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High fidelity preservation of fossil insects from the Crato Formation (Lower Cretaceous) of Brazil

Nathan Barling [a, *], David M. Martill [a], Sam W. Heads [b], Florence Gallien [a]

[a] School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK
[b] Illinois Natural History Survey, University of Illinois at Urbana-Champaign, 1816 South Oak Street, Champaign, IL 61820, USA

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ABSTRACT

Fossil insects from the Lower Cretaceous (Aptian) Crato Formation of north-east Brazil are preserved as goethite replacements in laminated limestones of lacustro-lagoonal origin. They display remarkable degrees of morphological detail down to the macromolecular level in some examples. We document the fidelity of preservation and reveal an astonishing variety of morphological detail comparable in some instances with that found in amber inclusions.

1. Introduction

The Crato Formation represents one of the richest Cretaceous fossil Konservat-*Lagerstätten* in the world, yielding an exceptionally well preserved and diverse palaeobiota (Martill et al., 2007a). Although the formation yields abundant vertebrates, including rare dinosaurs, crocodiles and abundant pterosaurs and fishes, it also preserves diverse crustaceans, arachnids, and plants. However, it is perhaps most famous for the astonishing diversity and remarkable preservation of its fossil insects (Grimaldi, 1990; Martill et al., 2007a; Heads et al., 2008).

The insects of the Crato Formation are extremely important for our understanding of insect evolution for a number of reasons. In particular, their Late Aptian (Early Cretaceous) age coincides with a time at which angiosperms were diversifying (Hochuli et al., 2006) and developing the complex relationships with insects that so strongly influenced their subsequent evolution and characterizes their biology to this day (Ehrlich and Raven, 1964; Labandeira et al., 1994; Hu et al., 2008). In addition, with other fossils, the overall assemblage provides a unique glimpse of an ancient biota that existed at this time. Understanding the development of these relationships is vital to understanding not only the Mesozoic record of plant-insect interactions, but ultimately the structure and stability of modern terrestrial ecosystems. Furthermore, the Crato Formation is the only well-documented insect Lagerstätte of its age from Gondwana, representing an extremely valuable source of data concerning diversification and austral biogeography during one of the most complex continent scale vicariance events in insect history (Amedegnato, 1993; Heads, 2008).

The Crato Formation boasts an extremely high diversity and abundance of fossil insects, with at least 18 different orders represented and over 350 named species described to date. In addition, many families are represented by as yet unnamed taxa (Bechly, 2007, 2010; Staniczek et al., 2011). These fossils are preserved exceptionally well, with details visible at the micrometer and sometimes nanometre scale. Despite this, little is known about the processes of preservation, and the high quality of preservation of Crato insects is often under-reported in species descriptions.

Here we illustrate the exceptional quality of preservation displayed by the Crato Formation insects, describe the preservational fabrics, and suggest possible mechanisms that resulted in such preservation.

2. Locality and geological background

The Crato Formation crops out on the northern flanks of the Chapada do Araripe, a ~150 km east-west plateau, located on the borders of the north-east Brazilian states of Ceará, Pernambuco and

* Corresponding author.
E-mail addresses: nathan.barling@port.ac.uk (N. Barling), david.martill@port.ac.uk (D.M. Martill), swheads@illinois.edu (S.W. Heads), fgallien@hotmail.com (F. Gallien).

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Piauí (Fig. 1). The formation is mined extensively for commercial purposes in the vicinity of Santana do Cariri and Nova Olinda in Ceará, and it is from these areas that most fossils are obtained.

The formation itself is a ~60 m thick heterolithic sequence dominated in its middle part by laminated limestones, interbedded at their base with claystones, siltstones, and sandstones (Martill and Heimhofer, 2007). The formation consists of four distinct members, though only the lowest Nova Olinda Member yields exceptionally preserved fossils (Martill et al., 2007a). The Nova Olinda Member is a finely laminated limestone, formed authigenically by algae (Heimhofer et al., 2010). The laminae average 1 mm in thickness, alternating between light and dark-blue grey colours when freshly exposed and likely represent wet and dry seasonal cycles (Heimhofer et al., 2010). The depositional environment represented is that of a restricted lacustrine or lagoonal setting with a stratified water column. The upper water column was likely brackish and well oxygenated, whereas the lower column and lake/lagoon bottom was hypersaline and anoxic (Heimhofer et al., 2010). More detailed geological and sedimentological information can be found in Martill et al. (2007a) and Heimhofer et al. (2010).

3. Materials and methods

3.1. Collection

Specimens used in this research were donated to the University of Portsmouth by Judith Wohlrabe in 2011. They were obtained via a German fossil dealer and, somewhat ironically, given to Ms. Wohlrabe on account of their perceived poor quality and lack of aesthetic appeal. They were made available to the senior author and assigned new research numbers. Some of the specimens were subjected to destructive analysis and no longer survive (NBRL034 and FLO27), but photographs of them are included within the text nonetheless.

The collection is dominated by specimens of Blattodea (cockroaches), but also includes examples of Orthoptera (grasshoppers and crickets), Odonata (dragon- and damselflies), Hymenoptera (wasps), Hemiptera (true bugs), Diptera (flies), Neuroptera (lacewings and antlions) and Coleoptera (beetles).

Ninety two specimens were studied for this analysis. The majority of unprepared specimens were stored in sealed plastic containers and specimens prepared for SEM viewing were either stored in desiccators or secured by foam in sealed plastic containers with cobalt chloride granules.

3.2. Preparation techniques

Many Crato Formation insects are damaged by the quarrymen collectors who routinely rub the specimens to 'clean' them, often severely damaging the exposed surface. Consequently, all specimens were initially examined under a light microscope for subjective evaluations of their quality of preservation. The unexposed surface of the insect adjacent to the limestone usually remains pristine. To examine the unadulterated surface we transferred the specimens to resin blocks (Walton, 1923; Cridland and Williams, 1966; Escapa et al., 2010).

Several techniques were used to prepare the insect specimens. In some cases, a simple wash with water was sufficient to reveal details of the specimen for light microscopy. In other examples excess matrix was removed using fine needles under the microscope. For examination by electron microscopy we employed three techniques: hydrochloric or acetic acid wash to expose the specimen on the limestone slab; acid transfer onto resin blocks, or in some cases the complete removal of the fossil from the matrix using acids. Acid etching and complete digestion of matrix were done with 10% acetic acid or 5–10% hydrochloric acid, depending on the degree of weathering.

Photomicrographs were taken using an Olympus SZ-STS light microscope with a mounted Nikon DS-Fi1 camera and a Nikon Digital Sight attachment. Images were saved as JPEG or Tiff files.

Two scanning electron microscopes were used for this project: a JEOL JSM-6100 Scanning Microscope and a JEOL JSM-6060LV Scanning Electron Microscope. Specimens were prepared by mounting on aluminium stubs with a black carbon pad or carbon cement (Conductive Carbon Cement Leit-C). They were then cleaned with a soft squeeze blower and/or acetone to remove any grease and dust. Any remaining gaps between the specimen and the stub were sealed with additional carbon cement and finally they were sputter coated with a gold-palladium alloy using a Quorum Q150RES Sputter Coater. Images were captured and analysed using PC digitiser and 'SemAfore' software. Image manipulation and construction of illustrations was performed using CorelDRAW X5 and Corel Paint-Shop Photo Pro X3.

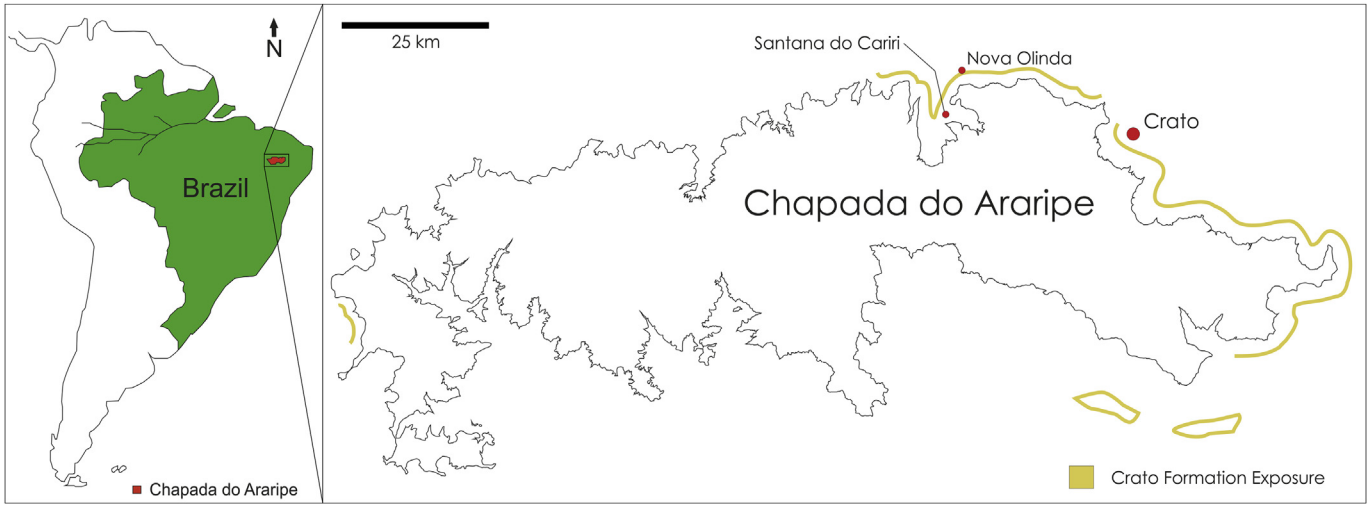

Fig. 1. Locality map showing the outcrop of the Crato Formation on the flanks of the Chapada do Araripe, north-east Brazil. The two most important localities for fossil insects are indicated: Santana do Cariri and Nova Olinda. The town of Crato is also indicated.