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Publisher: Taylor & Francis
Informa Ltd Registered in England and Wales Registered Number:
1072954 Registered office: Mortimer House, 37-41 Mortimer Street,
London W1T 3JH, UK



Journal of Natural History Series 8

Publication details, including instructions
for authors and subscription information:
<http://www.tandfonline.com/loi/tnah14>

XXII.—On the hyoidean apparatus of the lion (*F. leo*) and related species of *Felidæ*

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Version of record first published: 11 Sep
2009.

To cite this article: R.I. Pocock F.R.S. (1916): XXII.—On the hyoidean apparatus of the lion (*F. leo*) and related species of *Felidæ*, *Journal of Natural History Series 8*, 18:104, 222-229

To link to this article: <http://dx.doi.org/10.1080/00222931608693839>

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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.

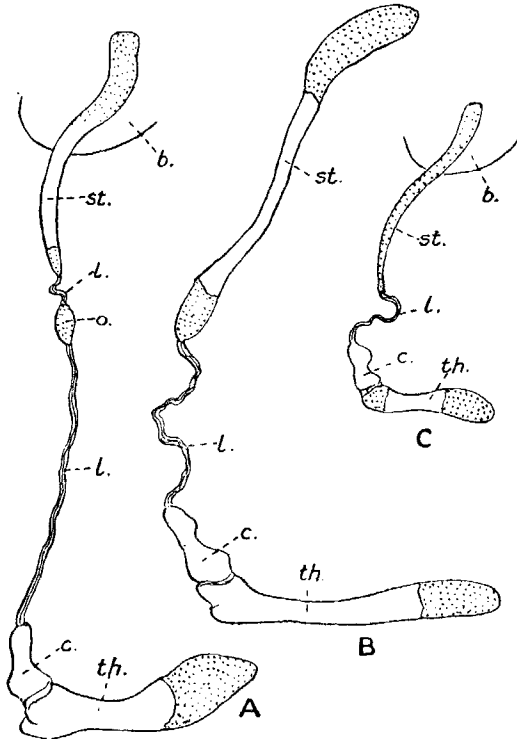
Blainville's figures (Ostéogr. Atlas, *Felis*, pl. xi.) of the hyoid in *F. leo*, *F. tigris*, and *F. pardus*, the only species known up to the present time to possess the modification of the suspensorium above described, show that the lower end of the suspensorium is represented by the ceratohyal and 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.

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.



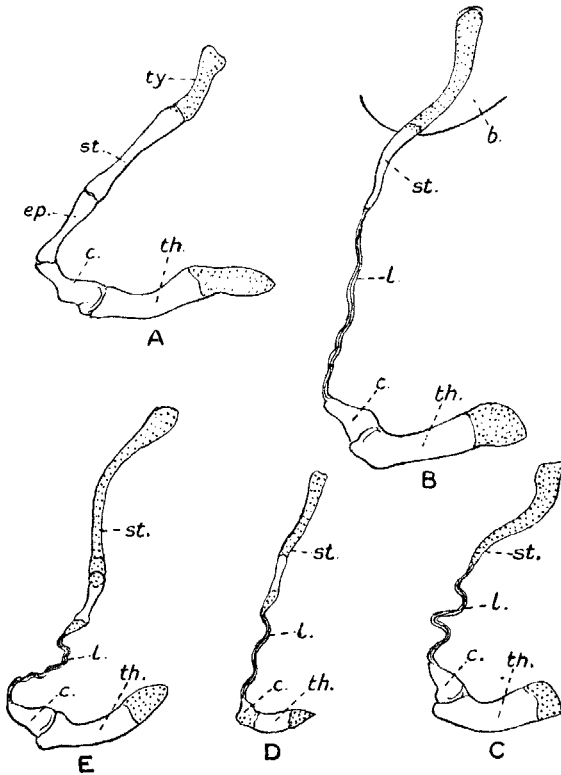
- A. Lateral view of hyoid apparatus of a young lion (*Felis leo*). *st.*, styloid process; *l.*, ligament with sesamoid cartilage (*o.*); *c.*, ceratohyal; *th.*, thyrohyal; *b.*, portion of bulla in profile.
 B. The same of adult tiger (*Felis tigris*). Lettering as in A.
 C. The same of immature ounce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

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.