

Evolutionary Morphology in Belgium

The Fortunes of the “Van Beneden School,” 1870–1900

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Abstract. In historical literature, Edouard van Beneden (1846–1910) is mostly remembered for his cytological discoveries. Less well known, however, is that he also introduced evolutionary morphology – and indeed evolutionary theory as such – in the Belgian academic world. The introduction of this research programme cannot be understood without taking both the international and the national context into account. It was clearly the German example of the Jena University that inspired van Beneden in his research interests. The actual launch of evolutionary morphology at his University of Liège was, however, also connected with the dynamic of Belgian university reforms and the local rationale of creating a research “school.” Thanks to his networks, his mastering of the rhetoric of the “new” biology, his low ideological profile and his capitalising on the new academic élan in late-19th century Belgium, van Beneden managed to turn his programme into a local success from the 1870s onwards. Two decades later, however, the conceptual underpinnings of evolutionary morphology came under attack and the “Van Beneden School” lost much of its vitality. Despite this, van Beneden’s evolutionary morphology was prototypical for the research that was to come. He was one of the first scientific heavyweights in Belgium to turn the university laboratory into a centre of scientific practice and the hub of a research school.

Keywords: evolutionary morphology, Edouard van Beneden, Ernst Haeckel, University reforms

Introduction

If the Belgian zoologist Edouard van Beneden (1846–1910) is still remembered today, it is principally because of his memorable

“discovery” of chromosome reduction in germ cell formation (“meiosis”).¹ Van Beneden described this reduction division in his own journal *Archives de Biologie* in 1883 and finalised his standpoints on the matter 4 years later in a one-page research report that was published by the Belgian Académie Royale.² Although his current international notoriety is almost entirely based on these two cytological papers, van Beneden was active in other fields of biology as well. The greater part of his published work did not concern cytological questions, but was dedicated to evolutionary morphology – the research programme that aimed at the reconstruction of phylogenetic trees by studying morphological characters of embryos and adult specimens. Van Beneden would actually introduce this programme in Belgium in the 1870s and subsequently attract a sizeable group of young zoologists and anatomists to evolutionary morphology in the following two decades. It is this little-researched but central part of the work of van Beneden (and his Belgian pupils) that constitutes the focus of this paper.

An investigation of the fortunes of van Beneden’s evolutionary morphology in Belgium can be instructive for several reasons. First, it is of importance because the success of his research programme largely coincided with the breakthrough of evolutionism in the Belgian sciences as such. It is true that in geological circles, gentlemen scientists (such as Jean-Baptiste d’Omalius d’Halloy or Henri Lehon) had already discussed evolutionary theory in the 1850s and the 1860s, but they did so only in general terms and without actually integrating evolutionism into their methodology.³ In the same period the zoologists at the Belgian universities – who were mostly physicians⁴ – ignored evolutionism or were openly averse to it.⁵ They were very much committed to the project of building a “Belgian science” that was focused on the national territory and their work was predominantly descriptive and classificatory.⁶ As such, Belgian science of the mid-19th century was characterised by a strong reluctance to integrate conceptual renewals.⁷ This can at least partly explain why it

¹ See e.g. Coleman, 1965, pp. 139–142; Churchill, 1970; Hamoir, 1994, passim.

² Van Beneden, 1883b; Van Beneden and Neyt, 1887.

³ The professionalisation of Belgian geology in the 1870s furthermore caused their “speculative” theorising to fade into the background. For the evolutionary ideas of d’Omalius and Lehon see e.g.: d’Omalius, 1850, 1858; Lehon, 1868.

⁴ In 1860, with one exception, all Belgian zoology professors were physicians.

⁵ A good example of a negative response to evolutionism in this period is: Hannon, 1872 [1864].

⁶ Vanpaemel, 1992, pp. 14–15.

⁷ Porter, 2001, p. 92.

took until the 1870s before attempts were made to integrate evolution theory into biological research. Of those attempts, van Beneden's was definitely the most important. Other endeavours in the same direction only had limited success. The few excursions into mathematical evolution studies by the Liège philosopher Joseph Delboeuf, for example, had little following, and the same was true of the evolutionary-inspired research in animal psychology by the traveller and astronomer Charles Houzeau.⁸ At this stage it was only in morphology that Belgian scientists saw a possibility of establishing a successful evolutionary programme.

Van Beneden's enterprise is, however, not only illuminating for the introduction of evolution theory in Belgium. It also offers a good case study for those interested in the creation of academic "schools" around one charismatic "master." Van Beneden managed to attract various students and followers to his research interests, despite the fact that evolutionary morphology was not institutionalised as a discipline. Of those students and followers many would play an important role in various Belgian universities. In this way, van Beneden managed to have a very strong impact on the world of Belgian biology, which was still a very small world in the late 19th century (with only four universities, each holding only two or three chairs related to the biological sciences).⁹ An analysis of the rise of evolutionary morphology in Belgium is therefore also a study of the "mechanics" behind the changes in academic research trends.

Third, a study of van Beneden's research programme is of interest because it can help us understand a pivotal era in the history of Belgian science. The period between roughly 1870 and 1900 not only witnessed a significant rise in the prestige of the natural sciences as such, but it also saw an important shift in the Belgian scientific infrastructure. Before the 1870s, the most prestigious centre of scientific debate was the Royal Academy in Brussels. The national character of this institution resulted in a striving for ideological neutrality and its multidisciplinary composition fed an aspiration for synthetic knowledge. In the final decades of the 19th century, however, the Academy (which did not have its own research facilities) gradually lost its central position within

⁸ Houzeau, 1872; Delboeuf, 1877.

⁹ Until the late 1870s there was usually one chair in botany and one in zoology at the Belgian science faculties. It was only towards the end of the century – particularly after the new laws on Higher Education of 1876 and 1890 – that more chairs were gradually created. Obviously, some chairs in the medical faculty, such as anatomy and from the 1880s onwards also embryology, also offered possibilities for a "zoological" approach.

Belgian science to the universities.¹⁰ This was only possible because these universities underwent structural changes themselves – inspired by the German example.¹¹ In the middle of the century they had basically been institutions of professional learning, only incorporating research responsibilities in the period between 1870 and the end of the century. The erection of university laboratories (which started in the 1870s, and reached a peak in the 1880s and 1890s) was of major importance in this respect and led to a growing disciplinary specialisation. Furthermore it also enhanced the international reputation of Belgian science, which had been rather meagre until then.¹² Van Beneden’s enterprise, which has to be situated in these crucial years, can be very revealing for the developments in the Belgian natural sciences outlined here. The success of van Beneden depended heavily on the changes in scientific infrastructure from the 1870s onwards; moreover, he was an important enough player to make these changes happen.

Finally, there is a truly international aspect to van Beneden’s evolutionary morphology: on both a practical and theoretical level his programme was clearly inspired by the German prototype. It took its inspiration from German evolutionary conceptions, German laboratory practice and German ideals of *Wissenschaft*. In particular, the research as it was carried out at the University of Jena served as a model for van Beneden and his students. The story of evolutionary morphology at this small university – which was initiated in the 1860s by zoologist Ernst Haeckel and anatomist Carl Gegenbaur – has been described in detail elsewhere.¹³ We also know that the Haeckelian model successfully spread throughout Europe from the 1870s on. According to Lynn Nyhart it was this foreign success that eventually led historians to an overestimation of the influence of the Jena programme in German biology itself.¹⁴ Whatever the case, the actual export of this Haeckelian model outside Germany has been little explored. Consequently, we know very little about the practicalities of how it was introduced abroad and how it fitted into other national scientific traditions. Here again, the Belgian “Van Beneden School” offers a valuable case study.

¹⁰ Vanpaemel, 2001, p. 257.

¹¹ Wachelder, 2001.

¹² Harsin et al., 1954, pp. 9–12, 46–48, 62–77; Halleux, 2001, pp. 17–47; Dhondt, 2005, pp. 345–350.

¹³ On the Jena tradition of evolutionary morphology, see: Nyhart, 1987, 1995; Di Gregorio, 1995; Hoßfeld et al., 2002. On its success (mainly in the Anglo-American world): Maienschein, 1991; Bowler, 1996.

¹⁴ Nyhart, 1995, p. 343.

The Road of Truth

The intellectual influences at the origin of van Beneden's programme were diverse. First, there was obviously his father, the internationally renowned zoologist Pierre-Joseph van Beneden (1809–1894).¹⁵ Van Beneden senior, who held the chair of zoology and comparative anatomy at the University of Leuven for no less than 58 years, was arguably the most influential Belgian biologist of the mid-19th century. Owing to great differences between the ideological and scientific profile of father and son, it would be easy to portray them as intellectual antipodes. It is not difficult to contrast the old taxonomist with the young, “modern” laboratory scientist, the Catholic with the agnostic, the (albeit moderate) creationist with the evolutionist. However, such a caricatured opposition neglects the important scientific initiatives with which Pierre-Joseph influenced future generations – and indeed his own son. It overlooks his important research in marine biology, for example, for which he founded a research station in Ostend in 1841 – the first in the world and an example for many others that were founded throughout Europe in the 1870s and 1880s.¹⁶ At the same time it ignores the fact that van Beneden senior showed great interest in embryology, a discipline in which his French master Etienne Geoffroy Saint-Hilaire had excelled, but which was very unpopular in mid-19th century Belgium.¹⁷

The scientific continuity from Pierre-Joseph to Edouard van Beneden is obvious (Figure 1). When Edouard was a young researcher, he worked at his father's research station, and later he would try to establish such a station himself – again in Ostend. Furthermore, with his stress on morphological research, Edouard continued a scientific enterprise that his father had basically put on the map in Belgium. Obviously, there was sustained interest in morphological questions in various European countries from the late 18th century onwards, especially in Germany, England and France.¹⁸ In the early decades of Belgian science, however, roughly between the country's independence in 1830 and 1850, most zoologists were working in systematics. Of those who showed an interest in comparative anatomy, Pierre-Joseph van Beneden was definitely the most prominent. In embryology – the discipline that would be taken further by his son – he was virtually alone. And even in the interpretation of their common discipline, there

¹⁵ On Pierre-Joseph: Kemna, 1897.

¹⁶ See a. o.: Partsch, 1980; Paul, 1985, pp. 103–117.

¹⁷ On the negative reactions to Van Beneden's embryology in the Belgian scientific world: Kemna, 1897, p. 21.

¹⁸ See e.g. Richards, 2002.



Figure 1. The van Benedens in their family garden in Louvain, ca. 1880. Pierre-Joseph (with hat) and Edouard (with cigar) are facing each other. (Personal papers Mme M. Duchesne, Résimont).

was a clear link between father and son. Already in 1840, Pierre-Joseph had stressed the importance of embryology in determining the “affinities” (“*affinités*”) between different species.¹⁹ His son would use exactly the same term, but would give it a different meaning.²⁰ In the work of Pierre-Joseph “affinities” referred to the relationships between the different species in the “Chain of Being.” Embryology therefore only gave him indications to develop a “natural” classification – an inventory of the hierarchy among the living beings. Edouard, however, interpreted “affinities” as precise phylogenetic relationships, which made embryology a central key in the reconstruction of the tree of life. The difference between the science of the father and the science of the son was thus on the conceptual level. The alteration in meaning of the term “affinity” was, however, less important for the scientific practice. Because of the growing professionalism of biology by the late 19th century, Edouard’s zoological activities *did* differ from those of his father, but he nevertheless worked along the same lines.

¹⁹ Van Beneden, 1840, p. 243.

²⁰ Van Beneden, 1876, p. 59.

As well as his father, Edouard van Beneden would later acknowledge two major sources of inspiration: the German cytologist Theodor Schwann and Charles Darwin. The former, a friend of the van Beneden family, was known for his revolutionary work in the late 1830s, in which he proclaimed that all tissues, both vegetable and animal, were composed of cells. Embryological development therefore had to be understood, according to Schwann, as the division of one first “mother cell.”²¹ With these conclusions, the German cytologist (who in 1848 was appointed to the chair of anatomy in Liège) not only deeply influenced van Beneden senior, but also his son.²² Edouard’s earliest work (on cell division) was very much in line with Schwann’s and contained an explicit homage to the cytologist.²³ Throughout his career, van Beneden would often return to the study of the structure and composition of reproduction cells and the early phases of cell division. Furthermore, he repeatedly stressed Schwann’s pioneering role in this field.²⁴ From the perspective of this paper, however, the influence of Charles Darwin is obviously of greater importance.

Van Beneden’s admiration for Darwin dated back to his student years, when he read *On the Origin of Species* in French translation (probably in 1863).²⁵ Although he was acquainted with the work of some Belgian preDarwinian evolutionists, it was above all Darwin’s masterpiece that actually convinced him of the evolutionist principles.²⁶ Seven years after his first reading of the book, the young Belgian biologist would actually come into personal contact with the author. When Darwin was elected as an associate member of the Académie Royale de Belgique in 1870, van Beneden – at that time the youngest correspondent of the institution – insisted on personally congratulating the English naturalist on his election.²⁷ In an effusive letter to Darwin, he expressed his joy that the French-speaking scientific circles of Belgium had happily distinguished themselves from the narrow-mindedness of neighbouring France – where Darwin had been nominated for

²¹ Florkin, 1960; Harris, 1999, pp. 98–105.

²² On the influence on the father, see: Kemna, 1897, p. 51.

²³ Van Beneden, 1869.

²⁴ Van Beneden, 1883a, p. 906; Hamoir, 2002, pp. 30–31.

²⁵ Hamoir, 2002, p. 131.

²⁶ In 1874, he would for example review the work of the deceased d’Omalius d’Halloy. On this occasion, however, he would hide his disagreement with the non-Darwinian aspects that typified the ideas of the grand old man of Belgian geology. Van Beneden, 1874, pp. 404–406.

²⁷ He did so on his own behalf. In addition to Van Beneden’s letter, Darwin also received an official notification from the permanent secretary of the Academy. Adolphe Quételet to Darwin, Dec. 15th, 1870, CUL, Darwin Papers, MS. DAR. 175:12.

a corresponding membership by the Académie des Sciences but had not been elected.²⁸ “In Belgium,” van Beneden stressed, “the young generation had hoisted the flag of intellectual independence and had blown away prejudice and preconceived ideas.”

By sending Darwin some publications in which he had incorporated Darwinian ideas van Beneden clearly presented himself as a good representative of this movement of the young.²⁹ Darwin, who only 6 months earlier had explicitly deplored the lack of response he had met with in the French-speaking world, was eager to return the kindness.³⁰ A signed exemplar of the (recently published) *Descent of Man* triggered a great deal of excitement in van Beneden’s Liège. “Never,” van Beneden wrote in his letter of thanks, “have I been so flattered by receiving a book, because there is, in our century, nobody that I respect more than the author of the selection theory.” To this, he immediately added his first impressions after a quick reading of the book. Van Beneden applauded the many qualities of the author, like his factual knowledge, his synthetic power and his logic – a quality, he added strategically, which Darwin’s colleague Alfred Russell Wallace often lacked. The young Belgian zoologist finally expressed the conviction that Darwin’s conclusions on intellectual evolution would revolutionise psychology, just as his earlier work had transformed the natural sciences. In a concluding paragraph of his exalted letter van Beneden finally sought to arrange a meeting in London with the great naturalist. His intellectual relationship with Darwin seems to have stopped short after a mutual exchange of friendliness, however.³¹ For van Beneden, Darwin would remain a scientific icon, more than an approachable colleague.³²

Darwin’s scientific conceptions appealed to van Beneden on two levels. On a general level, they endowed him with a new world view. With the theory of natural selection, Darwin had, according to van Beneden, demonstrated the truth of “the fundamental idea of filiation” and changed the basis of how scientists thought about nature.³³ On a more specific level, Darwin’s work provided him with a new line of approach with regard to embryology, his own discipline. It was through

²⁸ This ‘scandal’ is often seen as one of the clearest examples of the singular position of France in the reception of Darwinism. See e.g. Buican, 1982.

²⁹ Van Beneden to Darwin, Dec. 17th, 1870, CUL, Darwin Papers, MS. DAR. 160:132.

³⁰ Darwin to Armand de Quatrefages de Bréau, May 28th, 1870, cited in Molina, 1996, pp. 909–910.

³¹ Van Beneden to Darwin, Dec. 17th, 1870, CUL, Darwin Papers, MS. DAR. 160:133.

³² Van Beneden would only write to Darwin again to ask him for his support for a celebration in honour of his other scientific idol, Theodor Schwann, in 1878. Van Beneden to Darwin, April 29th, 1878, CUL, Darwin Papers, MS. DAR. 160:135.

³³ Van Beneden to Darwin, March 31st, CUL, Darwin Papers, MS. DAR. 160:133.

the study of Darwin's conceptions that Edouard would give new meaning to the "affinities" described by his father. Darwin's interest in embryology showed most clearly in the studies of the morphology of the *Cirrepedes* (barnacles) from the 1840s and 1850s. In those studies he stressed that early developmental stages of the embryo were less subject to adaptive modifications than adult specimens and therefore more suited for tracing evolutionary relationships between species.³⁴ In *On the Origin of Species* he would later write: "Embryology rises greatly in interest, when we thus look at the embryo as a picture, more or less obscured, of the common parent-form of each great class of animals."³⁵ Although Darwin therefore by no means underestimated the possibilities and the importance of embryology, he would not give the discipline a central place in his most influential publications. In *On the Origin of Species* he only devoted a dozen of pages to the subject and in *The Descent* he limited his ideas on embryology to a short introductory passage.³⁶ It was, however, precisely those passages that had convinced van Beneden. In his first reaction to *The Descent* he stressed that, to his mind, the arguments which Darwin had derived from ontogenesis were, "even more than the others," irrefutable.³⁷ In a letter to the English naturalist of the year before, he had already indicated that he was well-acquainted with Darwin's work on barnacles and that he saw his own research as an extension of the same ideas.³⁸

In the work of the English naturalist, van Beneden found a starting point for an evolutionary reading of embryology, but not a well-rounded research programme. Darwin was interested primarily in the mechanism of evolution and less in the factual reconstruction of the tree of life (for which the morphological study of embryos might be applied). Furthermore, Darwin was a gentleman scientist with eclectic interests, the type of "erudite" and "naturalist" which in the view of van Beneden himself would lose ground in the professionalising discipline of biology of the late 19th century.³⁹ Van Beneden was convinced that if he wanted to develop a contemporary academic and evolutionary discipline, it was not to Darwin's England that he had to address himself, but to the Germany of the new-fashioned academic laboratory research. Particu-

³⁴ Newman, 1993, pp. 349–434.

³⁵ Darwin, 1859, p. 368.

³⁶ Darwin, 1859, pp. 359–369; Darwin, 1874, pp. 9–11 and 25.

³⁷ Van Beneden to Darwin, March 31st, CUL, Darwin Papers, MS. DAR. 160:133.

³⁸ Van Beneden to Darwin, Dec. 17th, CUL, Darwin Papers, MS. DAR. 160:132.

³⁹ On Van Beneden's ideas about "naturalists" see: Van Beneden, 1883a, pp. 897–899. For a contemporary (and more nuanced) vision on the fate of naturalism in the late 19th century: Nyhart, 1996.

larly in Jena, he could find a young scientific tradition that integrated Darwin's ideas in a research programme with "modern" allure. It was there that van Beneden actually went in 1871.

By the end of the 19th century, Germany had become almost an obligatory destination for the ambitious Belgian science student. Whereas in the 1830s it had been a logical choice for Pierre-Joseph van Beneden to study zoology in Paris, 40 years later it was the German laboratories that served as shining examples.⁴⁰ Also, Edouard van Beneden was attracted to what he called the "central region of science." Like other students of his generation, he undertook several journeys to Germany, but thanks to the networks of his father, he also found an easy introduction to scientists with an international reputation. In 1867, he visited the reputed cytologist Max Schultze in Bonn and the physicist Hermann Helmholtz in Heidelberg. The next year he stayed in the laboratory of the histologist Rudolph von Kölliker in Würzburg and in Giessen he visited his father's friend, the morphologist and parasitologist Rudolf Leuckart. In 1871, only a short time after his appointment as a professor in Liège, van Beneden undertook a study tour to no fewer than eight German universities.⁴¹ One of the most important destinations this time was Jena. Van Beneden wanted to meet the well-known physiologist Wilhelm Preyer, but above all the great evolutionists Gegenbaur and Haeckel. A flattering epistle to the latter prepared his arrival. As well as complementing Haeckel's work ("Every step you take is a leap forward on the road of truth") the letter clearly expressed van Beneden's "very great desire" to visit the German morphologist.⁴² Only a month later, he arrived in Jena.

Edouard's networking in the small German university town was successful. To his parents he wrote: "Gegenbaur, Haeckel and Preyer have received me as one receives an old friend – we were accomplices and companions." Proudly, Edouard related how Haeckel initiated him in his research on sponges and how the German morphologist offered him a whole series of natural historical objects. He furthermore told how Gegenbaur – who turned out to be a great admirer of his father⁴³ – accompanied him during all his visits and set aside a full day to show him his discoveries and osteological collections. Van Beneden liked Gegenbaur, who proved to be friendly, knew what he was talking about, reasoned logically and only accepted theories

⁴⁰ Dhondt, in press.

⁴¹ Hamoir, 2002, pp. 47–48.

⁴² Van Beneden to Haeckel, July 11th, 1871, EHH, Haeckel papers.

⁴³ Gegenbaur had met Pierre-Joseph van Beneden in 1861 in the town of Speier. On that occasion he had already stressed how inspiring he found the work of the Belgian. 1886, *Manifestation en l'honneur de Monsieur P.J. van Beneden*, pp. 75–78.

when scientific data were available. Van Beneden's assessment of Haeckel, however, was not unambiguous. To his father, Edouard wrote that his German host had a "philosophical" and "boisterous" character – and among scientists these characteristics were definitely not compliments. Haeckel was said to be "essentially of German mind," which accounted for his "wildness" of character.⁴⁴ However, the critical stance taken by the young Edouard in the letters to his father seemed to mask a certain infatuation. With Haeckel, van Beneden definitely did not leave the impression of being a critical colleague. To his wife, Haeckel wrote: "The last week, I have really lived very restlessly – almost every day there was a foreign enthusiast that wanted to see the famous professor! You would have become completely annoyed by this kind of hero-worship. Twice I spent the night at Gegenbaur's with the Belgian professor Von Beneden [sic] – a special-admirer, according to whom I march in the avant-garde of science."⁴⁵

Although Haeckel and van Beneden wrote down their first impressions of each other with a certain irony, the two zoologists stayed in touch. Only a month after his visit, Van Beneden would write to Haeckel extensively about his activities. In an amicable tone, he told of his trip to Hamburg, his flirting with local women and his research on the north German coast – research that, completely within the Haeckelian tradition, aimed at an evolutionary interpretation of embryological material. In addition to an ode to the "masters of Jena," the letter also contained an alternative evolutionary tree of the trilobites, horseshoe crabs, scorpions and arachnids.⁴⁶ Van Beneden clearly showed himself to be an ambitious researcher and triggered Haeckel's interest. The latter gave van Beneden the advice he asked for, forwarded him (rare) zoological specimens and sent him his latest publications.⁴⁷ The two morphologists would work for a while on comparable material (sea squirts or *Ascidia*) and they exchanged scientific references.⁴⁸ Haeckel furthermore integrated van Beneden's conceptions about heredity in his own work.⁴⁹ In 1874 – van Beneden was not yet 30 – the Liège researcher received an honorary doctorate in Jena thanks to the mediation of Haeckel.⁵⁰

⁴⁴ Hamoir, 2002, pp. 49–50.

⁴⁵ Ernst to Agnes Haeckel, Aug. 3rd, 1871, see: Haeckel and Haeckel, 1950, pp. 86–91.

⁴⁶ Van Beneden to Haeckel, Sept. 27th, 1871, EHH, Haeckel Papers.

⁴⁷ See e.g. Van Beneden to Haeckel, Nov. 8th, 1871, June 2nd, 1872 and Aug. 9th, 1874, EHH, Haeckel Papers.

⁴⁸ Van Beneden to Haeckel, Nov. 8th, 1871, EHH, Haeckel Papers.

⁴⁹ Di Gregorio, 2005, pp. 224–225.

⁵⁰ Ironically, it was an honorary doctorate in philosophy. Van Beneden to Haeckel, Aug. 28th, 1874, EHH, Haeckel Papers.

Within a very short space of time, Haeckel's "special-admirer" developed into a scientist with a European reputation, something which his German "master" had to acknowledge. Van Beneden had achieved this status partially by using his father's networks, but also by extending them to the younger generation of zoologists. When in 1870 the young English morphologist Ray Lankester wrote to his mother about a European research journey and discussed the "big names" he had met, he mentioned van Beneden next to Haeckel himself.⁵¹ This growing reputation also increased van Beneden's self-confidence. Since the mid-1870s, the sheer admiration in his letters to Haeckel decreased and the critical notes grew in number.⁵² Furthermore, the frequency of his correspondence with Haeckel lessened as the latter lost interest in empirical research and concentrated more and more on his role as the "prophet" of a monistic world view.⁵³ However, in contrast to other "pupils" of Haeckel, van Beneden would never break with the Jena zoologist. Haeckel, for his part, continued to send his latest work to Liège.⁵⁴ Eventually, when van Beneden died in 1911 and various reputed scientists supported the call to erect a statue for the deceased, Haeckel (71 years old by now) took a seat on the organising committee.⁵⁵ In this way, he wanted to honour a man who had defended a research programme that also largely had been his own.

"Explicative" Embryology

Like Haeckel, van Beneden basically used evolutionary theory from the standpoint of a morphologist who wanted to reconstruct evolutionary trees. Only at the very beginning of his career, when a government-sponsored expedition brought him to Brazil in 1872, had he also shown an interest in broader evolutionary questions concerning adaptation, natural selection and biogeography – the very questions that Darwin had been most interested in. While crossing the Atlantic he had already

⁵¹ Lankester to his mother, May 1st, 1870, see: Lester, 1995, p. 30.

⁵² E.g. in Van Beneden to Haeckel, Feb. 17th, 1876, EHH, Haeckel Papers.

⁵³ On this metamorphosis: Holt, 1971, pp. 267–268; Weindling, 1989, p. 313.

⁵⁴ E.g. Van Beneden to Haeckel, June 6th, 1878 and Jan. 15th, 1891, EHH, Haeckel Papers.

⁵⁵ "Souscription pour l'Edification d'un Monument destiné à Perpétuer le Souvenir d'Edouard van Beneden." AEL, Fund Lesoine Family, P.J. and E. van Beneden Papers, 30.

tried to perform some oceanographic research (partly with material that Thomas Huxley had provided him with).⁵⁶ However, the commercial vessel on which he was travelling proved unsuitable for making accurate observations.⁵⁷ Despite the support of the Brazilian emperor Pedro II (incidentally a convinced anti-Darwinian), van Beneden's research on the South American east coast proved disappointing as well.⁵⁸ Due to various practical difficulties, he had to abandon his ambitious project to systematically study the fauna of the coasts around Rio de Janeiro. He toned down his ambitions to small-scale biogeographical and morphological studies in which he compared the fauna of the open sea with that in enclosed bays. His hope was to indicate how differences in environment had led to variation in form. To the home front he wrote: "What I hope to find there are some new arguments in the fauna for the grand scientific doctrine, to the triumph of which all my work is dedicated."⁵⁹ Judging from the very modest expedition report he published later, van Beneden seems to have failed in this objective as well (Figure 2).

Once he returned to Belgium in 1873 van Beneden abandoned "field biology" and "naturalism" altogether and focused completely on laboratory-based embryological research. Darwin remained an important reference point, but the Belgian zoologist did not retain a high esteem of the scientific culture of the "naturalists" in general, which he associated with an obsession for classification and "collection mania." The alternative programme that van Beneden defended was the "new" biology, which he identified with morphology and physiology. Its modernity lay mainly in the connection of this programme with evolutionary theory. While the old "natural history" had been merely "descriptive," van

⁵⁶ Van Beneden had contacted Huxley (who, again, was a scientific contact of his father) to provide him with fishing nets similar to those that the English morphologist had used in earlier expeditions. At the same time, he also asked him for a letter of recommendation to the German morphologist Fritz Müller, who happened to be in Brazil at that moment – and whom he would never visit. Van Beneden to Huxley, June 5th and 30th, 1872, ICL, T. Huxley Papers, 10: 283–286.

⁵⁷ The speed at which the ship travelled created too much pressure on the nets, so that Van Beneden could hardly collect any interesting specimens – just like Huxley, Haeckel and the Würzburg zoologist Karl Semper had predicted him on beforehand. Van Beneden, 1873, pp. 776–777.

⁵⁸ On his second meeting with Pedro II, Van Beneden wrote to his parents: "He has talked about various things and particularly about Darwin. He presented himself as very anti-Darwinian." Van Beneden to his parents, Aug. 16th, 1872, AEL, Fund Lesoine Family, P.J. and E. van Beneden Papers, 28.

⁵⁹ Van Beneden to Behr, Nov. 17th, 1872, AEL, Fund Lesoine Family, P.J. and E. van Beneden Papers, 28.



Figure 2. Edouard van Beneden in his château in Ramelot in 1889. On the wall one can see the trophies of his expedition to Brazil of 1872 – the only tropical expedition he would ever perform. (Personal papers Mme M. Duchesne, Résimont).

Beneden's morphological research was "explicative," because it indicated the genealogical connections between living beings. The separation that van Beneden constructed between the two types of life sciences was obviously of a strategic nature. It clearly had to support the growing will of governmental circles to sponsor the "new" biological laboratory research in the universities. According to van Beneden, natural history had always been generously funded in the past (implicitly referring to the funding of the Museum of Natural History).⁶⁰ Now, he suggested, the time had come to free some money for disciplines that were interested in something more than the mere "knowledge of Latin names."⁶¹ This rhetorical strategy is very comparable to the one that Huxley had used in the United Kingdom – and van Beneden would in fact refer explicitly to

⁶⁰ On the "descriptive" scientific activities of the early Museum of natural history: Gilson, 1914, pp. 159–182.

⁶¹ Van Beneden, 1883a, pp. 896–919.

Huxley's arguments in his own justification of the "new" biology.⁶² From the 1850s through to the 1870s, Huxley argued that the activities of well-funded museums (like that of his "preferred enemy" Richard Owen) were no longer in touch with "modern" biological research – which preferably had to be performed in German-inspired laboratories. In England, just as in Belgium, the conception of such laboratories was still in its infancy and it still had to be explicitly legitimised.⁶³ This is what Huxley and van Beneden tried to do.

The modernity of van Beneden's programme has to be put in perspective, however. Various historians have stressed already that there was an important continuity between the old morphology and its new evolutionary variant.⁶⁴ In the work of van Beneden, evolutionary morphology also largely remained a descriptive enterprise, which apart from some phylogenetic speculations was comparable to what morphologists had been doing for decades already. Furthermore, with the rising criticism of the Haeckelian programme since the 1880s, van Beneden's caution towards evolutionary theorising grew. This made him focus even more on the descriptive aspects of his work. The modern reputation of van Beneden's biology seemed largely due to the laboratory context in which it was conducted and the new techniques that were used there. The new fixative fluids and microtomes (the instruments used to cut specimens into very thin sections for microscopic examination) that he introduced after the German example, turned morphology into a largely microscopic science.⁶⁵ These technical developments in fact only reinforced the descriptive character of morphological practice. The emphasis was increasingly laid on the comparison of isolated microscopic pictures and less and less on the interaction between the development of an embryo and its environment.⁶⁶ Yet, the continuity with a descriptive (and institutionalised) tradition, combined with a reputation of modernity (based both on evolutionary theory and the use of new laboratory techniques), proved to be successful.

The "explicative" (and therefore "modern") aspect of van Beneden's research was intimately connected with Haeckel's conception of the biogenetic law. The idea that embryological development recapitulated the evolutionary history of the species was crucial in van Beneden's attempt to reconstruct the tree of life. Van Beneden associated ontogeny and phylogeny so closely that he used the same term to denote both

⁶² Van Beneden, 1883a, p. 904.

⁶³ Bowler, 1996, pp. 26–27; White, 2003, pp. 55–58.

⁶⁴ Coleman, 1976; Mayr, 1982, pp. 466–476; Bowler, 1988, pp. 80–84.

⁶⁵ See e.g. Van Beneden, 1871b.

⁶⁶ Nyhart, 1996, pp. 201–202; Hopwood, 1999, pp. 476–477.

phenomena. In doing so, he was again following his German “masters.” Whereas the English morphologists clearly distinguished “evolution” from “development,” their German colleagues referred to both using the term “Entwicklung.”⁶⁷ In the work of van Beneden this same identification between ontogeny and phylogeny returns – though in his case he used the term “evolution” to label both.⁶⁸ The development he observed in his embryological research was therefore interpreted as an access to the phylogenetic tree. Such reasoning did not in fact mean a complete breakaway from the older morphology. Van Beneden’s own father Pierre-Joseph had written (as early as 1860) that the embryological development “remembered” “the idea that had been realised throughout the diverse ages of the earth.”⁶⁹ Given the Christian world view of Pierre-Joseph van Beneden, this statement seems to refer to divine conceptions that are unfolded both in the history of life and the history of the individual. As Pierre-Joseph remained a sceptic of evolutionary theory in this period, it is clear that his words cannot be interpreted as an early version of the biogenetic law.⁷⁰ It was, however, not too hard for Edouard van Beneden to reformulate his father’s ideas in explicit evolutionary language – just as Haeckel had reformulated the conceptions of the early 19th-century idealist morphologists.⁷¹

Above all, Edouard van Beneden’s embryological studies had to elucidate particular parts of the evolutionary tree, namely the transitional stages or missing links. The credibility of the reconstruction of the “tree of life” after all depended completely on a good understanding of such transitional stages. In the 1870s, van Beneden focused in the first place on the transition between *protozoa* (unicellular organisms) and

⁶⁷ Nyhart, 1995, p. 139.

⁶⁸ Van Beneden, 1871a, pp. 325–359.

⁶⁹ Van Beneden, 1861, p. 71.

⁷⁰ In that respect, I do not follow Pierre-Joseph’s admirer and early biographer Adolphe Kemna, who was an evolutionary morphologist himself and who wanted to see the Louvain biologist as a precursor of the “modern” biology of his own period. Kemna, 1897, pp. 97–98.

⁷¹ On Haeckel’s mechanistic reformulation of older idealist conceptions of morphology, see Rinard, 1981, pp. 249–275; Di Gregorio, 2005, pp. 167–168. The lack of explicit references in the work of Pierre-Joseph van Beneden makes it difficult to trace his relationship with idealist morphologists of the early 19th century. It is not improbable, however, that Etienne Geoffroy St.-Hilaire, the idealist naturalist under whom he studied in Paris, was of importance in this respect. In a later period, Pierre-Joseph furthermore maintained good contacts with the German comparative anatomist Johannes Müller – who amongst other things would visit his marine laboratory in Ostend. Müller’s “conceptual empiricism” is often seen as a crucial link between earlier idealistic morphology and the more modern conceptions of Haeckel. On Geoffroy and Müller, respectively, see Laurent, 1987, pp. 335–336; Rinard, 1981, pp. 253–254 and 265–266. Also: Kemna, 1897, p. 15.

metazoa (multi-cellular animals). In an article from 1876 he indicated that he believed he had found this missing link in a primitive order of parasites (*Dicyemida*), which he came across in the kidneys of particular squids. He named this group “mesozoa” and interpreted them as living variants of Haeckel’s “Gastraea” – or the primeval evolutionary form consisting of a double-walled “sac” that was recapitulated in the embryonic “gastrula-stage” of all multi-cellular animals.⁷² Van Beneden had incorporated the “Gastraea-theory” in his work as soon as he became acquainted with it. In 1874, after reading Haeckel’s *Monographie der Kalkschwämme* (1872) he immediately wrote enthusiastically to its author: “Your Gastraea-theory will become a reference point in the history of the zoological sciences: In my view it is of capital importance from an evolutionary standpoint, because it *establishes*, using precise facts and a broad scope, the *convergence* of the great branches that so far has only been a mere hypothesis.”⁷³ By indicating that the *Dicyemida* were living fossils, very comparable to Haeckel’s theoretical “Gastraea,” the young Belgian tried to turn the theory of his German “master” into reality.⁷⁴

As well as the missing link between *protozoa* and *metazoa*, van Beneden also focused on another crucial transition in the animal kingdom, namely that between vertebrates and invertebrates. With this topic, which he would basically study in the 1880s and the 1890s, he brought up a theme that had already been heavily discussed by several reputed morphologists. In the 1860s the subject was first extensively dealt with by the Russian embryologist Alexandr Kovalevskii. Based on comparative embryology, he had defended the view that vertebrates originated from larvae of sea squirts (*Ascidia*), a theory that was supported by both Darwin and Haeckel. In the same period, however, other leading embryologists such as Franz Leydig and Anton Dohrn – both pupils of Haeckel – argued that the group of segmented worms (*Annelida*) had to be seen as the ancestral branch of vertebrate animals.⁷⁵ In the 1870s, van Beneden would follow the line of reasoning of Kovalevskii for a while.⁷⁶ It was with his hypothesis as a starting point that he also initiated an elaborate research project in the 1880s in which

⁷² Van Beneden, 1876, pp. 77–79. On the Gastraea-theory: Nyhart, 1995, pp. 181–187; Bowler, 1996, pp. 85–87; Di Gregorio, pp. 208–222.

⁷³ Van Beneden to Haeckel, Aug. 9th, 1874, EHH, Haeckel Papers.

⁷⁴ This interpretation of the place of *Dicyemida* in the animal kingdom was only refuted in the 20th century. The Belgian zoologist Auguste Lameere would indicate then that the “primitive” characteristics of the group were the consequence of ‘degeneration’ due to their parasitic way of life. He therefore refuted the idea that it was a species stuck in an early evolutionary stage. Lameere, 1916, pp. 1–35.

⁷⁵ Bowler, 1996, pp. 141–171.

⁷⁶ Van Beneden, 1875.

he compared the embryology of sea squirts, mammals and the lancelet (*Amphioxus*) – a species which in Kovalevskii's studies was seen as the closest living representative of the common ancestor of the vertebrates. Van Beneden's results ran counter to this original premise, however, and he abandoned Kovalevskii's hypothesis. The existing homologies between sea squirts and vertebrates, he argued on the basis of new material, were not to be ascribed to direct descent, but to a common origin in a (hypothetical) primitive segmented worm.⁷⁷

Even now, van Beneden was conscious of gaps in his argumentation and in the 1890s he studied the question of the vertebrate origin again (Figure 3). This time he focused his research on tube anemones (*Ceriantharia*) from the phylum of the cnidarians. The specimens of these, gathered during the prestigious Plankton expedition, were sent to the Belgian zoologist for description by the Kiel physiology professor Victor Hensen.⁷⁸ Van Beneden's embryological observations on Hensen's anemones brought him to a new phylogenetic vision. He observed that vertebrates and ascidians, but also annelids and arachnids, went through an embryological stage which in his view was comparable to the modern tube anemone. He described this phase (which followed the gastrula stage) using the term "cerianthula." The tube anemone was then seen as a living representative of the common ancestor of four major branches in the animal kingdom. This theory, which was close to earlier suggestions of the English zoologist Adam Sedgwick, was, however, never published as such by van Beneden.⁷⁹ To Albert Brachet, one of his pupils, van Beneden would confess that the discussions on the origin of the vertebrates had produced so many "hypothetical ancestors" that he actually recoiled from adding another one.⁸⁰

Despite this growing aloofness in the evolutionary debate, van Beneden's various morphological analyses had, according to Brachet, to be understood as part of a bigger project: the reconstruction of the tree of life that eventually led to Man. Unlike Haeckel, van Beneden did not publish an *Anthropogenie*, but such a broad evolutionary history of life was nevertheless the framework within which his specialised monographs had to be understood.⁸¹ Like his German "master," he interpreted evolution as a progressive process and he tended to see the tree of

⁷⁷ Van Beneden and Julin, 1887.

⁷⁸ He furthermore used specimens from Haeckel's personal collection. Van Beneden to Haeckel, 5th Sept. 1890, EHH, Haeckel Papers. For his actual description of the tube anemones, see: Van Beneden, 1897.

⁷⁹ On Sedgwick's theory: Bowler, 1996, pp. 183–184.

⁸⁰ Brachet, 1923, p. 208.

⁸¹ Brachet, 1923, p. 202.

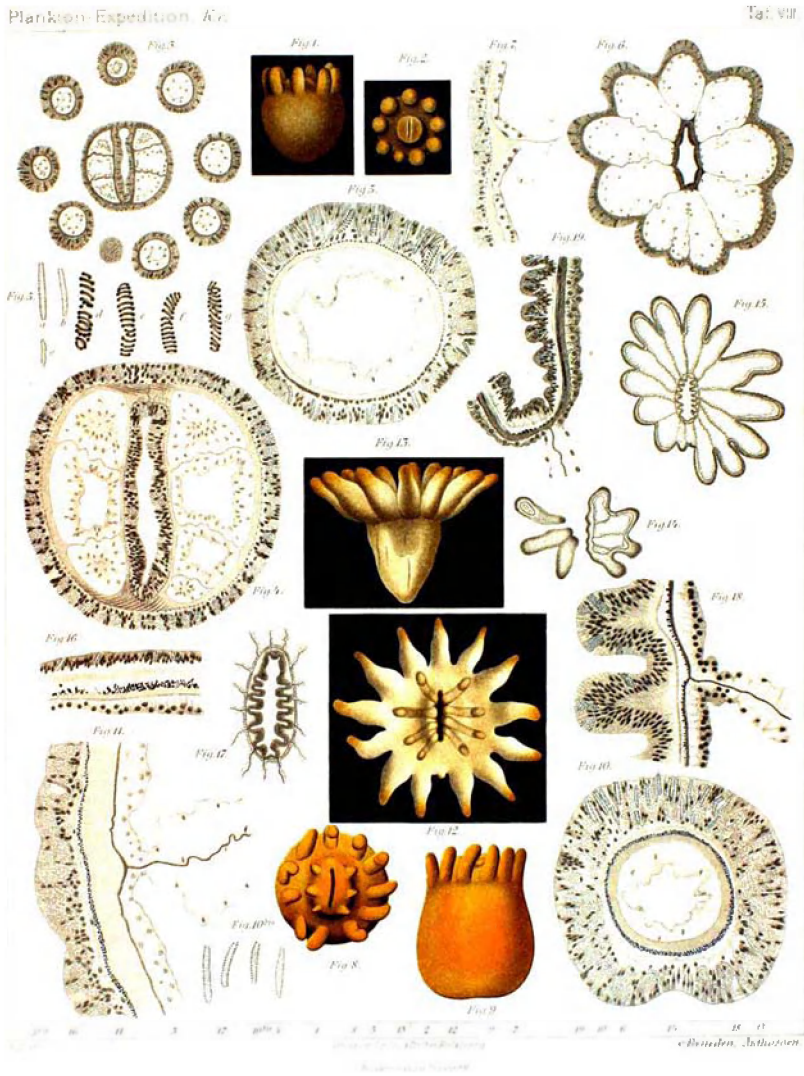


Figure 3. The tube anemones collected during the Plankton expedition brought van Beneden to new phylogenetic insights. On the illustration: cross-sections of *Dactylactis Elegans* (van Beneden, 1897, pl. VIII).

life as a hierarchical ladder.⁸² Nevertheless, he did not follow Haeckel without question. Like many morphologists of his generation, he would regularly distance himself from the “prophet of Jena.”⁸³ He did not

⁸² See e.g. Van Beneden, 1871a, p. 355; Van Beneden, 1902, p. 1088.

⁸³ E.g. in: Van Beneden, 1876, pp. 1202–1203 and Van Beneden to Haeckel, 17th Feb. 1876, EHH, Haeckel Papers.

only when technical morphological questions were involved, but also in his (scarce) general statements about what science should be. As indicated earlier, even while still young van Beneden assessed Haeckel's scientific approach as too "philosophical." In the view of the Belgian, Haeckel was "attracted more by philosophy than observation" and often let himself get carried away by the "tempestuousness of his imagination."⁸⁴ In spite of his admiration for German *Wissenschaft*, van Beneden always seemed uneasy with the holistic ambitions that are often ascribed to it.⁸⁵ In this sense he at least partly belonged to the more positivist tradition of French (and indeed Belgian) science.⁸⁶ He *did* support some of the major hypotheses of Haeckel, but would never follow him in his stress on theory and all-embracing synthesis. Van Beneden's phylogenetic reflections were usually only a small epilogue to very sophisticated and technical embryological comparisons. In many cases there was no such epilogue at all.

Towards the end of his career, van Beneden's aversion to hypotheses only seemed to increase. This did not, however, mean that he turned his back on evolutionary morphology as such – not even in the 1890s when the research programme was clearly past its peak. In Germany, a true *Kompetenzstreit* was raging under former figureheads of the movement in this period, in which embryologists and comparative anatomists faced each other. The Gastraea-theory was openly questioned, and later the biogenetic law also came under fire. The debates acquired a polemical, often very personal tone, and the methodological unanimity under evolutionary morphologists was gone.⁸⁷ In this context, van Beneden apparently felt a growing fearfulness to publish his phylogenetic trees, but he nevertheless kept gathering pieces of the puzzle.

The Creation of a School

The pinnacle of van Beneden's programme in evolutionary morphology clearly has to be situated in the late 1870s and the 1880s. This success was not only due to the internal aspects of his science, but also to a new dynamism in the Belgian academic world as such. This academic vitality of the late 19th century meant a drastic change from the state of

⁸⁴ Hamoir, p. 49. Van Beneden was, however, strategic enough to give a much more positive interpretation of Haeckel's "philosophical" tendencies in his letter to the German. Van Beneden to Haeckel, 27th Sept. 1871 EHH, Haeckel Papers.

⁸⁵ McClelland, 1980, pp. 124–125.

⁸⁶ On the positivist tradition in Belgian scientific and intellectual culture: Wils, 2005.

⁸⁷ Nyhart, 1995, pp. 243–277.

lethargy that had characterised Belgian universities in the period before then. Despite many attempts at reform in the middle of the century, universities met great difficulties in shifting their focus away from professional training towards scientific research. Particularly in Liège this had led to an atmosphere of disappointment in the 1860s. However, the return of many young doctors (like van Beneden himself) from study tours in Germany created a new élan for the reform movement around 1870.⁸⁸ This élan was subsequently endorsed by the Law on higher education of 1876, which gave the individual university authorities the power to assign grades (instead of an “independent” exam jury) and in this way enhanced academic freedom. The law was followed by the introduction of new courses, the establishment of the seminar system in various curricula and the creation of assistantships – all following the German example.⁸⁹ The fact that student numbers were on the rise only reinforced this new trend.⁹⁰ Finally, the government would also free up extra money for the state universities. The Liège rector, Louis Trasenster, proved a good advocate of “pure knowledge” and made use of his networks, which connected him closely to the liberal prime minister.⁹¹ When the government passed a budgetary law in 1879 which was intended to permit the state universities to renew their scientific infrastructure, Liège received a large slice of the pie. This permitted the university to implement the ambitious infrastructure plans of the young chemist Walthère Spring – a contemporary of van Beneden and an enthusiast of the German laboratory culture. In the period between 1883 and 1893 no fewer than seven modernly equipped institutes for the natural sciences were erected in Liège. One of these was the pompous Institute of Zoology, next to the river Meuse, that would be occupied by van Beneden.⁹²

The Liège Zoology Institute can be seen as the most tangible symbol of the success of van Beneden’s research programme (Figure 4). The huge complex (described in the press as “the palace of the beasts”) was built with precise instructions by van Beneden, and the architecture was an homage to *his* scientific heroes. Three frontons decorated the facade

⁸⁸ Harsin et al., 1954, pp. 62–64.

⁸⁹ Dhondt, 2005, pp. 271–272, 291–294, 334 and 347–349.

⁹⁰ In 1872 there were 762 students at the university. In 1885 this number had already risen to 1567.

⁹¹ The (very intimate) correspondence between Trasenster and Prime Minister Walthère Frère-Orban – both freemasons and prominent members of the Liberal party – is preserved in the Archives of the University of Brussels. AULB, Frère-Orban Papers, 2 PP.

⁹² New institutes were also constructed for the departments of pharmacy, botany, astronomy, anatomy, chemistry and physiology. Harsin et al., 1954, pp. 62–66; Hamoir, 1997, pp. 5–9; Despy-Meyer, 2001, pp. 76–77.



Figure 4. Van Beneden's impressive Zoological Institute.

of the Institute. In the one on the right, a medallion contained a portrait of his father. The one on the left was a similar homage to Theodor Schwann. The central and biggest fronton, finally, held a bust of Darwin – who had just died at the time that the building was being designed.⁹³ Contrary to the poisonous assertions in the Catholic press that the Institute was basically the luxury apartment of the freethinker van Beneden,⁹⁴ it was also home to the small research school that the professor had gathered around him during the previous decade. Almost since the moment he began his career, he would permanently have around five collaborators performing morphological research under his rigid guidance. In contrast to Haeckel – who ran a loose and unstructured laboratory and saw himself in the first place as an intellectual catalyst – van Beneden would involve his collaborators closely in his own research.⁹⁵ In this way, he could effectively create a “school” in which the ideas of “the master” were directional.⁹⁶

All this was possible thanks to the change of academic climate that van Beneden witnessed and capitalised on. Together with his colleagues from histology and anatomical pathology, he managed to convince the Minister of Internal Affairs as early as in 1873 of the need for a

⁹³ Hamoir, 2002, pp. 75–76 and 114.

⁹⁴ The Institute was typified this way in the Catholic *Gazette de Liège* of Dec. 7th, 1889. Extensively quoted in Florkin, 1967, pp. 379–380.

⁹⁵ Nyhart, 1996, pp. 158–166.

⁹⁶ The atmosphere in Van Beneden's laboratory in the 1870s has been described in: Julin et al., 1925, pp. 160–161.

microscopic laboratory on the Liège campus.⁹⁷ The actual space at his disposal (which was in the same building as the music conservatory) was small, but its dynamism as the first biological laboratory in the country was of importance. As soon as the laboratory was installed van Beneden introduced a free course in “comparative microscopy.” In 1876 a compulsory (and successful) course in embryology followed.⁹⁸ To attract students to new courses was one thing, however; to actually draw them to scientific research another. The fact that van Beneden managed to create a “school” was due in large part to the fact that the law of 1876 actively stimulated the appointment of assistants with doctoral degrees. The reform did not go so far as to introduce the system of *Privatdozenten* which was advocated by the German-inspired Trasenster, but it nevertheless created extra space for research and offered good students a first stepping stone in an academic career.⁹⁹

Many of van Beneden’s pupils actually managed to carve out such academic careers. His laboratory produced no fewer than nine university professors, seven in Liège and two in Brussels.¹⁰⁰ When the small scale of the Belgian academic world is taken into account, these numbers are without any doubt spectacular. Although two students from this group would later shift their focus of interest towards clinical work and pathophysiology, the majority remained faithful to the programme of the “master.” One (Hans de Winiwarter) would continue van Beneden’s research in reduction division; all the rest carried on his morphological studies of embryos – often studying the zoological groups that had occupied the “master” himself.¹⁰¹ In the end, van Beneden actually trained two generations of university professors to pursue research within the conceptual lines he had drawn. A first generation, born in the 1850s, would work in van Beneden’s laboratory in the late 1870s and obtain professorships in the late 1880s. A second generation was born in the 1870s and worked under van Beneden in the years between 1895 and 1905. After World War I, they would gradually replace the first generation. This cycle of academic appointments was a disadvantage for an

⁹⁷ Delcour, 1876, p. 8.

⁹⁸ 1923, *Commémoration Ed. van Beneden*, p. 23.

⁹⁹ Harsin et al., 1954, p. 62. On Trasenster’s admiration of the system of *Privatdozenten*: Dhondt, 2005, p. 287.

¹⁰⁰ Namely: Polydore Francotte (1851–1916), Charles Julin (1857–1930), Julien Fraipont (1857–1910), Paul Cerfontaine (1864–1917), Pierre Nolf (1873–1953), Hans de Winiwarter (1875–1949), Désiré Damas (1877–1959), Marc de Selys-Longchamps (1877–1963) and Jacques Roskam (1890–1977).

¹⁰¹ Cerfontaine would go more deeply into the study of tube anemones, while Damas, de Selys-Longchamps and Julin continued his research on sea squirts. The latter would also deepen his master’s work on mesozoa.

in-between generation, who were born between 1860 and 1875 and who had worked in the Liège laboratory between 1880 and 1895. From this group, only one researcher would manage to carve out an academic career – and only then because of the premature death of a colleague.¹⁰²

Despite the academic success of van Beneden's pupils, evolutionary morphology never became institutionalised as a branch of learning in Liège. It was more an approach that found its way into different academic disciplines (such as zoology, comparative anatomy and embryology), which were furthermore divided among different faculties (namely sciences and medicine). To defend his programme, van Beneden therefore had to fight on various fronts. He was appointed in the Science Faculty, but also used his networks to influence the policies in the Faculty of Medicine – where he attracted many students. To his mind, their training could not be finished without a thorough introduction to comparative and evolutionary morphology. In 1883 he stated: “Who cannot see that, when it is important for the physician to know the human organism objectively, he can not be permitted to neglect the science that focuses on the organisation and the structure of Man? This is why today in Germany all those who have been recently appointed to a chair of human anatomy are savants initiated in animal morphology, known for their work in comparative anatomy and embryology.”¹⁰³ Thanks to this reasoning (and to the good contacts van Beneden had among the medical staff), pupils of van Beneden could actually “colonise” chairs in the Medicine Faculty.¹⁰⁴ The “master” furthermore used his influence to change the curriculum of medical students, by adding “general biology” as a compulsory course to the prospectus.¹⁰⁵ The fact that evolutionary morphology did not itself become an institutionalised chair can be seen as a disadvantage; for a strong personality like van Beneden, however, it also opened up opportunities to spread his programme in various disciplinary contexts.

The fact that van Beneden was able to found his own journal was another important element in the success of his research programme. Together with Charles van Bambeke, an embryologist at the University of Ghent, he set up *Archives de Biologie* in 1880. The journal was aimed at an international audience (as well as Liège it was also published in Leipzig), but had a bias towards contributions from Belgian authors. It

¹⁰² On the pupils of van Beneden who had scientific careers as morphologists: Leplat, 1966; Brien, 1971–1972, 1973–1974, 1977–1978a, 1977–1978b; Ubaghs, 1973–1974; Mulnard, 1990.

¹⁰³ Van Beneden, 1883a, p. 927.

¹⁰⁴ The first was his pupil Charles Julin, who was not even trained as a physician.

¹⁰⁵ Damas, 1936, p. 88.

offered a forum for physiological research in line with the work of the Liège professor Léon Fredericq, but above all there was room for the evolutionary morphological programme of van Beneden. Van Bambeke, the Ghent co-founder of the journal, would not really go into evolutionary morphology himself, but he nevertheless defended evolutionism in his popular conferences and would later, in letters to Haeckel, explicitly show his admiration for both the scientific ideas and the monistic world view of his correspondent.¹⁰⁶ The atmosphere van Bambeke created in the Ghent sciences faculty at least made it possible for some of his students to engage in evolutionary morphology and to come into contact with van Beneden. In this way van Beneden managed to gain a foothold for his research programme amongst young scholars in the country's other state-run university.¹⁰⁷

The connection of van Beneden's programme with state universities can explain its rather low ideological profile. Unlike the Catholic University of Leuven or the (free-thinking) University of Brussels, these state-run universities were after all directly dependent on a government whose political composition could easily change. In contrast to Haeckel – who would connect his research programme successively with fierce anti-clericalism and a Darwinian and mystic pantheism – van Beneden therefore often stressed that his goals were merely scientific. He *did* believe that society could learn “lessons” from nature, but these were only minimal. Among these he stressed the importance of a “natural” division of labour and the negative impact of social privileges – both consistent with his liberal convictions. Furthermore, his belief in natural selection also caused him to casually reject “egalitarianism” – in this way distancing himself from the growing association between socialism and Darwinism in the German press.¹⁰⁸ He would not, however, actively promote his ideological standpoints through his scientific work.

Furthermore, although a confirmed agnostic, van Beneden did not openly speak about religion. He *would*, however, agitate against those

¹⁰⁶ See: Van Bambeke, 1893, p. 740; Goossens, 1992, p. 75; Van Bambeke aan Haeckel, Jan. 22nd, 1890, Nov. 15th, 1891 and Feb. 27th, 1892, EHH, Haeckel Papers.

¹⁰⁷ The most important were Hector Leboucq, whose comparative anatomy in line with Gegenbaur would become internationally respected, and the young Julius MacLeod, who would later leave evolutionary morphology for the physiology and geography of plants and – finally – sociology. For a more in-depth analysis of their work, see: De Bont, 2005, pp. 108–110 and 290–293. In the other Belgian universities, Van Beneden's programme was less successful. Until 1894, zoology in the University of Leuven was dominated by his father, who never completely converted to evolutionary ideas. In the Brussels University, finally, morphology was largely neglected in the period before 1890.

¹⁰⁸ Van Beneden, 1883a, pp. 903–909. On the link between socialism and evolutionary theory in Germany: Kelly, 1981.

who believed that science had to be in keeping with a literal interpretation of the Bible. In 1873, he caused a minor incident in the Academy with an offhand remark in which he dismissed the biblical story of Jonas and the whale as a fable.¹⁰⁹ The Catholic press would openly attack him thereafter, trying to portray him as the leading Belgian representative of an arrogant and anti-clerical Darwinism. In doing so, they liked to present him as the opposite of his father, who was seen as the symbol of successful Catholic science. Edouard's plea for better financing of biology could, in this context, be unkindly interpreted as the demands of a greedy man who had lost the Catholic morals of his father: "That is to say, one has to construct majestic buildings, provide them with sumptuous furniture, lodge Mr. van Beneden in it, give him an armchair and slippers, with a nice little pension, in order to prove that which is unprovable, namely that he springs from Darwin's Grandfather-monkey. Un-provable, because we all know that Mr. van Beneden's father and grandfather, great-great uncle and further back, were good, religious and learned men."¹¹⁰ Such commentaries confirmed van Beneden in his aversion to biblical literalism, but never prompted him to react against Catholic religion as such.

Van Beneden and his pupils explicitly tried to prevent the evolutionary debate from becoming contaminated by religious or political discussions. In the polarising Belgian society of the 1870s and 1880s, however, this was not always possible.¹¹¹ In 1883, van Beneden wrote irritatedly: "Everybody thinks he can pronounce for or against Darwinism, as if it were some kind of political opinion."¹¹² Van Beneden himself was convinced that the debate should be discussed in scientific terms only, and he tried to avoid ideological comments in his own work altogether. His oldest pupil, Charles Julin, would write in the same vein: "Evolutionism has nothing to do with religion and it shouldn't scare anyone, not even the most pious."¹¹³ Although the members of the Liège "school" moved in free-thinking liberal circles, they explicitly detached their ideological background from their work. This attitude of pragmatic tolerance also returned in van Beneden's private life. He not only had to take the religious feelings of his father into account, but also (just like Darwin) those of his wife. When he bought a castle in Résimont, van Beneden – agnostic or not – would hire the pew for the

¹⁰⁹ Van Beneden, 1873, p. 780. On the incident: Gilbert and Henry, 1873.

¹¹⁰ Duclos, 1884, pp. 92–95. For comparable comments, see Florkin, 1967, pp. 379–380 and 385.

¹¹¹ On this polarisation: Witte et al., 2005, pp. 365–371 and 477–499.

¹¹² Van Beneden, 1883a, p. 928.

¹¹³ Julin, 1888.

privileged on the front row of the local church for his wife and daughters.¹¹⁴ At the end of his life he nevertheless insisted on receiving a civil funeral – to the dismay of his family, who indulged his wish, but did everything to make the event pass unnoticed.¹¹⁵

Because he shunned religious-political profiling, van Beneden would, in contrast to Haeckel, never achieve the status of a prophet. In the institutional context in which he worked, such a reputation would obviously only have hampered support for his research programme. The success of evolutionary morphology at state-run universities was, after all, connected with van Beneden's sustained belief in keeping out the more polemical aspects of German *Darwinismus*. This attitude also seemed to have enhanced his personal reputation, in a country which was very much divided between free-thinkers and Catholics. When in 1920 (9 years after his death) a prestigious commemoration was arranged, this would appear under the patronage of the Catholic Minister of Sciences and Arts, Frans Schollaert – something that would have been unthinkable with a controversial figure like Haeckel.¹¹⁶ Van Beneden had never been a man of high-flown ideologies, but had instead devoted himself to the small-scale politics of academic life, its rhetoric and its networking. It was in the latter that his success has to be sought.

The End of the Dynamism

The vigour instigated by van Beneden's evolutionary morphology would not last. When in the late 1880s the conceptual underpinnings of his programme came under fire, he and his Liège followers basically started to elaborate on the more descriptive aspects of their work. In this way, van Beneden's pupils were able to perfect their technical qualities (for which they would be praised in posthumous biographies),¹¹⁷ but they hardly introduced any theoretical innovations. Consequently, they would no longer play the leading role in the evolutionary debate among Belgian biologists.

This role was taken over in around 1890 by a faction of young scientists, which has to be situated in the *milieus* around the University of Brussels. Although less coherent than “the Van Beneden School,” this group would develop a solid intellectual network, in which a shared interest in evolutionary theory served as an important connecting factor.

¹¹⁴ Hamoir, 2002, pp. 126–128.

¹¹⁵ Marc de Selys-Longchamps to Auguste Lameere, s.d., AULB, Lameere Papers, 104 PP.

¹¹⁶ 1923, *Commémoration Ed. van Beneden*, 5.

¹¹⁷ See note 98.

The group consisted of generational contemporaries, all born in the late 1850s and early 1860s. The most influential of them were probably the zoologists Auguste Lameere and Paul Pelseneer, the botanist Jean Massart and the palaeontologist Louis Dollo. Their careers would bring these men to different Belgian institutions, but they nevertheless kept in contact and although they lacked a strong leader figure like van Beneden, the ideas of this “Brussels Group” were not without coherence.¹¹⁸

In the beginning of their careers, the members of the “Brussels Group” worked very much in the same register of van Beneden’s evolutionary morphology. All of them furthermore published several times in his *Archives de biologie*. From the start, however, their interests were also broader than those of the “Van Beneden School.” They would criticise evolutionary research that was based on embryology only, and they actively broadened the field of evolutionary studies to include palaeontology, systematics, biogeography and “*éthologie*” (the discipline interested in the adaptation of organisms to their environment).¹¹⁹ Especially adaptation – a topic that had been largely neglected by van Beneden – became an important focus of interest in the work of the Brussels biologists.¹²⁰ They were largely inspired in this approach by the example the French zoologist Alfred Giard, whose marine station in Wimereux on the northern French coast was becoming an important stopping place for Belgian biologists.¹²¹ Under Giard’s influence, the members of the Brussels Group would in particular revalue the importance of field research. In their view, the study of microscopic slices, isolated from their environment, had led to a very one-sided view of nature.¹²² According to Massart, laboratory-trained botanists were so blinkered that they could recognise plants in their dried form only, while Lameere complained that zoologists had started to believe that formaline was the animal’s natural habitat.¹²³ They were all convinced of the importance of experimental laboratory science, but wanted to combine “modern” scientific tendencies with a “broad” view on natural phenomena.¹²⁴ In contrast to van Beneden, who saw his university

¹¹⁸ For biographical background on the different members of the Brussels Group, see: e.g. Marchal, 1927; Brien, 1951a, b; Selys-Longchamps, 1954. For a more in-depth analysis of their work: De Bont, 2005, pp. 221–268.

¹¹⁹ Lameere, 1902, pp. 5–11.

¹²⁰ See e.g. Dollo, 1909; Massart, 1912; Lameere, 1915; Pelseneer, 1920a.

¹²¹ On Giard’s cenacle: Bouyssi, 1998.

¹²² Pelseneer, 1910, pp. 305–322; Pelseneer, 1920a, pp. 63–69.

¹²³ Massart, 1912, p. 954; Lameere, 1915, p. 88.

¹²⁴ In this sense they can be seen as European representatives of “the new natural history” – a movement of which Robert Kohler has described the American variant. Kohler, 2002, pp. 23–59.

laboratory and the Academy as the most important places of scientific debate, the new generation Brussels biologist re-valued the naturalist societies (Figure 5). In doing so, they also restored the contacts with amateur naturalists, whom they accompanied on their field excursions.¹²⁵

Less allergic to speculation than van Beneden, the Brussels biologists would actively engage in the debates on the mechanism of evolution between neo-Lamarckians and neo-Darwinians – debates that had occupied the international scientific community since the 1880s.¹²⁶ Furthermore, they also developed the ambition to discover tendencies and “laws” in evolutionary history, which was again an interest with a certain speculative flavour.¹²⁷ It was not only in their preference for research topics that the Brussels evolutionists showed less prudence than van Beneden and his pupils, however. They were also less fearful of openly mixing evolution theory and ideology. Given their ties to the Free University of Brussels, various freethinkers’ organisations and the freemasonry, it is not surprising that they openly associated evolutionism with a mechanistic, materialist and liberal philosophy.¹²⁸ In an intellectual climate of growing ideological polarisation, this world view was aggressively propagated as an alternative to Catholic “obscurantism.”¹²⁹ To enhance the success of this alternative, the Brussels biologists furthermore actively engaged in various forms of scientific popularisation.¹³⁰ Again this distanced them from van Beneden, who had always addressed himself to the scientific community alone.

It seems above all important that, in addition to differences in style and ideological profiling, the Brussels biologists were faster at integrating new scientific developments than the members of the “Van Beneden School.” Van Beneden’s pupils kept very close to the morphological work as it had been conceived by their (dominant) master. They hardly underwent any influence from Giard’s *éthologie*, and the *Entwicklungsmechanik* of German embryologists like Wilhelm Roux and Hans Driesch also largely

¹²⁵ Pelseener, Lameere, Massart and Dollo played crucial roles in the Société entomologique, the Société royale malacologique, the Société royale de botanique and the Société belge de géologie, de paléontologie et de hydrologie, respectively.

¹²⁶ A.o.: Massart, 1906; Lameere, 1907; Pelseener, 1920b. On the international context of these debates: Bowler, 1985, pp. 38–43.

¹²⁷ Dollo, 1893; Pelseener, 1896; Lameere, 1904. See also: Gould, 1970; Bowler, 1996, pp. 339–352.

¹²⁸ Only Dollo had a Catholic background. After he was appointed at the University in Brussels in 1893, one can detect ever clearer expressions of his mechanistic world view in his writings, however.

¹²⁹ See for example Pelseener, 1902; Lameere, 1906.

¹³⁰ All of them would for example take part in the Brussels movement of University Extension. De Bont, 2005, pp. 259–261.



Figure 5. The Brussels biologists would re-establish contacts with the naturalist societies. On the illustration: Auguste Lameere (on the left, with butterfly net) and his colleagues from the Société entomologique (AUBL, Augste Lameere Papers).

passed them by. Neither Roux' defence of "experiment" nor his critique of the basic concepts of evolutionary morphology triggered much response in Liège, and when Driesch described Haeckel's *Gastraea* theory as "*eine lächerliche Geschichte*," this only led to indignation.¹³¹ It was only towards the end of their careers that some of the pupils of van Beneden would distance themselves from the type of morphology that they had pursued. In the 1920s, Julin – already close to retirement – would openly question the research programme that he had embraced as a young researcher. In an open-hearted lecture in 1921 he said that the evolutionary morphological programme had been "exaggerated" and "simplistic."¹³² In his letters the disappointment could be heard even more strongly. To the French anatomist Robert Picqué he wrote how sceptical he had become of evolutionary embryology. The disillusionment was complete because it related to the only discipline for which he was trained. "I lost my faith in the Gods that I adored," he wrote, "and I have nothing to put in their place."¹³³ Younger members of the "Van Beneden School"

¹³¹ De Selys-Lonchamps, 1948, p. 140.

¹³² Julin, 1921, pp. 21–31.

¹³³ Julin to Picqué, 23 July 1923, RAB, Personal Files, Charles Julin, 8028.

would also look back on their scientific lives with a certain frustration. At the end of his career, Marc de Selys-Longchamps wrote scornfully about the “pure” morphology he had practised, and the old Hans de Winiwarter talked regretfully about his lack of background to refocus on experimental research.¹³⁴ Van Beneden’s programme might have been embedded in his own “school,” but after a few decades it seemed to have lost much of its dynamism due to a lack of conceptual renewal.

Conclusion

Since his death, Edouard van Beneden has been characterised as the “hyphen” between Haeckel’s evolutionary morphology and August Weismann’s cytological research.¹³⁵ Only van Beneden’s contributions in the latter field have triggered the attention of historians of science, however. In this way the idea has arisen that the Liège zoologist had been “principally interested in the study of the cellular basis of life.”¹³⁶ Without seeking to downplay the importance of his cytological work, I have used this essay to shed light on a part of his activities that was at least as important to him, namely his research in evolutionary morphology. Van Beneden after all devoted the greater part of his publications to this discipline and oriented the majority of his students towards it. In the context of late 19th-century Belgian science, it was furthermore not without importance. In the case of van Beneden, launching a programme of evolutionary morphology also meant the practical creation of a research school, the introduction of evolutionary theory in Belgian academia, the promoting of a “new” biology and the reorganisation of existing academic traditions.

The reason for the (temporary) success of van Beneden’s programme has to be sought in a combination of factors. Obviously, the climate of university reform – in which he partook – was crucial. The introduction of new courses, the creation of laboratories and the appointment of assistants would have been impossible without a structural reformation of the universities supported by the Belgian government and the academic authorities. In this context, however, van Beneden was still one of the only Belgian scientists to actually found a “school” connected to his own research programme, which implies that he used the existing opportunities more efficiently than most of his colleagues. In this

¹³⁴ De Selys-Longchamps, 1948, p. 140; Gérard, 1949, p. 72.

¹³⁵ Lameere, 1913, p. 878.

¹³⁶ Coleman, 1965, p. 140.

respect, his contacts in the biological world, both nationally and internationally, were of importance. Virtually born into the world of zoology, van Beneden “inherited” the scientific networks of his father, but he also actively extended them to take in the new-style researchers of his time. In his own university, the zoologist maintained good contacts with the staff of the Medicine Faculty – where his own students would eventually “colonise” chairs – and he was furthermore well-acquainted with a (politically influential) rector like Trasenster.

Thanks to his international networks, van Beneden was able to secure a first-hand introduction to the new research interests at German universities. In the Haeckelian programme developed at Jena he found a good foreign example for what he wanted to realise in Liège – at a moment when German science in general had many admirers in the Belgian academic world. Van Beneden also showed himself to be flexible enough to smooth off the sharp ideological edges of Haeckelism, to make it acceptable in a state-run university. Refreshing in its interpretations, his programme was not entirely new as regards scientific practice and it could therefore be grafted onto existing university chairs. At the same time, van Beneden managed to give the programme an aura of “modernity,” precisely because of the place where it was practised: the modernly equipped university laboratory.

The heyday of evolutionary morphology in Belgium lasted for a limited time. Van Beneden and the “school” he dominated would not be able to revive the research programme once their conceptual paradigm came under international attack towards the end of the 19th century. His followers would basically direct their attention to descriptive morphological work, which they would perform well into the 20th century. Evolutionary interests largely disappeared from their publications, but others would pick up the theme. As such, evolutionism would never die out in Belgian academia after van Beneden had introduced it in the 1870s. The Brussels biologists, who had taken the lead in the evolutionary debate by the turn of the century, to some extent used different perspective from which to study the phenomenon, but they would still recognise van Beneden’s role as an intellectual catalyst.

Van Beneden’s evolutionism is not the only aspect of his work that survived his research programme. One can obviously point to the following that his cytological work would continue to attract in the following decades, but it was above all the actual setting of his science – both cytological *and* morphological – that had come to stay. Van Beneden was one of the first scientific heavyweights in Belgium who turned the university laboratory into his habitat and operating base.

Although the excesses of laboratory-oriented research in the universities were criticised towards the end of the 19th century, its rationale was never questioned. Van Beneden can therefore be seen as the “prototype” of a new kind of scientist – a type that still dominates the Belgian scientific landscape to this day.

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References

1886. *Manifestation en l'Honneur de Monsieur P.J. van Beneden à l'Occasion de son Cinquantenaire de Professorat (1836–1886)*. Louvain 20 juin 1886. *Compte-rendu*. Leuven: Peeters-Ruelens.
1923. *Commémoration Ed. van Beneden 24 mai 1920*. Liège: Vaillant-Carmanne.
- Bouyssi, F. 1998. *Alfred Giard (1846–1908) et ses Elèves. Un Cenacle de 'Philosophes Biologistes'. Aux Origines du Scientisme?* 2 vols. Paris: ANRT.
- Bowler, P. J. 1985. *The Eclipse of Darwinism. Anti-Darwinian Evolution Theories in the Decades around 1900*. Baltimore: Johns Hopkins University Press.
- 1988. *The Non-Darwinian Revolution. Reinterpreting a Historical Myth*. Baltimore and London: Johns Hopkins University Press.
- 1996. *Life's Splendid Drama. Evolutionary Biology and the Reconstruction of Life's Ancestry 1860–1940*. Chicago and London: University of Chicago Press.
- Brachet, A. 1923. “Notice sur Edouard van Beneden.” *Annuaire de l'Académie Royale de Belgique* 89: 167–242.
- Brien, P. 1951a. “Notice sur Paul Pelseneer.” *Annuaire de l'Académie Royale de Belgique* 117: 1–55.
- 1951b. “Notice sur Louis Dollo.” *Annuaire de l'Académie Royale de Belgique* 117: 69–138.
- 1971–1972. “Selys Longchamps (Marc-Aurèle-Gracchus, baron de).” *Biographie Nationale Suppl.* 9: 727–736.
- 1973–1974. “Damas (Philippe-Désiré).” *Biographie Nationale Suppl.* 10: 121–133.
- 1977–1978a. “Cerfontaine (Paul).” *Biographie Nationale Suppl.* 12: 122–125.
- 1977–1978b. “Julin (Charles).” *Biographie Nationale Suppl.* 12: 534–542.
- Buican, D. 1982. “L'Accueil de Darwin à l'Académie des Sciences.” *Revue de Synthèse* 103: 39–51.

- Churchill, F. B. 1970. "Hertwig, Weismann and the Meaning of Reduction Division circa 1890." *Isis* 61: 428–457.
- Coleman, W. 1965. "Cell, Nucleus and Inheritance: An Historical Study." *Proceedings of the American Philosophical Society* 109: 124–158.
- 1976. "Morphology between Type Concept and Descent Theory." *Journal of the History of Medicine* 31: 149–175.
- Damas, D. 1936. "Edouard van Beneden." L. Halkin and P. Harsin (eds.), *Liber Mémorialis. L'Université de Liège de 1867 à 1935. Vol. 2. Faculté des Sciences. Ecole Spéciale. Faculté Technique*. Liège: Rectorat de l'université, pp. 88–101.
- Darwin, C. 1859. *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*. London: Murray.
- 1874. *The Descent of Man, and Selection in Relation to Sex*, 2nd ed. London: Murray.
- De Bont, R. 2005. *Darwins Kleinkinderen. De Omgang met de Evolutieleer in België, 1865–1945*. Unpublished Doctoral Thesis, University of Leuven.
- Delboeuf, J. 1877. "Les Mathématiques et le Transformisme. Une Loi Mathématique applicable à la Théorie du Transformisme." *La Revue Scientifique de la France et de l'Étranger*, series 2, 6: 669–679.
- Delcour, C. 1876. *Situation de l'Enseignement Supérieur donné aux frais de l'Etat. Rapport triennal. Années 1871, 1872 et 1873*. Brussels: Gobbaerts.
- De Selys-Longchamps, M. 1948. "Notice sur Charles Julin." *Annuaire de l'Académie Royale de Belgique* 114: 130–188.
- De Selys-Longchamps, M. 1954. "Notice sur August Lameere." *Annuaire de l'Académie Royale de Belgique* 120: 63–118.
- Despy-Meyer, A. 2001. "Instellingen en Netwerken." R. Halleux, et al. (eds.), *Geschiedenis van de Wetenschappen in België 1815–2000*, vol. 1. Brussels: La Renaissance du Livre, pp. 71–89.
- Dhondt, P. 2005. *Een Tweevoudig Compromis. Discussies over Universitair Onderwijs in het Negentiende-eeuwse België*. Unpublished Doctoral Thesis, University of Leuven.
- In press. "Belgische Studenten an der Berliner Universität zwischen 1831 und 1914." *Jahrbuch für Universitätsgeschichte*.
- Di Gregorio, M. A. 1995. "A Wolf in Sheep's Clothing: Carl Gegenbaur, Ernst Haeckel, the Vertebral Theory of the Skull, and the Survival of Richard Owen." *Journal of the History of Biology* 28: 247–280.
- 2005. *From Here to Eternity. Ernst Haeckel and Scientific Faith*. Göttingen: Vandenhoeck & Ruprecht.
- Dollo, L. 1893. "Les Lois de l'Évolution." *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 7: 164–165.
- 1909. "La Paléontologie Ethologique." *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 23: 377–421.
- D'Omalius d'Halloy, J.-B. 1850. "Note sur la Succession des Êtres Vivants." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 13: 498–510.
- 1858. "Discours sur l'Espèce." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 5: 555–565.
- Duclos, A. 1884. "Darwinisme." *Rond den Heerd* 19: 92–95.
- Florkin, M. 1960. *Naissance et Déviation de la Théorie Cellulaire dans l'Oeuvre de Théodore Schwann*. Paris: Hermann.

- 1967. “Etat Belge contre van Beneden.” L.-E. Halkin and M. Florkin (eds.), *Chronique de l'Université de Liège*. Liège: Vaillant-Carmanne, pp. 377–385.
- Gérard, P. 1949. “Notice sur Hans de Winiwarter.” *Annuaire de l'Académie Royale de Belgique* 115: 61–92.
- Gilbert, P. and Henry, L. 1873. *La Baleine de Jonas et l'Université de Louvain*. Leuven: Peeters.
- Gilson, G. 1914. *Le Musée d'Histoire Naturelle Moderne. Sa Mission, son Organisation, ses Droits*. Brussels: Hayez.
- Goossens, N. 1992. *De Gentse Morfologenschool*. Gent: RUG.
- Gould, S. J. 1970. “Dollo on Dollo's Law. Irreversibility and the Status of Evolutionary Laws.” *Journal of the History of Biology* 3: 189–212.
- Haeckel, E. and Haeckel, A. 1950. *Ernst und Agnes Haeckel. Ein Briefweschel*. Ed. Konrad Huschke, Jena: Urania-Verlag.
- Halleux, R. 2001. “De Ontwikkeling der Ideeën.” R. Halleux, et al. (eds.), *Geschiedenis van de Wetenschappen in België 1815–2000*, vol. 1. Brussels: La Renaissance du Livre, pp. 17–36.
- Hamoir, G. 1994. *La Découverte de la Méiose et du Centrosome par Edouard van Beneden*. Brussels: Académie royale de Belgique.
- 1997. *Frère-Orban (1812–1896) et l'Université de Liège*. Liège: CURL.
- 2002. *La Révolution Évolutionniste en Belgique. Du Fixiste Pierre-Joseph van Beneden...à son Fils Darwiniste Edouard*. Liège: Les Éditions de l'Université de Liège.
- Hannon, J.-D. 1872 [1864]. “De la Certitude dans l'Étude des Sciences Naturelles à propos de l'Origine des Espèces. Discours prononcé à la Séance Solennelle de Réouverture des Cours, le 10 octobre 1864.” *Recueil des Procès-verbaux et Discours dédié à M. van Schoor. Séances Solennelles de 1834 à 1871, U.L. B*, vol. 2. Brussels: Archives de l'ULB, pp. 669–684.
- Harris, H. 1999. *The Birth of the Cell*. New Haven and London: Yale University Press.
- Harsin, P., et al. 1954. *Histoire des Universités Belges*. Brussels: Office de publicité.
- Holt, N. 1971. “Ernst Haeckel's Monistic Religion.” *Journal for the History of Ideas* 32: 265–280.
- Hopwood, N. 1999. “‘Giving Body’ to Embryos. Modelling, Mechanism and the Microtome in the late Nineteenth-Century Anatomy.” *Isis* 90: 462–496.
- Hoßfeld, U., Olson, L. and Breidbach, O. (eds.) 2002. *Carl Gegenbaur and Evolutionary Morphology*. Special Issue of *Theory of Biosciences*, p. 122.
- Houzeau, J.-C. 1872. *Études sur les Facultés Mentales des Animaux comparées à celles de l'Homme*, 2 vols. Mons: Hector Manceaux.
- Julin, C. 1888. “A propos de la Création d'une Chaire de Darwinisme à Paris.” *Journal de Liège*, Feb. 16th, 1888.
- 1921. “Séance du 22 février 1921.” *Bulletin de la Société Zoologique de France* 46: 21–31.
- 1925. “Notice sur Julien Fraipont.” *Annuaire de l'Académie Royale de Belgique* 91: 131–196.
- Kelly, A. 1981. *The Descent of Darwin. The Popularisation of Darwinism in Germany, 1860–1914*. Chappel Hill: University of North Carolina Press.
- Kemna, A. 1897. *P.J. van Beneden. La Vie et l'Oeuvre d'un Zoologiste*. Antwerp: Buschman.
- Kohler, R. E. 2002. *Landscapes and Labscapes. Exploring the Lab-Field Border in Biology*. Chicago: University of Cicago Press.

- Lameere, A. 1902. "Sur l'Origine des Siphonores." *Annales de la Société Royale Malacologique de Belgique* 37: 5–11.
- 1904. "L'Evolution des Ornaments Sexuels." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 4th series, 4: 1327–1364.
- 1906. "Les Ancêtres de l'Espèce Humaine. Discours Rectoral." *Revue de l'Université de Bruxelles* 12: 1–34.
- 1907. "Le Mécanisme de l'Evolution. Discours prononcé à l'Ouverture Solennelle des Cours le 14 octobre 1907." *Revue de l'Université de Bruxelles* 13: 1–27.
- 1913. "Edouard van Beneden (Résumé d'une Conférence)." *Revue de l'Université de Bruxelles* 19: 877–878.
- 1915. "Les Sociétés Animales." *Bulletin du Muséum d'Histoire Naturelle* 3: 1–17.
- 1916. "Contribution à la Connaissance des Dicémides." *Bulletin Biologique de la France et de la Belgique* 50: 1–35.
- Laurent, G. 1987. *Paléontologie et évolution en France, 1800–1860. De Cuvier-Lamarck à Darwin*. Paris: Comité des Travaux Historiques et Scientifiques.
- Lehon, H. 1868. *L'Homme Fossile en Europe. Son Industrie, ses Moeurs, ses Oeuvres d'Art*, 2nd ed. Brussels and Paris: Muquardt.
- Leplat, G. 1966. "De Winiwarter (Hans-Chrysostôme, chevalier de)." *Biographie Nationale Suppl.* 5: 750–753.
- Lester, J. 1995. *E. Ray Lankester and the Making of British Biology*. Oxford: British Society for the History of Science.
- Maienschein, J. 1991. *Transforming Traditions in American Biology, 1880–1915*. Baltimore: Johns Hopkins University Press.
- Marchal, E. 1927. "Notice sur Jean Massart." *Annuaire de l'Académie Royale de Belgique* 93: 69–158.
- Massart, J. 1906. *L'Evolution et ses Facteurs*. Brussels: J.-H. Moreau.
- 1912. "Les Naturalistes Actuels et l'Etude de la Nature." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 4th series, 11: 944–965.
- Mayr, E. 1982. *The Growth of Biological Thought. Diversity, Evolution and Inheritance*. Cambridge (Mass.): Harvard University Press.
- McClelland, C. E. 1980. *State, Society and University in Germany, 1700–1914*. Cambridge: Cambridge University Press.
- Molina, G. 1996. "Darwinisme Français." P. Tort (ed.), *Dictionnaire du Darwinisme et de l'Evolution*, vol. 1. Paris: PUF, pp. 909–954.
- Mulnard, J. 1990. "Francotte, Polydore." *Nouvelle Biographie Nationale* 2: 158–159.
- Newman, W. A. 1993. "Darwin and Cirrepedology." F. Truesdale (ed.), *History of Carcinology*. Rotterdam: Balkema, pp. 349–434.
- Nyhart, L. K. 1987. "The Disciplinary Breakdown of German Morphology, 1870–1900." *Isis* 78: 365–389.
- 1995. *Biology takes Form. Animal Morphology and the German Universities 1800–1900*. Chicago and London: University of Chicago Press.
- 1996. "Natural History and the 'New' Biology." N. Jardine, et al. (eds.), *Cultures of Natural History*. Cambridge: Cambridge University Press.
- Partsch, K. 1980. *Die Zoologische Station in Neapel. Modell internationaler Wissenschaftszusammenarbeit*. Göttingen: Vandenhoeck & Ruprecht.
- Paul, H. W. 1985. *From Knowledge to Power. The Rise of the Science Empire in France 1860–1939*. Cambridge: Cambridge University Press.

- Pelseneer, P. 1896. "L'Hermaphroditisme chez les Mollusques." *Archives de Biologie* 14: 33–62.
- 1902. "La Morale de la Science et la Morale de l'Eglise." *Bulletin des Travaux du Suprême Conseil de Belgique* 47: 39–47.
- 1910. "L'Enseignement des Etudes Biologiques." *Revue de Belgique*, 2nd series, 60: 305–322.
- 1920a. "La Nécessité des Etudes Ethologiques." *Annales de la Société Royale Zoologique et Malacologique de Belgique* 51: 63–69.
- 1920b. *Les Variations et leur Hérité chez les Mollusques*. Brussels: Lamertin.
- Porter, T. M. 2001. "Adolphe Quetelet, een Boegbeeld van de Wiskunde." R. Halleux, et al. (eds.), *Geschiedenis van de Wetenschappen in België 1815–2000*, vol. 1. Brussels: La Renaissance du Livre, pp. 90–98.
- Richards, R. J. 2002. *The Romantic Conception of Life. Science and Philosophy in the Age of Goethe*. Chicago: University of Chicago Press.
- Rinard, R. 1981. "The Problem of the Organic Individual. Ernst Haeckel and the Development of the Biogenetic Law." *Journal of the History of Biology* 14: 249–275.
- Ubaghs, G. 1973–1974. "Fraipont (Julien-Jean-Joseph)." *Biographie Nationale* suppl. 10: 221–224.
- Van Bambeke, C. 1893 "Les Matériaux de l'Organisme Humain." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 3, 26: 733–757.
- Van Beneden, E. 1869. "Recherches sur la Composition et la Signification de l'Oeuf." *Mémoires de l'Académie des Sciences, des Lettres et des Beaux-Arts* 34: 1–283.
- 1871a. "Recherches sur l'Évolution des Grégarines." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 2, 31: 325–359.
- 1871b. "Note sur la Conservation des Animaux Inférieurs." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 2, 32: 179–181.
- 1873. "Rapport sur les Résultats d'un Voyage au Brésil et à la Plata." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 2, 35: 775–792.
- 1874. "Le Transformisme d'après d'Omalius d'Halloy." *Revue de Belgique*, 6, 16: 404–406.
- 1875. "Recherches sur la Structure de la Corde Dorsale de l'Amphioxus, par M.C. Moreau. Rapport de M. Edouard van Beneden." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 2, 39: 250–257.
- 1876. "Recherches sur les Dycémides, Survivants Actuels d'un Embranchement des Mésozoaires." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 2, 41 and 42: 1160–1205 and 35–97.
- 1883a. "La Biologie et l'Histoire Naturelle." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 3, 6: 896–932.
- 1883b. "Recherches sur la Maturation de l'Oeuf, la Fécondation et la Division Cellulaire." *Archives de Biologie* 4: 265–640.
- 1897. *Les Anthozoaires de la Plankton Expedition*. Kiel and Leipzig: Lipsius and Tischer.
- 1902. "La Reproduction des Animaux et la Continuité de la Vie." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 4, 1: 1047–1089.
- Van Beneden, E. and Neyt, A. 1887. "Nouvelles Recherches sur la Fécondation et la Division Mitotique chez l'Ascaride Mégalocephale. Communication Préliminaire."

- Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, series 3, 6: 238.
- van Beneden, E. and Julin, C. 1887. "Recherches sur la Morphologie des Tuniciers." *Archives de Biologie* 6: 237–474.
- van Beneden, P.-J. 1840. "Recherches sur le Développement des Aplysies." *Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 7: 239–243.
- 1861. "Recherches sur les Crustacés du Littoral de Belgique." *Mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 33: 1–171.
- Vanpaemel, G. 1992. "Transformism and the Question of Species in Belgium before the Introduction of Darwinism." *Tractrix* 4: 13–37.
- 2001. "De Darwinistische Revolutie." R. Halleux, et al. (eds.), *Geschiedenis van de Wetenschappen in België 1815–2000*, vol. 1. Brussels: La Renaissance du Livre, pp. 256–268.
- Wachelder, J. 2001. "The German University Model and its Reception in the Netherlands and Belgium." R. Christoph Schwinges (ed.), *Humboldt International: der Export des deutschen Universitätsmodells im 19. und 20. Jahrhundert*. Basel: Schwabe, pp. 179–204.
- Weindling, P. 1989. "Ernst Haeckel, Darwinismus and the Secularization of Nature." J. R. Moore (ed.), *History, Humanity and Evolution. Essays for John C. Greene*. Cambridge: Cambridge University Press, pp. 311–327.
- White, P. 2003. *Thomas Huxley. Making the "Man of Science."* Cambridge: Cambridge University Press.
- Wils, K. 2005. *De Omweg van de Wetenschap. Het Positivisme en de Belgische en Nederlandse Intellectuele Cultuur 1845–1914*. Amsterdam: Amsterdam University Press.
- Witte, E., et al. 2005. *Nieuwe Geschiedenis van België, vol. 1. 1830–1905*. Tiel: Lannoo.