Earliest record of fossil insect oothecae confirms the presence of crown-dictyopteran taxa in the Late Triassic

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Abstract. Although dissimilar in their overall appearance and life habits, the praying mantises (Mantodea) and cockroaches (Blattodea, including their eusocial relatives, the termites [Isoptera]) are grouped within the clade Dictyoptera, based on – among other significant characteristics – the laying of eggs in a compound structure called an ootheca. The origin of the Dictyoptera and the currently recognized taxa within is, however, a controversial topic among entomologists. This has resulted from disparities in the divergence age estimates obtained from phylogenetic analyses based on molecular data together with the limited and controversial fossil evidence attributable to these groups. Here, we report two new oothecae ichnospecies found in a Carnian (237 to 227 mya. lowermost Upper Triassic) deposit from Argentina. Morphological comparisons and Scanning Electron Microscope and X-ray Energy Dispersive Spectroscopy analyses of fossil and extant oothecae of mantises and cockroaches were performed in an attempt to solve their systematic placement within Dictyoptera and fossil allies, such as †Alienoptera. In addition to being the earliest known record of oothecae, this discovery moves the origin of this specialized reproductive strategy back by 100 million years. As direct fossil evidence, these specimens provide an important calibration and reference point that can inform future research on the origins and timing of diversification of the Dictyoptera.

Introduction

Unravelling the evolutionary biology of taxa and their phylogenetic relationships is fundamental to answering questions in biodiversity, ecology and taxonomy. In this sense, the phylogeny of the Dictyoptera (Insecta) and its suborders, Mantodea (praying mantises) and Blattodea (cockroaches and termites), has generated considerable debate among researchers

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since Hennig's (1969) seminal work on the evolution of the group. Despite their contrasting external morphologies, praying mantises, cockroaches and termites are nested within the Dictyoptera on the basis of two main remarkable features: the perforation of the tentorium (an anatomical feature of the head) and the short ovipositor in females. The latter trait allows for the production of an ootheca, a specialized reproductive strategy particular to this group of insects (Grimaldi & Engel, 2005; Klass & Meier, 2006; Hörnig *et al.*, 2018).

The diverse and complex behaviours identified in the Dictyoptera, including parental care (some cockroaches and termites), castes and eusociality (termites), and predatory habits (praying mantises), also point to a rich evolutionary history of the group. However, the relationships, origin and diversification times within the Dictyoptera seem far from resolved, even after considerable advances in the molecular techniques

Table 1. SEM/EDS analysis of fossil and extant oothecae.

Specimen	Selected spot	Relative abundance of predominant elements ([a]wt%)											
		C	O	Si	Fe	S	N	Ca	P	K	Al	Na	Mg
IANIGLA-PI 3129 Fossil ootheca (isolated cuticle)	Emergence area	53.7	40.3	3.47	1.55	0.93	–	–	–	–	[b]	–	–
	Egg chambers	59.4	35.5	2.68	1.34	0.80	–	–	–	0.07	[b]	0.18	–
IANIGLA-PI 3132 Fossil ootheca	Emergence area	54.4	38.0	4.12	0.87	0.42	–	–	–	0.19	1.72	0.13	0.06
	Egg chambers	51.0	40.0	4.92	0.92	0.43	–	0.04	–	0.23	2.09	0.16	–
	Rock matrix	11.9	49.3	24.4	2.23	0.19	–	0.09	–	1.26	9.53	0.23	0.43
IANIGLA-PI 3136 Fossil ootheca	Emergence area	47.2	40.2	7.48	0.95	0.19	–	–	–	0.46	3.10	0.12	0.12
	Egg chambers	12.0	59.8	17.8	1.09	0.05	–	0.08	–	1.06	7.25	0.22	0.24
	Rock matrix	36.7	41.7	12.0	0.83	0.08	–	–	–	1.52	6.87	–	–
Extant mantid ootheca	Emergence area	48.5	37.8	0.15	–	0.70	9.90	2.25	0.42	0.15	–	–	0.08
	Egg chambers	55.1	35.6	0.33	–	1.40	–	4.09	0.95	0.47	2.09	–	–
	Residual process	54.8	37.3	1.86	0.55	1.10	–	2.68	0.80	0.40	–	–	–
Extant cockroach ootheca (oviparous)	Keel area	59.3	36.3	0.22	0.08	0.07	–	3.57	0.18	0.09	0.11	–	0.05
	Egg chambers	58.4	37.6	0.25	0.08	0.11	–	2.73	0.31	0.12	0.10	0.09	0.16
Extant cockroach ootheca (ovoviviparous)	Dorsal area	72.7	25.8	0.01	–	0.12	1.28	0.01	0.01	0.02	[b]	–	–
	Egg chambers	72.6	25.7	0.01	–	0.14	1.35	0.01	0.01	0.03	[b]	–	–

[a] wt%: percentage of atom weight.
[b] Aluminium (Al) excluded from EDS mapping since it measures the conductive paint used to glue the sample.

applied in phylogenetic studies over the last 30 years (Thorne & Carpenter, 1992; Klass, 1997; Deitz *et al.*, 2003; Klass & Meier, 2006; Legendre *et al.*, 2015; Hörnig *et al.*, 2018; Evangelista *et al.*, 2019; among many others).

Modern techniques combining morphological, molecular, environmental and behavioural data, with the addition of key fossil information, mostly gathered from mid-Cretaceous amber deposits, from which various new dictyopteran taxa have been described (Bai *et al.*, 2016, 2018; Kočárek, 2018), have allowed for the development of different evolutionary scenarios for the Dictyoptera (Grimaldi & Engel, 2005; Béthoux & Wieland, 2009; Legendre *et al.*, 2015; Wang *et al.*, 2017; Evangelista *et al.*, 2019). These analyses, however, resulted in incongruent age estimates for the origin and diversification of dictyopteran taxa, ranging from the Carboniferous to the latest Cretaceous. One reason for the divergent results obtained by different research groups is a lack of consensus on whether the fossils used for dating tree nodes should be considered stem- or crown-taxa (Forest, 2009; Evangelista *et al.*, 2017; Hörnig *et al.*, 2018; Giribet & Edgecombe, 2019).

Here we report two new ichnospecies of fossil oothecae recovered from the uppermost levels of the Potrerillos Formation, Carnian-aged deposits at the Quebrada del Durazno locality, in Mendoza, Argentina (Fig. S1). We assessed the taxonomic affiliations of the new specimens through morphological and chemical analyses and comparisons with extant and fossil oothecae from both Blattodea and Mantodea. Because of the current lack of consensus regarding the origin and diversification of stem-versus crown-dictyopteran taxa, we discuss the phylogenetic relevance of this material and encourage the use of these fossils as a calibration point in future dictyopteran phylogenies.

Lastly, we briefly discuss the paleoecological implications of these findings.

Results

A total of 20 fossil oothecae were identified, nine of which are almost complete, relatively well-preserved specimens (the holotype and paratype specimens described herein).

In an attempt to determine the systematic placement (i.e. Blattodea vs Mantodea) of our material, Scanning Electron Microscope and X-ray Energy Dispersive Spectroscopy (SEM/EDS) analyses were performed on the egg cases of three fossil specimens, which had cuticles preserved. The latter technique was used to characterize the elemental composition on a highly localized area ("spot mode") of the sample, allowing for the comparison with extant oothecae from both groups (Table 1).

Based on their different morphologies and apparent modes of attachment, two ichnospecies are identified.
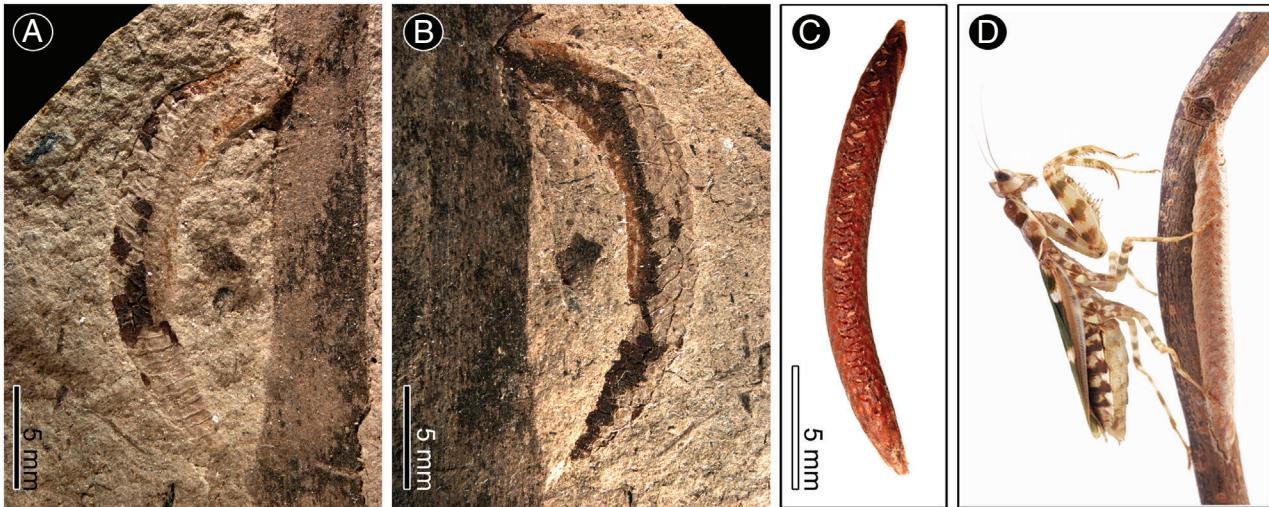
Systematic palaeontology

Order Dictyoptera Latreille, 1829.
† *Oothecichnus pensilis* ichnosp. n. (Fig. 1).

Holotype. IANIGLA-PI 3140.

Age and locality. Carnian (~232 mya, lowermost Upper Triassic); uppermost levels of the Potrerillos Formation, Quebrada del Durazno locality, Mendoza, Argentina.

Fig 1. † *Oothecichnus pensilis* ichnosp. n., characterized by its elongate shape with tapering ends and a proximal end mode of attachment. (A and B) Holotype specimen IANIGLA-PI 3140, part and counterpart. Note apparent proximal attachment to an indeterminate plant stem. (C) Extant ootheca of *Creobroter* sp. comparable to † *Oothecichnus pensilis* ichnosp. n. (Picture provided by D. Känel [http://www.macroscientifique.com/], used with permission). (D) *Creobroter gemmatus* praying mantis and its ootheca (Picture purchased from 123RF.com, used with permission). [Colour figure can be viewed at wileyonlinelibrary.com].

Etymology. "*pensilis*" meaning "hanging down" or "pendant" in Latin; referring to the attachment of the proximal end of the pendulous ootheca to a twig, branch or other substrates.

Diagnosis. Ootheca elongate, cylindrical, with rounded to acute proximal and distal ends. Ootheca attached to a substrate by the proximal end. Exhibiting approximately 60 egg chambers arranged in two ranks along the length of the ootheca, the chambers clearly delimited by transverse wall partitions visible on the lateral side of the ootheca. Egg chambers ranging from 2.4 to 1.6 mm long and 0.7 to 0.5 mm wide. Emergence area covering 3/4 of the dorsal surface of the ootheca.

Description. Specimen IANIGLA-PI 3140 (Holotype, Fig. 1A, B) consists of a part and counterpart adpression fossil preserved in dorso-lateral view, and was the largest ootheca found, measuring 24.8 mm long and 3.11 mm wide. It has an elongate, curved shape of constant width except at the ends, which gradually taper to a rounded tip. The proximal end appears to be attached to a plant fragment, whereas the remainder of the structure is free. The emergence area is 14.4 mm long and 1.4 mm wide, with no dorsal openings preserved. Approximately 30 egg chambers arranged in pairs (~60 in total) were counted based on the transverse wall partitions visible on the lateral wall (Fig. 1A), although the number of eggs contained in each chamber remains unknown.

† *Oothecichnus duraznensis* ichnosp. n. (Fig. 2).

Holotype. IANIGLA-PI 3130.

Paratypes. IANIGLA-PI 3129, IANIGLA-PI 3131, IANIGLA-PI 3132, IANIGLA-PI 3133, IANIGLA-PI 3136, IANIGLA-PI 3137, IANIGLA-PI 3138.

Age and locality. Carnian (~232 mya, lowermost Upper Triassic); uppermost levels of the Potrerillos Formation, Quebrada del Durazno locality, Mendoza, Argentina.

Etymology. "*duraznensis*" after the Quebrada del Durazno locality.

Diagnosis. Ootheca oblong to obovate in shape, slightly decreasing in width from proximal to the distal end. Proximal end rounded, distal end truncates, in some cases forming a short, residual process. Ootheca attachment along the entire ventral surface. Egg chambers ranging from 2.6 to 1.6 mm long and 0.6 to 0.4 mm wide, arranged in two longitudinal ranks, ranging from 10 to 24 chambers per side; walls well defined. Emergence area clearly defined, dorsal openings hexagonal to polygonal, arranged in two rows in an alternating zigzag pattern. Cuticle comprising contiguous polygonal structures (cells?) ~20−25 μm in diameter, with a central, circular dome and a wall 9 μm thick. Egg chamber surfaces covered in papillae, which are more densely clustered closer to the wall boundaries.

Description. The shape of these oothecae ranges from oblong to obovate, with the proximal end slightly larger than the distal end. The fact that these specimens were all found detached and isolated from any plant matter, and preserved mostly in dorsiventral and dorso-lateral views, points to a ventral attachment of the oothecae to the substrate.

Specimens IANIGLA-PI 3130 (holotype), IANIGLA-PI 3133 and IANIGLA-PI 3138 (Fig. 2A–C) were all preserved in dorsiventral view. These oothecae have an obovate shape, and range from 10.1 to 16.7 mm long, with a wider proximal end varying from 4.2 to 6.3 mm gradually decreasing to 2.3 to
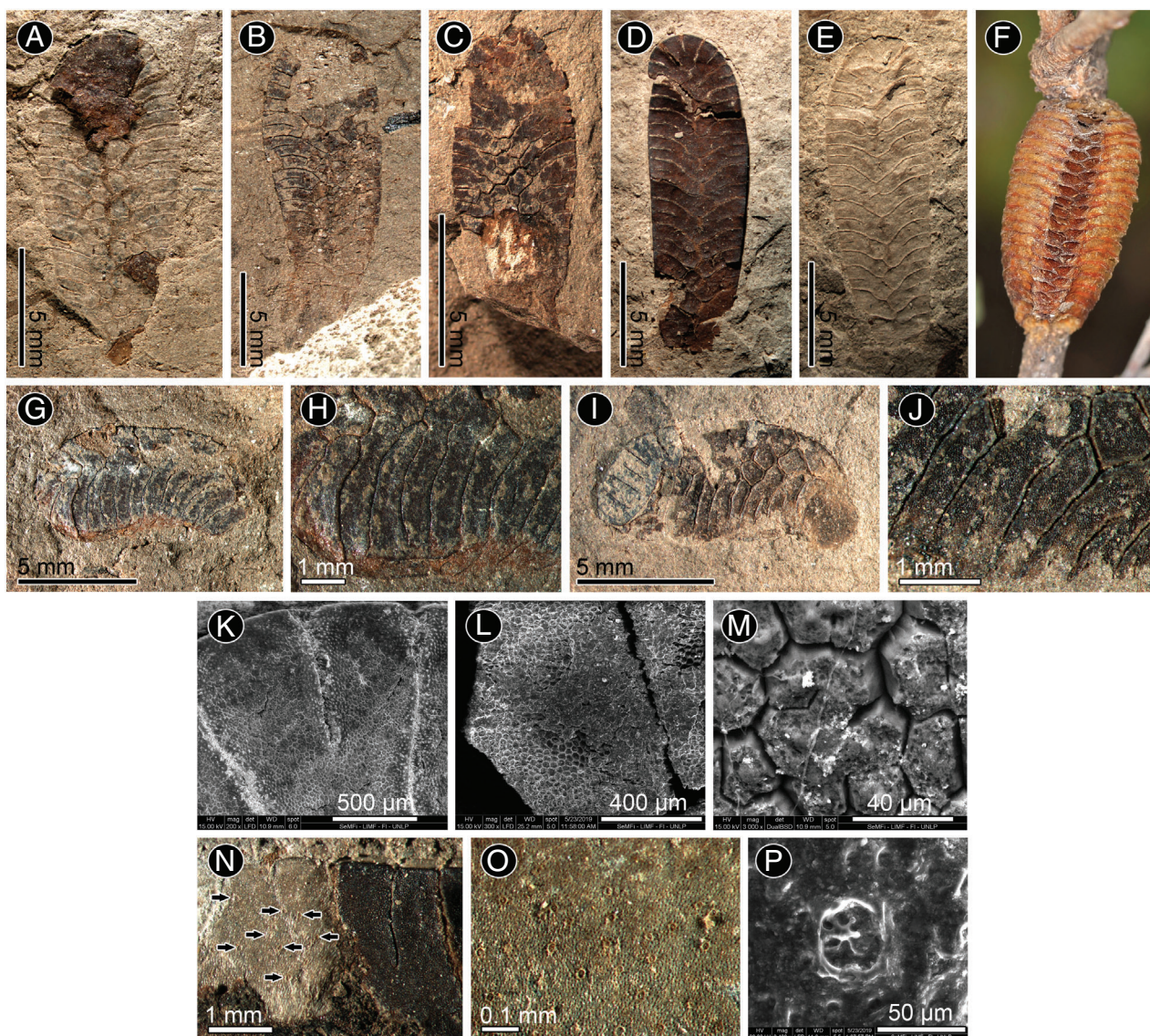
Fig 2. † *Oothecichnus duraznensis* ichnosp. n., characterized by an obovate shape and a ventral mode of attachment to a substrate. (A) Holotype specimen IANIGLA-PI 3130 displayed in dorsal view (Fig. S2); note the hexagonal emergence area openings and some of the residual process distally preserved. (B and C) Dorsal views of paratype specimens IANIGLA-PI 3133 and IANIGLA-PI 3138. (D and E) Part and counterpart of paratype specimen IANIGLA-PI 3129, with closed emergence area; note cuticle fully preserved on (D), later extracted from fossil for SEM/EDS analysis (Fig. S3). (F) Extant praying mantis ootheca morphologically comparable to † *Oothecichnus duraznensis* sp. nov. (Picture provided by C. M. Mancilla Canseco, used with permission). (G–J) Paratype specimens IANIGLA-PI 3131 and IANIGLA-PI 3132 preserved in lateral view (Fig. S2); note the emergence area openings dorsally and the egg chambers laterally. (H and J) Detail of emergence area and lateral egg chambers in (G) and (I), respectively; note the engrossment at the wall boundaries. (K–M) SEM images of cuticles preserved in IANIGLA-PI 3129 (K and M) and IANIGLA-PI 3132 (L), showing the polygonal arrangement of cells, giving the impression of a papillated surface. (N–P) Rimmed pores randomly arranged on the surface of specimen IANIGLA-PI 3137 where there is no cuticle preserved, (P) SEM image obtained from IANIGLA-PI 3136 (Fig. S5), showing the branched internal structure of one these pores. [Colour figure can be viewed at wileyonlinelibrary.com].

3.3 mm at the distal end. The emergence areas are well defined, arranged alternately in two longitudinal rows of openings, creating a distinctive zigzag pattern. These dorsal openings are typically hexagonal in shape and measure between 0.85 and 1.3 mm in diameter. Each egg chamber range from 2.4 to 1.6 mm long and 0.6 to 0.4 mm wide, visible to the side of each dorsal

opening, and the total number of chambers varies depending on the different sizes of the specimens. Specimen IANIGLA-PI 3130 (Fig. 2A) has some of the final residual processes distally.

Specimen IANIGLA-PI 3129 (Fig. 2D, E) consists of the part and counterpart of an oblong ootheca preserved in a dorsiventral view. It is 15.3 mm long and 4.7 mm wide, decreasing to 3.3 mm

wide towards the distal end. A total of 48 egg chambers were counted, each 1.8 mm long and 0.6 mm wide, whereas the emergence area is closed, with only a few, ill-defined, sealed hexagonal exits observed, ∼0.7 mm in diameter.

Lastly, specimens IANIGLA-PI 3131, IANIGLA-PI 3132 (Fig. 2G–J) were preserved in a lateral view, although the dorsal side is partially visible. These oothecae range in size from 7.7 to 9 mm long and 3.8 to 4.3 mm at their maximum width, decreasing to 1.8–2 mm distally. The egg chambers range from 2.6 to 2.3 mm long and 0.6 to 0.4 mm wide, with clearly visible transverse walls separating them, varying from 10 to 13 per side. The hexagonal dorsal openings are 0.8 mm in diameter.

SEM/EDS analysis. The high quality of preservation of these oothecae allowed for the identification of several microscopic features under both the stereo microscope and SEM. Detailed visualization under SEM of the cuticles in specimens IANIGLA-PI 3129, 3132 and 3136, showed a consistent pattern in all three fossils (Figs. S3–S5). The cuticle is composed of contiguous polygonal structures ranging from 20 to 25 μm in diameter, with a central dome, giving the impression of a papillated exterior (Fig. 2K–M). These polygonal structures are slightly bigger at the wall boundaries, being more densely arranged along the margins (Fig. 2H, J–L). Other remarkable features were observed in areas where there were no organic remains, characterized by circular pores arranged randomly on the surface, each with a thick, slightly elevated rim, ∼35 μm in diameter and a centrally branched structure visible in the interior (Fig. 2N–P). We interpret these structures as pores that possibly allowed the exchange of gases between the exterior and the egg chambers, or which might have helped with the regulation of water content within the ootheca.

Furthermore, the recovery and isolation of an almost complete cuticle from specimen IANIGLA-PI 3129 was possible (Fig. 2D, Fig. S3), and was chemically analysed (Table 1). Other two fossil specimens with cuticle remnants were included in the EDS compositional analysis (IANIGLA-PI 3132, 3136; Figs. S4, S5), but since these were embedded in the rock, extra care was taken when interpreting the values of each element, to compensate for the potential influence of the chemistry of the host rock. Whenever possible, two spots were chosen for the analysis, (i) emergence area, and (ii) egg chambers. Clean surface spots on the host rocks in which IANIGLA-PI 3132 and 3136 were preserved were also tested (Table 1).

The concentration of both carbon and oxygen was predominant (totalling more than 85%) in all fossil samples evaluated, with the remainder of detected elements occurring at different but considerably lower concentrations (Table 1). An exception to this was IANIGLA-PI 3136 (Fig. S5), in which a lower amount of carbon was detected at the egg chamber spot, maybe as a consequence of the thinned cuticle in that region (Table 1; Fig. S5b, d, k). In order of importance, silicon followed with values ranging from 2.68 to 7.48%, once again IANIGLA-PI 3136 showing a disparate 17.8% value in the spot where there was no cuticle preserved, therefore probably reflecting the host rock rather than the original composition of the cuticle. Iron, aluminium, sulfur, potassium and sodium, although present, were registered at very low concentrations, whereas concentrations of nitrogen, phosphorous, magnesium or calcium, if detected, were present at negligible values (Table 1). The highest elemental concentrations obtained from analysing clean rock surfaces in specimens IANIGLA-PI 3132 and 3136 were those of oxygen, silicon and aluminium; despite carbon concentrations being higher compared to the rest of the elements, values are still considerably lower than those obtained from spots in the fossils where cuticle was present. The combination of the above-mentioned elements points to predominantly Al-Si (alumino-silicate) as the major constituent of the matrix. This is probably a consequence of the weathering of feldspars, resulting in clays such as kaolinite.

## Discussion

Origins of oothecal oviposition

Despite being relatively hard structures, fossil oothecae are elusive, with only a few mentions in the literature (Table 2). In particular, presumed Paleozoic oothecae (Laurentiaux, 1951) have been later interpreted as fish teeth or parts of other organisms (Brown, 1957; Rasnitsyn & Quicke, 2002; Gao *et al.*, 2018). Among the possible explanations for the lack of oothecae in pre-Cretaceous deposits is the apparent prerequisite for small ovipositors to produce oothecae (Roth, 2003; Hörnig *et al.*, 2018). Cockroach-like insects were a common element in Carboniferous coal swamps, as reflected by the complete fossil specimens recovered from numerous localities around the globe (Rasnitsyn & Quicke, 2002; Grimaldi & Engel, 2005). However, these primitive roaches possessed a long ovipositor, therefore, precluding the formation of an egg case (Hörnig *et al.*, 2013 for discussion). By the Cretaceous, species with moderately long ovipositors were still present; although the structure underwent a gradual decrease in size throughout the Mesozoic, giving rise to the clade of modern cockroaches (Blattodea), characterized by a short or completely internalized ovipositor (Grimaldi, 1997; Vršanský *et al.*, 2002; Gao *et al.*, 2018; Hörnig *et al.*, 2018). Concomitant with the appearance of Cretaceous cockroaches with reduced ovipositors were reports of cockroaches preserved in the process of laying oothecae, as well as a number of isolated oothecae attributable to this group (Fig. 3 and Table 2).

Unlike the cockroach fossil record, no examples of praying mantises laying oothecae have been found to date. However, the short, broad ovipositors observed in some mantis specimens recovered from Cretaceous deposits suggest they could potentially lay oothecae similar to those of extant mantodeans (Grimaldi, 2003; Hörnig *et al.*, 2013). To date, only two isolated oothecae have been attributed to mantids in the literature (Table 2), both Cretaceous in age (Rasnitsyn & Quicke, 2002; Li & Huang, 2019).

The fossils described here are the earliest direct evidence of oothecae, and as such, they push back the origin of the ootheca-laying reproductive strategy in the fossil record by 100 million years, to the early Late Triassic. Dictyopterans with

Table 2. Comparison of fossil oothecae.

Specimen	Length of ootheca	Width of ootheca	Egg chambers (per side)	Other features	Affinity	Age	Ref.
n/a	Indet.	Indet.	15	Squared shape, slightly curved, compact ootheca. Top with sutural crest. Strong longitudinal and transverse striations. Preserved in amber.	Cockroach	Miocene	Poinar Jr, 2010
n/a	3 mm	2 mm	7	Squared shape. Top with sutural crest bordered by a narrow, undulant, notched flange. Preserved as adpression.	Cockroach	Eocene	Brown, 1957
Oothecichnus negevianus Anisyutkin and Rasnitsyn	11.4 mm	4.4 mm	34–40	Irregularly elongate, oval. Rounded narrow ends. Top with longitudinal zigzag suture. Preserved as adpression.	Mantis	Cretaceous	Rasnitsyn & Quicke, 2002
Blattaoothecichnus argenteus Hinkelman	8 mm	2 mm	15	Tubiform shape. Dorsal margin with strongly developed keel with distinct protrusions. Preserved in amber.	Cockroach	mid-Cretaceous	Hinkelman, 2019
n/a	6.6 mm (5.4 mm w/o residual process)	2.5 mm	12	Ovate, acuminate shape. Distal end tapering in a residual process. Ventral attachment. Preserved in amber.	Mantis	mid- Cretaceous	Li & Huang, 2019
n/a (7 isolated specimens)	3.53–8.32 mm; 7.20–13 mm	1.86–2.92 mm; 2.86–4.64 mm	<40; >60	Two groups recognized based on egg number: <40 (Group I); >60 (Group II). Serrated protrusions along the lateral border of the oothecae. Preserved in amber.	Cockroach	mid-Cretaceous	Gao *et al*, 2018
(belonging to) *Piniblatella yixianensis* Gao et al.	6.1–7.1 mm	1.5–2.4 mm	30–35	Slightly curved ootheca. Transverse lines (egg chamber walls) equally separated. Notched edge along ootheca, forming a relatively smooth keel. Preserved as adpression.	Cockroach	Mid-Lower Cretaceous	Gao *et al*, 2018
(belonging to) *Piniblatella limai* Pinto and Purper ("*Mesoblattina*")	3.9–4.6 mm	2–2.2 mm	Indet.	Two roaches retaining their ootheca are pictured, without further description provided. Preserved as adpression.	Cockroach	Lower Cretaceous	Hörnig *et al.*, 2013
Oothecichnus pensilis Cariglino et al.	24.8 mm	3.11 mm	30	Elongate, cylindrical ootheca, tapering towards the proximal and distal ends. Proximal end attachment. Preserved as adpression, with cuticle preserved.	Mantis	lower Upper Triassic	This work
Oothecichnus duraznensis Cariglino et al.	7.7–16.7 mm	3.8–6.3 mm	10–24	Oblong to obovate in shape. Proximal end is wider than the distal end. Ootheca attachment ventral. Distinct emergence area with hexagonal to polygonal dorsal openings aligned in two rows in a zigzag manner. Preserved as adpression, with cuticle preserved.	Mantis	lower Upper Triassic	This work
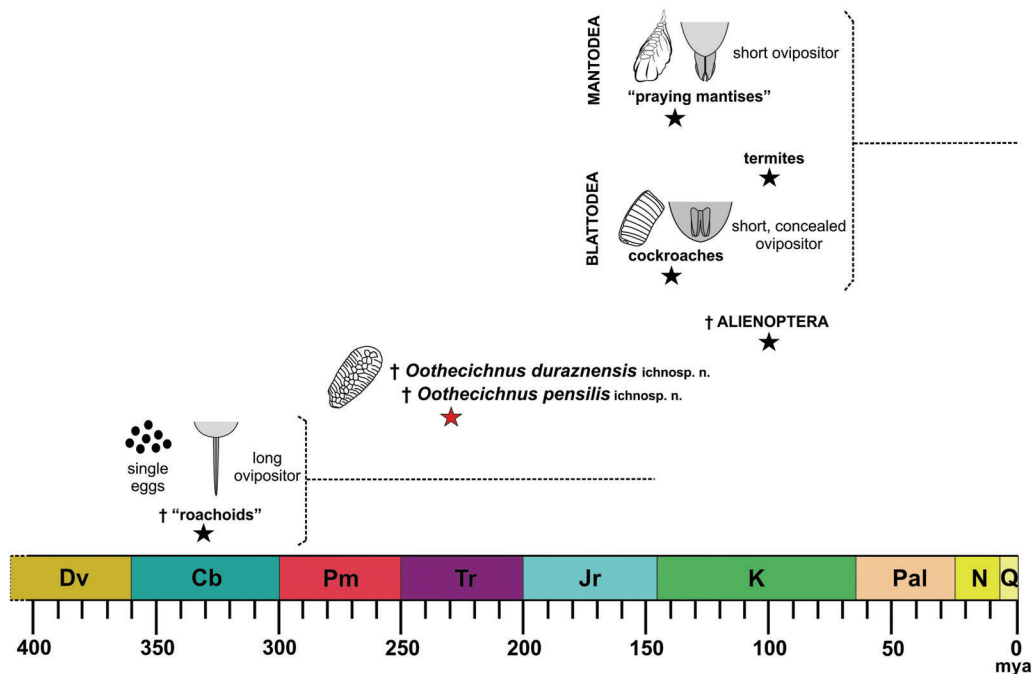
Fig 3. Origin of the ootheca and inferred ovipositor reduction (based on Hörnig *et al.*, 2018) according to the current fossil evidence (based on Gao *et al.*, 2018 and Li & Huang, 2019). [Colour figure can be viewed at wileyonlinelibrary.com].

short ovipositors are still unknown from pre-Cretaceous deposits (Hörnig *et al.*, 2013, 2018), but the discovery of the oothecae presented here strongly implies their presence at least since the Carnian (Fig. 3).

Plausible ootheca producers

To date, more than 300 fossils of insects belonging to numerous groups, including Hemiptera, Orthoptera, Odonata, Coleoptera, Miomoptera, Grylloblattida, Mecoptera and Diptera, have been recovered from the Triassic Quebrada del Durazno locality (Lara *et al.*, 2017). Unfortunately, despite their abundant and diverse occurrence, no direct body evidence (e.g. wings, legs, etc.) from mantids, cockroaches or proposed stem-dictyopterans have yet been identified, posing a dilemma when looking for the owner of the egg cases described here.

The presence of Grylloblattodea is worth consideration, as several researchers have proposed a close relationship with the Dictyoptera based on the presence of "enlarged coxae" in the former (Hennig, 1969; Kristensen, 1975; Boudreaux, 1979). For many years, the fossil record of Grylloblattodea in Argentina consisted of a single aquatic nymph recovered from the Potrerillos Formation (Marquat, 1991), which was later postulated to be similar to a stonefly (Aristov *et al.*, 2006). More recently, the first confident record of Grylloblattodea was described from the uppermost levels of the Potrerillos Formation, near the Quebrada del Durazno locality (Lara & Aristov, 2016). Based on the forewing of an adult specimen, † *Permoshurabia argentina* Lara and Aristov was assigned to the extinct Geinitziidae, a

family widely distributed during the Triassic, with representatives similar in appearance to extant cockroaches (Lara & Aristov, 2016). The current lack of knowledge about the reproductive biology of extinct members of this group precludes any useful clues as to the potential owner of these oothecae, but considering extant grylloblattids lay single, ellipsoidal eggs (Matsuzaki *et al.*, 1982; Wipfler *et al.*, 2014), we consider † *Permoshurabia argentina* to be an improbable candidate.

The reproductive strategies employed by other dictyopteran lineages are still barely understood. As a new extinct insect order considered to be a link between Blattodea and Mantodea, the † Alienoptera is based on few specimens recently recovered from mid-Cretaceous Burmese amber (Bai *et al.*, 2016, 2018; Kočárek, 2018). This group possessed a mosaic of characters that led to its placement within the Dictyoptera and to being more closely allied to Mantodea than to Blattodea. Among the new taxa, † *Alienopterus brachyelitrus* Bai *et al.* and † *Alienopterella stigmatica* Kočárek are male specimens, precluding any suppositions about the production of an ootheca; however, the male genitalia in † *A. brachyelitrus* closely concurs with those in Mantodea (Bai *et al.*, 2016). Another taxon attributed to † Alienoptera is † *Caputoraptor elegans* Bai *et al.*, based on nine specimens representing nymphs and adult females, characterized by a remarkable scissor-like feature on the posterior head, considered as a device to hold on the males during copulation (Bai *et al.*, 2018). The terminal sternite of the abdomen in † *C. elegans* is modified into a triangular subgenital plate, a feature also present in Mantodea and Blattodea. In the latter, this subgenital plate fully covers the short, internalized ovipositor, whereas, in female praying mantises, the ovipositor is short

but distally visible, similarly to what happens in † *C. elegans*, where the first segment ("valvula") of the ovipositor is longer than the subgenital plate (Bai *et al.*, 2018). The formation of an ootheca in † *C. elegans*, as well as any other † Alienoptera, is still unknown (Bai *et al.*, 2018); however, a mantis-like ootheca found at the same Burmese amber deposits could potentially belong to one of these taxa (Li & Huang, 2019).

As a consequence, the potential producers of these fossil oothecae remain a source of speculation, as the sole, direct evidence of this reproductive strategy is the oothecae themselves. We provide a measured proposal of their potential affinities through a comparison of the morphology and elemental composition of the specimens with other fossil and extant oothecae already described in the literature.

Oothecae morphology. The laying of eggs as a compound structure is found in numerous groups of insects, including the Orthoptera, Coleoptera, Mantophasmatodea and Phasmatodea (Goldberg *et al.*, 2015). However, the oothecae of the Dictyoptera are characterized by an ordered arrangement of the eggs and the absence of incorporated external elements, such as soil particles or twigs (Roth, 1968; Goldberg *et al.*, 2015; Brannoch *et al.*, 2017; Li & Huang, 2019).

Within Dictyoptera, the ootheca in praying mantises exhibits remarkable architectural variations at both specific and higher taxonomic levels, but they all share a consistent general structure, distinct from those of the Blattodea (Breland & Dobson, 1947; Rivera & Svenson, 2016; Brannoch *et al.*, 2017). The shape variations of the egg cases are considered diagnostic at the species level, whereas the differences in size seem to depend on the number of eggs contained within the ootheca. Overall, mantid oothecae consist of one or more eggs enclosed in a series of chambers arranged in rows, usually alternating. Each of the chambers exhibits a single, dorsal opening from where the young mantises will hatch, aligned longitudinally but in a slight and distinctive zigzag pattern (because of the off-set, alternate arrangement of the chambers) in two parallel rows forming the emergence area. Mantids lay their oothecae on a variety of substrates, typically being attached along the length of the ventral surface, although in some species attachment is only proximal.

The structure of oothecae in both termites and cockroaches differs from those typical of mantids, where two lateral ranks of egg chambers flank a dorsal emergence area. In Isoptera, only one termite species (*Mastotermes darwiniensis* Froggat) is oviparous, producing a reduced ootheca characterized by up to 24 eggs glued together in a double row, with no dorsal keel, and an irregular distal end (Rugg & Rose, 1984; Nalepa & Lenz, 2000; Grimaldi & Engel, 2005; Courrent *et al.*, 2008). On the other hand, cockroaches evolved oviparity and ovoviviparity, and even nonplacental viviparity in one group (Roth, 2003). Therefore, the morphology (i.e. size, shape, number of eggs) of the oothecae varies depending on the species. Overall, the ootheca of oviparous forms is a hardened, sometimes curved capsule bearing two rows of elongate, ovate eggs, externally divided by transverse furrows and bearing a conspicuous, linear dorsal keel that splits open when hatchlings arise

(Roth, 1968, 1970, 2003; Gao *et al.*, 2018). Short, curved oothecae, with varying numbers of egg chambers and a noticeable keel, have been associated with Cretaceous cockroaches (Hinkelman, 2019), demonstrating little morphological change in 100 million years. Ovoviviparous cockroaches belonging to extant Blaberidae, however, developed soft, flexible oothecae with numerous egg chambers, but lacking the characteristic keel of other cockroach groups. Although at first glance these egg cases exhibit similarities with those of Mantodea, in closer detail some differences arise: first, the width of the ootheca in cockroaches remains highly consistent along its full length, whereas in mantids they are usually wider in the proximal or middle sections; second, a residual process at the distal end of the ootheca has not been found in cockroaches, while it is typical of mantid oothecae; lastly, and most importantly, since the hatching of eggs in the Blaberidae occurs inside the brood sac of the carrying female, there is no distinct emergence area; whereas in mantids, hatching of the eggs occurs through a well-delimited emergence area in the ootheca, in the open environment.

Oothecae composition. The chemical composition of the oothecae is another feature that has been utilized to further characterize the suborders within extant Dictyoptera; however, there have been few studies on this topic (Roth & Willis, 1954; Hackman & Goldberg, 1960; Stay *et al.*, 1960; Kramer *et al.*, 1991; Courrent *et al.*, 2008). The ootheca is formed from the secretions of the colleterial glands, part of the reproductive apparatus in the females (Pryor, 1940; Hackman & Goldberg, 1960; Roth, 1968; Courrent *et al.*, 2008). In cockroaches, the secretions of these glands produce quinone, the hard, dark tannin that covers the oothecae, but no chitin. This chemical compound acts as a sex pheromone; however, it is also considered that quinone helps in the sclerotization of the oothecae (Pryor, 1940). Besides quinone, the oothecae of oviparous cockroaches have high concentrations of calcium oxalate crystals, which would add to the structural rigidity similar to that of chitin in other insects (Hackman & Goldberg, 1960). The ovoviviparous cockroaches (Blaberidae) are once again an exception, lacking all calcium oxalate content in their oothecae. Both, the loss of the keel and the lack of calcium oxalate crystals in Blaberidae are considered adaptations that give flexibility to allowing for the retraction of the oothecae into the brood sac to internally incubate the eggs (Roth, 1968).

Even fewer chemical analyses have been done on the oothecae of mantids. As in the Blattodea, mantid oothecae do not contain chitin; however, instead of calcium oxalate, calcium citrate and calcium carbonate crystals have been reported in the oothecae of mantids (Parker & Rudall, 1955; Kato & Kubomura, 1956). A different study on the ootheca of *Orthodera ministralis* Fabricius mantis did not detect the latter compounds, although an elemental composition of mainly nitrogen, calcium, aluminium, silicon and magnesium was observed (Hackman & Goldberg, 1960).

Inferring the chemical compositions through the analysis of adpression fossils is a difficult task, even if there is original organic material present. The fossils recovered from the uppermost levels of the Potrerillos Formation at the Quebrada del

Durazno locality presented in a few cases, well-preserved cuticles, allowing for SEM/EDS for their analysis (Figs. S3–S5). The same technique was applied to three oothecae from a living mantis (Fig. S6) and two extant cockroach species (oviparous vs ovoviviparous; Figs. S7, S8, respectively) for further comparisons (Table 1). Particular note was taken of the presence/absence of calcium, since it is a predominant element in extant cockroach oothecae (calcium oxalate crystals), and has been also noted in some fossils (Roth, 1968; Hinkelman, 2019). As expected from what was observed in previous studies, calcium was present in both the oothecae of mantid and oviparous cockroach, ranging from 2.25 to 4.09%, whereas almost none (0.01%) was detected in the ovoviviparous ootheca (Table 1). Regarding the fossils from the Quebrada del Durazno locality, with the exception of a meagre 0.04 and 0.08% measured at the egg chamber spots on IANIGLA-PI 3132 and 3136, respectively (Figs. S4, S5), none of the fossil oothecae yielded any calcium values at all (Table 1). Therefore, the presence of calcium cannot be used here as a defining characteristic that could assist in elucidating the taxonomic affinities of these fossils.

Since the elemental analysis of the composition in our fossils did not provide useful comparisons with extant examples of mantid and cockroaches oothecae, any inferences about the affinities of these egg cases must be confined to physiognomical analyses. The absence of the typical keel, and most importantly, the presence of a defined emergence area in both ichnospecies described here differ considerably from the oothecae of most fossil and extant cockroaches (Roth, 1968; Gao *et al.*, 2018; Hinkelman, 2019). The ascription of these fossils to representatives of Blaberidae or an unknown basal ovoviviparous blattoid seems remote, since ovoviviparity is considered an advanced trait in cockroaches (Roth, 1968, 1970, 2003), and the robust cuticle in the fossils is in contrast to the soft, internally born oothecae seen in ovoviviparous species. The numerous isolated egg cases assigned to † *Oothecichnus duraznensis* ichnosp. n. found at the Quebrada del Durazno also points to an oviparous producer; the presence of an ovoviviparous taxon would imply the retraction and posterior internal incubation of the oothecae in the female's body where the young hatch (Roth & Willis, 1954), reducing their chances of fossilization (see also Anisyutkin *et al.*, 2008). On the other hand, the different shapes (elongate vs obovate), attachment modes (proximal end vs ventral), the defined dorsal openings of the emergence area arranged in a distinctive alternating, zigzag pattern, and in a few cases, the residual processes observed in our fossils, are comparable to those of some extant mantid oothecae (e.g. *Creobroter* sp., Fig. 1C, D, or *Stagmomantis* sp., Fig. 2F) (Rivera & Svenson, 2016), and these variations suggest the presence of two different species at the Quebrada del Durazno.

Even though the general structure exhibited in our oothecae resembles more closely to those of Mantodea rather than Blattodea, a conclusive determination about the producers of these egg cases beyond Dictyoptera will not be possible until direct evidence of body parts from individuals belonging to either of these groups (or new evidence of the production of ootheca in another insect group), is found at the Quebrada del Durazno locality. Nevertheless, the possibility of these fossils belonging to Mantodea is not inconceivable, as we will discuss below.

Implications for the origin of Dictyoptera

There is presently no consensus about the morphological features that can be used to distinguish between basal ("stem" or primitive) and advanced ("crown" or modern) fossil Dictyoptera, and the same applies for its suborders (Hörnig *et al.*, 2013; Evangelista *et al.*, 2017). This has led to conflicting interpretations about the timing of the origins and diversification of the clade. In addition, age estimates have been obtained from molecular phylogenies that have in some cases utilized taxonomically questionable fossils (e.g. wings; see discussion in Evangelista *et al.*, 2017) as calibration points (Klass, 2001; Béthoux *et al.*, 2010; Gorochov & Гороxov, 2013; Hörnig *et al.*, 2013; Legendre *et al.*, 2015).

Numerous studies have estimated the origin of dictyopteran taxa, with ages ranging from the Late Paleozoic to Mesozoic. For example, a Paleozoic origin of Mantodea was proposed based on features of the forewing venation described in Carboniferous and Permian strephocladid (Polyneoptera) insects (Béthoux & Wieland, 2009; Béthoux *et al.*, 2010); whereas others suggested a late Carboniferous origin stemming from blattoids (Kukalová-Peck, 1991). Such hypotheses have been strongly opposed by other authors, who have maintained that basal mantises show a well defined transition from the Liberiblattinidae, implying that the origin of Mantodea could not have occurred earlier than the Mesozoic, and also, that they stemmed from ancient cockroaches (Vršanský *et al.*, 2009; Vršanský, 2010; Gorochov & Гороxov, 2013). Other studies in which cockroaches with long ovipositors were considered to be crown-Dictyoptera, yielded the latest Carboniferous (~300 mya) age estimate for the split between Mantodea and Blattodea (Svenson & Whiting, 2009), and either a Triassic/Jurassic (~200 mya) or Late Jurassic (~150 mya; Legendre *et al.*, 2015) appearance of crown-Mantodea. If the Paleozoic roachoids with long ovipositors are assumed to be stem-Dictyoptera instead, the age estimated for the split of Blattodea and Mantodea is sometime between the Middle Permian (~263 mya; Evangelista *et al.*, 2019) and Middle Triassic (~243 mya; Wang *et al.*, 2017), with crown-Blattodea appearing in the latest Triassic (~205 mya; Evangelista *et al.*, 2019). Based on the fossil evidence gathered so far, other researchers have proposed overall younger age estimates for the origins of dictyopteran taxa, assuming a Middle Jurassic origin for crown-Blattodea (Vršanský, 2000, 2002, 2010; Vršanský *et al.*, 2002; Grimaldi & Engel, 2005), or even a Cretaceous age for the origins of both Blattodea and Mantodea (Gao *et al.*, 2018; Hörnig *et al.*, 2018; Evangelista *et al.*, 2019; Hinkelman, 2019).

It is clear that fossils utilized to calibrate nodes in phylogenetic analyses must be carefully selected, preferably using only those for which taxonomically diagnostic characters are clearly identified. The discovery of the oothecae described here, makes a critical contribution to the fossil record, as these structures are considered a distinctive derived feature of the Dictyoptera

(Grimaldi & Engel, 2005). They represent the oldest indisputable evidence of modern dictyopteran taxa, from the early Late Triassic. Despite the overall mantodean morphological similarities of the oothecae, and even though some phylogenies do not rule out the possibility of their presence this early (or even earlier) in the fossil record, these fossils alone cannot be used to conclusively demonstrate the presence of mantids at the Quebrada del Durazno locality or a Triassic origin for the group. Our findings are; however, the first concrete evidence supporting the presence of crown-Dictyoptera in the Carnian, and as such, they provide a definite calibration point for use in future phylogenetic analyses.

Ecological importance of the ootheca

As a compound structure that offers offspring of a stable place to develop safely, the ootheca provides protection against environmental disturbances, potential predators, microorganisms and parasitoids (Goldberg *et al.*, 2015; Gao *et al.*, 2018).

Our fossil oothecae, recovered from the upper levels of the Potrerillos Formation, were found in association with a diverse and typical Gondwanan *Dicroidium* flora and profuse invertebrate fauna (Lara *et al.*, 2017) (Fig. 4). Based on paleomagnetic pole reconstructions, the Quebrada del Durazno locality was located in the middle latitudes (∼45°S), in the extratropical belt of Gondwana. The sedimentary analysis supports a deltaic environment with semi-permanent ponds developing under locally temperate to warm, humid conditions, but affected by the megamonsoonal climate of the Late Triassic (Lara *et al.*, 2017). As a consequence, dry seasons would have alternated with more humid ones. In such circumstances, the laying of eggs in an ootheca would have been a strongly advantageous strategy for protection against desiccation (Goldberg *et al.*, 2015). The pore-like structures described in these fossils (Fig. 2K, L) would have served to maintain a stable water balance in a fluctuating paleoenvironment, such as the one at the Quebrada del Durazno (Keller, 1998; Lara *et al.*, 2017; Hinkelman, 2019).

Conclusions

The two new ichnospecies described here – † *Oothecichnus pensilis* ichnosp. n. and † *Oothecichnus duraznensis* ichnosp. n. – are the earliest fossil evidence of oothecae, predating by 100 million years any previously known records of this reproductive strategy. Morphological comparisons of these structures with both fossil and extant oothecae from Blattodea and Mantodea, show closer similarities with the latter group; but the current lack of direct evidence of dictyopteran body fossils from the Quebrada del Durazno locality, prevents an unequivocal systematic assignation.

As an exclusive diagnostic feature of Dictyoptera, these oothecae represent fossils of significant phylogenetic importance, with implications for the origins of and relationships between

Fig 4. An artistic interpretation of the Quebrada del Durazno site (based on Lara *et al.*, 2017), with a hypothetic crown-Dictyopteran laying its ootheca on *Dicroidium* foliage (Paleoartistic reconstruction by M. Charnelli). [Colour figure can be viewed at wileyonlinelibrary.com].

the disparate suborders Mantodea and Blattodea. Interpretations of the cladogenesis of Dictyoptera remain disputed in part due to the sparse pre-Cretaceous fossil record of its suborders and the taxonomic uncertainties of alleged stem-dictyopterans. To date it has been assumed that the common ancestor of dictyopterans with a reduced ovipositor originated at the earliest in the Early Jurassic; the discovery of Triassic oothecae radically changes this view and reinforces previous hypotheses that place the crown-Dictyoptera earlier in the timescale. It is beyond the scope of this paper to discuss the phylogenetic relationships within Dictyoptera since most of the character sampling involves the analysis of wings and body parts, presently lacking at the Quebrada del Durazno locality. However, these fossils provide an indisputable calibration point that confirms the reduction and/or internalization of the ovipositor and the strategy of laying eggs in the form of an ootheca (an inherent trait of Dictyoptera) featured present at least since the early Late Triassic (Carnian).

Author Contributions

All authors participated in the fieldwork and collected the specimens for the study; B. Cariglino and M. B. Lara conceived the project and wrote the text; B. Cariglino photographed the specimens and organized the figures; M. B. Lara drafted the figures; A. M. Zavattieri provided the geological and sedimentological information on the fossil locality.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Supplemental Information.

Fig. S1. Aerial view of the uppermost levels of the Potrerillos Formation at the Quebrada del Durazno locality (Cuyo Basin), in Mendoza province, Argentina.

Fig. S2. General ootheca morphology. (a–c) Schematic representation of oothecae in (a) dorsal view, based on IANIGLA-PI 3130, (b) ventral view, based on IANIGLA-PI 3134, (c) lateral view, based on IANIGLA-PI 3131. (d) Internal(?) view of specimen IANIGLA-PI 3135 showing the egg chamber wall partitions. (e) Specimen IANIGLA-PI 3139, attributable to † *Oothecichnus pensilis* ichnosp. n. Note that despite it is detached, a fragment of plant stem is closely associated (lower right of picture).

Fig. S3. Scanning Electron Microscope and X-ray Energy Dispersive Spectroscopy analysis of the cuticle extracted and isolated from specimen IANIGLA-PI 3129. (a) Specimen with cuticle before its extraction for analysis. (b, d–g) Spot analysis of emergence area. (c, h–k) Spot analysis of egg chambers zone.

Fig. S4. Scanning Electron Microscope and X-ray Energy Dispersive Spectroscopy analysis of specimen IANIGLA-PI 3132. (a, b) Specimen's images, showing the selected preferential spots in (b). (c, e–h) Spot analysis of emergence area. (d, i–l) Spot analysis of egg chambers zone.

Fig. S5. Scanning Electron Microscope and X-ray Energy Dispersive Spectroscopy analysis of specimen IANIGLA-PI 3136. (a, b) Specimen's images, showing the selected spots in (b). (c, e–h) Spot analysis of preserved cuticle. (d, i–l) Spot analysis on an area with few remains of the cuticle (note cuticle in strong red colour in [k]).

Fig. S6. Scanning Electron Microscope and X-ray Energy Dispersive Spectroscopy analysis of extant praying mantis ootheca (species unknown). (a–c) Specimen's selected spots. (d, f–i) Spot analysis of emergence area. (e, j–m) Spot analysis of the distally preserved residual process.

Fig. S7. Scanning Electron Microscope and X-ray Energy Dispersive Spectroscopy analysis of extant oviparous cockroach oothecae (species unknown) (a–k). (a) Specimen's selected spots. (b, d–g) Spot analysis of dorsal keel. (c, h–k) Spot analysis of the egg chambers zone.

Fig. S8. Scanning Electron Microscope and X-ray Energy Dispersive Spectroscopy analysis of extant ovoviviparous cockroach ootheca (a–k) (*Blaptica dubia* Serville) (a) Specimen in dorsal and lateral views. Note lateral egg chamber breakage and potential egg (arrow). (b, d–g) Spot analysis

of the dorsal area. (c, h–k) Spot analysis of the egg chambers zone.

Data availability statement

The data that support the findings of this study are available in the supplementary material of this article.

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