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Review Article

George Poinar and the foundations of entomopathogenic nematology and amber paleobiology

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Abstract. George Poinar Jr. is widely recognized as a pioneering biologist, whose interdisciplinary career profoundly advanced insect nematology and amber paleobiology. His fundamental studies during the 1960s and 1970s on the entomopathogenic nematodes *Steinernema* and *Heterorhabditis* clarified their life cycles, infection pathways, bacterial symbioses, and transformed them into recognized biological control agents, establishing entomopathogenic nematology as a cornerstone of applied insect pathology. Similarly, his groundbreaking research on amber inclusions revealed evolutionary histories of insects preserved for millions of years, inspiring sci-fi stories, and standardizing paleobiological methodologies. Through bridging the modern ecological interactions with ancient evolutionary narratives, Poinar exemplified how innovation and careful observation can reshape scientific fields, leaving a lasting legacy in taxonomy, ecology, and biological control.

Keywords: Amber, Insect pathology, Nematology, Palaeoentomology, Pioneer entomologists

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We present a brief acknowledgment of the eminent biologist George Poinar Jr., whose remarkable career was foundational to advancing insect nematology and amber paleobiology. Long before his amber studies brought him global attention, Poinar established himself as one of the pioneering figures of insect nematology. His research during 1960s and 1970s laid the essential groundwork for what would later become a central branch of biological control science. His early investigations on the insect pathogenic nematodes, *Steinernema* and *Heterorhabditis* revealed the complexity of insect–nematode interactions with unparalleled clarity. He systematically documented the life cycles, infection pathways, and symbiotic bacterial partners of these nematodes at a time when much of the field remained unexplored. Only a few researchers have influenced the study of insects across such a broad temporal scale, examining the ecological dynamics of living insects and the evolutionary histories preserved in species that inhabited Earth, tens of millions of years ago. His studies went beyond the taxonomy of these organisms, laying both theoretical and practical foundations that transformed nematodes into effective biological control agents. Many of the concepts and methods used today in applied insect pathology and entomopathogenic nematology, as described by Poinar, continue to serve as reference points in taxonomy, ecological research, and pest management.

As entomology expands into molecular, ecological, and computational domains, recognizing figures whose insights enabled such progress remains crucial. Poinar's career exemplifies the impact of interdisciplinary vision, illustrating how careful observation, intellectual curiosity, and methodological innovation can transform entire areas of science. This paper provides a brief overview of his work, the subsequent advancements of entomopathogenic nematology, and why his contributions still matter for the development of insect pathology as a branch of biological pest control.

Entomopathogenic nematodes in biological control

Agricultural pest control underwent significant changes in the last century, driven by the discovery of chemical pesticides. Crop yields improved enormously; however, recognition of the adverse effects of pesticides resulted in the emergence of environmental efforts worldwide, that encompass various approaches to achieving biological

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control. Entomophagous microbial agents, and entomopathogenic nematodes (EPNs) are among the most effective biocontrol agents with a long list of products worth over $100 million annually worldwide. This market is expected to grow by 10% over the next ten years (Ramakuwela *et al*., 2025). Among microbial control agents (including EPNs), *Bacillus thuringiensis* leads in the number of products and the range of applications in different parts of the world. Similarly, the use of EPNs also increased during the last 50 years, and today they are used in agricultural, horticultural, and urban ecosystems (Ramakuwela *et al*., 2025).

Studies on EPNs began 100 years ago and have three distinct periods, according to Stock *et al.* (2025). During the initial phase (1923–1950), nematode discoveries were largely incidental, with research primarily directed toward describing species and resolving taxonomic issues. In 1917, Anton Krausse encountered an outbreak of webworm larvae on spruce. Some of the larvae were infected by nematodes, which he eventually sent to Gottold Steiner (later named the father of insect nematology), who described the nematode as a new species, *Aplectana kraussei* (Krausse, 1917; *Steiner,* 1923). A Brazilian researcher, Lauro Travassos considered the genus classification mistaken, first proposing *Steineria* and subsequently *Steinernem*a (Travassos, 1927). Steiner, who later emigrated to the USA, also described the second named EPN species *Neoaplectana glaseri* in 1929 (now *S. glaseri*). This nematode was collected from Japanese beetle larvae by R.W. Glaser (Glaser & Fox, 1930), who studied its effectiveness against white grubs on golf courses in New Jersey, USA. In mid–late 1930s, he began propagating the species in artificial culture media (Glaser, 1940) and his team documented its effectiveness on the Japanese beetle and several other species. In the following years, they released *S. glaseri* in the field as the first attempts of innundative control by EPN (Glaser *et al*., 1935). Istvan Filipjev, a Russian scientist, identified *Steinernema feltiae* (=*Neoaplectana feltiae*, =*Neoaplectana bibionis*) from a noctuid moth larva (*Agrotis segetum*) (Filipjev, 1934). He noticed similarities among *Steinernema* and *Neoaplectana*, so he created a subfamily of Steinernematinae in the Oxyuridae family where he placed both genera. After five decades, all species of *Neoaplectana* were transferred to the *Steinernema* genus, when Wouts (1982) contended there were no morphological differences between these two genera (Nguyen & Hunt, 2007).

A second recognizable era of exploration spanned roughly three decades (1950s–70s) during which the fundamental basis of EPN Biology was revealed. In 1955, *Steinernema carpocapsae* (Weiser) was isolated from codling moth larvae by both Jaroslav Wieser in Bohemia, Czech Republic, and by Dutky and Hough (who designated the isolate DD 136) in the USA (Dutky & Hough, 1955). Dutky (1959) proposed the role of bacteria in protecting the cadaver. Several years later, Poinar and Thomas (1965) described *Achromobacter nematophilus* from *S. carpocapsae,* the first known symbiotic bacteria from an EPN. Poinar and Thomas characterized the vesicle containing the bacterium the following year by light and electron microscopy (Poinar & Grewal, 2012). Poinar and Thomas (1966, 1967) also elucidated the dual role of symbiotic bacteria in inducing host mortality and supporting nematode growth and development. A further vital discovery in the following decade was the description of the family Heterorhabditidae (Poinar, 1976). The type species of this family, *Heterorhabditis bacteriophora*, was collected from the pupae of a butterfly species in Australia (Poinar, 1976). Poinar & Thomas (1965) described the symbiotic bacterium from *S. carpocapsae*, naming it *Achromobacter nematophilus*. Two years later, Poinar &Thomas (1967) erected the genus *Xenorhabdus*, to revise *A. nemtophilus* as *X. nematophilus* and described the bacterium associated with *H. bacteriophora* as *X. luminescens* (later transferred to *Photorhabdus luminescens*). Among other notable discoveries during this period, those of Bedding and Akhurst are perhaps the most durable. In 1975, they described the *Galleria* baiting technique, a simple yet widely used method for the collection of EPNs. They also presented the cross-breeding method used to test the biological species concept in *Steinernema* for species delimitation. They gained further international recognition for their groundbreaking research that identified the nematode *Deladenus siricidicola* (now known as *Beddingia siricidicola*) as an exceptionally effective biological control agent against the wood-boring wasp, *Sirex noctilio* (Bedding & Akhurs, 1974; Bedding & Iede, 2005; Bedding, 2009). A fitting bookend to this period was the publication of "*Nematodes for Biological Control*" by Poinar (1979), the inaugural comprehensive treatise on the subject (Fig.1).

Fig. 1. The books published by George O. Poinar on the Entomopathogenic nematodes and Paleobiology.

The "Golden Age" of Insect Nematology (Stock *et al.*, 2025), expands from 1980 to the end of the twentieth century. The study of the bactohelminth complex expanded across various fields (Goodrich-Blair, 2007; Goodrich-Blair & Clarke, 2007), the number of studies on the efficacy of EPNs against various pests increased, new products entered the market (Georgis, 1992), and the backbone documents on the ecology (Grewal *et al.*, 1994), behavior (Lewis *et al.*, 1992), taxonomy (Nguyen & Hunt, 2007; Hunt & Nguyen, 2016), mass production (Ehlers, 2001), and formulation of EPN (Shapiro-Ilan *et al.*, 2025; Nickel *et al.*, 1994) was largely elaborated. Two world symposia, both organized by Harry Kaya and Randy Gaugler, were held during these years: the first in 1989 at Asilomar, California, and the second in 1995 at the University of Hawaii (Poinar & Grewal, 2012). In 1980, Raymond Akhurst discovered the phenomenon of phase diversity in *Xenorhabdus*, which is critical in the mass production of the nematodes (Akhurst, 1980). His long term and continuous collaboration with Noel Boemare led to significant progress in understanding bacterial phase diversity and in facilitating the identification of the species and strains. With the increase in the number of EPN species in two nematode families, it became apparent that the classical methods that relied on characteristics of males and larvae were inadequate for species differentiation. A species concept and molecular methods were proposed (Adams, 1998), and a widely adopted guide for using DNA sequences as an essential basis for EPN studies was published (Hominick, 1997). Poinar's efforts at this time shifted noticeably to laboratory and field trials exploring the extent to which EPN can function effectively for insect management (Georgis *et al.*, 1982) (Figs 2, 3). He also published broadly on EPN biology, touching topics such as bioluminescence (Poinar *et al.*, 1980), effects of soil moisture and temperature on infectivity (Byers & Poinar, 1982; Georgis & Poinar, 1983), and interactions with organisms other than insects such as bacteriophages, other viruses, bacteria and nematophagous fungi (eg., Poinar *et al.*, 1989).

It was during this period too, that readers beyond the scientific world began to learn about Poinar's discoveries. Always intrigued by the amazing opportunity provided by amber inclusions to recover evidence traditionally missing from the evolutionary record, he published, beginning in 1977, the descriptions of several hundreds of species of insects, plants and microorganisms trapped in amber dating to the Cretaceous Period. He and his wife, the entomologist Roberta Poinar, wrote "A Life in Amber" describing a 45-million-year-old ecosystem based on Dominican amber, one in a series of five popular books about the secrets contained in that substance (Fig.4). The book "Jurasic Park" had its genesis in a 1982 Science paper Poinar published with Roberta describing fly organelles in amber and a 1993 Nature paper, published with his son Hendrik, describing efforts to sequence fossilized weevil DNA (Poinar & Hess, 1982; Cano *et al.*, 1992) (Fig. 5). After nearly half a century, he continues regularly reporting discoveries, most recently a description of nematode ectoparasites of ancient pseudoscopions (Poinar, 2025).

Applications and EPN-based commercial products

The new millennium has witnessed notable achievements in the discovery of new steinernematid and heterorabditid species (Adams & Nguyen, 2002; Hunt & Nguyen, 2016), the natural role of EPNs (Dilman & Sternberg, 2012; Griffin, 2015; Blanco-Pérez *et al.*, 2025), their utility as biological models (Campos Hererra *et al.*, 2012; Stock & Hazir, 2025), and their potential for pest management (Shapiro & Lewis, 2024). Some of the key figures involved in the discovery, development and use of EPNs during the past century are shown in Fig. 2-3.

New formulations to deliver EPN have been developed employing alginate and polyacrylamide gels, charcoal, clay, diatomaceous earth, paste, peat, polyurethane sponge, vermiculite, and water-dispersible granules (Shapiro *et al.*, 2025). The methodology can vary widely depending on the availability of the resource material. In some countries, such as China, Rwanda, Kenya, and Korea, semi-solid production systems for nematode propagation in abiotic environments have been employed (Holmes *et al.*, 2015; Ramakuwela *et al.*, 2025). However, most nematode production for biological products is done in bioreactors (Ramakuwela *et al.*, 2025).

The development of entomopathogenic nematodes (EPNs) reflects a century of progress in pest management. Advances in genomics, gene modification, precision farming, and material technology promise improved strain selection, efficacy, and broader crop applications. Collectively, EPNs exemplify sustainable pest management, with ongoing innovation ensuring their continued role in agriculture, forestry, and ecosystem resilience. Currently, 212 nematode-based biological products are produced and marketed around the world (Ramakuwela *et al.*, 2025). The species employed are dominated by *S. feltiae* (68), *S. carpocapsae* (57), and *H. bacteriophora* (49), with the manufacturing companies mainly located in Europe (Netherlands, Spain, Germany, Switzerland, England, Poland, Russia), the Americas (Canada, the United States, Colombia, Costa Rica), and Asia (China and Korea) (Dolinski *et al.*, 2012). In the African continent, South Africa and Kenya have also made initial efforts to develop EPN products (Hatting *et al.*, 2019; Duncan & Malan, 2024). There are also sectors of the production process in India and Cuba on living hosts (San-Blas *et al.*, 2019; Rodríguez, 2015). However, numerous countries, particularly in Asia and Africa have no local EPN production. High labor costs in Europe and North America make the utilization of those products economically impractical in less economically developed. Accordingly, semi-industrial production approaches should be established locally to ensure affordable access for the growers. New technologies such as the application of robotics and artificial intelligence to optimize the myriad conditions affecting the yield of bioreactors are critical in order to decrease product cost (Ramakuwela *et al.*, 2025). Corn represents one of the few major field crops for nematode application in some countries; however, pests on several other crops are also anticipated to be targeted in the coming years when costs and availability of EPN products become more favorable. Although these nematodes can play an important role in organic production, this issue has been inadequately addressed in the literature and related forums (Koppenhöfer *et al.*, 2020). Even in forest ecosystems, given the challenge posed by climate change, the successful application of these agents in Italy has shown potential for EPN integration into pest management programs (Ramakuwela *et al.*, 2025).

Fig. 2. Key scientists who have had leading role in the field of entomopathogenic nematology from 1923 to the present. **1.** Gottold Steiner; **2.** Lauro Travassos; **3.** Rudolf Glaser; **4.** Jaroslav Wieser; **5.** George Poinar; **6.** Robin Bedding, **7.** Raymond Akhurst; **8.** Randy Gaugler; **9.** Harry Kaya 10. Lawrence Lacey; **11.** Parwinder Grewal; **12.** William Hominick; **13.** Zdeněk Mráček; **14.** Itamar Glazer; **15.** Roman Georgis; **16.** Patricia Stock.

Fig. 3. Key scientists who have had leading role in the field of entomopathogenic nematology from 1923 to the present. 1. Ralf-Udo Ehlers; 2. Edwin Lewis; 3. Noel Boamare; 4. D. T.M. Manjunath; 5. Nobuyoshi Ishibashi; 6. David Shapiro-Ilan; 7. Albrecht Koppenhöfer; 8. Khong Nguyen; 9. Richou Han; 10. Sergei Spiridonov; 11. Christine Griffin, 12. Ann Burnell; 13. Heidi Goodrich-Blair; 14. Antoniette Malan;15. Mary Barbercheck, 16. Adler Dilman, 17. Raquel Campos-Hererra, 18. Selçuk Hazır, 19. Vladimir Půža, 20. Eustachio Tarasco.

Outlook for entomopathogenic nematodes

Beyond the overarching need to lower product cost and availability, key challenges remain to be investigated. Species diversity (currently more than 120 known EPN species) and biogeography should be addressed broadly. The various populations and species of EPNs collected from different parts of the world should be consolidated into living collections to prevent the extinction of known and undiscovered species and facilitate access to them by researchers. Accurate identification of entomopathogenic nematodes requires comprehensive molecular data, incorporating at least two loci, a nuclear gene (ITS or 18S), and mtDNA markers such as COI and ND4. For *Heterorhabditid* species, less sequence variation in ITS, D2-D3, and 18S genes, requires additional DNA markers, such as cox1, nad-4, fan-1, and ppfr-1 (Puzza *et al.*, 2025; Machado *et al.*, 2025). For *Steinernema* species, some genes, such as the D2-D3, provide low resolution of phylogenetic relationships, so markers such as 12S and COI, are recommended. For both genera, the whole-genome sequencing approach will be helpful. In the case of symbiotic bacteria, whole-genome sequencing is preferable, although multi-locus information can also be used for the identification (Puzza *et al*., 2025). When characterizing either nematodes or their associated bacteria, both organisms should be considered as a symbiotic entity. Recent methodological advances have significantly improved our understanding of nematode interactions with soil biota and plants (Blanco-Pérez *et al*., 2025). In the future, more focused application of OMICs disciplines combined with comprehensive data processing will enable more precise prediction of nematode function and performance across various ecosystems.

The commercial formulations of EPNs allow them to be used in combination with other inputs, such as fertilizers or other pest control agents. The integration of EPN with routinely used inputs will increase their cost-effectiveness, as would methods to employ them using precision agriculture methodology (Grewal *et al*., 2012; Ulu & Erdoğan, 2023).

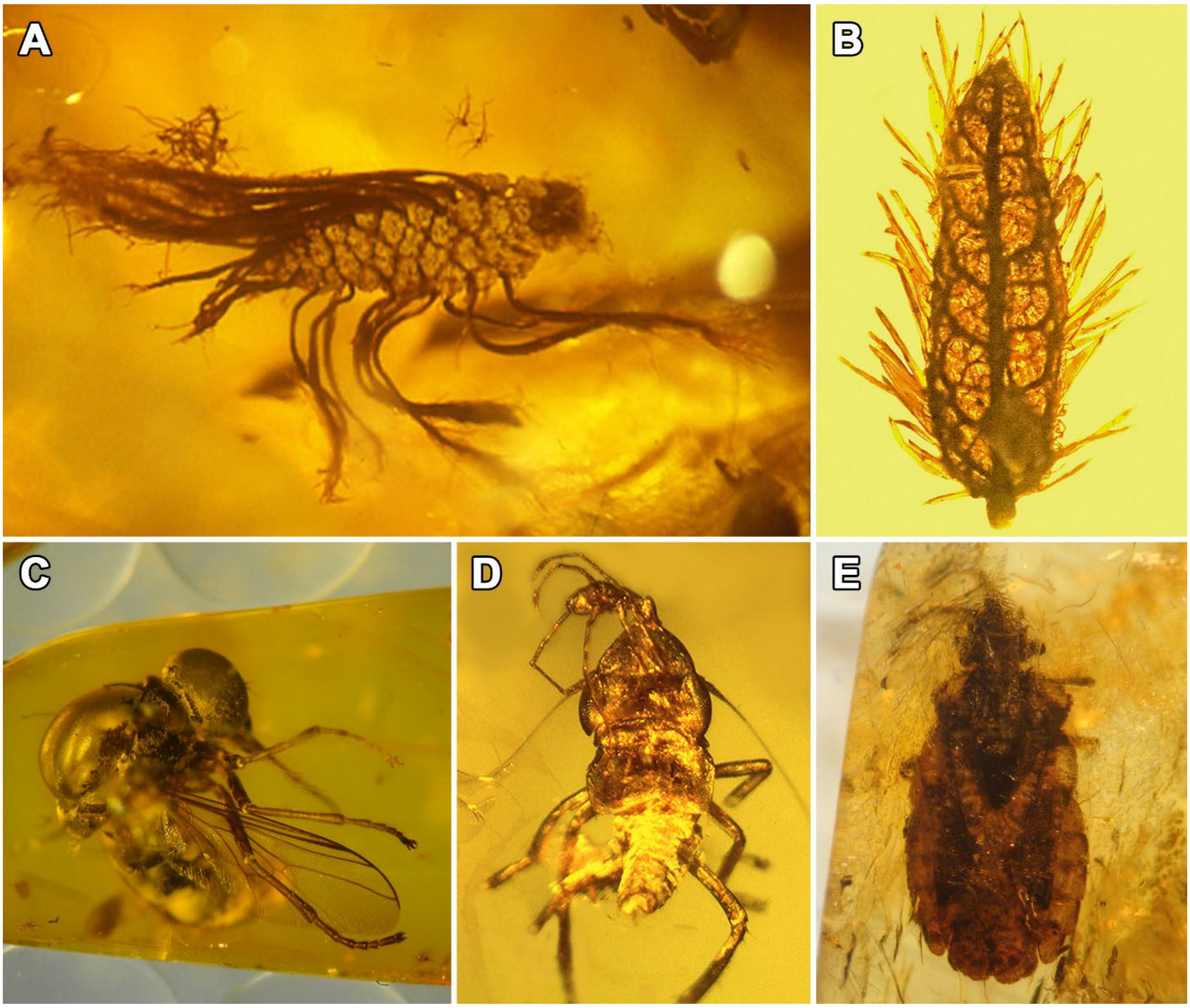

Fig. 4. The representative fossil taxa described by G. Poinar. A. *Gymnosperm*, Coniferales (Pinaceae, *Pinus* sp.); B. Possible fern leaf (Polypodiales, Polypodiaceae); C. A bibionid fly (Diptera, Bibionidae); D. A mite (Acari) on a leafhopper nymph (Hemiptera, Cicadellidae); E. A flat bug (Hemiptera, Aradidae).

Fig. 5. Prof. G. Poinar and his wife, Roberta Poinar, who collaborated with him in Amber paleontology studies and electron microscopy.

Product inconsistency ranks along with high cost as the main obstacles to the use of EPN for pest management. Superior strain/species selection and strain improvement (virulence, persistence in the environment, product shelf life) have been widely reported and should be continued in combination with powerful technologies such as RNAi and CRISPR (Mahushe *et al*., 2023; Ireri & Cao, 2025). Novel materials such as anti-desiccants, chitosan-based formulations, encapsulated material using alginate beads coated with lipid membranes, Super absorbent formulation (Zeba and Nu films), and silica-based formulations are among the materials used to improve EPN performances (Makirita *et al*., 2020; Shapiro-Ilan *et al*., 2025).

Concluding remarks

We prepared this note as part of an expanded JESI mission to document global entomological information and showcase scientific heritage and pioneering contributions. We intend to provide our readers with information about the evolution of insect nematology that may help to identify avenues for advancing biological control. We hope that readers find inspiration from the extent to which two scientific disciplines were shaped by George Poinar's visión, passion, and perseverance, and that students will recognize the potential rewards of delving so deeply into research and education.

Notable Discoveries and Contributions by George Poinar Jr.

Entomopathogenic nematology

Identification of the symbiotic bacterium (under the name *Achromobacter nematophilus*) associated with *S. carpocapsae*

Localizing the vesicle containing the bacteria in the infective juveniles using light and electron microscopy.
Exploring the role of the symbiotic bacterium in the development of the entomopathogenic nematode and the death of the host.
Description of the symbiotic bacteria of the genus *Xenorhabdus*.
Description of the Heterorhabditidae family and its symbiont, *Xenorhabdus luminescens*.
Taxonomic revisions using hybridization tests and morphological analyses to identify species of the genus *Steinernema*.
Innovative method for mass rearing of nematodes using axenic culture and addressing phase variations.
Discovery of the bioluminescent ability of *Photorhabdus*, a symbiont of Heterorhabditidae.

Palaeoentomology

Discovery of several new taxa from insects, nematodes, plants, fungi, protists and prokaryotes.
Successful DNA extraction from a Lebanese weevil in amber, 125 million years old.
Application of microtomy and applied chemical clearing techniques to study amber.
Discovery of a new plant species (*Strychnos electri*) with about 45-million-year-old amber (Poinar & Struwe, 2016).
Cataloging more than 10,000 amber inclusions, mainly on arthropods and plant materials from the Eocene to Miocene epochs.

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Author's Contributions

Javad Karimi: Conceptualization; compiling the background data; drafting the manuscript; final editing; **Ehsan Rakhshani**: Conceptualization, revising the text and sorting the illustrations and **Larry Wayne Duncan**: Conceptualization; drafting the manuscript; final editing.

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Consent for Publication

Not applicable

Conflict of Interest

The authors declare that there is no conflict of interest regarding the publication of this paper.

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جورج پوینار و پیشرفت مطالعات نماتدهای بیمارگر حشرات و زیست باستان‌شناسی کهربا

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چکیده: جورج پوینار، حشره شناسی پیشرو است که با تسلط بر حشره‌شناسی، نماتودشناسی و دیرینه‌شناسی، نقش چشمگیری در توسعه دیرینه‌شناسی کهربا داشته است. مطالعات بنیادی او در دهه‌های ۱۹۶۰ و ۱۹۷۰ روی نماتدهای *Steinernema* و *Heterorhabditis*، چرخه زندگی، مسیر بیماری‌زایی و نقش و محل همزیست باکتریایی را روشن کرد و در معرفی نماتودهای بیمارگر حشرات به عوامل کنترل بیولوژیک، نقشی کلیدی داشت. پوینار پایه گذاری مهم در توسعه مطالعه نماتودهای بیمارگر حشرات و تثبیت این زمینه در چهارچوب آسیب‌شناسی کاربردی حشرات بود. در دهه‌های بعدی، تحقیقات به روز وی روی موضوع کهربا، تاریخچه تکامل حشراتی که میلیون‌ها سال حفظ شده بودند را آشکار کرد. بدین ترتیب، او هم الهام‌بخش داستان‌های علمی تخیلی بود و هم پایه‌گذار روش‌های استاندارد در مطالعه دیرینه‌شناسی زیست‌شناسی شد. پوینار با پیوند بین پدیده های زیست‌شناختی در حشرات و نماتودها با روند تغییرات دیرینه‌شناسی، هم پنجره‌ای جدید در زیست باستان شناسی باز کرد و نیز میراثی جاودان در سیستماتیک، بوم‌شناسی و کنترل بیولوژیک باقی گذاشت. وی با فهمی که در موضوعات دیرینه‌شناسی، حشره‌شناسی، تکامل و میکروبیولوژی داشت، اطلاعات ارزشمندی را روی فسیل‌ها ارائــه کرد. این نوشته با هدف معرفی نقش و جایگاه پروفسور پوینار در مسیر تکامل نماتودهای بیمارگر حشرات به عنوان عوامل کنترل زیستی نگاشته شده است. امیدواریم خوانندگان این نوشتار، از میزان علاقه، تلاش، پشتکار و جامع نگری جورج پوینار الهام بگیرند و این رویکرد همه جانبه نگر و عمیق را در تحقیق، تحصیل و زندگی بکار گیرند.

کلمات کلیدی: بیماری‌شناسی حشرات، نماتودشناسی حشرات، زیست باستان‌شناسی، حشره‌شناسان پیشرو، فسیل شناسی

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