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The Arthropod Assemblage of the Upper Devonian Strud locality and its Ecology

LINDA LAGEBRO



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Abstract

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The Devonian (419-359 million years ago) is the geological period when the terrestrial biota fully established. Early representatives from a terrestrial and continental aquatic biota have previously been reported from the Upper Devonian (Famennian) Strud quarry in Belgium, in the shape of seed-bearing plants and vertebrates (fish and early tetrapods). The palaeoenvironment is interpreted as a floodplain with slow accumulation of sediment in the river channels and adjacent shallow pools, subject to seasonal flooding and desiccation. This thesis presents the upper Famennian Strud ecosystem with representatives from the largest animal phylum – the Arthropoda. Pancrustaceans are dominating the arthropod assemblage by two eumalacostracans (previously described), three groups of branchiopods, and a putative insect, all collected in fine shales likely deposited in the shallow pools. The branchiopods from Strud comprise new members from all three extant clades, i.e. notostracans, anostracans, and spinicaudatan diplostracans. The notostracan *Strudops goldenbergi* is remarkable for its close resemblance with the extant genus *Triops* by the overall body plan and telson morphology. A phylogenetic analysis including modern and extinct notostracans and anostracans was performed, where *Strudops* appears as the earliest undisputed notostracan ever found. In addition, new genera of Anostraca (*Haltinnaias serrata*) and Spinicaudata (*Gesvestheria pernegrei*) are described herein. The insect *Strudiella devonica* consists of a single specimen and is interpreted to have been a nymph due to its minute size and wingless appearance. The chelicerates are represented by one or several species of eurypterids. So far unnamed juvenile eurypterid remains have also been found within the pool strata, and fragments of adult individuals in the coarser river deposits. The branchiopod community displays a unique insight to the ecosystem that these crustaceans inhabited. This is partly because of their co-occurrence, but mainly because they are preserved in close association to draught-resistant encysted eggs, in the same manner as modern day branchiopods do to survive and disperse during periods of drought and freezing. Altogether, the arthropod assemblage offers insight to Late Devonian freshwater ecosystems, and provides further understanding of the evolution of respective groups.

Keywords: Branchiopoda, Hexapoda, Eurypterida, Strud, Famennian, ephemeral pool

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List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Garrouste, R., Clément, G., Nel, P., Engel, M.S., Grandcolas, P., D’Haese, C., **Lagebro, L.**, Denayer, J., Gueriau, P., Lafaute, P., Olive, S., Prestianni, C., and Nel, A. (2012). A complete insect from the Late Devonian period. *Nature*, **488**, 82-85 Reprints were made with permission from the respective publishers
- II Garrouste, R., Clément, G., Nel, P., Engel, M.S., Grandcolas, P., D’Haese, C., **Lagebro, L.**, Denayer, J., Gueriau, P., Lafaute, P., Olive, S., Prestianni, C., and Nel, A. (2013). Garrouste et al. reply. *Nature*, **494**(7437), E4-E5
- III **Lagebro, L.**, Gueriau, P., Hegna, T. A., Rabet, N., Butler, A., Budd G.E. (2015) The oldest notostracan (Upper Devonian Strud locality, Belgium). *Palaeontology* Published online 25 February 2015. DOI : 10.1111/pala.12155.
- IV Gueriau, P., Rabet, N., Clément, G., **Lagebro, L.**, Charbonnier, S., Olive, S., and Béthoux, O. (manuscript to be submitted to *Nature*). The ephemeral pool crustacean community unchanged since the Late Devonian
- V **Lagebro, L.**, Gueriau, P., Edgecombe, G. D., and Budd, G. E., (manuscript to be submitted to *Geologica Belgica*). Sty-lonurine eurypterids from the Upper Devonian Strud locality, Belgium.

Additionally, the following paper was prepared during the course of my PhD but not included in the thesis:

- VI Janssen, R., Jörgensen, M., **Lagebro, L.**, and Budd, G. E. (2015) Fate and nature of the onychophoran mouth-anus furrow and its contribution to the blastopore. *Proc. R. Soc.* <http://dx.doi.org/10.1098/rspb.2014.2628>.

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Statement of authorship

Paper I: R.G. and P.N. are first authors with equal rank. P.N., P.G., C.D'H., L.L., M.S.E., J.D., C.P., P.G. and S.O. drafted the manuscript and prepared figures. A.N. and P.N. coordinated the manuscript. G.C. coordinated and participated in fieldwork and contributed to the draft manuscript. L.L., J.D., P.G. and S.O. participated in fieldwork.

Paper II: R.G. and P.N. are first authors with equal rank; P.N., P.G., C.D'H., L.L., M.S.E., J.D., C.P., P.G. and S.O. drafted the manuscript and prepared figures. A.N. and P.N. coordinated the manuscript. G.C. coordinated and participated in fieldwork and contributed to the draft manuscript. L.L., J.D., P.G. and S.O. participated in fieldwork.

Paper III: L.L. collected data, prepared figures and wrote the manuscript; P.G. collected data, prepared figures and wrote the section on the Geological Setting; T.A.H. contributed to the cladistics analysis, A.B. performed the cladistics analysis. All authors contributed to the draft manuscript.

Paper IV: P.G. and N.R. are first authors with equal rank. G.C. and O.B. designed the project. P.G., N.R., G.C., L.L., S.C., S.O. and O.B. collected data and drafted the manuscript. P.G., N.R. and O.B. analysed the fossils and prepared figures.

Paper V: L.L. analysed the data, prepared figures and wrote the manuscript. P.G. photographed the specimens and prepared figures. All authors drafted the manuscript.

Disclaimer: The papers presented herein are for the purpose of public examination as a doctoral thesis only. They are not considered publications according to the ICZN. Accordingly, all new taxonomic names and emendations in papers IV and V are void. Authority for taxonomic work in papers I-III is by the original publications.

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1. Introduction to the Arthropoda

Morphology and phylogeny

Arthropods are the largest living animal phylum. The group consists of animals around us in our every day life - spiders, mites, ants, mosquitos, shrimps, myriapods, and many more. They are globally widespread and inhabit environments from the deep oceans to salt lakes and deserts, and even in the skin of the human face.

Arthropods are characterised by having a hard exoskeleton of chitin and protein, sometimes made even more rigid by mineralisation, often by calcite. The cuticle consists of sclerites, or separate plates, articulated together with softer membranes, and muscle attachments on the inner layer. The appendages, composed of several podomeres, have given the name to the phylum Arthropoda, simply meaning 'jointed limbs'. Arthropods are segmented and tagmatised, which means that they have a body composed of serially repeated compartments with similar or specialised functions.

The group as a whole is nowadays undisputedly regarded as being monophyletic with onychophorans, (or velvet worms), as their closest living ancestors (Campbell et al. 2011). Arthropods together with onychophorans (and tardigrades (water bears)) make up the Panarthropoda, a clade within the Ecdysozoa (panarthropods plus cycloneuralians). The *internal* phylogeny of arthropods on the other hand is an on-going and vivid matter. The combined studies of molecular and morphological analyses of various kinds (genes, HOX-genes, proteins, gene expression patterns and morphology of living and fossil arthropods) have led to a massive and still growing record of arthropod systematics.

There are three or four large clades within the phylum. These are the Chelicerata, e.g. spiders, scorpions, horseshoe crabs, the Myriapoda (millipedes and centipedes) and the Pancrustacea/Tetraconata, which includes crustaceans (shrimps, lobsters, branchiopods and many more) and hexapods with the insects and their entognathous relatives. The fourth clade is the Pycnogonida, or sea spiders, a group of chelicerate-bearing arthropods that either belongs within the Chelicerata, or constitutes a clade on their own (treating Pycnogonida as a separate clade leaves Xiphosura + Arachnida in Euchelicerata). Pancrustacea and Myriapoda are usually regarded as sister-groups in the Mandibulata, whereas some studies suggest a close relationship be-

tween Myriapoda and Chelicerata (= Myriochelata/Paradoxopoda) (e.g. Bitsch & Bitsch 2004; Giribet & Edgecombe 2013)).

Arthropods and terrestrialisation

Amongst the extant arthropods, myriapods, chelicerates and hexapods are primarily terrestrial, and crustaceans primarily aquatic. For an organism to adapt on land, whether it is an animal or a plant, it needs to overcome certain barriers, for example respiration, reproduction, dehydration and physical support. The hard exoskeleton and podomerised limbs were probably advantageous characters for allowing arthropods to leave aquatic environments (Dunlop et al. 2013).

The criteria for being a terrestrial versus an aquatic arthropod are not clearly defined and there are endless variations of how organisms cope with a terrestrial life style; in fact many arthropods occupy for example the interstitial water on sandy beaches (e.g. bristle tails) and in wet soils (e.g. woodlice), constituting a diverse micro- and meiofauna together with many other invertebrates. Certain insects for example, live their whole life on land but are destined to return to water during parts of their life cycle. Some crustacean groups have taken on a terrestrial life style with modifications like the land crabs and woodlice, and branchiopods, a few ostracods and copepods have invaded ephemeral aquatic habitats. These latter three groups cannot live above the water surface but they have evolved the ability to produce drought-resistant resting “eggs” (diapausing/dormant encysted embryos in the gastrula stage (Fryer 1996)), which can be transported over large distances via wind, terrestrial animals or human activity as a strategy for the species to survive and spread. The encysted embryos (resting eggs) can survive for decades, or even centuries before hatching. It is not clear *when* these embryos specialised for coping with dry seasons, but the earliest branchiopods (stem-groups) from the Rhynie chert are indeed found in a protected freshwater environment, albeit not ephemeral (Fayers and Trewin 2003).

Terrestrialisation as such is a highly complex matter beyond the scope of this thesis, but it is touched upon considering the continental and terrestrial arthropods described herein. Arthropods originated in the marine realm and were probably the first animals to conquer land with arthropod trace fossils dated back to the Late Ordovician (Wilson 2006) and the first body fossils from millipedes from middle Silurian rocks in Scotland (Wilson and Anderson 2004). It is not known what group or groups of arthropods were the first to adapt to a terrestrial life style, and also not what the driving force was behind such a change in environment. Furthermore not what route they took; was it via freshwater systems, if so, how and why did the first animals first colonise rivers and lakes? The hypothesis suggesting that the transition took place via freshwater environments agrees both with the co-occurrence of the

earliest branchiopod crustaceans and hexapods in the Early Devonian (Glennier et al. 2006), and with the suggested close relationship between branchiopods and hexapods (Rota-Stabelli et al. 2011). The last common ancestor of today's terrestrial arthropods was likely aquatic, but it is generally thought that arthropods explored land not once but several times. Morphology alone has shown to not be reliable in terms of phylogeny, as many of the "land-living structures" such as tracheae in hexapods and myriapods are similar but not homologous (Dunlop et al. 2013). Understanding the ecology and biology of fossil freshwater arthropods such as branchiopods could provide insight to the water-land transition.

Preservation

Arthropods moult when they grow and the leftovers, the exuviae, are often fossilised. Certain arthropods with mineralised cuticle retain the minerals prior to ecdysis, resulting in very fragile exuviae. It is sometimes difficult to tell whether a fossil represents the leftovers of a dead animal or a moult, and this fact can make it hard to draw ecological conclusions as one individual can leave behind several fossils. Since the process of shedding the exoskeleton exposes the animal to a greater risk of predation and other injuries (normally the exoskeleton protects the body from predators and drought), the animal often seeks a calm, protected environment for the ecdysis. Such assemblages of moulted exoskeletons are relatively common in the fossil record.

Mineralised arthropods, for example trilobites, have a very high preservation potential owing to their hard cuticle, and although they are now extinct, we know a lot about their morphology, diversity, and distribution. Other groups, like most mandibulates and chelicerates, have a non-mineralised cuticle or retain the minerals when they moult, and thus suffer harder from taphonomic processes. They are more frequently found in deposits with exceptional preservation, and we often only get a snap shot of their evolutionary history. For a terrestrial environment, preservation calls for exceptions for an arthropod in order to be fossilised; for example by being buried under sediment during a flooding event, being killed by hot springs, or getting trapped in resin.

This thesis contains descriptions of notostracan, anostracan, and spinicaudatan branchiopod crustaceans, an insect, and two types of eurypterids. These new fossils accounts for five of the seven outstandingly preserved arthropod taxa so far discovered in the Upper Famennian Strud locality in Belgium. The arthropod assemblage herein provides a better understanding of the evolution of freshwater arthropods and their ecosystems, in particular ephemeral pools.

2. The Strud locality

History and stratigraphy

The Strud outcrop is represented by a very small area, which is located in the village of Strud in the Namur region, Belgium. It was discovered by Hock (1878), and then investigated by Lohest (1888a, b) who described a fish-jaw that later turned out to be from an *Ichtyostega*-like tetrapod (Clément et al. 2004), and an amphibian that was re-described as a lungfish (Clément and Boisvert 2006). More than a century passed from its discovery until the outcrop received attention again in 2004 and it has since then yielded several publications and on-going studies on the biota and geological settings.

The stratigraphy of Strud displays a short succession of river and temporary pool deposits making up the Bois-des-Mouches Formation (Montfort-Evieux Group), overlying earlier marine deposits. The Strud section is dated to be Late Famennian (miospore assemblages (*Grandispora gracilis* - *Grandispora famennensis* biozone)) (Prestianni et al. 2007; Denayer et al. under revision). The material described in this thesis was found in a 1.4 m thick fining-upward channel-filling succession (Fig. 1). The succession begins with a conglomeratic sandy dolomite holding reworked plant remains, followed by fish bone beds with early tetrapod remains (Clément et al. 2004), interpreted as point-bar lag deposits of the main channel. These beds are overlaid by a fining-upward succession of arkosic micaceous sandstones, siltstones and shales. The hexapod, branchiopod and juvenile eurypterid fossils were found in the slowly accumulated floodplain dark-grey micaceous shales, corresponding to one of the last channel-filling phases, representing seasonally dried and flooded freshwater ponds (Garrouste et al. 2012; Hörschemeyer et al. 2013; Gueriau et al. 2014 a, b; Lagebro et al. 2015). Larger eurypterid fragments were found in slightly older, coarser layers together with vertebrate and plant remains. The channel ends with mudcracks and is covered by numerous meters of red micaceous sandstones.

The arthropod specimens are all preserved two-dimensionally flattened. Most cases represent dorso-ventrally flattened fossils, but a few lateral compressions occur, both preserved as a pale to dark brown carbonaceous film on the fine green-grey shales. This carbonaceous film easily flakes off from the rock, making the specimens rather fragile and vulnerable to investigation. Most of the studied specimens are more or less complete, although they

typically have undistinguishable proximal portions of the appendages at the point of attachment to the body (Figs. 3,8,9).

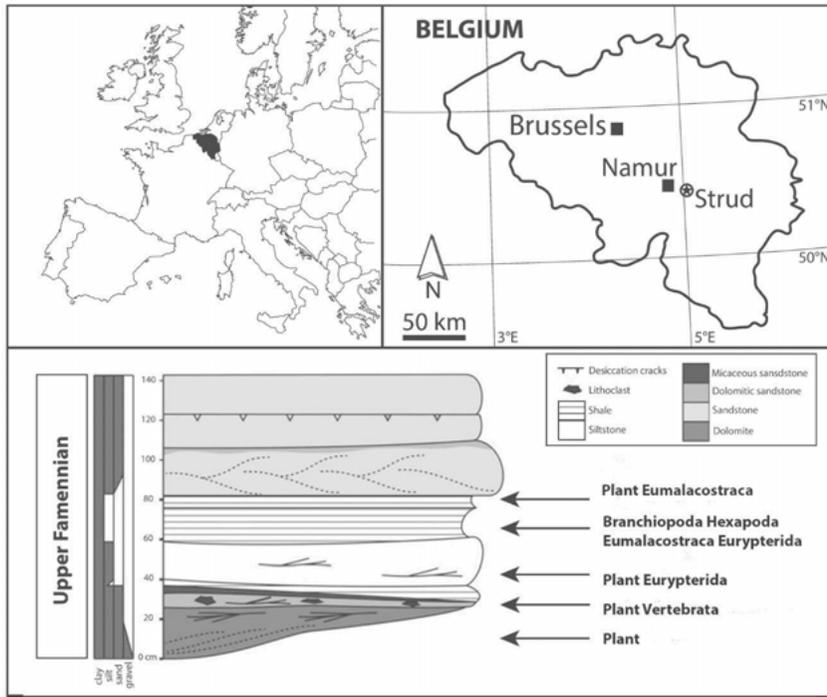


Fig. 1. Location and partial stratigraphy of the Strud quarry (Upper Famennian) with plant, vertebrate and arthropod bearing strata (modified from Gueriau et al. 2014a).

3. The arthropod assemblage

Pancrustacea

Branchiopoda

Branchiopods are crustaceans living in continental fresh water environments, apart from a few derived exceptions. They are united by phyllopodous limbs, the ability to produce drought-resistant resting eggs, and for possessing a so called ventral food groove in which food particles are being transported from the posterior to the mouth using sclerotised specialised proximal endites on the thoracic appendages. Typical habitats for branchiopods are ephemeral pools all over the globe (discussed below), but they do occur in larger lakes and river systems as well (Brendonck et al. 2008; Hegna 2012), and some groups have even explored the marine realm (Potts and Durning 1980).

Branchiopods have for long been thought to be one of the most basal crustacean clades with virtually no change since their appearance (Fryer 1985), but recent studies by for example Casane and Laurenti (2013), Lloyd et al. (2013), and Mathers et al. (2013) indicate that they in fact are no less derived than any other modern crustacean. Branchiopods display a strong morphological stasis since at least the Upper Devonian and they are often referred to as “living fossils”. The term “living fossils” was first used by Darwin (1859) as a description of lungfish as organism with no apparent morphological change through evolutionary time, and since then the term has been applied to several groups, e.g. coelocanths (Friedman et al. 2007), ginkgo (Royer et al. 2003), and as discussed here, branchiopods, and in particular notostracans (e.g. Maeda-Martínez et al. 2000). Lately, many authors have come to question this concept as a valid and appropriate label for these taxa, and point out that these groups only show stasis on a phenotypic level, but that they actually have evolved genotypically. The fossil record reveals on one hand early branchiopods with many shared morphological characters with the modern day taxa, but on the other hand some groups that definitely differ from their modern descendants. The first occurrence of the Branchiopoda is the stem-group *Rehbachella kinnekullensis* Müller, 1983 in the upper Cambrian, and mandibular remains from the mid-upper Cambrian have been interpreted as belonging to crown-group Branchiopoda (Harvey et al. 2012). The Lower Devonian (Pragnian) Rhynie chert deposits have in addition to the first insects (see below), yielded what are probably stem-

groups Notostraca and Anostraca (Scourfield 1926; Fayers and Trewin 2003; Olesen 2007). The Mesozoic Kazacharthra were a group of intriguing branchiopods that are either considered as an ingroup Notostraca, or their sister-group. Kazacharthrans were restricted to central Asia (China, Mongolia, and Kazakhstan) during the Late Triassic – Early Jurassic, and they differ considerably from modern notostracans. They had large flat carapaces of variable shapes and often with pronounced ornamentation, small biramous second antennae, up to 11 thoracic limb bearing segments, a long limbless abdomen and a telson with furca and often a prominent ornamented supra-anal plate or flap (McKenzie et al. 1991). Although sharing many characters with the Notostraca, Kazacharthra was distinctly different (Olesen 2009) and is preferably regarded as the sister-group to the former, constituting the monophyletic clade Calmanostraca. The modern notostracan species *Triops cancriformis* Bosc, 1801 is popularly referred to as the oldest living species on Earth, with representatives in the Triassic (*T. cancriformis minor* Trusheim, 1937) and in the Permian (*T. cancriformis permiensis* Gand et al., 1997). The genus *Triops* has been pushed down to the Carboniferous with *Lynceites ornatus* Goldenberg, 1870, a preserved carapace that was later synonymised as *Triops ornatus*. One character uniting all living members of the family Triopsidae (comprising the two extant genera *Triops* and *Lepidurus*) is the elongated distal endites on the first thoracic appendage, adapted to have a sensorial function after the reduced antennae. An elongated distal endite has never been unambiguously shown in any fossil material (Hegna 2012), indicating that extant and fossil notostracans cannot belong to the same family, even less so the same species.

The branchiopods from Strud comprise members from all three extant clades, i.e. notostracans, anostracans, and spinicaudatan diplostracans (tadpole shrimps, brine shrimps, and clam shrimps, respectively). They all share remarkable similarities to their modern descendants, but differ clearly from their supposed ancestors.

Notostracans (Fig. 2) are the largest member of the group in terms of size, up to 10 cm, although most forms are a couple of centimetres long. They have a large carapace attached on the head, covering the head, thorax and their appendages. The two compound eyes and the single nauplius eye are situated on the dorsal surface of the carapace. The carapace carries small spines on the posterior notch and a prominent mandibular groove and dorsal carina. The head carries, apart from the head shield, only one pair of small antennae, contrasting to the (for crustaceans) usual set of two pairs of antennae. Among notostracans, some have either lost the second antennae completely, or drastically reduced them as in some species (McLaughlin 1980). Further they possess a pair of large, sturdy mandibles. The thorax carries 11 pairs of appendages. The first thoracic appendage is specialised with elongated distal endites with a sensory function and the remaining appendages

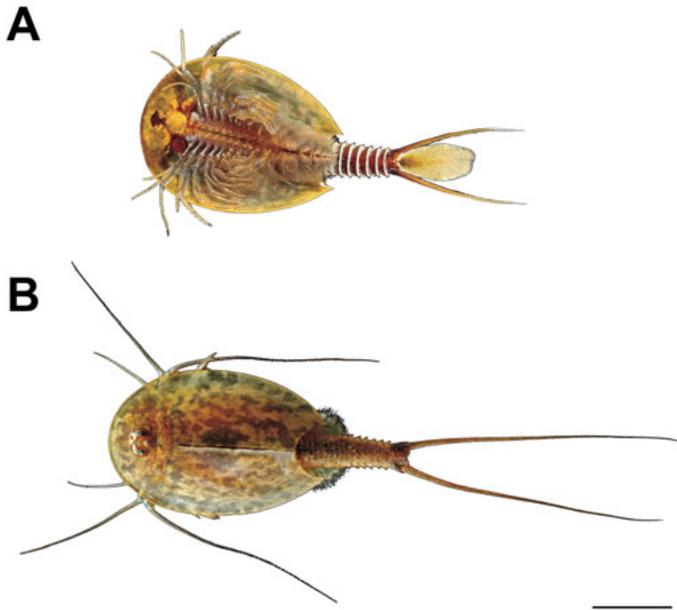


Fig. 2. The two extant notostracan genera. A, *Lepidurus*, ventral view. B, *Triops*, dorsal view. Scale bar ca. 10mm. Photo courtesy of Jean-François Cart.

are undifferentiated but decreases in size posteriorly. The abdomen consists of fused tergites and sternites (exoskeletal plates) to form “body rings”. The abdomen ends with a spine-bearing telson with a caudal furca. The Notostraca comprises two extant genera: *Triops* and *Lepidurus*. These two genera are very similar in morphology and occurrence, distinguished mainly by the presence of a supra-anal plate in *Lepidurus* (Fig. 2).

The notostracans from Strud, *Strudops goldenbergi* (Fig. 3), were recently described as the oldest notostracans in the fossil record, in a study in which 23 fossil and living branchiopod taxa were included (Lagebro et al. 2015)(Paper III). *Strudops* is a significant fossil in having the same outline, or habitus, as modern notostracans, but lacking certain key characters, either phenotypically or due to taphonomy. *Strudops* possessed a large carapace, with no ornamentation such as spines, mandibular groove, or dorsal carina. It carried 11 pairs of undifferentiated thoracic appendages and a limbless abdomen terminating in a telson lacking a supra-anal plate.

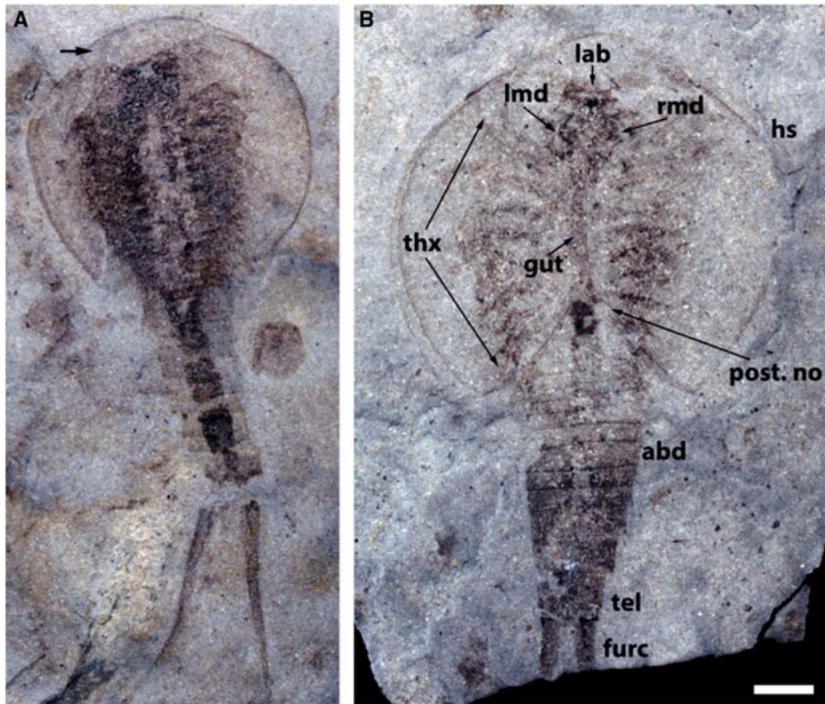


Fig. 3. *Strudops goldenbergi* A, complete specimen in ventral view. The arrow highlights the prominent subfrontal plate/frontal doublure of the carapace. B. complete specimen in dorsal view. Abbreviations: abd, abdomen; furc, caudal furca; hs, head shield; lab, labrum; lmd, left mandible; post. no, posterior notch; rmd, right mandible; tel, telson; thx, thorax. Scale bar represents 1 mm and applies for both specimens (Lagebro et al. 2015).

Anostracans (Fig. 4) differ from all other branchiopods by the absence of a carapace. It remains unclear whether the lack of a carapace is a plesiomorphic character for the Branchiopoda, or if the anostracans have secondarily lost it (Hegna 2012). They generally have 11 trunk limbs and a limbless abdomen with a small caudal furca. The compound eyes are large and stalked, the nauplius eye is small and anterior. The first antennae are short and thin, and where the notostracans have reduced their second antennae, male anostracans carry a large specialised pair of appendages that are used for clasping the female during mating. Anostracans have a very sparse fossil record probably due to the lack of a hard carapace as opposed to notostracans and diplostracans, with the stem-group in the Lower Devonian, and undisputed crown-group representatives in the Upper Jurassic (Huang 2006; Huang et al. 2006) and Lower Cretaceous (Trusova 1971; 1975).

The anostracans found in Strud, *Haltinnaias serrata* (Gueriau et al. in prep), occur as a female and a male individual. The female possessed a

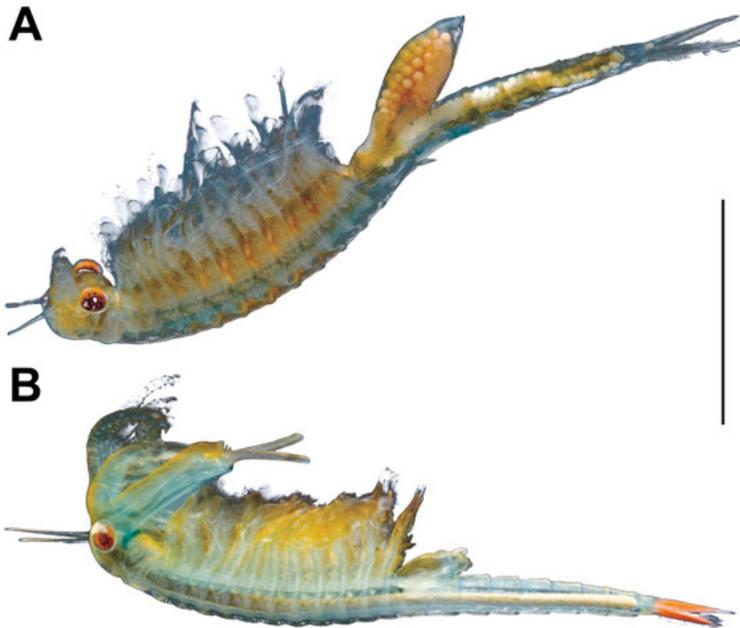


Fig. 4. Extant Anostraca. A, female with egg-filled brood-pouch. B, male with large clasping antennae. Scale bar 5mm. Photo courtesy of Jean-François Cart.

protruding spine-bearing brood pouch, and the male was equipped with enlarged antennae used for clasping the female, typical for the group.

Spinicaudatans (Fig. 5) are bivalved branchiopods. Together with the similar laevicaudatans and cycletheridans, and the smaller morphologically different cladocerans, they belong to the branchiopod ingroup Diplostraca. Since the only diplostracans found in Strud are spinicaudatans, the remaining groups will not be discussed herein. The body of spinicaudatans is not subdivided in thorax and abdomen, but has a long trunk consisting of 32 or more segments.

The spinicaudatan *Gesvestheria pernegrei* (Gueriau et al. in prep) is very abundant in the Strud fine shales, not unexpected as they are enclosed in a bivalved hard carapace, but softer parts of the body are somewhat surprisingly preserved in a few specimens as well. The carapace valves are united by a straight hinge line and each valves has prominent growth lines. Internally, the head, thorax, abdomen and telson are preserved although without detailed anatomy.



Fig. 5. Extant Spinicaudata. Scale bar 5mm. Photo courtesy of Jean-François Cart.

Although branchiopod monophyly is well supported (Regier et al. 2005; 2010; Olesen 2007; 2009; Regier and Zwick 2011; von Reumont et al. 2012), their internal phylogeny is not yet resolved (Olesen 2007). Synapomorphies uniting the group and defining its internal clades concern mainly appendage morphology and larval characters (fig 3. *in* Olesen 2009), many of which are naturally difficult to apply to fossil taxa. At the moment, the phylogeny of the branchiopods appears as illustrated in Fig. 6. Since *Castracollis* Fayers and Trewin, 2003 shares characters with both notostracans and diplostracans, and since the extant notostracans end up within the Diplostraca in some molecular analyses (Stenderup et al. 2006), the position of the whole clade Calmanostraca (extant Notostraca, the extinct Kazacharthra, +/- *Castracollis*) is not fully resolved.

Lagebro et al. (2015) published a tree of living and fossil branchiopods (excluding Diplostraca) in an attempt to resolve the phylogeny of early notostracans. 23 taxa and 60 characters were included in the analysis and this resulted in a tree with a defined crown- and total group Notostraca (Fig. 7).

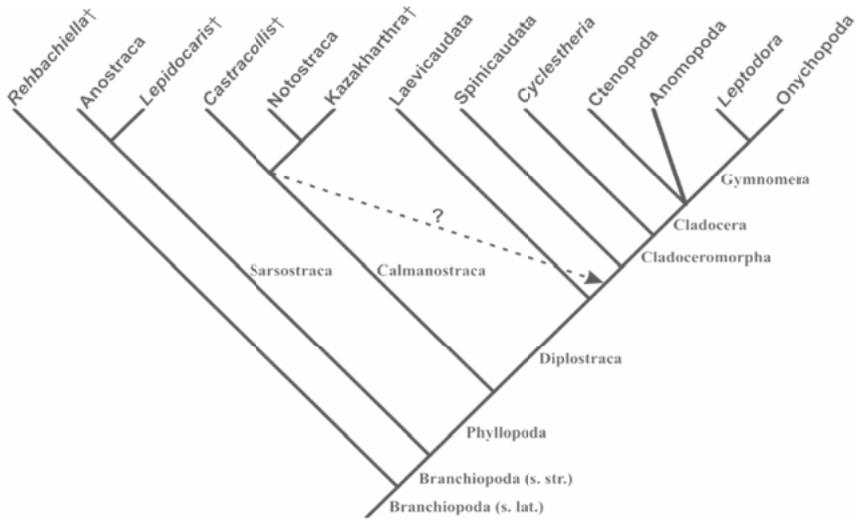


Fig. 6. Morphology-based phylogenetic tree of living and fossil Branchio-poda (modified from Olesen 2007).

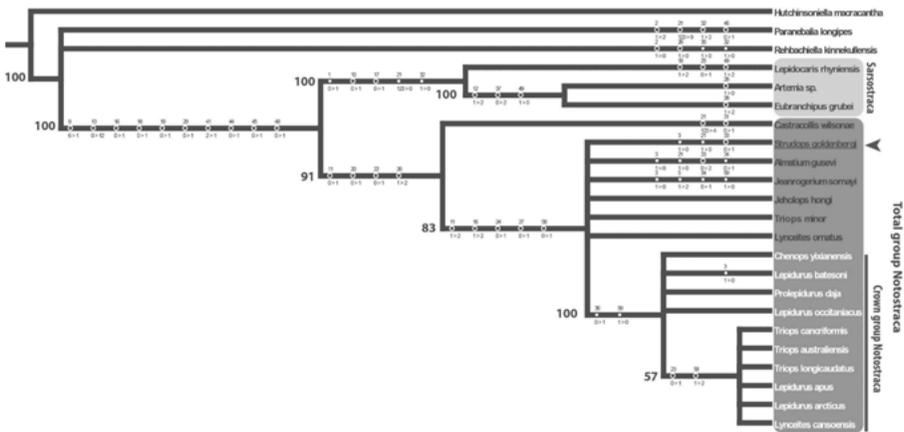


Fig. 7. Majority-rule tree of 168 most-parsimonious trees analysed under equal weights, using living and fossil taxa. White circles indicate synapomorphies or autapomorphies for respective characters. White dots show homoplasies. *Hutchinsoniella*, *Rehbachiella* and *Paranebalia* are outgroup taxa on which the tree is rooted (Lagebro et al. 2015).

Malacostraca

Malacostracan crustaceans from Strud were described by Gueriau et al. (2014a) and (2014b). The malacostracans will only be mentioned here as they constitute to the Strud arthropod fauna but are not a part of this thesis. Gueriau et al. (2014a;b) reported the findings of two fresh water malacostracans; the decapod (*Tealliocaris walloniensis* and the angustoniid *Schramidontus labasensis*), and showed that although decapods originated in deep marine environments, they were established also as a continental group by the time of the Upper Devonian.

Hexapoda

Although hexapods are the most abundant and widespread animals today, their terrestrial life style prohibits a good preservation potential. The very earliest fossil hexapod is the collembolan (springtail) *Rhyniella praecursor* Hirst and Maulik, 1926, from the Lower Devonian hot spring chert deposits in Rhynie, Scotland. Rhynie chert displays an arthropod fauna with exceptional three-dimensional preservation of arachnids, eurypterids, crustaceans, centipedes, and hexapods in translucent chert (Shear et al 1987; 1998; Anderson and Trewin 2003; Anderson et al. 2003; Fayers and Trewin 2003; 2005) From the same locality, a pair of dicondylic mandibles has been interpreted by Engel and Grimaldi (2004) as remains from the first definite winged insect, *Rhyniognatha hirsti* Tillyard, 1928. From the time when these two first hexapods were found there is a large hiatus of insects in the fossil record. Until recently, the second earliest pterygote (winged) hexapod (apart from hitherto undescribed cuticular remains from Gilboa (Grimaldi and Engel 2005)), is an undetermined forewing belonging to the Archaeorthoptera (Béthoux and Nel 2002) from the late Early Carboniferous (Prokop et al 2005). By the time of the Early Carboniferous the group Hexapoda was already diversified and abundant.

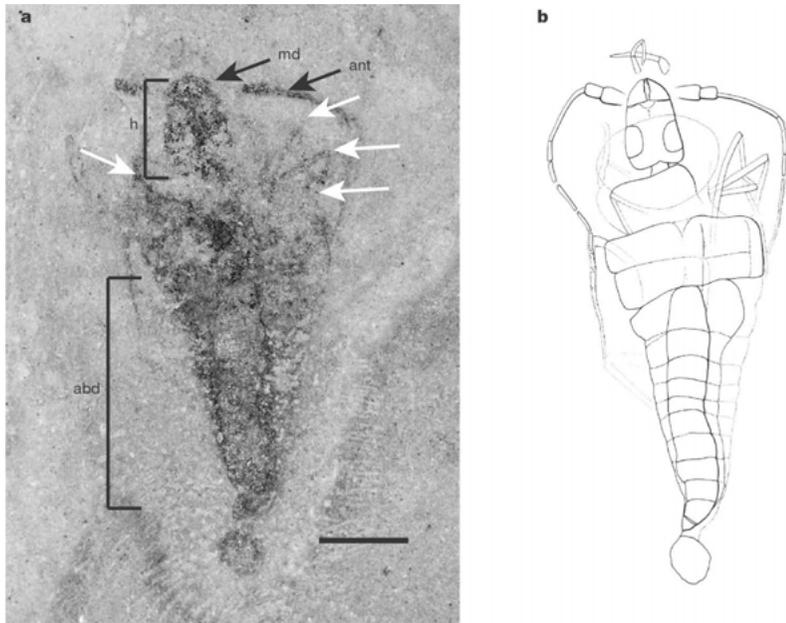


Fig. 8. General habitus of the Strud insect *Strudiella devonica* A. Photograph of the part. B. Reconstruction of general habitus. White arrows indicate legs visible on part. Abbreviations: abd, abdomen; ant, antenna; h, head; md, mandible. Scale bar represent 1 mm (Garrouste et al. 2012).

Garrouste et al. (2012) (Paper I) reported a complete insect from the Strud biota, minimising the hexapod gap. The study by Garrouste et al. (2012) comprises a description of *Strudiella devonica*, a fossil preserved as a single specimen, part and counterpart, in fine shale deposited in a fresh water river system (Fig. 1). The specimen is 8 mm long and possesses a head with compound eyes, dicondylic mandibles, maxillary palps and uniramous antennae; a thorax with three pairs of uniramous appendages; and a 10-segmented limbless abdomen (Fig. 8). The combination of characters and their details led to the initial conclusion of this specimen being a metapterygotan insect. The small size, and the absence of wings could suggest that *S. devonica* from Strud is a juvenile.

Hörschemeyer et al. (2013) replied to the original report with a different explanation of *Strudiella*, where they questioned the hexapodan affinities of the fossil. They report additional post-thoracic appendages and claim that Garrouste et al. (2012) over-interpreted structures such as the eyes, mandibles, and antennae. Instead, they suggest that the fossil belongs to some other arthropod group, for example an undefined decayed crustacean (Hörschemeyer et al. 2013). Garrouste et al. (2013) (Paper II) replied to the reply by Hörschemeyer et al. (2013) with a clarification of how *Strudiella*

cannot be a crustacean, pointing to the differences between the head and trunk appendages.

Eurypterida

Eurypterids are an extinct group of aquatic predatory arthropods common in the Palaeozoic oceans and rivers, belonging to the Chelicerata (spiders, mites, scorpions, horseshoe crabs, and more). Their fossils have been found in deposits from the early Late Ordovician to the late Permian and are more or less globally distributed (Tetlie 2007). The eurypterids are subdivided into two major clades; the basal walking form *Stylonurina* Diener, 1924, and the derived, much more abundant, swimming form *Eurypterina* Burmeister, 1843). Eurypterids are characterised by having a body divided into an anterior prosoma and a posterior opisthosoma. The prosoma consists of fused cephalic and thoracic segments, dorsally covered by a carapace. Eurypterids have six pairs of prosomal appendages, traditionally labelled I-VI. The first appendage is the chelicera, which is either very small or extremely large, depending on the eurypterid type. The following four appendages were used for prey capture and/or walking and are often equipped with spines. The sixth and last either had the function of a walking limb, as in the basal form *Stylonurina*, or was developed into a swimming paddle in *Eurypterina*.

The group is believed to have originated in the marine realm, but they were common in fresh waters and are often found in river deposits such as the Strud settings; they are even believed to have been able to take short excursions onto land (e.g. Vrazo and Braddy 2008). Eurypterids have no extant members, but a substantial fossil record. Unfortunately, the group has a history of being over-split, meaning that some specimens have been assigned new species or genera when they should in fact have been placed in already existing taxa (Dunlop et al. 2008; Vrazo and Braddy 2011). This is causing problems when estimating both the abundance and ecological significance of eurypterids, as well as their phylogeny. Further, there are also difficulties in distinguishing exuviae from dead individuals, and juveniles from adults. Juvenile eurypterids are rather rare in the fossil record, however eurypterids are believed to have nine ontogenetic stages, which is also the case in the xiphosuran (horseshoe crab) *Limulus* (Braddy, 2001). In juvenile eurypterids, the eyes are larger relative to the size of the carapace, the carapace is more rounded anteriorly, and the opisthosoma is shorter (can consist of less than 12 segments) (Braddy, 2001). The outline of the carapace changes during ontogeny and is therefore not a reliable character for taxon determination (Tollerton, 1989; Braddy, 2001).

The eurypterids found in Strud are preserved both as juvenile body specimens based on the criteria mentioned in the previous section, and as isolated larger fragments (Lagebro et al. in prep. Paper V). The juveniles (body spec-

imens) have a smooth surface without spines, scales or other ornamentation often displayed in adult eurypterids. Two semi-articulated specimens, one isolated prosoma/carapace) and four isolated fragments have been recovered from the locality. The juveniles are represented by two semi-articulated specimens, almost complete bodies, and one isolated carapace. (Figs. 9, 10) The juveniles are estimated to have been 3-4 cm long, preserved with the dorsal side up (Fig. 10), and as a cast of the ventral side (Fig. 9). The carapace carries a pair of large oval or crescentic eyes. Ocelli are not preserved.

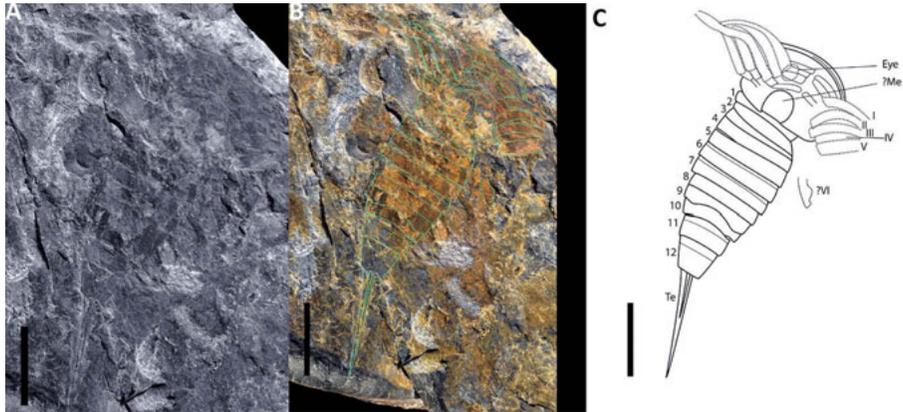


Fig. 9. Complete specimen of a juvenile stylonurid eurypterid from Strud. A. Photograph. B. and C. Interpretative drawing of the specimen. Arabic numbers indicate opisthosomal segments 1-12, roman numbers indicate prosomal appendages I-IV, Abbreviations: eye, compound eye; me, metastoma; tel, telson. Scale bars represent 10 mm. Drawing by Pierre Gueria. (Lagebro et al. in prep.).

The prosomal appendages are poorly preserved. One specimen (Fig. 10) shows the proximal part of what is believed is the sixth appendage, but as discussed earlier, the Strud arthropod assemblage tends to disarticulate at the region of attachment. Also the distal part is missing in this specimen, however, the shape and size of this small part of appendage VI implies a walking type. The opisthosoma, slender and not visually divided into a pre- and post-abdomen, terminates in a styliform to lanceolate telson. The isolated fragments have all knobs or scales (Fig. 11) and they are also significantly larger than the juveniles. They have therefore been interpreted as adult remains but it is not clear which part of the body they represent.

The eurypterids from Strud probably belong to the Stylonurina based on the apparent shape of appendage VI (walking form) and the undifferentiated opisthosoma. However, up to this point, these eurypterid remains have not been systematically defined below the level of suborder.



Fig. 10. Juvenile eurypterid from Strud (Lagebro et al. in prep.).

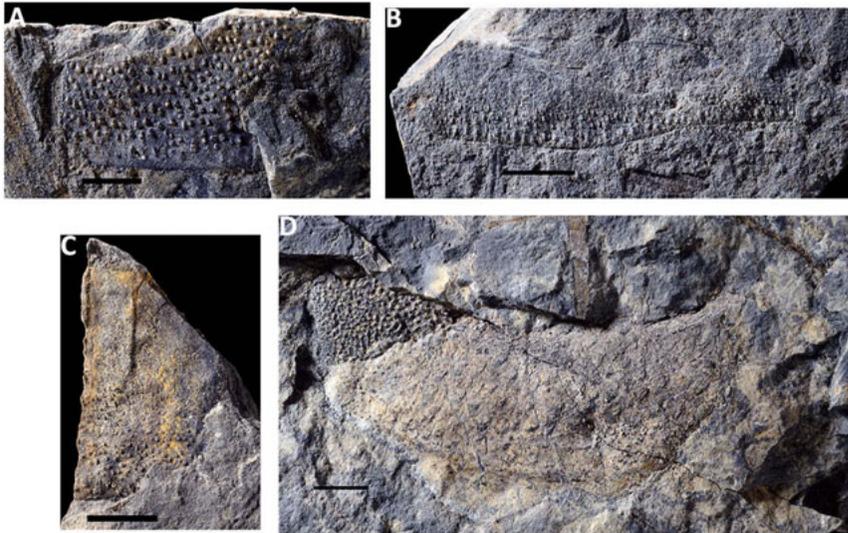


Fig. 11. A-D-. Isolated fragments from adult eurypterids from Strud. Scale bars represent 10 mm (Lagebro et al. in prep.).

4. Ecological significance of the Strud arthropod assemblage

Ponds and pools are continental ecosystems differing immensely from all other aquatic realms. Compared to most river or perennial lake environments for example, which have a high diversity with a lot of biotic factors to affect individual groups (Lindholm 2014), ephemeral pools comprise distinct habitats on their own, and are not merely “tiny lakes”. The definition of an ephemeral pool (or pond) varies regionally. Within this thesis the terminology *sensu* Meester et al. (2005) and references therein is adopted, with both ponds and pools being small and shallow, but ponds permanent and pools temporary. The definition “small and shallow” is of course relative, but ponds can broadly be distinguished from small lakes mainly by the absence of larger predators such as fish, in the former (Meester et al. 2005). Although, and paradoxically perhaps due to, the fact that they are widely occurring, temporary pools have received substantial interest from ecologists only relatively recently and are therefore still somewhat enigmatic (Blaustein and Schwartz 2013). Sedimentary deposits corresponding to such environments are much less abundant, or at least less investigated. The Strud quarry represents one of the oldest fresh water ephemeral pool environments, with a modern day arthropod assemblage.

Ephemeral pools offer a protected yet unstable habitat that few organisms are able to cope with. The fauna in these environments consists of fully aquatic animals such as branchiopod, some copepod and ostracod crustaceans together with many terrestrial arthropods and amphibian vertebrates, which require a water body for completing their reproductive cycle. Ponds and pools are common all over the globe; wherever there is a small submerision in the landscape with an impermeable bottom, rain water, spring water, or water flooded from adjacent rivers (just to mention a few) can stay for some period of time short enough to prevent certain predators to establish, and long enough (a couple of months) for the pool-specific biota to inhabit (Blaustein and Schwartz 2001; Meester et al. 2005; Lindholm 2014).

Branchiopod crustaceans are well adapted to these types of environments by the possession of draught- and freeze-resistant resting eggs (and have been since at least the Upper Devonian as shown in Paper IV within this thesis. Crown-group branchiopods have been found in continental waters since the Early Devonian (Rhynie) and they have thus had a long time span

of adapting to the environments, but yet not been considerably prone to morphological changes. They are restricted to shallow waters with little or no predation, but less so to temperature and salinity, which means that they live on all latitudes and in varied salinity (*Lepidurus arcticus* occurs in temperatures down to 4°C and some species of *Artemia* tolerate hyper-saline water (Longhurst 1955; Vanhaecke et al. 1984)). Although they are spatially widely separated from each other, they have all retained the morphology of their Devonian ancestors, probably as a result of the lack of predation pressure and the dispersal of diapausing eggs, as suggested by Gueriau et al. (in prep). The short-life ecosystem that constitutes temporary pools, actually appear to be one of the most stable and long-lived in terms of global distribution and morphologically static inhabitants. The branchiopod assemblage in Strud provides significant and remarkable clues to the ecosystem in which they lived – an ephemeral pool in close proximity to a floodplain environment. This assemblage is fascinating in many aspects; the animals show apparent differences to the earlier (stem-groups) from the Lower Devonian Rhynie chert, but remarkable similarities to the modern respective taxa. Further, they are not only preserved as two-dimensionally flattened body fossils, but they also have their eggs preserved in and around them (Gueriau et al. in prep).

There are no “intermediate steps” between the marine putative stem-group branchiopod *Rehbachella* from the upper Cambrian, the stem-group notostracan and stem-group anostracan from the Lower Devonian, and the crown-group representatives in the Upper Devonian. Anostracans and notostracans are only found on continental waters, whereas diplostracans have occurred in marine environments in the past, with a few returning more recently (Hegna 2012). As the internal phylogeny of branchiopods is not yet resolved, it is difficult to draw any conclusions about when and what groups abandoned the marine realm – whether the last common ancestor of the crown-group Branchiopoda was marine or continental, are questions that remain unanswered. As said, the diapausing eggs found in Strud confirm that this ability was present already in the Late Devonian. The reason why these cysts evolved is not clear. The diapausing eggs are not only useful for dry seasons but also functions to spread the population either by wind, or animals which for example can carry the egg-containing mud under their feet. Wind is not an effective way for branchiopods to disperse, since the eggs are typically stuck in the dry mud on the ground. At the time of the Late Devonian there were no large terrestrial animals that could take the eggs with them to unexplored areas, so the initial benefits must have been solely for surviving desiccation.

For the Chelicerata, it is strongly suggested that one eurypterid genus could occupy a range of different habitats, depending on their ontogenetic stage, moulting and mating behaviour (see Braddy 2001 for a review). Juvenile eurypterids are found more often in near-shore and lagoonal waters, whereas adults often inhabited environments such as rivers and open marine.

Juveniles initially living in the ponds could have been wandering up on land to get to the adjacent rivers when becoming old enough to compete with larger animals. This could explain why the small eurypterid specimens in Strud are found in association with the branchiopod crustaceans whereas the adult fragments are found deeper down in the succession together with plant and vertebrate remains, in a coarser deposit in a higher energy environment such as a river. The advantage of living in small shallow ponds is obvious – here the young and vulnerable eurypterids were safe from predators (fish) but had access to prey (the smaller branchiopods and/or their eggs). There is no evidence of the Strud eurypterids seeking calm waters solely for moulting, i.e. a mass moult assemblage, but this could be a preservational artefact.

5. Conclusions and future perspectives

- The Upper Devonian Strud quarry has delivered various vertebrate fossils (fish and early tetrapods). It also encompasses an outstandingly well-preserved and complex fossil arthropod fauna in terms of composition of taxa, appearance in geologic time, and preservation. A reconstruction of the Famennian Strud environment displays a calm freshwater floodplain environment with a slow accumulation of sediments. As result there is a short succession of sediments embedding arthropods in various layers; eurypterids within the river deposits, and pancrustaceans represented in adjacent ponds and ephemeral (temporary) pools.
- Notostracans collected in the fine shales have provided a much broader understanding of the evolution of the group in the way that they are morphologically different from the Early Devonian suggested member *Castracollis*, but very similar to the later and extant forms. *Strudops goldenbergi* described in Paper III is the earliest undisputed member of the total group Notostraca, as shown in the phylogeny of early notostracans.
- Anostracan and spinicaudatan branchiopods, sampled from the same layer as the notostracans, demonstrate notable similarities to modern members of their groups, for example the spinicaudatan external carapace morphology and encysted eggs, and the anostracan stalked eyes and enlarged antenna in the male individual.
- The encysted eggs associated with the branchiopod fossils strongly suggest that branchiopods were adapted to ephemeral pools already in the Late Devonian. This trait probably allowed branchiopods to survive more or less unchanged until now, since they could survive in and spread to areas where many other animal groups could not.
- The insect, *Strudiella devonica*, described herein is an important find as it minimises the “hexapod hiatus”. Insects have been long searched for in Middle to Upper Devonian strata, but until recently (Garrouste et al. 2012) without a convincing outcome.
- *Strudiella* is composed of a head region, a thorax bearing three pairs of uniramous limbs part and an abdomen. The relatively poor preservation of the insect fossil *Strudiella devonica* lacking a detailed morphology, and the fact it is represented by a single specimen, led to immediate criticism of the original description (Hörschemeyer et al. 2013), met by Garrouste et al. (2013) in an attempt to clarify why *Strudiella* is indeed

an insect and not a crustacean as suggested by Hörnschemeyer et al. (2013).

- The eurypterids from Strud are of two categories; body fossils found in the branchiopod-bearing layer, interpreted as juveniles, and the larger isolated fragments from the lower, coarser, river deposits. The body fossils have a subquadrate carapace, slightly rounded anteriorly, with oval or crescentic eyes, six pairs of prosomal appendages, and non-subdivided opisthosoma consisting of up to 12 segments and a lanceolate to styliform telson.
- At this point, the affinities of the eurypterids herein are not clear, i.e. it remains unresolved whether the specimens belong to the same group of eurypterids, and where they should be placed systematically. Based on the morphology of the body fossils with the non-subdivided opisthosoma, the shape and position of the eyes, and the apparent walking form of the sixth prosomal appendage, they suggestively belong within the *Stylonurina*.
- Studies herein have, together with additional analyses by other research groups, substantially modified the image of the upper Famennian Strud locality regarding both sedimentology and ecology of the biota. However, the ecosystem is complex and at this point not a fully resolved matter. The still on-going study of the locality and potentially newly discovered quarries nearby will provide further knowledge of Late Devonian freshwater ecosystems.

6. Svensk sammanfattning

Leddjuren (Arthropoda), utgör den absolut största gruppen av flercelliga djur på jorden. Uppskattningsvis tre fjärdedelar av alla nu levande (recenta) arter hör till detta framgångsrika fylum, i vilket kräftdjur (Crustacea), insekter (Hexapoda), mångfotingar (Myriapoda) och palpkäkar (Chelicerata) ingår. Gemensamt för gruppen är en segmenterad kropp, ledade extremiteter, och ett hårt yttre skelett (exoskelett) uppbyggt av ”plåtar” bestående av kitin och protein, ibland även med mineralet kalcit för extra härdning. Exoskelettet ger stöd åt djurets muskler vilka är fästa på insidan, men framförallt fungerar det som ett effektivt skydd mot uttorkning och predatorer. Att kroppen är segmenterad är viktig då det innebär att vissa delar av kroppen är anpassade för specifika funktioner (tagmatisering), ofta utrustade med specialiserade extremiteter. Leddjurens huvud har gett upphov till livliga debatter bland olika forskargrupper inom ämnet, segmenten på huvudet är nämligen sammaväxta med varandra och det är svårt att peka ut vilken struktur (extremitet) som hör till vilket segment. Detta är något enklare när det gäller recenta leddjur där man kan studera t ex embryoutveckling och neurologi, jämfört med hos fossil där man uteslutande får förlita sig på morfologin. Att kunna härleda dessa huvudstrukturer är av stor vikt när man ska rekonstruera släktträd (fylogener), något som alltså inte är helt lätt. Mångfotingarna, kräftdjuren, och insekterna (ofta kallade Mandibulata med ett gemensamt namn) har alla ett huvud med antingen två par antenner (kräftdjuren) eller ett (insekterna och mångfotingarna). De skiljer sig åt i många aspekter men gemensamt för alla tre grupper inom Mandibulata är deras mandibler, eller käkdelar, vilka är modifierade benpar specialiserade för att bearbeta föda. Palpkäkarna å andra sidan har huvud och mellankropp sammansmälta till ett så kallat prosoma. Vidare saknar palpkäkarna både antenner och mandibler men har istället gripklor, chelicerer, som främsta födobearbetande extremitet. Leddjuren var vanligt förekommande i haven redan under kambrium, och var förmodligen de första djuren att lämna marina habitat någon gång under ordovicium. Under devon, när de fyrfota ryggradsdjuren tog sina första trevande steg på land, var leddjuren redan där väl etablerade med alla sina undergrupper.

Denna avhandling behandlar sen-devonska (ca. 360 miljoner år gamla) representanter från tre av de fyra undergrupperna (kräftdjur, insekter och palpkäkar) från en liten geologisk lokal i Strud i provinsen Namur, Belgien. Avlagringarna i Strud avsattes i långsamt strömmande sötvattendrag utan

några marina inslag. Detta fluviala system tros ha utsatts för periodvisa översvämningar och uttorkningar vilket visar sig i stratigrafien som både grövre avsättningar i strömmande vatten och som finkorniga, långsamt avsatta sediment i närliggande grunda stillastående vattensamlingar. De rester av djur och växter som hittats här utgör ett nästintill komplett ekosystem i form av tidiga fröbärande växter, tetrapoder (fyrfota ryggradsdjur) lungfiskar, kvastfeningar och leddjur (räkor, bladfotingar, havsskorpioner och en presumtiv insekt). Nedan följer en kort sammanfattning av respektive artikel som alla handlar om leddjuren från Strud, ur ett ekologiskt och evolutionärt perspektiv, men en kort inledning till varje leddjursgrupp.

Artikel I och II

I artikel I och II (Garrouste et al. 2012;2013) beskrivs den nästintill kompletta insekten *Strudiella devonica* Garrouste et al. 2012 från de finkorniga skifferlagren i Strud. Insekterna tillhör klassen Hexapoda och karakteriseras som namnet antyder av sex ben, vilka är icke-grenade och är placerade på mellankroppen (thorax). På huvudet har de bland annat ett par antenner, maxiller och mandibler (käkdelar).

Fossilet, som utgörs av endast ett exemplar, är ca. 8 mm långt, har ett huvud med bevarade mandibler, ett par antenner, en benbärande tresegmenterad mellankropp och en tio-segmenterad bakkropp (abdomen). *Strudiella* tolkades som en nymf på grund av avsaknaden av vingar trots att mandiblerna tros ha varit av samma typ som hos vingbärande insekter. Artikeln tilldrog sig mycket uppmärksamhet då de tidigaste beskrivna insekterna kommer från tidig-devonska avsättningar och inga övertygande insekter tidigare hittats förrän i tidig karbon (Engel & Grimaldi 2004; Garrouste et al. 2012). Man har hittills utan framgång sökt efter insekter i mellan- och sen-devonska terrestriella sedimentära lager, och fyndet av *Strudiella* rapporterades som en viktig pusselbit i insekternas utvecklingshistoria. Dock möttes Garrouste et al. (2012) av massiv kritik och Hörnschemeyer et al. (2013) publicerade ganska omgående en artikel där de pekade ut brister i den ursprungliga beskrivningen, till exempel att Garrouste et al. (2012) övertolkat flera strukturer, men ignorerat andra. Garrouste et al. (2013) mötte kritiken med ett kort förtydligande svar där det framhävdes att *Strudiella*, trots sin ringa storlek och icke välbevarade exemplar faktiskt är mer likt en insekt än någon annan leddjursgrupp.

Artikel III

Artikel III (Lagebro et al. 2015) handlar om exceptionellt bevarade sköldbladfotingar (Notostraca), funna i samma lager som *Strudiella*. Branchiopo-

derna, eller bladfotingar på svenska, är en grupp tillhörande kräftdjuren (Crustacea) som uppvisar en del relikta egenskaper, t ex icke-specialiserade kroppsben. De har fått både sitt svenska och sitt vetenskapliga namn från sina bladlika ben. Benen är delade i två grenar, som hos alla kräftdjur. Hos bladfotingarna bär den yttre grenen stora bladlika utskott (gälar, därav namnet Branchiopoda, som betyder ”gäl-fot”). Deras senaste gemensamma stamfader (last common ancestor) förmodas vara *Rehbachella kinnekullensis* Müller 1983 från över-kambriska marina avsättningar från Västergötland, Sverige.

Den mest utmärkande karaktären för sköldbladfotingar jämfört med andra bladfotingar, är deras stora, platta huvudsköld (carapace) men också deras drastiskt reducerade antenner. Den allra tidigaste sköldbladfotingen tros vara *Castracollis wilsonae* Fayers & Trewin, 2003 från tidig devon i Rhynie i Skottland. *Castracollis* skiljer sig markant från både *Strudops* och alla senare och recenta Notostraca med sin avvikande form, detaljer av benen, och genom att *Castracollis* inte helt övertygande bar en huvudsköld.

Fossil av sköldbladfotingar är relativt vanligt förekommande i Strud och de hör alla till samma art, *Strudops goldenbergi* Lagebro et al. 2015. Förutom en grundlig beskrivning av det nya släktet *Strudops* med dess typart *S. Goldenbergi* innehåller artikel III en fylogenetisk analys inkluderande 23 fossila och recenta taxa och 60 karaktärer. Analysen resulterade i ett kladogram där *Strudops* bevisligen är den allra tidigaste faktiska sköldbladfotingen (jmf. *Castracollis*). *Strudops* är utmärkande inte bara för sin tidiga uppkomst, utan också för sin tydliga likhet med nu levande sköldbladfotingar.

Artikel IV

Artikel IV (Gueriau et al. in prep) innehåller beskrivningar av ytterligare två nya bladfotingar *Gesvestheria pernegrei* och *Haltinnaias serrata* (Diplostraca (Spinicaudata, musselräkor) respektive Anostraca (gälbladfotingar)). Vidare innehåller artikeln en hypotes om hur det till synes instabila ekosystem som en temporär vattensamling (ephemeral pool) utgör lyckats bibehålla samma typ av organismer sedan sena devon. Här diskuteras de morfologiska och ekologiska likheterna mellan bladfotingarna från Strud och deras recenta motsvarigheter, med extra fokus på de ”viloägg” som hittats i anslutning med själva fossilerna. Äggen i fråga är bevarade dels inuti fossilerna och hopklistrade i klumpar utanför, så kallade ”äggbanker”. Både äggens utseende och sättet de läggs i äggbanker i omgivande sediment är mycket likt tillvägagångssättet idag.

Artikel V

I den sista artikeln, artikel V (Lagebro et al. in prep) presenteras lämningar av havsskorpioner funna i Strud. Havsskorpionerna, Eurypterida, tillhör klassen Chelicerata (palpkäkar) och är alltså besläktade med skorpioner, spindlar, kvalser m.fl. Trots sitt svenska namn levde havsskorpionerna både i marina miljöer och i sötvattendrag. Havsskorpioner var rovdjur som i vissa fall kunde bli enormt stora (mer än två meter) och var vanligt förekommande från ordovicium till perm, då gruppen helt dog ut. Som namnet antyder visar havsskorpionerna vissa likheter med recenta landlevande skorpioner, men deras inbördes släktskap har inte helt kunnat påvisas. Gemensamt för alla palpkäkar är som nämnts ovan deras prosoma (jmf. med mandibulaterna), som hos havsskorpionerna täcks av en dorsal huvudsköld på vilken ögonen är integrerade. Havsskorpioner bär sex par extremiteter på prosomat; första paret är griplorna, chelicerna som ofta är mycket mindre än de övriga extremiteterna, men kan också vara gigantiska som hos undergruppen Pterygotidae. De följande fyra benparen var ej kloförsedda, men en del av dem bar taggar. Det sjätte och sista benparet var antingen utvecklat till att gå med som hos gruppen Stylonurina, eller, som hos Eurypterina, till en simpaddel (Lamsdell et al. 2010). Om det sjätte benparet finns bevarat hos ett fossil är det en viktig karaktär för en första klassificering, men för närmare analyser tittar man på detaljer på prosomat; dess form, strukturer på dess ventrala sida, på ögonens form och placering, samt bakkroppens och stjärtens utformning.

I Strud har två typer av havsskorpioner hittats. Dels förekommer nästintill kompletta små (upp till ett par cm) kroppsossil från vad som tolkas vara juvenila individer, dels större enskilda fragment av plåtar med för gruppen typiska ornamenteringar ("knölar"). De juvenila exemplaren kommer från samma lager som *Strudiella* och *Strudops*, medan fragmenten hittats i ett något äldre, grovkornigare lager avsatt i strömmande vatten. Enligt vissa forskare kunde havslevande havsskorpioner söka sig till grundare strandnära vatten för att lägga sina ägg och låta avkomman växa till sig i en relativt lugn miljö innan de begav sig ut på djupare hav (Braddy 2001). Denna hypotes stöder sig på förekomsten av vuxna individer i sediment avsatta på djupt vatten och av juvenila individer av samma art i strandnära sediment. Inte nog med att havsskorpioner kunde ta sig mellan olika typer av vatten, de tros också ha kunnat vistats korta stunder på land. Detta verkar vara tillämpligt även i Strud i och med att de stora fragmenten och juvenilerna förekommer i lager avsatta i energirika respektive lugna vatten. När denna avhandling trycks är det ännu inte klart till vilken grupp havsskorpionerna från Strud hör, eller om de ens hör till samma art. Baserat på karaktärer som hunnits analyserats (extremiteternas, huvudsköldens och bakkroppens form) verkar de tillhöra gruppen Stylonurina, dvs de havsskorpioner med sitt sjätte benpar anpassat för gång.

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