Assessment on the Late Devonian fauna of Strud, Belgium

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The Late Devonian Strud locality from the Namur Province, Belgium, was known for over a century for its faunal and floral content (Hock, 1879; Lohest, 1888; Leriche, 1931; Stockmans, 1948). Then forgotten, this locality was rediscovered in 2004 by geologists of the Liege University and regular field collecting for the last 10 years has resulted in a unique continental floral and faunal assemblage which give a glimpse of Euramerican environment and biogeography during the Late Devonian phase of the processes of tetrapod and arthropod terrestrializations. Fieldwork at the Strud locality has now come to its end.

The Strud locality has yielded a diversified flora including seed-plants (Prestianni *et al.*, 2007) and fauna including crustaceans (anostracans, notostracans, conchostracans, and decapods), eurypterids, a putative insect, placoderms (groenlandaspids, phyllolepidids, antiarchs), actinopterygians, acanthodians, sarcopterygian fishes (porolepiformes, osteolepiformes, lungfishes) and tetrapods. This fossil assemblage is one of the oldest continental – probably freshwater – ecosystems with a consequent vertebrate and invertebrate diversity.

The exceptional preservation of arthropods and plants in the main fossiliferous layers is explained by a quick burial in the fine-grained sediment of a calm and confined flood plain and temporary ponds environment. Recent stratigraphic correlations allow to review the age of the fossiliferous horizon that is now definitely considered to be Late Famennian (VCo "rad" zone) (Denayer *et al.*, 2015).

Invertebrate fauna: The crustacean fauna is composed of two decapod shrimps (Gueriau *et al.*, 2014a, 2014b). *Tealliocaris walloniensis* documents the earliest occurrence of continental decapod crustaceans and indicates that decapods are part of continental ecosystems at least since the Late Devonian. *Schramidontus labasensis* documents the first occurrence of angustidontids in continental environment whereas it was previously only known from marine (pelagic) environments and enlarges the geographical distribution of angustidontids from North America and Eastern Europe to Western Europe. Angustidontida fills the gap between Amphionidacea and Decapoda *sensu stricto*.

The Strud locality also yielded an ephemeral pool branchiopod community comprised of anostracan (fairy shrimps), notostracan (tadpole shrimps) and spinicaudatan (clam shrimps). The fossil notostracan *Strudops goldenbergi* bears a close resemblance to modern notostracans in possessing a large, simple head shield covering almost half of the whole body, a set of phyllopodous thoracic appendages and a legless posterior abdomen with a telson bearing a caudal furca. The differentiation and relative size of mouthparts and limbs suggest that these specimens are all adults (Lagebro *et al.*, 2015). These notostracans are the earliest clear members of the total group Notostraca.

A unique complete insect, *Strudiella devonica*, which was probably a terrestrial species, was recently discovered associated with notostracans (Garrouste *et al.*, 2012, 2013). Its dicondylic mandibles are of an omnivorous type, clearly not modified for a solely carnivorous diet. This discovery narrows the 45-Myr gap in the fossil record of Hexapoda, and demonstrates further a first Devonian phase of diversification for the Hexapoda, as in vertebrates, and suggests that the Pterygota diversified before and during Romer's gap.

Vertebrate fauna: The placoderm fauna includes the antiarch *Grossilepis rikiki*, the groenlandaspidid *Turrisaspis strudensis* and the actinolepidoideid *Phyllolepis undulata* (Olive, 2015; Olive *et al.*, 2015). Based on morphological and morphometric evidences, this material is characterized, with rare exceptions, as juvenile

material. Since the abundant placoderm material from Strud did not suffer of size sorting and is nearly exclusively composed of juvenile individual remains, this locality may be identified as a fish nursery. This nursery from Belgium, one of the rare known placoderm nurseries so far, sheds light on the ecology of the earliest fish nurseries.

Remains attributed to the sarcopterygian rhynchodipterid lungfishes *Soederberghia groenlandica* and ?*Jarvikia*, two taxa previously known in the late Devonian of East Greenland, have also been recovered from Strud (Clément & Boisvert, 2006).

A tetrapod jaw, found in the nineteenth century at Strud, was initially presumed to be from a fish (Lohest, 1888; Clément *et al.*, 2004). It shows typical tetrapod characters in its bone ornamentation and chamfered ventral margin of the dentary. The teeth are widely spaced and strongly curved posteriorly, as in the corresponding jaw portion of *Ichthyostega* from East Greenland. Although the find cannot be referred with certainty to *Ichthyostega*, it is strong evidence for the existence of a close relative of this tetrapod genus outside Greenland.

Supplementary tetrapod material from Strud has been recently collected. It consists of an isolated postorbital, fragment of two maxillae and one cleithrum.

The vertebrate occurrences, especially of placoderms, lungfishes and tetrapods, provide additional evidence for paleobiogeographical links between East Greenland and the central southern coast (Pennsylvania, Belgium) of the Euramerican continent during the Late Devonian.

Our knowledge of the paleoenvironment of the Strud locality is crucial because it recorded the earliest phase of tetrapod evolution that took place after their emergence and before their terrestrialization. It raises the question of the environmental and ecological conditions for the Devonian aquatic ecosystem and the selection pressures occurring at the onset of the tetrapod and hexapod terrestrializations.

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