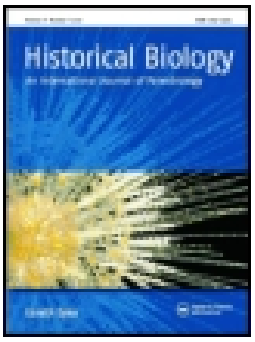

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ARTICLE

A review of the concepts of 'axony' and their bearing on tetrapod ichnology

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ABSTRACT
Two meanings of the term axony are found in the ichnological literature. Multiple meanings may prove to be a double-edge sword, complicating scientific communication. In vertebrate ichnology the first meaning of axony relies on aspects of locomotion related to the body weight support and propulsive thrust. A second one concerns axony as a purely geometric and dimensional descriptor. These approaches are based on a static view of the impression process, implying the loss of much important information. Here we report an analysis of shallowly impressed footprints referred to the ichnotaxa *Ichniotherium sphaerodactylum* and *Dimetropus osageorum*. The analysis was carried out by considering the track registration as a dynamic process and attempting to identify and describe axony conditions during movements. Variations in the axony conditions can be understood in the light of the producer's foot anatomy and the reciprocal relations between foot bone elements. The concept of axony can be a useful tool in ichnological practice only when it is related to the complex dynamic of locomotion and the resulting track registration. It can help in restoring the interconnections between track and track-maker, re-establishing the biological significance of tetrapod footprints.

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Introduction

A problem afflicting all areas of knowledge is attribution of different meanings and different uses to the same word or to conventional terms commonly used in the context of a specific discipline (Romano 2015, 2016; Romano and Cifelli 2015). Tetrapod ichnology is not immune to such issues and a good example is the multifaceted meaning of the term 'axony', which may have several implications (i.e. anatomical, behavioral and related to the dynamic of locomotion) in the context of track analysis and trackmaker identification. The term 'axony' originally constituted an indicator of the functionality of the track producer, in particular identifying the main axis accomplishing body weight support during locomotion and thrust. In the ichnological literature the term is commonly used to identify the greatest relative length of digit impressions, even when the longest trace does not correspond to the most functional digit in the trackmaker autopod (Figure 1). Losing its original meaning, the term becomes simply a morphological and geometrical descriptor.

The same dichotomy is maintained in other disciplines: in general zoology and in the study of body fossils, the term 'axony' is adopted with a functional meaning and is linked to the osteological elements bearing maximum loads during a single step cycle. Within the same context, a different meaning is adopted in mammalian studies, where the term 'axony' is closely related to size and particularly a digits relative length and robustness. Both of the meanings are seemingly useful in the field of tetrapod ichnology, providing at first glance meaningful information for describing and interpreting tetrapod footprints in the light of different perspectives: from the merely morphological to the one focused on dynamic of track formation and possible attribution to putative (palaeo-) zoological categories.

Besides affecting the ability of scientific communication in general, the current apparent ambiguity within the term 'axony', regarding both its meaning and its use, obviously impacts the quality and reliability of track description, ichnotaxa diagnoses and descriptions, as well as attempts at trackmaker identification. The history surrounding the different meanings of axony is here briefly summarized and discussed, together with the proposal of a more integral view based on a dynamic conception of the footprint impression process.

The term axony in tetrapod ichnology

A quite exhaustive definition and discussion of the term axony in the field of tetrapod paleoichnology is the one provided by Leonardi (1987, p. 47–48): '*The fact or the effect of a footprint having the axis in a determinate direction. The axis in this case, is not the long axis (the basis for the measurement [...]) but rather the axis of the most important digit. This corresponds generally to the axis that receives the greatest load and, at times, coincides with the long axis.*'

According to this author, the term axony primarily pertains to information about the functionality of the trackmaker's foot during the cycle of locomotion, on the basis of digit trace configuration; coherently, different axony conditions (e.g., entaxony, mesaxony, paraxony, ectaxony) can be recognized

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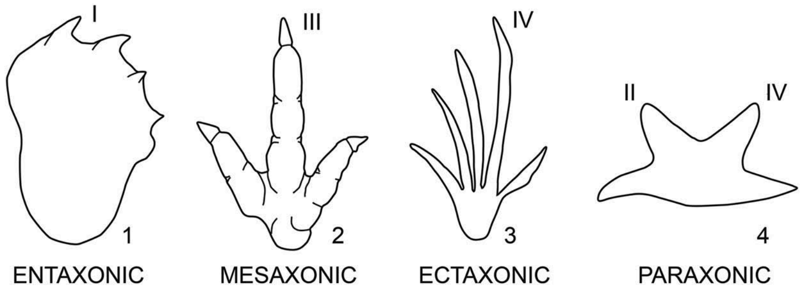

Figure 1. Classical subdivision of axonies purely based on a geometric criterion. **(1)** Entaxony in a sauropod pes footprint (redrawn from Thulborn 1990); (**2**) Mesaxony in a theropod pes footprint (redrawn from Thulborn 1990); **(3)** Ectaxony in a lacertoid pes footprint (redrawn from lockley and Jackson 2008); **(4)** Paraxony in a lacertoid manus footprint (redrawn from Leonardi 1987).

Figure 2. Different axony conditions on the light of differential depth of impression in *Ichniotherium sphaerodactylum* pes. **(1)** MNG-10072; **(2)** Interpretative drawing; **(3)** Entaxony (trackmaker medial functional prevalence) during the touch-down phase; **(4)** Entaxony (trackmaker centro-medial weight support) during the weight-bearing phase; **(5)** Entaxony during the kick-off phase. Solid lines indicate footprint outline; dashed lines indicate pad traces. For each phase, red to orange areas indicate pad traces with maximal functional prevalence; yellow ones indicate pad traces with minimal functional prevalence. Scale bar represents 5 cm. Institutional abbreviation: MNG, Museum der Natur, Gotha, Germany.

on the basis of the most important digit (i.e. the one receiving the greatest load). At the same time, the author referred to a geometrical significance for such axony conditions, identifying footprint symmetry/asymmetry (Leonardi 1987). In this framework, the functional and the morphological/dimensional meanings imply establishing a direct and unambiguous relation between functionality on one side, and size and morphology on the other. A similar approach can be found in Thulborn (1990), with a discussion of the term axony, primarily based on functionality and only later related to digits' morphology and size.

In other cases, the term axony was characterized in a purely morphological/dimensional fashion, without direct hints on the dynamic of locomotion and on different roles that pedal elements can play in body weight support and propulsive thrust (e.g., Schulp and Brokx 1999; Whyte and Romano 2001; Gierlinsky and Sabath 2002; Thulborn 2006; Mateus and Milàn 2010; Voigt et al. 2010; Klein et al. 2011; Meldrum et al. 2011; Costa Da Silva et al. 2012; Kim et al. 2012) (Figure 1).

Under this meaning, axony was also adopted as a two dimensional descriptor. In discussing mesaxony in bipedal dinosaurs and ground-dwelling birds, Lockley (2009; see also Weems 1992) adopted axony to describe the digit III protrusion with respect to the medial and lateral digits; in these cases the term could lose the geometrical meaning related to footprint symmetry/asymmetry (e.g., Kim et al. 2013).

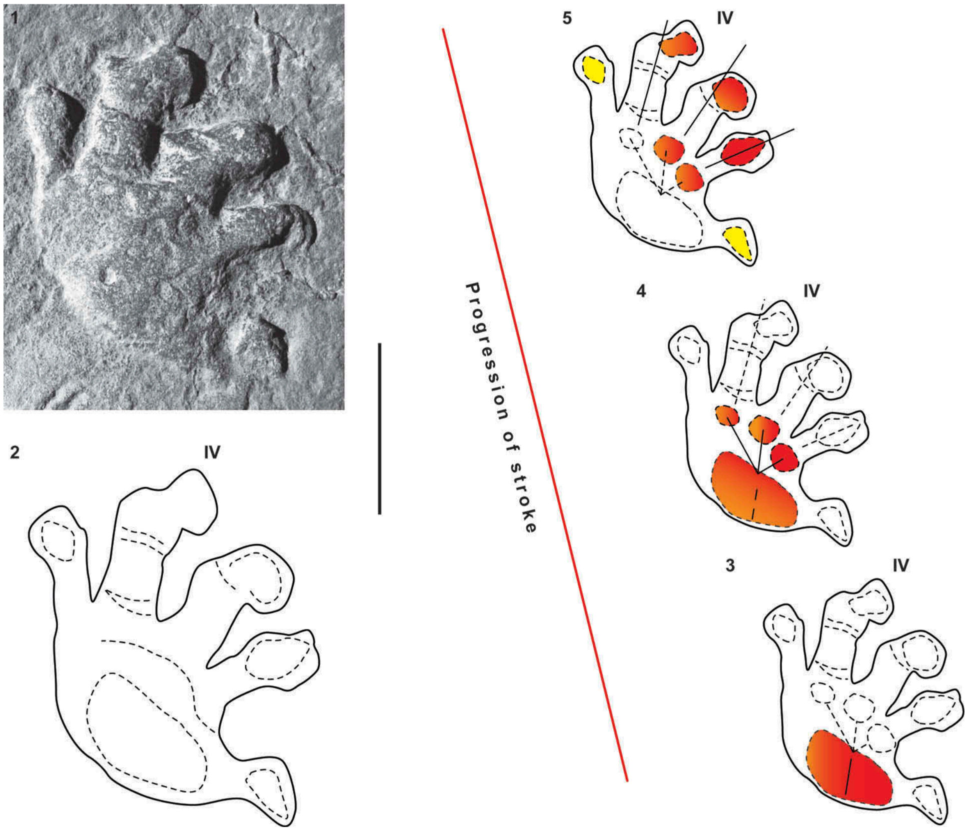

Figure 3. Different axony conditions on the light of differential depth of impression in *Ichniotherium sphaerodactylum* manus. **(1)** MNG-1351; **(2)** Interpretative drawing; **(3)** Entaxony (trackmaker medial functional prevalence) during the touch-down phase; **(4)** Mesaxony (trackmaker central weight support) during the maximum load phase; **(5)** Entaxony during the kick-off phase. Solid lines indicate footprint outline; dashed lines indicate pad traces. For each phase, red to orange areas indicate pad traces with maximal functional prevalence; yellow ones indicate pad traces with minimal functional prevalence. Scale bar represents 5 cm. Institutional abbreviation: MNG, Museum der Natur, Gotha, Germany.

Although the term axony is often adopted as a morphological and dimensional descriptor, thus potentially obscuring functional meaning and the chance to describe in detail the locomotion dynamics, in other cases the term axony is explicitly used to indicate the footprint functional prevalence (by means of impression depth), clearly separating this concept from a footprint's two-dimensional outline (e.g., D'Orazi Porchetti and Nicosia 2007; Valentini et al. 2007; Avanzini et al. 2008). In this case, provided descriptions are firmly based on the comprehension of the dynamic of track formation, at least taking into account different phases making up the locomotion cycle. The functionality of different digits during subsequent locomotion phases can be highlighted (Avanzini 1998), thus allowing a more careful description of the dynamics of the track registration process and the different locomotion styles of trackmakers.

The term axony in body fossils and general zoology studies

In the study of body fossils and zoological groups in general, the term axony has taken on different nuances, making the semantic problem even more complex. As for ichnology, the first interpretation of the term is purely functional in nature and regards the axis of maximum load during locomotion.

One of the first examples of a functional meaning of the term axony is found in Osborn (1904), which connected weight distribution to the digits of the hand in Sauropoda. Other examples bearing the same functional meaning of the term are provided by Allaby (1999) and Yates et al. (2010). According to these authors, different conditions of axony (e.g., entaxony and mesaxony) are completely independent from morphology and/or size and do not show relations with a more developed length of internal digits or with the autopod symmetry.

Conversely, in some areas of zoology the term axony seems to be related to the digits' relative length rather than to a particular functional significance (at least with regard to the weight support and propulsive thrust during locomotion). In particular, this approach is found in the study of mammals (mainly in hominids and primates) and originates mainly from the use of the terms introduced by Lessertisseur and Jouffroy (1973, 1978). These authors defined entaxony as the condition in which the second digital ray is longer than the fourth, mesaxony if the second and the fourth are of the same length, ectaxony if the fourth is longer than the third and paraxony in the case where the axis is positioned in the space between two interdigital rays characterized by the same strength and length (regardless of their functional importance). Examples of such use of the term may be found in Hamrick (1997), Weisbecker and Schmid (2007), Weisbecker and Warton (2006) and Morgan and Verzin (2011).

In addition to the existing terminology, Weisbecker and Schmid (2007) added more terms within the concept of

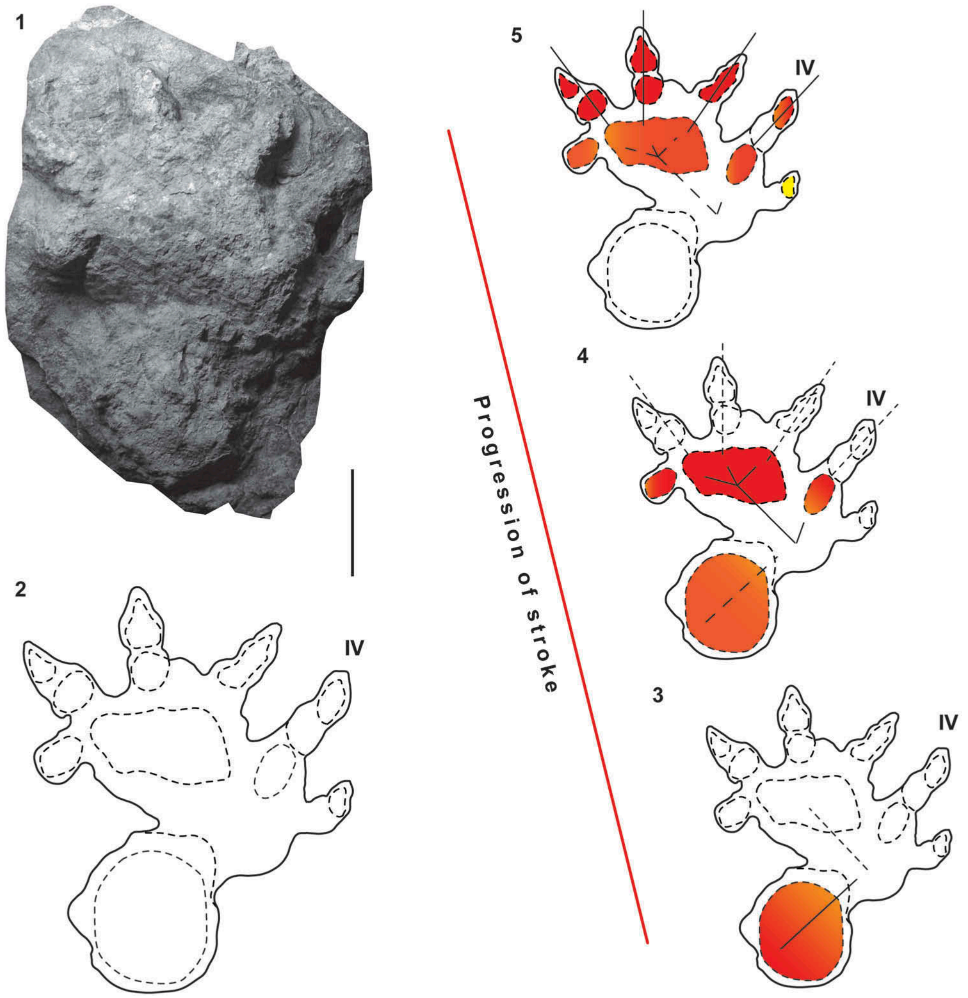

Figure 4. Different axony conditions on the light of differential depth of impression in *Dimetropus osageorum* pes. **(1)** MPUR NS 160/8; **(2)** Interpretative drawing (redrawn and slightly modified from Sacchi et al. 2014); **(3)** Ectaxony (trackmaker lateral functional prevalence) during the touch-down phase; **(4)** Entaxony (trackmaker medial weight support) during the weight-bearing phase; **(5)** Entaxony during the kick-off phase. Solid lines indicate footprint outline; dashed lines indicate pad traces. For each phase, red to orange areas indicate pad traces with maximal functional prevalence; yellow ones indicate pad traces with minimal functional prevalence. Scale bar represents 5 cm. Institutional abbreviation: MPUR NS, Museo di Paleontologia Sapienza Università di Roma Nuova Serie, Rome, Italy.).

axony, fundamentally linking it to the digits' relative length rather than to the autopod functionality, and only subsequently searching for a match between digit length/strength and alleged functionality (not necessarily linked to locomotive habits but also to other attitudes, such as burrowing, climbing, or grasping – Jouffroy 1962; Cartmill 1974). In extreme cases, the term axony was adopted with both a purely geometrical and a functional meaning at the same time, further complicating this specific issue and discussing different axonies from different standpoints (e.g., morphological, geometrical, functional; Reghem et al. 2012). As an example, a hand defined as ectaxonic on an exclusively morphological level, is actually mesaxonic or entaxonic if functionality is considered.

How many axonies? a different perspective from the tetrapod track record

As highlighted above, the significance and meaning of the term axony sometimes is referred to a static and 2D view of the footprint and the process leading to its formation. Considering only a static view of the dynamics of track registration, a lot of information related to functional and behavioral aspects, most of which relevant for trackmaker identification, could be lost.

A concept of a footprint as the result of a dynamic process of formation (e.g. Baird 1957; Cobos et al. 2016) could instead offer the opportunity to define different axonies according to a specific phase of the locomotion cycle (see Padian and Olsen 1984), and then to the particular footprint portion involved in each locomotion phase. For example, in describing footprints attributed to sauropods, Mateus and Milàn (2010) correctly defined the pes as entaxonic, considering that the medial digits are the most deeply impressed. However, by analyzing the differential depth (as far as possible) from the figures presented in the paper (Mateus and Milàn 2010), the footprint proximal portion seems to be more deeply imprinted laterally, thus defining a condition of ectaxony during a specific phase of the locomotion cycle. In the same paper, the authors defined the studied theropod footprints as mesaxonic; the material, however, should be regarded as ectaxonic (i.e. more

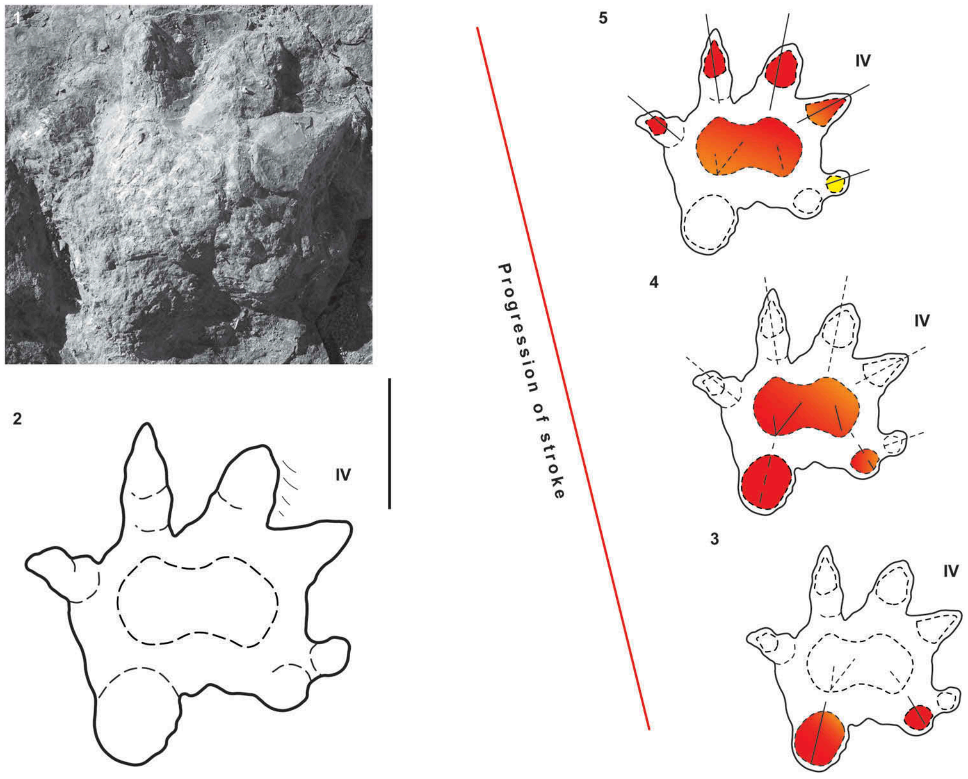

Figure 5. Different axony conditions on the light of differential depth of impression in *Dimetropus osageorum* manus. **(1)** OMNH 76702; **(2)** Interpretative drawing (redrawn and slightly modified from Sacchi et al. 2014); **(3)** Ectaxony (trackmaker lateral functional prevalence) during the touch-down phase; **(4)** Entaxony (trackmaker medial weight support) during the maximum load phase; **(5)** Entaxony during the kick-off phase. Solid lines indicate footprint outline; dashed lines indicate pad traces. For each phase, red to orange areas indicate pad traces with maximal functional prevalence; yellow ones indicate pad traces with minimal functional prevalence. Scale bar represents 5 cm. Institutional abbreviation: OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma.

imprinted laterally) at least in the initial touch down phase (Mateus and Milàn 2010, p. 250, fig. 7). Thus, if dynamic of locomotion cycle is considered, the material turns out to indicate two different axonies.

Different axonic conditions can be distinguished by taking into account gait mechanics. These conditions can be highlighted, for example, by the path that the trajectories of the center of pressure show during the movement and the distribution of plantar pressures providing loading patterns and locomotor function of specific anatomical structures (comprising bones, cartilaginous tissues and/or fleshy pads, see Michilsens et al. 2009). The recognition of the complex dynamics of locomotion is obviously an arduous task; it should be attempted when preservation history of the track under study is known and does not preclude a reliable evaluation of the three-dimensional footprint morphology in relation to the dynamic foot pressure, considering substrate properties and type (Falkingham et al. 2011; Bates et al. 2013).

A dynamic concept of track registration is crucial in enabling connection between the term axony and the different dynamic forces acting on the autopods during a locomotion cycle. As already stated by Thulborn (2013), a footprint is a complex object developed in four dimensions. Reduction of a footprint to a two-dimensional object (disregarding time and depth of impression), as often happens, leads to the loss of a large amount of information. These lost data, concerning primarily time in which different autopod portions contact the substrate and differential depth of impression within a footprint (Thulborn 1990), are considered the basis for a multifaceted approach in comprehending biomechanics and in defining trackmaker functionality directly from tracks.

Regarding time of impression, Thulborn and Wade (1989) proposed a model consisting of three main phases in which a foot interacts with the substrate during a locomotion cycle: the touch down phase, the weight-bearing phase and the kick-off phase. The touch down includes the forward motion of the foot until it contacts the sediment surface. Afterwards, the weight-bearing phase occurs; it consists of the transition of the animal's centre of gravity over the animal's foot, subsequently registered on the substrate. The final phase, that is the kick-off, concerns the transfer of body weight to the acropodium and the forward impulse of the body; then the foot is lifted off the ground. As stated by several authors, these phases are more complex and the footprint formation is, actually, the result of multiple and *in continuum* interaction between foot and substrate (e.g., Gatesy et al. 1999; Gatesy 2003). So, in a dynamic conception of ichnology, tetrapod footprints, representing a powerful tool to understand the locomotion capabilities of different trackmakers, must be considered as a complex record of a multiphase interaction between autopods and substrate, where, instant by instant, only some foot portions are functionally active, transferring the load from the limbs to the ground (Avanzini 1998).

An analogous concept is found in Baird (1980, p. 224), which stated '…a footprint is not the natural mold of a morphological structure but is, instead, the record of that structure in dynamic contact with a plastic substrate', highlighting the intrinsic diachrony of each impression (see Romano et al. 2016). Studying human footprints, D'Août et al. (2010, p. 515) stated: 'We conclude that footprint topology cannot be related to a single variable, but that different zones of the footprint reflect different aspects of the kinesiology of walking.', and '…morphology of a footprint is the result of a highly complex interaction between multiple factors, most of which being not well known. For the example of fossilized hominin footprints, at least the following static and dynamic factors can be assumed to contribute and interact: the shape of the foot, the mechanical properties of the foot, its kinematics, and its kinetics. In addition, the mechanical properties of the substrate… …will probably play an important role… …All these factors ultimately result in a dynamic distribution of pressures at the foot/substrate interface and a footprint with a complex topology.' (D'Août et al. 2010; p. 516; see also Citton et al. 2017a; Avanzini et al. 2018).

The use of differential depth of impression, to gather information about gait mechanics, is found several times in the literature. An early example is found in Tilton (1931). In describing *Dimetropus berea* from the Waynesburg Sandstone, West Virginia, the author discussed the depth of impression in different footprint portions, continuously referring to trackmaker autopodium and zeugopodium features inferable from tracks. Another example is found in the analysis of footprints related to sauropod trackmakers carried out by Farlow (1992). According to this author, the deepest impression along the inner margin of pes tracks in *Brontopodus* would indicate a weight support on the inner side of the hindfoot, 'a conclusion consistent with the stout construction of the inner metatarsales of the sauropod pes.' (Farlow 1992, p. 108).

Observations of different depth at which digits penetrated the sediment has allowed researchers to reconstruct the walking dynamics of small ceratosaurs in the different movement phases (Avanzini 1998), highlighting an inward twist of digit II and the proximal portion of the trackmaker's foot during the weight-bearing phase. Another example is supplied by Gatesy et al. (1999), in the reconstruction of theropod foot movement performed on the basis of deep tracks from the Greenland Triassic, compared to those of living birds. According to the authors, traces of stable metatarsals suggest that '…the initial foot posture was maintained during the early part of the stance phase…' (Gatesy et al. 1999, p. 142) and that '…these theropods powered the early stance phase by femoral retraction…' (Gatesy et al. 1999, p. 143). In addition, analysis of digits' depth of impression in Late Triassic, Early Jurassic and Late Jurassic tracks indicated different penetration geometries of foot distal portions into the substrate, '…with implications for different geometries and mechanics of the limbs between Late Triassic and Late Jurassic theropods.' (Milàn et al. 2006, p. 362).

Once a dynamic view of the impression process and a dynamic footprint registration process is established, the term axony can be used with respect to trackmaker functionality and gait mechanics, and not as a mere geometrical or dimensional descriptor. Obviously, transferring the concept of a dynamic impression process into the resulting three-dimensional morphology of the footprint is a hard task, bringing a reliable result when dealing with detailed footprints and when the dynamic of track registration is known. As a result, if on the one side this approach is applicable depending on the track detailing, on the other side a very informative perspective, potentially useful for both ichnological description and trackmaker identification, can be achieved.

A case study

A possible different use of the term axony in the context of functional analysis can be exemplified by considering detailed shallow footprints assigned to the Permian ichnotaxa *Ichniotherium sphaerodactylum* (sensu Voigt et al. 2007) and *Dimetropus osageorum* (Sacchi et al. 2014), recently the subject of a careful functional analysis (Romano et al. 2016). For the sake of brevity, these case studies will be discussed taking into account two fore foot and two hind foot impressions for each considered ichnotaxon.

Ichniotherium sphaerodactylum. – A medial functional prevalence during the entire locomotion cycle can be recognized in the pes footprint of *Ichniotherium sphaerodactylum* (Figure 2.1 and 2.2). During the touch-down and weight-bearing phases, a condition very close to entaxony is highlighted by a single transversely wide and antero-posteriorly narrow sole pad characterizing the proximal margin of the track. In fact, the sole pad, well imprinted posterior to all five digits, shows a greater depth of impression behind digits I-III (and a maximum behind digits I-II, Figure 2.3).

The deeper portion of the sole pad likely derives from a well-developed fleshy pad below the trackmaker's astragalus, hitting the ground and unloading the body weight in the stroke's initial phase and during the weight-bearing phase. This configuration clearly indicates that the weight was supported by a main functional axis acting medially in the trackmaker hind autopods, producing entaxony in the resulting footprint. With the progression of the weight-bearing phase, the sole pad's distal portion and, to a lesser extent, the metatarsal-phalangeal pad behind digit II (the deepest) and III, were imprinted, suggesting the shifting of the functional prevalence in a centro-medial position (Figure 2.4). In the kick-off phase, a medial functional prevalence (i.e. entaxony) is observed, since digit II and, to a lesser extent, digit III, are the more deeply impressed, although the fourth is the longest. The terminal kick-off phase is instead accomplished by all five digit distal tips, which were equally deeply registered, suggesting a powerful final propulsion immediately before the limb recovery (Figure 2.5).

Regarding the manus (Figure 3.1 and 3.2), the touch-down and the initial weight-bearing phases are highlighted by a medial functional prevalence, as in the pes. The palm pad is divided into a bigger ellipse behind digits I-III, more deeply imprinted in respect to the shallow area posterior to digits IV and V, so defining an entaxonic condition for the footprint proximal margin (Figure 3.3). During the weight-bearing phase, the centro-medial distal portion of the palm pad and the metacarpal-phalangeal pad of digit II, III (the deepest) and IV, are imprinted, indicating a mesaxonic functionality (Figure 3.4). At the end of the stroke (i.e. kick-off phase), the functional prevalence are distributed on digit II, III and, to a lesser extent, on digit IV. Among these, digit II is the more deeply imprinted, so the footprint can be considered as entaxonic in the final phase of the locomotion cycle (Figure 3.5).

Dimetropus osageorum. – The footprints assigned to *Dimetropus osageorum* (Sacchi et al. 2014) show a completely different functionality and axony configuration during the locomotion cycle in respect to those of *Ichniotherium sphaerodactylum.*

Regarding the pes impression (Figure 4.1 and 4.2), during the touch-down phase an antero-posteriorly elongated sole-pad, compatible in shape and position to a fleshy pad likely positioned below the trackmaker calcaneum, is impressed with a maximum depth at the track lateral margin, which gradually decreases medially. Such a configuration suggests a lateral functional prevalence of the trackmaker hind autopods and, then, a strong ectaxony for this footprint portion (Figure 4.3). In the subsequent phase the functional prevalence moves medially; among the metatarsal-phalangeal pads, those behind digits I-III, with a slight prevalence of that of digit II, are more deeply impressed, suggesting an entaxonic condition for this footprint portion and a medial weight support during the maximum load (Figure 4.4). The final kick-off phase is likely performed by all the free digits, with a greater involvement of the medial digits I and II, which result the most deeply impressed (and relatively more proximally), identifying a clear entaxony (Figure 4.5).

As in the pes, even in the forefoot impression (Figure 5.1 and 5.2) the proximal portion, which is the first that hits the ground during the touch-down phase, is most deeply impressed laterally. The lateral pad trace is deeper in respect to the medial one, defining an ectaxonic condition during the initial stroke (i.e. lateral functional prevalence of ulnar and related fleshy pad; Figure 5.3). In the subsequent phase (i.e. weight-bearing), a second functional axis is activated, involving trackmaker distal basipodials and metapodials. Metacarpal phalangeal pads behind digit II, and sometimes III, seem to be the most deeply imprinted in this footprint portion, with depth decreasing both medially and laterally, suggesting a footprint medial functional prevalence (i.e. entaxony) during the maximum load (Figure 5.4). In the locomotion cycle terminal phase all digits are involved, with particular emphasis of digit II, which results the most uniformly and deeply impressed, indicating a final functional prevalence acting medially (i.e. entaxony; Figure 5.5).

Discussion

From the cases reported above, it is evident how:

(i) a functional definition of axony is rooted in the trackmaker biomechanical pattern; when it is clearly mirrored in well preserved prints, it can be refined;

(ii) the differential axony can be ideally defined even from a single isolated footprint, however, a large number of footprints/trackways should be considered in a comparative analysis to reconstruct a general axony (or a series of discrete axonies) for a putative trackmaker;

(iii) an analysis focused on the differential depth of impression, to obtain information about axony, can be carried out only on detailed footprints and, particularly, when the mode of preservation and the dynamic of track registration are understandable;

(iv) a firm definition of axony is important in order to rationalize and describe tracks. Keeping in mind that the track registration process is continuous, ideally many different axony conditions (at the time of footprint impression) could be detected, by carefully analyzing the differential depth of impression. In this framework, the realization and use of photogrammetric models represents a new powerful and cutting edge approach to infer differential depth in tetrapod footprints, also enabling more objective communication and preservation of ichnological data (see Castanera et al. 2013; Lallensack et al. 2015; McCrea et al. 2015; Romano and Citton 2016; Citton et al. 2015, 2016, 2017a, 2017b, 2018; Falkingham et al. 2018).

Conclusions

The above reported brief review of the multifaceted meaning that axony assumed over time and under different methodological approaches highlights the possibility of operatively choosing from three basic systems.

(i) In a first approach and use of the term, axony could simply indicate – both in the zoological and ichnological fields – the more developed digits (i.e. simply the longest or largest and most robust), therefore without any direct reference to the actual trackmaker functionality. Thus, in this view, a simple interpretive footprint outline with a dominant fourth digit (the longest in the digit series) could be defined ectaxonic, even if the differential depth analysis indicates a marked functional prevalence in correspondence of medial digits (e.g., *Ichniotherium* pes). Therefore, in this case, the terminology would simply represent geometrical shape descriptors (footprints with symmetrical outline or more developed medially/laterally), without any indication about functionality and locomotive capability of the putative trackmaker.

(ii) In a second approach, the term axony is correlated to the functionality – and in particular, the main support axis – using the maximum load phase (i.e. weight-bearing) to define footprints respectively as entaxonic, mesaxonic, ectaxonic and so on. Therefore, in this case, a footprint can be defined entaxonic if the internal portions (whether basipodial, metapodial or acropodial) are decidedly deeper, thus indicating a maximum load and a corresponding functional axis displaced medially during the weight-bearing phase. Therefore, in this sense, the term would not be just a pure geometric descriptor, but it would indicate specific functional and biomechanical information. With this approach, however, the term would continue to be used as part of a static (2D) view of the footprint, only describing a discrete period of the locomotion cycle.

(iii) In a third and final approach, the terms can be diversified in relation to the three main recognized impression process phases, recognizing a particular axony (and then a principal functional axis) for the touch down, weight-bearing, and kick-off phases. In this case, footprints such as *Dimetropus* can be considered ectaxonic in the touch-down, and entaxonic in the weight-bearing and kick-off phases (Sacchi et al. 2014; Romano et al. 2016). Then, axony would assume a purely functional meaning, and the refined differentiation in at least three phases would represent substantial additional information, both as a simple descriptor and in relation to the possibility of inferring particular osteological and functional patterns.

Although all these approaches can be considered valid in principle (once clearly defined), the second and third conception should be favoured if one wants to associate a clear functional significance with the term axony. In about all ichnotaxa diagnoses, the digits' relative length (in both manus and pes) is conventionally reported as a taxonomic character. Therefore, it follows that the use of axony to simply report information about digit trace dimensions is an unnecessary repetition, self-evident and deducible also from the simple interpretive outline reported in the paper. Differently, a functional sense of the term could provide additional information, since the differential depth of impression is not represented or difficult to derive in most of the papers found in literature.

As a conclusion, both in ichnology and generally in zoology, the meaning of the term that is embraced from time to time should be clearly explained, absolutely avoiding the use of axony with different meanings even in the same research or paper. In particular, the re-establishment of the original meaning given by Leonardi (1987) makes the third approach ideal in order to establish a more direct cognitive interconnection between footprints and the respective trackmaker, with analysis and description of objects that have in all respects a biological significance and not geometric shapes to be described.

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