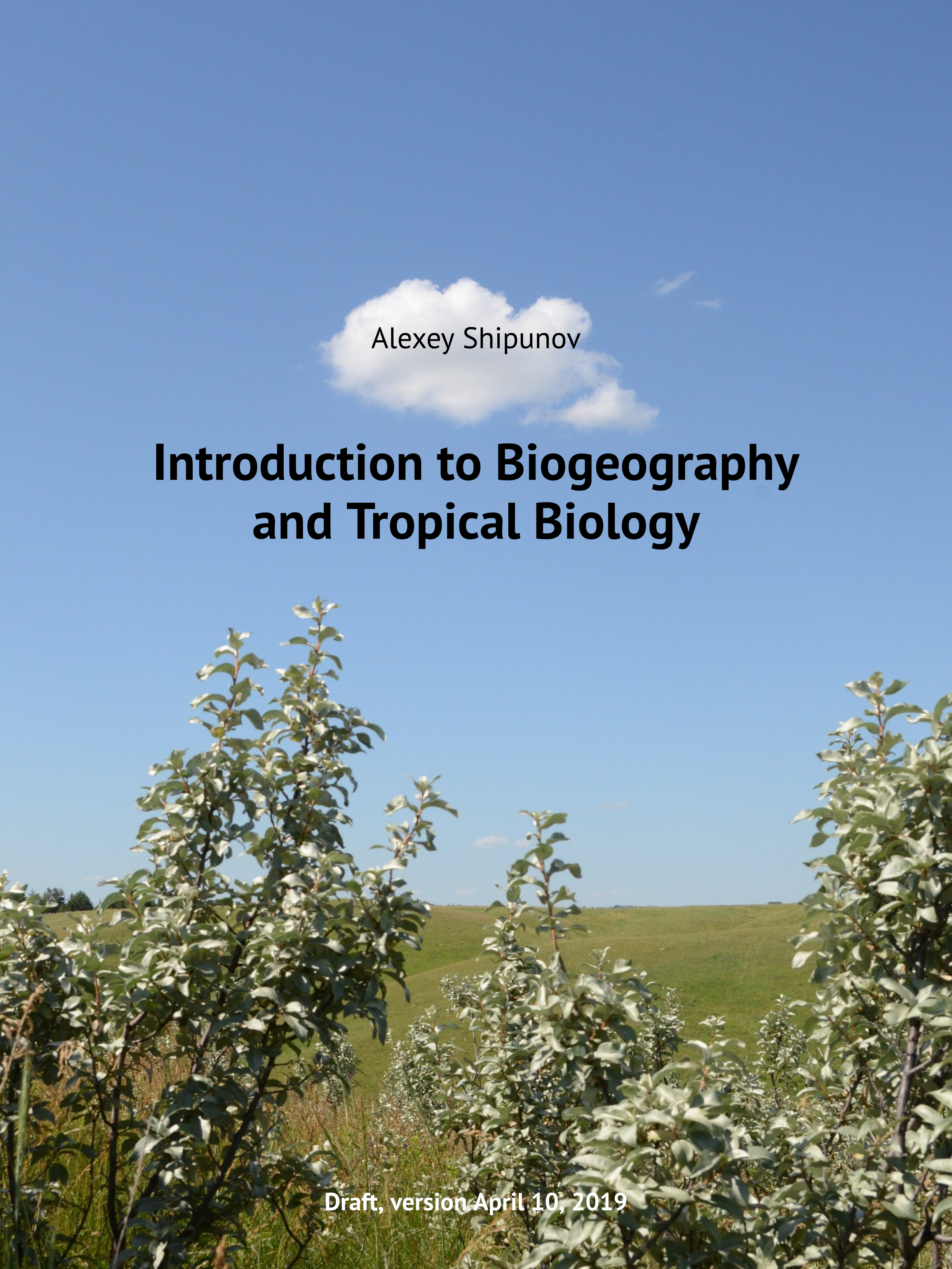


Alexey Shipunov

Introduction to Biogeography and Tropical Biology

Draft, version April 10, 2019

Shipunov, Alexey. *Introduction to Biogeography and Tropical Biology*. This at the moment serves as a reference to major plants and animals groups (taxonomy) and descriptive biogeography ("what is where"), emphasizing tropics.
April 10, 2019 version (draft). 101 pp.

Title page image: Northern Great Plains, North America. *Elaeagnus commutata* (silverberry, Elaeagnaceae, Rosales) is in front.

Contents

What

Chapter 1

Diversity maps

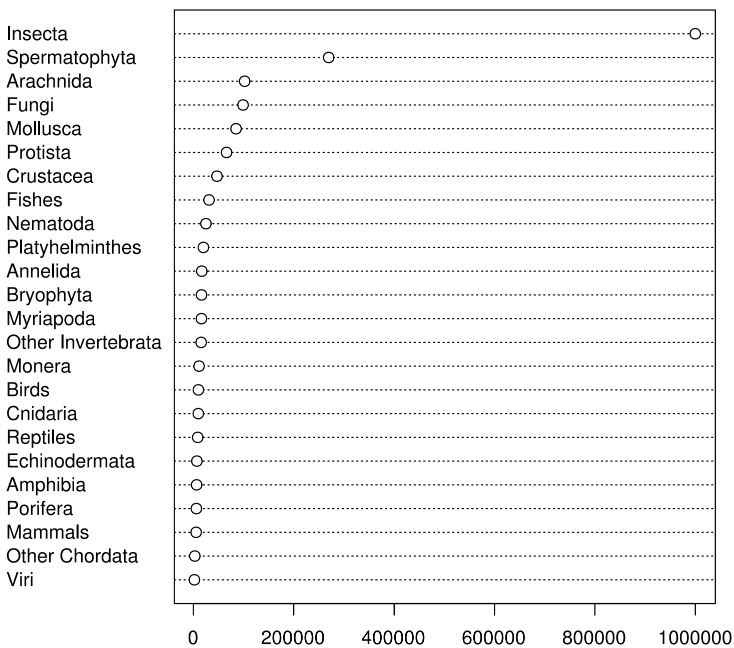
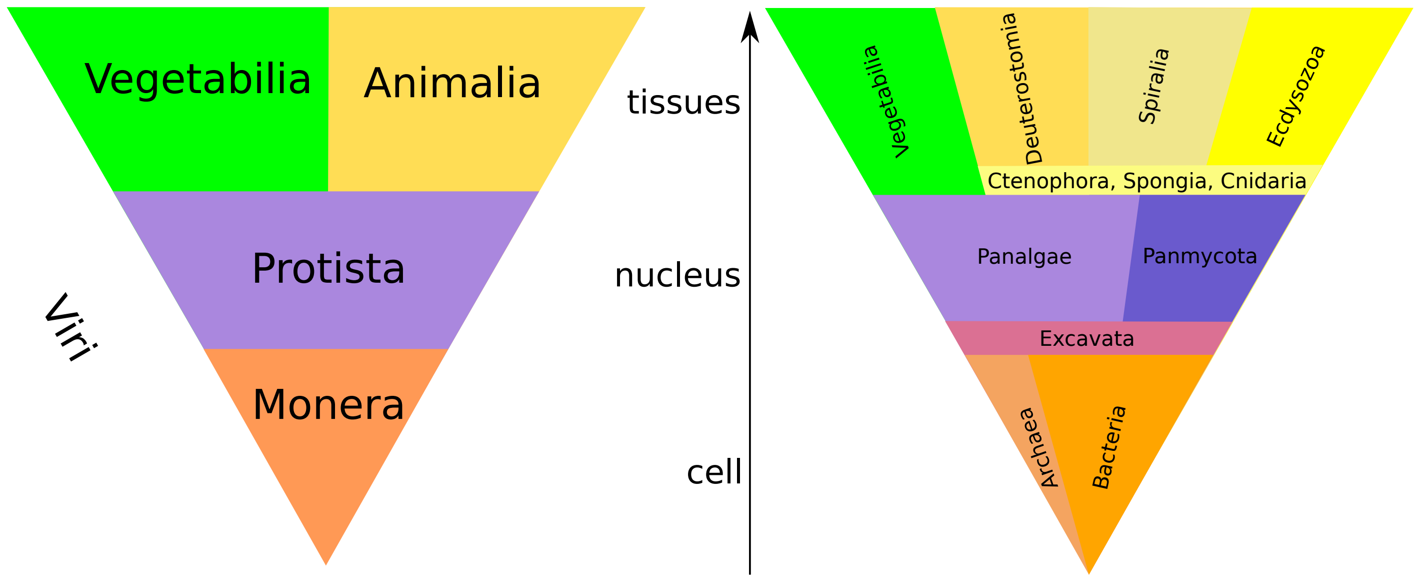
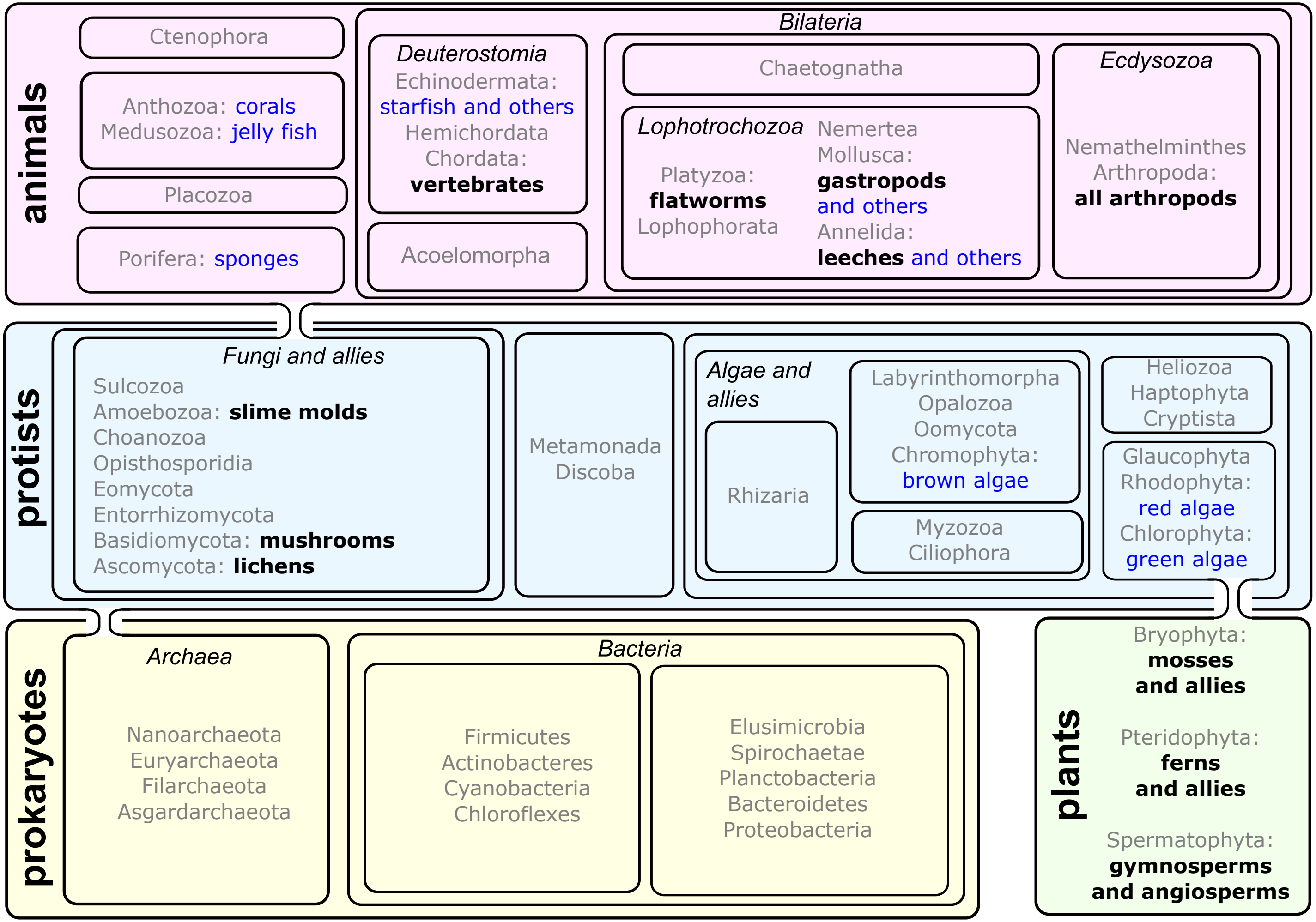


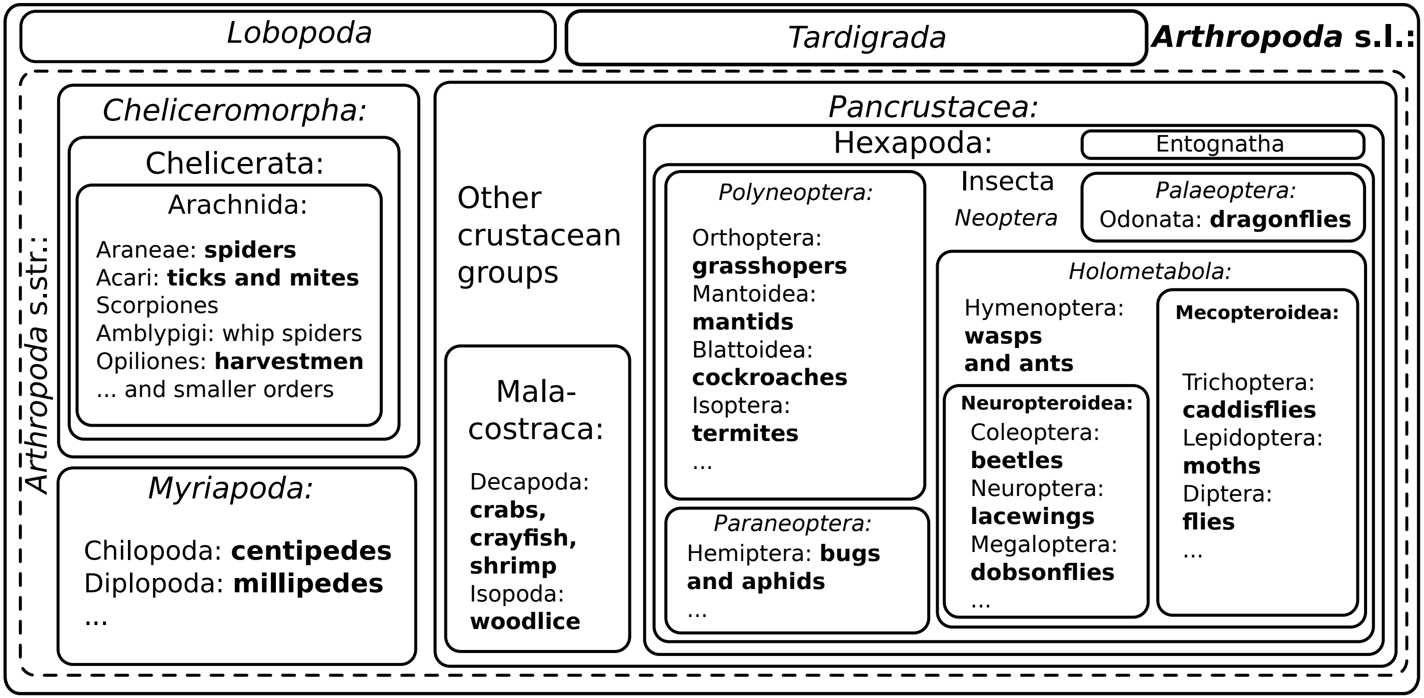
Figure 1. The most diverse groups of living things.



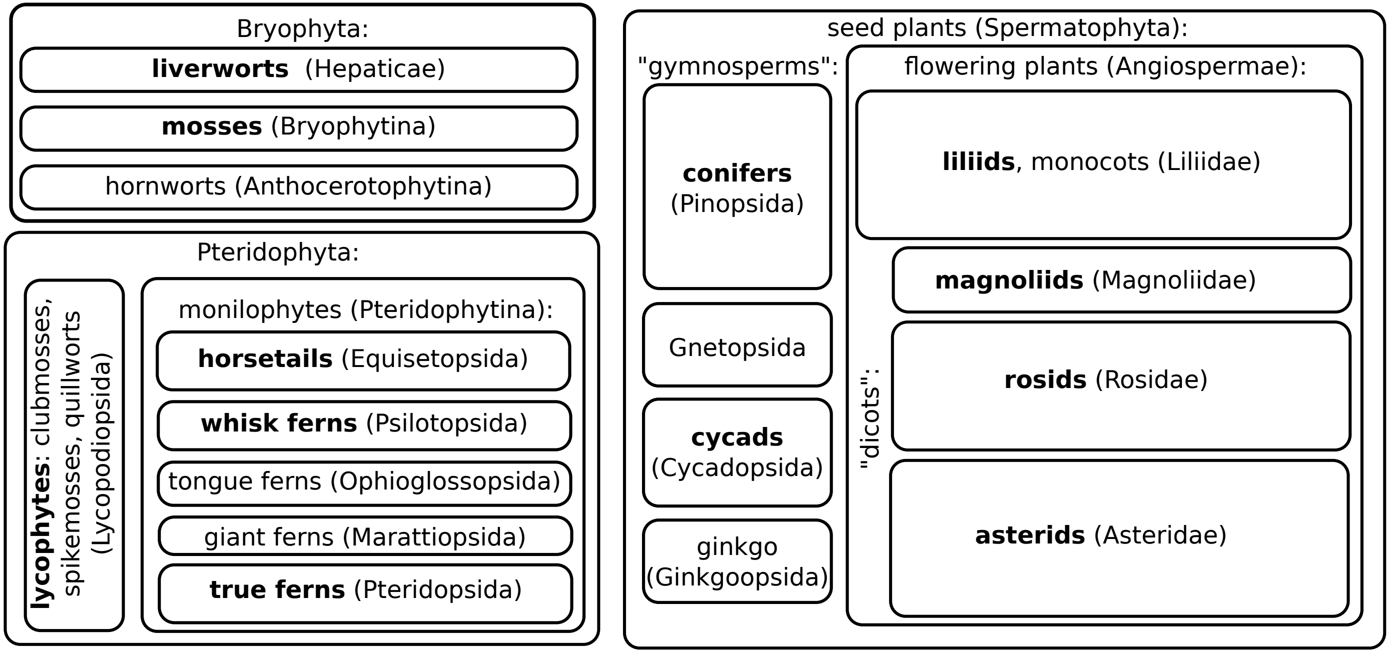
"Pyramids of Life."



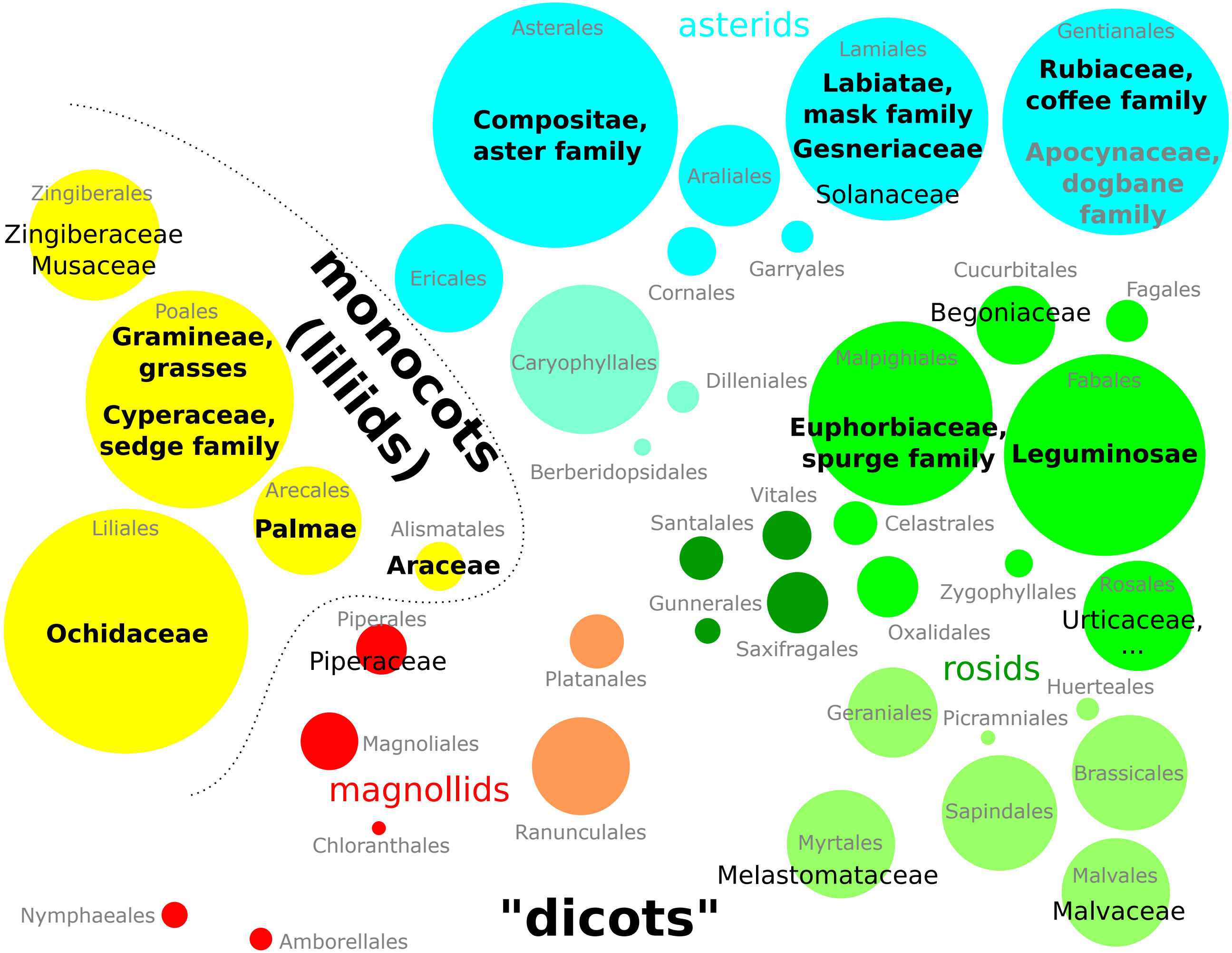
Treemap of Life.



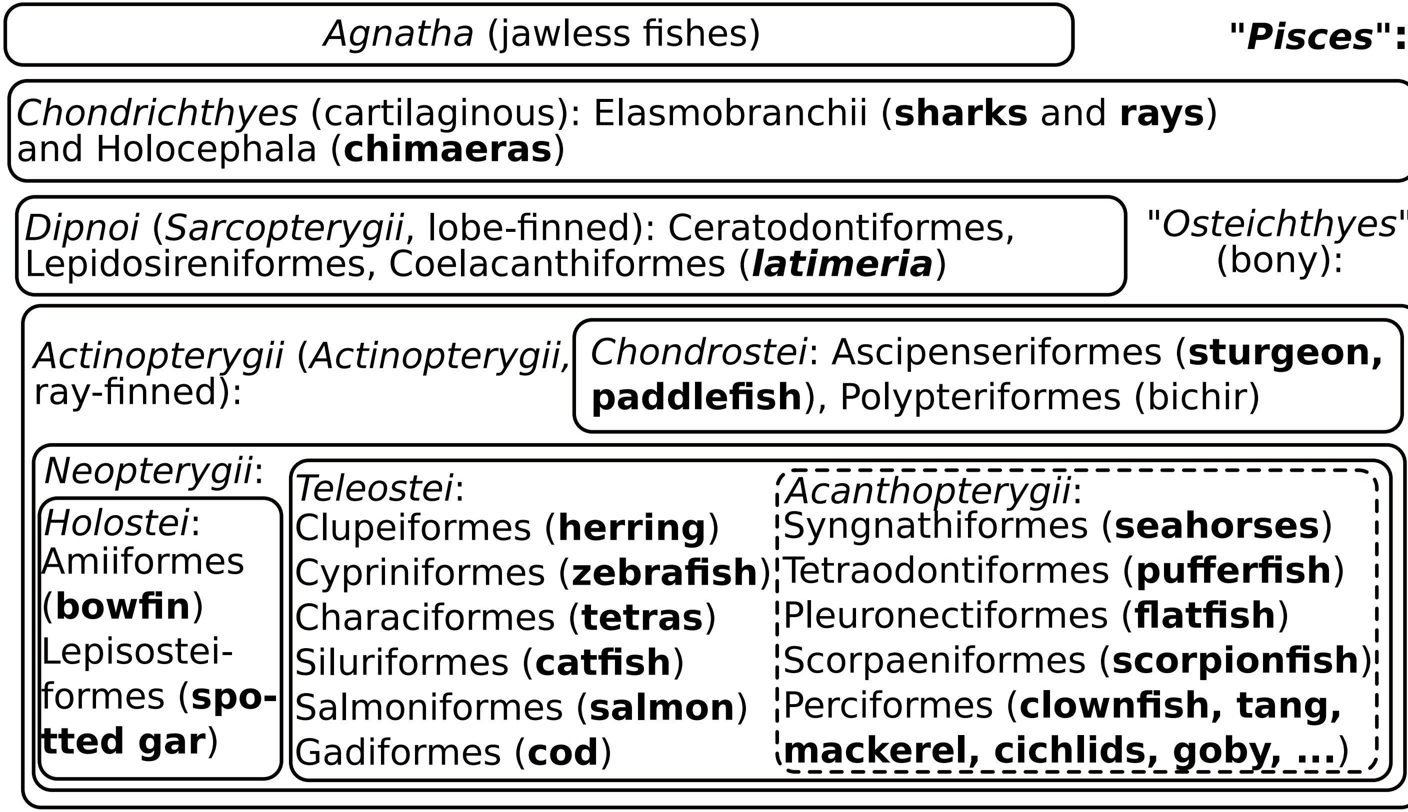
Treemap of arthropods.



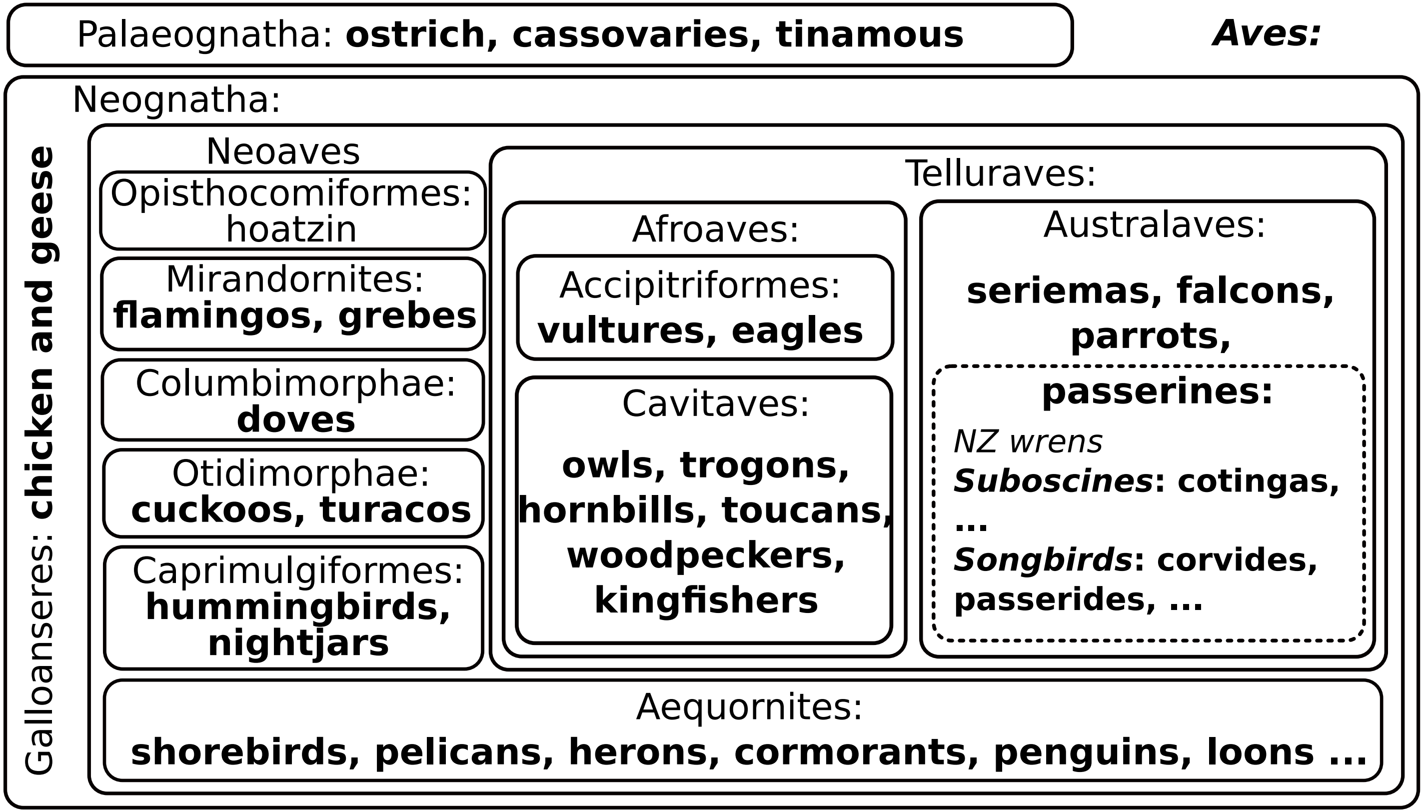
Treemap of plants.



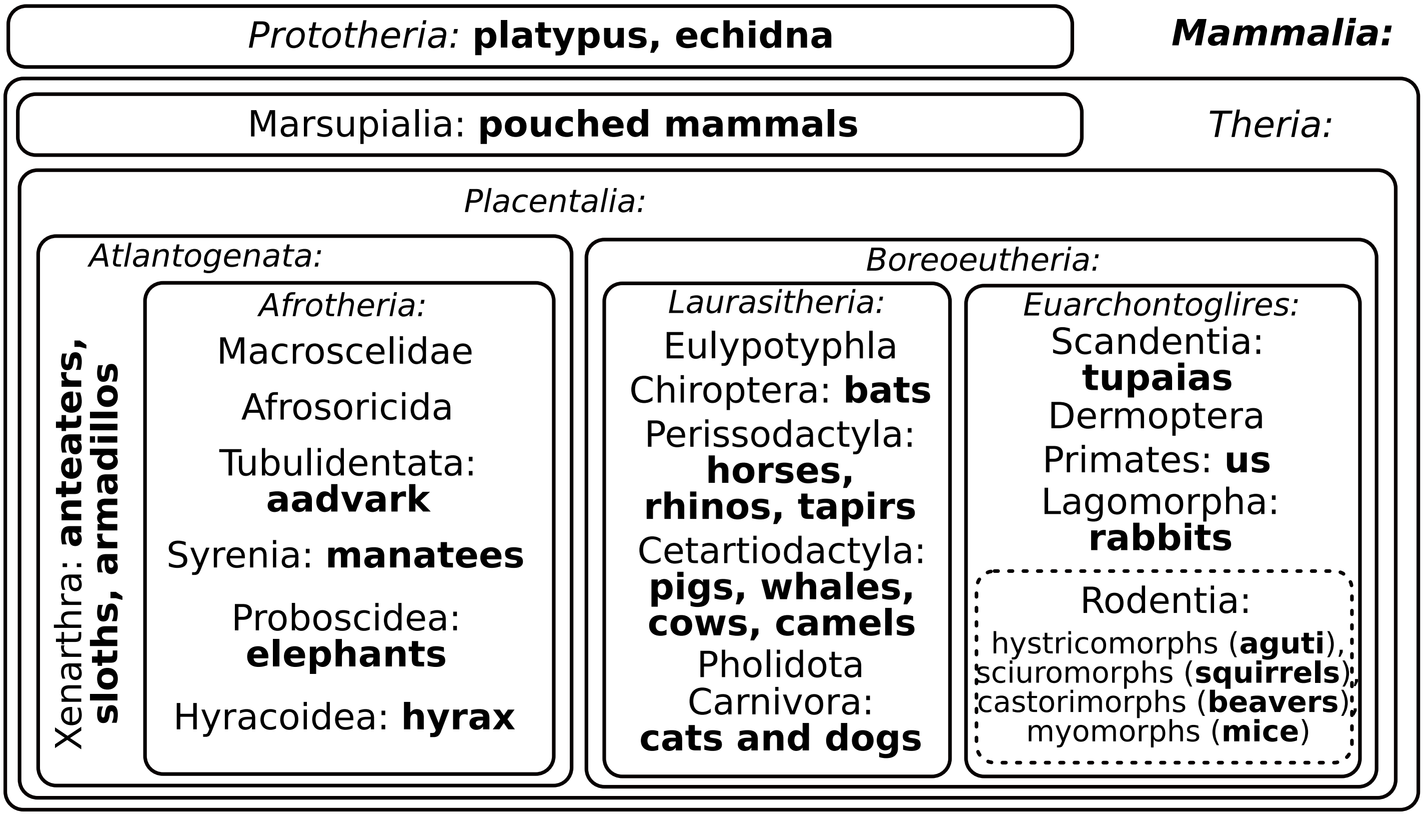
Treemap of angiosperms.



Treemap of fishes.



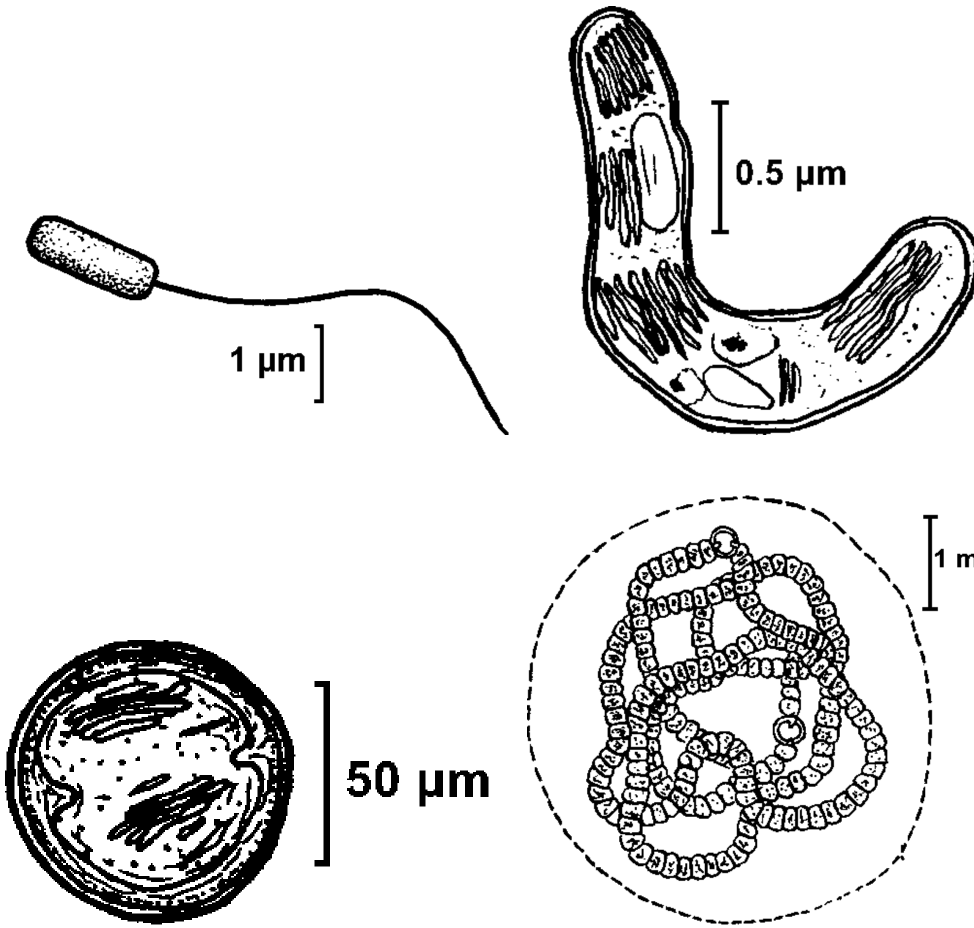
Treemap of birds.



Treemap of mammals.

Diversity atlas

All black and white illustrations in this section were provided by Georgij Vinogradov and Michail Boldumanu.



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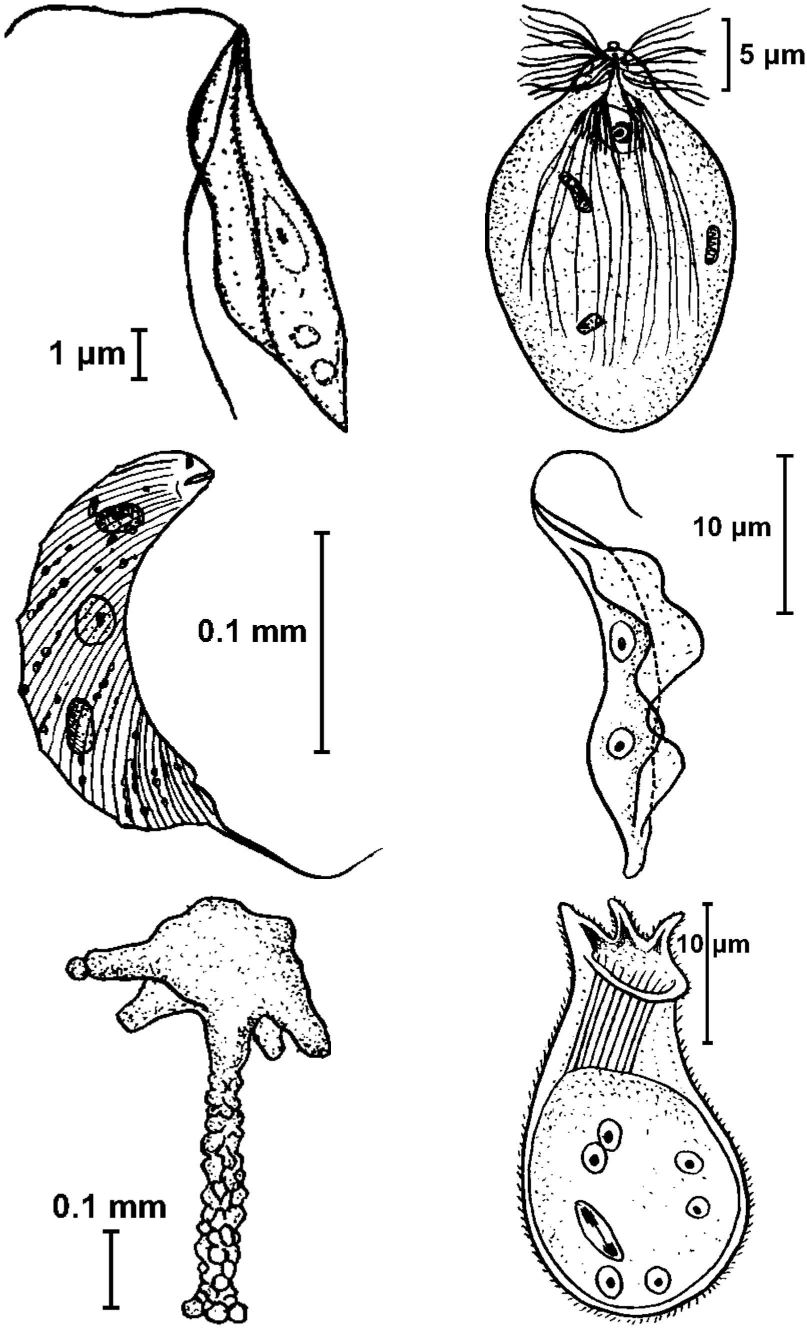

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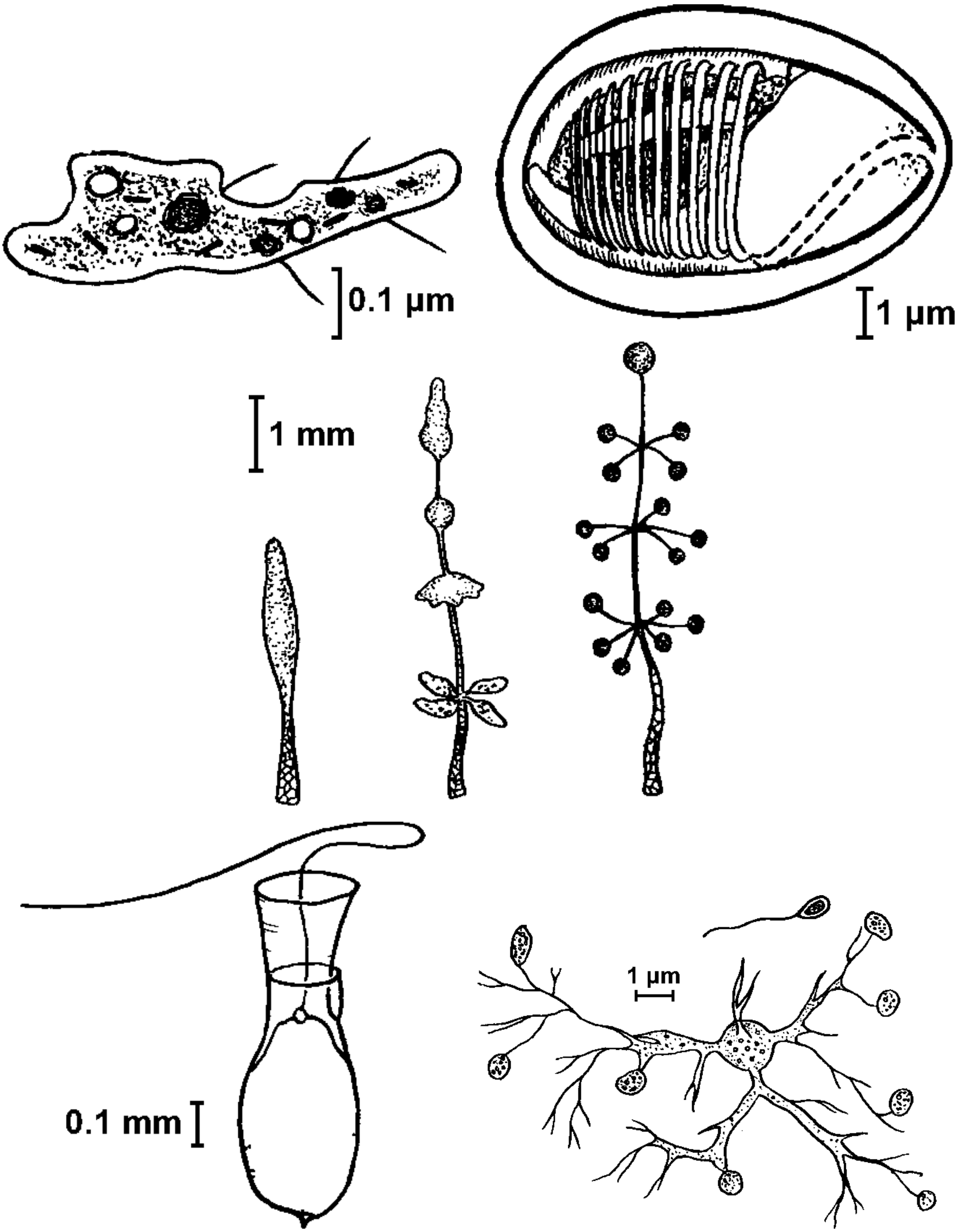

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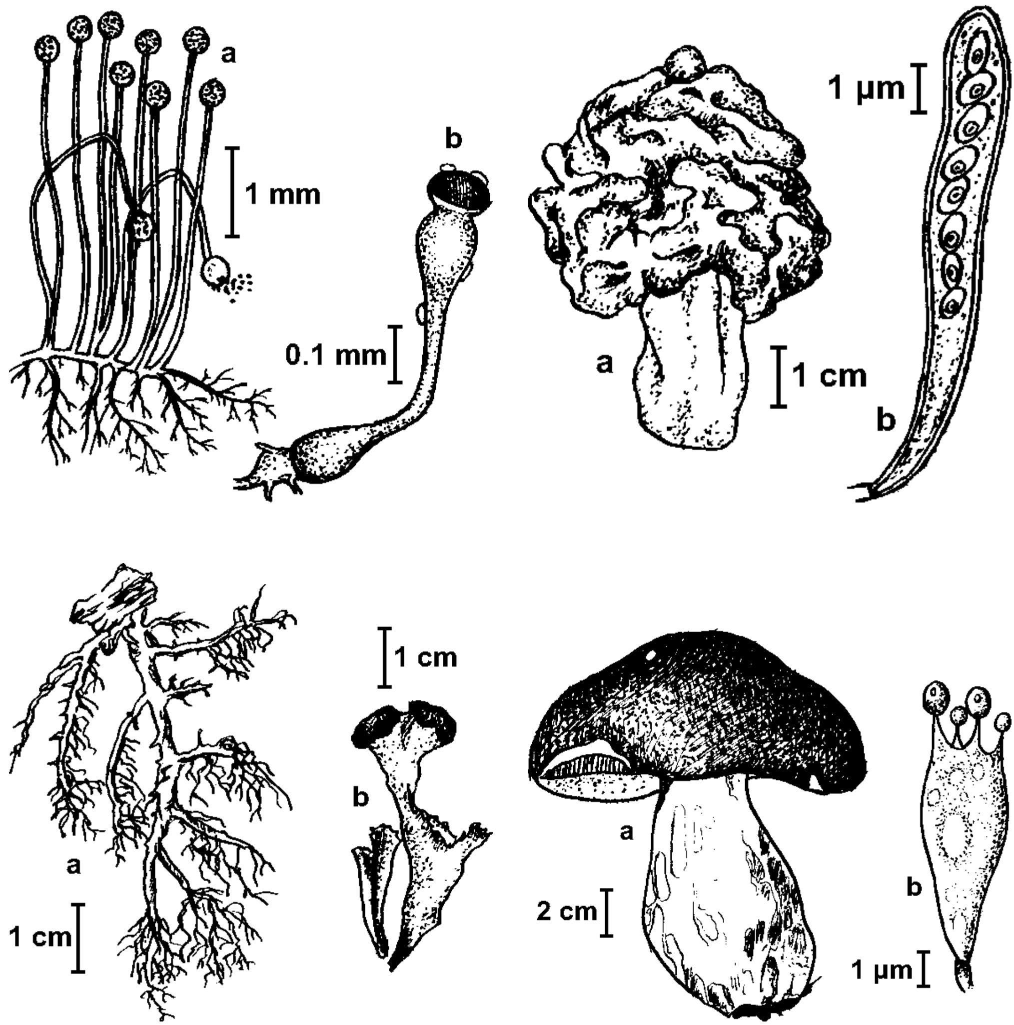

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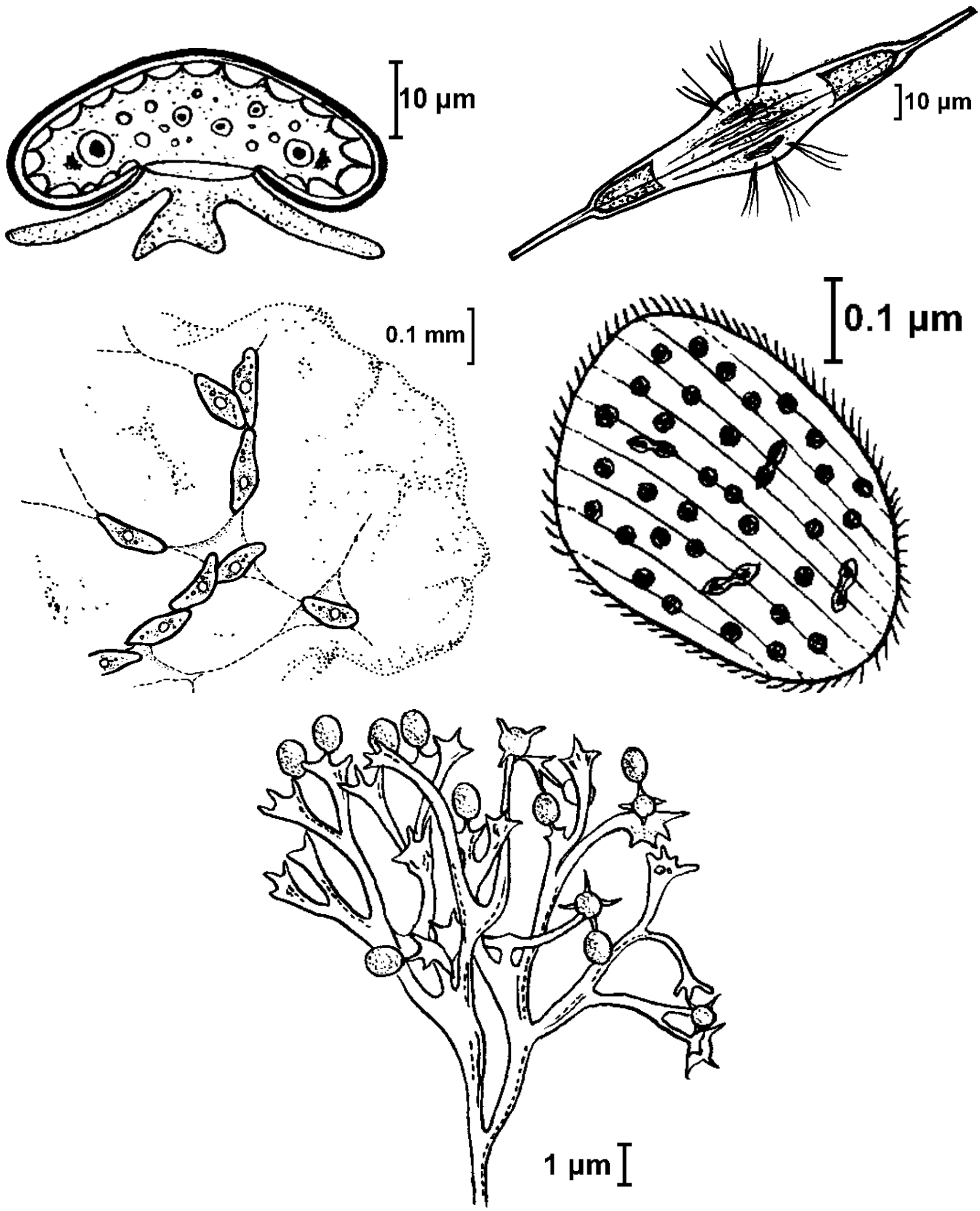

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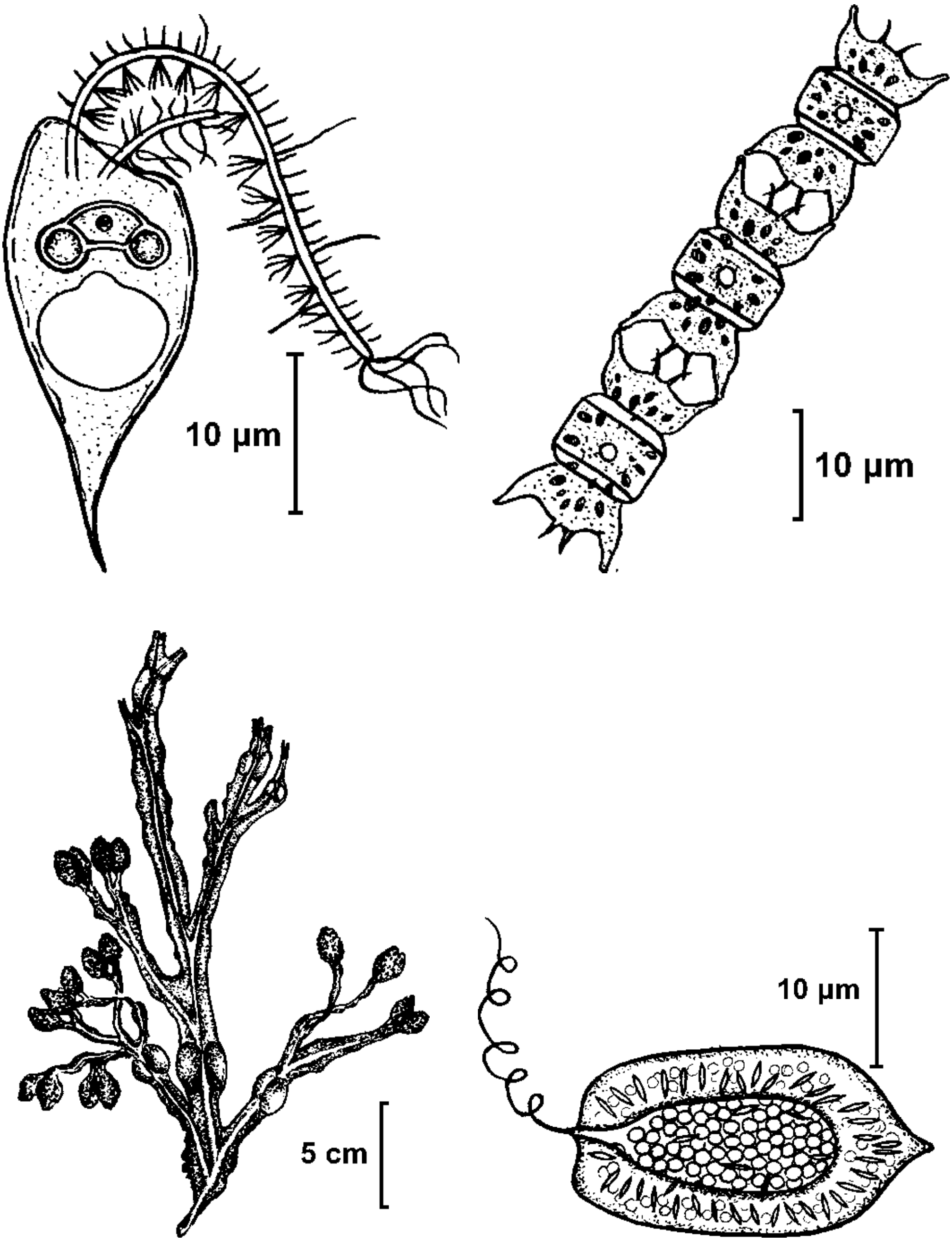

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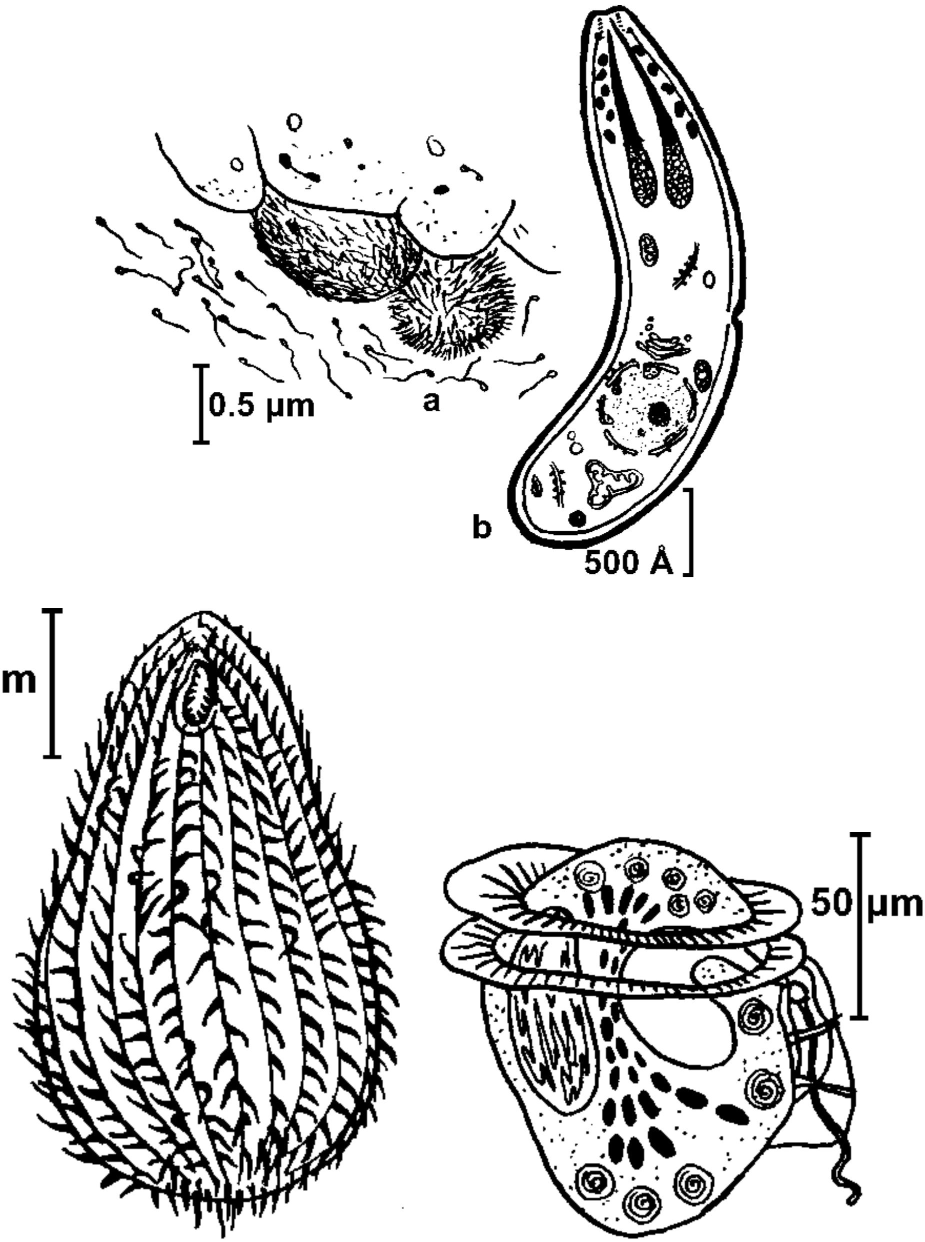

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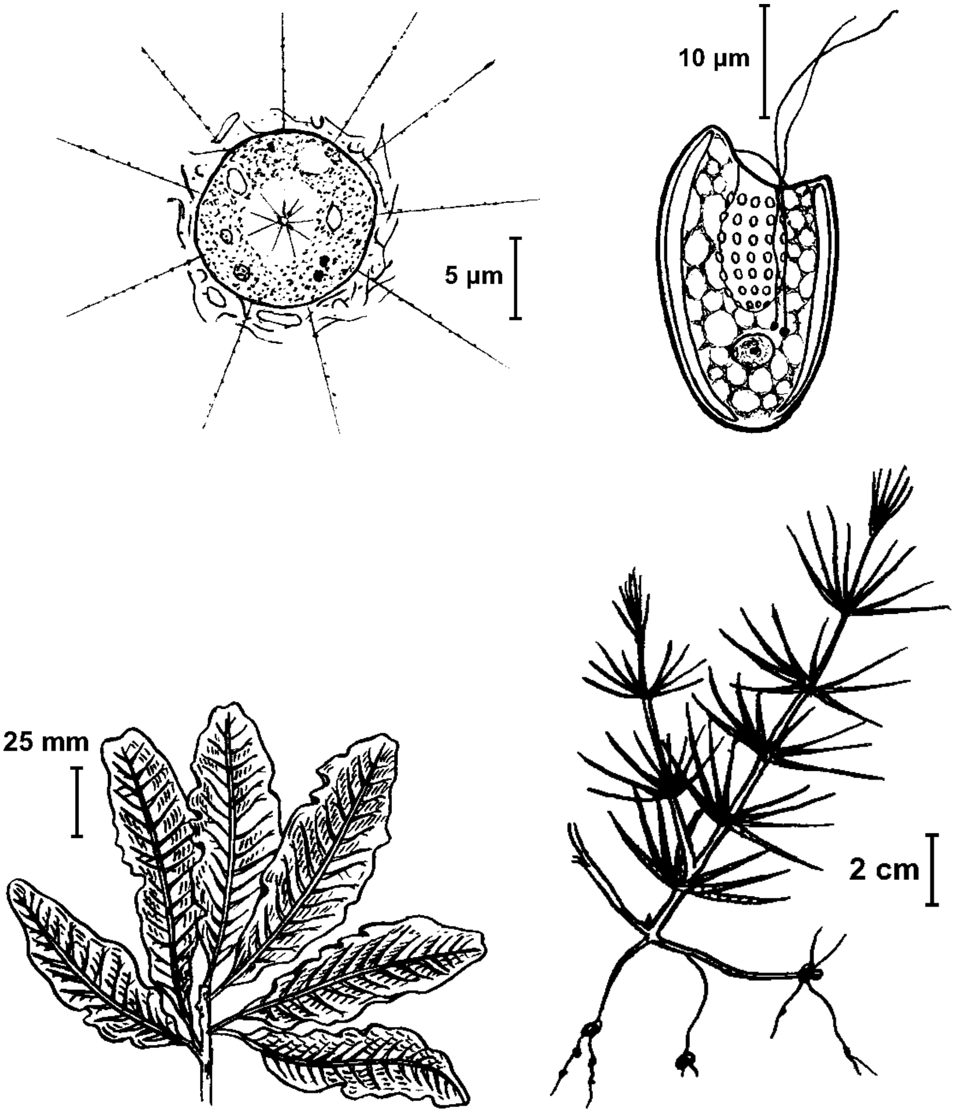

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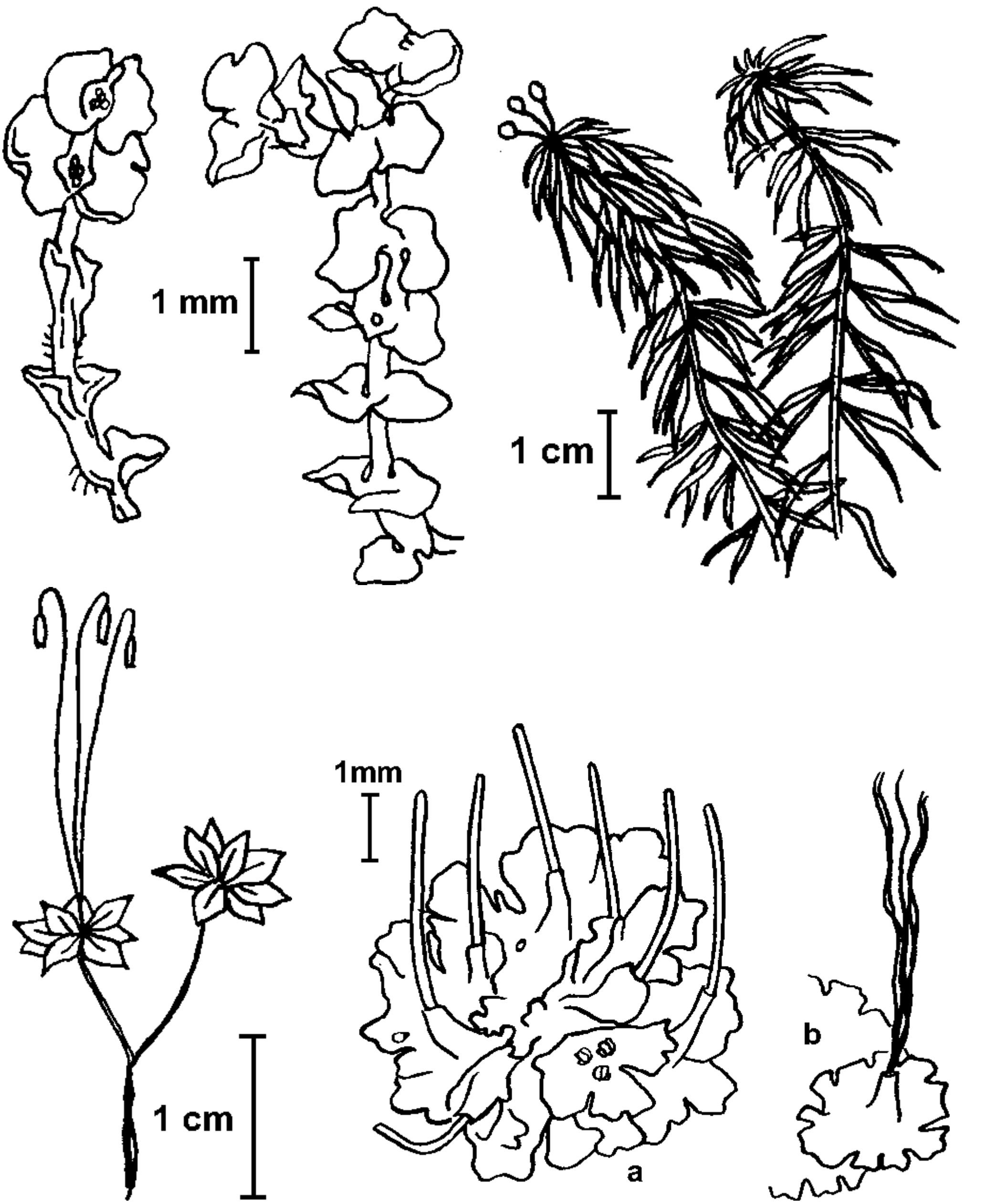

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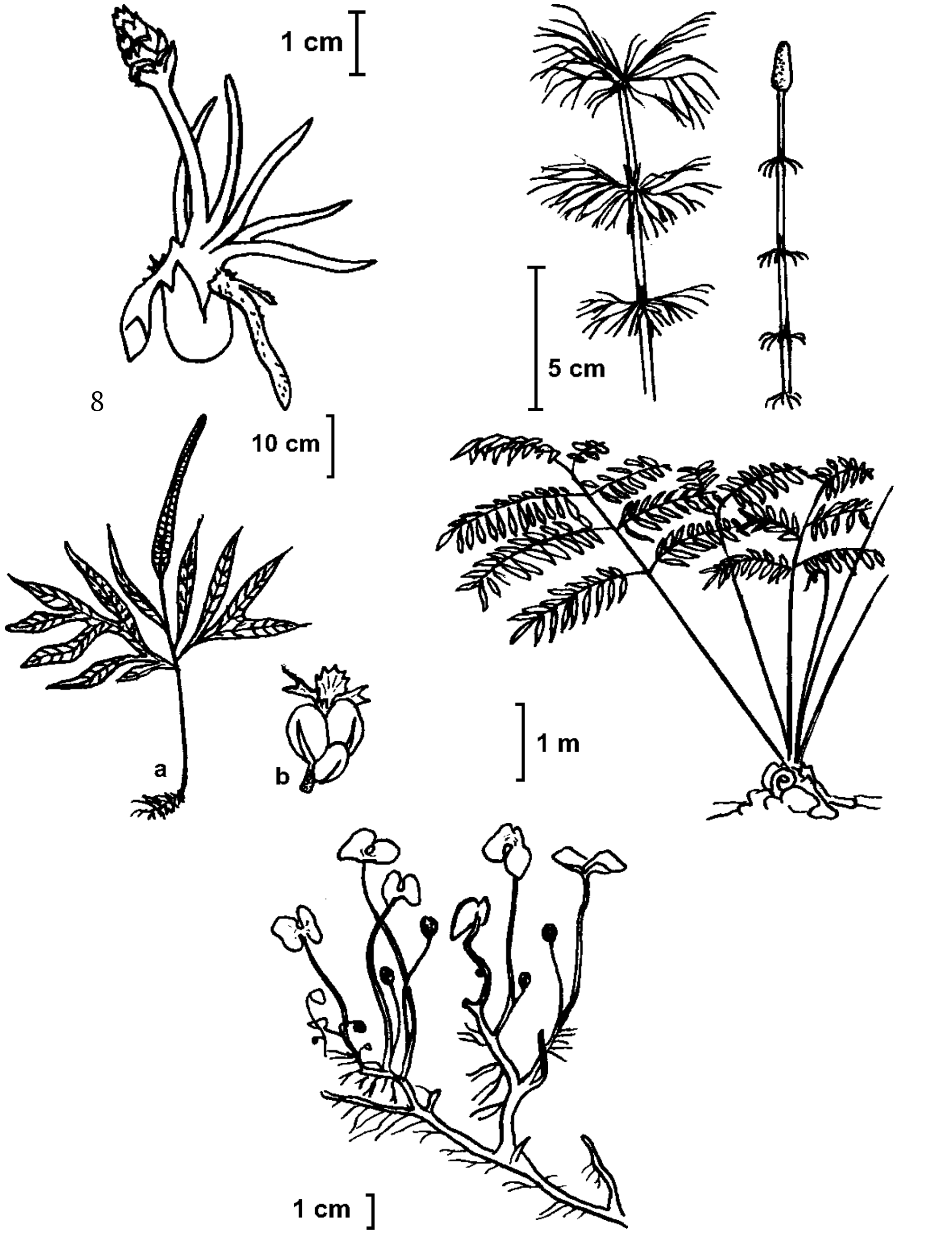

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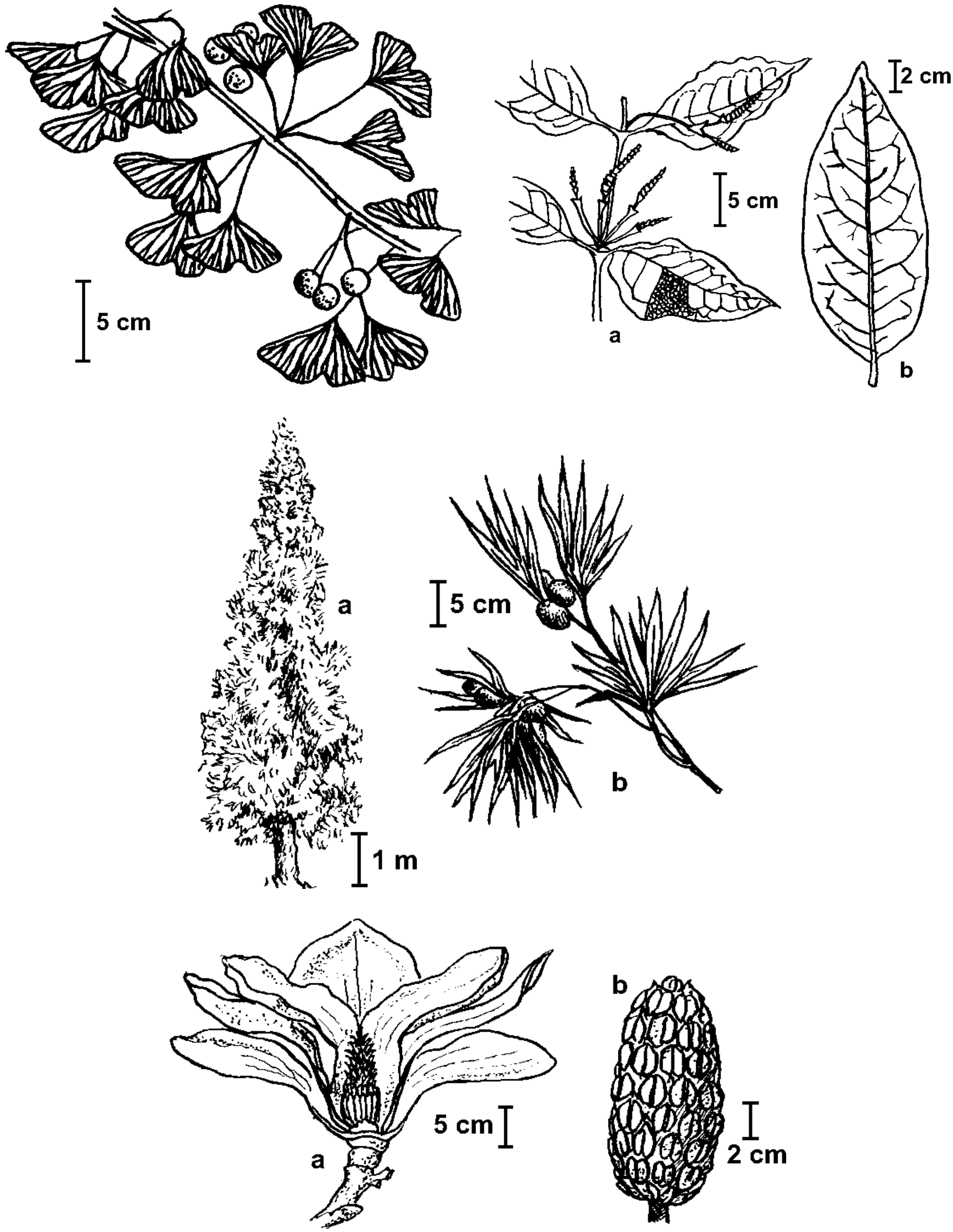

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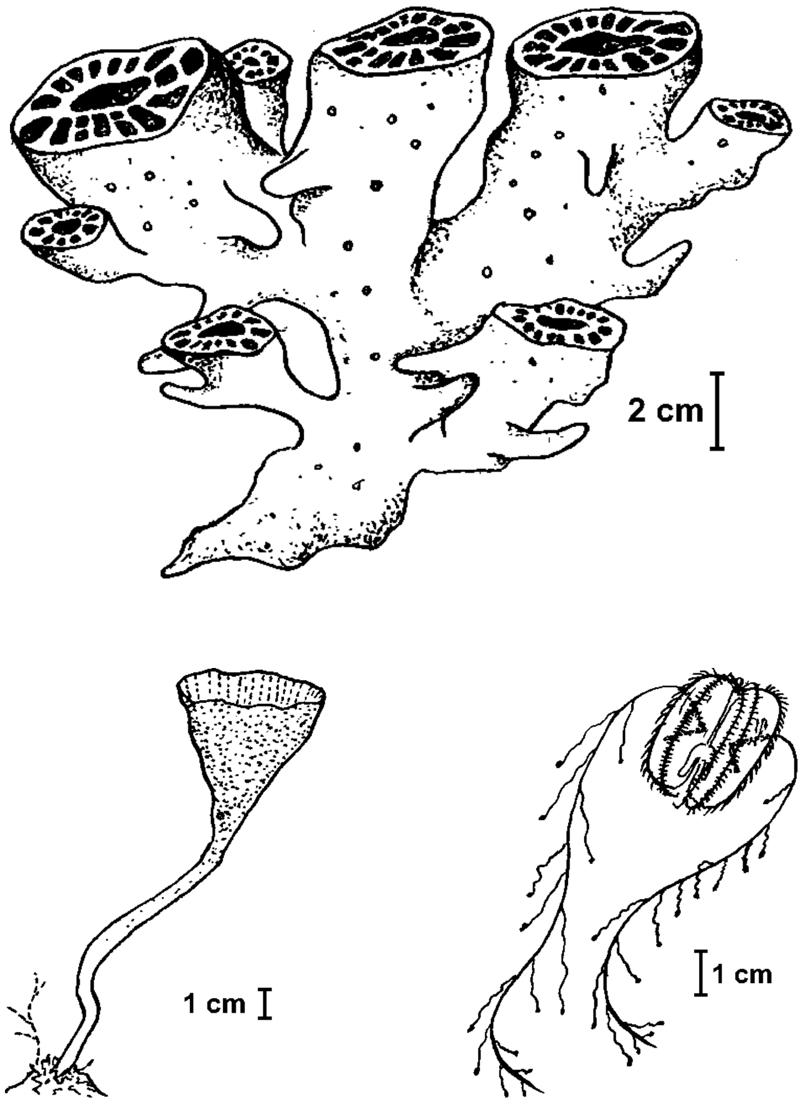

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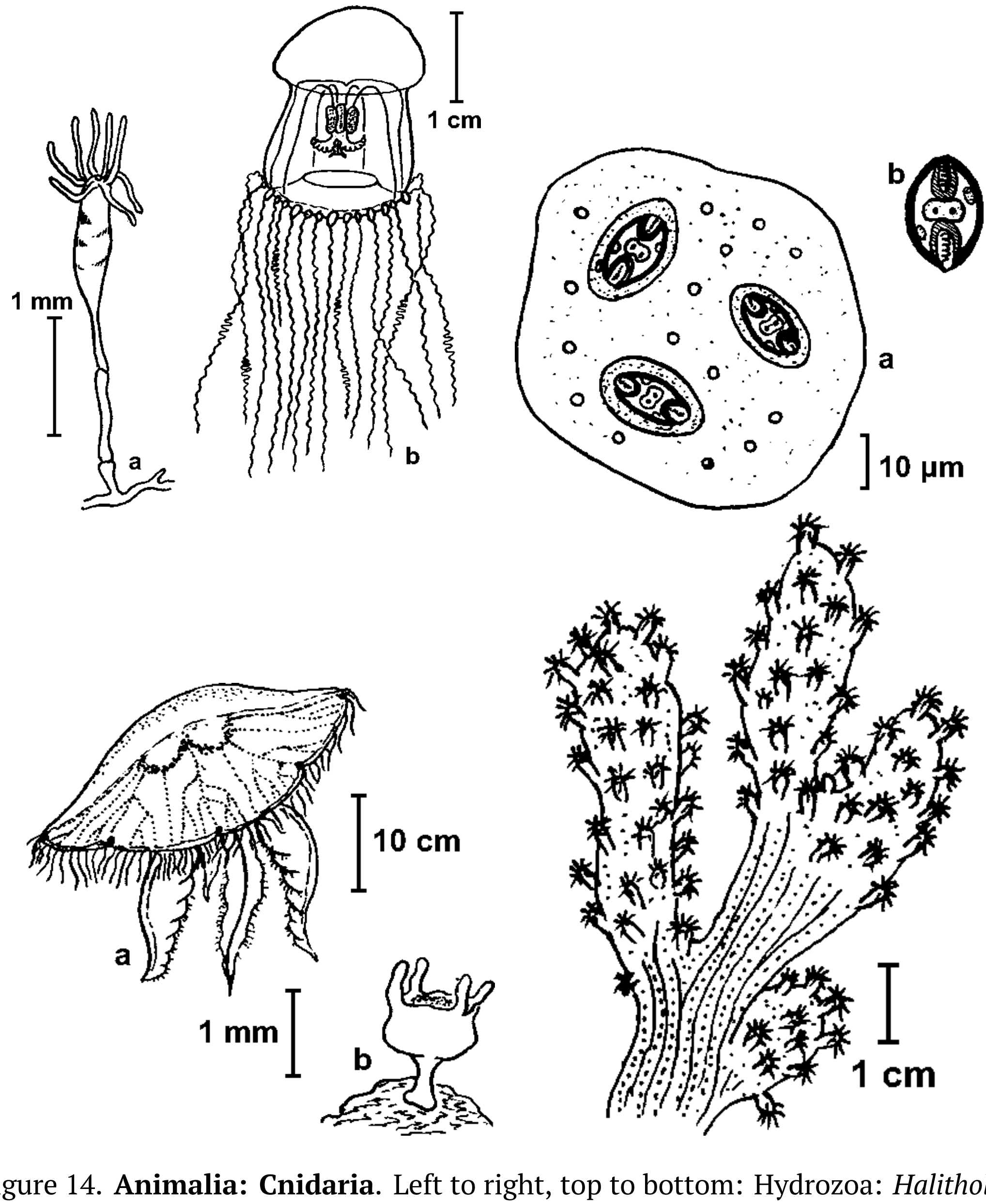

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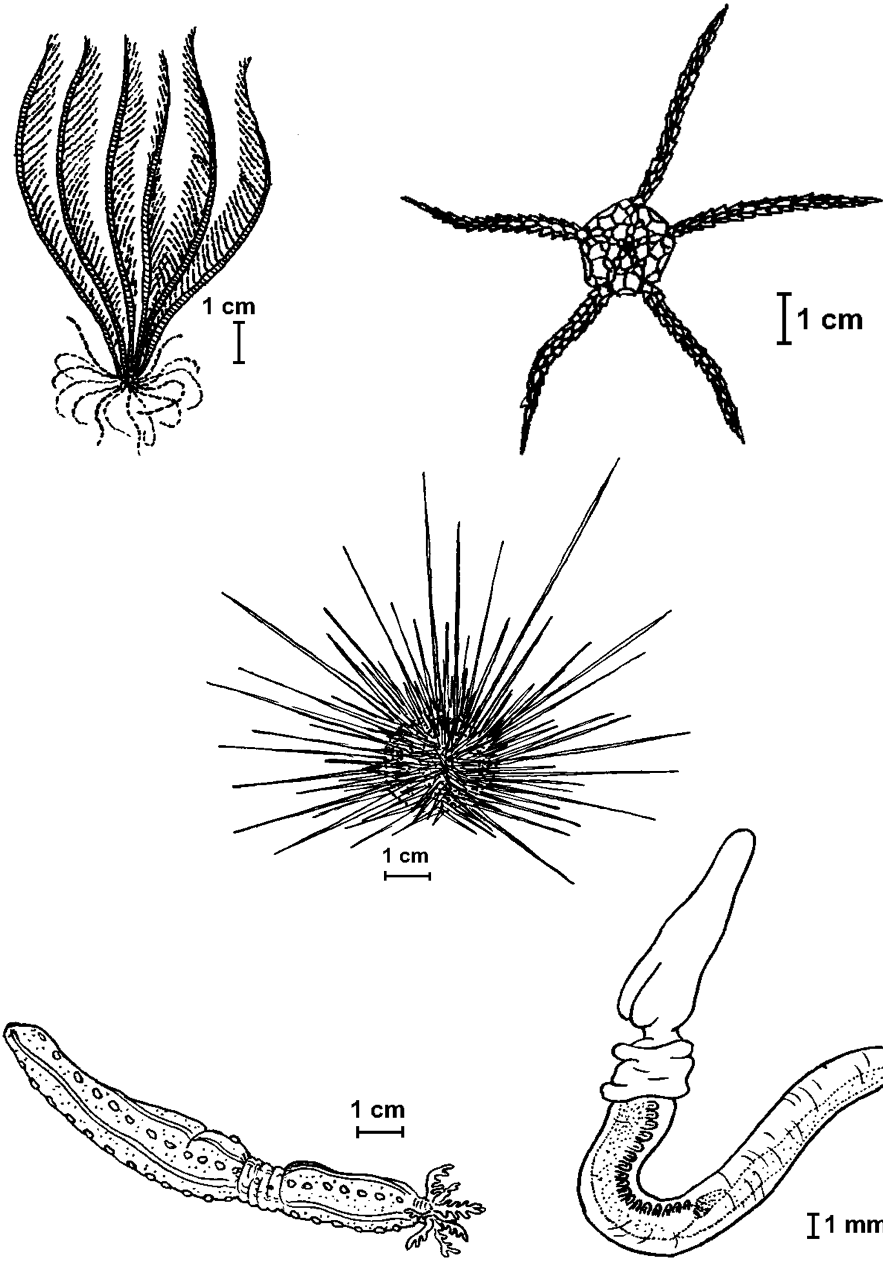

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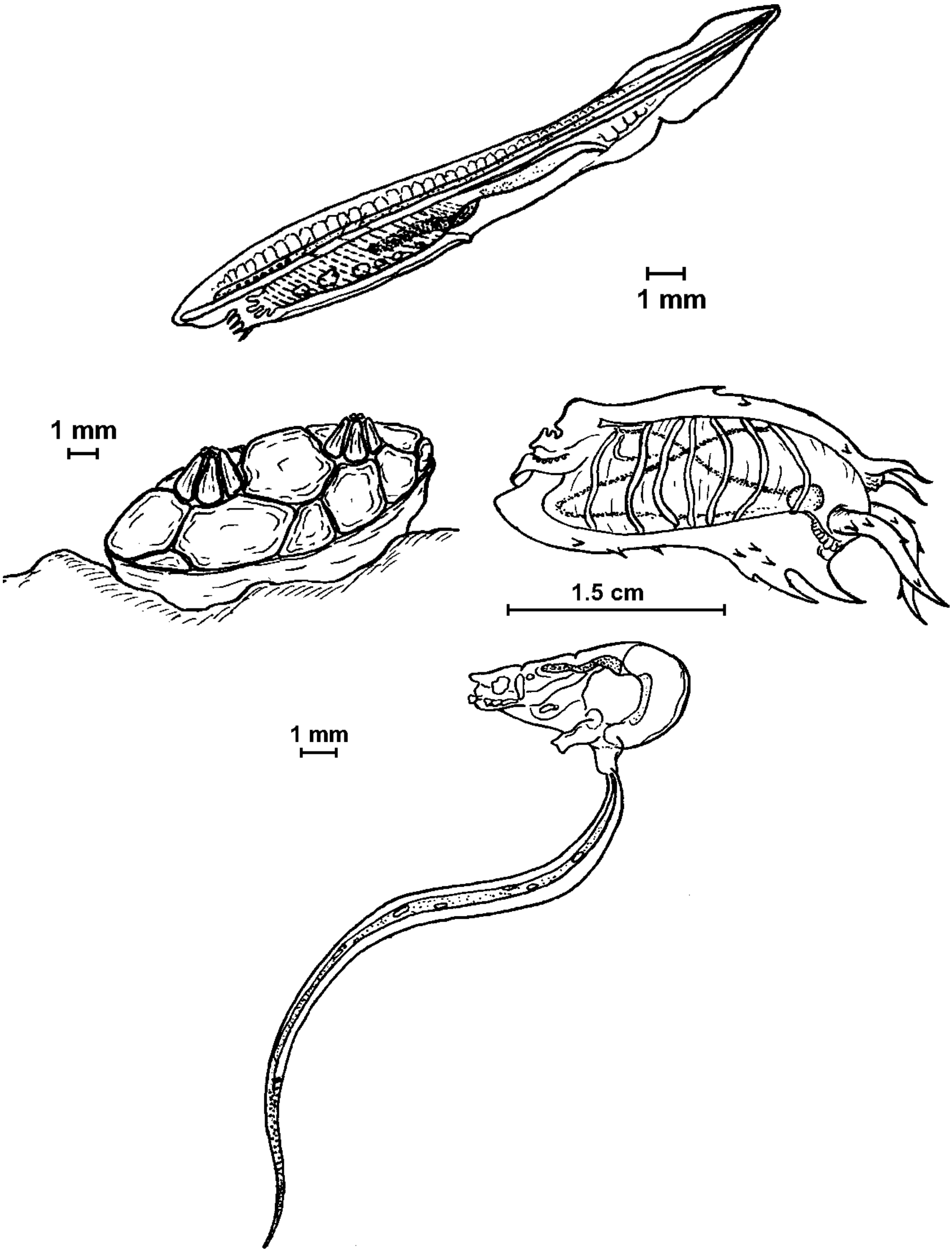

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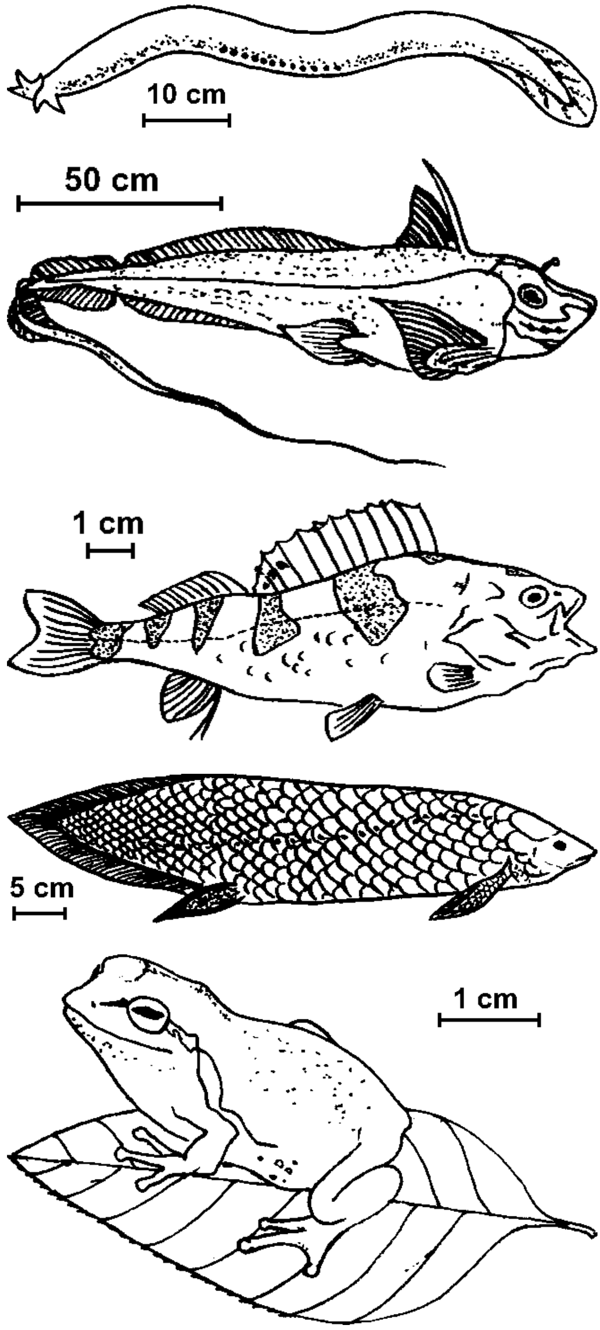

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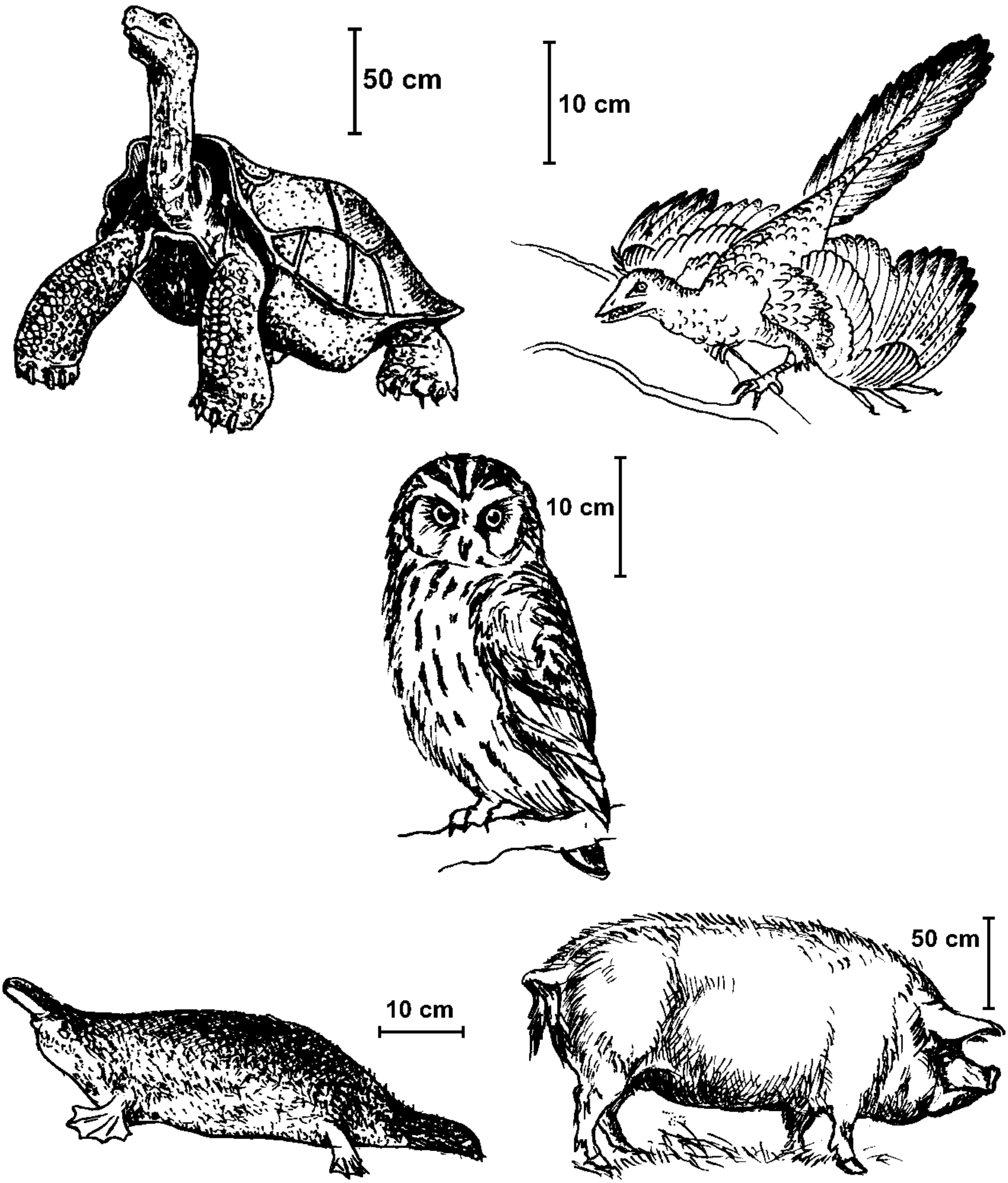

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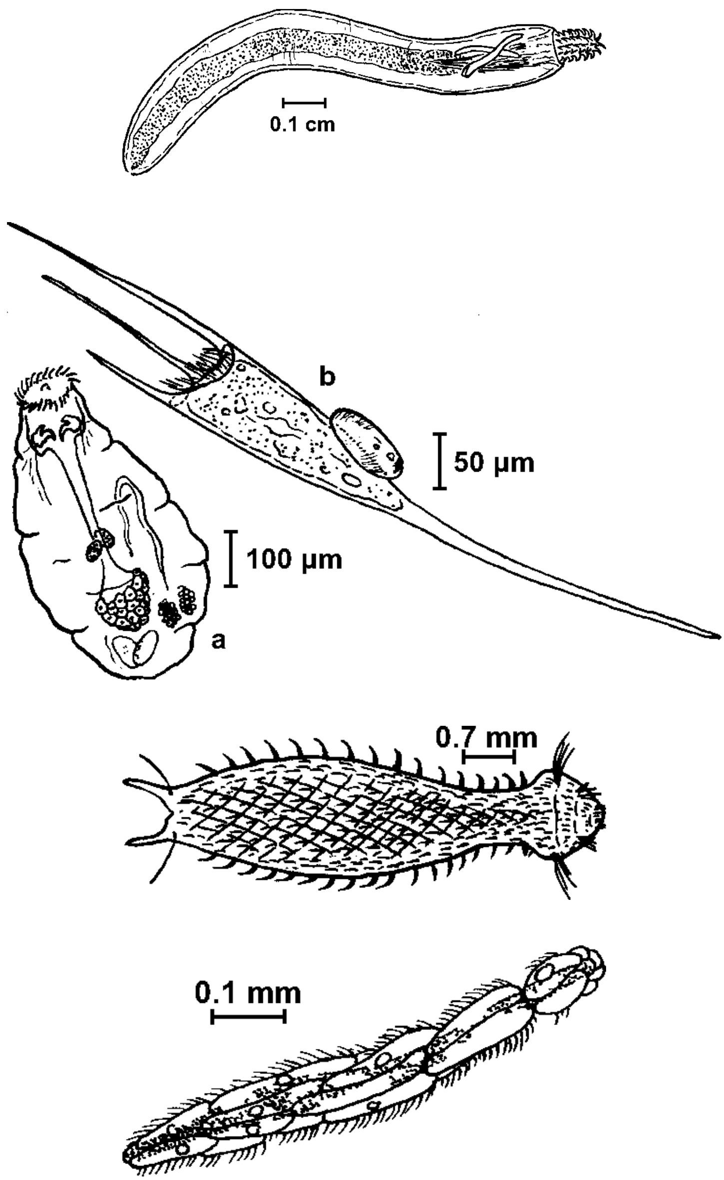

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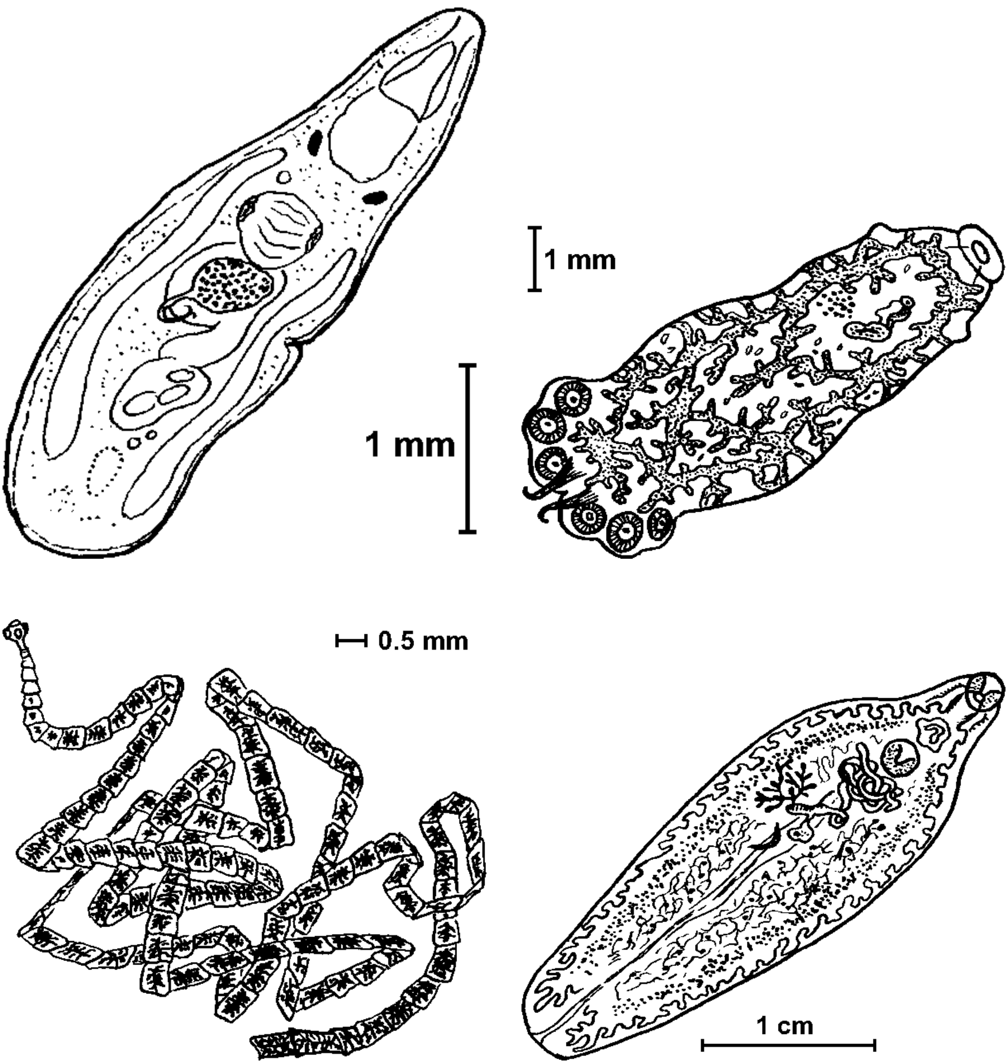

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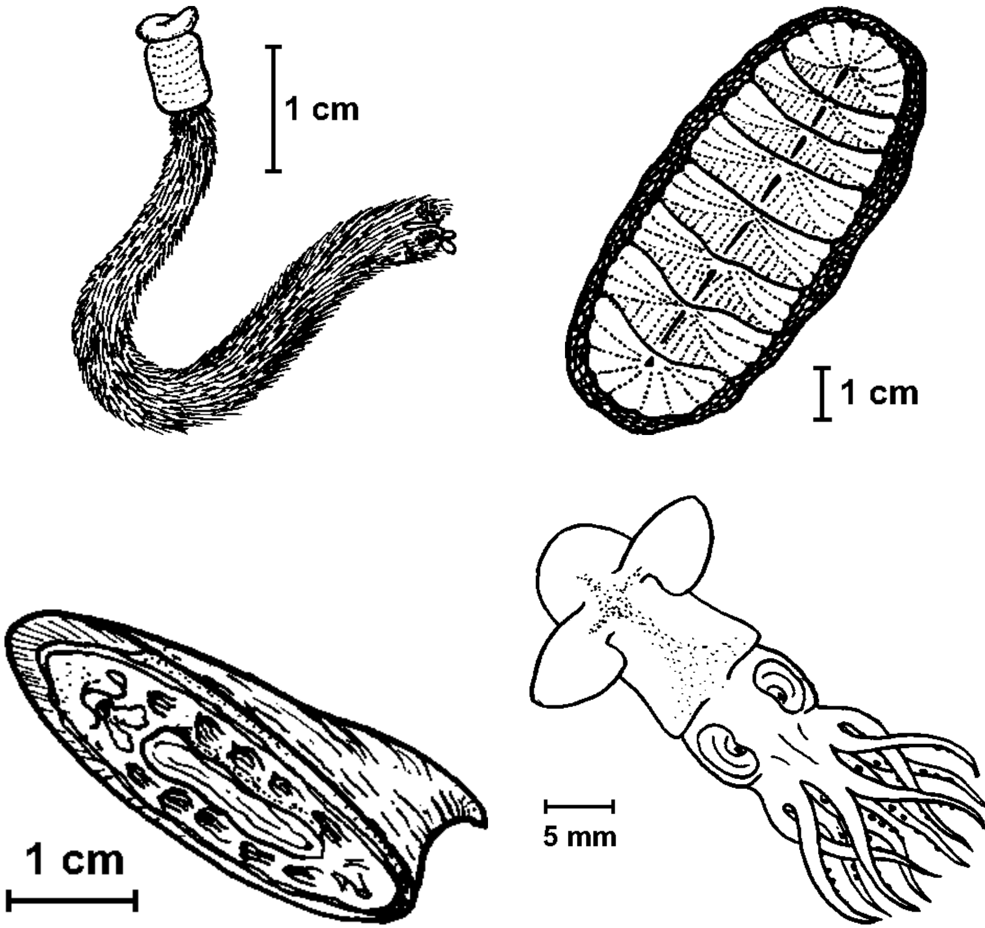

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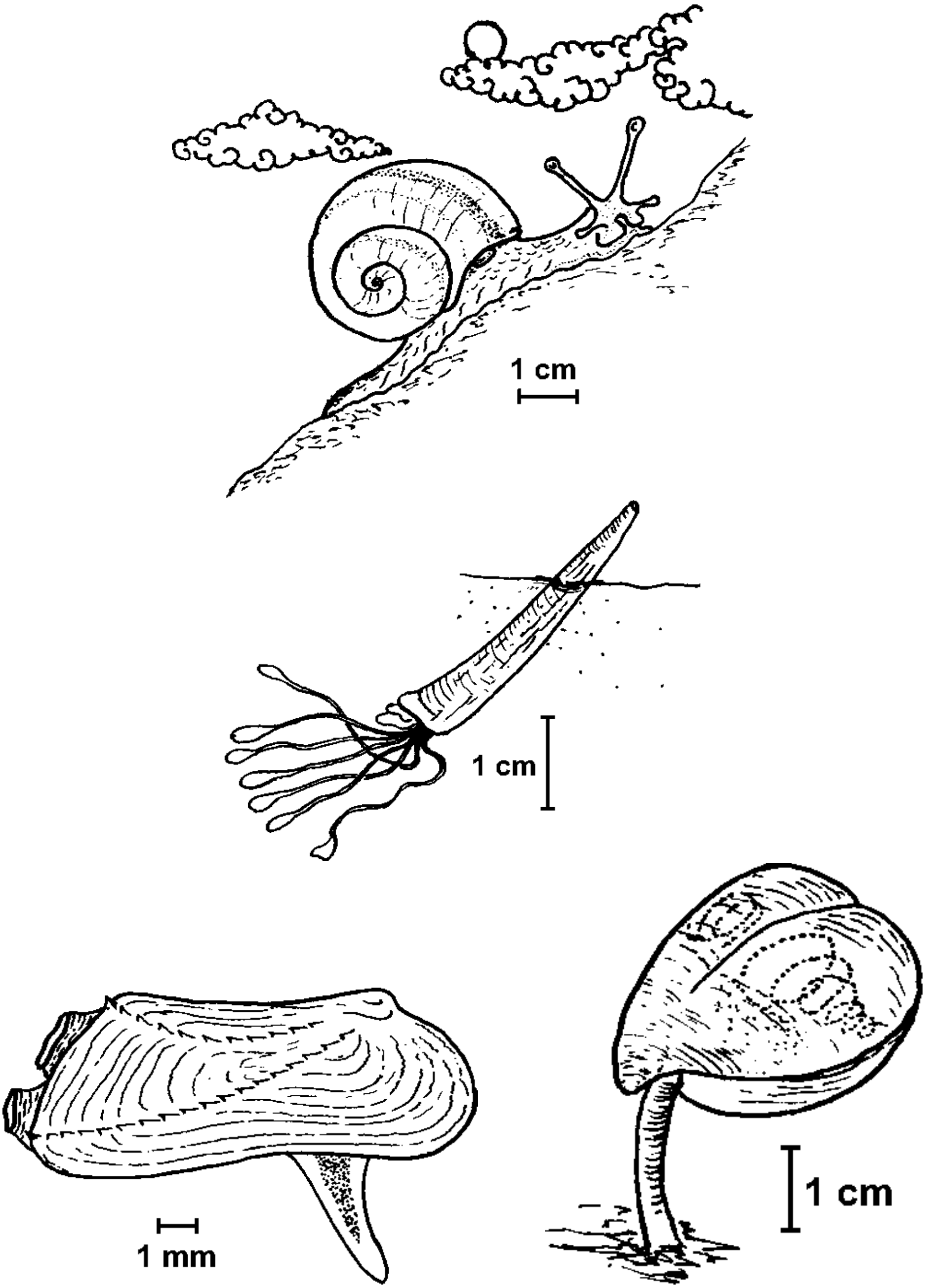

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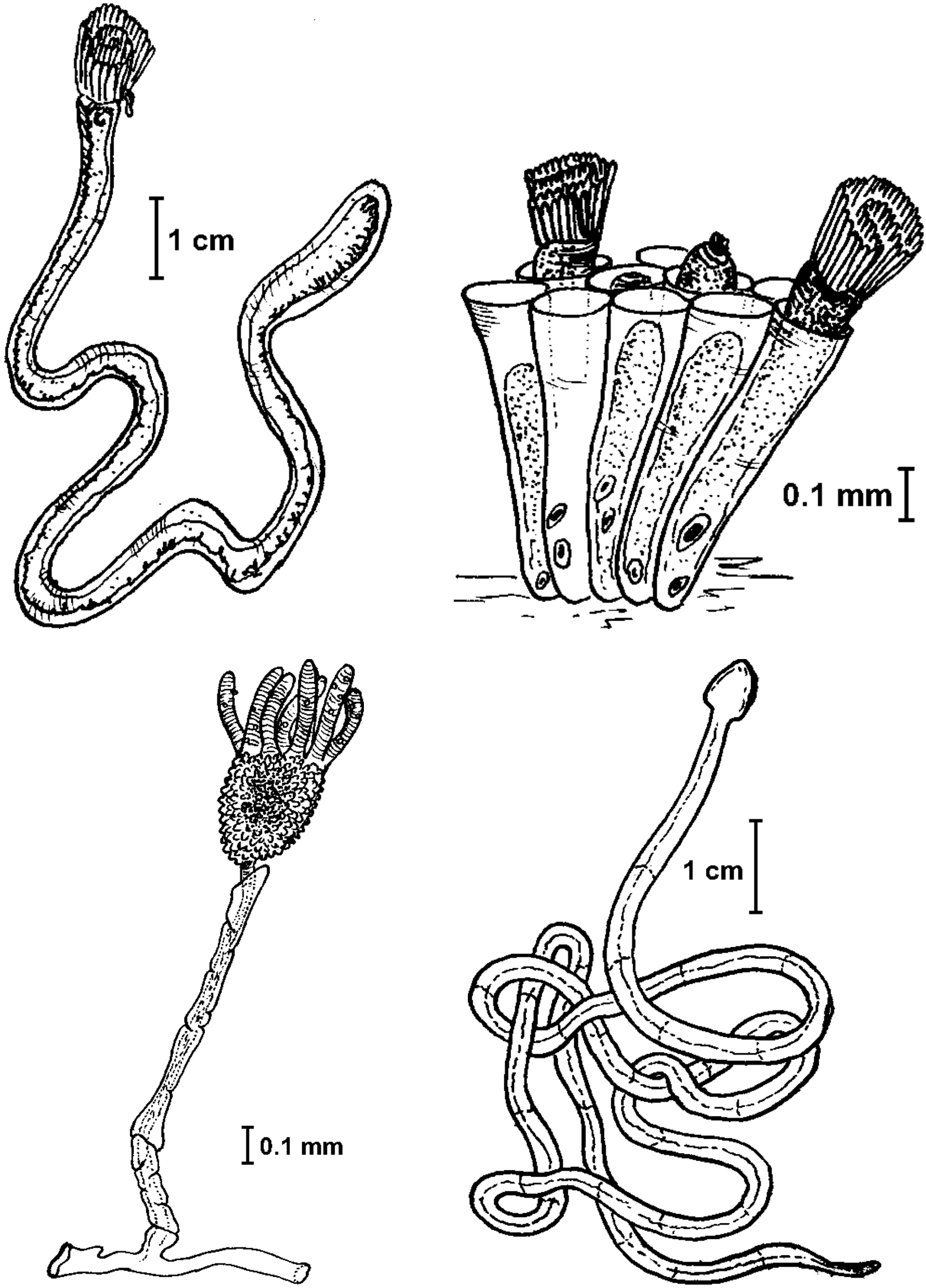

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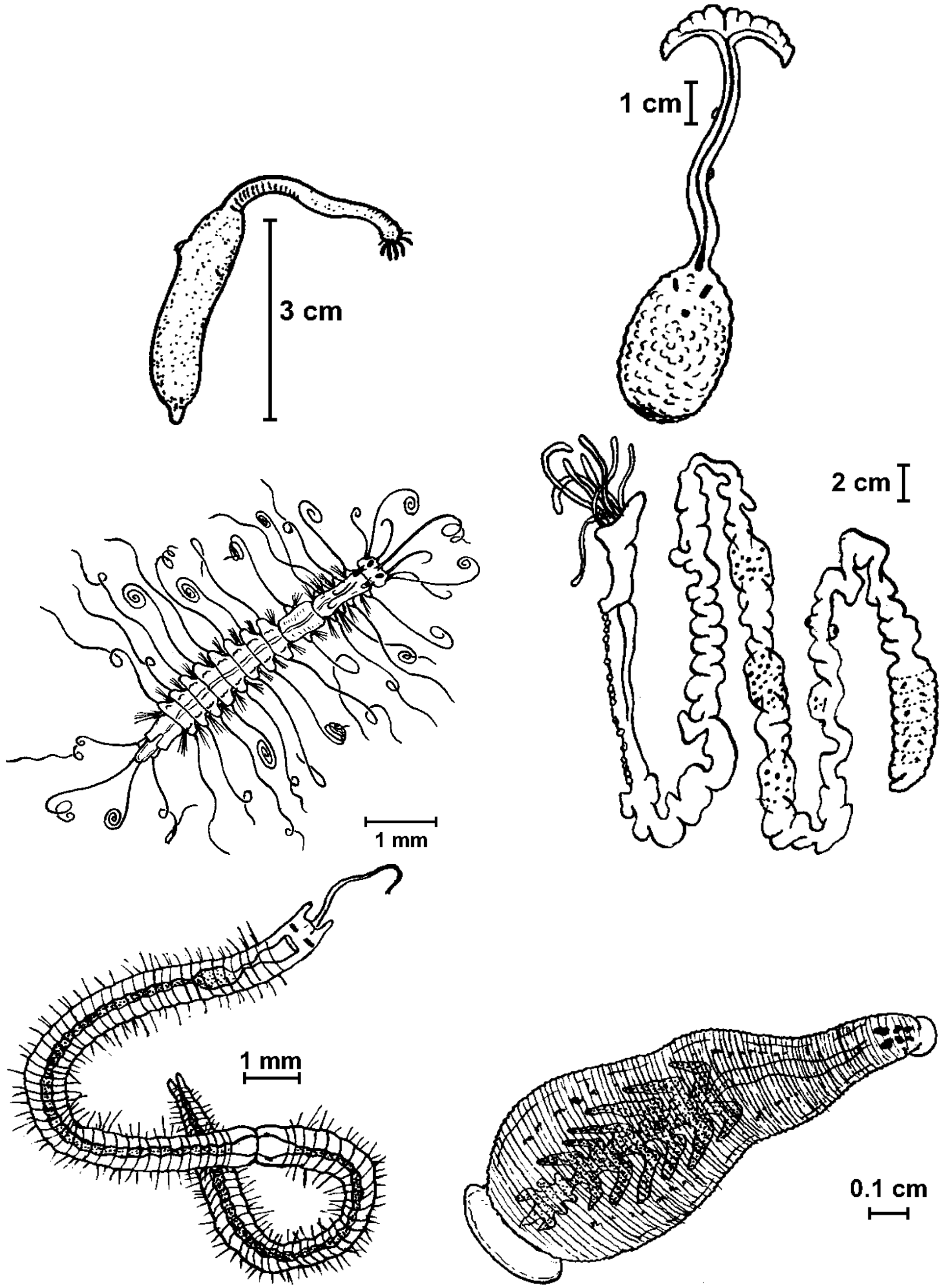

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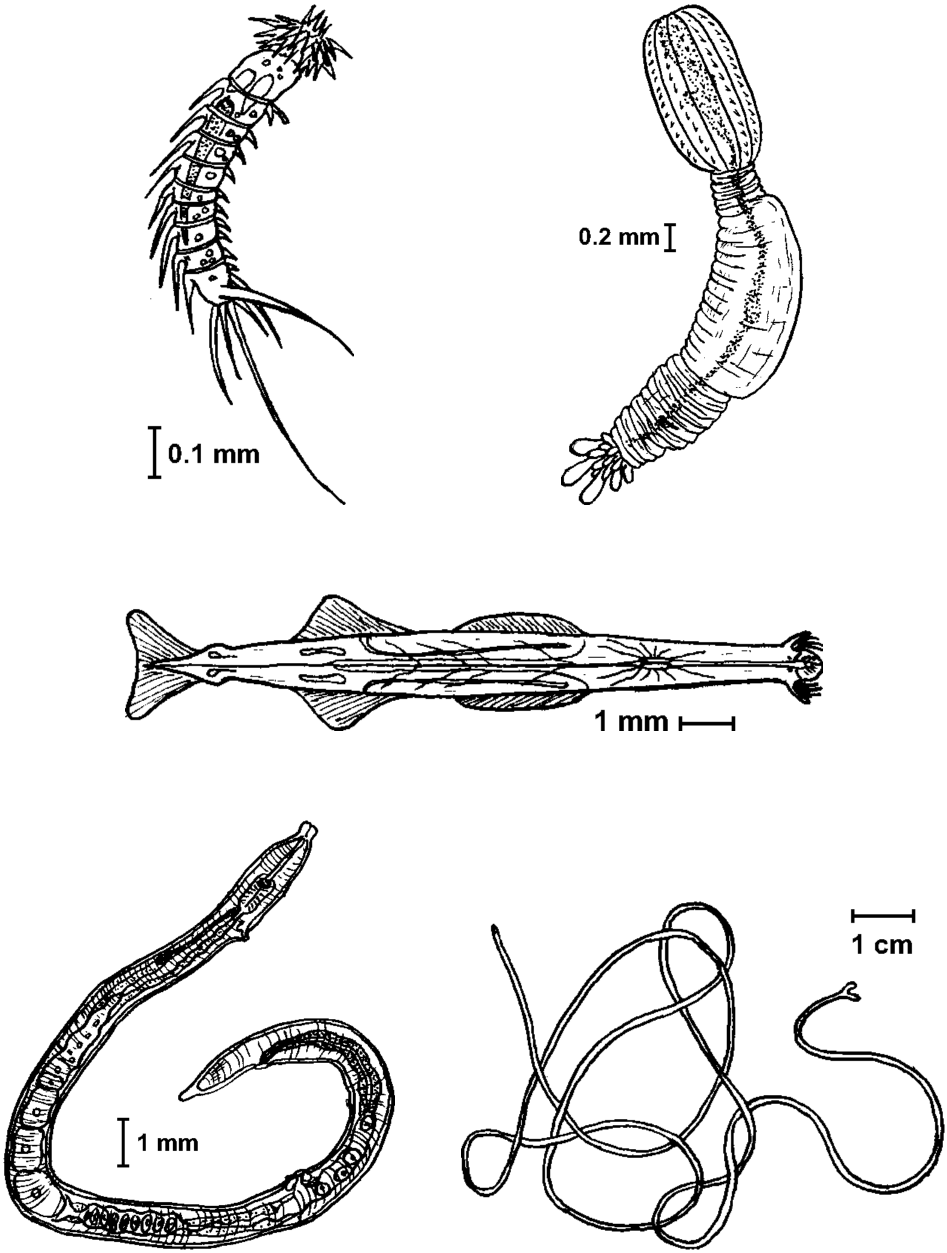

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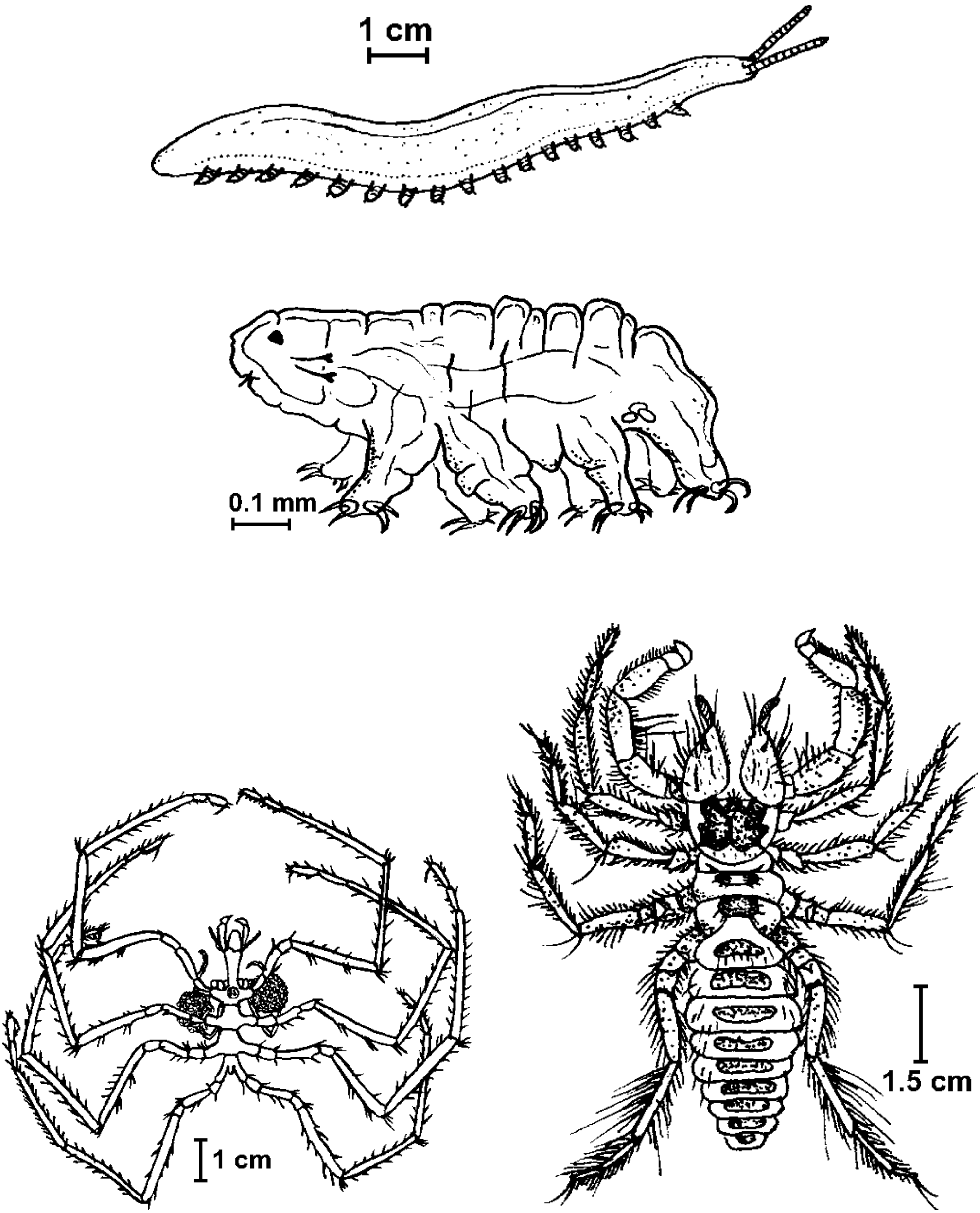

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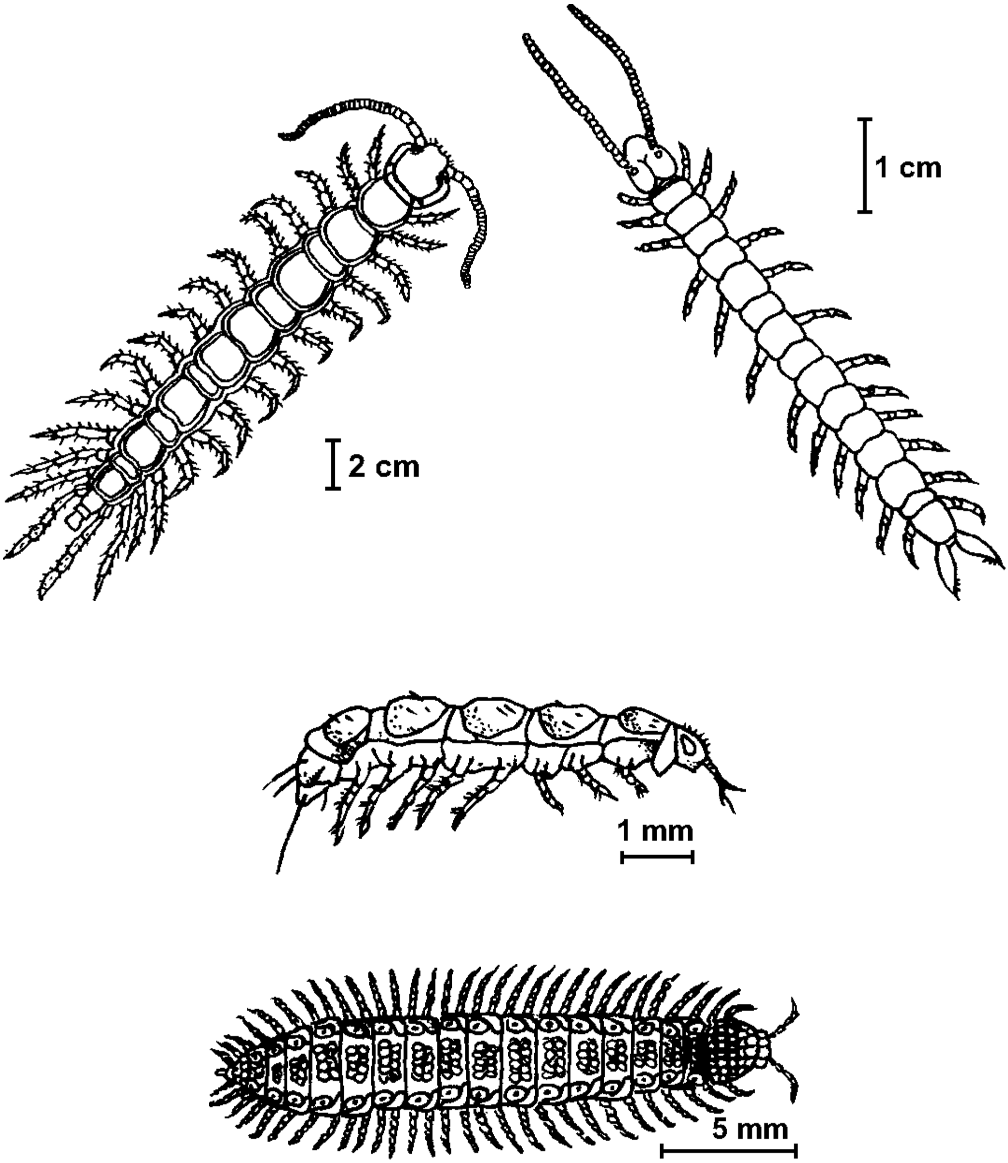

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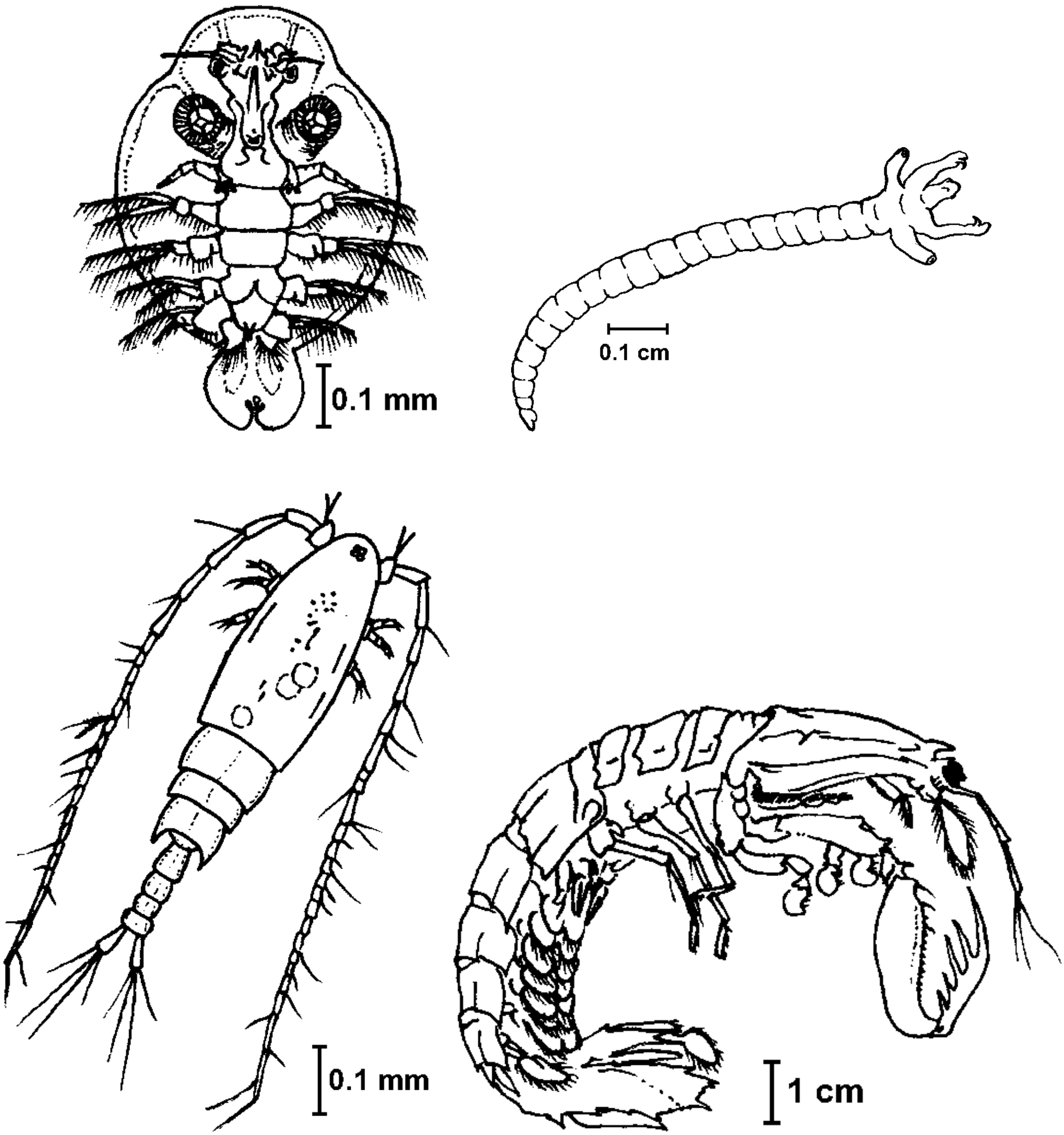
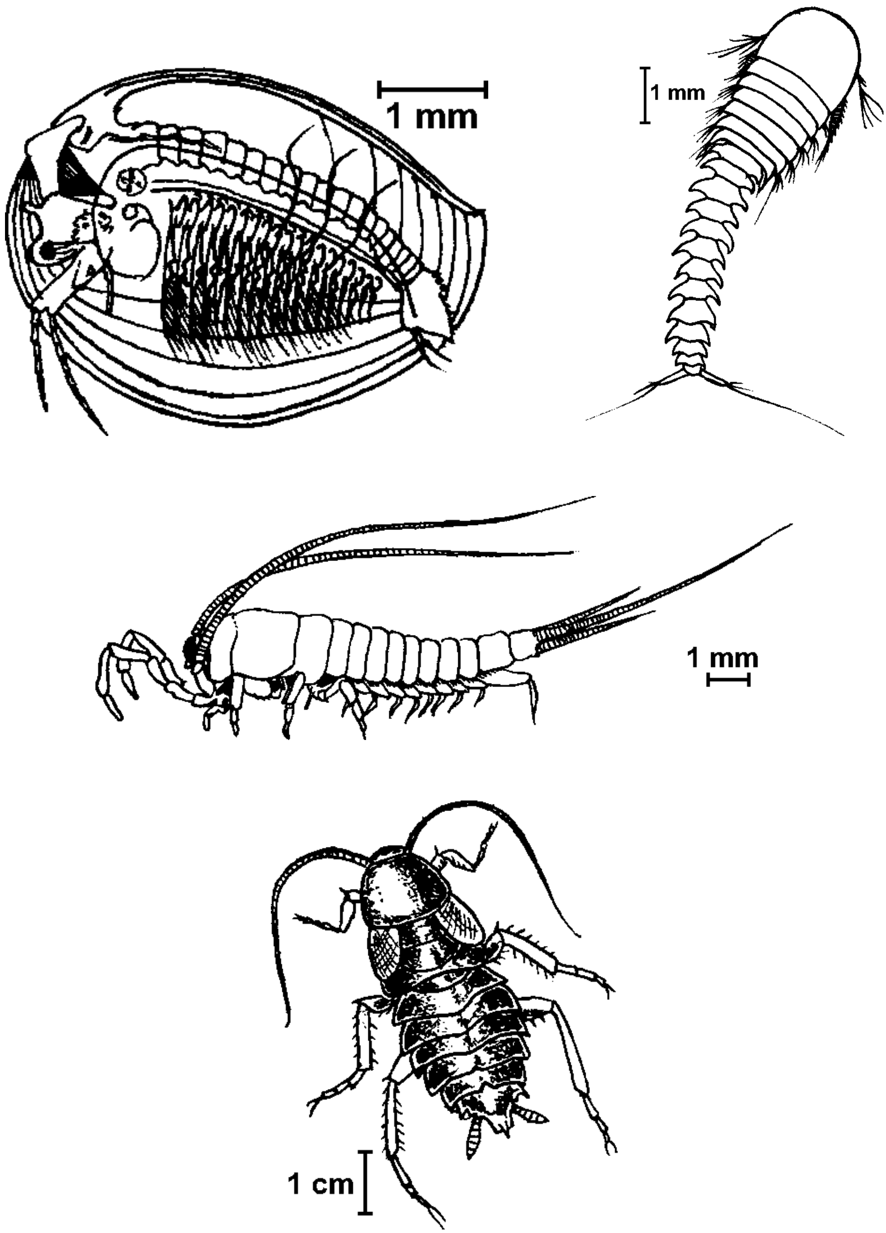


Figure 28. **Animalia: Ecdysozoa IV (Pancrustacea I)**. Left to right, top to bottom: Branchiura: *Argulus* sp.; Pentastomida: *Cephalobaena tetrapoda*; Copepodoidea: *Calanus* sp.; Malacostraca: *Squilla mantis*.



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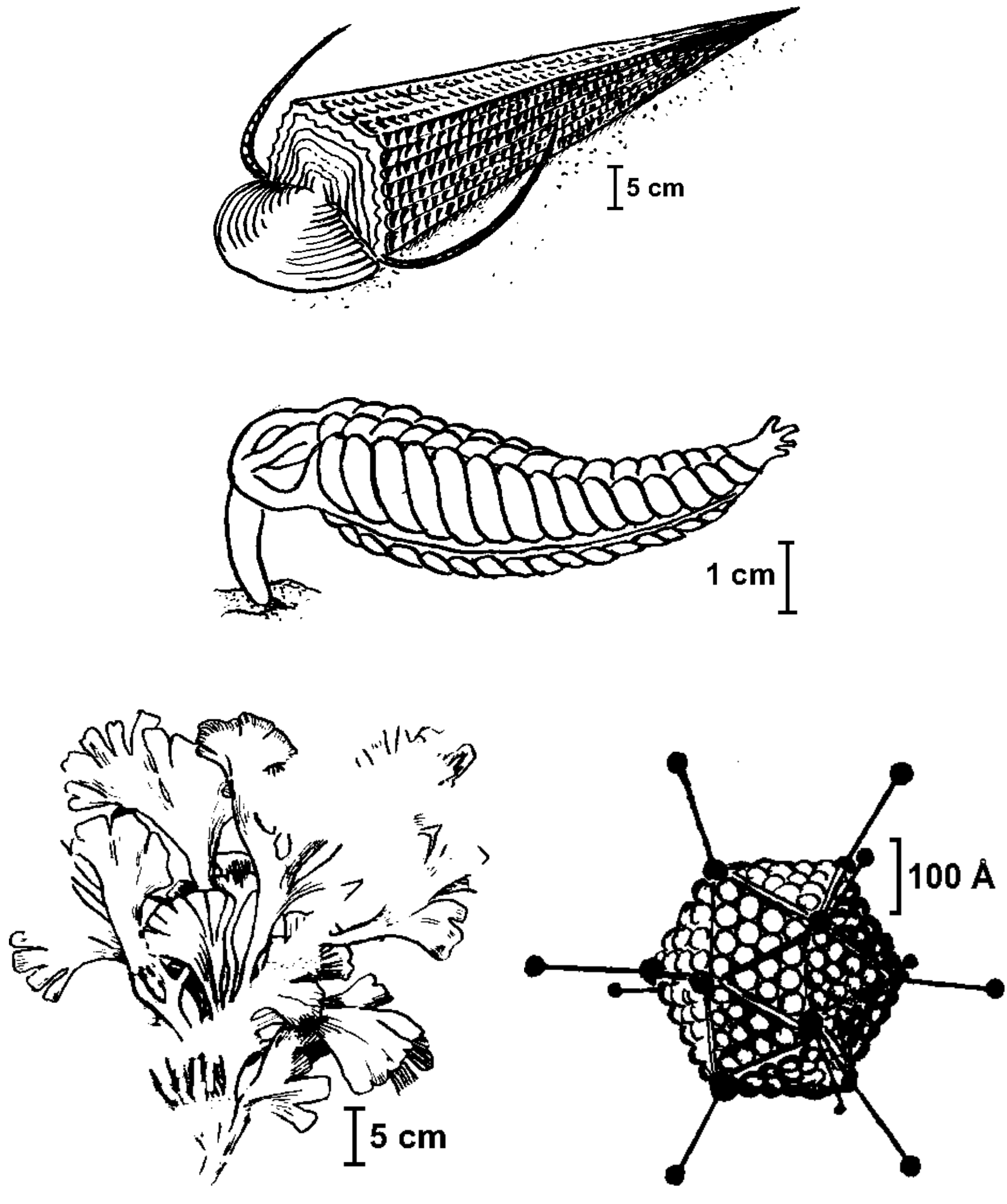


Figure 30. ***Problematica* and Viri**. Left to right, top to bottom: Hyolitha gen. sp.; Erniettiomorpha: *Pteridinium* sp.; "Nematophyta": *Prototaxites* sp.; Viri: *Adenovirus* sp.

Chapter 2

Vegetabilia

Bryophyta

Pteridophyta

Spermatophyta

Chapter 3

Animalia

Arthropoda

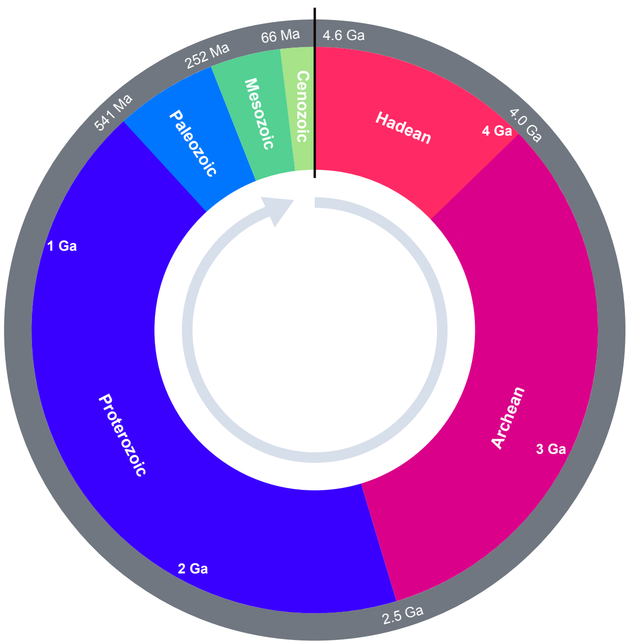
Mollusca

Chordata

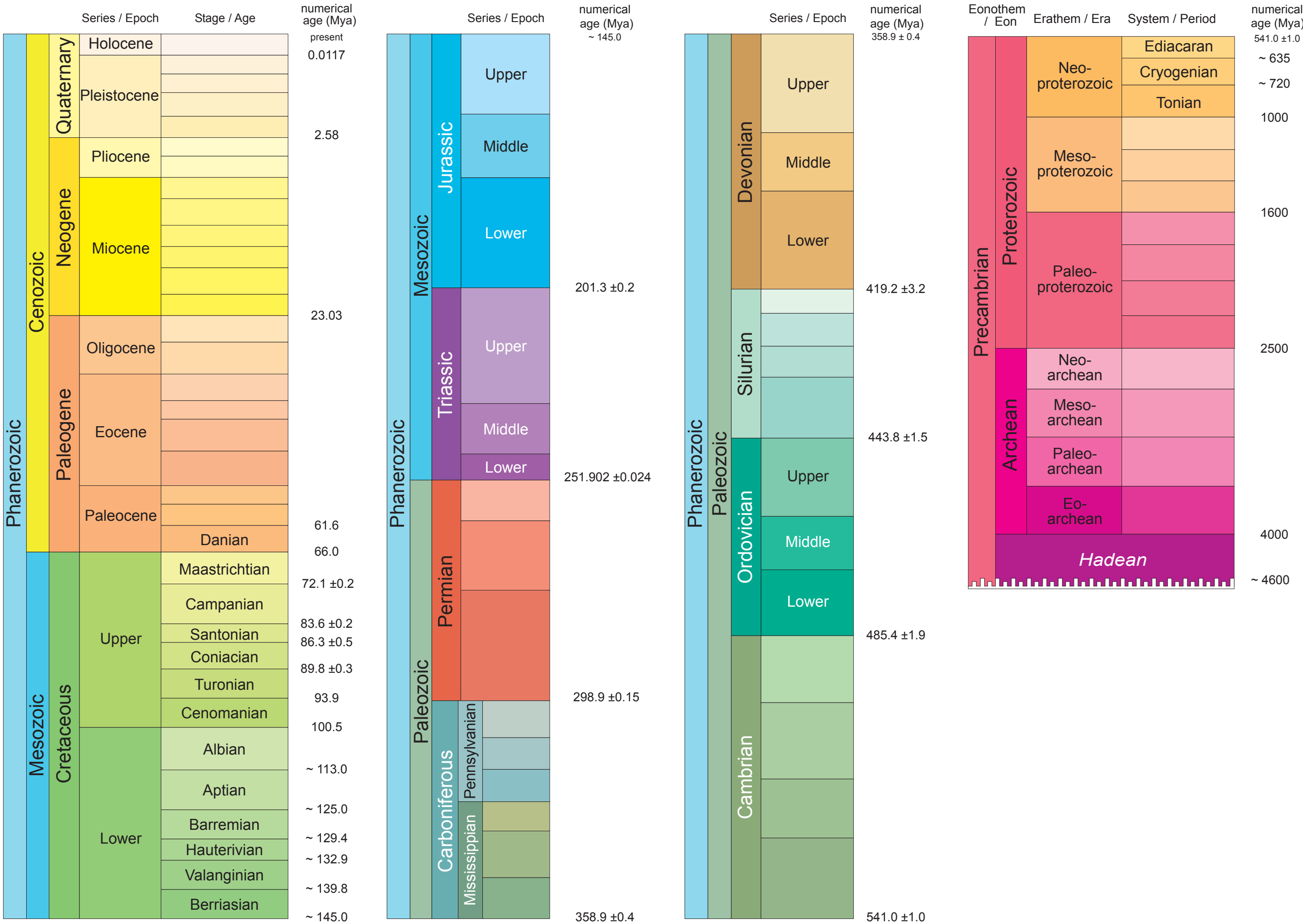
When

Chapter 4

The Really Short History of Life



Geologic clock.



Chronostratigraphic chart. Simplified from `http://www.stratigraphy.org/index.php/ics-chart-timescale`.

Origin of Life

Nikolaj Zinovjev, "Archeozoic Era" (1968)

In the strict sense, origin of life does not belong to biology. In addition, biologists were long fought for the impossibility of a spontaneous generation of life (which was a common belief from Medieval times to the end of 19 century). One of founders of genetics, Timofeev-Resovsky, when he was asked about his point of view on the origin of life, often joked that "he was too small these times, and do not remember anything".

However, the contemporary biology can guess something about these times. Of course, such guesses are no more then theories based on common scientific principles, **actuality** and **parsimony**.

First, Earth was very different. For example, atmosphere had no oxygen, it was much closer to atmosphere of Venus then to atmosphere of contemporary Earth and contained numerous chemicals which are now poisonous for most life (like CS_2 or HCN). However, by the end of Archean first oxygen appears in atmosphere, and in early Proterozoic it started to accumulate rapidly. The process is called "oxygen revolution" and it had many consequences. But what the reason of oxygenation was nothing else than appearance of first photosynthetic organisms, most likely **cyanobacteria**.

Second, the first traces of life on Earth are suspiciously close to the time of Earth origin (4,540 mya)— **molecular clock** place **LUCA** about 4,000 mya, and recently found first traces of cyanobacteria are 3,700 mya. Altogether, life on Earth was most of the time of its existence!

Third, first living things were most likely **prokaryotes** (Monera, bacteria). These could be both photosynthetic (cyanobacteria) and **chemotrophic** bacteria as evidenced from isotope analysis of Isua sedimentary rocks in Greenland, and now also from the presence of **stromatolites**, the traces of cyanobacteria in the same place.

What was the first living thing? It has a name LUCA, Last Universal Common Ancestor but only a little could be estimated about its other features. It was probably a cell with DNA/RNA/proteins stream, like all current living things. Unclear is how this stream appeared, and how happened that it was embedded into the cell. One of helpful ideas is "RNA world", speculation about times when no **DNA** yet exist, and even **proteins** did not function properly but **RNA**s already worked as information source as well as biological machines. Another possibility is that **lipid** globules, some other organic molecular and water formed **coacervates**, small droplets in which these RNAs could dwell. If this happened, then resulted structure could be called "proto-cell".

Prokaryotic World

Most of Proterozoic prokaryotes (Monera) dominated the living world. Typical landscape these times was high, almost vertical rocks and very low plains which should be covered with tide for dozens of kilometers. This is because there were no terrestrial organisms decreasing erosion. Ocean was low oxygenated, only water surface contained oxygen.

In that conditions, ancestor of eukaryotes appeared. First eukaryotes could probably remain contemporary heterotrophic Excavata (Fig. 3) like *Jacoba* but there are no fossils of this kind. However, there are number of fossils which could be treated as **algae**, photosynthetic protists. These fossils remind contemporary red and green algae (Fig 9, the bottom row). It is possible that some other Proterozoic fossils (acritarchs) belong to other protist groups, for example, unicellular Dinozoa (Fig. 8).

Ecosystems of these times were similar to Archean and mostly consisted of cyano- and other bacteria, and represented now by stromatolites. No one can say anything about terrestrial life in Proterozoic, but it possible that Monera dominated there as well.

In the end of middle Neoproproterozoic, continents of Earth joined in one big continent Rodinia, this triggered the most powerful glaciation in history, “snowball Earth”, Cryogenian glaciation.

The Rise of Nonskeletal Fauna

This mentioned above glaciation possibly, in turn, triggered evolution of Earth, because in Ediacarian period (the last period of Proterozoic), animals and other multicellular organism appear. There are three most unusual things about Ediacarian ecosystems. First, they were filled with creatures as similar to contemporary life as would (not yet discovered) extra-terrestrial life be. In other words, they (like *Pteridinium*, see Fig. 30) had no similarity with the recent fauna and flora. Second, all these Ediacarian creatures were evidently soft, nonskeletal. This is even more striking because in the next period (Cambrian), almost all animals and even algae had skeletal parts.

There were different types of ecosystems in Neoproterozoic, but in essence, they all consisted of these soft creatures (it is not easy to say what they were, animals, plants of colonial protists). They thrived for about 90 million years and then suddenly declined (some left-overs existed in Cambrian, though). This is the third, really weird thing. Weird because later ecosystems almost always left descendants, even famous dinosaurs went extinct but left the great group of birds, their direct “offspring”.

Why they went extinct, it is not clear. Several factors could be blamed: oxidization of ocean, appearance of macroscopic carnivores, increased transparency of water. The last could relate with two first by means of *pellet production*. Many recent small plankton invertebrates pack their feces in granules (pellets) which speedily fall to the ocean bottom. In Ediacaran, there was probably no pellet production and therefore ocean water was mostly muddy. When first pellet producers appear, water start to be increasingly more transparent which raised oxygen production by algae, and, as the next step, allowed more and bigger animals to exist. Bigger plankton animals mean that it start to be rewarding to hunt them (remember ecological pyramid). These hunters were probably first macroscopic carnivores which caused the end of Ediacaran “soft life”.

After Ediacaran great extinction (this is the first documented great extinction), one can observe the rise of very different creatures, small, **skeletal** Cambrian organisms. They appear in big diversity and represent many current phyla of animals. This is called “Cambrian revolution”, or “Cambrian explosion” (see below).

Filling Marine Ecosystems

Nikolaj Zinovjev, "Silurian Period" (1968)

This happened due Cambrian and Ordovician periods which jointly continued for almost 100 million years. Most of this time Earth climate was relatively warm, but continents were concentrated in the Southern hemisphere. In the end of Ordovician, Africa hit the South Pole, and this resulted in a serious glaciation.

The sea in large degree prevailed over the land, and thus created exceptionally favorable conditions for the development of marine communities which in this epoch became finally similar to what we see around now. For some groups, there was not "enough space" in the sea, and, as a consequence, the *colonization of land* from higher organisms started.

At this time, all main types and even classes of invertebrates and vertebrates and terrestrial plants already existed. Stromatolites went to the "background" of ecosystems, and were replaced with other builders of bioherms (reef-like organic structures) like archaeocyaths (Fig. 13, group probably close to the sponges) and calcareous red and green algae. Archaeocyaths went extinct in the end of the Ordovician, but calcareous algae have survived.

In Cambrian, there was a great variety of different groups of animals, usually *small size and with a skeleton* of different types (phosphate, calcareous, organic): that was a consequence of "skeletal revolution". some of them were crawlers, some swimmers, and some burrowers.

Among the sea floor bilaterians, trilobites (an extinct group of arthropods) dominated, there were also many other groups of arthropods and lobopods (intermediates between ecdysozoan nematode-like "worms" and arthropods), plus various spiralians, namely brachiopods and mollusks (Fig. 21, 22) including cephalopods which played the role of pelagic predators, preceding sea scorpions and armored fish. There were also plenty of echinoderms, mostly sea lilies and many other, now extinct, classes (Fig. 15). First jawless fishes (Fig. 17, top row) were also the part of pelagic life.

It can be assumed that at this time started the mass "exodus" of invertebrates to the land. Perhaps, at this there were already some soil fauna, consisting of nematodes, small arthropods and other similar organisms.

Green algae were gradually replaced red algae in communities. For some of them, like for some invertebrates, there were "not enough space" in the ocean, and they proceeded to conquer the land. The living conditions outside of ocean were much more stringent for plants than for the animals, so the process of adaptation took a long time. The first land plants are known from the Ordovician, they probably were liverworts (Fig. 10, top left). Land conquest for plants was concerted with the development of symbiosis with mycorrhizal fungi (Fig. 5). Apparently, among the first terrestrial photosynthetic organisms were symbioses both with a predominant fungus and predominant alga. The first gave rise to the lichens, who took the most extreme habitats, and the second to the contemporary terrestrial plants.

Terrestrial plants had to solve many problems. There were, in particular, water supply (so they developed vascular system), gas exchange (acquired stomata), competition for light (body began to grow vertically with the help of supportive tissues), and spore dispersal (diploid stage, sporophyte, began to form sporangia on a long stalk containing spores covered with thick envelope).

A very serious plant problem was also in the optimization of the **life cycle**. Putative ancestors of land plants, charophyte green algae, did not have any sporophyte as their zygote proceed to meiosis almost immediately after fertilization. New sporophyte could arise in connection with the need to disperse the spores from plants growing in the shallow water, where the wind acted as the most efficient dispersal agent. First sporophytes served likely only for the storage of the haploid spores, but later most of gametophyte functions were transfered to sporophyte.

It is important to note also that the colonization of the land by plants was to happen after formation of **soil**, the process involved bacteria, fungi, and invertebrates. Furthermore, the term “colonization of land” is not accurate since the actual land in the usual sense in those days did not exist, it was in fact huge, often completely flooded wetlands / sea bottom space, interspersed with rock formations; there were no permanent freshwater. We can say that *animals and plants made the land themselves*, stopping erosion that once ruled the earth surface. Land type familiar to us was formed slowly; we can, for example, assume that until Jurassic watersheds were completely devoid of vegetation.

First Life on Land

This epoch (spans Silurian and Devonian periods) began more than 440 million years ago and took about 85 million years. The Earth’s climate was gradually warmer, starting with a small glaciation of Gondwana (South Pole was in Brazil), climatic situation slowly reversed, and during the Devonian period, the world was dominated by abnormally high temperatures and extremely high ocean level. This time was ended with Caledonian orogeny, the result of proto-North America and proto-Europe collision, when mountains of Scandinavia, Scotland, and eastern North America have been risen.

On land, there was a **radiation** (i.e., evolution in different directions) of terrestrial plants. There were already several **biomes**: bog communities, semi-aquatic ecosystems, and more dry plant associations with domination of mosses. Once the plants have “learned” how to make chemicals which make their cell walls much stronger (**lignin** and **suberin**), they started to make “skyscrapers” to escape competition for the light; this allowed them to grow up to the almost unlimited height. By the end of epoch, first **forests** appeared which consisted of marattioid ferns (Fig. 11, middle left), giant horsetails, mosses and first **seed plants**.

Origin of seed was most likely connected with origin of trees. Ancestors of the seed plants (it is possible that they were close to modern tongue ferns, Fig. 11) were among the first plants acquired the **cambium**, “stem-cell” tissue, and, consequently, the ability of the secondary thickening their trunk. After that, growth in height was virtually unrestricted. But there was another problem: the huge ecological gap between the giant sporophyte and minuscule, short-lived gametophyte dramatically reduced protection capabilities of the sporophyte the overall plants viability (similar thing happened with dinosaurs in the late Cretaceous).

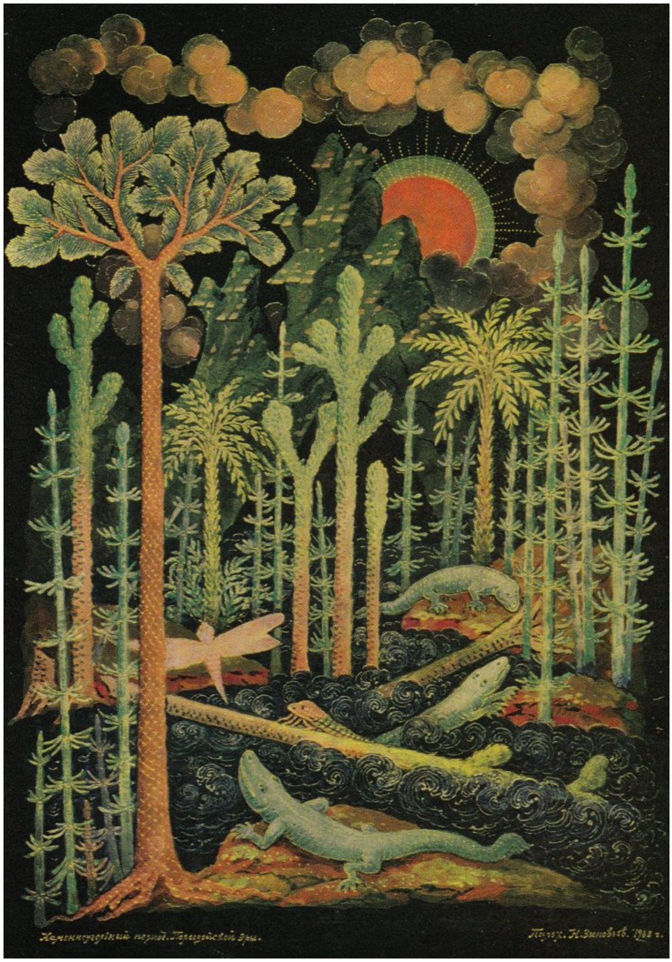
Seed plants solved the problem and found the room for gametophyte right **on the sporophyte**. However, this change required plenty of coordination in the development (e.g., pollination), and initially, seed plants (like contemporary gingo, Fig. 12, top left, and cycads) were not much better then their sporic competitors.

At the seas, predatory vertebrates, armored fish "pushed" the old dominants, chelicerates (Fig. 26, bottom right) into the land. The last group became **first terrestrial predators**. Apparently, there was already plenty of prey in the terrestrial fauna, in particular, millipedes and wingless proto-insects (Fig. 29, the middle). The last group (in order to escape predators) was likely forced to migrate to live **on trees**, and there true insects appeared in the next epoch.

Shallow-water communities were dominated by advanced fish groups. The most important were ancestors of terrestrial vertebrates, lobe-finned fish (Fig. 17, 4th from top). These predatory animals, probably in order to "catch up" with the retreating water (as the tides at that time apparently extended for kilometers into the "land"), and also in the search for more food, started to develop adaptations to the terrestrial lifestyle. At the end of epoch, they "made" organisms similar to modern amphibians, labyrinthodonts. They had many characters of terrestrial animals but likely spent most of their life time in water.

From that time, most of changes in marine ecosystems were only regrouping, reduction or increase of particular group. As an example, corals (existed from Cambrian) started to become the main builders of bioherms (as they are now). Role of trilobites decreased. Among mollusks prevailed ammonoids and nautiloids, cephalopods (Fig. 21, bottom right) with heavy shells. Vertebrates were represented not only with lobe-finned, but with many other groups of fish-like animals, including jawless and different cartilaginous and boned fish. This epoch is often called "**the age of the fish**."

Coal and Mud Forests



Nikolaj Zinovjev, "Carboniferous Period" (1968)

This epoch took about 60 millions of years and is often described as the kind of tropical world, with warm and humid climate, plenty of CO_2 in the atmosphere, and the predominance of ferns. In fact, in the world at that time the climate was quite variable. For example, the Arctic continent Angarida (or "Siberia", it corresponds with recent East Siberia) had really cold and dry climate. In contrast, the Euro-North-America was on the equator and had tropical climate.

However, there was a little carbon dioxide and lots of oxygen; in fact, much more oxygen then it was on the whole history of Earth, both earlier and later. One of proofs is an existence of giant **palaeodictyopteroidean insects**, some of them had more then a meter wingspan! As insects depend on tracheal system for ventilation, is safe to guess that there were plant of oxygen in the atmosphere to supply these big bodies.

The raise of oxygen is probably explained with appearance of forest biomes. Accumulation of coal is also related, the more carbon accumulated, the less should go into CO_2.

These Carboniferous forests were dominated with primitive woody ferns, tree-like horsetails and basal seed plants (they have quite misleading name "seed ferns" but in fact, belonged to groups which now include ginkgo and cycads). There were also related to conifers (**cordaites** and, finally, **woody lycophytes** which now exist only as small water quillworts (*Isoëtes*).

Forests of this epoch were really peculiar, and more similar to mangroves then to "normal" forests. They were systematically flooded with the tides and surf waves, and at the same time, decomposition of organic matter was slow (as there were no phytophagous insects and little fungi). Consequently, bottom of such forest was probably covered with mud. This mud was threaded with numerous rhizomes of woody lycophytes.

They, as many other trees of these times, had imperfect thickening, and sooner or later would break and fall down. In addition, sporic trees had no control over their microscopic gametophytes, and this resulted in periodical outbursts when many young plants of the same age started to compete and eliminate each other. All of these factors add to the existing mess, and lower levels of these forests were literally inundated with large size wood litter.

This was the basic ground of the origin of reptiles and flying insects. These two groups might origin "together", as elements of the one food chain included also trees. In the beginning of their evolution, many insect groups probably feed on generative organs of plants. Then dragonflies formed the first flying predators, and as the response, cockroaches and crickets went into the litter layer.

Some amphibians slowly evolved toward feeding on terrestrial invertebrates (like insects, slugs and millipedes), and as a consequence, developed the full independence from water. This required substantial restructuring of the organization, in particular the improvement of the respiratory system, skin, fertilization and embryogenesis. Taken together, these changes resulted in appearance of new group, *reptiles*.

Seas in this epoch were dominated by mollusks, primitive arthropods, cartilaginous and lobe-finned fishes.

Pangea and Great Extinction

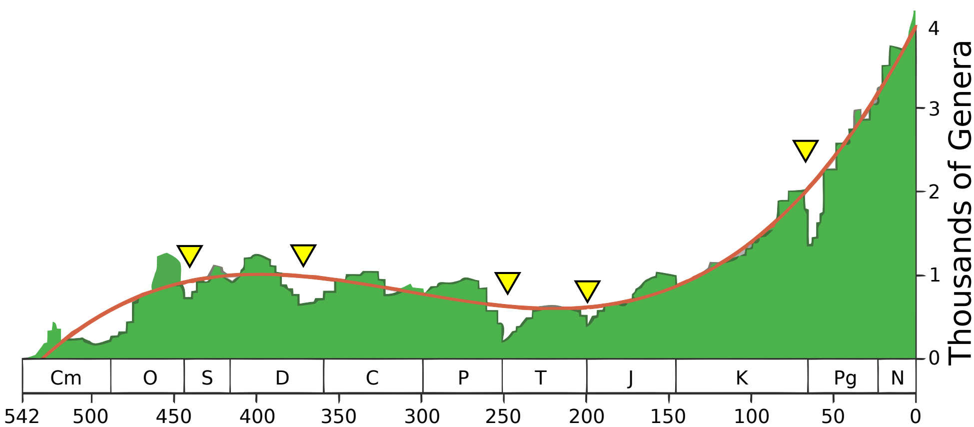
Nikolaj Zinovjev, "Permian Period" (1969)

At the end of the Carboniferous period there have been several important events. Firstly, all Earth continents collided in a single continent Pangea. Second, an active mountain building started; this orogeny formed Urals, Altai, the Caucasus, Atlas, Ardennes. Then part of Pangaea (namely, Australia) "drove" to the South Pole, thus started the Great glaciation. Temperatures on Earth were thus even lower than it is now, in the epoch of Great Cenozoic glaciation.

Interesting is that these processes were not strongly affected the evolution of the biosphere, at least in the beginning. Of course, there are were new types of vegetation, conifer forests, savannas and deserts. Three ferns declined, cycads (rare now) appeared. But the fauna has not changed. The role of reptiles increased greatly, many of them were insectivorous, and some reptiles (synapsids) started to acquire characters of the future mammals. Amphibian stegocephalians were still thrived. Higher insects (insects with metamorphosis) were close to modern Hymenoptera and lived on conifers, they played an important role in the further evolution of the seed. In a forest litter lived multiple herbivorous and predatory cockroach-like insects.

Reptile metabolism is quite compatible with water life, so in Permian some reptilian groups “returned” to water (this process continued in Mesozoic): there were marine, fish-eating mesosaurs, and freshwater hippo-like pareiasaurs.

At the end of the Permian period, about 270 million years ago, glaciation stopped. But orogeny intensified, half of Siberia were covered with volcanic lava (famous Siberian Traps), and that event probably was reason of the *great extinction of marine life*: trilobites did not survive Permian, as well as 40% of cephalopods, 50% echinoderms, 90% brachiopods and bryozoans, almost all corals and so on. More or less happily escaped were only sponges and bivalvians. However, some groups appeared first at this time, for example, contemporary bony fishes and decapod crustaceans.



Five “great” extinctions. Great extinction of marine life is the third triangle from left.

Renovation of the Terrestrial Life

In the Triassic and early Jurassic, Pangea begins to disintegrate. The Atlantic Ocean (which still grows) opened. The climate was warm at first, but very dry, and by the end of the era it gradually became more convenient to the terrestrial life.

Among the seed plants there appeared more advanced groups like bennettites, which participate in making savanna type vegetation (without grasses though, role of grasses was likely played with ferns, mosses and lichens). Seeds of many plants were protected by scales or were embedded in an almost closed cupula. Apparently, this was the “answer” of seed plants to the appearance of numerous phytophagous insect groups. Some other groups of insects began to adapt to pollination of seed plants, this was an additional factor to facilitate growing of seed covers.

Reptilian were still dominated but gradually replaced with various groups of arhosauromorphs, the most advanced reptiles by that time, able to move very quickly, typically using only two legs.

Simultaneously run there were processes of “mammalization” and “avification” of reptiles. Ancestors of mammals were now in a small dimensional class and became insectivorous; this is because small herbivorous reptiles were simply physiologically impossible. Plant food is not very nutritional, and reptile feeding apparatus was unable to extract enough calories to support small, presumably more active animal. Large herbivorous reptiles have less relative surface and therefore need less calories, and they of course existed. Only turtles are an exception, because of their “superprotection”, which however has closed all further ways to improve the organization.

Ancestors of mammals were animals of the size of a hedgehog or less; they continued to improve their dental system, the thermal insulation system, and increase the size of the brain. The result was the emergence at of first the first true mammals.

Among “true” reptiles, dinosaurs (birds’ ancestors), crocodiles and pterosaurs (which dominate the air for the next 70 million years) have appeared.

In the seas, there are first diatom algae, that stimulated the zooplankton, and in turn, cephalopods, which dominated throughout the Mesozoic. In addition, to replace the extinct by this time mesosaurs, appeared new groups of marine reptiles, for example, notosaurs and molluscivorous placodonts.

Jurassic Park: World of Reptiles

The climate on Earth in this epoch (Jurassic and Early Cretaceous) approached the optimum, the split of the continental plates led to its humidification. A new flourishing of fauna and flora began. The sea strongly prevailed over the land, even high continental platforms such as the Russian and North African, were flooded.

The abundance of phytoplankton and zooplankton caused the thrive of marine fauna, including sponges, corals, bivalve mollusks (who took an active part in the construction of bioherms), echinoderms, etc. Ichthyosaurs and plesiosaurs were the largest marine predators.

Interestingly that in fossil deposits, pregnant females of ichthyosaurs are often found. Therefore, the ichthyosaurs were not only viviparous but gave birth in conditions ‘promoted” fossilization. This is probably because they could not give birth as modern cetaceans: a tail up, this was not allowed with their vertical (like in fish, but not like in cetaceans) caudal fin. Then it seems that they were forced to give birth in shallow water, probably forming large groups (like modern seals).

On land there were forests similar to the recent temperate taiga, composed mainly of representatives of the ginkgo class. Many of them were technically also angiosperms as their seeds were well protected by additional covers. These forests were mostly inhabited by insects, and primitive mammals hunted for them.

In open spaces, savanna forests were maintained (as modern grasslands exist only due to the constant pressure of ungulates) by giant herbivorous dinosaurs, replacing all the other groups with size of modern cow and bigger. There also lived numerous predatory dinosaurs, both large and small bird-like insectivorous forms.

Flight of ancient birds was still very imperfect. Apparently, the ancestors of birds needed feathers mainly for thermal insulation, and the flight occurred from the jumping movements required to catch flying insects. There is no much difference between archosauromorph reptiles and birds; in fact, flying is the only radical difference of birds.

The other group of flying arhosaurs, pterosaurs, dominated the water and land borders. Apparently, ancestors of pterosaurs were fish-eating animals, and their flight arose as an adaptation to catching prey from the water.

The Rise of Contemporary Ecosystems

Nikolaj Zinovjev, "Cretaceous Period" (1969)

Cretaceous and Paleogene periods are usually referred to different eras, but here we join them in one epoch, as the development of the biosphere between the Cretaceous and the Paleogene did not change its direction.

The climate on Earth at that time was generally favorable for the life, at in the end of the Cretaceous period, one of an absolute maximum of temperatures on Earth was observed. Continents gradually acquired modern positions and outlines. **Alpine** orogeny began, then **Andes** and the **Rocky Mountains** arose, and then the **Himalayas**.

The main event of this epoch was the *Aptian revolution*. At the very end of the Lower Cretaceous almost simultaneously appeared those groups of animals and plants which are dominant to this day: flowering plants, eupolypod ferns, placental mammals, higher (tailless) birds, social insects (bees, ants and termites), butterflies, and higher bony fishes.

The origin of flowering plants for a long time was considered enigmatic. However, they do not radically differ from the rest of the seed plants: neither double fertilization, nor protection of ovaries, much less the presence of a flower are unique attributes of flowering plants.

On the other hand, recent studies of both fossil and modern flowering plants indicate that the first flowering plants were *herbaceous perennials*, and some of them even aquatic. It is possible that during the previous epochs, some smaller primitive “gymnosperms”, so-called “seed ferns” gradually acquired a herbaceous appearance, together with the capacity for easy vegetative reproduction (“partiality”), and a much shorter and more optimized life cycle. In the same direction, many other groups of seed plants were evolved, pushing each other’s evolution, but the ancestors of flowering plants were the first to achieve this level.

Flowering plants colonized the land quickly, first at herbaceous storeys where ferns and mosses could not compete with them (and there were no other seed plants, too). Then secondary woody flowering trees were formed and apparently they began to interfere with the woody “gymnosperms”. By the end of the era, angiosperms forced out all other plants (except conifers) on the periphery of the ecosystems. As the climate gradually differentiated (becoming colder in high latitudes and warmer in the lower latitudes), tropical forests arose (they did not exist from the Carboniferous period).

An important event in the middle of the Upper Cretaceous was the occurrence of graminoids (grass-like plants). Capable of firmly retaining captured territory, they began to play an increasing role in communities.

The leaf litter of flowering plants, which is much copious than that of other seed plants (remember their fast life cycle), dramatically changed the carbon regime of freshwater ecosystems. Most of the oligotrophic (as modern sphagnum bogs) places have become mesotrophic or eutrophic, rich in organic substances. This is associated with strong changes in the fauna of insects (the emergence of higher forms of Diptera and beetles), and in turn associated with the previous event the emergence of numerous insectivorous lizards, as well as with the radiation of tailed amphibians. Another consequence was probably a change of the outflow of some elements to the sea, possibly having an influence on the further development of the marine communities.

In the seas, various crocodiles, hampsosaurs and giant mosasaur lizards dominated, and then extinct, likely due to the rapid radiation of fast-swimming higher bony fishes. At the end of the era, cetaceans appeared. Cephalopods began to decline, but the role of gastropods and bivalves significantly increased.

* * *

Extinction of dinosaurs is usually called the main event of this era. It must be said, however, that many dinosaur groups died out much earlier than the end of the Cretaceous, and many faded gradually so Cretaceous extinction was only the “last stroke” of their decline.

On the other hand, the often-named *exogenous* causes of extinction (meteorite, etc.) do not not explain why it touched practically only dinosaurs and having little effect on the evolution of the other tetrapods and almost nothing on the evolution of insects and plants. In the most of Earth history, exogenous influences cannot be firmly tied to any evolutionary event, for example, the time of the appearance of the most large meteorite craters of the Phanerozoic cannot be clearly associated with any extinction.

Apparently, one of the *endogenous* causes of extinction was the appearance of a predator capable of feeding on small and medium-sized prey (Rautian’s hypothesis). The fact is that before the Cretaceous period, the animals of the small-sized class were represented only by insectivorous forms. However, gradually improving the dental apparatus, some mammals finally switched to plant food. This led to the emergence of predatory forms capable of feeding on this herbivorous mammals. (Note that insectivorous animals of small size could not serve as a regular food for any predator according to the law of the ecological pyramid.)

Since such a predator (they could be small predatory lizards, snakes, birds, and other mammals that appeared in this era) *could not be specialized only in one kind of prey*, it was necessarily the main enemy of small offspring of large dinosaurs.

The other point is that the average size of adult dinosaurs increased dramatically by the end of the Cretaceous (this is the typical race of arms between prey and predator), but *young dinosaurs simply could not be large*! Dinosaur eggs had an upper limit of size because they (1) must be warmed to the center and also (2) be reasonably easy to hatch.

So small carnivores added a lot of pressure to the gradual extinction of herbivorous, and after them, predatory large dinosaurs. Small dinosaurs evolve into birds, and whoever was left, did not have any significant advantages over mammals and birds, and therefore lost in the competition.

It is curious that the extinction of large predatory forms led to a kind of “vacuum” in terrestrial communities, and the most unexpected groups pretended to be predators before the advent of real predatory mammals (at the end of epoch): there were terrestrial crocodiles, giant predatory birds and carnivorous ungulates.

Pterosaurs formed more and more large forms, and at the end of the era, were unable to withstand competition with increasingly better flying birds. But the first flying mammals appeared: bats, whose flight arose, perhaps, as a means to save themselves from tree-ridden predators. Bats and birds safely divided the habitat, which is why they co-exist today.

Winning groups started extensive radiation. In the described epoch several hundreds order-level groups of mammals, birds and bony fishes appeared, and the the most orders of flowering plants.

Nikolaj Zinovjev, "Tertiary" (1969)

Last Great Glaciation

Movements of continents in this epoch led to very adverse consequences. Panama and Suez isthmus closed, Antarctica gradually shifted to the area of the South Pole, and the northern continents surrounded the Arctic region as a ring. Everything now was ready for for *new Great Glaciation*.

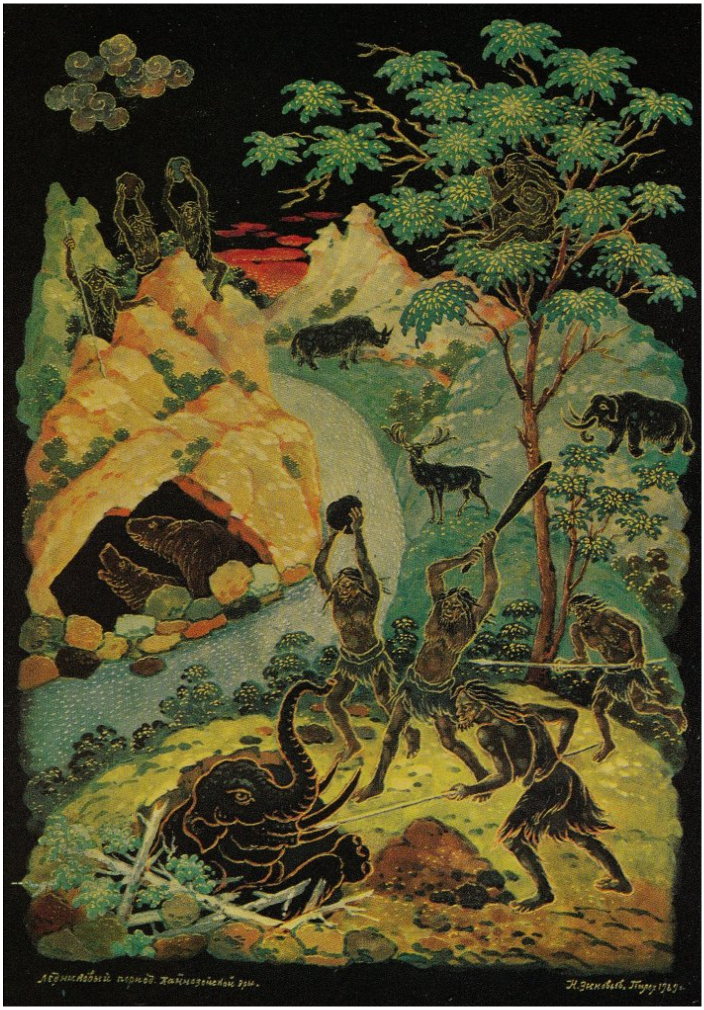
Life in the seas has not changed much. At the beginning of the epoch, due to the dryer climate and the progressive development of herbivorous mammals, *grasslands* were extensively expanded. These areas were inhabited by a fauna in which various proboscis, ungulates, rodents and predatory mammals dominated.

One of the most curious episodes of this era was the *Great Inter-American Exchange*, the result of the formation of the Panama Isthmus. South America, isolated so far from all other continents (like Australia now), experienced the invasion of more advanced North American groups. Some South American animals have successfully withstood this onslaught and even advanced far to the north (opossums, armadillos, porcupines). However, the greater part of the South American fauna went extinct.

After the formation of the glaciers, the rich Antarctic fauna and flora also died out, the last remnants (refugia) of which are now in the remnants of flooded Zealandia continent: now islands New Zealand, Lord Howe and New Caledonia.

The advent of the glacier led to the formation of another type of community, *arctic steppe*: **tundra**, which advanced or retreated along with the ice.

The final accord of the development of the biosphere in this era was the appearance (most likely in East Africa) of representatives of the species *Homo sapiens* L.



Nikolaj Zinovjev, "Ice Age" (1969)

How

Chapter 5

Basics of Ecology

Ecological Interactions: Two-Species Model

Two-species model allows to describe how two theoretical species might influence each other. For example, Species I may facilitate Species II: it means that if biomass (sum of weight) of Species I increases, biomass of Species II also increases (+ interaction). There are also + and 0 interactions. Two species and three signs make **six** combinations:

	+	0	–
+	mutualism	commensalism[1]	exploitation[2]
0	...	neutralism	amensalism
–	...	...	interference[3]

[1] Includes phoresy (transportation), inquilinism (housing) and "sponging".
[2] Includes predation, parasitism and phytophagy.
[3] Includes competition, allelopathy and aggression.

Mutualism It sometimes called "symbiosis". Two different species collaborate to make each other life better. One of the most striking example is lichenes which is algae-fungus mutualism.

Commensalism Remember "Finding Nemo"? Clown fish lives inside actinia. This type of commensalism is called "*housing*". Another example is suckerfish and shark, this is *phoresy*. *Sponging* happens when scavengers feed on what is left after the bigger carnivore meal.

Exploitation This is the most severe interaction. *Predation* kills, but *parasitism* or *phytophagy* (the only difference is that second uses plants) do not.

Neutralism Rare. Philosophically, everything is connected in nature, and if Species I and II live together, they usually interact, somehow.

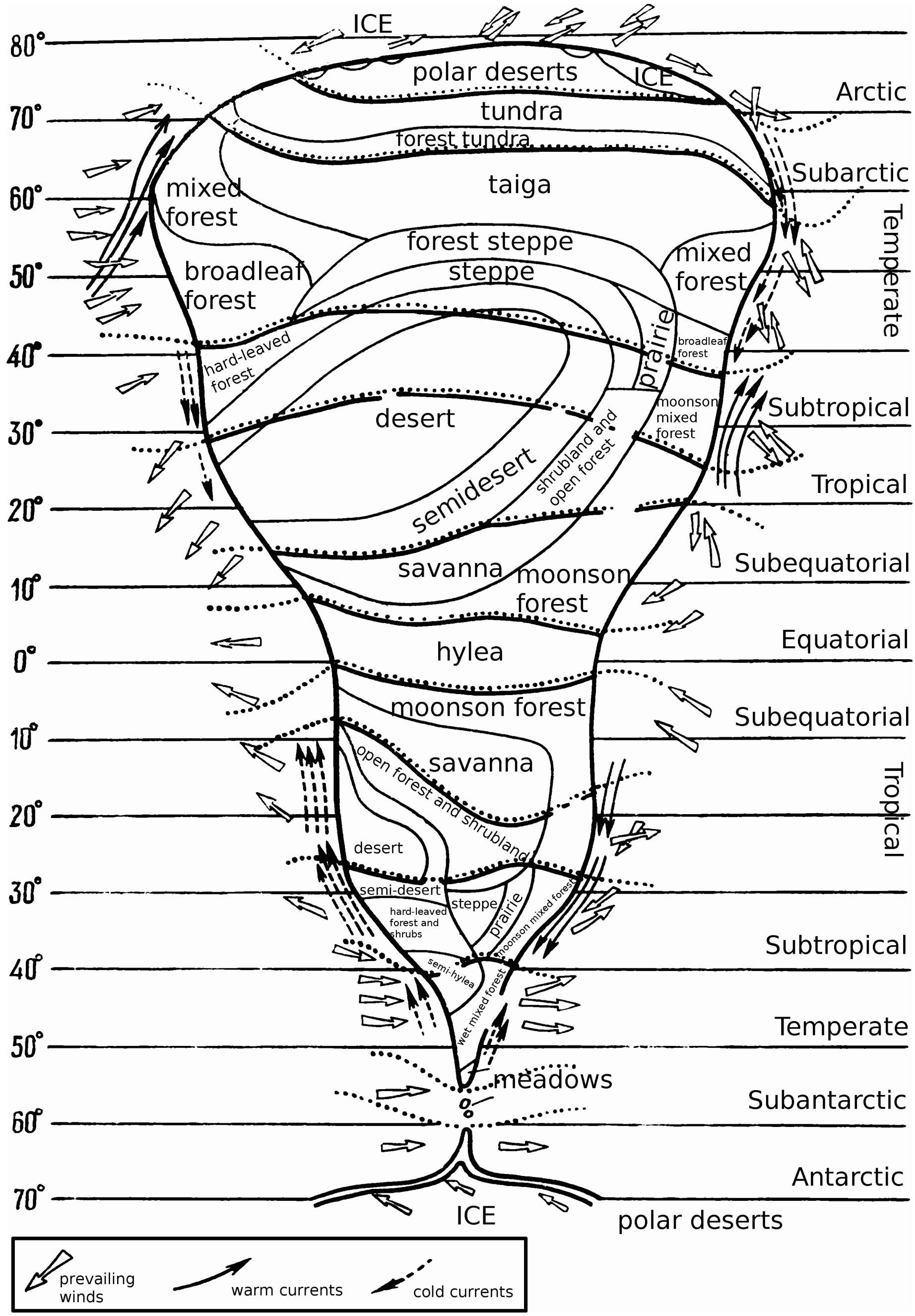
Amensalism This happens when suppressing organism is, for example, much bigger then the "partner". Big trees often suppress all surrounding smaller plants.

Interference *Competition* happens when Species I and II share same ecological niche, have similar requirements. *Gause's Principle* says that sooner or later, one of them wins and another looses. *Allelopathy* is a mediated competition, typically through some chemicals like antibiotics. Most advanced (but least pleasant) is the direct *aggression* when individuals of one species physically eliminate the other one.

Where

Chapter 6

Ecological geography and taxonomical geography



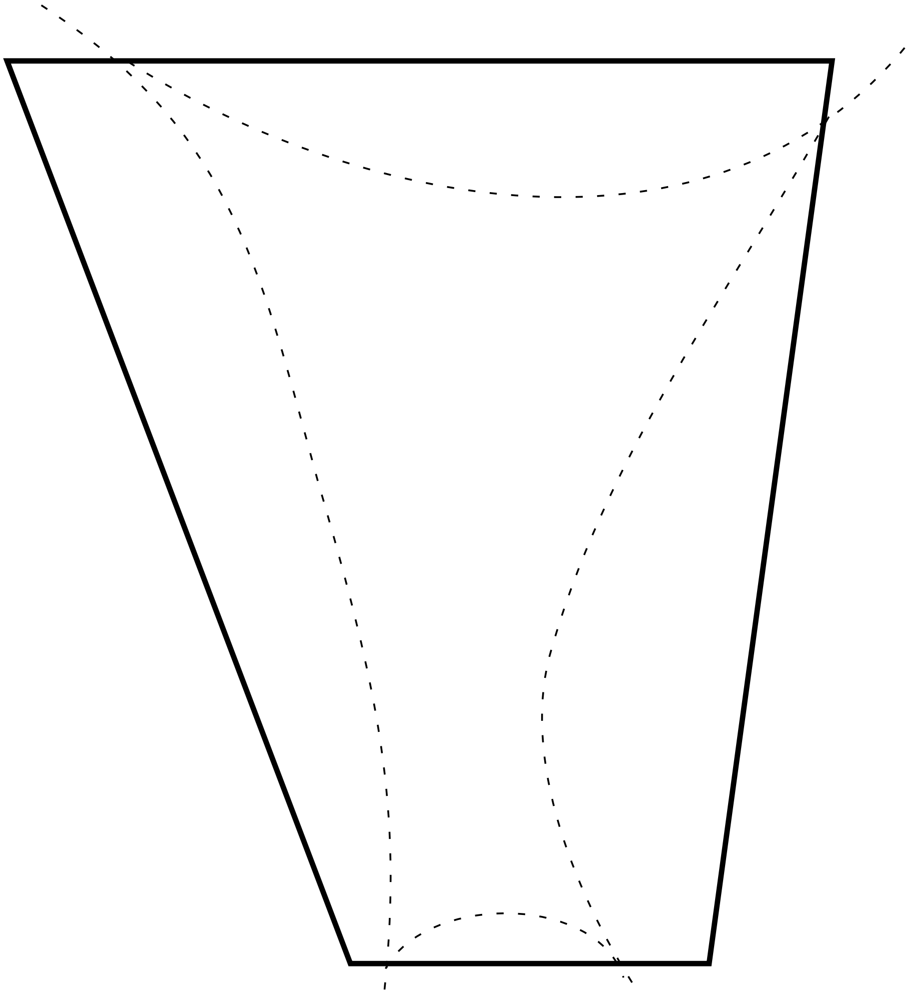
“Ideal continent” representing the Earth landmasses, ocean currents, climates and ecoregions (according to Rjabchikov, 1960).

Chapter 7

Regions

Chapter 8

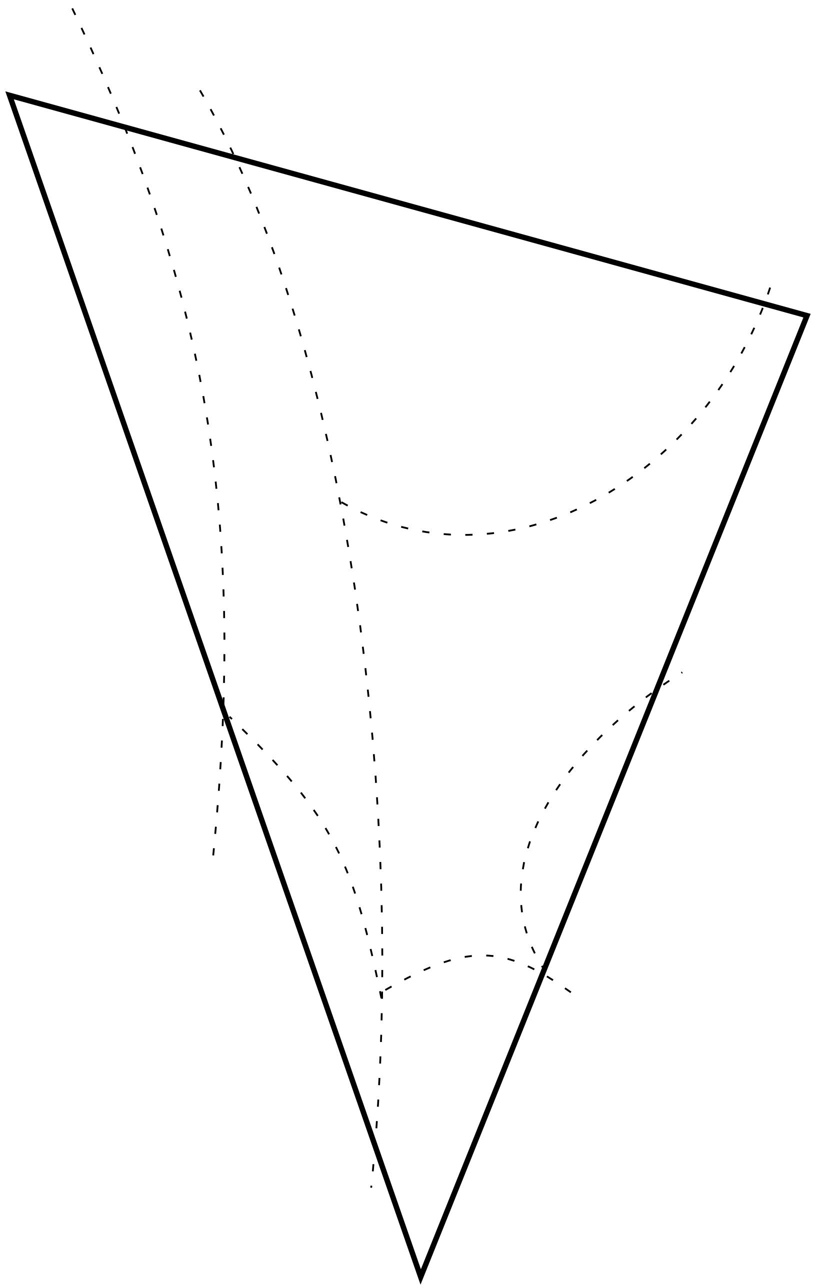
Holarctic



The most simple biogeographic map of North America.

Chapter 9

Neotropics

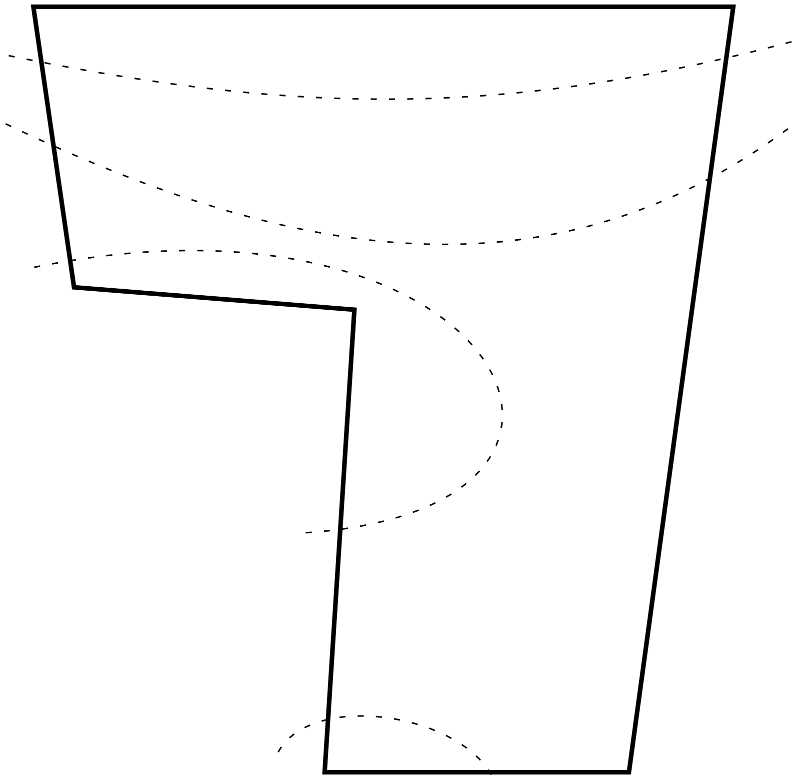


The most simple biogeographic map of South America.

Chapter 10

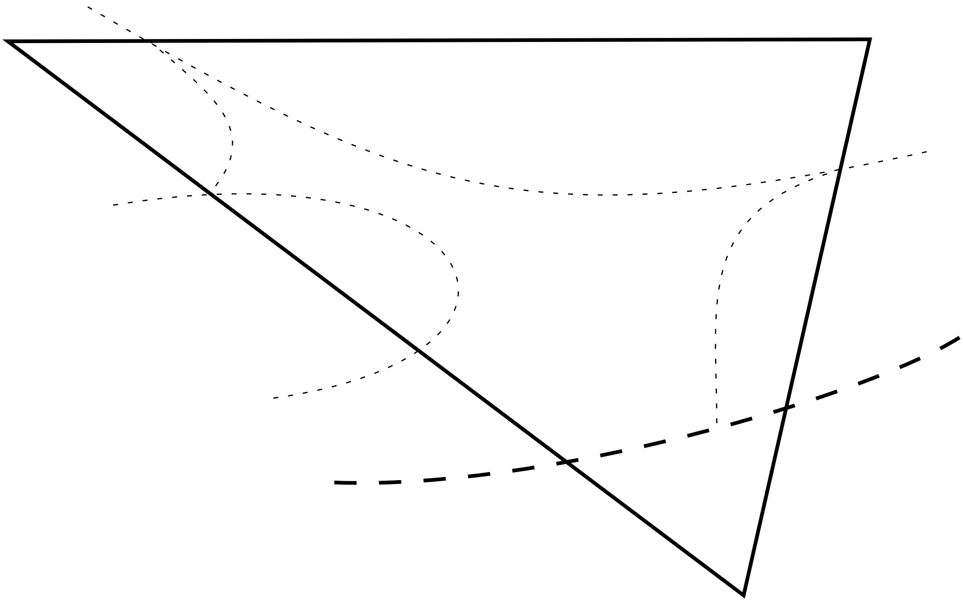
Palaeotropics

Africa



The most simple biogeographic map of Africa.

Asia



The most simple biogeographic map of Eurasia.

Chapter 11

Australia and Pacific Islands

Tropical Biology

Chapter 12

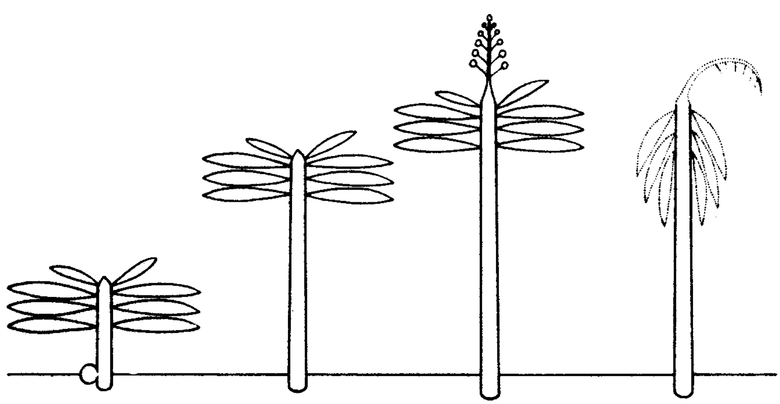
Architecture of Tropical Forest

Illustrated Key to the Architectural Models of Tropical Trees

The following key is based on Halle, Oldeman and Thomlinson (1978) "Tropical Trees and Forests" (pp.84–97).

1. Stem strictly unbranched (Monoaxial trees) .... 2.
– Stems branched, sometimes apparently unbranched in Chamberlain's model (polyaxial trees) .... 3.

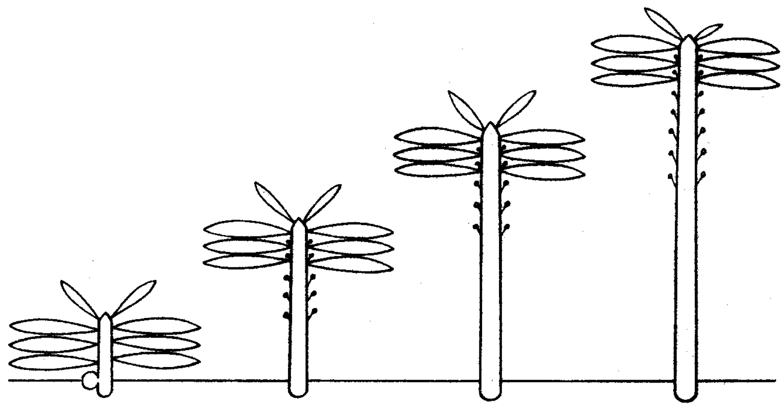
2. Inflorescence terminal .... **Holttum's model**.



Monocotyledon: *Corypha umbraculifera* (Talipot palm—Palmae). Dicotyledon: *Sohnreyia excelsa* (Rutaceae).

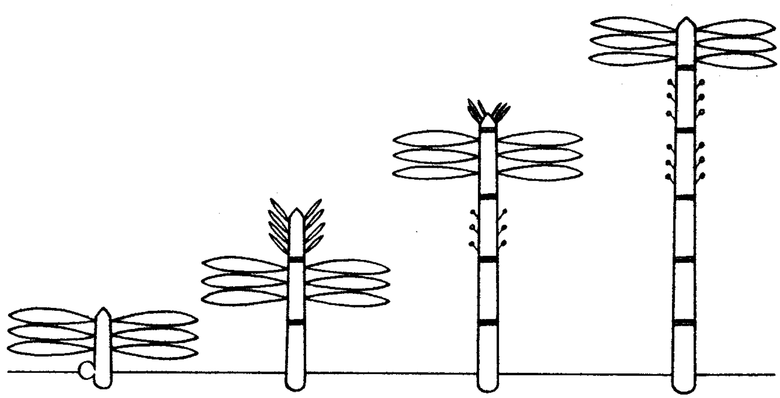
– Inflorescences lateral .... **Corner's model**.

(a) Growth continuous:



Monocotyledon: *Cocos nucifera* (coconut palm—Palmae), *Elaeis guineensis* (African oil palm—Palmae). Dicotyledon: *Carica papaya* (papaya—Caricaceae).

(b) Growth rhythmic:



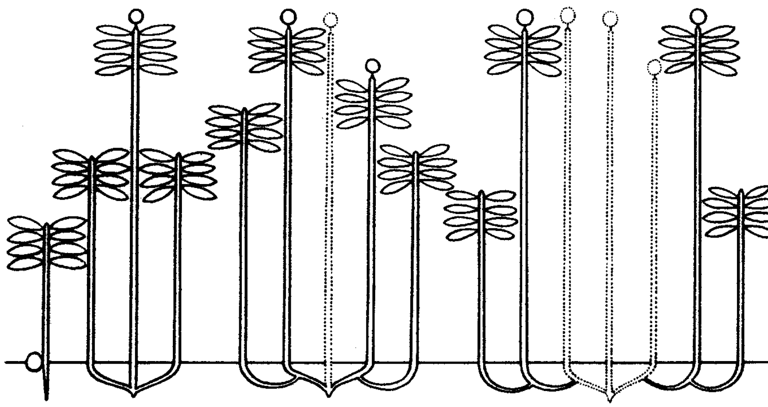
Gymnosperm: Female *Cycas circinalis* (Cycadaceae). Dicotyledon: *Trichoscypha ferntginea* (Anacardiaceae).

3 (1). Vegetative axes all equivalent, homogenous (not partly trunk, partly branch), most often orthotropic and modular .... 4.

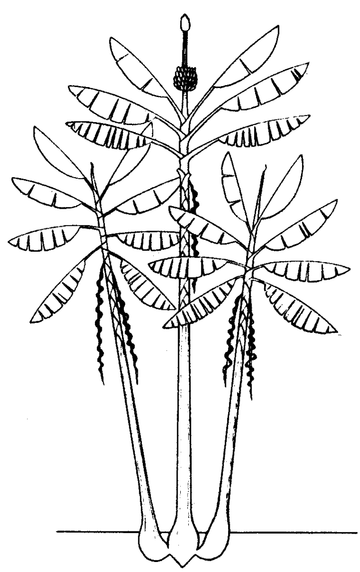
– Vegetative axes not equivalent (homogenous, heterogenous or mixed but always clear difference between trunk and branches) .... 7.

4. Basitony, i.e., branches at the base of the module, commonly subterranean, growth usually continuous, axes either hapaxanthic or pleonanthic .... **Tomlinson's model**.

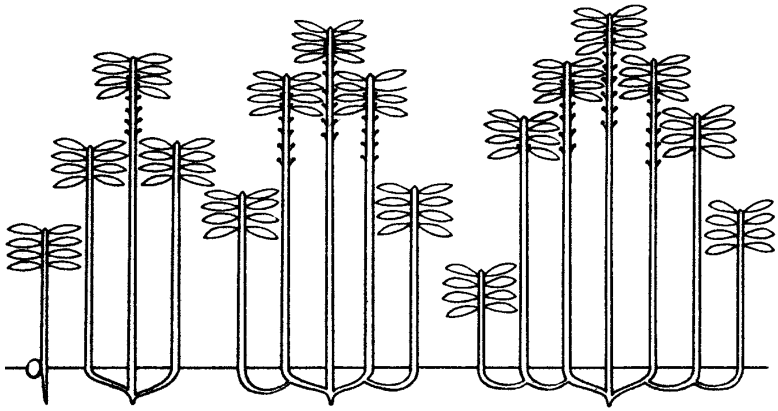
   (a) Hapaxanthy, i.e., each module determinate, terminating in an inflorescence:



Monocotyledon: *Musa* cv. *sapientum* (banana—Musaceae). Dicotyledon: *Lobelia gibberoa* (Lobeliaceae).



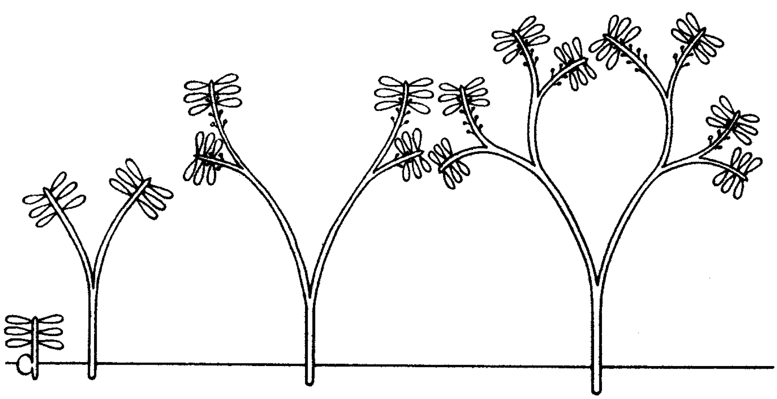
(b) Pleonanthy, i.e., each module not determinate, with lateral inflorescences



Monocotyledon: *Phoenix dactylifera* (date palm—Palmae).

– Acrotony, i.e., branches not at the base but distal on the axis .... 5.

5. Dichotomous branching by equal division of apical meristem ....
.... **Schoute's model**.



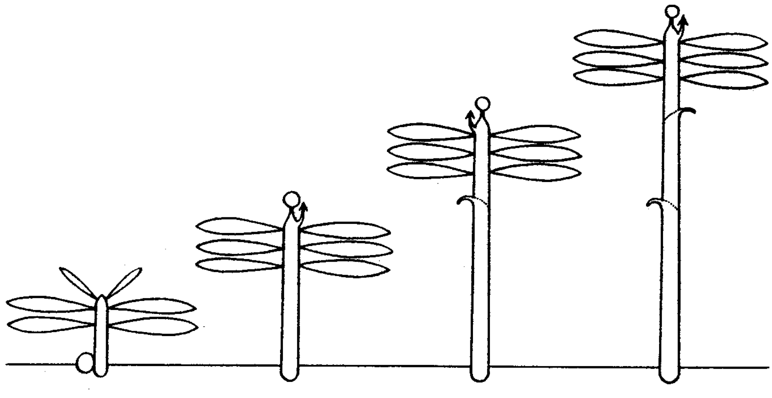
Monocotyledons:

Vegetative axes orthotropic: *Hyphaene thebaica* (doum palm—Palmae).

Vegetative axes plagiotropic: *Nypa fruticans* (nipa palm—Palmae)

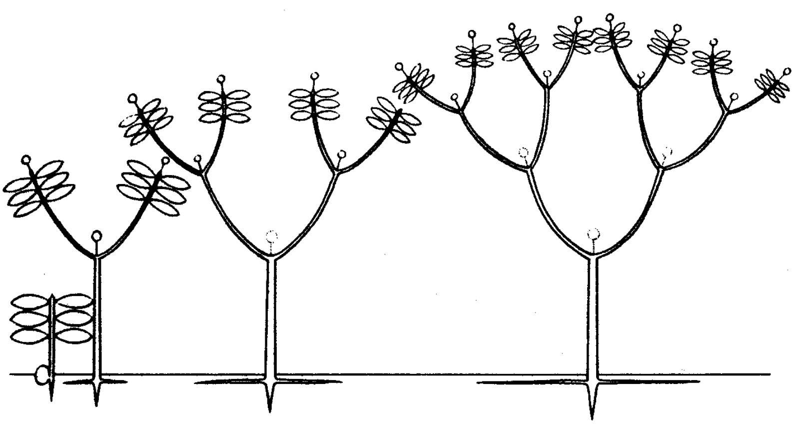
– Axillary branching, without dichotomy .... 6.

6. One branch per module only; sympodium one-dimensional, linear, monocaulous, apparently unbranched, modules hapaxanthic, i.e., inflorescences terminal . . . . **Chamberlain's model**.



Gymnosperm: Male *Cycas circinalis* (Cycadaceae). Monocotyledon: *Cordyline indivisa* (Agavaceae). Dicotyledon: *Talisia mollis* (Sapindaceae).

– Two or more branches per module; sympodium three-dimensional, nonlinear, clearly branched; inflorescences terminal . . . . **Leeuwenberg's model**.

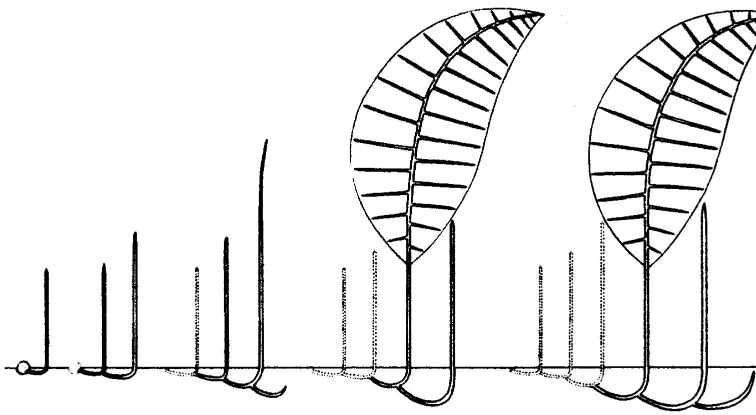


Monocotyledon: *Dracaena draco* (dragon tree—Agavaceae). Dicotyledon: *Ricinus communis* (castor-bean), *Manihot esculenta* (cassava), both Euphorbiaceae.

7 (3). Vegetative axes heterogeneous, i.e., differentiated into orthotropic and plagiotropic axes or complexes of axes . . . . 8.

– Vegetative axes homogeneous, i.e., either all orthotropic or all mixed . . . . 18.

8. Basitonic (basal) branching producing new (usually subterranean) trunks . . . . **McClure's model**.



Monocotyledon: *Bambusa arundinacea* (bamboo—Gramineae / Bambusoideae). Dicotyledon: *Polygonum cuspidatum* (Polygonaceae).

– Acrotonic (distal) branching in trunk formation (never subterranean) . . . . . . 9.

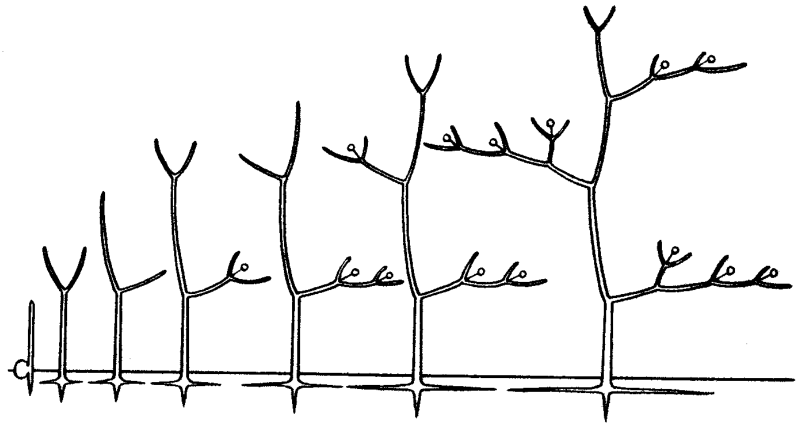
9. Modular construction, at least of plagiotropic branches; modules generally with functional (sometimes with more or less aborted) terminal inflorescences . . . . 10.

– Construction not modular; inflorescences often lateral but always lacking any influence on main principles of architecture . . . . 13.

10. Growth in height sympodial, modular . . . . 11.

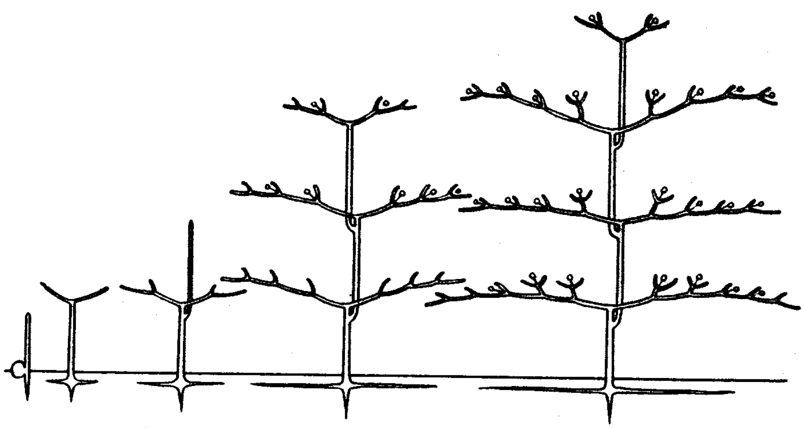
– Growth in height monopodial, modular construction restricted to branches . . . . 12.

11. Modules initially equal, all apparently branches, but later unequal, one becoming a trunk . . . . **Koriba's model**.



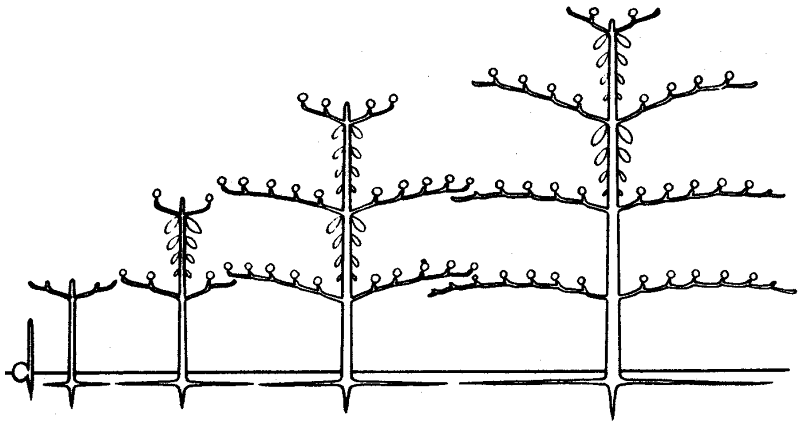
Dicotyledon: *Hura crepitans* (sand-box tree—Euphorbiaceae).

– Modules unequal from the start, trunk module appearing later than branch modules, both quite distinct .... **Prevost's model**.

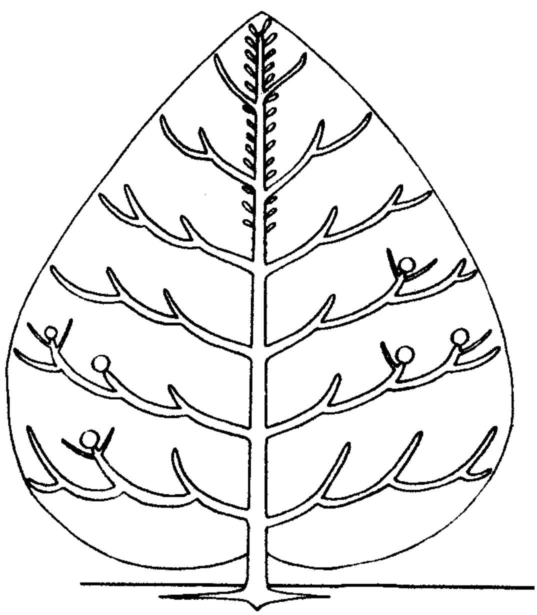


Dicotyledon: *Euphorbia pulcherrima* (poinsettia—Euphorbiaceae), *Alstonia boonei* (emien—Apocynaceae).

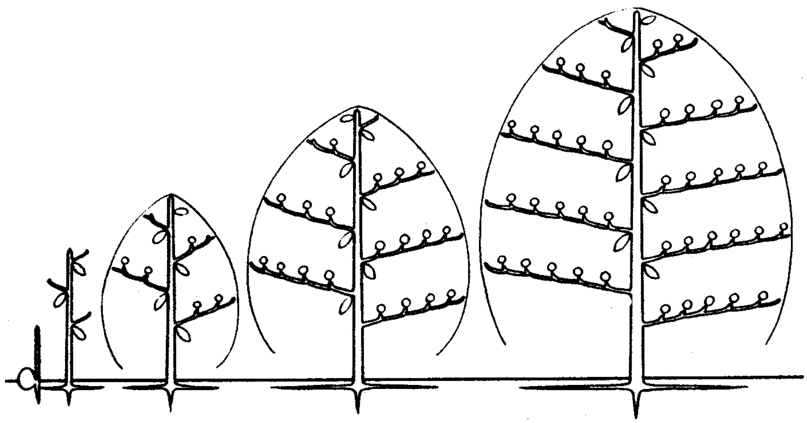
12 (10). Monopodial growth in height rhythmic .... **Fagerlind's model**.



Dicotyledon: *Cornus alternifolius* (dogwood—Cornaceae), *Fagraea crenulata* (Loganiaceae), *Magnolia grandiflora* (Magnoliaceae):

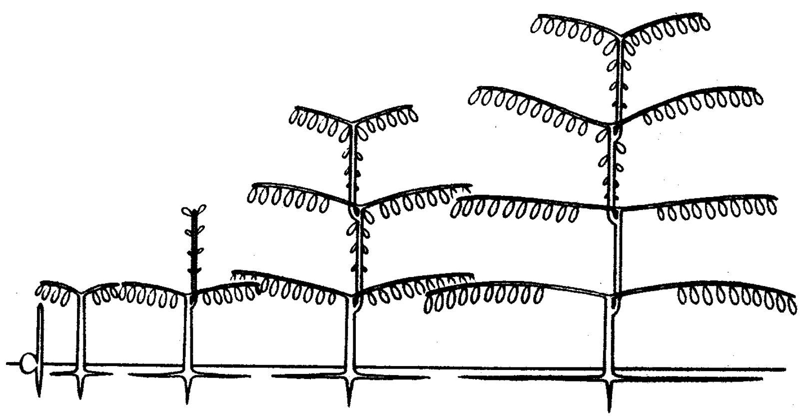


– Monopodial growth in height continuous .... **Petit's model**.



Dicotyledon: *Gossypium* spp. (cottons—Malvaceae).

13 (9). Trunk a sympodium of orthotropic axes (branches either monopodial or sympodial, but never plagiotropic by apposition) .... **Nozeran's model**.



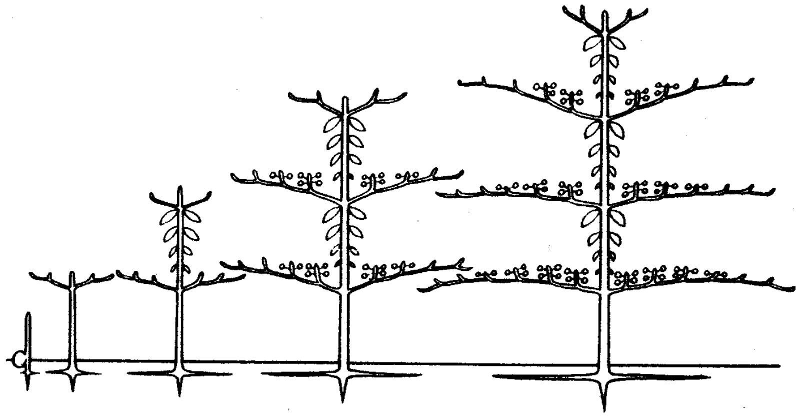
Dicotyledon: *Theobroma cacao* (cocoa—Sterculiaceae).

– Trunk an orthotropic monopodium .... 14.

14. Trunk with rhythmic growth and branching .... 15.

– Trunk with continuous or diffuse growth and branching .... 16.

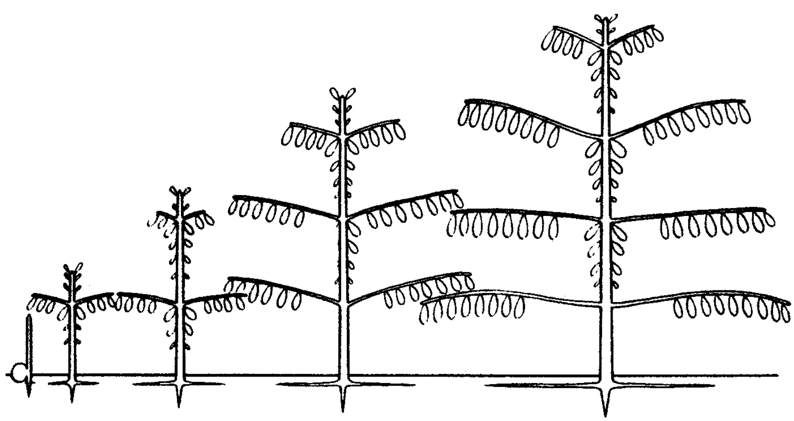
15. Branches plagiotropic by apposition .... **Aubreville's model**.



Dicotyledon: *Terminalia catappa* (sea-almond—Combretaceae).

Theoretical Model II defined as an architecture resulting from growth of a meristem producing a sympodial modular trunk, with tiers of branches also modular and plagiotropic by apposition, has still not been recognized in a known example. It would occur here, next to Aubreville's model from which it differs in its sympodial trunk.

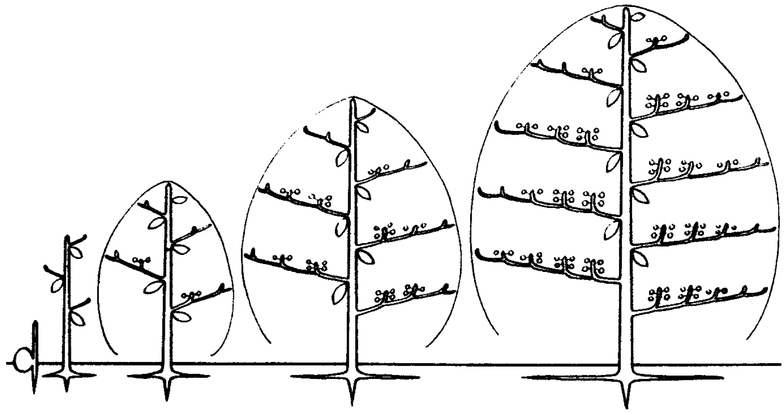
– Branches plagiotropic but never by apposition, monopodial or sympodial by substitution .... **Massart's model**.



Gymnosperms: *Araucaria heterophylla* (Norfolk Island pine—Araucariaceae). Dicotyledon: *Ceiba pentandra* (kapok—Bombacaceae), *Myristica fragrans* (nutmeg—Myristicaceae).

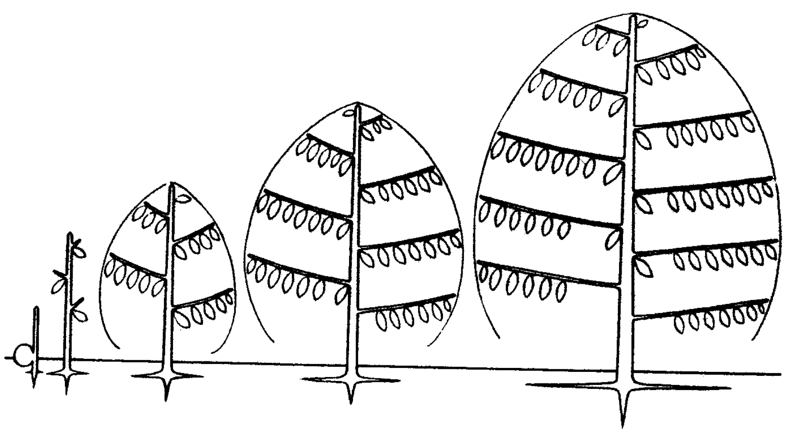
16 (14). Branches plagiotropic but never by apposition, monopodial or sympodial by substitution .... 17.

– Branches plagiotropic by apposition . . . . **Theoretical model I**.

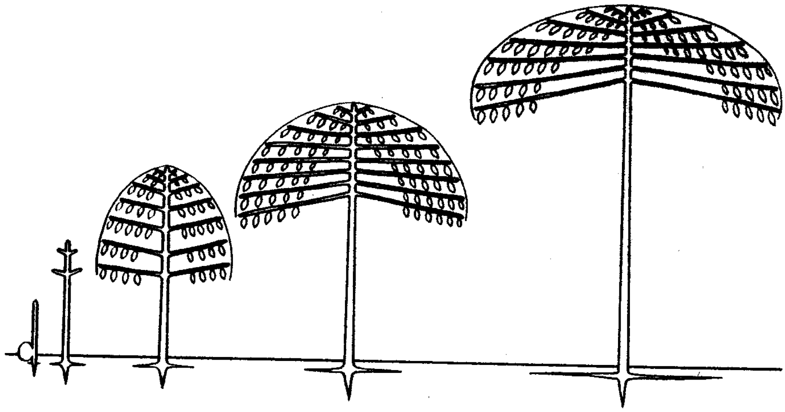


Dicotyledon: *Euphorbia* sp. (Euphorbiaceae)

17. Branches long-lived, not resembling a compound leaf . . . . **Roux's model**.



Dicotyledon: *Coffea arabica* (coffee—Rubiaceae), *Bertholletia excelsa* (Brazil nut—Lecythidaceae).



– Branches short-lived, phyllomorphic, i.e., resembling a compound leaf .... **Cook's model**.

Dicotyledon: *Castilla elastica* (Ceara rubber tree—Moraceae)

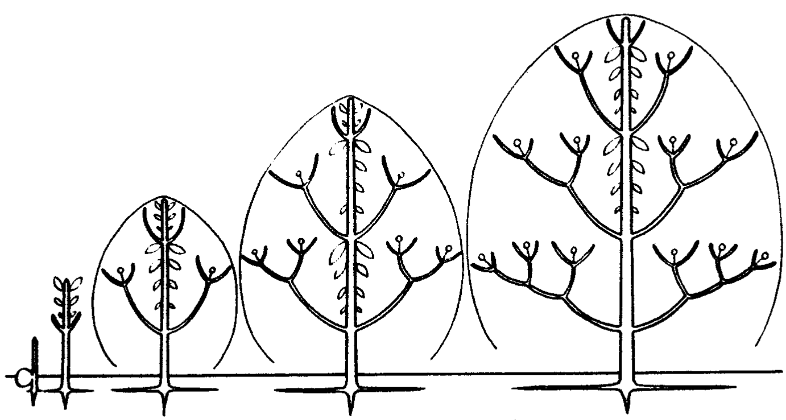
18 (7). Vegetative axes all orthotropic .... 19.

– Vegetative axes all mixed .... 22.

19. Inflorescences terminal, i.e., branches sympodial and, sometimes in the periphery of the crown, apparently modular .... 20.

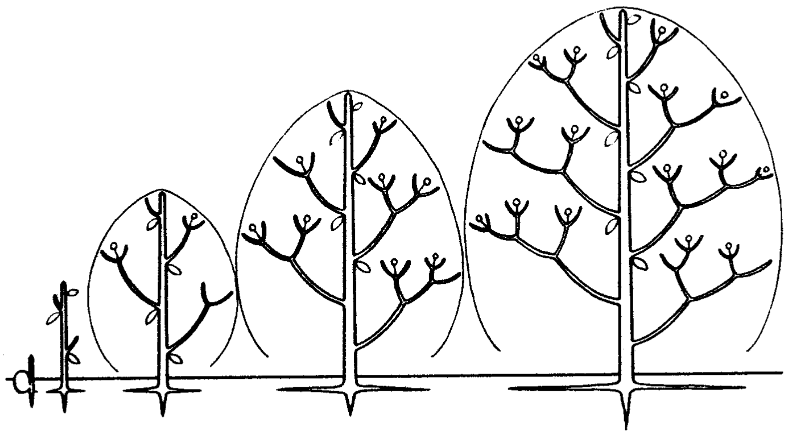
– Inflorescences lateral, i.e., branches monopodial .... 21.

20. Trunk with rhythmic growth in height .... **Scarrone's model**.



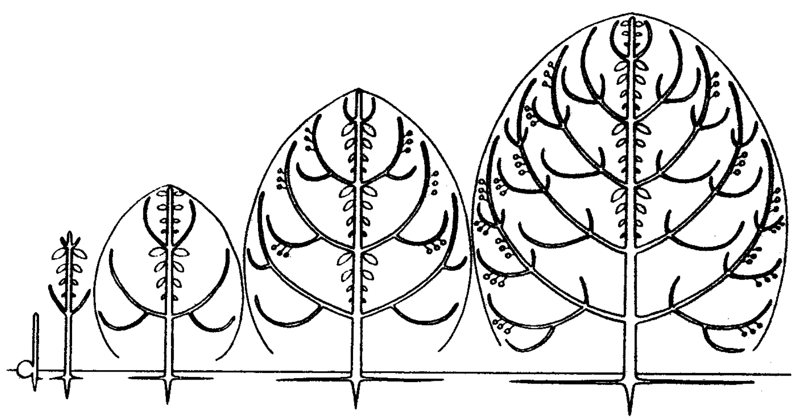
Monocotyledon: *Pandanus vandamii* (Pandanaceae). Dicotyledon: *Mangifera indica* (mango—Anacardiaceae).

– Trunk with continuous growth in height .... **Stone's model**.



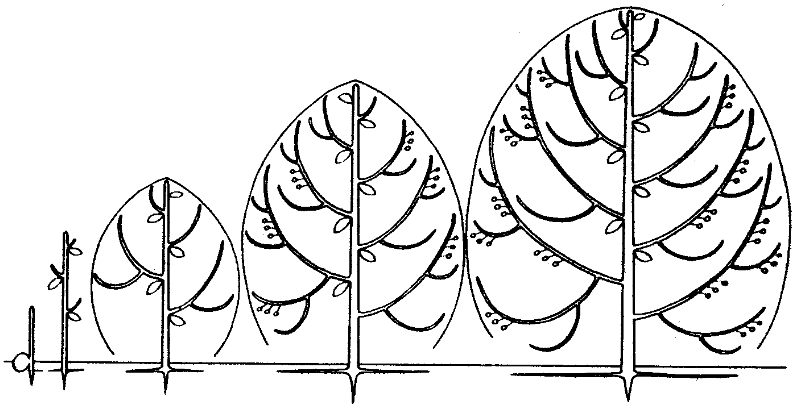
Monocotyledon: *Pandanus pulcher* (Pandanaceae). Dicotyledon: *Mikania cordata* (Compositae)

21 (19). Trunk with rhythmic growth in height .... **Rauh's model**.



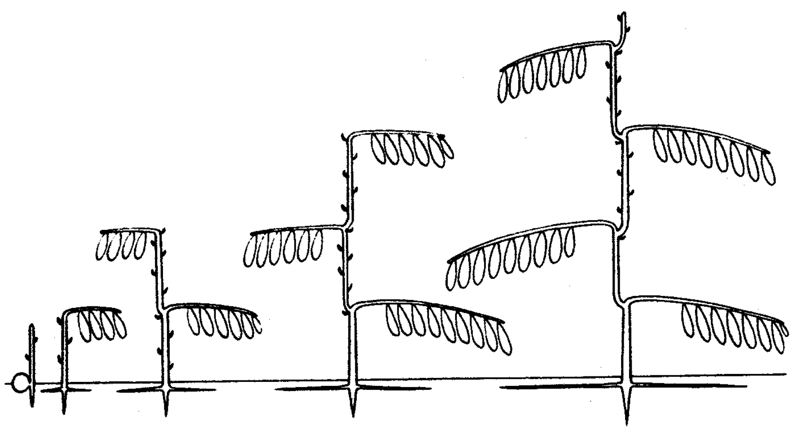
Gymnosperm: *Pinus caribaea* (Honduran pine—Pinaceae). Dicotyledon: *Hevea brasiliensis* (Para rubber tree—Euphorbiaceae).

– Trunk with continuous growth in height .... **Attims'model**.



Dicotyledon: *Rhizophora racemosa* (Rhizophoraceae)

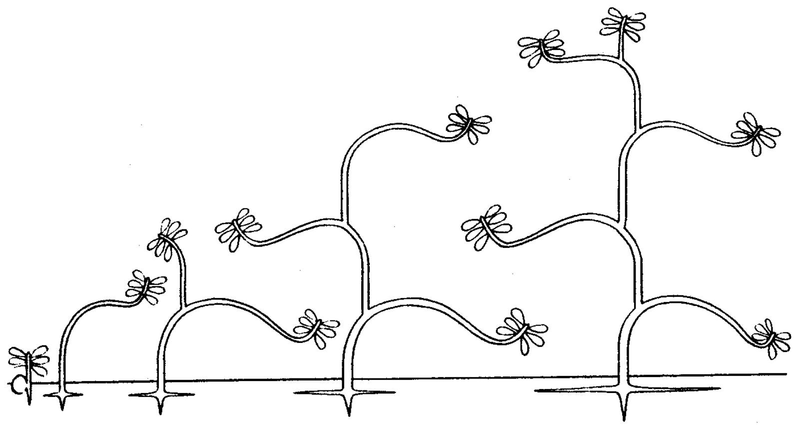
22 (18). Axes clearly mixed by primary growth, at first (proximally) orthotropic, later (distally) plagiotropic .... **Mangenot's model**.



Dicotyledon: *Strychnos variabilis* (Loganiaceae).

– Axes apparently mixed by secondary changes .... 22.

23. Axes all orthotropic, secondarily bending (probably by gravity) .... **Champagnat's model**.

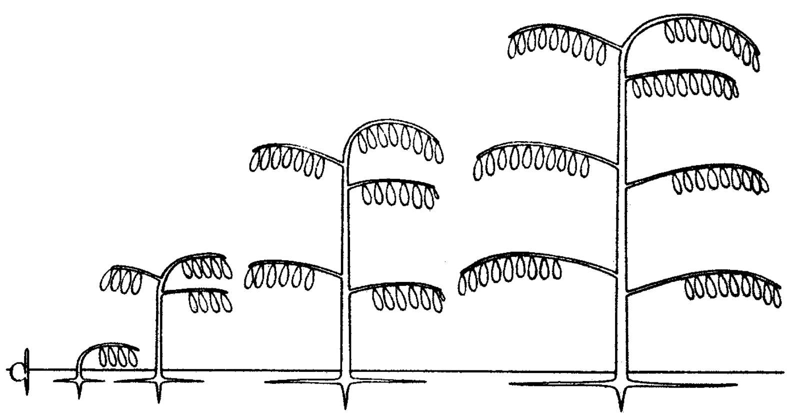


Dicotyledon: *Bougainvillea glabra* (Nyctaginaceae).

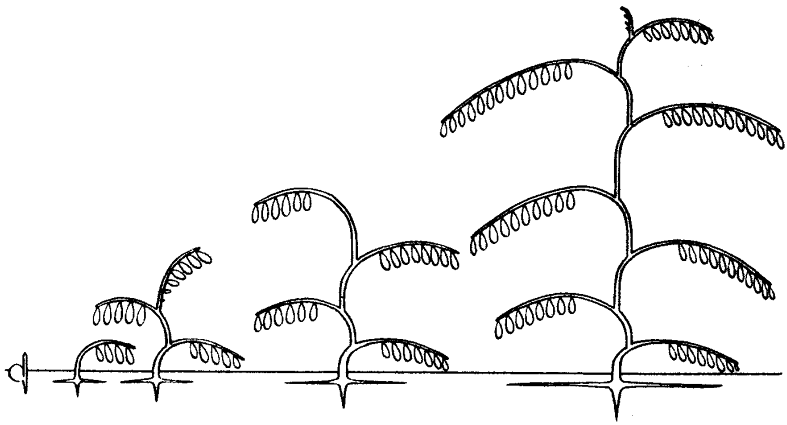
– Axes all plagiotropic, secondarily becoming erect, most often after leaf-fall . . . . **Troll's model**.

Dicotyledon: *Annona muricata* (custard apple—Annonaceae), *Averrhoa carambola* (carambola—Oxalidaceae), *Delonix regia* (poinciana—Leguminosae / Caesalpinioideae)

(a) Trunk a monopodium (e.g., *Cleistopholis patens*—Annonaceae):



(b) Trunk a sympodium (e.g., *Parinari excelsa*—Rosaceae):



* * *

Some woody vines do not conform with known tree models, e.g. *Triphyophyllum pellalum*, *Ancistrocladus abbreviatus* and *Hedera helix*: