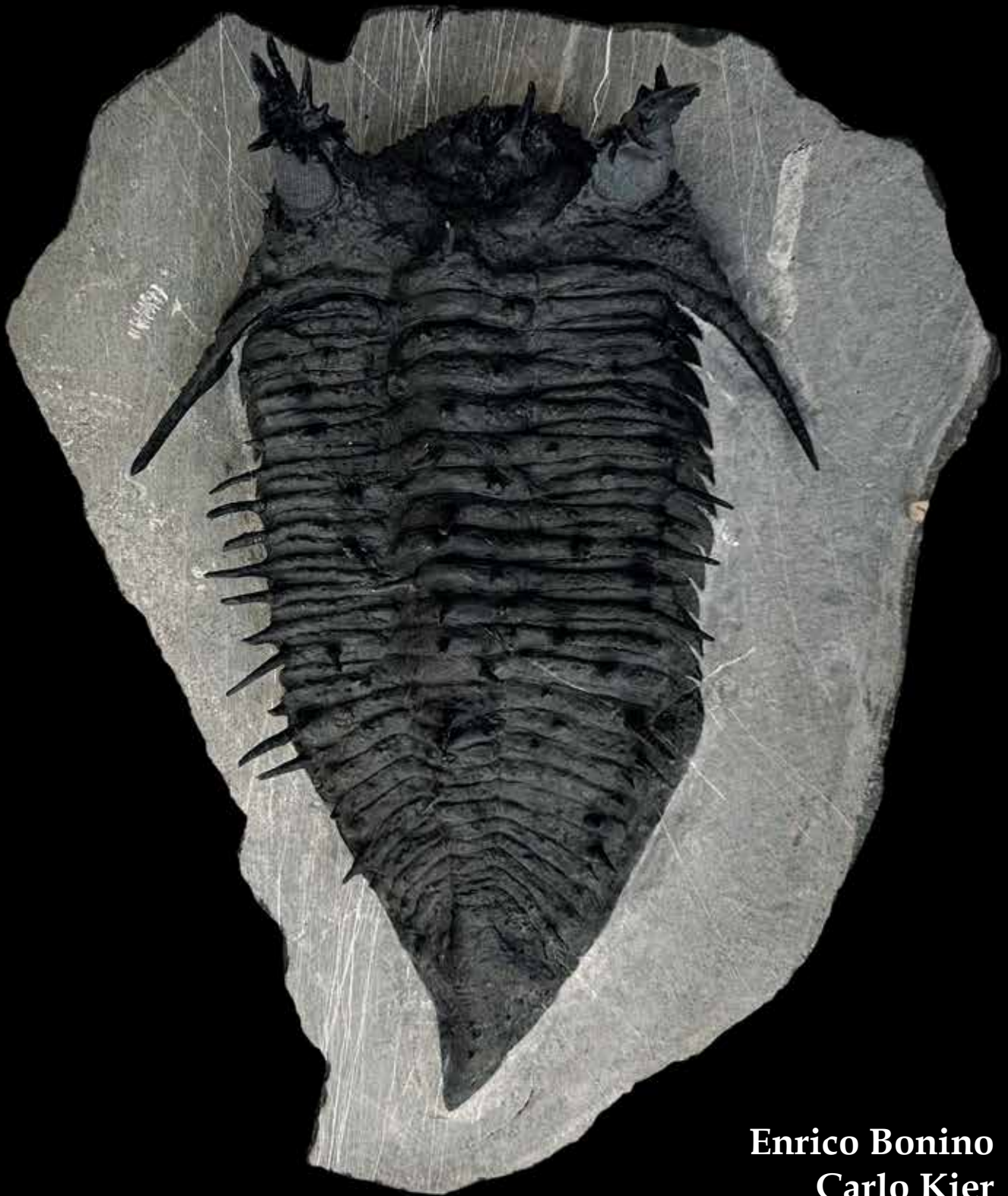


The Back to the Past Museum Guide to  
**TRILOBITES II**



**Enrico Bonino**  
**Carlo Kier**

# The Back to the Past Museum Guide to **Trilobites II**

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Conceived by Enrico Bonino and Carlo Kier with contributions by Jason Cooper, Ben Cooper, Dave Comfort, and Allart van Viersen

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Front cover: *Godzillaspis cooperi* (n.n.), undescribed trilobite from the Devonian Wenban Formation, Nevada, USA.  
This exceptional specimen was found and donated by Jason Cooper to the Back to the Past Museum.

To my parents, to my son Alessio that support me with interest, patience and enthusiasm, to Diana that she carried me through long working days.

(E.B.)

Dedicated to my parents, Vittorio and Marinella, to my family. Alice, wonderful wife and Vittorio and Carlotta , my sons, for nourishing my passion, even to the farthest corners of our beautiful planet.

(C.K.)

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*Olenellus* sp., Cambrian, Carrara Formation, Marble Mountains, California, USA, 13.5cm, (BPM coll.)

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Enrico Bonino & Carlo Kier

# Preface

---

Almost fifteen years have passed since the printing of the first volume in the Italian language published by the Back to the Past Museum on trilobites.

Encouraged by its success in Italy and abroad, we decided to publish the following year the translated version in English (The Back to the Past Museum Guide to TRILOBITES). This new tome, enlarged with updated plates, became a best seller in the paleontological field, obtaining an important worldwide distribution and a particularly positive evaluation by the professional sector.

This overwhelmingly positive response allowed for our project to continuously expand the museum's collections. Additionally, we began implementing research campaigns (always respecting international rules and laws), started an intense collaboration with professionals in the field and consequently, have published in high impact scientific journals.

It is no coincidence that the museum's collections contain holotypes and paratypes of specimens of considerable paleontological importance.

Much has happened since the publication of the first edition. We cannot fail to recall the sad demise of scientific eminences who dedicated their lives to paleontological research (Riccardo Levi-Setti, Dolf Seilacher, Tom Whiteley), and of friends who were collectors and preparators of the highest order (Harald Prescher and Dieter Holland).

We are proud to have been able to work and exchange discussions with these men of science; they actively and enthusiastically participated in the writing and critical evaluation of the volumes we published.

We dedicate to them the chapters in which they shared their professionalism and gracious availability.

It seemed important to us to resume the discourse "interrupted" a decade ago to publish an update of this book. Initially, a simple reprint was planned, given the pressing demand for the volume in Italian, and it has been sold out for some time now. From an initial reprint, we then moved on to an update: a new edition with new plates and a much-improved iconography.

The techniques of preparation have evolved almost exponentially in this last decade, and new specimens with extraordinary ornamentation have come to light.

Moreover, in these years the discovery of new deposits and new species (15.000 in 2009, today estimated at more than 25.000) has evolved the interpretation on the distribution, ecology, classification, morphology of these arthropods.

In conclusion, the volume compared to the previous one has not only been enriched with new tables and iconographic sources, but it has also been updated regarding the classification of trilobite orders, in accordance with the latest interpretations and studies. Studies that will lead to new interpretations, and consequently new reorganizations of Families and genera within the class of Trilobites.

What we hope is that this text will attract the interest of the "warned" collector, the professional or simply the passionate. We would also like to dedicate this work of ours to each one of them, in the hope of reinforcing the thin bridge that exists between public and private, both interdependent for study, field research, the discovery of new species and the evolution of scientific thought.

Enrico Bonino & Carlo Kier

# Presentation by Loren E. Babcock, Ph.D

---

## *A Treasure Trove of Trilobites*

Trilobite. The word immediately conjures up a range of mental images. Apart from dinosaurs, few animals known from the fossil record create such excitement in people. With their extraordinary visual appeal, their seemingly endless diversity in form, and their worldwide occurrence, trilobites are one of the most recognizable and sought-after invertebrate fossils.

Human fascination with trilobites has roots extending back at least 15,000 years. Among the early records of human interaction with trilobite fossils, some people of the First Nations in North America used specimens of the Cambrian *Elrathia kingii* from Utah for adornment or as charms long before the arrival of Europeans in the New World; and pygidia, or tail shields, of *Drepanura* were known as “bat stones” to the Chinese since antiquity. Trilobites were first illustrated in scientific literature by Edward Lhwyd in 1699. One of the first to bring trilobites to the forefront of science, however, was none other than the great Swedish naturalist Carolus Linnaeus. In 1753, Linnaeus introduced ‘*Entomolithus paradoxus*,’ and in 1768 he described an agnostoid, an olenid, and an asaphid as ‘subspecies’ of that form. Not long afterward, in 1771, Johann Walch coined the word “trilobite,” and we have used this word to the present day. The beginnings of a concerted effort to collect, describe, and interpret trilobites began in the early 1800s in Dudley, England, where for many years people have collected the Silurian *Calymene blumenbachii*, better known as the “Dudley locust,” or the “Dudley bug.” The original coat-of-arms of Dudley County is emblazoned with a “Dudley bug,” and this symbol still adorns the Dudley family’s coat-of-arms. Today, it seems that nearly every shop around the globe that sells rocks, minerals, and fossils has trilobites on the shelves. Some of the biggest attractions in natural history museums are the displays featuring trilobites. Among invertebrate fossils, trilobites are the leading subjects of books intended for a wide audience. Trilobites are boundlessly popular, and those who have had the pleasure of collecting specimens themselves always seem to delight in relating the heroic tales of their trilobite-collecting experiences.

Covering the vast range of paleontologic topics that trilobites offer, and presenting a variety of these wondrous fossils in a useful and aesthetic manner, is an enormous undertaking. In an almost unfathomable labor of love, Enrico Bonino and Carlo Kier present these ancient arthropods in ways that will appeal to all who strive to understand the history and evolution of life on Earth. This volume, “The Back to the Past Museum Guide to Trilobites II,” expands on one of the most ambitious projects to document the diversity and scientific relevance of any invertebrate fossil group.

The result is a dazzling array of breathtaking photographs, and an interesting, well-rounded, up-to-date, introduction to the paleobiology of trilobites and some of their close relatives. Major topics addressed in the text include the classification, evolutionary origins, morphology, paleoecology, and biogeography of trilobites, as well as field work and laboratory preparation of specimens. The highlight of this tour de force, however, is more than 160 pages of awe-inspiring trilobite photographs, organized by localities and within periods/systems of the Paleozoic.

Most of the photographs in this beautifully and profusely illustrated volume are of specimens in the magnificent collection of the Back to the Past Museum (BPM). The BPM houses what is perhaps the world’s most spectacular collection of trilobite fossils. Supplementing the illustrations of BPM specimens are ample illustrations of fine specimens housed in other collections. Together with preceding volumes by Enrico Bonino and Carlo Kier, “Trilobiti: il Libro del Museo” (2009), and its English translation, “The Back to the Past Museum Guide to Trilobites” (2010), “Trilobites II” represents the most comprehensive and most diverse suite of trilobite photographs ever assembled. Those who marveled at the tremendous illustrations in the earlier compilation will be gratified to find an extensive new set of extraordinarily preserved and exquisitely prepared fossils in “Trilobites II.”

This book is an invaluable introduction and guide to almost everything we now know about trilobites. Stunning photographs that fill page after page are embellished by compelling, readily comprehensible explanations and text. The observations and insightful interpretations made through many years by generations of dedicated naturalists, academic scientists, and citizen-scientists are compiled, synthesized, and compared with what we now know of these remarkable ancient arthropods. Enrico Bonino, Carlo Kier, and the contributors to “Trilobites II,” all of whom have been integral to important modern research on trilobites, show us just how far the science of trilobites has come since the early days of study in Europe and the United Kingdom.

This volume, like its predecessors, is certain to stimulate even more research, and inspire more collecting, as we seek ever more detailed answers to evolutionary and geological questions. This book is an absolute must-have for every trilobite enthusiast the world over.

Loren E. Babcock, Ph.D  
*School of Earth Sciences*  
*Orton Geological Museum*  
*The Ohio State University*  
*Columbus, Ohio 43210, USA*

# Presentation by Allart P. van Viersen, BSc.

---

My family lived in a land house on the edge of a forest. As a child I would be out a lot, exploring, observing and learning. I developed a broad interest for archaeology, biology and geology. In due time I gravitated towards fossils and dinosaurs were top of the bill.

In 1991, my parents took me to Natura Docet, one of the oldest natural history museums in the Netherlands, where the very successful “Dinosauriërs in Denekamp” exposition was held. Little did I know, I would meet my true love on a fossil market at the end of our visit: a calymenid trilobite from the Ordovician of Morocco – a creature so ancient and fascinating that I had to know all about it. That knowledge came from many books but in retrospective, only few were truly memorable.

Close to heart has always been the second edition of the Trilobites book by Ricardo Levi-Setti. I vividly recall the countless beautiful photographs filled with a world of details. In the late 1990s I moved to Maastricht for my studies. It was the time of first broad use of the Internet. Sam Gon launched his celebrated website on the (eight) orders of trilobites and there were two subsequent Yahoo discussion groups which Sam kindly permitted me to co-moderate.

Trilobites were on a roll.

But life changing decisions had to be made. I chose geographical information systems (GIS) as a professional career and carried out my research activities on regional trilobites from the Ardennes and Eifel in my leisure time.

One could say that a meeting with Enrico was bound to happen. A fellow GIS specialist with a passion for trilobites, living some 25 km away. We got acquainted through a mutual friend, Paul Hille, at the Interminéral fossil market in Liège. One day we met up with Harald Prescher and others in the old Resteigne quarry, at the heart of the Ardennes. Enrico found a trilobite cephalon of an aulacopleurid species unknown to science, which he generously donated for description. The species would later be formally named *Cyphaspis boninoi* (Bonino’s Cyphaspis).

Enrico has the extraordinary gift of sparking unparalleled enthusiasm in people. So when he told me that he was working with Carlo Kier on a comprehensive trilobite book (the first version in Italian, which would later be translated to English) there was no doubt in my mind that this would become significant.

Enrico and Carlo were in a unique position, as eminent members of a worldwide network of trilobitophiles – professionals and nonprofessionals alike– affording access to a vast pool of knowledge and trilobite specimens. It is safe to say that they delivered more than any of us had expected.

The first books embodied everything there was to love about trilobites, explaining all the essential aspects to know about them, while illustrating rare and exotic specimens from the most remote corners in the world. As in all active research fields, our knowledge of trilobites continues to develop. Like a treatise, regardless of its comprehensiveness, no work can remain up to par and so at some point in time an updated version is necessary.

This new book by Enrico and Carlo offers the status quo, effectually incorporating the past 15 years of trilobite research. A great deal of time was invested in expanding the original chapters, all furnished with exquisite illustrations.

No effort was spared to revise the systematic part including the Eodiscida, Olenida and Trinucleida as well as contemporary perspectives on Nektaspida, Agnostida, Ptychopariida and Aulacopleurida.

The second part of the book is yet another gem. It is a complete overhaul of the gallery of trilobite photos to encompass all new localities and specimens. Seeing so many beautiful trilobites from befriended collectors adds a familiar touch to the book.

I congratulate Enrico and Carlo for outdoing themselves with this masterful new edition of one of the world’s most iconic and integral works on trilobites of our time, and I humbly thank them for letting many of us be a part of it.



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# The Back to the Past Museum

Cancún, Mexico, located on the east coast of the Yucatán Peninsula and bathed by the blue waters of the Caribbean Sea, provides the setting for the Back to the Past Museum. Here, not far from the famous Chicxulub Crater, the impact site of a meteorite that struck the Earth some sixty-five million years ago, is housed the first museum dedicated entirely to trilobites. The rarity, quality, and scientific importance of the specimens on display at the Back to the Past Museum (more than three hundred species are represented) make this one of the most important collections of trilobites in the world.

The acronym “BPM coll.” indicates specimens drawn from the Museum’s collections.

These jewels, which have found their way to the Museum literally from the four corners of the globe, are the culmination of years of field research, acquisitions, or exchanges by the Museum’s director, Carlo Kier, the co-author of this book. The individuals whose work has made the Museum’s projects possible include Enrico Bonino (geologist, and the Museum’s scientific consultant and artistic director), Jake Skabelund (an American biologist and well known professional fossil hunter), and Carlo Kier. Behind the wings are specialists such as Dave Comfort, Bob Carroll, and Scott Vergiels who are responsible for the preparation of display specimens and whose contributions are literally indispensable. It hardly needs to be said that nothing of what visitors see at the Museum would be visible without their patient, professional preparation of the Museum’s invaluable fossil specimens.

The Museum, in addition to providing a careful scientific description of each of the specimens on display, is especially committed to its educational function as well. Each display case contains a reconstruction of the environment at the time the organisms lived, as well as photographs and illustrations that explain the geology of the sites where trilobites are found and the flora and fauna that shared an ecological niche with them.

A visit to the Museum begins at the dawn of the Paleozoic and continues in a virtual voyage through time across the millennia, from the Cambrian to the Permian. Each geological period is richly illustrated with specimens that are often one-of-a-kind, and the background of each display case follows the color standards established by the International Commission

on Stratigraphy for the official geological time scale. The Museum is constantly being updated as new specimens are acquired and integrated into the displays. Our main goal is to inspire new generations of collectors and future paleontologists and to expand awareness of these ancient and fascinating organisms which colonized almost all Paleozoic oceans for nearly three hundred million years.



Fig. 1. Welcome to the new section of the museum.



Fig. 2. The museum not only allows visitors to explore the new collections but also provides a space for extensive research and bibliographic research.





Fig. 3. A new section of the museum not only allows visitors to explore the newly illuminated collections but also provides a space for extensive research and bibliographic inquiry.

## Some Notes on Classification and Terminology

(based upon *LEBRUN, 2002; modified*).

With the intention of establishing order in the complex diversity of the animal and plant kingdoms, the publication of the tenth edition of Carl Von Linné's *Systema Naturae* (1758) gave rise to the creation of an elaborate hierarchical classification system—the beginning of zoological nomenclature.

The basic unit of this hierarchy was the species, and the system's purpose was to group organisms together according to their interrelationships. Each species was given a two-part or “binomial” scientific name composed, first, of the name of the genus to which an organism belonged.

The genus name was followed by the species or “specific” name, which is the hierarchical level just below the genus.

The genus (or generic name) is always written with an initial capital letter, while the specific name is always written in lower case.

Both names are printed in italics (for example, *Selenopeltis buchii*). If the name has been mentioned previously in a text—or in the case of a list of species that belong to the same genus—the generic name may be abbreviated using its first letter (*S. buchii*), but it can never be omitted.

In general, scientific names are presumed to have Latin or Greek roots, such as in the case of the trilobite *Asteropyge longispina*. The generic name is formed from the Greek words *asteros* (star) and *pyge* (buttocks) and the species name is a combination of *longi* (long) and *spina* (spine).

This rule, however, has more recently been abandoned in large part, and zoological naming has been left to the liberal interpretations of the specialists who study and describe new taxa.



Fig. 4. *Asteropyge longispina*, RÜCKERT & KLEVER, 2007, x2.9, (A. Rückert coll.). Note the long spines on either side of the cephalon and the spinose pygidium.

The name of the “author” or authors follows the binary or Linnaean classification; these are the workers who first named and described the organism—for example, the trilobites *Isotelus gigas* DE KAY, 1824 or *Crozonaspis kerfornei* CLARKSON & HENRY, 1970.

When the author's name appears within parentheses, such as, for example, in the case of *Panderia beaumonti* (ROUAULT, 1847)—this indicates that the fossil had originally been given a different name. ROUAULT, for example, first called the trilobite in question *Illaeus beaumonti*, though it was later assigned to a different genus.

Abbreviations such as “cf.” (*confere* or “compare with”) or “aff.” (*affinis* or “akin to”) are used to signal uncertainty regarding the classification of a particular organism—for example, *Calymene* cf. *breviceps* and *Lonchodomas* aff. *pennatus*. Finally, the abbreviation “sp.” following the genus name (e.g., *Phacops* sp.) indicates that the genus has been identified but not the species.

A genus (the plural is “genera”) includes one or more species that share a number of characteristics. Moving up the taxonomical hierarchy, a group of genera with shared features are contained within a family, whose name ends in the suffix “-idae.” Groups of families, in turn, may be placed within superfamilies (suffix “-oidea”), suborders (suffix “-ina”), and collected into orders (suffix “-ida”), orders into classes, and classes into phyla (the singular is phylum). At the very top of the hierarchy is the Kingdom.

To take a concrete example: *Neseuretus* (*Neseuretus*) *tristani tardus* HAMMANN, 1983 belongs to the Family Calymenidae HAWLE & CORDA, 1847, the Order Phacopida SALTER 1846, the Class Trilobita WALCH, 1771, the Phylum Arthropoda SIEBOLD & STANNIUS, 1845 and, finally, to the Kingdom Animalia. Within these basic taxonomic categories, we find intermediate subdivisions: subspecies, subgenera, subfamilies (suffix “-inae”), and so on.

## Cladistics

Cladistics, or cladistic taxonomy (from the Greek word *klados* = branch), is a systematic scheme for classifying living organisms. Cladistics, also known as phylogenetic systematics, originated in the work of WILLI HENNIG (1913-1976), and its system is based upon the degree of inferred kinship between and among organisms—or, to say it another way, on their temporal distance from their last shared ancestor. In the cladistic classification method, animals and plants are divided into monophyletic taxonomic groups (clades) that comprise the common ancestor and all its descendents.

The evolutionary relationships within a clade are established on the basis of shared features (homologies) and on the assumption that such features indicate the presence of a common ancestor. Classification is also based upon the presumption that two new species may be formed by the sudden separation from a common ancestor rather than through gradual evolutionary change. A clade that is included in a larger unit is said to be “nested” within that clade.

A clade possesses a single ancient member in common, and the phylogenetic lines of descent from that branch are called monophyletic groups. A taxon is said to be polyphyletic, on the other hand, if it does not share a common ancestor with another taxon, and polyphyletic groups have little pertinence to cladistics.

Frequently, they reflect a sort of popular association of organisms that share some features (the algae, for instance), though, in fact, they actually represent a number of clades with distinct origins.

A monophyletic group is characterized by one or more autapomorphies (features that are uniquely present in the terminal phase of a group). Autapomorphies are observed exclusively in one member of a clade and not elsewhere, not even in closely related organisms, and it is essential to point out that such autapomorphies may, in some cases, be lost in adulthood, even if they are maintained at an embryonic level following paedogenesis (that is, sexual development that is accelerated with respect to a normal individual).

Paedogenesis contrasts with neoteny, the more-or-less marked retention, by adults in a species, of traits previously seen only in juveniles.

The term pedomorphosis is used, instead, when features are present in a sexually mature adult that are typical of earlier stages of development. In a practical sense, we are speaking of adult forms that retain aspects reminiscent of juvenile stages of life.

A clade is differentiated from others by derived features that do not appear in other clades (apomorphy), though it may be evolutionarily related to other clades through a common ancestor and exhibit shared derived characters (synapomorphies). If a clade does not include all the descendents of a common ancestor (that is, it includes most of the species derived from the ancestral progenitor but excludes some branches), the clade is called paraphyletic. A symplesiomorphy is a primitive feature shared by two or more taxa; that feature may appear in other taxa as well if they share an ancestor with the taxon in question, but cannot be used to define a clade.

All of these relationships are represented in diagrams called cladograms, formed of a series of two-pronged branches. Each point of branching represents a divergence from a common ancestor. A cladistic analysis may be based on a wide variety of data, including DNA sequencing (so-called “molecular data”) and on biochemical and morphological information.

In addition, the reader may come across the following terms in the scientific literature, which we describe here as a matter of thoroughness.

- The *nomen nudum* (plural: *nomina nuda*) or “naked name” is printed in normal characters (i.e., not in italics) to indicate that an organism’s name has not yet been accepted and standardized by the International Commission on Zoological Nomenclature (ICZN).

If the organism’s name is later formalized, it is then written in italics (e.g., *Canis latrans*, the coyote). The formal scientific name given to an organism may or may not correspond to its previous *nomen nudum*.

- The *nomen oblitum* (from Latin, “forgotten name”) refers to names that have not been used by the scientific community since 1899 and when a name has either been replaced by a more recent name (called the *nomen protectum*) or when a formally accepted homonym exists.

The former name, no longer in use, is said to be “forgotten” and the *nomen protectum* takes precedence.

- The *nomen dubium* (“doubtful name”) is used to indicate fossils that have no distinct or unique features that permit them to be classified according to rigorous scientific standards. This may happen when the holotype (the physical specimen upon which a species description is originally based) has been lost or lacks all the information necessary for a true taxonomic classification.

- The *nomen novum* (“new name”) is a scientific name created specifically to replace a name that is already in use but which is no longer considered legitimate (e.g., because it is a homonym or is spelled the same as an existing, older name). A *nomen novum* is not applied, however, when a name is changed on the basis of a new taxonomic interpretation.

# Trilobites (Class Trilobita)

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Biota (*Classification by Systema Naturae 2000*)

Domain: **Eukaryota** WHITTAKER & MARGULIS, 1978

Realm: **Animalia** LINNAEUS, 1758

Subkingdom: **Bilateria** HATSCHKE, 1888 (**Bilaterians** CAVALIER-SMITH, 1983)

Branch: **Protostomia** GROBBEN, 1908

Infrakingdom: **Ecdysozoa** AGUINALDO *et al.*, 1997

Superphylum: **Panarthropoda** CUVIER

Phylum: **Arthropoda** LATREILLE, 1829

Subphylum: **Arachnomorpha** HEIDER, 1913

Infraphylum: **Trilobita**

Class: **Trilobita** WALCH, 1771

**Distribution:** Cambrian, Series 2 (~521Ma) - Upper Permian (251Ma).

**Environment:** marine, all ecological niches were occupied.

**Feeding:** full alimentary pyramid.

**Exoskeleton:** calcitic at lower concentration in magnesium.

**Dimensions:** from less than a millimeter to near one meter long.

**Importance:** paleoecological, paleobiogeographical, and partially biostratigraphic.

## PLATE 6

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The following tables illustrate (non-exhaustively) the trilobites that appeared in the lower Cambrian, and that possessed a stratigraphic distribution during Series 2. **1-** *Archaeaspis* cf. *macropleuron* LIEBERMAN, 2002, x1.7, Montenegro Member, Campito Formation, Fallotaspis Zone, Esmeralda County, Nevada, USA, (BPM coll.); **2-** *Eofallotaspis* sp., x1.8, Campito Formation Montezuma Range, Nevada, USA, (M.R. Haensel coll.); **3-** *Fallotaspis plana* HUPÉ, 1953, R50885, x1.1, Tazemmourt, AntiAtlas, Morocco, (MNHN coll., Paris, France); **4-** *Nevadella perfecta* WALCOTT, 1913, x0.9, *Nevadella perfecta* zone, Poleta Formation, Nevada, USA, (photo courtesy: G. Di Silvestro); **5-** *Daguinaspis ambroggi* HUPÉ, 1953, x1.8, Amouslek Formation, Morocco, (G. Huot-Marchand coll.); **6-** *Fallotaspis tazemourtensis* HUPÉ, 1952, x0.6, Isaffen, Morocco, (M.A. Rojo coll.); **7-** *Perrector* (*Richterops*) cf. *falloti* HUPÉ, 1953, x1.3, Tazemmourt, Morocco, (photo courtesy: M. Caldeira Pais); **8-** *Choubertella spinosa* HUPÉ, 1953, x0.9, Formation d'Amouslek, Anti-Atlas, Morocco, (G. Huot-Marchand coll.); **9-** *Zhangshania typica* LI & ZHANG, 1990, x1.8, Hongjingshao Formation (Xiaoshiba Biota), Kunming, China, (M. Haensel coll.); **10-** *Lemdadella linaresae* LINAN & SDZUY, 1978, x0.6, Atdabanian, Pedroche Formation, Member 1, Puente de Hierro, Cordoba, Spain, (J. Cuevas coll.); **11-** *Dolerolenus zoppii* MENEGHINI, 1882, Membro di Punta Su Pranu, Punta Manna Formation, Sardegna, Italy, (photo courtesy: G.L. Pillola); **12-** *Metadoxides armatus* MENEGHINI, 1881, Membro di Punta Su Pranu, Formazione di Punta Manna, Porto di Canalgrande, Sardegna, Italy, (photo courtesy: G.L. Pillola); **13-** *Jakutus primigenius* IVANTSOV, 2005, PIN 4349/813 (holotype), x0.4, Sinsk Formation, Lena River, Siberia, (Paleontological Institute coll., PIN, Russian Academy of Sciences, Moscow); **14-** *Bigotinops dangeardi* HUPÉ, 1954, x7.0, Amouslek Formation, Morocco, (G. Huot-Marchand coll.); **15-** *Yunnanocephalus yunnanensis* MANSUY, 1912, x4.4, Che-f-6-4-50, x2.5, Yu'anshan member, Chiungchussu Formation, Haikou, Kunming, China;

## PLATE 7

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**16-** *Megapharanaspis nedini* PATERSON & JAGO, 2006, SAMA P45206a, x4.3, Emu Bay Shale, Big Gully, Kangaroo Island, Australia, (photo courtesy: J. Paterson); **17-** *Holmia* cf. *kjerulffi* LINNARSSON, 1871, x0.9, Holmia Shale, Tomten farm, Ringsaker, Norway, (BPM coll.); **18-** *Olenellus clarki* RESLER, 1928, x1.5, Pioche Formation, Marble Mountains, California, (BPM coll.); **19-** *Eoredlichia intermedia* LU, 1940, x1.0, Yuanshan Formation, Maotianshan Shale Member, Haikou, Kunming, (photo courtesy: L. Hennion); **20-** *Redlichia rex* HOLMES, PATERSON & GARCÍA-BELLIDO, 2019, SAMA P40181, x0.4, Emu Bay Shale, Big Gully, Kangaroo Island, Australia, (photo courtesy: J. Paterson); **21-** *Tsuniyidiscus* cf. *acutus* SUN, 1983, x20.0, Shujingtuo Formation, Yichang, Hubei, southern China, (M. Haensel coll.); **22-** *Estaingia bilobata* POCOCK, 1964, SAMA P14955, x1.7, Emu Bay Shale, Big Gully, Kangaroo Island, Australia, (photo courtesy: J. Paterson); **23-** *Elliptocephala* sp., x0.5, Poleta Formation, Montezuma Range, Esmeralda County, Nevada, USA, (BPM coll.); **24-** *Wanneria* sp., x0.6, Fort Steel Formation, Cranbrook, British Columbia, Canada, (BPM coll.); **25-** *Balcoracania dailyi* POCOCK, 1970, x6.6, SAMA P14568, Billy Creek Formation, Reaphook Hill, South Australia, (South Australian Museum coll.), Palaeontological collection, Adelaide, Australia); **26-** *Ellipsocephalus hoffi* SCHLOTHEIM, 1823, x2.1, (Geosvět Galerie Minerálu a Fossilii coll., Praga); **27-** *Peachella iddingsi* WALCOTT, 1884, x6.2, Carrara Formation, Emigrant Pass, California, (photo courtesy: J. Skabelund); **28-** *Bristolia insolens* RESSER, 1928, x1.6, Carrara Formation, Nevada, (BPM coll.); **29-** *Bathynotus kueichowensis* LU in WANG ET AL., 1968, x8.3, Kaili Formation, Jianhe County, Guizhou, China, (private coll.); **30-** *Protolenus* (P.) cf. *densigranulatus* GEYER, 1990, x2.8, Jbel Wawrmast Formation, Tarhoucht, Jbel Ougnat area, Anti-Atlas, Morocco, (E. Bonino coll.); **31-** *Hamatolenus* (H.) *marocanus* NELTNER, 1938, x0.5, Jbel Wawrmast Formation, Tarhoucht, Jbel Ougnat area, Anti-Atlas, Morocco, (E. Bonino coll.); **32-** *Myopsalenites* cf. *boutiouiti* GEYER & LANDING, 2004, x1.6, Anti-Atlas, Morocco, (photo courtesy: G. Di Silvestro); **33-** *Oryctocephalus indicus* REED, 1910, x0.5, GM9-4-2139, Kaili Formation, Jianhe County, Guizhou, China, (Guizhou Museum Archive, Guizhou University, Guiyang, China).





# Trilobite morphology

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*Cyphaspis heissae* VAN VIERSEN & PRESCHER, 2014, PWL-2014 02, Ahbach Formation, Germany, (photo courtesy: A. van Viersen).



Fig. 36, a-b. **a)** The “turret” eyes of *Erbenochile erbeni* ALBERTI, 1981, lower-middle Devonian, Morocco, (P. Cameron coll.); **b)** Detail of the lens arrangement and the peculiar morphology of the “visor”, in *Godzillaspis cooperi* (n.n.), Undescribed trilobite, Devonian (Pragian), Wenban Limestones, Eureka, Nevada, USA, (BPM coll.)

## Evolution of the Visual Apparatus

Large schizochroal eyes appeared late in the evolution of trilobites (in the Order Phacopida, specifically, which evolved between the lower Ordovician and the upper Devonian). Only these species possessed a well-defined doublet lens. Ancestral species, conversely, possessed holochroal eyes composed of single prismatic calcite lenses, while the abathochroal eye represents an intermediate position between the two. According to HORVÁTH *et al.* (1997), the following evolutionary trends occurred in the visual apparatus of trilobites:

a) an initial stage was marked by the development of holochroal eyes composed of calcite crystals in which the c-axis was aligned perpendicular to the surface of the eye (and, thus, parallel to the optical axis of the lens) in order to resolve the problem of calcite birefringence (or double refraction);

b) a later stage led to the development of abathochroal eyes, with larger lenses in comparison to the holochroal model and a profile that might be called “Huygensian,” as ZHANG & CLARKSON (1990) observed. This more evolved variety of lens, though it permitted light loss via internal reflection, is found exclusively in the Suborder eodiscina (Order Agnostida) and is limited to the lower and middle Cambrian;

c) The visual problem of inefficiency in capturing light rays is resolved in the schizochroal eye, the culmination of trilobite evolution. The result was likely an improved



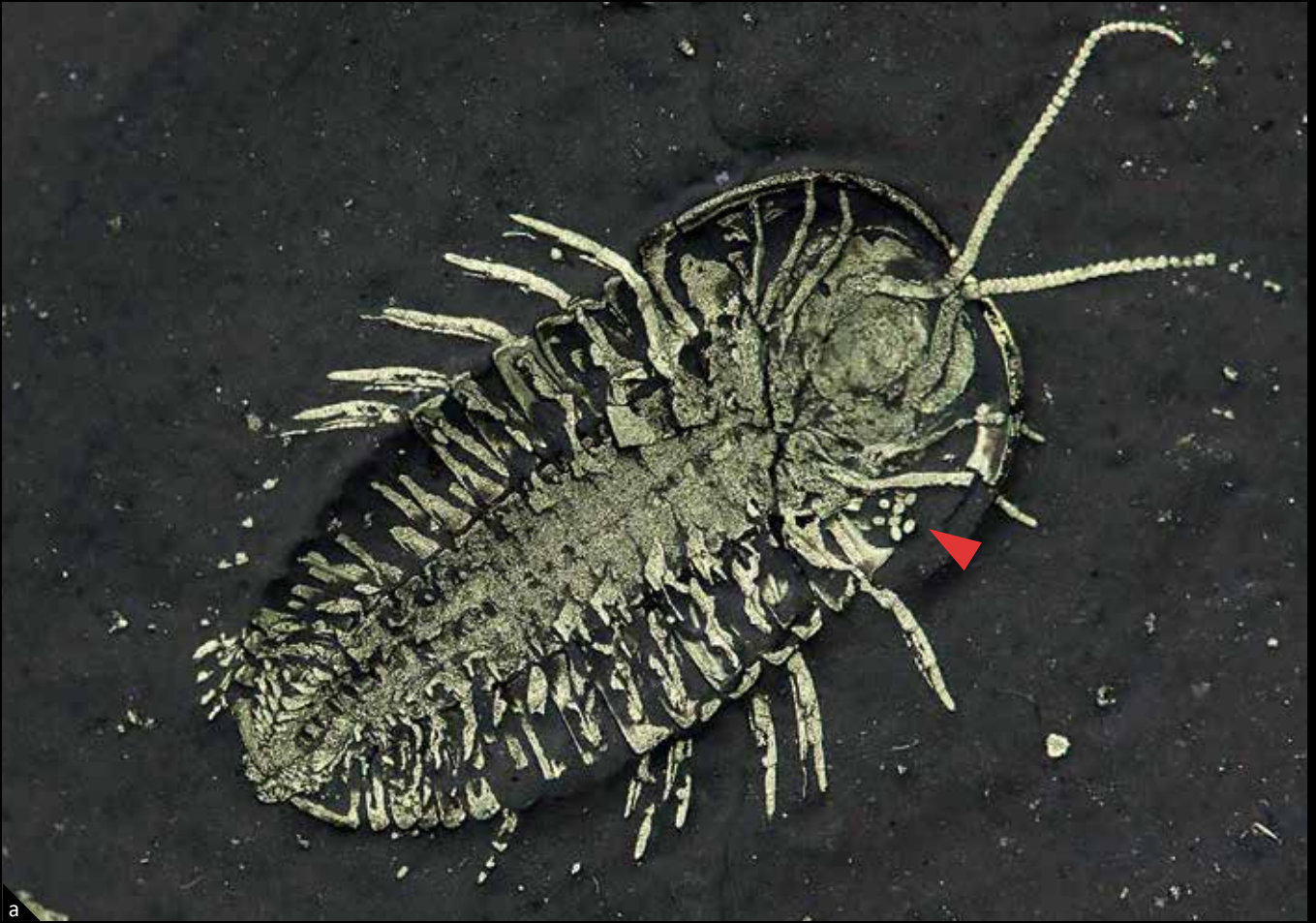
visual acuity connected with the need to develop more active behaviors both as predators and in defense from predators and an increase in daytime activity. The structure of individual lenses is improved by the addition of a lens with a different refraction index. This eliminates internal reflection and increases the capacity of the doublet lens to transmit light.

## Blindness

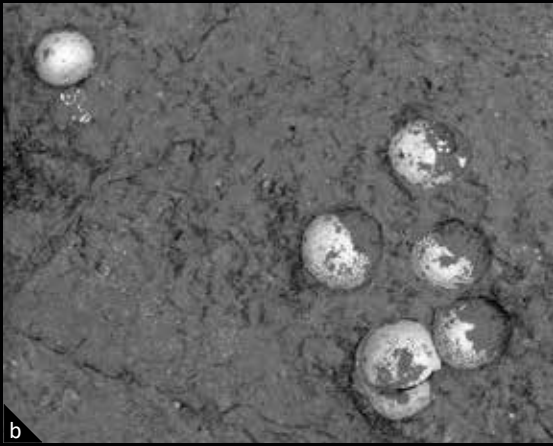
Many trilobite species had no visual organs and are considered blind. The absence of eyes is rare in the Cambrian but becomes more frequent in a number of families during the Ordovician.

In the Devonian, the proetid species *Pteroparia coumiacensis* FEIST, 1976 and the phacopid *Trimercephalus*





a



b



d



c



e





Spectacular Niobinae with antennae, gills and gut preserved, 11cm (sagittal length), Early Ordovician (Tremadocian), Fezouata Formation, Zagora, Morocco, (S. Piérard coll.)



# Paleoecology

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*Cyphaspis heissae* VAN VIERSEN & PRESCHER, 2014, PWL-2014 02, Ahbach Formation, Germany, (photo courtesy: A. van Viersen).



a



b



c



d



e



# Faunal Provincialism

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*Cyphaspis heissae* VAN VIERSEN & PRESCHER, 2014, PWL-2014 02, Ahbach Formation, Germany, (photo courtesy: A. van Viersen).

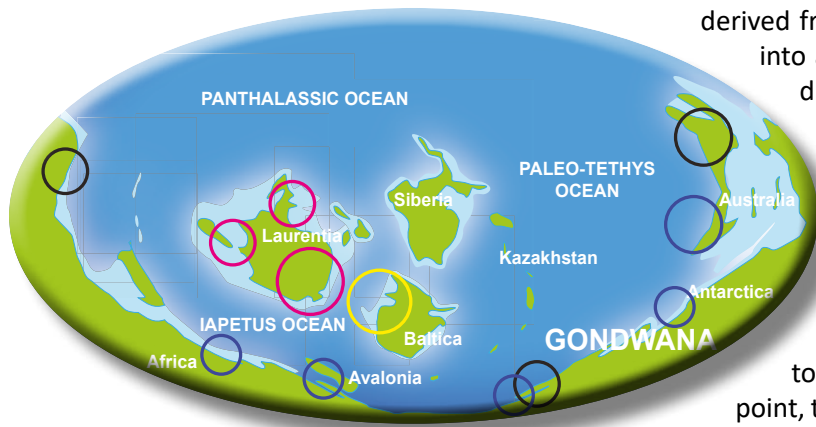


Fig. 107. Distribution of faunal provinces during the lower Ordovician. Red indicates the province occupied by the bathyrurids; blue, the calymenid-dalmanitids; black, the dikelocephaliids; and, finally, yellow represents the province occupied largely by the asaphids.

In the Ashgillian (upper Ordovician), a marine regression and a notable reduction in temperature took place as a consequence of a period of glaciation. During the Hirnantian (final stage; RONG & HARPER, 1988), these changes became co-factors in a significant biological crisis that is considered one of the primary reasons for the end of trilobite faunal provincialism (as well as that of many other organisms) during the Ordovician-Silurian transition. A major anoxic phase followed that crisis, which led to the definitive extinction of the Orders Asaphida (with the exception of some of the Trinucleoidea), Agnostida, and Ptychopariida. While benthic Ordovician platform faunas seem to have followed the model of provincialism we've discussed here, the same is not necessarily true for deeper-ocean faunas, less directly influenced by latitude and by the positions of the continents.

## Silurian

The global cooling and glaciation that occurred at the end of the Ordovician, with resultant mass extinctions, gave way to the proliferation and widespread distribution of brachiopods at the beginning of the Silurian. In many cases, brachiopods differentiated into significant faunal provinces (such as the *Clarkeia* zone, typical of cold-water environments), a phenomenon that is particularly well documented in the Malvinokaffric Realm (South America, the Falkland Islands, and the southernmost part of Africa). The same cannot be said for trilobites, however. Silurian trilobites seem to have become more-or-less cosmopolitan, and faunal provinces are generally less easy to distinguish. It is known that trilobite faunas

derived from the acastids (Order Phacopida) migrated into a faunally impoverished region and began to diversify to the point of constituting a distinct faunal province (ELDREDGE & ORMISTON, 1979).

In consequence, Silurian trilobites are represented substantially by benthic and epicontinental species belonging to the Orders Phacopida, Lichida, Harpetida, Odontopleurida, Proetida, and Corynexochida. At this point, they made up only 5% of marine invertebrates and demonstrated only a weak provincialism (COCKS & FORTEY, 1990; SCHRANK, 1977). Numerous cosmopolitan forms such as *Sphaerexochus* (Superfamily Cheiruroidea) were widely distributed geographically (North America, Europe, Japan, and Australia). Other species, such as *Coronocephalus* (Family Encrinuridae), conversely, were much more limited in distribution to the east of Gondwana (Southern China, eastern Australia, and Japan).

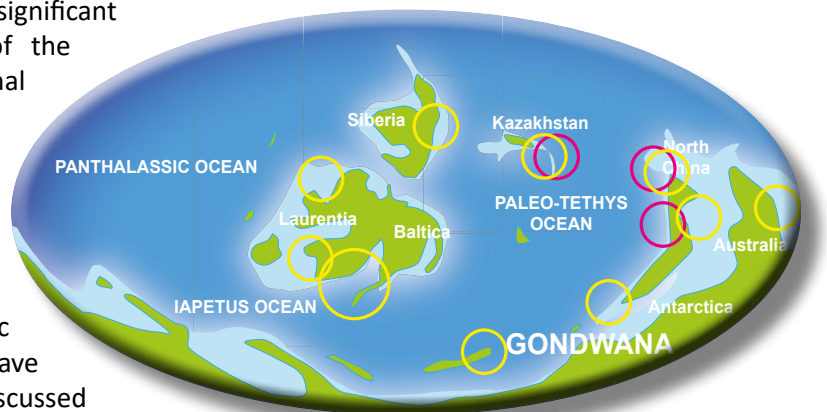


Fig. 108. Distribution of faunal provinces during the middle Silurian. Yellow indicates cosmopolitan Cheiruroidea genera; *Coronocephalus* is represented by red.

## Devonian

The trilobites' decline proceeded at an accelerated pace during the Devonian. As a result of a series of planet-wide sea-level changes and consequent extinctions, the hundred or so genera present at the Lochkovian (earliest Devonian) gave way to not more than twenty. Four mass extinctions, associated with eighteen significant eustatic sea-level changes (SANDBERG *et al.*, 2002), are known from the middle and upper Devonian (FEIST, 1991). These extinctions very nearly marked the end of trilobites:

- the Kacák/Otomari Event, which separated the Eifelian from the Givetian;
- the Taghanic-Pharciceras Event in the Givetian;



# Trilobite Classification

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*Cyphaspis heissae* VAN VIERSEN & PRESCHER, 2014, PWL-2014 02, Ahbach Formation, Germany, (photo courtesy: A. van Viersen).



# Order Lichida



MOORE, 1959

**Distribution:** Cambrian (Miaolingian Series) - upper Devonian (Frasnian)

**Families:** Lichakephalidae TRIPP, 1957, Lichidae HAWLE & CORDA, 1847



Fig. 132. *Lichas marocanus* DESTOMBES, 1968, x0.3, lower Ashgill, upper Ordovician, upper Ktaoua Group, Jbel bou Degane, east of Tagounite, Central Anti-Atlas, Morocco, (BPM coll.)

In this Order, the glabella broadens at the occipital ring and extends frontally to reach the anterior cephalic margin. The suture lines are opisthoparian. The lateral and occipital lobes of the glabella are developed

frontally and run alongside and/or are merged with smaller lobes.

The hypostome is conterminant and broad. The rostral plate is separated laterally by sutures that converge in a posterior direction, and the doublure is ornamented with terraces. The thorax is composed of ten or eleven segments.

A terminal spine is present on the pleurae, which bend retrograde at the fulcrum. The pygidium is broad, generally flat, and equipped with pleural furrows that vary in number from two to six.

The pygidial pleurae may be leaf-shaped (*Lichas*, *Oinochoe*, *Arctinurus*).

The surface of the exoskeleton is typically covered with granules or tubercles in two different size categories.



Fig. 133. *Metopolichas* cf. *platyrhinus*, SCHMIDT, 1907, lower Llanvirnian, lower Ordovician, Saint Petersburg, Russia, (BPM coll.)



## Suborder CALYMENINA

SWINNERTON, 1915

**Distribution:** lower Ordovician - upper Devonian

**Families:** Calymenidae BURMEISTER, 1843, Bathycheilidae PŘIBYL, 1953, Bavarillidae SDUZY, 1957, Calymenidae BURMEISTER, 1843, Homalonotidae CHAPMAN, 1890

The Suborder Calymenina includes the Superfamily Calymenoidea HUPÉ, 1945.

The Suborder Calymenina includes the most ancestral structures of the order, including suture lines and the presence of a circumocular suture. The coherence of the Clade Phacopida was partly disputed by ELDREDGE (1977), who emphasized features that would bring the

The glabella narrows in the anterior direction to become bell-shaped or trapezoidal; there may be as many as four glabellar furrows of varying depth. The eyes are holochroal and often tiny. The hypostome is conterminant and subrectangular and is marked by small anterior swellings (wings). Genal spines are absent with the exception of some species known from the Ordovician



Fig. 138. *Devononeseuretus beichti* ALBERTI, 2023, early lower Emsian, Devonian, Hunsrück Slate, Bundenbach, Germany, 7cm, (M. Alberti coll.)

Calymenina closer to the Order Ptychopariida. It is plausible that these phacopids descended from ancestral species belonging to the Librostoma, but no evidence has emerged to date that could correlate these two orders with a common ancestor.

The cephalon is semicircular or subtriangular in shape with either opisthoparian or gonatoparian suture lines.

(*Prionocheilus*, *Bathycheilus*, *Bavarilla*). The thorax is composed of a minimum of eleven to a maximum of thirteen segments, and the pleural extremities tend to narrow toward the posterior. The pygidium is of medium size with a variable number of axial elements. It may be elliptical or triangular in shape. Spines are not present. Primitive species were by and large micropygous.



Fig. 139, a-c. a) *Dipleura deckayi* GREEN, 1832, x0.5, middle Devonian, Moscow Fm., New York, USA; b) *Salterocoryphe salteri* ROUAULT, 1851 and *Colpocoryphe rouaulti* HENRI, 1970, x1.0, middle Ordovician, Brittany, France; c) *Flexicalymene retrorsa* FOERSTE, 1910, upper Ordovician, Cincinnati series, Kentucky, USA, (BPM coll.)



*Lonchodomas volborthi* SCHMIDT, 1894, lower Ordovician, Expansus Limestone, Ljungbro, Sweden, (BPM coll.)

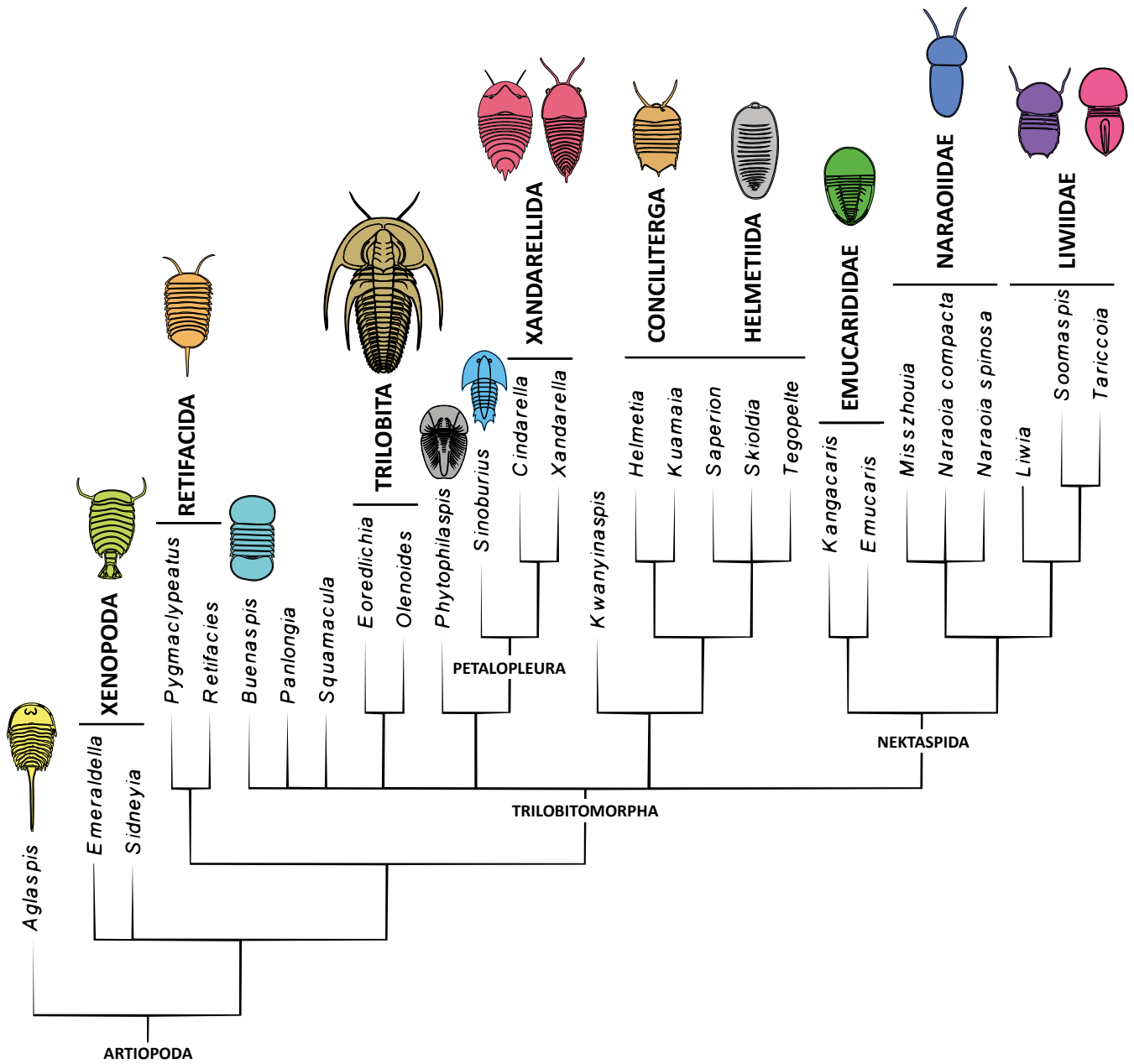


Fig. 175. The Clade Trilobita includes species that do not possess a caudal spine (telson) and in which each thoracic segment may cover more than one pair of legs (the pygidium of trilobites may be considered a tergite that covers numerous pairs of podomeres); cladogram after PATERSON ET AL. 2010, simplified.

2006 and *Panlongia spinosa* LIU & LUO, 2006 (the latter currently considered synonymous with *P. tetranudosa*) and considered as belonging to the Helmetiida (LUO ET AL., 2008), or according to other authors to an intermediate form between the Liwiida and Helmetiidae.

Clearly, the classification of this clade remains subject to significant revision, interpretation, and debate by specialists, and it is not out of the question that major modifications will be made in future to the phyletic relationships among the families we've briefly mentioned here.

Another arthropod with features that are very near those of trilobites was described by IVANTSOV (1999)

and assigned to the Subclass Xandarellida.

This species has a cephalon with suture lines, well-developed eyes, a wide if reduced thorax (with four axial segments), and a large pygidium.

The suture lines are not connected to the eyes as they are in trilobites, and traces of segmentation are visible in the librigenae, evidence of a probable fusion of the pleurae located directly posterior to the cephalon. Unlike trilobites, however, the exoskeleton shows signs of only slight or absent mineralization.

This arthropod, discovered in a significant Siberian Lagerstätte (Cambrian Series 2 or lower Cambrian, Sinsk Formation, near the town of Sinsk on the Lena River), was named *Phytophilaspis pergamena* IVANTSOV, 1999.



# Field work and Preparation techniques

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*Cyphaspis heissae* VAN VIERSEN & PRESCHER, 2014, PWL-2014 02, Ahbach Formation, Germany, (photo courtesy: A. van Viersen).



Fig. 180. Near the center of the photograph the reddish Latham Shales (Cambrian) is exposed in the Marble Mountains, Mojave Desert, southeast California near the towns of Chambless and Cadiz. This locality provides an ideal opportunity to find olenellid trilobites.

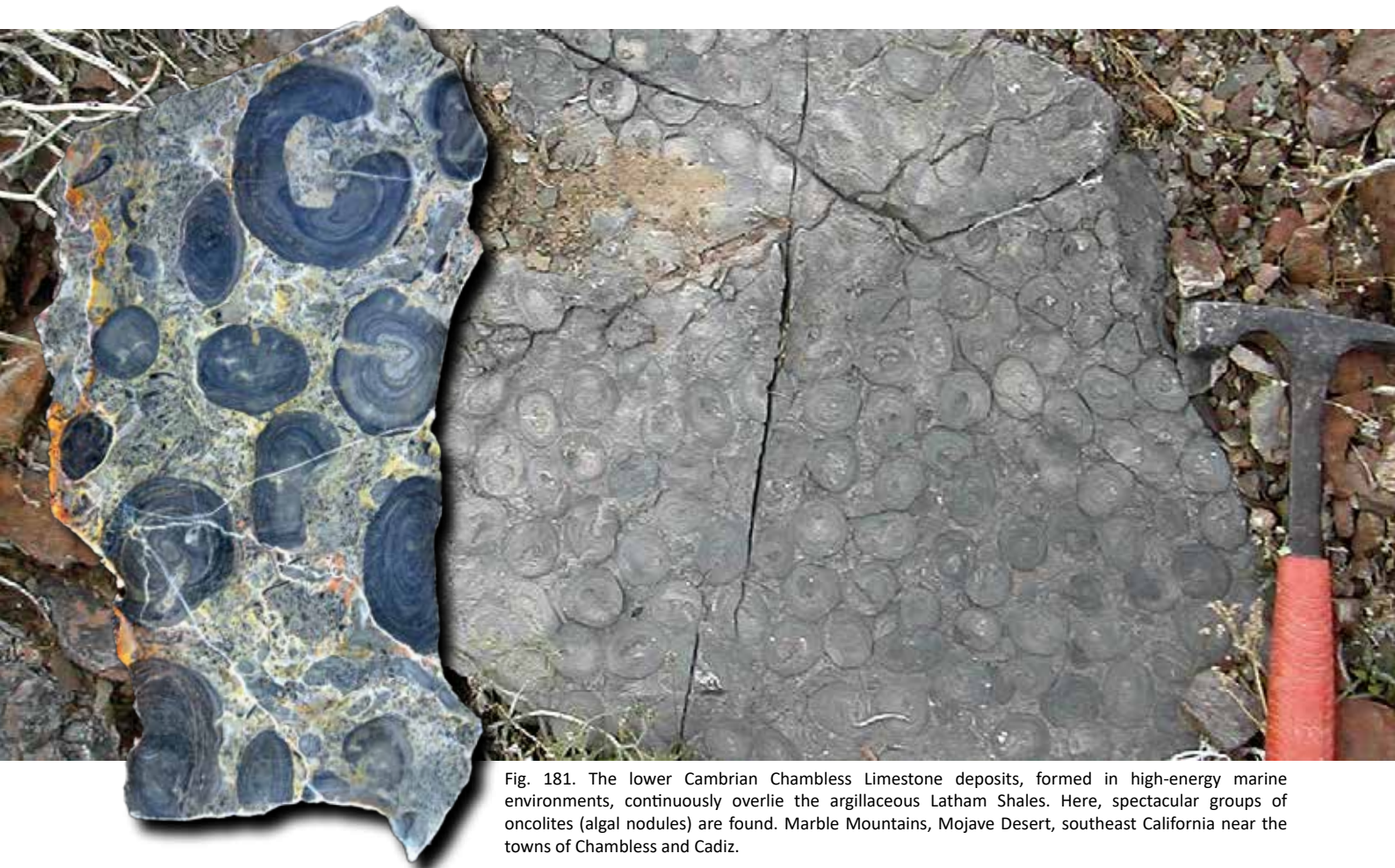


Fig. 181. The lower Cambrian Chambless Limestone deposits, formed in high-energy marine environments, continuously overlie the argillaceous Latham Shales. Here, spectacular groups of oncolites (algal nodules) are found. Marble Mountains, Mojave Desert, southeast California near the towns of Chambless and Cadiz.



# Introduction to the plates

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a



b



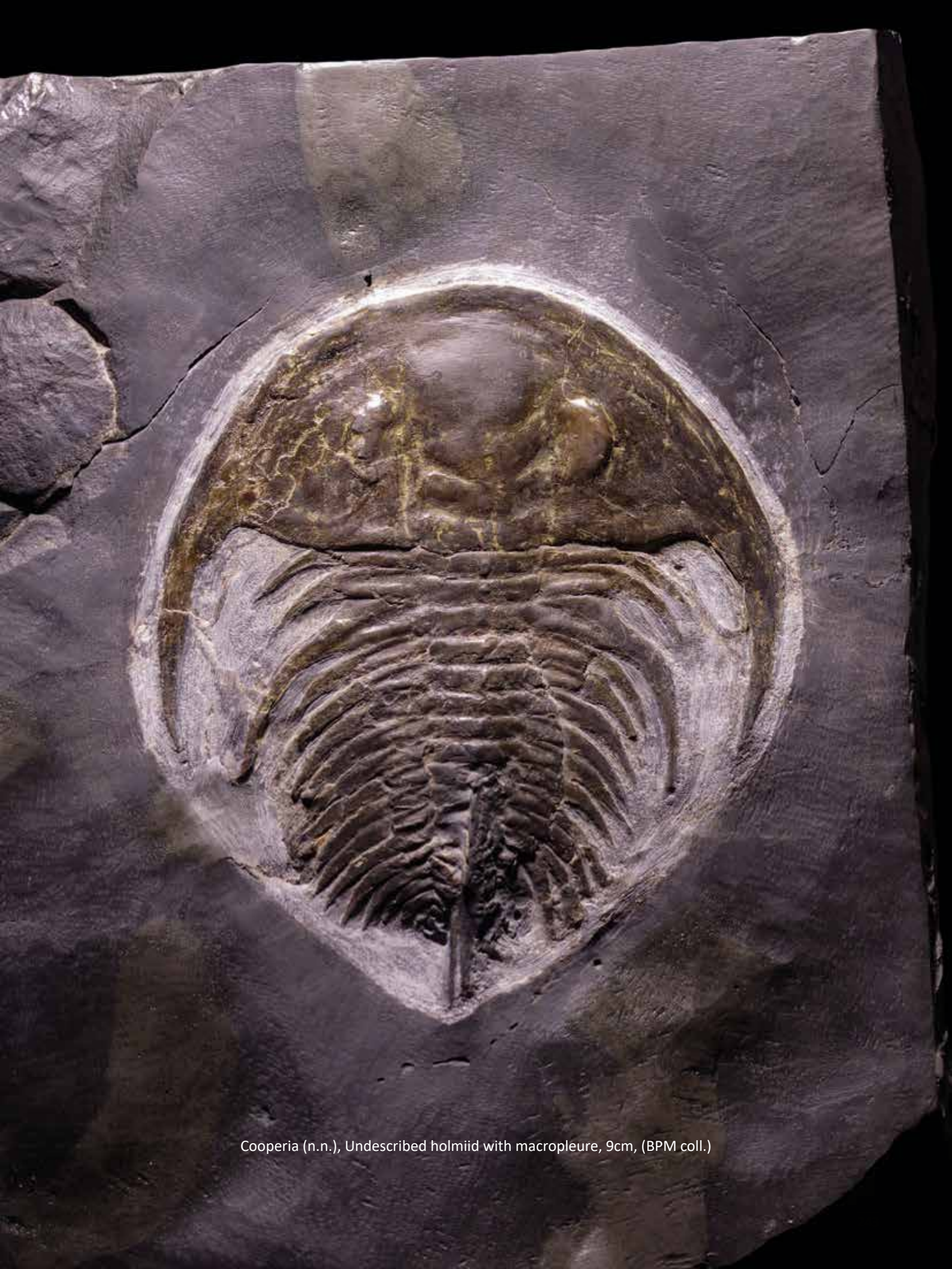
c



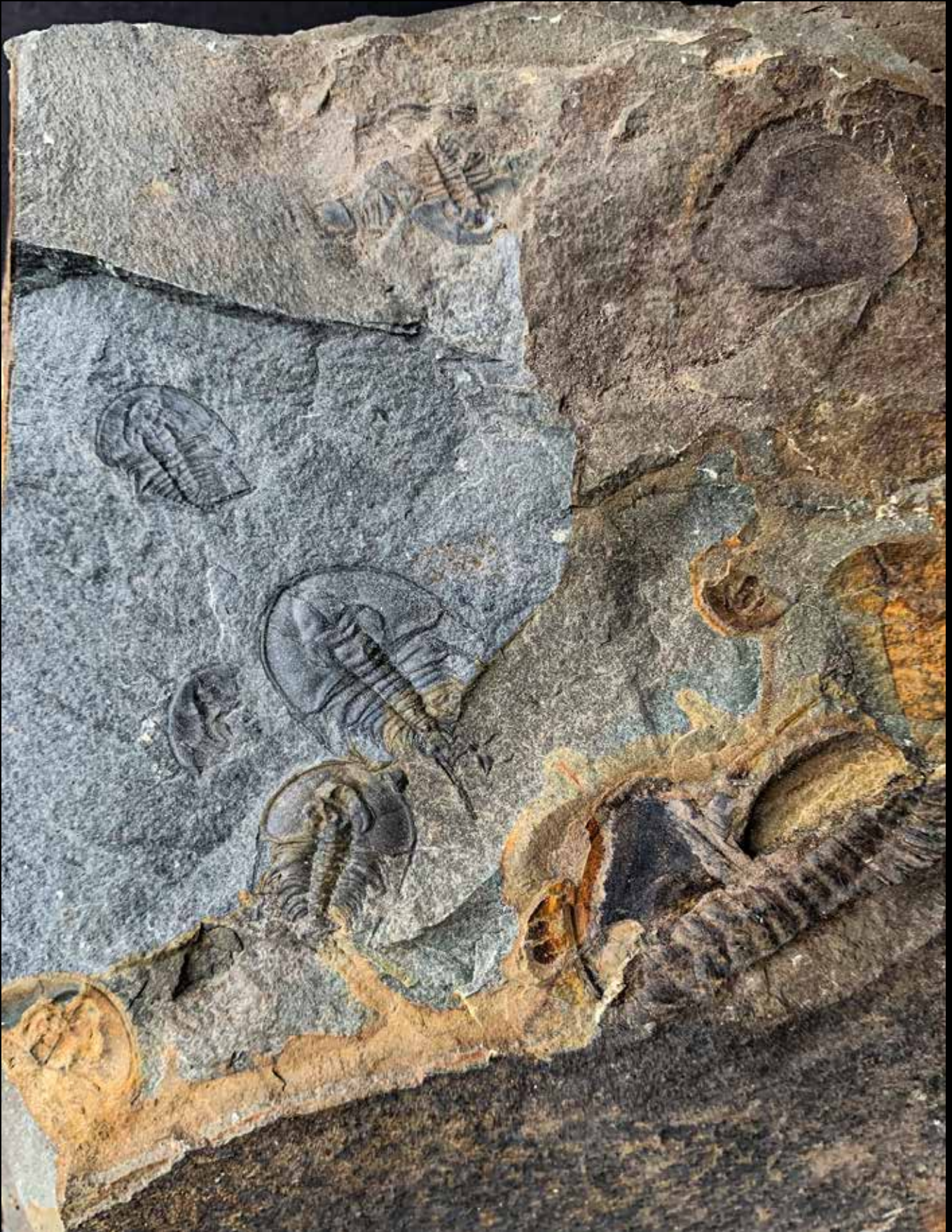
d

- a) *Lochmanolenellus subquadratus*, WEBSTER & BONACH, 2014, 5cm and 8.1cm wide tip-to-tip of the genal spines, (BPM coll.);  
b) *Keeleaspis* sp. FRITZ, 1972, 2.9cm, (BPM coll.);  
c) *Lochmanolenellus trapezoidalis*, WEBSTER & BONACH, 2014, 18cm, (BPM coll.);  
d) *Esmeraldina (Palmettaspis)* sp., 8cm, (BPM coll.)





*Cooperia* (n.n.), Undescribed holmiid with macropleure, 9cm, (BPM coll.)



d) *Olenellus cf. gilberti* MEEK in WHITE, 1874, 1.5 to 3cm, (C. New coll.)



a-b) *Olenellus* sp., 2.9cm and 2.7cm respectively, (BPM coll.);  
c) *Olenellus schucherti* RESSER & HOWELL, 1938, 3cm, (BPM coll.)



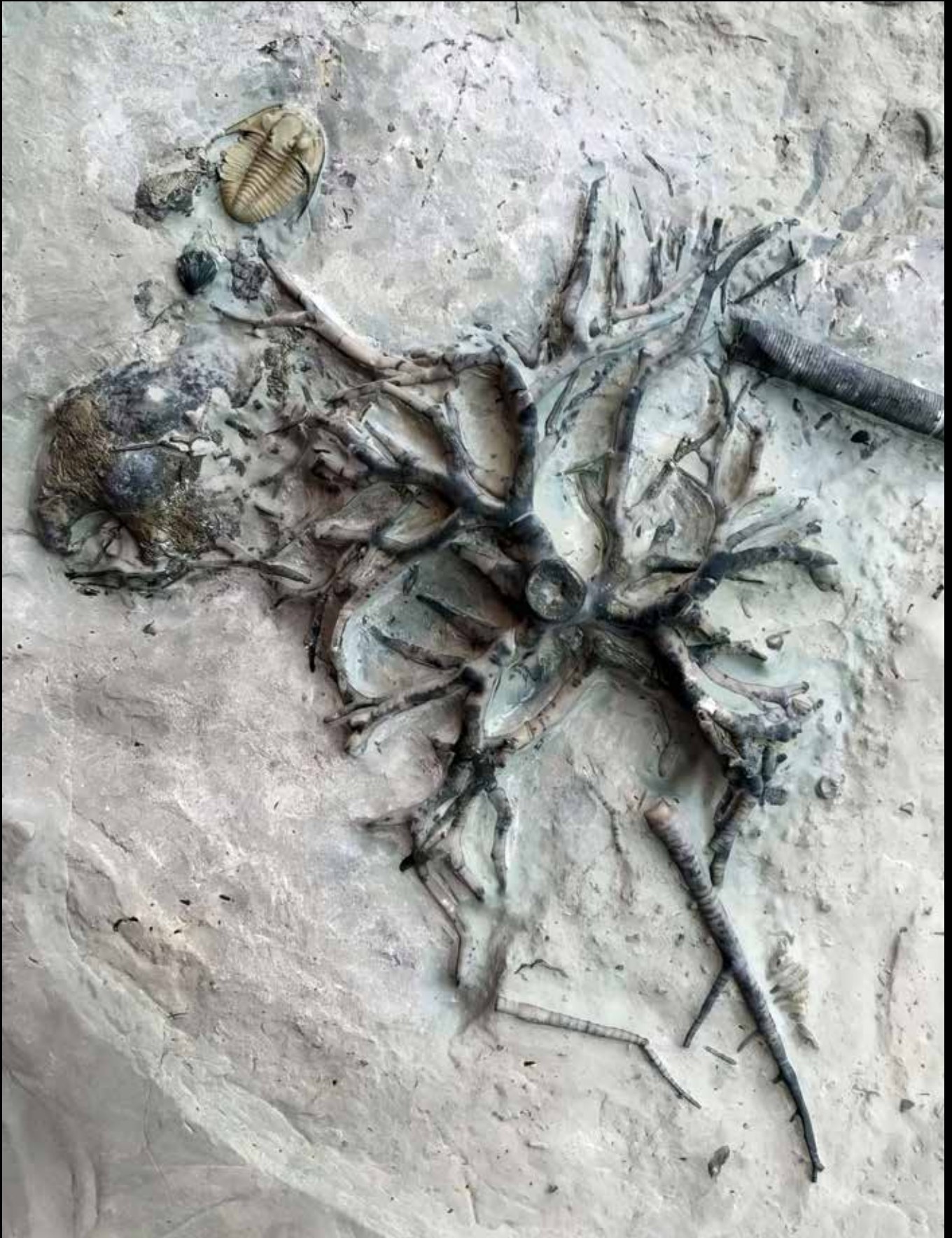
*Paradoxides davidis davidis* SALTER, 1863, 16cm, (BPM coll.)



*Parabailiella languedocensis* THORAL, 1946, 6cm, (BPM coll.)



a) *Ptychopyge orientalis* KOBAYASHI, 1951, 8.5cm, (BPM coll.);  
b) *Ptychopyge* sp., 7cm, (BPM coll.);  
c) *Illaenus sarsi* JAANUSSON, 1954 and two Orthoceratids, 5cm and 21cm respectively, (BPM coll.)



*Maurotarion christyi* HALL, 1864, 2.3cm and *Eucalyptocrinites crassus* HALL, 1863, (BPM coll.)



Lichida (Undescribed), 39cm, (BPM coll.)  
As of today, the biggest known trilobite found in the USA.





a



b



c



d



e



f

- a) *Pedinopariops* sp., (P. Taghon coll.);  
 b) *Neomethacanthus stellifer* BURMEISTER, 1843, (P. Taghon coll.);  
 c) *Pedinopariops richterianus geminus* VAN VIERSEN, TAGHON & MAGREAN, 2019 (top) and *Geosops icovellaunae* VAN VIERSEN, TAGHON & MAGREAN, 2019 (bottom), (P. Taghon coll.);  
 d) *Radiaspis* cf. *comes* BASSE, 2003, (P. Taghon coll.);  
 e) *Goldius endelsi* VAN VIERSEN, 2015, and *Dohmiella pooka* VAN VIERSEN, 2021, (P. Taghon coll.);  
 f) *Tropidocoryphe insciens* VAN VIERSEN, TAGHON & MAGREAN, 2019, 1cm, (B. Magrean coll.)

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*Megistaspis (Ekeraspis) hammondi* CORBACHO & VELA, 2010, early Ordovician (Tremadocian), Fezouata Formation, Zagora, Morocco, 26cm, (BPM coll.)

*“The Back to the Past Museum Guide to Trilobites is a unique compilation of trilobites from different localities all over the world that shows like no other why we are so fascinated by these creatures. Fortunately, it is continuing with a new volume. Coming along with more unseen and spectacular specimens and new sites, the new volume is again a real must-have for every trilobite enthusiast.”*

*Mirco Alberti (Geologist)*

*“The second edition of the Back to the Past Museum Guide to Trilobites is not a repackaging of the first edition. It has intellectual heft but is still incredibly fun to flip through. The introductory material (the first half of the book) has been thoroughly updated with many new illustrations. And, to the delight of every trilobitologist and enthusiast, the book contains an ENTIRELY NEW set of exquisitely-illustrated vignettes on trilobite-bearing localities—42 in all! This book deserves a place of respect on our bookshelves right next to the first edition!”*

*Thomas A. Hegna  
Associate Professor*

*State University of New York at Fredonia, USA*

*“The Back to the Past Museum Guide to TRILOBITES II is an excellent complementary volume to the first. The chapters on morphology, palaeoecology, and classification have been updated, based on the recent scientific literature. Perhaps the biggest highlight is the showcase of spectacular specimens from Cambrian to Permian deposits from around the world that were not included in the first volume. TRILOBITES II should be an essential addition to the library of anyone with a passion for these ancient arthropods.”*

*John R. Paterson  
Professor of Earth Sciences*

*University of New England, Armidale, Australia*



**Enrico Bonino**

was born in the province of Bergamo in 1966. He received his degree in Geology from the Department of Earth Sciences at the University of Genoa. He currently lives in Belgium where he works as a cartographer specialized in the use of satellite images and geographic information systems (GIS). His proficiency in the use of digital-image processing, a healthy dose of artistic talent, and a good knowledge of desktop publishing software have provided him with the skills he needed to publish books in the paleontological domain. In addition to his passion for trilobites, Enrico is particularly interested in the life forms that developed during the Precambrian, and his avid interest in micropaleontology and amber inclusions, push him to explore the possibilities of extreme macrophotography for microfossils and paleoentomology.

**Carlo Kier**

was born in Milan in 1961. He holds a degree in law and is currently the director of the Azul Hotel chain. He lives in Cancún, Mexico, where he is involved in efforts to preserve the marine environment. At the age of sixteen, he began a long collaboration with Milan’s Museum of Natural History, but it wasn’t until 1970 that his true passion for trilobites began to take shape. Today, that passion has become the impetus behind one of the most important collections in the world. His tireless field research across the globe and his involvement with professionals in paleontology have given him the opportunity to describe new species of trilobites and other arthropods. His personal determination and the development of the Azul Sensatori hotel complex finally brought his dream to fruition: the Back to the Past Museum, the world’s first museum dedicated entirely to trilobites.

