Rend. Fis. Acc. Lincei
s. 9, v. 7:277-302 (1996)

Zoologia. — *Remarks on the skull morphology of the endangered Ethiopian jackal,* Canis simensis *Rüppel 1838.* Nota di Lorenzo Rook e Maria Luisa Azzaroli Puccetti, presentata (*) dal Socio A. Azzaroli.

Abstract. — The study of a skull of *Canis simensis* Rüppel 1838, an endangered species endemic to the Ethiopian highlands, belonging to the old collections of the Museo Zoologico «La Specola» of the University of Florence, gave us the starting stimulus for this research. The results of morphological and biomethrical analyses carried out on a sample of 13 skulls of this rare and little known species are reported here. Although characterized by peculiar features, *Canis simensis* is closely related with jackals.

Key words: *Canis simensis*; Mammalia; Carnivora; Skull morphology; Ethiopia.

Riassunto. — *Note sulla morfologia craniale dello sciacallo etiopico in pericolo di estinzione*, Canis simensis *Rüppel 1838*. Lo studio di un cranio di *Canis simensis* Rüppel 1838, una specie endemica degli altipiani etiopici, appartenente alle vecchie collezioni del Museo Zoologico «La Specola» ha fornito lo spunto per questa ricerca. Vengono qui riportati i risultati di uno studio morfologico e biometrico su un campione di 13 cranii di questa specie rara e poco conosciuta. Sebbene presenti caratteristiche peculiari, *Canis simensis* risulta in stretta relazione con gli sciacalli.

Introduction

The concept of the family Canidae has never been challenged. The same cannot be asserted for its genera and species, which are still the source of argument, particularly at generic level.

This is the case of the Simien jackal. Gray (1868) placed this species in the monospecific genus *Simenia*, with the combination *S. simensis*, and was followed by some students (*e.g.*: Allen, 1939; Thenius, 1969), while others place it within the jackals in *Canis*. Clutton-Brock *et al.*(1976), basing on a numerical analyses of external and osteometric characters, obtained a high similarity in cranial and dental characters of this species with those of the side-striped jackal *Canis adustus*. These authors therefore do not accept the generic separation and retain the Simien jackal in the genus *Canis*. Placing the Simien jackal in a separate genus would express a great uncertainty on the affinities of this species, as it would imply that this form is philogenetically distant from the wolf, as well as from jackals.

De Beaux (1922) remarked that in the Simien jackals living on the western side of the Rift Valley (Simien and Gojjam) the nasals do not reach the line joining the posterior margins of the maxillofrontal sutures, while the nasals of Simien jackals from eastern populations (Arrsi and Bale) extend back of this line. Basing on this skull structure De Beaux considered these populations as taxonomically separate and named the first one *Canis simensis simensis* and the second one *Canis simensis citernii*. His conclusion was substantiated by Yalden *et al.* (1980).

The species is still poorly known and the number of specimens in Museum collections is scanty, we thought therefore that more detailed information would be of inter-

(*) Nella seduta del 13 giugno 1996.

est. Most papers about the Simien jackal, or «Simien fox», as it is currently called, deal with its distribution and behaviour (cf. Morris and Malcom, 1977; Yalden *et al.*, 1980; Hillman, 1986; Gottelli and Sillero-Zubiri, 1992) but so far the skull morphology has been dealt with brief generic remarks or little more. In order to fill this gap we tried a morphological comparison of the skull of *Canis simensis* ssp. with African jackals and European wolf and fox, with the aim to assert the closest systematic relationships among these species. For such comparison we were able to study 13 skulls of *Canis simensis*. While the present paper was almost concluded we received the last two papers by Gottelli *et al.* (1994) and by Sillero-Zubiri and Gottelli (1994), in which biochemical analyses associate *C. simensis* to the European wolf rather than to African jackals. We are bound to say that the result of our research does not agree with Gottelli and Sillero-Zubiri's conclusions.

Materials and methods

In the present research 13 *Canis simensis* skulls were considered (tab. I). Comparison was made with the following species: *Canis adustus* (Sundevall 1846), *Canis me-*

Table I. – *List of studied skulls of* Canis simensis.

	Museum	Inventory umber	Locality	Sex
I	Zool. Mus., Florence University	13718	Senneti plateau	—
II	The British Museum (N.H.), London	23.10.10.1	Arssi, Bale	—
III	The British Museum (N.H.), London	24.8.7.11	Arssi, Bale	M
IV	The British Museum (N.H.), London	36.5.20.4	Arssi, Bale	F
V	The British Museum (N.H.), London	24.8.7.10	Gojjam	F
VI	The British Museum (N.H.), London	24.8.7.12	Argin, Simien	F
VII	The British Museum (N.H.), London	42.8.15.11	Abissinia	— Type (Gray, 1868)
VIII	The British Museum (N.H.), London	ex PCM A.99	Lake Tana	M
IX	Mus. Civ. St. Nat. «G. Doria», Genoa	C.E. 818	Arssi, Bale	M Type *C. s. citernii* (De Beaux, 1922)
X	Mus. Civ. St. Nat. «G. Doria», Genoa	C.E. 17800	Dabarif	F
XI	Mus. Civ. St. Nat. «G. Doria», Genoa	C.E. 17801	Dabarif	M
XII	The British Museum (N.H.), London	22.1.24.1	Lake Zwai	F
XIII	Nat. History Mus., Addis Ababa Univ.	M 1987 105 M 600	Arssi, Bale	—

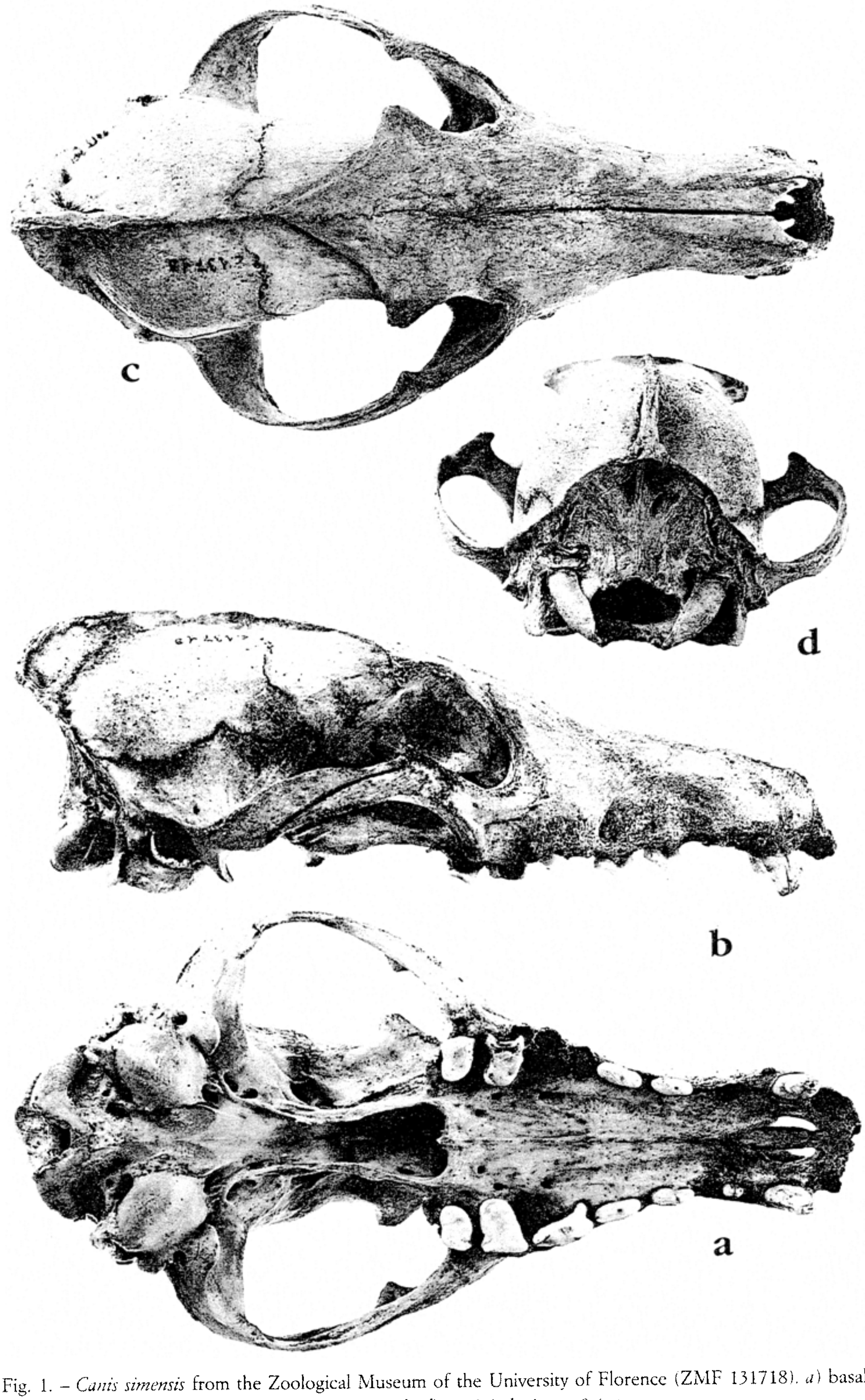

Fig. 1. – *Canis simensis* from the Zoological Museum of the University of Florence (ZMF 131718). *a*) basal, *b*) lateral, *c*) cranial, *d*) occipital views. 0.6×.

somelas Drake Brockman 1910, *Canis aureus* L. 1758, *Canis lupus* L. 1758 and *Vulpes vulpes* L. 1758. Data were obtained by the study of collections in the Natural History Museum, Dpt.s of Zoology and Palaeontology in London, Musée Guimet d'Histoire Naturelle in Lyon, Naturhistorisches Museum in Basel, Addis Ababa University Natural History Museum, Museo Civico di Storia Naturale «Giacomo Doria» in Genoa and Zoological Museum of the Florence University «La Specola».

All the *Canis simensis* skulls considered in the present research are well preserved, with no breaks nor missing parts and belong to young/adult animals, with the exception of the skull in Florence University (fig. 1) which belongs to an old animal and was presumably collected on the ground long after death: the bone is whitish and porous, the distal extremity of the maxillaries was probably gnawed by animals, all incisors, right upper carnassial and P^1 are missing; only the left mandible is present with the tip slightly eroded, all incisors, carnassial and the small M_3 are missing.

Cranial and dental measurements were taken by dial slide gauges, with the accuracy of 0.05 mm. The study was carried out through the analyses of logarithmic ratio-diagrams (L.R.), and through the morphological study and comparison of the skulls (M.L.A.P.). Resolution came accordingly.

Morphological description and comparisons

Skull and mandible. – A simple look at the skull of *C. simensis* shows that the species belongs under the jackals; even considering its larger size, its closest affinities are with *C. aureus*, *C. mesomelas* and *C. adustus*, while it differs from *V. vulpes* and from *C. lupus*. Notwithstanding its similarities with the jackals, *C. simensis* shows definite differentiations: it is of large size, though not as large as *C. lupus*, and has a greatly elongated muzzle (figs. 2-5); this has caused its anterior premolars P 1/1, P 2/2, and to some extent also P 3/3 to be more or less widely spaced (figs. 2, 3, 6, 7): an obvious adaptation to chase small, swift animals. In what concerns the frontal bones a morphological analysis of the Simien jackal excludes this species from the fox group: in the Simien jackal the postorbital processes of the frontal bone do not have the small depression which characterizes the lack of frontal sinuses (figs. 4, 5): within the living canids this character is only found in the genera *Vulpes*, *Alopex* and *Otocyon*. Frontal sinuses mark the difference also between *C. simensis* and *Canis lupus*, as in this last species the frontals appear almost inflated. The postorbital processes of the frontal bones are triangular in shape and less convex than in jackals and wolf, while in the fox they terminate in short protruding rods (figs. 4, 5).

The zygomatic arcade in *C. simensis* is more slender than in jackals and distinctly less protruding than that of the wolf; the palate is also narrow (figs. 2-7). The nasals of the specimens considered extend cranially beyond or behind the line joining the margins of maxillofrontal sutures, according to De Beaux assertion concerning the variations of this character in the two subspecies of *C. simensis*: in the type specimen of *C. s. citernii* (CE 318; fig. 5) the nasals extremities lie slightly beyond the maxillofrontal sutures while in specimen MF 13718 the nasals extend well beyond the maxillofrontal sutures; both animals were collected in the Bale Mountains; in all specimen of *C. s. simensis* from Gojjam the nasals extremities lie behind the above said sutures (cf. also Yalden *et al.*, 1980).

The profile of the skull is almost linear on the forehead, slightly concave on the nose and the snout is elongate; it does not show the bulging forehead nor the facial angle (deflection of the braincase relative to the muzzle) which characterizes the wolf (figs. 3, 4).

The braincase is elongated as compared with fox and jackals, though not so elongated as in the wolf; the general shape differs from that of the wolf and is similar to jackals, though more slender. In the bregma region the sagittal crest splits frontally into two ridges. In *C. simensis* as well as in jackals these ridges diverge from the bregma with an angle of approximately 65°, proceeding laterally and downward to form the posterior margin of the postorbital processes; in *C. simensis*, in jackals and fox these ridges are well defined, while in the wolf they appear smoothly rounded. Still in the wolf the two ridges start from the bregma, proceed parallel and diverge on the parietal bones only after 15-20 mm. In the fox the splitting of the sagittal crest begins more backwards, from the lambdoid suture. In the occiput of *Canis simensis* the sagittal crest protrudes strongly from the back of the braincase and appears very elongated as compared with jackals and fox and different in shape; the infraorbital foramina are elongated, though not as much as in other jackals, where they are narrow (a fissure in *C. aureus* and in *C. mesomelas*), and not as widely open as in *C. lupus*. The bullae are nearly oval but proportionally smaller as compared with the skull, and also smaller than in the wolf (figs. 6, 7).

The mandible is slender, its depth at the posterior edge of the carnassial is contained 12 times in the total length; the lower profile is straight all along the dental row and starts rising gently below M_3 (fig. 9).

Teeth. – Dental formula: I 3/3, C 1/1, P 4/4, M 2/3. The incisors form a regular row of closely spaced teeth, they increase a little in size from I 1/1 to I 3/3 whose length is about 1/3 of the length of the canines. Both upper and lower canines are well developed. There are four premolars in the maxilla and four in the mandible, both upper and lower premolars are widely spaced, the diastema between them gradually increases in rostral direction; the premolars immediately preceding the carnassials are almost in contact with them. P 1/1 are very small, nearly conical and single rooted, the other premolars are larger, with a trenchant profile, and double rooted; their size increases in caudal direction. The upper carnassial P^4 is smaller than the lower carnassial M_1 (figs. 2, 3, 6, 7, 9).

C. simensis does not share the distinctive dental characters of *Canis lupus*. In fact, since the Middle Pleistocene, dogs with wolf-like affinities show as a derived character a lower carnassial with a strongly developed paraconid (Torre, 1967; Rook and Torre, 1996*a*); this cusp of M_1 increases in size and rises above the main cups of the lower premolars. Jackals and foxes bear a plesiomorphic lower carnassial with the paraconid relatively low, which never rises above the main cusps of the lower premolars.

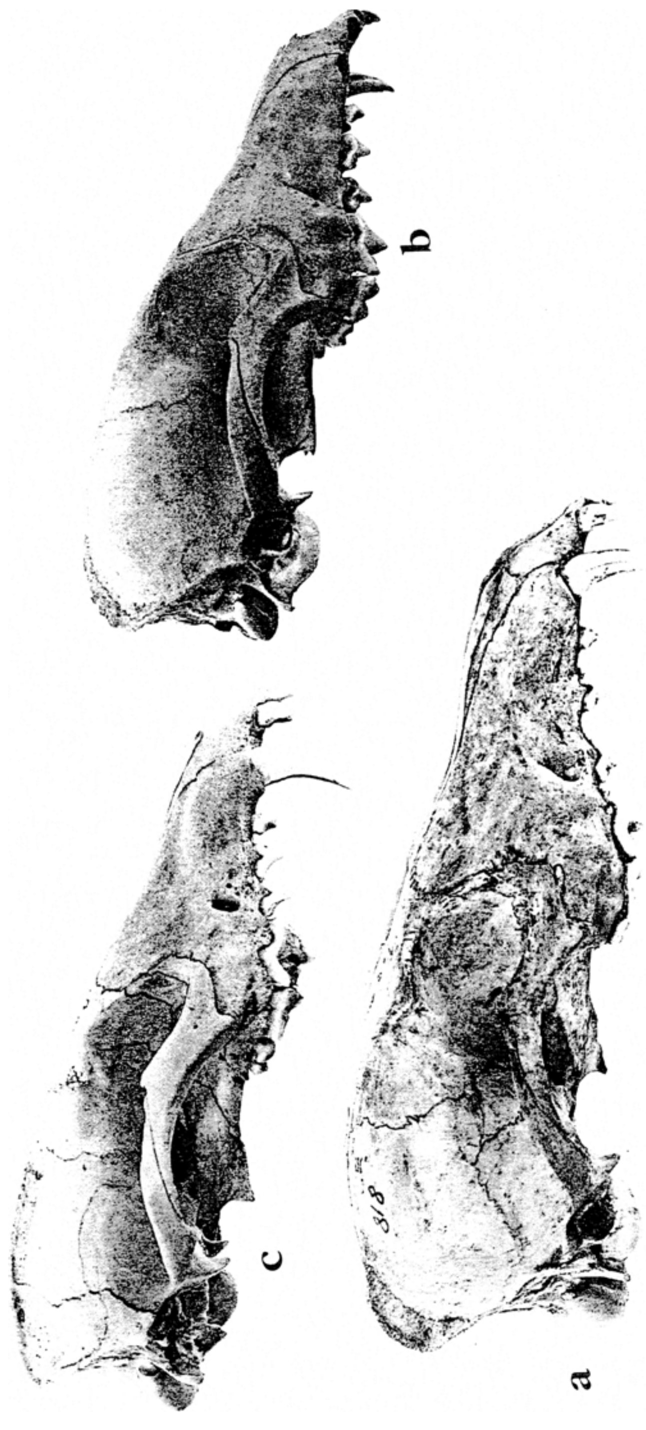

Fig. 2. - Skulls in lateral view: *Canis lupus* ZMF 11874 (*a*); *Canis aureus* ZMF 2110 (*b*); *Vulpes vulpes* ZMF 4141 (*c*). 0.6×.

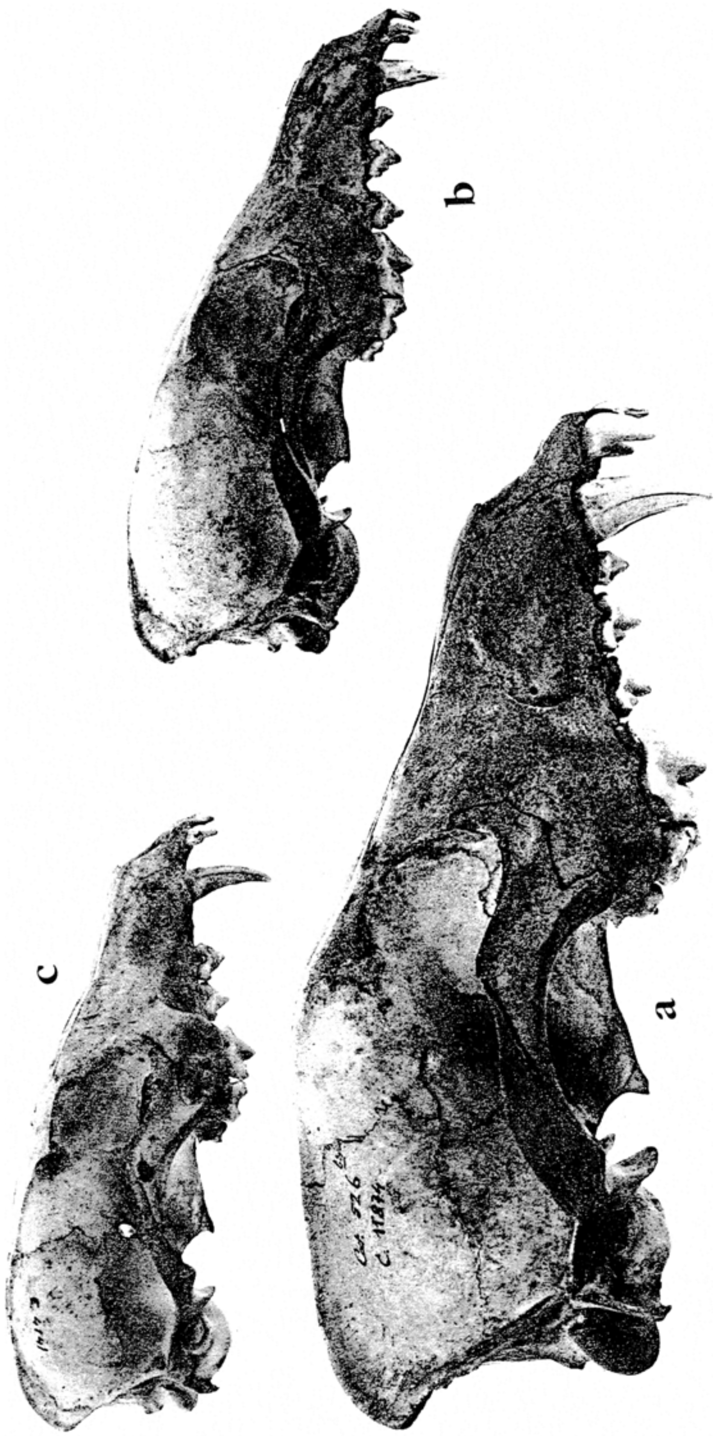

Fig. 3. – Skulls in lateral view: *Canis simensis* CE 818 (*a*); *Canis mesomelas* ZMF 1898 (*b*); *Canis adustus* ZMF 8496 (*c*). 0.6×.

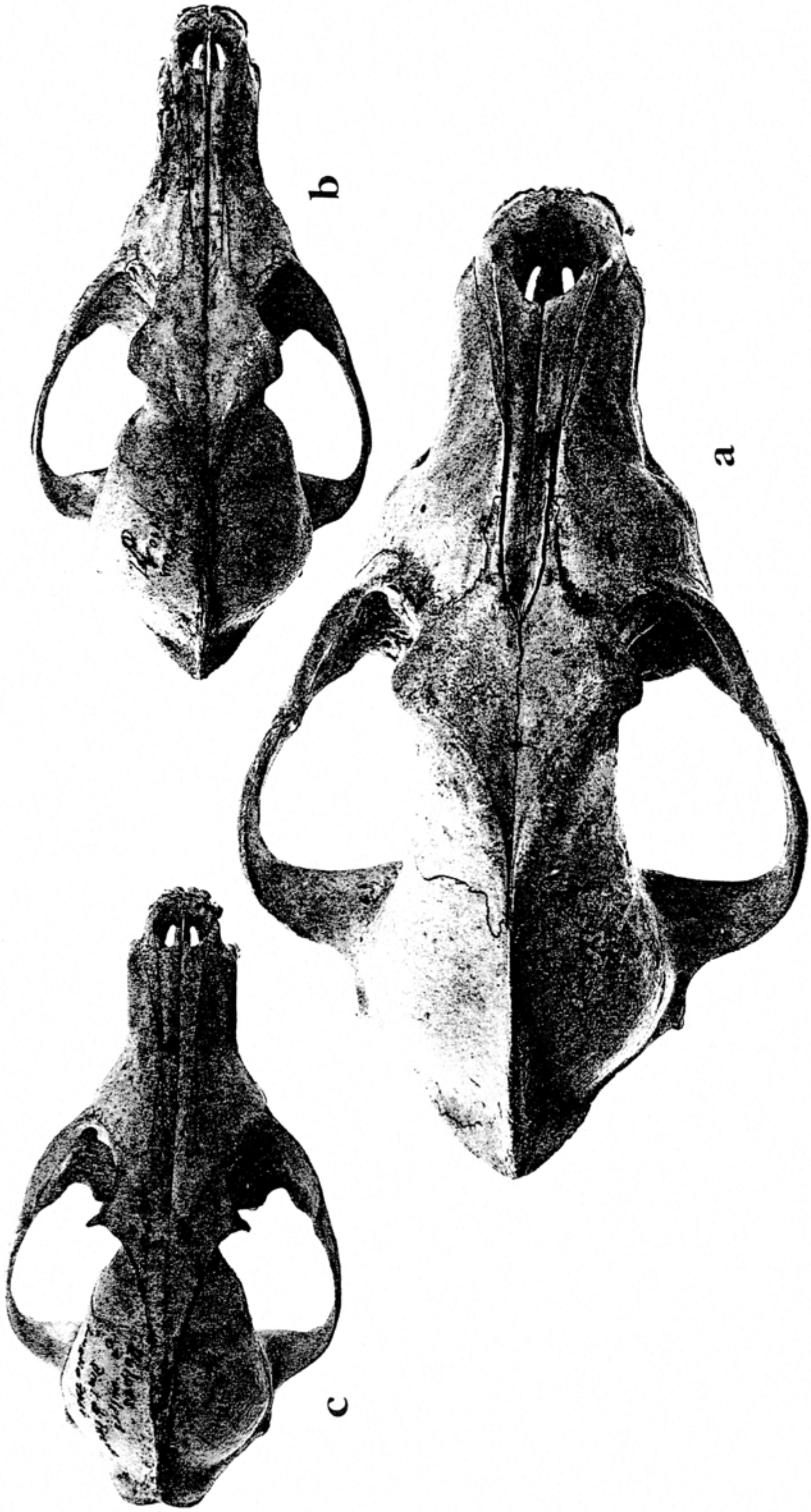

Fig. 4. - Skulls in cranial view: *Canis lupus* (*a*); *Canis aureus* (*b*); *Vulpes vulpes* (*c*). 0.6×.

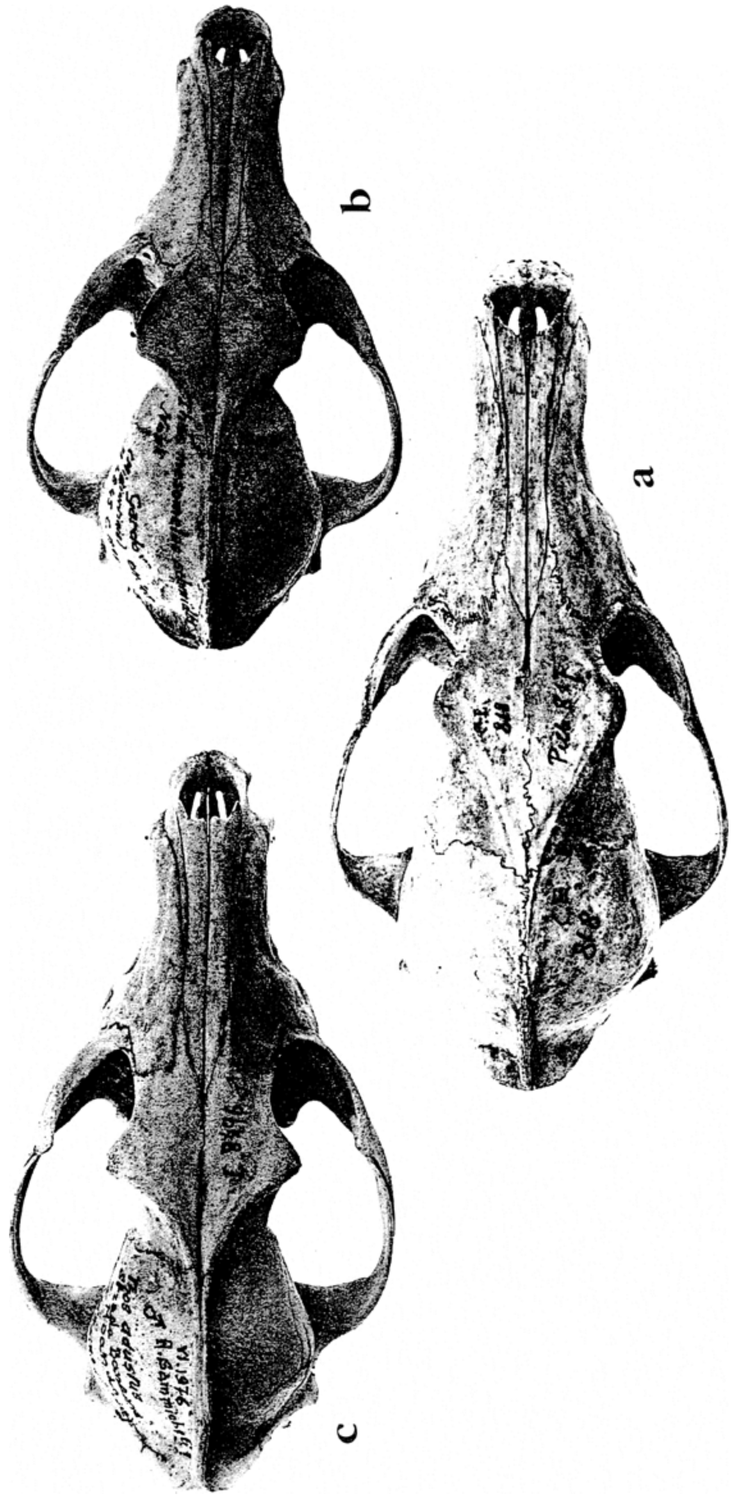

Fig. 5. – Skulls in cranial view: *Canis simensis* (*a*); *Canis mesomelas* (*b*); *Canis adustus* (*c*). 0.6×.

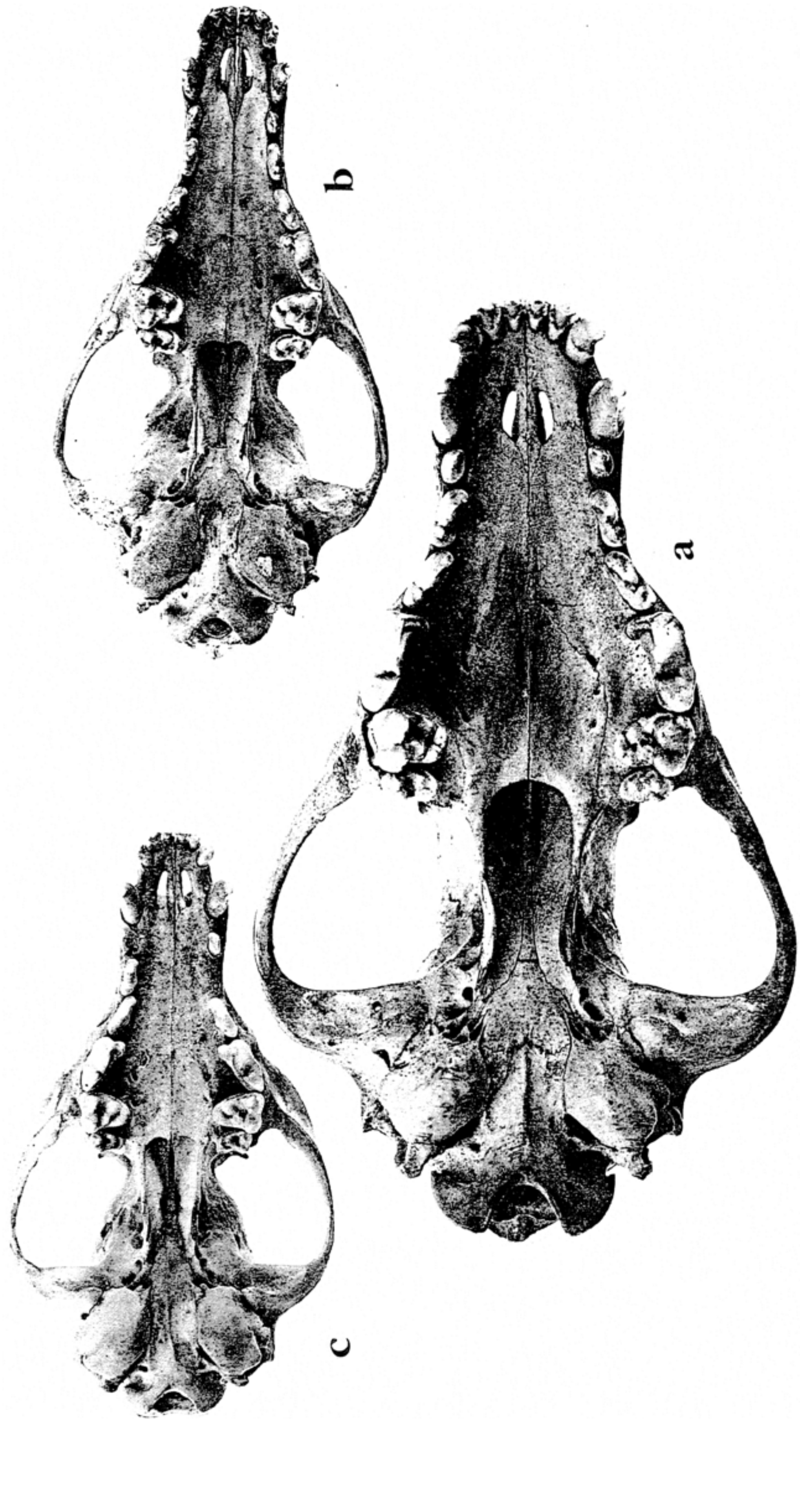

Fig. 6. - Skulls in basal view: *Canis lupus* (*a*); *Canis aureus* (*b*); *Vulpes vulpes* (*c*). 0.6×.

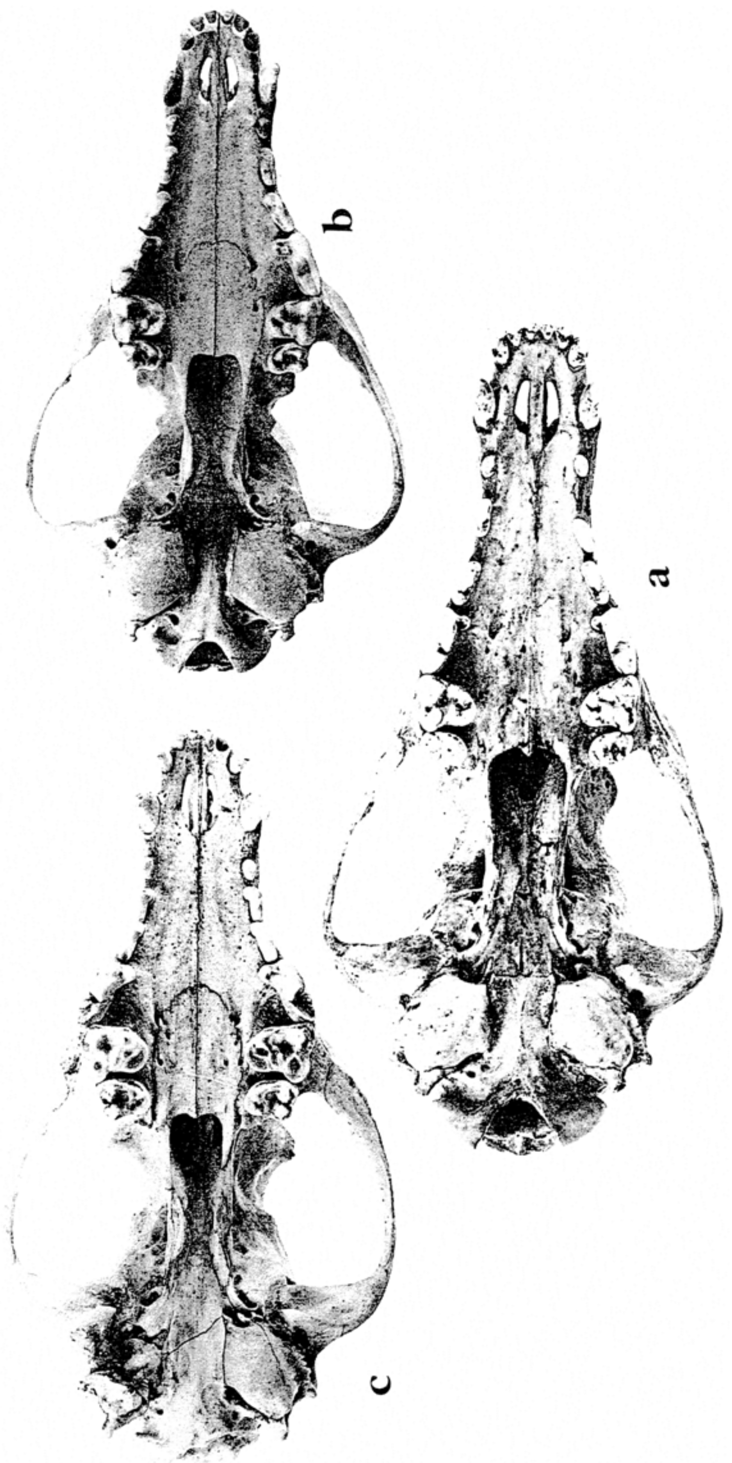

Fig. 7. – Skulls in basal view: *Canis simensis* (*a*); *Canis mesomelas* (*b*); *Canis adustus* (*c*). 0.6×.

Fig. 8. – Skulls in occipital view: *Canis lupus* (*a*), *Canis aureus* (*b*), *Vulpes vulpes* (*c*), *Canis simensis* (*d*), *Canis mesomelas* (*e*), *Canis adustus* (*f*). 0.7×.

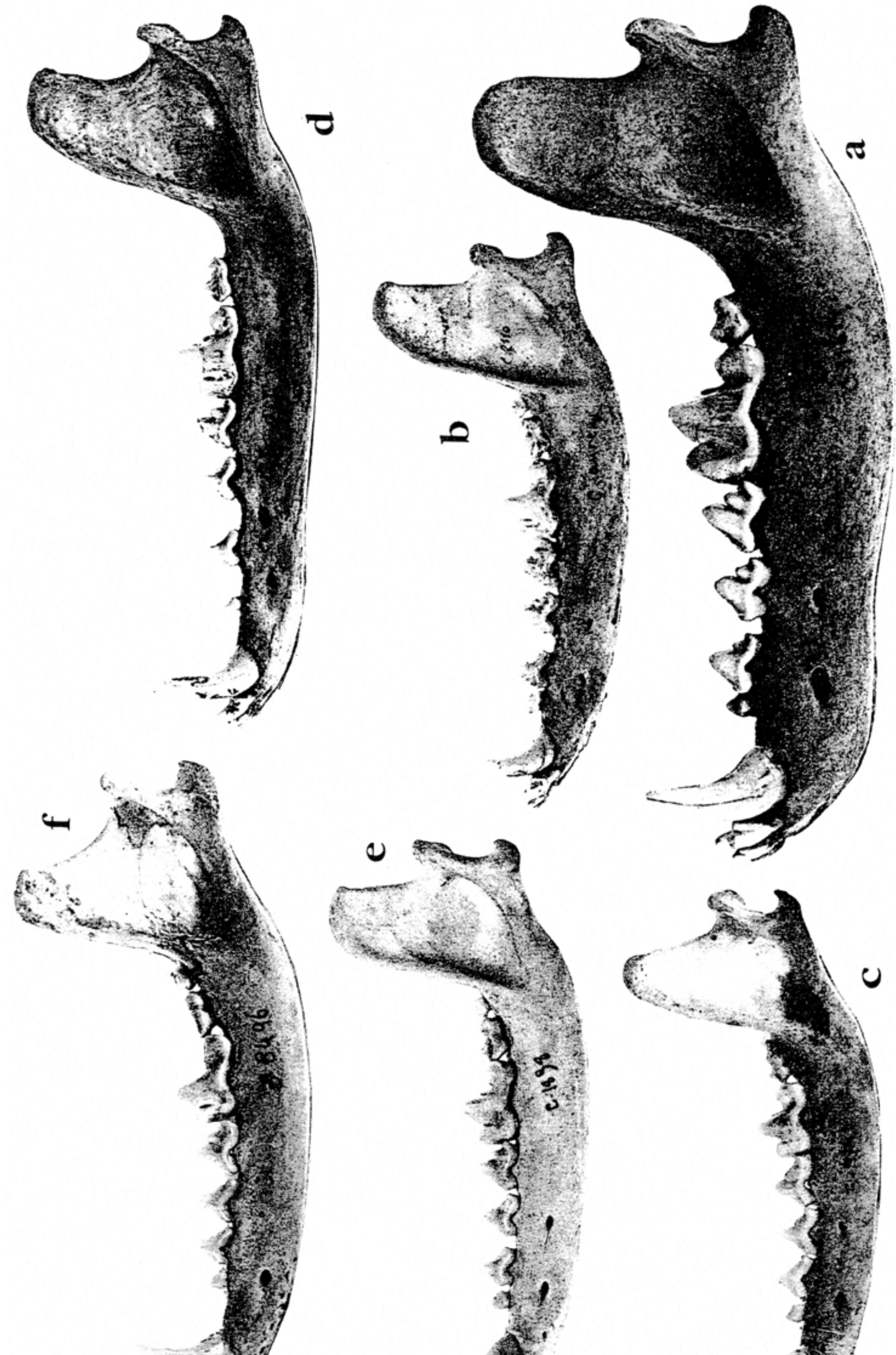

Fig. 9. – Mandibles in labial view: *Canis lupus* (*a*), *Canis aureus* (*b*), *Vulpes vulpes* (*c*), *Canis simensis* (*d*), *Canis mesomelas* (*e*), *Canis adustus* (*f*). 0.7×.

ANALYSES THROUGH LOGARITHMIC RATIO-DIAGRAM

The comparisons of *Canis simensis* carried out through logarithmic ratio-diagrams are limited to the wolf (*Canis lupus*) and to the three species of jackals: the golden jackal (*C. aureus*), the black backed jackal (*C. mesomelas*) and the side-striped jackal (*Canis adustus*). As a standard for comparison in the analyses by ratio-diagram, the mean of the studied sample for golden jackal was used. The set of measurements is the one used by Berta (1988), with some additions. Description of the measurements are given in tabs. II-IV and illustrated in fig. 10. In tabs. V-VII is given the complete set of measurement for the studied sample.

TABLE II. – *Description of cranial measurements. See also fig.* 1.

1. Maximal height. Greatest height from the basal plain to the highest point of the interparietal conjunction.
2. Length, posterior C/to foramen magnum notch. Distance from posterior border of canine alveolus to foramen magnum notch.
3. Greatest length. Length from anterior tip of premaxillae to posterior point of inion.
4. Length of nasals.
5. Maxillary toothrow length. Distance from anterior edge of alveolus of P^1 to posterior edge of alveolus of M^2.
6. Maxillary and premaxillary length. Distance from anterior edge of alveolus of I^1 to posterior edge of alveolus of M^2.
7. Length M^2 to bulla. Minimum distance from posterior edge of alveolus of M^2 to depression in front of bulla.
8. Length P^4 to M^2. Maximum distance between outer sides of P^4 to M^2.
9. Zygomatic width. Greatest distance across zygomata.
10. Width of occipital condyla.
11. Braincase width. Maximum breadth of braincase across level of parietotemporal sutures.
12. Occipital shield width. Maximal breadth of the occipital shield at the paraoccipital processes.
13. Orbital constriction. Width across frontals at constriction behind orbita.
14. Frontal shield width. Maximum breadth across postorbital processes of frontals.
15. Postorbital constriction. Width across frontals at constriction behind postorbital processes.
16. Maximum skull width across cheek teeth. Greatest breadth between outer sides of P^4s.
17. Palatal width at P^1s. Minimum width between inner margins of alveoli of first upper premolars.
18. Facial depth, maxillary toothrow to orbit. Minimum distance from alveolar margin of M^1 to most ventral point of orbit.
19. Jugal depth. Minimum depth of jugal anterior to postorbital process, at right angles to its anterio-posterior axis.
20. Rostrum length. Length from anterolateral margin of infraorbital canal to anterior tip of premaxillae.
21. Suborbital length. Length from anterolateral margin of infraorbital canal to orbit margin.
22. Bulla length. Length from medial lacerate foramen to suture of bulla with paraoccipital process.
23. Bulla width. Width of bulla, measured at right angles to length (22).
24. Bullae width. Distance between the two more external point of bullae.
25. Length of mandible. Distance from posterior edge of alveolus of I_1 to posterior edge of angular process.
26. Mandibular toothrow. Length distance from anterior edge of alveolus of canine to posterior edge of M_3.
27. Height of mandible. Maximum distance between highest point of coronoid process and base of angular process perpendicular to the toothrow.
28. Depth of mandible below M_1. Distance from alveolar margin of M_1 at protoconid to ventral border of mandible transverse to long axis ramus.

TABLE III. – *Description of upper dentition measurements.*

P^1 P^2 P^3	L	Maximum length
	W	Maximum width measured at right angles to length
P^4	L	Maximum length
	W	Maximum width measured from protocone to anterolabial extremity of the tooth
M^1 M^2	L	Maximum length. Distance from anterior margin of the paracone to posterior margin of the metacone
	W	Maximum width. Distance from labial margin of the anterolabial corner of the crown to lingual margin of the tooth
P^1-P^4		Length from the anterior margin of P^1 to posterior edge of P^4 protocone
M^1-M^2		Distance from anterior margin of the paracone of M^1 to posterior margin of the metacone of M^2

TABLE IV. – *Description of lower dentition measurements.*

P_1 P_2 P_3 P_4	L	Maximum length
	W	Maximum width measured at right angles to length
M_1	L	Maximum length. Distance from anteriormost point on the paraconid to posterior margin of the talonid
	W	Maximum width measured at right angles to length
	Trig	Trigonid length. Distance from anteriormost point on the paraconid to posterior base of metaconid
	Tal	Talonid length. Distance from the posterior base of the metaconid to the posterior edge of the tooth
M_2 M_3	L	Maximum length
	W	Maximum width measured at right angles to length
P_1-Trig		Length from the anterior margin of P_1 to the posterior base of carnassial metaconid
Tall-M_3		Length from the posterior base of carnassial metaconid to the posterior edge of M_3

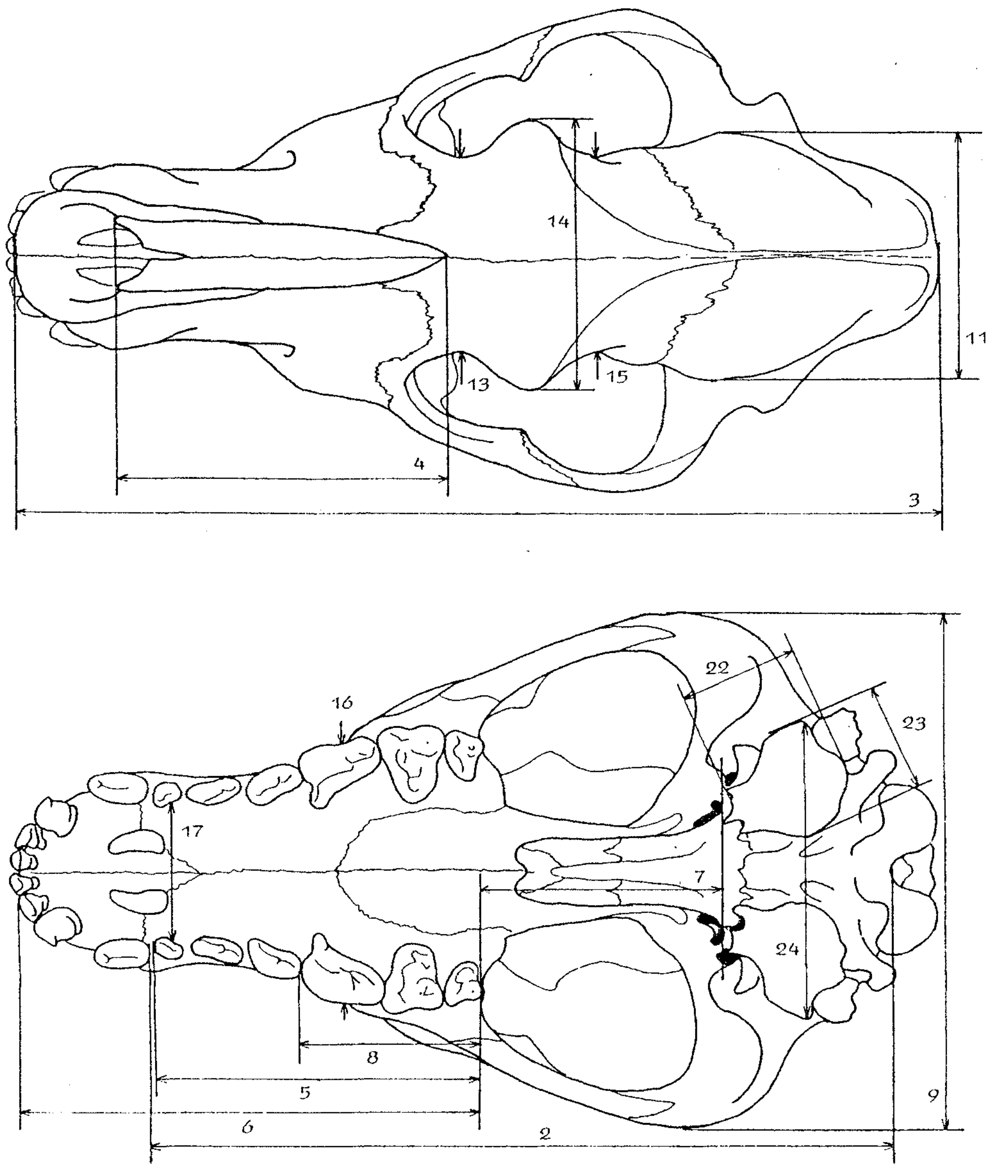

Fig. 10*a*. – Diagram of *Canis* skull, illustrating cranial measurements.

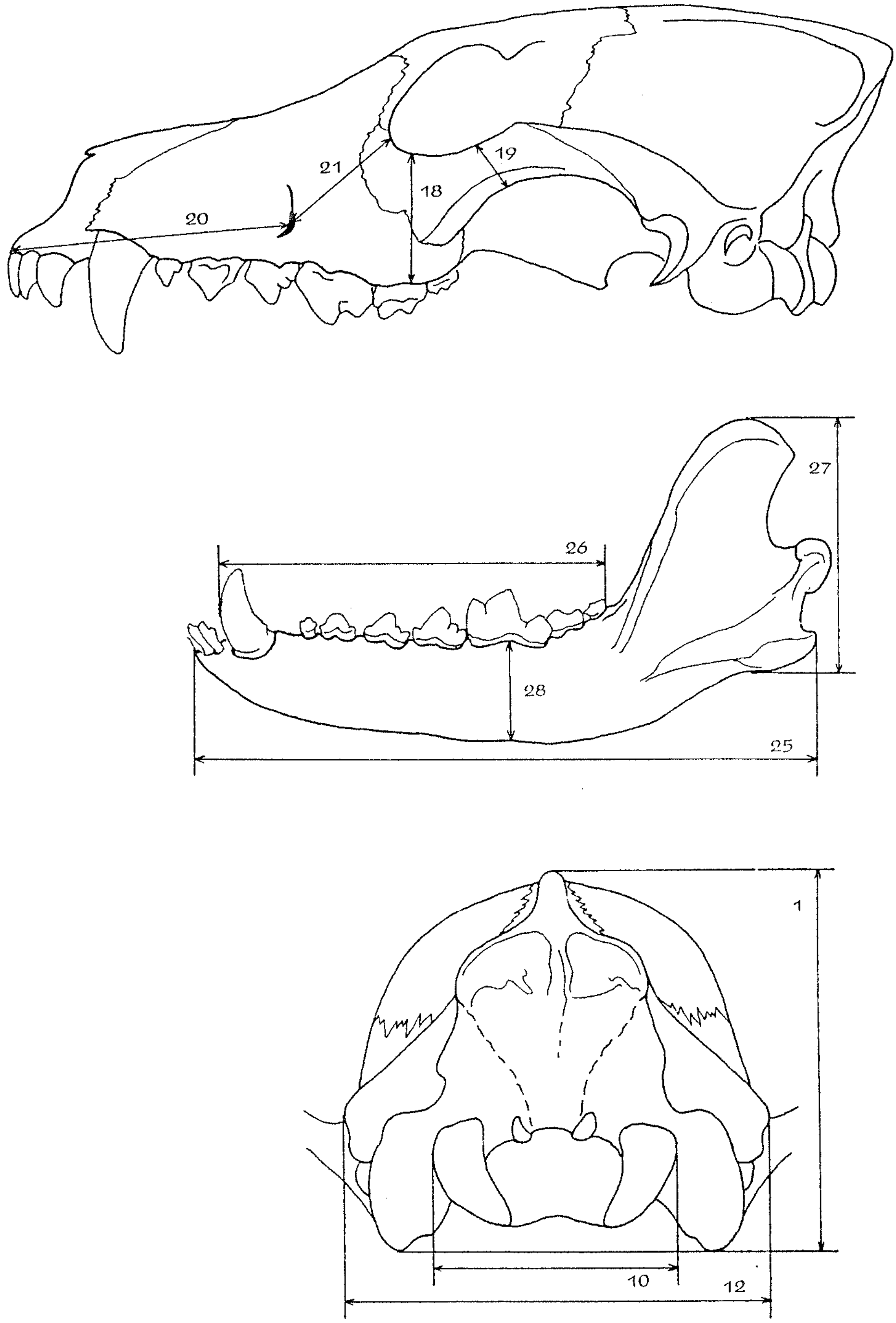

Fig. 10*b*. – Diagram of *Canis* skull and mandible, illustrating cranial and mandibular measurements.

TABLE V. – *Cranial measurements of the studied sample of* C. simensis *and means of the comparison samples for the different* Canis *species*. I-XI: Canis simensis *as listed in tab.* I; Au: Canis aureus (*n* = 20); Me: Canis mesomelas (*n* = 15); Ad: Canis adustus (*n* = 8); Lu: Canis lupus (*n* = 22). *The first column refers to the cranial measurements as given in tab.* II *and fig.* 10.

	C. simensis											Mean values of living samples			
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Au	Me	Ad	Lu
1	67.35	67.00	62.40	66.50	63.40	59.50	68.60	68.80	64.60	62.10	59.00	53.11	52.43	46.80	78.20
2	165.30	160.00	151.40	157.50	147.00	146.00	165.20	159.60	147.70	142.00	—	124.87	123.67	133.05	185.21
3	205.60	200.00	188.80	197.50	183.70	187.30	208.60	204.80	187.20	193.90	192.40	159.81	151.75	164.15	235.65
4	—	83.90	78.10	83.60	71.60	74.50	87.00	84.40	70.10	77.70	79.10	53.81	49.80	67.25	85.50
5	71.40	79.10	68.20	79.20	65.70	66.40	73.20	70.10	72.80	69.50	68.60	56.45	55.47	56.10	81.04
6	102.70	102.80	91.00	93.80	92.70	94.60	105.30	104.40	97.60	97.30	97.80	77.34	76.38	86.00	112.80
7	55.70	51.70	44.10	51.40	46.10	46.90	52.90	50.20	46.10	48.10	47.70	37.76	36.69	45.75	60.71
8	—	33.80	31.90	32.70	31.20	30.50	34.30	32.40	32.80	33.90	31.80	30.55	30.18	34.90	42.50
9	105.65	104.70	97.40	94.10	93.50	89.60	104.80	103.50	89.40	95.30	90.40	84.22	84.28	86.50	132.84
10	41.70	40.10	38.80	39.00	36.40	34.50	39.60	38.60	38.70	—	—	33.89	28.25	28.80	42.50
11	59.90	60.40	57.90	58.90	58.40	57.60	61.00	59.90	58.20	58.40	57.60	50.58	52.27	51.50	68.36
12	63.25	63.50	61.50	62.40	58.20	57.50	64.70	61.90	58.60	59.40	58.80	49.28	49.65	53.10	74.90
13	39.40	34.80	31.40	33.20	28.90	29.00	33.10	34.50	31.20	30.80	30.10	25.19	26.70	29.55	42.90
14	53.70	49.20	44.40	44.90	41.60	43.00	46.70	47.50	42.10	13.40	43.10	40.26	42.05	42.85	61.19
15	40.40	36.50	34.50	36.30	35.50	33.80	35.30	35.70	36.40	32.10	33.10	28.88	32.14	28.60	42.69
16	46.70	47.40	44.00	44.10	40.90	39.50	46.60	45.70	43.50	42.10	42.40	42.69	42.14	45.30	73.53
17	19.20	19.50	17.50	18.50	16.70	17.10	18.90	19.90	17.00	17.10	16.20	17.24	17.67	19.20	30.43
18	26.40	24.20	21.40	23.40	22.40	19.20	25.20	24.80	23.40	22.10	21.10	20.46	18.96	18.65	37.25
19	10.90	9.80	9.00	9.70	8.90	10.00	10.50	11.60	8.70	9.90	9.40	11.07	9.36	11.15	18.64
20	63.60	62.10	62.10	65.00	65.00	63.40	66.80	67.10	60.10	60.60	62.10	48.08	46.24	52.55	68.33
21	—	25.70	23.20	26.40	22.70	23.30	30.90	26.00	25.60	26.60	25.50	17.24	16.20	17.25	30.80
22	23.20	24.70	26.20	24.40	26.20	23.80	26.30	27.70	23.20	24.30	23.10	22.49	21.91	21.45	28.14
23	16.60	—	16.15	—	16.00	17.00	20.90	—	17.30	16.70	15.10	13.90	12.38	14.20	18.10
24	53.45	52.80	51.30	50.70	47.80	47.20	55.00	50.10	49.70	51.50	45.20	43.42	40.20	43.75	60.70
25	152.90	149.80	144.70	144.90	135.10	137.50	157.90	143.70	138.30	139.70	139.30	115.24	113.50	125.80	174.35
26	97.70	99.60	94.50	96.90	91.30	92.60	102.60	97.60	92.40	95.00	94.30	76.87	71.54	81.50	112.61
27	54.50	48.50	47.90	46.80	65.80	42.10	55.20	47.40	45.30	47.40	44.70	42.29	40.49	44.75	71.14
28	18.10	21.10	17.60	20.50	17.60	16.60	22.40	19.40	15.70	16.60	17.60	16.96	16.22	16.45	29.60

TABLE VI. – *Upper tooth measurements. See tab.* V *for explanation. The first column refers to the dentition measurements as given in tab.* III.

	C. simensis											Mean values of living samples			
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Au	Me	Ad	Lu
P^1 L	4.70	4.90	4.90	5.20	4.90	4.80	4.50	4.50	4.90	4.70	4.80	5.58	4.47	4.55	7.40
P^1 W	3.45	3.40	3.50	3.20	3.20	2.90	2.90	3.30	3.20	3.20	3.10	3.33	2.90	3.10	4.99
P^2 L	9.80	9.30	9.40	8.50	8.40	8.40	8.90	8.00	8.10	8.20	8.75	9.95	8.13	8.05	13.30
P^2 W	4.05	4.00	4.00	3.90	3.50	3.40	3.70	4.00	3.50	3.50	3.55	3.93	3.13	3.50	5.69
P^3 L	11.10	10.80	10.70	10.50	9.70	9.50	10.20	9.90	10.15	9.45	10.30	11.08	9.00	9.55	15.17
P^3 W	4.65	4.30	4.30	4.30	3.80	3.80	3.90	4.20	3.95	3.80	4.05	4.52	3.70	3.40	6.47
P^4 L	15.15	16.50	16.20	15.70	15.30	14.70	11.50	15.70	15.65	14.90	15.30	17.88	16.10	16.20	24.74
P^4 W	7.55	7.90	7.70	7.70	7.90	6.90	7.70	7.70	7.80	7.80	7.80	9.40	7.63	8.45	13.47
M^1 L	11.40	12.60	12.50	12.30	12.20	11.50	12.80	11.80	12.70	11.90	12.50	11.20	11.03	13.15	16.53
M^1 W	15.50	16.30	16.30	16.10	15.40	14.20	15.50	15.70	15.25	15.70	16.10	16.77	14.97	16.20	21.61
M^2 L	7.60	8.60	7.90	8.30	7.60	7.50	8.50	7.80	6.95	7.80	8.10	7.70	7.30	9.15	8.63
M^2 W	11.50	12.00	11.20	12.30	10.40	10.50	11.90	11.70	10.45	11.00	11.40	11.68	10.43	12.35	13.49
P^1-P^4	57.45	54.70	51.40	50.90	49.10	50.00	55.00	53.50	50.05	51.60	50.60	44.88	41.80	39.80	62.47
M^1-M^2	19.95	21.30	20.60	20.80	19.70	18.80	21.20	20.00	19.95	19.60	20.30	17.27	16.17	22.45	21.56

TABLE VII. – *Lower tooth measurements. See tab. V for explanation. The first column refers to the dentition measurements as given in tab. IV.*

	C. sinensis											Mean values of living samples			
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Au	Me	Ad	Lu
P_1 L	—	4.20	3.70	3.80	3.80	3.70	4.20	3.90	3.90	3.90	3.90	4.40	3.60	4.00	5.65
P_1 W	—	3.10	3.20	3.20	2.80	2.80	2.80	3.10	3.00	3.10	3.10	3.07	2.60	2.75	4.40
P_2 L	8.20	8.10	8.20	7.10	8.10	7.70	8.10	7.70	7.20	7.90	7.40	8.93	7.60	8.10	11.70
P_2 W	4.30	4.50	4.30	4.10	3.80	3.50	4.00	3.90	4.20	3.70	3.90	4.12	3.40	3.35	5.77
P_3 L	9.80	10.40	9.50	9.40	9.10	8.70	9.10	9.40	8.90	9.10	9.20	9.78	8.37	9.15	13.26
P_3 W	4.40	4.70	4.50	4.50	4.00	3.80	4.00	4.00	4.20	3.90	4.10	4.38	3.63	3.50	6.36
P_4 L	10.20	11.00	10.60	10.50	9.90	9.80	10.60	9.80	10.40	9.90	10.10	11.30	9.53	10.80	15.30
P_4 W	5.40	5.50	5.30	5.40	4.60	4.70	4.90	4.60	5.00	4.50	4.70	5.45	4.30	4.50	7.44
M_1 L	—	19.60	18.90	19.80	18.50	17.00	19.40	18.30	19.30	18.50	19.10	20.45	18.17	17.45	26.81
M_1 W	—	7.50	7.00	7.00	6.50	6.30	6.90	6.70	7.00	4.50	7.10	7.60	6.70	7.35	11.11
Trig	—	13.50	13.30	12.80	12.30	11.50	13.30	12.70	13.10	12.70	12.70	13.65	12.37	10.60	19.59
Tal	—	6.10	5.60	7.00	6.20	5.50	6.10	5.60	6.20	5.80	6.40	6.80	5.80	6.85	7.23
M_2 L	10.00	9.80	9.70	10.30	9.60	9.20	10.50	9.10	9.20	9.20	9.90	9.70	8.23	10.15	11.83
M_2 W	6.40	6.90	6.50	6.80	6.50	6.00	6.50	6.30	6.50	6.00	6.40	6.62	5.67	6.95	8.60
M_3 L	—	4.40	4.70	4.40	4.50	4.10	3.90	5.20	—	4.70	3.80	4.92	3.43	5.40	5.83
M_3 W	—	4.20	4.40	3.90	4.20	3.60	3.80	4.60	—	3.70	3.60	4.35	3.47	4.40	5.23
P_1-Trig	—	57.90	56.60	58.30	54.10	56.10	61.30	57.10	55.70	57.70	57.00	48.30	44.27	43.45	66.46
Tal-M_3	—	20.60	19.70	21.60	20.20	19.50	20.60	20.00	—	20.00	20.10	20.18	18.20	22.40	25.63

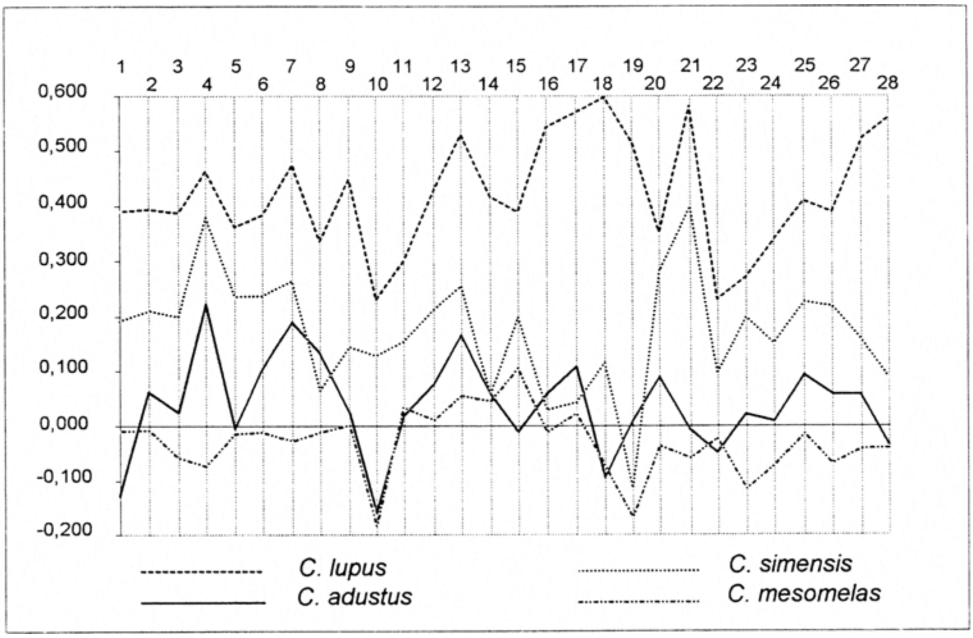

Fig. 11. - Logarithmic ratio-diagrams for cranial measurements. See tab. II and fig. 10 for cranial measurement description.

Skull and mandible (fig. 11). – On an overall view of this diagram, *C. simensis* seems to be somewhat closer, on the average, to *C. adustus*. Conversely, *C. mesomelas* shows characters closer to *C. aureus*. *C. simensis* shows an overall size larger than that of other jackals, especially in the total length of the skull (measurements 1, 2, 3 and 9) and has a greatly elongated facial region (measurements 20, 21); the nasals (measurement 4) are also elongated (like in *C. adustus*). As mentioned in the Introduction a subspecific division of the Simien jackal based on the relative length of this bone was suggested by De Beaux (1922); in early phases of this study, the two subspecies were retained as separate samples but, as they did not differ significatively, we grouped all *C. simensis* specimens into one specific sample. Upper and lower toothrow length is significant (measurements 5, 6, 26). The occipital condyles (measurement 10) and the orbital (measurement 13) and postorbital (measurement 15) constrictions are wide. The rostral tapering of the skull is given by the narrow width of the skull across cheek teeth (measurements 16, 17), the relatively small facial depth (measurement 18) and by the very small jugal depth (measurement 19). Upper and lower carnassials are very short, as well as the P^4-M^2 length (measurement 8). Bullae are broad (measurement 23). The mandible ramus is greatly elongated (measurement 25) and shows a reduced depth (measurement 28).

Dentition. – The Simien jackal is characterized by relatively short upper carnassials (fig. 12*A*) and by an elongated trenchant part of the cheek-teeth (P^1-P^4). The diagram further evidences the great development of crushing teeth M^1 and M^2 in *C. adustus*. The

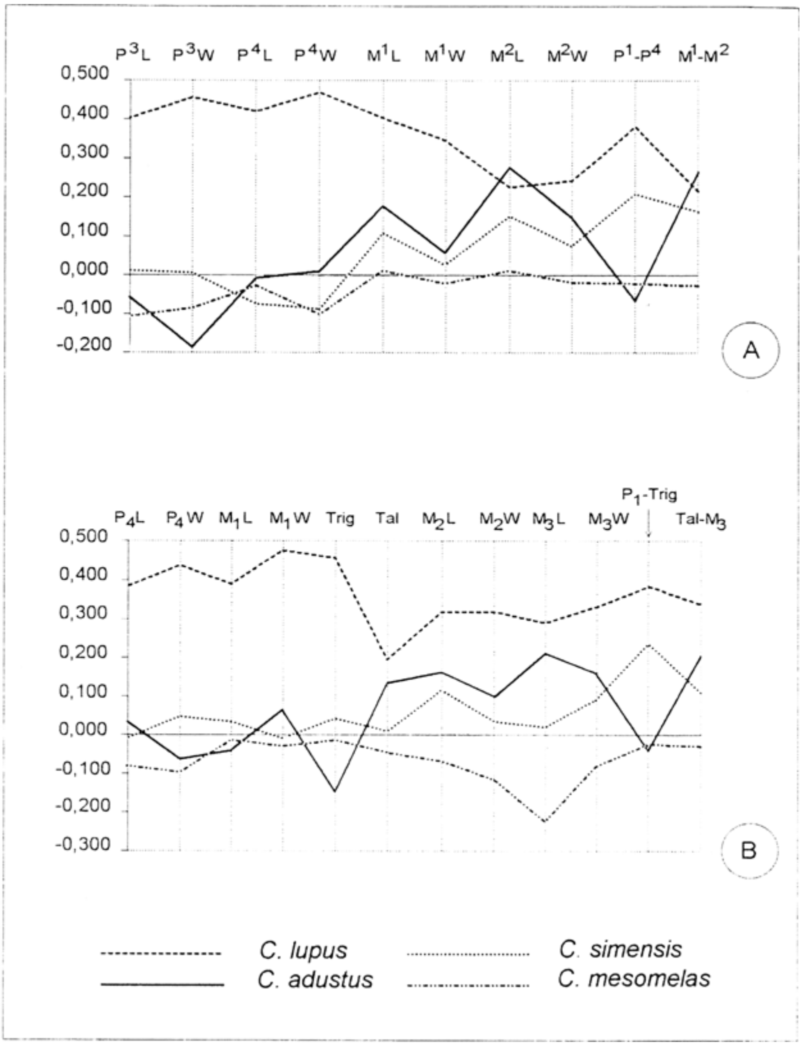

Fig. 12. - Logarithmic ratio-diagrams for dental measurements. *A*: upper dentition. *B*: lower dentition. See tabs. III and IV for dentition measurement description.

ratio between P^1-P^4 and M^1-M^2 in *C. simensis* and *C. adustus* are inverted, as in the lower toothrow.

On the whole the lower dentition of *C. simensis* is close to that of other jackals. The diagram (fig. 12*B*) shows the relative shortening of second and third molar in *C. mesomelas*. About *C. adustus*, this form is peculiar for its very short trigonid in the carnassial and the well developed crushing part of the toothrows; *C. simensis* has a ratio P_1-Trig/Tal-M_3 greater than that of other jackals. It is interesting to note the inversion of proportion in P_1-Trig (trenchant part of the cheek-teeth) and Tal-M_3 (crushing part of the cheek-teeth) between *C. simensis* and *C. adustus*.

CONCLUSIVE REMARKS

Nothing is practically known about the origin of the Simien jackal, which is geographically restricted to small areas on the Ethiopian plateaux. Some hypotheses may be made on the basis of the distribution of fossil canids in the Old World.

It is clear from the fossil record that dogs originated during the Miocene in North America (cf. Tedford, 1978). A first spread of dogs into Eurasia and Africa occurred in the Turolian (latest Miocene) with forms comparable to the North American *Eucyon davisi*. More or less sporadic finds throughout Europe indicate that these forms survived into the Pliocene, represented by the species *Eucyon adoxus* and *Eucyon odessanus*, until the Perpignan faunal unit, the MN 15 unit of the European mammal biochronologic scale (Rook, 1992, 1993). Forms closely related to this group have also been found in Pliocene deposits in China (Tedford and Qiu, 1996) and in Early Pliocene of Transbaikalia (Sotnikova and Kalmipov, 1991). This group of dogs does not belong to the genus *Canis* «*sensu stricto*» but rather to a stem characterized by some primitive features. The conclusion that this group of dogs represents a new genus was reached independently by Tedford and Taylor (unpublished; personal communication in Berta, 1988) and by one of the writers (Rook *et al.*, 1991; Rook, 1992, 1993) and has been formalized with the new generic name by Tedford and Qiu (1996).

The earliest known *Canis* «*s.s.*» occurs in North America in latest Hemphillian (Early Pliocene) deposits with the species *Canis lepophagus*. The dispersal of *Canis* in the Old World occurred during the middle Pliocene. According to Flynn *et al.* (1991), Tedford *et al.* (1991) and to direct study of the Frick collection in the American Museum of Natural History, New York (Rook, 1993), the occurrence of a *Canis* ex gr. *C. etruscus* (a primitive wolf-like form) is documented in China from deposits dated 3 m.y., while the smaller *Canis* ex gr. *C. arnensis* occurs in slightly younger deposits.

The early form of middle sized dog in North America (*C. lepophagus*) has been interpreted as a direct ancestor of the extant coyote (Johnston, 1938; Kurtén, 1974). The more or less contemporaneous forms of Eurasia (*Canis* ex gr. *C. arnensis*) were at first regarded as early jackals (Torre, 1967, 1979; Kurtén, 1968) and later, given that they are closely related with the North American contemporary forms, as Eurasian representatives of the coyote (Kurtén, 1974; Torre, 1979). Obviously *C. lepophagus* and *C. arnensis* are closely related and could at least be recognized as semispecies, thus representing the extremes of the geographic range of one taxon (*C. arnensis* representing the spread in the Old World of *C. lepophagus* populations). However neither is a true coyote or a true jackal; they are the ancestors of both: coyote and jackals represent the evolution in North America and in Old World of forms which were originally very close.

In Central and Western Asia, in Europe and in Africa the first occurrence of true dogs is documented later than in the East Asia. Basing on Sotnikova (1989 and personal communication) a jackal-like dog (*Canis kuruksaensis*) occurs at Kuruksai (Tadzikistan), a locality dating back about 2.5 m.y. In Africa the first confirmed occurrence of jackals (*Canis mesomelas*) is recorded in Member 4 at Sterkfontein, a locality dated about 2.6 m.y. (Turner, 1990).

It appears clear that modern dogs occurred in East Europe and Africa since the early Late Pliocene. Ecological reasons or geographical barriers were supposed to explain the delay of dogs arrival in Western Europe, until the Early Pleistocene (beginning of Late Villafranchian, at approximately 1.8 m.y.). Actually, recent findings and reconsideration of old collections allow to recognize the occurrence of modern dogs (the wolf-like *Canis etruscus* and the smaller *Canis arnensis*) in western Europe in Middle Villafranchian faunal assemblages (latest Pliocene), at the time of the Senèze faunal unit (Rook and Torre, 1996*b*).

African fossil dogs are unfortunately poorly known. It appears however evident that during Early and Middle Pleistocene at least two *Canis* species were present in Africa, one close to *C. mesomelas*, and the second one of a large size form closely related to the European *Canis (Xenocyon) falconeri* group (Turner, 1990; Rook, 1994). *C. adustus* was tentatively identified only from one site in South Africa (Ewer, 1956; Turner, 1990), while there is no evidence of the occurrence of *C. aureus* South of the Sahara before the end of the Pleistocene (Turner, 1990).

Lacking further evidence from fossil records, it may only be inferred that in the highlands of Ethiopia some jackal population gave rise to forms adapted to montane environments and specialized for hunting small mammals, especially rodents and lagomorphs. It is interesting to note that most of the grass rats and hares which are the main prey of the Simien jackal, are also endemic to the Ethiopian mountains (cf. Morris and Malcom, 1977; Azzaroli Puccetti, 1987; Azzaroli Puccetti *et al.*, 1996).

On the basis of either morphological comparisons and of fossil evidence, a close relationship of *C. simensis* with the gray wolf or the coyote more than to the jackals (as suggested on the basis of biochemical analyses) sounds unsatisfactory. We can only note as conclusive remark that when animals with deep differences in morphology and behaviour appear genetically very similar, this requires reconsideration of further genetical and phenetical approach.

Acknowledgements

The authors express their gratitude to Dr. Marco Corti for the kind collaboration in the field, to Profs. Augusto Azzaroli and Danilo Torre for useful discussions and suggestions since the early stages of this work. For the loan of speciments we are grateful to the curators of the Museo Zoologico «La Specola» (Università di Firenze) and of the Museo Civico «G. Doria» (Genova). M.L.A.P. thanks Ato Goitom Redda of the Natural History Museum of Addis Ababa University for unvaluable assistance. For the access to fossil and extant collections L.R. is deeply indebted to Burkhart Engesser (Naturhistorisches Museum, Basel), Andy Currant and Paula Jenkins (British Museum, Natural History, London), Michel Philippe (Musée Guimet d'Histoire Naturelle, Lyon), Marina Sotnikova (Geological Institute, Moscow), Richard H. Tedford (American Museum of Natural History, New York). Photos by Mr. Francesco Landucci (Dipartimento di Scienze della Terra, Università di Firenze).

Work financially supported by: Accademia Nazionale dei Lincei (M.L.A.P.); Ministero dell'Università e della Ricerca Scientifica e Tecnologica (responsabile Dr. Marco Corti, Dip. Biologia Animale e dell'Uomo, Università di Roma «La Sapienza»); Ministero dell'Università e della Ricerca Scientifica e Tecnologica and Consiglio Nazionale delle Ricerche (L.R. under the direction of Prof. D. Torre).

References

Allen G. M., 1939. *A checklist of African mammals*. Bull. Mus. Comp. Zool. Harvard, 83: 1-736.

Azzaroli Puccetti M. L., 1987. *The systematic relationships of hares (genus* Lepus*) of the Horn of Africa*. Cimbebasia, ser. A, 9: 1-22.

Azzaroli Puccetti M. L., Corti M., Scanzani A., Civitelli M. V., Capanna E., 1996. *The caryotypes of two endemic species of hare from Ethiopia*, Lepus habissinicus *Henprich & Ehrenberg (1832) and* Lepus starcki *Petter (1963), with a comparison with* Lepus europaeus *Pallas (1778)*. Mammalia, in press.

Berta A., 1988. *Quaternary evolution and biogeography of the larger South American Canidae (Mammalia, Carnivora)*. Univ. California Publ. Geol. Sci., Berkeley, 132: 1-149.

Clutton-Brock J., Corbet G. B., Hills M., 1976. *A review of the family Canidae with a classification by numerical methods*. Bull. Brit. Mus. (Nat. Hist.), zool., 29: 117-199.

De Beaux O., 1922. *Mammiferi abissini e somali*. Atti Soc. Ital. Sci. Nat., 61: 21-34.

Ewer R. F., 1956. *The fossil carnivores of the Transvaal caves: Canidae*. Proc. zool Soc. London, 126: 97-119.

Flynn J. L., Tedford R. H., Qiu Z., 1991. *Enrichment and stability in the Pliocene mammal faunas of North China*. Paleobiology, 17: 246-265.

Gottelli D., Sillero-Zubiri C., 1992. *The Ethiopian wolf: an endangered endemic canid*. Oryx, 26: 205-214.

Gottelli D., Sillero-Zubiri C., Applebaum G. D., Roy M. S., Girman D. J., Garcia-Moreno J., Ostranders E. A., Wayne R. K., 1994. *Molecular genetics of the most endangered canid: the Ethiopian wolf* Canis simensis. Molecular Ecology, 3: 301-312.

Gray J. E., 1868. *Notes on the skulls of the species of dogs, wolves and foxes (Canidae) in the collection of the British Museum*. Proc. zool. Soc. London: 492-525.

Hillman J. C., 1986. *Conservation in Bale Mountains national Park, Ethiopia*. Oryx, 20: 89-94.

Johnston C. S., 1938. *Preliminary report on the vertebrate type locality of Cita Canyon, and the description of an ancestral coyote*. Amer. Journ. Sci., s. 5, 35: 383-390.

Kurtén B., 1968. *Pleistocene Mammals of Europe*. Weidenfield & Nicolson, London, 317 pp.

Kurtén B., 1974. *A history of coyote-lyke dogs (Canidae, Mammalia)*. Acta Zool. Fennica, 140: 1-38.

Morris P. A., Malcom J. R., 1977. *The Simien fox in the Bale Mountains*. Oryx, 14: 151-160.

Rook L., 1992. «Canis» monticinensis *sp. nov., a Canidae (Carnivora, Mammalia) from the Late Messinian of Italy*. Boll. Soc. Paleont. It., 31: 151-156.

Rook L., 1993. *I cani dell'Eurasia dal Miocene superiore al Pleistocene medio*. Doctoral Dissertation, Florence, 154 pp., 29 tabb.

Rook L., 1994. *The Plio-Pleistocene Old World* Canis (Xenocyon) *ex gr.* falconeri. Boll. Soc. Paleont. It., 33: 71-82.

Rook L., Ficcarelli G., Torre D., 1991. *Messinian carnivores from Italy*. Boll. Soc. Paleont. It., 30: 7-22.

Rook L., Torre D., 1996*a*. *The latest Villafranchian-early Galerian small dogs of the Mediterranean area*. Acta Zool. Cracov, in press.

Rook L., Torre D., 1996*b*. *The wolf-event in western Europe and the beginning of the Late Villafranchian*. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1996, (8): 495-501.

Rüppel E., 1838. *Neue Wirbelthiere zu der Fauna von Abyssinien gehörig, Säugethiere*. Siegmund Schmerber, Frankfurt am Main, 40 pp.

Sillero-Zubiri C., Gottelli D., 1994. Canis simensis. Mammalian Species, 485: 1-6.

Sotnikova M., 1989. *Late Pliocene early Pleistocene carnivora stratigraphyc significance*. USSR Academy of Sciences Transactions, 440: 1-121 (in russian).

Sotnikova M., Kalmipov N. P., 1991. *Pliocene carnivora from Udunga locality, Transbaikal, URSS*. In: E. Vangengeim (ed.), *Pliocene and Anthropogene Paleoecology and Biostratigraphy*. USSR Academy of Sciences, Geological Institute, Moscow: 146-160 (in russian, with english abstract).

TEDFORD R. H., 1978. *History of Dogs and Cats, a view from the fossil record*. In: *Nutrition and Management of Dogs and Cats*. Ralston Purina Company, St. Louis, Cap. 23: 1-10.

TEDFORD R. H., FLYNN J. L., QIU Z., OPDYKE N., DOENS W. R., 1991. *Yushe basin, China: Paleomagnetically calibrated mammalian biostratigraphic standard for the Late Neogene of eastern Asia*. J. Vert. paleont., 11: 519-526.

TEDFORD R. H., QIU Z., 1996. *A new Canid genus from the Pliocene of Yushe, Shanxi Province*. Vertebr. PalAsiatica, 34: 27-20.

THENIUS E., 1969. *Stammesgeschichte der Säugtiere (einschlieslich der Hominiden)*. Handb. Zool., 8: 1-722.

TORRE D., 1967. *I cani villafranchiani della Toscana*. Palaeontogr. Italica, 63: 113-138.

TORRE D., 1979. *The Ruscinian and Villafranchian dogs of Europe*. Boll. Soc. Paleont. It., 18 (2): 162-165.

TURNER A., 1990. *The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa*. Géobios, 23: 349-368.

YALDEN D. W., LARGEN M. J., KOCK D., 1980. *Catalogue of the mammals from Ethiopia. 4. Carnivora*. Monitore zool. Ital., n.s., 8: 169-272.

M. L. Azzaroli Puccetti:
Museo di Storia Naturale dell'Università di Firenze
Sezione Zoologica «La Specola»
Via Romana, 17 - 50125 FIRENZE

L. Rook:
Dipartimento di Scienze della Terra
Università degli Studi di Firenze
Via G. La Pira, 4 - 50121 FIRENZE