The Strud crustacean fauna (Late Devonian, Belgium): updated review and palaeoecology of an early continental ecosystem

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ABSTRACT: Arthropods were the first known animals to colonise land habitats, with myriapods and arachnids having done so at least by the Silurian. Much later, several lineages of Pancrustacea (hexapods and the paraphyletic crustaceans) also ventured onto land; the hexapods by the Early Devonian, and later at least four other groups of crustaceans, namely isopods, amphipods, ostracods and decapods, most of which generally colonised the continental water bodies. All faced a series of challenges (in particular: gas exchange; desiccation; reproduction; osmoregulation; and exposure to ultraviolet radiation), resulting in many morphological, physiological and ecological adaptations. Nonetheless, whether they reached land via saltwater or freshwater remains poorly documented, mainly because relevant localities are few. The Famennian (Late Devonian) Strud locality in Belgium provided an exceptional source of information on early aquatic continental ecosystems and their plant, vertebrate and arthropod colonisers at a crucial step in the terrestrialisation process. Here, we review and update its crustacean fauna, which inhabited floodplain and temporary pool waters. New anatomical details of the notostracan *Strudops goldenbergi* Lagebro *et al.*, 2015, as well as a new genus and species of spinicaudatan, are described. We also discuss the ecology of this unique, early continental ecosystem and the insights it gives into the terrestrialisation process.

KEY WORDS: Famennian, floodplain habitats, fossil branchiopods, fossil eumalacostracans, temporary pools, terrestrialisation

Arthropods are the most diverse group of animals in terms of species number, as well as, together with molluscs and annelids, body plan disparity. Zhang (2011) reported 1,214,295 extant species, comprising 1,023,559 hexapods, 111,937 chelicerates (arachnids and horseshoe crabs), 66,914 crustaceans (all pancrustacean lineages excluding hexapods) and 11,885 myriapods. Although the total number of fossil arthropods is impossible to estimate, they have probably been a major component of the Earth's fauna since the Cambrian (541–485.4 Ma), in which they diversified greatly (e.g. Edgecombe & Legg 2014; Lee *et al.* 2013). Arthropods are also the first animals to venture on land, by at least the Silurian (443.8–419.2 Ma) with myriapods and arachnids (acarids, spiders and scorpions among others; see Dunlop *et al.* 2013 for a review; Waddington *et al.* 2015).

But terrestrial arthropods may have existed earlier, as suggested by trackways in coastal dune strata from the Middle Cambrian of New York (*c.*500 Ma; Hagadorn *et al.* 2011) and the Late Cambrian–Early Ordovician of Ontario (MacNaughton *et al.* 2002; Braddy 2004; Collette & Hagadorn 2010; Collette *et al.* 2012), and by molecular time trees (Rota-Stabelli *et al.*

2013). The earliest hexapods are documented from the Early Devonian Rhynie locality (Scotland, *c.*410 Ma), with the springtail (Collembola) *Rhyniella praecursor* Hirst & Maulik, 1926 (Scourfield 1940), the possible bristletail (Zygentoma or Archaeognatha) *Leverhulmia maria* Anderson & Trewin, 2003 (Fayers & Trewin 2005) and *Rhyniognatha hirsti* Tillyard, 1928 interpreted as the oldest true insect (Engel & Grimaldi 2004). Modern phylogenies (e.g., Regier *et al.* 2010) suggest that all these land-living arthropod clades evolved independently, and at least seven separate terrestrialisation events may have occurred within arthropods: in myriapods, arachnids, and at least five times in pancrustaceans. Amongst the latter, hexapods and at least four groups of crustaceans (namely isopods, amphipods, ostracods and decapods), colonised terrestrial environments independently (Dunlop *et al.* 2013).

Unfortunately, the morphological evolution of these lineages in the Late Silurian to the Late Devonian is very poorly known, because the fossil record for early continental arthropods is extremely scarce; mainly due to the very few continental sedimentary localities at this time. The complex and diverse continental ecosystem from the Late Devonian of Strud, which
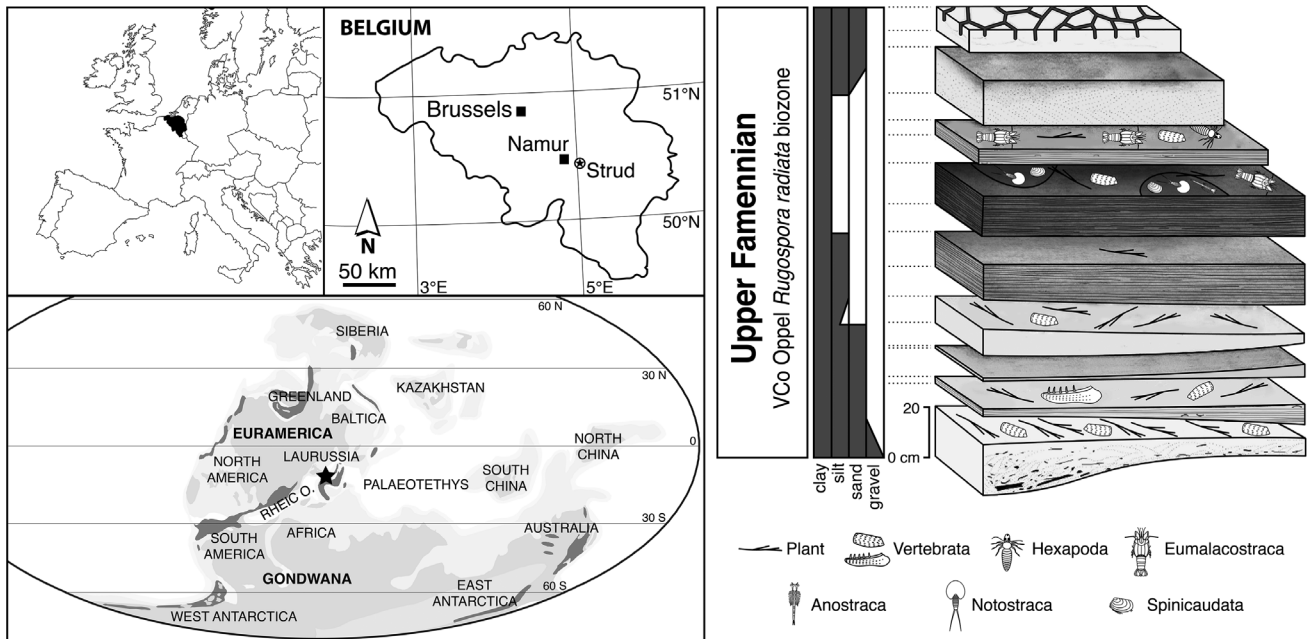
Figure 1 Geography, palaeogeography (modified from the Late Famennian to early Viséan (359–338 Ma) (map from Golonka 2000) and stratigraphy of the Strud channel-filling deposits, showing their main fossiliferous content (Late Devonian, Belgium). Modified from Gueriau *et al.* 2014a and Denayer *et al.* 2016.

yields an abundant and diverse flora (including early cupulate seed plants (Prestianni *et al.* 2007), vertebrate fauna including early tetrapods (Clément *et al.* 2004; Blieck *et al.* 2007, 2010), various placoderms (Olive 2015; Olive *et al.* 2015a), actinopterygian, acanthodian and sarcopterygian fishes (Clément & Boisvert 2006), and well-preserved aquatic crustacean fauna), appears as a unique snapshot of the terrestrialisation processes. Here, we review and update this crustacean fauna. This article also describes a newly discovered species of spinicaudatan.

Institutional abbreviations. IRSNB, Royal Institute of Natural Sciences, Brussels, Belgium; MNHN, Muséum national d'Histoire naturelle, Paris, France.

1. Geological setting

1.1. History and depositional environments
Strud is a village in the Belgian municipality of Gesves (Wallon Region, Namur Province). The outcrop that yields the fossils (50°26′, 43″N, 5°03′, 24″E) results from the extraction of sandstone layers for local building stone during the second half of the 19th Century, and corresponds today to a small quarry of a few dozen square metres exposing oblique and vertical deposits. Since the first paleontological investigation by the palaeobotanist Hock in 1878, who mentioned the finding of well-preserved *Rhacophyton condrusorum* Crépin, 1875 (Hock 1879), this quarry has yielded various other fossil remains of plants (Stockmans 1948) as well as 'fishes' (Lohest 1888; Leriche 1931) from the Late Devonian. Amongst this vertebrate material, Clément *et al.* (2004) recognised a tetrapod ichthyostegid jaw fragment, misidentified as a fish by Lohest. Clément and collaborators then started looking for this new early tetrapod-bearing locality, in order to find additional material. The quarry was finally rediscovered in October 2004, after having been abandoned for over a century (Clément & Boisvert 2006).

The fossil-bearing quarry of Strud is only the younger part of a longer section, beginning in the Lower Famennian greyish to greenish shales with one or more layers of oolitic ironstone deposited as tempestites in a muddy shallow marine environment. The beds yielding the fossils are precisely located in

the upper part of the overturned section, dipping at 80° to the south. The depositional environment is characterised by a 1.4 m-thick fining-upward channel-fill that preserves distinct but synchronous, continental fossil assemblages (Fig. 1). The succession begins with yellow to brown arkosic sandstones, deposited in a flood channel, that yielded isolated remains of vertebrates, including early tetrapods (Clément *et al.* 2004; Clément & Boisvert 2006; Olive 2015; Olive *et al.* 2015a, 2016), and plant macrofossils (Prestianni *et al.* 2007). Arthropods have been found in fine shales corresponding to the last channel-fill phases. Complete eumalacostracans (Gueriau *et al.* 2014a, b), a putative insect (Garrouste *et al.* 2012, 2013; Hörnschemeyer *et al.* 2013), eurypterid remains and plant microfossils, including the first seeds (Prestianni *et al.* 2007), are found in black to green shales, indicating a low energy, restricted floodplain habitat. Well-preserved branchiopods (notostracans, spinicaudatans and anostracans; Lagebro *et al.* 2015; Gueriau *et al.* 2016) were recovered, together with plant microfossils from small (a few tens of centimetres in width) lenses of fine, dark grey shale lying on a dark siltstone exhibiting millimetre-thick sandy laminae, interpreted as fresh to brackish, shallow-water pool deposits which periodically dried out.

Denayer *et al.* (2016) precisely described the stratigraphy and palaeoenvironments of the locality. According to regional stratigraphic correlations, these deposits belong to the Upper Famennian Bois des Mouches Formation. A miospore assemblage (VCo Oppel *Rugospora radiata* interval biozone) confirms a late Famennian age (Denayer *et al.* 2016).

1.2. Taphonomy of the well-preserved arthropods
The preservation of soft-bodied or lightly skeletised organisms such as arthropods in the fossil record requires exceptional physical and chemical conditions (Seilacher *et al.* 1985). The occurrence of well-preserved crustaceans (eumalacostracans, spinicaudatans, notostracans and anostracans) in the Upper Famennian sedimentary rocks of the Strud locality is thus remarkable and attests to exceptional depositional and taphonomic processes. They are preserved as a pale to dark brown carbonaceous film consisting of "shadows" of organic origin and tending to flake-off in patches, as revealed by scanning
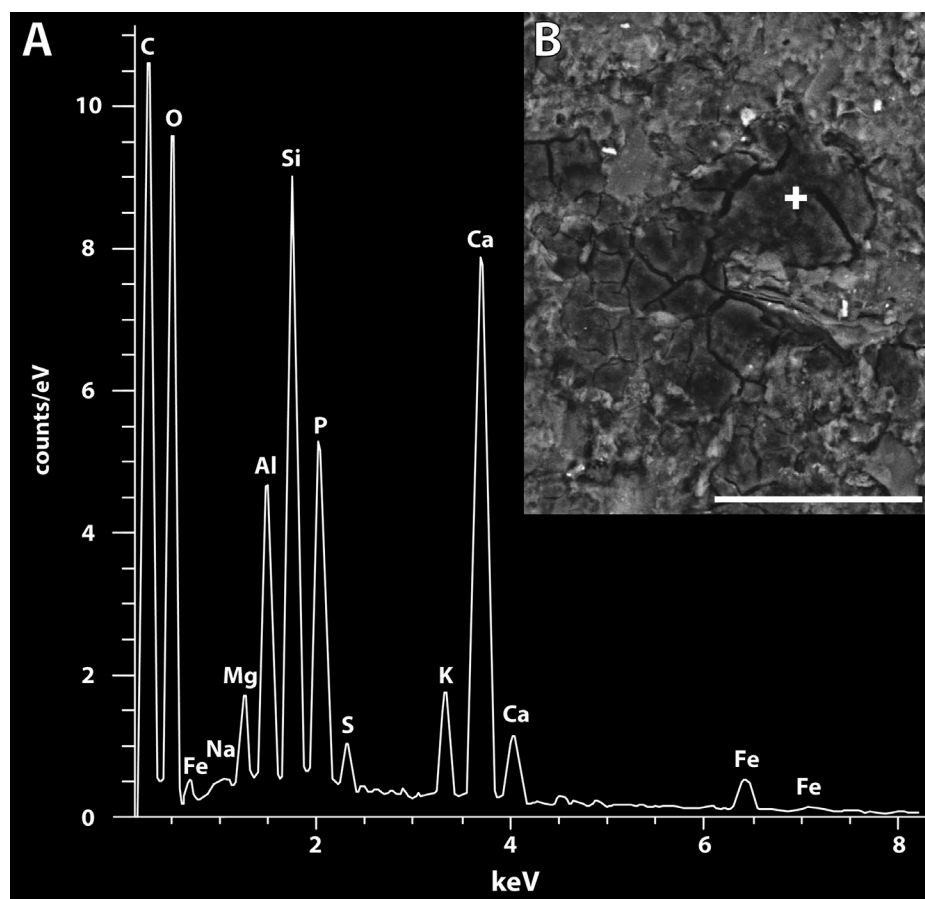
Figure 2 SEM-EDX point spectroscopy from the head of *Strudiella devonica* Garrouste *et al.*, 2012: (A) EDX spectra showing presence of carbon, oxygen and phosphorous within the fossil (LV 30 Pa, 20 kV); (B) SEM photograph of the precise area investigated; white cross indicates exact location of chemical analysis. See Fig. 3G for a view of the complete specimen. Scale bar = 50 μm.

electron microscopy and energy-dispersive X-ray (SEM-EDX) spectroscopy (Fig. 2).

A large majority of specimens presents a dorso-ventral compression, with only a few preserved in lateral aspect. They are mostly disarticulated, but many were found nearly complete in the finer green and grey shales (carapace, pleon and telson articulated; Fig. 3), which is evidence of the absence of – or very limited – transport in the calm and confined environment of the floodplain. Such conditions allowed the minute preservation of delicate anatomical structures, such as the cephalic and thoracic appendages. The best-preserved legs, antennae and mandibles have been found isolated within the sediment; whereas their morphologies and connections with the body are often hardly distinguishable in the articulated specimens, due to compacted superimposition of the different anatomical structures. Many specimens preserve traces of the gut, suggesting that they represent carcasses rather than moults (see Tetlie *et al.* 2008).

Only decay-resistant gut and cuticular structures fossilised here. This corresponds to the decay stages 4–5 proposed by Butler *et al.* (2015), with substantial autolysis and microbial decay of the labile soft-tissues, such as musculature and other internal organs, before fossilisation. The preservation of the arthropods is then interpreted as the result of rapid burial in fine-grained sediment before complete decay occurred.

2. Material and methods

Specimens were collected during the successive field campaigns organised each year since the rediscovery of the locality in 2004. The material is housed at the IRSNB (Brussels, Belgium). The fossils were observed under a binocular microscope with polarised light, both dry and covered in 95 % ethanol, to see cuticular remains with a low angle light to reveal relief. Drawings were produced using a camera lucida. Specimens were photographed covered in ethanol with cameras coupled with macro lens equipped with polarising filters. Anatomical measurements were performed using ImageJ software. Statistical analysis was performed using the 'R' statistical environment (R Development Core Team 2011). Scanning electron microscopy (SEM) imaging and spectroscopy were carried out in back scattered electrons (BSE) mode using the Tescan SEM (VEGA II LSU) associated with a Bruker SD[3] energy-dispersive spectrometer (EDS) detector of the microscopy platform of the MNHN, Paris (France).

3. Systematic palaeontology of the Strud crustacean fauna

Malacostraca Latreille, 1802
Eumalacostraca Grobben, 1892
?Eucarida Calman, 1904
?Decapoda Latreille, 1802
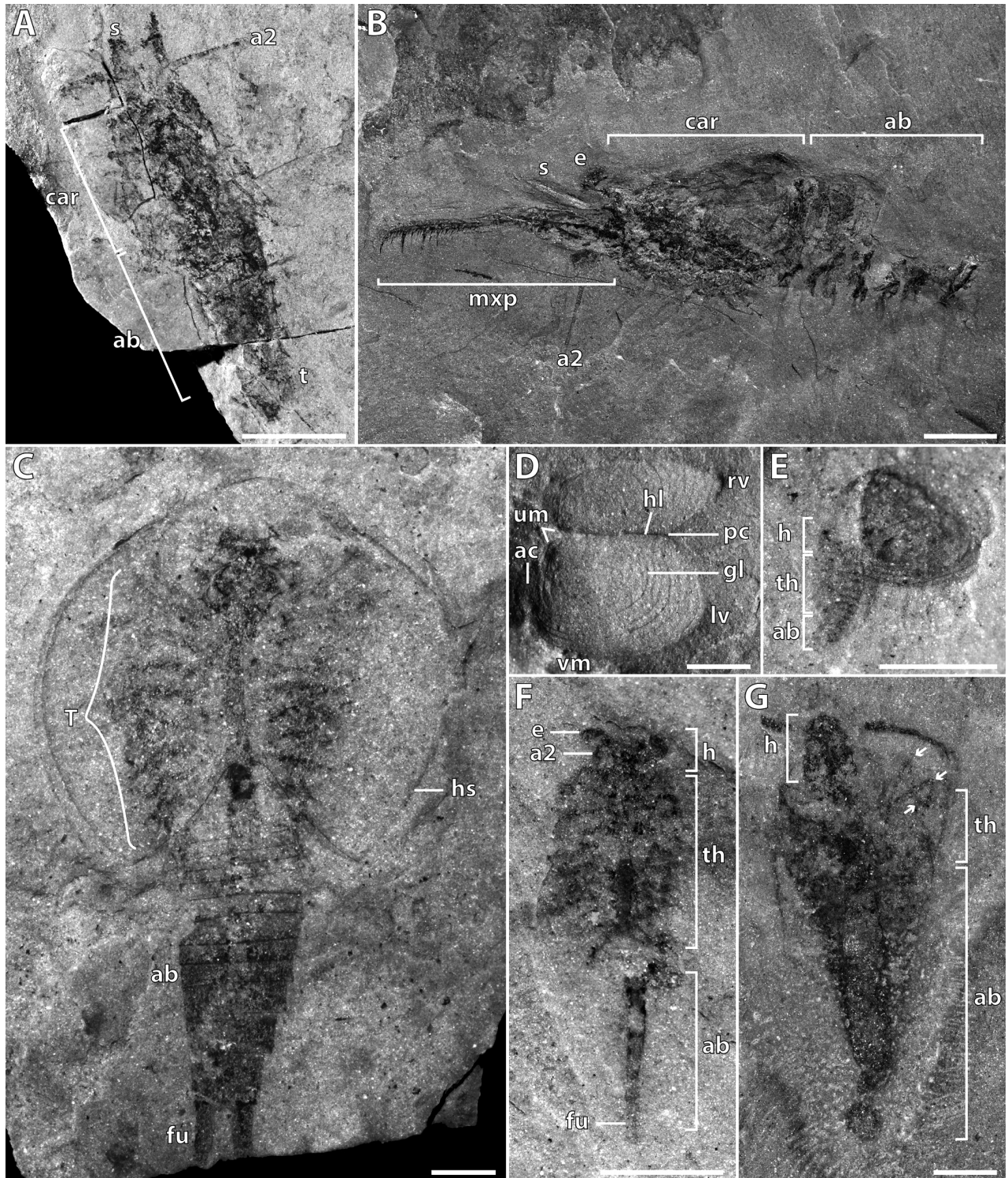Tealliocarididae Brooks, 1962
Tealliocaris Peach, 1908

Figure 3 Arthropod fossils from Strud, Belgium: (A) *Tealliocaris walloniensis* Gueriau, Charbonnier & Clément, 2014a, paratype IRSNB a 12869a, nearly complete specimen in ventral view; (B) *Schramidontus labasensis* Gueriau, Charbonnier & Clément, 2014b, paratype IRSNB a 12878a, anterior part in lateral view; (C) *Strudops goldenbergi* Lagebro *et al.*, 2015, paratype IRSNB a 12859, complete specimen in dorsal view. (D–E) *Gesvesia pernegrei* Gueriau *et al.*, 2016: (D) holotype IRSNB a 12932, external morphology of the carapace; (E) paratype IRSNB a 12934a, juvenile specimen in lateral view. (F) *Haltinnaias serrata* Gueriau *et al.*, 2016, paratype, IRSNB a 12930, male in dorsal view; (G) *Strudiella devonica* Garrouste *et al.*, 2012, holotype IRSNB a12818a. Abbreviations: a2 = antenna; ab = abdomen; ac = anterior corner; car = carapace; e = pedunculate eye; fu = caudal furca; gl = growth line; h = head; hl = hinge line; hs = head shield; lv = left valve; mxp = maxillipeds; pc = posterior corner; rv = right valve; s = scaphocerite; T = thoracopods; th = thorax; um = umbo; vm = ventral margin. Scale bars = 5mm (A, B); 1 mm (C–G).

Tealliocaris walloniensis Gueriau, Charbonnier & Clément, 2014a
(Fig. 3A)

Holotype. IRSNB a 12866a–b, isolated carapace.

Paratypes. IRSNB a 12867a–b, isolated carapace; IRSNB a 12868a–b, IRSNB a 12869a–b, IRSNB a 12870a–b, nearly complete specimens; IRSNB a 12871a–b, IRSNB a 12872a–b, articulated pleons; IRSNB a 12873a–b, posterior part of the pleon showing telson and uropods; IRSNB a 12874a–b, isolated cephalic appendages (antennula, antenna and scaphocerite).

Discussion. The total material includes more than 50 specimens. *Tealliocaris* was previously only known from the Carboniferous. Clark (2013) ascribed it to Decapoda, based upon a suite of characters indicating a closer relationship to decapod crustaceans (in particular, Astacida, Homarida and Glypheoidea) than to any other eumalacostracan clade. *Tealliocaris walloniensis* then enlarges the stratigraphical distribution of the genus to the Late Devonian, and represents the third Devonian decapod known, after the rather derived lobster-like *Palaeopalaemon newberryi* Whitfield, 1880 (Schram *et al.* 1978) and *Aciculopoda mapesi* Feldmann & Schweitzer, 2010 from Famennian marine deposits of the USA. *T. walloniensis* was, therefore, thought to document the earliest occurrence of continental decapod crustaceans and to indicate that decapods have been part of continental ecosystems at least since the Late Devonian. However, the phylogenetic affinities of *Tealliocaris* remain under debate, as its assignment to Decapoda has recently been contested by Jones *et al.* (2016), who transferred it back to Peracarida: Pygocephalomorpha, based particularly on the presence of an oostegite marsupium in females (interpreted by Clark (2013, fig. 6) as phyllobranchiate gills), a distinct terminal telson lobe and a pair of lateral telson lobes (shown by Clark (2013, fig. 12) to be an artefact of compaction of a larger single terminal lobe).

Eucarida Calman, 1904
Angustidontida Gueriau, Charbonnier & Clément, 2014b
Angustidontidae Cooper, 1936
Schramidontus Gueriau, Charbonnier & Clément, 2014b
Schramidontus labasensis Gueriau, Charbonnier & Clément, 2014b
(Fig. 3B)

Holotype. IRSNB a 12880a–b, thoracic appendages in ventral view.

Paratypes. IRSNB a 12878a–b, nearly complete specimen; IRSNB a 12879a–b, isolated cephalic and first thoracic appendages.

Discussion. Besides the type material, only one additional fragment of maxilliped has been collected. Angustidontid remains have been known for more than 80 years, but their crustacean affinity was only recently established (Rolfe & Dzik 2006). These fossils, recognisable by their peculiar first pair(s) of thoracopods modified into long, slightly curved maxillipeds bearing elongated teeth of alternating sizes (Fig. 3B), have been recovered from Upper Devonian marine deposits through most of Euramerica (Rolfe & Dzik 2006; Shpinev 2010) and are interpreted as pelagic predators. Gueriau *et al.* (2014b) ascribed them to Eucarida, based upon their carapace being fused to thoracic segments 1–7, and erected the new order Angustidontida, based upon the absence of autapomorphies of each of Euphausiacea, Amphionidacea and Decapoda. *Schramidontus labasensis* documents the first occurrence of angustidontids in a continental environment. Unlike *Angustidontus seriatus* Cooper, 1936 (Rolfe & Dzik 2006), *S. labasensis* possess two pairs of maxillipeds, suggesting that angustidontid crustaceans fill the gap between Amphionidacea (Decapoda *sensu lato*; characterised by a unique pair of thoracopods modified into maxillipeds) and Decapoda *sensu stricto* (three maxillipeds) (Gueriau *et al.* 2014b). This implies that early decapods may have had autapomorphically at least one pair of maxillipeds that were further modified in Decapoda *sensu stricto*.

Branchiopoda Latreille, 1817
Notostraca Sars, 1867
Strudops Lagebro *et al.*, 2015
Strudops goldenbergi Lagebro *et al.*, 2015
(Figs 3C, 4)

Holotype. IRSNB a 12858a–b, nearly complete specimen.

Paratypes. IRSNB a 12854, IRSNB a 12856, IRSNB a 12857, IRSNB a 12859, IRSNB a 12877, nearly complete specimens; IRSNB a 12855, IRSNB a 12860a–b, carapace with cephalic and thoracic appendages; IRSNB a 12861a–b, IRSNB a 12864, posterior part of the abdomen with telson; IRSNB a 12862a–b, IRSNB a 12863, carapace with mouth parts.

New material. IRSNB a 13055, nearly complete specimen; IRSNB a 13056a–b, incomplete carapace with thoracic appendages.

Discussion. *Strudops goldenbergi* is the earliest unequivocal member of total-group Notostraca (Lagebro *et al.* 2015). It is morphologically very similar to modern notostracans, but differs from extant Triopsidae in the absence of dorsal carina, the spineless posterior notch and the larger size, but smaller number, of abdominal segments (Fig. 3C). More than 40 specimens have been collected and most preserve soft-tissues, such as the phyllopodous thoracic appendages, the mouthparts and even clusters of resting eggs. Since the original description, two newly excavated specimens show additional, fine anatomical details of the thoracopods (Fig. 4). One specimen preserves serrated, trapezoidal structures at the tip of the thoracopods (Fig. 4A, C–D) that strongly resemble the 4th and 5th endites and endopod of extant notostracans (see Longhurst 1955, fig. 10 for comparison with extant taxa). However, the morphology of the first thoracopod appears different, with more elongated, articulated "antenna-like" structures (Fig. 4A–B; and see Longhurst 1955, fig. 10), suggesting limb differentiation. Specialisation of the first thoracopods in most extant notostracans consists of elongated 4th–5th endites (Longhurst 1955). Such a type of thoracopods had never before been recorded in fossils (Hegna 2011), but our data suggest that differentiation of the first legs could be as ancient as the Late Devonian. Furthermore, another specimen displays "hockey-stick" setae in the thoracic region, in the same area as the endites and endopods (Fig. 4E–F). Very similar, but smaller, structures were extracted from shale of the early Cambrian Mount Cap Formation, Canada (Harvey & Butterfield 2008, fig. 1a–c). The latter authors suggest a scraping function, based on their proportions and spatial arrangement, and found strong similarities with scraping armatures that are located along the margins of the distal endites in many branchiopod crustaceans (T. H. Harvey, pers. comm. 2015), particularly in the laevicaudatan *Lynceus* (*L. gracilicornis* Packard, 1871 and *L. simiaefacies* Harding, 1941) (Fryer & Boxshall 2009).

Anostraca Sars, 1867
Haltinnaias Gueriau *et al.*, 2016
Haltinnaias serrata Gueriau *et al.*, 2016
(Fig. 3F)

Holotype. IRSNB a 12928a–b, nearly complete specimen, female.

Paratypes. IRSNB a 12930, nearly complete specimen, male; IRSNB a 12929, IRSNB a 12931a–b, nearly complete specimens.
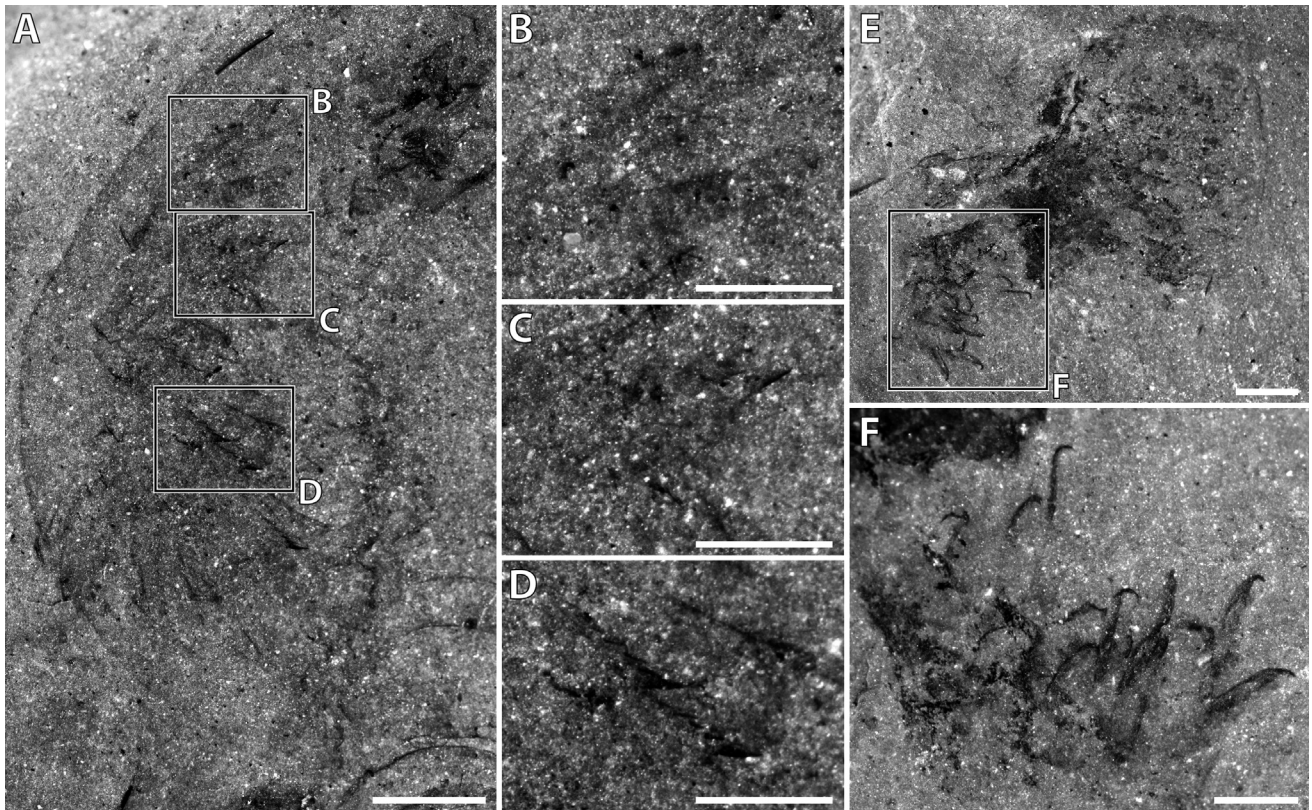
Figure 4 Thoracopod morphology of *Strudops goldenbergi* Lagebro *et al.*, 2015: (A) close-up of the right thoracopds of IRSNB a 13055, complete specimen in dorsal view; (B–D) enlargements of the articulated 4th and 5th endites of the first thoracopod (B), and of endites and endopods (C, D) of following thoracopods, from boxed areas in (A); (E) IRSNB a 13056a, partially preserved anterior thoracic region; (F) enlargement on the "hockey-stick" setae. Scale bars = 1mm (A, E); 500 μm (B–D, F).

Discussion. *Haltinnaias serrata* is the earliest member of total-group Anostraca with a modern morphology, whilst the Early Devonian stem-group anostracan *Lepidocaris rhyniensis* Scourfield, 1926 from Scotland is morphologically distinct in having locomotory biramous antennae. The fossil record for anostracans is extremely limited, due to their small size, delicate nature and lack of a carapace, and no other specimens have been excavated from this locality. Exceptionally, *H. serrata* preserved details of most cephalic and thoracic appendages (Fig. 3F), which bear diagnostic characters of the Anostraca (i.e., pedunculated eyes and phyllopodous thoracic legs). Although it differs from all extant anostracans, it is not possible to assign it to any extant family (Gueriau *et al.* 2016).

Spinicaudata Linder, 1945
Gesvesia Gueriau *et al.*, 2016.
Gesvesia pernegrei Gueriau *et al.*, 2016.
(Fig. 3D–E)

Holotype. IRSNB a 12932, bivalved carapace.
Paratypes. IRSNB a 12933, carapace with preserved digestive system; IRSNB a 12934a, b, IRSNB a 12935a, b, nearly complete specimens with preserved internal anatomy; IRSNB a 12936, carapace with resting eggs.
Discussion. *Gesvesia pernegrei* is the main constituent of the branchiopod community, and hundreds of specimens have been found. The affinities of bivalved branchiopod fossils are usually difficult to assess precisely because their carapaces, which are most often the only remains preserved, display highly homoplastic features that provide little systematic information. Carapace morphology, the presence of growth lines on the whole carapace, and a small head with a relatively

long trunk in *G. pernegrei* (Fig. 3D–E) are features similar to those in extant Spinicaudata, but clearly different from extant Laevicaudata (Gueriau *et al.* 2016). Further research has begun to determine the phylogenetic relationships between extant and fossil spinicaudatans (Astrop & Hegna 2015), but many points still need clarification, and it is not possible to confidently assign *G. pernegrei* to any subclade of Spinicaudata.

Spinicaudata Linder, 1945
Vertexioidea Kobayashi, 1954 sensu Zhang *et al*., 1976
Undulatesta gen. nov.

Etymology. The name is derived is from "undulata" (Latin for wavy) and "testa" (Latin for carapace), referring to the sinuous growth lines on the bivalved carapace.
Type species. *Undulatesta bounonensis* sp. nov. by monotypy.
Diagnosis. Bivalved branchiopod with limnadiform carapace, covered only in the anterior half by growth lines connecting the hinge line sinuously backward.

Undulatesta bounonensis sp. nov.
(Fig. 5)

Etymology. From Bounon, the name of the street just next to the Strud quarry.
Holotype. IRSNB a 13057a–b (Fig. 5A–D), carapace with growth lines.
Paratype. IRSNB a 13058a–b (Fig. 5E), IRSNB a 13059a–b (Fig. 5A, right), incomplete carapaces.
Type locality. Strud, Gesves municipality, Namur Province, Belgium (50°26′43″N, 5°03′24″E).
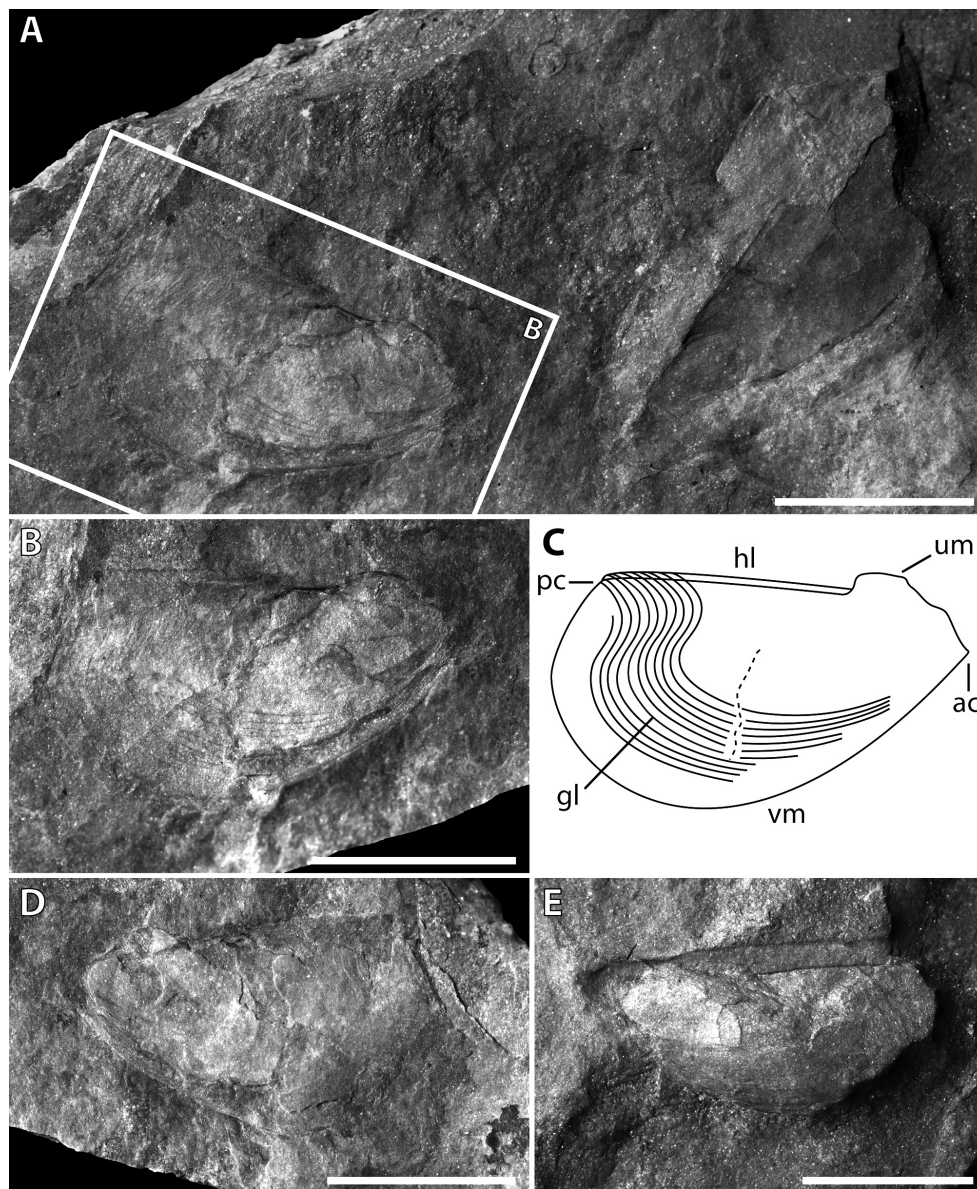
Figure 5 *Undulatesta bounonensis* gen. et sp. nov.: (A) left: holotype, IRSNB a 13057a, right valve in lateral view, head oriented to the left; right: paratype IRSNB a 13059a, left valve in lateral view, head to the right; (B) close-up of the holotype from boxed area in (A); (C) line drawing of holotype, not to scale; (D) holotype, counterpart, IRSNB a 13057b, head to the right; (E) paratype, IRSNB a 13058a, left valve in lateral view, head oriented to the right. Abbreviations: ac = anterior corner; gl = growth line; hl = hinge line; pc = posterior corner; um = umbo; vm = ventral margin. Scale bars = 5mm.

Stratigraphic age. Late Famennian (age based upon miospore assemblages and regional stratigraphic correlations; Denayer *et al.* 2016).

Occurrence. Known only from the type locality.

Description. Bivalved limnadiform carapace (length = 10.66 mm and 11.02 mm, and width = 5.26 mm and 5.29 mm, respectively, for IRSNB a 13057 and IRSNB a 13058, which are the only two specimens that could be confidently measured); mean length/height ratio 2.05 ± 0.04; umbo slightly pronounced; first larval valve unornamented; numerous growth lines forming narrow concentric ribs on the anterior half surface of the valve, connecting dorsally to the hinge line sinuously backward, and converging ventrally at the anterior cardinal angle (Fig. 5A–C); growth lines more closely spaced further from this angle; straight hinge line about two thirds the total length of the carapace; anterior and posterior cardinal angles 140° and 120°, respectively; no internal anatomy is preserved.

Discussion. *Undulatesta bounonensis* gen. et sp. nov. is ascribed to Spinicaudata Linder, 1945, based upon the presence of growth lines on the carapace. Indeed, previous external laminae remain during moulting in Spinicaudata, overlying the youngest (larger) plates, whereas the carapace is smooth in other bivalved branchiopods (Laevicaudata and most of Cladoceromorpha), because the oldest laminae are not retained during moulting (Roessler 1995). It differs from *Gesvesia pernegrei* in its larger size and higher mean length/height ratio (Fig. 6), but most importantly in its striation pattern, which involves growth lines that only cover the marginal part of the carapace, suggesting a different development, with complete valve moulting during the early developmental stages followed by conservation of external laminae later in the development. This type of development is characteristic of the extant family Limnadiidae (Rogers *et al.* 2012) and found in many fossils clustered with limnadiids in Vertexioidea Kobayashi, 1954 *sensu*
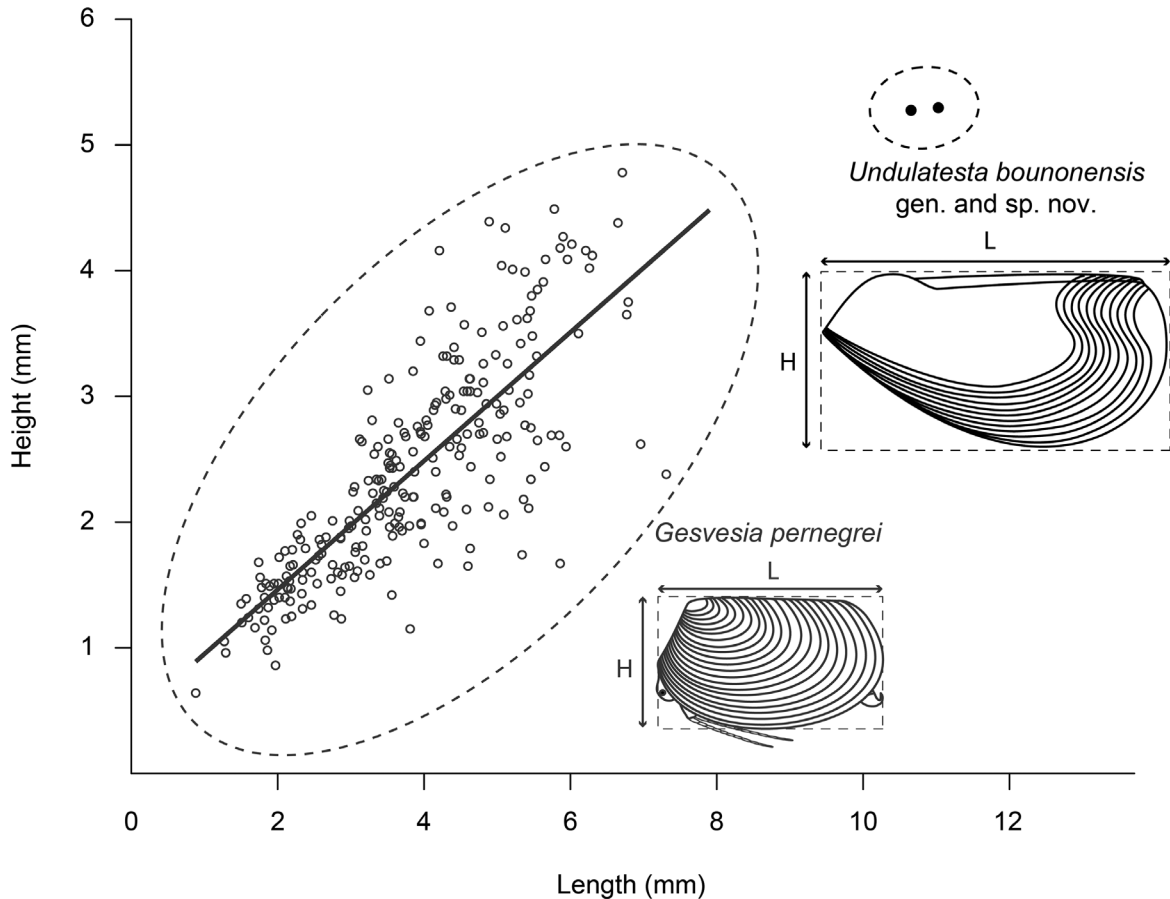
Figure 6 Length/height distributions of the spinicaudatans *Gevesia pernegrei* (circles) and *Undulatesta bounonensis* gen. et sp. nov. (black dots) from Strud, Belgium. Mean L:H ratio in *G. pernegrei* = 1.629 ± 0.390 (n = 251), shown with linear model (intercept = 0.440; slope = 0.512; *p-value* < 2.2e-16; R^2 = 0.637). Mean L:H ratio in *U. bounonensis* gen. et sp. nov. = 2.055 ± 0.040 (n = 2).

Zhang *et al.*, 1976 (See Astrop & Hegna 2015). Recent molecular clock estimates suggest that limnadiids are no older than 200 Ma (Bellec & Rabet 2016), which is not compatible with the assignation of *Undulatesta* to the Limnadiidae. *Undulatesta* is, therefore, here assigned to the more inclusive Vertexioidea.

Remark. Interestingly, the general morphology of *U. bounonensis* gen. et sp. nov. looks very similar to that of the Silurian marine bivalve *Pteronitella retroflexa* Wahlenberg, 1821 (see Walmsley 1962). However, the latter fossils are significantly bigger and bear growth lines covering the whole valves. Moreover, the organic preservation of *U. bounonensis* is not consistent with the calcareous shells of molluscs.

4. Discussion

4.1. A complex Late Devonian floodplain ecosystem

Terrestrialisation of land by plants and animals is the second most important event in the history of multicellular life, after the Cambrian and Ordovician radiations that led to the colonisation of the marine realm and to the first modern-looking trophic webs. The first complex continental ecosystems were settled by the Middle to Late Devonian, after plants, arthropods and tetrapods ventured onto land, respectively, in the Ordovician (*c.* 470 Ma) (Rubinstein *et al.* 2010; Wellman 2014), Late Silurian and Late Devonian (433.8–358.9 Ma) (Shear & Selden 2001; Giribet & Edgecombe 2013; Dunlop *et al.* 2013; Clack 2012). They included some high-diversity forest communities (although forests were not typical in the Mid to Late

Devonian) (DiMichele *et al.* 1992; Stein *et al.* 2012) and irreversibly changed atmospheric pCO_2 and pO_2, climate and sedimentation patterns (Algeo & Scheckler 1998; Dahl *et al.* 2010; Godderis *et al.* 2014).

The Late Devonian Strud locality, together with the Red Hill locality in Pennsylvania (see Cressler *et al.* 2010 for a review of this locality), constitute unique examples of early complex and diversified continental biocenoses, with ecological partitioning of the floodplain biotopes at a high taxonomic level. At Strud, vertebrates, including early tetrapods, placoderms, acanthodians and sarcopterygians, inhabited a deltaic flood channel. Eumalacostracan crustaceans, as well as acanthodian and actinopterygian fishes, were collected from fine shales witnessing a calm and confined floodplain habitat, but were probably more generally living both in floodwaters and in river branches. A community of branchiopod crustaceans (notostracans, anostracans and spinicaudatans) colonised calm, fresh to brackish temporary ponds that seasonally dried and flooded. They overcame constraints of the terrestrial environment, such as seasonal desiccation, by the production of resting (drought-resistant) eggs, which accumulate as an egg bank in sediment and are resistant for long periods of drought, allowing them to await favourable conditions (Gueriau *et al.* 2016). Eurypterid remains have been recovered from all depositional environments and were living in, or exploiting, all the aquatic biotopes. The only unequivocal terrestrial organisms were abundant and diversified plants, including early cupulate seed plants. Garrouste *et al.* (2012) suggested that the putative insect *Strudiella devonica*

Garrouste *et al.*, 2012 was a terrestrial species, but the affinities and lifestyle of this fossil remain under debate (Hörnschemeyer *et al.* 2013; Garrouste *et al.* 2013).

4.2. Freshwater bodies as key environments for terrestrialisation

It must be considered that the new continental niches available in the Middle to Late Devonian continental realm were harsher and less stable than the long-colonised fluvial and marine ones. This results in many morphological and physiological transformations in plants and animals. The most important palaeobotanical innovations were the development of arborescence (tree stature) and the production of seeds which, respectively, increased root penetration and rhizoturbation, resulting in intensified pedogenisis (and consequently in major changes in weathering processes), and allowed colonisation of drier upland and primary successional areas (see Algeo & Scheckler 1998).

When they managed to colonise the land, animals faced an identical series of challenges, namely gas exchange, reproduction, osmoregulation and exposure to ultraviolet radiation (Little 1990). Tracheae enable air breathing in insects, myriapods and some arachnids (whereas others use book lungs as respiratory organs for atmospheric gas exchange). The enlargement and thickening of the jointed legs present in aquatic arthropods living on the substrate probably gave arthropods a great advantage in ensuring their water-to-land transitions (Dunlop *et al.* 2013; Waddington *et al.* 2015). Another advantageous adaptation of arthropods is their exoskeleton, the waxy epicuticle of which controls water loss and facilitates osmoregulation (Moussian 2013). Dunlop *et al.* (2013) further point out that osmoregulation is a central challenge that constrained arthropods' terrestrialisation; in particular, it may also indicate whether it occurred directly from the marine environment or via freshwater. In this regard, the colonisation of the ephemeral pool habitat by branchiopods during the Late Devonian, together with the presence of early tetrapods in surrounding deltaic rivers, suggests that ephemeral pools and more generally freshwater bodies may have been key environments in the terrestrialisation process.

Another central question that still remains to be settled is why some taxa rather than others risked venturing onto land, as the continental realm offers only limited environmental stability. Of the pressures that may have driven multiple lineages to exploit continental ecosystems, ecological pressure, and especially predation (avoidance of predators), has been proposed both for arthropods (Dunlop *et al.* 2013) and for tetrapods (McNamara & Selden 1993).

4.3. Palaeogeographical considerations

The poor fossil record of soft-bodied fossils in the Late Devonian makes palaeogeographical considerations very difficult, since we need localities with exceptional preservation. It is easier for vertebrates because they have a much greater fossilisation potential, and do not require exceptional conditions to enter the fossil record. Most of the fossil vertebrates recovered from the Late Devonian worldwide consist mostly of isolated bones, bony plates, teeth or scales. Nevertheless, strong similarities have been highlighted between the vertebrate fauna from Belgium and that of the Red Hill site, Pennsylvania, USA (Cressler *et al.* 2010). By looking for faunal relationships and similarity between the different tetrapod localities worldwide, using cluster analyses based on taxonomic and anatomical datasets, Delgehier (2014) showed faunal similarities between both areas at the species level. Olive *et al.* (2015a) also pointed out this pattern in their study of material of the placoderm *Phyllolepis* from Belgium, which they identified as *Phyllolepis undulata* Lohest, 1888, and is also known from Red Hill.

However, from comparing the Strud and Red Hill arthropod fauna, no links can be established between both sites. Strud has exclusively yielded aquatic crustaceans, whereas only the trigonotarbid *Gigantocharinus szatmaryi* Shear, 2000 and the millipede *Orsadesmus rubecollus* Wilson, Daeschler & Desbiens, 2005 have been described from Red Hill; although greater diversity is evidenced by enigmatic body impressions, burrow traces and walking traces (Cressler *et al.* 2010).

At the regional levels, strong similarities exist between the Strud flora and fauna and other localities from Belgium; in particular, the Becco locality in Liège Province, eastern Belgium (Olive *et al.* 2015b). Moreover, several taxa found in Strud are also present in the Pont-de-Bonne Modave locality; in particular, the lungfishes *Soederberghia cf. S. groenlandica* Lehman, 1959 and *Jarvikia* Lehman, 1959 (Clément & Boisvert 2006) and some placoderms (Olive 2015). It is not surprising to find such similarities between the Strud, Becco and Modave assemblages, since the whole Condroz area consisted of a single deltaic unit during the Late Famennian, therefore suggesting that vertebrates and arthropods may have colonised all the river branches.

4.4. The fate of this early continental ecosystem

One of the "Big Five" mass extinctions (Raup & Sepkoski 1982) occurred within the Late Devonian, marked by two extinction pulses: the Kellwasser Event at the Frasnian–Famennian boundary (374 Ma); and the Hangenberg Event at the Devonian–Carboniferous boundary (359 Ma) (Raup & Sepkoski 1982; McGhee 1996; Caplan & Bustin 1999; Bambach 2006). This end-Devonian extinction is associated with important losses in marine diversity, and has been particularly recognised as a bottleneck in the evolutionary history of vertebrates (Sallan & Coates 2010). According to the stratigraphical distribution of genera listed in Sepkoski's fossil marine animal database (Sepkoski 2002), these important biotic crises also strongly affected marine crustaceans. However, very few data exist with regard to the continental realm, due to the scarcity of continental fossil animals collected between the Late Devonian and the middle-to-late early Carboniferous, leading to the definition of two fossil gaps, known as "Romer's gap" for vertebrates (360–345 Ma), and the "arthropod gap" for continental arthropods, particularly myriapods, arachnids and hexapods (385–325 Ma). Both fossil-poor intervals have long been interpreted as resulting from global atmospheric change affecting early continental ecosystems (Ward *et al.* 2006), but a series of recent discoveries suggests that they rather derive from a preservational artefact (Garrouste *et al.* 2012; Smithson *et al.* 2012).

Regarding the fate of the Strud crustacean taxa, *Tealliocaris* is widespread in Euramerica after the Devonian–Carboniferous boundary, and has been recorded from marginal marine, brackish, lagoonal, hypersaline and freshwater environments (see Gueriau *et al.* 2014a). No occurrence of angustidontids is known after the Late Devonian, nor of the branchiopod genera *Strudops*, *Haltinnaias*, *Gesvesia* or *Undulatesta*. Nevertheless, branchiopods survived the end–Devonian mass extinction, as well as the following ones, as demonstrated by their exceptional morphological and ecological stasis since the Late Devonian, with recurrent associations of anostracans, notostracans and spinicaudatans typically inhabiting temporary freshwater bodies worldwide today (Gueriau *et al.* 2016). It is very likely that their reproductive strategy involving the production of drought-resistant eggs, like seeds in plants, made these lineages far less vulnerable and better equipped to survive crises and extinctions than other lineages lacking the adaptations to survive stressful periods.

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6. References

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