THE TAXONOMY AND TAPHONOMY OF FOSSIL SPIDERS FROM THE CRATO FORMATION OF BRAZIL

by

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ABSTRACT

In order to develop a clearer picture of the paleoenvironment of the Crato Formation, an early Cretaceous Fossil-Lagerstätte, the taphonomy and taxonomy of fossil spiders were examined. The Crato Formation is represented by deposits of thinly laminated limestones with abundant terrestrial invertebrate fossils. One aspect of the Crato Formation depositional environment that has been debated is the salinity of the ancient lake in which this unit was deposited. To investigate the paleosalinity, the leg orientations of fossil spiders from the Crato, Green River, and Florissant formations were examined as well as the leg orientations of modern spiders drowned in varying salinities. The leg orientations of drowned modern spiders suggest hypersalinity produces a tightly curled leg orientation and fresh water produces an extended leg orientation. The results of drowned modern spiders are comparable to the fossil spiders preserved in lacustrine deposits of similar salinity, and thus, suggest the Crato Formation was deposited in hypersaline water. In addition, the taxonomy of the fossil spiders from the Crato Formation was elucidated. The abundant araneoids previously named *Cretaraneus martinsnetoi* Mesquita, 1996 have been redescribed and placed in a new genus, *Olindarachne*, within Araneidae. Two other families of spider have been described, Nephilidae and Palpimanidae. The age range of Palpimanidae is extended back nearly 90 million years from a previous specimen from Dominican amber (Neogene), and the geographic range for Araneidae, Nephilidae, and Palpimanidae has been expanded to the South American continent during the Early Cretaceous.

ACKNOWLEDGEMENTS

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INTRODUCTION

This thesis is composed of two projects focusing on fossil spiders from the Crato Formation of Brazil in order to make inferences about the depositional environment, specifically the salinity, and to describe the biodiversity of spiders present in the early Cretaceous. Reconstructing the biotic and abiotic components of such environments is important in understanding geologic history, climate, and the history and evolution of life. Fossil-Lagerstätten provide an extraordinary opportunity for reconstructing past environments due to the exceptionally preserved fossils for which they are known (Briggs, 2003; Nudds and Selden, 2008). The Crato Formation is one such example from the Early Cretaceous with an abundance of well-preserved fossils, including spiders, and thus received great attention in reconstructing the geologic history of the deposit and the biological communities present during deposition. The Crato Formation also presents the unique opportunity to study the biogeography of spiders during the breakup of Gondwana, and is one of the few localities in which spiders are preserved in the Southern Hemisphere. Many studies have investigated different aspects of the Crato Formation, however, there are several controversies surrounding the depositional environment and the taxonomy of spiders preserved in this locality.

Environmental reconstruction is typically done through analysis of lithology and environment-sensitive organisms preserved as fossils. Benthic organisms are absent and ostracods that are commonly used as proxies for salinity are scarce (Martill and Wilby, 1993; Schweigert et al., 2007). Multiple hypotheses have been proposed for the salinity of the ancient lake in which the Crato Formation was deposited. Maisey (1990) suggested freshwater conditions based on aquatic larval forms of insects that only live in fresh water. In contrast,

hypersalinity has been suggested based on the occurrence of pseudomorphs after halite present in the Crato Formation (Martill et al., 2007).

The first chapter of this thesis examines the problem of elucidating the salinity of the Crato Formation by using the post-mortem leg orientation of spiders as an indicator for salinity, a previously unused method in paleosalinity reconstruction. This study compares the leg orientations of modern spiders to the leg orientations of fossil spiders preserved in lacustrine deposits. Three distinct salinities (fresh, saline, and hypersaline) are tested in the modern spider drowning experiments to see if salinity is a taphonomic control on leg orientation after death. In addition, some spiders were allowed to expire in air and subsequently submerged in a solution of hypersaline water or fresh water. These results are compared to the fossil record in which spiders from the Crato, Green River, and Florissant formations are preserved. Salinity for the Green River and Florissant formations has previously been interpreted as stratified saline and fresh, respectively (Cole, 1985; Meyer, 2003). The results reveal that death in fresh water produces an extended leg orientation in spiders, a pattern that is supported by the extended leg orientation of fossil spiders from the Florissant Formation. Similarly, spiders drowned in saline water have extended and curled leg orientations in near equal abundance, which is consistent with fossil spiders from the Green River Formation. Conversely, leg orientations of spiders drowned in hypersaline conditions produces a strong pattern of tightly curled legs similar to what is observed of fossil spiders in the Crato Formation. Spiders allowed to expire in air have an initial curled leg orientation. Once submerged, the legs of spiders begin to uncurl in fresh water and stay tightly curled in hypersaline water. The modern taphonomy experiments on the relationship between salinity and leg orientation are consistent with what is observed in the fossil record, suggesting hypersaline conditions present during deposition of the Crato Formation to produce the curled

leg orientation trend in fossil spiders, although death on land cannot be ruled out as a possible scenario.

The second chapter of this thesis revisits the taxonomy of spiders preserved in the Crato Formation. Fossil spiders are relatively rare compared to other groups of arthropods, and most are preserved in amber of Cenozoic age (Selden et al., 2009). Most Mesozoic spiders are preserved in rock, and the Crato Formation is one out of a handful of units in which spiders of this age can be studied and, therefore, is important in reconstructing the biogeographic and evolutionary history of these arachnids. Few spiders have been described from the Crato Formation, and include *Cretadiplura ceara* Selden, 2006 and *Dinodiplura ambulacra* Selden, 2006 belonging to the suborder Mygalomorphae, and *Cretaraneus martinsnetoi* Mesquita, 1996, the first formally described spider from the Crato Formation (Mesquita, 1996; Selden et al., 2006).

Cretaraneus martinsnetoi was assigned to the genus *Cretaraneus*, previously described by Selden, 1990 from an early Cretaceous spider from the Sierra de Montsech, Spain. Most of the spiders of the Crato Formation appear to be the same species, which was placed in *Cretaraneus*. This classification was later questioned, and *C. martinsnetoi* was thought to not be congeneric with *Cretaraneus* (Dunlop et al., 2007). A re-examination of the Crato fossil spiders and the *C. martinsnetoi* holotype has shown this classification to be incorrect. This group, previously described as *C. martinsnetoi,* is a distinct genus justified by the extremely long first pairs of legs, robust femurs, and spines on the patellae, traits unlike *Cretaraneus*. *Cretaraneus* was later placed in the family Nephilidae, the golden orbweavers, based on size of the male and by a long, slightly twisted, embolus on the pedipalps (Selden and Penney, 2003). Four fossil

spiders described in this thesis closely resemble family Araneidae, the true orbweavers, suggested by leg length, squarish endites, the absence of a cribellum, and a globose abdomen.

A new genus, *Olindarachne*, is erected for the four Crato Formation specimens and is placed in the family Araneidae, expanding the geographic distribution of this family during the Cretaceous. Previously, fossil Araneidae were only known to exist in the Northern Hemisphere; however, this study has shown araneids were also present in South America during this time and suggests the family would have been distributed throughout Pangaea before the continents separated. In addition, two other fossil spiders have been described to the family level, and represent families Nephilidae and Palpimanidae. This extends the known age range of Palpimanidae back nearly 90 million years from a previously described palpimanid in Neogene Dominican amber (Wunderlich, 1988).

This project has amended previous interpretations about the taxonomy of the abundant araneoid spiders present in the Crato Formation and provided further evidence for hypersaline conditions during deposition. The results from this project suggest a relationship between salinity and the leg orientation of fossil spiders in ancient lacustrine environments. The erection of a new genus for the araneid *Olindarachne martinsnetoi* and the presence of two additional families, Nephilidae and Palpimanidae, expand pre-existing knowledge spider diversity during the Mesozoic Era.

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CHAPTER 1: SPIDER LEG ORIENTATION AS A PROXY FOR ESTIMATING SALINITY IN LACUSTRINE PALEOENVIRONMENTS

Abstract

The Crato Formation of Brazil is a Fossil-Lagerstätte and a significant source of Early Cretaceous fossil spiders. The Crato Formation contains alternating heterolithic beds and laminated limestone deposited in a lacustrine setting. Two other lacustrine deposits in which spider-bearing beds are present are the Green River and Florissant formations of the early to mid-Eocene and late Eocene age, respectively. While these three formations are the result of similar depositional settings, the proposed salinity for the Florissant, Green River, and Crato spider-bearing beds differ as fresh, stratified saline, and multiple interpretations that range from fresh to hypersaline, respectively. The leg orientations of fossil spiders preserved in each of the three formations also vary. Florissant spiders commonly display legs extended outward from the body, Green River Formation spiders display a mix of curled and extended legs, and those in the Crato Formation typically have legs curled under the body. To investigate the differences in leg orientation among the three formations, the leg orientation for over 200 fossil spiders from the Florissant, Green River, and Crato formations was determined and compared to the leg orientations of modern postmortem spiders. Modern spiders were either allowed to expire in air and subsequently submerged in a solution or drowned in water of three different salinities: fresh (<0.5 ppt), saline (35 ppt), and hypersaline (160 ppt). Spiders expired in air exhibited curled legs, but most decayed; however, three spiders were subsequently placed in fresh water and three were placed in hypersaline water. The legs of subaerial death spiders submerged in fresh water uncurled but did not fully extended. Conversely, subaerial death spiders submerged in hypersaline water did not exhibit any change from the tightly curled leg orientation. The leg

orientations of spiders drowned in fresh, saline, and hypersaline water were extended, mixed, and curled, respectively. These results suggest the difference in leg orientation appears to be driven by salinity. This trend was also recognized in fossil spiders: Florissant, Green River, and Crato formations exhibited extended, mixed, and curled leg orientations. The results suggest an increase in curled leg orientation with salinity and, therefore, suggest hypersalinity present during deposition of the spider-bearing units in the Crato Formation, as opposed to spider-bearing units in the Green River and Florissant formations.

Keywords: Araneae, Taphonomy, Crato Formation, Paleosalinity, Hypersalinity

Introduction

Body and trace fossils are used to reconstruct ancient environments, providing information regarding past 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, such benthic organisms as ostracodes are used commonly in paleoenvironmental reconstruction because they are abundant and sensitive to surrounding conditions (Rosenfeld and Vesper, 1977; Chivas et al., 1986; De Deckker et al., 1988). In addition, 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 such delicate features as hairs. These deposits, termed Fossil-Lagerstätten, provide a more complete view of organism morphology and ecosystems by preserving organisms and 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).

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The Lower Cretaceous Crato Formation of Brazil is one example of a Konservat-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. Benthic organisms are absent and ostracodes are generally scarce, although there are a few horizons within the Crato Formation with abundant ostracodes (Martill and Wilby, 1993; Schweigert et al., 2007). The Crato Formation presents a unique view of an Early Cretaceous terrestrial ecosystem during the breakup of South America and Africa.

Paleontological, geochemical, and stratigraphic studies suggest deposition in a low-energy lake in a semiarid to arid climate (Heimhofer et al., 2010). Though general aspects of the environment of deposition for the Crato Formation have been determined, the water salinity is still debated, in part due to the absence of such indicators as benthic organisms and ostracodes. Multiple hypotheses have been proposed for the salinity of the ancient Crato Lake, ranging from fresh to hypersaline (Maisey, 1990; Neumann, 2003; Martill et al., 2007). Most recently, Martill et al. (2007) suggested pseudomorphs after halite as evidence for hypersalinity, focusing on geochemical data rather than paleontological evidence. The Crato Formation presents a unique opportunity to use a fossil assemblage dominated by terrestrial organisms as a potential proxy for salinity.

The Crato Formation fossils are predominantly insects and 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 saline water and fresh

water, respectively (Cole, 1985; Meyer, 2003). A connection likely exists between the unique curled leg pattern of Crato Formation spider fossils and the unknown salinity, suggesting the leg orientation of fossil spiders can be used as a potential indicator of salinity in the ancient lacustrine deposits in which they are preserved. This paper seeks to determine if an increase in the amount of curled legs observed is related to elevated levels of salinity, and proposes 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 analyses of fossil spiders.

Geologic Setting

The Crato Formation is a series of alternating heterolithic beds and carbonate deposits located northeastern Brazil (Martill and Wilby, 1993, Neumann et al., 2003; Fig. 1). Theses beds were deposited in the Araripe Basin, one of several fault-bounded intracratonic rift basins controlled by extensional tectonics during the break up of South America and Africa (Heimhofer et al., 2010). At the base of the Crato Formation is the Nova Olinda Member—the focus of this work—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. The laminated limestones are represented by the fossil-rich plattenkalk, thinly laminated limestones with little to no bioturbation, in which terrestrial arthropods are abundant. 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). Other members of the Crato Formation, listed in increasing stratigraphic order, include the Casa de Pedra, Jamacaru, and Caldas (Fig. 1). The Crato Formation is overlain by the Ipubi Formation, a unit composed of evaporites (Martill and Wilby, 1993).

GROUP	FORMATION	MEMBER	LITHOLOGY
ARARIPE	IPUBI		Mainly gypsum
		CASA DE PEDRA	Heterolithic - including black shales and muddy sandstones
		JAMACARU	Laminated limestones
	CRATO	CALDAS	Heterolithic - inlcuing silty mudstones, silts and fine to medium sandstones. Some thin laminated limestones
		NOVA OLINDA	Laminated limestones
		Transition beds	
	CASA DE PEDRA		
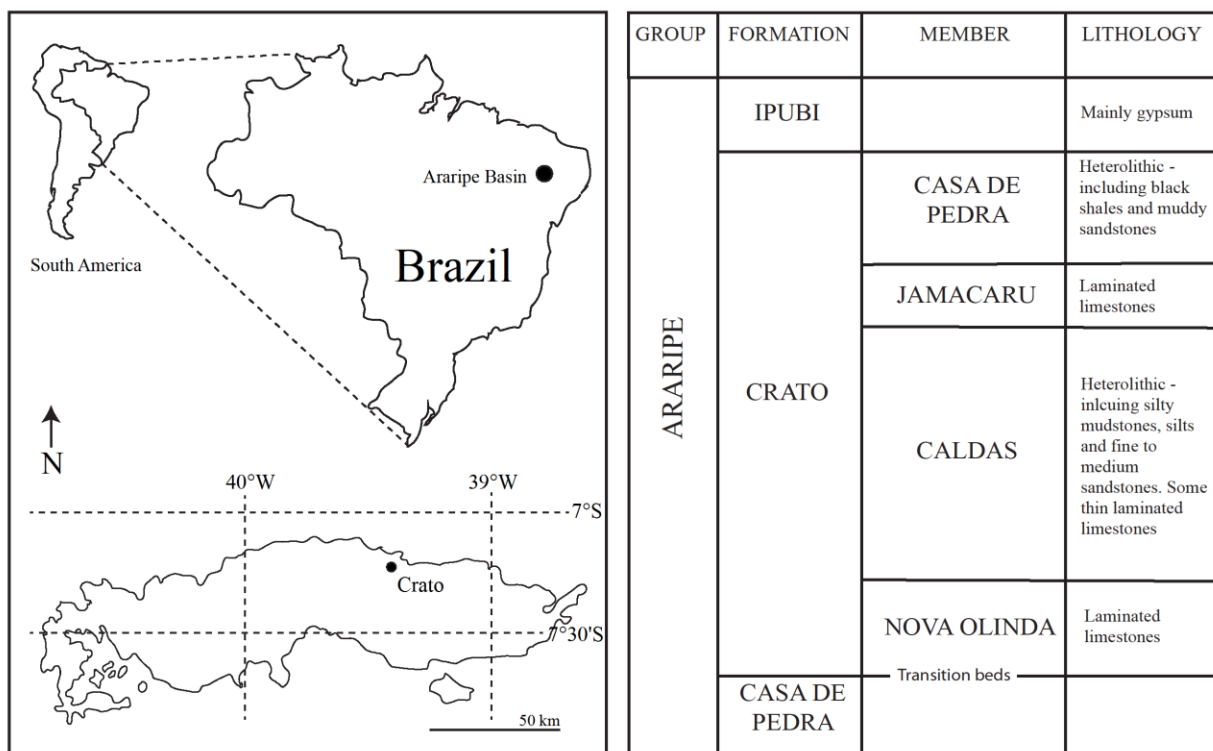
Figure 1.1– Location and stratigraphy of the Araripe Basin. Araripe Basin located in northeastern Brazil near the town of Crato for which the Crato Formation is named (modified from Heimhofer et al., 2010). Stratigraphic column showing lithologies of the Crato Formation within the basin (modified from Martill et al., 2007).

The age of the Crato Formation has been interpreted as Aptian (Early Cretaceous) based on ostracode and palynomorph studies (Coimbra et al., 2002; Batten et al., 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; Barbara et al., 2007). Fossil camel spiders (Solpugida) have also been found in the

Crato Formation, and modern-day representatives typically live in desert or semiarid climates

(Selden and Shear, 1996; Punzo, 1998; Dunlop and Martill, 2004).

Although there is general agreement about a lacustrine interpretation, the salinity of the

lake in which the Nova Olinda Member was deposited is unclear. Estimates of paleosalinity

range from fresh to hypersaline. The absence of benthic organisms used as salinity indicators,

such as ostracodes, has made salinity interpretations ambiguous in the Nova Olinda Member. A

freshwater interpretation has been proposed based on such fossils of freshwater organisms as

aquatic insect larval forms and fish (Maisey 1991). In marked contrast, hypersalinity is suggested

by hopper-cast pseudomorphs after halite throughout the laminated limestones (Martill et al.,

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 from the Parachute Creek Member (49–50 Ma), which is an oil

shale likely deposited in a chemically stratified lake in which saline bottom waters were overlain

by tongues of fresh water (Brobst and Tucker, 1973; Cole, 1985). 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,

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and aquatic angiosperms, existed during the deposition of the lacustrine sediments (Meyer, 2003).

Materials and Methods

Paleontological

Spider fossils were examined and photographed from the Crato, Green River, and Florissant formations. Ninety-five 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. One hundred twenty-five Green River Formation spiders and 42 Florissant Formation spiders were photographed at the University of Colorado, Boulder Natural History Museum. Leg orientations of the fossil spiders from all formations were determined from the photographs in Adobe Photoshop using the measure tool. Femur-patella and tibia-metatarsus joint angles were measured and leg orientation 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 positions 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. Leg orientation and joint measurements were recorded for each fossil specimen.

Modern spider taphonomy experiments

This study utilized a comparison with modern spiders to explore possible causes for differences in spider leg angles. One hundred seven spiders were collected at Clinton Lake State Park, Lawrence, Kansas during July to August 2013. Most spiders were *Mangora maculata*, a small (2–3 mm) green araneid spider, typically found in low brush. *Mangora maculata* is distinguished by abundant spines and prominent cluster of trichobothria on the femur of the third pair of legs (Levi, 1975). Twenty-five spiders were selected to be left in vials and expire in air for subsequent submersion in solutions of varying salinity. Eighty-two 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, 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 Great Salt Lake, a large hypersaline lake (Nicholson and Marcarelli, 2004).

Each spider was placed in a glass beaker and solution was poured over it. The spider and the solution were then poured into a glass vial. The vial was filled with more solution until it was full, and 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 float just beneath the surface. In either case, the vial was then turned upside down repeatedly to sink the spider. If the spider was still floating, it was left overnight and turned upside down 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 orientations were recorded over a period of five days. Spiders were left in the vials longer to monitor for further changes in leg orientation. Once spiders attained a consistent leg orientation they were photographed from the anterior, dorsal or ventral, and lateral views to capture the range of the arrangement of the legs. The leg orientation for each drowned spider was measured from the photographs in Adobe Illustrator CS5, and subsequently recorded as curled or extended, using similar criteria as the fossil specimens.

Statistical tests

Data collected from each of the fossil spiders and modern spiders was analyzed in Minitab 15 Statistical Software. For raw leg angle data, recorded in degrees, an arcsine transformation was used. After the transformation, a one-way analysis of variance (ANOVA) was conducted to test for a significant difference in the means between 1) the fossil groups and 2) the modern spider groups. In addition, a Chi-Square Goodness-of-Fit test was performed on each individual group: Florissant, Green River, Crato, Fresh, Saline, and Hypersaline, with leg orientation data categorized as curled or extended to test if leg orientation was significantly curled or extended within each group.

Results

Leg orientation of fossil spiders in lacustrine deposits

Fossil specimens include a range of femur-patella joint angles within and among the formations (Fig. 2). A one-way ANOVA performed using the leg angles of fossil spiders showed 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 fossil spiders from the Crato Formation display a statistically significant consistency in curled leg orientation, $p < 0.05$. The legs are curled under the body in 96% of the Crato Formation samples. 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 the other formations (Figs 2, 3; Table 1). Green River Formation fossil spiders showed a much more variable pattern in leg orientation than the other two formations. The legs are extended in 58% of the samples with a p-vale 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 were curled as tightly as what was observed in the Crato Formation, where joint angles are typically acute. Many specimens from the Green River Formation have a leg arrangement near the boundary distinguishing between curled and extended. At the other end of the spectrum, spiders from the Florissant Formation exhibit a dominant leg orientation in which legs in 98% of the specimens are extended. Many samples included fully 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°).

Taphonomy experiments and leg orientation

All of the 25 spiders that were allowed to expire in subaerial conditions exhibited a curled leg orientation, but 19 of the spiders quickly decayed beyond recognition while sealed in the vials before submersion. The six spiders that did not completely decay were submerged in vials of fresh water and hypersaline water. The legs of subaerial death spiders placed in fresh water began to uncurl, but still maintained a curled leg orientation. Subaerial death spiders placed in hypersaline water did not change from the tightly curled leg position.

For the 82 drowned spiders, the leg orientation of spiders varied greatly, immediately following submersion, with no consistent trend in leg orientation. After a period of three days when all spiders had expired, leg orientations had changed from their initial pose, and no further changes beyond three days were observed. An one-way ANOVA for fresh, saline, and hypersaline, revealed that the means of 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 large 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, $p = 0.493$. A statistically significant number of spiders, p-value < 0.05, drowned in hypersaline conditions had legs that were tightly curled under the body with small femur-patella joint angles 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. $= 22.52°$).
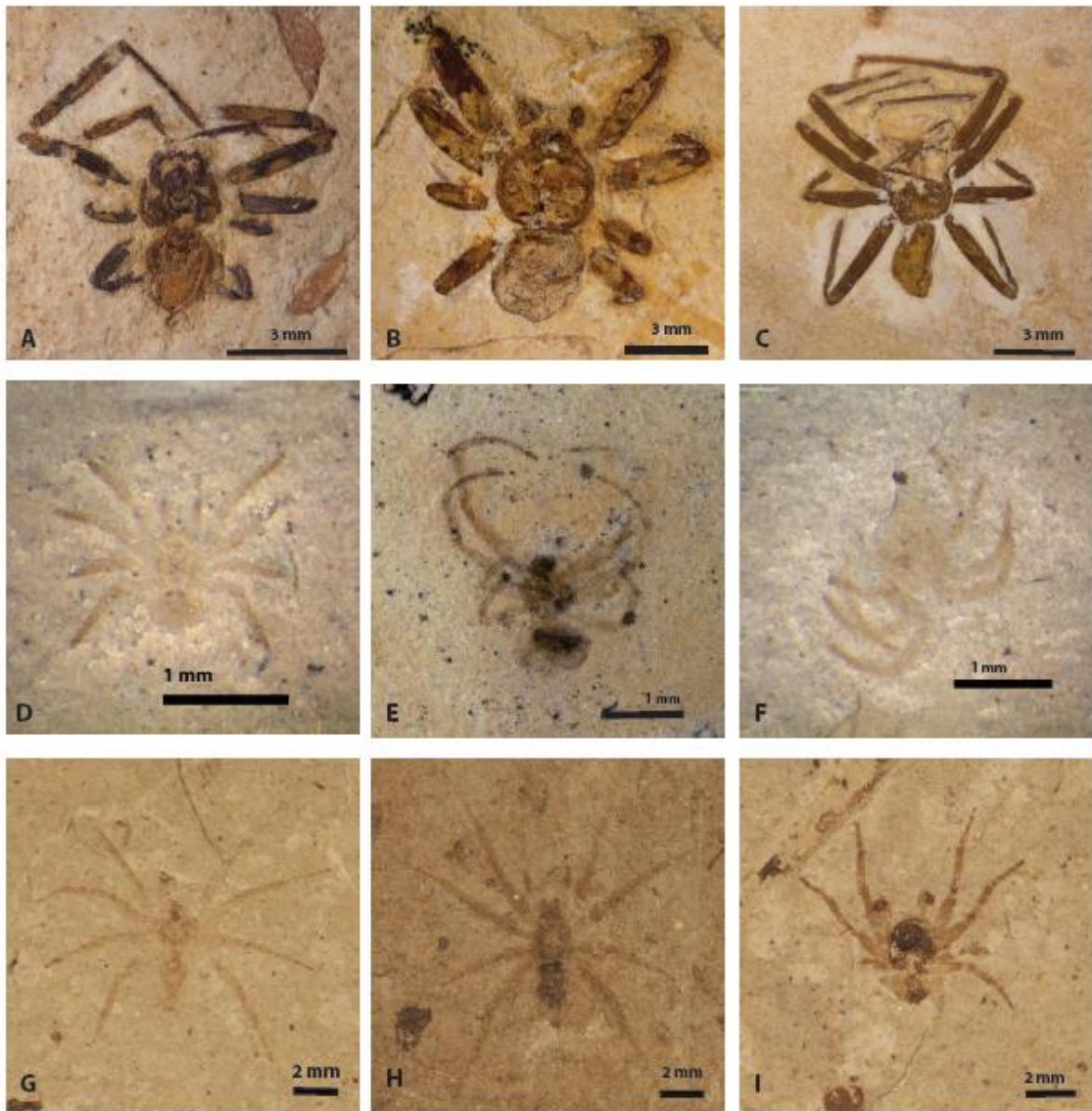
Figure 1.2 – Fossil spiders from the Crato (A–C), Green River (D–F), and the Florissant (G–I) formations.
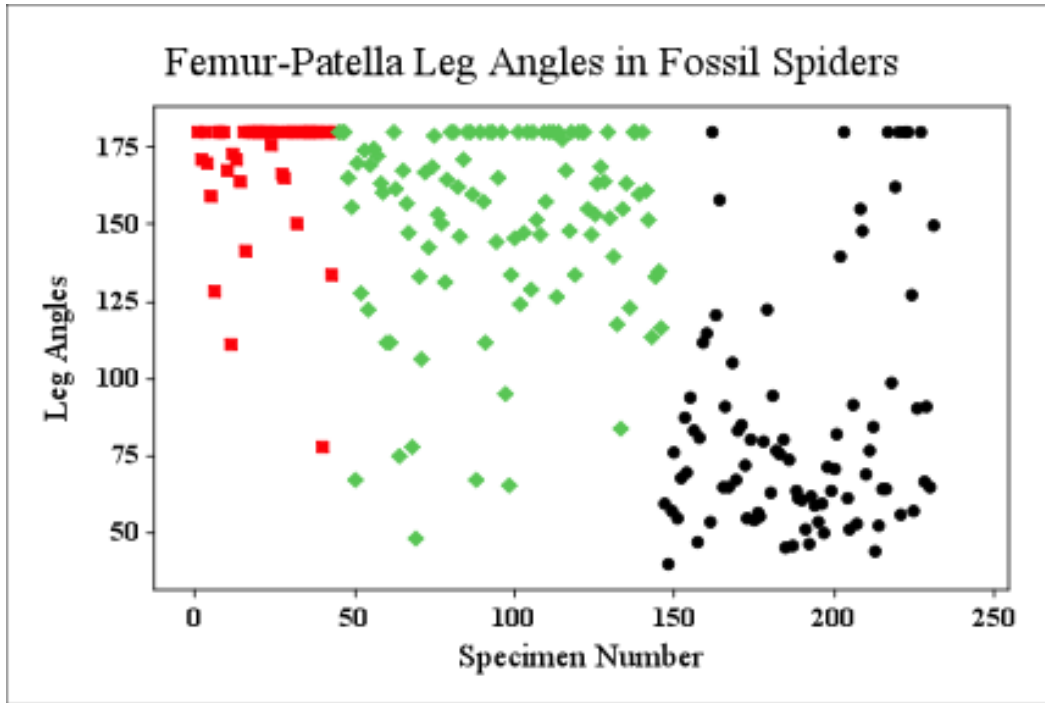
Figure 1.3 – Femur-patella leg angles within the three formations. The Florissant Formation is dominated by leg angles near 180° indicating fully outstretched legs. The Green River Formation also has many 180° but populates a wider range of angles. The Crato Formation leg angles are concentrated at lower, mostly acute, leg angles indicating curled legs. Black = Crato Formation, Red = Florissant Formation, Green = Green River Formation.
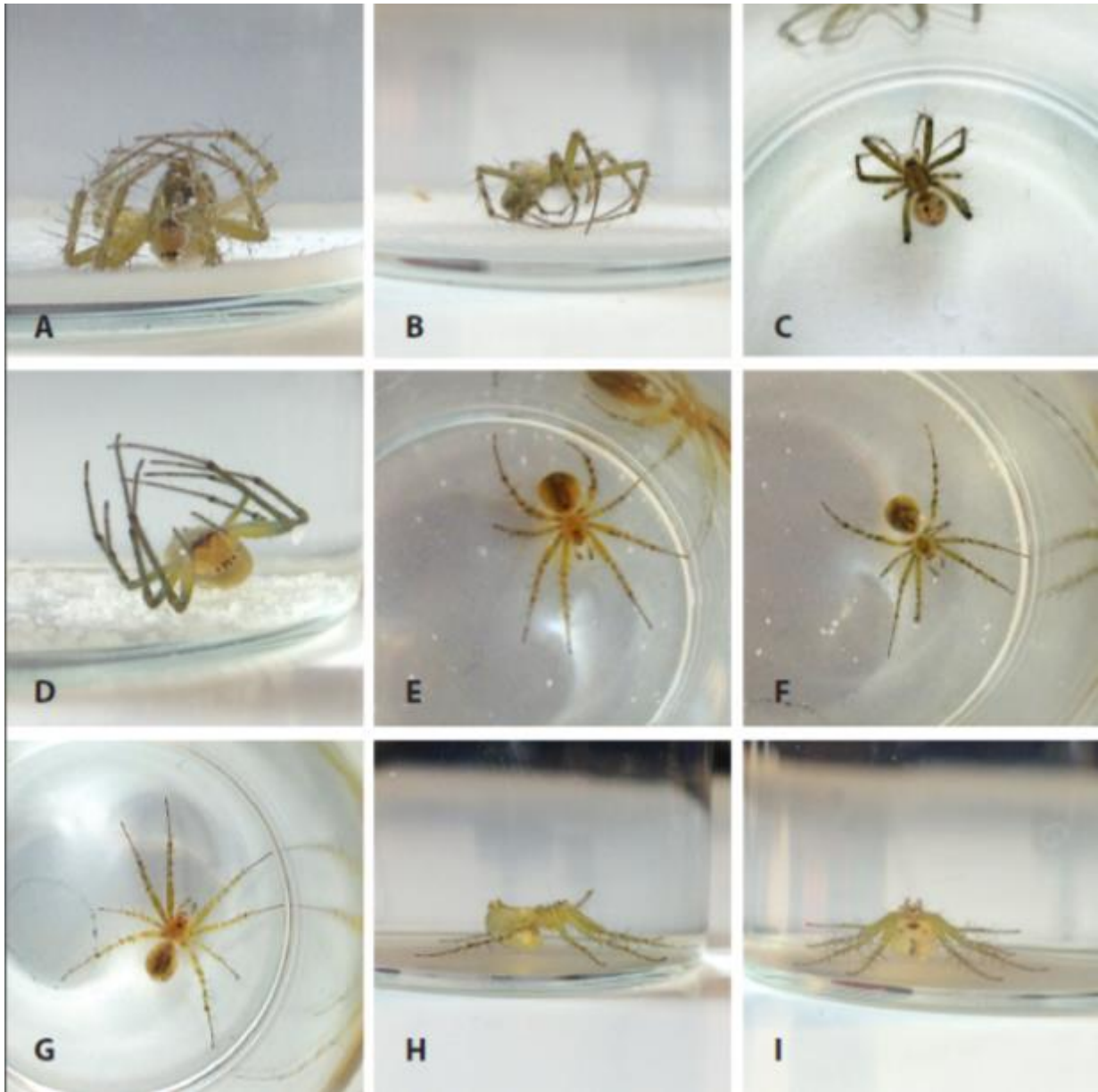
Figure 1.4 – Drowned spiders in various salinities. (A-C) Hypersaline water. Spiders typically have strongly curled legs. (D-F) Saline water. D shows a curled leg orientation in saline water. The femur-patella joint angle is acute, but the tibia-metatarsus joint in not bent significantly resulting in a curled leg orientation that is weak compared to hypersaline conditions. (G-I) Fresh water. Leg orientation is dominated by an extended leg pattern.
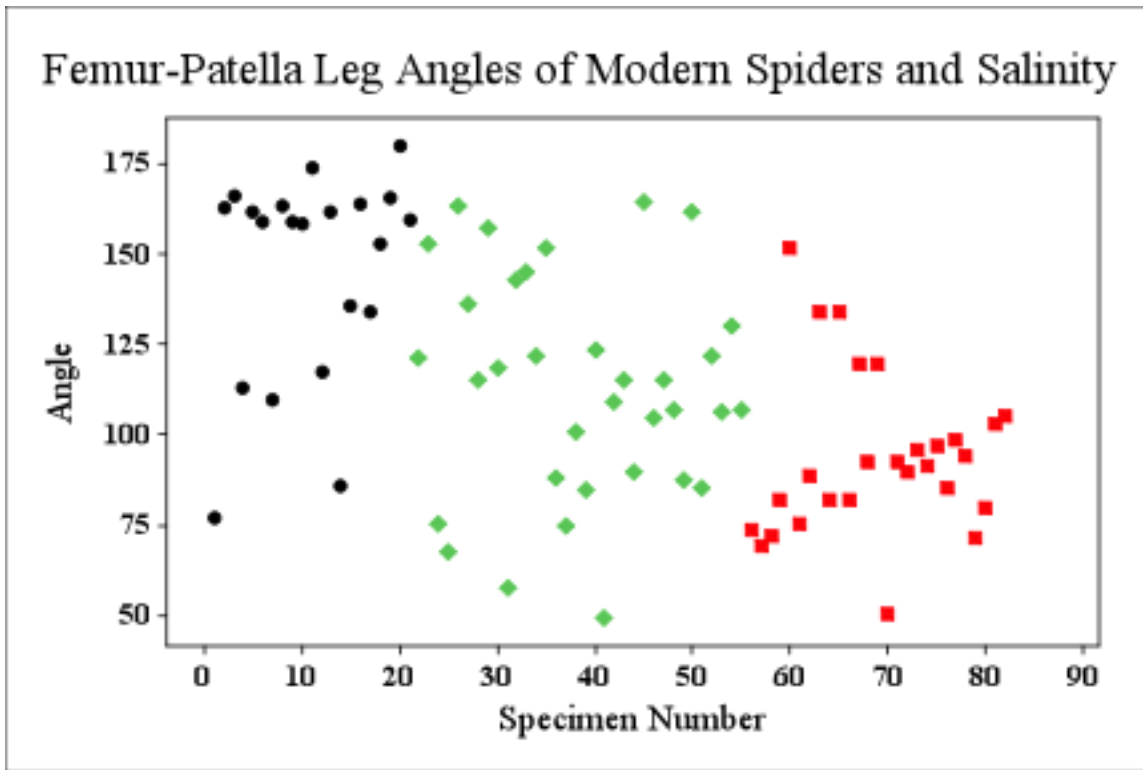
Figure 1.5 – Femur-patella leg angles for the three salinities. Black = Fresh Water, Green = Saline, Red = Hypersaline.

Discussion

The curling of spider legs after subaerial death is the result of physiological processes. Spiders have muscles for the contraction of legs, but lack extensor muscles. Extension of spiders legs is instead, controlled by a hydraulic mechanism (Ellis, 1944; Parry and Brown, 1955). Spider hemolymph, the fluid in the circulatory system of arthropods, is pumped into the legs, thus increasing the fluid pressure, and results in extension of the legs. After death in subaerial conditions, this hydraulic mechanism ceases and gives way to contraction of the legs via the flexor muscles.

Spiders clearly did not live in the lake in which the Crato Formation was deposited, although they were deposited with lacustrine sediment. Several observations during the course of the experiments provided insight on taphonomic processes affecting the 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 requires quick deposition (Smith et al., 2002). Smith et al. (2002) 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. O'Brien et al. (2002) proposed that microbial mats aided insect in 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 et al., 2002). 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 decay, although, the spiders allowed to expire in air quickly decayed. The rapid decay of spiders allowed to expire in air could be attributed to humidity and favorable conditions for decomposers sealed in the vials. To better test a death on land scenario, spiders should be allowed to expire in air and subsequently desiccated, which would likely reduce the risk of complete decay and be more consistent with the hypothesized semiarid climate of the paleolake in which the Crato Formation was deposited. The legs of the three spiders placed in fresh water after subaerial death began to uncurl, but did not fully extend, and exhibited a leg orientation similar to spiders drowned in saline water. In contrast, the legs of three spiders placed in hypersaline water after subaerial death did not uncurl, and were similar to the spiders drowned in hypersaline water. Thus, the death on land scenario cannot be fully ruled out for spiders preserved in the Crato Formation, as a curled leg orientation is possible after death on land and subsequent submersion in hypersaline water.

For spiders that have expired in water, leg extension and contraction are likely controlled by osmosis, the diffusion of water across semipermeable membranes. In a freshwater solution, water diffuses into the spider, 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 used by spiders to extend their legs. In a hypersaline solution, water moves from the spider into the area of higher solute concentration (the solution surrounding the spider) and allows for the contraction of the legs tightly under the body, creating a smaller angle at the femur-patella and tibia-metatarsus joints. Although water does permeate the spider body and void spaces are filled with water in high salinity, sufficient pressure is not created to fully extend

the legs as observed in fresh water. Evidence for this phenomenon was observed when spiders that had shrunk after dying in air were later placed in a solution and swelled after absorbing water.

Modern spiders in this study that died in fresh water revealed that the legs of spiders were predominantly extended (curled = 2 and extended = 19). In contrast, spiders that drowned in saline water included specimens with curled legs and others with extended legs in roughly equal abundance (curled = 55.2% and extended = 44.8%), suggesting salinity hinders the action to produce spiders with fully extended legs (Table 1). Most spiders of those that had a curled leg orientation did not have legs that were curled very tightly—legs positioned under the body with joint angles > 100 (Fig. 4 – D). In hypersaline water, most spiders had a curled leg orientation (84.2% curled), with most of the legs being curled tightly under the body—femur-patella joint angles ~90° and tibia-metatarsus joint angles ~113° (Table 1; Figs. 4, 8). The average femur-patella angle of curled spiders in hypersaline water was 91.56°, and 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. The angle at both joints, the femur-patella and tibia-metatarsus, give the appearance of extended or curled legs. Smaller angles at both joints produce a more tightly curled leg.

These patterns provide insights that can be applied to understand the fossil samples. Previous explanations for patterns in the leg orientation of fossil spiders include acidity and temperature. 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 were also suggested as a leg extension mechanism for Florissant spiders by Licht (1896) suggested high water temperatures produced leg extension in Florissant Formation

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spiders based on experiments with spiders placed in warm, hot, and boiling water, each

producing extended legs; no specific water temperatures were reported. Each of these

experiments was likely conducted in fresh water, as no addition of salts were reported, which

would explain the extended legs. Boiling water may have also resulted in denaturing proteins in

the muscles of the legs of spiders, removing the ability of legs to contract (Wu and Wu, 1925).

Instead, the osmotic mechanism for leg extension and curling can also be applied to the

fossil specimens. For example, 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 orientations 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 orientation have legs that

were not curled very tightly—legs were curled under the body, but joint angles were typically

>100° (Fig. 2 – E, F). The joint angles of fossil spiders from the Green River Formation suggest

an intermediate salinity between fresh and hypersaline because they are not fully extended, yet

not contracted close to the body. At the other end of the spectrum, 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 average femur-patella joint angle. These results from fossil spiders from the Crato

Formation suggest they are very similar to the spiders drowned in hypersaline conditions (Figs. 4, 6, Table 1).
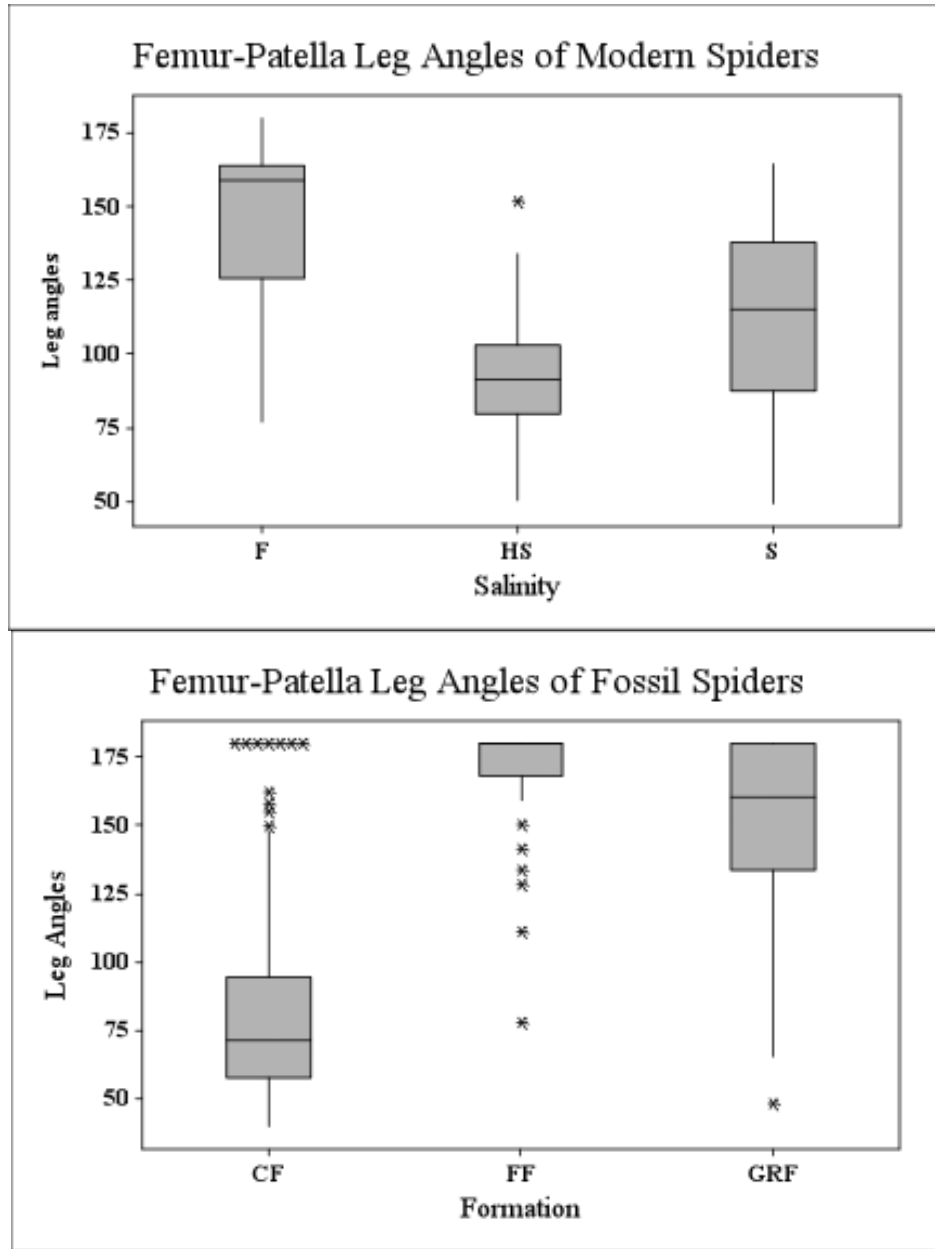
Figure 1.6 – Box plots of leg angles from fossil spiders (top) and modern spiders (bottom). Fresh water and the Florissant Formation have the largest leg angles. Saline water and the Green River

formation leg angles represent the middle part of the spectrum, but still have leg angles greater

than hypersalinity and the Crato Formation, which are represented by smaller leg angles.

Formation Salinity	Sample size	Curled (C)	Extended (E)	% C	% E	Av. F-P	F-P sd	Av. T-M	T-M sd	P-value
FF	42	3	39	7.1	92.9	168.98	21.69	173.59	14.15	<0.05
GRF	125	56	69	44.8	55.2	151.57	31.02	149.46	32.66	0.089
CF	95	80	15	84.2	15.8	85.84	39.4	120.75	26.79	<0.05
FW	21	2	19	9.5	90.5	145.84	28.96	157.84	27.73	<0.05
S	34	19	15	55.2	44.8	113.34	30.9	147.4	20.92	0.493
HS	27	26	1	96.3	3.7	93.79	22.52	113.8	22.02	<0.05
Test				F				P		
ANOVA Fossil Groups				$F(2,288) = 130.76$				< 0.05		
ANOVA Drowning Groups				$F(2,77) = 17.52$				< 0.05		

Table 1 – Summary of the leg orientations of fossil and modern spiders. FF = Florissant

Formation, GRF = Green River Formation, CF = Crato Formation, FW = Fresh Water, S =

Saline, HS = Hypersaline, F-P = Femur-patella joint angle, T-M = Tibia-metatarsus joint angle,

sd = standard deviation, Av. = average

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 and fish from the genus *Dastilbe* (Maisey, 1990). Mayfly larvae are

exclusively freshwater inhabitants. Fossils of these insects occur in the thousands, and are the

most common insect fossil within the Crato Formation (McCafferty, 1990; Martins-Neto, 1996).

These insects were most likely not inhabitants of the actual ancient lake, but instead, inhabitants

of freshwater rivers and streams 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 gonorhynchiform

fish are known to tolerate high levels of salinity (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 or temperature and 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 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; Stephen Hasiotis, personal communication, November 14, 2014).

Previous evidence for hypersalinity is based primarily on sedimentological and

stratigraphic evidence rather than paleontological 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., 2007b). These halite pseudomorphs are

present in the Nova Olinda Member at the bottom of the Crato Formation, and also in the

Jamacaru 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 (Martill and Wilby, 1993). The sequence throughout the

Crato Formation and the Ipubi Formation suggest 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.

Salinity is a common environmental parameter determined when studying bodies of

water, with 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 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 region are particularly sensitive to changes in climate (Last and

Selzak, 1988). Lakes are also relevant to the carbon cycle. Large amounts of carbon can be

stored in lakes and, conversely, released from lakes into the atmosphere (Tranvik et al., 2009).

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 need highly oxygenated water

(Hammer 1986). 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.

Conclusions

This study suggests that a relationship exists between the leg orientation of drowned spiders and salinity of the water in which they were accumulated. Osmosis is likely the mechanism responsible for the differences in leg orientations 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 fresh and the hypersaline conditions tested, suggesting increasing salinity results in an increase in the curled leg orientation.

Application of these results to the spider-bearing strata in the geologic record reveals a similar pattern of leg orientation with respect to salinity. Spider fossils from the Florissant Formation were deposited in a freshwater lacustrine environment and show the same out-stretched leg pattern as freshwater experiments. Spider fossils from the Parachute Creek Member of the Green River Formation were deposited in saline conditions, and the pattern in leg orientations for those fossils is similar to 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. Spiders that die in subaerial conditions will also produce a curled leg orientation, even after subsequent

submersion in hypersaline water, and thus, cannot be ruled out as a possible scenario to produce curled leg pattern in fossil spiders. Spiders that die in air and are subsequently submerged in fresh water produce an initial curled leg orientation that slightly uncurls.

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 orientation where salinity indicators are otherwise ambiguous. Future studies could focus on other potential scenarios including death in fresh water followed by submersion in hypersaline water and desiccation flowed by submersion in water. In addition, further experiments finding the threshold where different leg orientations 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. Although fossil spiders are considered rare, they occur in many deposits around the world including Daohugou, China (Selden et al., 2013), Montsech 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, would allow for more discrete interpretations of salinity for paleoenvironments reconstructed from spider-bearing strata.

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CHAPTER 2: SPIDER DIVERSITY IN THE CRATO FORMATION, A LOWER CRETACEOUS FOSSIL-LAGERSTÄTTE OF BRAZIL

Abstract

The Crato Formation is a Fossil-Lagerstätte, and an important source of Cretaceous spiders, but from where few specimens have been formally described (Mesquita 1996; Selden et al. 2006). Examination of 95 fossil spiders reveals three new families of spiders present in the Crato Formation: Araneidae, Nephilidae, and Palpimanidae. Although the spiders are preserved in exceptional detail, many characteristics used to differentiate taxa are absent in the specimens, so identification is only possible to family level for Nephilidae and Palpimanidae. The majority of spider specimens present in the Crato Formation deposits can be ascribed to *Cretaraneus martinsetoi* Mesquita 1996, a genus of nephilid. A redescription of the holotype and other specimens has resulted in the erection of a new genus, *Olindarachne* n. gen., for this species, and its placement in Araneidae. The recognition of these families presents a clearer picture of spider biodiversity on the South American continent during the break up of Gondwana in the Early Cretaceous.

Keywords: Mesozoic, Araneidae, Nephilidae, Palpimanidae

Introduction

Herein, the abundant orbweaving araneoid in the Lower Cretaceous Crato Formation in Brazil, *Cretaraneus martinsnetoi* Mesquita 1996, is redescribed and placed into a new genus in Araneidae. Other fossil spiders described for the first time from the Crato Formation include members of Nephilidae and Palpimanidae. This study, thus, extends the paleogeographic distribution of Araneidae, Palpimanidae, and Nephilidae to the South American continent during the breakup of Gondwana in the Early Cretaceous, and extends the fossil record of the Palpimanidae back by almost 90 million years.

The orbweavers, Araneidae, are one of the most common groups of spiders with over 3,000 species. The orb web likely played a major role in insect evolution along with flowering plants during the Cretaceous (Volrath & Selden, 2007). The oldest known true orbweaver (Araneidae) is *Mesozygiella dunlopi* Penney & Ortuño 2006, from the Lower Cretaceous of Spain. Other spiders that produce orb webs, including Tetragnathidae and Uloboridae, have been found in Cretaceous deposits. The origin of all orbweaving spiders is hypothesized dates to be Jurassic or even earlier (Penney & Ortuño 2006).

Nephilids are some of the largest web-weaving spiders, and typically live in tropical to subtropical regions (Kuntner & Coddington 2009). Currently, the fossil record of Nephilidae extends back to the Early Cretaceous (Selden 1990). A supposed nephilid, *Nephila jurassica* Selden, Shih & Ren 2011, was recently redescribed and placed in the new genus *Mongolarachne* Selden, Shih & Ren 2013, family Mongolarachnidae. The fossil record of Mesozoic nephilids is therefore currently limited to the Cretaceous, including *Cretaraneus liaoningensis* Cheng, Meng, Wang & Gao, 2008, from the Jehol Biota of China, *Geratonephila burmicana* Poinar & Buckley

2012, from Myanmar amber, *Cretaraneus vilaltae* Selden 1990, from Spain, and *Cretaraneus*

martinsnetoi and an unnamed *Nephila* sp. (figured in Dunlop & Penney 2012) from the Crato

Formation. The first of these, *C. liaoningensis*, shows no characters of *Cretaraneus* (Selden et al.

2011), and the last two are the subject of this paper. Cenozoic nephilids are predominantly

preserved in Dominican and Baltic ambers (Wunderlich 2004) with the exception of one

nonamber fossil nephilid from the Florissant Formation (34 Ma) of Colorado, *Nephila*

pennatipes Scudder 1885.

    Palpimanids are ground-dwelling araneophagous spiders that live in tropical to

Mediterranean regions. There is a single fossil specimen from Cenozoic Dominican amber,

Otiothops sp. Wunderlich 1988 (Wunderlich 1988). There are many spiders representative of

superfamily Palpimanoidea from the Mesozoic, however, including Baltic ambers and Myanmar

ambers and others, although no Mesozoic fossil of Palpimanidae has previously been described

(Penney 2005; Wunderlich 2006, 2008, 2011, 2012).

    Fossil spiders are relatively abundant in the Crato Formation, and most appear to be the same

species. Only a few species of spider from the Crato Formation have been formally described:

Cretadiplura ceara Selden 2006 and *Dinodiplura ambulacra* Selden 2006 belong to the suborder

Mygalomorphae (Selden et al. 2006). The majority of Crato spiders appear to be araneomorphs.

The first spider described from the Crato Formation was *Cretaraneus martinsnetoi* Mesquita

1996. The generic assignment was based on an earlier description of an araneomorph spider of

the genus *Cretaraneus* from the Lower Cretaceous of Spain (Selden 1990). *Cretaraneus* is

currently placed in family Nephilidae (Selden & Penney 2003). The commonest Crato spider is

C. martinsnetoi, but its characters suggest the assignment to *Cretaraneus* is incorrect. So, the

species is redescribed here after examination of the holotype and additional specimens from the Crato Formation.

Geologic Setting

During the Early Cretaceous, the Crato Formation was being deposited in the Araripe Basin in modern-day Brazil. The Crato Formation is a series of alternating heterolithic beds and laminated carbonates (Martill & Wilby 1993). The age of the formation has been interpreted as late Aptian, based on ostracodes and palynomorphs (Coimbra et al. 2002; Batten 2007). At the base of the Crato Formation is the Nova Olinda Member. The Nova Olinda Member is a fossil-rich Plattenkalk, laminated limestones, with two types of laminated carbonate facies: clay-carbonate rhythmites and laminated limestones (Neumann et al. 2003). Bioturbation, traces, and fossils of benthic organisms are absent in this member, suggesting anoxic bottom conditions (Martill & Wilby 1993).

The Araripe Basin was positioned ~10° south of the paleoequator, and thus located within the tropics (Hallam 1984, 1985; Chumakov et al. 1995; Föllmi 2012). In addition, the fossil flora within the Crato Formation possess characteristics of extant plants that live in areas of limited rainfall and dry conditions, suggesting a semiarid to arid climate (Alvin 1982; Selden & Shear 1996; Dunlop & Martill 2004; Martill et al. 2007). The thin laminations suggest a low-energy environment during deposition of the Nova Olinda Member. Salinity of the lake in which the Crato Formation was deposited has been debated, and interpretations range from fresh water to hypersaline (Maisey 1991; Neumann et al. 2003; Martill et al. 2007). Recently, the paleosalinity was reinvestigated using spider taphonomy experiments that support hypersaline conditions present in the ancient lake that deposited the spider-bearing member (Downen & Selden 2013).

This is in congruence with evidence of hypersalinity suggested by the presence of pseudomorphs after halite (Martill et al. 2007). A hypersaline lake with overlapping tongues of freshwater is the most supported and most likely scenario (Martill & Wilby 1993).

Materials and Methods

The holotype of *Cretaraneus martinsnetoi*, UnG/1T-50, was studied by PAS in 2002 at the Universidade Guarulhos, São Paulo, Brazil. Photographic slides of the holotype were scanned with an Epson scanner at 24-bit color and 4800 dpi resolution for study at the University of Kansas. The Crato fossil spider collection at the University of Kansas consists of 90 specimens, 79 of which are considered to be conspecific with *C. martinsnetoi*. Three of these were selected for the redescription: Crato 012, Crato 033, and Crato 071, as they are the best well preserved. Another specimen, Crato 096, was selected for describing Nephilidae, and a single specimen of Palpimanidae, Crato 098. 3 few spiders in the collection resemble mygalomorphs, and others have not been determined. Specimens were photographed with a Canon EOS 5D Mark II digital camera attached to a Leica M650C microscope. Seventy percent ethanol was used to wet the surfaces of the fossils and enhance details not easily seen in the dry specimens. Measurements were made from the photographs using the measurement tool in Adobe Photoshop, and drawings were made from the photographs using Adobe Illustrator CS5. Abbreviations are as follows: BL = book lung, cl = claw, cx = coxa, EF = epigastric furrow, at = anal tubercle, fe = femur, pa = patella, ti = tibia, mt = metatarsus, ta = tarsus, pr = prosoma, op = opisthosoma, st = sternum, lb = labium, pd = pedipalps, cy = cymbium, AT = Anal Tubercle, ch = chelicerae, en = endite, sp = spinnerets. All measurements are in millimeters. A "+" following a measurement indicates a body part that is not fully visible.

Interpretation of the Fossils

Taphonomy.—The Crato Formation fossil spiders exhibit excellent preservation, and many are preserved in three dimensions. The spiders have been replaced by dark brown goethite, (FeO(OH)), and are supported by a matrix of light-colored, fine-grained lime mudstone (Barling et al., 2014). Cavities in the body of the spiders have been infilled with white crystalline CaCO3. Pyrolusite (MnO_2) speckles many of the samples, and in Crato 071 clusters of pyrolusite are present on the abdomen and legs. Spiders preserved in the Crato Formation typically display a curled arrangement of legs making total leg length difficult to calculate. This curled leg orientation is related to hypersaline conditions present in the environment in which they were deposited (Downen et al., 2014, in prep.).

Morphological interpretation.—The holotype of *C. martinsnetoi*, UnG/1T-50, is preserved dorsal side up, and with extended legs (Fig. 1). Pedipalps are visible and unmodified, indicating the specimen is female. Parts of the opisthosoma and the coxae are obscured by matrix. The carapace appears mostly intact, but eyes cannot be seen.

Crato 012 is preserved dorsal side up in the matrix with legs and pedipalps curled tightly under the body (Fig. 2). Although the pedipalps are curled, they are distinctly swollen, indicating the specimen is male. Hairs and spines are not visible. Part of the carapace has been removed and/or crushed.

Crato 033 is preserved dorsal side up in the matrix (Fig. 3). Chelicerae and pedipalps are visible. Part of the carapace appears removed. Coxae 2–4 are clearly visible on both sides of the spider, but coxae 1 are not easily visible on either side. Hairs and spines are most easily seen as dark brown impressions where part of the cuticle has broken away. A circular spot near the end

of the abdomen where the spinnerets would be present has weathered out. Two book lungs are present and discolored yellow in the specimen. The opisthosoma of many of the Crato Formation spiders have a wrinkled appearance. All eight legs are present, but only the anterior two pairs are mostly visible, as the others are truncated by the sample or curled under the body. Crato 071 is preserved dorsal side up (Fig. 4). Part of the carapace has been removed to reveal the sternum and coxae. The pedipalps are unmodified indicating the specimen is female. Crato 071 displays extended legs, but the metatarsi and tarsi of some legs disappear into the matrix.

Crato 096 is preserved in lateral view, with the left side facing upward, and is one of the largest spiders in the collection (Fig. 5). Preparation around the specimen has removed most pre-existing hairs, spines, or trichobothria, with the exception of a single pedipalp preserved as an impression and a few scattered hairs. Only the first two pairs of legs are fully visible, as well as one of the last posterior legs. The other legs are either completely absent or only partially preserved.

Crato 98 is preserved ventral side up, with the end podomeres of some legs disappearing into the matrix and, therefore, a walking leg formula cannot be determined (Fig. 6). Pedipalps and chelicerae are either hidden by matrix or truncated by the sample, but no swelling is visible in the pedipalps, so the specimen is assumed female. The abdomen appears crushed, and pieces of the cuticle are not preserved. Some parts of the abdomen are exceptionally preserved, but appear disturbed either through a taphonomic process or preparation of the fossil, separating the spinnerets from the rest of the abdomen. The specimen is strongly preserved in three dimensions.

Eyes are not visible in any of the specimens examined due to preservation ventral side up or partial removal of the carapace. Trichobothria, presumed to have been present during life, are not seen in any of the specimens.

Systematic Paleontology

Order Araneae Clerck 1757

Suborder Opisthothelae Pocock 1892

Infraorder Araneomorphae Smith 1902

Suborder Araneoidea Latreille 1806

Family Araneidae Simon 1895

Genus *Olindarachne* new genus

Diagnosis.—Araneid spider with very long first two pairs of legs (twice the length of the body); robust femora; femur I length to body length ratio of ~1.58; spines present on patella.

Etymology.—After the Nova Olinda Member of the Crato Formation, the strata in which the specimens are found.

Type species.—*Cretaraneus martinsnetoi* Mesquita 1996.

Olindarachne martinsnetoi new combination

Figures 1–3.

Material studied.—Holotype, UnG/1T-50, female specimen in the paleontological collections at

the Department of Geosciences, Universidade Guarilhos, São Paulo, Brazil. Crato 012 (male), Crato 033, Crato 071 (females), in the Department of Invertebrate Paleontology, University of Kansas Natural History Museum. Lawrence, Kansas. All specimens come from the Lower Cretaceous (Aptian) Nova Olinda Member of the Crato Formation, northeast Brazil.

Description of holotype.—Adult female. Carapace longer than wide (ratio 1.16), length 1.82, width 1.56; narrows anteriorly. Raised eye region. Opisthosoma subelliptical, longer than wide (ratio 1.33), length 2.83, width 2.13. Walking leg formula 1243. Legs I and II robust. Leg III noticeably shorter than others. Macrosetae on fe, pa, ti, mt. Leg I fe length to carapace length ratio 1.58. Leg I twice as long as body length. Podomere lengths: Leg I fe 2.88, pa 1.04, ti 2.42, mt 1.92, ta 0.81, Leg II fe 2.74, pa 0.85, ti 1.87, mt 1.97, ta 0.87, Leg III fe 1.61, pa 0.41, ti 1.16, mt 0.97, ta 0.41, Leg IV fe 1.42, pa 0.56, ti 1.49, mt 1.36, ta 0.57.

Description of Crato 012. —Adult male. Subrounded carapace bulging laterally, narrows anteriorly, length 2.48, width 2.88 (raio 0.86). Opisthosoma oval, slightly tapering toward posterior, length 3.03, width 2.33. Walking leg formula 1243. Legs I and II robust. Femur length to carapace length ratio 1.50. Podomere lengths: Leg I fe 3.72, pa 1.05, ti 2.67, Leg II fe 3.11, pa 0.89, ti 2.20, mt 1.36+, Leg III fe 1.58, Leg IV fe 2.19, pa 0.73, ti 2.27, mt 0.88+.

Description of Crato 033.—Adult female. Carapace longer than wide (ratio 1.14), length 1.62, width 1.42. Labium wider than long, rhombus-like shape with rounded edges. Sternum subtriangular, longer than wide, concave toward chelicerae, tapering toward abdomen. Setae and macrosetae present on fe, pa, ti, mt. Opisthosoma oval, longer than wide (ratio 1.19), length 1.87, width 1.56 . Walking leg formula 1243. Legs I and II robust. Femur I length to carapace length ratio 1.58. Leg I nearly twice as long as body. Podomere lengths: Leg I fe 2.70, pa 0.52, ti 2.16,

mt 0.97+, Leg II fe 1.94, pa 0.34, ti 1.56, mt 0.86, ta 0.44, Leg III fe 1.18, pa 0.39, ti 0.49+, Leg IV fe 1.25.

Description of Crato 071.—Adult female. Rounded carapace outline, longer than wide, narrows anteriorly, length 4.00, width 3.79. Raised eye region. Chelicerae project down. Opisthosoma oval, length 4.64, width 3.03. Leg formula 1243. Left Leg I longest (18.17) and Leg III shortest (9.13). Legs I and II more robust than III and IV. Two tarsal claws on right leg III and right leg IV. Setae and macrosetae present on legs including patella. Femur I length to carapace length ratio: 1.52. Leg I twice as long as body length. Podomere lengths: Leg I fe 6.08, pa 1.95, ti 0.73+, Leg II fe 4.66, pa 1.54, ti 3.7, mt 4.01, ta 1.65, Leg III fe 2.81, pa 1.05, ti 1.93, mt 2.21, ta 1.13, Leg IV fe 3.38, pa 1.34, ti 3.55, mt 2.89, ta 1.21.
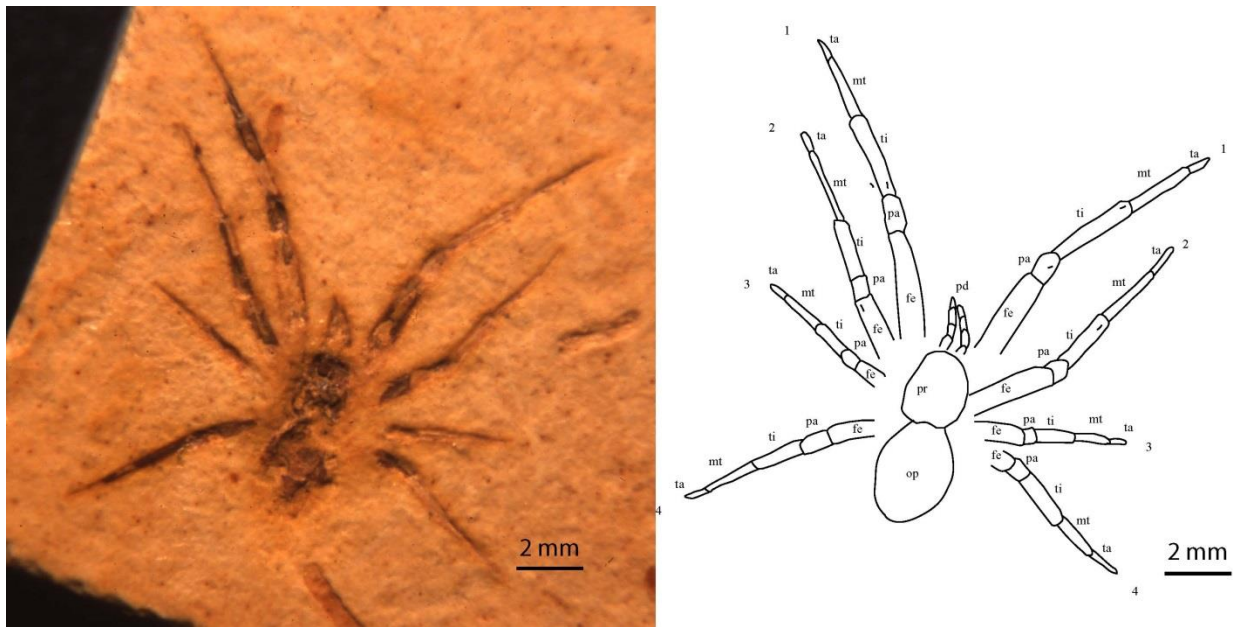
Figure 2.1 – Olindarachne martinsnetoi n. gen., holotype UnG/1T-50, photograph and interpretative drawing.
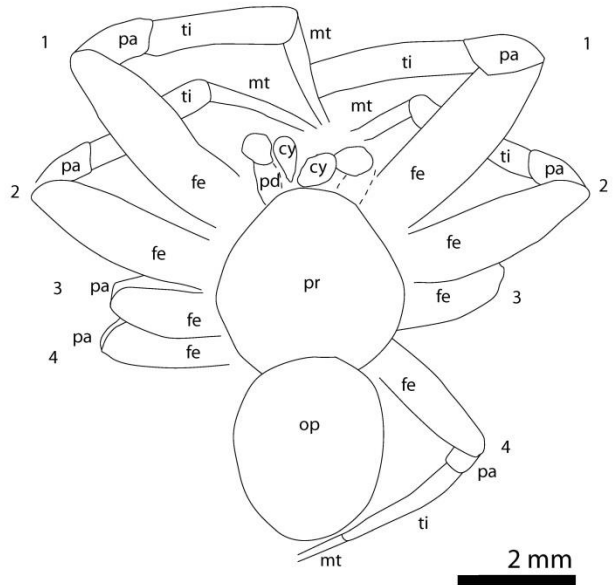
Figure 2.2 – *Olindarachne martinsnetoi* n. gen., Crato 012, photograph and interpretative drawing.
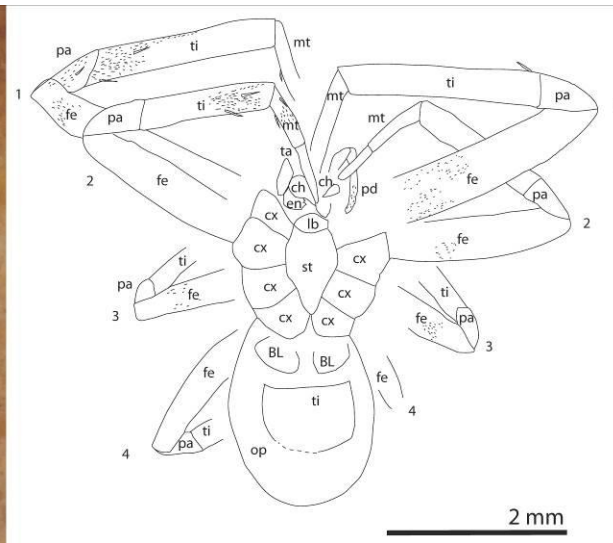
Figure 2.3 – Olindarachne martinsnetoi n. gen., Crato 033, photograph and interpretative drawing.
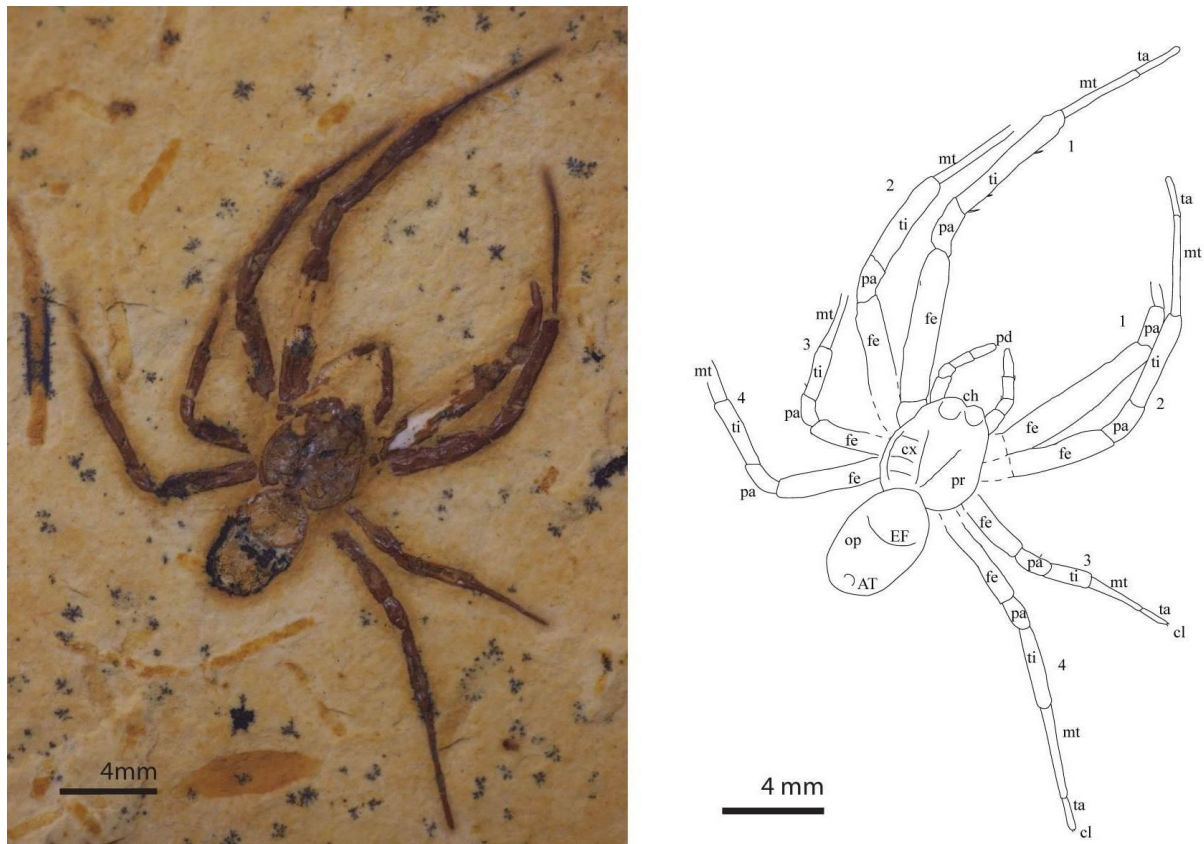
Figure 2.4 – Olindarachne martinsnetoi n. gen., Crato 071, photograph and interpretative drawing.

Remarks.—The previous interpretation of these abundant spiders in the Crato Formation was by Mesquita (1996), who placed them in the genus *Cretaraneus*. Selden (1990) described *Cretaraneus vilaltae* from an Early Cretaceous locality at Sierra de Montsech, Spain. The diagnosis of *Cretaraneus* is as follows: "Araneoid spider with subelliptical carapace bearing raised cephalic area and no fovea; subtriangular sternum; small, subtriangular labium; serrate setae covering all parts of body. Chelicerae relatively large (0·4 × length of carapace), forwardly directed (at least in adult male), with inner and outer row of denticles (not peg-teeth), and mesal ridge; male palp with long embolus, and small, proximal ?paracymbium; legs relatively equal in

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length, about three times the length of carapace; femora, tibiae and metatarsi with spines; tarsi with pectinate paired claws, small median claw, and associated serrate bristles; no true trichobothria globose abdomen." (Selden 1990, p. 270).

The definition of *Cretaraneus martinsnetoi* Mesquita (1996, p. 25) is as follows "afora os caracteres listados para o gênero, esta espécie apresenta diferenciação das quelíceras, com formato arredondado e presença de espinhos na patela"; i.e., apart from the characters listed for the genus, this species is differentiated by the chelicerae with rounded shape and the presence of spines on the patella." In addition, Mesquita (1996 p. 26) mentioned further differences, in that the chelicerae being of rounded shape in *C. martinsnetoi*, they are turned back over the carapace and lack a claw ("O espécime em discussão difere na posição das queliceras, que se encontram voltadas sobre o abdome, possuem o formato arredondado e sem garras"). The Crato fossil spiders do share traits in common with *Cretaraneus vilaltae* Selden 1990, including a raised cephalic area, abundant setae and large chelicerae. Several differences exist, however, that suggest the Crato spiders do not represent *Cretaraneus*. The carapace is rounded and narrows anteriorly. The legs are not relatively equal in length. The first two pairs of legs (I and II) of the Crato spiders described here are much longer compared to legs III and IV. The femur/carapace length ratio is approximately 1.58 whereas the femur/carapace length ratio of *Cretaraneus vilaltae* is 1:1. The holotype has a leg I length to carapace ratio of 4.98, and specimen Crato 071 has a leg I length to carapace ratio of 4.54, whereas *Cretaraneus vivaltae* has a ratio of 3.54, indicating much longer legs in the specimens described here. The third pair of legs (III) is noticeably shorter than the others. Spines are present on the patellae of the Crato spiders, unlike *Cretaraneus vilaltae*, a difference also noted by Mesquita (1996).

At the time of the description of *C. martinsnetoi*, *Cretaraneus* was not placed in a family, but the genus was later recognized as belonging to Nephilidae based on morphology of the male pedipalp (Selden & Penney 2003). Though the Crato spider shares some characteristics with Nephilidae, several characteristics of the spiders described here suggest they instead belong to family Araneidae: the first pair of legs is the longest and the third pair of legs is the shortest, the carapace is longer than wide and has a narrowed raised cephalic region, the sternum is longer than wide, there is a short, stout cheliceral fang, there are abundant setae and macrosetae, the globose abdomen is longer than wide, a cribellum is absent, the labium is wider than long, and the endites are squarish. Nephilids possess a wider than long sternum and endites that widen anteriorly, suggesting the holotype, Crato 033, and Crato 071 do not belong to Nephilidae. In addition, male nephilids are typically much smaller in size compared to females (Coddington et al. 1997). The male *O. martinsnetoi* (Crato 012) is not greatly reduced in size compared to females. Some characteristics are shared with the family Tetragnathidae, but tetragnathids typically possess longer, forward-projecting chelicerae, endites that widen distally, a labium longer than wide, and slender legs.

Family Nephilidae Simon 1894

Nephilidae *incertae sedis*

Material.—Crato 096 (female) in the Department of Invertebrate Paleontology, University of Kansas Natural History Museum. Lawrence, Kansas; from the Lower Cretaceous (Aptian) Nova Olinda Member of the Crato Formation, northeast Brazil.

Description.—Adult female. First pair of legs very long. Three tarsal claws. Opisthosoma elongate, subelliptical, raised higher than carapace at anterior, tapered toward posterior,

Opisthosoma length: 12.56, width: 6.99. Walking leg formula: 1243. Podomere lengths: Left Leg

I fe 19.07, pa 4.74, ti 16.51, mt 17.91, ta 4.35, Left Leg II fe 14.31, pa 2.82, ti 12.32, mt 12.00, ta

3.40, Left Leg 4 fe 7.76, pa 2.81, ti 11.30, mt 7.63, ta 3.71.

Remarks.—The extremely large size of the spider and subelliptical, tapering opisthosoma are

suggestive of Nephilidae. The specimen here is female, but sexual dimorphism cannot be

confirmed until a male is found.
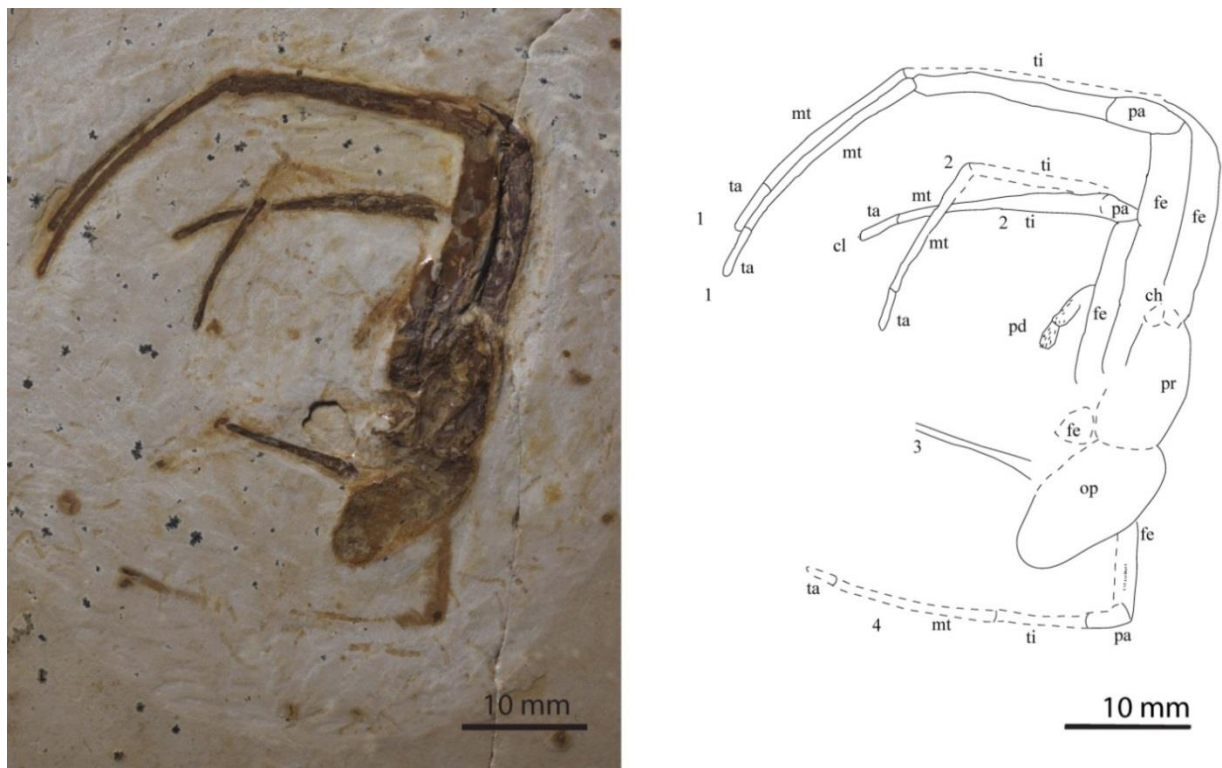
Figure 2.5 – Nephilidae *incertae sedis*, Crato 096, photograph and interpretative drawing.

Superfamily Palpimanoidea *sensu* Agnarsson et al. 2013

Family Palpimanidae Thorell 1870

Palpimanidae *incertae sedis*

Material.—Crato 098 (female) in the Department of Invertebrate Paleontology, University of Kansas Natural History Museum. Lawrence, Kansas; from the Lower Cretaceous (Aptian) Nova Olinda Member of the Crato Formation, northeast Brazil.

Description.—Female spider. Body length 3.2. Sternum shield-shaped, nearly as wide as long. Labium triangular. Endites short and close together. Opisthosoma oval with heavily sclerotized epigastric region forming a ring shape around pedicle. Epigastric region with dotted pattern. Two spinnerets. Robust first pair of legs. Three tarsal claws on right leg III. Podomere lengths: Leg I fe 1.69, pa 0.80, ti 0.73, Leg II fe 0.74, pa 0.30, ti 0.61+, Leg III fe 0.91, pa 0.26, ti 0.94, mt 0.66, ta 0.35, Leg IV fe 1.53, pa 0.43, ti 1.17, mt 1.10, ta 0.15+.

Remarks.—Crato 098 is easily recognized from other spiders preserved in the Crato Formation by its distinct enlarged front pair of legs, which are characertistic of the superfamily Palpimanoidea. The enlarged front pair of legs could suggest the family Stenochilidae, but Crato 098 most closely resembles Palpimanidae based on the triangular shape of the labium, a reduced number of spinnerets, and a heavily sclerotized, ring-shaped part of the epigastric region, which is suggestive of further classification into subfamily Palpimaninae. A specific genus cannot be determined due to a lack of diagnostic details.
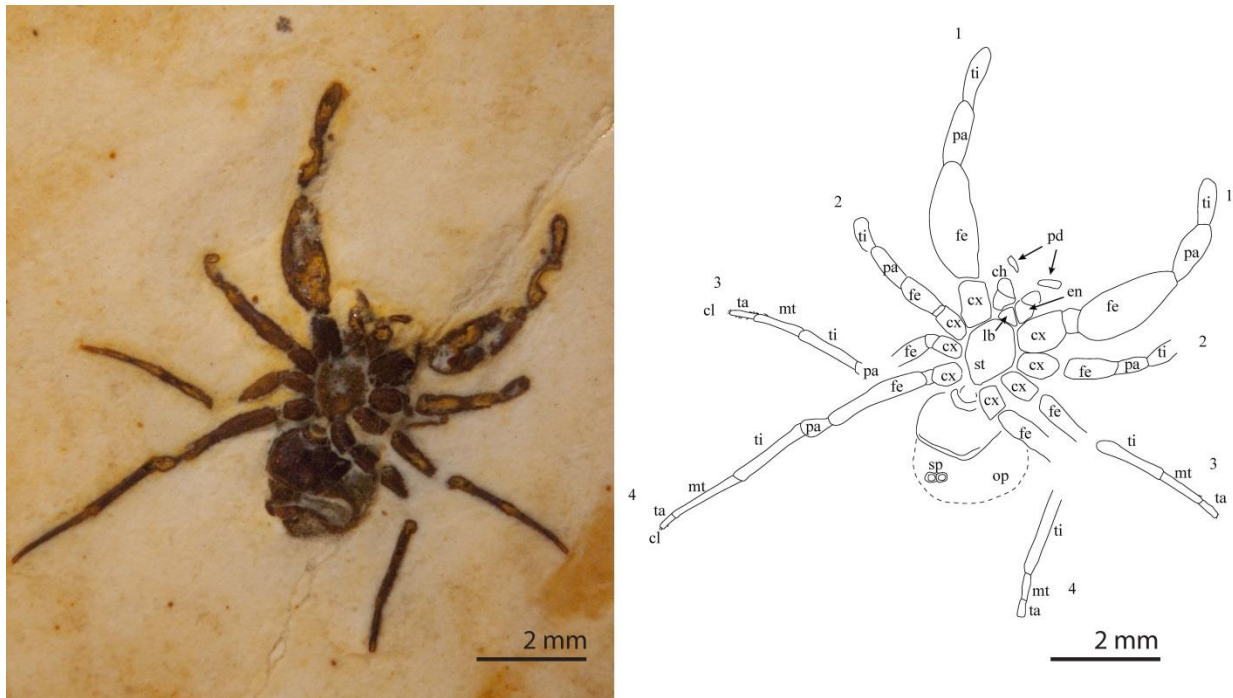
Figure 2.6 – Palpimanidae incertae sedis, Crato 098, photograph and interpretative drawing.

Discussion

The placement of *Olindarachne* in Araneidae does not extend the age of the family because

the araneid *Mesozygiella dunlopi* was described from the Aptian (Penney & Ortuño, 2006), and

the Crato Formation is considered to be late Aptian in age (Batten 2007). This placement does

expand the known paleogeographic distribution of araneids during the Mesozoic. *M. dunlopi*

comes from Spain, and would have been separated from South America during the Early

Cretaceous by a young North Atlantic Ocean. One other Mesozoic araneid spider has been

described: a juvenile from Late Cretaceous amber in New Jersey (Penney 2004). Possibly,

araneids were distributed across parts of Pangaea before its breakup beginning in the Mesozoic.

Other araneids have been reported or suggested, but are either questionably identified or not

formally described (Dunlop et al. 2014). Araneids would have likely constructed orb webs in the vegetation surrounding the ancient lake in which the Crato Formation was deposited. Extant nephilids also weave orb webs, sometimes up to 1.5 m in diameter (Kuntner & Coddington 2009). The insect fossil assemblage of the Crato formation is dominated by mayflies, dragonflies, and grasshoppers, and these insects would have likely been common prey for the araneid and nephilid spiders (Maisey 1990). Specimen Crato 098 extends the age range of Palpimanidae back nearly 90 million years. Palpimanids are ground-dwelling spiders that prey upon other spiders, and likely would have lived relatively close to the shoreline or a stream entering the ancient lake to be washed in during flooding events (Jocqué & Dippenaar-Schoeman 2007).

Conclusions

The area surrounding the ancient lake in which the Crato Formation was deposited supported a variety of life, evidenced by a diverse fossil assemblage. The fossils are dominated by terrestrial arthropods including insects and spiders. Previously, only a few spiders had been described: *Cretaraneus martinsnetoi* Mesquita 1996 and a few mygalomorphs. A redescription of the spider described by Mesquita and examination of other specimens has shown the presence of three new families: Araneidae, Nephilidae, and Palpimanidae, that existed in the Early Cretaceous of present-day Brazil. Many more fossil spiders have been found and await description, and have the potential to further increase our understanding of spider biodiversity in the early Cretaceous.

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CONCLUSION

Two common aspects of paleontological research are reconstruction of depositional environments and the description and classification of ancient organisms. Study of past life can reveal constraints on the physical environment and insight into the ecological communities present during times which cannot be directly observed. The purpose of this thesis was to illustrate the practicality of fossil spiders for interpreting salinity in lacustrine depositional environments, and to rectify previous interpretations of the taxonomic status of an abundant spider taxon preserved in the Crato Formation. An important abiotic factor, salinity, and biotic factor, the type of spiders, have been made clear and expand upon pre-existing knowledge of the paleoenvironment of the Crato Formation.

The results of these projects have provided evidence of a relationship between post-mortem leg orientations and variations in salinity based on leg joint angle measurements. Spiders deposited in freshwater typically display fully extended legs. As salinity increases, the legs become increasingly curled. When hypersaline conditions are present, the legs of spiders curl tightly under the body. Leg orientations were quantified by measuring angles at the femur-patella and tibia-metatarsus joints to show that smaller angles (~90°) are present in hypersaline conditions and larger angles are present in fresh conditions (~180°). The results of the modern taphonomy experiments are consistent with observations of fossil spiders preserved in lacustrine deposits. For example, fossil spiders deposited in the Florissant Formation, which has been interpreted as deposition in fresh water, have similar leg orientations as modern spiders drowned in fresh water. Using the results of this study, the unique pattern of tightly curled legs of fossil spiders in the Crato Formation is suggestive of hypersaline conditions existing during deposition. This conclusion concurs with previous studies suggesting evidence of hypersalinity and aims to

remedy the controversy surrounding an interpretation of salinity for the Crato Formation. Additional observations on spiders allowed to expire in air showed a tightly curled leg orientation can also be produced by death on land and subsequent submersion in hypersaline water. Further experiments are needed to constrain salinity levels and understand other possible scenarios including death on land after desiccation and changes in salinity for an individual spider.

The spider taphonomy experiments show that fossil spider leg orientation may be a useful proxy for salinity for other lacustrine deposits in which fossil spiders are present. These conclusions are already supported by two such localities, the Green River Formation and the Florissant Formation. Other ancient lacustrine environments to which similar studies can be applied include, but are not limited to, deposits in Spain, China, Russia, France, and New South Wales. Expanding upon the taphonomy experiments, salinity could potentially be constrained further to more precise measurements by discovered thresholds in which specific leg angles and orientations are present. This type of data could be useful to paleoclimate studies in which salinity may allow inference for rates of evaporation and/or precipitation in lacustrine settings.

In addition to understanding a previously ambiguous abiotic constraint of the Crato Formation depositional environment, insight into a biotic component of this ancient lacustrine setting was achieved. The previously interpreted *Cretaraneus martinsnetoi* Mesquita, 1996 has been revised through redescription, the erection of the new genus *Olindarachne*, and placement in the family Araneidae. *Olindarachne martinsnetoi* (Mesquita, 1996), was previously described as genus *Cretaraneus* in the family Nephilidae. Several characteristics of the Crato spiders described here support assignment to family Araneidae, the true orbweavers, including leg length, squarish endites, short stout fangs, the absence of a cribellum, and a globose abdomen. In

addition, redescription revealed that the Crato spiders do not belong in *Cretaraneus*, but instead, belong to a new genus diagnosed by robust femurs, an extremely long first two pair of legs, and the presence of spines on the patellae. *Olindarachne* martinsetoi (Mesquita, 1996) suggests an expanded distribution of araneids shortly after the breakup of Gondwana in the early Cretaceous improving our knowledge of spider biogeography. In addition, the families Nephilidae and Palpimanidae have been shown to be present during the early Cretaceous of South America as well, and extended the range of Palpimanidae back nearly 90 million years.

Both projects have aided in further reconstructing the paleoenvironment of the Crato Formation by clarifying paleosalinity and the types of spiders present in this area during deposition. A more complete reconstruction of this environment includes deposition in a calm stratified hypersaline lake with freshwater lenses situated in a semi-arid to arid setting. Vegetation that thrives in limited water would have likely bordered the lake, and been home to araneid and nephilid spiders capturing prey such as crickets and flying insects in their orb-shaped webs. Palpimanid spiders are ground-dwellers, and would have preyed upon other spiders. Precipitation would have been limited, but occasional storms and flash flooding events would have likely blown and/or washed spiders into the lake. After sinking though the water column, spiders would subsequently be deposited and preserved as part of the exceptional fossil assemblage for which the Crato Formation is known.

Appendix

TABLE A1—Fossil spiders, leg angles, and leg orientations. CF = Crato Formation, Sp = specimen, Or = orientation, F-P = Femur-patella joint angle, T-M = Tibia-metatarsus joint angle, E = extended, C = curled, U = unknown, unknown = no specimen number, blank = no data.

CF Sp	CF F-P	CF T-M	CF Or
374670	79.7	142.9	C
374671	59.8	136.4	C
374672	40	150.9	C
AMNH 48338			C
374673	57	91.8	C
374674	75.9	116.2	C
Wun001	54.8	128.5	C
8	68	99.3	C
374675	87.4	120	C
374676	69.6		C
DM X94.2	94.1	101.7	C
F18871/SAN/AP/JW	83.5		C
DM 002B	47.3		E
374677	80.6	117.3	C
DM X94.1	111.8	115.9	C
Wun005	114.8	53.9	C
374678	53.7		C
BD7DM	180		E
Berlin009	120.9	102.9	C
Wun009	157.9	172.5	E
374679	65.1	91.8	C
BD6DM	90.8		C
374680	64.7	112.9	C
BD1DM	105.3	91.4	C
BD12DM	67	80.8	C
BD11DM	83.1		C
BD8DM	85.2	109.6	C
28	71.7	114.6	C
BD13DM	54.5	107.7	C
DM003			C

374681	80.5	100.8	C
BD15DM	54.4	127.1	C
Wun002	56.6	96	C
BD4DM	55.2	101.4	C
801W	79.7	123.8	C
374682	122.5	111.9	C
Wun003	62.9	137.3	C
Wun007	94.7	112.5	C
Wun006	76.9	91.2	C
374683	75.8		C
MJS6	80.1	112.1	C
MBA 983	45.1	95.1	C
374684	74	100.8	C
374685	46.1	108	C
374686	63.9	108.5	C
374687	61.2	135.7	C
374688	60.6	92.4	C
374689	51.1		C
MJS1	46.5	111.1	C
374690	61.7	101.4	C
51	58.8		C
374691	53.6	100.2	C
BD3DM	59.3	92.6	C
BD17DM	50.3	101.4	C
374692			C
Berlin005	71.4	119.5	C
374693	63.4		C
Wun004			C
DM001			C
JS133	70.8	116	C
61	81.9	116.1	C
DM X94.3	139.6		C
374694	180	180	E
374695	61.4		C
DM X94.5	51.1	117.7	C
DM X94.4			C
374696	91.8	122.6	C
DM2A	52.9	153.1	E
DM004	155.1	123.5	E

DM005	148.2	155.9	E
374697	68.8	141.9	C
73	76.5	105.6	C
374698			C
374699			C
374700	84.3	153.5	C
BD16DM	44.2	123.8	C
BD20DM	52.6	103.3	C
BD14DM	64	111.5	C
374701	64.4	96.8	C
MJS2	180	146.1	E
83	98.8	107.7	C
Berlin006	162.3	141.1	E
374702	180	180	E
DM X94.6	56.2		C
374703	180	180	E
MBA 984	180	180	E
B2 2 DM	127.3	159.6	E
BD18DM	56.9	103.6	C
DM 4	90.5	157.7	C
374704	180	180	E
D43?	66.9		C
Berlin004	91	144.8	C
BD19DM	65	110.7	C
374705	150		E

TABLE A2—Fossil spiders, leg angles, and leg orientations. FF = Florissant Formation, GRF = Green River Formation, Sp = specimen, Or = orientation, F-P = Femur-patella joint angle, T-M = Tibia-metatarsus joint angle, E = extended, C = curled, U = unknown, unknown = no specimen number, blank = no data.

FF Sp	FF F-P	FF T-M	FF Or	GRF Sp (UMC)	GRF F-P	GRF T-M	GRF Or
35035	180	180	E	45166	180	180	E
4111	171.3	146.5	E	45891	180	180	E
35048a	180	180	E	46131	180	180	E
29634b	170.2	180	E	46143b	180	180	E
34338	159.1	142.7	E	46134	165.3	148.1	C
29641	128.2	158.6	E	46142	155.9	180	E
4941	180	180	E	unknown	67.4	162.5	C
29642	180	180	E	46140	169.8		E
35040	180	174.5	E	46123	127.8	146.9	C
29639	167.7	180	E	46126	174	178.1	U
35034			C	45078	122.6	112	C
34337	111.1	131.6	C	45166	169.3	172.3	E
29636	172.8	180	E	45891	175	180	E
36540	171.4	169.8	E	45193	172.2		E
35033	164	160.7	E	46170	163.6	95.3	C
37471	180	180	E	46172	160.4	167.2	E
35036	141.7	160.7	E	46161	111.9	58.7	C
29633	180	180	E	43654	111.6	117.3	C
35050	180	180	E	46496	180	180	
35049	180	180	E	46497	161.5	159	E
29638	180	180	E	46494	74.8	107.4	C
35051	176.1	180	E	48344		139.8	C
29635	180	180	E	46425	167.8	180	E
35042	180	180	E	46423	157.2	134.5	C
35037	166.5	180	E	46426			E
34342b	165.5	180	E	46427	147.2		E
35044	180	180	E	unknown		180	E
25052	180	180	E	51642	77.8	116.2	C

35041a	180	180	E	51569	48.2	142.3	C
35043	150.5		E	46483	132.9	164	C
35045	180	180	E	51499		90.2	C
29631	180	180	E	46499	106.5	147.7	C
35038	180	180	E	46501	166.9	118.2	E
36092	180	180	E	46502	142.5	170.1	C
35047	180	180	E	37624	168.7	132.4	E
34339	180	180	E	46414	178.6	180	E
35035a**	180	180	E	37736	153.5	180	E
35046	78.2	125.1	C	42908	150.1	143.5	C
4110	180	180	E	46155	131.6	70.4	C
35054	180	180	E	37141		112.8	C
35056a	133.9		E	37142	164.5	106.1	E
17705	180	180	E	39615	180	180	E
				39957			E
				39583	180	180	E
				40643	162.3	162.2	E
				40150			C
				40615		125.2	E
				40614	146.2	151.2	U
				40613			U
				39963	171.1	147.7	C
				unknown	180	180	E
				46159	180		E
				43018	159.9	165.9	C
				46143	67.2	142.2	C
				43202		135.4	C
				46489		180	E
				46490	180	180	E
				53498	157.3	107.1	C
				46446	112	121.6	C
				46165	180	166.4	E
				40073	180	180	E
				42730	144.7	180	C
				42729	165.4	180	E
				42737	180	180	E
				42670	95.3	116.7	C
				46487		176	E

				47192	65.6	165.6	E
				47193	133.9	144.8	E
				46440	145.4	119.8	C
				unknown	180	180	E
				unknown			C
				unknown			C
				46435	124.4	99.9	C
				46436	147.6	122.9	C
				46451	180	180	E
				46452	129.3	97.2	C
				46416	180	180	E
				46418	151.6	159.2	C
				46417			C
				46453			C
				46419	147.1	168.3	E
				46420			C
				46428	180	180	E
				46430	157.8	174.7	E
				unknown			E
				46431	180	180	E
				46432	180	180	E
				46460	126.5	141.8	C
				46463		84.7	C
				46465	180	180	E
				46457		104.6	C
				46458			C
				46459	177.6		E
				46471		150	C
				46472	167.4	180	E
				46467			U
				46468	147.9	180	E
				46475		112.9	C
				GRF0074a	180	180	E
				GRF0074b	133.5	180	E
				GRF0074c	180	180	E
				GRF0078a	180	180	E
				GRF0078b		137.5	C
				GRF0079a	180	180	E

				GRF0079b			E
				GRF0103	155.2	137.7	E
				GRF0104	146.9	90.7	C
				GRF0105	153.2	169.1	E
				GRF0106	163.5	154.4	E
				GRF0109	168.7	162.6	E
				GRF0110	163.8	174.1	E
				GRF0125	180		E
				YWS29	152.4		E
				YWS49	139.7	147.7	C
				YWS18			C
				YWS11	117.7	112.8	C
				YWS10	83.7		C
				YWS14	155.3	99.2	C
				YWS5	163.2		E
				YWS7	123.1	109.3	C
				YWS54	180	180	E
				YWS8	180	180	E
				YWS9	160.1		E
				YWS17	180	180	E
				YWS2	161.2	164.9	E
				YWS16	151.6	92.3	C
				YWS37	113.7	109.7	C
				YWS45	133.4	102.7	C
				YWS34	134.8	91.3	C
				YWS55	116.8		E

TABLE A3— Modern spider drowning experiments. FW = fresh water. S = saline, HS = hypersaline, see Table 2 for further abbreviations.

FW Sp	FW F-P	FW T-M	FW Or	S Sp	S F-P	S T-M	S Or	HS Sp	HS F-P	HS T-M	HS Or
1	76.8	106.1	C	1	121.4	149.3	C	1	73.7	81.3	C
2	163	180	E	2	152.7	180	E	2	69.2	125.7	C
3	166.5	180	E	3	75.6	96.1	C	3	72.1	116.4	C
4	113.3	139.9	E	4	67.7	149.1	C	4	82.1		C
5	161.7	164.2	E	5	163.4	173.8	E	5	151.9	123.7	E
6	159		E	6	136.1	180	E	6	75.4	99.7	C
7	109.6	94.5	E	7	115.1	109.7	C	7	88.6	151.7	C
8	163.7	124.3	E	8	157.5	169.6	C	8	134.2	92	C
9	159.3	180	E	9	118.5	125.9	C	9	81.9	130.1	C
10	158.6		E	10	57.8	159.4	E	10	134.2	59.2	C
11	174	167	E	11	142.8	154.6	E	11	81.8	115.3	C
12	117.6	162.3	E	12	145.2	128.3	E	12	119.9	135.6	C
13	161.7	175.7	E	13	122.1	134.3	E	13	92.8	116.3	C
14	85.7	125.4	C	14	151.6	180	E	14	119.5	143.4	C
15	135.7	180	E	15	87.9	126.5	C	15	50.3	150.2	C
16	163.8	180	E	16	74.6	149.2	C	16	92.6	106.9	C
17	134.2	165.3	E	17	101	148	E	17	89.6	91.3	C
18	153.2		E	18	84.7	130.1	C	18	95.7	128.1	C
19	165.6	180	E	19	123.7	139.4	E	19	91.4	126.9	C
20	180	158.3	E	20	49.4	154.4	C	20	97.2	98.2	C
21	159.6	178.2	E	21	109.2		C	21	85.6	120.5	C
				22	115	160.9	E	22	98.8	99.3	C
				23	89.6	134.4	C	23	94.4	121.2	C
				24	164.3	173.4	E	24	71.6	135.6	C
				25	104.5	142.1	C	25	79.6	95.3	C
				26	115.1	157.3	C	26	103	101.1	C
				27	107.1	142.4	C	27	105.3	96	C
				28	87.3	130.7	C				
				29	161.7	174.9	E				
				30	85.2	166.8	C				
				31	122.1	135.5	E				
				32	106.3	124	C				
				33	130.3	151.7	E				
				34	107	132.3	C				

Chi-Square Goodness-of-Fit Tests

Chi-Square Goodness-of-Fit Tests for Florissant Formation (FF), Green River Formation (GRF), Crato Formation (CF), Freshwater solution (Fresh_1), Saline solution (Saline_1), Hypersaline solution (Hypersaline_1).

Chi-Square Goodness-of-Fit Test for Categorical Variable: FF

Category	Observed	Test Proportion	Expected	Contribution to Chi-Sq
curled	1	0.5	21	19.0476
extended	41	0.5	21	19.0476

N	N*	DF	Chi-Sq	P-Value
42	0	1	38.0952	0.000

Chi-Square Goodness-of-Fit Test for Categorical Variable: GRF

Category	Observed	Test Proportion	Expected	Contribution to Chi-Sq
curled	53	0.5	62.5	1.444
extended	72	0.5	62.5	1.444

N	N*	DF	Chi-Sq	P-Value
125	0	1	2.888	0.089

Chi-Square Goodness-of-Fit Test for Categorical Variable: CF

		Test		Contribution
Category	Observed	Proportion	Expected	to Chi-Sq
curled	80	0.5	47.5	22.2368
extended	15	0.5	47.5	22.2368

N	N*	DF	Chi-Sq	P-Value
95	0	1	44.4737	0.000

Chi-Square Goodness-of-Fit Test for Categorical Variable: Fresh_1

		Test		Contribution
Category	Observed	Proportion	Expected	to Chi-Sq
curled	2	0.5	11	7.36364
extended	20	0.5	11	7.36364

N	N*	DF	Chi-Sq	P-Value
22	0	1	14.7273	0.000

Chi-Square Goodness-of-Fit Test for Categorical Variable: Saline_1

		Test		Contribution
Category	Observed	Proportion	Expected	to Chi-Sq
curled	19	0.5	17	0.235294
extended	15	0.5	17	0.235294

```
 N  N*  DF    Chi-Sq  P-Value

34   0   1  0.470588    0.493
```

Chi-Square Goodness-of-Fit Test for Categorical Variable: Hypersaline_1

```
                     Test           Contribution

Category  Observed  Proportion  Expected    to Chi-Sq

curled          26         0.5      13.5      11.5741

extended         1         0.5      13.5      11.5741
```

```
 N   N*  DF   Chi-Sq  P-Value

27   0   1  23.1481    0.000
```

ANOVA Statistical Tests

One-way ANOVA for fossil groups using arcsine transformed data in minitab: Florissant Formation (Florissant Transformed), Green River Formation (grf trans), and Crato Formation (cf trans). One-way ANOVA for drowning experiment groups: freshwater solution (fresh trans), saline solution (saline trans), and hypersaline solution (hyper trans).

One-way ANOVA: Florissant Transformed, grf trans, cf trans

```
Source    DF       SS       MS       F       P

Factor     2  211.345  105.673  130.76  0.000

Error    228  184.260    0.808

Total    230  395.605


S = 0.8990   R-Sq = 53.42%   R-Sq(adj) = 53.01%



Level                    N    Mean   StDev

Florissant Transformed  44  7.4654  0.5211

grf trans              102  7.0177  0.8055

cf trans                85  5.1983  1.1289


                        Individual 95% CIs For Mean Based on

                        Pooled StDev

Level                   --------+---------+---------+---------+-

Florissant Transformed                              (---*--)

grf trans                                       (-*--)

cf trans                  (-*--)

                        --------+---------+---------+---------+-

                            5.60      6.30      7.00      7.70


Pooled StDev = 0.8990
```
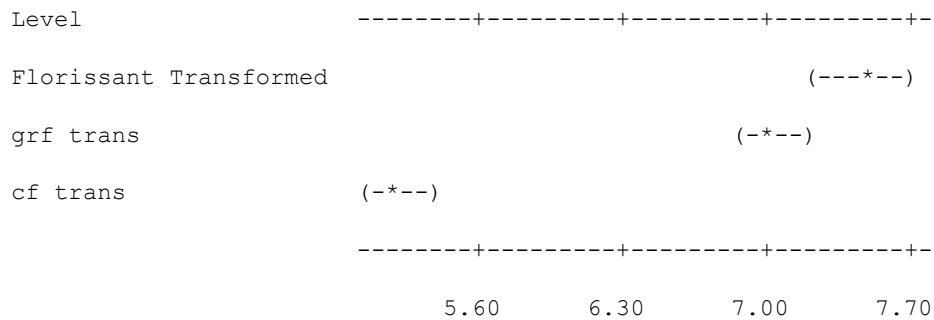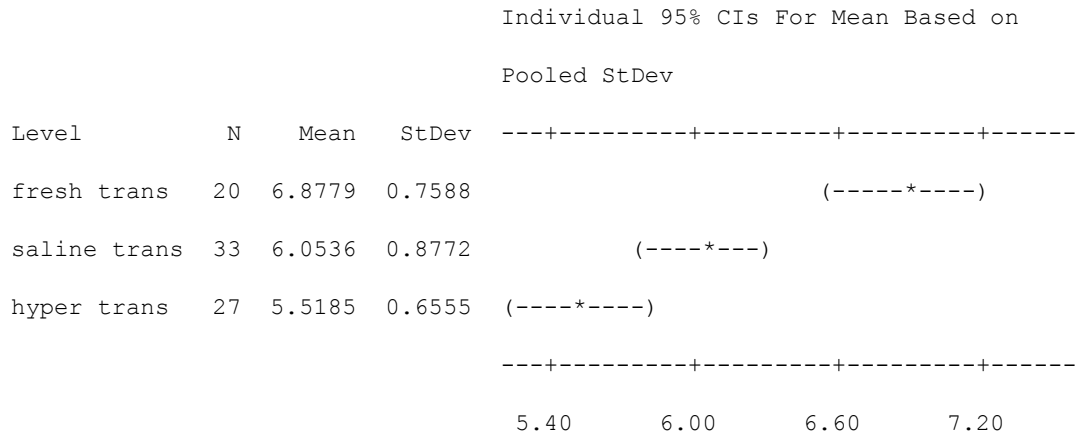
One-way ANOVA: fresh trans, saline trans, hyper trans

```
Source  DF      SS      MS      F      P

Factor   2  21.269  10.635  17.52  0.000

Error   77  46.734   0.607

Total   79  68.003
```

```
S = 0.7791   R-Sq = 31.28%   R-Sq(adj) = 29.49%
```

```
                                  Individual 95% CIs For Mean Based on

                                  Pooled StDev

Level          N    Mean   StDev  ---+---------+---------+---------+------

fresh trans   20  6.8779  0.7588                              (-----*----)

saline trans  33  6.0536  0.8772              (----*---)

hyper trans   27  5.5185  0.6555  (----*----)

                                  ---+---------+---------+---------+------

                                   5.40      6.00      6.60      7.20
```

```
Pooled StDev = 0.7791
```