



Spider leg flexure as an indicator for estimating salinity in lacustrine paleoenvironments



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ABSTRACT

Spider fossils are rare outside of amber but do occur in lacustrine Fossil-Lagerstätten. In general, spiders preserved in lacustrine beds show splayed legs; however, those in the Crato Formation of Brazil are commonly curled up. It is hypothesized that the post-mortem flexure of spider legs is related to the salinity of the lake water. To investigate this, we measured the flexure (at the two main leg joints: femur–patella and tibia–metatarsus) of spider legs in three Fossil-Lagerstätten: the Crato Formation of Brazil (Cretaceous), the Green River Formation of the western USA (Eocene), and the Florissant Formation of Colorado (Eocene). In addition, we drowned living spiders in water of three salinities: fresh (<0.5 ppt), saline (35 ppt), and hypersaline (160 ppt). Our results show that spiders drowned in fresh water show predominantly extended legs, those in hypersaline water curled legs, and those in saline water intermediate values of flexure. In the Florissant Formation, spiders show extended legs; in the Crato Formation, the spider legs are predominantly flexed, while those in the Green River Formation show a mixture of flexure types. These results concur with ideas about the salinities of these formations: that the Florissant Formation is a freshwater lake, the Crato Formation represents a hypersaline lake (at least at times), and the Green River lakes varied from fresh to various higher salinities. The reason for this phenomenon is likely that spider legs, uniquely, lack extensor muscles at the femur–patella and tibia–metatarsus joints, relying on hemolymph pressure for leg extension. Hence, post-mortem osmosis determines whether the legs become outstretched (fresh water) or flexed (hypersalinity). While further work is necessary to determine more taphonomic details of this phenomenon, there is sufficient evidence that spider leg flexure may be a useful indicator of salinity in lacustrine paleoenvironments.

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1. Introduction

Body and trace fossils are used to reconstruct past environments and provide information about ancient organisms including their morphology, ecology, and biogeography and can act as environmental indicators of such parameters as temperature, water chemistry, and many others (e.g., Goodfriend, 1992; Hasiotis, 2004). For example, benthic organisms such as ostracodes are used commonly in paleoenvironmental reconstruction because they are abundant and sensitive to environmental conditions (Rosenfeld and Vesper, 1977; Chivas et al., 1986; De Deckker et al., 1988). Trace fossils are also used in reconstructing paleoenvironments (e.g., Bromley, 1996; Hasiotis, 2002). In rare cases, fossils can be exceptionally preserved to include soft tissues and delicate features such as hairs. These deposits, termed Fossil-Lagerstätten, provide a more complete view of organism morphology and ecosystems

by preserving parts of organisms that would not normally become fossilized (e.g., Allison and Briggs, 1993; Brett et al., 1997; Briggs, 2003; Nudds and Selden, 2008). Many Fossil-Lagerstätten have a lacustrine origin.

The Lower Cretaceous Crato Formation of Brazil is an example of a lacustrine Fossil-Lagerstätte: a deposit with exceptional preservation that includes soft tissues, represented by laminated limestones with an abundance of terrestrial arthropods, fish and other vertebrates, and plants (Martill et al., 2007). Terrestrial arthropods include insects, spiders, and other arachnids and represent an allochthonous assemblage (Barling et al., 2015). The Crato Formation presents a unique view of an Early Cretaceous terrestrial ecosystem during the diversification of angiosperms and the breakup of South America and Africa.

The Crato Formation fossils are predominantly insects, with relatively common spiders (Maisey, 1991). Spiders in the Crato Formation are of particular interest due to their curled legs, an attribute unlike fossil spiders from other lacustrine localities, which usually have legs extended outward (Meyer, 2003; Dunlop et al., 2007). This extended leg pattern is evident in lacustrine deposits of the Green River and Florissant formations, which were likely deposited in a stratified saline lake and freshwater lake, respectively (Cole, 1985; Meyer, 2003).

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Multiple hypotheses have been proposed for the salinity of the ancient Crato environment, ranging from fresh to hypersaline (Maisey, 1990; Neumann et al., 2003; Martill et al., 2007). Most recently, Martill et al. (2007) offered pseudomorphs after halite as evidence for hypersalinity, thus focusing on geochemical data rather than paleontological evidence. The Crato Formation presents a unique opportunity to investigate a fossil assemblage dominated by terrestrial organisms as a potential proxy for salinity. This paper seeks to determine if an increase in the amount of curling of the legs is related to elevated levels of salinity. The results suggest hypersaline conditions during the deposition of the spider-bearing beds in the Crato Formation, based on taphonomy experiments conducted on modern spiders, as well as comparative studies of fossil spiders.

2. Geologic setting

The Crato Formation is a series of alternating heterolithic beds and carbonate deposits located in northeastern Brazil (Martill and Wilby, 1993; Neumann et al., 2003). These beds were deposited in the Araripe Basin, one of several fault-bounded intracratonic rift basins formed and controlled by extensional tectonics during the break up of South America and Africa (Martill, 2007; Heimhofer et al., 2010). At the base of the Crato Formation is the Nova Olinda Member—the focus of this work—which is composed of a series of laminated carbonates in which the vast majority of the well-preserved fossils are found. Neumann et al. (2003) described two types of laminated carbonate facies: clay-carbonate rhythmites and laminated limestones. Clay-carbonate rhythmites are approximately 0.5–0.8 mm with high detrital content. The laminated limestones are represented by the fossil-rich Plattenkalks: thinly laminated limestones (3.0–6.0 mm), with little to no bioturbation and less detrital material, in which terrestrial arthropods are abundant (Martill et al., 2007). Bioturbation and fossils of benthic organisms are absent in the Nova Olinda Member (Martill and Wilby, 1993). Carbon and oxygen stable-isotopic composition of the carbonates have confirmed a lacustrine origin for these deposits (Heimhofer et al., 2010). The ubiquitous thin laminations suggest that the lake in which the Crato Formation was deposited experienced low-energy conditions, in relatively deep water, below storm wave base (Heimhofer et al., 2010). The carbonates of the Crato Formation have been interpreted as biologically induced or mediated precipitation from the water column (Heimhofer et al., 2010). The higher members of the Crato Formation are the Caldas, Jamacaru, and Casa de Pedra members (Martill and Heimhofer, 2007). The Crato Formation is overlain by the Ipubi Formation, a unit composed of evaporites (Martill and Wilby, 1993).

The age of the Crato Formation has been interpreted as Aptian (Early Cretaceous) based on ostracode and palynomorph studies (Coimbra et al., 2002; Batten, 2007). During the late Aptian, the Araripe Basin was positioned 10–15°S in the tropics and experienced mostly arid conditions (Hallam, 1984, 1985; Chumakov et al., 1995; Föllmi, 2012). Additional support for a semiarid climate is fossil plant life that likely thrived in areas with limited water based on morphological characteristics including sunken stomata and reduced leaves (Alvin, 1982; Ziegler et al., 2003; Mohr et al., 2007). Fossil camel spiders (Solpugida) have also been found in the Crato Formation, whose modern-day representatives live in desert or semiarid climates (Selden and Shear, 1996; Punzo, 1998; Dunlop and Martill, 2004). It is likely, however, that a variety of habitats existed around the Crato depositional environment based on fossil organisms that lived in humid environments (Menon, 2007).

Two other well-known localities for spider fossils in lacustrine deposits are the Green River Formation (early to mid-Eocene) in Utah, Colorado, and Wyoming and the Florissant Formation (late Eocene) in Colorado (Meyer, 2003; Smith et al., 2008). Green River Formation fossils used in this study are preserved in shales and siltstones from the Parachute Creek Member (49–50 Ma), deposited in a chemically stratified lake in which saline bottom waters were overlain by tongues

of fresh water (Brobst and Tucker, 1973; Cole, 1985; Smith et al., 2008). The Florissant Formation (34 Ma) is composed of shales and volcanic tuffs, deposited in a volcanically dammed lake (Evanoff et al., 2001; Meyer, 2003). Freshwater conditions, based on freshwater diatoms, mollusks, algae, and aquatic angiosperms, existed during the deposition of its lacustrine sediments (Meyer, 2003).

3. Materials and methods

3.1. Paleontology

Initial observations came from fossils that were examined and photographed from the Crato, Green River, and Florissant formations. 95 Crato Formation spiders were photographed at the University of Kansas, Lawrence, Kansas, using a Canon 5D Mark II digital camera attached to a Leica M650C microscope. 125 Green River Formation spiders and 42 Florissant Formation spiders were photographed at the University of Colorado Natural History Museum, Boulder, Colorado. Leg flexures of the fossil spiders from all formations were determined from the photographs in Adobe Photoshop CS5 using the measuring tool. Femur–patella and tibia–metatarsus joint angles were measured from the front right leg (Fig. 1). The front left leg was measured if the front right leg was obscured. Joints on the second, third, and fourth pairs of legs were not measured as they are typically obscured by the legs being folded in ventral view and disappearing into the matrix in dorsal view. Leg flexure was categorized as extended or curled for each individual specimen. A curled leg was defined as any leg with an angle formed at the femur–patella joint and coinciding tibia–metatarsus joint that positioned the leg under the body. Smaller femur–patella joint angles, usually <100°, and smaller tibia–metatarsus joint angles, usually <130°, result in a leg positioned under the body. Individual specimens with four or more of their legs meeting this criterion were considered curled. In contrast, both femur–patella and tibia–metatarsus joint angles that are exceptionally obtuse, approach 180°, do not position legs under the body and are considered extended. Overall leg flexure was recorded for 245 fossil specimens, and joint angles were recorded for 82 specimens.

3.2. Taphonomy experiments

This study utilized a comparison with modern spiders to explore possible causes for differences in spider leg angles. 107 spiders were collected at Clinton Lake State Park, Lawrence, Kansas, during July and August 2013. Spiders were *Mangora maculata*, a small (2–3 mm), green, araneid spider, typically found in low brush. *M. maculata* is distinguished by abundant spines and a prominent cluster of trichobothria on the femur of the third pair of legs (Levi, 1975, 2005). *M. maculata* are similar in size to the majority of spiders preserved in the Crato Formation and likely belong to the same family. 25 were selected to be left in sealed vials and expire by controlled atmospheric killing (CAK), asphyxiation in carbon dioxide, for subsequent submersion in solutions of varying salinity. 82 spiders were placed in solutions of varying salinities and allowed to drown immediately after being caught.

The live spiders were drowned in solutions of three distinct salinities: freshwater (<0.5 ppt), saline water (35 ppt), and hypersaline water (160 ppt). Freshwater solution used tap water, such as is commonly used in freshwater aquariums and has negligible salinity (chemicals were not added to remove chlorination). Saline and hypersaline solutions were created using Instant Ocean® Sea Salt (Spectrum Brands, Inc.), a mix commonly used in saltwater aquariums. Saline solutions consisted of 35 ppt (average seawater salinity) and hypersaline conditions consisted of 160 ppt, a concentration of salts much greater than that of ocean water. Saline lakes have previously been defined as lakes containing >5 ppt salinity, a value based on biological tolerances; however, multiple classifications for salinity based on solute concentration exist (Williams, 1967; Beadle, 1974; Carpenter, 1978; Hammer,

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