

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,

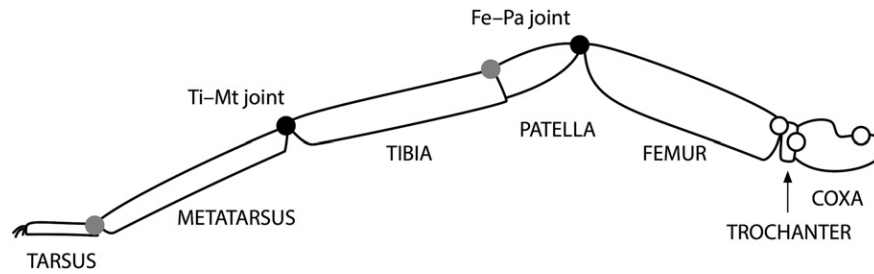


Fig. 1. Diagram of a typical spider leg showing podomere names and joints. Black circles mark hinge joints without extensor muscles; open circles are joints with both flexor and extensor muscles, and gray circles are other joints. After Foelix (2011) and Weihmann et al. (2012).

1986; Last, 2002; Last and Ginn, 2005). Hypersalinity is generally considered greater than the salinity of seawater (35 ppt); however, the Venice Classification System (1959) for salinity, a standard used by many scientists for classifying salinity, considers 40 ppt and above hyperhaline (hypersaline). In this experiment, 160 ppt was chosen to test hypersalinity that is observed in other large hypersaline lakes such as Great Salt Lake (Nicholson and Marcarelli, 2004).

Each spider was placed in a glass beaker and solution was poured over it to break the surface tension. The spider and the solution were then poured into a glass vial. The vial was filled with solution until it was full, then sealed with a plastic cap. In some cases, the spider would sink immediately. Usually, the spider would either be floating on the surface or the water or hang suspended beneath the surface. In either case, the vial was then rotated repeatedly to sink the spider. If the spider was still floating, it was left overnight and rotated the next day until it sank. Once all spiders were fully submerged, they were not subjected to further agitation. During this time period, vials were maintained at room temperature, and leg flexures were recorded after 5 days, the time after which all spiders had drowned and no further movement was noted in the spiders. After 5 days, the spiders were also photographed from the lateral views. For each drowned specimen, the femur–patella and tibia–metatarsus joints of the front right leg were measured from the photographs in Adobe Photoshop CS5. The front right leg was chosen because those legs were able to be measured in the fossil specimens, whereas the joint angles in the other legs were typically obscured. In addition, each specimen was categorized as either curled or extended. A spider was considered curled if 4 or more of its legs were positioned under the body.

3.3. Statistical tests

Data collected from each of the modern and fossil spiders were analyzed in Minitab 15 Statistical Software. For raw leg angle data, recorded in degrees, an arcsine transformation was used to normalize the data. After the transformation, a one-way analysis of variance (ANOVA) was conducted to test for a significant difference in the means of joint angles between two groups: 1) the three solutions in which modern spiders were drowned and 2) the three formations with fossil spiders. The null hypothesis for the ANOVA test on the salinity treatments was that there is no significant difference in the means between the salinity treatments (fresh, saline, and hypersaline). The null hypothesis for the ANOVA test on the fossil spiders was that there is no significant difference in the means between the fossil formations (Florissant, Green River, and Crato). The alternative hypothesis for each group is that at least one of the means differs from the others. In addition, a chi-square goodness-of-fit test was performed on each individual salinity treatment and formation: Fresh, Saline, Hypersaline, Florissant, Green River, and Crato, with leg flexure data categorized as curled or extended to test if leg flexure was significantly curled or extended within each group. The null hypothesis for each test was that the number of curled legs would equal the number of extended legs. The alternate hypothesis for each test was that the number of curled legs would be different from the number of extended legs.

4. Results

4.1. Taphonomy experiments

All of the 25 spiders that were allowed to expire by CAK exhibited a curled leg flexure, but 19 of the spiders quickly decayed beyond recognition while sealed in the vials before submersion. Only the modern spiders from the drowning experiments will be included for the remainder of the results. For the 82 drowned spiders, their leg flexure varied greatly with no consistent trend immediately following submersion. After a period of 5 days when all spiders had expired, leg flexures had changed from their initial pose, and no further changes were observed. The leg flexure of drowned spiders varied between the three salinities tested (Fig. 2). An one-way ANOVA for fresh, saline, and hypersaline revealed that the means of the joint angles from the three groups are significantly different, $F_{2,77} = 17.52$, $p < 0.05$. Spiders drowned in fresh water typically displayed extended legs, $p < 0.05$, and obtuse femur–patella joint angles with an average of 145.84° (s.d. = 28.96°). Spiders drowned in saline conditions had a wide range of femur–patella joint angles, ranging from 49.4° to 180° , and had nearly equal abundance of curled (55.2%) and extended (44.8%) legs with an average of 113.34° (s.d. = 30.9°). Curling was not statistically significant in spiders drowned in saline water, $p = 0.493$, based on the nearly equal amounts of curled and extended flexures. A statistically significant number of spiders, $p < 0.05$, drowned in hypersaline conditions had legs that were tightly curled under the body with acute femur–patella and tibia–metatarsus joint angles smaller than those spiders drowned in saline and fresh water (Table 1). The average femur–patella joint angle in spiders drowned in hypersaline water was 93.79° (s.d. = 22.52°).

4.2. Fossil spiders in lacustrine deposits

Fossil specimens include a range of femur–patella joint angles within and among the formations (Fig. 3). A one-way ANOVA test performed using the leg angles of fossil spiders shows a significant difference in the means of the Crato, Florissant, and Green River formations, $F_{2,228} = 130.76$, $p < 0.05$ (Table 1). The categorical data (curled vs extended) reveal that 96% of fossil spiders from the Crato Formation display a curled leg flexure, $p < 0.05$. The average angle formed at the femur–patella joint is 85.85° (s.d. = 39.63°). The spiders from the Crato Formation have legs that are curled more closely to the body than those in the other formations (Fig. 3; Table 1). Green River Formation fossil spiders show much more variety in leg flexure than the other two formations. The legs are extended in 58% of the samples with a p value of 0.089, and thus curling is not statistically significant. The average femur–patella joint angle is 151.57° (s.d. = 31.04°). In nearly all of the cases where the legs of spiders are considered curled, very few of the legs of specimens are curled as tightly as in those observed in the Crato Formation, whose joint angles are typically acute. Many specimens from the Green River Formation have a leg arrangement near the boundary between curled and extended. Spiders from the Florissant Formation exhibit a dominant leg flexure in which the legs in 98% of the specimens are extended. Many samples include fully

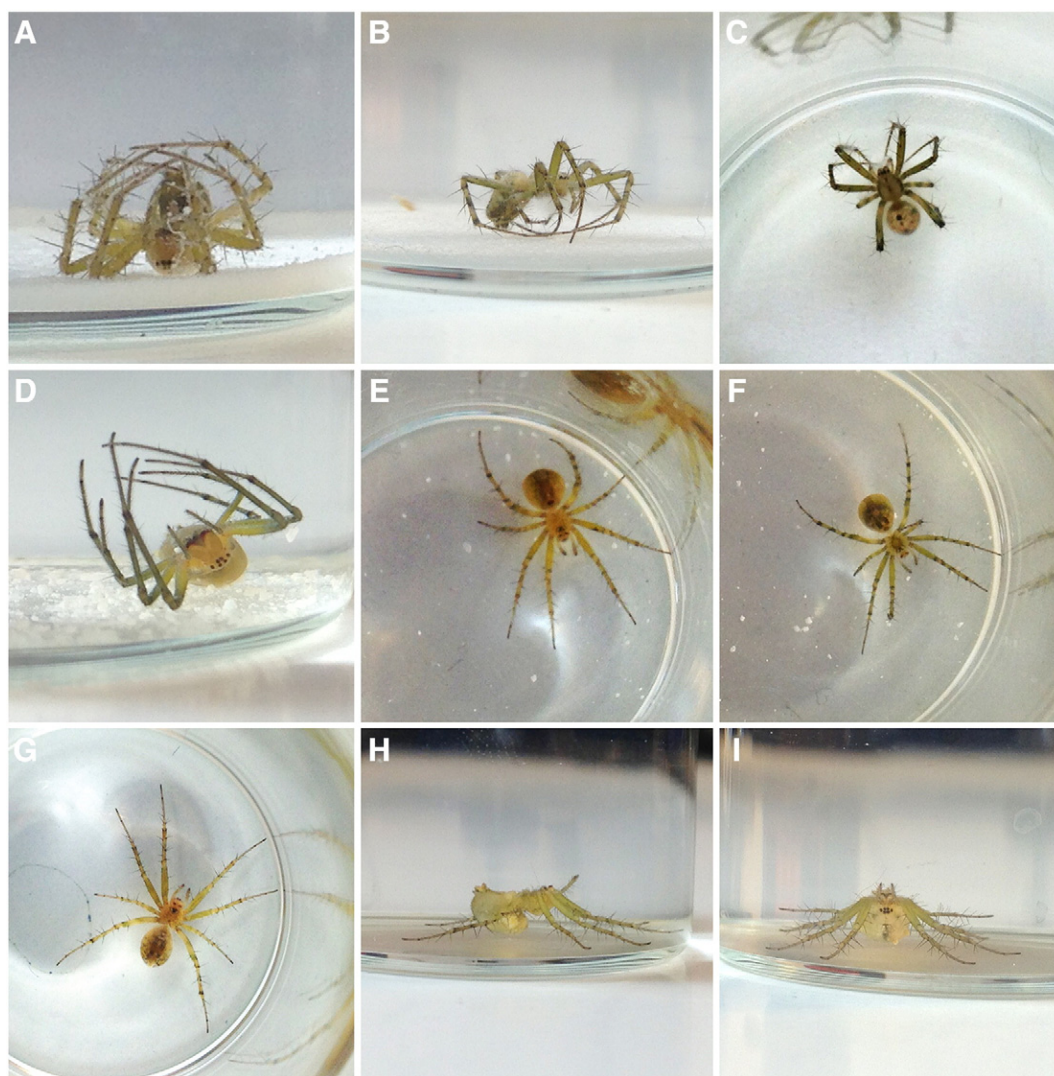


Fig. 2. Drowned spiders in various salinities. (A–C) Hypersaline water; spiders typically have strongly curled legs. (D–F) Saline water; D shows a curled leg flexure in saline water; the femur–patella joint angle is acute, but the tibia–metatarsus joint is not bent significantly, resulting in a curled leg flexure that is weak compared to hypersaline conditions. (G–I) Fresh water; leg flexure is dominated by an extended leg pattern.

outstretched legs, at nearly 180° , resulting in a p value < 0.05 and a statistically significant proportion of extended legs. The average femur–patella joint angle in the Florissant fossil spiders is 169.73° (s.d. = 21.11°).

5. Discussion

The curling of spider legs after death is the result of physiological processes. Spider legs have promotor–remotor and levator–depressor muscles at the coxa–trochanter–femur joints, but the femur–patella and tibia–metatarsus joints lack extensors (Foelix, 2011) (Fig. 1).

Extension at femur–patella and tibia–metatarsus joints occurs by a hydraulic mechanism (Ellis, 1944; Parry and Brown, 1959). Hemolymph, the fluid in the circulatory system of arthropods, is pumped into the legs, thus increasing the fluid pressure, and resulting in their extension (Kropf, 2013). After death on land, in normal conditions, this hydraulic mechanism ceases and the legs contract through the action of the flexor muscles through rigor mortis.

Being terrestrial, the spiders did not live in the lake in which the Crato Formation was deposited, despite being deposited within lacustrine sediment. Several observations during the course of the experiments provided insight into taphonomic processes affecting the

Table 1

Summary of the leg flexures of fossil and modern spiders with p values (P) for the chi-square goodness-of-fit test for each formation and salinity experiment. C = curled, E = extended, Fe–Pa = femur–fatella joint angle, Ti–Mt = tibia–metatarsus joint angle, sd = standard deviation.

Formation salinity	n	Curled	Extended	% C	% E	Mean Fe–Pa	Fe–Pa sd	Mean Ti–Mt	Ti–Mt sd	P
Florissant	42	3	39	7.1	92.9	168.98	21.69	173.59	14.15	<0.05
Green River	125	56	69	44.8	55.2	151.57	31.02	149.46	32.66	0.089
Crato	95	80	15	84.2	15.8	85.84	39.4	120.75	26.79	<0.05
Fresh	21	2	19	9.5	90.5	145.84	28.96	157.84	27.73	<0.05
Saline	34	19	15	55.2	44.8	113.34	30.9	147.4	20.92	0.493
Hypersaline	27	26	1	96.3	3.7	93.79	22.52	113.8	22.02	<0.05

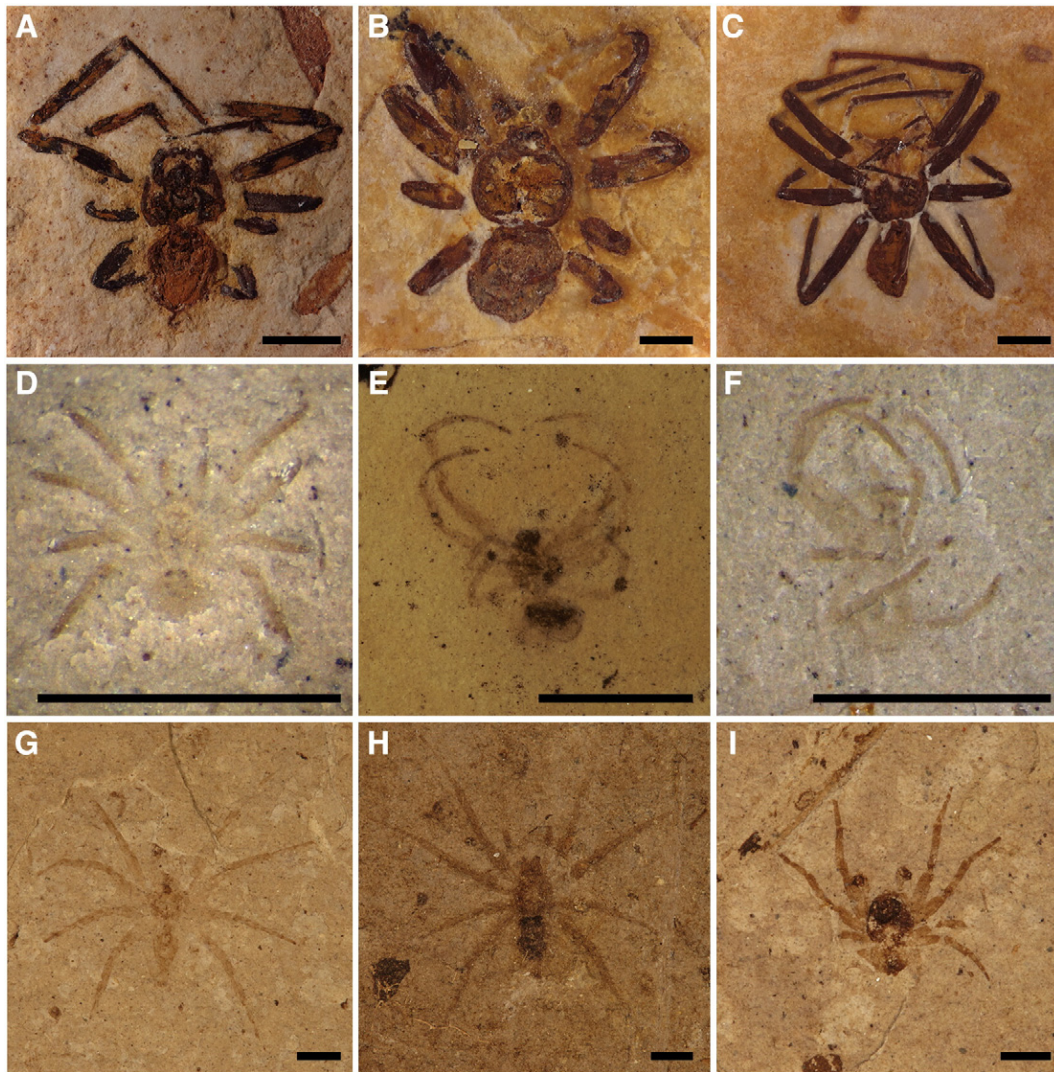


Fig. 3. (A–C) Fossil spiders from the Crato, (D–F) Green River, and the (G–I) Florissant formations. Scale bars = 2 mm.

spiders. One possible explanation for the curled legs observed in the Crato Formation is death either on land or floating on the surface of the water, in which the legs would curl, followed by subsequent deposition in the lake. Death on land or the surface of the water, however, would also increase the chance of decay or removal by predators and scavengers, as exceptional preservation generally requires reduced decay (Allison, 1986; Smith, 2012). Smith (2012) provided an explanation of the pathway leading to fossilization for insects in the Florissant Formation. This included insects making it to the lake, submerging, and sinking through the water column to a burial environment in which the insects can be preserved. Many taphonomic controls exist along this pathway to preservation, including predators, scavengers, decomposers, disarticulation, and microbial action that can hinder preservation. In contrast, O'Brien et al. (2002) proposed that microbial mats aided insect preservation in the Florissant Formation by forming a protective coating that hinders decomposition during sinking through the water column. For exceptional insect preservation, three conditions are crucial: 1) a fast sinking rate to limit removal by scavengers, 2) bottom water anoxia, and 3) microbes that facilitate preservation (Smith, 2012). A similar possible pathway exists for spiders and can be applied to fossil spiders of the Crato Formation. Dunlop and Martill (2004) suggested a mechanism of transport for nonflying terrestrial biota, in which such organisms as spiders were washed in through rivers and streams during flash-flood events, an interpretation suggested

by the presence of whole plants preserved with roots, stems, leaves, and surrounding soil attached to roots. Other methods of transport to the ancient Crato lake are possible and include spiders blown in or falling on the lake surface during ballooning events, a method of areal dispersal used by some spiders, or strong winds (Humphrey, 1987).

Spiders preserved in the rock record obviously did not completely decay, yet the spiders allowed to expire in air quickly decayed. This could be attributed to humidity and favorable conditions for decomposers sealed in the vials. To test a death on land scenario, spiders should be allowed to expire in air and subsequently be desiccated, which would likely reduce the risk of complete decay and be more consistent with the hypothesized semiarid climate of the Crato Formation paleoenvironment. Thus, the death on land scenario cannot be fully ruled out for spiders preserved in the Crato Formation, and further experiments are needed to understand this taphonomic pathway. Future research should focus on the different taphonomic and taxonomic variables that may influence leg flexure. Death on land, desiccation, transport, decay, agitation, and changes in water chemistry are just some of the variables that need to be investigated. In addition, taxonomy and morphology may play a role in leg flexure as well. For example, how different families of spider compare to each other, juveniles compared to adults, males to females, large spiders (several centimeters in size) compared to small spiders (millimeters in size), and robust spiders compared to more delicate spiders. A comprehensive investigation of

these variables and how they influence spider taphonomy will provide a clearer of the relationship between salinity and leg flexure.

For spiders that have expired in water, leg extension and contraction are likely controlled by osmosis: the diffusion of water from a weak to a strong solution across a semipermeable membrane. During drowning in arthropods, water is taken in through the tracheal system and can permeate the body (Martínez-Delclòs and Martinell, 1993). In fresh conditions, water will diffuse into the spider (whose body fluids have a higher ion concentration than the water) through osmosis, creating a pressure that causes the legs to extend, overpowering the flexor muscles for contraction. The pressure of the water mimics the hemolymph pressure employed by spiders to extend their legs. In a hypersaline solution, on the other hand, water will move from the spider into the environment of higher solute concentration and allow the contraction of the legs tightly under the body, creating a smaller angle at the femur–patella and tibia–metatarsus joints.

Modern spiders in this study that died in fresh water revealed that their legs will predominantly extend (curled = 2 and extended = 19). In contrast, spiders that drowned in saline water produced specimens with curled legs and others with extended legs in roughly equal abundance (curled = 55.2% and extended = 44.8%), suggesting that salinity hinders the action to produce spiders with fully extended legs (Table 1). Most spiders of those that had a curled leg flexure did not have legs that were curled very tightly—legs positioned under the body with joint angles $>100^\circ$ (Fig. 2D). In hypersaline water, most spiders had a curled leg flexure (84.2% curled), with most of the legs being curled tightly under the body: femur–patella joint angles $\sim 90^\circ$ and tibia–metatarsus joint angles $\sim 113^\circ$ (Table 1; Fig. 2). The average femur–patella angle of curled spiders in hypersaline water was 91.56° , whereas the average for curled spiders in saline water was 98.09° . The tibia–metatarsus joint also differed between hypersaline and saline water in curled spiders at 113.49° and 138.33° , respectively. Smaller angles at both joints produce a more tightly curled leg.

Previous explanations for patterns in the leg flexure of fossil spiders include acidity and temperature (Licht, 1986; Meyer, 2003). Meyer (2003) speculated that the extended legs of spiders in the Florissant Formation were the result of acidic or warm waters, due to volcanic ashfall or thermal vents. High temperatures have also been suggested as a leg extension mechanism based on experiments with spiders placed in warm, hot, and boiling water, each producing extended legs; however, no specific water temperatures were reported (Licht, 1986). Each of these experiments was likely conducted in fresh water, as no addition of salts was reported, which could explain the extended legs. Boiling water may have also denatured the proteins within the spider's leg muscles, removing the ability of legs to contract (Wu and Wu, 1925).

Patterns in leg flexure from the salinity experiments provide insight that can be applied to understand the fossil samples (Fig. 4). The Florissant Formation has been interpreted to represent an ancient freshwater lake environment (Meyer, 2003). Most of the spider fossils in the Florissant Formation display extended legs, consistent with the observations in the freshwater drowning experiments (Table 1). In contrast, the Parachute Creek Member of the Green River Formation has been interpreted to reflect an ancient stratified saline lake environment (Cole, 1985). Fossil spiders from this unit display more curled leg flexures than the Florissant Formation based on measurements herein. The fossil spiders of the Green River Formation are similar to the modern spiders in saline drowning experiments in two ways: 1) the ratio of spiders with curled to extended legs is about equal; and 2) most spiders with a curled leg flexure have legs that were not curled very tightly—legs were curled under the body, but joint angles were typically $>100^\circ$ (Fig. 3E, F). The joint angles of fossil spiders from the Green River Formation suggest an intermediate salinity between fresh and hypersaline as they are not fully extended, yet not contracted close to the body. The Crato Formation has an abundance of spider fossils with legs curled tightly under the body. These specimens exhibit a narrow range of femur–patella joint angles (mostly acute) in spiders with curled legs, and a smaller

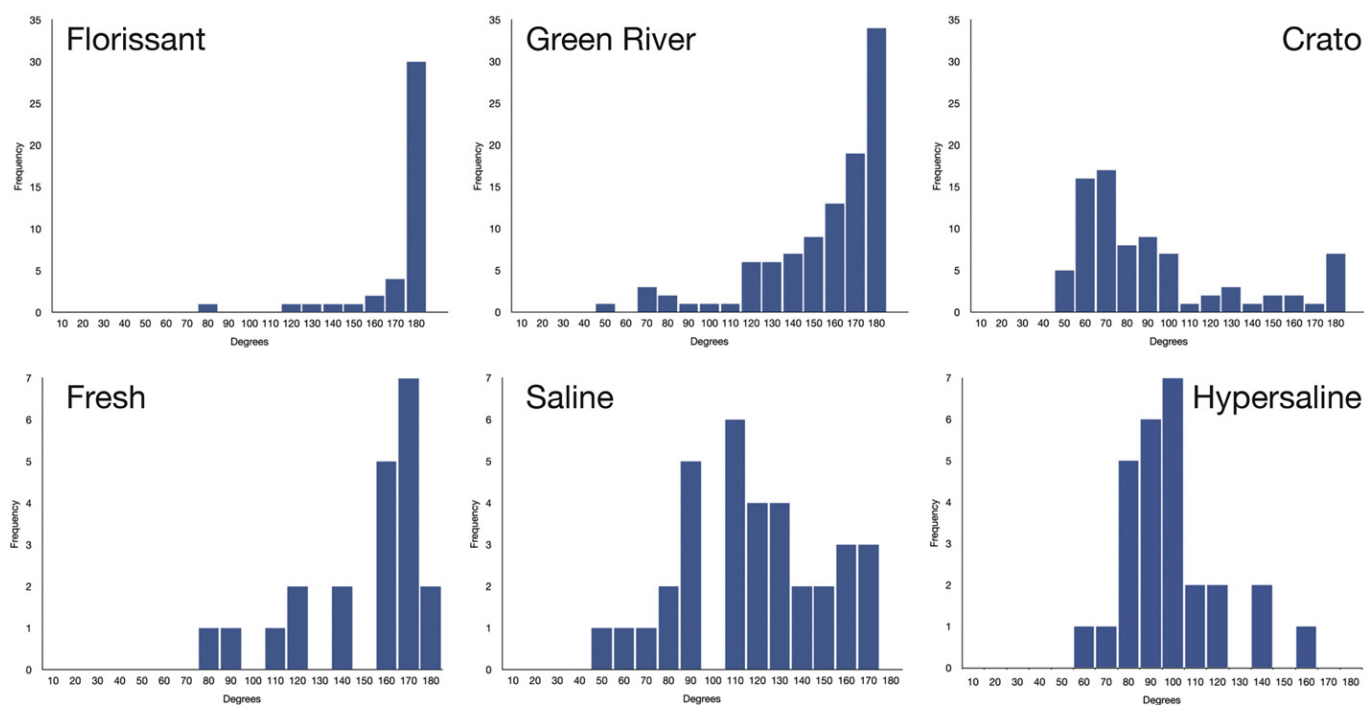


Fig. 4. Femur–patella leg angles for spiders in the three formations (top row) and the three salinity experiments (bottom row) with joint angle degrees on the x-axis and the frequency of occurrence on the y-axis. The Florissant Formation is dominated by leg angles of 180° , indicating fully outstretched legs. The Green River Formation also has many 180° but populates a wider range of angles. The Crato Formation leg angles are concentrated at lower, mostly acute, leg angles, indicating curled legs. Among the drowned spiders, a noticeable shift from high Pa–Ti angles to low angles can be seen from the fresh (<0.5 ppt), through the saline (35 ppt), to the hypersaline (160 ppt) solutions, indicating increasing leg flexure with higher salt concentrations.

average femur–patella joint angle. These measurements from fossil spiders from the Crato Formation suggest that they are very similar in leg position to the spiders drowned in hypersaline conditions (Fig. 4; Table 1).

The paleosalinity of the lake in which the Crato Formation was deposited has been a subject of debate for the last 20 years. The main evidence for freshwater conditions includes the presence of mayfly larva (Maisey, 1990). Mayfly larvae are exclusively freshwater inhabitants. Fossils of these insects occur in the thousands in the Crato Formation (McCafferty, 1990; Martins-Neto, 1996). However, these insects were most likely not inhabitants of the actual ancient lake but, instead, lived in freshwater rivers that drained into the lake (Martill and Wilby, 1993). *Dastilbe* also occur in large numbers, and the majority appears to be juveniles (Davis and Martill, 2003). These fish are widely assumed to have been freshwater fish; however, extant goniorhynchiform fish are known to tolerate high levels of salinity, and *Dastilbe* were likely anadromous (Herald, 1961; Patterson, 1984; Davis and Martill, 2003). Large concentrations of juveniles preserved within the same layer are suggestive of mass mortality episodes (Martill et al., 2008). A number of mechanisms can result in fish mass mortality events, including changes in salinity, temperature, oxygen depletion by algal blooms, or the overturn of bottom waters (Marti-Cardona et al., 2008; Martill et al., 2008; Rao et al., 2014). Martill and Wilby (1993) suggested that the fish likely lived above the halocline within a surface layer of fresh water and died en masse brought on by the breakdown of the halocline as a result of storms or seasonal overturn. Another possible scenario responsible for the presence of freshwater organisms is freshening episodes that lowered the salinity of the paleolake to a suitable level for survival of the organisms during brief periods, and a later increase in salinity through evaporation that resulted in mass mortality events as is observed in Lake Eyre of Australia (Croke et al., 1996; Hasiotis, pers. obs.).

Previous evidence for hypersalinity is also based on sedimentological and stratigraphic evidence. A variety of pseudomorphs after hopper-face halite morphologies occur throughout the Crato Formation and indicate widespread hypersalinity (Martill and Wilby, 1993; Martill et al., 2007). These halite pseudomorphs are present in the Nova Olinda Member at the bottom of the Crato Formation, and also in the Jamaru Member further up in the section. Immediately above the Crato Formation lies the Ipubi Formation, a series of bedded and massive evaporite deposits, indicating high rates of evaporation and high levels of salinity throughout the basin's history (Martill and Wilby, 1993). The sequence throughout the Crato Formation and the Ipubi Formation suggests a lake environment with episodes of fluctuating salinity and hypersalinity. Hypersaline conditions are in congruence with the semiarid to arid climate interpretation based on paleogeography and the fossil terrestrial plant and animal life. Based on paleontological and stratigraphic evidence, the water body in which the Crato Formation was deposited was likely stratified with well-mixed surface waters and hypersaline bottom waters (Martill et al., 2007; Heimhofer et al., 2010).

Salinity is a common environmental parameter determined when studying bodies of water, and it has strong ties to climate and ecology (e.g., Williams et al., 1990; Henderson, 2002). Many climate studies focus on oceanography; however, lakes are also important proxies for climate change (Street-Perrot and Harrison, 1985; Winter and Woo, 1990; Mason et al., 1994; Cohen, 2003). Fluctuations in salinity can provide insight on rates of evaporation and rainfall for an area. Saline lakes, for example, are dependent on a rate of evaporation that exceeds the rate of precipitation resulting in a higher concentration of salts (e.g., Eugster and Hardie, 1978; Horne and Goldman, 1994). Lakes in semiarid to arid regions are particularly sensitive to changes in climate as an increase in precipitation can greatly alter the conditions of the lake (Last and Selzak, 1988). With respect to ecology, salinity influences what types of plants and aquatic life can be present in a certain environment (Hammer, 1986; Grande, 1994). High levels of salinity result in lower levels of dissolved oxygen, restricting the types of organisms that require highly oxygenated water (Hammer, 1986).

6. Conclusions

This study suggests that a relationship exists between the leg flexure of drowned spiders and salinity of the water in which they were deposited. Osmosis is likely the mechanism responsible for the differences in leg flexures in varying salinity. High levels of salinity produce more acute femur–patella and tibia–metatarsus joint angles, resulting in more tightly curled legs. In freshwater conditions, legs typically are extended out from the body with obtuse joint angles approaching 180°. Solutions of saline water produce a wide range of leg angles that fall in between the fresh and the hypersaline conditions tested, suggesting that increasing salinity results in an increase in the curled leg flexure.

Application of these results to the spider-bearing strata in the geologic record reveals a similar pattern of leg flexure with respect to interpreted salinity. Spider fossils from the Florissant Formation were deposited in a freshwater lacustrine environment and show the same outstretched leg pattern as seen in freshwater experiments. Spider fossils from the Parachute Creek Member of the Green River Formation were deposited in saline conditions, and the pattern in leg flexures for those fossils is similar to that seen in the saline experiments. These results suggest spiders preserved in spider-bearing beds of the Crato Formation were deposited in hypersaline conditions to produce the dominant curled leg pattern observed in the spider fossils.

This study has revealed that salinity is a taphonomic control on spiders, and thus a new potential proxy for salinity in lacustrine environments is proposed based on spider leg flexure where salinity indicators are otherwise ambiguous. Future studies need to focus on other potential scenarios including death in fresh water followed by submersion in hypersaline water and desiccation followed by submersion in water. In addition, further experiments finding the threshold where different leg flexures are represented in more specific salinities, especially between 35 ppt and 160 ppt, constraining salinity to distinct values, and thus be applied to other aquatic paleoenvironments where fossil spiders can be found. This could further be applied to the Green River Formation, where multiple horizons with fossil spiders exist, to track fluctuations in salinity throughout deposition. Although fossil spiders are considered rare, they occur in many deposits around the world including Daohugou, China (Selden et al., 2015), Montsec and Las Hoyas, Spain (Selden and Penney, 2003), and the Isle of Wight, England (Selden, 2014). Investigating the fossil spiders from deposits of this nature, after further salinity experiments on modern spiders, might allow for more discrete interpretations of salinity for these paleoenvironments. Finally, proxies for salinity in ancient lake environments are valuable, but when these are ambiguous, such as in the Crato Formation, other methods must be used to determine salinity.

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References

- Allison, P.A., 1986. Soft-bodied animals in the fossil record: the role of decay in fragmentation during transport. *Geology* 14, 979–981.
- Allison, P.A., Briggs, D.E.G., 1993. Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* 21, 527–530.
- Alvin, K.L., 1982. Cheileropodiaceae: biology, structure and paleoecology. *Rev. Palaeobot. Palynol.* 37, 71–98.
- Batten, D.J., 2007. Spores and pollen from the Crato Formation: biostratigraphic and palaeoenvironmental implications. In: Martill, D.M., Bechley, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge.
- Beadle, L.C., 1974. *The Inland Waters of Tropical Africa: An Introduction to Tropical Limnology*. Longman, London.

- Barling, N., Martill, D.M., Heads, S.W., Gallien, F., 2015. High fidelity preservation of fossil insects from the Crato Formation (Lower Cretaceous) of Brazil. *Cretac. Res.* 52, 605–622.
- Brett, C.E., Baird, G.C., Speyer, S.E., 1997. Fossil Lagerstätten: stratigraphic record of paleontological and taphonomic events. In: Brett, C.E., Baird, G.C. (Eds.), *Paleontological events: stratigraphic, ecological, and evolutionary implications*. Columbia University Press, New York.
- Briggs, D.E.G., 2003. The role of decay and mineralization in the preservation of soft bodied fossils. *Annu. Rev. Earth Planet. Sci.* 31, 275–301.
- Brobst, D.A., Tucker, J.D., 1973. X-Ray Mineralogy of the Parachute Creek Member, Green River Formation, in the Northern Piceance Creek Basin, Colorado. US Government Printing Office, Washington DC.
- Bromley, R.G., 1996. *Trace Fossils: Biology, Taphonomy and Applications*. Chapman and Hall, London.
- Carpenter, A.B., 1978. Origin and chemical evolution of brines in sedimentary basins. *Oklahoma Geol. Surv. Circ.* 79, 60–77.
- Chivas, A.R., De Deckker, R., Shelley, J.M.G., 1986. Magnesium and strontium in non-marine ostracod shells as indicators of paleosalinity and palaeotemperature. *Hydrobiologia* 143, 135–142.
- Chumakov, N.M., Zharkov, M.A., Herman, A.B., Doludenko, M.P., Kalandadze, N.M., Lebedev, E.L., Ponomarenko, A.G., Rautian, A.S., 1995. Climatic belts of the mid-Cretaceous time. *Stratigr. Geol. Correl.* 3, 241–260.
- Cohen, A.S., 2003. *Paleolimnology: The History and Evolution of Lake Systems*. Oxford University Press, Oxford.
- Coimbra, J.C., Arai, M., Careno, A.L., 2002. Biostratigraphy of Lower Cretaceous microfossils from the Araripe Basin, north-eastern Brazil. *Geobios* 35, 687–698.
- Cole, R.D., 1985. Depositional environments of oil shale in the Green River Formation, Douglas Creek Arch, Colorado and Utah. In: Picard, M.D. (Ed.), *Geology and Energy Resources, Uinta Basin of Utah*. Utah Geological Association, Salt Lake City, Utah, pp. 211–225.
- Croke, J.C., Magee, J.M., Price, D.M., 1996. Major episodes of Quaternary activity in the lower Neales River northwest of Lake Eyre, central Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 124, 1–15.
- Davis, S.P., Martill, D.M., 2003. The goniorhynchiform fish *Dastilbe* from the Lower Cretaceous of Brazil. *Paleontology* 42, 715–740.
- De Deckker, P., Chiva, A.R., Shelley, J.M.G., Torgersen, T., 1988. Ostracod shell chemistry: a new paleoenvironmental indicator applied to a regressive/transgressive record from the gulf of Carpentaria, Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 66, 231–241.
- Dunlop, J.A., Martill, D.M., 2004. Four additional specimens of the fossil camel spider *Cratosolpuga wunderlichi* Selden, 1996 (Arachnida: Solifugae) from the Lower Cretaceous Crato Formation of Brazil. *Revista Ibérica de Aracnología* 9, 143–156.
- Dunlop, J.A., Menon, F., Selden, P.A., 2007. Arachnida: spiders, scorpions and allies. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge.
- Ellis, C.H., 1944. The mechanism of extension in the legs of spiders. *Biol. Bull.* 86, 41–50.
- Eugster, H.P., Hardie, L.A., 1978. *Saline Lakes*. In: Lerman, A. (Ed.), *Lakes*. Springer, New York.
- Evanoff, E., McIntosh, W.C., Murphey, P.C., 2001. Stratigraphic summary and $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology of the Florissant Formation, Colorado. In: Evanoff, E., Gregory-Wodzicki, K.M., Johnson, K.R. (Eds.), *Fossil flora and stratigraphy of the Florissant Formation, Colorado*. Denver Museum of Nature and Science Proceedings 4, pp. 1–16.
- Foelix, R.F., 2011. *Biology of Spiders*. fourth ed. Oxford University Press, Oxford.
- Föllmi, K.B., 2012. Early Cretaceous life, climate, and anoxia. *Cretac. Res.* 35, 230–257.
- Goodfriend, G.A., 1992. The use of land snails in paleoenvironmental reconstruction. *Quat. Sci. Rev.* 11, 665–685.
- Grande, L., 1994. Studies of paleoenvironments and historical biogeography in the Fossil Butte and Laney members of the Green River Formation. *Contrib. Geol.* 30, 15–32.
- Hallam, A., 1984. Continental humid and arid zones during the Jurassic and Cretaceous. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 47, 195–223.
- Hallam, A., 1985. A review of Mesozoic climates. *J. Geol. Soc. Lond.* 142, 433–445.
- Hammer, U.T., 1986. *Saline Lake Ecosystems of the World*. Dr W. Junk Publishers, Dordrecht.
- Hasiotis, S.T., 2002. Continental Trace Fossil Short Course Number 51. SEPM—Society for Sedimentary Geology, Tulsa, Oklahoma.
- Hasiotis, S.T., 2004. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA. Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnoconos. *Sediment. Geol.* 167, 177–268.
- Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S.P., Martill, D., Rios-Netto, A.M., 2010. Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous, Araripe Basin, North-eastern Brazil). *Sedimentology* 57, 677–694.
- Henderson, G.M., 2002. New ocean proxies for paleoclimate. *Earth Planet. Sci. Lett.* 203, 1–13.
- Herald, E.S., 1961. *Living Fishes of the World*. Doubleday and Company, London.
- Horne, A.J., Goldman, C.R., 1994. *Limnology*. McGraw-Hill, New York.
- Humphrey, J.A.C., 1987. Fluid mechanic constraints on spider ballooning. *Oecologia* 73, 469–477.
- Kropf, C., 2013. Hydraulic system of locomotion. In: Nentwig, W. (Ed.), *Spider Ecophysiology*. Springer, Berlin, pp. 43–56.
- Last, W.M., 2002. Geolimnology of salt lakes. *Geosci. J.* 6, 347–369.
- Last, W.M., Ginn, F.M., 2005. Saline systems of the Great Plains of western Canada: an overview of the limnogeology and paleolimnology. *Saline Systems* 1 (10), 1–38.
- Last, W.M., Slezak, L.A., 1988. The salt lakes of western Canada: a paleolimnological overview. *Dev. Hydrobiol.* 44, 301–316.
- Levi, H.W., 1975. The American orb-weaver genera *Larinia*, *Cercidia*, and *Mangora* north of Mexico (Araneae, Araneidae). *Bull. Mus. Comp. Zool. Harv. Coll.* 147, 101–135.
- Levi, H.W., 2005. The orb-weaver genus *Mangora* of Mexico, Central America, and the West Indies (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* 158, 139–181.
- Licht, E.L., 1986. Araneid taphonomy: A paleo thermometer. In: Eberhard, W.G., Lubin, Y.D., Robinson, B.C. (Eds.), *Proceedings of the Ninth International Congress of Arachnology*, Panama, 1983. Smithsonian Institution Press, Washington DC, pp. 163–165.
- Maisey, J.G., 1990. Stratigraphy and depositional environment of the Crato Member (Santana Formation, Lower Cretaceous) of northeast Brazil. *Bull. Am. Mus. Nat. Hist.* 195, 15–19.
- Maisey, J.G., 1991. *Santana Fossils: An Illustrated Atlas*. T.F.H. Publications, Neptune City, New Jersey.
- Marti-Cordano, B., Steissberg, T.E., Schladow, S.G., Hook, S.J., 2008. Relating fish kills to upwellings and wind patterns in the Salton Sea. *Hydrobiologia* 604, 85–95.
- Martill, D.M., 2007. The geology of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge, pp. 8–24.
- Martill, D.M., Heimhofer, U., 2007. The stratigraphy of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge, pp. 25–43.
- Martill, D.M., Wilby, P.R., 1993. Stratigraphy. In: Martill, D.M. (Ed.), *Fossils of the Santana and Crato Formations, Brazil*. The Palaeontological Association, London, pp. 20–50.
- Martill, D.M., Loveridge, R., Heimhofer, U., 2007. Halite pseudomorphs in the Crato Formation (Early Cretaceous, Late Aptian–Early Albian), Araripe Basin, northeast Brazil: further evidence for hypersalinity. *Cretac. Res.* 28, 613–620.
- Martill, D.M., Brito, P.M., Washington-Evans, J., 2008. Mass mortality of fishes in the Santana Formation (Lower Cretaceous, ?Albian) of northeast Brazil. *Cretac. Res.* 29, 649–658.
- Martínez-Delclòs, X., Martinell, J., 1993. Insect taphonomy experiments. Their application to the Cretaceous outcrops of lithographic limestones from Spain. *Kaupia* 2, 133–144.
- Martins-Neto, R.G., 1996. New mayflies (Insecta, Ephemeroptera) from the Santana Formation (Lower Cretaceous), Araripe Basin, northeastern Brazil. *Revista Española de Paleontología* 11, 177–192.
- Mason, I.M., Guzikowska, M.A.J., Rapley, C.G., Street-Perrott, F.A., 1994. The response of lake levels and areas to climate change. *Clim. Chang.* 27, 161–197.
- McCafferty, W.P., 1990. Chapter 2: Ephemeroptera. In: Grimaldi, D. A. (Ed.), *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bulletin of the American Museum of Natural History v. 195, pp. 20–50.
- Meyer, H.W., 2003. *The Fossils of Florissant*. Smithsonian Books, Washington, DC.
- Menon, F., 2007. Higher systematics of scorpions from the Crato Formation, Lower Cretaceous of Brazil. *Paleontol.* 50, 185–195.
- Mohr, B.A.R., Bernardes de Oliveira, M.E.C., Loveridge, R.F., 2007. The macrophyte flora of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge, pp. 537–565.
- Neumann, V.H., Borrego, A.G., Cabrera, L., Dino, R., 2003. Organic matter composition and distribution through the Aptian-Albian lacustrine sequences of the Araripe Basin, northeastern Brazil. *Int. J. Coal Geol.* 54, 21–40.
- Nicholson, B., Marcarelli, A., 2004. The paradox of a Great Salt Lake. *Southwest. Hydrol.* 3, 24–25.
- Nudds, J., Selden, P., 2008. Fossil-Lagerstätten. *Geol. Today* 24, 153–158.
- O'Brien, N.R., Meyer, H.W., Reilly, K., Ross, A., Maguire, S., 2002. Microbial taphonomic processes in the fossilization of insects and plants in the late Eocene Florissant Formation, Colorado. *Rocky Mt. Geol.* 37, 1–11.
- Parry, D.A., Brown, R.H., 1959. The hydraulic mechanism of the spider leg. *J. Exp. Biol.* 36, 423–433.
- Patterson, C., 1984. Family Chaniidae and other teleostean fishes as living fossils. In: Eldredge, N., Stanley, S.M. (Eds.), *Living fossils*. Springer, New York.
- Punzo, F., 1998. *Biology of camel-spiders (Arachnida, Solifugae)*. Kluwer Academic Publishers, Norwell, Massachusetts.
- Rao, Y.R., Howell, T., Watson, S.B., Abernathy, S., 2014. On hypoxia and fish kills along the north shore of Lake Erie. *J. Great Lakes Res.* 40, 187–191.
- Rosenfeld, A., Vesper, B., 1977. The variability of sieve-pores in recent and fossil species of *Cyprioides torosa* (Jones, 1850) as an indicator for salinity and palaeosalinity. In: Löffler, H. (Ed.), *Aspects of Ecology and Zoogeography of Recent Fossil Ostracoda*. Dr. W. Junk Publishers, Dordrecht.
- Selden, P.A., 2014. Spiders (Arachnida: Araneae) from the Eocene Insect Limestone of the Isle of Wight. In: Ross, A. (Ed.) *Paleontological studies on the Insect Limestone of the Isle of Wight. Earth & Environmental Science Transactions of The Royal Society of Edinburgh* 104, pp. 275–282 (for 2013).
- Selden, P.A., Penney, D., 2003. Lower Cretaceous spiders (Arthropoda: Arachnida: Araneae) from Spain. *Neues Jb. Geol. Paläontol. Monat.* 2003, 175–192.
- Selden, P.A., Shear, W.A., 1996. The first Mesozoic Solifugae (Arachnida), from the Cretaceous of Brazil and a redescription of the Palaeozoic solifuge. *Paleontology* 39, 583–604.
- Selden, P.A., Ren, D., Shih, C.-K., 2015. Mesozoic cribellate spiders (Araneae: Deinopoidea) from China. *J. Syst. Palaeontol.* 14, 49–79.
- Smith, D.M., 2012. Exceptional preservation of insects in lacustrine environments. *Palaios* 27, 346–353.
- Smith, M.E., Carroll, A.R., Singer, B.S., 2008. Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. *Geol. Soc. Am. Bull.* 120, 54–84.
- Street-Perrott, F.A., Harrison, S.P., 1985. Lake levels and climate reconstruction. In: Hecht, A.D. (Ed.), *Paleoclimate Analysis and Modeling*. Wiley, Chichester, pp. 291–340.
- Weihmann, T., Gunther, M., Blickhan, R., 2012. Hydraulic leg extension is not necessarily the main drive in large spiders. *J. Exp. Biol.* 215, 578–583.

- Williams, W.D., 1967. The chemical characteristics of lentic surface waters in Australia. In: Weatherley, A.H. (Ed.), *Australian Inland Waters and Their Fauna*. Australian National University Press, Canberra, pp. 18–77.
- Williams, W.D., Boulton, A.J., Taaffe, R.G., 1990. Salinity as a determinant of salt lake fauna: a question of scale. *Dev. Hydrobiol.* 59, 257–266.
- Winter, T.C., Woo, M.K., 1990. Hydrology of lakes and wetlands. In: Wolman, M.G., Riggs, H.C. (Eds.), *Surface Water Hydrology*The Geology of North America. Geological Society of America, Boulder, Colorado, pp. 159–187.
- Wu, H., Wu, D.Y., 1925. Nature of heat denaturation of proteins. *J. Biol. Chem.* 64, 369–378.
- Ziegler, A.M., Eshel, G., McAllister Rees, P., Rothfus, T.A., Rowley, D.B., Sunderlin, D., 2003. Tracing the tropics across land and sea: Permian to present. *Lethaia* 36, 227–254.