ISSN (print): 1698-6180. ISSN (online): 1886-7995
www.ucm.es/info/estratig/journal.htm

Journal of Iberian Geology 34 (1) 2008: 115-122

Journal of Iberian Geology
AN INTERNATIONAL PUBLICATION OF EARTH SCIENCES

The Odonatoptera of the Late Permian Lodève Basin (Insecta)

Odonatoptera del Pérmico Superior de la Cuenca de Lòdeve (Insecta)

A. N. Nel[1*], G. Fleck[1], R. Garrouste[1], G. Gand[2]

[1]CNRS UMR 5202, Muséum National d'Histoire Naturelle, CP 50, Entomologie, 45 rue Buffon, F-75005, Paris, France
e-mail: anel@mnhn.fr
[2] Laboratoire de Biogéosciences, CNRS, Université de Bourgogne, Centre des Sciences de la Terre; 6, boulevard Gabriel, F-21000 Dijon, France

Received: 15/07/06 /Accepted: 27/12/06

Abstract

The discovery of numerous and very diverse Odonatoptera in the Red Late Permian Lodève Basin questions its current reconstructions of a dry to very dry palaeoclimate and palaeoenvironment. It rather suggests the presence of more or less permanent water bodies, surrounded by a diversity of terrestrial biotas. The discovery of large to very large Meganeuridae contradicts the alleged relations between the decrease of body and wing sizes of the insects during the late Permian as a direct consequence of the decrease of the oxygen atmospheric concentrations at that time.

Keywords: Insecta, Odonatoptera, Late Permian, Lodève Basin, diversity, palaeoecology, gigatism, oxygen atmospheric concentrations.

Resumen

El descubrimiento de una numerosa y variada fauna de Odonatoptera en el Pérmico Superior rojo de la cuenca de Lodève pone en cuestión la hipótesis de un paleoclima seco a muy seco para este yacimiento. Sugiere la presencia de masas de agua más o menos permanentes, rodeadas por una importante diversidad de medios terrestres. El descubrimiento de grandes a muy grandes ejemplares de Meganeuridae contradice la existencia de una relación directa entre la disminución de la talla de cuerpo y de las alas de los insectos durante el Pérmico Superior, y el decrecimiento de la tasa de oxígeno atmosférico en esta época.

Palabras clave: Insectos, Odonatoptera, Pérmico Superior, Cuenca de Lòdeve, diversidad, paleoecología, gigantismo, concentraciones de oxígeno atmosférico.

1. Introduction

The Late Permian Lodève Basin has given a very rich and diverse fauna of the superorder Odonatoptera, with about 60 specimens in five families, i.e. the large dragonfly-like Meganeuridae Handlirsch, 1908 (Paleozoic Meganisoptera) and Lapeyridae Nel *et al*., 1999 (sister group of Nodialata, only known from Lodève), and the small damselfly-like Saxonagrionidae Nel *et al*., 1999 (oldest representative of the modern clade Panodonata), Permepallagidae Martynov, 1938, and Permolestidae Martynov, 1932 (both belonging to the Permian-Early

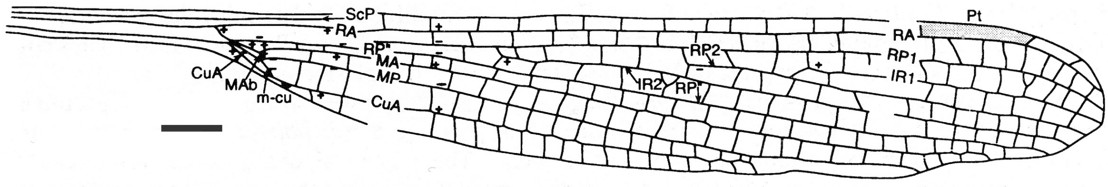

Fig. 1.- *Lodevia longialata* Nel *et al*., 1999 (Protozygoptera). Wing, Pt, Pterostigma; ScP, Subcosta Posterior; RA, radius Anterior; RP, Radius Posterior; MA, Media Anterio; MP, Media Posterior; CuA, Cubitus Anterior; m-cu, cross-vein between MP and CuA (scale bar represents 2 mm).

Fig. 1.- *Lodevia longialata* Nel *et al*., 1999 (Protozygoptera). Ala, Pt, Pterostigma; ScP, Subcosta Posterior; RA, radio Anterior; RP, Radio Posterior; MA, Media Anterior; MP, Media Posterior; CuA, Cubito Anterior; m-cu, sección entre MP y CuA (la barra de escala representa 2 mm).

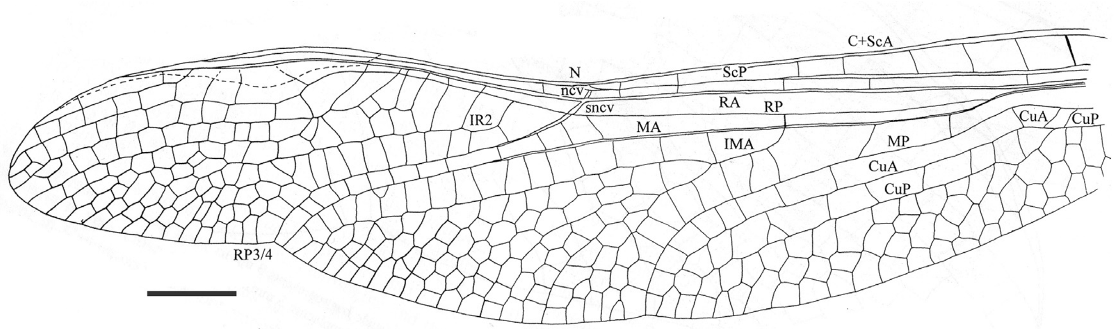

Fig. 2.- *Permaeschna dolloi* Martynov, 1931 (Protanisoptera). Forewing, C+ScA, Costal vein; N, Nodus; Ncv, nodal cross-vein; sncv, subnodal cross-vein; IR, intercalary radial vein; IMA, intercalary median vein; CuP, Cubitus Posterior (scale bar represents 5 mm).

Fig. 2.- *Permaeschna dolloi* Martynov, 1931 (Protanisoptera). Forewing, C+ScA, vena costal; N, nodo; Ncv, vena transversa nodal; sncv, vena transversa (sub-) nodal; IR, vena radial intercalar; IMA, vena media intercalar; CuP, Cubito Posterior (la barra de escala representa 5 mm).

Cretaceous clade Protozygoptera) (Nel *et al*., 1999a,b,c) (Fig. 1). The diverse Permian clade Protanisoptera Carpenter, 1931 is lacking in the Lodève Basin (Fig. 2). This group, known from the Early Permian of Elmo (USA), Early Permian and Late Permian (Kazanian) of Russia, Late Permian of Brazil, and Late Permian of Australia, is clearly widespread (Huguet *et al*., 2002). Its real (or apparent?) absence in the Lodève Basin is very surprising. It could correspond to particular ecological preferences, but the presence of a Protanisoptera in the Elmo Formation, supposed to have a similar palaeoenvironment, would contradict this hypothesis.

2. The Lodève Basin: a 'desert' with numerous aquatic odonatopteran insects?

The Odonatoptera of the Lodève Formation are all adult specimens, mainly isolated wings, or fragments of body. Some meganeurid specimens have their four wings disposed in life position but with the body almost missing. These insects have been disarticulated after their death by necrophagous animals, by the Triopsidae (Crustacea: Branchiopoda), which are extremely frequent and associated to the fragments of body of Meganeuridae (Fig. 3).

The wings of the Meganeuridae from Lodève can be easily separated into five categories, corresponding to at least five different species, i.e. a small species with wings 6-7 cm long, two medium species with wings 8-11.5 cm long (respectively with hind wings 16 mm wide and 26 mm wide), one large species with wings 16-17 cm long, and one very large species with wings 21-23 cm long (Figs. 4-9). Therefore this formation has the highest known diversity for a meganeurid fauna. It is more diverse than those of the Late Carboniferous, currently alleged period of highest diversity for this family. These species with very different wing sizes certainly had different life habits (different types of flight and sizes of preys), as for the recent Odonata: Anisoptera (dragonflies). Small species probably lived in zones with vegetation (forest, bush), while the largest ones lived in open environments.

The larvae of all Odonatoptera (except few particular cases of recent taxa with terrestrial larvae) eat and breathe

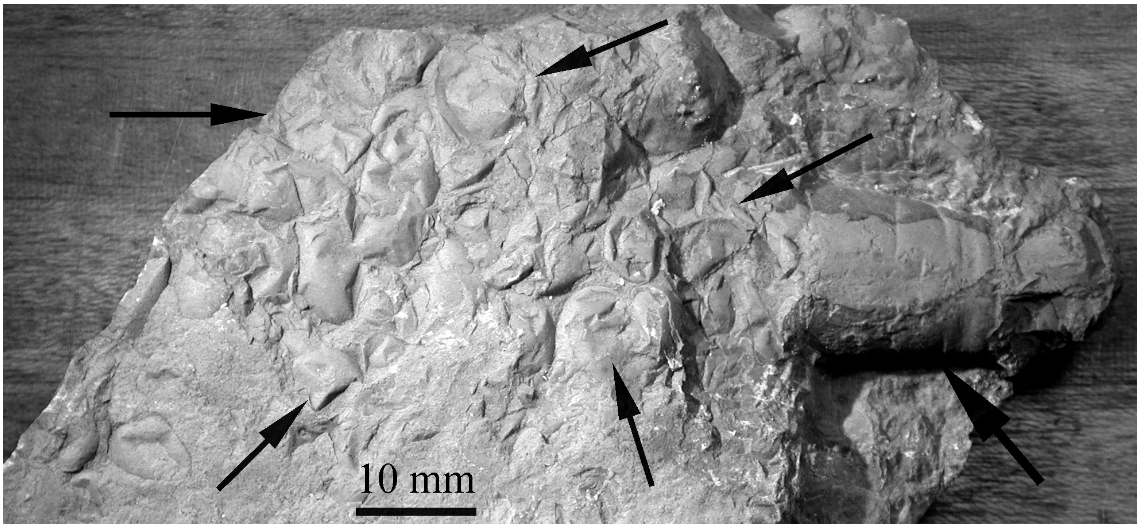

Fig. 3.- Part of an abdomen of a Meganeuridae, specimen Ld LAP 537, with numerous specimens of *Triops* (Crustacea) (scale bar represents 10 mm).

Fig. 3.- Parte de un abdomen de Meganeuridae, espécimen Ld LAP 537, con numerosos especimenes de *Triops* (Crustacea) (la barra de escala representa 10 mm).

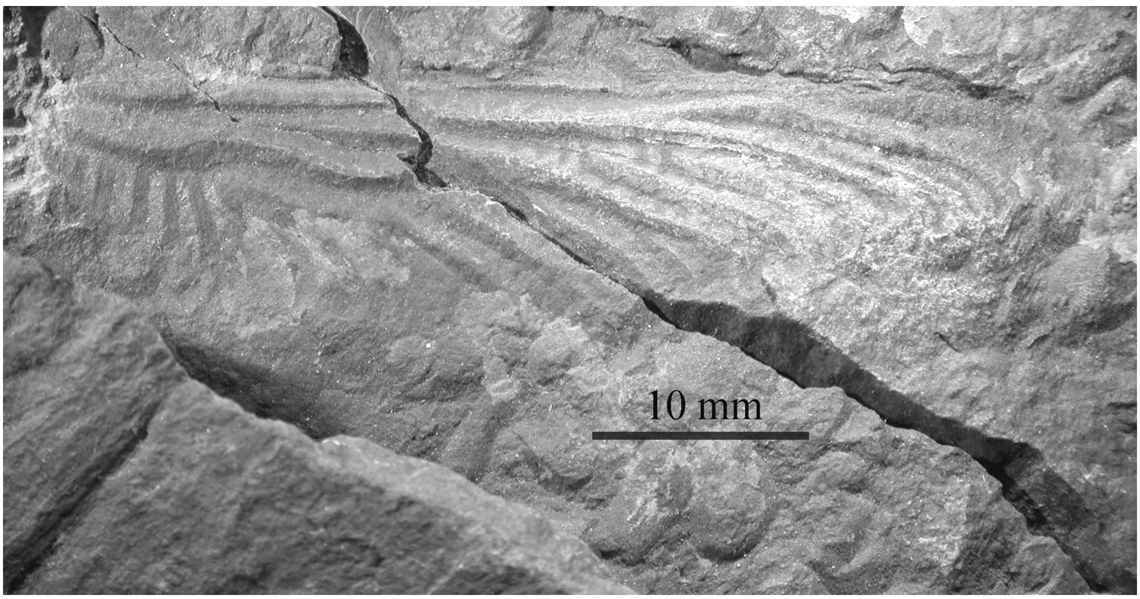

Fig. 4.- Smallest Meganeuridae from Lodève, specimen Ld LAP 33, fore wing, 48 mm long (scale bar: 10 mm).

Fig. 4.- El Meganeuridae más pequeño de Lodève, espécimen Ld LAP 33, ala externa 48 mm de longitud (la barra de escala representa 10 mm).

in water. The great majority of the recent species develop within several months but some in few weeks. Nothing is known on the early stages of the Palaeozoic Odonatoptera, except for an undescribed record of a large Late Carboniferous aquatic larva attributable to a Meganeuridae (Kukalová-Peck, pers. comm.; Grimaldi and Engel, 2005: Fig. 2.42). As the recent Odonata have primitively aquatic larvae and as the potential sister groups of the Odonatoptera (Ephemeroptera and Paleodictyopteroid orders) have aquatic larvae, the situation was probably the same for the Paleozoic Odonatoptera. The recent Odonata are attracted by humid environments suitable for their life cycle. Some females can erroneously lead their eggs in the sea.

Therefore, the presence of a diverse odonatopteran fauna at Lodève implies the presence of more or less close water bodies (pool, pond, lake, stream, etc.). The palaeoenvironment is supposed to be dry with episodic

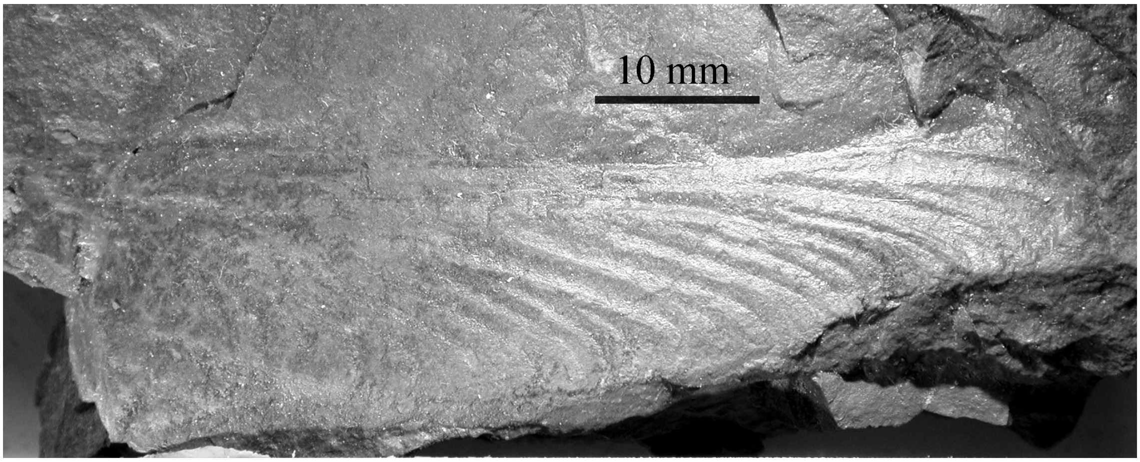

Fig. 5.- Medium Meganeuridae from Lodève, specimen Ld LAP 379, fore wing, 65 mm long (scale bar represents 10 mm).

Fig. 5.- Meganeuridae de tamaño medio de la Cuenca de Lodève, espécimen Ld LAP 379, ala exterior de 65 mm de longitud (la barra de escala representa 10 mm).

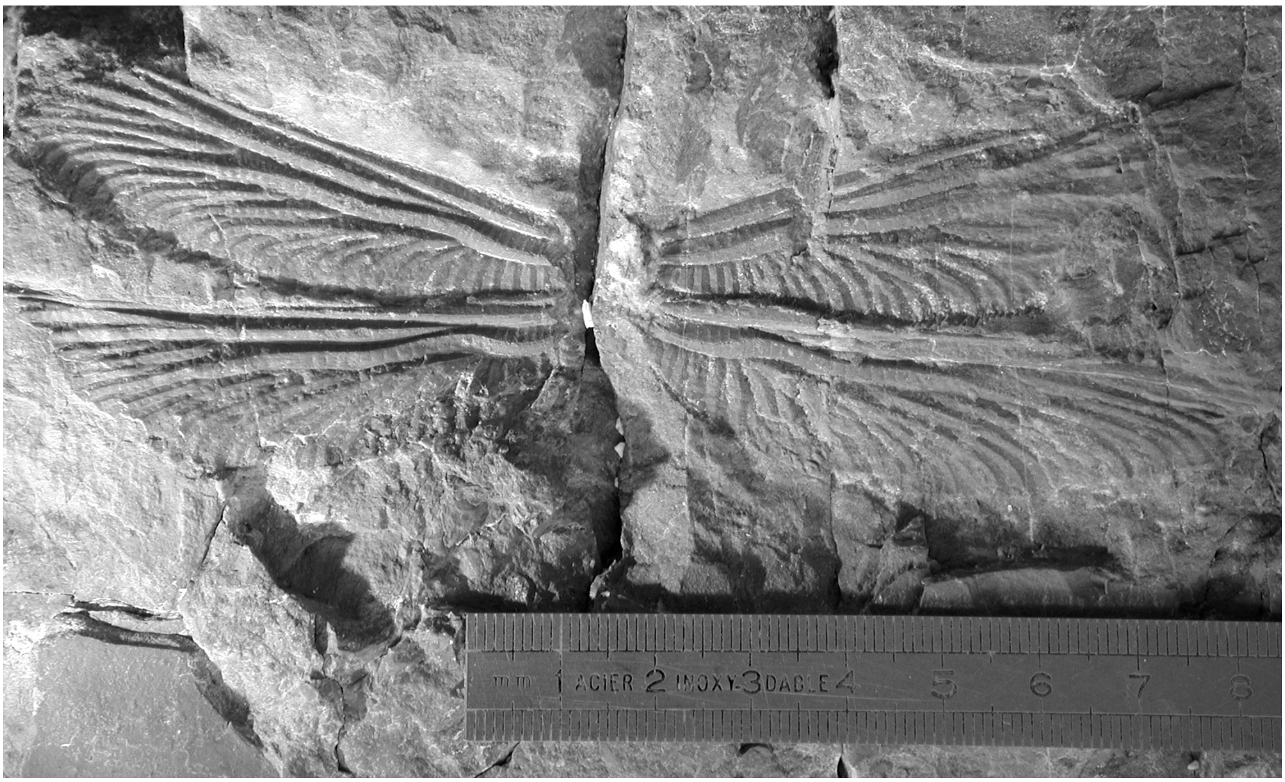

Fig. 6.- Large Meganeuridae from Lodève, specimen Ld LAP 568, four wings, wing 77 mm long (scale bar represents 10 mm).

Fig. 6.- Meganeuridae grande de la Cuenca de Lodève, espécimen Ld LAP 568, cuatro alas, la longitud del ala es de 77 mm (la escala de la barra representa 10 mm).

and more or less short rainy periods, with the presence of waters. The presence of a diverse and rich odonatopteran fauna would contradict this reconstruction. These dragonfly- and damselfly-like insects could have migrated periodically from another more humid place, and reached this area when it was filled with temporary water bodies. This hypothesis of a migratory origin for all these Odonatoptera could explain the frequent presence of adults and the total absence of larvae. But the absence of fossilised larvae does not exclude that they could not occasionally or regularly develop there, with very rapid growth. The presence of five adult specimens of the same species of Meganeuridae on the same slab of rock also suggests that numerous specimens could fly all together, falling and dying in the wet mud in the same time (Fig. 10). A similar recent situation occurs in Mauretania, where several Odonata migrate along the ocean beach and are attracted by the water bodies after the erratic rains.

Another hypothesis could be that every year, at the end of the wet period, the adults mate and led eggs in soft mud, then died massively. After the eggs stay in dry mud still next rain season, and then developed quickly. This implies a regular alternation of rainy and dry seasons. Note that Sheldon (2005) recently questioned the current interpretation of the red Late Permian beds as desert deposits, but could be the result of a good drainage of the soils, under warm and humid conditions (red Late Permian of Sardinia).

3. The Late Permian 'giant' Meganeuridae ignored that they could not be!

Atmospheric composition greatly changed during the Phanerozoic (Beerling, 1999). In particular, the Late Carboniferous is supposed to be the period of highest oxygen and lowest carbon dioxide atmospheric concentrations but on the contrary, the Late Permian shows a minimum of oxygen atmospheric concentration (Dudley, 1998; Berner *et al*., 2000; Berner, 2005). These changes are currently supposed to have induced the development of 'giant' arthropods during the former period, and their extinction during the latter (Graham *et al*., 1995; Dudley, 1998; 2001; Spicer and Gaston, 1999; Chapelle and Leck, 1999; Gans *et al*., 1999; Berner *et al*., 2000). Increased oxygen concentration would have permitted insects to become larger by increasing diffusive permeation (Graham *et al*., 1995).

'Gigantism' affected myriapods, scorpions, mayflies, palaeodictyopterids, and Odonatoptera (Grimaldi and Engel, 2005). Some of these alleged 'giants' were erroneous considered as terrestrial, viz. Selden *et al*. (2005) recently demonstrated that *Megarachne servinei* is an aquatic Eurypterida. The giant Odonatoptera: Meganeuridae are the 'symbol' and best known of these 'giant' Car-

Fig. 7.- Very large Meganeuridae from Lodève, specimen Ld LAP 445, hind wing, 105 mm long (scale bar represents 10 mm).
Fig. 7.- Meganeuridae de gran tamaño de la Cuenca de Lodève, espécimen Ld LAP 445, ala posterior de 105 mm de longitud (la barra de la escala representa 10 mm).

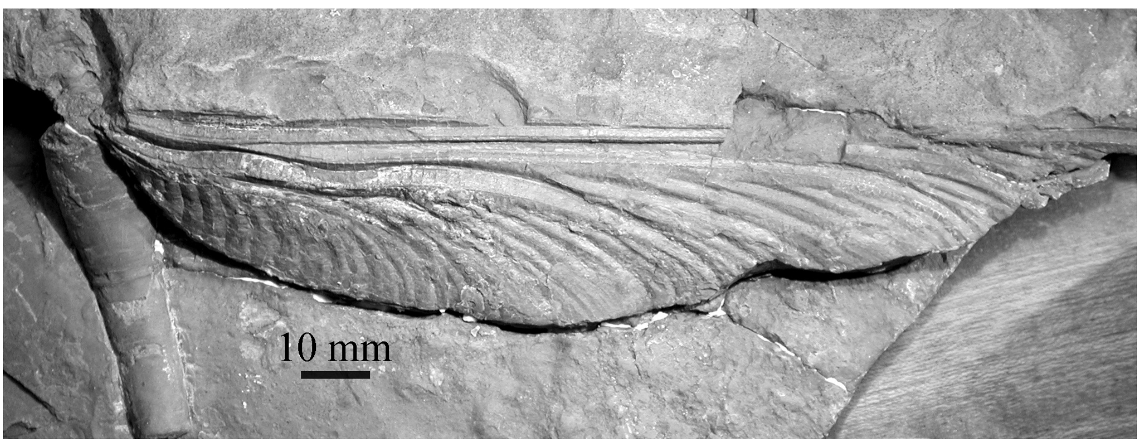

Fig. 8.- Very large Meganeuridae from Lodève, specimen Ld LAP 569, hind(?) wing 155-160 mm long (scale bar represents 10 mm).
Fig. 8.- Meganeuridae de gran tamaño de la Cuenca de Lodève, espécimen Ld LAP 569, ala posterior (?) de155-160 mm de longitud (la barra de escala representa10 mm).

Fig. 9.- Largest Meganeuridae from Lodève, specimen Ld LAP 497, wing fragment, arculus region, estimate wing length 210-230 mm (scale bar represents 10 mm).

Fig. 9.- El Meganeuridae mas grande de la Cuenca de Lodève, espécimen Ld LAP 497, fragmento de ala,"región arculus", estimación de la longitud 210-230 mm (la escala de la barra representa 10 mm).

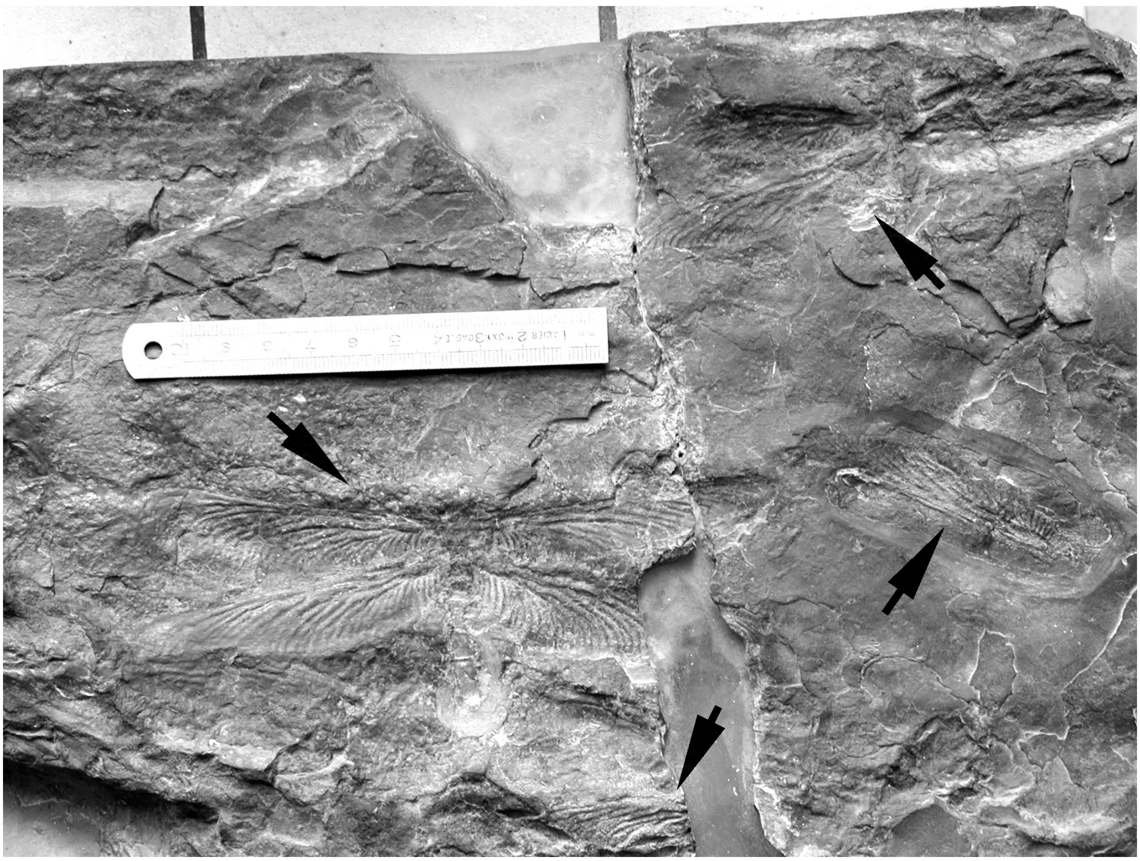

Fig. 10.- Group of four meganeurid specimens from Lodève (black arrows), wings 70 mm long.

Fig. 10.- Grupo de cuatro especimenes de meganeurid de la Cuenca de Lodève (flechas negras), alas de 70 mm de longitud.

boniferous and Early Permian insects, with 34 described species. The largest representatives are *Meganeura monyi* (Brongniart, 1884) (wing length about 320 mm), *Meganeuropsis permiana* Carpenter, 1939 (wing length about 330 mm), *Meganeuropsis americana* Carpenter, 1947 (wing length 305 mm), and *Megatypus shucherti* Tillyard, 1925 (wing 195 mm long) (Carpenter, 1947, 1992; Rasnitsyn and Pritykina, 2002; Grimaldi and Engel, 2005). The Meganeuridae are supposed to have decreased in size and diversity during the Late Permian. The family is absent in the Triassic and probably became extinct somewhere during a period of 20 M.a. between

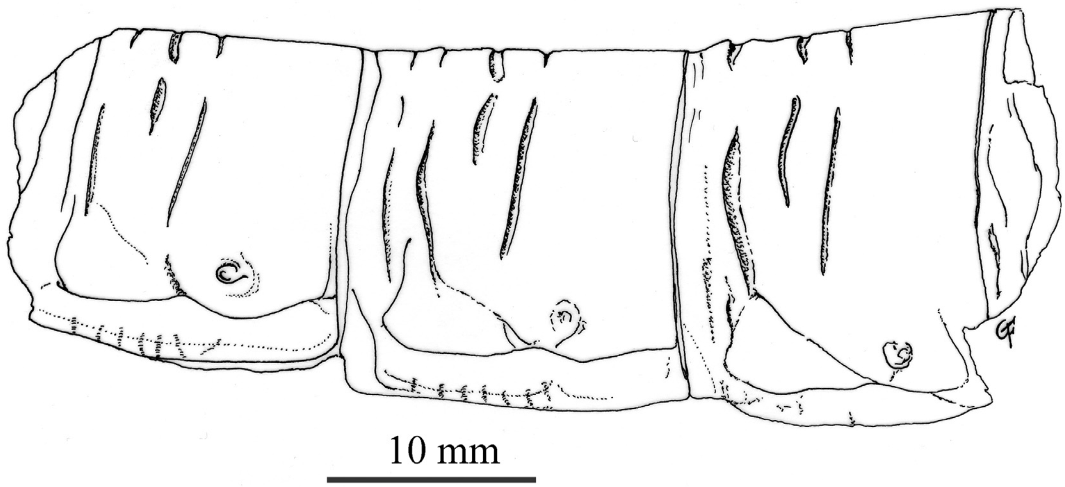

Fig. 11.- Abdomen of a Meganeuridae, with large spiracles. Specimen Ld LAP 536 (scale bar represents 10 mm).
Fig. 11.- Abdomen de un Meganeuridae con grandes espiráculos. Espécimen Ld LAP 536 (la escala de la barra representa 10 mm).

the Late Permian and the Early Triassic.

The Late Permian is supposed to be the period with lowest oxygen atmospheric concentrations. Thus after the preceding theory, large to very large Meganeuridae should be already extinct during this period. But the present discoveries alienate this theory:

The inference of wing length for the incomplete specimen Ld LAP 497 gives a wing length of 210-230 mm and a wing span of about 430-470 mm. The two specimens Ld LAP 569 and Ld LAP 567 have wings 160-170 mm long and a body 10 mm wide (wing span 330-350 mm). Therefore 'giant' Meganeuridae were still present in the Late Permian of Lodève (Figs. 7-9).

Furthermore, if the Meganeuridae had the largest known wing span, their bodies were not very large, less than 30 mm wide and 70 mm long for *Meganeura monyi*. They were smaller than some recent large Coleoptera: Scarabaeidae or Cerambycidae. Therefore, they cannot be qualified as 'giant' insects in term of body size and weight, except by comparison with the recent Odonata. One very well preserved abdomen of Meganeuridae from Lodève has large, clearly functional respiratory spiracles (Fig. 11). Nothing is known on the abdominal spiracles of the Late Carboniferous Meganeuridae. It is not possible to definitively establish these structures were secondarily developed by the Late Permian Meganeuridae, as a response to the decrease of the oxygen or if they belong to the ground plan of the Odonatoptera. Similar abdominal spiracles are also present in recent Anisoptera: Gomphidae or Austropetaliidae, but not in the more derived family Libellulidae. Therefore the latter solution is the most probable.

4. Conclusions

The large to very large Carboniferous and Permian Meganeuridae were not dependent of a high oxygen atmospheric concentration for their flight capacities or their body metabolism. The appearance and diversification of very large insects and arthropods during the Late Carboniferous could have very different origins, i.e. the absence of flying vertebrate predators, and the pressure of selection related to the increasing of the prey and predator sizes.

References

Beerling, D.J. (1999): Quantitative estimates of changes in marine and terrestrial primary productivity over the past 300 Million years. *Proceedings of the Royal Society*, London, (B), 266: 1821-1827.

Berner, R.A. (2005): The carbon and sulfur cycles and atmospheric oxygen from middle Permian to middle Triassic. *Geochimica et Cosmochimica Acta,* 69 (13): 3211–3217.

Berner, R.A., Petsch, S.T., Lake, J.A., Beerling, D.J., Popp, B.N., Lane, R.S., Laws, E.A., Westley, M.B., Cassar, N., Woodward, F.I., Quick, W.P. (2000): Isotope Fractionation and Atmospheric Oxygen: Implications for Phanerozoic O_2 Evolution. *Science*, 287: 1630-1633.

Carpenter, F.M. (1947): Lower Permian insects from Oklahoma. Part 1. Introduction and the orders Megasecoptera, Protodonata, and Odonata. *Proceedings of the American Academy of Arts and Sciences*, New York, 76 (2): 25-54.

Carpenter, F.M. (1992): Superclass Hexapoda. In: Moore, R.C., Kaesler, R.L. (eds.), *Treatise on Invertebrate Paleontology*. The Geological Society of America and the University of Kansas, Boulder, Colorado, (R), Arthropoda 4, 3/4: 655 pp.

Chapelle, G., Peck, I.S. (1999): Polar gigantism dictated by oxygen availability. *Nature*, 399: 114-115.

Dudley, R. (1998): Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. *The Journal of Experimental Biology*, 201 (8): 1043-1050.

Dudley, R. (2001): From Paleozoic giants to contemporary miniatures: trends in the evolution of insect body size. *2nd International Congress on Palaeoentomology*, Krakow, Poster: 11-12.

Gans, C., Dudley, R., Aguilar, N.M., Graham, J.B. (1999): Late Paleozoic atmospheres and biotic evolution. *Historical Biology*, 13: 199-219.

Graham, J.B., Dudley, R., Aguilar, N.M., Gans, C. (1995): Implications of the Late Palaeozoic oxygen pulse for physiology and evolution. *Nature*, 375: 117-120.

Grimaldi, D.A., Engel, M.S. (2005): *Evolution of the insects*. Cambridge University Press: 755 pp.

Huguet, A., Nel, A., Martínez-Delclòs, X., Bechly, G., Martins-Neto, R. (2002): Preliminary phylogenetic analysis of the Protanisoptera (Insecta: Odonatoptera). *Geobios*, 35: 537-560.

Nel, A., Gand, G., Fleck, G., Bethoux, O., Lapeyrie, J. 1999a. *Saxonagrion minutus* nov. gen. et sp., the oldest damselfly from the Upper Permian of France (Odonatoptera, Panodonata, Saxonagrionidae nov. fam.). *Geobios*, 32 (6): 883-888.

Nel, A., Gand, G., Garric, J. (1999b): A new family of Odonatoptera from the continental Upper Permian: the Lapeyriidae (Lodève Basin, France). *Geobios*, 32 (1): 63-72.

Nel, A., Gand, G., Garric, J., Jarzembowski, A.E., Lapeyrie, J. (1999c): The first Insecta Odonata Protozygoptera from the Upper Permian of France. *Palaeontology*, 42 (1): 83-97.

Rasnitsyn, A.P., Pritykina, L.N. (2002): Superorder Libellulidea Laichartin, 1781. Order Odonata Fabricius, 1792. The dragonflies. pp. 97-106. In: A.P. Rasnitsyn, D.L.J. Quicke (eds.), *History of insects*. Kluwer Academic Publishers, Dordrecht, Boston, London: 517 pp.

Selden, P.A., Corronca, J.A., Hünicken, M.A. (2005): The true identity of the supposed giant fossil spider *Megarachne*. *Biology Letters*, 1 (1): 44–48.

Sheldon, N.D. (2005): Do red beds indicate paleoclimatic conditions?: a Permian case study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 228: 305-319.

Spicer, J.I., Gaston, K.J. (1999): Amphipod gigantism dictated by oxygen availability? *Ecology Letters*, 2: 397-403.