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Systematic palaeontology (invertebrate palaeontology)

New fossil arthropods (Notostraca and Insecta: Syntonopterida) in the Continental Middle Permian of Provence (Bas-Argens Basin, France)

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Abstract

Apart frequent and relatively common ichnites, only a few body fossils (Ostracoda) have been mentioned in the Red Continental Permian formations of Provence till these last years. During 2006 and 2007 field researches, new arthropods have been discovered in the Pradineaux Formation of the Bas-Argens. They are Triopsidae (Crustacea, Notostraca) and an insect wing (Syntonopteridae) corresponding to a new genus and species *Gallolithoneura butchlii* gen. et sp. n. This latter is the first insect record in the Permian of Provence and the youngest one of this enigmatic Carboniferous paleopteran family. As in the other French Permian basins (Lodève, Saint-Affrique), these discoveries demonstrate that the Permian Provençal paleofauna was rich and diverse. For the Upper part of the Pradineaux Formation, Capitanian (Upper Guadalupian) in age, the Triopsidae mean the presence of periodical ponds settled in a playa environment evolving under a xerophytic climate. *Gallolithoneura butchlii* suggests also the presence of aquatic habitats. ***To cite this article: R. Garrouste et al., C. R. Palevol 8 (2009).***

Résumé

Nouveaux arthropodes fossiles (Notostraca, Insecta : Syntonopterida) du Permien moyen continental de Provence (Bas-Argens, France). Jusqu'à ces dernières années, hormis les diverses traces d'activités animales, très peu de fossiles corporels furent trouvés dans les bassins permiens provençaux. Seuls des Ostracodes et des restes indéterminables étaient connus dans des niveaux carbonatés du bassin de l'Estérel. Les découvertes d'Arthropodes nouveaux dans la partie supérieure de la Formation des Pradineaux du bassin du Bas-Argens, datée du Capitanien (Guadaloupien supérieur) comblent donc cette lacune. Elles laissent espérer de nouvelles observations en provence à l'égal de ce qui a été réalisé dans celui de Lodève (Languedoc). En Provence, les nouveaux fossiles correspondent à des Crustacés Triopsidae et à un insecte. Les premiers permettent d'imaginer des environnements de playas se développant sous un climat aride. Le second représenté par une aile d'insecte a été nommée *Gallolithoneura butchlii*

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gen. et sp. n. Elle correspond au dernier représentant connu de la famille des Syntonopteridae et suggère aussi la présence d'étendues d'eaux plus ou moins permanentes. ***Pour citer cet article : R. Garrouste et al., C. R. Palevol 8 (2009).***

Keywords: Arthropoda; Notostraca; Insecta; Syntonopterida; Middle Permian; Var; France

Mots clés : Arthropoda ; Notostraca ; Insecta ; Syntonopterida ; Permien moyen ; Var ; France

1. Introduction

Before 1997, the French Red Permian outcrops were supposed to be devoid of fossil insect bodies and with very few arthropods except for the single study of a meganeurid wing from the French Alpes-Maritimes, Dôme de Barrot deposits [31]. The large deposits of the Lodève and Provence Basins were first known only for ichnites [19,22,23]. This situation completely changed after 1997, thanks to the discoveries by Dr. J. Lapeyrie and the studies of a very rich fauna of Arthropoda, mainly insects [1–11,25,26,35–40].

The South Provence in the Var Department shows large Red Permian Formations located in a depression between the crystalline Massif des Maures (Variscan basement) and the Provencal Mesozoic foothills (Fig. 1). Formations were deposited in several basins arranged from west to east along 150 km. Despite palaeontological researches [12,13,15,18,21,22,24,28,29,45], except ichnofossils frequent and relatively abundant and some stromatoliths [20], body fossils found were exceptional, only mentioned by ostracods [13,45]. It is the reason why, one of us (RG) led field researches in several basins: le Luc, le Muy and Bas-Argens.

In this latter basin, RG found for the first time a little slab bearing Notostraca (Crustacea: Branchiopoda). Likewise, a Swiss naturalist (Lorentz Buchli, LB) discovered almost in the same place a remarkable insect wing of the Carboniferous family Syntonopteridae that he gave to RG. Both fossils are quite new in the Provençal Permian basins (from Var to Maritimes Alps). They will allow to precise the palaeoenvironment and to describe a new insect.

2. Geology settings and age of the fossiliferous sites

2.1. Location

These fossils have been found by surface prospecting at several hundred meters of distance, near a site already known for footprints and invertebrates traces [15,46]. It is the fossiliferous site F7 of the Coulet-Redon hill, located to the north of Roquebrune-sur-Argens. The new sites belong to the upper part of the Pradineaux Formation (Fig. 1) overlying in this area by that of Mitan [46].

The **F7n** (F7 for the Collet-Redon fossiliferous site and n for Notostraca) having supplied triopsid carapaces is situated in the east side of the hill, close to it summit but as the plane bedded mudstone fossiliferous slabs were collected in a small ravine, we do not know exactly the corresponding layer. Nevertheless, clearly, this bed is located above the δ 2 dolerit, equivalent of the B3 trachyandesit, this latter being described from the Esterel basin by Boucarut [13]. In this site **F7n,** some sheeted silstones show also large plants stem prints (Fig. 2).

The **F7i** (i for insect) site is settled on a slope of the "Petit Coulet". Herein, large red laminites show ripple marks (Fig. 3) and plant imprints lightly displaced from the original beds by gravity. The wing fragment was found in this place by M. Butchlii above layers bearing the footprints *Microsauripus acutipes* Moodie, 1929 similar to those of *Varanopus curvidactylus* Moodie, 1929 but smaller (Gand in [16,17,23]) (Fig. 4) and *Dromopus didactylus* Moodie, 1930 (Fig. 5). These ichnites were collected in the quarry by the third author [15]. Stromatolitic-like structures were also remarked by RG and LB (Fig. 6). All these fossiliferous beds underlay the local black δ 2 dolerite.

2.2. Age of fossiliferous sites

The Pradinaux Formation [33,45–47] is on average 100 m thick. It begins by conglomerates with many rhyolitic pebbles coming from the underlying A7 flow, dated from radio-isotopes of 272, 5 ± 0, 3 Ma [34,49]; for example, Upper Kungurian. The above following beds are fluvial greenish to beige-brownish sandstones. Overlying are finer and often sheeted sandstone/siltstones in which sedimentological, biological marks (ripples, rain-drops, dessication, footprints, burrows, invertebrate trackways, etc.) and macroflora are rather frequent [15,45] (Fig. 2). All meaning deposits in shallow water environment. In the Upper part of the Formation are green to brown lacustrine carbonate-rich mudstones, decimetric thick [45,47]. Some carbonate rolls are also met. They were made in marsh environment.

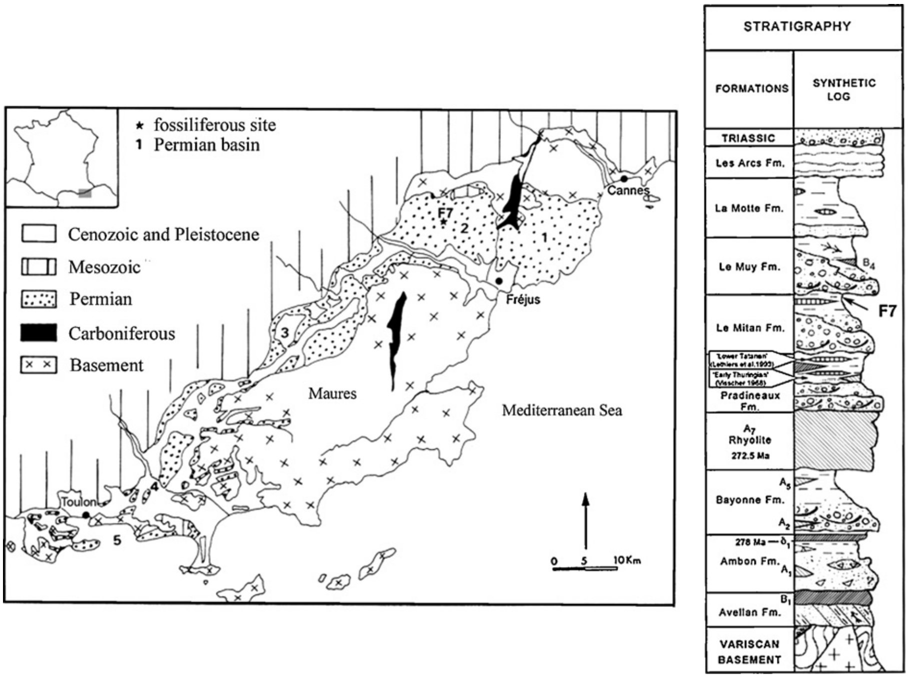

Fig. 1. Var (France) Permian basin location. F7: Coulet Redon site. 1: Esterel; 2: Bas-Argens; 3: Le Luc; 4: Cuers-Sollies; 5: Toulon; modified from Demathieu et al. [15]; stratigraphy of the Bas-Argens Permian sedimentary, after Gand and Durand [23] and Toutin et al. [46]. F7: Coulet Redon fossiliferous site.

Fig. 1. Localisation des bassins sédimentaires permiens du Var (France). F7 : Coulet Redon. 1 : Esterel ; 2 : Bas-Argens ; 3 : Le Luc ; 4 : Cuers-Sollies ; 5 : Toulon ; modifié d'après Demathieu et al. [15] ; coupe stratigraphique des formations sédimentaires du bassin permien du Bas-Argens d'après Gand et Durand [23] et Toutin et al. [46]. F7 : localisation du site fossilifère de Coulet Redon.

In the neighbor Esterel basin (Fig. 1), some of the carbonates beds, located above the B3 trachy-andesit flow, equivalent of the δ 2 dolerite of the Bas-Argens basin) supplied ostracods. From Lethiers et al. [32], these fossils allow to date Early Tatarian (= Midian) the fossiliferous beds; for example, Capitanian (265.8 to 260.4 Myr) sensu the global scale (ICS 2004) and sensu Menning et al. [34] (265 to 262 Myr). The Notostraca beds of the Pradineaux Formation would be Late Capitanian (Guadalupian) in age.

3. Systematic palaeontology

3.1. Triopsids (from F7n)

The triopsids belong to the following class, order and family respectively (Figs. 7 and 8),

Class Branchiopoda Latreille, 1817

Order Notostraca Sars, 1867

Family Triopsidae Keilhack, 1909

Material. Specimen MNHN-LP-R 63918, stored at the Muséum national d'histoire naturelle, Paris, France. A piece of siltstones (around 20 μm grain), 4 × 5 cm, 1 cm thick, with triopsid carapaces prints. In one face of the slab, imprints of carapaces are easily identifiable (Fig. 7), but there are also more poorly preserved prints and counterimprints on its back, possibly indicative of a multilayer deposit of carapaces.

The Fig. 7 shows the silstone slab with external cephalothoracic carapaces (or dorsal shield) of a dozen of individuals, some of them recovered with sediments. The reconstitution of this animal is proposed in Fig. 8. One can see that the ovoid-shaped shield is characteristic, with a streamlined dorsal carapace with prints of the strong lateral maxillary glands [25,42,43,44].

These fossils are attributed to notostracan Branchiopodae (Crustacea) of the family Triopsidae [42], which is known for its exceptional morphological stability from Carboniferous to Holocene, suggesting also a great ecological stability. The three best visible individuals (specimens a, b, c in Fig. 7) are about 9 to 11 mm long. The others being of the same length, we suppose that all the individuals were from the same cohort (same age). The distribution of these imprints on the slab, with at least three shields in dorsal position, and one concave imprint in ventral position, together with the absence of abdomen and telson suggest that they correspond to

Fig. 2. Plant stem from the F7n (Pradineaux Formation, rPx).
Fig. 2. Tige de plante, site F7n (formation des Pradineaux, rPx).

postmortem disarticulated bodies, deposited in a water depression.

We cannot assign these fossils to a precise triopsid species or genus because of the absence of diagnostic characters, all located on the telson or on the thoracic appendages. Gand et al. [25,26] described *Lepidurus occitaniacus* and *Triops cancriformis permiensis* from the Permian Lodève basin thank to the presence of thoracic-abdominal segments and supra-anal plates fossilised with carapaces.

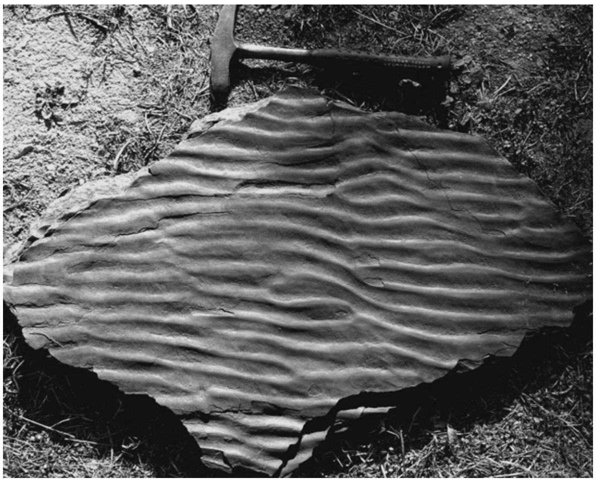

Fig. 3. Wave ripples confirming the shallow water bodies, F7i (Pradineaux Formation, rPx).
Fig. 3. Rides d'oscillation confirmant la faible profondeur des nappes d'eau, F7i (formation des Pradineaux, rPx).

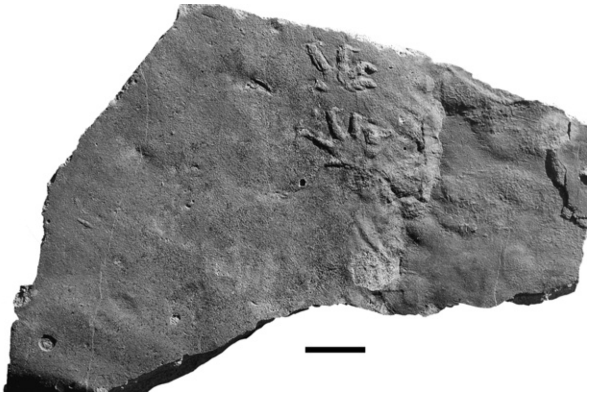

Fig. 4. *Microsauripus acutipes* counterprints, F7i (Pradineaux Formation, rPx) (scale bar represents 1 cm).
Fig. 4. Contre-empreintes de *Microsauripus acutipes*, F7i (formation des Pradineaux, rPx) (échelle : 1 cm).

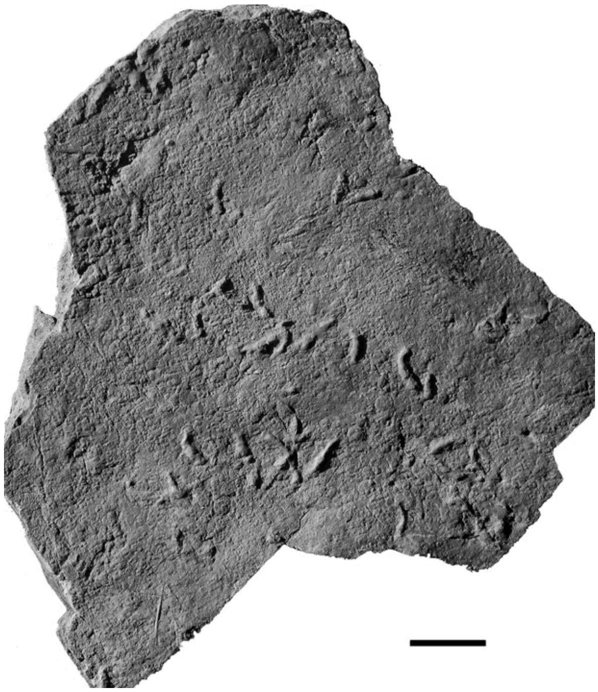

Fig. 5. *Dromopus didactylus* counterprints, F7i (Pradineaux Formation) (scale bar represents 2 cm).
Fig. 5. *Dromopus didactylus*, contre-empreintes, F7i (formation des Pradineaux) (échelle : 2 cm).

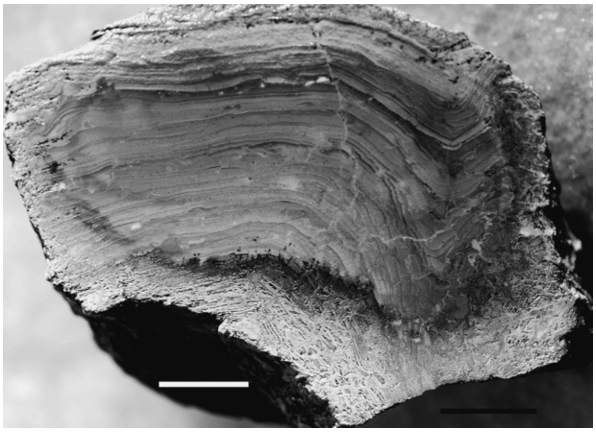

Fig. 6. Structure stromatolithique, F7i (Pradineaux Formation, rpx) (scale bar represents 1 cm).
Fig. 6. Structure stromatolithique, F7i (formation des Pradineaux, rpx) (échelle : 1 cm).

3.2. Insect wing (from F7i)

We follow the wing venation nomenclature of Kukalová-Peck [30] and Willmann [48], with the reserves concerning the possible fusion and relative positions of CuP and AA1 + 2, already indicated in Prokop et al. [41].

Class Insecta L., 1758

Order Syntonopterida Handlirsch, 1911 and/or Superfamily Syntonopteroidea Kukalová-Peck, 1985

Family Syntonopteridae Handlirsch, 1911

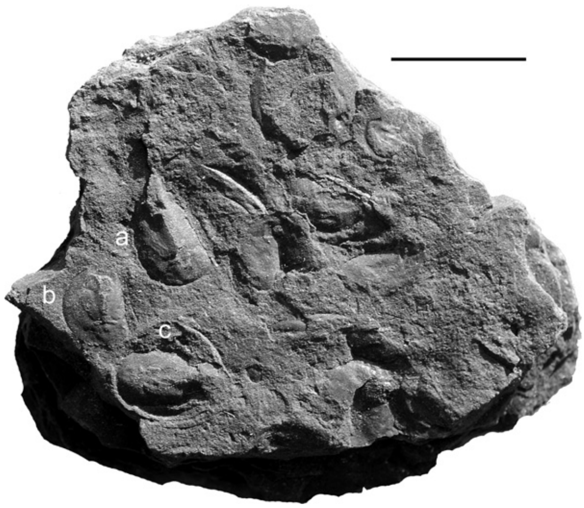

Fig. 7. Slab with Notostraca sp., LP-R63918, F7n (Pradineaux Formation, rPx) (scale bar represents 1 cm).
Fig. 7. Laminite à Notostraca sp., LP-R63918, F7n (formation des Pradineaux, rPx) (échelle : 1 cm).

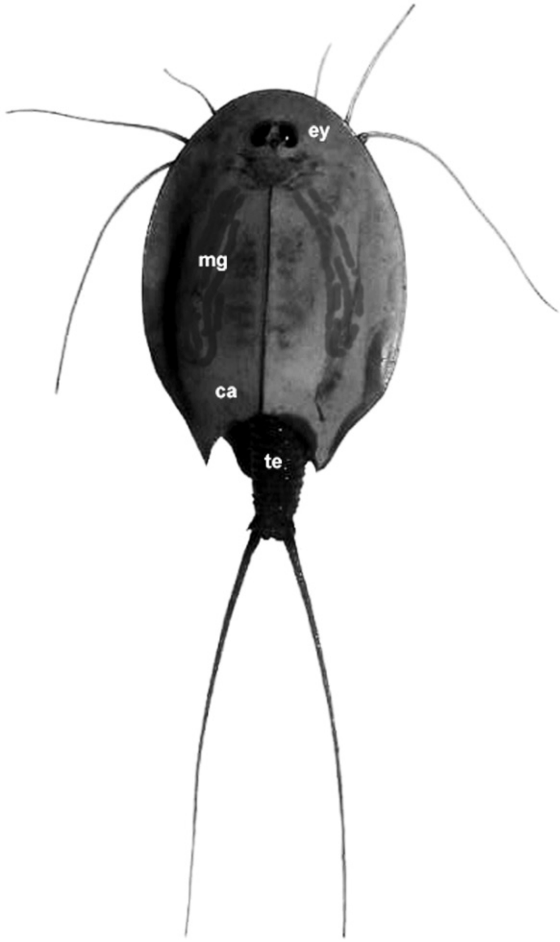

Fig. 8. Notostraca sp., body reconstruction (extant species). mg: maxillary gland; ca: carapace; ey: eyes; te: telson.
Fig. 8. Reconstitution d'un Notostraca sp. d'après une espèce actuelle. mg : glandes maxillaires ; ca : carapace ; ey : yeux ; te : telson.

List of included genera, after Prokop et al. [41]. *Syntonoptera* Handlirsch, 1911 (type species: *S. schucherti* Handlirsch, 1911 by monotypy); *Lithoneura* Carpenter, 1938 (type species: *L. lameeri* Carpenter, 1938); a new genus and species described by Prokop et al. [41]; *Gallolithoneura* gen. nov. (type species: *Gallolithoneura butchlii* sp. nov.)

Genus *Gallolithoneura* gen. n.

Type species. *Gallolithoneura butchlii* sp. n.

Derivation of name. Named after the Latin name *Gallia* for France, and *Lithoneura*.

Diagnosis. Apex of ScP probably near wing apex; forks of RP and MA at the same level, well distal of that of MP; fork of MP distal of that CuA; MP and CuA with single forks into two branches, with areas between them triangular in shape and rather reduced.

Gallolithoneura butchlii sp. n. (Figs. 9 and 10)

Fig. 9. *Gallolithoneura butchlii* gen. et sp. n., photograph of holotype, LP-R 63893 (scale bar represents 1 cm).
Fig. 9. *Gallolithoneura butchlii* gen. et sp. n., photographie de l'holotype, LP-R 63893 (échelle : 1 cm).

Description. Print of the median part of a wing with apex and base missing, no trace of coloration preserved; broadest part at about midwing; precostal area of CA and CP not preserved; simple concave ScP nearly parallel to anterior wing margin and reaching it distal forks of RP into branches, probably near wing apex; numerous straight and simple crossveins in area between ScP and C, not aligned with crossveins in area between ScP and RA; RA and RP probably fused a little basal of preserved part of wing; RA strong, convex, simple, parallel to ScP and ending probably in wing apex; R and MA strongly approximate in their basal parts; MP clearly concave, distally forked into two strong posterior branches, 8.4 mm basal of fork of MA, both branches of MP slightly curved posteriorly and ending on posterior wing margin well distal of level of fork of RP, area between branches of MP rather broad, with probably one secondary longitudinal vein; MA convex with two long branches and an intercalary veins between them; base of first posterior branch of RP opposite fork of MA, first branch of RP concave, apparently simple and weakly curved, at least in its preserved part; a convex and simple intercalary vein between branches of RP; CuA clearly convex, with a strong distal fork 4.1 mm basal of level of fork of MP, anterodistal branch of CuA parallel to posterior branch of MP, posterobasal branch of CuA the shortest and more curved than the other one; area between branches of CuA triangular with a secondary concave longitudinal vein in it; concave CuP simple, weakly curved; AA convex but only its apex is preserved; wing membrane between main veins with straight, simple crossveins perpendicular to main veins.

Dimensions. Length of wing fragment about 40 mm, probable total length about 65 to 70 mm; wing width about 15.4 mm. Wingspan probably around 15 to 16 cm.

Material. Holotype specimen MNHN-LP-R 63893 (median part of a single wing; supposed folded on another wing), on a small siltite slab, 1 cm thick (laboratoire de paléontologie, Muséum national d'histoire naturelle, Paris, France).

Derivation of name. Named after Mr Lorentz Butchli who found and donated the type specimen.

Age and outcrop. Permian, Capitanian, Capitanian (Upper Guadalupian), Pradineaux Formation, Petit Coulet Redon Hill, La Bouverie, Roquebrune-sur-Argens, Var, France.

Diagnosis. As for the family.

Discussion. The presence of only simple crossveins perpendicular to main longitudinal veins in the wing membrane (archaedictyon reduced and transformed into a regular polygonal meshwork of crossveins) excludes affinities with the palaeodictyopteroid orders and many Palaeozoic Ephemeroptera. The general pattern of wing venation would be compatible with an attribution to the Odonatoptera, but under this hypothesis, the vein that we call here “MA” would be in fact “IR2” and in that case, it would be distally forked, which is unlikely in all Palaeozoic

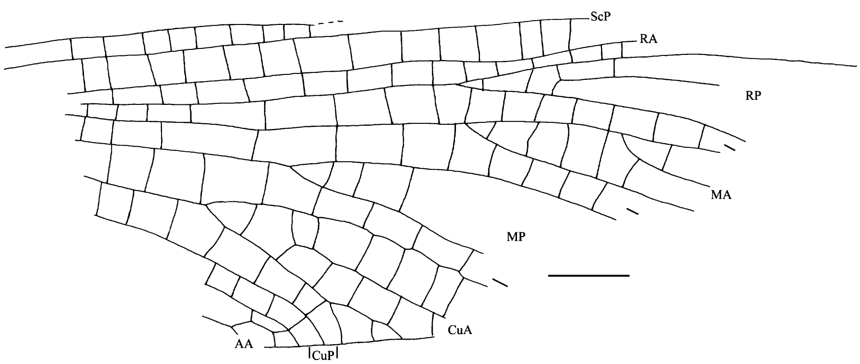

Fig. 10. *Gallolithoneura butchlii* gen. et sp. n., wing venation, holotype, LP-R 63893 (scale bar represents 1 cm).
Fig. 10. *Gallolithoneura butchlii* gen. et sp. n., nervation, holotype, LP-R 63893 (échelle : 1 cm).

Odonatoptera. Thus, an attribution to this order is to be rejected.

The preserved parts of the wing venation of *Gallolithoneura* are very similar to that of a Syntonopteridae Handlirsch, 1911. It especially shows a striking resemblance to *Syntonoptera schucherti* Handlirsch, 1911 (Upper Carboniferous of Mazon Creek, USA) in the relative positions of the forks of RP and MA nearly at the same level and those of MP and CuA in a distinctly more basal position [14]. The only differences concern the broader cubital area in Syntonoptera with four branches instead of two in our fossil. The new genus and species that Prokop et al. [41] recently described from the English Upper Carboniferous differs from our fossil in the less distant forks of MP and MA, MP with five branches, instead of two in our fossil, and CuA with four branches, instead of two [41]. The third syntonopterid genus *Lithoneura* Carpenter, 1938 (Upper Carboniferous of Mazon Creek, USA) differs from *Gallolithoneura* in the position of fork of MP distinctly basal of that of CuA, instead of being slightly distal in *Gallolithoneura* [48].

4. Palaeoenvironmental implications

The tadpole shrimps extant species, all belonging to genus *Lepidurus* L., 1758 and *Triops* Schrank, 1803 are characteristics of the presence of shallow, temporary freshwater, neutral to slightly alkaline, soft muddy substrate at the ground and a depth of usually less than 0.3 m [42,43]. They are sensitive to pH and salinity. The life cycle is long and needs three to five months of submersion. The range of food is wide and they can be considered as predators, herbivores or detritivores. In turbid waters they are scavengers. They dig up the mud with the front part of the carapace and with appendices [43]. Many ichnites (*Acripes, Rusophycus, Cruziana*) can be attributed to walking, digging, ploughing, and resting behaviors of Triopsidae in Permian deposits [25,26].

Feeding can vary during the growth of the animal, which can pass from a strictly phytoplanktonophagous regime when it measures less than 5 mm, to a herbivorous regime. When it is larger than 1 cm, they also feed dead congeners and living small animals [43]. It was probably so for our Coulet-Redon fossil specimens, 10 to 12 mm long. Population outbreaks are sometimes observed, with circa 300 individuals per square meters and are very important as trophic resources for many vertebrates (herptiles, fishes).

The triopsid imprints observed in the Coulet-Redon sample would have reached the necrophorous and predatory stage, on other crustaceans, dead insect bodies, young insect larvae or amphibian tadpoles and eggs. Massive death can be easily considered if environmental conditions quickly deteriorated (drought, temperature higher than 35 °C, lack of oxygen, etc.). In these conditions, only the carapaces can potentially be fossilized after body decomposition by bacteria, saprophagous organisms, and mechanical effects of flows.

On the basis of the preferences and biology of the modern triopsids, we infer that the sedimentary conditions of the Pradineaux Formation include the presence of ephemeral neutral to alkaline water bodies, in an arid climate (desiccation cracks, etc.), in a playa like environment with a mosaic of habitats and scarce vegetation, along a river with large meanders or on the shore of a temporary lake.

The fossil insect wing is quite new in the Continental Permian of Provence. It corresponds to a rather large animal with 14 to 16 cm wingspan. This fossil demonstrates the persistence of the Carboniferous syntonopterid lineage in the Middle Permian, under palaeoclimatic and palaeoenvironmental conditions strikingly different from those of the Carboniferous greenforest; for example, drier and probably outside of forest environments, but certainly near to aquatic environments. After the probable phylogenetic relationships of Syntonopteridae with Ephemeroptera and Odonatoptera, we can infer that syntonopterids had aquatic larvae [27].

These discoveries, made during short field researches, show the promising palaeontological potential of the Permian of Provence. Further prospecting shall be necessary to precise the stratigraphy and find new fossils necessary to understand the palaeoclimate and the palaeoecology of this area during the Permian. Our research into the paleontology of the Permian Continental deposits needs to improve in light of strong urbanistic pressure in the center of the Var department, before destruction of the known fossiliferous and potential sites.

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