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Onychophorology, the study of velvet worms, historical trends, landmarks, and researchers from 1826 to 2020 (a literature review)

Onicoforología, el estudio de los gusanos de terciopelo, tendencias históricas, hitos e investigadores de 1826 a 2020 (Revisión de la Literatura)

Onicoforologia, o estudo dos vermes aveludados, tendências históricas, marcos e pesquisadores de 1826 a 2020 (Revisão da Literatura)

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Abstract

Velvet worms, also known as peripatus or onychophorans, are a phylum of evolutionary importance that has survived all mass extinctions since the Cambrian period. They capture prey with an adhesive net that is formed in a fraction of a second. The first naturalist to formally describe them was Lansdown Guilding (1797-1831), a British priest from the Caribbean island of Saint Vincent. His life is as little known as the history of the field he initiated, Onychophorology. This is the first general history of Onychophorology, which has been divided into half-century periods. The beginning, 1826-1879, was characterized by studies from former students of famous naturalists like Cuvier and von Baer. This generation included Milne-Edwards and Blanchard, and studies were done mostly in France, Britain, and Germany. In the 1880-1929 period, research was concentrated on anatomy, behavior, biogeography, and ecology; and it is in this period when Bouvier published his mammoth monograph. The next half-century, 1930-1979, was important for the discovery of Cambrian species; Vachon's explanation of how ancient distribution defined the existence of two families; DNA and electron microscopy from Brazil; and primitive attempts at systematics using embryology or isolated anatomical characteristics. Finally, the 1980-2020 period, with research centered in Australia, Brazil, Costa Rica, and Germany, is marked by an evolutionary approach: from body and behavior to geographic distribution; the discovery of how they form their adhesive net; the reconstruction of Cambrian onychophoran communities, the first experimental taphonomy; the first country-wide map of conservation status (in Costa Rica); the first model of why they survive in cities; the discovery of new phenomena like food hiding, parental feeding investment, and ontogenetic diet shift; and the birth of a new research branch, onychophoran ethnobiology. While a few names often appear in the literature, most knowledge was produced by a mass of researchers who entered the field only briefly.

Keywords: history of science, the study of invertebrates, research patterns, studies on onychophorans.

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Resumen

Los gusanos de terciopelo, peripatos u onicóforos, son un filo de importancia evolutiva que ha sobrevivido a todas las extinciones masivas desde el Cámbrico. Capturan sus presas con una red adhesiva que se forma en una fracción de segundo. El primer naturalista que los describió fue Lansdown Guilding (1797-1831), un sacerdote británico de la isla caribeña de San Vicente Su vida es tan poco conocida como el campo científico que él inició, la onicoforología. Este artículo es la primera historia general de la Onicoforología, aquí dividida en periodos de 50 años. Los primeros estudios, de 1826 a 1879, fueron publicados por estudiantes de naturalistas famosos como Cuvier y von Baer. Entre estos estudiantes estaban Milne-Edwards y Blanchard, y los estudios se hicieron mayormente en Francia, Gran Bretaña y Alemania. En el período 1880-1929, el trabajo se concentró en anatomía, comportamiento, biogeografía y ecología, y es en este período cuando apareció la gran monografía de Bouvier. El siguiente periodo, 1930-1979, fue importante por el descubrimiento de fósiles cámbricos; la explicación de Vachon de cómo la distribución antigua definió la existencia de dos familias; estudios en Brasil con ADN y microscopía electrónica; e intentos primitivos de sistemática utilizando embriología o características anatómicas aisladas. Finalmente, el período 1980-2020, con investigaciones centradas en Australia, Brasil, Costa Rica y Alemania, está marcado por un enfoque evolutivo de todos los campos, desde el cuerpo y el comportamiento, hasta la distribución geográfica; el descubrimiento de cómo forman su red adhesiva; la reconstrucción de las comunidades del Cámbrico, la primera tafonomía experimental; el primer mapa del estado de conservación en todo un país (de Costa Rica); el primer modelo de porqué sobreviven en las ciudades; el descubrimiento de nuevos fenómenos, como ocultar alimentos, inversión en alimentación parental y el cambio ontogenético de dieta; así como el nacimiento de una nueva rama de investigación, la etnobiología de onicóforos. Si bien algunos nombres aparecen a menudo en la literatura, la mayoría del conocimiento fue producido por una masa de investigadores que ingresaron al campo brevemente.

Palabras clave: historia de la ciencia, estudio de invertebrados, patrones de investigación, estudio de onicóforos.

Resumo

Os vermes aveludados ou onicóforos, são um filo de importância evolutiva que sobreviveu a todas as extinções massivas desde o período cambriano. Capturam suas presas com uma rede adesiva que se forma em uma fração de segundo. O primeiro naturalista que os descreveu foi Lansdown Guilding (1797-1831), um sacerdote britânico da ilha caribenha de San Vicente. Até o momento, nenhuma história sobre o estudo destes animais tinha sido escrita: este artigo é a primeira História Geral da Onicoforologia. Os primeiros estudos, de 1826 a 1879, foram publicados por estudantes de naturalistas famosos como Cuvier e von Baer. Dentre esses estudantes estavam Milne-Edwards e Blanchard, e os estudos foram feitos, em sua maioria, na França, Alemanha e Grã-Bretanha. No período de 1880-1929, o trabalho se concentrou na anatomia, comportamento, biogeografia e ecologia, e apareceu a grande monografia de Bouvier. O período seguinte, 1930-1979, foi importante pelo descobrimento de fósseis cambrianos; a explicação de Vachon sobre como a distribuição antiga definiu a existência de duas famílias; estudos no Brasil com DNA e microscopia eletrônica; e tentativas primitivas de sistemática utilizando embriologia ou características anatómicas isoladas. Finalmente, o período de 1980-2020, com pesquisas focadas na Austrália, no Brasil, na Costa Rica e Alemanha, está marcado por um enfoque evolutivo de todos os campos, desde o corpo e o comportamento, até que a distribuição geográfica; o descobrimento sobre como formam sua rede adesiva;

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a reconstrução das comunidades do Cambriano, a primeira tafonomia experimental; o primeiro mapa do estado de conservação em todo um país (da Costa Rica); o primeiro modelo do porquê sobrevivem nas cidades; o descobrimento de novos fenômenos, como ocultar alimentos, investimento em alimentação parental e a alteração ontogenética de dieta; como também o nascimento de um novo ramo de pesquisa, a etnobiologia de onicóforos. Embora alguns nomes apareçam com frequência na literatura, a maior parte do conhecimento foi produzida por uma massa de pesquisadores que entraram brevemente em campo.

Palavras-chave: história da ciência, estudo de invertebrados, padrões de pesquisa, estudo de onicóforos.

INTRODUCTION

Velvet worms, or onychophorans, include placental species and, as a phylum, have survived all mass extinctions since the Cambrian (Hutchinson, 1930; Hou, & Bergström, 1991). They capture prey with an adhesive net that is formed in less than a second (Dendy, 1889; Concha *et al*., 2015). There is not a single general history of this branch of science called onychophorology; the word does not even appear in dictionaries at the time I write this (May 2020, the year of the COVID 19 pandemic), but it has been used for decades by the Centre International de Myriapodologie in Paris (https://myriapodology.org/). A definition is in order, so here is mine: **Onychophorology is a field of biology that studies the phylum Onychophora and all subjects related to onychophorans in all fields of research**. These animals are important in the study of evolution, but only interest a minuscule fraction of the scientific community. If all the onychophorologists active in the year 2020 were inside a bus, there would be many empty seats.

Here I summarize the historical trends, landmarks and researchers who have defined the history of Onychophorology for almost two centuries. This analysis of the literature is based on reading and selecting, based on my experience of many years in the field; from my personal perspective, I have chosen articles based on three criteria: being the first on a particular subject (e.g. Peters, 1880, the first to focus on leg variation); being comprehensive (the large monograph by Bouvier, still used today: Bouvier, 1905, 1907); or marking a decade (e.g. the article by Hill, 1950, which was followed by several other popularization articles around the world in that decade). The comprehensive bibliography that I used to select the papers listed here is the General Bibliography of Onychophora, available online under a Creative Commons license: https://zenodo.org/record/3698134#.XmEuBBP0nOQ

A new phylum is discovered among humble plants: 1826 to 1879

Other people probably saw onychophorans before Guilding (Costa Rican farmers refer to them as "slugs with legs"), but he was the first to describe them in a scientific paper (Guilding, 1826). It is hard to imagine the world in which he lived, where slavery was legal, Beethoven was still alive and no one knew that bacteria existed and caused disease. The Reverend Lansdown Guilding (1797-1831) was a British naturalist from the Caribbean island of Saint Vincent. He was mainly a botanist, a brilliant young

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man who corresponded with Darwin and Hooker; Hooker described him as "an arrogant, demanding, ambitious, and often conceited individual, all too ready to ask for unusual favors" (Howard & Howard, 1985). We know little else about Guilding, other than his first wife died "in childbed" leaving five children behind and that he died of unknown causes in 1831 while on vacation in another island (Howard & Howard, 1985).

Of the first and only onychophoran he ever saw, he wrote "it inhabits primary forests in Saint Vincent, often walks backward. If pressed, it releases viscous liquid from the mouth. Among the plants that I collected at the foot of mount 'Bon Homme´, I, astonished, discovered by chance the only specimen" (Monge-Nájera, 2019).

Seven years after the publication, and two after Guilding's death, two French zoologists, Jean Victor Victoire Audouin (1797-1841) and Henri Milne-Edwards (1800-1885; a student of Georges Cuvier) moved onychophorans from mollusks to annelids (Audouin & Milne-Edwards, 1833). Soon afterwards, the scientific world received the news that the animal was also found half a world away, in South Africa (Gervais, 1836). Some pioneers in the field appear in Figure 1.

During the 1840s the animals were studied by classical French luminaries Jean de Quatrefages and Émile Blanchard (Quatrefages, 1848; Blanchard, 1847). Blanchard also wrote the onychophoran chapter for the monumental book series *Historia Física y Política de Chile* edited by Claude Gay (1800-1873) a French naturalist who did natural history in Chile (Blanchard, 1849).

The raising of onychophorans to their own phylum was done in 1853 by Adolf

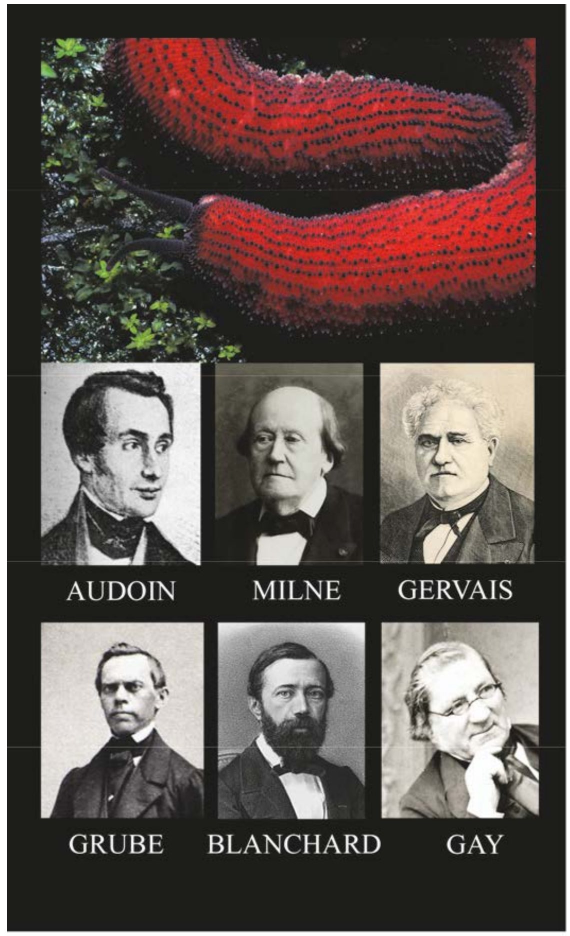

Fig 1. *A giant onychophoran from Costa Rica, and six pioneers of Onychophorology.*
Source: Alejandro Solórzano (worm) and, for the portraits, https://commons.wikimedia.org/

Eduard Grube (1812-1880), then a lecturer in zoology in Dorpat, Germany. Grube, a student of the famous von Baer, father of embryology, was himself a recognized authority on invertebrates and specialized in Mediterranean polychaete worms (Grube, 1853).

The 1860s were poor in production, characterized by short notes, but for the first time in Europe (because it had been done earlier in Chile) we see the inclusion of the new animals in a general zoology, in this case, the *Leipzig Handbuch der Zoologie* (Carus, 1863).

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The 1870s had a marked increase in productivity, mostly about anatomy, but also with a study about the embryology of *Peripatopsis capensis* (Grube, 1866) from South Africa (Gegenbaur, 1874) and an early attempt on the evolutionary history of the group and its possible relationship with the origin of insects (Wood-Mason, 1879).

They are all over the world! Bouvier enters the scene: 1880 to 1929

The already notable growth in publications from the previous decade was followed by an even more spectacular increase in the 1880s, with papers on anatomy, embryology, ecology, geographic distribution and behavior. It was also the time of the oldest thesis on these animals that I could find: a study on the anatomy and histology of "peripatus" from the University of Breslau, in what is now Wrocław, Poland (Gaffron, 1883).

The embryology papers were about species from South America (Sclater, 1888), South Africa (Balfour, 1883; Sedgwick, 1884) and New Zealand (Sheldon, 1887). Others dealt with compared anatomy of the brain (Saint-Remy, 1889) and the pharynx (Nicolas, 1889), the origin of metamerism (Sedgwick, 1884), and the first study focused on how the number of legs varies, this one from South Africa (Peters, 1880).

Ecological papers described the habitat of species from New South Wales (Bell, 1887) and New Zealand (Kirk, 1883), and Reverend Adam Sedgwick, Darwin's geology teacher, published the first monograph of species and their geographic distribution (Sedgwick, 1908a). Smaller papers expanded the known distribution of the phylum in Asia and Oceania (e.g. Horst, 1886).

The Onychophora report from the H.M.S.Challenger was also published in this decade (Anonymous, 1885) as well as the first study about the animal's movements (Haase, 1889).

The decade of 1890 was marked by many natural history notes, as more specimens were found around the globe; there was less embryology and more ecology.

A study compared ovum development in South Africa and New Zealand (Sheldon, 1890) and Prenant (1890) described the seminal vesicles, which would prove important in understanding evolutionary pressures upon these animals (Monge-Nájera, Barquero, & Morera, 2019f), just like hypodermic impregnation, which was first described by Whitman (1891). Curiously, this decade also produced work on the presence of corpuscles in the adhesive that the animal uses to hunt (Dendy, 1889); the adhesive would remain mostly forgotten as a study subject for over a century, until it became a leading-edge subject in the 21st century (Concha *et al*., 2015).

The first studies on onychophoran eggs and hatching (a still poorly known subject) were also written by Dendy (1889) and discussed by Fletcher (1891) in these late years of the 19th century.

Of particular interest is the fact that even at this early period, Caribbean onychophorans were so rarely seen that a note of the "rediscovery" of one was published by Grabham and Cockerell (1892), and that they were included in the reports of "noteworthy findings" by a natural history club that operated in the island of Trinidad (Anonymous, 1895).

Misidentification of species, still a problem in 2020, was mentioned as a problem over a century ago by Fletcher (1895) regarding Australian species. Other papers followed and dealt with the evolution of the onychophoran body (Goodrich, 1897) and

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their relationships with other invertebrates (Boas, 1898; Packard, 1898).

An unjustly forgotten author, Italian zoologist and alpinist Lorenzo Camerano (1856-1917), published several papers on the species of Panama and the Andes (e.g. Camerano, 1896), and around this time we also find the first papers by French zoologist Bouvier (Figure 2), the founding father of modern onychophorology, who dealt with their origin, evolution, variation and biogeography (e.g. Bouvier, 1902).

The 1900s started well, with the first paper on spermatogenesis (Montgomery, 1900) and the first one dealing about population density (Duerden, 1901). But undoubtedly what marks this period is the appearance of a large mass of literature by Bouvier, including evolution (Bouvier, 1902), and his monumental monograph (Bouvier, 1905, 1907), where he summarized all that was known about the animals, with emphasis on formal species descriptions. His species descriptions may be insufficient according to the standards of the 21st century, but are good if one considers the equipment and resources available to him at the time, and the fact that Eugène Louis Bouvier (1856-1944) was a busy man working mostly on crabs at the time. Son of a watchmaker, Bouvier moved up the social ladder through hard work, first as a teacher in a primary school, then by teaching about mosses and lichens in a Pharmacy School (Anonymous, 2012). It was only in 1895 that he got the chair of entomology at the National Museum of Natural History in Paris; the chair was previously occupied by Émile Blanchard (who had written the onychophoran section for the Chilean monograph mentioned earlier; Anonymous, 2012).

At the museum, Bouvier established what today would be called a "citizen science" program to enlarge the collections, and he also wrote a textbook of natural history for colleges that came out at the same time as his onychophoran monograph. He was then with the Prince of Monaco expedition, studying deep water crustaceans from the Sargasso Sea (Anonymous, 2012).

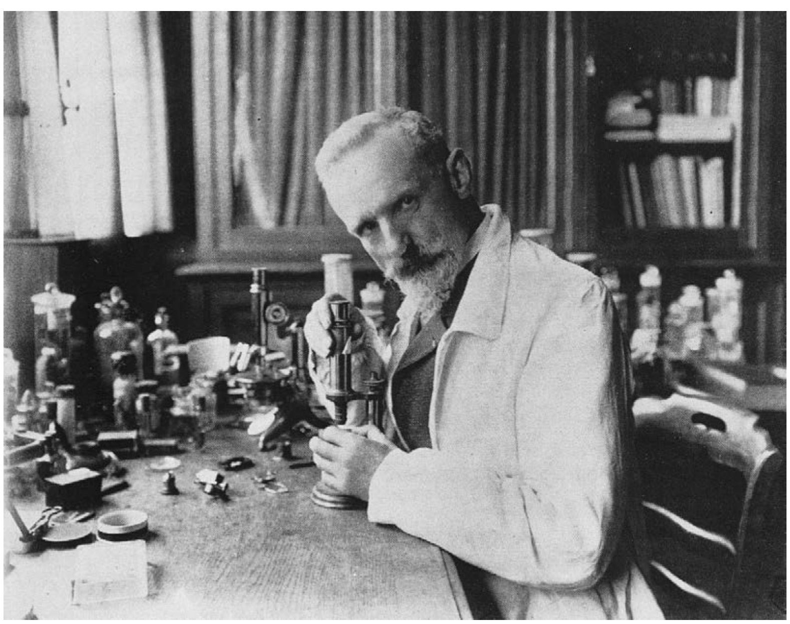

Fig. 2. *Eugène Louis Bouvier, who at the beginning of the twentieth century wrote the general monograph of the phylum Onychophora.*
Image source: https://commons.wikimedia.org/wiki/File:Louis_Eug%C3%A8ne_Bouvier.jpg

Later in his life, Bouvier wrote popular books about insect behavior (perhaps under pressure, because he had written little in the field of insects, despite keeping the entomology chair), but in science he is best remembered for his studies of crabs and onychophorans, which appeared

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to have been his real love (Blanckaert & Hurel, 2017).

This is also the decade in which researchers studied how onychophoran bodies process waste (Bruntz, 1903) and did more comparative studies, considering the parapodia of onychophorans and millipedes (Lankester, 1904); at the same time Sedgwick made the first attempt to associate the systematic relationships of onychophorans with their distribution around the world (Sedgwick, 1908a, b). This period included the work of C. E. Porter, in which he taught the natural history of onychophorans to students of the Naval Officers School of Chile, his lessons were later collected in the Chilean Journal of Natural History (Porter, 1905) and that probably are not part of the curriculum in naval schools today.

Their known distribution in Asia and Oceania was expanded in the decade of 1910 (Horst, 1910; Annandale, 1912); a curious observation on the discharge of mitochondria from the spermatozoon was reported (Montgomery, 1912) and Clark (1915) analyzed their world distribution, while the natural history and bibliography of the Chilean species were reviewed by two authors (Johow, 1911; Porter, 1917). An interesting finding from the time was that they could also be found in the forest canopy, according to Costa Rican microbiologist Clodomiro Picado (Picado, 1911).

The 1920s produced the first report of an onychophoran birth in captivity (for specimens kept in England: Dakin & Fordham, 1926); and the first study of their diet, from Chile (Janvier, 1928). Bouvier published an "answer to Claude-Joseph" about Chilean species (Bouvier, 1928), but most of the work from this period focused on the head parts of onychophorans: the eye (Dakin, 1921); infra-cerebral organs (Dakin, 1922), ventral brain organs (Duboscq, 1920) and the evolution of the head in relationship with other invertebrates (Crampton, 1928). This period even has a rare Soviet contribution, a general morphology of the brain, read during the Second Congress of Zoologists, Anatomists, and Histologists of the USSR (Fedorov, 1927).

A new look into physiology: 1930 to 1979

The 1930s had the first papers on Cambrian onychophorans (Hutchinson, 1930; Walcott, 1931), as well as a study of the local variation of a species which showed that, what appeared to be one species, could vary in color and in small body characteristics throughout its geographical range (Brues, 1935). A rare report on the parasites of onychophorans (Vincent, 1936) has not, unfortunately, been followed by much work afterwards, leaving this as an almost virgin territory for exploration.

This period is marked by the first papers by authors that would become better known in next decade, such as Marcus in Brazil and Manton in England (Marcus, 1937; Manton, 1937), as well as by Snodgrass classic work on the compared evolution of onychophoran and arthropod bodies (Snodgrass, 1938).

The decade of 1940 is important because it has the first studies about a region that would later become a center of onychophoran research, Central America; the articles mostly resulting from strong research activity in the Panama canal area during, and after, World War II (Brues, 1941; Dunn, 1943; Clark & Zetek, 1946; Hilton, 1946; Arnett, 1947).

The 1950s was characterized by articles in popular magazines from London (Hill, 1950), South Africa (Lawrence,

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1950), New Zealand (Wenzel, 1950), Germany (Zilch, 1955), New York (Milne & Milne, 1954; Alexander, 1958), Philadelphia (Bellomy, 1955), Malaysia (Hendrickson, 1957) and Belgium (Darteville, 1958). All of these popular accounts highlighted the use of the adhesive secretion to capture prey, the strange distribution on the animals in isolated regions but always within the same latitudinal belt, and what at the time was considered as their position as missing links between annelids and arthropods.

Studies from the period considered how onychophorans produce leukocytes (Arvy, 1954), "muscle pharmacology" and possible uses of these animals in pharmacology (Ewer & van der Berg, 1954; Trindade, 1958); crural gland microanatomy (Gabe, 1956); brain secretions (Sanchez, 1958; Mendes & Sawaya, 1958); oxygen consumption in relation to size, temperature and oxygen tension (Mendes & Sawaya, 1958) and the formation of sperm cells (Tuzet & Manier, 1958; Gatenby, 1959). Perhaps the most innovative study from this decade was the first biogeographic analysis that explained the division into two families, as the results of historical separation at the time of Gondwana and Laurasia (Vachon, 1954).

In the 1960s, Brazil produced the first study of DNA (Simoes, Marques da Silva, & Schreiber, 1964), the first observation with the electron microscope (Lavallard, 1965), and detailed studies on molting (Campiglia, 1969). Reassessments of the fossils *Xenusion* (onychophoran or coelenterate?) and *Aysheaia* are also from this period (Tarlo, 1967; Hutchinson, 1969).

The 1970s were characterized by an increase in anatomical and physiological work. The anatomy of the body wall (Birket-Smith, 1974), giant fibers in the ventral nerve cord (Schürmann & Sandeman,

Fig. 3. *The electron microscope presents the onychophoran surface more clearly than the light microscope and greatly facilitates taxonomic work. This is an example from the giant species that lives in the Caribbean of Costa Rica.*
Source Morera-Brenes & Monge-Nájera (2010).

1976), sarcoplasmic reticulum of smooth muscle (Heffron, Hepburn & Zwi, 1976), the sensilla (Storch & Ruhberg, 1977), the salivary glands (Ruhberg, 1979), and synaptic zones of nephrids (Storch, Alberti, Lavallard, & Campiglia, 1979).

Physiology studies analyzed cuticular chemistry and hardening (Krishnan, 1970); skeletal collagen (Hepburn & Heffron, 1976); enzymic activities of the smooth body-wall muscle (Heffron, Hepburn, & Zwi, 1977); the presence of monoamines in the nervous system (Gardner, Robson, & Stanford, 1978), and neuromuscular transmission (Hoyle & del Castillo, 1979).

Attempts were also made to disentangle systematics by comparing isolated aspects, such as locomotion (Manton, 1972), cuticle (Hackman & Goldberg, 1975), compared anatomy (de la Fuente, 1975) hemolymph (Gowri & Sundara Rajulu, 1976), and the Golgi complex (Locke & Huie,

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1977). These attempts had little chance of succeeding because the resulting phylogenetic trees produced by any particular character were incompatible with the trees produced by other characters.

This is also the time of the first general study about the habitat (Lavallard, Campiglia, Parisi Alvares, & Valle, 1975). Lawrence (1977) summarized research in South Africa, while Peck (1975) reviewed the species of the American continent and Delle Cave and Simonetta (1975) added new information on the morphology and taxonomic position of the fossil *Aysheaia*.

An exciting period of unveiled secrets and conservation worries: 1980 to 2020

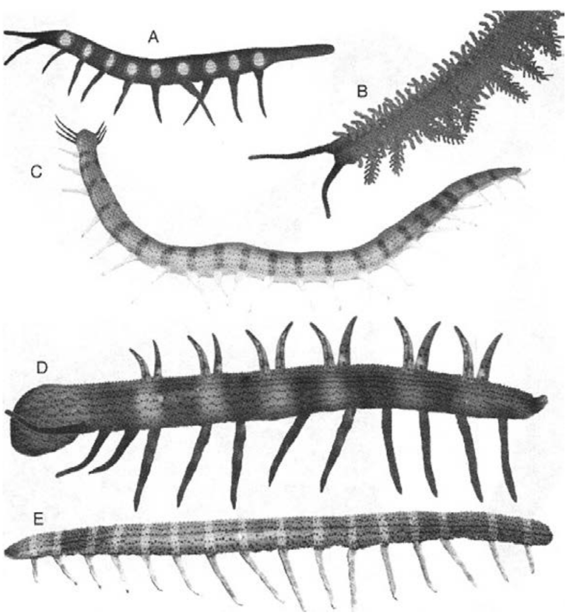

Fig. 4. *Digital reconstructions of fossil onychophorans (Monge-Nájera & Xianguang, 2002). A: Microdictyon sinicum, B: Onychodictyon ferox, C: Cardiodictyon catenulum, D: Hallucigenia fortis, E: Luoishania lingicruris. Not to scale.*

Much study was done in the 1980s on the anatomy of onychophorans: musculature and innervation (Hoyle & Williams, 1980); morphometry of the tracheal system (Pereira, Bicudo & Campiglia, 1985); the application of scanning electron microscopy to systematics (Read, 1988); and the curious cephalic pits and palps of some Australian species (Ruhberg, Tait, Briscoe, & Storch, 1988).

This period is also marked by the first strongly evolutionary focus on their reproduction (Morera, Monge-Nájera, & Saenz, 1988; Havel, Wilson, & Hebert, 1989), and seems to also be the first time that onychophorans appear in the IUCN Invertebrate Red Data Book (Wells, Pyle, & Collins, 1983). New possible onychophoran fossils were reported from Illinois (Thompson & Jones, 1980) and France (Rolfe, Schram, Pacaud, Sotty, & Secretan, 1982), and the second monograph on the family Peripatopsidae (Ruhberg, 1985) was also published in this period.

The 1990s was characterized by research in genetics and systematics. RNA and DNA sequences were combined with morphological data to assess systematics, using antennal circulatory organs (Pass, 1991; de Haro, 1998), and a paper recommended rejection of the "Uniramia" hypothesis, in which Sidney Manton joined Hexapoda, Myriapoda and Onychophora as a single monophyletic group (Wägele, 1993).

Overall, researchers in several regions of the world discovered the large genetic variation hidden in what seemed to be a relatively simple phylum (Grenier, Garber, Warren, Whitington, & Carroll, 1997; Curach & Sunnucks, 1999; Hebert *et al.*, 1991; Morera-Brenes, Herrera, Mora, & Leon,1992; Ballard *et al.*, 1992; Briscoe & Tait, 1995; Gleeson, 1996).

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The second area of this decade, by productivity, was ecology and biogeography. Findings from Singapore showed that recent introductions could complicate the reconstruction of onychophoran historical biogeography (van der Lande, 1991), and computerized techniques were used to understand how climate and paleo-vegetation define their current world distribution (Monge-Nájera, 1994a), as well as how climate affects body characteristics (Monge-Nájera, 1994b).

This decade was also marked by the first detailed study of the geographic variation of habitats (Monge-Nájera & Alfaro, 1995), and a model of onychophoran biogeographic history from the Jurassic through the Pliocene (Monge-Nájera, 1996). Other studies were a comparative analysis of evolutionary trends in onychophorans and scorpions (Monge-Nájera & Lourenco, 1995), and the first in-depth studies of the onychophoran adhesive secretion, with electrophoresis (Mora, Herrera, & León, 1996); chemical characterization (Benkendorff, Beardmore, Gooley, Packer, & Tait, 1999) and a comparison with arthropod silk secretions (Craig, 1997).

In the field of conservation, the finding of a single large aggregation in New Zealand (Harris, 1991) and an unconfirmed estimate that the population of a single species reached millions, led to the unjustified generalization that these animals "are not rare" (Mesibov, 1998), an error that can lead to dangerous implications for conservation (Monge-Nájera, 1995).

In ethology, this period is marked by the first experimental study of general behavior (Monge-Nájera, Barrientos, & Aguilar, 1993) and of the pheromonal function of crural glands (Eliott, Tait, & Briscoe, 1993).

In fossils, publications included the reinterpretation of *Hallucigenia*, now thought to be an onychophoran that was originally interpreted upside-down by Morris (1977) and corrected by Hou and Bergström (1991); and the opposite case, a Palaeozoic "onychophoran" reinterpreted as a stalked echinoderm (Rhebergen & Donovan, 1994). But perhaps the most unfortunate error of the time was G. Poinar's creation of new "onychophoran families" with specimens that lacked the body parts needed to define families (Poinar, 1996, 2000).

This decade was also marked by the first "modern synthesis" that proposed evolutionary explanations for the origin of all known onychophoran characteristics and summarized their history since the Cambrian, including anatomy, physiology, behavior, distribution, reproduction and systematics (Monge-Nájera, 1995).

The decade of 2000 had an eclectic production. Papers dealt with how population structure and genetic constitution are related (Laat, 2006; Santana, Almeida, Alves, & Vasconcellos, 2008); the rediscovery, after more than a century, of *Oroperipatus eisenii* in Mexico (Cupul-Magaña & Navarrete-Heredia, 2008); and a revival of the ancient debate about the origin of head parts (e.g. Eriksson & Budd, 2003; Mayer & Whittington, 2009).

In paleoecology, a quantitative study of an exquisitely preserved Cambrian community from China found similarities with an extant community in Costa Rica (Monge-Nájera & Hou, 2000), and experimental taphonomy identified which fossil onychophoran "structures" are real and which can be just artifacts (Monge-Nájera & Xianguang, 2002).

Other reports included the use the head to insert the spermatophore (Tait &

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Norman, 2001) and that female-dominated hierarchies (Reinhard & Rowell, 2005).

This decade was also marked by the first study of the inflammatory process in onychophorans (Silva, Coelho, & Nogueira, 2000) and the identification of immune inducible genes (Altincicek & Vilcinskas, 2008), but perhaps the most innovative work was the first study of the physics of the adhesive secretion (Jerez-Jaimes & Bernal-Pérez, 2009).

The most recent decade, the 2010s, has been marked by the discovery of the largest species ever and by the first study of the mechanism by which onychophorans produce their adhesive "hunting nets" (Morera-Brenes & Monge-Nájera, 2010). The adhesive skin exudate of some frogs was found to be similar to that of onychophorans (Graham, Glattauer, Li, Tyler, & Ramshaw, 2013), and the adhesive net mechanism was finally cracked and found to be produced by passive hydrodynamic instability (Concha *et al*., 2015).

Other studies from this time dealt with the nanostructures of the solidified adhesive secretion (Corrales-Urena *et al*., 2017), the assembling of fibers by electrostatic interactions in phosphoproteins (Baer, Hänsch, Mayer, Harrington, & Schmidt, 2018), and a mimic of onychophoran skin, which is slippery to the adhesive, produced with microporous porphyrin networks (Ryu *et al*., 2018).

In the field of genetics, the genome size and chromosome numbers were reviewed (Jeffery, Oliveira, Gregory, Rowell, & Mayer, 2012), and new morphological characters were added to the arsenal used in taxonomy (Oliveira, Read, & Mayer, 2012). Other studies dealt with genes related to head and eye development (Eriksson, Samadi, & Schmid, 2013); endoderm marker-genes during gastrulation and gut-development (Janssen & Budd, 2017); the conserved and derived cell death in embryonic development (Treffkorn & Mayer, 2017); and the report that fluorescence *in situ* hybridization of telomers indicate chromosome fusions (Dutra, Cordeiro, & Araujo, 2018).

In this decade, onychophorans were found in unexpected places, like Vietnam (Bai & Anh, 2012), lava tubes (Espinasa *et al*., 2015) and urban vegetation (Barrett, 2013), and the first model to explain and predict their survival in highly disturbed habitats, based on their size and habits, was published (Monge-Nájera, 2018). The only tropical African species was collected again after more than a century (Costa & Giribet, 2016), and the period was also marked by advances in the study of onychophoran genetics and conservation in Brazil (Lacorte, De Sena Oliveira, and Da Fonseca, 2011; Costa, 2016; Cunha *et al*., 2017; Costa *et al*., 2018).

Costa Rica became the first country to fully map the distribution of its onychophorans and to indicate where they were preserved and the strength of conservation measures for each species (Morera, Monge-Nájera, & Mora, 2018). The first field monitoring study covering "several years" found that the relationship between onychophoran hunting activity, humidity and light, was not as expected (Barquero-González, Morera-Brenes, & Monge-Nájera, 2018). Food hiding, parental feeding investment and ontogenetic diet shift were also reported for the first time for the whole phylum (Barquero-González, Vega-Hidalgo, & Monge-Nájera, 2019).

A new branch of Onychophorology was also born in this decade, the Ethnobiology of Onychophorans, with the first study of onychophoran representations in folklore and art (Monge-Nájera

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& Morera-Brenes, 2015). The period ends with a series that proposes evolutionary explanations for several previously unexplained anatomical, physiological, behavioral and ecological characteristics, such as why onychophoran spermatozoa swim for years, why some Australian males have bizarre heads, why there are no onychophorans in Cuba and why ovoviviparity may be the ancestral form of reproduction in velvet worms (Monge-Nájera, Barquero, & Morera, 2019a, b, c, d, e, f, g).

In a period of climatic change and fear of mass extinctions, in which undescribed species need protection and long term conservation, Sosa-Bartuano and his colleagues suggested the use of common names, an idea taken from bird watchers, to rapidly and cheaply distinguish new onychophoran species until they are formally described (Sosa-Bartuano, Monge-Nájera, & Morera-Brenes, 2018).

CONCLUSION

In these two centuries, Onychophorology has been built by contributions from many men and women. A few stayed long enough in the field to write numerous contributions (e.g. Barquero-González, Bouvier, Campiglia, Daniels, Mayer, Monge-Nájera, Morera-Brenes, Lavallard, Oliveira, Ruhberg, Sedgwick, Storch, Sunnucks, & Tait), but we ought the bulk of our knowledge to the mass of men and women who entered the field only briefly. There is a lesson here: for Onychophorology to prosper, we need to attract as many researchers from other fields as possible, even if each produces only one paper: the future of Onychophorology will be born in their minds.

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AUTHOR CONTRIBUTION STATEMENT

The total contribution percentage for the conceptualization, preparation, and correction of this paper was J.M.N. 100 %.

DATA AVAILABILITY STATEMENT

The data supporting the results of this study are fully and freely available here: https://zenodo.org/record/3698134#.XmEuBBP0nOQ.

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