WALKING KINEMATICS PARAMETERS IN SOME PALEOGNATHOUS AND NEOGNATHOUS NEOTROPICAL BIRDS

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Resumo. – Parâmetros cinemáticos da marcha em aves paleognatas e neognatas neotropicais. – Foram estudados os parâmetros cinemáticos da marcha de tinamídeos (*Tinamus solitarius*, *Crypturellus obsoletus* e *Rhynchotus rusfescens*) e cariamídeos (*Cariama cristata* e *Chunga burmeisteri*) com o objetivo de verificar se a duração da fase de elevação dos membros é um parâmetro discriminante para as aves paleognatas e neognatas. Os tinamídeos, assim como as ratitas, são aves paleognatas e os cariamídeos, que compartilham com as grandes ratitas a adaptação cursora, são neognatas. As mensurações dos ossos longos dos membros posteriores, bem como a análise imagem por imagem de vídeo registrado em alta velocidade de aves marchando em condições normais, permitiram comparar a duração da fase de elevação dos membros em duas categorias funcionais: aves com os membros posteriores longos e esticados vs aquelas com membros posteriores curtos e flexionados. Foram também comparadas as aves pertencentes a dois grupos filogeneticamente distintos: Neognathae vs Palaeognathae. Os resultados indicam que existe uma correlação entre a fase de elevação dos membros e os dois clados estudados: as paleognatas exibem uma fase mais longa do que as neognatas pertencentes à mesma categoria funcional. No entanto, apenas este parâmetro não permite discriminar os dois grupos. As categorias funcionais estão também correlacionadas à duração da fase de elevação dos membros: aves com membros flexionados têm esta fase mais curta do que aquelas com membros esticados. Assim, esses dados são congruentes com os resultados de várias análises filogenéticas recentes, que colocam os Tinamidae como grupo-irmão das ratitas no táxon Palaeognathae.

Abstract. – The walking parameters of the tinamous (*Tinamus solitarius, Crypturellus obsoletus* and *Rhynchotus rusfescens*) and cariamids (*Cariama cristata* and *Chunga burmeisteri*) were studied with the aim of verifying whether the duration of the swing phase is a discriminant parameter for paleognathous and neognathous birds. Tinamous are paleognathous birds as are the ratites, whereas the cariamids are neognathous birds sharing a cursorial adaptation with the large ratites. Osteological measurements of the long bones of the hind limbs, and frame by frame analysis of high speed video records of the birds walking under usual conditions, allowed for comparing duration of the swing phase in two functional categories: birds with long stretched-hind limbs versus those with short flexed-limbs. In addition were compared birds of two distinct phylogenetic groups: Neognathae vs Palaeognathae. Results indicate that there is a correlation between the duration of the swing phase and two studied clades, the paleognathous birds having a longer swing phase duration than neognathous birds belonging to the same functional categories. However, this parameter alone does not allow for discriminating between groups. The functional categories are also correlated to the duration of the swing phase as flexed-limb birds have a shorter swing phase than the stretched-limb ones. These data are congruent with several recent phylogenetic analysis results, placing the Tinamidae as a sister group of ratites within the Palaeognathae taxon. *Accepted 23 May 2005.*

Key words: Tinamidae, Cariamidae, terrestrial locomotion, kinematics.

INTRODUCTION

Terrestrial locomotion plays an important role in the ecology of many birds for foraging or collecting nesting material (Verstappen & Aerts 2000). Several aspects, such as mechanics, energetics or kinematics of bipedal locomotion of birds, have previously been studied [see Verstappen *et al.* (2000) and Reilly (2000) for a review]. These studies show that birds use locomotor patterns similar to those existing among biped mammals: walking, running and hopping (Hayes & Alexander 1983, Alexander & Jayes 1983, Gatesy & Biewener 1991). Strategies for increasing velocity have been studied by Gatesy & Biewener (1991), Gatesy (1999), Reilly (2000), Verstappen *et al.* (2000) and Abourachid (2000). Velocity can be raised by increasing either the frequency of limb movements or the stride length. Relatively to their size, large birds with stretched hind limbs increase their speed mainly by increasing the frequency, whereas small species with flexed hind limbs achieved this by the length of the stride (Gatesy & Biewener 1991, Abourachid 2001). In the phases of the limb rhythmic cycle, i.e., the stance (contact phase) and the swing (no contact phase), only the duration of the latter is not related to animal velocity (Alexander & Ker 1990, Abourachid 2001) but seems to vary a little bit according to species. Abourachid (2001), in a sample of ratites and Galloanseres, noted that the duration of the swing phase is significantly longer among the paleognathous [(Brown Kiwi (*Apteryx australis*) and Great Rhea (*Rhea americana*)] than among the neognathous [(Mallard Duck (*Anas platyrhynchos*), Quail (*Coturnix coturnix*), Guineafowl (*Numida meleagris*)]. Phylogenetically related species could then show slightly different locomotion features from those of more distantly related species. In the swing phase, the absence of force exchange between the foot and the ground reduces external sensorial informa-

tion (exteroreceptive returns). The swing phase duration is controlled by a medular oscillator (Grillner *et al.* 2000) and is probably modulated by the amplitude of oscillation (McGeer 1992) imposed by the limb length (pendulum effect). The aim of this paper is to verify the initial results obtained by Abourachid (2001) when other paleognathous, the Tinamidae, and neognathous with long limbs adapted for running, the Cariamidae, were included in the comparison. Does the swing duration of the limb rhythmic activity during bipedal progression allow for establishing a link between the phylogenetic groups of birds and the morphology of the species?

MATERIAL AND METHODS

The Tinamidae and Cariamidae are exclusively Neotropical birds. The first family is more diversified, including 9 genera and 47 species; the second has only two species placed in two different genera (*Cariama* and *Chunga*). Tinamous occur in a wide range of habitats. The Solitary Tinamou (*Tinamus solitarius*) occupies tropical and subtropical forests, preferably warm and moist, but also areas with a cold dry season, typically in the Atlantic rain forest of Brazil; the Brown Tinamou (*Crypturellus obsoletus*) occurs in tropical and subtropical forests; and the Red-winged Tinamou (*Rhynchotus rusfescens*) lives in tropical lowlands, mainly damp grasslands and savanna woodlands (Cabot 1992). Tinamous have discrete habits, avoid flying and, when disturbed, prefer to escape by running, except for the *Tinamus* species. Most of the time, flight is in a straight line, with few maneuvers due to the small size of the rectrices (Silveira & Höfling 2001).

The two species of Cariamidae, the Red-legged (*Cariama cristata*) and the Black-legged (*Chunga burmeisteri*) seriemas, inhabit open woodlands. Red-legged Seriemas also occur in
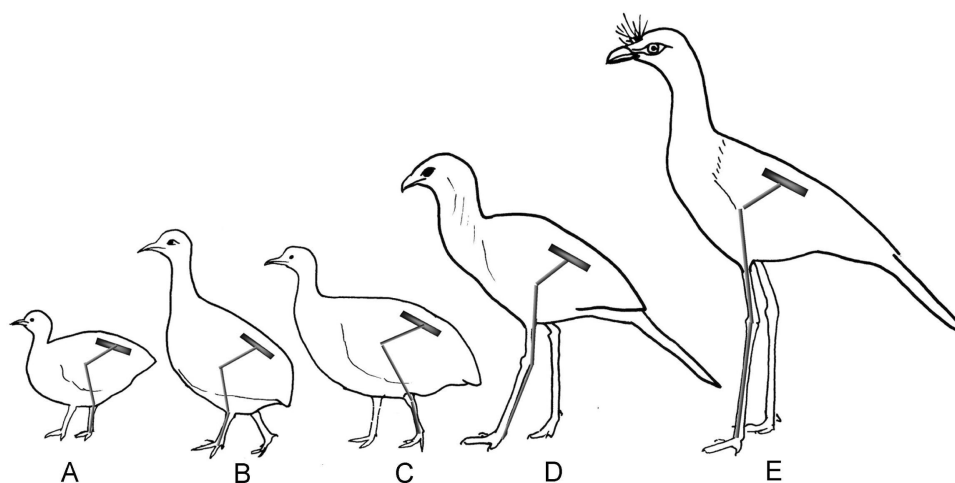
FIG. 1. Scheme of the Tinamidae and Cariamidae, with the bones of the pelvic appendage (pelvis, femur, tibiotarsus and tarsometatarsus). A: Brown Tinamou; B: Red-winged Tinamou, C: Solitary Tinamou, D: Black-legged Seriema, E: Red-legged Seriema.

thorny scrubland, ranchland and hilly grassland near woodlands in southestern Brazil and Uruguay; typical habitats include caatinga, cerrado and chaco. Black-legged Seriemas typically occur in the chaco and woodlands, being apparently restricted to lower altitudes. Seriemas are among the largest ground-dwelling neognathous birds. They possess cursorial adaptation and are swift runners. Red-legged Seriemas, when chased, may attain speeds of 25–40 or even 70 km/h. Seriemas rarely fly (Gonzaga 1996).

We filmed 4 individuals of Solitary Tinamou, 5 of Brown Tinamou, 15 Red-winged Tinamou, 3 Red-legged Seriema and 2 Black-legged Seriema. In the latter there were both a male and a female, the male walking more slowly than the female. The Tinamidae were in their usual enclosure at the "Criadouro Científico e Cultural Poços de Caldas" (Poços de Caldas, MG, Brazil). This enclosure was 7.5 m wide x 10 m long and 3.5 m high, half covered with high grass, the other half with sandy ground. The Cariamidae were

filmed in a 7.5 m wide x 13 m long and 6 m high enclosure, with sandy ground, at the "Fundação Parque Zoológico de São Paulo" (São Paulo, SP, Brazil).

All the birds were filmed under the same experimental conditions: free locomotion in front a wall of the enclosure. A 3 m long ruler with marks at each 5 cm was placed close to one of the sides of the cage. At each 25 cm of this rule, the marks were continued on the ground by parallel lines, being clearly visible on the records. The birds were incited to move parallel to the side on which the rule was placed, so they crossed the lines on the ground. It was then easy to evaluate the walk distance. Sequences of 8 s were recorded at 250 fields/s with the use of a high-speed video camera (Redlake MotionScope), and afterwards on a numerical cassette (DVCAM Sony DSR-PD100P).

Measurements ($\pm$ 0.01 mm) of the long bones of the hind limbs (femur, tibiotarsus and tarsometatarsus) of the studied species
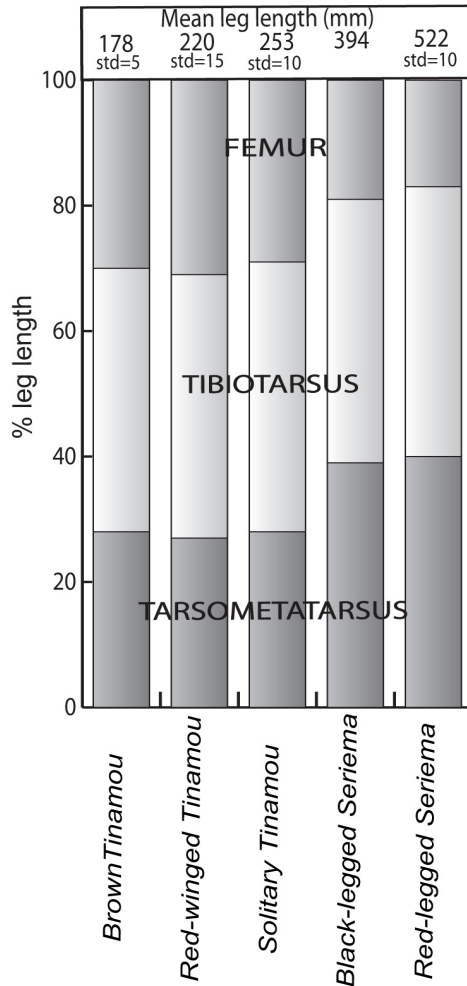
FIG. 2. Hind limb long bones (femur, tibiotarsus and tarsometatarsus) in the Tinamidae and Cariamidae) as a percentage of total hind limb length. The mean hind limb length is presented for each species on the top.

(Fig. 1) were taken with a caliper on isolated pieces of skeletons of adult specimens from collections of the Museu de História Natural de Taubaté (MHNT), of the Departamento de Zoologia, Instituto de Biociências, of the Universidade de São Paulo (AZ), in Brazil, and of the British Museum of Natural History (BMNH), in UK. The osteological material was represented by seven skeletons of Solitary Tinamou (MHNT: 8, 497, 801, 1016, 1022; AZ: 137, 139), five of Brown Tinamou (MHNT: 7, 832, 1135, 1163, 1233), nine of Red-winged Tinamou (MHNT: 9, 220, 689, 719; AZ: 148, 149, 151, 152, 155), four of Red-legged Seriema (MHNT: 78, 1136, 1214, 1267) and two of Black-legged Seriema (BMNH: 1870.10.5.1, 1891.7.20.91). Data on body mass were taken from Sick (1997).

The films were analysed frame by frame, and sequences with birds moving straight and perpendicularly to the camera were selected. Kinematic parameters were recorded on 43 cycles for Solitary Tinamou, 46 for Brown Tinamou, 68 for Red-winged Tinamou, 68 for Red-legged Seriema and 60 for Black-legged Seriema.

The times of touchdown, when all the toes contact the ground, and takeoff, when the last toe leaves the ground, were noted (precision $\pm$ 0.01 s). Stride lengths ($\pm$ 0.05 m) were measured between two identical successive positions of the same foot, using the lines marked on the ground. Stride duration is the time lag between two successive touchdowns. Absolute speed was calculated by dividing the stride length by the stride duration. In order to compare species with various sizes and lengths of hind limbs, absolute speeds were converted into relative speeds (Alexander & Jayes 1983), relative speed being absolute speed divided by (gh^2), where g corresponds to gravity acceleration (9.81 m/s) and h to hip height. The position of the hip on the living birds was found by palpation, so that we were able to estimate the hip height on the frames at the middle of the stance. Swing duration corresponds to the time lag between limb takeoff and its next touchdown whereas, inversely, stance duration represents the time lag between limb touchdown and its next takeoff. These two parameters were recorded
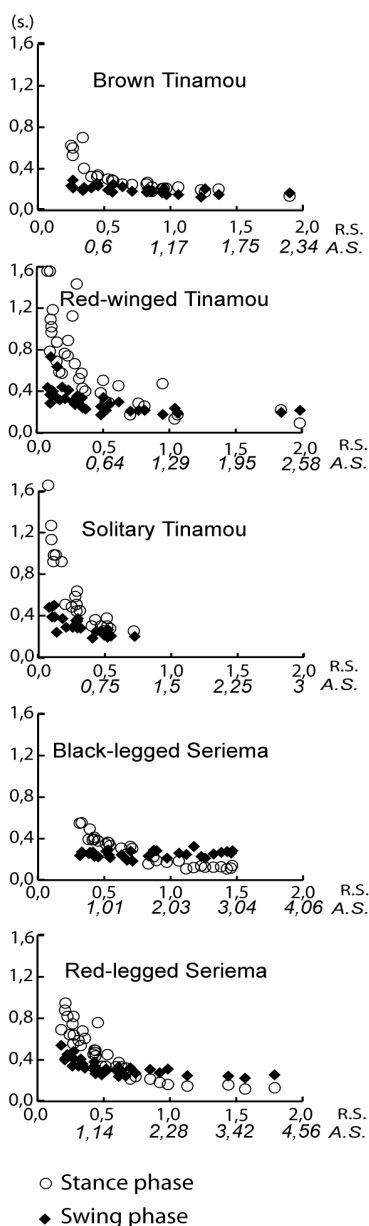
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○ Stance phase
◆ Swing phase

FIG. 3. Duration of the stance and swing phase (s) vs speed of the Tinamidae and Cariamidae. A.S.: absolute speed (m/s), R.S.: relative speed.

in seconds. Comparisons of means were undertaken using the Student t-tests.

RESULTS

Inside each group, the length of the hind limb reflects the size of the animal (Fig. 2). In the Tinamidae, the Brown Tinamou (500 g) has shorter limbs than both Red-winged Tinamou (800 g) and Solitary Tinamou (1300 g), and in the Cariamidae, the Black-legged Seriema (1300 g) has shorter limbs than Red-legged Seriema (1500 g). The proportions of the three long bones are comparable within each group. Amongst the Tinamidae, the femura, tibiotarsi and tarsometatarsi correspond to 30%, 42% and 28% of the total length of the legs, respectively. Amongst the Cariamidae, the femura, tibiotarsi and tarsometatarsi represent 19 and 17%, 42 and 43%, and 39 and 40% of the total length of the hind limbs. The Cariamidae have proportionally shorter femora and proportionally longer tarsometatarsi than the Tinamidae, whereas the tibiotarsi have the same proportions in the two groups.

The Red-legged Seriema, a larger bird, reaches a speed up to 14.5 km/h whereas the Brown Tinamou, smaller, moves at the maximum speed of around 8 km/h. However, the relative speeds calculated using hip height (14 cm in Brown Tinamou, 17 cm in Red-winged Tinamou, 23 cm in Solitary Tinamou, 42 cm in Black-legged Seriema and 53 cm in Red-legged Seriema) are comparable. In Figure 3, absolute and relative speeds are indicated. The birds do not behave the same under our experimental conditions. Red-winged Tinamou and Solitary Tinamou sometimes walk very slowly (relative speed less than 0.25). Solitary Tinamou never walks rapidly and its relative speed does not exceed 0.72. This result is explained by the fact that Solitary Tinamou is the only species of our sample that escape flying.

Three kinds of speed can be distinguished considering the duration of swing and stance phases (Fig. 3). For relative speeds under 0.5, stance duration is long, decreasing with
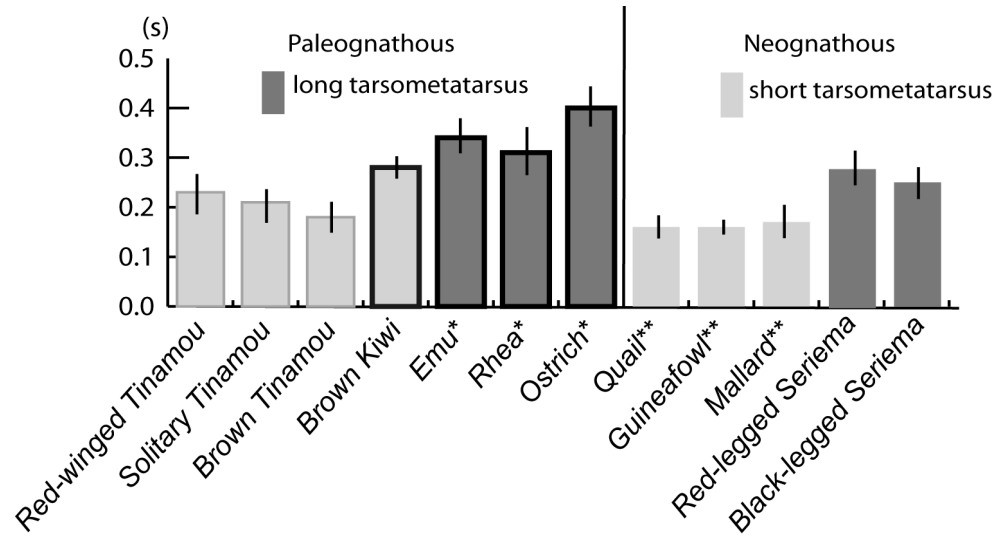
FIG. 4. Mean swing duration (s) for walking in the paleognathous and neognathous birds. * : from Abourachid & Renous (2000); ** : from Abourachid (2001).

increase of speed. Duration of the swing phase is shorter, decreasing more moderately with speed, and showing great variability. Relative speeds lower than 0.5 are very slow and occur mainly when birds are exploring or foraging rather than when moving directly from one point to another. For relative speeds over 0.5, duration of the stance phase still decreases slightly with speed whereas duration of the swing phase reaches a plateau. Stance duration is comparable to swing duration at a relative speeds over 0.8 in the Tinamidae, although it becomes shorter than the swing amongst the Cariamidae. The duty factor [the stance duration expressed in percent of the cycle duration (swing+ stance)] is less than 50% when the swing duration is longer than the stance and, according to Alexander & Jayes (1983), the Cariamidae are running for relative speeds over 0.8, whereas the Tinamidae are still walking for those relative speeds. Nevertheless, this difference arises from a decrease of the stance duration and not from an increase of the swing duration.

In order to compare swing duration in different species, we used the mean plateau value reached at relative speeds over 0.5. Mean duration of the swing phase is 0.18 s (SD = 0.03) in Brown Tinamou, 0.23 s (SD = 0.05) in Red-winged Tinamou, 0.22 s (SD = 0.03) in Solitary Tinamou, 0.25 s (SD = 0.04) in Black-legged Seriema, and 0.28 s (SD = 0.03) in Red-legged Seriema. Comparison of the means shows that the values for Black-legged Seriema and Red-winged Tinamou are not different, as neither are those between Red-winged Tinamou and Solitary Tinamou (*P* = 0.1).

DISCUSSION

The aim of this work is to verify whether or not the swing phase duration is higher in paleognathous than in neognathous birds (Abourachid 2001). With this in mind, we added to the species object of this previous paper , other species of paleognathous birds, the Tinamidae, and cur-

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sorial neognathous birds, the Cariamidae. Does this postulate remain relevant with the amount of data suggesting the presence of phylogenetic relationships between the two groups, or does it also concern morphofunctional features without relationships with the phylogeny?

Taking into account the length of the long bones as a portion of the total hind limb length among the paleognathous and neognathous species studied, it appears that the Cariamidae, cursorial birds such as the large ratites (Abourachid & Renous 2000), have a longer tarsometatarsus than the latter (37% vs 40%). Nevertheless, when the proportions of the hind limbs in our sample are inserted into the ternary diagram used by Gatesy & Middleton (1997) for all theropod groups (including 23 orders of birds), the tarsometatarsus of the Cariamidae and large ratites are within the range for long tarsometatarsus animals (> 35%). The other birds of our sample, the Tinamidae, Brown Kiwi and non cursorial neognathous share a shorter tarsometatarsus (< 30%). In our sample, this means that cursorial birds share a longer tarsometatarsus, whatever their phylogenetic relationship.

Abourachid (2001) found a significant difference between the swing phase duration of paleognathous ratites [Ostrich (*Struthio camelus*), Great Rhea , Emu (*Dromaius novaehollandidae*) and Brown Kiwi] and neognathous birds [Quail, Mallard Duck and Guineafowl]. These new data include this information in all the paleognathous groups: ratites and tinamous, and also paleognathous and neognathous birds with either long or short tarsometatarsus (Fig. 4). The paleognathous birds could not be differentiated from the neognathous based on duration of the swing phase alone because it is longer in the Cariamidae than in the Tinamidae so that we took into account the morphological type. We compared the mean swing length in the paleognathous with long tarsometatarsus (0.35 s ± 0.06 s), paleognathous with short tarsometatarsus excluding the Brown Kiwi (0.20 s ± 0.05 s), neognathous with long tarsometatarsus (0.26 s ± 0.04 s) and neognathous with short tarsometatarsus (0.16 s ± 0.02 s). The means are significantly different in the four groups ($P > 0.05$). We can thus observe that inside a morphological group, the paleognathous birds have a longer swing duration than the neognathous birds. On the other hand, the Brown Kiwi, presenting a very different functional type with a short tarsometatarsus (23%) and very flexed limbs (Abourachid & Renous 2000), share high swing duration (0.28 s ± 0.01 s) with the large ratites with long tarsometatarsus (0.35 s ± 0.05 s), so that the ratites are distinguished from the Tinamidae (0.207 s ± 0.042 s) by longer swing duration.

Lengthening of the tarsometatarsus in cursorial birds that increase the length of the most mobile part of the limb and the stride length could be also related to mechanical properties, allowing an efficient use of an inverse pendulum system even at medium velocity (Rubenson *et al.* 2004). The short tarsometatarsus and thus a short limb mobile part may on the contrary not be very efficient for a pendular effect, and spring-driven hind limb protraction mechanism (Roberts *et al.* 1997) could be use, allowing a spring mass system functionning even during walking as found in the Tinamidae (Hancock *et al.* 2004).

Based on our data, the ratites thus always form the more homogeneous group and the Tinamidae show high duration of swing phase values compared to the neognathous belonging to the same functional category, this being congruent with results of recent phylogenetic analyses (e. g., Groth & Barrowclough 1999, van Tuinen *et al.* 2000, Livesey & Zusi 2001, Mayr & Clarke 2003). Theses analyses place the Tinamidae as a sister taxon of the ratites,

within a monophylelic group, the Palaeognathae. Nevertheless, the Tinamidae have been established (e.g., Houde 1988) as a sister taxon of the Neognathae, and amongst this latter group, Livesey & Zusi (2001) consider the Cariamidae as a basal group in the Neoaves.

CONCLUSIONS

Duration of the swing phase in the paleognathous and neognathous clearly discriminate two morphofunctional categories: birds with long tarsometatarsus, having a longer swing phase, and birds with short tarsometatarsus, with a shorter swing phase. However, on the whole, and if taking into account functional category, the paleognathous present a longer swing duration than that of the neognathous. Therefore, there seems to be a trend for a longer swing duration in the paleognathous than in the neognathous birds. This could be related to a difference at the nervous system but further studies are needed indeed to examine this hypothesis.

ACKNOWLEGMENTS

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