

A PEAFOWL FROM THE PLIOCENE OF PERPIGNAN, FRANCE

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ABSTRACT. A tarsometatarsus from the Pliocene of Serrat-d'en-Vacquer, Perpignan, attributed to *Gallus bravardi* Gervais, actually belongs to the recent genus *Pavo*, and hence is designated as *Pavo bravardi* (Gervais). Fossil Peafowls are also present in other Pliocene and Lower Pleistocene localities in France and Moldavia. The Perpignan form is very similar to the recent species of *Pavo* and differs from the African form *Afropavo*, suggesting that these two genera diverged from a common ancestor prior to the Pliocene.

THE species *Gallus bravardi* was described by Gervais (1849, 1848-1952) from a fragment of tarsometatarsus bearing a strong spur, which came from the site of Ardé, or Ardes, in the 'Montagne de Perrier', near Issoire (Puy-de-Dôme, France). This specimen, collected by M. Bravard, was deposited in the collection of the Paris Muséum national d'Histoire naturelle, but it has not been possible to locate it again in this collection.

Depéret (1890) described from the Pliocene of Perpignan, in Roussillon, an upper part of a right coracoid and an almost complete left tarsometatarsus which he referred to *G. bravardi* Gervais. The part of the tarsometatarsus which bears the spur resembles in all its details the specimen described by Gervais as *G. bravardi*, its size being just a little smaller. However, the morphological characters of the proximal and distal parts indicate that this tarsometatarsus does not correspond to the recent genus *Gallus*, the Junglefowl, but to the recent genus *Pavo*, the Peafowl. The species *bravardi* is therefore transferred to the genus *Pavo*. However, the coracoid from Perpignan is morphologically similar to the genus *Gallus* and can be provisionally referred to as *Gallus* sp.

The specimen from the Roussillon Pliocene, illustrated by Lambrecht (1933, p. 875, fig. 193H) as *G. bravardi* Gervais, is actually *G. aesculapi* Gaudry, from Pikermi.

The Perpignan tarsometatarsus, described as complete, was made up of two fragments stuck together in such a way that the dorsal face of the proximal part was in continuity with the plantar face of the distal part, as can be seen in Depéret's illustration. This tarsometatarsus has been restored by placing its dorsal and plantar faces correctly in line and, by comparison with recent forms, its shaft has been lengthened by plaster so that its present length is 158 mm. This is an estimate of its minimal size (its previous length was 143 mm).

The occurrence of a fossil Peafowl in the European Pliocene and Lower Pleistocene is confirmed by the fact that the specimens from Senèze (Stehlin 1923) and Saint-Vallier (Viret 1954), referred to as ?*G. bravardi*, also have the morphological characteristics of *Pavo* and differ from *Gallus*. They can also be attributed to the species *P. bravardi* (Gervais). Another Peafowl, *P. moldavicus*, recently described by Bochenski and Kurochkin (1987) from the Moldavian Roussillon is here placed in synonymy with *P. bravardi*.

SYSTEMATIC PALAEOLOGY

Order GALLIFORMES (Temminck, 1820)

Family PHASIANIDAE Vigors, 1825

Subfamily PHASIANINAE (Vigors, 1825)

Genus PAVO Linnaeus, 1758

Pavo bravardi (Gervais, 1849)

Plate 50, figs 1-3, 7, 8

- 1844 'Gallinacé' Gervais, p. 22.
 1849 *Gallus Bravardi* Gervais, p. 220.
 1848-1852 *Gallus Bravardi* Gervais; Gervais, t. 1, p. 238; t. 2, explanation of pl. 51; t. 3, pl. 51, fig. 1-1a.
 1859 *Gallus Bravardi* Gervais; Gervais p. 418, pl. 51, fig. 1-1a.
 1869-1871 *Gallus Bravardi* Gervais; Milne-Edwards, t. 2, p. 250.
 non 1890 *Gallus Bravardi* Gervais; Depéret, p. 134, pl. 13, fig. 11-11a (= *Gallus* sp.).
 1890 *Gallus Bravardi* Gervais; Depéret, p. 138, text-fig. 3a, b.
 non 1892 *Gallus Bravardi* Gervais; Depéret, p. 691 (= *Gallus* sp.).
 1923 ?*Gallus Bravardi* Gervais; Stehlin, p. 278.
 1933 *Gallus Bravardi* Gervais; Lambrecht, p. 443.
 non 1933 *Gallus Bravardi* Gervais; Lambrecht, p. 875, text-fig. 193H (= *Gallus aesculapi* Gaudry).
 1954 ?*Gallus bravardi* Gervais; Viret, p. 173.
 1964 *Gallus bravardi* Gervais; Brodkorb, p. 318.
 1987 *Pavo moldavicus* Bochenski and Kurochkin, p. 89, pl. 18, figs 13 and 14.

Holotype. Middle part of the shaft of a left tarsometatarsus with a spur. This specimen was in the collection of the Muséum national d'Histoire naturelle de Paris but, as yet, it has not been possible to find it.

Type stratum and locality. Lower Villanyium or Lower Villafranchian, Neogene Mammal Unit 16 (Mein 1975). Ardé near Issoire, Puy-de-Dôme, France.

Additional material. An almost complete left tarsometatarsus from Serrat-d'en-Vacquer, near Perpignan, Pyrénées-Orientales, France. Upper Ruscinium, Neogene Mammal Unit 15. This specimen is in the collection of the Musée Guimet d'Histoire naturelle de Lyon (Pp 269). Other specimens referable to the same species are known from the sites of Saint-Vallier, Drôme, France, Upper Villanyium, Neogene Mammal Unit 17 (Collection Musée Guimet d'Histoire naturelle de Lyon), Senèze near Brioude, Haute-Loire, France, Lower Biharium, Neogene Mammal Unit 18 (Collection Museum of Natural History of Basel), and Lucheshty, Kagul district, Moldavian SSR, Upper Pliocene, Moldavian Roussillon (Collection of the Palaeontological Institute of the USSR Academy of Sciences in Moscow).

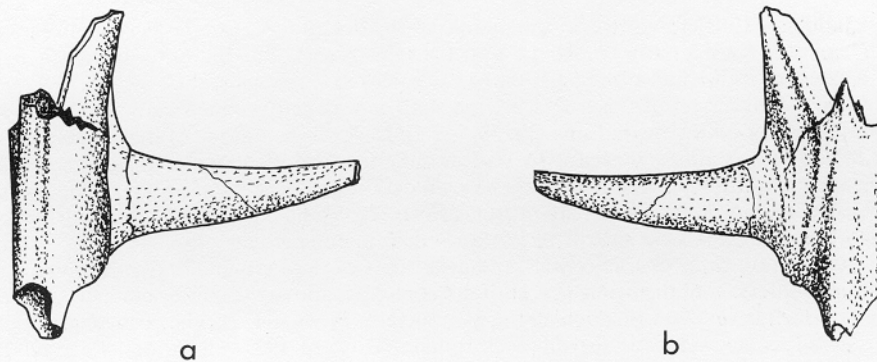
Original diagnosis (Gervais 1848-1852). 'Portion intermédiaire du tarse de Gallinacé. . . . Ce fragment est la partie la plus voisine de l'éperon. Celui-ci est long de 0m,021, quoique son sommet ait été cassé; sa base a 0m,013 de hauteur verticale. Cet éperon est assez comprimé; il est creusé en gouttière près de sa base, pour le passage des tendons. A cet endroit la face externe du tarse a 0m,015 et elle diminue brusquement à 0m,05 au dessous de la base de l'éperon par la cessation de la crête postérieure de l'os, qui n'est que la soudure au canon du métatarsien du pouce. Ce fragment a plus de rapport avec la partie correspondante du canon du Coq qu'avec la même partie chez le Paon ou les autres Gallinacés auxquels je l'ai comparé. Il indique un oiseau voisin des Coqs, et dont la taille était intermédiaire à celle du Paon et du Coq ordinaire, mais que je ne crois pas de la même espèce que ce dernier, quoiqu'il lui ressemble plus qu'aux autres oiseaux du même ordre.'

Remarks. This specimen is illustrated in natural size and there are probably two misprints in the dimensions given by Gervais in its description. On the figure the spur length, as preserved, is 31 mm instead of 21 mm, and the lateral face of the tarsometatarsus below the level of the bony spur core is 5 mm deep instead of 50 mm (0.05 m).

Description and comparisons

The anatomical descriptions follow the terminology of Baumel (1979).

Comparison with Ardé specimen (text-fig. 1). The spur of the Perpignan specimen looks very similar to the Ardé one. It is long, slightly curved and elliptical in section. It arises on the medial face of an intertendinal ossified septum running down the plantar face of the tarsometatarsus. This septum disappears a little below the level of the bony spur core so that the depth of the medial face of the shaft decreases considerably. On the base of the bony spur core and on its medial side, one can see a tendinal groove which is very similar to the tendinal groove illustrated in the Ardé specimen (Gervais, 1848-1852, pl. 51, fig. 1a). Although the shaft of the latter looks a little more robust than the Perpignan one, the dimensions are very close (Table 1).



TEXT-FIG. 1. *Pavo bravardi*, holotype, left tarsometatarsus, central part of the shaft, with the spur, from Ardé, Puy-de-Dôme, France (after Gervais 1848-1852, pl. 51, fig. 1-1a).
a, lateral view; b, medial view. Natural size.

Comparison with the recent genera Gallus and Pavo. The general shape of the Perpignan bone is slender, the shaft in the middle is rather thin while in the large-sized *Gallus* (which are artificially produced by selection, the wild *Gallus* being much smaller) the bone is proportionally shorter, and the shaft more robust. The Perpignan form has the same general outline as the two recent species of Peafowls, *P. muticus*, the Green peafowl, and *P. cristatus*, the Blue one.

In the proximal part the disposition of the hypotarsal calcaneal ridges is different in Peafowls and Junglefowls (Pl. 50, figs. 6 and 7). In Peafowls the medial calcaneal ridge (crista medialis hypotarsi of Baumel 1979) (Pl. 50, fig. 7, a) is prolonged by an ossified intertendinal septum along the medio-plantar corner of the bone and bears the bony core of the spur. In Junglefowls the medial calcaneal ridge is short and completely separated from the septum upon which the bony core arises (Pl. 50, fig. 5). In *Pavo* the lateral calcaneal ridge (crista lateralis hypotarsi of Baumel 1979) projects very little and is more or less included in the hypotarsal block (Pl. 50, fig. 7, b); in *Gallus* this ridge is well developed, flattened on its plantar face, and enlarged at its distal part (Ballmann 1969) (Pl. 50, figs. 5 and 6, b). The groove between these two ridges is deeper in *Gallus* than in *Pavo*. On the lateral side of the hypotarsus there is a short accessory lateral ridge, more developed in *Gallus* (Pl. 50, fig. 6, c) than in *Pavo* (Pl. 50, fig. 7, c). On the Perpignan tarsometatarsus the shape of the calcaneal ridges is similar to *Pavo*. The medial one was probably prolonged down to the spur by an ossified intertendinal septum which has been preserved but is no longer *in situ*.

In the proximal part the shaft narrows considerably below the articular part in Peafowls, while in Junglefowls it narrows gradually (Pl. 50, figs. 1 and 4). In Peafowls the sulcus extensorius is situated nearer

TABLE 1. Measurements of the bony spur core in *Pavo bravardi* and in recent *P. muticus*, male, in mm.

	<i>Pavo bravardi</i>		<i>P. muticus</i> male		
	Ardé	Perpignan	MNHN Paris		
		Pp 269	1891-1022	1875-50	1880-1397
Length of the bony spur core	31 (1)	31 (1)	30.0	26.0	31.0
Height of the spur core at its base	13	12	11.0	11.0	11.5
Depth of the spur core at its base	—	7.3	8.0	6.5	c. 8.0
Depth of the medial face of the tarso-metatarsus, above the spur core	15	11	—	—	—
Depth of the medial face of the tarso-metatarsus, below the spur core	5	6	—	—	—

(1) as preserved.

the medial side while in Junglefowls it is in the middle of the dorsal face. On the Perpignan tarsometatarsus the shaft also narrows considerably below the upper articular part, but the bone has been damaged and restored and it is not possible to see the position of the sulcus extensorius.

In the distal part, at the level of the trochleae, the shaft is widened symmetrically in *Pavo* (Pl. 50, fig. 2) while in *Gallus* it is wider on the medial side (Pl. 50, fig. 5). In *Pavo* the outline of the lateral side of the bone curves, while in *Gallus* it is almost straight. In Peafowls the trochlea metatarsi tertii projects with regard to the dorsal face of the shaft, while in Junglefowls it is almost on the same plane. The trochlea metatarsi tertii is also proportionally larger in Peafowls than in Junglefowls (Pl. 50, figs. 1-2 and 4-5). The trochlea metatarsi secundi is less strongly directed backwards in Peafowls than in Junglefowls.

Taking into account all these characteristics, the distal part of the Perpignan tarsometatarsus agrees with the genus *Pavo* and differs from the genus *Gallus*. It also presents, above the incisura intertrochlearis medialis, a small foramen, which is very conspicuous on the plantar face (Pl. 50, fig. 2). The occurrence of this foramen has been considered as characteristic for the Meleagrinae (Howard 1927; Olson and Farrand 1974) but it can also be seen in *Pavo* and in some specimens of *Gallus*. Steadman (1980) indicates that it may be present in several other genera of Phasianinae.

The bony spur core of the Perpignan form is long, elliptical in section, and slightly curved. In Peafowls the spur is often not very developed and variable in shape but several individuals of *P. muticus* in the collection of the Paris MNHN bear a spur very similar in shape and size to the Perpignan one (Table 1). Milne-Edwards (1867-1871) also illustrated a tarsometatarsus of *P. muticus* with a strong, elongated, and curved bony spur core. In Turkeys spur length increases with age and is fully developed only in 2-3-year-old individuals (Steadman 1980); it is probably the same in Peafowls. By this feature the Perpignan form is also similar to Junglefowls which have long, sharply pointed spurs (Pl. 50, figs. 4 and 5).

In its absolute dimensions the Perpignan Peafowl is very close to the male specimens of the Green peafowl, *P. muticus*, which are generally larger than the Blue ones, *P. cristatus*. It is also nearer to the Green peacocks by the ratios between the different measurements. In recent Peafowls the spur position differs in males and females, the spur being situated lower in Peacocks than in Peahens. The only difference between the recent and the fossil forms is that in the fossil the spur is situated in a lower position than in the recent males (Table 2). The mean distance between the middle of the spur core and the distal part of the bone, expressed as a percentage of its total length, is 40.1% in the Green peacocks and 33.3% in the Blue peacocks. In *P. bravardi* the minimal total length being 158 mm, the percentage of 29.7% for the position of the spur is a maximal value. In this form the bony spur core is situated immediately above the fossa metatarsi I, while in the recent Peafowls there is some distance between them.

Comparison with the recent genus Afropavo. Another Peafowl, *Afropavo congensis* from Africa (Chapin 1936) seems from osteological, myological, and karyological evidence to be more closely related to the genus *Pavo* than to any other gallinaceous bird (Lowe 1939; Hulsemans 1962; de Boer and van Bockstaele 1981). I compared the Perpignan Peacock with two specimens of *A. congensis* males from the American Museum of Natural History in New York, and one female from the Lyon Collection which was presented to me by the Royal Zoological Society of Antwerp. The Perpignan tarsometatarsus differs from the African ones by its much larger size (Table 2). In the two males there is a supplementary ridge between the crista medialis and the crista lateralis hypotarsi, which does not reach the distal part of the hypotarsus, but this supplementary ridge does not exist in the female specimen. This supplementary ridge also exists in some specimens of

EXPLANATION OF PLATE 50

Figs. 1-3. *Pavo bravardi* (Gervais). Musée Guimet d'Histoire naturelle de Lyon, n^o. Pp 269. Upper Ruscium of Serrat-d'en-Vacquer, near Perpignan (Pyrénées-Orientales), France. Left tarsometatarsus. 1, dorsal view, $\times 1$. 2, plantar view, $\times 1$. 3, medial view, $\times 1$.

Figs. 4-6. *Gallus gallus* (Linnaeus). Département des Sciences de la Terre de Lyon, n^o. 456-2. Recent. Left tarsometatarsus from a wild bird. 4, dorsal view, $\times 1$. 5, plantar view, $\times 1$. 6, proximal view, $\times 2$, a—crista medialis hypotarsi, b—crista lateralis hypotarsi, c—accessory lateral ridge.

Figs. 7 and 8. *P. bravardi* (Gervais). Left tarsometatarsus, n^o. Pp 269. 7, proximal view, $\times 1.5$, a, b, c, same as in fig. 6. 8, distal view, $\times 1.5$.

Fig. 9. *Afropavo congensis* Chapin. Département des Sciences de la Terre de Lyon, n^o. 1988-1. Recent. Left tarsometatarsus, proximal view, $\times 2$, a, b, c, same as in fig. 6, d—tubercle on the latero-plantar corner of the external cotyla.

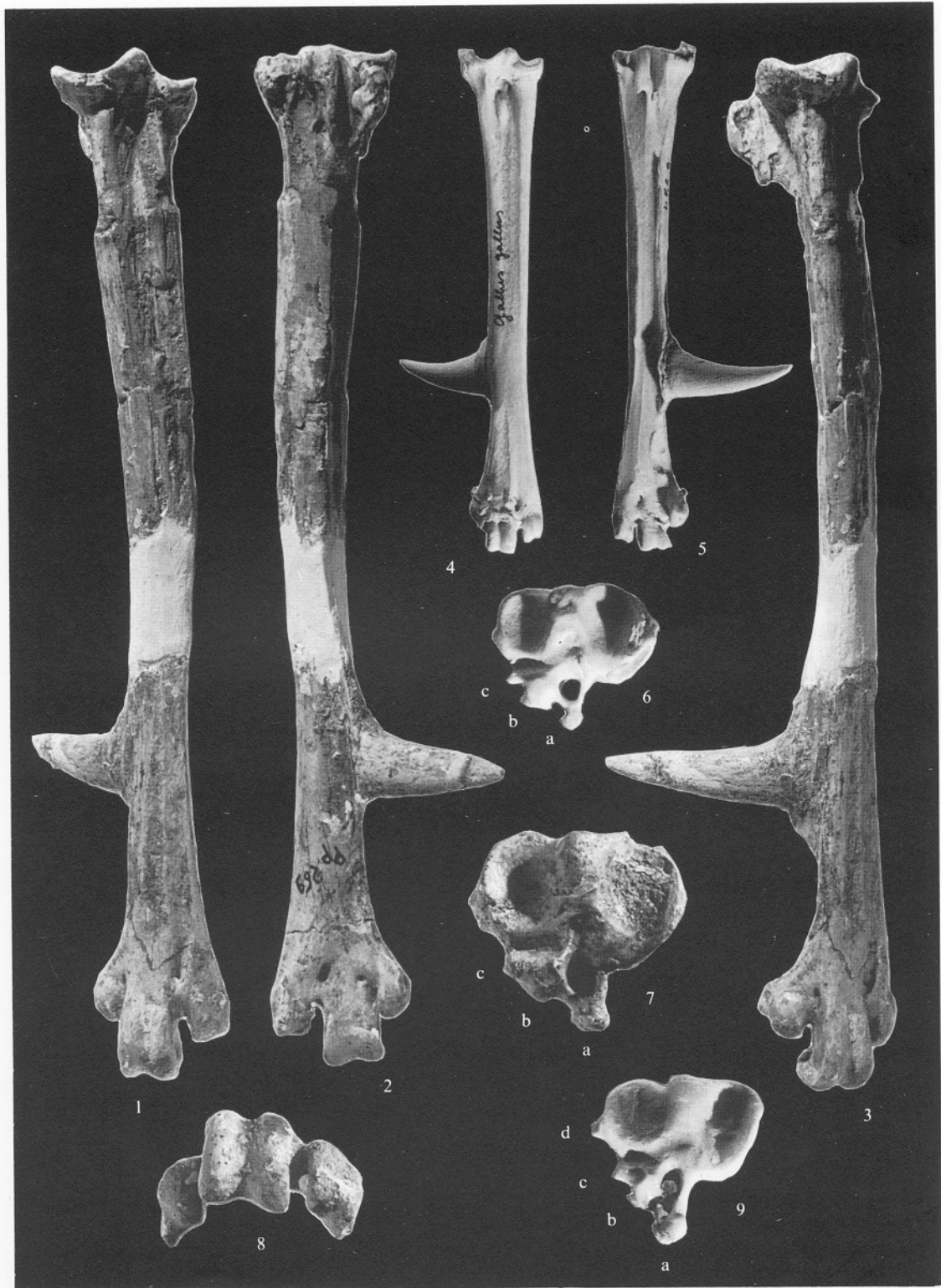


TABLE 2. Measurements of the tarsometatarsus in *Pavo bravardi* and in recent Peafowls, in mm.

	Total length 1	Proximal width 2	Proximal depth 3	Distal width 4	Distal depth 5	Width of the midshaft 6	Distance from the middle of the spur core to distal end 7	Ratio $\frac{7 \times 100}{1}$
<i>Pavo muticus</i> , male	extremes	139.4-167	19.0	19.3	19.5	8.2-9.8	46.5-54.0	31.1-35.5
	mean	152.5	—	—	—	9.1	50.7	33.3
	n	5	1	1	1	5	5	5
<i>P. muticus</i> , female	extremes	126.8-133.4	18.4-20.4	16.0-17.3	18.8-20.6	8.2-9.0	45.0-49.0	34.1-37.9
	mean	130.7	19.4	16.7	19.7	8.6	47.3	36.3
	n	3	2	2	2	3	3	3
<i>P. cristatus</i> , male	extremes	127.3-138	20.6-21.3	18.0-19.0	20.3-23.0	8.8-9.7	50.0-56.0	39.3-40.8
	mean	130.9	21.1	18.3	21.1	9.1	52.5	40.1
	n	4	4	4	4	4	4	4
<i>P. cristatus</i> , female	extremes	109-112.4	17.6-19.0	15.3-16.8	17.6-19.6	7.9-8.6	45	42.3
	mean	109.3	18.4	16.1	18.5	8.3	—	—
	n	3	3	3	3	3	1	1
<i>P. bravardi</i> , Perpignan Pp 269	min.	158	23.3	21.6	22.0	c. 10.5	47.0	max. 29.7
<i>Afropavo congensis</i> , male	extremes	104.5-112	15.1-15.9	14.0-14.1	13.9-15.2	5.8-6.3	38.0-40.5	33.9-38.8
	mean	108.25	15.5	14.05	14.55	6.05	39.25	36.35
	n	2	2	2	2	2	2	2
<i>A. congensis</i> , female, n = 1	79.0	13.0	12.6	11.3	9.1	4.4	34.0	43.6

Pavo (Howard 1927). It is generally present in the Meleagrinae (Steadman 1980). The medial intertrochlear foramen is absent in the two males but is present in the female.

In *A. congensis* there is a strongly developed tubercle on the latero-plantar corner of the lateral cotyla (Pl. 50, fig. 9, d). This tubercle exists also in *Pavo* but is smoother. At the distal part the trochlea metatarsi tertii, which is very wide in *Pavo*, is proportionally narrower in *Afropavo*. The ossified intertendinal septum which extends from the hypotarsus to the fossa metatarsi I and from which the bony spur core arises exists also in *Afropavo*, as in *Pavo* and many other phasianids. The spur core is long, tapered, elliptical in section, and slightly curved. It is situated proportionally higher in the female than in the male, and at the same level as in the Asiatic Peafowls, i.e. proportionally higher than in *P. bravardi* (Table 2).

In conclusion, the Perpignan form is more similar to the Asiatic Peafowls, and particularly to the Green one, than to the Congo Peafowl.

Comparison with P. moldavicus *Bochenski and Kurochkin*. This species was described from an incomplete lower part of a coracoid, from the locality Lucheshty, in Moldavia. Its age 'Moldavian Roussillon' is the same as the Perpignan fauna. Its size is indicated as being larger than any living species of the genus *Pavo* (15% larger than the largest bone of *P. muticus*). It is not possible to compare *P. bravardi* and *P. moldavicus* directly. The Perpignan specimen, as well as the other specimens from Saint-Vallier and Senèze, share the same size as the recent individuals of *P. muticus*. Moreover, in the collection of the Paris MNHN, one specimen of *P. muticus*, male, is larger than the Moldavian Peafowl. The medial part of its facies articularis sternalis is 10.4 mm thick on the left coracoid, and 11.9 mm on the right one, while in *P. moldavicus* this dimension is 7.5 mm (Bochenski and Kurochkin 1987).

Given that the Moldavian specimen is the same age as the Perpignan one, and considering the great variation in size in the recent Peafowls, I think that they probably belong to the same species.

PALAEOBIOGEOGRAPHICAL AND PALAEOECOLOGICAL IMPLICATIONS

It is necessary to emphasize the occurrence of an element of eastern Asiatic affinities in the Perpignan avifauna. Southern and eastern Asiatic elements, such as *Cathaya*, *Sciadopitys*, *Pterocarya*, *Parrotiopsis* cf. *jacquemontiana*, and *Microtropis fallax*, have also been found in the palynological study of the hill of Serrat-d'en-Vacquer, Sondage Fl de la Mutualité agricole de Perpignan (Cravatte *et al.* 1984). The genus *Pavo* is now restricted to Pakistan, India, Nepal, Bangladesh, Sri Lanka, south-west China, Burma, Thailand, Indochina, the Malay Peninsula, and Java, but its occurrence in the Pliocene and Lower Pleistocene of France and Moldavian SSR shows that it was much more widespread in the past. The discovery of a form related to it and isolated in Africa seems therefore much easier to understand. However, the Perpignan form is more closely related to the Asiatic form than to the African one, so the separation from an ancestral Peafowl into the two recent genera must have occurred before the Pliocene, and probably during the Miocene.

Recent Peafowls live in dense jungles or open forests, near water. Thus the presence of a Peafowl in the Perpignan fauna confirms that the environment was mainly forested, as has already been established by palynological data.

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Typescript received 4 July 1988

Revised typescript received 2 September 1988