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KINEMATIC DESCRIPTION OF THE VERTICAL CLIMBING OF *Dasypus novemcinctus* (XENARTHRA, DASYPODIDAE): THE FIRST REPORT OF THIS ABILITY IN ARMADILLOS

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ABSTRACT. Armadillos are well-known quadrupeds whose digging abilities classify them differently into many fossorial categories. This is the first time a kinematic description is provided on the vertical climbing sequences performed by these animals, more specifically by the nine-banded armadillo *Dasypus novemcinctus*. After an opportunistic observation of climbing behavior, video recording sessions were setup to document wire mesh climbing. The individuals climbed up to its top showing four distinct ways of vertical progression, such as lateral and diagonal-sequences as well as few styles that resemble the asymmetrical motions used by quadrupeds on land. Sharp claws were used as strategic points of attachment on a substrate, and tails provided additional support during vertical progression. Thus, the locomotory repertoire of armadillos is far more diverse than previously considered.

RESUMO. Descrição cinemática da escalada vertical de *Dasypus novemcinctus* (Xenarthra, Dasypodidae): o primeiro registro desta habilidade em tatus. Tatus são quadrúpedes bem conhecidos cujas habilidades escavatórias classificam-nos de forma diferenciada em diversas categorias fossoriais. Esta é a primeira vez que a descrição cinemática de sequências de escalada vertical realizada por estes animais, mais especificamente pelo tatu de nove-bandas *Dasypus novemcinctus*, é feita. Após uma observação oportunística de escalada, sessões de gravação em vídeo foram realizadas a fim de documentar a escalada em grade. Os indivíduos escalaram-na até o topo exibindo quatro maneiras distintas de progressão vertical, tais como sequências laterais e diagonais e alguns estilos que se assemelhavam aos movimentos assimétricos usados por quadrúpedes em terra. Garras afiadas foram usadas como pontos estratégicos de adesão ao substrato, e as caudas forneceram suporte adicional durante a progressão vertical. Assim sendo, o repertório locomotor dos tatus é bem mais diverso do que até então considerado.

Key words: Behavior. Cingulata. Locomotion. Nine-banded armadillo. Xenarthra.

Palavras-chave: Comportamento. Cingulata. Locomoção. Tatu-de-nove-bandas. Xenarthra.

Climbing ability allows animals to perform upward or downward locomotion on vertical or very steep substrates (Maderson 1965; Gallardo-Santis et al. 2005). Within the superorder Xenarthra, climbing is mostly known among Pilosa (sloths and anteaters), rather than Cingulata (armadillos). Sloths are particularly adept at climbing vertical surfaces as they bear long limbs with long claws that allow the ascending/descending movement along tree branches and lianas. There are descriptions of climbing behavior of sloths (Mendel 1981, 1985; Nyakatura et al. 2010), as well as records of the climbing ability of anteaters (Shaw et al. 1987; Redford 1985; Young et al. 2003; Rodrigues et al. 2008).

In contrast, armadillos are well known for their digging ability. These mammals are indeed fossorial to varying extents, and digging is mediated by a strong forearm extension (Vizcaíno et al. 1999; Vizcaíno & Milne 2002). Other than their powerfully-built limbs, the rigidity of their axial skeleton, partially braced against a strong carapace (Vaughan et al. 2000) may have contributed to the development of a digging capability instead of a cursorial competence (Superina & Loughry 2012). The climbing activity of armadillos has not been reported.

The nine-banded armadillo *Dasybus novemcinctus* Linnaeus, 1758 is widely distributed from the lowlands of temperate South America to the southern USA. If startled, this species jumps straight up (Hoffman 2005), but whether it is capable of climbing (i.e., a vertical ascension on a perpendicular plane to the ground) remained unrecorded. The aim of this study is to provide the first report of climbing behavior in nine-banded armadillos, providing the kinematic description of vertical climbing activity for *D. novemcinctus*.

This study was held at Lauro de Souza Lima Institute (ILSL) at Bauru County in São Paulo State, Brazil, in June, 2015. The behavior here reported was initially observed by chance during a study performed to describe the digging behavior of *D. novemcinctus*, which was conducted in accordance with the Research Ethics Committee of the Federal University of São Paulo (UNIFESP) under procedural number 1701280316. When confined at a wire mesh-lined vivarium (about 3 m x 2 m x 2.5 m), the

individuals spontaneously jumped against the mesh walls and climbed them, which thus led us to perform this. These walls were typically formed by rhombic wire mesh fences (6 m x 2 m) with knuckle-twist top mesh finishing. The diameter of wire mesh is 3 mm, with 4 cm openings. Each fence of the vivarium was sustained by two cylindrical steel bars at about 1 m intervals (**Fig. 1**). Adult individuals of *D. novemcinctus* (n=5; three males and two females) had been recently captured from a savannah reserve, where this institute is placed. After the experiment, the animals were released.

During the experiments, individuals were placed at the basis of the mesh walls and released as soon as they grabbed it with the four paws. Once released, the act of climbing the walls was recorded with a digital camera (SONY Cyber-shot DSC-H50 model, 9.1 Megapixels) at 30 frames/s until the individual stopped as the vivarium was closed at its top. The same individual was then taken off the grid and placed again at the basis for a new performance (n=19 records in total). The observations were then based on the succession in which paws grabbed the walls during climbing.

After all the video recordings were produced, the locomotor patterns were detailed and described. Herein, the terms used to describe the patterns noted were taken from kinematic approaches used for analyzing gaits of quadrupeds in the context of horizontal displacements (Dagg 1973; Hildebrand 1976, 1977). Since these definitions are essentially assigned for different patterns of limbs coordination, their use seems adequate for our purpose of describing vertical progression. Accordingly, the climbing activity performed by *D. novemcinctus* was illustrated by taking representative sequences of symmetrical and asymmetrical gait-analogs.

When placed at the mesh walls, all the animals climbed up to its top (about 2.5 m high). Nineteen sequences were recorded, and through the analysis of the video recordings the movement sequences were then described. Four main sequences (1-4) were identified and are described as follows:

1. The right hindlimb (RH) was used as a reference for this sequence, which then starts with the stance phase of this limb. The right

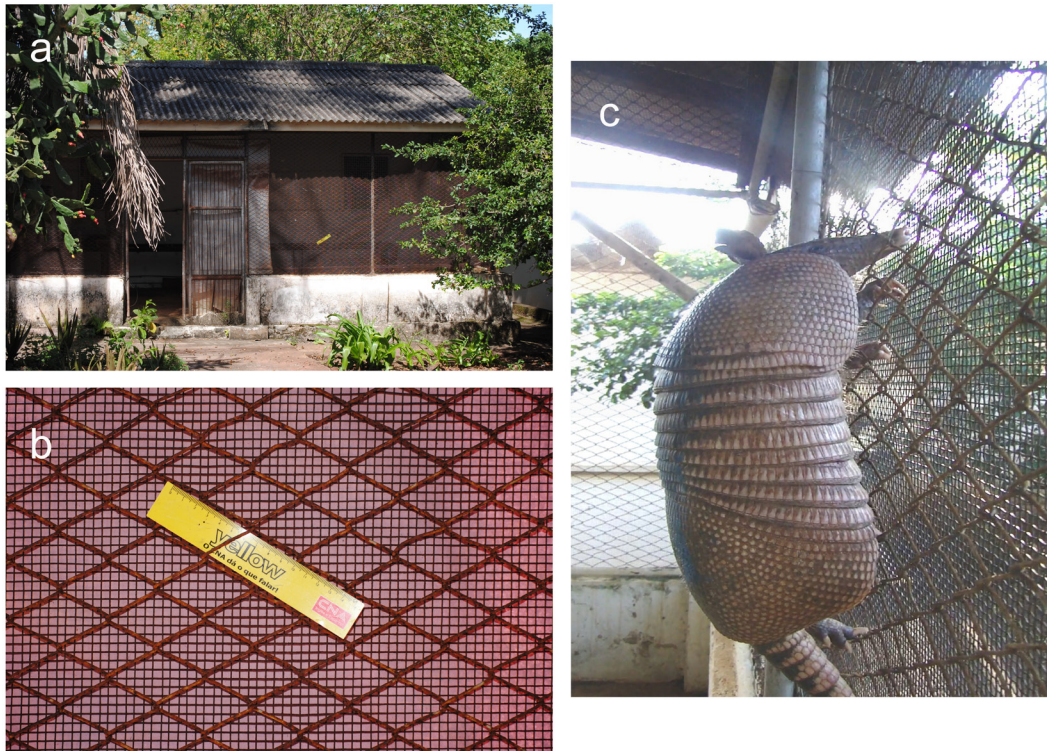


Fig. 1. Wire mesh fenced vivarium at ILSL where the experiment was held. (a) External view of the whole structure. (b) Detail of the mesh fence (scale: 15 cm) that was used for recording climbing behavior. (c) One of the armadillos during the climbing movement to the top of the vivarium.

forelimb (RF) starts the swing phase, and after grabbing the mesh the left hindlimb (LH) lifts off the mesh, moves and returns to the stance phase. Then the left fore limb (LF) swings and returns to the mesh. At this sequence just one limb at a time was in motion, while the others remained grabbed to sustain the body on the vertical surface. The pattern of this sequence (RH-RF-LH-LF) is known as lateral walk (Hildebrand 1976) (**Fig. 2**).

2. The sequence begins with the RF in motion, while the other limbs remain grabbed to the mesh. After the RF grabbing the mesh the LF repeats this movement, going through the swing phase and returning to the stance phase. With the fore limbs on the mesh (and here the claws are more attained to the mesh) the animal pulls up both hind limbs that move and return to the mesh at the same time. This sequence (RF-LF-RH/LH or LH + RH) is analogous to the half-bound sequence

on terrestrial flat ground, an asymmetrical gait in which pairs of fore and hind limbs alternately contact the ground (Hildebrand & Goslow 2001).

3. The LF starts the movement lifting off the mesh and then advancing to it, while the others remain grabbed. As follows, the RF repeats the sequence, while the others remain on the mesh. The animal then moves both hind limbs up by curving the body; following this the LF moves and advances to the mesh (the same for the RF) and then the motion ceases with the animal straightening the body and buttressing all the limbs on the mesh. The pattern of this sequence (LF-RF-LH-RH) is known as gallop (Hildebrand 1977) (**Fig. 3**).

4. The LH was used as a reference for this sequence that begins with the LH on the mesh. After that, the RF swings and advances to the mesh (the same for the RH, followed by the LF and finally the LH). The pattern of this

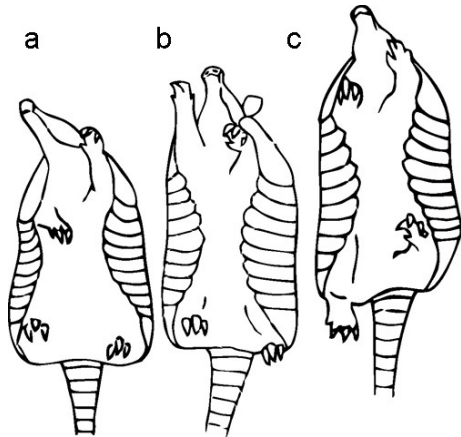


Fig. 2. Ventral view of the climbing phases during the lateral sequence of *D. novemcinctus*. The cycle initiates with one of the fore limbs being brought to an upper position (a), followed by both the contralateral hind and the remaining fore movement upwards (b). The cycle finally ends with the repetition of the first movement (c). Drawings based on the video recordings.

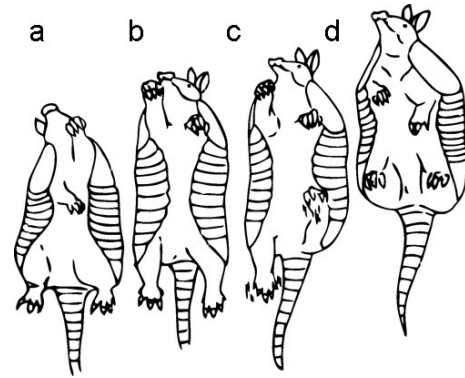


Fig. 3. Ventral view of the climbing phases during the gallop of *D. novemcinctus*. First the individual moves one of the fore limbs towards a higher anchorage point at the vertical plane (a) followed by the other fore limb (b); then the hindlimbs are brought upwards (one after another) so that the body is momentarily sustained just by both fore limbs (c); the hindlimbs lean on consecutively (d). Drawings based on the video recordings.

sequence (LH-RF-RH-LF) is known as diagonal walk (Hildebrand 1976).

Some variation on these sequences were also observed, such as: LH-RH-RF-LF, in which the animal reverses the fore limbs sequence relative to the gallop sequence, and LH-LF-RF-RH, in which it reverses the right limbs sequence of the lateral walk sequence. It is worth mentioning that, once in motion, the individuals did not change directions or attempted a downward movement once they reached the top of the mesh, where they stopped and were removed or jumped to the ground. Moreover, during all the sequences the tail alternated from buttressing on the mesh to swinging during the climbing. No degree of maneuverability was observed during this kind of locomotion.

As mentioned above, armadillos have never been reported to be capable of vertical climbing. Other related behaviors have been reported for armadillos (climbing and vertical displacement; Cortés et al. 2015), none of them entailed climbing along substrates at angles greater than 45° relative to a horizontal plane, as described by Maderson (1965) and Gallardo-Santis et al. (2005).

Dasybus novemcinctus presented distinct ways of moving upwards, displaying coordination

styles that resembled the symmetrical as well as the asymmetrical gaits used by quadrupeds on land and other horizontal substrates. In the first case, each hindlimb is followed by one of the fore limbs integrating a four-beat sequence (i.e., a sequence in which each foot in a step cycle hits the ground at a different time). If the fore unit (which comes next in time) is on the same side of its hind precursor, then we refer this pattern as a lateral-sequence. Similarly, a diagonal-sequence is characterized when the fore unit lies on the opposite side of the previous hind/by contralateral limbs in phase. The remaining types can be depicted by the alternation between the actions of the fore and hindlimbs, with both the forepaws reaching an upper position before the hind ones.

When employing a lateral or a diagonal sequence, the animals had at least three paws holding the mesh to support their weight. Both these patterns were often used by *D. novemcinctus* during our observations, possibly reflecting a more stable ascension. On the other hand, the asymmetrical styles exhibited a period of support in which only the forepaws were seen grabbing the mesh. At this very moment, while the animal brings its hind legs up, the trunk experiences a move-

ment of dorsiflexion that probably increases the length of the step. Here, the foreclaws seemed to have an important role in preventing the animal to fall.

In this context, some morphological characters, such as sharp claws to offer strategic points of attachment on a substrate (Cartmill 1974; Mc Neil 2003; Crandell et al. 2014), and tails to be used as additional support or even as a prehensile structure, as found in primates (Schmidt 2010), are important. The sharp claws of *D. novemcinctus* anchor the limbs on the holes of the grid and thus help stabilizing the animal at a vertical position, providing support. Bent digits assume a hook-like position that tie the animal to the mesh and prevents it from falling. Early mammals are presumed to have used their claws to grip, in lack of opposable toes (Taylor et al. 1972).

Armadillos also have long tails, although they are not prehensile (a character that is used to aid climbing in mammals; Gallardo-Santis et al. 2005). However, the presence of a long tail can suggest arboreal habits in other animals such as rodents (Earl & Nel 1976), primates (Schmidt 2010) and marsupials (Antunes et al. 2016). The tail of the individuals of *D. novemcinctus* here studied seems to be used as a support during the climbing, thus offering an extra buttress point when moving upwards. However, further observation is needed to confirm the role of the tail during climbing in armadillos.

Although *D. novemcinctus* is able to climb as here reported, its performance appears to be restricted to the ability of moving upwards, with limited maneuverability. Likewise, the act of climbing up and clinging on the top has also been observed in the indian pangolin (*Manis crassicaudata* Geoffroy 1803), an armored mammal that shares behavioral traits with armadillos. This behavior has been associated with fleeing, even though the pangolin has shown the ability to perform downward displacement (Mohapatra & Panda 2014). The ability to climb down head-first noticed in some mammals seems to be related to anatomical features such as highly flexible ankle joints in squirrels (Nations & Olson 2015) or the presence of a prehensile tail, which provides stability (Montgomery & Lubin 1977; Lubin 1983) and

can be found in rodents (Earl & Nel 1976), primates (Schmidt 2010), marsupials (Antunes et al. 2016) and even in xenarthrans such as the semi-arboreal collared anteater (*Tamandua tetradactyla* Linnaeus, 1758) (Hayssen 2011). These traits are lacking in armadillos.

In conclusion, we can state that the nine-banded armadillo *D. novemcinctus* is capable of climbing, possibly as an escape strategy. Further research is required to confirm the use of climbing in the field and its possible role as an escape strategy in armadillos.

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