Evolution of reproductive strategies in dictyopteran insects —clues from ovipositor morphology of extinct roachoids

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Dictyoptera, which comprises cockroaches, termites and mantids, is a quite successful group of insects in evolutionary terms with a long fossil record—roachoid insects were already abundant 315 million years ago in the Carboniferous forests. One of the most remarkable autapomorphies of extant dictyopterans, and possibly a major factor for their persisting success, is the ability to produce oothecae. Despite the robustness of this sort of egg package, fossils of oothecae are very rare, the oldest direct evidences being from the Cretaceous Crato Formation in Brazil (115 mya). The ability to produce oothecae is presumably linked to a specific ovipositor morphology, including a significant length reduction. Hence, ovipositor morphology can indirectly inform about the reproductive strategy of a species. Herein we describe the ovipositor morphology of various fossil forms of dictyopteran insects. Early fossil roachoids, in contrast to the modern forms, possessed a very long and prominent ovipositor, reminiscent of the ovipositor in orthopterans (Ensifera), indicating that these forms laid individual, rather small eggs into a substrate. We present examples from different fossil deposits, which show the entire range of ovipositor morphologies, from very long forms over forms with ovipositors partly reduced in length to modern-appearing morphologies. Most remarkably, different shapes of ovipositors seem to be present in roachoids in the fauna of the 115 million years old Crato Formation—species with long prominent ovipositors co-existed with species with a reduced short and broad ovipositor. Additionally, females that carry oothecae attached to their abdomen indicate a third type of ovipositor: a further reduced ovipositor as seen in modern forms, which already allowed the internal production of oothecae.

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Introduction

There are at least 7570 extant species of blattodeans reported (including 4641 species of cockroaches and 2929 species of termites) (Beccaloni and Eggleton 2013), which are almost ubiquitously distributed, and about 2500 species of mantodeans (2425 in 2013; Zhang 2013). Hence, Dictyoptera, the monophyletic group including these morphotypes, comprises more than 10,000 species, making it a comparatively successful group among non-holometabolous insects.

At present, the consensus scenario of the relationships between these three groups within extant dictyopterans contains Isoptera as sister group of *Cryptocercus* (wood roaches) deeply nested within Blattodea, and Mantodea as the sister group of Blattodea (Lo et al. 2003, 2007; Grimaldi and Engel 2005; Klass and Meier 2006; Inward et al. 2007; Djernæs et al. 2012, 2015; Legendre et al. 2015). Early representatives of Dictyoptera were roach-like in appearance and are therefore referred to as "roachoids" (see Discussion). These latter forms possess a fossil record extending back to at least the Pennsylvanian (e.g., Scudder 1895; Schneider 1978a, b, 1984; Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005; Hörnig et al. 2014).

It is assumed that mantodeans and termites evolved by the Jurassic or early in the Cretaceous (Rasnitsyn and Quicke 2002; Grimaldi 1997, 2003; Grimaldi and Engel 2005; Svenson and Whiting 2009; for different interpreta-

tions see Béthoux and Wieland 2009; Béthoux et al. 2010; discussed in Hörnig et al. 2013; Legendre et al. 2015), hence modern dictyopterans must have evolved before this time. The stem species (more or less equal to the "last common ancestor") of extant dictyopterans evolved a very notable autapomorphy: the eggs were deposited in a kind of package, the so-called "ootheca", which is made of secretions from asymmetrical true accessory glands of abdominal segment nine (e.g., McKittrick 1964; Klass 1998; Bohn and Klass 2003; see also Goldberg et al. 2015 for similarities of oothecae in different insects). This characteristic is shown by all representatives of Mantodea, Blattodea, and one species of Isoptera, *Mastotermes darwinensis* Froggatt, 1897, consensually regarded as sister group to the rest of termites. Indeed all other termites deviate secondarily from this strategy and produce single eggs (Nalepa and Lenz 2000; Courrent et al. 2008; Klass et al. 2008; Wieland 2013).

Genuine fossil oothecae are very rare, with only five specimens in total so far (Grimaldi and Engel 2005; Anisyutkin et al. 2008; Poinar 2010; Hörnig et al. 2013). Some further specimens of putative oothecae are described in the literature, but their interpretation is controversial (see discussion of ovipositor morphology and oothecae of Paleozoic roachoids). Additionally, the inference of reproductive strategies based on hatchling morphology of fossil species has been proposed, as it is known for extant species of cockroaches that the presence and form of broodcare can be mirrored in the developmental status of the nymphs (Arillo 2007; Hörnig et al. 2016). But this is currently not yet possible in a wide taxonomic range due to the lack of hatchlings, or better small nymphs in general (see discussions e.g., in Haug et al. 2013; Hörnig et al. 2014, 2016). Therefore, one might conclude that it is quite challenging to infer the reproductive strategies in the majority of extinct representatives of Dictyoptera based on fossil remains. Yet, for example, the ability to produce oothecae is presumably linked to a specific morphology of the posterior part of the abdomen, and especially to the length of the ovipositor. While insects with short ovipositors do not obligatorily produce oothecae, it seems likely that a long ovipositor can be seen as contraindication for producing this kind of egg package. Hence, aspects of ovipositor morphology represent a useful tool to infer details of reproductive strategies of extinct dictyopterans.

A relatively long ovipositor is likely the plesiomorphic condition of pterygotes (see e.g., Sharov 1966; Scudder 1971; Grimaldi and Engel 2005; discussion in Hädicke et al. 2014), which was reduced several times within Pterygota (Klass 2007), but seems to be retained in early dictyopterans. With such long ovipositors, it is generally admitted that early roachoids were not able to produce oothecae (Laurentiaux 1951; Grimaldi 1997; Grimaldi and Engel 2005; Hörnig et al. 2013). Extant representatives of Mantodea have an externally visible ovipositor (at least its distal part), reduced into a rather short and broad form, allowing the formation of oothecae and their attachment to the substrate (e.g., Levereault 1936; Preston-Mafham 1990). Ovipositors of

modern species of Blattodea are further specialised, being reduced in length and covered by the so-called "subgenital plate", which is formed by post-ocular segment 15 (abdominal sternite 7) (Marks and Lawson 1962; Bohn 2003; Deitz et al. 2003; Klass and Meier 2006; Bell et al. 2007). This results in the ability to internally produce the ootheca and carry it by attaching it to the abdomen (McKittrick 1964; Scudder 1971). In Mantodea the subgenital plate is in fact present but not that large (as in Blattodea; Levereault 1936).

Herein we describe ovipositor morphologies of different fossil dictyopterans and discuss possible conclusions about their reproductive strategies. Based on that, we provide an evolutionary reconstruction of the transformation of the ovipositor within Dictyoptera and, consequently, the presumed evolution of the reproductive strategies within this group.

Institutional abbreviations.—KUP, Institute of Geology and Palaeontology of the Charles University, Prague, Czech Republic; NHMS-WP, Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen, Germany; ROMIP, Royal Ontario Museum Invertebrate Palaeontology, Toronto, Canada; YPM IP, Invertebrate Paleontology collection of the Yale Peabody Museum of Natural History, New Haven, USA.

Other abbreviations.—CuP, vein cubitus posterior.

Material and methods

We investigated several examples of dictyopteran fossils with preserved ovipositors from different localities and different geological periods: the late Carboniferous Mazon Creek locality, the early Permian Cabarz and Obora localities and the Early Cretaceous Crato Formation.

Carboniferous material (Mazon Creek).—The specimens from the Carboniferous Carbondale Formation of Mazon Creek, USA (YPM IP 000057, YPM IP 027870, YPM IP 027872) are preserved in ironstone concretions and determined to an age of ca. 309 mya (Moscovian, middle Pennsylvanian).

The selected specimens were first described and figured by Sellards (1904). He placed the nymphs into genera and species erected by Scudder in 1882 and 1895 based on isolated wings. As there is no further support so far which nymph correlates to which winged imago, we use collection numbers for specimen designation.

Permian material (Cabarz, Obora).—The specimen from the Cabarz quarry, Goldlauter Formation, Thuringian Forest Basin, Germany (NHMS-WP 5045) comes from lacustrine laminated claystone of early Permian (Cisuralian, Asselian) age, which is of about 295 mya (Schneider and Werneburg 2012; Schneider et al. 2013). This specimen is not described in detail in the present study, but included for comparison.

The specimen from the renowned Obora insect site, Bačov Horizon, Letovice Formation, Boskovice Graben, Czech

Republic (KUP 114a,b) is preserved in a lacustrine claystone of early Permian (Cisuralian, Artinskian/Kungurian) age, which is about 285 to 280 mya (Schneider and Scholze 2016).

Cretaceous material (Crato Formation).—The specimens from the Cretaceous Crato Formation, Brazil, formerly addressed to as part of the Santana Formation (for details see Martill 2007) (ROMIP64634, ROMIP64635, ROMIP64636, ROMIP64637, ROMIP64638, ROMIP64639, ROMIP64640, ROMIP64641) are on long term loan to the Royal Ontario Museum, Toronto (ROM). They are preserved in a limestone, which is assigned to the Aptian stage (115 mya; Grimaldi 2003).

Data collection.—All specimens were photographed with a Canon Eos Rebel T3i camera equipped with a MP-E 65 mm objective and a MeiKe LED Macro Ring Flash FC 100 or a Canon Twin Flash MT-24. To reduce reflections, cross-polarised illumination was used (e.g., Haug et al. 2011a, b; Kerp and Bomfleur 2011; Hörnig et al. 2014, 2016). Different adjacent image details were stitched to panoramas with the photomerge-function of Adobe Photoshop CS3. To generate stereo images (red/cyan), two photographs from different angles were recorded, subsequently edited and arranged with Adobe Photoshop CS3 (e.g., Haug et al. 2011a).

Morphological terminology.—Terminology should represent an important issue to be thought of in scientific procedures, leading to well-founded, broadly applicable and unambiguous terminologies (e.g., Richter et al. 2010).

Insects appear to be especially challenging in this aspect. Many terms were coined for structures appearing only for specific ingroups. While this is not only the case in insects, the group, as being so morphologically diverse, is clearly vulnerable for such practices. One could argue that highly specialised terminology leads to less ambiguous descriptions. Yet, this comes at the cost of broader understandability. Moreover, many terminologies imply hidden meanings about the origins of certain structures (see e.g., discussion of Hädicke vs. Haug in Hädicke et al. 2014). Therefore, we opt for a neutral terminology in the following. This should allow also non-expert readers to access more easily specialised literature. Specialist terminology is given in brackets to keep the reference to ingroup specific literature. Descriptions use general arthropod terms and follow a strict pattern of describing segment by segment (Haug et al. 2012).

To assist the reader we provide data on the external morphology of selected extant dictyopterans (Figs. 1, 2). We selected females of the extant species *Hierodula* cf. *grandis* (Burmeister, 1838) and *Periplaneta americana* (Linnaeus, 1758) for documentation. Specimens of *P. americana* were taken from the breeding of the Zoological Institute and Museum of the Ernst-Moritz-Arndt-University of Greifswald. One female of *H.* cf. *grandis* came from a private breeding and was kindly provided by Marc Bierling, Munich.

The ovipositor of polyneopteran insects, including dictyopterans, is composed of 3 pairs of so-called "valves" (gonapophyses 8, 9/gonopod 8, 9 = valves 1, 2; gonoplaque = valves 3) and are transformed parts of appendages of abdominal segments 8 (valve 1) and 9 (valve 2) (Klass et al. 2012; Figs. 1, 2), but the exact identity of valves 3 is still unclear to some degree (in comparison to non-insect arthropods; e.g., Marks and Lawson 1962; Grimaldi and Engel 2005; Hädicke et al. 2014). In fossils it is not always possible to clearly identify which of these is preserved. In some cases the orientation of the fossil (dorsal versus ventral, lateral versus medial) can give some hints, but only if more than one pair can be seen. In case of doubt, we treat these structures under "open" terminology.

Results

All specimens have a blattoid habitus. The body is divided into presumably 20 segments. The head capsule is formed by the ocular segment and post-ocular segments 1–5. The thorax with walking appendages includes post-ocular segments 6–8. The abdomen without walking appendages includes (presumably, as the fossil is an insect) post-ocular segments 9–19. As in all specimens at least parts of the ovipositor are preserved, we assume that all described specimens are females.

Carboniferous roachoid dictyopteran nymphs from Mazon Creek

Figs. 3–8.

Locality: Mazon Creek, Illinois, USA.

Horizon: Carbondale Formation, Moscovian, middle Pennsylvanian, upper Carboniferous.

YPM IP 000057 (?phylloblattoid type).—The specimen (Figs. 3, 5A, 8A), original to Sellards (1904: fig. 13, pl. 1: 2) is preserved in ventral position. The total body length is about 16 mm, and width (without appendages) is about 9 mm. Shape of head capsule in ventral view is relatively stout, about 3 mm wide. Exact length unclear as posterior part concealed by pronotum; visible part 1.5 mm. Compound eyes are not preserved.

Post-ocular segments 6–8 each with a separate, well sclerotised lateral extruded tergite (pro-, meso-, and metanotum). Pronotum is about 4 mm long and 6.5 mm wide and partly overhanging the posterior region of the head capsule. Mesonotum is strongly curved in dorsal view; medially 2 mm long, up to 6 mm long laterally, 9 mm wide. Metanotum is strongly curved in dorsal view; medially 2.5 mm long, up to 5.5 mm long laterally, 7 mm wide. The entire medial length of thorax (post-ocular segments 6–8) is about 8.5 mm. Appendages of post-ocular segments 6–8 developed as walking legs; only parts of legs preserved (Fig. 5A$_3$, A$_4$). Post-ocular segments 7 and 8 additionally bear dorsally anlagen of fore- and hindwings (continuous with the tergites).

The visible abdominal sternites are well sclerotised. The sternites of post-ocular segments 10–15 are clearly identi-
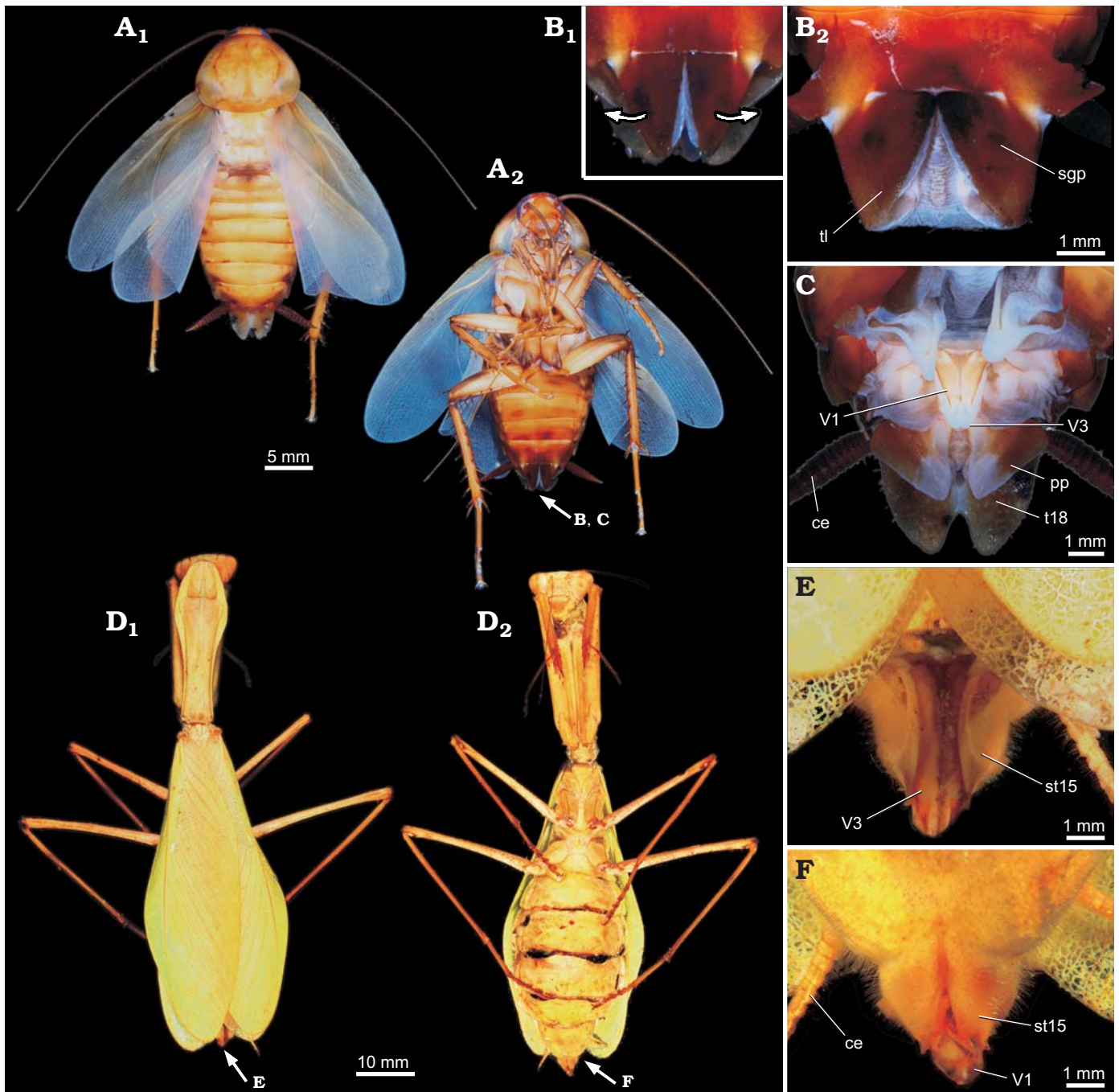
Fig. 1. General external morphology of extant Dictyoptera. **A–C**. American cockroach *Periplaneta americana* (Linnaeus, 1758). **A**. Overview in dorsal (A₁) and ventral (A₂) views. **B**. Close-up of subgenital plate in ventral view (B₁, B₂). **C**. Close-up of the ovipositor, subgenital plate ventrally bent for exposition of the ovipositor valves. **D–F**. Giant Asian mantis *Hierodula* cf. *grandis* (Burmeister, 1838). **D**. Overview in dorsal (D₁) and ventral (D₂) views. Close-up of ovipositor in dorsal (**E**) and ventral (**F**) views. Abbreviations: ce, cercus; pp, paraproct; sgp, subgenital plate; st15, sternite of post-ocular segment 15 (abdominal sternite 7; subgenital plate); tl, terminal lobes; t18, tergite of the post-ocular segment 18 (abdominal segment 10); V1, V3, valves 1, 3.

fiable. Post-ocular segment 9 is not visible but it is unclear whether this is the original condition or due to the incomplete preservation. The visible abdominal sternites are about 0.5 mm long respectively, sternite of post-ocular segment 15 is about 1 mm in length.

Distal parts of appendages of post-ocular segment 16 or 17 (valves of ovipositor) are well developed (Fig. 5A₁, A₂); in ventral view, one pair of valves is visible which is about

2.7 mm long and 0.6 mm wide at the base and tapers to a fine point on the distal end. Appendages of post-ocular segment 19 (cerci) are not preserved.

YPM IP 027872 (part/counterpart).—The specimen (Figs. 4, 5B, 8B), original to Sellards (1904: fig. 11) is preserved in dorso-lateral view. The total body length is about 16 mm, body width (without appendages) is about 6.5 mm. The head is not visible (covered by pronotum or not preserved).
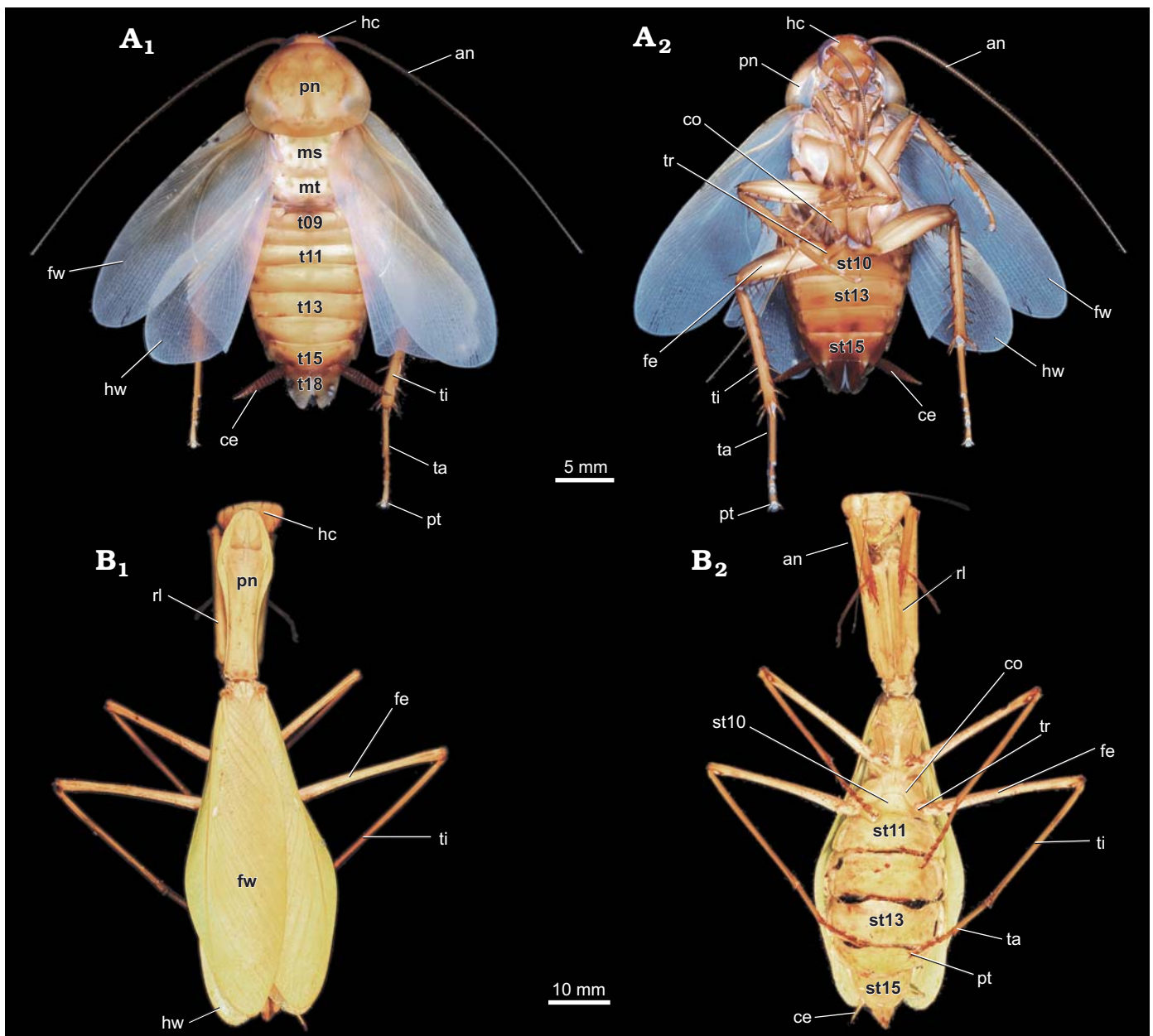
Fig. 2. General external morphology of extant Dictyoptera. **A**. Female of American cockroach *Periplaneta americana* (Linnaeus, 1758), in dorsal (A₁) and ventral (A₂) views. **B**. Female of giant Asian mantis *Hierodula* cf. *grandis* (Burmeister, 1838), in dorsal (B₁) and ventral (B₂) views. Abbreviations: an, antenna; ce, cercus; co, coxa of metathoracic leg; fe, femur of metathoracic leg; fw, forewing; hc, head capsule; hw, hindwing; ms, mesonotum; mt, metanotum; pn, pronotum; pt, pretarsus of metathoracic leg; rl, raptorial leg (prothoracic leg); st10–15, sternite of post-ocular segment 10–15 (abdominal sternite 2–7); t9–18, tergite of the post-ocular segment 9–18 (abdominal segment 1–10); ta, tarsus of metathoracic leg; ti, tibia of metathoracic leg; tr, trochanter of metathoracic leg.

Post-ocular segments 6–8 dorsally each with a separate, well sclerotised tergite (pro-, meso-, and metanotum). Pronotum is about 4 mm long and 6 mm wide. Mesonotum is curved in dorsal view; medially 2 mm long, up to 3 mm long laterally, 6 mm wide. Metanotum is curved in dorsal view; medially 2 mm long, up to 3.5 mm long laterally, 6.5 mm wide. The entire medial length of thorax (post-ocular segments 6–8) is about 8 mm. Appendages of post-ocular segments 6–8 developed as walking legs; only parts of legs preserved (parts of the coxae are visible because of erosion of the median parts of the thoracic tergites). Post-ocular segments 7 and 8 appear to bear anlagen of fore- and hindwings (continuous with the tergites).

The visible abdominal tergites are well sclerotised, each about 1 mm long. Clearly identifiable are tergites of post-ocular segments 13–17. The tergites of post-ocular segment 9–12 and 18 are not visible but it is unclear in which cases this is the original condition or caused due to incomplete preservation.

Appendages of post-ocular segments 16 and 17 (ovipositor; Fig. 5B): one pair of valves is clearly recognisable (spread apart). The valves are about 4 mm long and 1 mm
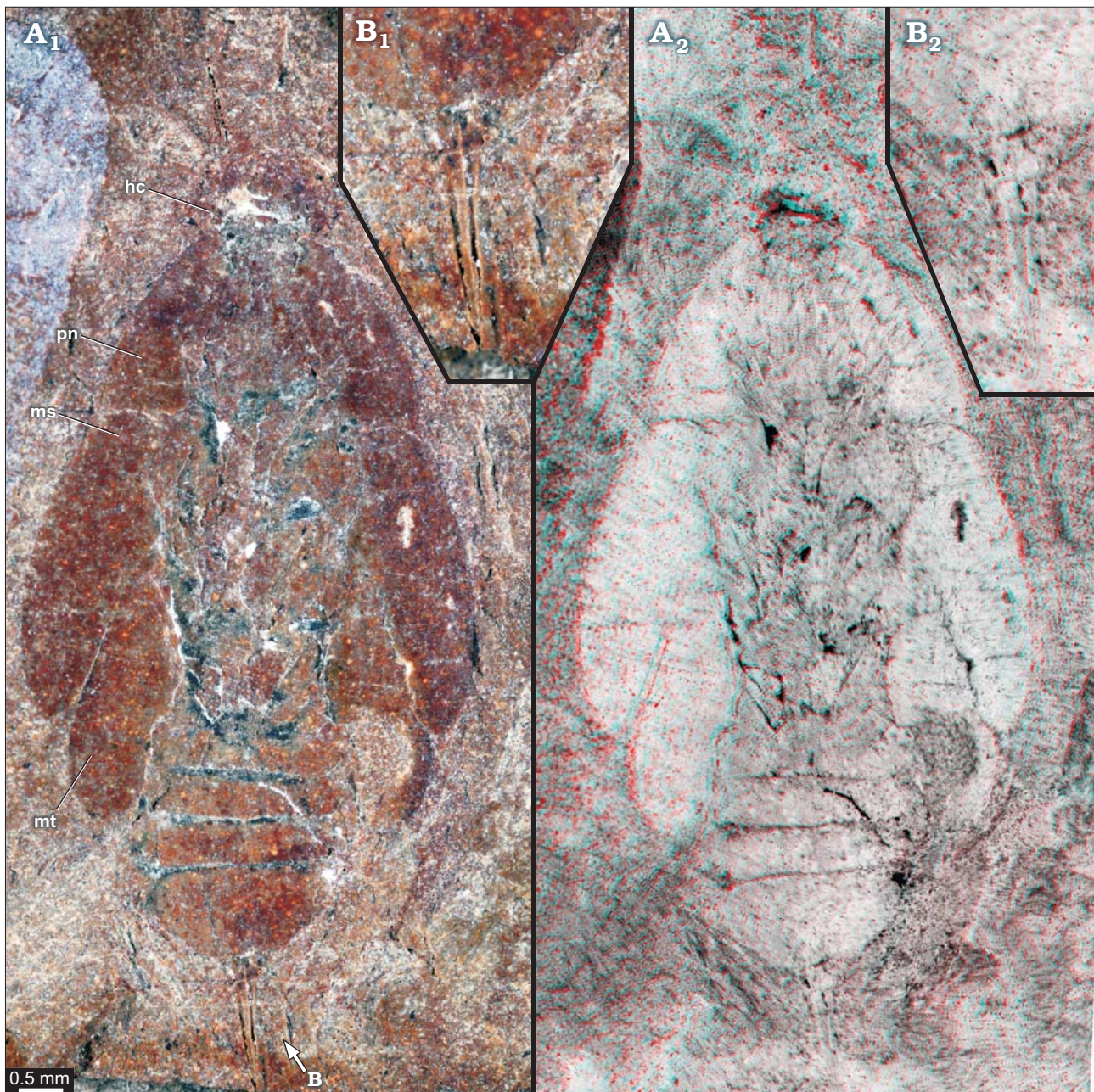
Fig. 3. Roachoid nymph YPM IP 000057 from the Carboniferous Carbondale Formation of Mazon Creek, USA; in ventral view. Overview (**A**) and close-up images of ovipositor (**B**); A₁, B₁, photographs without stereo information; A₂, B₂, red-cyan stereo-anaglyphs (please use red-cyan glasses to view). Abbreviations: hc, head capsule; ms, tergite of mesothorax; mt, tergite of metathorax; pn, tergite of prothorax.

wide at the base. Appendages of post-ocular segment 19 (cerci) are not preserved.

YPM IP 027870 (mylacrid type; part/counterpart).—The specimen (Figs. 6, 7, 8C), original to Sellards (1904: figs. 6, 7) is preserved in dorsal position. The total body length is about 25 mm and body width is about 15 mm (without appendages). The head is not visible (covered by pronotum or not preserved).

Post-ocular segments 6–8 dorsally each with a separate, well sclerotised tergite (pro-, meso-, and metanotum). Pronotum is about 8 mm long and 14 mm wide.

Mesonotum is strongly curved in dorsal view; medially 2.5 mm long, up to 9 mm long laterally, 15 mm wide. Metanotum is curved in dorsal view; medially 3 mm long, up to 4 mm long laterally, 12 mm wide. The entire medial length of thorax (post-ocular segments 6–8) is about 13.5 mm. Appendages of post-ocular segments 6–8 developed as walking legs; only parts of legs preserved (parts of the coxae are visible because of erosion of the median parts of the thoracic tergites). Post-ocular segments 7 and 8 bear anlagen of fore- and hindwings (continuous with the tergites).

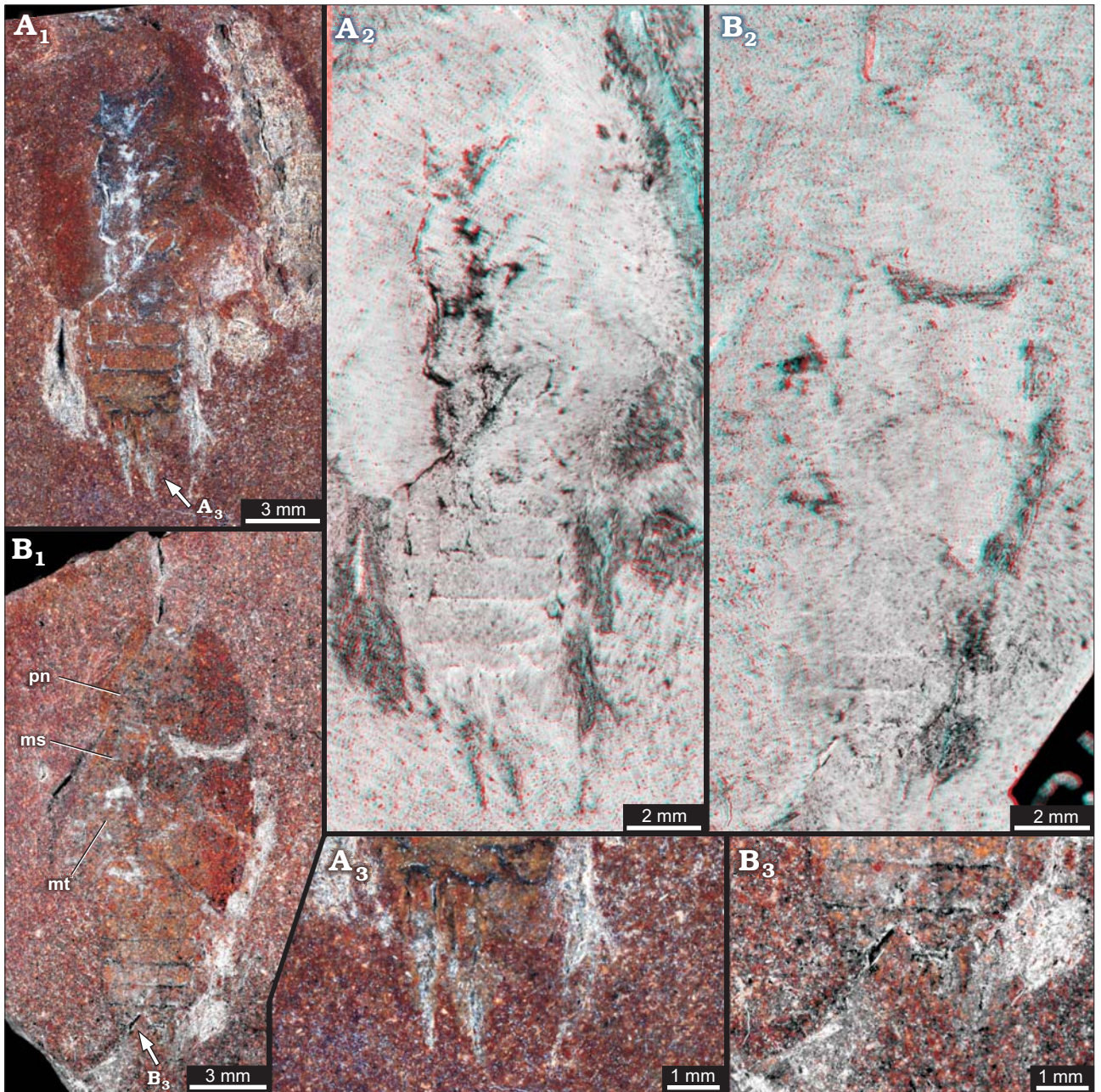Post-ocular segments 9–18 dorsally with a separate, well

Fig. 4. Roachoid nymph YPM IP 027872 from the Carboniferous Carbondale Formation of Mazon Creek, USA; in dorso-lateral view. Part (**A**) and counterpart (**B**). A₁, B₁, overview images; A₂, B₂, red-cyan stereo-anaglyphs (please use red-cyan glasses to view); A₃, B₃, close up images of ovipositor. Abbreviations: ms, tergite of mesothorax; mt, tergite of metathorax; pn, tergite of prothorax.

sclerotised and about 1 mm long tergite each. On post-ocular segment 16 or 17 a deltoid-shaped dent is visible (see stereo images; Fig. 7), which could be interpreted as insertion point of an ovipositor. Appendages of post-ocular segment 19 (cerci) are only fragmentarily preserved.

Permian roachoid from Obora

Fig. 9.

Locality: Obora insect site, Boskovice Graben, Czech Republic.

Horizon: Lacustrine claystone, Letovice Formation, Bačov Horizon, Cisuralian, Artinskian/Kungurian, early Permian.

KUP 114a, b (part/counterpart), Syscioblatta *sp.*—The specimen (Fig. 9) is preserved in dorsal view and nearly complete. The total body length is about 15 mm (without appendages).

Shape of head capsule in dorsal view is drop-shaped and about 2 mm long. Compound eyes are not preserved. Post-ocular segment 6 dorsally with a separate, well sclerotised tergite (pronotum). Pronotum about 4.7 mm long and has a maximum width of about 5.2 mm. Pronotum is not overhanging the head capsule. Meso- and metanotum (post-ocular segments 7 and 8) are concealed by the wings. Appendages of post-ocular segments 6–8 (legs) are
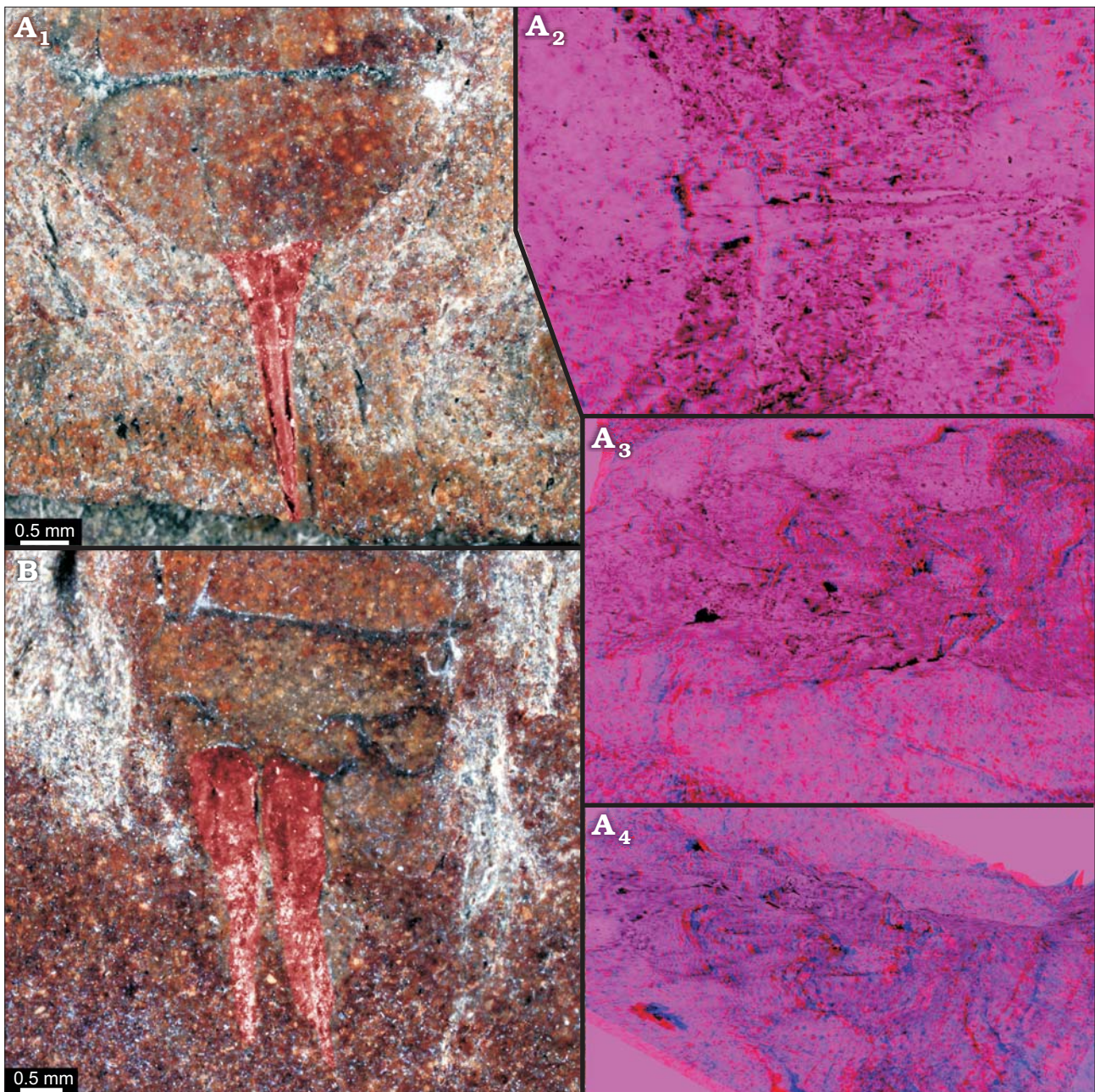
Fig. 5. Roachoid nymphs YPM IP 000057 (**A**) in ventral view and YPM IP 027872 in dorso-lateral view (**B**) with interpretations of preserved structures. A₁, B, colour-marked close-up image of ovipositor; A₂, stereo close-up image of the ovipositor; A₃, A₄, stereo close-up images of thorax with visible parts of the coxae (red-cyan stereo-anaglyphs; please use red-cyan glasses to view).

well preserved. Prothoracic leg (appendage of post-ocular segment 6): coxa is about 2.5 mm long and 1 mm wide, femur is about 2.5 mm long and 0.8 mm wide, tibia is about 3 mm long and 0.3 mm wide, tarsus is about 3.5 mm long and about 0.1 mm wide. Mesothoracic leg (appendage of post-ocular segment 7): coxa is not visible, femur is about 2.7 mm long and 0.5 mm wide, tibia is about 3.1 mm long and 0.4 mm wide, tarsus is about 3.7 mm long (including pretarsus with claw) and about 0.3 mm wide. Metathoracic leg (appendage of post-ocular segment 8): coxa is not visible, femur is about 2.5 mm long and 0.9 mm wide, tibia is about 7.7 mm long and 0.4 mm wide, tarsus is about

3.1 mm long and about 0.3 mm wide. Fore- and hindwings on post-ocular segments 7 and 8 protrude beyond the abdomen about one third of the entire body length. The forewings are about 14 mm long and about 5 mm wide (maximum width). The wings have a characteristic color pattern, schematically shown in Schneider et al. (2013: fig. 4, top right). Post-ocular segments 9–19 (abdominal segments) are not visible (concealed by wings).

Appendages of post-ocular segments 16 and/or 17 (valves of ovipositor) are well developed (Fig. 9A₂), the visible part of the ovipositor is about 5 mm long and 1.2 mm wide at the base. Two parts of the ovipositor are identifiable, which
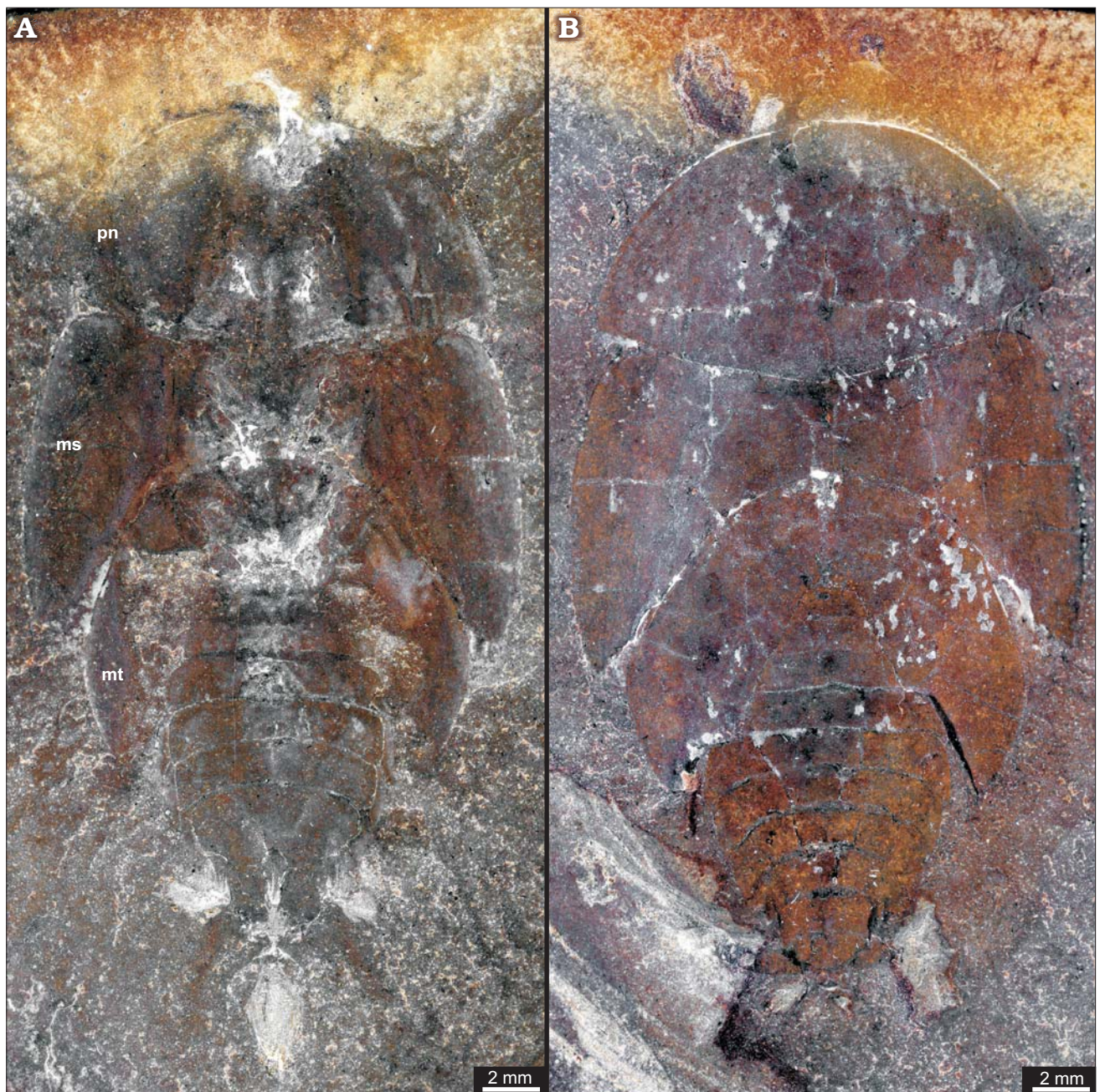
Fig. 6. Roachoid nymph YPM IP 027870 from the Carboniferous Carbondale Formation of Mazon Creek, USA; in dorsal view. Overview of part (**A**) and counterpart (**B**), thorax with visible parts of the coxa because of erosion of the median parts of thoracic tergites. Abbreviations: ms, tergite of mesothorax; mt, tergite of metathorax; pn, tergite of prothorax.

is interpreted as valves 1 and 3. The surface seems to be partly structured, but we cannot rule out for sure that this is a preservation artefact. Appendages of post-ocular segment 19 (cerci) are not visible.

Cretaceous blattodean-like dictyopterans from the Crato Formation

Figs. 10–13.

Locality: Araripe Basin, Brazil.

Horizon: Crato Formation (formerly part of Santana Formation), Aptian, lower Cretaceous.

ROMIP64635.—Specimen (Figs. 10A$_1$, 11A$_1$) is preserved in ventral position. The total body length is about 6.5 mm and body width is about 3.5 mm (without appendages).

Head is fragmentarily preserved. Post-ocular segments 6–7 (pro- and mesothorax) are not preserved. Post-ocular segment 8 (metathorax) ventrally with a separate, well sclerotised sternite. The individual lengths of pro-, meso-, metathorax and abdomen are undeterminable due to the incomplete preservation. Forewings on post-ocular segment 7 are about 8 mm long (insertion points are not visible because of incomplete preservation) and 2.5 mm wide. The
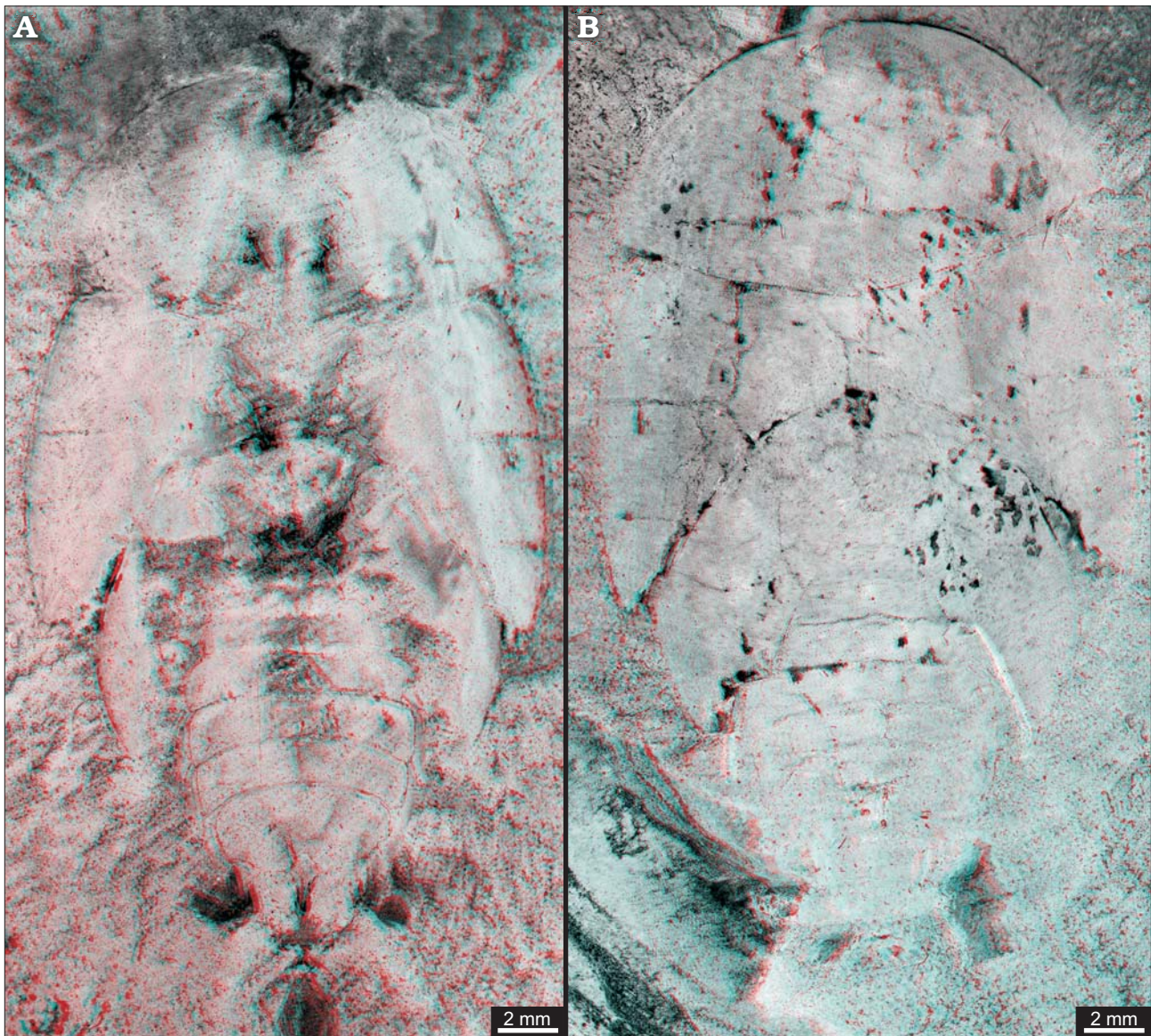
Fig. 7. Roachoid nymph YPM IP 027870 from the Carboniferous Carbondale Formation of Mazon Creek, USA; in dorsal view. Overview of part (**A**) and counterpart (**B**). Red-cyan stereo-anaglyphs (please use red-cyan glasses to view).

vein cubitus posterior (CuP) is strongly curved. Hindwings on post-ocular segment 8 are about 7.5 mm long (insertion points are not visible) and about 3.5 mm wide. Fore- and hindwings protrude beyond the abdomen about one third up to one half of the entire body length.

The visible abdominal sternites are well sclerotised. Sternites of post-ocular segments 10–15 are clearly identifiable. Post-ocular segment 9 is not visible, but it is unclear whether this is the original condition or caused by the incomplete preservation. Appendages of post-ocular segments 16 or 17 (valves of ovipositor) are well developed (Figs. 10A$_2$ and 11A$_2$). One pair of valves of the ovipositor is visible (spread apart). Each valve is about 1.5 mm long and 0.1 mm wide at the base and tapers to a fine point on the distal end. Appendages of post-ocular segment 19 (cerci) are about 0.7 mm long and at the base 0.1 mm wide and subdivided into several elements.

ROMIP64634.—The specimen (Figs. 10B$_1$, 11B$_1$) is preserved in dorsal view. The total body length is about 8.3 mm and body width is about 4 mm (without appendages).

Shape of head capsule in dorsal view is relatively stout and about 2.2 mm wide. Exact length unclear as posterior part concealed by pronotum; visible part 0.6 mm. Compound eyes are well preserved with a diameter of about 1 mm. Post-ocular segment 6 dorsally with a separate, well sclerotised tergite (pronotum). Pronotum is about 2.5 mm long, 3 mm wide and partly overhanging the head capsule posteriorly. Meso- and metanotum (post-ocular segments 7 and 8) are concealed by the wings. Appendages of post-ocular segments 6–8 (legs) are not preserved. Fore- and hindwings on post-ocular segments 7 and 8 protrude beyond the abdomen about one quarter of the entire body length. Tergites of post-ocular segments 9–18 (abdominal segments) are not visible (concealed by wings).
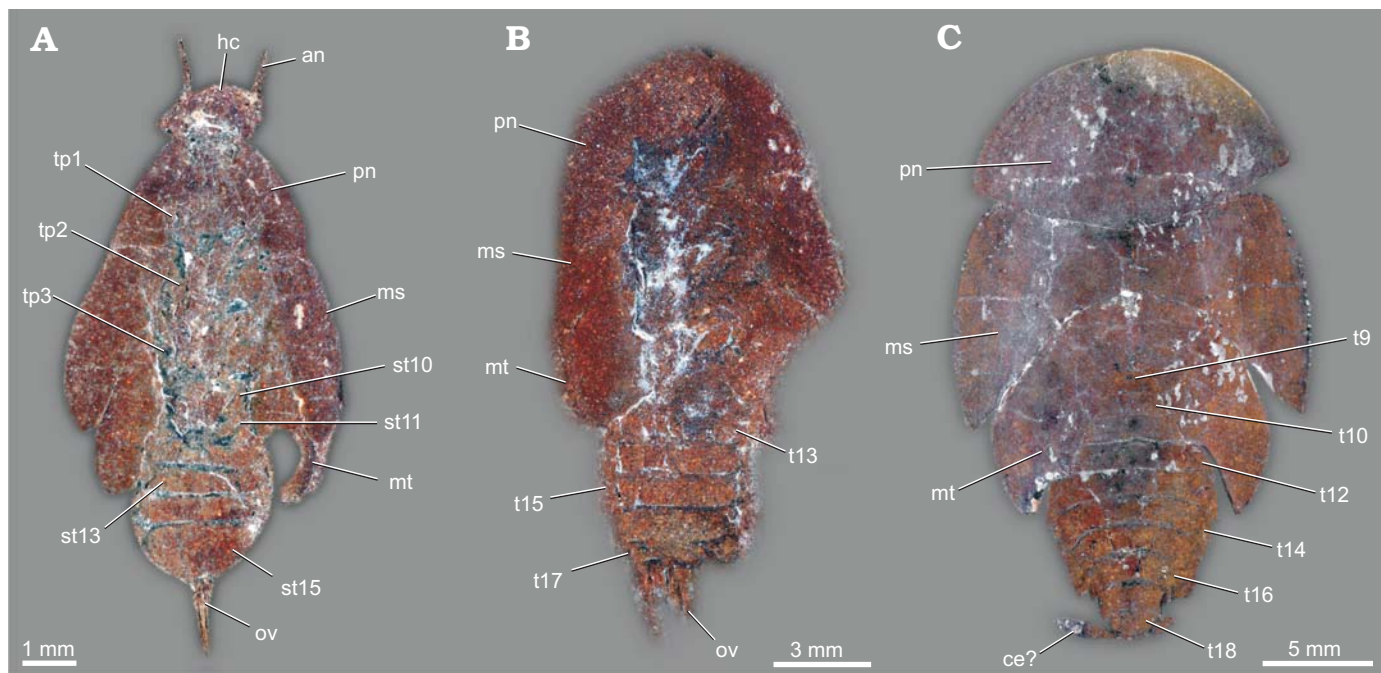
Fig. 8. Roachoid nymphs from the Carboniferous Carbondale Formation of Mazon Creek, USA; with interpretations of preserved structures. **A**. YPM 000057. **B**. YPM IP 027872. **C**. YPM IP 027870. Abbreviations: an, antenna; ce, cercus; hc, head capsule; ms, tergite of mesothorax; mt, tergite of metathorax; ov, ovipositor; pn, tergite of prothorax; st10–15, sternite of post-ocular segment 10–15 (abdominal segment 2–7); t9–18, tergite of post-ocular segment 9–18 (abdominal segment 1–10); tp1–3, thoracopod 1–3 (pro-, meso- and metathoracic legs).

Appendages of post-ocular segments 16 or 17 (valves of ovipositor) are well developed (Figs. 10B$_2$, 11B$_2$). One pair of valves is visible (spread apart due to preservation), each valve about 1.5 mm long and 0.1 mm wide at the base. Appendages of post-ocular segment 19 (cerci) are about 1.7 mm long and at the base 0.3 mm wide and taper to a fine point on the distal end. The cerci are subdivided into several elements and are preserved with numerous setae.

ROMIP64636.—The specimen (Figs. 10C$_2$, 11C$_2$) is preserved in ventro-lateral position. The total body length is about 6.2 mm without head (head not preserved) and total body width is about 3 mm (without appendages).

Post-ocular segments 6–8 (pro-, meso-, metathorax) and post-ocular segments 9–15 (abdominal segments) presumably ventrally with a separate, well sclerotised sternite (segments only partly preserved and not individually identifiable). The individual lengths of the pro-, meso-, metathorax and abdomen are undeterminable due to their incomplete preservation. Appendages of post-ocular segments 6–8 (legs) are not preserved. Fore- and hindwings on post-ocular segments 7 and 8 protrude beyond the abdomen about one quarter of the entire body length.

Appendages of post-ocular segments 16 and/or 17 (valves of ovipositor) are well developed (Figs. 10C$_2$, 11C$_2$), about 1.2 mm long and 1.2 mm wide at the base. Inner valves (valves 2) are about 0.2 mm wide and 1.2 mm long. Lateral valves (presumably valves 3) are about 0.5 mm wide at the base and about 1 mm long. Appendages of post-ocular segment 19 (cerci) are not preserved.

ROMIP64638.—The specimen (Figs. 10D$_1$, 11D$_1$) is preserved in ventral position. The total body length is about 14 mm and body width is about 6.5 mm (without appendages). The head is very weakly preserved (width presumably about 2.7 mm), but compound eyes are partly recognisable with a diameter of about 0.8 mm.

Post-ocular segments 6–8 (pro-, meso-, metathorax) each ventrally with separate, well sclerotised sternite. Prothorax is about 3 mm long. Lengths of meso- and metathorax are undeterminable due to their weak preservation. Appendages of post-ocular segments 6–8 (legs) are not preserved. Fore- and hindwings on post-ocular segments 7 and 8 protrude beyond the abdomen about one fifth of the entire body length.

Abdominal segments (post-ocular segments 9–15) are only partly identifiable due to the incomplete preservation. Appendages of post-ocular segments 16 and/or 17 (valves of ovipositor; Figs. 10D$_2$, 11D$_2$) are well developed. Two pairs of valves are visible. Inner valves (valves 2) are about 0.2 mm wide at the base and about 2.5 mm long. Lateral valves (presumably valves 3) have a maximum width of 0.7 mm and are about 2.5 mm long. Appendages of post-ocular segment 19 (cerci) are not preserved.

ROMIP64637.—The specimen (Figs. 12A$_1$, 13A$_1$) is preserved in ventral position. The total body length is about 8 mm and body width is about 3.5 mm (without appendages). Head and compound eyes are fragmentarily preserved. The width of the head is about 2.2 mm (length not determinable due to the weak preservation). Compound eyes have a diameter of slightly more than 1 mm.
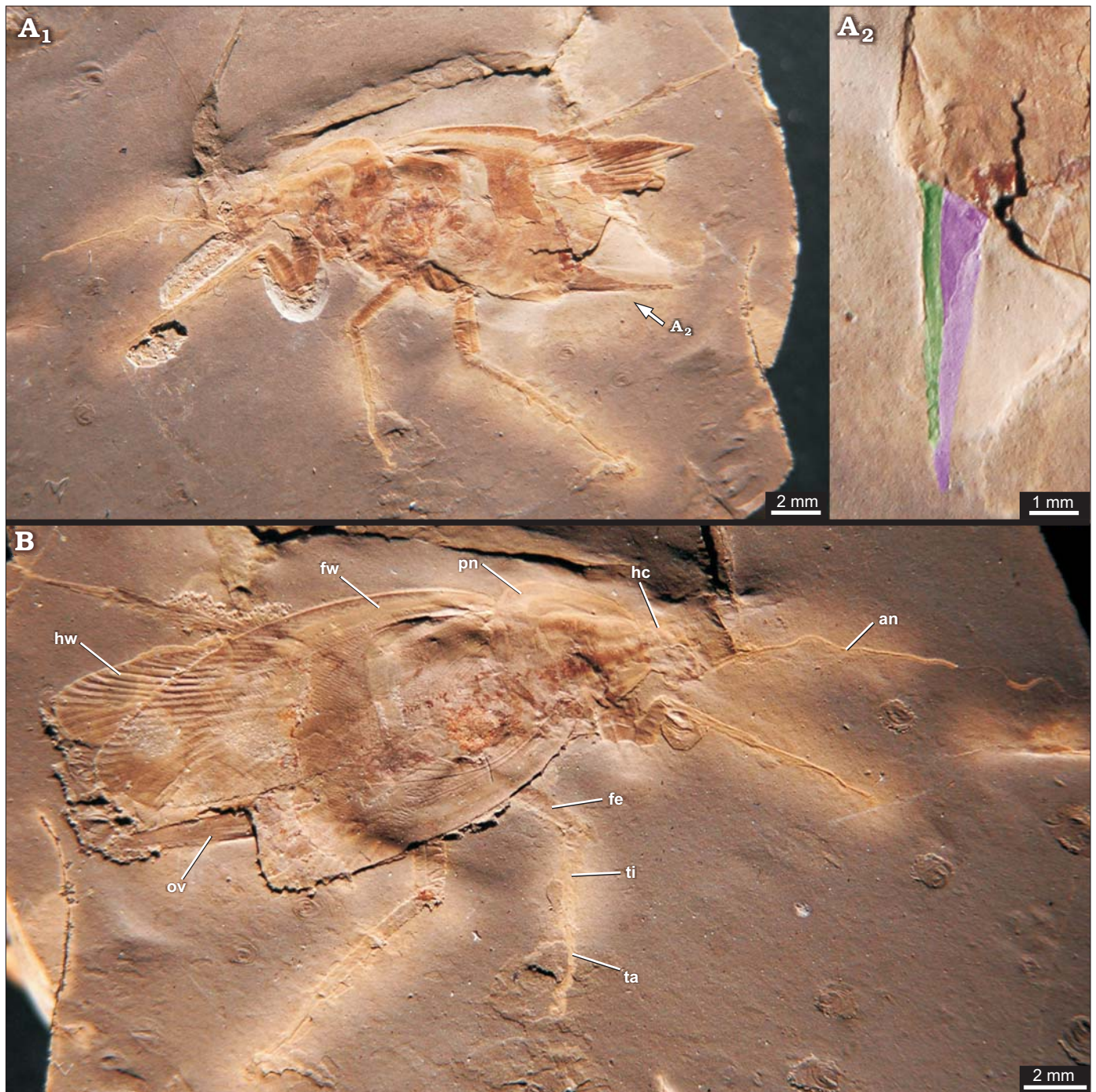
Fig. 9. Roachoid *Syscioblatta* sp. from early Permian of Obora, Czech Republic; in dorsal view. **A**. Part KUP 114a. **B**. Counterpart KUP 114b. A$_1$, B, overviews; A$_2$, close-up of the ovipositor (green, valve 1; purple, valve 3). Abbreviations: an, antenna; fe, femur of prothoracic leg; fw, fore wing; hc, head capsule; hw, hind wing; ov, ovipositor; ta, tarsus of prothoracic leg; ti, tibia of prothoracic leg.

Sternites of post-ocular segments 6–8 (pro-, meso-, metathorax) are only fragmentarily preserved. Prothorax is about 1.3 mm long (width is not determinable due to incomplete preservation). Mesothorax about 1 mm, and metathorax about 0.8 mm long. Appendages of post-ocular segments 6–8 (legs) are fragmentarily preserved; parts of the tibia preserved with several spines. Forewings on post-ocular segments 7 are about 9 mm long and 3 mm wide. CuP (vein) is strongly curved. Hindwings on post-ocular segment 8

are about 7.5 mm long (insertion points are not visible) and about 3.8 mm wide. Fore- and hindwings protrude beyond the abdomen about one quarter up to one third of the entire body length.

The visible abdominal sternites are well sclerotised. The sternites of post-ocular segments 10–15 are clearly identifiable. The sternite of post-ocular segment 9 is not visible but it is unclear whether this is the original condition or caused by incomplete preservation, but putative parts of the terg-
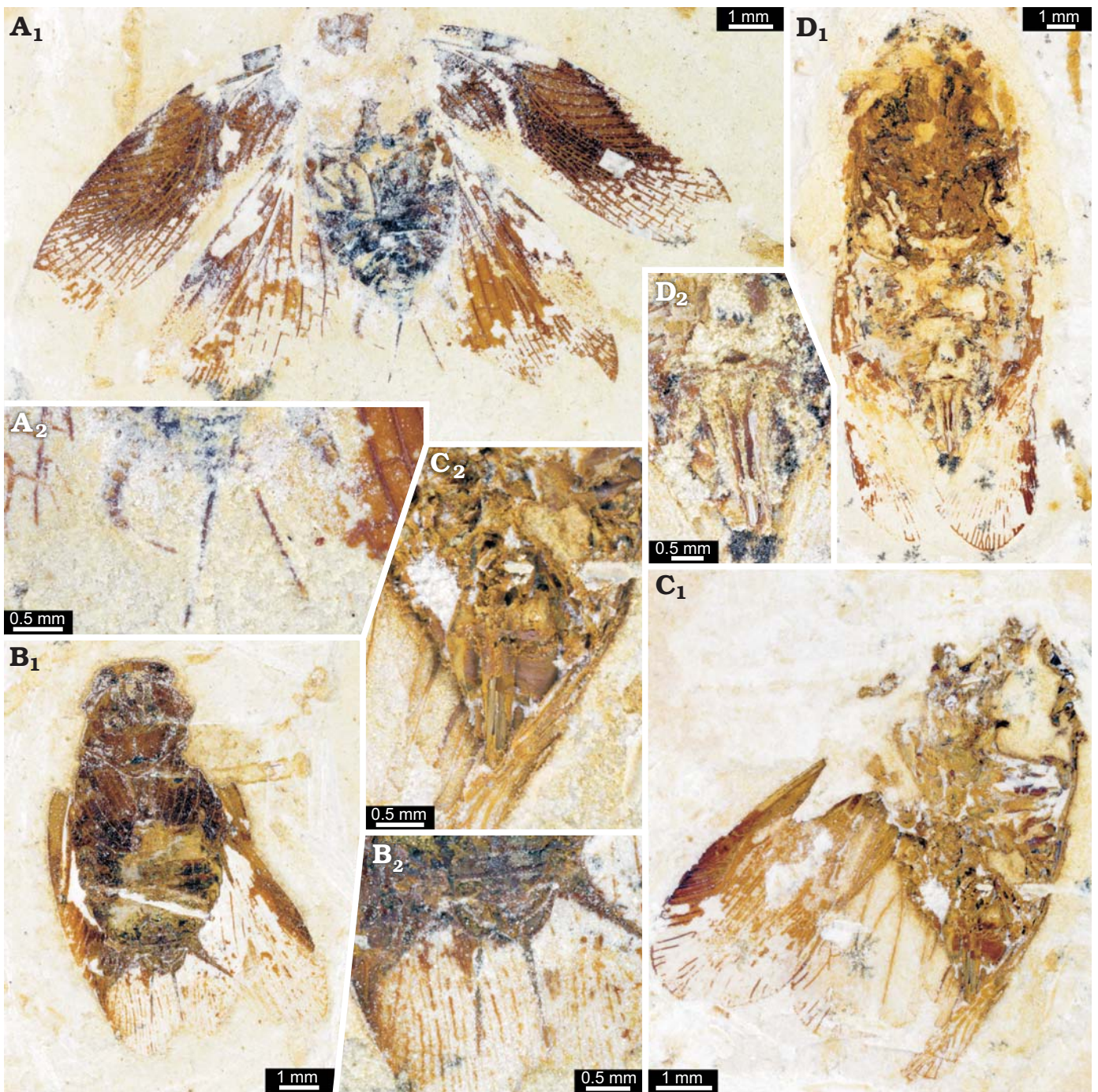
Fig. 10. Undescribed cockroaches or roachoids from the Aptian, Cretaceous Crato Formation of Brazil. **A**. ROMIP64635 in ventral view. **B**. ROMIP64634 in ventro-lateral view. **C**. ROMIP64636 in dorsal view. **D**. ROMIP64638 in ventral view. A_1–D_1, overviews; A_2–D_2, close ups of the ovipositor.

ite 9 are visible laterally. Post-ocular segment 15 (sternite 7) is drawn out posteriorly into two lobes.

Appendages of post-ocular segments 16 and or 17 (valves of ovipositor; Figs. $12A_2$ and $13A_2$) are well developed. One pair of valves is recognisable. Valves 1 protrude beyond post-ocular segment 15 (sternite 7) about 0.4 mm (insertion point on post-ocular segment 17 not visible) and are less than 0.1 mm wide. The visible part of the elongated post-ocular segment 15 (sternite 7) is about 1 mm wide at the base and about 0.6 mm long. Appendages of post-ocular

segment 19 (cerci) are partly preserved; subdivided into several elements.

ROMIP64639, Ponopterix maxima *Bechly, 2007.*—The specimen (Figs. $12B_1$, $13B_1$) is preserved in ventral position. Total body length is about 10 mm and body width is about 4 mm (without appendages). Head has a diameter of 2.5 mm. Compound eyes are well preserved; diameter about 1 mm.

Post-ocular segments 6–8 (pro-, meso-, metathorax) each ventrally with separate, well sclerotised sternite. Prothorax
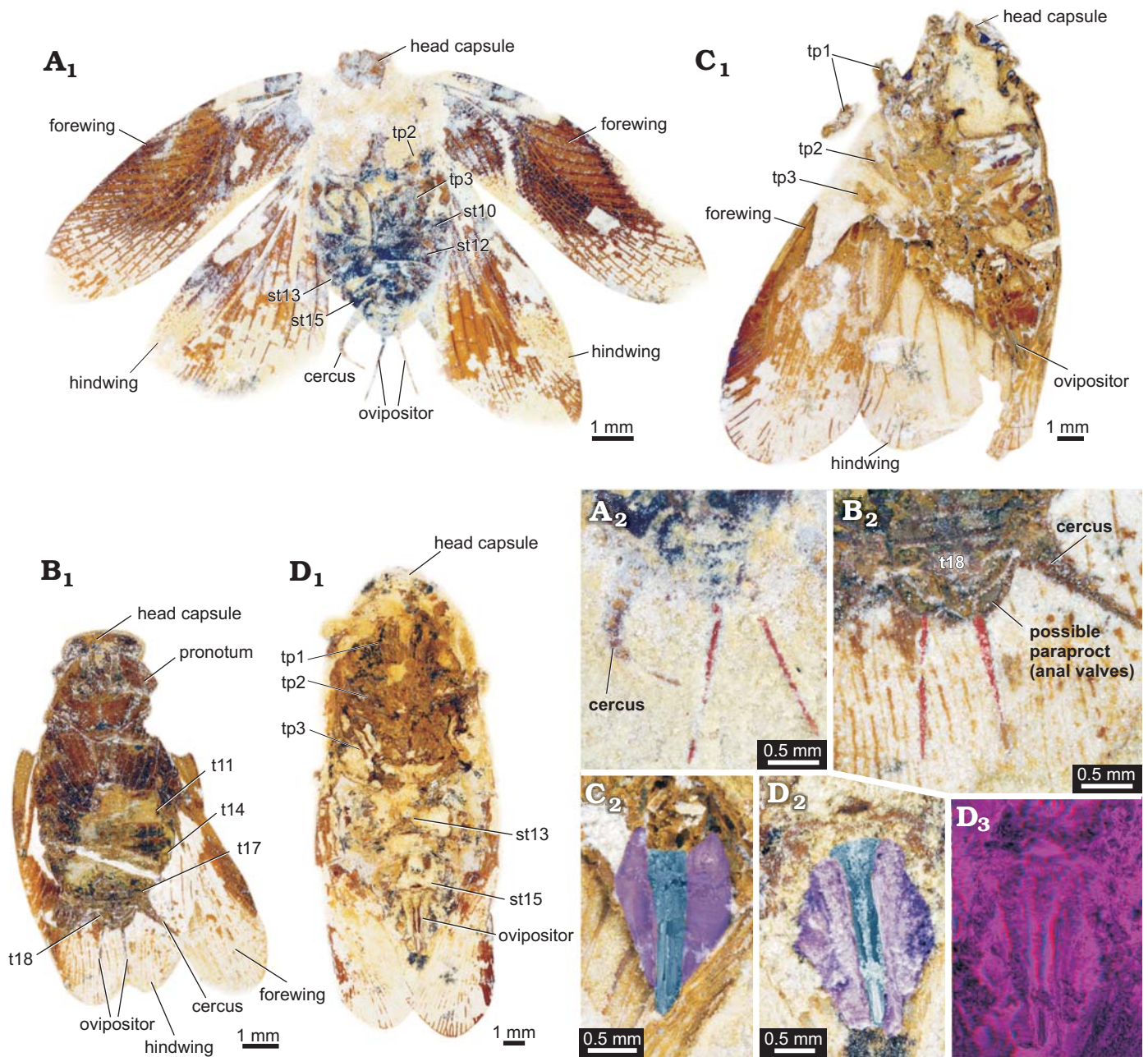
Fig. 11. Undescribed cockroaches or roachoids from the Aptian, Cretaceous Crato Formation of Brazil; with interpretations of preserved structures. **A**. ROMIP64635 in ventro-lateral view. **B**. ROMIP64634 in dorsal view. **C**. ROMIP64636 in ventral view. **D**. ROMIP64638 in ventral view. A_1–D_1, overviews; A_2–D_2, colour-marked close ups of the ovipositor (red, undeterminable valves; blue, valves 2; purple, valves 3); D_3, red-cyan stereo-anaglyph (please use red-cyan glasses to view). Abbreviations: st10–15, sternite of post-ocular segment 10–15 (abdominal segment 2–7); t11–18, tergite of post-ocular segment 11–18 (abdominal segment 3–10); tp1–3, thoracopod 1–3 (pro-, meso-, and metathoracic legs).

is about 2 mm long and 2 mm wide. Mesothorax is about 2 mm and metathorax is about 1.5 mm long. Appendages of post-ocular segments 6–8 (legs) are not preserved. Fore- and hindwings (post-ocular segments 7 and 8) slightly protrude beyond the abdomen.

The visible abdominal sternites are well sclerotised. The sternites of post-ocular segments 11–15 are clearly identifiable. Post-ocular segments 9 and 10 are not visible but it is unclear whether this is the original condition or caused by incomplete preservation.

Appendages of post-ocular segments 16 or 17 (valves of ovipositor; Figs. $12B_2$, $13B_2$) are well developed, about 0.7 mm long and 0.5 mm wide at the base (no individual valves determinable; presumably valves 1 visible because of the fossils position). Appendages of post-ocular segment 19 (cerci) taper to a fine point, are subdivided into several elements, about 1.2 mm long and 0.3 mm wide at the base.

ROMIP64640, Ponopterix maxima Bechly, 2007.—The specimen (Figs. $12C_1$, $13C_1$) is preserved in ventral position. Total body length is about 11 mm and body width is about 4
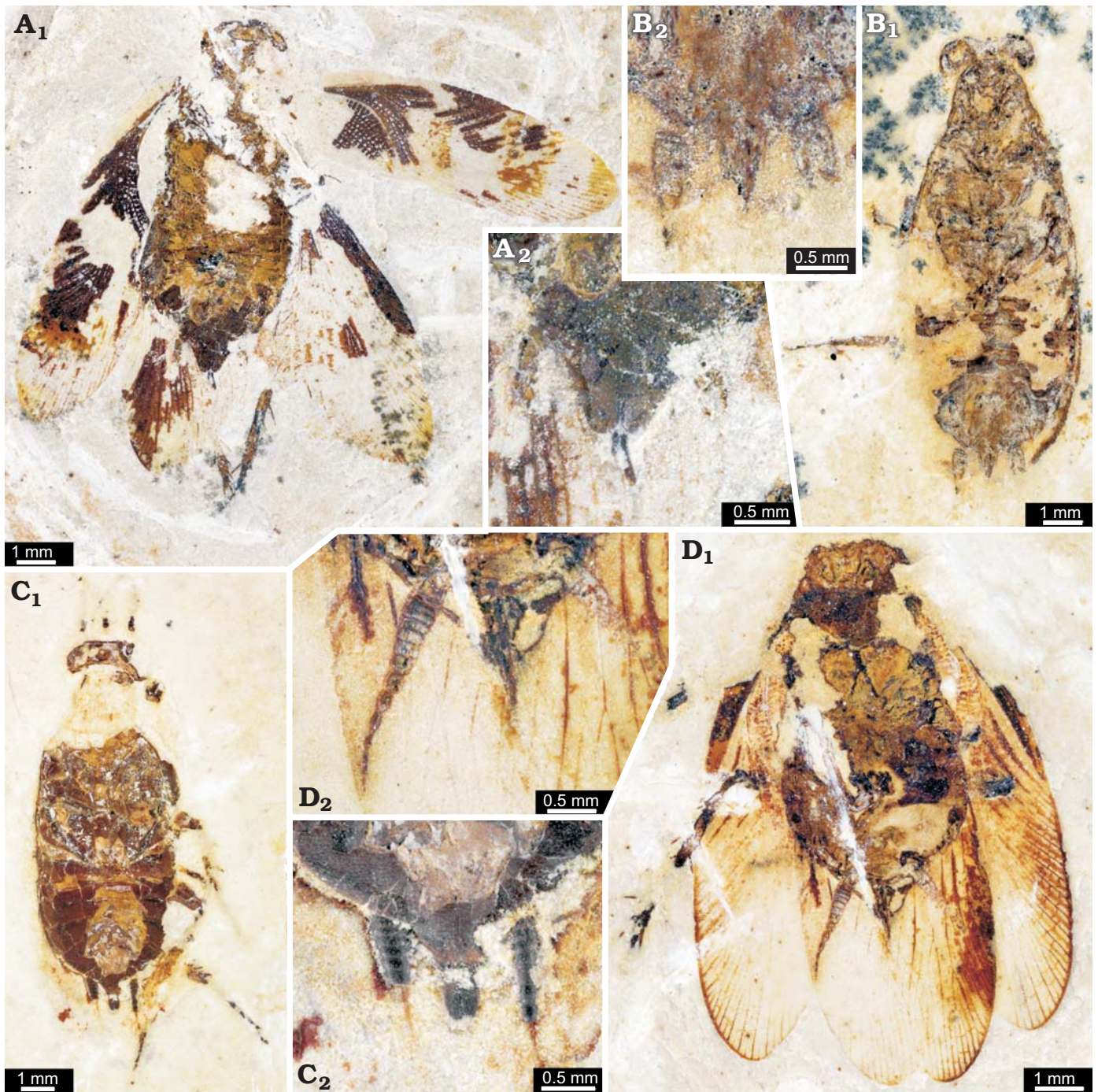
Fig. 12. *Ponopterix maxima* Bechly, 2007 (B, C) and undescribed cockroaches or roachoids (A, D) from the Aptian, Cretaceous Crato Formation of Brazil; in ventral views. **A**. ROMIP64637. **B**. ROMIP64639. **C**. ROMIP64640. **D**. ROMIP64641. A_1–D_1, overviews; A_2–D_2, close ups of the ovipositors.

mm (without appendages). Head has a diameter of 2.5 mm. Compound eyes and antennae are fragmentarily preserved.

Post-ocular segments 6–8 (pro-, meso-, metathorax) each ventrally with separate, well sclerotised sternite. Prothorax is about 2.5 mm long and 2 mm wide. Mesothorax is about 2 mm and metathorax is about 1.5 mm long. Appendages of post-ocular segments 6–8 (legs) are fragmentarily preserved; spines visible. Fore- and hindwings (post-ocular segments 7 and 8) not overhanging the abdomen, details are not visible (due to preserved position).

The visible abdominal sternites are well sclerotised. The sternites of post-ocular segments 10–15 are clearly identifiable. Post-ocular segment 9 is not visible, but it is unclear whether this is the original condition or caused due to incomplete preservation.

Appendages of post-ocular segments 16 or 17 (valves of ovipositor; Figs. $12C_2$, $13C_2$) are well developed. One pair of valves is visible (presumably valves 1); each valve is about 0.8 mm long and 0.5 mm wide at the base. Appendages of post-ocular segment 19 (cerci) taper to a fine point on the
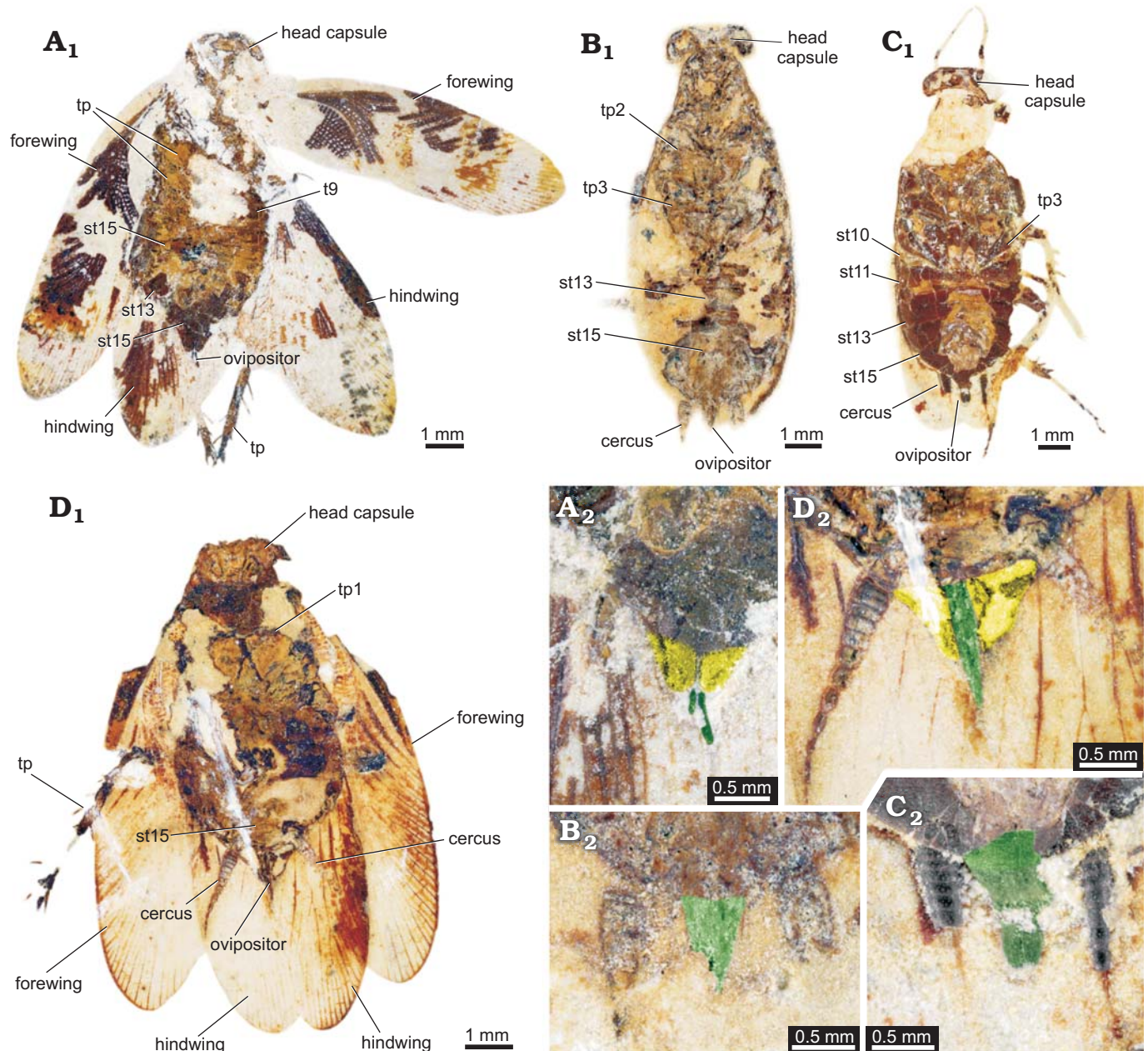
Fig. 13. *Ponopterix maxima* Bechly, 2007 (B, C) and undescribed roachoids (A, D) from the Aptian, Cretaceous Crato Formation of Brazil; in ventral views with interpretations of preserved structures. **A**. ROMIP64637. **B**. ROMIP64639. **C**. ROMIP64640. **D**. ROMIP64641. A_1–D_1, overviews; A_2–D_2, colour-marked close ups of the ovipositor (green, valves 1; yellow, part of post-ocular segment 15 [sternite 7; subgenital plate]). Abbreviations: st10–15, sternite of post-ocular segment 10–15 (abdominal segment 2–7); t9, tergite of post-ocular segment 9 (abdominal segment 1); tp1–3, thoracopod 1–3 (pro-, meso-, and metathoracic legs).

distal end, are subdivided into several elements and about 1.2 mm long and 0.2 mm wide at the base.

ROMIP64641 (undescribed).—The specimen (Figs. $12D_1$, $13D_1$) is preserved in ventral position. The total body length is about 8.5 mm and body width is about 3.5 mm (without appendages). The head has a diameter of about 2 mm. Compound eyes are not determinable.

Post-ocular segments 6–8 (pro-, meso-, metathorax) each ventrally with separate, well sclerotised sternite. Prothorax is about 1.2 mm long and 2.7 mm wide. Mesothorax is not well preserved, presumably about 1 mm long. Length of metathorax is undeterminable due to the incomplete preservation. Appendages of post-ocular segments 6–8 (legs) are fragmentarily preserved; spines visible. Forewings on post-ocular segment 7 are about 9.5 mm long and 2.7 mm wide. Insertion points of hindwings on post-ocular segment 8 are not visible. Fore- and hindwings protrude beyond the abdomen about one half of the entire body length. Sternites of abdominal segments (post-ocular segments 9–15) are not clearly identifiable due to the incomplete preservation. The supposed post-ocular segment 15 (sternite 7) is drawn out posteriorly into two lobes.

Appendages of post-ocular segments 16 or 17 (valves of ovipositor; Figs. 12D$_2$, 13D$_2$) are well developed. One pair of valves is determinable. The valves (presumably valve 1) are about 1.1 mm long and about 0.1 mm wide. The visible part of the elongated post-ocular segment 15 (sternite 7) is about 0.5 mm long (median part seems to lack, presumably due to incomplete preservation). Appendages of post-ocular segment 19 (cerci) taper to a fine point on the distal end and are subdivided into several elements. Cerci are about 2 mm long and about 0.3 mm wide at the base.

Discussion

Palaeozoic specimens

Identification.—There has been a debate about whether the Palaeozoic roachoids should be treated as blattodeans or "further down the tree" as non-blattodean dictyopterans (e.g., Sellards 1904; Hennig 1969; Bohn and Klass 2003; Grimaldi and Engel 2005). Apomorphies that characterise modern dictyopterans, such as a shortened ovipositor and presumably the production of oothecae appear to be clearly absent in Palaeozoic species. Thus, it is important to clearly differentiate between two different evolutionary levels:

(i) Dictyoptera sensu stricto (sensu Béthoux et al. 2009), with a short ovipositor and the ability to produce oothecae, including the two sister groups Blattodea (which itself also includes Isoptera as an ingroup) and Mantodea (Béthoux and Wieland 2009).

(ii) Dictyoptera sensu lato (sensu Béthoux et al. 2009), the larger group including Dictyoptera sensu stricto and the roachoids with (plesiomorphically) long ovipositors.

Several of the recognised apomorphies of Dictyoptera sensu lato are ambiguous or difficult to evaluate in fossils, as the preservational condition often only allows the identification of parts of these features. Characteristics for identifying a roachoid are flattened, splayed, and elongated coxae; a flattened body; tegminous forewings; in some instances, forewings with a distinctive and strongly curved CuP vein, or a claval furrow (Grimaldi and Engel 2005). An additional important feature characterising Dictyoptera sensu lato is the large pronotum (tergum of the first thoracic segment), which may partly conceal the head capsule. We consider this as a relevant character. Representatives of other groups with large pronota, such as Palaeodictyoptera, differ in their detailed morphology, as they possess a notch exposing the head. As all here treated specimens possess a large pronotum partly covering the head and, where preserved, rather long coxae, we consider all of them as ingroup representatives of Dictyoptera sensu lato. More exact phylogenetic placement of most specimens is hampered by different factors and will be discussed below.

Developmental status.—The specimens YPM IP 000057, YPM IP 027870, and YPM IP 027872 were already depicted by Sellards (1904; see above). A very remarkable feature on this specimens is the long ovipositor, which is especially well preserved in YPM IP 000057. Sellards (1904) assumed that these specimens represent roachoid nymphs and assigned them to specific species, for some of which he also described assumed adults. Reconstructing ontogenetic sequences of fossil arthropods, especially insects, is a challenging task (e.g., Haug et al. 2013) and usually depends on having a large sample available for reconstructing (more or less) continuous parts of ontogenetic sequences.

At the moment, we still have very few comparable Carboniferous specimens available. In most of these, only the large discoid pronotum allows the identification as Dictyoptera sensu lato because, apart from tergites and ovipositor, neither many details of wings, legs or further structures are preserved.

Hence, the ascription of fossil nymphs to adult-based species as done by Sellards (1903, 1904) is plausible, but not exclusive. Two interpretations can explain the morphological features of the herein described specimens:

(i) The Carboniferous specimens described here could represent paedomorphic adults not possessing fully functional wings. Such paedomorphic-appearing adults are known among extant cockroach species, such as *Macropanesthia* spp. or *Cryptocercus* spp. (Nalepa and Bandi 2000; Bell et al. 2007: 35–36). There are also rare cases of species with paedomorphic females and non-paedomorphic males in cockroaches, such as *Nocticola termitophila*, or at the population level e.g., in *Paratemnopteryx howarthi* and *Alluaudellina cavernicola* (Nalepa and Bandi 2000) (yet, it seems to be more often occurring in other extant insect groups, such as beetles, e.g., Lampyridae: McDermott 1964; Branham and Wenzel 2003; Jeng 2008; *Duliticola* (= *Platerodrilus*), Lycidae: Mjöberg 1925; Kazantsev 2002). However, in cases in which larger numbers of forewings of one species of Palaeozoic roachoids are known, a distinct dimorphism in the wing geometry is visible—a long slender type and a short wider type with identical venation patterns. This was interpreted by Laurentiaux (e.g., 1951, 1963) and Schneider (1978b) as an expression of sexual dimorphism, hence as fully developed wings of males and females, contradicting the lack of functional wings in one of the sexes (see also discussion below). However, we cannot fully exclude that already in the Carboniferous roachoid species occurred in which neither adult females nor adult males possessed wings.

(ii) If the specimens indeed represent nymphal stages of roachoids, their morphology is remarkable, as they possess a long external ovipositor. In this case, genital structures usually present at (and defining) the adult stage would be already developed in the nymph. This interpretation is also supported by modern counterparts, such as nymphs of Orthoptera already possessing a (long) external ovipositor (Ensifera: Sperber et al. 2003; Moon et al. 2009), as well as in nymphs of Grylloblattodea (Nagashima 1991). Given the extreme ovipositor length in definite adult roachoid specimens (e.g., Figs. 9, 14), the presence of the ovipositor at
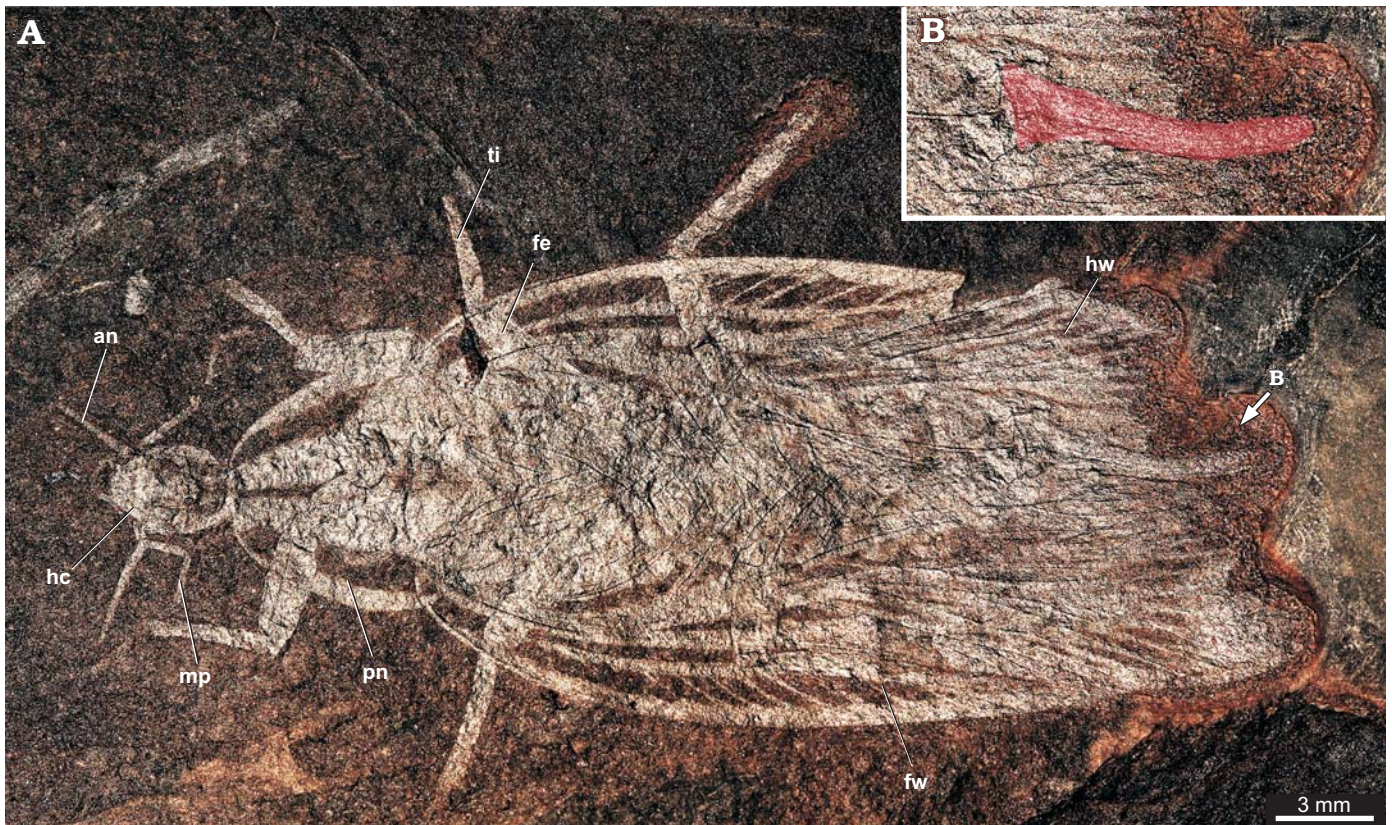
Fig. 14. Roachoid *Sysciophlebia balteata* (Scudder, 1879) (NHMS-WP 5045) from the early Permian Goldlauter Formation, Thuringian Forest basin, Cabarz quarry, Germany. **A**. Overview (composite photograph of part and counterpart). **B**. Close-up of the ovipositor (red-coloured). Abbreviations: an, antenna; fe, femur of prothoracic leg; fw, forewing; hc, head capsule; hw, hind wing; mp, maxillary palpus; pn, pronotum; ti, tibia of prothoracic leg.

least in late nymphal stages is likely. In this case, these long valves would develop gradually, gaining length with each molt. Yet, we do not know the exact length of the valves of the nymphs as they all appear to be broken off distally. We can therefore only conclude that this second interpretation is rather plausible but cannot further validate it.

As externally visible ovipositors in nymphs are known from different groups of Polyneoptera (see above) and are possibly developed in early dictyopterans, this character might be considered a plesiomorphy. Alternatively, it is also possible that in this group the ovipositor development is pre-displaced (peramorphic heterochrony), resulting in a larger ovipositor in the adult, i.e., the large size of the ovipositor is achieved by an evolutionary change to an early onset of the development of the ovipositor.

Ovipositor morphology.—The ovipositor of specimen YPM IP 000057 is preserved prominently and clearly recognisable, but also in specimens YPM IP 027870 and YPM IP 027872 structures are visible which can be interpreted as parts of an ovipositor. As the exact insertion areas are mostly difficult to assess, the identification of the valves remain ambiguous.

In specimen YPM IP 000057, the first pair of valves is visible thanks to the exposure of the ventral side in the fossil. In specimen YPM IP 027870 one pair of valves is almost exclusively visible in the stereo image, as the colour contrast to the matrix is rather low. In specimen YPM IP 027872, the situation is more complex. Sellards (1904) assumed the presence of more than a single pair of valves. Based on the specimens, this is difficult to evaluate. One pair can be verified. The presumed further lateral valves of Sellards (1903, 1904) are very incompletely preserved and in fact, may well represent a different structure. Sellards (1904) interpreted YPM IP 000057 and YPM IP 027872 as conspecific, representing different developmental stages. Although YPM IP 027872 is not too well preserved, it indeed resembles YPM IP 000057 in the outlines of the thoracic nota, hence, it is at least plausible that both specimens are conspecific. Yet, both specimens are of the same size and are therefore unlikely representing two successive instars. Hence, it can be considered as more likely that only a single pair of valves is represented in YPM IP 027872 and that the ovipositor morphology is similar to what we find in YPM IP 000057.

Carboniferous roachoids which are preserved with an ovipositor are rarely reported in the literature (e.g., Brongniart 1893; Laurentiaux 1951; Schneider 1978a, 1984; Wei et al. 2013). Meanwhile, numerous new finds are known (but are poorly described) which indicate that for nearly all Palaeozoic major groups of roachoids, an external long ovipositor was typical (Figs. 9, 14, 15).

It can be assumed that roachoids with long ovipositors did not have the ability to form oothecae. Compared to
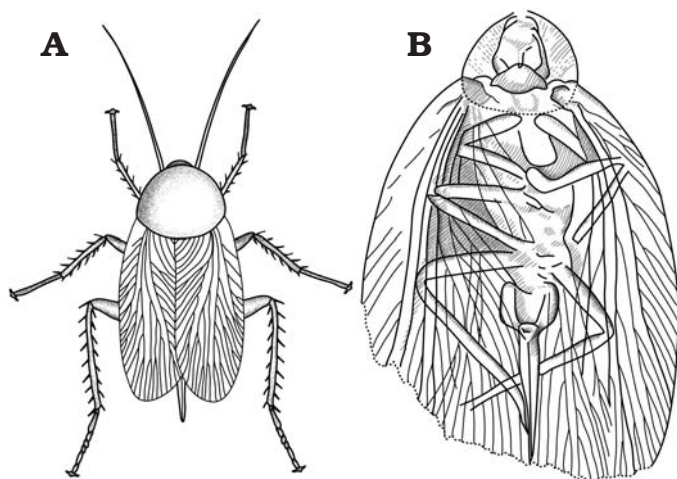
Fig. 15. Adult Carboniferous roachoids. **A**. Reconstruction of *Etoblattina mazona* Scudder, 1882, redrawn from Sellards (1904), primarily based on a specimen from Mazon Creek showing the pronotum, two forewings, and below them parts of the hindwings, but no ovipositor. Sellards (1904: figs. 10–14) assumed that the nymphs from Mazon Creek are conspecific with *E. mazona*. The here shown reconstruction based on his assumption is not provable. **B**. Drawing of *Anthracoblattina ensifera* Brongniart, 1894, redrawn from Laurentiaux (1951). Brongniart (1889) was the first who noted the presence of an external ovipositor in late Palaeozoic blattoids in his description of *A. ensifera* (hence the given specific epithet). Not to scale.

observations of modern polyneopterans, it is likely that these early dictyopterans laid single eggs into a substrate like many species of Orthoptera (about egg deposition of Orthoptera see e.g., Masaki 1986; Masaki and Walker 1987; Preston-Mafham 1990).

Direct evidences of the egg deposition mode cannot be provided yet, and fossil oothecae are very rare, with only a few definitive specimens in total so far (Grimaldi and Engel 2005; Anisyutkin et al. 2008; Poinar 2010; Hörnig et al. 2013). Beside these Cretaceous and Miocene specimens, five fossils from the Carboniferous are described in the literature as oothecae-like and are discussed to be remains of putative oothecae of Carboniferous roachoids by Sellards (1904: fig. 25), Schlechtendal (1912: pl. 4: 32, without description), Handlirsch (1906: 181, pl. 18: 47–49, the specimen of Sellards 1904 and Schlechtendal 1912), Pruvost (1919: text figs. 34, 35, pl. 22: 15, 16; 1930: 164, not figured). Yet, clear evidence cannot be provided that these fossils indeed represent oothecae or, even if that would be the case, that they were produced by dictyopterans.

Laurentiaux (1951, 1963) and Laurentiaux and Laurentiaux (1981) discussed possible links between sexual dimorphism of the geometry of the wings of Carboniferous representatives of Mylacridae, such as the presence of extremely long ovipositors in *Anthracoblattina ensifera* of Commentry, France, and the supposed presence of oothecae in the Carboniferous. Laurentiaux concluded a split into two evolutionary linages of Dictyopera in the early late Carboniferous (Laurentiaux 1959: fig. 3): the Eoblattodea, which possess long ovipositors, and the Neoblattodea, which are able to produce oothecae. He also argued that Eoblattodea,

which includes Anthracoblattina (Phyloblattidae Schneider, 1983), became extinct in the Permian, and Mylacridae, as representatives of Neoblattodea, already became extinct in the late Carboniferous (Laurentiaux 1959). Representatives of Poroblattinidae of Laurentiaux' (1959), i.e., "Série Poromesoblattinide", occur up to the Triassic, while from his "Mesoblattinidea" arose the modern groups of Dictyoptera (Laurentiaux 1959).

Meanwhile, based on further fossil findings of representatives of all groups of Palaeozoic dictyopterans listed by Schneider (1983) except Archimylacridae und Mylacridae, an extremely long ovipositor can be observed in these groups (JS, personal observation). This includes also representatives of Poroblattinidae, which furthermore do not occur up to the Mesozoic, as assumed by Laurentiaux (1959) and Vršanský et al. (2002), but became extinct in the early Permian (Schneider 1983). New completely preserved fossil findings of roachoids from the Carboniferous and Permian (JS, personal observation) allow the conclusion that the males did not possess long and slender forewings, as discussed by Laurentiaux (1951, 1959, 1963), Laurentiaux and Laurentiaux (1981), and Schneider (1977) with comparison to modern groups. Instead, the described long and slender forewings belong to the females, which cover partially the long ovipositor with the wings; the broader forms of the fore wings belong to males (JS, personal observation). This relation of the length of the fore wings of males and females is first reversed in modern groups, in which females possess relatively broader forewings than visible in males.

Therefore, the dimorphism in the wing geometry of the Carboniferous to Jurassic roachoids was possibly misinterpreted in the context of the distinction between roachoid males and females with a reduced ovipositor. Hence, it cannot be seen as argument for a possible presence of the ability to produce oothecae of Palaeozoic representatives of Dictyoptera sensu lato.

Cretaceous specimens

Ascription of the specimens to Dictyoptera/Blattodea.— Compared to the Carboniferous specimens, those from the Cretaceous Crato Formation appear much more similar to Recent species in terms of general morphology. The specimens with the elongate, but not far laterally extending pronotum can be determined to the species level as *Ponopterix maxima* Bechly, 2007. All other specimens are more problematic. They distantly resemble modern cockroaches, especially representatives of Blattellidae, but differ markedly in the morphology of the ovipositors. Therefore, we will treat these under open nomenclature as the aim of the present study was not taxonomic, but focused on the ovipositor morphology.

Ovipositor morphology.—*Type 1*: Among the specimens of the Cretaceous Crato Formation of Brazil, several principally different shapes of ovipositors are recognisable. Two types can be directly observed, a third type is indirectly inferred.
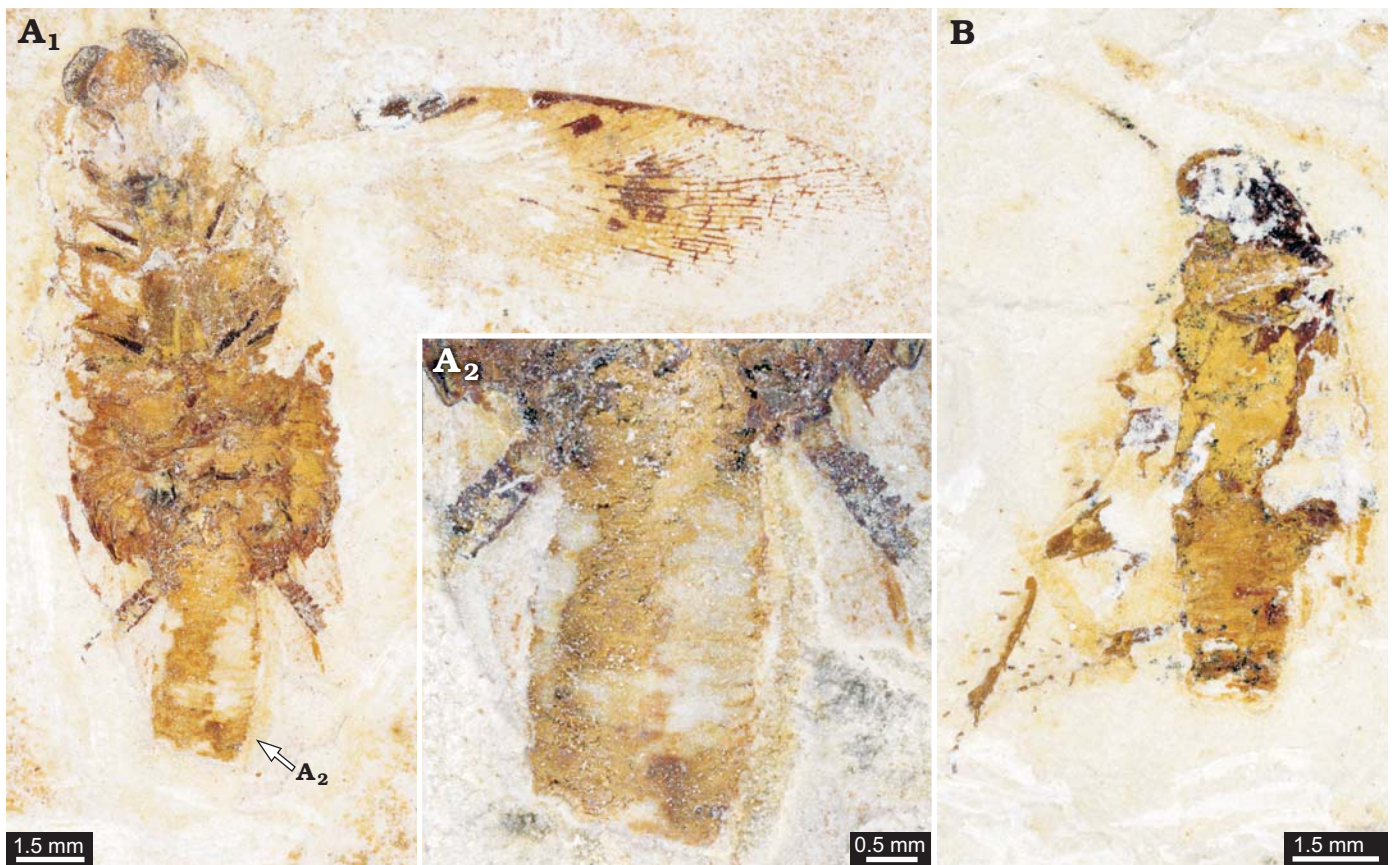
Fig. 16. Cockroaches with oothecae from the Aptian, Cretaceous Crato Formation of Brazil. **A**. AI 3208, "*Mesoblattina*" cf. *limai* Pinto and Purper, 1986. Overview (A$_1$), close-up of ootheca (A$_2$). **B**. Undescribed cockroach AI 292 (from Hörnig et al. 2013: fig. 4).

The ovipositor type 1 is represented by two specimens: ROMIP64635 (Figs. 10A$_1$, 11A$_1$) and ROMIP64634 (Figs. 10B$_1$, 11B$_1$). One pair of valves is apparent, which cannot be exactly identified. The valves are quite long and slender, but prominent, comparable to those of Carboniferous dictyopterans, although not as long. The two valves appear separated in both specimens, which is most likely caused by the incomplete preservation.

Until now, long and slender ovipositors have been recognised only in one case for Cretaceous roachoids; one representative of ?*Mesoblattina* from Cretaceous (Mongolia) is depicted by Vishnikova (1986: 167 and 203). The specimen was interpreted (see drawing in Vishnikova 1986: 167) to bear a long prominent ovipositor. The next oldest described roachoid specimens with long ovipositors are represented by the Jurassic species *Karataublatta longicaudata, Rhipidoblattina maculata, R. brevivalvata* (Vishniakova 1968; Liang et al. 2017), and *Solemnia alexandri* (Vršanský 2008). While not as long as in these older forms, ovipositor type 1 in the Crato specimens is significantly longer than that of type 2 (see below). This morphology indicates that these forms, despite their modern appearance, retained the plesiomorphic strategy of laying single eggs into a substrate.

Type 2: Specimens that have a protruding, but rather short and broad ovipositor (here, called type 2) co-occur with specimens featuring the long ovipositor type 1. Most likely, the second pair of valves is rather elongate, and the first and third pairs of valves are rather broad. In some specimens, the ovipositor valves are partly protruded by an elongated, but rather broad structure on the most distal part of the abdomen. In comparison with the ovipositor morphology of modern representatives of Mantodea, it is plausible that these structures represent an elongated part of post-ocular segment 15 (sternite 7).

This type of ovipositor is found in specimens of *Ponopterix maxima* Bechly, 2007 (Figs. 12B$_1$, C$_1$, 13B$_1$, C$_1$), but also in specimens which appear like modern forms in general morphology (ROMIP64636, Figs. 10C$_1$ and 11C$_1$; ROMIP64638, Figs. 10D$_1$ and 11D$_1$, ROMIP64637, Figs. 12A$_1$ and 13A$_1$; ROMIP64641, Figs. 12D$_1$ and 13D$_1$). While in the here described specimens of *P. maxima*, the first pair of valves is more difficult to spot, a specimen depicted in Bechly (2007) has a well preserved first and second pair of valves. Similar ovipositors have been described for most Cretaceous dictyopteran species (Rasnitsyn and Quicke 2002), including specimens of another species of the Crato Formation, *Ponopterix axelrodi* Vršanský and Grimaldi, 1999 (Vršanský 2003).

Bechly (2007) already compared this type of ovipositor to that of Mantodea. From a functional point of view, it is unlikely that these roach-like dictyopterans with ovipositor

type 2 could produce oothecae like modern blattodeans. Yet, it could well be possible that a protruding ovipositor facilitated the production of an ootheca, presumably in a mode that is comparable to that of Mantodea. Thus, these early forms might well have produced oothecae attached to a substrate.

Type 3: A third type of ovipositor is indicated by specimens with preserved oothecae attached to the abdomen (Fig. 16; Grimaldi and Engel 2005; Hörnig et al. 2013). It must be assumed that these forms had a rather short ovipositor concealed by the elongated post-ocular segment 15 (abdominal sternite 7). Only this structure would allow roaches to "grab" the ootheca and carry it with them. Yet, it must be noted that these specimens strongly resemble most of the specimens with ovipositors of morphotype 1 and 2 in general body morphology.

Evolutionary reconstruction

Although the present data cause some challenges concerning taxonomy and identity of the here described specimens, we can infer an evolutionary reconstruction of the transformation of the ovipositor. Coupled to this, it is also possible to infer the evolutionary changes of the reproductive strategies within Dictyoptera sensu lato.

Dictyoptera sensu lato.—The ancestral condition for Dictyoptera sensu lato is a long and slender ovipositor, which most likely already started to develop in the late nymphs. Whether this condition is (aut-)apomorphic for Dictyoptera sensu lato or a plesiomorphy is currently unclear. These early forms did not yet produce oothecae but laid single eggs, presumably into substrate. The long ovipositors must have caused evolutionary costs, as it constraints the female's mobility. These costs were counterbalanced by the advantage of the protection of the eggs. The extremely long ovipositors at least persisted from the Carboniferous into the Jurassic (Vishniakova 1968, 1982; Schneider 1984); in the Cretaceous, still moderately long ovipositors were present, and the strategy to lay single eggs co-existed with further derived ones.

Dictyoptera sensu stricto.—Autapomorphic for Dictyoptera sensu stricto is a shorter ovipositor with a still rather elongate and slender second pair of valves and a broader first and third pair of valves; the second pair of valves could be protruded from the first and third pair of valves, but were at equal length in resting position.

This principal type of ovipositor is still found in modern mantodeans (Figs. 1D–F, 2B). The stem species of Dictyoptera sensu stricto might have produced oothecae attached to the substrate, e.g., branches or leaves. While the case material is still viscid, single eggs are deposited in a specific arrangement (as indicated in modern mantodeans; Preston-Mafham 1990; Grimaldi and Engel 2005; Leong 2009; Wieland 2013). If representatives of Mantodea were indeed already present in the Jurassic, this strategy, which
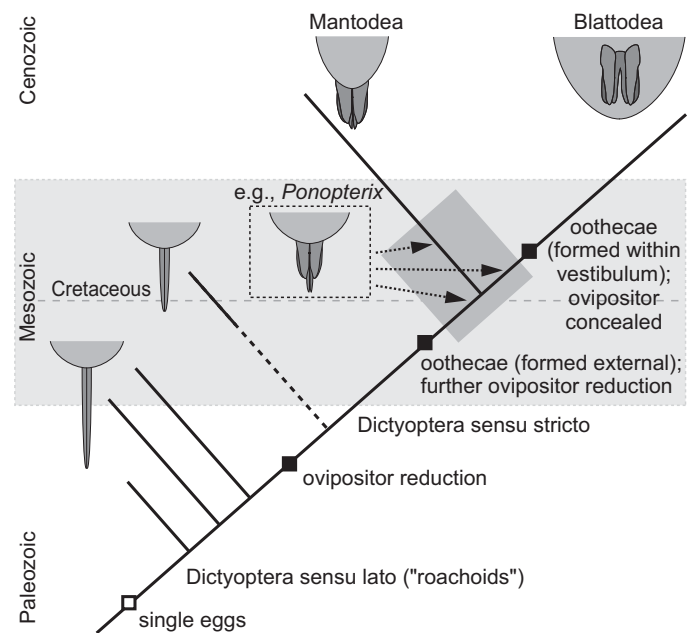

Fig. 17. Proposed evolution of ovipositor morphology in Dictyoptera.

persists until today in Mantodea and was further derived in the blattodean linage, must have been already developed before.

Blattodea.—A further shortened ovipositor concealed by the elongate post-ocular segment 15 (abdominal sternite 7; subgenital plate; Figs. 1A–C, 2A) is considered autapomorphic for Blattodea (Fig. 17). This facilitates the production of free (non-adhesive) oothecae and active maternal transport (at least for some time). This strategy was at least present since the Cretaceous and persists until today (and was further derived in representatives of ovoviviparic and viviparic blattodean species; see e.g., Bell et al. 2007).

Evolution of the subgenital plate.—An important structure in the genital apparatus of female modern representatives of Dictyoptera sensu stricto is the specialised sternite of post-ocular segment 15 (abdominal sternite 7), the so-called sub-genital plate. In all modern female representatives, it is elongated in anterior-posterior axis (compared to other sternites). It is furthermore drawn out posteriorly into two distinct lobes, which partly (Mantodea) or fully (Blattodea) cover the genitalia, forming the ventral border, the so-called vestibulum in the latter.

It has been suggested that this specialisation of the sternite of post-ocular segment 15 characterises a larger group within Polyneoptera including not only Dictyoptera but also Dermaptera (Ax 2000). This evolutionary interpretation clearly ignores fossil dictyopterans. Neither already known specimens from the Carboniferous, nor specimens re-investigated here show a specialisation of the sternite of post-ocular segment 15. From a functional point of view, this seems barely surprising. With an elongate ovipositor, a drawn out sternite of post-ocular segment 15 would not pro-

vide any support. Only in combination with a shortened ovipositor, such a specialisation of the sternite has advantages.

Therefore, it would be interesting if we could demonstrate that shortening of the ovipositor and specialisation of the sternite of post-ocular segment 15 was indeed also evolutionarily coupled, or which character evolved first. Unfortunately, our fossils are only of limited value for this discussion. Two specimens with a type 2 ovipositor (ROMIP64637, Figs. 12A, 13A; ROMIP64641, Figs. 12D, 13D) clearly possess already a specialised sternite of post-ocular segment 15, being drawn out into two distinct lobes. Other specimens are less informative in this region. At least, it seems that all specimens that have a longer ovipositor do not have a specialised sternite of post-ocular segment 15. However, due to the difficulties of preservation and interpretation in this region, this cannot be stated with certainty. With this type of data, we can only conclude that a specialised sternite of post-ocular segment 15 (sub-genital plate) evolved within Dictyoptera sensu lato.

Conclusions

The phylogenetic consequences from the data presented here are limited as we did not deal with other characters besides the ovipositor. Yet, we can point out possible character conflicts which will need to be addressed in future studies:

(i) The ovipositor morphology of type 1 makes it unlikely that species with such an ovipositor are an ingroup of Dictyoptera sensu stricto.

(ii) Specimens with ovipositor morphology of type 2 are (likely) representatives of ingroups of Dictyoptera sensu stricto. Yet, their exact position could be either before the branching off of Mantodea, i.e., below the "crown-group"; hence, Dictyoptera sensu stricto is not necessarily identical to the "crown-group", on the lineage towards Mantodea, or on the lineage towards Blattodea (see also Fig. 17). This principal discussion has been put forward (at least in part) for *Ponopterix*, but also applies for other forms with ovipositor type 2 (see Vršanský 2003; Grimaldi and Engel 2005; Bechly 2007). We consider it as unlikely that these forms are ingroups of Blattodea as it would demand for a parallel evolution of the blattodean ootheca (Vršanský 2003; Bechly 2007).

(iii) Specimens with ovipositor type 3 are likely an ingroup of Blattodea.

(iv) A fossil ootheca from the Cretaceous of Israel (Anisyutkin et al. 2008) is not necessarily that of a mantodean. It might well be the product of a non-mantodean dictyopteran with an ovipositor of type 2.

(v) The Cretaceous is a time in which all three reproductive strategies (single eggs, substrate-attached ootheca, "mobile" ootheca) existed at the same time slice (and in the same fauna), all in otherwise very similar-appearing cockroach-like morphotypes.

Acknowledgements

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