strongly contrasted dark and light, the dark line along its upper side narrower and with less black in it.

Skull with the posterior nares narrowed and closed in to a sharp angle, level with the front edge of the pits in the parapterygoid fossæ, just as in *cuniculoides* and *hatcheri*, not as in *typicus*. Colour of incisors darker than in *cuniculoides*.

Dimensions of the type (measured in flesh):—

Head and body 145 mm.; tail 85; hind foot 29; ear 23.

Skull: greatest length 35·5; condylo-incisive length 32·6; zygomatic breadth 19·8; nasals 15; palatilar length 16·8; palatal foramina 9; postforaminal palate 7; upper molar series 6·7.

Hab. Southern pampas of Buenos Ayres Province. Type from Peru, F.C.P., about 200 kilometres N.W. of Bahia Blanca.

Type. Young adult male. B.M. no. 13. 11. 1. 1. Original number 3. Collected 20th July, 1913, and presented by F. H. F. Parkes, Esq. Three specimens. Others obtained by A. W. Whyte and W. A. Smithers.

This seems to be the northern representative of the *R. cuniculoides* of Patagonia, differing from *R. typicus* of Uruguay and Corrientes by more essential characters than any that separate the southern forms from each other. On this account I should consider *hatcheri* also as a subspecies of *cuniculoides*, although I confess I have not for comparison modern topotypes of the latter. But, according to the describer of *R. hatcheri*, the differences are mainly in colour.

XXXVI.—*On the Tooth-change, Cranial Characters, and Classification of the Snow-Leopard or Ounce* (Felis uncia).

By R. I. Pocock, F.R.S., Superintendent of the Zoological Society's Gardens.

This paper is based mainly upon a series of skulls in the collection of the Zoological Society. Two of the series are those of the snow-leopard or ounce (*Felis uncia*), whose cranial characters have never been fully described, so far as I am aware. The animals themselves lived only a few months in captivity. Hence the features the skulls present may be regarded without hesitation as normal. Neither animal was mature, and since by chance these skulls show very clearly the successive steps in the tooth-change, an account of that process may be interesting. Of greater interest, however, are certain characteristics shown

by the occipital region, more particularly those connected with the tympanic bullæ, when compared with those parts in *F. leo*, *tigris*, *pardus*, and *onca*.

The Succession of the Teeth.

There is nothing noteworthy in the structure of the teeth of the deciduous set.

In the smaller of the two skulls, measuring 125 mm. in basal length, the tooth-change has just started. In the upper jaw the two inner pairs of deciduous incisors have been shed and replaced by those of the permanent set, which are fully erupted; but the deciduous outer incisors are still in place, with the tips of the corresponding teeth of the permanent set appearing through the bone just behind them.

The first deciduous premolar has been shed, pushed out by the crown of the permanent tooth, which, however, lies deep in its alveolus.

The canines and second and third premolars of the deciduous set are in place and fully functional; but the molar, lying some distance behind the last deciduous premolar, is through the bone, but not quite fully erupted.

In this stage, therefore, the four median incisors, the first premolars, and the molars of the permanent set are cut, while the outer incisors, the canines, and second and third premolars of the deciduous set are still in full use.

In the next stage, shown by the larger skull measuring 131 mm. in basal length, the outer deciduous incisors have been replaced by those of the permanent set, which are slightly higher than the rest of the series.

The deciduous canines are shed and the permanent canines are half-erupted.

The first permanent premolar and the molar are fully erupted, and the third permanent premolar (carnassial) has pushed out its small predecessor and is erupted nearly to the level of the deciduous second premolar, which is fully functional just in front of it, and is the only tooth of the deciduous set still retained.

On each side of the upper jaw, therefore, the permanent teeth become functional approximately in the following order:—(1) the two inner incisors; (2) the first premolar and the molar together; (3) the outer incisors; (4) the canine and the third premolar (carnassial) at the same time; (5) the second premolar. The deciduous teeth are shed in corresponding order, the last to fall being the second premolar (carnassial). Thus the carnassials of the deciduous and permanent sets are functional at the same time.

In the *mandible* of the smaller skull the deciduous incisors are shed, those of the permanent set being in place, although the outer teeth are shorter than the rest. The canines and premolars (pm_2, pm_3) of the deciduous set are fully functional, but the alveolus of the molar (carnassial) is open, the posterior cusp projecting just above the bone.

In the second and older skull all the incisors are fully erupted, the deciduous canines are shed, and the permanent canines half up. The cheek-teeth on one side consist of the two deciduous premolars and the molar (carnassial), which is as high as the deciduous milk-premolar, but, on the other side, the first deciduous premolar (pm_2) has been pushed out by the tip of its successor, which is just level with the rim of the alveolus.

In each ramus of the mandible, therefore, the permanent teeth become functional approximately in the following order:—(1) the two inner incisors; (2) the outer incisor; (3) the molar (carnassial); (4) the canine; (5) the first premolar; (6) the second premolar.

The change in the upper and lower jaws closely coincides, allowance being made for the complete absence in the mandible of a tooth representing the first premolar of the maxilla and for the functional correspondence of the second and third premolars of the maxilla with the second premolar and molar of the mandible. Of the cheek-teeth, the first of the permanent set to erupt above and below are the molars, and the last to erupt are the teeth immediately preceding the permanent carnassials—that is to say, pm^3 of the maxilla and pm_4 of the mandible of the normal mammalian series.

The Cranial Characters of F. uncia.

The main sources of information known to me about the skull of *F. uncia* are the figure and description published by Gray *, and derived from a specimen with defective occiput and base, which was then, as it is now, the sole example available for examination in the collection of the British Museum.

In the Zoological Society's collection there are two perfect skulls of animals from Kashmir. The larger of the two, almost in the final stage of tooth-change, is only slightly smaller than the adult described by Gray, the total length in the latter being 6½ inches and the zygomatic width 4⅞ inches, whereas in mine the total length is 6½ inches, the zygomatic width 4⅜, and the basal length 5¼. *

* P. Z. S. 1867, p. 262; Cat. Carn. Mamm. etc. p. 8 (1869).

* in mm	Totale Länge	Zygomat. Breite	Basale Länge
Gray	165.1	123.8	–
Pocock	165.1	111.1	133.3

1 Zoll = 25.4 mm

The only obvious differences between the two skulls are the greater elevation of the forehead between the postorbital processes and the deeper depression at the base of the muzzle above in Gray's example. These differences are probably attributable to differences of age. However that may be, the closeness of the resemblances suggests that the specimen in the Zoological Society had attained practically its permanent form in the characters mentioned below, the more important of which are those cited as distinctive of *F. uncia* in comparison with *F. leo*, *tigris*, *pardus*, and *onca*, the species to which, as I have recently shown*, *F. uncia* is affiliated by the structure of the hyoid bone.

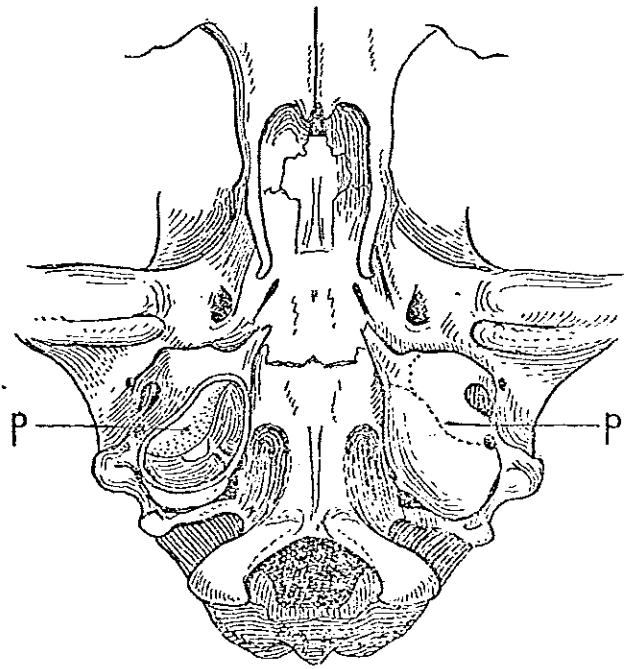
The principal cranial features of *F. leo*, *tigris*, *pardus*, and *onca* can be verified in any museum of repute. Those of *F. uncia* are, generally speaking, similar, but the skull is relatively broader, shorter, and more vaulted, being elevated between the postorbital processes and sloped and somewhat lynx-like in the muzzle, which is depressed posteriorly above. There is no evidence of the development of a strong sagittal crest or of a deep constriction behind or in front of the short blunt postorbital processes. The orbits are comparatively large in relation to the temporal fossæ and the posterior portions of the zygomata are not markedly salient. The upper end of the maxilla is long, acutely angled, and projects very noticeably farther back than the broad and short nasals. The straightness and inclination of the fronto-maxillary-nasal suture, the form of the premaxillæ, the plane of the anterior nares, the flatness of the cheek above the carnassial, the height of the lacrymal bone above the foramen, the large size of the anteorbital foramen as compared with the palatal foramen of the orbit, are practically as in the other species mentioned above. The mesopterygoid fossa is nearly parallel-sided, the hamulars only converge slightly posteriorly, the anterior angles are rounded, the anterior border transverse, with two small spines and a small median notch. The palate is moderately prolonged and narrow posteriorly, and the postero-lateral borders of the palate show an angular emargination passing in front of the line of the molar (fig. 1).

The most marked characters of the skull are found in the occipital region. The basioccipital is deeply excavated up against the bulla, the anterior end of the excavation deepening into a pit holding a thick muscular tendon (fig. 1). The foramen magnum is higher than wide, with a very thick

* Ann. & Mag. Nat. Hist. (8) vol. xviii. p. 221–229 (1916).

inferior border, and the condyles are everted, so that the distance between their inner edges exceeds the width of the foramen. The bullæ are separated by a very narrow valley from the vertical glenoid ridge of the squamosal (fig. 2 A, *v*), the groove on the bulla marking the line of the partition passes from the styloid to a point behind the basioccipital suture on the inner side and lies a long way below the

Fig. 1.



Base of skull of *Uncia uncia* with bulla of right side (left of figure) cut open to show the inner chamber and the partition (*p*) separating it from the outer or auditory chamber. On the left bulla *p* marks the groove showing the line of origin of the partition. Depressions on basioccipital also shown.

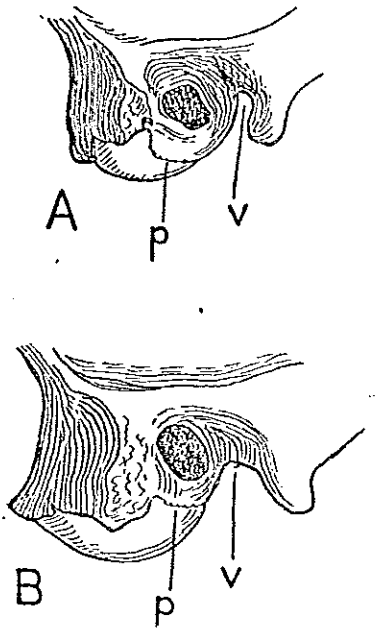
auditory meatus (figs. 1, 2, *p*). Thus the auditory chamber is comparatively very large and antero-internally passes in front of the extremity of the posterior chamber (fig. 4 C), the cavity of which is still further reduced by the convex bulging of the partition (fig. 1, *p*).

In the mandible the chin is nearly vertical in its anterior two-thirds and sharply curved backwards inferiorly.

In the sum total of its characters the skull of *F. uncia* differs considerably from the skulls of *F. leo*, *tigris*, *pardus*, and *onca*; but, as stated above, the most marked differences are found in the occipital region, which does not appear to have been previously described in *F. uncia*.

In *F. leo*, *tigris*, *pardus*, and *onca* the foramen magnum is wider than high, its inferior edge is comparatively thin, the width between the inner edges of the condyles is equal to

Fig. 2.

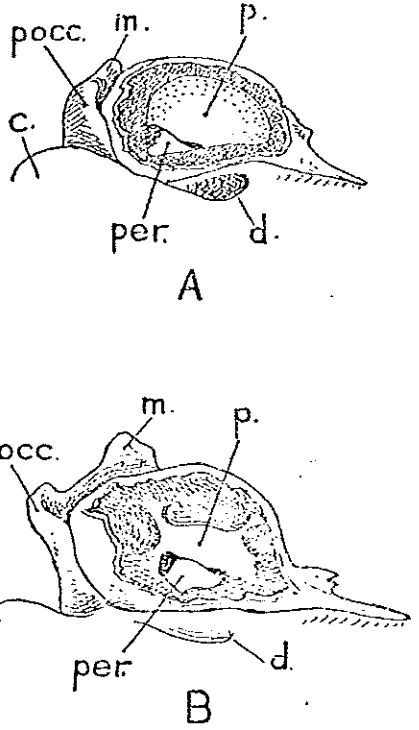


A. Right tympanic bulla of *Uncia uncia* seen obliquely from behind, showing the narrow valley (*v*) between the bulla and the glenoid ridge of the squamosal and the line of origin of the partition (*p*).
B. The same of *Panthera onca*.

the width of the foramen, there is no deep depression, deepening in front, up against the bullæ on the basioccipital, and there is a comparatively wide valley between the bullæ and the glenoid ridge of the squamosal (fig. 2 B, *v*). Finally, the partition of the bulla is low, rises tolerably close to the auditory meatus, the line of its origin running from a point just in front of the stylomastoid foramen to a point on the anterior face of the bulla (fig. 2 B, *p*); and when the bulla

is cut open the posterior chamber is seen to be much larger than the anterior or auditory chamber, and its auditory portion extends forwards along the inner part of the bulla approximately as far as, or farther than, the anterior part of the auditory chamber (fig. 4 A, B).

Fig. 3.



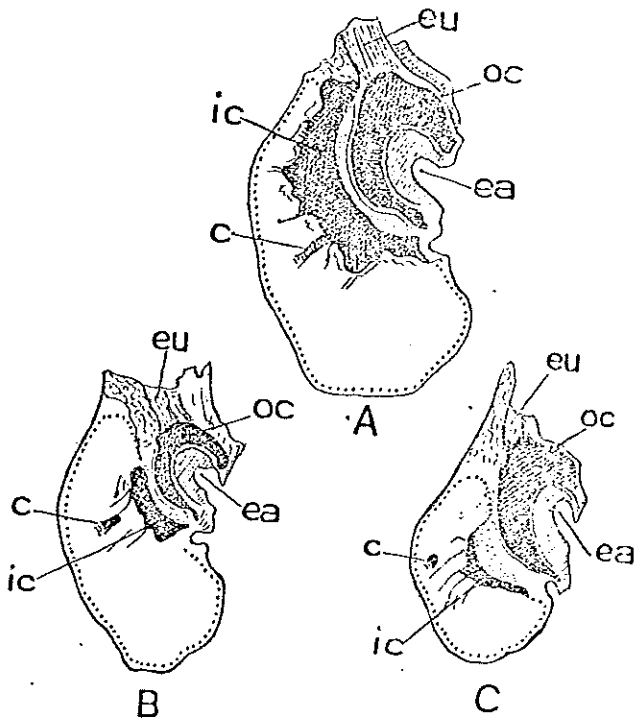
A. Right tympanic bulla of *Uncia uncia* seen from the inner side, with the wall of the inner chamber cut open from the summit to the basioccipital. *p*, partition between the chambers; *per*, periotic bone against which the partition abuts; *m*, mastoid; *pocc*, paroccipital; *c*, condyle; *d*, depression on basioccipital.

B. The same of *Panthera onca*. The crest rising from the posterior end of the partition marks the stylomastoid groove.

In some half-dozen skulls of *F. pardus* from Asia and Africa there is no great variation in the internal structure of the bulla. In all cases the ridge formed on the wall of the

posterior chamber by the stylomastoid groove is distinct from the low partition and runs upwards, when the skull is inverted, from its posterior end. The same applies to two skulls of *F. onca* (fig. 3 B) and to four of *F. tigris*. But in

Fig. 4.



A. Right bulla of *Panthera leo* extracted and viewed from its upper, or attached, surface, part of the roof of the inner chamber cut away. *c*, carotid groove; *eu*, floor of eustachian tube; *ea*, external auditory meatus with horseshoe-shaped tympanic bone; *oc*, outer or auditory chamber separated by the partition from inner chamber (*ic*), the extent of which is indicated by the dotted line following the contour of the bulla.
B. The same of *Panthera pardus* (from India), but the roof left intact.
C. The same of *Uncia uncia*.

three skulls of *F. leo* the partition is somewhat higher and longer, and the auditory chamber consequently a little larger relatively (fig. 4 A).

The Classification and Generic Nomenclature of F. uncia *and its Allies.*

In the paper already quoted, I have shown that the five species here discussed differ from other existing species of Felidæ in the structure of the hyoid apparatus. To this character, at all events, generic value should be given. But it appears to me that the combination of cranial features exhibited by *F. uncia*, particularly in the occipital and auditory bones, entitles that species to generic separation from *F. leo*, *tigris*, *pardus*, and *onca*, the skulls of which differ in comparatively minor points from each other and show many cross-resemblances.

The view that the external differences observable between these species in coloration and hair-growth are worth generic recognition does not appeal to me. For example, Gray adopted the generic name *Leo* for *F. leo* mainly on the strength of the secondary sexual characters, which he knew to be exceedingly variable in development racially or individually, although he was not aware that they are sometimes not developed at all *; and, as regards pattern, I have elsewhere shown † that the markings of *F. leo*, as exhibited by the cubs, sometimes show a complete transition between the stripes of *F. tigris* and the spots of *F. onca* or *pardus*, although usually, when visible, which is not always the case, approaching the rosette type exhibited by the two last mentioned species.

Nevertheless, since the tendency of modern systematic mammalogy has found in the present instance expression in the admission of many species of leopard, lion, jaguar, and tiger, it is possible, perhaps probable, that the logical outcome of that process—namely, the ascription of generic rank to each of these animals—will be followed in the future. If that be so, nominal symbols are available for them.

Rejecting the validity of *Leo* and *Tigris*, published by Frisch in 1775 ‡, it seems that Oken was the first author to introduce generic terms for the leopard, tiger, and lion. By pagination the following is the order of their publication:—

Panthera, Oken, Lehrb. Zool. 2nd Abth. pp. 1052–1066

* Col. Patterson's man-eating lions of Tsavo were described as maneless, and, judging from his photographs, they were not distinguishable, so far as the mane is concerned, from lionesses.

† Ann. & Mag. Nat. Hist. (7) xx. p. 436 (1907).

‡ Following the decision of Sherborne and of Thomas and Miller, Ann. & Mag. Nat. Hist. (7) xvi. p. 461 (1905).

(1816). With other species were included *vulgaris*=*pardus*, Linn.; *americana*=*onca*, Linn.; *alba*=*uncia*, Schreb. Of these, *pardus* is the type, according to Allen's decision (Bull. Amer. Mus. Nat. Hist. xvi. pp. 377–378, 1902).

Tigris, Oken, *tom. cit.* pp. 1066–1070; type by tautonymy *tigris*, Linn. (Palmer, 1904).

Leo, Oken, *tom. cit.* pp. 1070–1076; type by tautonymy *leo*, Linn. (Palmer, 1904).

Furthermore, the following names are available for the remaining two species of large cats which come into this group:—

Uncia, Gray, Ann. & Mag. Nat. Hist. (2) xiv. p. 394 (1854); type by tautonomy *uncia*, Schreb.

Jaguarius, Severtzow, Rev. Mag. Zool. (2) x. pp. 386 & 390 (1858), proposed as a subgenus of *Panthera* for *F. onca*, Linn., which is its type.

It does not appear to me that these conclusions, which are set forth in Palmer's 'Index Generum Mammalium,' 1904, are open to dispute.

Adopting, then, the view here advocated, that *F. uncia* is entitled to generic distinction from *F. leo*, *tigris*, *pardus*, and *onca*, it will take the name *Uncia*; while, for the category composed of the remaining four species, *Panthera* is by page priority in Oken's work the correct title, with *Tigris*, *Leo*, and *Jaguarius* as synonyms according to the system I adopt *.

The only other name which might possibly be claimed as superseding *Panthera* is *Leopardus*, Forskål (Descr. Anim. etc. p. v, 1775). This name, however, was published without citation of genotype. It was followed merely by the Arabic name *nimr*, which clearly cannot be regarded as a specific title in a zoological sense. In the Arabic tongue it probably embraces both the leopard (*pardus*) and the cheetah or hunting leopard (*jubatus*). At all events, according to Tristram ('Nat. Hist. of the Bible,' ed. 9, 1898, p. 114) the Hebrew term *namer* "doubtless comprehended both these species" †.

* In Agassiz's 'Nomenclator' and Palmer's 'Index' the name *Panthera* is alleged to have been given by Hübner to a genus of Lepidoptera in 1816, thus synchronizing with Oken's publication. I am indebted, however, to Mr. Oldfield Thomas for the information that 1816 for Hübner's work is a misprint for 1826. Thus the way is cleared for the adoption of *Panthera*, Oken.

† Mr. Oldfield Thomas and Mr. Knud Andersen concur in the rejection of *Leopardus*, Forskål.

It may be added that Matschie's classification of these large Felidæ as *Uncia* for *leo*, *tigris*, and *concolor* and *Leopardus* for *pardus*, *uncia*, and *onca* (SB. Ges. Nat. Fr. Berlin, 1895, pp. 198–199)—a classification which was adopted by Trouessart in 1904 (Cat. Mamm., Suppl. p. 265)—is quite indefensible both from the zoological and nominal standpoints. The valuelessness of Matschie's opinion on the question of the affinities of the species concerned is attested by his regarding *uncia* as a subspecies of *pardus* and by his placing *concolor* with *tigris* and *leo* in a genus from which *pardus* and *onca* are excluded. It cannot be doubted that the relationship between *onca* and *pardus* is greater than that between *uncia* and *pardus*, and that *tigris* is much more nearly akin to *pardus* than it is to *concolor*. Yet Matschie's classification implies the precise opposite of these conclusions. And as regards his choice of names, *uncia* by tautonymy, let alone the selective actions of Severtzow and Gray, is the type of *Uncia* and *Leopardus*, rejecting Forskål's work, is not admissible either for *pardus* or *onca* or *uncia*, since none of these species was included when it was first proposed by Gray in 1842 (Ann. & Mag. Nat. Hist. x. p. 260). It was applied to *griseus*, *pictus*, *ellioti*, and *horsfieldi*. Since one of these must be the type, I select *griseus*, which probably connotes a subspecies of *pardalis*. That Gray intended *pardus* to come into *Leopardus* is shown by his subsequent writings; but there seems to be no defensible pretext for its admission, gratifying as it would be to relegate *Leopardus* to the synonymy of *Panthera*.

The principal cranial differences between *Uncia* and *Panthera* may be briefly contrasted as follows:—

a. Outer chamber of the bulla very large and involving the whole of the anterior portion of its cavity, the line of the partition remote from the meatus and running from the stylomastoid foramen to a point on the inner surface close to the basioccipital suture; a narrow valley between the bulla and the glenoid joint; basioccipital deeply excavated laterally, a deep pit at the anterior end of the excavation ..... *Uncia.*

b. Outer chamber of bulla comparatively small, not involving the whole of the anterior portion of the cavity; the partition-line close to the meatus and ceasing towards the anterior edge of the bulla; a wide valley between the bulla and the glenoid joint; basioccipital at most shallowly excavated laterally ..... *Panthera.*

1916 a

XXII.—*On the Hyoidean Apparatus of the Lion* (F. leo) *and Related Species of* Felidæ. By R. I. Pocock, F.R.S., Superintendent of the Zoological Society's Gardens *.

In typical members of the Felidæ the suspensorium (fig. 2, A), or anterior cornu, of the hyoid consists of four elements—the ceratohyal, epihyal and stylohyal (which are ossified in the adult), and the tympanohyal (which generally, if not always, remains cartilaginous through life up to its point of attachment with the bulla) †. But it is well known that the hyoid apparatus of some of the larger species of Felidæ—*F. leo* and *F. tigris*, for example—differs from that of the majority of species in the defective ossification of parts of the suspensorium, so that the larynx, clamped though it be by the basihyal and thyrohyals, is not held close up to the base of the skull by a comparatively short series of contiguous and jointed bones, but is imbedded in the muscles of the throat, and is susceptible of much greater range of movement than is ordinarily the case. The missing portion of the suspensorium is represented by a long and slender "ligament," the course of which it is by no means always easy to follow through the muscles it traverses.

Blainville's figures (Ostéogr. Atlas, *Felis*, pl. xi.) of the hyoid in *F. leo*, *F. tigris*, and *F. pardus*, the only species known up to the present time to possess the modification of the suspensorium above described, show that the lower end of the suspensorium is represented by the ceratohyal and the upper by a styloid process which is undivided in *F. pardus*, but divided into a proximal cartilaginous portion, and a distal osseous portion in *F. leo* and *F. tigris*. The ligament, moreover, carries one bead-like ossicle in *F. leo* and *F. pardus* and two in *F. tigris*. Thus, the suspensorium in the lion, tiger, and leopard consists of two main bones instead of three, the ligament with the ossicles taking the place of the epihyal. But, according to Blainville (Ostéogr. vol. ii., *Felis*, p. 32),

* The facts recorded in this paper are based upon dissections made in the Society's Prosectorium.

† Flower applied the term "tympanohyal" to the ossicle of the hyoid which is embedded in the styloid foramen of the skull. Mivart ('The Cat,' pp. 77–78) extended the term to include the longish cartilage depending from that bone. In this paper, without prejudice, I follow Mivart's terminology, leaving open the question as to whether or not this cartilage is a separate element from the tympanohyal. It may belong to the stylohyal. At all events, before ossification of the latter sets in, it appears to form with the tympanohyal a continuous cartilaginous rod, which, for convenience, I speak of as the styloid process.

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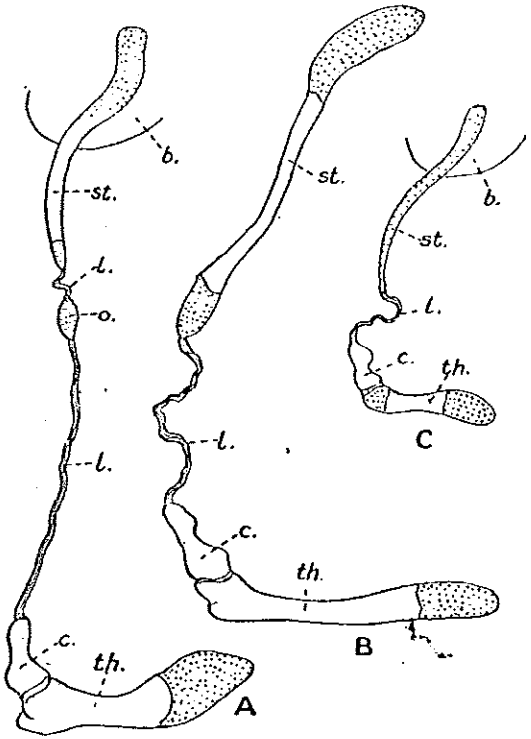
the suspensorium in the jaguar (*F. onca*), which on *à priori* grounds might be expected to resemble that of the leopard, is like the suspensorium of typical cats in consisting of three

Fig. 1.



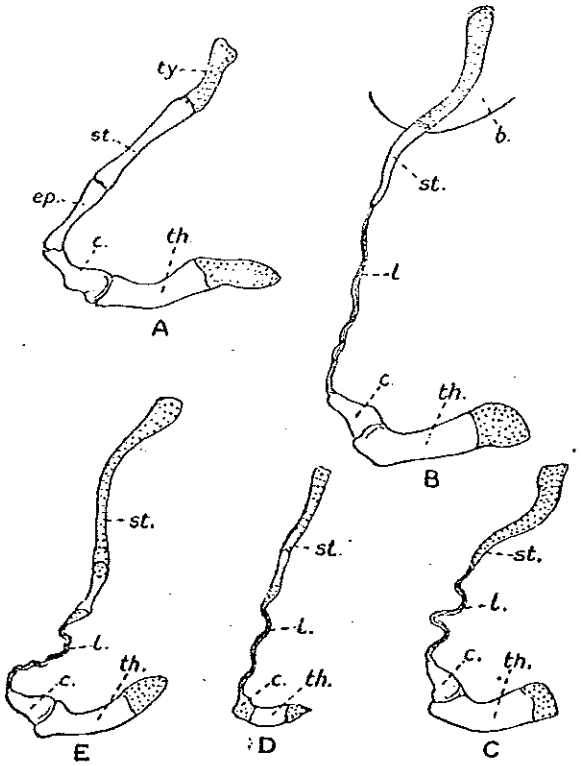
A. Lateral view of hyoid apparatus of a young lion (*Felis leo*). *st.*, styloid process; *l.*, ligament with sesamoid cartilage (*o.*); *c.*, ceratohyal; *th.*, thyrohyal; *b.*, portion of bulla in profile.
B. The same of adult tiger (*Felis tigris*). Lettering as in A.
C. The same of immature ounce or snow-leopard (*F. uncia*). Lettering as in A and B.

Fig. A is approximately natural size; figs. B and C are two-thirds natural size. Cartilaginous elements are dotted. The ligaments are not represented their natural length, but shortened and twisted by the action of alcohol.

bones joined end to end, without the intervention of a ligament. It will be noticed, however, that his figure of the hyoid of this species, although agreeing with the text in

indicating three distinct bones, shows the second bone from the top joined to the inferior bone by a dotted line. I

Fig. 2.



A. Lateral view of hyoid of hunting leopard (*Acinonyx jubatus*), showing the structure of this apparatus in normal species of Felidæ. *ty.*, tympanohyal cartilage; *st.*, stylohyal; *ep.*, epihyal; *c.*, ceratohyal; *th.*, thyrohyal.

B. The same of the adult common leopard (*Felis pardus*). Lettering as in fig. 1, A.

C. The same in immature leopard (*Felis pardus*). Lettering as in fig. 1, A.

D. The same in very young jaguar (*Felis onca*). Lettering as in fig. 1, A.

E. The same of one-year-old jaguar (*Felis onca*). Lettering as in fig. 1, A.

All two-thirds natural size. Ligament and cartilages represented as in fig. 1.

supposed at one time, as probably others have done before, that the elements of the suspensorium in this case were

separated on the plate, so as to be fitted into it, although there was no very obvious reason for selecting this particular figure to be treated in that way. But I now believe that in the preparation from which the figure in question was taken the hyoid at the point indicated was divided by the interposition of a ligament which was lost in maceration; and, secondly, that Blainville's assertion that the two bones were connected was nothing but an inference based upon the assumption that when the ligament is present the suspensorium contains only two bones, and that when the suspensorium is composed of three bones the ligament is absent.

The reasons given above for the opinion that Blainville's interpretation of the hyoid of *F. onca* was erroneous is supported by the presence of the ligament in two examples of this bone that I possess. In one, taken from a young cub (fig. 2, D), there is a long cartilaginous styloid process, broad above and tapering below, with a single cylindrical ossification in its lower half a little less than its own length from the cartilaginous inferior extremity. From this extremity a longish ligament passes to the summit of the ceratohyal. In this example the hyoid is rather smaller than that of a domestic cat (*F. catus*). In a second, much larger example of the hyoid taken from a jaguar about one year old (fig. 2, E) the styloid process is divided into two distinct portions—an upper, long, and somewhat curved cartilaginous piece and a lower piece, consisting of a slender cylindrical bone with a cartilaginous epiphysis at each end. From the short inferior epiphysis the ligament runs to the ceratohyal.

The correspondence between the elements of the two hyoids just described is quite clear from the figures (fig. 2, D, E); and if the figure of the more advanced of the two be compared with that of the adult hyoid of *F. onca* depicted by Blainville, it will, I think, be evident that the two long bones constituting the upper end of the suspensorium in the adult are the homologues of the long cartilaginous element and the shorter bony element in the one-year-old example above described, the only difference being that the upper portion of the suspensorium is ossified in the adult and cartilaginous in the young.

In a very young leopard (fig. 2, C) I find that the suspensorium consists of a long, cartilaginous, curved, styloid process, broad at the top and tapering at the point, a longish ligament, and a short weakly ossified ceratohyal. In a full-grown example (fig. 2, B) it is composed of the same elements, but the inferior half of the styloid is ossified, its superior, broader, and more flattened half remaining cartilaginous. It

is noticeable that the ligament is distinctly longer in this species than in the jaguar, but in the examples examined there is no trace of the oval sesamoid bone on the ligament depicted by Blainville.

In an adult tiger (fig. 1, B) the suspensorium broadly resembles that of the leopard, except that the broad upper cartilaginous portion of the styloid bar is only about half the length of the slender ossified portion and the latter has a cartilaginous epiphysis at its lower extremity. From this a long ligament, without oval ossification, passes to the summit of the ceratohyal. Except for the absence of the ossicles on the ligament and its longer styloid, this suspensorium tolerably closely resembles that of the same species figured by Blainville.

In the hyoid of a young lion (fig. 1, A) I find a long partly cartilaginous styloid, with a distinct cartilaginous epiphysis at its lower end, and long ligament passing to the ceratohyal, and furnished near its upper end close to the tip of the styloid with an oval cartilage.

Finally, in a young ounce (*F. uncia*) the suspensorium is composed of a long, tapering, cartilaginous, styloid process, a comparatively short ligament, and the ceratohyal. The structure of the hyoid in this species has not been previously described (fig. 1, C).

Comparison between the hyoids of an adult leopard (*F. pardus*), tiger (*F. tigris*), and cheetah (*A. jubatus*) suggests that the cartilaginous tympanohyal and the ossified stylohyal in the last are represented by the partly cartilaginous and partly ossified proximal end of the suspensorium in the other two; and since the ceratohyal is the distal end of the suspensorium in the three forms, it seems obvious that the epihyal of the cheetah is the part that is missing in the tiger and leopard, its place being taken by the elastic ligament.

But in the case of the jaguar (*F. onca*) this is not so clear. In the adult of this species, according to Blainville, the upper end of the suspensorium consists of two mutually jointed bones, the proximal of which is long and slender. In the young animal a year old (fig. 2, E) the upper bone is represented by a cartilage correspondingly long, and forms a definite joint with the cartilaginous upper epiphysis of the partially ossified lower element, and is at the same time more sharply separated from the lower bony element than is the proximal cartilage of the suspensorium, the tympanohyal cartilage, from the bony stylohyoid element in the cheetah,

leopard, and tiger. The great length, indeed, of the upper cartilaginous element in the young jaguar and its mode of articulation with the second bony element suggest that it is the homologue of the partly cartilaginous, partly ossified upper element—that is to say, of the tympanohyal cartilage and of the stylohyoid bone—in the cheetah, leopard, and tiger. In that case, the second element in the jaguar corresponds to the epihyal of the cheetah, and the comparatively short ligament is interposed between the epihyal and the ceratohyal, and does not replace the epihyal.

From the data available it does not appear to me that this point can be settled; but I incline to the opinion that that interpretation is correct, and that Blainville, although wrong in stating that the ligament is absent in the jaguar, was right in saying that the suspensorium in that animal consists of the same bony elements—namely, the stylohyal, epihyal, and ceratohyal—as in the normally constructed hyoids of Felidæ. If this be so of the five species—namely, the lion, tiger, leopard, ounce, and jaguar—which have an elastic ligament in the hyoidean suspensorium, the jaguar is the most primitive in retaining the three bony suspensorial elements in the hyoid, and at the same time shows the first step in the modification of the hyoid to have been the interposition of an elongated elastic ligament between the ceratohyal and the epihyal, and the second step, as illustrated in the leopard, lion, and tiger, to have been the suppression of the epihyal element. The obvious suggestion here arises that the bony nodule, or nodules, sometimes present near the upper end of the ligament in these three species may be the remnant of the epihyal.

Whichever of the two above-suggested interpretations proves ultimately to be correct, the important fact remains that in the lion, tiger, leopard, ounce, and jaguar there is a longish or very long elastic ligament interposed between the ceratohyal and the upper element of the hyoidean suspensorium.

All the other species of the Felidæ that I have examined, including *F. concolor*, *pardalis*, *wiedii*, *geoffroyi*, *jaguarondi*, *pajeros*, *nebulosa*, *viverrina*, *bengalensis*, *serval*, *aurata*, *chaus*, *ocreata*, *nigripes*, *sylvestris*, *caracal*, *lynx*, *rufa*, and *Acinonyx* (*Cynælurus*) *jubatus*, bear out the observations of others, that there is no long elastic ligament in the suspensorium in any form but the five enumerated above.

In his paper on the anatomy of the cheetah (*Acinonyx jubatus*) Owen (Tr. Zool. Soc. i. p. 129, 1834) wrote as follows:—"In their internal structure the differences of the

Felis one from another are less easily appreciable than in their outward form. Perhaps the most marked among the anatomical variations obtains in the mode of attachment of the *os hyoides* to the cranium; and this difference is evinced in the living animal by a difference in the variety and power of the voice. In the lion an elastic ligament, about 6 inches in length, connects on each side the lesser cornu [ceratohyal] of the *os hyoides* with the styloid process; this ligament can be stretched to 8 or 9 inches. The larynx is consequently situated at a considerable distance from the posterior margin of the bony palate; but the soft palate is prolonged backwards to opposite the aperture of the glottis, and the tongue is proportionately increased in length. Thus a gradually expanding passage leads from the glottis, where the air is rendered sonorous, to the mouth, and it is not unlikely that the strong transverse ridges upon the bony palate may contribute, with the preceding trumpet-like structure, to give that intonation which is so aptly denominated 'the roar of the lion.'

"In the domestic Cat, in *Felis planiceps*, and in *Felis caracal* the *os hyoides* is connected with the cranium . . . . by an uninterrupted chain of bones . . . . The same structure obtains in the Cheetah. From the difference in the voice, the feline animals might have been expected, *à priori*, to present some differences in that part of their anatomy which relates to it."

In this passage Owen was, I believe, the first to point out the connection between the resonance of the voice and the looseness of the hyoid in the lion. The same applies to the tiger, the roar of which, used solely, I believe, as a sexual call, is deceptively like that of the lion at times. On the other hand, the roars of the jaguar and leopard are quite different from those of the lion and tiger, but remarkably like one another. It is not easy to describe them, but I have elsewhere (P. Z. S. 1907, p. 677) compared the sound to "a series of hoarse barking coughs, an interval of about one second separating each expiratory effort. It very much resembles the sound produced by sawing a piece of thin wood with a coarse-toothed saw" *. The voice of the ounce is unknown to me. The only sound I have heard these animals make results from puffing through the nostrils. The tiger has a similar habit when pleased. The voice of other members of the Felidæ cannot be described as a roar. The

* The name "jaguar" is, I presume, derived from the roar of the animal, of which it is not a bad representation.

Hemmer (1968: 236)

call of the cheetah is a most decided mew, hardly distinguishable from that of domestic cats.

Apart from the roar there is another very distinctive feature about the voice of the cats with a normal hyoid. This is the familiar "purr." Lions, tigers, leopards, and jaguars never purr; on the other hand, such widely different species as cheetahs, pumas, caracals, jaguarondis, and others that could be named, always, when sufficiently tamed, express pleasure or content by that sound. These are interesting differences correlated with the differences in the hyoidean apparatus above described.

Conclusion.

The following are the main points this paper seeks to establish:—

1. The hyoid of the jaguar (*Felis onca*) resembles that of the lion (*F. leo*), tiger (*F. tigris*), and leopard (*F. pardus*) in having the suspensorium lengthened by an elastic ligament interposed between the ceratohyal and the upper elements of the suspensorium. Blainville, therefore, was wrong in denying the existence of the ligament in the jaguar.
2. The hyoid in the ounce (*F. uncia*) resembles that of the above-mentioned species.
3. The species in which the hyoid is provided with this ligament roar, but do not purr. All the other species of Felidæ with normally constructed hyoid purr, but never roar.

XXIII.—Triæschna gossi, *a new Genus and Species of Odonata from the Eocene of Bournemouth.* By Herbert Campion.

[Plate XI.]

In the 'Entomologist' for 1878 (vol. xi. p. 193) H. Goss figured the right fore-wing of a fossil Æschnid dragonfly, and made some general remarks concerning it. The specimen was in a very fine state of preservation, and was obtained by J. Starkie Gardner from the leaf-beds (Bagshot Sands) of Bournemouth, Hampshire. It was referred to the genus *Æschna*, but no specific name was proposed, no measurements of the wing were stated, and no description of the venation was given.