GRAPTOLITES

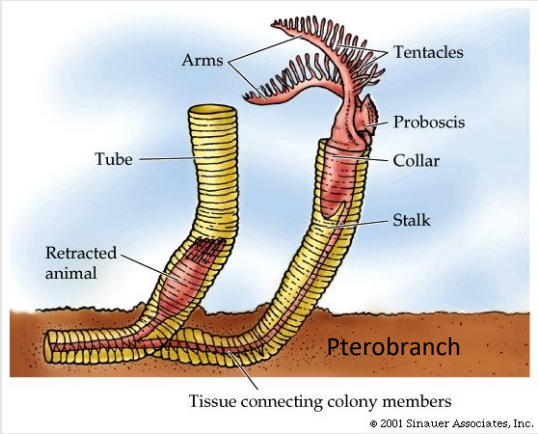
INTRODUCTION TO HEMICHORDATA

Phylum	Hemichordata
Class	Graptolithinia (Graptolites)
Order	Graptoloidea (graptoloids)
Now Extinct	Early Ordovician (with continuing abundance until the Middle Silurian) to Early Devonian

Hemichordata (the phylum) is a very small phylum of animals with bilateral symmetry. They first appear in the lower/Middle Cambrian (with Graptoloids appearing in the **early Ordovician**). *Hemichordata are considered the sister group to Echinodermata.*

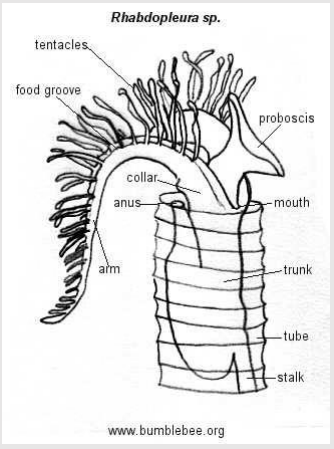
The phylum Hemichordata also includes extant classes such as Pterobranchia. **Pterobranchs** are modern-day **worm-like** animals.

Graptolites (**The class**) include the **order Dendroidea**, a **multi-stiped ancestral version of the graptoloids**. The fossils are most commonly found **as two dimensional**, flattened specimens. **Rare three-dimensional** fossils have allowed palaeontologists to reconstruct the skeleton, showing that it was a **colonial organism**.



- **Sicula**: the conical structure in which the first member of the colony lived
- **Thecae:** the individual cups in which the zooids lived (later members of the colony). The thecae form a tube built onto the sicula.
- **Stipe**: a branch of the theca, it is a stack of thecae built up to form a colony.
- **Nema**: A long extension to the top of the sicula, possibly for attachment to a floating object i
- n planktonic forms.
- **Rhabdosome** is the whole graptoloid's skeleton, which may consist of one or several stipes.
- **Aperture**: The terminal ring to a theca where the zooid protruded to filter feed.
- **Virgella**: The spine at the end of the sicula
-

Pterobranchs are **filter-feeders** removing **plankton** from the water via **tentacle cilia**. They are primarily colonial, living in interconnected tubes on the ocean floor.

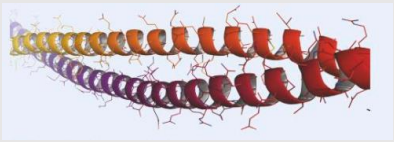


These have a **primitive notochord** (flexible rod-like body found in the embryo of all chordates). This makes them a possible ancestor of chordates.

GRAPTOLOIDS MORPHOLOGY AND MODE OF LIFE

They had **benthonic and planktonic modes of life.** They are **marine, colonial** organisms with a similar format to corals.

A single organism is called **a zooid** and shares a common exoskeleton **Rhabdosome** (which is the colonial organism as a whole). True graptolites had varying numbers of stipes making up their entire skeleton.



They build their skeleton from fibrous proteins also called **scleroproteins**.

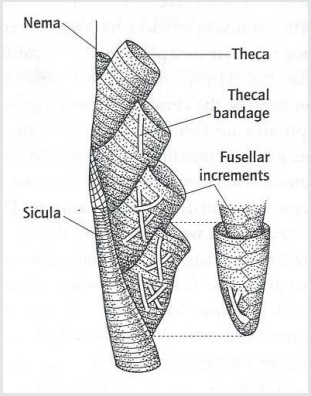
Zooids lived in and build up tubes called thecae. The **first zooid** secreted a tube called the **sicula**, which often had a **long tapering point**. This may have been due to asexual budding from the first zooid.

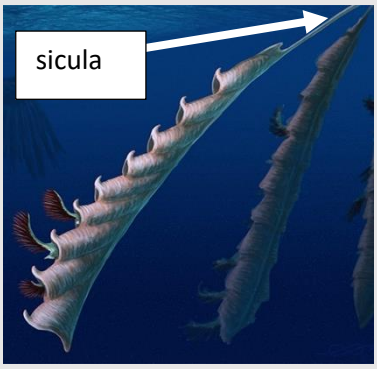
Graptoloids were successful, abundant and diverse, globally and throughout most of the Palaeozoic, forming important communities in the **Ordovician and Silurian**.

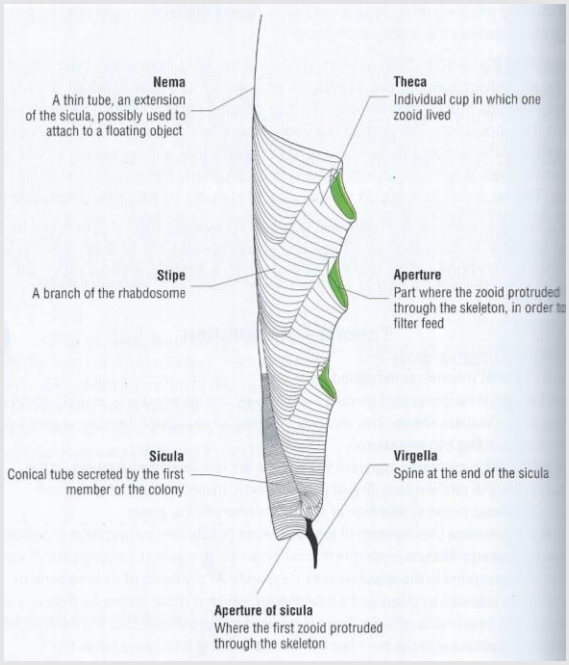
A single zooid inhabited a t**heca** (**tube-shaped protective cup**).

As the colony grew, additional theca are stacked on top of each other and the sicula. This stacking forms the stipes (a branch of the overall skeleton, the **Rhabdosome**). The colony grew by **asexual budding** and may have been linked by a communal soft part connection.

Most graptoloids either had a **holdfast** for attachment to the substrate (**benthonic epifaunal species)** or a **nema** (a thin tubular extension to the sicula) which may have attached to floating objects (**Pelagic, planktonic forms**).







The Most ancestral (primitive) graptoloids were benthic, sessile forms found living in shallow water fossil assemblages. Benthonic forms were widespread but relatively rare throughout the Ordovician.

The ancestral dendroids were attached to the sea floor (sessile, benthonic, epifaunal) but the graptoloids lived within the water column and were probably pelagic, planktonic.

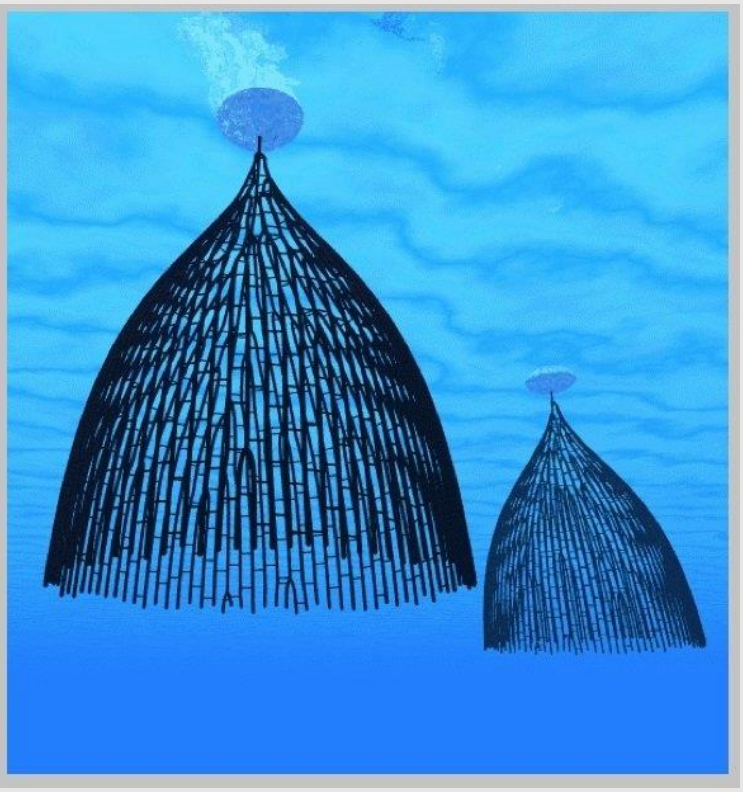
The aperture of the sicula would have faced downwards and the whole organism floated or at least attached to a floating object by the nema.

Some forms show evidence that they were arranged around a gas-filled membrane that acted as a buoyancy aid.

Models of graptoloids often spiral. This is to increase the efficiency of filter feeding as they sank, however, it is not known how they rose again.

Most appear to be planktonic but some are actually nektonic (active swimmers).

Planktonic forms

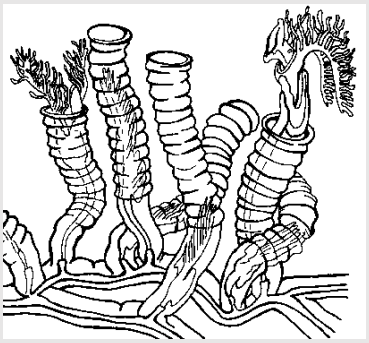


Graptoloids diversified in the early Ordovician giving rise to planktonic forms with a **global distribution**. These were v**ery abundant, successful and diverse.**

Planktonic Graptolites are considered **psuedoplanktic** since they did NOT naturally float **but attached themselves to floating debris** via the **nema.**

SIMILARITIES TO PTEROBRANCHS

It is due to the close similarity between the rare-extant Pterobranchs and the graptoloids that has lead to the suggestion that graptolites filter fed.



Modern Pterobranchs attach to substrates as deep as 600m, as small colonies (2cm - 3cm), filter feeding. Each zooid lived in a tube or depression, varying from species to species. The zooids emerged from their tubes made of collagen (a fibrous/scleroprotein) to filter food particles form the water. The presence of cilia shows us that the Pterobranchs maybe closely related to the echinoderms.

PRESERVATION AND IMPORTANCE AS A ZONE FOSSIL

Index (or zone) fossils used to define and identify geologic periods (or faunal stages). These fossils work on the premise that, sedimentary rocks will contain **fossils unique to that time period**.

Graptoloids appeared in the early Ordovician and rapidly became the dominant marine fauna. The success continued into the Silurian but they began to decline after the mid-Silurian and were extinct by the end of the Devonian. Their **rapid evolution, abundance, global distribution (due to the planktonic mode of life)** and **short geological** range makes them ideal zone fossils.

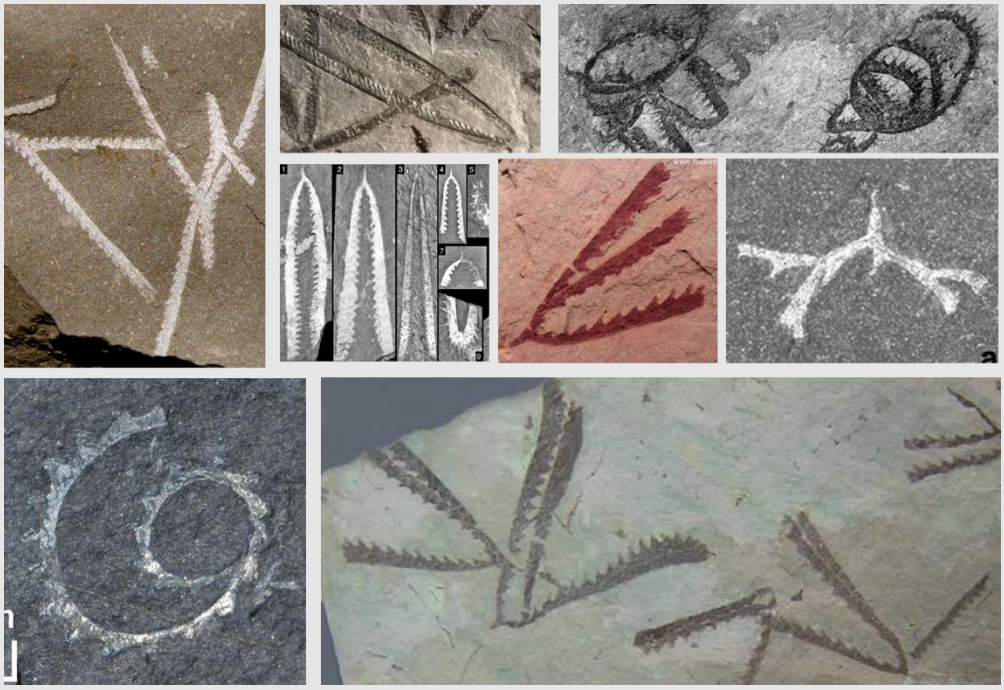
The rhabdosome was **protein based and insoluble** so they did not dissolve into solution as they sank into deep waters. However, they are **delicate** and **vulnerable to scavengers or decay in the shallow oxygenated waters** of **high energy.** They collected in vast quantities in the **anoxic mud of the seafloor**. It is assumed that the fossil

record is biased as they would have **inhabited many environmental niches** but are only preserved well in the low-energy conditions.

Graptoloids became **extinct when fish first evolved** but it is not certain whether the events are linked.

Why are graptoloids so good as zone fossils? -summary

Abundant, so easily found.
Rapid evolutionary turner, gives a short stratigraphic range, precise dating
Easily identified to genera/species level, so confident assessment of locality age
Readily preserved/fossilized, little time spent searching for specimens, practical
Globally distributed, biostratigrpahic methods are suitable and consistent everywhere
Occupy a planktic mode of life, allowing recovery from a variety of rock types.



Some currents on the seafloor aligned graptolites that sunk. This makes the good **paleocurrent indicators**.

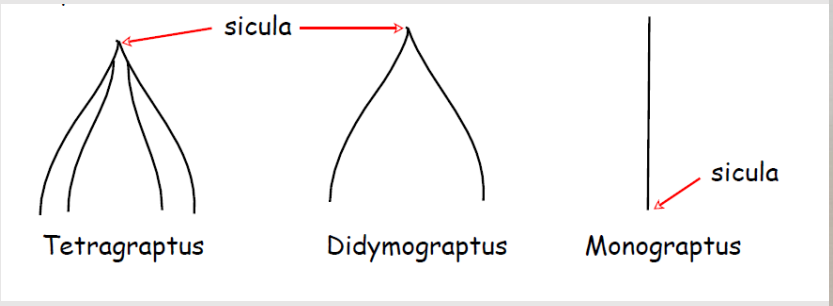
GRAPTOLOID EVOLUTION

REDUCTION IN THE NUMBER OF STIPES

Early graptoloids had up to 8 stipes, but later Ordovician forms more commonly had 2.

The dominant form during the Silurian were single stiped graptolites.

Period	Generic name of graptoloid
Silurian	Monograptus (1 stipe)
Silurian	Diplograptus (1 stipe)
Ordovician	Dicellograptus (2 stipes)
Ordovician	Didymograptus (2 stipes)
Ordovician	Tetragraptus (4 stipes)



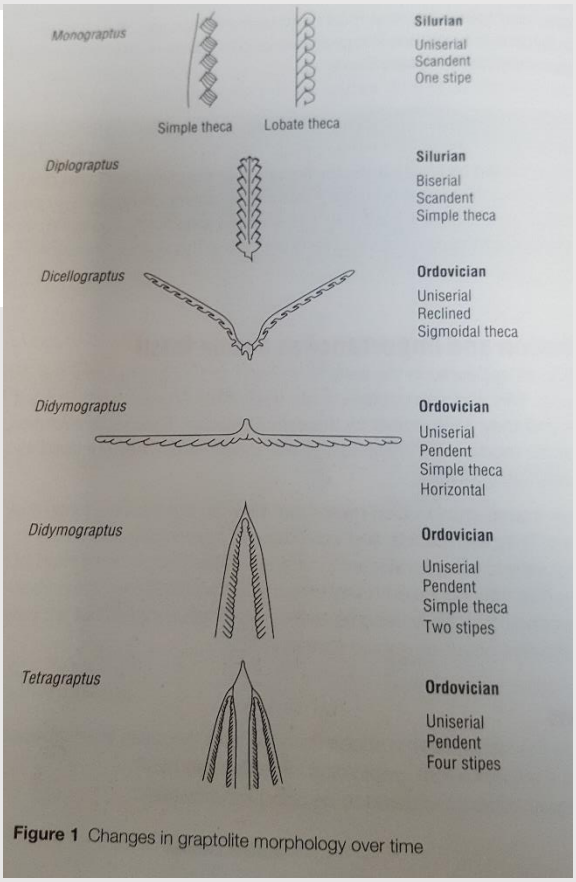


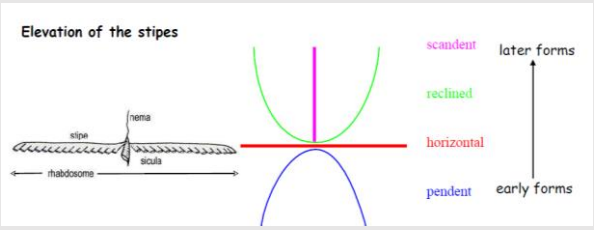
Figure 1 Changes in graptolite morphology over time

CHANGES IN THE ORIENTATION (ATTITUDE) OF STIPES

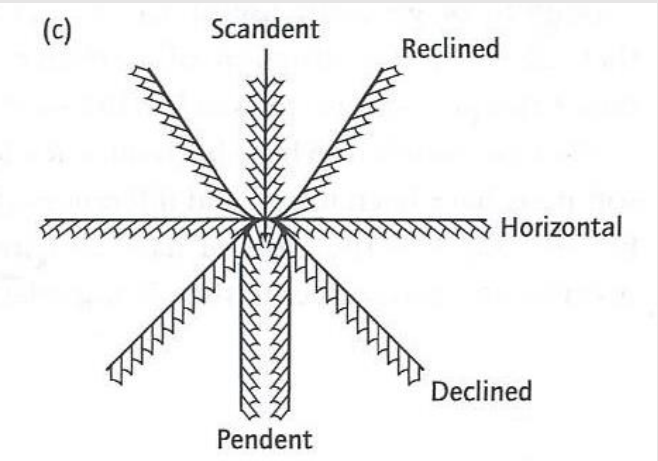
- **Pendent:** the thecae are added downwards from the sicula
- **Declined**: thecae are added growing downwards at an angle/sideways
- **Horizontal:** the thecae are added outwards from the sicula
- **Reclined:** thecae are added growing upwards at an angle/sideways
- **Scandent:** thecae are growing vertically upwards from the sicula

The attitude of stipes described their **angle relative to the sicula** (which always has the aperture pointing downwards and the nema pointing upwards).

The general trend through geological time (Ordovician to Silurian) that **stipes went from pendent to scandent.**



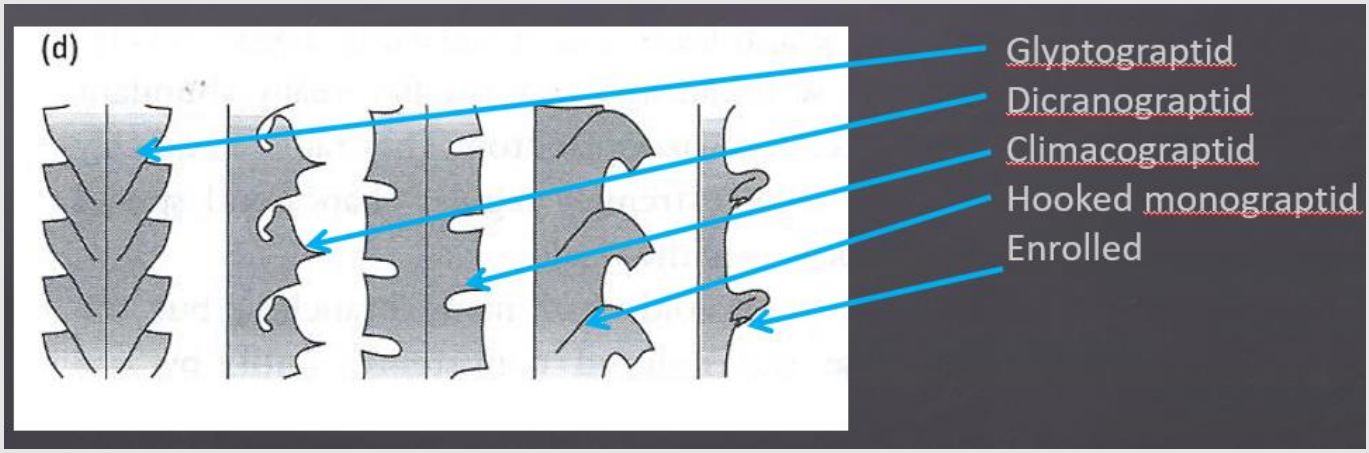
*Early graptoloids were **pendent or horizontal (although scandent biserial forms were around at the same time)**, and later graptolites appeared with **reclined stipes**. By the late Silurian **scandent** forms were most common.*



INCREASED COMPLEXITY OF THECAE

Over time the complexity of the thecae increased, this evolutionary trend is suspected to result in more efficient filter feeding by **reducing the competition between zooids** for the **same suspended nutrients**.

Early forms typically had simple **cup-shaped theca**, **overlapping each other** and although this arrangement persisted through graptolite history, **elaborate thecae** appeared in the late Ordovician and Silurian.



Early forms had **simple thecae with uncomplicated apertures**, which were arranged along the **stipe close together** or with only **slight overlap**. Although, simple forms persisted, **elaborate** thecae were found later in the Ordovician and in the Silurian. Many of these had **hooked or curved** ends to their aperture or were **more widely separated along the stipe.**

The detail found in well preserved 3-dimensional forms has greatly improved our understanding of their morphology.

ARRANGEMENT OF THECAE ON THE STIPE

- **Uniserial:** the thecae are arranged on only one side of the stipe.
- **Biserial:** the thecae are added on two sides of the stipe.

Some species of graptoloids show an **intermediate stage** between uniserial and biserial in which **two uniserial stipes are half-zipped** together to give a **biserial lower-half.**

The general trend is that early forms were **uniserial** and became **biserial towards the late Ordovician**. The trend then reverted in the Silurian forms **became uniserial again.**

It is not a simple progression with one group being replaced by the next; some groups, such as **diplograptids**, **coexisted** with all the other examples shown.

Characteristics of different species often overlapped with others or appeared out of order. However, the general tendency towards fewer stipes that are more spread out, curved, scandent attitudes and complex thecae are a good working guide.