The avian femur: morphology and terminology of the lateral condyle

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ABSTRACT – In the dinosaurs, the lateral condyle of the femur is subdivided into two parts, here termed semicondyles: cranial semicondyle which articulates primarily with the fibula, and caudal semicondyle which is known in the theropods as the ectocondylar tuber and articulates with the tibia. Modern birds also have two semicondyles, fibular and tibiofibular ("tibiofibular crest"), which roughly correspond in position to the non-avian theropod semicondyles. However, the basal birds have a single rounded lateral condyle which must have undergone differentiation into two modern avian semicondyles independently of those in the non-avian theropods. Since extrapolating anatomical terms for details of the femoral lateral condyle between modern birds and theropods seems unwarranted, I propose to use two separate, consistent sets of terms, both based on the subdivision of the lateral condyle into two semicondyles, as implemented for modern birds in Table 1.

Key words: *Aves, femur, morphology, terminology*

Le fémur avien: morphologie et terminologie du condyle latéral – Chez les dinosaures, le condyle latéral du fémur est divisé en deux parties, appelées ici semicondyles : le semicondyle cranial, qui s'articule principalement avec la fibula, et le semicondyle caudal, connu chez les théropodes sous le nom de tuber ectocondylaire, qui s'articule avec le tibia. Les oiseaux modernes ont aussi deux semicondyles, fibulaire et tibiofibulaire (« crête tibiofibulaire »), qui correspondent à peu près par leur position aux semicondyles des théropodes non-aviens. Cependant, les oiseaux basaux ont un condyle latéral unique arrondi, qui doit s'être différencié en deux semicondyles chez les oiseaux modernes indépendamment de ceux des théropodes non aviens. Comme il semble injustifié d'extrapoler les termes anatomiques décrivant les détails du condyle latéral du fémur entre les oiseaux modernes et les théropodes, je propose d'utiliser deux groupes de termes distincts, tous deux fondés sur la subdivision du condyle latéral en deux semicondyles, comme le montre le tableau 1 pour les oiseaux modernes.

Mots clés: *Aves, fémur, morphologie, terminologie*

INTRODUCTION

In contrast to the mammalian lineage, the reptilian fibula maintains its primitive tetrapod articulation with the femoral lateral condyle. In the lepidosaurs (Haines, 1942), notably varanids (Fig. 1A, see also Romer, 1956: fig. 172), crocodiles (Fig. 1B, see also Haines, 1942: fig. 1), basal archosaurs (Ewer, 1965: fig. 34/31; Sennikov, 1989: fig. 3), and the Triassic Tecovas formation femoral fragments which were assigned by Chatterjee (1991) to *Protoavis*, but are better comparable to lizards than to either *Protoavis* holotype or any birds, the femoral lateral condyle (in the comparative meaning of the term) is differentiated into the fibular groove or sulcus fibularis (Haines, 1942), which receives the fibular head, and the tibiofibular condyle which bears a tibial and a fibular facet separated by a tibiofibular crest, and thus reminds of the modern avian tibiofibular semicondyle (tibiofibular crest autt., see below).

The details of the femoral lateral condyle in the dinosaurs are surrounded by a paramount terminological confusion which calls for clarification. For the nonavian dinosaurs I propose to subdivide the lateral condyle into two semicondyles (new general term). The anterolaterodistal *semicondylus cranialis* (new term) articulates primarily with the fibula and has occasionally been labelled as "fibular condyle", a term originally used for the entire lateral condyle as the opposite of the tibial condyle. The posteromedioproximal *semicondylus caudalis* (new term) articulates primarily with the tibia and has been referred to by various names including "ectocondylar tuber" and "tibiofibular crest".

NONAVIAN THEROPODS

The caudal semicondyle was first identified in *Allosaurus* as the "outer condyle" (Gilmore, 1920) and then as "blocky protuberance" (Madsen, 1976). The term "ecto-

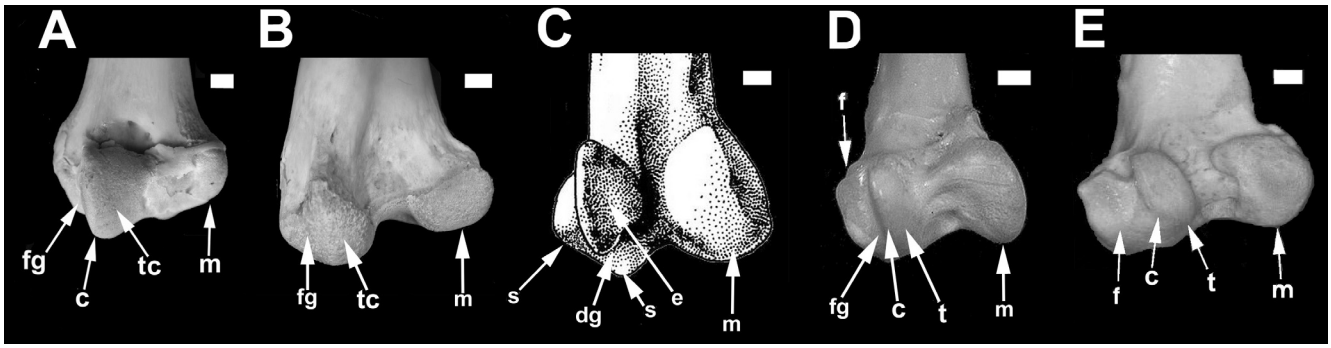

Figure 1 – Distal ends of left femur in caudal view: A, a monitor lizard (*Varanus* sp.); B, a crocodile (*Crocodilus rhombifer*); C, a coelurosaurian theropod (*Bagaraatan ostromi*) (Osmolska, 1996); D, a typical neornithine bird (*Fulica americana*); E, a diving, foot-propelled neornithine bird (*Phalacrocorax capensis*). Abbreviations: c, tibiofibular crest; dg, distal groove; e, caudal semicondyle (ectocondylar tuber); f, fibular semicondyle; fg, fibular groove; m, medial condyle; s, cranial semicondyle; t, tibiofibular semicondyle; tc, tibiofibular condyle. Scale bars equal 2 mm in A, D, and E and 6 mm in B and C.

condylar tuber" comes from Welles (1984) who referred to the lateral condyle as the ectocondyle, hence the term "ectocondylar" for a projection of the lateral condyle. Surprisingly, Madsen and Welles (2000) used another ad hoc term "tuberous process" instead of any of their previous terms. The caudal semicondyle has also been occasionally referred to as the lateral condyle (Molnar et al., 1990: p. 184; Langer 2004: figs. 2.7-2.8), and, rather surprisingly, as the fibular condyle in *Marasuchus* (Sereno & Arcucci 1994: fig. 10).

After Ballmann (1969) and Baumel (1979) reinstated the old Milne-Edwards's (1868) term crista tibiofibularis for birds, Rowe (1989) applied it to the caudal semicondyle in *Syntarsus*, and many others followed, especially for non-maniraptoriform theropods, in which, paradoxically, the tuber tends to be prima facie more crest-like than in the maniraptorans. Rowe (1989) apparently assumed that the tibiofibular semicondyle of birds evolved from the ectocondylar tuber as subsequently proposed by Chiappe (1996) and accepted by Farlow et al. (2000).

BIRDS

In the basal birds including *Archaeopteryx* (pers. obs.), *Confuciusornis* (pers. obs.), all Enantiornithes that are known in this respect (Chiappe and Walker, 2002: fig. 11.12: Lamanna et al. 2006), and *Vorona* (Forster et al., 2002: figs. 12.2 and 12.3), there is a single rounded lateral condyle, expanding distally, without any clear groove or crest and thus any indication of subdivision into a tibiofibular and fibular semicondyles. Since all the named basal bird taxa are extremely unlikely to form a monophyletic group with respect to the modern birds, the undivided rounded lateral condyle seems to be primitive for birds. Judging from its distal position, the single lateral condyle of the basal birds seems to incorporate the cranial semicondyle of non-avian theropods whereas the contribution of the caudal semicondyle (ectocondylar tuber) is unclear.A new set of anatomical terms for the lateral condyle of modern birds (Euornithes, Ornithurae *sensu* Chiappe) is provided in Table 1. The lateral condyle comprises two semicondyles enclosing a fibular groove (Fig. 1D): the cranial and lateral labrum-shaped fibular semicondyle and the caudal and medial tibiofibular semicondyle, the latter once described as "a ridge which plays between the heads of the tibia and fibula" (Lydekker, 1879) and bears articular facets for both.

The tibiofibular semicondyle has been widely referred to as tibiofibular crest. This name goes back to Milne-Edwards (1868:p. 32 and pl. 2), who distinguished *condyle interne ou tibial* and *condyle externe ou péronéen* (= fibular), corresponding, respectively, to the medial condyle and lateral condyle in the present, comparative terminology. Within the lateral condyle he identified two structures: *crête péronéotibiale* (fibulo-tibial crest) and the *gorge péronière* (fibular groove). However, in his figure 2/9, the line from the label "condyle externe" extends to the fibular semicondyle, which is not incorrect since the fibular semicondyle is part of the lateral condyle (Table 1), but seems to have engendered an inadvertent divergence of meanings and inevitable confusion of the terms "fibular" (*péronéen*) and "external", which Milne-Edwards used as synonyms.

Following Milne-Edwards's labels rather than writing, Howard (1929) set the usage of "internal condyle", "external condyle" and "fibular condyle" as three *equivalent* terms for the three projections of the avian distal femur without recognizing the entire lateral condyle as a morphological entity. She labelled the fibular semicondyle as "fibular condyle" and the tibiofibular semicondyle as "external condyle". Although clearly in conflict with current standards, Vickers-Rich et al. (2002) apparently applied Howard´s scheme to *Avimimus* except that the terms "internal" and "external" have been replaced by "medial" and "lateral", leading to a highly confusing concept of a "lateral condyle" being only the medial part of the lateral condyle in the widely used, comparative sense.

Stresemann (1934: fig. 83, p. 76) was the first to explicitly correct, in the last single-authored comprehensive

Present proposal	Baumel & Witmer (1993)	Howard (1929)[1]	Ballmann (1969)	Milne-Edwards (1868)
Condylus medialis	condylus medialis	internal condyle	condylus internus	condyle interne (= tibial)
Condylus lateralis	condylus lateralis	----------	condylus fibularis[2]	condyle externe (=péronéen)
Semicondylus tibiofibularis+	----------	external condyle	crista peroneo-tibialis	crête péronéo-tibiale
Facies articularis tibialis+	----------	----------	----------	----------
Facies articularis fibularis+	----------	----------	----------	----------
Crista tibiofibularis*[3]	crista tibiofibularis	----------	----------	----------
Sulcus fibularis	trochlea fibularis[4]	fibular groove	sulcus fibularis	gorge péronière
Semicondylus fibularis	----------	fibular condyle	----------	----------

Table 1 – New (+), emended (*), and old anatomical terms for the femoral condyles in modern birds.
[1]Howard (1929) used her terms as labels without defining them otherwise.
[2]It is unclear why Ballmann (1969) translated Milne-Edwards´s condyle externe to condylus fibularis but the condyle interne to condylus internus. However, subsequently Ballmann (1976: 19) returned to the term condylus externus, which shows that he considered these two terms as synonyms.
[3]In the proposed emended meaning, this term refers to the crest marking the boundary between the tibial and fibular facets of the tibiofibular semicondyle.
[4]The use this term as a synonym of sulcus fibularis seems inappropriate. The anatomical term trochlea refers to an entire pulley-like structure (such as the phalangeal head, the term caput phalangis being a synonym of trochlea phalangis) rather than a groove alone, and thus implies the inclusion of projections adjacent to the groove, which is neither intended nor desirable in this case (the inclusion of both semicondyles would make this term synonymous with the entire lateral condyle).

handbook of ornithology, the 19th century usage of terms internus-externus to the modern terms medialis-lateralis, which was in compliance with the developments in the formal anatomical nomenclature. Unfortunately, avian palaeontologists largely ignored these developments and continued with the terminological confusion. Ballmann (1969) adopted a latinized version of Milne-Edwards´s terms and his basic distinction of two condyles, internal and fibular, the latter being a synonym of external condyle (Balmann 1976).

It was only the Nomina Anatomica Avium (Baumel 1979), followed by Butendieck et al., (1981) and Baumel & Witmer (1993: fig. 4.16), that effectively applied the comparative concept of the lateral condyle to the avian femur, but lost what had been gained in Howard`s (1929) terminology, that is, a term ("fibular condyle") for the fibular semicondyle. Baumel & Witmer (1993: 108) defined the tibiofibular crest as the "crest on the lateral condyle of the femur that separates its tibial articular facet from that for the fibula". Unfortunately, their intended meaning of the term crista tibiofibularis is not clear. A rigorous understanding of their definition suggests that they really mean only the crest, as adopted here (Table 1), because the tibiofibular semicondyle bears both the tibial and the fibular facet. However, they did not provide a specific term for the entire tibiofibular semicondyle nor did they otherwise indicate a new, restricted usage of the term crista tibiofibularis. With the term crista tibiofibularis as the only specific label attached to the external condyle, their fig 4.16 (p. 64) is conducive to using this term for the entire tibiofibular semicondyle, which is in agreement with Milne-Edwards (1868) but not with the usual naming of condylar structures and not with the known diversity of this structure in birds.

The usage of the term "crista tibiofibularis" for the entire tibiofibular semicondyle is misleading on pure anatomical grounds. It is a convex, caudally protruding condylar structure rather than a crest which is a term normally used for non-articular surface structures. In addition, even in some modern birds, such as the cormorants (Phalacrocoracidae), the tibiofibular semicondyle is broad and does not look at all like a crest (Fig. 1E). Therefore, the term "tibiofibular crest" is here (Table 1) reserved for the ridge that separates the fibular groove from the tibial articular facet of the tibiofibular semicondyle, in agreement with the letter of the definition provided by Baumel & Witmer (1993: 108) rather than its traditional understanding by most authors.

CONCLUSIONS

The fibular and tibiofibular semicondyles of modern birds approximately correspond in their respective craniolateral and caudomedial positions to the cranial and caudal semicondyles of the non-avian theropods and the derivation of the modern avian form the non-avian theropod semicondyles has been widely accepted following Rowe (1989) and Chiappe (1996). However, since the tibiofibular semicondyle is located at the tip of the lateral condyle, that

is, more distally than the caudal semicondyle, Farlow et al. (2000) hypothesized a distal migration of the caudal semicondyle in the avian lineage. While this remains a possibility, much more obvious is the incorporation of the cranial semicondyle which has already occupied the distal position in the non-avian theropods.

No matter whether and how the single lateral condyle of basal birds may have originated from any of the non-avian theropod semicondyles, the two modern avian semicondyles originated from the single-condyle condition which makes an isomorphic (one-to-one) transformation of the theropod semicondyles into modern avian ones and thus their (structural) homology next to impossible, and the widely accepted extrapolation of terms between non-avian theropods and birds unwarranted.

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