, we feel that the idea of a wolf-like form with shorter legs is basically correct. We also made the feet more compact and the toes shorter than in the wolf. Finally, we decided to give *H. hyaenoides* basically the same coat pattern as *I. viverrinum*, but with lessened contrasts, indicating an animal living in more open and perhaps drier terrain than in the previous reconstruction. To emphasize this we have given *H. hyaenoides* a uniform facial coat pattern.

The third hyaenid reconstructed is *Palinhyaena reperta.* The investigations reported in the main text of this monograph have shown that this species lies at the base of the lineage leading to the three larger of the extant hyaenids. For this reason we have reconstructed the species using a composite of these species as a guide (Fig. 45). The postcranial skeleton of this species is at present unknown, but we have made the difference in length of the front and hind legs less marked than in the extant species. In other features we have purposely made the reconstruction close to the extant forms in order to emphasize the phylogenetic position of the species. Since nearly all specimens of this species are juveniles, we have made the reconstructed individual a juvenile as well, giving it relatively long limbs, large eyes, and a generally 'gawky' appearance. This individual has just been taking a bath, and the fur has not yet dried, hence the groomed appearance of the fur.

We have included this appendix in order to cast deserved light on the reconstruction of fossil mammals. This type of work has advanced far in some groups of animals, most notably dinosaurs, but is somewhat lagging behind in mammals. We hope that the future will see more skilled reconstructions of fossil mammals in scientific publications. It is important to emphasize that the animals we work on were once living, breathing, functioning animals, and there is no better way to show this than in a scientifically based life reconstruction.

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Contact the editor at an early stage regarding suitability of topic, technical requirements, and financing. Final acceptance for publication, however, will not be made until the manuscript has been refereed. Submit the manuscript initially as one paper copy for refereeing and eventually as word-processor text files. Figure and plate originals should not be submitted until the paper has been accepted for publication. After return of the final revised manuscript, the paper will normally be published within 4–6 months. Read galley and page proofs carefully, making only necessary corrections, and return them promptly to the editor. Twenty copies of the publication will be given free of charge to the author(s).

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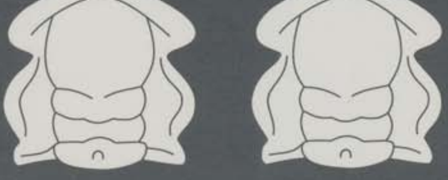

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