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THE HATCHING MECHANISM OF 130-MILLION-YEAR-OLD INSECTS: AN ASSOCIATION OF NEONATES, EGG SHELLS AND EGG BURSTERS IN LEBANESE AMBER

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Abstract: Hatching is a pivotal moment in the life of most animals. Diverse chemical, behavioural and mechanical methods have evolved in metazoans to break the egg membranes. Among them, many arthropod and vertebrate embryos hatch using ephemeral, frequently convergent structures known as egg bursters. However, the evolutionary processes by which hatching mechanisms and related embryonic structures became established in deep time are poorly understood due to a nearly complete absence from the fossil record. Herein we describe an exceptional *c.* 130-million-year-old association in Lebanese amber composed of multiple neonate green lacewing larvae, *Tragichrysa ovoruptora* gen. et sp. nov. (Neuroptera, Chrysopoidea), and conspecific egg remains. Egg bursters with a serrated blade bearing a short process are attached to three longitudinally split egg shells. Embryos of extant green lacewing relatives (Chrysopidae) utilize this egg burster morphotype to open a vertical slit on the egg, after which the burster is moulted and left joined to the empty egg shell. Additionally, the new larval species has extremely elongate dorsal tubercles, an adaptation to carry exogenous debris for protection and camouflage also known from other Cretaceous chrysopoids but absent in modern relatives. The present discovery demonstrates that the hatching mechanism of modern green lacewings was established in the chrysopoid lineage by the Early Cretaceous and proves through direct fossil evidence how some morphological traits related to hatching and linked behaviours, at least in insect embryos, have been subject to a high degree of evolutionary conservatism.

Key words: hatching, egg burster, fossil insects, Neuroptera, Cretaceous, amber.

Hatching is a universal process in animals by which an embryo emerges from various encapsulating egg membranes (Oppenheim 1973). This can occur at different developmental stages which can substantially differ even between closely related species (Warkentin 2011). Hatching usually entails a suite of physiological, morphological and/or behavioural mechanisms acting together. The secretion of enzymes that dissolve the egg membranes is one of the most generalized hatching methods across metazoans (Yamagami 1981). Other mechanisms involve the osmotic entrance of water into the egg due to the secretion of chemicals or the active swallowing of air or amniotic fluid by the embryo, both resulting in an increased internal egg pressure and finally bursting of the membranes (Sikes & Wigglesworth 1931).

Mechanically, the embryo can assist hatching by muscular action or using structures such as the mouthparts, for instance grinding the egg membranes with the radula in gastropods or chewing them with the mandibles in some insects (Davis 1961; Hinton 1981). However, specialized structures for cutting, piercing or tearing the egg membranes present in the embryo tend to disappear soon during post-embryonic life can be used. These can be referred to as egg bursters (EBs) and have received different names depending on the group; for example, egg-

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teeth, caruncles, hatching spines or oviruptor/ruptor ovi, among others (Hermyt *et al.* 2017). In a wide diversity of insects, including the Neuroptera, the EB is frequently shed with the embryonic cuticle on hatching, leaving it attached to the empty egg shell (Kobayashi & Suzuki 2016). As EBs are present in different metazoan phyla (i.e. chordates, arthropods and a few molluscs) and known to have multiple embryonic origins and anatomic positions, their morphofunctionally convergent nature is not questioned (Oppenheim 1973; Beutel 1994; Wang *et al.* 2017). However, regardless of the fact that EBs have been studied for more than a century, their evolution is still far from being understood (Mashimo *et al.* 2014). This lack of knowledge is largely due to the fact that the fossil record of EBs is almost entirely lacking, which is certainly not aided by the small size and relatively ephemeral nature of these structures. Indeed, the only previous fossil records of EBs were limited to tetrapods, that is, 'egg-tooth-like' structures in several titanosaur embryonic premaxillaries from the Upper Cretaceous of Argentina (García 2007) and a highly dubious 'egg-tooth' reported in a mesosaur embryo from the Permian of Uruguay (Piñeiro *et al.* 2012).

Within the staggering modern diversity of holometabolous insects, the superorder Neuropterida, including snakeflies (Raphidioptera), alderflies and dobsonflies (Megaloptera), and lacewings, antlions and relatives (Neuroptera), accounts for one of the so-called minor radiations, with almost 6000 extant species (Engel *et al.* 2018). However, both the past diversity and disparity of the group (known since the Permian) was greater than it is today (Engel *et al.* 2018). With about 1400 known living species, green lacewings (Neuroptera, Chrysopidae) are the second most speciose of the 20 living neuropterid families currently recognized, and one of the most studied non-social insect groups from an ecological standpoint due to the prominent role that their predatory, often debris-carrying (camouflaging) larvae have in biological pest control (McEwen *et al.* 2001). The fossil record of green lacewing immatures is scarce and only known from amber (see Pérez-de la Fuente *et al.* 2012, 2018*a*; Liu *et al.* 2016, 2018; Wang *et al.* 2016).

Here we present a fossil assemblage composed of nine neonate green lacewing larvae bearing extremely elongate setose tubercles and therefore of the debris-carrying (camouflaging) morphotype. The neonates are preserved together with 12 conspecific egg shell (= chorion) remains, three of which bear the EBs that the lacewing embryos used to crack a longitudinal slit in the egg and hatch. This extraordinary association has allowed us, for the first time, to elucidate the hatching mechanism of a long extinct organism through multiple, direct evidence. Previously, only an isolated fossil larva, originally described as a chrysopid but most parsimoniously assignable to beaded lacewings (Berothidae) (Wedmann *et al.* 2013) was known to be associated with any egg remains, although EBs were not described from the single preserved chorion (Engel & Grimaldi 2008). The studied assemblage is included in Early Cretaceous (early Barremian) Lebanese amber, representing the oldest amber known providing abundant biotic inclusions (Azar *et al.* 2010), and was originally contained in a single amber piece that was divided into three different preparations for improved visibility.

MATERIAL AND METHOD

The specimens were isolated within small amber pieces by removing most of the surrounding amber, and then prepared between two circular cover slips in Canada balsam medium (Azar *et al.* 2003). The original relative arrangement of each preparation in the amber piece from which they were isolated is unknown. Preparation NHMLU-AC S-7 contains six larvae (four of them complete, NHMLU-AC S-7a, S-7b, S-7c and S-7d, plus two partially preserved, S-7e and S-7f) and four semicomplete egg chorions (plus traces of three more); preparation NHMLU-AC S-1 has two complete larvae (NHMLU-AC S-1d and S-1e) and three semicomplete egg chorions (with traces of at least two more eggs); and preparation NHMLU-AC S-2 contains an isolated specimen lacking the distal part of the tubular tubercles and without associated egg remains. Preparation NHMLU-AC S-7 has a fracture that transversally cuts three of the larvae, and S-1 shows another fracture that affects one specimen.

A Discovery.V12 Zeiss stereomicroscope, and two compound microscopes (an Olympus BX51 and a Zeiss AXIO) were used to study the specimens in the two views that each preparation permits. Specimens were drawn using a drawing tube Olympus U-DA attached to the Olympus BX51 and were photographed using an Axiocam 105 colour digital camera attached to both the stereomicroscope and the Zeiss AXIO. Extant, hatched chrysopid eggs arranged in two clusters of about 20 eggs each were imaged for comparison. Each individual egg has its stalk glued together with the others in each cluster and its base attached to a bark fragment. The egg clusters belong to an undetermined chrysopid species and they are held at the Life Collections of the Oxford University Museum of Natural History, Oxford, UK, labelled 'Ex. Hope-Westwood colln. Pres 1849–1857 OX.UNI.MUS.NAT.HIST. (OUMNH).'

Nomenclature used for the larval descriptions follows that of C.A. Tauber and co-workers (e.g. Tauber *et al.* 2014). Measurements provided are taken from the holotype (except for tubercle setae).

SYSTEMATIC PALAEONTOLOGY

Class INSECTA Linnaeus, 1758
Order NEUROPTERA Linnaeus, 1758
Superfamily CHRYSOPOIDEA Schneider, 1851
Family INCERTAE SEDIS

Genus TRAGICHRYSA nov.

LSID. urn:lsid:zoobank.org:act:39A05937-623B-4C64-9C1B-A0F3DA0299AD

Derivation of name. Latin *tragicum* (= dramatic), after the entrapment of multiple specimens together, and *chrysa* (gender: feminine), a traditional stem to chrysopoid genus-group names.

Type species. Tragichrysa ovoruptora sp. nov.

Diagnosis (immature, first instar). Cephalic capsule subsemicircular. Antennae about as long as the mandibulomaxillary stylets. Antennal flagellum short, constant in diameter and with an elongate terminal bristle. Palpi rather stout, distal palpomere slightly swollen at midlength and terminating in a cylindrical papilla. Prothorax lacking tubular tubercles (TT); mesothorax with lateral and laterodorsal TT pairs; metathorax only with a lateral TT pair. TT pairs present on abdominal segments 2–5, lateral in position; abdominal segment 4 bearing additional pair of TTs, dorsolateral in position. TT setae lacking morphological specializations. Pretarsal claws mildly recurved, lacking basal expansions.

Tragichrysa ovoruptora sp. nov.
Figures 1–5

LSID. urn:lsid:zoobank.org:act:103FD874-9838-4322-86DF-BC459BB239AF

Derivation of name. A combination of the prefix *ovo-* (derived from the Latin *ōvum* = egg) and the Latin *ruptor* (= breaker), following the EBs associated with the specimens of the new species.

Type material. Holotype NHMLU-AC S-7a. Paratypes NHMLU-AC S-7b, S-7c, S-7d; NHMLU-AC S-1d and S-1e; NHMLU-AC S-2. Additional material: NHMLU-AC S-7e, S-7f. All specimens are deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II (Azar Collection), Fanar (abbreviated to NHMLU-AC). All specimens originally belonged to the same amber piece, which was divided into three preparations (i.e. NHMLU-AC S-1, NHMLU-AC S-2 and NHMLU-AC S-7).

Diagnosis (immature, first instar). As for genus (see above).

Description. First instar larva. Body campodeiform, only slightly gibbous, 1.65 mm long (excluding mandibulomaxillary stylets). Cephalic capsule subsemicircular, rather short, 0.41 mm wide, 0.27 mm long; frons barely concave. Mandibulomaxillary stylets recurved, 0.43 mm long, with several sensillae; coupling structures absent. Labial palpi stout, 0.26 mm long; basal palpomere shortest, with a few setae; medial and distal palpomeres subequal in length, 0.10 mm long, without annulations; medial palpomere with a long seta dorsodistally; distal palpomere slightly swollen at midlength, bearing a terminal cylindrical papilla. Antenna about as long as mandibulomaxillary stylets; scape elongate, 0.05 mm long; pedicel cylindrical, 0.28 mm long; flagellum rather stout (not filiform), 0.08 mm long, constant in diameter, surface regularly annulated; flagellum with a very long bristle, 0.23 mm long. Ocular tubercles not prominent, distolaterally on cephalic capsule, with six stemmata. Cephalic setae relatively short, at least five emerging from lateral sides of head, curving anteriorly; some elongate setae present on longitudinal head axis. No apparent colour patterns or epicranial marks preserved.

Elongate, setigerous TTs present on meso and metathorax (lacking on prothorax) and abdominal segments 2–5. TTs setose on their distal half. TT setae emerging from tuberculate bases, without serrations or specialized apices, not especially tapering apically, up to *c.* 0.20 mm long. Chalazae not distinct. Mesothorax with lateral and laterodorsal TT pairs, 0.65–0.80 mm long, 0.03–0.04 mm thick; metathorax with only a lateral TT pair. Legs relatively large and robust; prothoracic leg 0.92 mm long (coxa 0.12 mm, trochanter 0.07 mm, femur 0.27 mm, tibia 0.33 mm, tarsus 0.13 mm); mesothoracic leg 0.99 mm long (0.15, 0.06, 0.29, 0.35, 0.14 mm); metathoracic leg 1.13 mm long (0.15, 0.07, 0.29, 0.45, 0.17 mm). Trochanters without a conspicuous process. Ratio tarsus/tibia length *c.* 0.4. Tibiae with two larger setae ventrodistally. Pretarsal claws mildly recurved, without basal expansions. Trumpet-shaped empodia well developed, 0.09 mm long. Pulvilli absent.

Abdominal segments 2–5 with TT pairs in lateral position, slightly shorter and thinner than thoracic TTs. Abdominal segment 4 with an additional pair of smaller TTs, less than half as long as lateral TTs, dorsolateral in position. Abdominal segments 6–10 without TTs, subcylindrical, gradually becoming narrower and more elongate. Abdominal segments 6–9 with brief distolateral projections bearing a few setae, perhaps corresponding to weakly developed setose tubercles.

Egg remains half ellipsoid as preserved, 0.60 mm long as preserved, 0.42 mm in diameter (Fig. 3A–C). Colour uniform. Chorion without macro-ornamentation but finely granulate (Figs 3G, 4C). Disk-like micropylar area located at centre of egg pole; diameter 0.04 mm, height 0.02 mm, apparently darker (Fig. 3A–C). Egg burster 0.14 mm long; anterior process short, triangular, straight, with about six irregular serrations, 0.04 mm long (Fig. 3D–F). Some chorions with further internal contents, probably embryonic moults, but structures not distinctive (Fig. 3C).

FIG. 1. *Tragichrysa ovoruptora* gen. et sp. nov. neonate larvae and associated egg remains, photograph and drawing. Preparation NHMLU-AC S-7, bearing six specimens (a–f, NHMLU-AC S-7a–f) including the holotype (NHMLU-AC S-7a) and remains of seven eggs. This preparation (together with NHMLU-AC S-1 (Fig. 2) and NHMLU-AC S-2 (Fig. 4D)) originally belonged to the same amber piece. Egg remains are depicted in grey and each is marked with an asterisk. The numbers 1 and 2 refer to details shown in Figure 3A and G. The head of specimen NHMLU-AC S-7e (partially preserved) has not been depicted for clarity and is visible from the opposite angle. Scale bar represents 1 mm.

Locality and age. Early Cretaceous, early Barremian (Maksoud *et al.* 2017), Sarhmoul, Caza Aley, Mohafazat Jabal Loubnan, Central Lebanon (Azar *et al.* 2003).

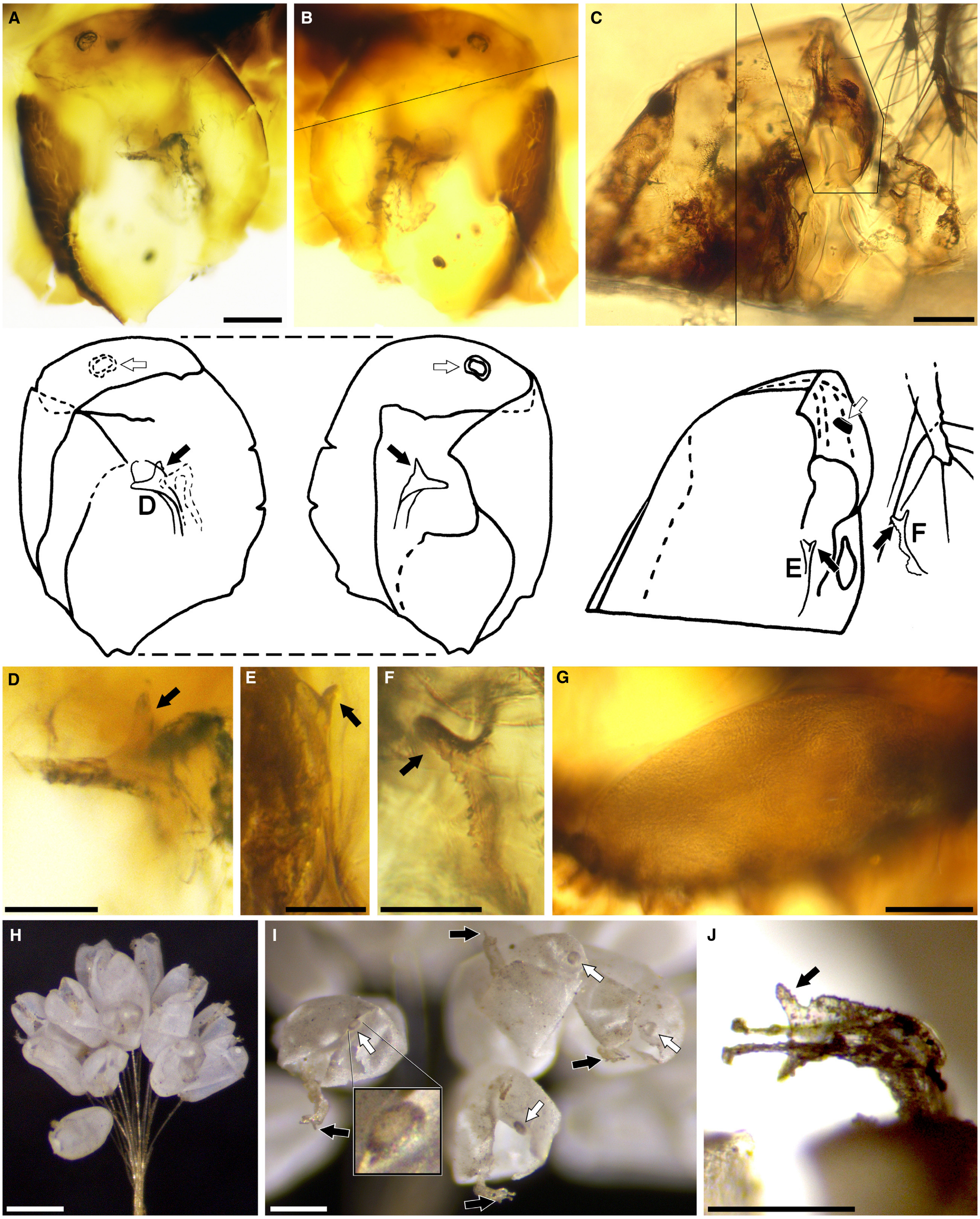
DISCUSSION

Some modern green lacewing (Chrysopidae) larvae are debris carriers; they camouflage and protect themselves using a self-gathered accumulation of exogenous elements, or debris packet, retained among setose dorsal tubercles (McEwen *et al.* 2001; Tauber *et al.* 2014). *Tragichrysa ovoruptora* gen. et sp. nov. fits this morphotype due to the presence of setose tubular tubercles (TTs) on its dorsum. These extremely elongate tubercles are only known from Cretaceous debris-carrying chrysopoids, including *Hallucinochrysa diogenesi*, the first named

FIG. 2. *Tragichrysa ovoruptora* gen. et sp. nov. neonate larvae and associated egg remains, photograph and drawing. Preparation NHMLU-AC S-1, bearing two specimens (d–e, NHMLU-AC S-1d and S-1e) and the remains of five eggs. This preparation (together with NHMLU-AC S-7 (Fig. 1) and NHMLU-AC S-2 (Fig. 4D)) originally belonged to the same amber piece. Egg remains are depicted in grey and each is marked with an asterisk. Antennal annulations have only been depicted in NHMLU-AC S-1d. The number 3 refers to a detail shown in Figure 3C. Scale bar represents 0.5 mm.

species of this kind (Pérez-de la Fuente *et al.* 2012, 2018*a*; Wang *et al.* 2016). Indeed, TTs are absent in extant green lacewing larvae, in which setose tubercles are never as dramatically elongate. This characteristic is the primary reason why *T. ovoruptora* and other Cretaceous chrysopoid larvae are tentatively not classified in Chrysopidae and left unplaced at the familial level. *Tragichrysa ovoruptora* is distinct from the only previously known fossil neonate described as a green lacewing (known from Canadian amber and clutching to the egg from which it probably emerged; Engel & Grimaldi 2008) in the morphology of the head and the mandibulomaxillary stylets as well as the lack of distinct setose tubercles in the latter taxon. These features actually more consistently place that specimen within beaded lacewings (Berothidae) (see Wedmann *et al.* 2013). The new species also clearly differs from *H. diogenesi* (an advanced instar), in the morphology of the head (subsemicircular vs banana-shaped), the antennae (about as long as the mandibulomaxillary stylets vs clearly longer and filiform), the labial palpi (rather stout, with terminal palpomere swollen at the middle vs very gracile, with terminal palpomere slightly club-shaped), the claws (without laminar basal expansions in *T. ovoruptora*), and the TT setae (lacking specialized setal endings in the new species, with trumpet-shaped endings in *H. diogenesi*) (Pérez-de la Fuente *et al.* 2012). *Tragichrysa ovoruptora* could have been the immature form of one of the multiple chrysopoid lineages described from the Cretaceous based on adult material (Nel *et al*. 2005). In any case, more records and descriptions of Cretaceous larval chrysopids with TTs are needed to determine the phylogenetic relationships among stem-groups of modern chrysopids.

All of the specimens represent first instars (neonates) due to their morphology when compared to more advanced chrysopoid instars (Pérez-de la Fuente *et al*. 2012, 2018*a*; Wang *et al*. 2016): the relatively large size of



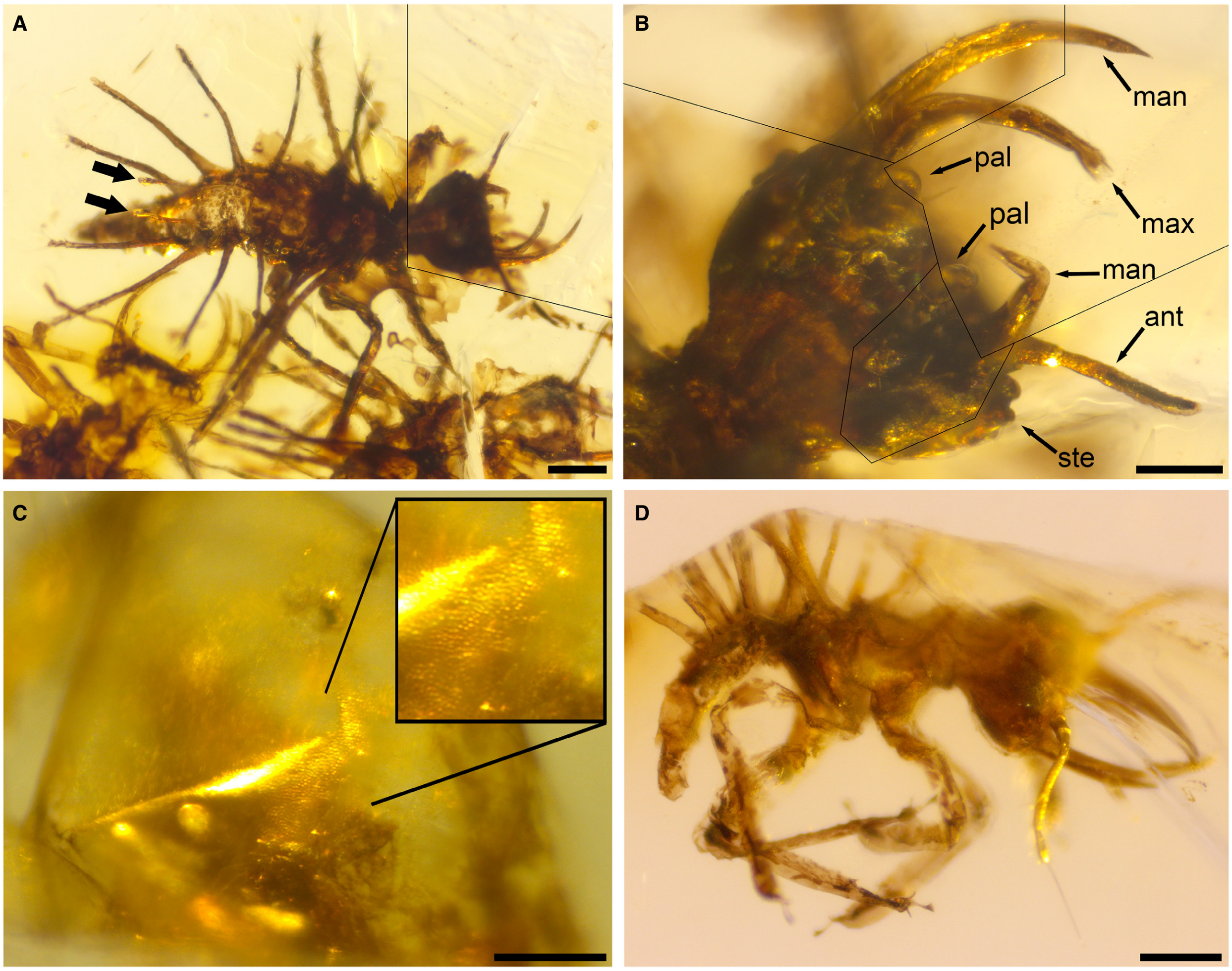


FIG. 4. Morphological details of *Tragichrysa ovoruptora* gen. et sp. nov. and associated egg chorions, and habitus of the isolated paratype specimen. A, dorsal habitus of NHMLU-AC S-7a, holotype of *T. ovoruptora*; arrows indicate the additional pair of tubular tubercles present in abdominal segment 4, dorsolateral in position. B, detail of head of the holotype (NHMLU-AC S-7a) in ventral view, showing the dislodged mandibles and maxillae that form the sucking stylets when conjoined. C, microsculpturing of egg chorion preserved in preparation NHMLU-AC S-1, marked as 3 in Figure 2. D, habitus of paratype NHMLU-AC S-2, a specimen prepared in isolation and without associated egg remains. *Abbreviations*: ant, antenna; man, mandible; max, maxilla; pal, labial palp; ste, stemmata (eyes). Scale bars represent: 0.2 mm (A, D); 0.1 mm (B, C).

head, legs, antennae, flagellar bristle and palps, the low TT development and setation, and the only slightly gibbous body. Moreover, in half of the *T. ovoruptora* specimens the maxillary and mandibular mouthparts that form the stylets when conjoined are not yet fully interlocked to form functional sucking, predatory stylets

FIG. 3. Egg remains associated with *Tragichrysa ovoruptora* gen. et sp. nov. larvae and comparison with extant green lacewing hatched eggs. Black arrows indicate the anterior process of the egg burster from its anterior (serrated) edge. White arrows indicate the disk-like micropylar area of the egg chorion. A, photograph and drawing of remains of egg marked 1 in Figure 1; a distal portion of an egg chorion showing micropylar area and egg burster attached to chorion. B, same as A but seen from the opposite side. C, photograph and drawing of remains of two eggs marked 3 in Figure 2, representing the distal portions of egg chorions showing one micropylar area and two egg bursters, each attached to a chorion. D, detail of egg burster shown in A, in frontolateral view. E, detail of first egg burster shown in C, in ventrolateral view. F, detail of second egg burster shown in C, in dorsolateral view; note the dorsal serrations. G, egg chorion marked as 2 in Figure 1, showing microsculpturing (surface ornamentation). H–J, Recent cluster of hatched green lacewing eggs with details; I, four micropylar (distal) poles of egg chorions showing disk-like micropyles (including inset) and egg bursters, in different views; J, detail of an egg burster, in lateral view. Scale bars represent: 0.1 mm (A–C, G, J); 0.05 mm (D–F); 0.5 mm (H); 0.2 mm (I).

FIG. 5. Reconstruction of two *Tragichrysa ovoruptora* gen. et sp. nov. neonates clutching the eggs from which they hatched. This behaviour typically occurs in modern green lacewing neonates while their cuticle hardens and mouthparts become functional. Note that the presence of egg stalks, almost universal in extant chrysopids, remains speculative in the new extinct species as it cannot be determined from the present fossils. Colouration is conjectural and based on modern forms.

(Figs 1, 2, 4B) indicating that these were probably still hardening. New-born chrysopids cling to their egg chorions for hours until their cuticle hardens and mouthparts become operational (Withycombe 1925). Lastly, the absence of debris packet elements on the specimens further suggests that they had recently hatched, as constructing the debris packet appears to be a priority of extant debris-carrying chrysopid neonates, even over feeding (Canard *et al.* 1984).

All but one of the partly preserved egg chorions and traces of additional ones have the same orientation in each amber preparation, respectively, with their poles aligned (Figs 1, 2). This indicates that their original relative position was not significantly altered by resin entrapment, probably because the eggs remained fixed to the substrate. The specimens of *T. ovoruptora* are equally separated from the egg chorions in each respective amber preparation and have their body axes aligned with each other, probably due to a moderately intense drag in the fresh resin.

The size and overall morphology of the egg, the number, morphology and location of the micropyles, and the macro and/or micro-ornamentation of the chorion show a wide diversity in insects, these differences varying sometimes even between closely related species (Hinton 1981). All these characters are clearly diagnostic of the chrysopoid affinity of the studied egg chorions. Recent chrysopid eggs are almost always ellipsoidal in shape, having a single disk-like micropylar area at their distal end (Fig. 3H, I) (Mazzini 1976; Canard *et al.* 1984; Gepp 1990). Chrysopid egg chorions lack the macro-ornamentation found on many insect eggs, including other neuropterids, but have a distinct microsculpturing (Figs 3, 4C) (Mazzini 1976; Canard *et al.* 1984; Gepp 1990). As

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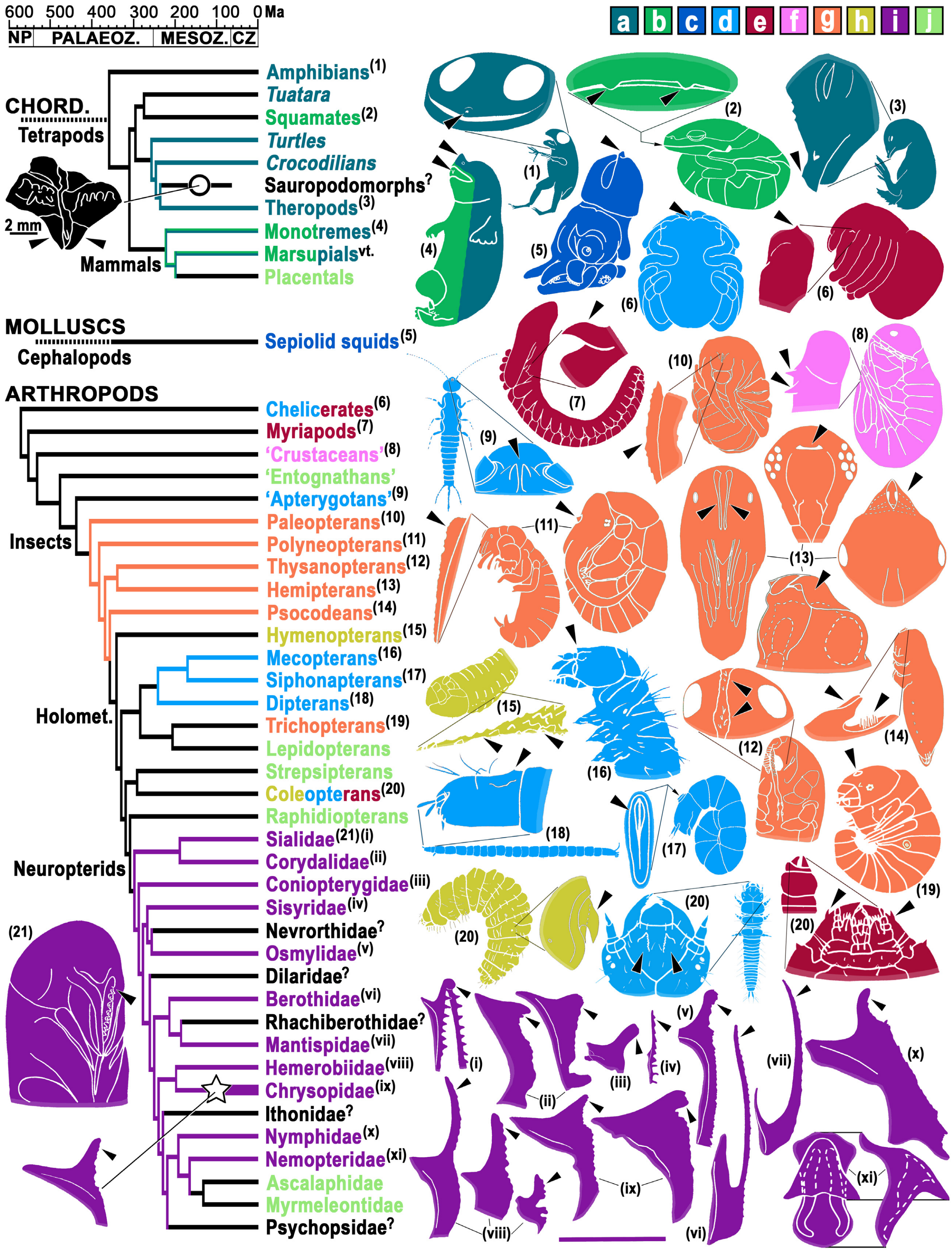
FIG. 6. Occurrence of egg bursters (EBs) across Metazoa, with emphasis on insects and, more particularly, lacewings and relatives (neuropterids, bottom). The only two known fossil records of an EB have been plotted (a Permian tentative record in a mesosaur has been excluded): several titanosaur embryonic premaxillaries from the Upper Cretaceous (Santonian) of Argentina preserving an ‘egg-tooth-like structure’ (circle), and three EBs attached to separate egg chorion remains of *Tragichrysa ovoruptora* gen. et sp. nov. in Early Cretaceous (Barremian) Lebanese amber (star, this report). Taxon names, drawings and some phylogenetic ranges are colour-coded (top right) for the following EB categories, which are not intended to unite homologous structures and may encompass convergences even within Phyla, as the evolutionary history of EBs within and across metazoan groups is not well-understood: a, caruncle (keratinous projection on rostrum); b, true egg-teeth (dentinous origin); c, EB on mantle; d, cephalic (frontal) EB retained by the first instar larva/nymph; e, EB on the anterior appendages (mandibles, maxillae or pedipalps); f, EB on caudal appendages (telson); g, cephalic (frontal or frontoclypeal) EB moulted with embryonic cuticle; h, thoracico-abdominal EB retained by the first instar larva; I, cephalic (labial) EB moulted with embryonic cuticle; j, no EB. Thin coloured lines indicate the alleged presence of EB categories in deep time as informed by phylogenetic inference due to sufficient embryonic/larval knowledge. Thick coloured line indicates the presence of an EB in deep time supported by the fossil record. Question marks show groups in which the presence of an EB is unknown. Paraphyletic groups are shown between quotation marks. Taxon names used *sensu lato* (i.e. including extinct stem-group relatives) are shown in italics. All arrowheads point to the EB; for neuropterids (i–x and *T. ovoruptora*), arrowheads also point to the anterior process of the EB from its anterior (usually toothed) edge. Sources used for the creation of this figure are provided in Pérez-de la Fuente *et al.* (2018*b*). *Abbreviations*: Chord., Chordates; CZ, Cenozoic; Holomet., Holometabolans; Mesoz., Mesozoic; NP, Neoproterozoic; Palaeoz., Palaeozoic; vt., vestigial EB. Scale bar for neuropterids (including *T. ovoruptora*) represents 0.1 mm; other drawings not to scale.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only the micropylar (distal) portions of the egg chorions are preserved in the fossils described herein, the elongate silky stalks typically found in chrysopid eggs proximally, an adaptation to minimize egg predation and parasitism (Canard *et al.* 1984), are not visible (if present). The egg-laying spatial pattern is generally fixed in chrysopid species: most species are known to lay their eggs individually or in loose and small groups (two to six), but some species are known to do so in tighter and larger groups of up to *c.* 40 eggs (Canard *et al.* 1984; Gepp 1990). In the latter, eggs form batches often arranged in more or less defined rows or in clusters in which egg stalks become intertwined (Canard *et al.* 1984; Gepp 1990). Laboratory experiments have demonstrated the importance of larva–egg and larva–larva cannibalism in chrysopids (Duelli 1981; Ye *et al.* 2014), and laying eggs in batches or clusters has been interpreted as an adaptation enhancing larval cannibalism. This behaviour has been hypothesized as favouring the offspring's survival in fluctuating environments, where prey availability is unstable (Duelli 1981; Canard *et al.* 1984). More sophisticated means to provide food reservoirs for the progeny are present in the specialized (trophic) eggs laid by other insects, including neuropterans (Henry 1972; Perry & Roitberg 2006).

In the studied samples, three semicomplete micropylar portions of egg chorions are longitudinally cracked and preserve their respective EBs attached to them in the same fashion as modern chrysopid hatched eggs (Fig. 3). In Neuropterida, the ventral side of the cephalic capsule of the late embryo possesses a toothed EB (Konopova & Zrzavý 2005; Möller *et al.* 2006), which most recent embryological studies regard as labial in origin (Kobayashi & Suzuki 2016). The neuropterid EB is almost always composed of a median plate forming a ventral cephalic 'mask' bearing a serrated single (or paired) blade projecting posteriad (backwards) to a greater or lesser extent (Pérez-de la Fuente *et al.* 2018*b*; Fig. 6). This type of EB probably represents a synapomorphy of the clade Megaloptera + Neuroptera (= Eidoneuroptera), as cephalic EBs known from other insects are always more frontodorsal in position and derive from the frons or the frontoclypeus (Pérez-de la Fuente *et al.* 2018*b*; Fig. 6). Neuropterid hatching embryos almost always use the cephalic EB to crack the egg in a more or less longitudinal slit that goes from the micropylar region of the egg towards the equatorial area. Chrysopid hatching embryos first liberate the dorsum of the head through said slit, subsequently pushing the thorax and abdomen out while the head appendages and legs remain held together within the embryonic moult, partially inside the egg. Once the thorax and most of the abdomen are out of both the egg chorion and the embryonic moult in a C-shape fashion, the appendages become free and the almost hatched neonate arches backward while being only attached to the egg by the tip of its abdomen, finally grasping the chorion with the freshly-hatched legs to liberate the tip of its abdomen (Pariser 1917; Withycombe 1925). During the hatching process, the neuropterid EB is shed with the embryonic moult, which is therefore left associated to the egg chorion (Fig. 3H–J) (Canard *et al.* 1984). This condition is not present in all insects, as EBs can also be retained in first (or even older) nymphal/larval instars (Pérez-de la Fuente *et al.* 2018*b*). The preserved EBs have a single median blade with an anterior process that is triangular in lateral view and relatively short (Fig. 3D–F). This morphology falls within the EB diversity found in modern Chrysopidae (Monserrat & Díaz-Aranda 2012) and distinguishes it from EBs known in the remaining neuropterid families (Pérez-de la Fuente *et al.* 2018*b*; Fig. 6).

The characteristics of the EBs are not as evolutionarily conservative as one would anticipate because of the key ontogenetic role that they play. First, the morphological disparity of EBs is remarkable, and includes piercing or tearing structures, cutting or serrating edges or even bursting eversible membranes (Pérez-de la Fuente *et al.* 2018*b*; Fig. 6). Moreover, EBs have diverse embryonic origins and different anatomical locations within the metazoan head, different appendages or the body. Generally speaking, the morphology and, above all, the location of the EBs (when present) tend to be consistent within groups that are often equivalent to the family rank (Pérez-de la Fuente *et al.* 2018*b*). However, the hatching mechanism can be drastically different between closely-related lineages, namely entailing the loss of the EB. In insects, EBs are known to be absent in major lineages, such as lepidopterans or most brachyceran dipterans (Pérez-de la Fuente *et al.* 2018*b*), or more minor lineages than can go down to species-group level as for example is known to occur in some bombardier and leaf beetles (Erwin 1967; Cox 1988) or in boreid mecopterans (Cooper 1974; Russell 1982). Within Neuroptera, EBs have been lost in owlflies and antlions (clade Ascalaphidae + Myrmeleontidae); the loss in these green lacewing relatives correlates with a substantially different hatching mechanism in these groups in which the egg opens through a transverse circular slit along a weak line that leaves a lid (= operculum), rather than the longitudinal slit mentioned above which lacks a preset area of weakness and is characteristic of the remaining Neuropterida (Pérez-de la Fuente *et al.* 2018*b*). An intermediate, allegedly transitional condition is found in some spoon-winged lacewings (Nemopteridae), where the embryo opens a transverse circular slit in the egg but using an EB, different to that of other neuropterids in that it lacks a median longitudinal blade but instead bears a plate with two denticles oriented transversally (Fig. 6). Further cases of transitioning from an egg-burster mediated hatching to an opercular egg dehiscence, with reduced or lacking EB, are found in stick insects (Phasmatodea) (Mashimo *et al.* 2014). Overall, these losses and transitions, together with the disparity of EB morphologies and embryonic origins, demonstrate how the hatching mechanism can be altered at multiple levels through the course of evolution and thus that its long-term stability in a given lineage should not be taken for granted. Potential selective pressure factors that might explain the change in the hatching mechanism could theoretically include temporal or spatial constraints in embryonic development, as well as changes in oviposition ecology or pattern.

The present fossil assemblage corresponds to a recently hatched egg lay. Indeed, the morphological and taphonomic data noted above indicates that the neonates of *Tragichrysa ovoruptora* were caught together by resin while clutching the eggs from whence they had freshly emerged (Fig. 5). These eggs were laid in a tight group, probably the stereotypical egg-laying pattern of the females of the new species and which could have favoured sibling cannibalism. The preservation as syninclusions of conspecific neonates, longitudinally split chorions, and serrated EBs bearing a short anterior process represents direct evidence of the late embryos of *T. ovoruptora* hatching from the egg through a slit cut from the micropylar region to the egg equator by a cephalic (labial) EB, as occurs in extant green lacewings. It is exceedingly rare to find direct fossil evidence of an early developmental event, particularly one as ephemeral and key as the transition from embryonic to post-embryonic life. This finding demonstrates a *c.* 130-million-year-old stasis in the embryo hatching mechanism in the lineage of green lacewings (Chrysopoidea) and proves the considerable ontogenetic and ethological conservatism to which some embryonic features related to hatching have been subject to, at least in insects. Conservatism is usually the result of long-term stability in local habitats (Hamilton 1978) but this would not be the case for green lacewings. Instead, such bradytely may reflect the early evolution of a successful life strategy not being altered in the succeeding eons. The evolutionary history of egg bursters within and across metazoan groups is complex and largely unknown. Further embryological studies are still required to gain a deeper understanding on the true diversity and variability of egg bursters in the extant fauna, but, above all, increased and targeted palaeontological efforts are needed to detect these ephemeral hatching structures on eggs, embryos and early immature stages from extinct taxa.

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DATA ARCHIVING STATEMENT

Data and additional supporting text for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.bd203r4.

This published work and the nomenclatural acts it contains have been registered in ZooBank: http://zoobank.org/References/0FB0072E-DB2D-48A6-8FDC-DEEE09718692.

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