Global Acritarch Database (>110 000 occurrences)

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4	Abstract. Acritarchs, are microfossils with of unclear biological affinities, mostly considered to be algalean algal affinity, are
5	of with great significance for studying the origin and evolution of early life on Earth. Acritarch data are currently dispersed
6	across various research institutions and databases worldwide, lacking unified integration and standardization. Palynodata was
7	the largest database of acritarchs, containing 1415 fields, 111 382 111 295 entries, 812 238 812 061 metadata items, and 7385
8	7369 references. However, it lacked references post-2007 and excluded geographic data. Here, we collected and organized
9	previous data, adding 2429 fields, 4531 entries, 1 882 0812 238 366-metadata points, and 424-415 references, to build a
0	"Global Acritarch Database" (GAD). The expanded database now contains a total of 39-43 fields, covering genera, species,
1	and related geological information (geological timescale, location, modern latitude and longitude, paleolatitude and
2	paleolongitude, stratum, and others), amounting to <u>115 947 115 860</u> entries, <u>2 694 6713 050 852</u> metadata, and <u>7816 7791</u>
3	references. Each entry is associated with fields that facilitate a better understanding of the geographical distribution and
4	changes over geological timescales of acritarchs, thereby revealing their temporal and spatial distribution patterns and
5	evolution throughout the history of the Earth. This article describes GAD version 1.0, which is available at
6	https://doi.org/10.5281/zenodo.13828633-https://doi.org/10.5281/zenodo.15208303 (Shu et al., 20252024).
7	1 Introduction
8	Acritarchs are organic-walled cysts of unicellular protists, first defined by Evitt (Evitt, 1963) as a group of "unknown and
9	possibly varied biological affinities consisting of a central cavity enclosed by single or multiple layers of walls, mainly
0	composed of organic materials" (Yin, 2018). Evitt (1963) also noted that acritarchs are an informal, practical classification
1	category with no taxonomic ranks above the genus level, suggesting the use of the International Code of Botanical

32 Nomenclature to name morphological genera and species without assigning them to a specific biological phylum (Wicander, 33 2002). Morphologically, acritarchs are typically single-celled microfossils ranging in size from a few micrometers to one 34 millimeter. The most common shape is spherical, and they can be either smooth or covered with spines (Mendelson, 1987). 35 Among these, Most of them have been interpreted as algal cysts (e.g., Colbath and Grenfell, 1995; Grey, 2005; Moczydłowska 36 and Liu, 2021)2022) only while a few are related to non-algal origins -(e.g., Butterfield, 2005; Schrank, 2003; Servais et al., 1997). Particularly for Precambrain acritarchs, some specimens with dividing cells have been attributed to animal possibly 37 38 representing eggs or exoskeletons of higher crustaceansembryos/diapause cysts (Cohen et al., 2009; Xiao et al., 1998; Yin et 39 al., 2007), giant sulphur bacteria (Bailey et al., 2007), plant spores, fungal spores, cyanobacterial remains, and or other groups holozoan affinity ((Butterfield, 2005; Colbath and Grenfell, 1995; e.g., Huldtgren et al., 2011; Yin et al., 2020Schrank, 2003; 40 41 Servais et al., 1997)., which are important for understanding the origin and early evolution of animals. Following the foundational work of earlier researchers, Fensome et al. (1990) made significant advancements by compiling a comprehensive 42 43 taxonomic index of acritarchs at the genus, species and infraspecific levels, thereby significantly enhancing the standardization 44 of classification criteria within the field. Evitt (Evitt, 1963) also noted that acritarchs are an informal, practical classification 45 category with no taxonomic ranks above the genus level, suggesting the use of the International Code of Botanical 46 Nomenclature to name morphological genera and species without assigning them to a specific biological phylum (Wicander, 47 2002). Morphologically, acritarchs are typically single celled microfossils ranging in size from a few micrometers to one 48 millimeter. The most common shape is spherical, and they can be either smooth or covered with spines (Mendelson, 1987). 49 genuslevels, thereby Acritarchs have been discovered in sedimentary rocks from marine and terrestrial aquatic environments, 50 with records from all continents, spanning from the Proterozoic to the present. The oldest and most well-preserved acritarchs 51 are derived from approximately 1.8 billion years ago in Mesoproterozoic rocks (Buick, 2010), with evidence suggesting these 52 rocks existed as far back as 2.5 billion years ago (Buick, 2010; Gaucher and Sprechmann, 2009). Due to their abundance, high 53 diversity, and widespread distribution in marine sediments (Lei et al., 2012), acritarchs Acritarchs are valuable for determining 54 chronological ages and biostratigraphic correlations for their high abundance, taxonomic diversity, and global distribution 55 patterns (Lei et al., 2012), particularly especially in Proterozoic and Paleozoic strata, where they are sometimes probably the 56 only preserved fossils present (Beraldi-Campesi, 2013; Wicander, 2002; Xiao and Narbonne, 2020). Aeritarehs have been discovered in sedimentary rocks from marine and terrestrial aquatic environments, with records from all continents, spanning 57 58 from the Proterozoic to the present. They are particularly valuable when combined with other fossil groups for regional and 59 global paleobiogeography and paleoecology research (Dale, 2023; Lamb et al., 2009; Mudie et al., 2001). Finally Additionally, 60 acritarchs represent primary producers at the base of the marine food chain in the Proterozoic and Paleozoic Eras (Wicander, 61 2002), and played an important role in the evolution of global marine ecosystems (Falkowski and Knoll, 2011). Given their 62 significance, it is crucial to establish a global database.

The compilation history of acritarch databases datesdean be traced back to the 1970s. Tappan and Loeblich (Tappan and Loeblich, 1973) pioneered systematic statistical work in this field, by publishing a dataset covering the interval from spanning

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0-700 Ma. However, this early compilation exhibited relatively coarse temporal resolution, and limited datathe data were apparently not abundant. Even for the Ordovician, which had the highest data density, fewer than 500 species were recorded the number of recorded species was less than 500. Between 1971 and 2010, John Williams compiled the "John William Index of Palaeopalynology", which documented 1577 genera. AThe digitized version of this catalog is now archived in the Acritax online database (https://www.mikrotax.org/Acritax). In the 1990s, with support from the Geological Survey of Canada (GSC), the Palynodata database was developed, integrating extensive acritarch records. Its final version, released in 2006, was published Its final updated version (2006) was released **GSC** Open (http://geopub.nrcan.gc.ca/moreinfo e.php?id=225704), containing 144 fields, 111 295-350 entries, 812 061-450 metadata items, and 736972 references.

Despite advances in acritarch research, several challenges remain. First, the morphological diversity and complex classification of acritarchs have limited our understanding of this group (Agić et al., 2015; Arouri et al., 1999; Bernard et al., 2015; Butterfield and Rainbird, 1998; Javaux and Marshal, 2006; Moldowan et al.,1996; Wang et al., 2022; Williams, 1998). Second, although many acritarchs have been discovered, global spatial and temporal distribution remains uneven, with certain regions experiencing relatively weak research (Gray and Boucot, 1989; Huntley et al., 2006; Jacobson, 1979; Lei et al., 2013; Schreck et al., 2017). Additionally, existing acritarch databases are often limited to specific regions or periods and lack comprehensive, systematic, and complete global coverage (Anderson et al., 2017; Bernardi et al., 2011; Chamberlain et al., 2016; Servais et al., 2003; Williman and Moczydłowska, 2011). These limitations hinder further research on acritarchs in geological history.

 Here, we introduced a database that integrates global acritarch data from various geological periods, including genus, geographical distribution, and geological timescales. In the following sections, we provide information regarding data sources and selection criteria, review and clean the definitions behind entries, fields, and metadata, and outline the process. We explored the extensive compiled spatial and temporal trends, discussed the future uses and limitations of the dataset, and addressed the ongoing goals of the database. By leveraging this global database, we can better understand the diversity and evolutionary patterns of acritarchs and reveal the structure and function of biological communities in geological history. It not only provides references for oil and gas exploration but also promotes interdisciplinary research. Through in-depth data mining and analysis, we can explore the acritarchs' stratigraphy, and environmental and ecological issues throughout the history of the Earth, ultimately providing new research ideas across different fields.

2 Methods

2.1 Compilation purpose

The affinities of acritarchs are primarily linked to algae, suggesting that acritarchs were the main contributors to primary productivity in early oceans, paving the way for the subsequent rise of consumers (Agić, 2016; Daners et al., 2017). This implies that they played a crucial role in early marine environments and were important for maintaining ecological balance

and carbon cycling. Quantitative analysis of fossils (e.g., acritarchs) from different strata allows better understanding of past changes in marine environments, including shifts in marine productivity, redox conditions, and carbon cycling. This aids in exploring the evolution of deep-time biological pumps and enhances our understanding of the processes and mechanisms behind the modern marine carbon cycle (Jia et al., 2022). Previous databases (Table 1), such as Palynodata (https://paleobotany.ru/palynodata, last access: 10 December 20244 April 2025), containing a large number of acritarchs, exhibit several shortcomings: 1) the database only includes literature from 1842 to 2007, with no records for the following 17 years; 2) the numeric ages of strata in the database have not been updated; 3) despite including 1415 fields, Palynodata lacks critical information such as latitude, longitude, lithology, stratigraphy, and paleogeography. In contrast, the Paleobiology Database (PBDB, https://paleobiodb. org/, last access: 4 April 202510 December 2024) only collects a small amount acritarch data (866 entries). In summary, previous databases exhibit issues such as incomplete data, difficulty in addressing fossil sampling biases, and inapplicability for studying spatiotemporal changes. Therefore, we aim to build a global acritarch database (GAD) to advance research in this field.

Table 1. GAD: Comparison of data sources from Palynodata, PBDB, this study.

Data base	N of all entries (i.e., rows)	Proportion	N of all metadata (i.e., cells with content)	Proportion
Palynodata	111 382 <u>111 295</u>	96.06%	<u>812 238</u> 812 061	30.15
				<u>26.62</u> %
PBDB	34	0.03%	<u>352425</u>	0.01%
This study	4531	3.91%	1 882 081 <u>2 238 366</u>	69.84
				<u>73.37</u> %
GAD	115 947 <u>115 860</u>	100%	2 694 671 3 050 852	100%

2.2 Metadata fields and criterion

GAD data come from PBDB, Palynodata, and published literature. From PBDB, 34 entries and 352-425 metadata points are sourced from seven studies. The main component of the database was derived from Palynodata (Kroeck et al., 2022; Palynodata Inc. and White, 2008; Strother, 2008) contains 1415 fields, 111 382111 295 entries, and 812 238812 061 metadata points, but it has not been updated since 2007 and its location information is limited to textual descriptions. In this study, we searched recent publications through Google Scholar using keywords (such as acritarchs, organic-walled microfossils) and collected 424-415 additional literatures from 2008 to 2023. This collection includes 24-29 new fields, i.e. geological timescale (with uniform high-to-low levels: Eon, Era, Period, Epoch, and Age), modern latitude and longitude, paleolatitude and paleolongitude, stratigraphy, and lithology, totaling 4531 entries and 2 238 3661 882 081 metadata points. We have revised and updated the numeric age to the latest International Chronostratigraphic Chart (2023/09) (https://stratigraphy.org/). Some of the entries that have not been updated include data without temporal information, entries spanning multiple periods, and ambiguously described Precambrian data. The aforementioned three sources together form a new database, GAD, containing

125 <u>115 860115 947</u> entries, <u>39 43</u> fields, and <u>3 050 8522 694 671</u> metadata. The database <u>did not don't include contains exclusively</u>
126 any unpublished data. The metadata primarily originated from original journal articles, supplements, or public repositories
127 containing data tables. The included fields were organized to facilitate future updates of speciation/extinction models,
128 taxonomic nomenclature corrections, data additions, and other research directions such as genus and species information,
129 lithological details, geological timescales, and sampling locations, thereby enabling continual data updates.

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2.3 Data cleaning

To maintain clarity and consistency in data description, an "entry" refers to each genus and species along with its related metadata as reported in the literature (i.e., a row), while a "field" refers to the metadata collected for each entry (i.e., a column) (Judd et al., 2022).

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136 To ensure accurate publishing and better utilization of the data, we have cleaned the data using the following steps.

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138 (1) All entries are integrated into a single data table, including entries that lack at least one type of information such as "genus 139 name without species name", "genus and species name without temporal information" or "genus and species name without 140 location information". These were treated as separate entries to preserve them for possible future data replacements. Many acritarch data from Cambrian were compiled by Palacios et al., (Palacios et al., 2009, 2012, 2014, 2017, 2020, 2021), 141 142 Ordovician data by Le Hérissé et al. (Le Hérissé et al., 2007, 2014, 2015, 2017; Paris et al., 2007; Vecoli and Le Hérissé, 2003), 143 and Silurian and Devonian data by Vavrdová et al. (Vavrdová and Dašková, 2011; Vavrdová and Svobodová, 2010; Vavrdová 144 et al., 1996, 2011). Wherever possible, these compiled datasets were cross-checked with their original publications to ensure 145 completeness, avoid errors, and fill in missing data or applicable fields.

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147 (2) Taxonomic field: acritarchs are generally considered form-taxa and are morphologically identified at the genus/species 148 level the classification of acritarchs was used to name morphological genera and species. During data cleaning, we regulated 149 the representation of "sp." and punctuation marks, such as question marks, commas, parentheses, and minor spacing issues 150 were removed to standardize the naming format and ensure proper characterization (Fig. 1). Considering that this database 151 containsed biological fossils, outdated taxonomies or misspellings may have led to analytical errors. We traced back to original 152 publication to validate taxonomic reliability for each taxonomic entry (those questionable or illegitimate taxa, invalidly named 153 taxa, taxa retained in open nomenclature, etc.) and implemented PyRate to check for spelling errors and inconsistencies among 154 the listed species (Silvestro et al., 2014, 2019). The function check names was utilized, which requires a text file with one 155 species name per line. In the returned file, ranks 0 and 1 indicated the most likely spelling errors, whereas ranks 2 and 3 156 represented genuinely different names. It is noteworthy that this algorithm does not check for synonyms. Ultimately, species 157 data accounted for 90.7% of the database, with 19.4% represented by "sp.".

(3) Time-Age field (includes 12 separate columns collectively): during data integration, several entries lacked temporal information or had insufficient resolution. Therefore, temporal information at the stage level was supplemented to ensure consistent information retrieval (Fig. 2). If precise data were unavailable, the highest possible resolution level was retained, using the stage level as the primary reference, including numeric ages (in Ma), Period, and Stage information to provide relative ages. Ages were assigned by entering a numeric age and automatically matching to fill in relative age information, or retaining manually entered numeric and relative ages. If the numeric age was not recorded in the literature, it was manually set the age of the top and bottom of its strata using the latest International Chronostratigraphic Chart (2023/09). In the absence of a precise numeric age, a stage position (i.e., early, middle, or late) was used to further define the relative age and match it with the numeric age. Entries with numeric age records accounted for 89.9% of the database, and the remaining 11.1% (11-73811726 entries) lacked numeric age data (Table 2). Additionally, entries with genus and species names were resolved to the stage level once supplemented, and they accounted for 34.8% of the total data (excluding entries in which the numeric age could not be determined).

(4) Location field (includes 9 separate columns collectively): during data integration process, it has been observed that only broad location information was available. To enhance the application of the data in the geospatial field, a minor location information field was added, specifically the "point" (the center point of text location information) determined by latitude and longitude (Fig. 1). After supplementation, latitude and longitude information accounted for 82.0% of the database. Modern latitude and longitude information were derived from detailed references to Google Satellite Electronic Maps (http://www.gditu.net). If location information was not recorded in the literature, it was left blank. When it was impossible to determine the precise location, the latitude and longitude information of the center point of the broader location were added to the remarks field. affecting entries. Paleolatitude conversion primarily relied G-Plates (https://www.gplates.org/download/, version 2.5), and map alignment was performed using QGIS (https://qgis.org/download/, version 3.32.3). All maps were based on Scotese (Scotese, 2021).

(5) Lithology and stratigraphy information covered only 0.11% and 2.7% of the total entries in the database, respectively, accounting for a very small proportion. The data on lithology and stratigraphy is the next priority for addition.

(6) The reference field achieved 100% coverage in the database. It included the main (first) author, publication year, and journal. DOI of relevant literature were supplemented through Crossref (https://www.crossref.org/).; however, the DOI for each publication was not retained. The corresponding information is expected to be completed in future updates and replacements. Concurrently, for the convenience of machine reading, special characters, and garbled combinations in other applicable fields were deleted.

192 Each field was evaluated based on a set of standardized criteria to ensure consistency throughout the process (Fig. 1). Any

issues discovered during this process were corrected. A summary of entries by fields is shown in Table 2.

Site

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- Do we need to select a detail location?
- · Is longitude and latitude represented in the literature?
- Is there a map of the selected location in the original report?
- · Is the symbol correct?

iteratur

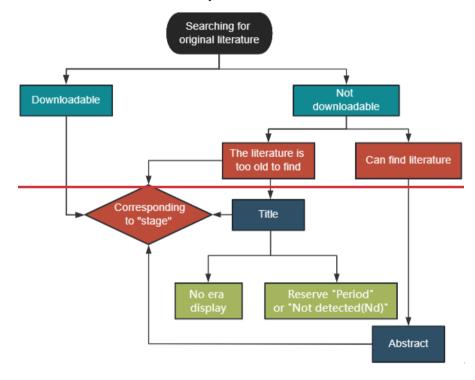
- · Can we download the original literature?
- · Can we find the DOI?
- · Is the spelling of the first author's surname correct?
- · Is the publication year correct?
- Is there any error in the format?

Are there any spelling errors?Is there any formatting error?

Others

- Can it correspond to the times?
- Is there a description in the original publication?

Figure 1. Criteria are used to evaluate whether each entry matches a field.



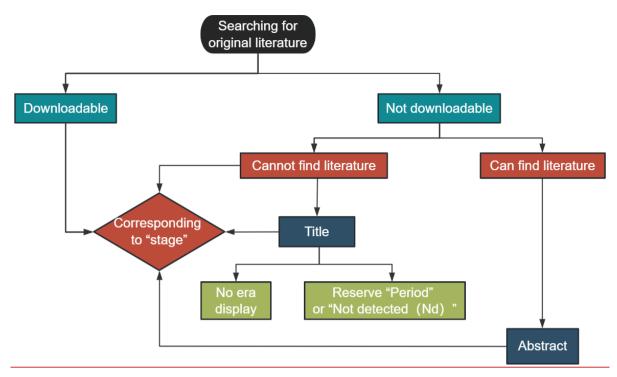


Figure 2. Specific supplementary process for stage level.

Table 2. Summary of entries by fields.

Fields		N of all entries	Proportion	Notes		
Taxon	With species name	105 191 <u>105 103</u>	90.7%	There are 20 395 2	20 374 inde	finite species,
filed				accounting for 19.49	% of "With s	pecies name".
	Without species name	10 75 76	9.3%	Refers to the genus	level.	
Total		115 947 <u>115 860</u>	100%			
Time	With age	104 209 <u>104 134</u>	89.9%	Include	Entries	
Age field					N	Proportion
				Eon level	104 134	100%
					104-209	
				Era level	<u>101 149</u>	97.1%
					101-224	
				System level	91 476	87.8%
					91 538	
				Series level	60 286	57.9%

						60-325	
					Stage level	<u>36 187</u>	34.8%
						36 233	
					Substage level	<u>5996</u>	5.7%
						5999	
	Without age		11 738 <u>11 726</u>	10.1%	This includes all e	entries that car	nnot detect the
					numeric age.		
					Include	Entries	
						N	Proportion
					Eon level	2082	17.7%
						<u>2070</u>	
					Era level	<u>415403</u>	3.5%
					System level	12	0.1%
					Cross level	2525	21.5%
						<u>2520</u>	
					Not detected	7131	60.8%
Total			<u>115 860</u> 115 947				
Location	With modern	latitude and	95 084 <u>94 997</u>	82.0%	This contains 17	96 entries fro	om oceans or
field	Without modern latitude and longitude records				seas, accounting f	or 1.9%, and	9 3 288 93 201
					entries from contin	nents, account	ing for 98.1%.
			20 - <u>20</u> 863	18.0%	This includes 626	4 entries that	have location
					names but canno	ot determine	latitude and
					longitude, account	ting for 30.0%	•
Total			<u>115 860</u> 115 947				
Others	Lithological f	field	128	0.11%			
	Occurrence	Incomplete	50 311 <u>50 288</u>	43.4%	Judgment principl	e: whether the	ere is a species
	status	Complete	65 636 <u>65 572</u>	56.6%	name, numeric ag	ge, and moder	n latitude and
					longitude.		
	Stratigraphic field		3122	2.7%			
	Reference field		115 860	100%			
	Reference field DOI		<u>20 903</u> 115 947	100 18.1%			

3.1 Data statistics

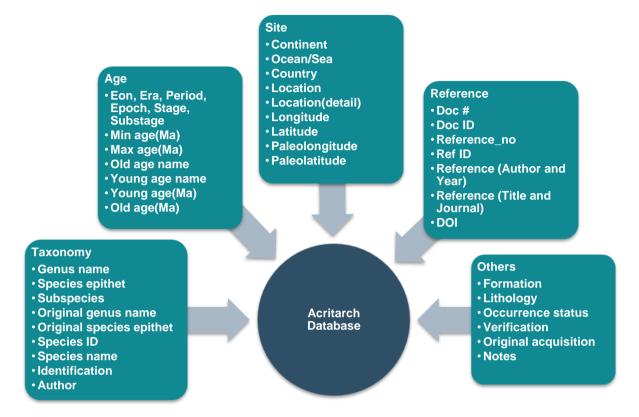


Figure 3. Classification of each field in database settings.

Each entry in the GAD is associated with a set of fields, all of which represent information related to fossils. There are 39 fields can be broadly divided into five categories (Fig. 3): (1) taxonomy, (2) time, (3) site, (4) reference, and (5) others. A basic description of these fields can be observed in Table 3, with details on how and why each field was assigned.

Table 3. Detailed description and notes for each field.

Category name	Description of Category (Individual fields)	Notes
Taxonomy		
Genus name	Genus names of biological fossils.	Unified format, all data available.
Species epithet	Species epithetname of biological fossils.	It may contain blank spaces or sp.
Species		
Subspecies	Subspecies names of biological fossils.	It may contain blank spaces.

Original genus	Record of genus name				
name					
Original Species	Record of species epithetname.				
epithet name					
Species name	Species name of biological fossils.				
Species ID	The serial number of the species.				
Author	The name of indefinite species.	It may contain blank spaces.			
Identification	Used to explain "aff. /cf. /certain/".	•			
TimeAge					
Eonothem/Eon	The unit of time representing the longest time, typically used	Source: International			
	to describe geological periods exceeding billions of years.	Chronostratigraphic Chart			
Erathem/Era	A unit of time under the Eon, typically referring to a large	(2023/09)			
	period lasting several hundred million years.	(https://stratigraphy.org/)			
System/Period	A unit of time under the Era, typically indexed to a period of	•			
	tens of millions year.				
Series/Epoch	A unit of time under the Period, typically measured in				
	millions to tens of millions of years.				
Stage/Age	A unit of time under the Epoch, each stage typically	•			
	represents a time span of several million years.				
Substage	A unit of time under the Stage, usually used to describe a	•			
	shorter period within the stage.				
Min Age (Ma)	Numeric age of the lower boundary of stratigraphic age.	•			
Max Age (Ma)	Numeric age of the upper boundary of stratigraphic age.	•			
Old Age Name	The lower boundary of stratigraphic age.	Keep the original division.			
Young Age Name	The upper boundary of stratigraphic age.	•			
Old Age (Ma)	Numeric age of the lower boundary of stratigraphic age.	•			
Young Age (Ma)	Numeric age of the upper boundary of stratigraphic age.	•			
Site					
Continent	The continent where the geographical location is located.				
Ocean/Sea	The sea area where the geographical location is located.				
Country	The country where the geographical location is located.				
Location	The major locations where the original data is used.	Including sectors, may be precise			
		to a province or country.			

Location (Detail)	Fixed point determined by longitude and latitude.	
Longitude	Longitude determined by location.	If it is not represented in the
Latitude	Latitude determined by location.	literature, use the center of the "location" to represent it.
Paleolongitude	The longitude of a certain period and location in geological history.	According to modern latitude and longitude conversion.
Paleolatitude	The latitude of a certain period and location in geological history.	-
Reference		
Doc#	The serial number of literatures in Palynodata.	Unified format, All data available
Reference (Author	Literature information includes author, year, title, and journal.	-
and Year)		
Reference (Title and		
<u>Journal)</u>		
DOI	A permanent link to the literature.	-
Ref ID	The serial number of literatures in GAD.	-
Doc ID	The serial number of literatures in the database (Supplement for 2008-2023).	-
Reference_no	The serial number of literatures in PBDB.	-
Others		
Formation	Stratigraphic information of fossils.	Insufficient data volume.
Lithology	Lithological information of fossils.	-
Occurrence status	Whether the information records are complete or not.	
Verification	Returning to the original to verify information.	
0::1::::::	Acquisition status of original literature.	
Original acquisition	requisition states of original increase.	

3.2 Statistics of the GAD Statistics

The GAD contains 115-115 860947_entries from 7816-7791 references, representing 2993-1146 different sampling locations and records throughout geological history. Among these, 36 18736-233 are marked as "stage level", covering 101 out of the 102 stages in the Phanerozoic. In terms of biological fossil records, the database included 1456 genera and 98653 species (excluding those classified as sp.). During the process of correcting the numeric age, 7131 data points lacked a numeric age due to the inability to obtain geologic age from the original literature. The Paleozoic is the most well-represented, accounting for 70.9% of total entries (Table 4), followed by Mesozoic (13 04413-071 entries) and Neoproterozoic (90403 entries). Regarding the spatial distribution of acritarchs, 93 28893 201 entries originated from the continent, with a small portion from oceanic or marine areas accounting for 1.9%.

The sections below focus on fossil classification, literature sources, paleogeographic and spatiotemporal distribution trends. These examples illustrate the unique aspects of this compilation method and demonstrate the potential of the database for promoting research in paleoproductivity, paleoenvironment, and biological evolution.

Table 4. Summary of the proportion of entries and sites by geologic era.

Era	All entries	All sites			
	N	Proportion	N	Proportion	
Cenozoic	600 4 <u>5997</u>	5.9%	54 <u>66</u> 73	6.2%	
Mesozoic	<u>13 044</u> 13 071	12.9%	<u>11 911 11 938</u>	13.5%	
Paleozoic	72 074 <u>72 024</u>	70.9%	<u>61 717</u> 61 767	69.6%	
Neo-Proterozoic	904 <u>0</u> 3	8.9%	816 <u>2</u> 5	9.2%	
Meso-Proterozoic	1251	1.2%	1167	1.3%	
Paleo-Proterozoic	196	0.2%	191	0.2%	
Total	<u>101 552</u> 101 639	100%	<u>88 614</u> 8 8 701	100%	

3.3 Taxonomy statistics

At the genus level, the database included 1456 genera and 98653 species (excluding sp.). The top ten genera, in terms of quantity that account for 36.0% of the total data volume, are *Baltisphaeridium* (7.0%), *Micrhystridium* (6.7%), *Veryhachium* (5.7%), *Leiosphaeridia* (3.9%), *Multiplicisphaeridium* (2.7%), *Cymatiosphaera* (2.7%), *Tasmanites* (2.1%), *Leiofusa* (1.8%), *Acanthodiacrodium* (1.8%), and *Lophosphaeridium* (1.5%), the specific number of entries can be obtained in the Figure 4. *Baltisphaeridium* (including 647 species accounting for 8076 entries in the database, with 337 entries having only the genus name and 1049 entries classified as sp.), the most abundant genus, has been present since the Precambrian (approximately 1600 Ma) and was is most prolific during the Paleozoic Era (including 647 species accounting for 8079 entries in the database, with 337 entries having only the genus name and 1050 entries classified as sp.).

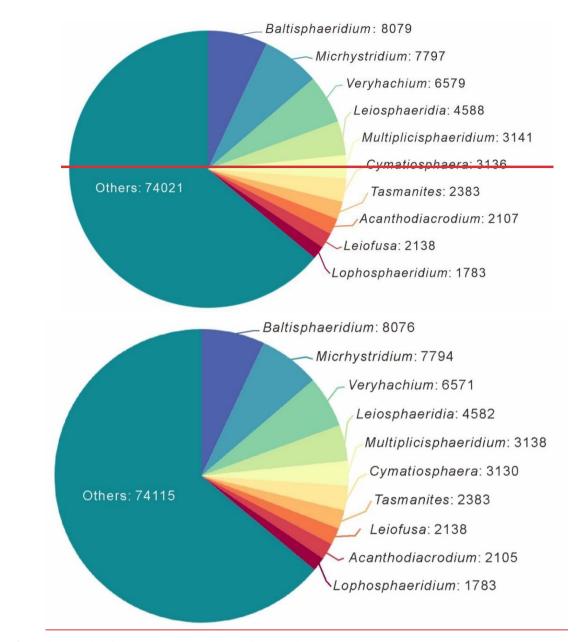
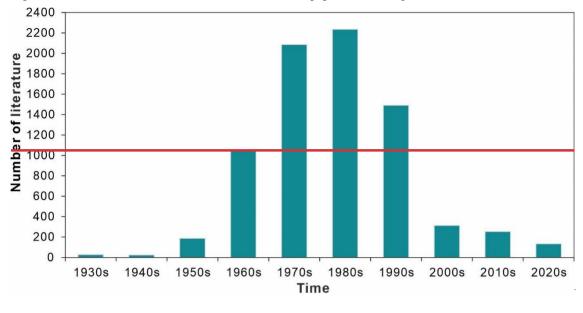


Figure 4. Statistical pie of the occurrence number of genera in the database.

3.4 Literature sources and statistics

Data in this database were obtained from 7816-7791 references, spanning from 1842 to 2023. The temporal distribution of publication years is presented in Fig. 5. The average number of research outputs after 1930 (83.9 papers/per year) is an order of magnitude greater than that before 1930 (0.12 papers/per year). This difference is not significant in the overall context number and was thus not displayed on the graph. Even the relatively lower research outputs of the 1950s and 2020s

were more than 2.5fold higher than the total output from the 1930s and 1940s combined over 20 years. More than half of research output occurred in the 1970s and 1980s, with 4322-4320 papers accounting for 55.355.4% of the total.



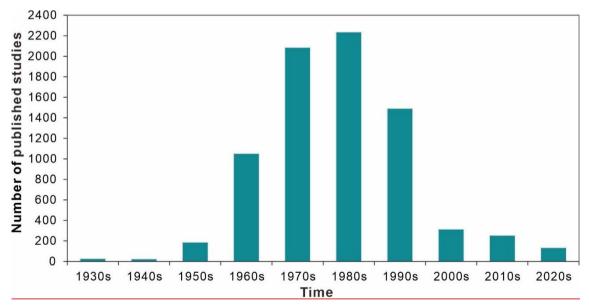


Figure 5. Statistics of publication distributions in the database.

3.5 Temporal distribution

Figure 6a indicates that over a long timescale, data volume steadily increases during the Proterozoic but remains below 5000 entries, peaking in the Ediacaran with 3137 entries. However, there are almost no records for the Paleoproterozoic, accounting

for only 1.9% of the Proterozoic data. The Ordovician (Paleozoic) exhibits the highest number of entries at-21 88021-898, followed by a decline to the Carboniferous low point of 1682 entries. Subsequently, a minor peak occurs during the Cretaceous (595984 entries) before the data volume dropped below 5000 entries. Figure 6b presents the maximum data volume of 4442 4431 entries during the Tremadocian Darriwilian (Ordovician), whereas the minimum is zero during the Jiangshanian (Cambrian). Two significant increases in data density occur at the intersections of Stage 10 and the Tremadocian Darriwilian (Cambrian-Ordovician) and between the Dapingian and Darriwilian (Ordovician). Four significant decreases occur at the transition between the Darriwilian and Floian (Ordovician), Darriwilian and Sandbian (Ordovician), Lochkovian and Pragian (Devonian), and Famennian and Tournaisian (Devonian-Carboniferous). Such data distribution may be attributed to 1) limited research intensity and 2) low temporal resolution in the study area, both of which constrain the availability of material for analysis.

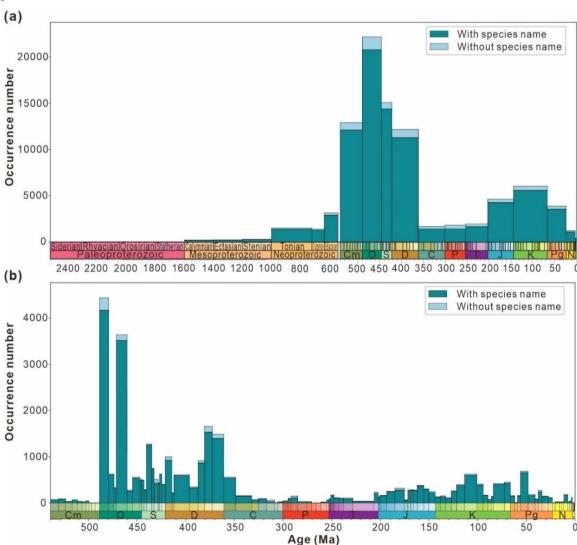


Figure 6. The number of entries from "have digital age" data split the "timescales include 2500 Ma" (a) and Phanerozoic (b) and binned by geologic stage. Each stage is divided into data with species name and data without species name for statistics according to the storage type of the genus and species field in the database.

3.6 Spatial distribution

The spatial distribution of data collection was inherently uneven. In terms of its modern distribution (Fig. 7), the peak in the longitudinal distribution lies primarily between -10° to 30°, with a small amount collected between -50° to -90° and 90° to 130°. According to the latitudinal distribution, most of the data are from the Northern Hemisphere, from (Europe, China, and North America) and predominantly between 25° and 65°, accounting for 82.0% of the GAD. Figure 8 presents the modern geographic distribution by Era. Most Precambrian data, primarily source from China and Europe, accounted for 86.4% of the total, whereas most Phanerozoic data are from North America, Europe, Australia, and China, accounting for 93.2%. The Cenozoic and Paleozoic data exhibit the widest spatial distribution (-176.2° to 176.1°), with the Paleozoic containing the highest quantity of data (61 717 61.767 entries, representing 69.6% of the total geographic data).

The paleogeographic distribution of data across periods (Fig. 9) highlights how data are concentrated in different regions over time. The diagram indicates that most of the data from the Cambrian to the Quaternary are from shallow marine environments, favoring continental edges. As the continents migrated northward from the Mesozoic to the Cenozoic, records begin to concentrate in the mid-latitude regions in the Northern Hemisphere. Taking the peak values of each period as examples and starting with the Cambrian, the highest data concentration is observed between -35° and -45° (3688 entries), mainly in Gondwana and the Baltic, which shifted to -25° and -35° (3638-3708 entries) by the Ordovician. In the Carboniferous, the highest data concentration is near ±5° to -15° (468 entries) in the North American and Eurasian plates. In the Permian, data are evenly distributed across the mid-latitude regions near the coast of the Tethys Ocean in both hemispheres. Thereafter, fossil records start to tilt towards the mid-latitude regions of the Northern Hemisphere (such as North America, Europe, and Asia) during the Mesozoic and Cenozoic. The highest data concentrations were between 25° and 35° during the Triassic, and moved to between 35° and 45° and between 45° and 55° during the Jurassic-Cretaceous and Paleogene-Quaternary periods, respectively.

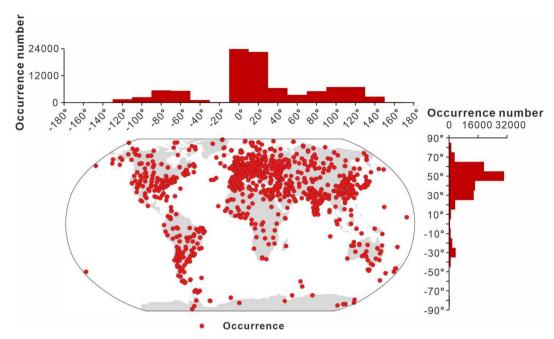


Figure 7. Spatial distribution of all data from the GAD.

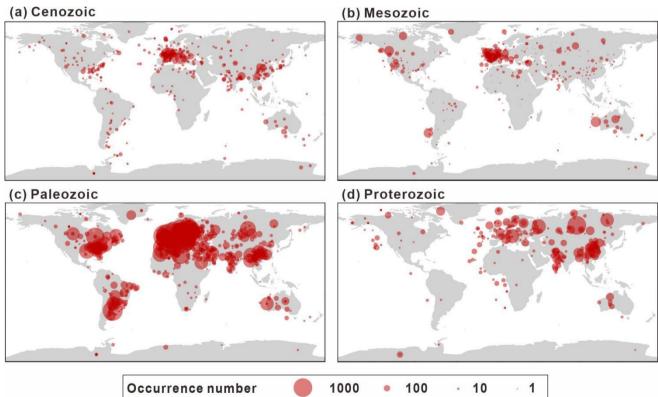


Figure 8. Summary of the spatial distribution of sampling sites by era (**a**–**d**), with the size of each point scaled to the number of occurrences at each site. All panels are plotted on the same scale.

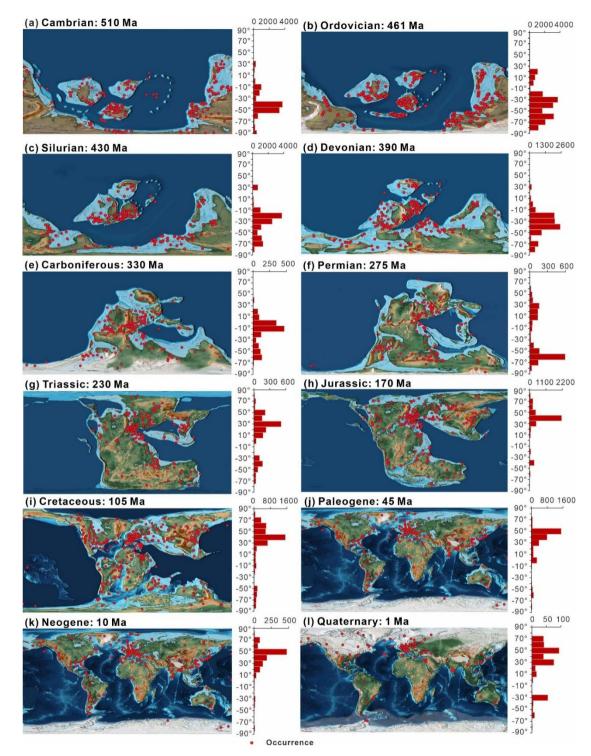


Figure 9. Summary of the paleogeographic spatial distribution of sampling sites, (a-1) separated by geologic period. Histograms to the right of each map show the relative latitudinal distribution of all unique sampling sites within 10° bins, with

the horizontal axis representing the number of occurrences. The chronology number indicates the exact point in time for the map selection. For example, Ordovician: 461 Ma, representing the Middle Ordovician. All maps were based on Scotese (Scotese, 2021).

3.7 Spatial-temporal trends in proxy values

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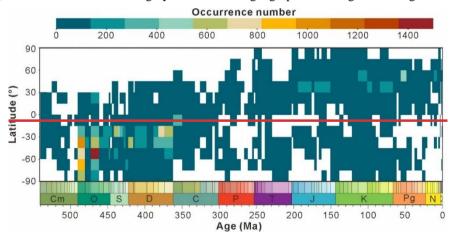
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The large volume and consistent structure of data in GAD provide opportunities to investigate research trends in acritarchs (e.g., regional research focus, taxonomic variations). allow for a comprehensive analysis of acritarch evolution over geological timescales. Figure 10 presents heatmaps for each time interval from database entries, where the data is temporally averaged by stage level and spatially into 4510° paleolatitude bins. Vertical trends indicate the latitudinal gradient for any given "stage", while horizontal trends indicate the temporal evolution of entries within latitudinal intervals. Notably, the data volume is predominantly observed in the mid-to-low latitudes of the Southern Hemisphere during the Paleozoic, with over 400 entries and peaks reaching above 1400. A clear migration pattern is observed, as the majority of data shift from the Southern Hemisphere to the Northern Hemisphere over time. On one hand, this may stem from sampling bias due to uneven research distribution; on the other hand, tTectonic movements appear to be a significant contributing factor This is related to tectonic plate movement as since the formation of Pangaea about 250 million years ago, the Gondwana gradually split apart. The plates of South America, Africa, Antarctica, Australia, and India have been drifting northward progressively, affecting the geographical pattern and biodiversity of the Earth (Park, 1988). However, spatial-temporal trend may be influenced by sampling biases arising from uneven research distribution, as well as inherent taxonomic uncertainties associated with acritarchs. The heat map (Fig. 10) clearly indicates that all entries exhibited discontinuous spatial and temporal coverage, but the Mesozoic (Cretaceous), Paleozoic (Ordovician and Devonian) generally exhibited good coverage, extending from 30° to -90°. During the Mid-Cretaceous, coverage reached 10090%. In contrast, the Paleozoic (Middle to Late Cambrian and Permian), Mesozoic (Jurassic), and Cenozoic exhibited highly discontinuous geographic coverage with a significantly reduced range.



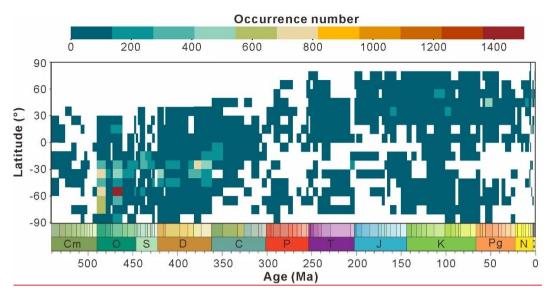


Figure 10. Summary of the spatial-temporal trends binned temporally by stage and spatially by 4510° paleolatitudinal bins, cooler colors correspond with lower number of occurrence and vice versa.

4 Data availability

- 325 All data for GAD (version 1.0) can be found on Zenodo: https://doi.org/10.5281/zenodo.15208303 (Shu et al.,
- 326 <u>2025</u>).https://doi.org/10.5281/zenodo.13828633 (Shu et al., 2024).

5 Code availability

- 328 All available example code and auxiliary functions have been uploaded on Zenodo: https://doi.org/10.5281/zenodo.15147118
- 329 (Shu, 2025)10.5281/zenodo.14350992(Shu, 2024).

6 Conclusions

Global Acritarch Database (GAD) is a global acritarch database that integrates data from Palynodata and Paleobiology Database (PBDB), and additional published literature not included in previous collections. Building on the foundation of Palynodata, which originally contained 1415 fields, 111 295 111 382 entries, 812 061 812 238 metadata points, and 7385 7369 references, GAD added 24-29 new fields, 4531 new entries, 1 882 081 2 238 366 new metadata points, and 424 415 new references, resulting in a database comprising 115 947 115 860 entries, 39 43 fields, 2 694 671 3 050 852 metadata points, and 7816 7791 references. GAD represents records from 2993-1146 different sampling sites spanning geological history from the Precambrian to Phanerozoic. The fossil records include 1456 genera and 98653 species (excluding sp.). Additionally, the database records information related to occurrences such as stratigraphy, lithology, and paleogeography. Among all entries, Paleozoic data are the most abundant, accounting for 70.9% of the total, followed by 13 07113 044 Mesozoic, 90403 Neoproterozoic, 59976004 Cenozoic, 1251 Mesoproterozoic, and 196 Paleoproterozoic entries. Regarding the spatial

distribution of acritarchs, 93 288 93 201 are derived from continents and primarily concentrated in Europe, North America,

342 China, and India, with the remaining 1.9% originating from oceanic or marine regions.

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Although substantial efforts have been made, the dataset remains incomplete. For example, information regarding the size dimensions of acritarchs, lithology, and strata are lacking and will be continuously supplemented in the future. Additionally, while meticulous care was taken to ensure accuracy, some errors may have been overlooked due to the sheer volume of data. When reusing GAD, we recommend citing both the GAD and original data sources to ensure proper attribution. Any issues or omissions discovered by the end users can be reported to us, and the relevant information will be updated in future versions of the database. GAD is expected to remain a valuable resource for ongoing and future research.

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Author contributions

- 352 Xiang Shu: Collected data, conducted database statistical analysis, and drafted a manuscript; Haijun Song, Daoliang Chu,
- 353 Yuyang Wu, Xiaokang Liu, Enhao Jia, Yan Feng, Yong Du, Wenchao Yu, Huyue Song: They have done a lot of work in
- 354 expanding and adjusting metadata structures, fields, and other information during the data collection process; Hanchen Song:
- 355 Technical guidance on ancient and modern geographic maps; Lai Wei, Xiaokang Liu, Qingzhong Liang, Xinchuan Li, Hong
- 356 Yao: Technical support for computer language writing, literature collection, semi-automatic data extraction, data cleaning and
- 357 screening; Haijun Song, Yong Lei, Jacopo Dal Corso, Qin Ye. Yuyang Wu, Xiaokang Liu, Enhao Jia: Provided valuable
- 358 revision suggestions for the manuscript.

359 Competing interests

360 The author has declared that there are no competing interests.

361 **Disclaimer**

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372 Review statement

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References

- 375 Agić, H.: Fossil focus: Acritarchs. Palaeontology Online, 6, 1-13, 2016.
- 376 Agić, H., Moczydłowska, M., and Yin, L. M.: Affinity, life cycle, and intracellular complexity of organic-walled microfossils
- from the Mesoproterozoic of Shanxi, China. Journal of Paleontology, 89(1): 28-50, https://doi.org/10.1017/jpa.2014.4,
- 378 2015.
- Anderson, R. P., Macdonald, F. A., Jones, D. S., McMahon, S., and Briggs, D. E. G.: Doushantuo-type microfossils from
- latest Ediacaran phosphorites of northern Mongolia. Geology 45, 1079–1082, https://doi.org/10.1130/G39576.1, 2017.
- Arouri, K., Greenwood, P. F., and Walter, M. R.: A possible chlorophycean affinity of some Neoproterozoic acritarchs-
- 382 Organic Geochemistry, -30(10), 1323-1337, https://doi.org/10.1016/s0146-6380(99)00105-9, 1999.
- Bailey, J. V., Joye. S. B., Kalanetra, K. M., Flood, B. and Corsetti, F. A.: Evidence of giant Sulphur bacteria in
- Neoproterozoic phosphorites. Nature 445, 198–201, https://doi.org/10.1038/nature05457, 2007.
- Beraldi-Campesi, H.: Early life on land and the first terrestrial ecosystems. Ecological Processes, 2(1): 1,
- 386 https://doi.org/10.1186/2192-1709-2-1, 2013.
- Bernard, S., Benzerara, K., Beyssac, O., Balan, E., and Brown Jr., G. E.: Evolution of the macromolecular structure of
- sporopollenin during thermal degradation. Heliyon 1, e00034, https://doi.org/10.1016/j.heliyon.2015.e00034, 2015.
- Bernardi, M., Petti, F. M., Kustatscher, E., Franz M., Hartkopf-Fröder, C., Labandeira, C. C., Wappler, T., van Konijnenburg-
- 390 van Cittert, J. H., Peecook, B. R., and Angielczyk, K. D.: Late Permian (Lopingian) terrestrial ecosystems: A global
- 391 comparison with new data from the low-latitude Bletterbach Biota. Earth-Sci. Rev. 175, 18-43,
- 392 https://doi.org/10.1016/j.earscirev.2017.10.002, 2017.
- 393 Buick, R.: Ancient acritarchs. Nature 463, 885–886, https://doi.org/10.1038/463885a, 2010.
- Butterfield, N. J.: Probable Proterozoic fungi. Paleobiology, 31, 165–182, https://doi.org/10.1666/0094-
- 395 8373(2005)031<0165:PPF>2.0.CO;2, 2005.
- 396 Butterfield, N. J. and Rainbird, R. H.: Diverse organic-walled fossils, including "possible dinoflagellates," from the early
- 397 Neoproterozoic of arctic Canada. Geology. 26, 963-966, https://doi.org/10.1130/0091-7613(1998)0262.3.CO;2, 1998.
- 398 Chamberlain, J., Chamberlain, R., and Brown, J. A.: Mineralized alga and acritarch dominated microbiota from the Tully
- Formation (Givetian) of Pennsylvania, USA. Geosciences 6, 57, https://doi.org/10.3390/geosciences6040057, 2016.

- 400 Cohen, P. A., Knoll, A. H. and Kodner, R. B.: Large spinose microfossils in Ediacaran rocks as resting stages of early animals.
- 401 Proceedings of the National Academy of Sciences U.S.A. 106, 6519–6524, https://doi.org/10.1073/pnas.0902322106,
- 402 2009.
- 403 Colbath, G. K. and Grenfell, H. R.: Review of biological affinities of Paleozoic acid-resistant, organic-walled eukaryotic
- algal microfossils (including "acritarchs"). Review of Palaeobotany and Palynology, 86(3-4): 287-314,
- 405 https://doi.org/10.1016/0034-6667(94)00148-d, 1995.
- 406 Dale, B.: Paleontological evidence for dinoflagellates and ciliates as early eukaryotes. J. Mar. Sci. Eng. 11, 533,
- 407 https://doi.org/10.3390/jmse11030533, 2023.
- Daners, G., Herisse, A. L., Breuer, P., and Veroslavsky, G.: Pragian–Emsian palynomorphs from the Cordobés Formation,
- Norte Basin, Uruguay: Stratigraphically restricted and regionally correlative palynological events in the cool-water
- 410 Malvinokaffric Realm. Palynology 41, 121–137, https://doi.org/10.1080/01916122.2017.1366115, 2017.
- Evitt, W. R.: A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs, I. Proceedings
- 412 of the National Academy of Sciences, 49(3), 298-302, https://doi.org/10.2307/71700, 1963.
- 413 Falkowski, P. and Knoll, A. H. (Eds.).:_-Evolution of primary producers in the sea. Academic Press,
- 414 https://doi.org/10.5860/choice.45-3183, 2011.
- 415 Fensome, R. A., Williams, G. L., Barss, M. S., Freeman, J. M. and Hill, J. M.: Acritarchs and fossil prasinophytes: an index
- 416 to genera, species and infraspecific taxa. AASP Contribution Series, 25, 1–771, 1990.
- 417 Gaucher, C. and Sprechmann, P.: Neoproterozoic acritarch evolution—Developments in Precambrian Geology, 16, 319-326,
- 418 https://doi.org/10.1016/S0166-2635(09)01622-3, 2009.
- 419 Gray, J. and Boucot, A. J.: Is Moyeria a euglenoid? Lethaia 22, 447–456, https://doi.org/10.1111/j.1502-
- 420 3931.1989.tb01449.x, 1989.
- 421 Grey, K.: Ediacaran palynology of Australia, Memoir of the Association of Australasian Palaeontologists 31, 1–439,2005.
- Huldtgren, T., Cunningham, J., Yin, C., Stampanoni, M., Marone, F., Donoghue, P. C. J. and Bengtson, S.: Fossilized nuclei
- 423 and germination structures identify Ediacaran "animal embryos" as encysting protists. Science 334,1696–1699,
- 424 https://doi.org/10.1126/science.1209537, 2011.
- 425 Huntley, J., Xiao, S., and Kowalewski, M.: 1.3 billion years of acritarch history: An empirical morphospace approach.
- 426 Precambrian Res. 144, 52–68, https://doi.org/10.1016/j.precamres.2005.11.003, 2006.
- 427 Jacobson, S. R.: Acritarchs as paleoenvironmental indicators in Middle and Upper Ordovician rocks from Kentucky, Ohio
- 428 and New York. J. Paleontol. 53, 1197–1212, 1979.
- 429 Javaux, E. J. and Marshal, C. P.: A new approach in deciphering early protist paleobiology and evolution: Combined
- 430 microscopy and microchemistry of single Proterozoic acritarchs. Rev. Palaeobot. Palynol. 15,
- 431 https://doi.org/10.1016/i.revpalbo.2006.01.005, 2006.
- 432 Jia, E., Song, H., Lei, Y., Luo, G., and Jiang, S.: Paleozoic-Mesozoic turnover of marine biological pump and Mesozoic
- plankton revolution (in Chinese). Chin Sci Bull, 67:1660–1676, https://doi.org/10.1360/TB-2021-1220, 2022.

- Judd, E. J., Tierney, J. E., Huber, B. T., Wing, S. L., Lunt, D. J., Ford, H. L., Inglis, G. N., McClymont, E. L., O'Brien, C.
- 435 L., Rattanasriampaipong, R., Si, W., Staitis, M. L., Thirumalai, K., Anagnostou, E., Cramwinckel, M. J., Dawson, R. R.,
- Evans, D., Gray, W. R., Grossman, E. L., Henehan, M. J., Hupp, B. N., MacLeod, K. G., O'Connor, L. K., Sanchez
- 437 Montes, M. L., Song, H., and and Zhang, Y. G.: The PhanSST global database of Phanerozoic sea surface temperature
- 438 proxy data. Sci. Data, 9, 753-753, https://doi.org/10.1038/s41597-022-01826-0, 2022.
- 439 Kroeck, D. M., Mullins, G., Zacaï, A., Monnet, C., and Servais, T.: A review of Paleozoic phytoplankton biodiversity: Driver
- for major evolutionary events? Earth-Sci. Rev. 232, 104113, https://doi.org/10.1016/j.earscirev.2022.104113, 2022.
- 441 Lamb, D. M., Awramik, S. M., Chapman, D. J., and Zhu, S.: Evidence for eukaryotic diversification in the ~1800 million-
- 442 year-old Changzhougou Formation, North China. Precambrian Res. 12, https://doi.org/10.1016/j.precamres.2009.05.005,
- 443 2009.
- Le Hérissé, A., Al-Ruwaili, M., Miller, M., and Vecoli, M.: Environmental changes reflected by palynomorphs in the early
- 445 Middle Ordovician Hanadir Member of the Qasim Formation, Saudi Arabia—Revue de micropaléontologie—50(1), 3-
- 446 16, https://doi.org/10.1016/j.revmic.2007.01.010, 2007.
- Le Hérissé, A., Molyneux, S. G., and Miller, M. A.: Late Ordovician to early Silurian acritarchs from the Qusaiba-1 shallow
- 448 core hole, central Saudi Arabia. Review of Palaeobotany and Palynology, 212, 22-59,
- 449 https://doi.org/10.1016/j.revpalbo.2014.08.016, 2015.
- 450 Le Hérissé, A., Steemans, P., Wellman, C., and Vecoli, M.: Darriwilian (Middle-Ordovician) elements of primitive
- vegetation, marine palynomorphs and problematic microfossils, from the Sag/Qasim transitional beds in core OSIM 801,
- 452 central Saudi Arabia. Discussion with eustatic and climatic events. In 9th European Palaeobotany-Palynology conference,
- 453 2014.
- 454 Le Hérissé, A., Vecoli, M., Guidat, C., Not, F., Breuer, P., Wellman, C., and Steemans, P.: Middle Ordovician acritarchs and
- 455 problematic organic-walled microfossils from the Saq-Hanadir transitional beds in the QSIM-801 well, Saudi Arabia.
- 456 Rev. Micropaléontologie 60, 289–318, https://doi.org/10.1016/j.revmic.2017.08.001, 2017.
- 457 Lei, Y., Servais, T. and Feng, O.: The diversity of the Permian phytoplankton, Rev. Palaeobot. Palynol. 198, 145–161,
- 458 https://doi.org/10.1016/j.revpalbo.2013.03.004, 2013.
- 459 Lei, Y., Servais, T., Feng, Q. and He, W.: The spatial (nearshore–offshore) distribution of latest Permian phytoplankton from
- 460 the Yangtze Block, South China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 363–364, 151–162,
- 461 https://doi.org/10.1016/j.palaeo.2012.09.010, 2012.
- 462 Mendelson, C. V.: Acritarchs. Series in Geology, Notes for Short Course. 18, 62-86,
- 463 https://doi.org/10.1017/S0271164800001500, 1987.
- 464 Moczydłowska, M. and Liu, P.: Ediacaran algal cysts from the Doushantuo Formation, South China. Geological Magazine
- 465 <u>159: 1050–1070, https://doi.org/10.1017/S0016756820001405, 2022.</u>
- Moldowan, J. M., Dahl, J., Jacobson, S. R., Huizinga, B. J., Fago, F. J., Shetty, R., Watt, D. S., and Peters, K. E.:
- 467 Chemostratigraphic reconstruction of biofacies: Molecular evidence linking cyst-forming dinoflagellates with pre-

- Triassic ancestors-_Geology-_24(2), 159-162, https://doi.org/10.1130/0091-7613(1996)024<0159:CROBME>2.3.CO;2,
- 469 1996.
- 470 Mudie, P. J., Aksu, A. E., and Yasar, D.: Late Quaternary dinoagellate cysts from the Black, Marmara and Aegean seas:
- 471 Variations in assemblages, morphology and paleosalinity. Mar. Micropaleontol. 24, https://doi.org/10.1016/S0377-
- 472 8398(01)00006-8, 2001.
- 473 Palacios, T., Högström, A. E., Ebbestad, J. O. R., Agić, H., Høyberget, M., Jensen, S., Meinhold, G., and Taylor, W. L.:
- 474 Acritarchs from the Duolbagáisá Formation (Cambrian Series 2, Miaolingian) on the Digermulen Peninsula, Finnmark,
- 475 Arctic Norway: Towards a high-resolution Cambrian chronostratigraphy. Geol. Mag. 157, 2051–2066, 2020.
- Palacios, T., Jensen, S., Álvaro, J. J., Zaldeugui, J. S., Eguiluz, L., Corfu, F., and Ibarguchi, J. G.: Acritarch-based
- 477 chronostratigraphic and radiometric calibration of the Cambrian volcanosedimentary Vallehondo and Playón formations
- in the Cambrian Ossa-Morena Rift, Spain. -Palaeogeography, Palaeoclimatology, Palaeoecology, 565, 110216,
- 479 https://doi.org/10.1016/j.palaeo.2021.110216, 2021.
- 480 Palacios, T., Jensen, S., Barr, S. M., and White, C. E.: Acritarchs from the MacLean Brook Formation, southeastern Cape
- 481 Breton Island, Nova Scotia, Canada: New data on Middle Cambrian-Lower Furongian acritarch
- zonation. Palaeogeography, Palaeoclimatology, Palaeoecology, -273(1-2), 123-141,
- 483 https://doi.org/10.1016/j.palaeo.2008.12.006, 2009.
- 484 Palacios, T., Jensen, S., Barr, S. M., White, C. E., and Miller, R. F.: Acritarchs from the Hanford Brook Formation, New
- Brunswick, Canada: New biochronological constraints on the Protolenus elegans Zone and the Cambrian Series 2–3
- 486 transition. Geol. Mag. 154, 571–590, https://doi.org/10.1017/S0016756816000224, 2017.
- 487 Palacios, T., Jensen, S., Sánchez, I. C., and Mus, M. M.: First Lower Cambrian record of Wiwaxia from north- west
- 488 Gondwana: Small carbonaceous fossils from the Lancara Formation, Cantabrian Mountains, northern Spain. Programme,
- 489 Abstracts and AGM Papers, 58th Annual Meeting of the Palaeontological Association, University of Leeds, Leeds, UK,
- 490 16, 2014.
- 491 Palacios, T., Jensen, S., White, C. E., and Barr, S. M.: Cambrian acritarchs from the Bourinot belt, Cape Breton Island, Nova
- 492 Scotia: Age and stratigraphic implications. Can. J. Earth Sci. 49(1), 289–307, https://doi.org/10.1139/e11-010, 2012.
- 493 Palynodata Inc. and White, J. M.: Palynodata Datafile: 2006 version, with Introduction by J. M. White. Geological Survey
- 494 of Canada Open File 5793, 1 CD-ROM, https://doi.org/10.4095/225704, 2008.
- 495 Paris, F., Hérissé, A. L., Monod, O., Kozlu, H., Ghienne, J. F., Dean, W. T., Vecoli, M., and Günay, Y.: Ordovician
- 496 chitinozoans and acritarchs from southern and southeastern Turkey. Revue de micropaléontologie, 50(1), 81-107,
- 497 https://doi.org/10.1016/j.revmic.2006.11.004, 2007.
- 498 Park, R. G.: Geological structures and moving plates. Springer Science & Business Media, 1988.
- Schrank, E.: Small acritarchs from the Upper Cretaceous: Taxonomy, biological affinities and palaeoecology-. Review of
- Palaeobotany and Palynology, 123(3-4), 199-235, https://doi.org/10.1016/S0034-6667(02)00228-2, 2003.

- 501 Schreck, M., Nam, S. I., Clotten, C., Fahl, K., De Schepper, S., Forwick, M., and Matthiessen, J.: Neogene dinoflagellate
- 502 cysts and acritarchs from the high northern latitudes and their relation to sea surface temperature. Mar. Micropaleontol.
- 503 136, 51–65, https://doi.org/10.1016/j.marmicro.2017.09.003, 2017.
- 504 Scotese, C. R.: An atlas of Phanerozoic paleogeographic maps: The seas come in and the seas go out. Annual Review of
- 505 Earth and Planetary Sciences. 49(1), 679-728, https://doi.org/10.1146/annurev-earth-081320-064052, 2021.
- Servais, T., Brocke, R., Fatka, O., Herisse, A. L., and Molyneux, S. G.: Value and meaning of the term acritarch. In O. Fatka,
- and T. Servais, (Eds.), Acritarcha in Praha 1996. Acta Universitatis Carolinae, Geologica, 40, 631–643, 1997.
- 508 Servais, T., Li, J., Molyneux, S., and Raevskaya, E.: Ordovician organic-walled microphytoplankton (acritarch) distribution:
- The global scenario. Palaeogeogr. Palaeoclimatol. Palaeoecol. 195, 149–172, https://doi.org/10.1016/S0031-
- 510 0182(03)00306-7, 2003.
- 511 Shu, X., Song, H., Lei, Y., Chu, D., Dal Corso, J., Liu, X., Song, H., Wei, L., Jia, E., Feng, Y., Du, Y., Song, H., Yu, W.,
- 512 Liang, Q., Li, X., Yao, H., and Wu, Y.: Global Acritarch Database [data set],
- 513 https://doi.org/10.5281/zenodo.1520830310.5281/zenodo.13828633, 20252024.
- 514 Shu, X.: Code encountered during the drawing process. Zenodo... https://doi.org/10.5281/zenodo.15147118,
- 515 <u>202510.5281/zenodo.14350992, 2024</u>.
- 516 Silvestro, D., Salamin, N., Antonelli, A., and Meyer, X.: Improved estimation of macroevolutionary rates from fossil data
- using a Bayesian framework—Paleobiology—45(4), 546-570, https://doi.org/10.1017/pab.2019.23, 2019.
- 518 Silvestro, D., Salamin, N., and Schnitzler, J.: PyRate: A new program to estimate speciation and extinction rates from
- 519 incomplete fossil data. Methods Ecol. Evol, https://doi.org/10.1111/2041-210X.12263, 2014.
- 520 Strother, P. K.: A speculative review of factors controlling the evolution of phytoplankton during Paleozoic time. Revue de
- 521 Micropaleontology, 51, 9–21, https://doi.org/10.1016/j.revmic.2007.01.007, 2008.
- 522 Tappan, H. and Loeblich Jr, A. R.: Evolution of the oceanic plankton. Earth-Science Reviews, 9(3), 207-240,
- 523 https://doi.org/10.1016/0012-8252(73)90092-5, 1973.
- 524 Xiao, S., Zhang, Y. and Knoll, A. H.: Three-dimensional preservation of algae and animal embryos in a Neoproterozoic
- 525 phosphorite. Nature 391, 553–558, https://doi.org/10.1038/35318, 1998.
- Xiao, S., Narbonne, G.M.: The Ediacaran Period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), Geologic
- 527 Time Scale 2020 (Volume 1). Elsevier, Oxford, pp. 521–561, https://doi.org/10.1016/B978-0-12-824360-2.00018-8,
- 528 <u>2020.</u>
- 529 Vavrdová, M., Bek, J., Dufka, P., and Isaacson, P. E.: Palynology of the Devonian (Lochkovian to tournaisian) sequence,
- Madre de Dios Basin, northern Bolivia—Vestnik Ceskeho geologickeho ustavu—71(4), 333-349, 1996.
- 531 Vavrdová, M. and Dašková, J.: Middle Devonian palynomorphs from southern Moravia: An evidence of rapid change from
- terrestrial deltaic plain to carbonate platform conditions. Geol. Carpathica 62, 109–119, https://doi.org/10.2478/v10096-
- 533 011-0010-2, 2011.

- Vavrdová, M., Isaacson, P. E., and Díaz-Martínez, E.: Early Silurian-Early Devonian acritarchs and prasinophytes from the
- Ananea and San Gabán Formations, southern Peru and their paleogeographic implications, 43, 2011.
- Vavrdová, M. and Svobodová, M.: Amphitheca isaacsonii gen. et sp. nov. (Acritarcha) from the Ananea Formation
- 537 (Silurian/Devonian transition), southern Peru. Journal of the National Museum (Prague), Natural History Series 179, 189-
- 538 196, 2010.
- Vecoli, M. and Hérissé, A. L.: Biostratigraphy, taxonomic diversity and patterns of morphological evolution of Ordovician
- 540 acritarchs (organic-walled microphytoplankton) from the northern Gondwana margin in relation to palaeoclimatic and
- palaeogeographic changes—Earth-Science Reviews—67(3-4), 267-311, https://doi.org/10.1016/j.earscirev.2004.03.002,
- 542 2004.
- Wang, K., Xu, H. H., and Yin, L. M.: A palynological assemblage from the Cambrian (Series 2, Stage 4) of Shandong
- Province, China, and its implications to the transition from algae to land plants. Rev. Palaeobot. Palynol. 301, 104645,
- 545 https://doi.org/10.1016/j.revpalbo.2022.104645, 2022.
- Wicander, R.: Acritarchs: Proterozoic and Paleozoic enigmatic organic-walled microfossils-__Conference on instruments,
- methods, and missions for astrobiology. https://doi.org/10.1117/12.454771, 2002.
- Williams, G. L.: Dinoflagellates, acritarchs and tasmanitids. In Introduction to Marine Micropaleontology. 293–326,
- 549 https://doi.org/10.1016/B978-044482672-5/50013-1, 1998.
- 550 Willman, S. and Moczydłowska, M.: Acritarchs in the Ediacaran of Australia Local or global significance? Evidence
- 551 from the Lake Maurice West 1 drillcore. Rev. Palaeobot. Palynol. 166, 12–28,
- 552 https://doi.org/10.1016/j.revpalbo.2011.04.005, 2011.
- Yin, L.: Illustrated book of organic-walled microfossils., Zhejiang: Zhejiang University Press. 978, 2018.
- Yin, L., Zhu, M., Knoll, A. H., Yuan, X., Zhang, J. and Hu, J.: Doushantuo embryos preserved inside diapause egg cysts.
- Nature 446, 661–663, https://doi.org/10.1038/nature05682, 2007.
- 556 Yin, Z., Sun, W., Liu, P., Zhu, M. and Donoghue, P. C. J.: Developmental biology of Helicoforamina reveals holozoan
- affinity, cryptic diversity, and adaptation to heterogenous environments in the early Ediacaran Weng'an biota
- (Doushantuo Formation, South China) Science Advances 6, 1–10, eabb0083, https://doi.org/10.1126/sciadv.abb0083,
- 559 <u>2020.</u>