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TREE HISTORY WORKBOOK

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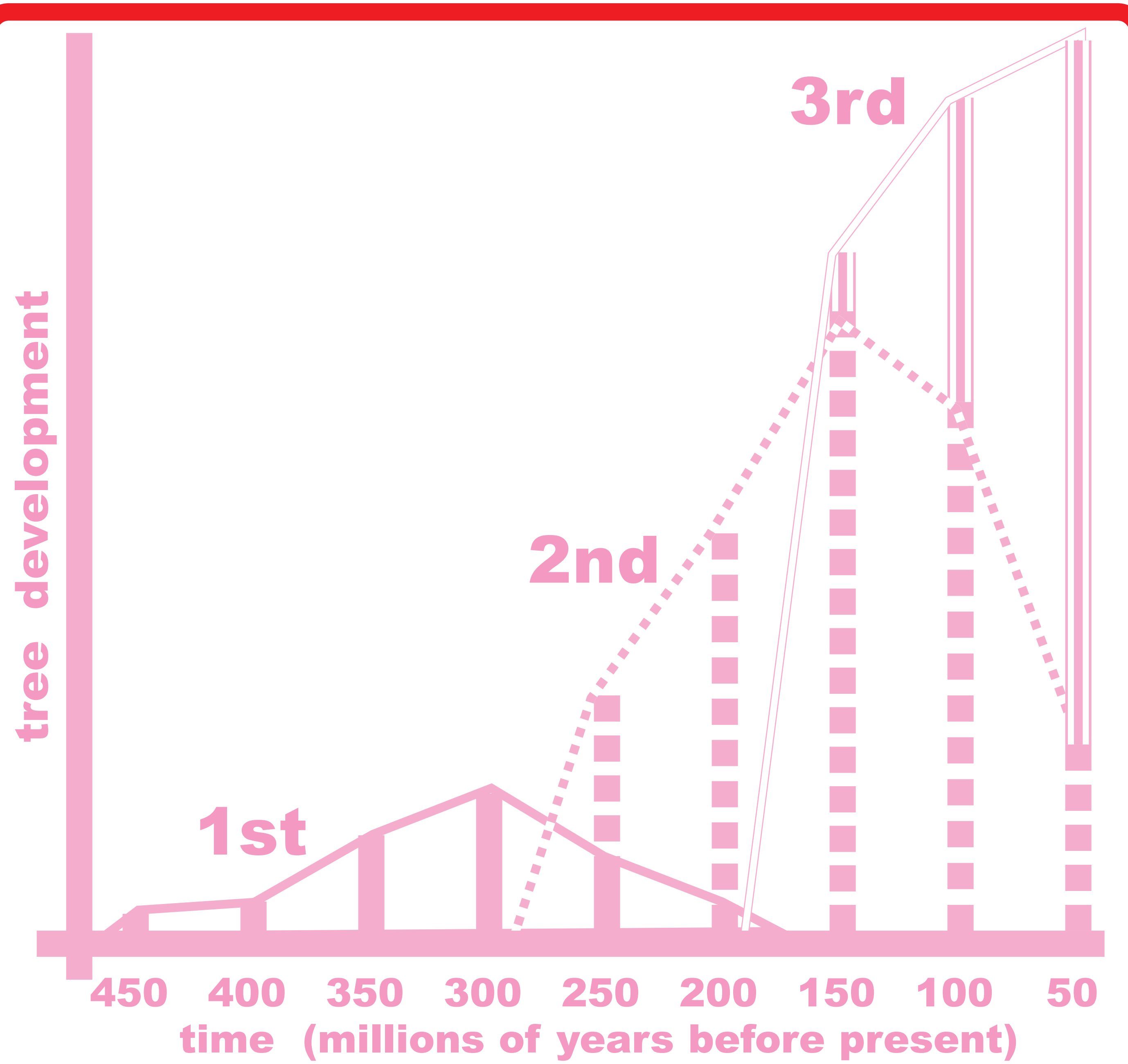


This workbook is an educational product designed for helping people interested in trees to appreciate and understand how modern trees developed across long time periods. This product is a synthesis and integration of research and educational concepts regarding tree evolution and species inception. This educational workbook was designed for awareness building and foundation training of professional tree health care providers.

At the time it was finished, this workbook contained educational materials and models concerning tree development thought by the author to provide the best means for considering the most basic understandings of time impacts on tree species creation, extinction, and tree biological and mechanical fundamentals. The University of Georgia, the Warnell School of Forestry & Natural Resources, and the author are not responsible for any errors, omissions, misinterpretations, or misapplications stemming from this educational product. The author assumed all users would have some basic tree biological, structural, and ecological background. This product was not designed, nor is suited, as a literature or research review. Please use the selected literature section at the back of this workbook to find scientific sources.

contents:

Introduction

An arborescent or tree growth form has developed across time in many different groups of plants. Diversity of unrelated tree forms suggest elevating leaves to catch sunlight is valuable in many ecological systems. There was not a single ancient relative from which all trees are derived, but many. What is the lineage of trees we use today in parks, yards, plantations, and along streets? To understand the history of trees it is critical to define a tree.

Trees?

Trees grow all around us in rural and community forests -- in stands, clumps and as single stems. What is a tree? The most effective definition of a tree, gathered from 155 descriptors and 45 definitions, is a "large, tall, woody, perennial plant with a single, basally unbranched, erect, self-supporting stem greater than 10 feet in height and larger than 3 inches in diameter holding an elevated and distinct crown of branches." Figure 1.

Trees of today are shaped by an environment filled with continually changing resources and other living things. Historically, the anvil of time upon which trees have been forged used five primary tools:

1. stress (including pests)
2. site disturbance
3. interference (allelopathy and competition)
4. effective reproduction, and
5. efficient defensive systems.

A history of tree-forms is all about reacting to change -- adapt or die. The geologic time scale of evolution and the human time scale of succession have generated the trees and forests we see around us today.

Delving Back

Trees have developed many features over time which allow success in hostile environments filled with other interfering living things. Trees developed in a similar way to how automobiles developed over the last 100 years – innovation and market success leading to new features and attributes of speed, safety, luxury, style, and amenities. A new car has its foundation in the past with Ford's first model. Modern trees have their foundation in trees of the geologic past.

Children know what dinosaurs looked like through media representations. What did trees and forests of the distant past look like? To explore the history of trees, the past must be examined through tree fossils. National and state petrified wood preserves of the Western United States provide a glimpse back in time to ancient trees and forests. Worldwide the fossil record is disjunct, untidy, and occasionally contradictory, but shows how a progression of time pushed trees into modern forms. To examine where trees began and developed is a study of ancient lands, seas, pollen, leaves, wood, and seeds.

Keeping Time

One key feature of tracking trees through time is understanding how time of the geologic / ecological past is kept. There are two ways used here to keep track of time: millions of years before the present abbreviated as "MY" with the MY truncating the time before present to a three digit or less time span; and, Coder tree time units, abbreviated by "TT," a natural logarithm designed to emphasize Earth's past which developed and supported tree forms.

Figure 2 provides the mathematical formula for interconversion of the MY and TT system. Because the fossil record is not accurate nor precise, use of one or the other system is not critical, as much is unknown about actual times of tree formation events. Figure 3 provides a comparison between MY and TT values in measuring tree history. For example, tree forms were thought to have been generated around 6.0TT or 410MY.

Cradle

Most of the history of Earth involves lava, rocks, and meteorites. For almost all of its existence (89%), the continents of Earth have been barren places of heat, cold, and geology irradiated by a merciless sun. Figure 4. Terrestrial biology began to be important late in the life of Earth. Depending upon source, Earth is considered to be approximately 4,600 million years old (i.e. 4.6BY or 4,600MY or 8.4TT). More than a billion years passed from Earth's formation until the first evidence of ocean life could be found. More than two billion years more passed before the land was colonized.

Earth's past has been divided by humans neatly into small time divisions millions of years in length. Figure 5 shows the four large time divisions or eons since the Earth was formed. The earliest time division was the Hadean eon spanning 800 million years. The Archean eon covered 1,300 million years and the Proterozoic covered almost 2,000 million years. The Proterozoic witnessed the development of marine life. The eon of trees and of humans is the Phanerozoic time period covering only the last 543 million years.

Our Eon

The subdivisions of time in the Phanerozoic eon is provided in Figure 6. The eon is divided into three large time spans called eras: Paleozoic lasting 295 million years; Mesozoic lasting 183 million years; and, Cenozoic lasting 65 million years up to today. Each era is further divided into other subdivisions where tree forms first developed, boomed to great success, and froze in icy times. Note the era names with the suffix "-zoic" refer to milestones in animal development.

The time subdivisions in the Phanerozoic eon are more closely examined in Figure 7. Some time periods are much shorter than others. The duration of each time period is given in the figure. Some of these period names have become familiar to animal-centric education programming, like the Jurassic and the Cambrian. A tree-centric period was the Carboniferous period, a time of vast swampy forests, generated almost all of the coal mined today. The whole of our eon is critical to appreciate from where trees came.

Drifting Around

One feature of land life is where it developed. Figure 8 traces the relative location of Eastern North America over the last 600 million years. Two massive supercontinents have formed and have broken apart over this time frame sending continent sized chunks of land skidding off in different directions. North America's animals and plants developed across time in many different neighborhoods, at one point straddling the equator.

Continuing into modern times, continents are still moving across the face of the globe. Figure 9 shows idealized land mass movements for the last 225 million years. The second supercontinent of Earth is called Pangaea and started to break apart about 200 million years ago. The two resulting landmasses were called Laurasia and Gondwana, and became separated by 180 million years ago. This separation essentially split land which would be in the Southern Hemisphere of modern times from land which would be in the Northern Hemisphere.

Continental drift greatly impacts ocean currents and wind patterns. Massive climatic changes occur when seas open up between land areas, or where land mass collisions occur pushing up high mountains. Some land mass drift velocities can be relatively high speed. The physical features of Earth are under constant change, and so are the living things clinging to its surfaces and suspended in its oceans.

What About Us?

Closer to home for humans is keeping track of time in the Cenozoic era. The last era of Earth time when we live is divided into two major time periods (Tertiary and Quaternary), and further into seven smaller subdivisions. Figure 10. Compared to the history of Earth, humans are short-timers and ephemeral. Our current time subdivision is called the Holocene and represents the last 10,000 to 12,000 years of Earth history.

Rules & Regulations

For tree history, most of Earth time is not critical. The Phanerozoic eon is the time period when land was first colonized by plants. It is with the first ocean plants splashed onto rocks (and survived!) where tree history begins. Trees are a conglomerate of Earth plant life histories on land. To appreciate tree history given here, several constructs must be recognized:

A. The first construct is the dating system in millions of years before today – here denoted as MY. A number followed by "MY" or "my" represents a time millions of years in the past. Here a million years is treated quite flippantly. It must be remembered humans have been in-residence for a trifle of Earth time, but trees have been present (using one human term for time passage) for 10.9 million tree generations. A lot can happen (and did!). Remember, treat any given time as a rough value (give or take 10 million years), not as an accurate time.

B. A second construct here of tree history is how past geologic time is divided. Many time periods of the past begin and end with major Earth or animal life events. These time period names are used to keep ecological time linear. Here, additional plant based terms are coupled with traditional time period names.

C. A third construct used here of tree history is understanding all dates are estimates taken from fossil and coal based records. Remember, the fossil record is disjunct and incomplete. It is heavily biased by Northern hemisphere sites, and by those species easy to find and identify. Scientists have an extremely limited view of trees from the past and must make terrible, error-prone guesses regarding old tree forms and forests based upon limited data.

Rocky Beginnings

The history of trees begins in the distant past when Earth was relatively new and quite different than today. Earth is estimated to have been formed around 4,600my, with the moon formed 100 million years later. Solar system bombardment and massive volcanic eruptions were winding down. Earth was cooling and water was condensing out of a low oxygen atmosphere. Oceans formed about 4,400MY ago with continental crusts present by 4,200MY.

Around 3,800MY, telltale signs of anaerobic carbon based photosynthesis were present in oceans. Bacteria chlorophyll developed for sensing infrared light energy coming from hydrothermal vents in on the ocean floor. This bacteriochlorophyll was the precursor to chlorophyll a of trees. By 3,700MY there is clear fossil evidence of ocean microbes living in colonies. The oldest individual fossil cell of what appears to be a anaerobic photo- or chemi-synthetic bacteria is seen by 3,600MY. There was beginning to be free oxygen in the atmosphere by 3,400my. Unmistakable evidence of aerobic photosynthesis is presented in the fossil record by 3,300MY.

Landing

Earth continued to form large landmasses (supercontinents) and break them apart. This cycling of clumping and splitting terrestrial environments seems to occur on a 200-500 million year cycle. When the land is clumped together, a massive global ocean exists. When land is split up into smaller units, intercontinental seas exist. These seas and oceans develop currents, differentially heat and cool the land, and can bring precipitation or desertification. Land masses pulling apart generate great rifts while land masses colliding pushing up great mountain ranges. New mountains mean new weather patterns, as does huge continental land areas.

Across Earth history when life was present, there has been more than six land mass gathering events. These life altering continent coalescent events are termed supercontinents: Gondwana 180my - 30my; Laurasia 180my- 60my; Pangaea 300my -180my; Pannotia (Vendian) 600my-540my (a relatively short-lived amalgamation); Rodinia 1,100- 750my; and, Columbia (Nuna) 2,000-1,500my.

Wet Beginnings

The edge of these most ancient oceans, and barren land masses raised above them, were nurseries of life. Over two billion years, resource availability and interactions between living things in the ocean propelled innovation of new attributes. After almost a billion years, atmospheric oxygen contents reached a significant concentration and aerobic photosynthesis was widespread. Algae are identified by 2,100MY. Bacteria, and green, blue-green and red algae were among the first living witnesses to ancient Earth. Continents pushed together into a supercontinent called Rodina by 1,100MY.

Rodinia

Probably the critical supercontinent to establishment of terrestrial life was Rodinia. Rodinia formed about 1,100 million years ago from residual continental pieces of the last supercontinent Columbia. Rodinia formed in the Southern hemisphere and near its end had developed a South polar ice cap. Rodinia was completely barren and inhospitable to life for a single major reason – severe ultraviolet solar radiation not blocked by an atmospheric ozone layer. Earth entered a rapid cooling phase as Rodinia was starting to break up around 750my. This massive change in environment triggered a rapid increase in the diversity of life, especially along the newly expanding coastlines.

Oxygenated

The first record of multicelled organisms occurred around 1,375my. Extensive algal mats existed along the shore by 1,200my. By 850my, photosynthetic plant life had began to significantly modify oxygen contents in the atmosphere. Increasing oxygen contents in sunlight started to initiate a ultraviolet light protective ozone layer. By 800MY multicelled algae are present along ocean edges. The first marine plant communities were present by 640my. A great explosion of marine species erupted in 595my providing many new species and families. The first plant life on the beach and around edges of tidal pools could be seen by 560my.

With demise of one supercontinent were made the pieces of the next supercontinent. Rodinia broke apart and by 600my had reassembled into supercontinent Pannotia. From 610MY to 590MY, the interior of Pannotia underwent a long ice age. Pannotia, for supercontinents, was a short-lived landmass which broke up by 540my. Continental portions later reassemble by 300my into supercontinent Pangaea. It is around and over Pannotia and Pangaea where much of Earth's tree history takes place. The ocean-centered part of early tree history ends.

descriptor	percent	cumulative percent
PLANT	20%	
WOODY	16	
SINGLE STEM	14	
TALL / HEIGHT	13	63%
BRANCHED	9	
PERENNIAL	8	
GIRTH / DIAMETER	7	87%
ELEVATED CROWN	4	
DISTINCT CROWN	3	94%
SELF-SUPPORTING	3	
LOWER STEM CLEAR	2	
ERECT STEM	1	100%

Figure 1: Examining definitions for trees from reference and regulatory sources with 155 descriptors in 45 formal definitions. (legal, regulatory, dictionary, reference)

$$TT = \log_e MY$$

$$MY = e^{(TT)}$$

Figure 2: Mathematical definition and conversion formulae between Coder tree time (TT) and millions of years before present (MY). For example: 486my = 486,000,000 years. The shortened 486my is used in the formulae above, not the full number.

	8.5 TT	**=**	**4,915 MY**
	7.5 TT	**=**	**1,808 MY**
trees	**6.5 TT**	**=**	**665 MY**
	5.5 TT	**=**	**245 MY**
boom	**4.5 TT**	**=**	**90 MY**
	3.5 TT	**=**	**33 MY**
	2.5 TT	**=**	**12 MY**
	1.5 TT	**=**	**4.5 MY**
burr	**0.5 TT**	**=**	**1.65 MY**

Figure 3: Time scale comparision between Coder tree time (TT) and millions of years ago (MY). $MY = \boldsymbol{e}^{(TT)}$; $TT = \log_e(MY)$

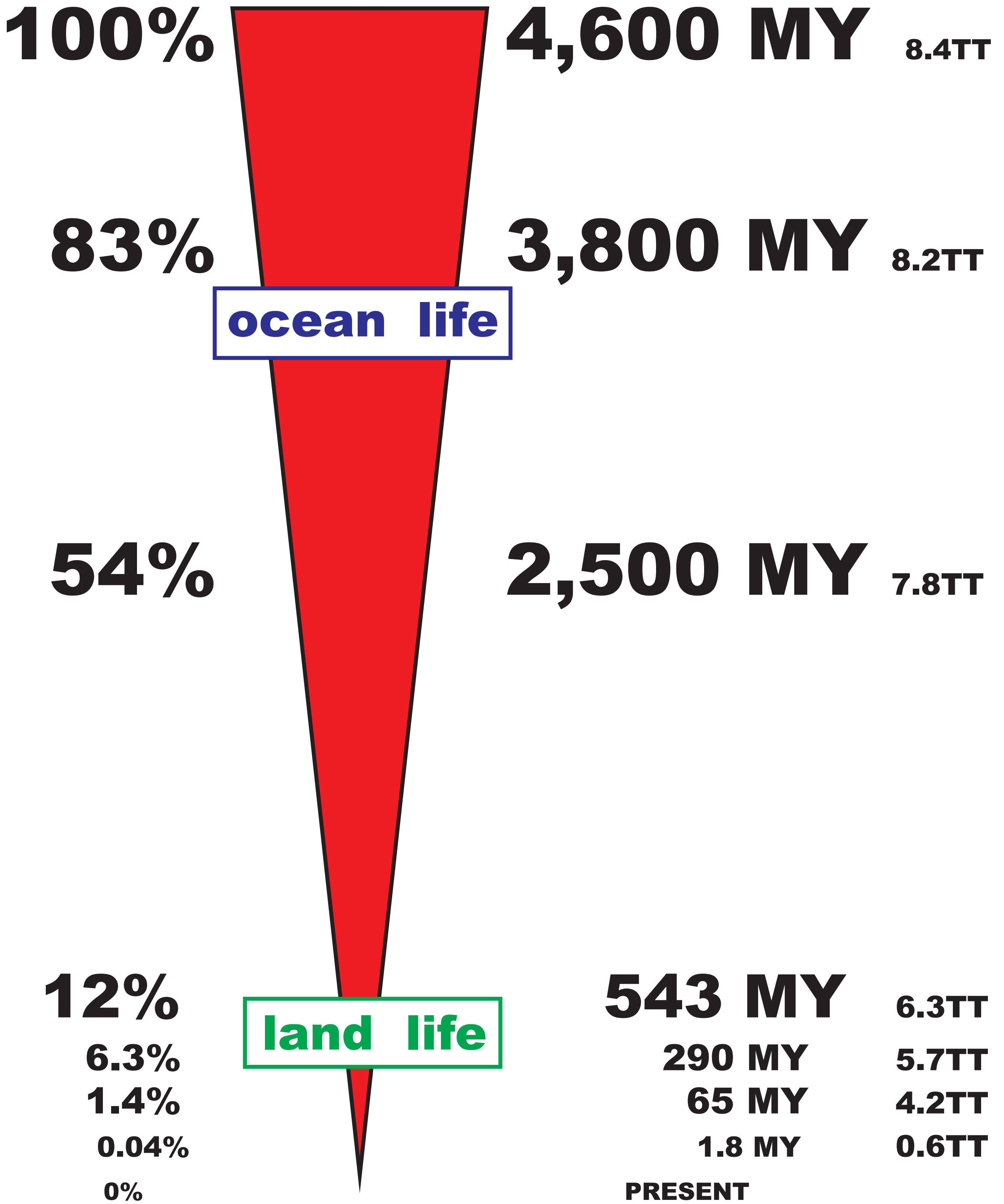


Figure 4: Timeline illustrating development of life on Earth in percent of Earth's total age, millions of years (MY), and Coder tree time units (TT).

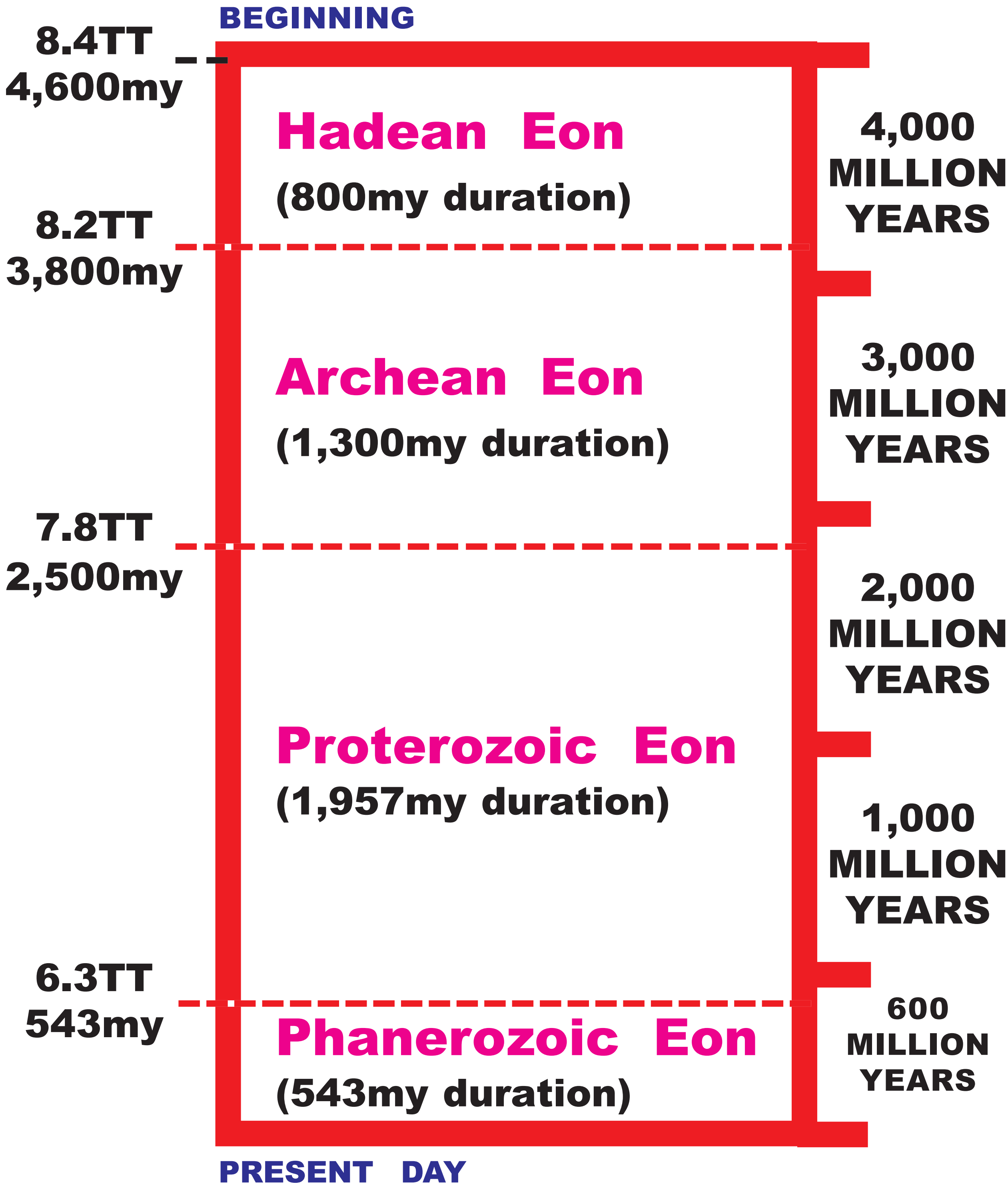


Figure 5: Illustration of duration for each eon period of Earth in millions of years, and rough starting / ending point in Coder tree time (TT) and millions of years before present (my).

Phanerozoic Eon				
Cenophytic – Age of Angiosperms (Age of Flowering Plants)				
Cenozoic era				
(Quaternary sub-era)				
	Neogene	**Holocene epoch**	**0.01MY**	
		Pleistocene	**1.8MY**	**0.6TT**
(Tertiary sub-era)		**Pliocene**	**5.4MY**	**1.7TT**
		Miocene	**24MY**	**3.2TT**
	Paleogene	**Oligocene**	**34MY**	**3.5TT**
		Eocene	**55MY**	**4.0TT**
		Paleocene	**65MY**	**4.2TT**
Mesophytic – Age of Gymnosperms (Age of Seed Plants)			**140MY (4.9TT)**	
Mesozoic era				
	Cretaceous		**142MY**	**5.0TT**
	Jurassic		**206MY**	**5.3TT**
	Triassic		**248MY**	**5.5TT**
Palaeaphytic – Age of Pteridophytes (Age of Vascular Plants)			**280MY (5.6TT)**	
Palaeozoic era				
	Permian		**290MY**	**5.7TT**
	Carboniferous	**Pennsylvanian**	**323MY**	**5.8TT**
		Mississippian	**354MY**	**5.9TT**
	Devonian	**Late**	**378MY**	**5.94TT**
		Middle	**386MY**	**5.96TT**
		Early	**417MY**	**6.03TT**
Proterophytic – Age of Land Plants			**420MY (6.0TT)**	
	Silurian		**443MY**	**6.1TT**
	Ordovician		**490MY**	**6.2TT**
	Cambrian		**543MY**	**6.3TT**
Archaeophytic – Age of Ocean Plants			**550MY (6.3TT)**	
Proterozoic Eon			**550MY (6.3TT)**	

Figure 6: Names and beginning times in millions of years (MY) before the present and in Coder tree time units (TT) for discrete time periods in the Phanerozoic Eon of Earth.

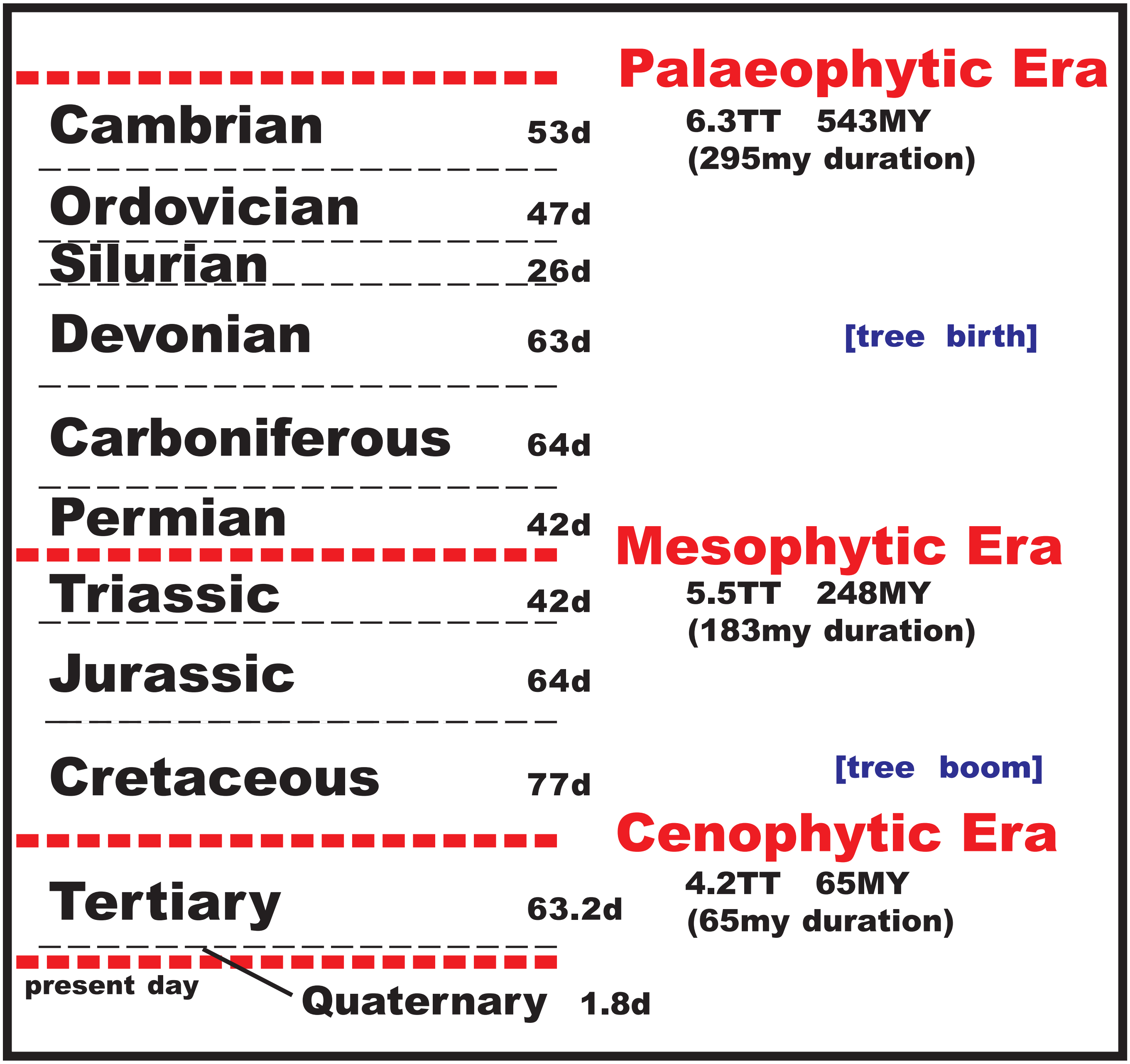


Figure 7: Timeline showing proportional duration of time periods in the Phanerozoic Eon. Duration (d) is in million of years.

Earth

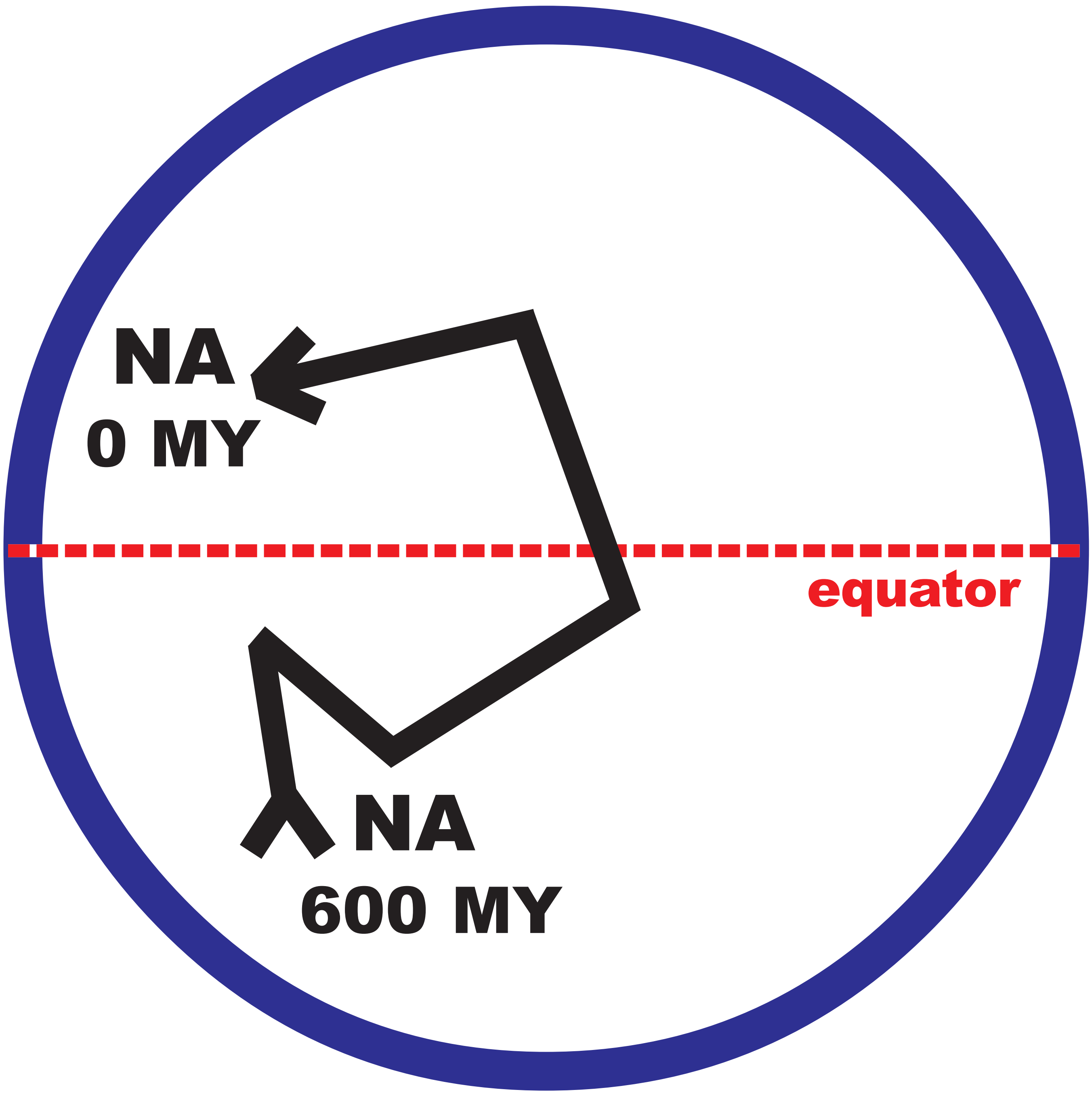


Figure 8: North America's continental drift across the face of Earth over 600 million years.
(MY = millions years)

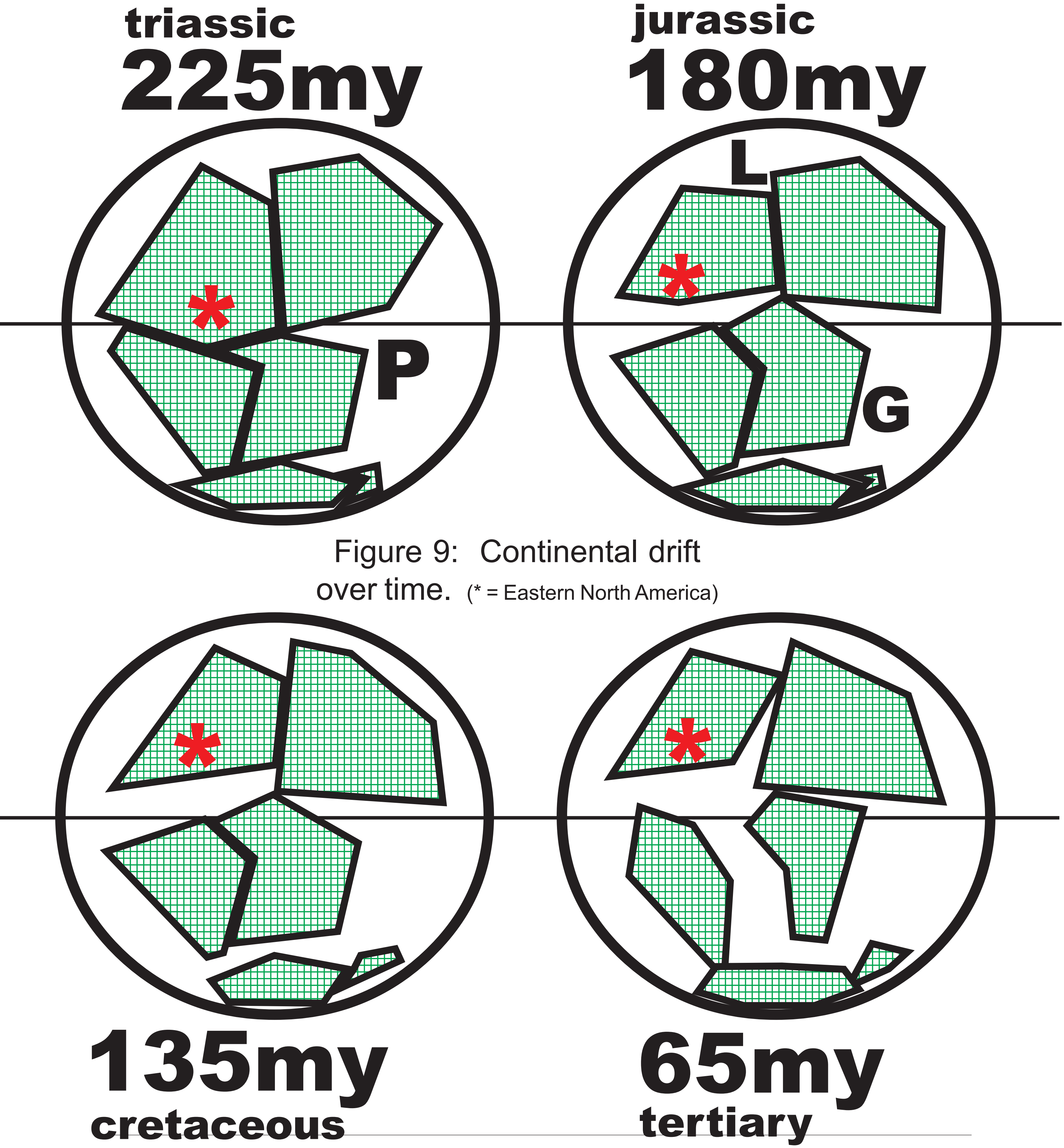


Figure 9: Continental drift over time. (* = Eastern North America)

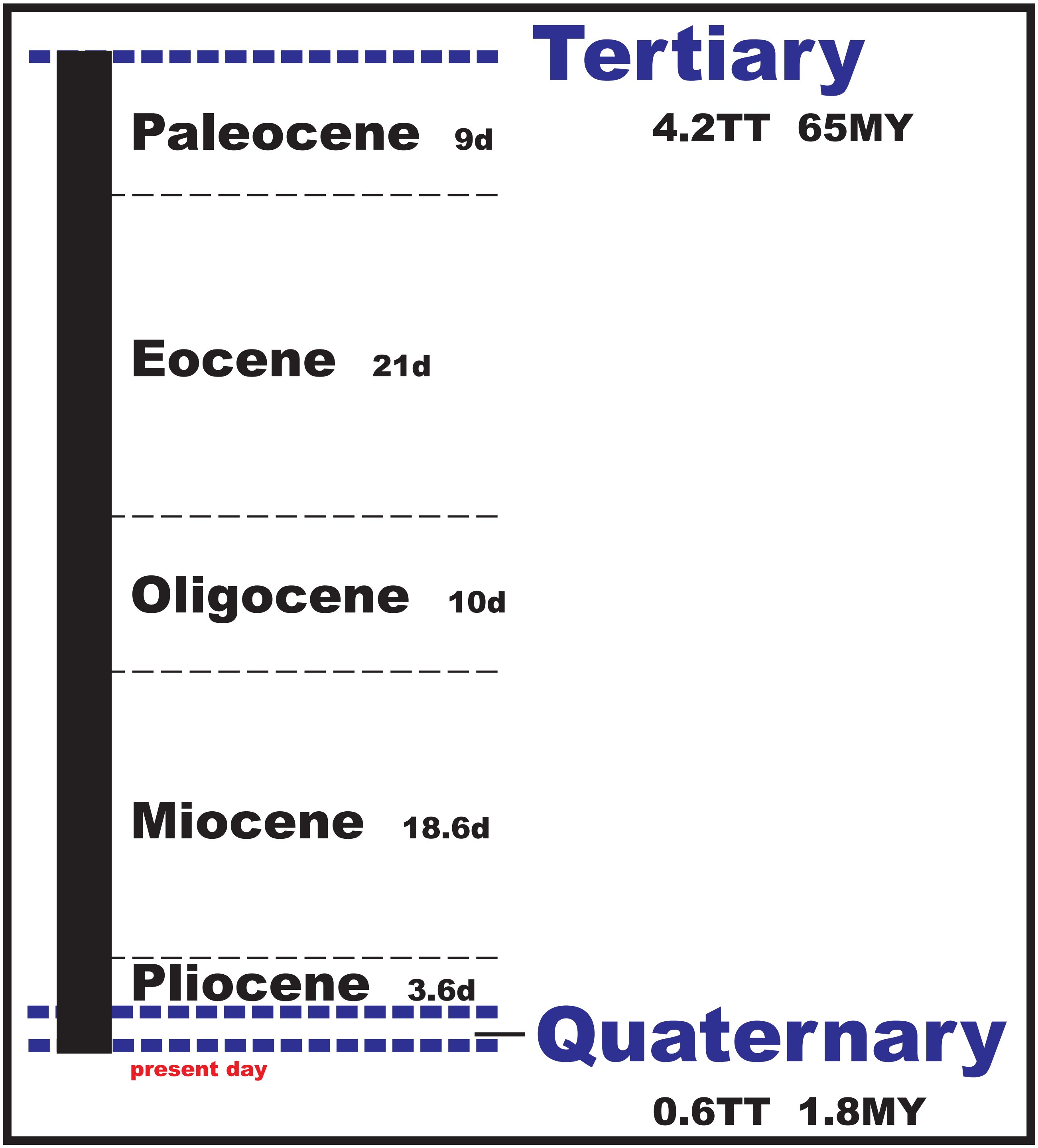


Figure 10: Timeline showing proportional duration of time periods in the Cenozoic Era. Duration (d) is in million of years. The Quaternary is composed of the Pleistocene (1.79d) and Holocene (0.01).

Proterophytic Age of Plants -- Age of Land Plants

Earth begins to warm up out of its deep freeze. The Proterophytic Age of Plants begins – the Age of Land Plants -- around 550MY. At 543MY the Paleozoic era Cambrian period begins with oceanic plants messing with edges of dry land. By this time oceans had many life-forms. New ways of capturing energy and reproducing allowed some organisms to be successful. Most could not compete well with others, or change with the times, and became extinct. Sexual reproduction of plants began around this time, instead of simply splitting or budding.

Beachfront Real Estate

By 510my plants derived from green algae which were filamentous and branched grew in fresh water pools near the shores. These pools had widely fluctuating water levels leaving pool edges dry for extended times.

The Ordovician period begins in 490MY with margins of continents invaded by plants. For over 50 million years beachfront communities of plants clambered farther onto land where light was plentiful and competitors few. New structures and processes were needed to be successful on land. The first land plants were green algae films laying over sand and rocks 485MY ago. Fossil records show land plant spores were present by 470MY.

Green Scum

Between 458MY and 443MY, carbon-dioxide (CO2) concentrations in the atmosphere were low, Earth was cooling, and glaciers were present. In this time of general cooling, the first plants make permanent colonies on land. It took some time for these first thin films of green slime on rocks to yield trees. From these flat, mat-like photosynthetic surfaces, a third dimension developed pushing upward. These unbranched, green, upright tissues or stubs grew to greater and greater heights (i.e. ½ to 2 inches). Height growth required new structural and vascular components.

Tiny green stems grew upward, as well as across the ground surface. Essential resources were gathered using localized surface filaments (epidermal cells) growing from undersides of horizontal stem segments (rhizomes). By 450MY many land plant spores were present and new primitive land plants developed specialized surface cells (epidermis) and an associated protective wax cuticle. The Ordovician ends with building levels of plant colonization of the land.

Silurian

In 443MY the Silurian period begins and new plant innovations for living on dry land (in dry atmosphere) quickly become visible. By 440MY the first tracheid cells (specialized hardened, stiff, water conducting cells) are found, along with more extensive surface cuticles. New materials developed for conserving and moving water.

By 435my a few land plants had reached 2-3 feet in height. Two milestones were reached around 428MY when: 1) the first vascular land plants develop called tracheophytes (meaning they use tracheids to move water within their tissues) – arising from about the last 9% of Earth's existence; and, 2) the atmosphere reaches ~13% oxygen concentration which can sustain wildfire. From this time onward, organic carbon derived from photosynthesis was recycled back into the atmosphere by surface fires.

Rhynios

By 425MY small, thin, 3 inch tall, stick-like erect plants grow upward from a ground-hugging rhizome exist. These plants are called rhyniophytes. They have generated elevated green stems supplied with water moving through dedicated vascular tissue and generated a specialized organic compound for stiffening cell walls called lignin. By 425MY, specialized gas exchange ports with opening and closing cells (guard cells) were present on plant cuticles. Not everything was an idealized step forward for vascular plants, as there was a major extinction event during this time period, followed immediately by a period of increasing diversification of many species groups.

Land Plants

Through this age of plants, several ancestral lines split apart. Some plants went on to be represented in modern flora and some became extinct. Figure 11 demonstrated some of the lineages generated in terrestrial plants. The first split was between lower and vascular plants. Vascular plants split into green stem plants and plants with leaves. Both these groups generated tree forms. The leafy plants split into spore generators and seed producers. Seed producers generated a number of evolutionary tree lines which survive today, almost 99% are conifers and angiosperms.

Tree Concepts

As mentioned previously, tree forms were generated in a number of different vascular plant groups, many of which became extinct. The key for tree developement and survival was dealing with, in order:

A. surviving a dry terrestrial environmnet -- invaders of land working against constraints of dehydration and dessication, sunlight impacts, and gas exchange processes;

B. moving water effectively agianst inceasing height above soil -- dedicated water conduction and control machinery against constraints of gravity and an extremely dry atmosphere;

C. devloping a better and more efficient light capture systems -- specialized light capture organs tuned for light quantity and quaility, while being elevated and disposible;

D. mechanically resisting gravity and wind with increasing height above surroundings -- stiff, strong, but light weight structural components for additional height against constraints of shading competition, gravity compression, and lateral wind force tension, compression, and torque (twist);

E. generating a protective and easily distributable device for reproduction (the seed) -- seed designed for effective distribution and germination; and,

F. nurturing and protecting seeds from damage and consumption while assuring distribution to appropriate sites (flowers and fruit) -- assures effective fertilization and survivability of seed within a container (fruit).

The constraints and inovations can be summarized as a single word sequence of -- land, water, transport, support, leaf, seed, and flower. This is the guantlet of developement from which modern trees have exited.

Land Plants

Bryophytes lower plants
(liverworts & mosses)

Tracheaphytes vascular plants

Lycophytes clubmosses & quillworts
(tree forms 360MY to 270MY)

Euphyllophytes leaf plants
(began to split ~400MY)

Monilophytes spore plants
tree ferns, horsetails, ferns, protoconifers

Spermatophytes seed plants
(by ~360MY)

Spermatophyte Tree Forms
5 evolutionary lines into today
99% conifers & angiosperms

Figure 11: General description of land plants roughly in order of development.

Palaeaphytic Age of Plants
Age of Vascular Plants / Age of Pteridophytes

In 420MY a new plant age arrives. The Palaeaphytic Age of Vascular Plants or the Age of Pteridophytes begins. The first vascular plants had wide spreading rhizomes (horizontal stems) growing across the surface of soil through any organic matter available. Every so often, the rhizome would send up a green photosynthetic shoot above the ground and send out small single celled absorbing cells across the soil surface. The fiirst vascular plants usually lacked a single main stem, but had multiple clumps of stems over particularly rich soil areas. These plants lacked a cambium and could not grow in diameter. Their height was limited by simple water movement through pressurized stem cells and mechanical support of an upright untapered stem against gravity and wind forces.

The first vascular land plants of note were clubmosses. By 418MY a clubmoss called Asteroxylon had developed simple, small, stem-hugging, scale leaves. The photosynthetic system used by these small land plants was a C3 system used today by most trees under cold, cool, and warm temperate or tropical conditions. The Silurian ends with an evolutionary starting gun ready to fire in a race forward to trees of today. Also around this time, the first land animals develop.

Devonian

In 417MY the Devonian period begins. The Devonian is a period when great tree forms developed. The Devonian is usually divided into three sections or epochs, early, middle and late. The early Devonian saw many innovations occur in plant forms. Figure 12. Actual dedicated plant roots, rather than rhizomes, first appear around 415MY. Gas exchange ports controlled by the plant called stomates were present on stems by 410MY. Small upright lycopsids (clubmosses) were common in the fossil record by 410MY. The average height of vascular land plants reached knee high by 400MY. An early ecological interaction was also visible by 400MY -- large plant rhizomes and roots infected with symbiotic fungi.

The early Devonian held the rise of euphyllophytes (leaf plants) by 400MY. Leaves generated were small points of green tissue with vascular tissue in the center. Up to this time, only stem and branches were green and photosynthesizing. The euphyllophyte group was the basis for an ecological split leading to spore and seed plants going separate ways.

Toward Leaves

A leaf is a photosynthetic organ held on stems for some period of time. The pathway to modern tree leaves began with the most primitive of photosynthetic organs -- a green stem. Figure 13 shows a progression toward a specialized organ dedicated to photosynthesis. Green stems became flattened with a more divided structural stem leading to long strap-like leaves. A continued finer and finer division of vascular tissue allowed intervienal tissues to photosynthesize. Figure 14 present a functional view of leaf development with a green stem generating green nubs which expand into clustered small branches which flatten and laterally expand to generate a leaf blade.

Around 391MY, an small extinction event occurred eliminating some pteridophytes (early vascular plants). This extinction event did not impact animal species. From 390MY to 360MY, Earth had a warm, humid period with elevated CO_2 concentrations. This period saw an explosion of vascular land plant species and families. Large forest expanses (altough short in stature) were present by 395my. In 390MY, progymnosperm trees were present (example is spore producing Archaeopteris, 25 feel tall and 5 feet in diameter with features intermediate between ferns and gymnosperms).

Living Dry

The Devonian period was dedicated to plants living without being immersed in water while developing features to effectively use and conserve any water which was present. It is here the first trunks of trees begin to rise above swamps, riversides and coasts, and the rate of tree-form development began to accelerate. Figure 15 provides a list of tree-form plant developments leading directly to modern trees.

All different tree-forms (shapes, sizes, morphology) which have existed can be created using computer models which optimize three primary biological requirements: mechanical stability; light gathering; and, reproductive success. All of these must exist in an environment of biological and ecological water contrainst, and temperature fluctuations. Figure 16. Optimizing these items generate a number of different tree-forms, depending upon water availability and temperature in the environment. Structure, light, and sex across a wet to dry, and warm to cool landscape gradients helped form trees of the past, and so, trees of today. The key downsize to optimizing is it propels tall tree forms to being more prone to damage / disturbance on a small scale, and to extinction.

Height vs. Light

An important resource for a tree to capture and control is sunlight. Several strategies developed to optimize light capture and are given in Figure 17. Key components included: greater extent and reach toward light associated with supporting structural improvements; interfering (competition and allelopathy) with neighboring plant forms to capture more light; long leaf forms perpendicular to sunlight impact angles; and, flattened, spreading leaf arrays.

One complex optimization pattern involves increasing height to over-top neighboring competitors. Increased height requires resistance to gravity and lateral forces, plus a continuous supply of water for photosynthetic arrays. Figure 18 presents six increasing advanced development stations gaining height, reach and extent for more effective light capture. Note increasing height, branching, diameter (taper), and rooting all yielded a variety of tree forms.

Being Tall

Although height was gained in many plant groups, tallness alone was not successful in all plant groups. Height in feet squared (ft^2) is roughly equal to success at spore or seed distribution -- a little taller is much better for reproduction. Height increases in tree forms began slowly, but rapidly (i.e. over ~33 million years) pushed up toward physical and biological limits. Figure 19. The downsize of height is being tall is a successful strategy in sable environments, but is detremental in unstable, radically changing environments. Environmental changes usually have a disproportional negative impact on tall tree forms.

Pushing Up

There was much coming and going of families and species over time. Since 391 MY to the present, there has been ten major tree-form extinctions. Few of these extinction events match-up with major animal extinctions. The cause of tree-form extinctions are usually global and continent changes in moisture avaiability (along dry to wet gradient), and global and continent changes in temperature (cool to warm gradient). If a species group is local and isolated, sudden catastrophic point events can disrupt survival and reproduction.

The middle Devonian period begins in 386MY. By 385MY tree horsetails were quickly developing. Vascular plant innovations around 380MY included: secondary xylem & phloem generated from a vascular cambium; more laterally extensive and greater depth of roots (i.e.<8 inches in depth with minimal soil disruption); a majority of upright plants growing from greatly thickened horizontal rhizomes; wood formation; protective periderm over vascular cambium; and, more effective leaves. The lycopsids (tree clubmosses) were growing taller. Around this time, another innovation was attempted -- production of a device for reproducing called a "seed" which would germinate upon release.

Sultry

The late Devonian (378MY) began with a massive extinction event in 377MY. This extinction event lead to the loss of many pteridophytes and large number of animals. Around 375MY, Earth reached its greatest concentration peak of atmospheric CO2 since life began, amounting to almost 17 times present day values. Earth was warm and moist.

Massive forests of green stem lycopod trees (tree clubmosses) covered large areas of land in 375MY. Common lycopsid trees, which were 100 feet tall by now were Lepidodendron. Fern understories in these forests developed by 370MY. Archaeopteris (progymnosperm) forests were widespread by 370MY. Tree ferns reached 25 feet tall and increased their diameter with secondary growth of the stem base. Hidden in among these more primitive tree forms, the fossil record shows gymnosperm wood around 370MY and gymnosperm pollen present around 364MY.

Accelerating Change

The late Devonian held many different tree form related events and develpments. The first event was a minor extinction event in 362MY which saw loss of some pteridophytes (early vascular plants). After this extinction event, the world of trees rapidly started to change. Seed plants called spermatophytes got started. Across the landscape in 360MY, there were massive swamp forests which would lead to coal of our time. Tree ferns called filicopsids (i.e. Psaronius tree fern up to 30 feet in height) were midstory forest trees. The last of a primitive evolutionary split with lycopsids (tree clubmosses) many millions of years before, the zosterophyllophyte trees, became extinct.

The new competitive advantage of better (more efficient) leaf arrays and added height led to an end of the first period for vascular plant development with the extinction of most first generation land plants by 360 MY. Events in the late Devonian would impact trees for the next 80 million years. From 360MY to roughly 280MY, lycophytes (tree clubmosses) were common. Lepidodendron remained a dominant tree clubmoss which grew to be 120 feet tall and 3 feet in diameter. The calamites (tree horsetails) were common, growing 60 feet tall with a diameter of one foot. Tree ferns were also common. As these trees were covering the land, atmospheric CO2 levels dropped and a new series of glacial events from 360MY to 290MY occurred.

Cool & Seedy

As cooler temperatures became more prevalent and CO2 levels dropped, trees developed (355MY) large flat leaves held away from the stem while growing dedicated root tissues deeper into soil (>20 inches). Because of this biological activity in soil from big and extensive roots, forested soil profiles began to develope. As the late Devonian closed in 354MY, trees and forests could be found all over the land.

Seed fern gymnosperms (pteridosperms) developed and grew to 30 feet tall and 30 inches in diameter (355 MY). Pteridosperms were similar to older tree ferns but with a more effective means of reproduction –

seeds not spores. Other major tree precursors of this time were cordaites, a primitive conifer-like tree growing 45-90 feet tall with many branches and stilt-like roots. Forests of this age were thick patches of stems with dense canopy branch clusters concentrated at the very top of straight stems. Trees of this age were simple green stems of the lycophytes, seedless progymnosperms, seed fern gymnosperms, and cordaites. These tree-forms are called "primitive" forms and represented the first wave of tree development.

Different Stems

Within all tree-forms are generally four types of stem structure responsible for meeting mechanical and biological requirements. Figure 20 provides a cross-sectional view of basic stem types developed to raise leaves while opposing gravity and wind. Basic stem types included:

1. Tough structural tube with either vascular tissue or a pressurized (hydrostatic) tissue filling the inside. In this stem type there is a distinct division of duty between structure and transport. This stem form is effective for small crowns on short stems like tree clubmosses;
2. Hollow trunk reinforced by longitudinal fluting. This stem form is susceptible to lateral forces causing local buckling of the exterior wall. This stem form is effective for small crowns on short stems in low wind environments as found in tree horsetails;
3. Fibrous composite with leaf bases sheathing stems providing limited increases in taper toward the base. This stem form is effective at opposing gravity but not lateral forces. This form also has mechanical problems with holding branches. This stem form was found in tree ferns.; and,
4. Solid cylinder with cellulose / lignin composite (wood). This stem form is effective for tall and large crowns with many branches, as in conifers.

All four of these stem forms could have a photosynthetic surface or rind. The fourth form could also bear a protective external periderm (i.e. generic bark) which minimized water loss while providing for gas exchange and a mechanical barrier over internal living tissue.

Coal Land

The Carboniferous (362 MY) is a time period when most people understand great forests existed and were buried to yield today's coal. Shallow warm seas and many low lying but separated landmasses provided huge areas of tropical swamps. Tropical swamp forests were dominated by a number of seedless and seed-bearing tree types, especially lycopods.

The Carboniferous period is divided into roughly two halves, the early Mississippian epoch and the late Pennsylvanian epoch. The Carboniferous' Mississippian epoch began in 354MY and showing a continuation of tree developments. There were many different tree species with vascular cambium, periderms and root systems. The sphenopsids or tree horsetails, and the pteridosperms or seed ferns (i.e. <u>Medullosa</u> 30 feet tall, 2 feet in diameter with large leaves), both grew in ecological importance. Seed fern tree forms derived from progymnosperms existed for about the next 110 million years.

Mississippi

The Mississippian epoch moved forward large tree species diversification, as well as an expansion of land coverage by 350MY. Forests were filled with older spore producers like filicopsids (ferns), progymnosperms (100 feet tall Archaeopteris derived from trimerophytes), sphenopsids (tree horsetails >30 feet tall called calamites), and lycopsids (tree clubmosses), as well as new seed producers like cordaites (90 feet tall and 3 feet in diameter), and pteridosperms (seed tree ferns).

Average forest height across many sites reached 60 feet for a codominant canopy. Seed production in these trees occurred at the end of a short, rapidly growing, no flowering, tree life -- then the tree died. By 350my an acceleration of speciation was occurring. By 348my lycopod trees had reached 160 feet in height and 4 feet in basal diameter. A great expansion of forested occurred by 345my. It was here that new seed types with dormancy developed to help tree reproduction to get through times with poor growing conditions.

Pennsylvania

The second half of the Carboniferous period, the Pennsylvanian epoch, began in 323MY and saw extinction of primitive progymnosperms. Swamp forests were laying down what would become coal in great layers of organic matter. By 320MY, tree clubmosses (remember these are closer to ferns and conifers than to mosses), and tree horsetails are at their ecological peak. Roughly 2/3s of wet forests are lycopsids. One successful type of tree horsetail around this time (315MY) were calamites (60 feet tall) growing erect from a huge creeping rhizome in wet swamps. Hidden among the dominant tree forms in 315MY was the first conifer (<u>Swillingtonia</u>). By 310MY tree species were again expanding and gaining more ecological space.

Around 305MY the Pennsylvanian epoch had a moderate extinction event with most tree lycopsids, and trees reproducing by spores were lost. Earth was cycling through a much more arid, droughty and warm period (300MY through 286MY) across the supercontinent Pangaea, even though atmospheric CO_2 concentrations were low, similar to today. These days gave rise to changes among seed ferns which would lead to cycads. 300MY presented fossils of <u>Utrechia</u>, a conifer (15 feet tall) similar to the present day Norfolk Island pine (an araucaria). By 295MY cycads were expanding.

Innovators

Innovations over the next 70 million years within tree forms continued. Attributes developed included: secondary xylem and phloem in woody stems (360 MY), tremendous diversity of seed types (350 MY), and appearance of a tree dormancy process (295 MY). A older type of tree-form rapidly dominated some areas, a type of calamite or giant horsetails (300 MY). These calamites reach 50 feet tall and 15 inches in diameter. The primitive lycophytes dominate many areas with their tall stems (30-120 feet tall) and their secondary growth, expanding stem diameters up to three feet. Dominant lycophytes had straight green stems with sparse, forked-type (dichotomous) branching concentrated at the top (290 MY).

At this time, tree-form spore ferns arose but lacked secondary growth. These tree spore ferns grew to between 25 and 75 feet tall holding 15 feet long leaf fronds on one foot diameter stems. With increasing climatic dryness, seed fern gymnosperms began their dominance of forests as the lycophytes and calamites move to extinction. Extensive forests of the world were being progressively more dominated by seed fern gymnosperms and gymnosperms. Hidden within all these changes were a slow expansion of conifers (300 MY). The supercontinent Pangaea formed and would change world climate for the next 100 million years. Figure 21. The coalescing of continental sized parts into Pangaea occurred by 300 my. It started to rift itself apart by 185my.

Endings

As the Permian began in 290MY, the climate was colder and drier, and many tree changes were in the works. An extinction event occurred which impacted many pteridophytes (early vascular trees) and some gymnosperms. The calamites (tree horsetails) were in full decline in swamps, and the lycopsid (tree clubmoss) forests were shrinking in size. It is at this time most organic matter accumulation, which will become coal, comes to an end. By 290MY mant tree heights had reached 120 feet tall in forests. On the Southern continents, glossopterid trees (seed tree ferns) are common and reach 30 feet tall. Along with all these changes, one change will lead to modern trees – there is a split in a common ancestor between gymnosperms and what will become angiosperms.

	innovation	plant group
1	chlorophyll	algae
2	cuticle	bryophytes
3	stomates	bryophytes
4	rhizomes	mosses & pteridophytes
5	water moving cells (tracheids)	pteridophytes
6	lateral branches	pteridophytes
7	non-dicotomous branching	pteridophytes
8	small leaf points	pteridophytes
9	roots	pteridophytes
10	periderm	pteridophytes
11	vascular tissue	pteridophytes
12	webbed leaves	pteridophytes
13	seeds	gymnosperms
14	flowers	angiosperms

Figure 12: Life innovations made by plants leading to trees. All except the last one (#14) developed in the Silurian and Devonian (443my to 353my) time periods. (Niklas 1997)

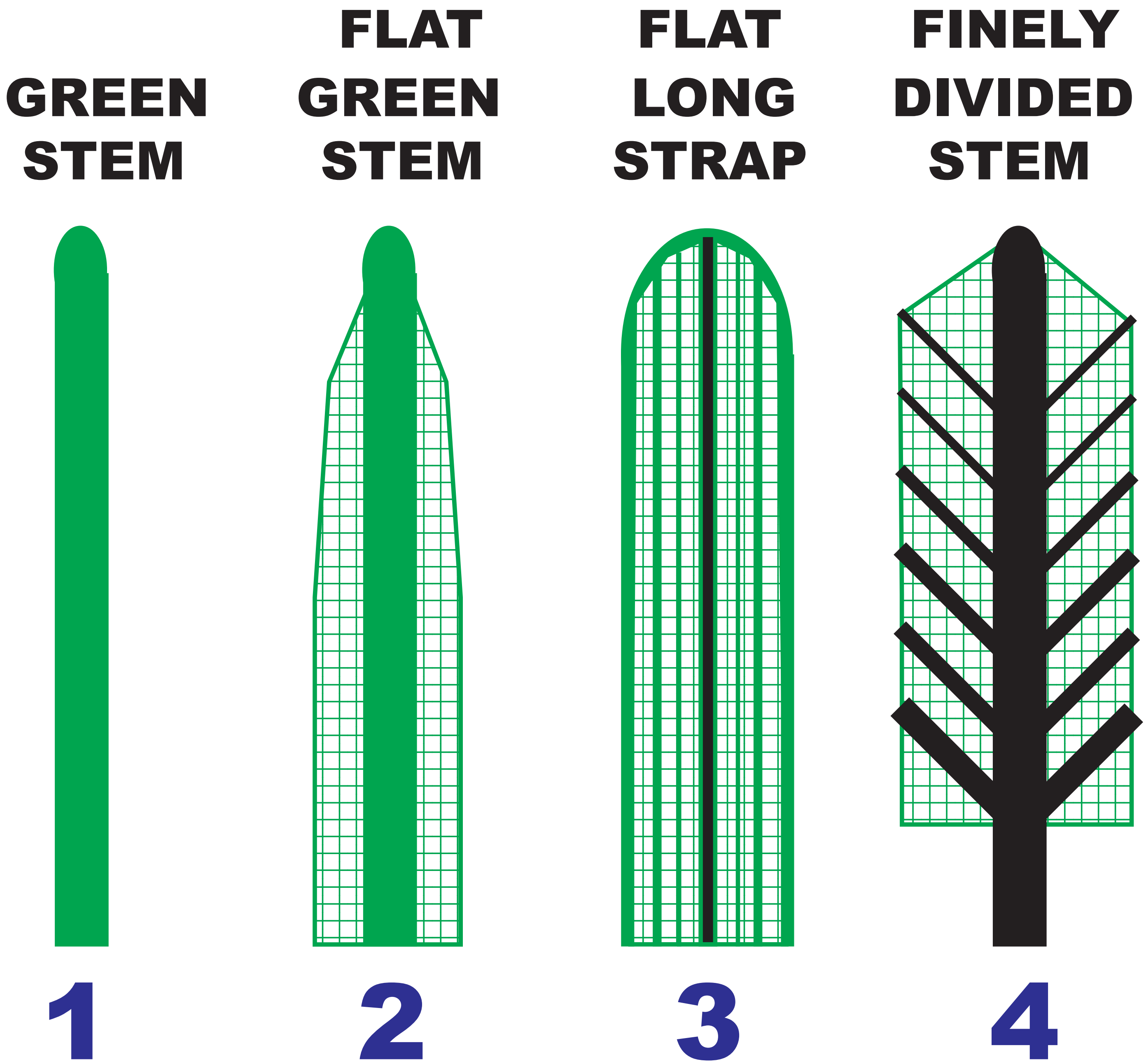


Figure 13: Progression of first tree leaf forms. Spores would have been formed on edges and along stems.

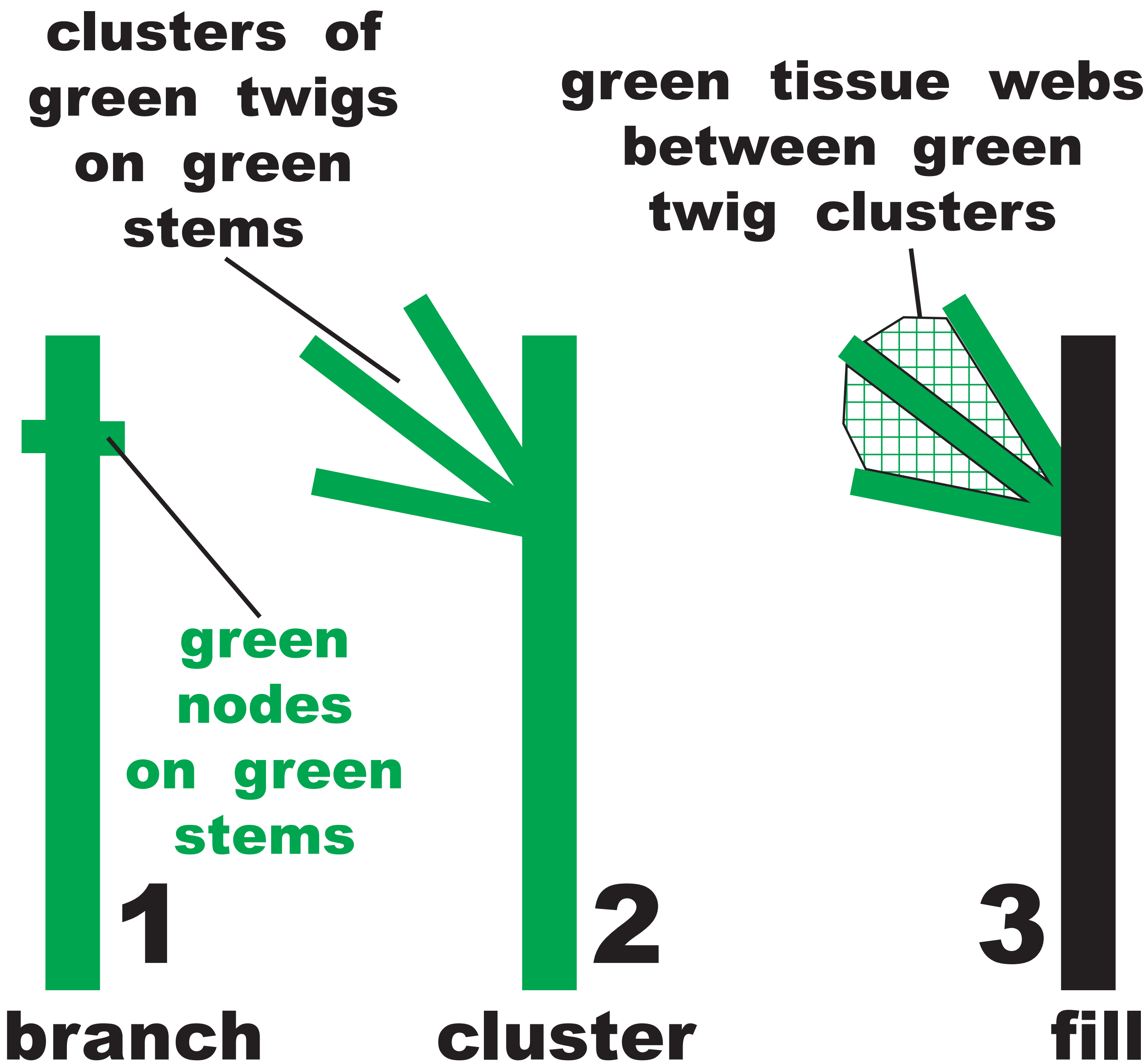


Figure 14: Three stage progression toward tree leaf development.

Tree-Form Plant Developments

Photosynthetic & accessary pigment arrays
Growth upward from horizontal mats into vertical spikes for sunlight
Increased surface area for photosynthesis
Expansion of horizontal stems (rhizomes)
Specialization of roots

Surface protection with water conserving epidermis & cuticle
Stomates on green stems for more efficient water use control
Rigid tracheids for withstanding stomate generated water tensions
Specialization of water conducting vessels and food transport elements
Greater height possible from rigid vascular materials

Lignin formation (component of wood)
Secondary growth & diameter growth to structurally support stem
Circumferential vascular cambium generating xylem & phloem
Phellogen generating thicker, suberized periderm
Specialized chemicals used in defense and protection

Reproduction no longer dependent upon water immersion
Multiple reproductive units on each individual
Seeds as unit of reproduction
Unisexal wind pollinated flowers & showy flowers
Shortened reproductive cycles

Codominant branching & forking
Branch & stem confluence union formed
Short and long shoot development specialization
Increased surface areas of subordinated shoots
Flattening and webbing of shoot clusters leading to leaf blades

Cold and drought tolerance
Dormancy
Deciduous habit especially in cool, dry areas
Flowers specialization

Figure 15: Estimated progression of tree-form developments leading to tree success.

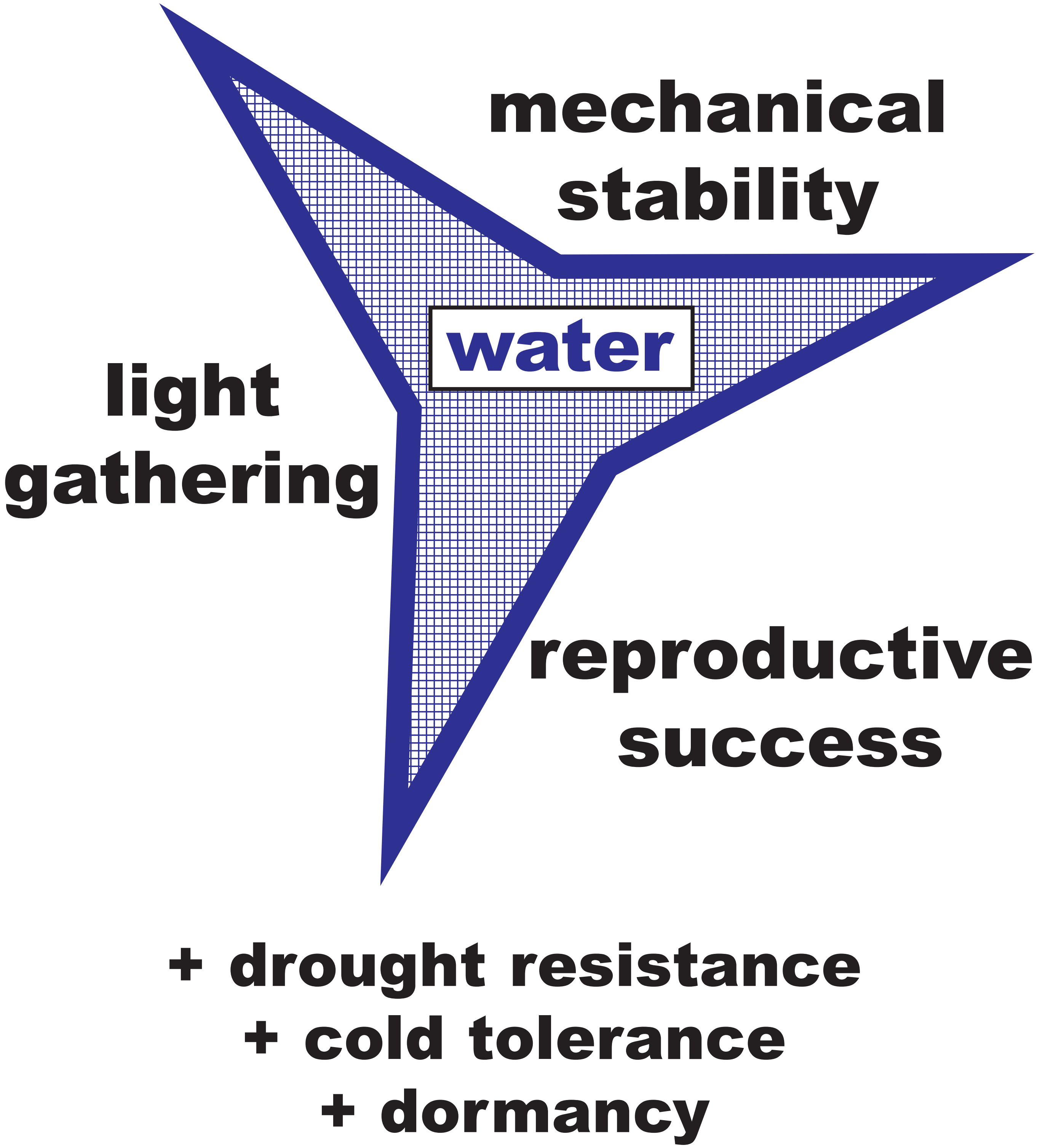


Figure 16: Primary and secondary optimizations needed for tree form success. (Niklas 1997)

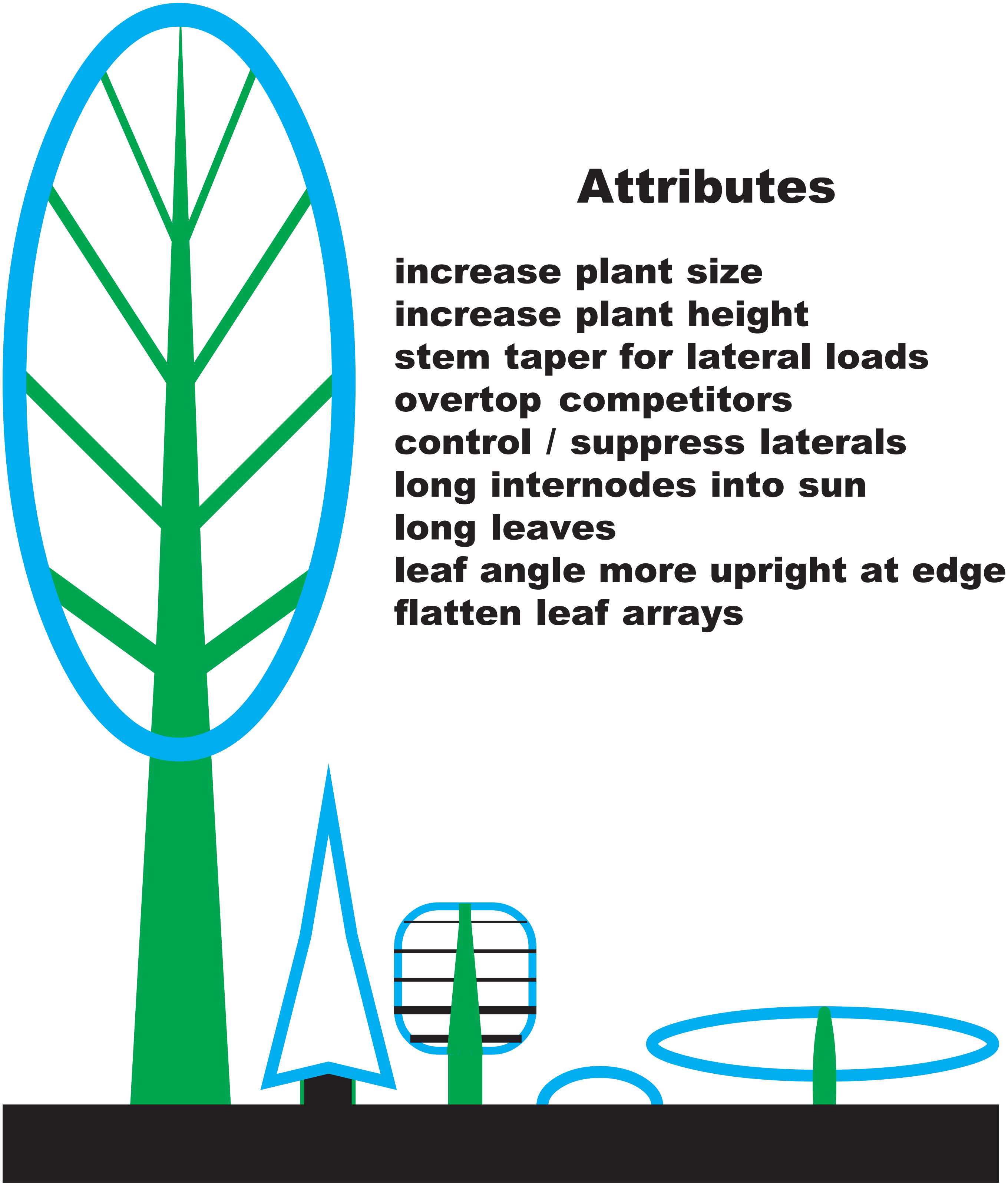
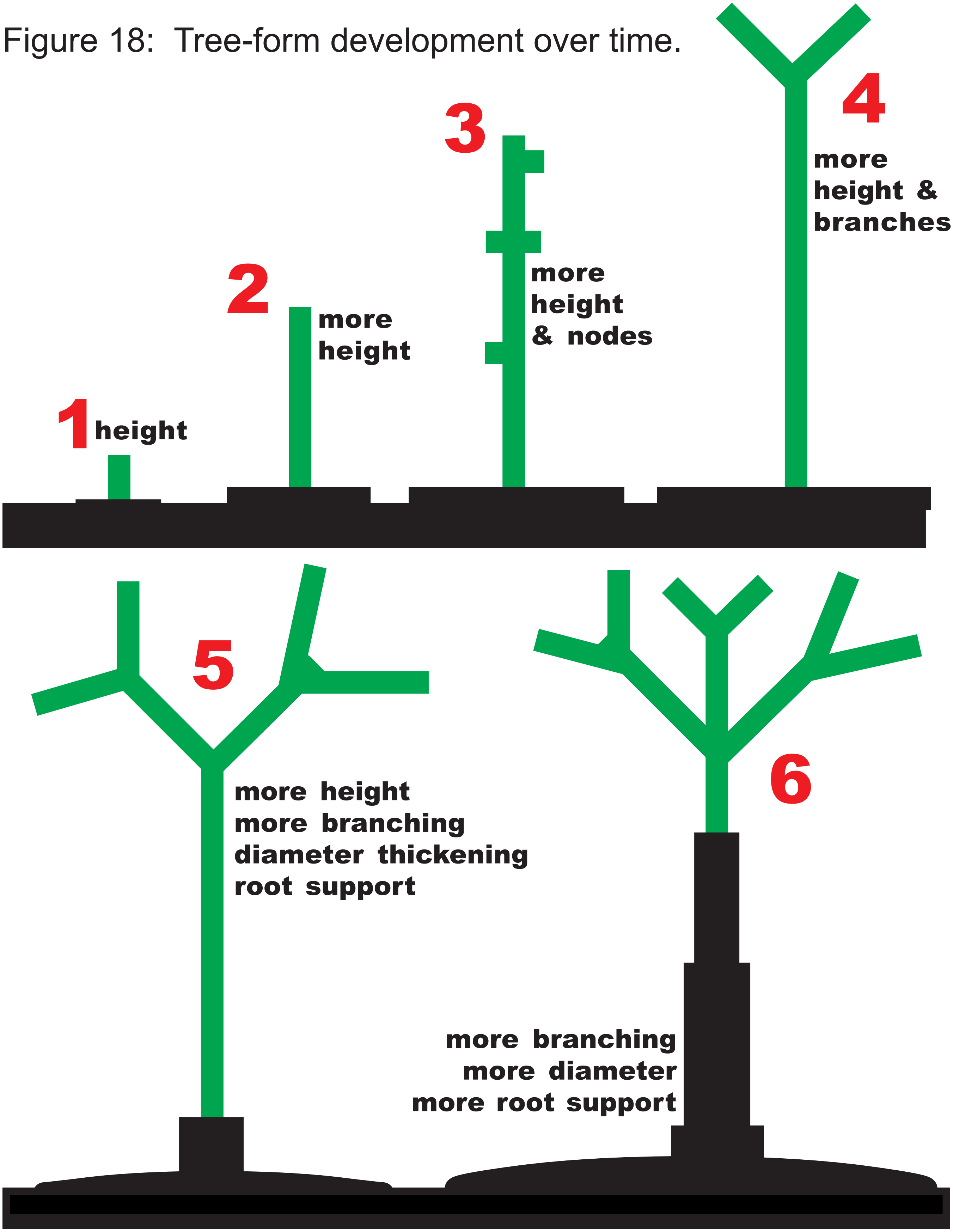


Figure 17: Plant developments to optimize light capture.

Figure 18: Tree-form development over time.



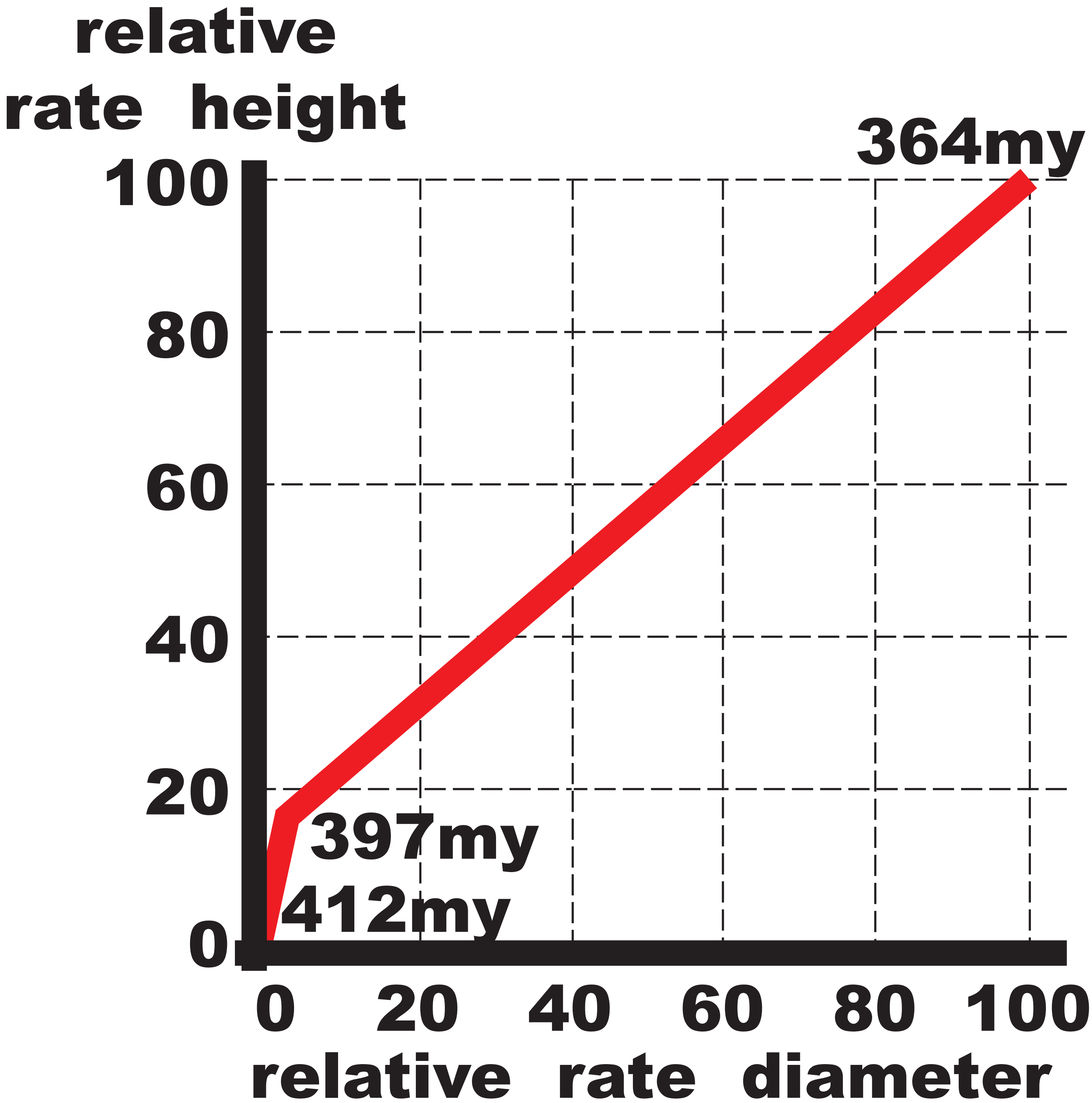


Figure 19: Relative growth of height and diameter over 50 million years. Tree heights and diameters would eventualy expand from a flat film with no diameter to 200 feet tall and 5 feet in diameter (dbh).
(derived from Niklas 1997)

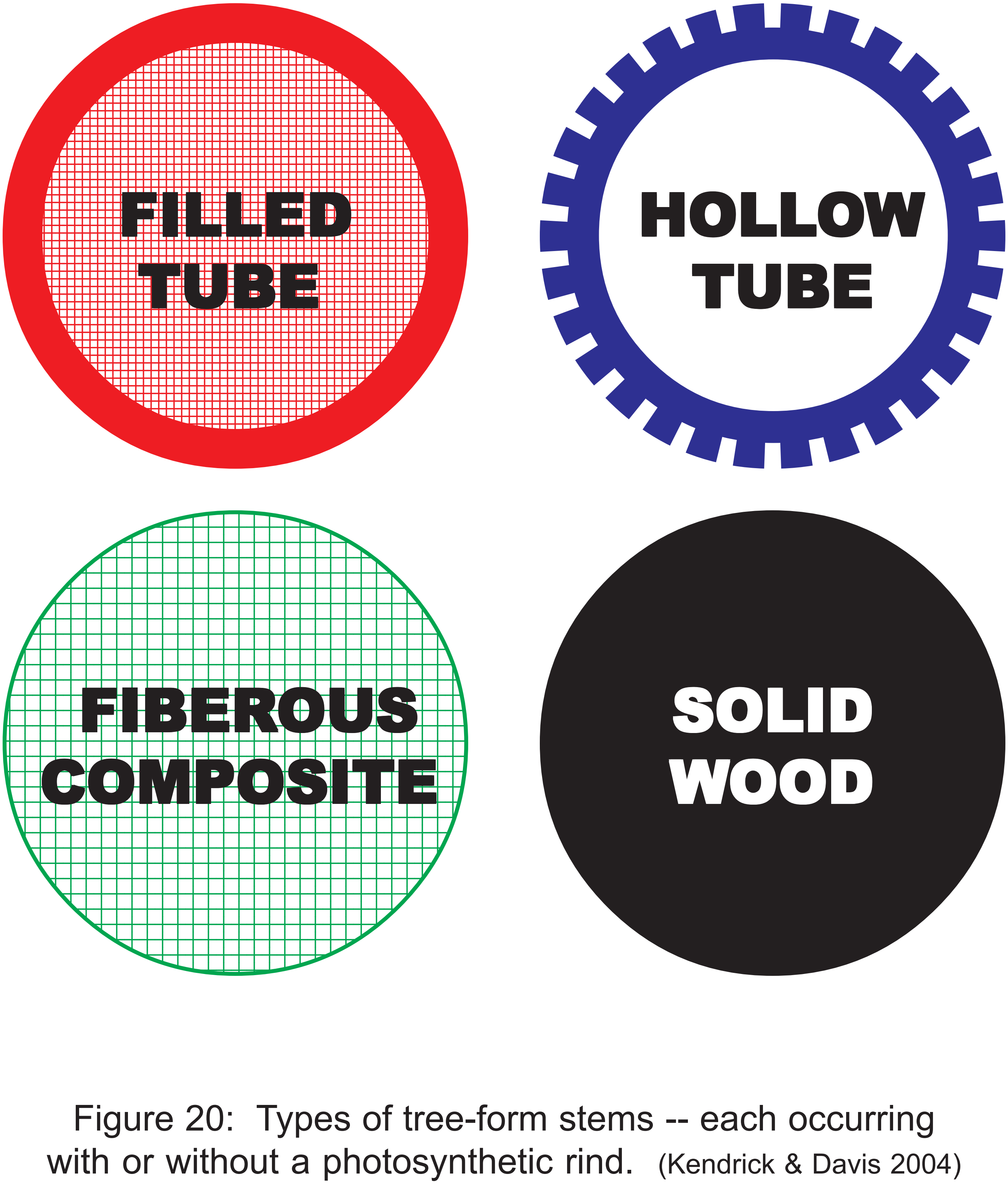


Figure 20: Types of tree-form stems -- each occurring with or without a photosynthetic rind. (Kendrick & Davis 2004)

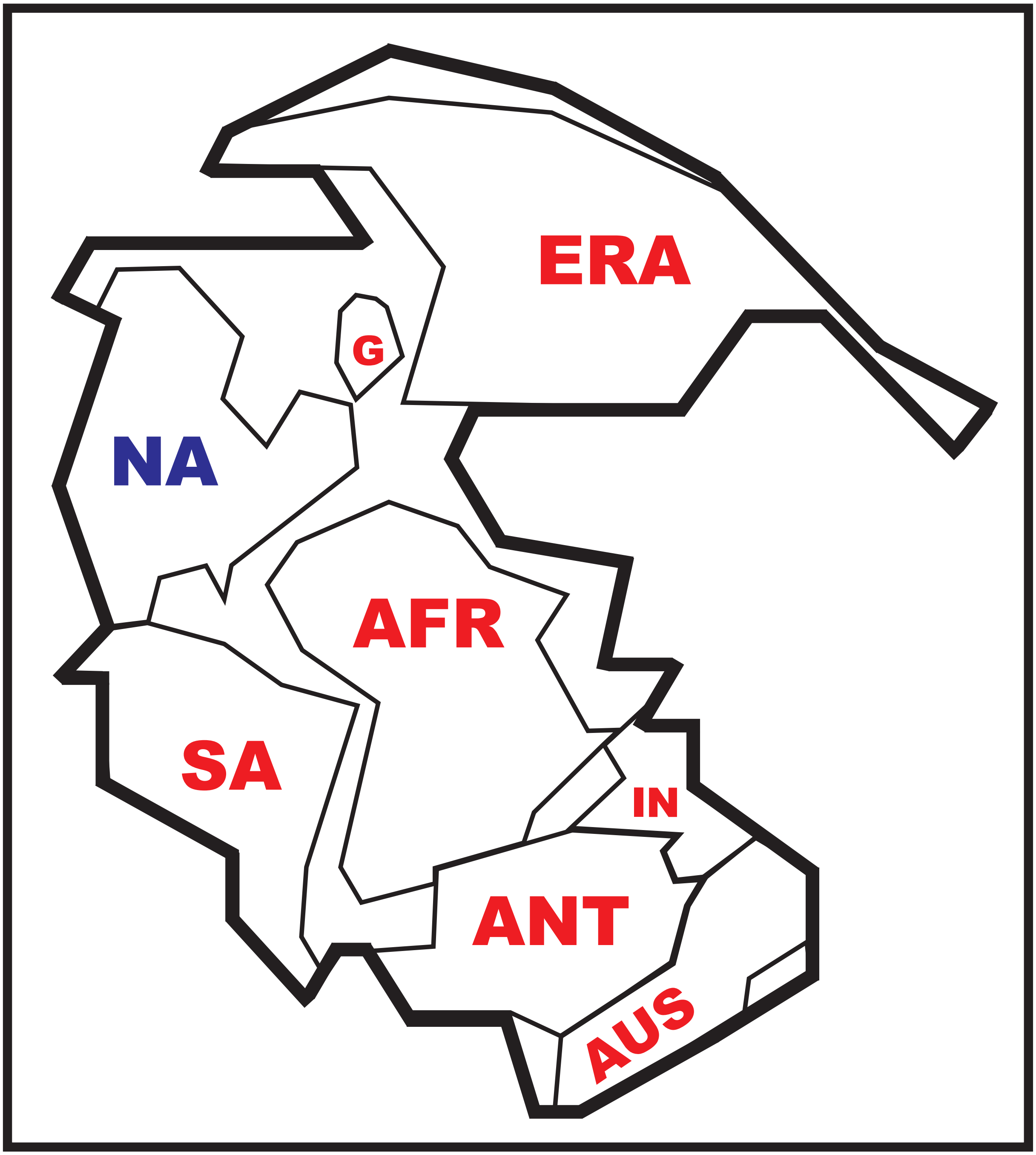


Figure 21: Idealized form of supercontinent Pangaea (300my-175my) with general locations of current continents.
AFR = Africa; ANT = Antarctica; AUS = Australia; ERA = Eurasia;
G = Greenland; IN = India; NA = North America; SA = South America.
(redrawn from Kenrick & Davis 2004).

Primitives Tree Forms

The first wave of tree-forms were a mix of species types most of which generated spores for reproduction. Figure 22. A number of unrelated groups of plants developed tree forms at one time or another. Many of these primitive tree-forms were well designed for wet, warm, swampy areas under stable climatic conditions. Extinction events for primitives usually involved significant climatic changes. Most of these primitive tree forms can be called by a generic name pteridophyte.

Other than being in the first wave of tree development together, these tree forms did not share much in common. Pteridophytes were vascular, spore producing ferns, horsetails, and clubmoss (sometime called ferns and fern allies). Pteridophytes (a multiple family grouping) should not be confused with pteridosperms (a single generic group of early gymnosperm seed ferns). Pteridosperms were early seed plants with fern-like foliage derived from progymnosperms.

Tree Clubmosses

The lycopods or clubmosses unfortunately share a name with a non-vascular, small, lower plant (i.e. moss). Tree lycopods reached at least 90 feet tall and 3 feet in diameter by 370my. The maximum size was a record 150 feet tall and 6 feet in diameter. Tree lycopods reproduced by spores and unlike ferns, do not have true leaves. They are descended from one of the most ancient plant groups the Zosterophylls (400my-355my). Fossil lycopods groups included Drepanophycales, Lepidodendrales, and Pleuromeiales. There are about 1,200 current species today divided into two class: Lycopodiopsida the clubmosses and firmosses; and, Isoetopsida the quillworts, scale trees, and spikemosses. All have outlived their giant tree forms by more than 100 million of years.

One of the most common fossil tree lycopods found is Lepidodendron (390my - 250my), partially because of its long life time on Earth. Lepidodendron was a spore producer with dichotomous (equal forking) branching and rooting patterns. The crown had many small branches holding three foot long strap-like leaves which were deciduous with age. The exterior surface was covered with diamond shaped indentations from old leaf scars. Roots grew shallowly and were highly branched and subdivided into tiny rootlets. The trunk had a massive, thick, hard, stiff exterior cylinder of supportive cortex fibers with xylem tissue inside (produced by a one-sided cambium). This tree form stem was supported by its hard, stiff periderm rind.

Lepidodendron generated on its trunk lateral leaf-like appendages which dichotomously branched and grew downward to form roots. The trunk stayed straight and unbranched for 10 to 15 years then branched profusely, reproduced and died. This tree form had extremely rapid growth and grew at a high density of stems per acre. Tree lycopods were invaders and colonizers of disturbed sites. It had formed extensive dense tropical forests by 345my. Its ecological peak was around 275my.

Progymnosperm

Progymnosperms were the woody, spore producing, full vascular cambium ancestors of all seed plants (gymnosperms and angiosperms). Progymnosperms came from the trimerophytes. They developed by 380my and lasted until about 350my, with an ecological peak around 365my. Progymnosperms were composed of three primary groups: Aneurophytales (375my-355my), Protopityales, and Archacopteridales (360my-335my). Progymnosperms led to pteridosperms or seed producing tree ferns (Lyginopteridales). Progymnosperms were an intermediate between ferns and gymnosperms reaching 26 feet in height and 4 feet in diameter. An example of a progymnosperm was Archaeopteris, a large tree-form with fern-like, spore bearing leaves on a conifer-like stem considered an ancestor of modern trees.

Tree Fern

Spore producing tree ferns of the cladoxylates lived a short time between 360my and 340my, with an ecological peak around 350my. Psaronius was a 30 feet tall spore-producing tree fern with a tough lightweight trunk. It held its 5-9 feet long leaf fronds at the trunk top. Leaf fronds unrolled like fern fiddle-heads (crosiers). The trunk has a central vascular tissue area and was covered with overlapping root mantles making the trunk larger in diameter toward the ground. Modern spore producing tree ferns are in the Cyatheales (175my to present), and includes tree ferns of the Polypodiopsida (tree fern families are Dicksoniaceae & Cyatheaceae). These tree ferns have trunk-like stems growing to 60 feet in height with multiple strands of vascular tissue, no periderm, and rare dichotomist branching.

Tree Horsetails

Calamites were 40-60 feet tall tree horsetails growing from a large horizontal, ground-hugging rhizome. The rhizome would continue to grow and branch, sending up shoots, making old rhizomes immense (possibly the largest single organisms on Earth.) Trunks were thick with long segments covered with longitudinal fluting or ribbing. The trunk had many air-filled longitudinal canals with small pockets of secondary xylem produced from a one-sided cambium, surrounding a central air-filled pith canal. This tree form stem was supported by secondary xylem columns throughout the tissue. All branching and leaves in calamites were at segment nodes. Leaves and branching occurred in whirls only at stem segment ends. Leaves were needle-like up to 25 per whorl and were clustered at the top of the trunk. Calamites reached a species importance peak around 275my just before their extinction. Calamites are considered "protoconifers."

Tree Seed Ferns – Pteridosperms

The name pteridosperm is generic term for extinct seed plants with fern-like leaf fronds which are not angiosperms, conifers, cordaites, ginkgo, cycads, or cycadoides. The name is also used for pteridosperm tree ferns (360my to 265my), which reproduced by seed dispersed by wind. They had huge fern-like leaf fronds up to 21 feet long. Seeds were borne on leaf surfaces. The trunk was made of earlier discarded leaf bases on top of , and overlapping, each other. Woody tissues were rich in resin. This seed tree fern reached its ecological peak around 275my.

Other early seed tree fern groups included Lyginopteridales, Medullosales, Callistophytales, and Peltaspermales. Later developing groups of seed tree fern included Corystospermales, Calamopityales, and Leptostrobales. Glossopterids (Arberiales) and gigantopterids were seed fern trees, but generated smooth entire leaves, not fern-like. Some later developed tree seed ferns survived in small refuges until 75my.

Ferns

Ferns of one form or another have been on Earth since about 360my, although most of today's ferns have appeared in the last 145my, with an explosion of new fern species around 75my. Ferns are spore producing vascular plants with true leaves. Fern species currently number around 12,000 . Ferns are pteridophyta, filicopsides, or monilophytes. Ferns include modern horsetails (sphenopsids), whisk ferns, marattioid ferns, ophioglossoid ferns, and leptosporangiate ferns (the largest fern group). Fossil fern groups include Cladoxylopsida, Rhacophytales, Stauropteridales, and Zygopteridales, and contained some tree forms.

Primitive Timeline

Figure 23 shows the duration and peak times of primitive plants. Some primitives existed for only a short time -- all were functionally gone by 220my. Figure 24 provides a breakdown of primitive vascular plants remaining into today.

primative group	time range	peak time
rhyniopsids	**420-365my**	**(398my)**
zosterophyllopsids	**400-355my**	**(375my)**
trimerophytes	**390-355my**	**(373my)**
(Psilophyton)		
protolepidodendids	**390-350my**	**(365my)**
lepidodendron	**390-250my**	**(275my)**
(tree lycopods)		
progymnosperms	**380-350my**	**(365my)**
(Archaeopteris)		
cladoxylates	**360-340my**	**(350my)**
(tree ferns)		
archaeoclamites	**355-325my**	**(330my)**
(tree horsetails)		
calamites	**350-270my**	**(275my)**
(tree horsetails / protoconifers)		
pteridosperms	**350-265my**	**(275my)**
(tree seed ferns – Medullosa)		

Figure 22: Primitive plant and tree forms which generated innovations to maximize light capture, mechanical stability, and reproduction over millions of years leading to modern trees.

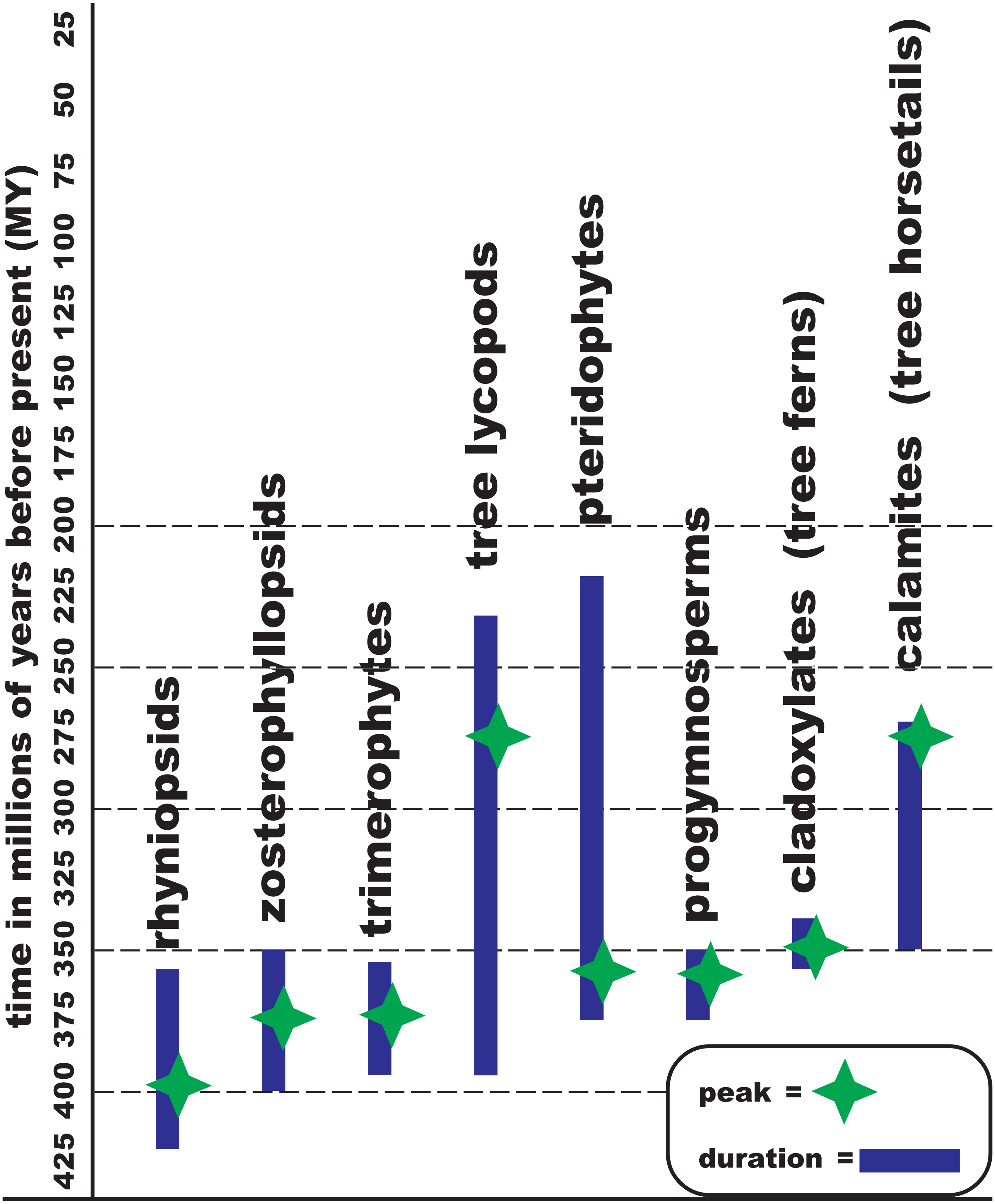


Figure 23: Duration and peak times of primatives.
(Stewart & Rothwell 2009; Niklas et.al. 1985)

Mesophytic Age of Plants
Age of Conifers / Age of Seed Plants

At 280MY, the Mesophytic age of plants began, known as the Age of Conifers or the Age of Seed Plants. At this point in time, seed plants began a massive diversification. For the next 70 million years conifers diversified and expanded, dominating forests. Cycads and cycadeoids reached 50 feet in height with giant, thick-stocked woody stems and a large seed bearing "strobilus." Ginkgoes by 280MY had at least 16 genera and multiple species. By 275MY lycopsids (tree clubmosses) were well pass their ecological peak and continued to decline. Forests of 275MY were rapidly changing species mixes with tree ferns (36 feet tall and 1.5 feet in diameter), primitive conifers, and tree horsetails occupying many sites.

Climatic and landmass changes led to many tree and forest changes. Ginkgoes continued to develope and diversify (270 MY), as are cycads and transition conifers -- Voltzales (260 MY). By 270MY, the Medullosales (seed ferns) and Cordaitales (protoconifers) become extinct. The sphenopsids (tree horsetails) were minimized in ecological importance. Seed fern gymnosperms of the early days are now declining rapidly (250 MY). New conifer groups are beginning to gain dominant positions in many areas.

Super Kill

Trees enter a period of great expansion and diversification in 260MY. But, at the end of Permian and beginning of the Triassic time periods (252my), and responsible for the change in time period names, was a cataclysmic event, probably tied to new volcanism and climatic shifts. This Permian / Triassic extinction event was the most severe ever on Earth. This extinction event was 70% more catastrophic than the K-T extinction of 65.5my which ended the dinosaurs.

The greatest of extinctions impacted marine and terrestrial life, including insects, vertebrates, and plants. About 83% of all genera became extinct. This extinction lead directly to a fast decline of cordaite and glossopterid species. Lycophytes recolonized and held disturbed areas after the extinction event. This major tree extinction event witnessed the demise of many spore tree ferns, seed tree ferns, lycopsids, and protoconifers. The tree winners at this time are the primitive conifers, cycads, and ginkgo.

Triassic

The Palaeozoic Permian period ends in 248MY and the Mesozoic Triassic period begins. Glossopterid trees (tree seed ferns) of Southern lands become extinct. Conifers continue to expand and diversify, generating podocarps by 248MY and araucarias by 245MY. Within a few million years, (241MY to 240MY) a major extinction event occurs which ends many pteridophytes and some gymnosperms, as well as a significant associated loss of animal species.

The Triassic (240 MY) sees the end of the first wave of tree-forms -- tree spore producers, and the beginning of a second wave of tree seed producers – gymnosperms. The Triassic is known for its wide spread gymnosperm forests with extensive fern understories. A number of modern gymnosperm tree groups arise and gain dominance. Taxodiaceae (baldcypress, redwood, and sequoia) develops, as does cypress. Ginkgoes dominate many places in the Northern hemisphere. In 225MY yews are present in the fossil record, as well as many araucaria. Pine-like woody seed cones develop around 215 MY. Hidden in all these forest changes are a small group of pre-angiosperms (225 MY). In 206MY the Jurassic period begins. The genus Pinus (pine) arises, followed in 200MY by Cephalotaxus.

Pangaea

Pieces of the supercontinent Pangaea begin to break up by 185my changing ocean circulation and isolating land areas from each other. This is just before the time when the third wave of tree development (angiosperms) was beginning. Pangaea was falling apart into two large subunits: Gondwana (Southern hemisphere lands); and, Laurasia (Northern hemisphere lands). By 155my Gondwana began to break apart. By 140my Africa - South America broke away from Gondwana, then split from each other by 120my. A separated landmass portion of India and Madagascar separated by 95my, with India rapidly moving North to impact Asia by 35my and pushing up the Himalayan mountain range.

Among other Gondwana land portions, New Zealand and New Caledonia broke away from Australia by 90my. By 55my Australia broke away from Antarctica. South America was the final landmass to break away from Antarctica by 30my, which caused Antarctica to be isolated and ecologically lost behind a strong, climate modifying Southern ocean current. It developed a substantial polar ice cap and a multitude of glaciers. Laurasia broke up with North America and Greenland rifting away from Eurasia by 60my. The globe of tree development has never looked as it does today, and will continue to change.

Clumping & Splitting

Part of tree development was powered by climatic change factors and location on each supercontinent where trees grew. As Pangaea began to breakup, tree homelands were divided with species and families being isolated. Some species are now known as Southern hemisphere trees or Northern hemisphere trees because . of which portioin of splitting Pangaea they successfully survived and thrived upon in the past.

For example, araucaria and podocarps are known as primarily Southern hemisphere trees, while pines are known to be almost exclusively Northern hemisphere trees. This survival location is directly related to the first separation of Pangaea into a Northern and Southern half, and to associated climate changes involved. Continental drift initiated large climatic changes and stimulated great gymnosperm speciation from 240-140my.

Gymno Doom

By 180MY, the ginkgo of our time, Ginkgo biloba is present. From 180MY to 100MY pines, and pinophytes in general, diversify and expand. Note conifers still generated new species well into the angiosperm explosion (i.e. 140MY - 100MY).

By 176MY primitive angiosperms, possibly derived from one of the gymnosperms with a flower-like strobili or cone, emerged. Generation of the first angiosperm is from a single genetic line of gymnosperms. Candidates from gymnosperms leading to flowering plants include three primary (#1 - #3) and one secondary group (#4) who had flower-like reproduction structures:

1. glossopterids -- tree seed ferns (290my-180my -- 225my peak);
2. claytonids -- tree seed ferns (230my-135my -- 170my peak); and
3. cycadeoids -- related to both cycads and ginkgoes (210my-80my -- 130my peak).
4. gnetophytes (220my today -- 100my peak).

The first primitive angiosperm group was represented by Amborella, a streamside tropical shrub (175my). The second group of primitive angiosperms was water lilies (170my). The gymnosperms had spawned a new and better version of tree which would diversify and exapnd, ecologically displacing gymnosperms and driving them farther along a path into decline and extinction.

Giants

The Jurassic was the culmination of all things gymnosperm. Forests of Earth at this time were almost completely dominated by gymnosperms. The conifer Cunninghamia was in the fossil record by 160MY.In the gymnosperm group were early pinophytes we would recognize just getting their start (fir, spruce, Douglas-fir, and hemlock -- 158my). Later the rest of the pinophytes developed (larch, cedar, cypress, and juniper -- 154my). Cycads continued to occupy understory and mid-story positions in forests dominated by Taxodiaceae (redwood family). Figure 25 shows the gymnosperm groups of today roughly in their order of development. Seed fern gymnosperms (pteridosperms) were pushed to extinction but left pro-angiosperms in their place. Araucarias start to dominate sites in the Southern hemisphere.

The lineage of gymnosperms leading to modern conifers is provided in Figure 26. Early tree forms of this line became extinct relatively early. The result was a strong contingent of pinophytes growing over many million of years into the present day. Figure 27.

Figure 28 shows when a number of species were generated. Figure 29 presents members in the pinophyte group with generation time, duration, and peak period. Some gymnosperms like ginkgo barely survived to modern times. Gymnosperms remain on an accelerating road to extinction as more efficient angiosperms take over more ecological niches.

Last of the Middle Times

Another extinction event for both plants and animals occurred between 155MY and 152MY. For trees, some of the last remaining pteridophytes (early trees) and some gymnosperms are driven to extinction. Animals are much more impacted by this event than plants. Tree loss bottoms-out by 148MY and a new wave of tree forms develop. By 145MY angiosperms (flowering plants) are present. The fossil record suggests there is a single ancestor for all angiosperm trees to come. This first ancestor was a medium sized tropical shrub. It was possibly descended from an extinct gymnosperm with insect pollinated cones. In 142MY the Jurassic ends and the Cretaceous period begins with mild temperatures and local spots of semiarid to arid conditions.

vascular plants (410my)

- **lycopodiaphytes (clubmoss) (405my)**
  - **lycopsids**
    - **Lycopodiales**
    - **Drepanophycales** ***extinct***
  - **isoetopsids**
    - **Selaginellales**
      - **Lepidodendrales** ***extinct***
        - **Pleuromeiales** ***extinct***
        - **Isoetales**
- **euphyllophytes (leaf plants) (385my)**
  - **seed plants (320MY)** →
  - **monilophytes -- ferns (370my)**
    - **eusporangiate ferns (360my)**
    - **leptosporangiate ferns (370my)**
      - **Cyatheales (tree ferns)**

Figure 24: Relationships among current primative trees.

Gymnosperms (tree-forms)

Pinophytes (Conifers)

6 families remain

araucaria, plum yews, cypress, juniper, baldcypress, redwood, celery pines, pine, fir, spruce, cedar, larch, hemlocks, podocarps, yews
(300MY - 50MY / declining since 100MY)

Sciadopty
Pine
Araucaria
Podocarp
Cypress
Yew

Ginkgoes

(270MY)

Cycads

thick-stocked, upright woody stems with large reproductive "strobilus" (230MY)

Cycadeoids

(210MY-70MY) ***extinct***

Gnetales

shrubby trees, large thick leathery leaves

Figure 25: List of gymnosperm tree-form groups in roughly their order of development.

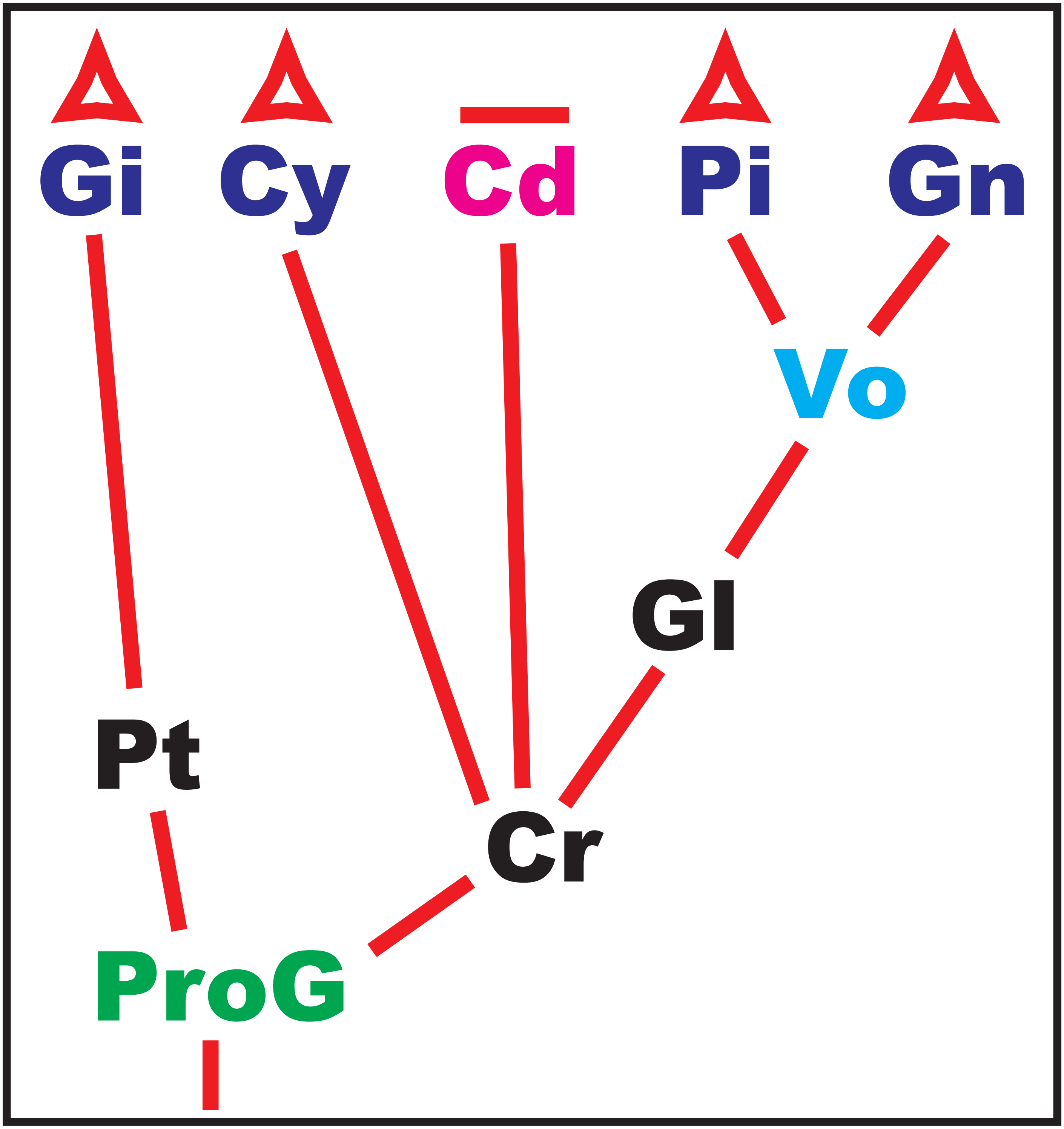


Figure 26: One proposed general pathway of gymnosperm tree development.

Cd = cycadoid; Cr = cordaite; Cy = cycad; Gi = ginkgo; Gl = glossopterids; Gn = gnetales; Pi = pinophyte; ProG = progymnosperms; Pt = pteridosperms; Vo = voltzales; .

1. 425my-365my rhyniophytes

-- 400my-355my zosterophyllophytes

2. 380my-350my trimerophytes

3. 375my-355my progymnosperms (aneurophytes)

3. 360my-335my progymnosperms (archacopterids)

-- 365my-280my giant tree clubmosses (Lepidodendron)

-- 360my-340my tree ferns (Cladoxylates)

-- 360my-325my tree horsetails (Calamites)

4. 360my-265my seed fern (pteridosperms) (Medullosa)

4. 290my-245my glossopterid (seed tree ferns)

4. 290my-200my gigantopterids (seed tree ferns)

5. 325my-270my cordaites (primitive conifer)

6. 295my-185my voltziates

7. 230my-135my claytonids (seed tree ferns)

Figure 27: General order of tree development from primarily primitive species groups (first wave) into the secong wave of seed plants (gymnosperms). (-- failed line to modern trees)

320my-	**Sciadopity (C)**
270my-	**ginkgo (from seed fern)**
250my-	**cycads (from seed fern)**
248my-	**podocarps (C)**
245my-	**araucarias (C)**
240my-	**redwood family (C)**
225my-	**yews (C)**
206my-	**pines (C)**
200my-	**Cephalotaxus (C)**
190my-	**gnetophytes**
180my-	**Ginkgo biloba**
160my-	**Cunninghamia**
158my-	**fir (C)**
158my-	**spruce (C)**
157my-	**Douglas-fir (C)**
157my-	**hemlock (C)**
154my-	**larch, cedar (C)**
154my-	**cypress, juniper (C)**
140my-	**Metasequoia (C)**

Figure 28: General order of tree development among current gymnosperm species groups (second wave).
((C) = conifers or pinophytes)

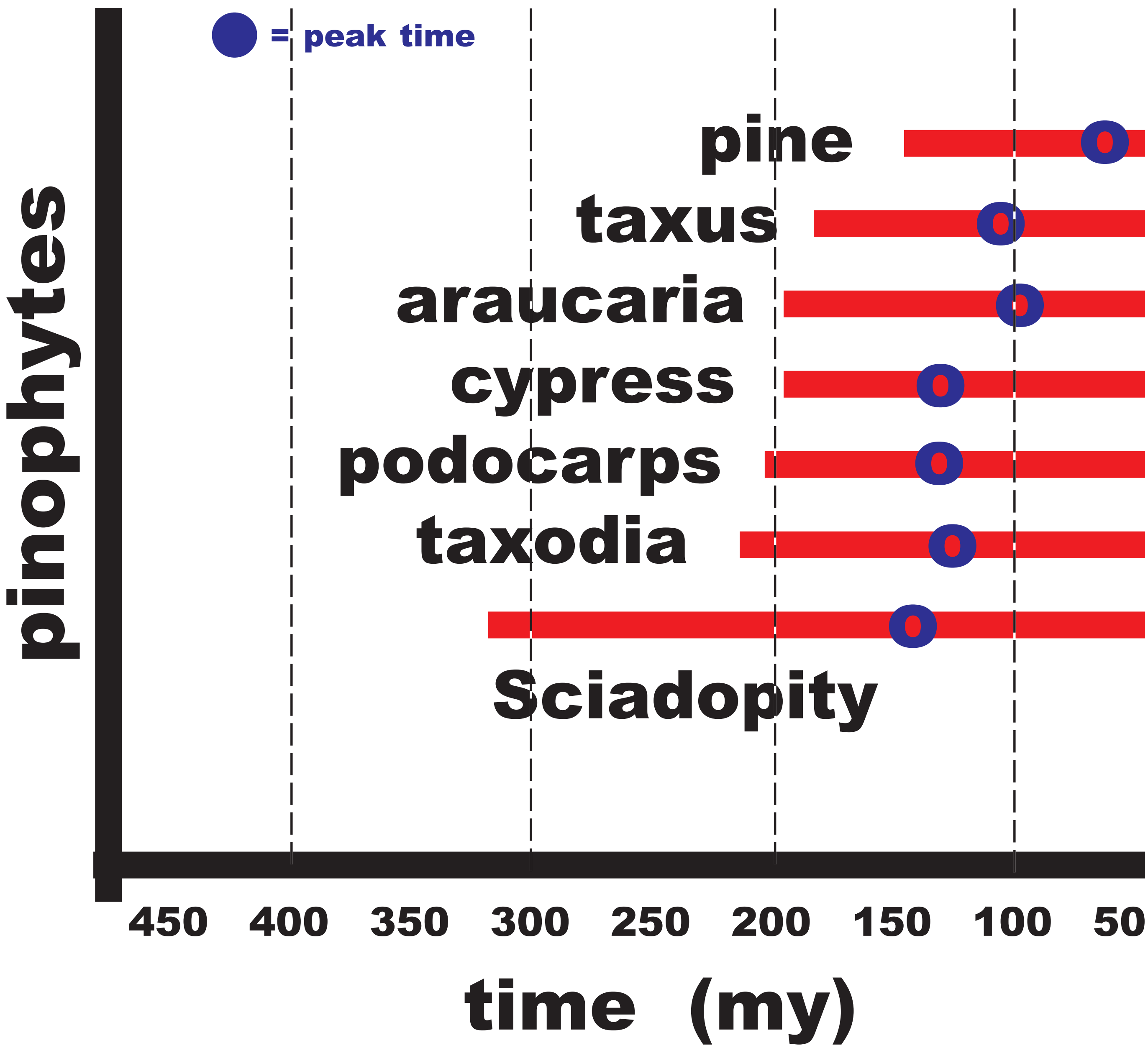


Figure 29: Timeline of pinophyte tree group development with duration time in millions of years (MY) and ecological peak point.
(derived from Miller 1984; Willis & McElwain 2002)

Gymnosperm Tree Forms

The second wave of tree development was seed producing trees (320my) of which most were gymnosperms. Figure 30. Gymnosperms bear their seeds open to the environment. Modern tree groups within the gymnosperms include cycads, ginkgo, gnetophytes, and conifers (pinophytes), and contain a total of almost 1,000 species. Figure 31 lists the relationships among modern gymnosperms.

Cycads

Cycads are a large group of gymnosperms with around 305 species. This group includes cycads and an extinct group cycadeoids. Cycads reached a maximum of 50 feet tall. Cycads have a thick, short , squat barrel-shaped, unbranched woody trunk with a crown of large, hard, stiff, evergreen palm-like or fern-like leaves. Cycads are dioecious. This group began around 230my and was both important and widespread during the Jurassic.

Most current species of cycads today developed since 12my. Cycads are related to ginkgoes. Modern cycad families include: cycad family with 105 species (Cycas genus); zamia family with 216 species (Ceratozamia, Chigua, Dioon, Encephalartos, Lepidozamia, Microcycas, Macrozamia, and Zamia, genera); and, stangeria family with three species (Bowenia and Stangeria genera).

Ginkgo

Ginkgo is one of the lost trees from the past rediscovered by science in the last century. Myths abound about its finding and about its historic uses. It produces a valuable and tasty toasted seed called a white nut. Ginkgo is represented among modern gymnosperms by a single species, Ginkgo biloba. It arose about 270my from pteridosperms (seed ferns) in the Peltaspermales. Ginkgoes are most closely related to cycads. We are fortunate to have saved one of the many ancient species of ginkgo.

Gnetophytes

One of the most enigmatic groups in gymnosperms are the gnetophytes. Gnetophytes are the third largest species group in gymnosperms after pinophytes and cycads, with about 78 species in three genera. This group is visually diverse and unique belying true interrelationships. Of the three genera, Ephedra, Gnetum, and Welwitschia -- the first genera is by far oldest.

Pinophytes

The largest group of gymnosperms is the pinophytes (conifers) with 6 families, 68 genera, and 550 species. This group was derived from extinct groups cordaites (seed plant with cone-like structures), Vojnovskyales, and Voltziales. Pinophytes began around 300my and received great benefits from the Permian / Triassic (252my) mass extinction event. Pinophytes are represented by six modern families of trees: pine, araucaria, podocarps, cypress, yew, and a single species family (Sciadopitys) with a very unique species, Sciadopitys verticillata.

Members of the pine family are familiar to most and include genera Abies, Cathaya, Cedrus, Larix, Nothotsuga, Keteleeria, Picea, Pinus (pine genus for which the family and order are known), Pseudolarix, Pseudotsuga, and Tsuga.

The araucaria order contains two families of trees, araucaria and podocarps. Family araucaria include genera Agathis, Araucaria, and Wollemia (the lost pine). The podocarp family, include genera Acmopyle, Afrocarpus, Dacrycarpus, Dacrydium, Falcatifolium, Halocarpus, Lagarostrobos, Lepidothamnus, Manoao, Microcachrys, Nageia, Parasitaxus, Pherosphaera, Phyllocladus, Podocarpus, Prumnopitys, Retrophyllum, Saxegothaea, and Sundacarpus.

The cypress order of pinophytes include three families: cypress, yews, and Sciadopitys. The Sciadopitys family contains one species called a koyamaki or Japanese umbrella pine, Sciadopitys verticillata (which means "shadow pine"). This family began around 320my making it the oldest of the pinophytes. This unique tree is rare in collections and arboretums. It is evergreen, 50-80 feet tall, and grows 3-5 inch long cladode (flattened green stems, not leaves or needles). Cones are 2.3 - 4.3 inches long. This family's long history is represented in the modern world by its fossilized resin, Baltic amber.

The cypress family is relatively large in number and composed of the genera Athrotaxis, Austrocedrus, Callitris, Calocedrus, Chamaecyparis, Cryptomeria, Cunninghamia, Cupressus (cypress genera for which the family is known), Diselma, Fitzroya, Fokienia, Glyptostrobus, Juniperus, Libocedrus, Metasequoia (a last remnant species once covering large portions of the colder portions of Northern hemisphere lands), Microbiota, Neocallitropsis, Papuacedrus, Pilgerodendron, Platycladus, Sequoia, Sequoiadendron, Taiwania, Taxodium, Tetraclinis, Thuja, Thujopsis, and Widdringtonia. The cypress family holds some of the last giant tree forms – redwoods, giant sequoia, and baldcypress. Notice a number of cypress genera have root names incorporating the term "cedrus," which is the name of true cedars from the pine family.

The yew family is composed of six genera and 30 species. Yew genera include Amentotaxus, Austrotaxus, Cephalotaxus, Pseudotaxus, Taxus (the yew genus for which the family is know), and Torreya. The yews began around 165my, peaking around 110my.

Ancient Gymnos

Modern gymnosperms are derived from progymnosperms (380my). The progymnosperms were woody spore producing plants with a full vascular cambium. Progymnosperms came from the trimerophytes. Progymnosperms are composed of three primary groups: Aneurophytales (375my-355my), Protopityales, and Archacopteridales (360my-335my). Progymnosperms led to pteridosperms or seed producing tree ferns (Lyginopteridales), and to a large tree form called Archaeopteris which is considered an ancestor of modern trees.

With the passage of time, early gymnosperm trees developed and then became extinct, but leaving a remnant heritage of gymnosperms into today. The fossil record is littered with fossil gymnosperms. Figure 32 lists the duration and peaks of gymnosperm groups. Early fossil gymnosperms included the cycadeoids, caytonids, and glossopterids groups. Early fossil conifers included cordaites, Vojnovskyales, and Voltziales (with two families Utrechtiaceae & Voltziaceae).

Cordaites & Voltziales

One of the first fossil gymnosperms were the cordaites. Cordaites were primitive conifers growing to 90 feet in height. Cordaites were tall woody trees with stilt-like roots similar to modern mangroves. Their woody cones, pollen, and seeds were all similar to modern conifers. Leaves were three foot long straps of photosynthetic surface. Cordaites grew in swampy or wet areas.

Another predecessor to modern gymnosperms, particularly conifers, were the Voltziales. These trees were considered the first true conifers and were similar to modern araucarias. They were large trees holding woody cones on tips of branches. Voltziales had needle-like leaves. It is thought modern conifers are directly derived from the Voltziales family Utrechtiaceae.

gymnosperm	time range	peak time
pteridosperms	350-200my	(275my)
cordaites	335-240my	(250my)
glossopterids	290-190my	(225my)
voltziales	290-185my	(200my)
claytonids	230-135my	(170my)
cycads	230my-today	(150my)
ginkgoes	230my-today	(130my)
pinophytes (conifers)	210my-today	(140my)
cycadeoids	200-75my	(150my)
gnetophytes	190my-today	(100my)

Figure 30: Current and fossil gymnosperm group names, time of beginning and end, and peak time (in millions of years before present (my)).

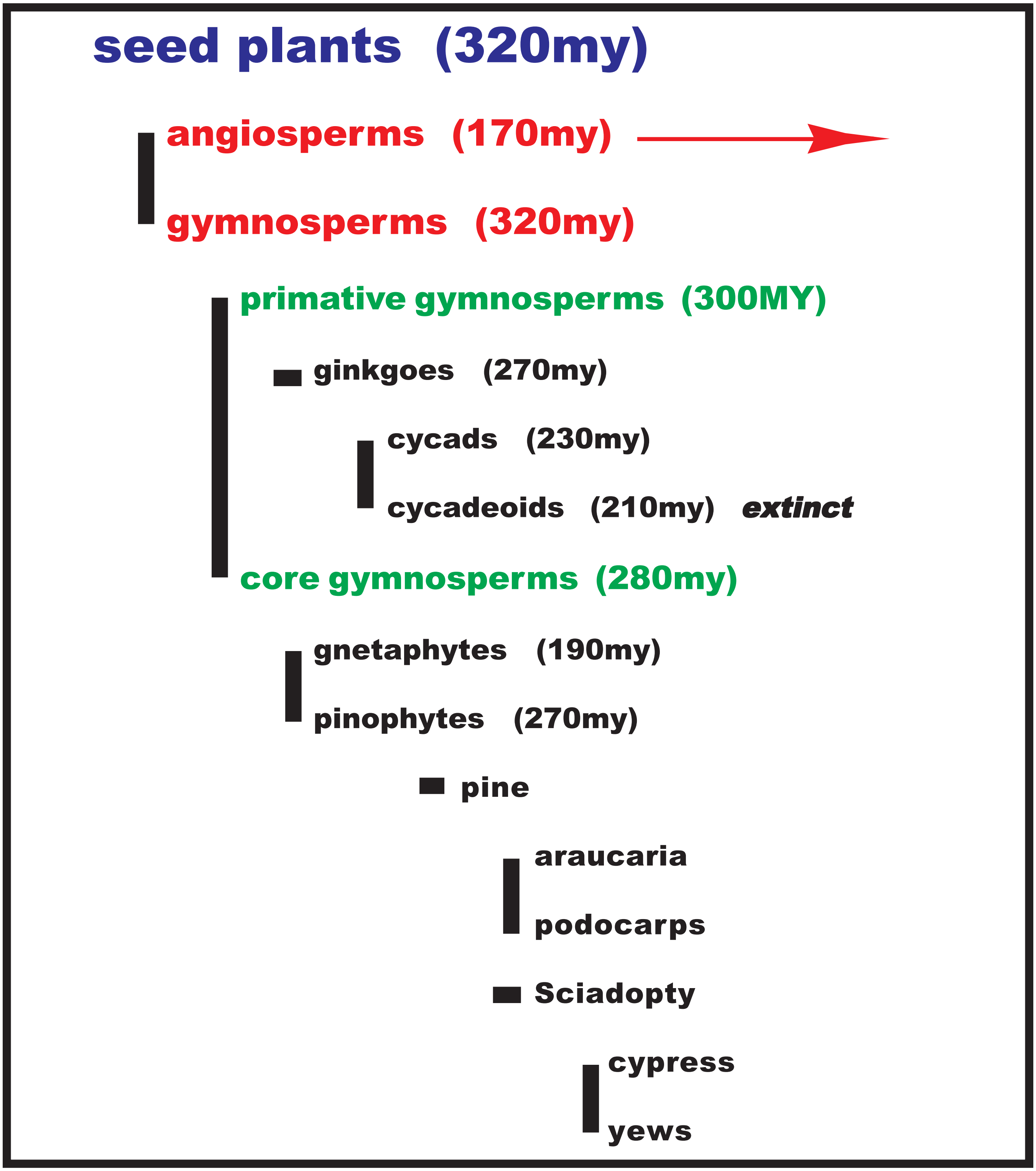


Figure 31: Relationships among current gymnosperm trees.

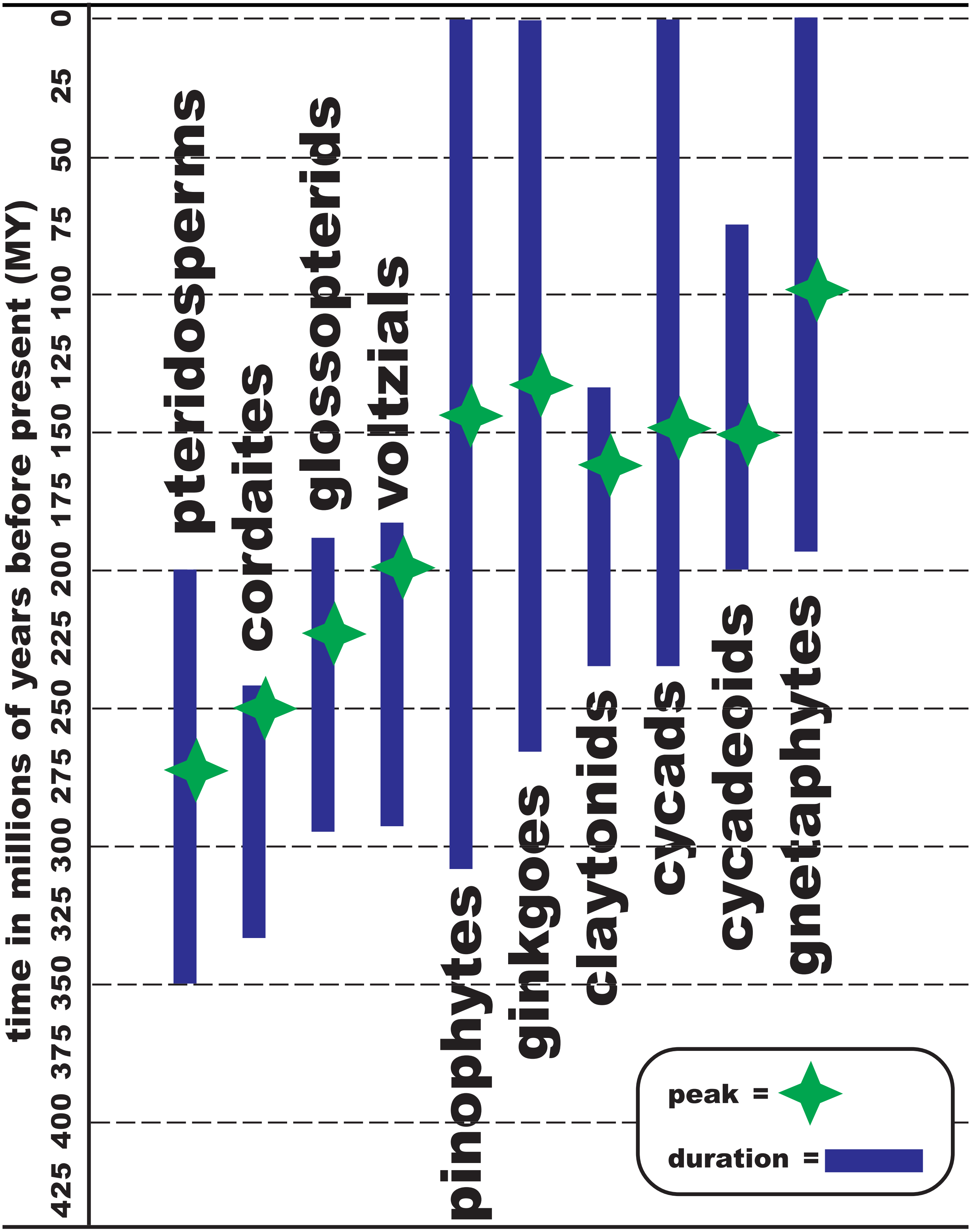


Figure 32: Duration and peak times of select gymnosperms.
(Stewart & Rothwell 2009; Niklas et.al. 1985)

Cenophytic Age of Plants
Age of Angiosperms / Age of Flowering Plants

The Cenophytic age of plants begins in 140MY, referred to as the Age of Angiosperms or Age of Flowering Plants. Angiosperms, which started in equatorial tropics, expanded and diversified, moving toward each pole over the next 30 million years. 140MY also saw the conifer Metasequoia and more podocarps develop. Primitive angiosperm trees were soon followed by magnoliids, monocots, and eudicots rapidly diversifying by 140MY. Figure 33 lists the outline of angiosperm types. Proportional primary segments of angiosperms are given in Figure 34.

Third Wave

By 134MY core eudicot angiosperms were present and diversifying. In 132MY another extinction event occurred which removed some angiosperm and gymnosperm diversity. The first fossil flower found dates to about 130 MY. Angiosperm trees seem to have arisen along stream in warm and dry areas of conjoined North Africa and Northern South America. Angiosperms began as successional pioneer on wetland sites. Within 30my , they had moved to both early and late successional ecological positions.

The second wave of tree-form development (gymnosperms) came to an end around 120MY, when the third wave -- angiosperms -- began to expand. Figure 35 presents the three waves of tree form development.

New & Improved

Angiosperm tree traits leading to success include a protected seed, a special food storage material in seeds for the new embryo, densely netted leaf venation, open water conducting vessels not tracheids, food transport assist cells (companion cells), and a diverse and potent set of secondary compounds which minimize herbivory and interference, while allowing animal (primarily insect) coevolution for pollination and seed dispersal. Early angiosperms trees have seeds which are water and wind dispersed. Latter angiosperms trees have seeds which are large and fruity, encouraging animal dispersion.

Did It Have To Be Sweetgum?

Angiosperms witchhazel, sycamore, and sweetgum were first seen in 127MY. Starting in 125MY and ranging into 83MY there were periods of significant volcanic activity, atmospheric CO2 concentration increases up to five times present day concentrations, and global warming. It is around 121MY angiosperm fruit, leaves, and wood can be commonly found in the fossil record. Modern magnolia tree forms (genera) were present by 120MY.

The next 19 million years generated many recognizable species groups. These species groups (with their development time) include: boxwood (112MY); Sequoia, redwood (>12 species 107my); pine (105my); oaks, Nothofagaceae (100MY); and, willows, maples, Ericaceae, holly, hackberry (95MY).

Angio Rising

By 100MY ginkgoes were significantly declining, and overall conifers were being pushed out by angiosperms. Gymnosperm dominance faded (100 MY) except in the far North where Metasequoia dominated forests until 20MY. Angiosperms (flowering trees) diversify species and dominate most forests by 100 MY in the Northern hemisphere and 80 MY in the Southern hemisphere.

Another major angiosperm diversification push began in 95MY. In 90MY, the rosiid angiosperm group took-off. Angiosperm species groups arising (around this time) include: buckeyes (89MY); chestnut, alder (87MY); waxmyrtle (85MY); walnut (83MY); birch, elm (80MY); and, sandalwood, screwpines (pandans), olives, dogwoods, Bombaceae, Symplocaceae, Rhamnaceae, Clethraceae, and aralia (71MY). Figure 36.

Monocots like grasses (80 MY) and palms (75 MY) arise. By 70MY angiosperms were represented by a great diversity of large trees and finished pushing out gymnosperms trees in many forest types. 69MY saw the first legumes.

K-T Boundary

In roughly 65.5MY, marking the end of the Mesozoic era Cretaceous period, and the beginning of the Cenozoic era, Tertiary sub-era, Paleogene period Paleocene epoch (called the K-T boundary instead of the C-T boundary), disaster struck. This was a mass extinction (~50% of all species) initiated by few long term climatic changes reaching critical levels, and several short-term sudden events. Volcanic events and a meteor strike serve to darken, chill, and disrupt climate for many years. Short-term events help intensify long term climatic changes already occurring.

The toll among trees was great but less than for animals. This extinction event terminated the dinosaurs, and saw the rapidly rising angiosperm diversity devastated (which has yet to recover) with many of the more primitive magnoliids (the magnolia / laurel group) reduced. Hardest hit of the plants were tree forms in general, and insect pollinated broad-leaved evergreens trees in particular. Araucarias were sent into decline, becoming extinct in the Northern hemisphere.

Survivors

Trees surviving best had deciduous leaves. Lowland swamps and river valleys dominated for so long by gymnosperms were quickly taken over by angiosperms. Ginkgoes and cycads rapidly declined and barely held-on until today. Forests of North America after the K-T boundary can be generally divided into four types: tropical coastal forest of the Southeast; semitropical coastal and inland forest of the West; broad-leaved evergreen forest of the Northwest; and, broad-leaved, inland deciduous forest of the central and North.

After 64my, angiosperm trees quickly dominate again, but with a much greater number of deciduous species, especially in areas with cold and dry conditions. Angiosperm trees, which had dominated early and mid-successional positions in landscapes before now developed into late-successional, stable communities. Many birds and mammals were enticed (coevolved) to disperse fruit and seeds. Over the next 40 million years, eudicot trees diversified and dominated forests, expanding ecological space all over Earth. The period between 60MY and 50MY was particularly good for angiosperm diversity as the climate was relatively warm and moist. Grass diversity swelled after 60MY (herb trees like bamboo), as do the modern oaks (first in what is Southeast Asia and then moving North).

Heat It Up

Conifers are not completely out of the ecological equation. The pine family (Pinaceae) continued to diversify and hold many forest systems, while other pinophytes decline in more temperate and cold areas of the Northern hemisphere. In 55.5MY there was a minor extinction event impacting trees but not animals. Afterwards, angiosperm diversity came back even stronger than before.

In 55MY the Eocene begins. The next 10 million years will be the warmest in the ecological history of Earth and had roughly two times present-day atmospheric CO_2 levels. Oaks have spread and are common in many areas. Specialized myrtles and eucalypts arise, as do a number of species specialized for arid conditions (Asteraceae & Agavaceae). Grass species, due to many and continual fires, coupled with dry continental climates, thrive.

Big Mountains

The face of Earth is changed over 50MY-35MY with uplifting of the Himalayas and Rocky Mountains. Continued warm, droughty and arid conditions plague many areas, but angiosperms continue to diversify. By 45MY, and continuing until roughly 5MY, mountain building activities cause temperatures to drop and drought periods to increase. Large areas of continents are more arid than in previous periods. 45MY sees Metasequoia widespread around the globe in cooler regions, and sees birches reach their greatest diversity. In 38my, angiosperm tree speciation accelerates further.

Many desert types of angiosperms develop due to more dry climatic conditions. Acacia is present by 38MY, as are many types of desert trees and shrubs. In 35MY the Pyrenees, Caucasus, and Carpathian mountains are uplifted and the South pole ice sheets grow. At this time, grasslands and savannas are expanding, and oaks continue to diversify.

Ecological Loss of Antarctica

In 34MY the Oligocene begins with major climatic limitations (cold and dry) on warm forest systems. Podocarps are pushed out of the Northern hemisphere completely. The rise of grass species into forest areas leads to expansive savannah systems, and closed canopy forests decline. By 30MY Antarctica is separated as a continent, and a cold ocean current begins to flow through the Southern ocean, isolating the continent. In 29MY a major extinction event for both trees and animals occurs. Many gymnosperms and some angiosperms are lost. After this extinction event in 28MY, and stretching to roughly 10MY, grass greatly expands and diversifies species.

Miocene

In 24MY the Paleogene Oligocene ends and the Neogene Miocene begins. As continents continue to drift, the Mediterranean Sea is created as Africa and Asia meet with Arabia in-between (21.5MY). Angiosperms continued to diversify and spread. The period between 20MY and 15MY sees a number of grass dominated ecological systems during a global warming period. Alders greatly diversify and expand (18MY). By 16MY more gymnosperms were becoming extinct.

The period between 15MY and 12.5MY has Earth undergoing a significant cooling period. At 15my, a great new acceleration of angiosperm speciation occurs. Within this period (14MY) many oaks develop. By 10MY specialized Northern cold boreal trees develop including species of willow, birch, and alder. The Miocene ends in 5.4MY and the Pliocene begins. In 5MY, the Mediterranean Sea is dry and global ocean levels are low. At the North pole ice sheets are large (3MY). Tundra ecological system develop (2.5MY). Extensive grasslands cover large areas of Earth (2MY) and forests retreat.

A Little Ice

As the Tertiary Pliocene period ends and the Quaternary Pleistocene begins (1.8MY) temperatures are falling, atmospheric CO2 is falling, and large ice sheets are expanding. Earth, between 1.8MY and today undergoes 10 glacial / interglacial cycles with most (~80%) of the time spend in a glacial cooling period.

Pleistocene glaciation in the Northern hemisphere causes loss of many tropical and sub-tropical angiosperms. The last remnants of giant redwoods and sequoias (Taxodiaceae) are driven to small refuges and almost to extinction. Glacial refuges in Eastern North America were either on the Coastal Plains of Georgia, Florida, and the Carolinas, or in the lower Mississippi valley. After many glacial advances and retreats, the last glacial cleansing of North America occurred around 18,000 years ago (0.018MY). The Pleistocene brought six major glacial periods to Europe and caused the loss of 2/3s of all tree species.

Climate Changes

Over the time of tree development, great swings in climate have occurred caused primarily by: large scale continental drift, and associated modification of dominant atmospheric and ocean currents; volcanism changing atmospheric gas and particulate contents with associated atmospheric transmission and reradiation of energy; and, individual catastrophic events like meteor impacts. Climatic changes of hot to cold and wet to dry completely alter rates of speciation and extinction among tree forms.

Global temperature have cycled between warm and cool periods around a global temperature average. Figure 37 shows the intensity and duration of warm and cool periods. Note by far the coldest and warmest periods in Earth history occurred from 400 million years ago to 250 million years ago.

Glaciers

Glacial events lead to great changes in tree speciation and extinction. Figure 38 provides the intensity and duration of glaciation periods since 500 million years ago. Note glaciation in the last 40 million years has been the second greatest of the last one-half billion years. It should also be noted the quickness of glacial period onset can occur much faster than trees can shift growing ranges. For example in Eastern North America, glaciers shifted climate quickly enough to drive a number of tree species into the sea, and then receded quickly enough allowing tree species Northern range limits to not have been reached after 12,000 years. Many trees are still genetically headed to Canada.

Carbon-Dioxide

Much is modelled and discussed regarding carbon dioxide (CO2) contents in the atmosphere providing a thermal blanket over Earth. Figure 39 shows how CO2 concentration have changed compared with today's level. Note the great range of CO2 over the last 500 million years including high levels as land plants became established, and a low point (not counting current conditions) around the glacial events of 300 million years ago. As a general rule with terrestrial plants, low (falling) CO2 levels tend to help diversify angiosperms, hurts gymnosperms, and is neutral on speciation of primitives.

New Species

New tree development has occurred in a number of spurts and steps, then remained steady for millions of years. Species diversity developes in short interludes between long stable periods. These speciation interludes usually occur when CO2 increases and continental shifts global climatic changes. Figure 40 demonstrates one way of showing species formation periods for primitive, gymnosperms and angiosperm species. Figure 41 presents another way of examining species diversity developement in primitive, gymnosperm and angiosperm species. There is a marked difference in time periods and intensity due to fossil record vulgarities and researchers. Both figures are valuable in showing general trends of species formation.

Dead Species

Extinction is the usual fate of any species. Tree forms are no exception, and some would argue the tall and large are more easily singled out for destruction. Figure 42 lists the nine primary terrestrial plant extinction events. Only four represent major catastrophic species losses. The rest represent significant reshuffling of genetic components and general species loss. Figure 43 presents ten terrestrial plant extinction periods with the plant forms lost. Note only four of the plant extinction events were associated with corresponding animal extinction events.

If species formation events are placed with species extinction events, Figure 44 is the result. The speciation and extinction events show major changes to terrestrial plant species numbers. Note the earlier periods of both species formation and loss were much greater in intensity and duration than latter periods.

Forest Changes

Earth offers a multitude of climatic zones for trees. Over time tree forms have taken advantage of these climates. Figure 45 shows how tree forms have moved toward cooler climates -- closer to the poles -- with time and species development. The tropics remain the last refuge of primitive tree forms from the early days of land plants. Gymnosperms comprise a majority of tree species living in the cold.

Figure 46 provides a simple summary for the progression to modern angiosperm trees. Much debate and fossil analysis remains to enable researcher to keep families and lineages together.

Angiosperms

1. Primitive Angiosperms

2. Magnoliids

3. Eudicots

A. Primitive Eudicots

B. Core Eudicots

1) Madagascar thorny trees, cactus, sandalwood

2) Rose Group

  a) Primitive Rosids

  b) Core Rosids

3) Aster Group

  a) Primitive Asterids

  b) Core Asterids

4. Monocots

Figure 33: Major angiosperm groups. Last three primary group devloped around the same time (150my).

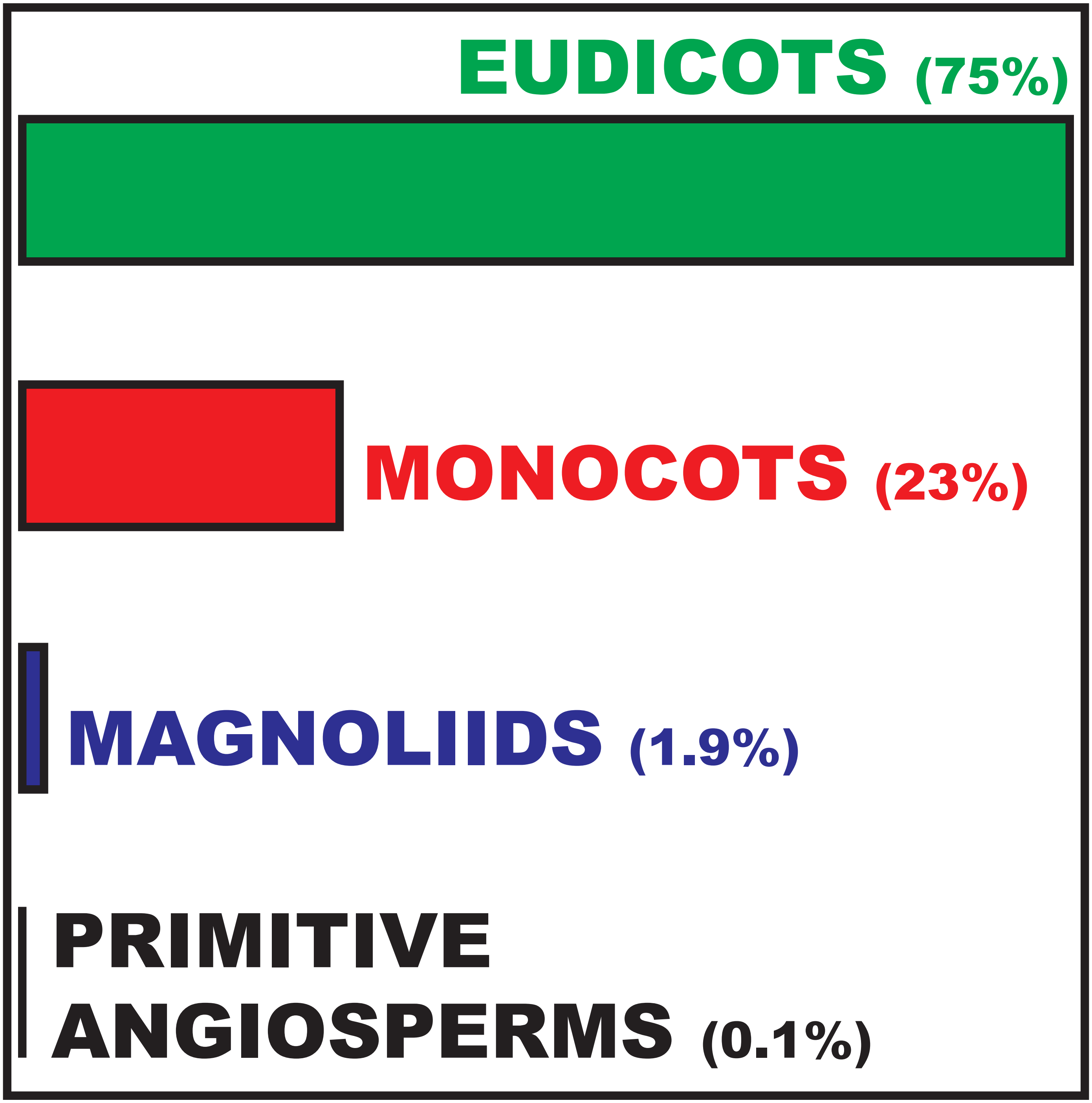


Figure 34: Relative proportions among primary divisions in angiosperms.

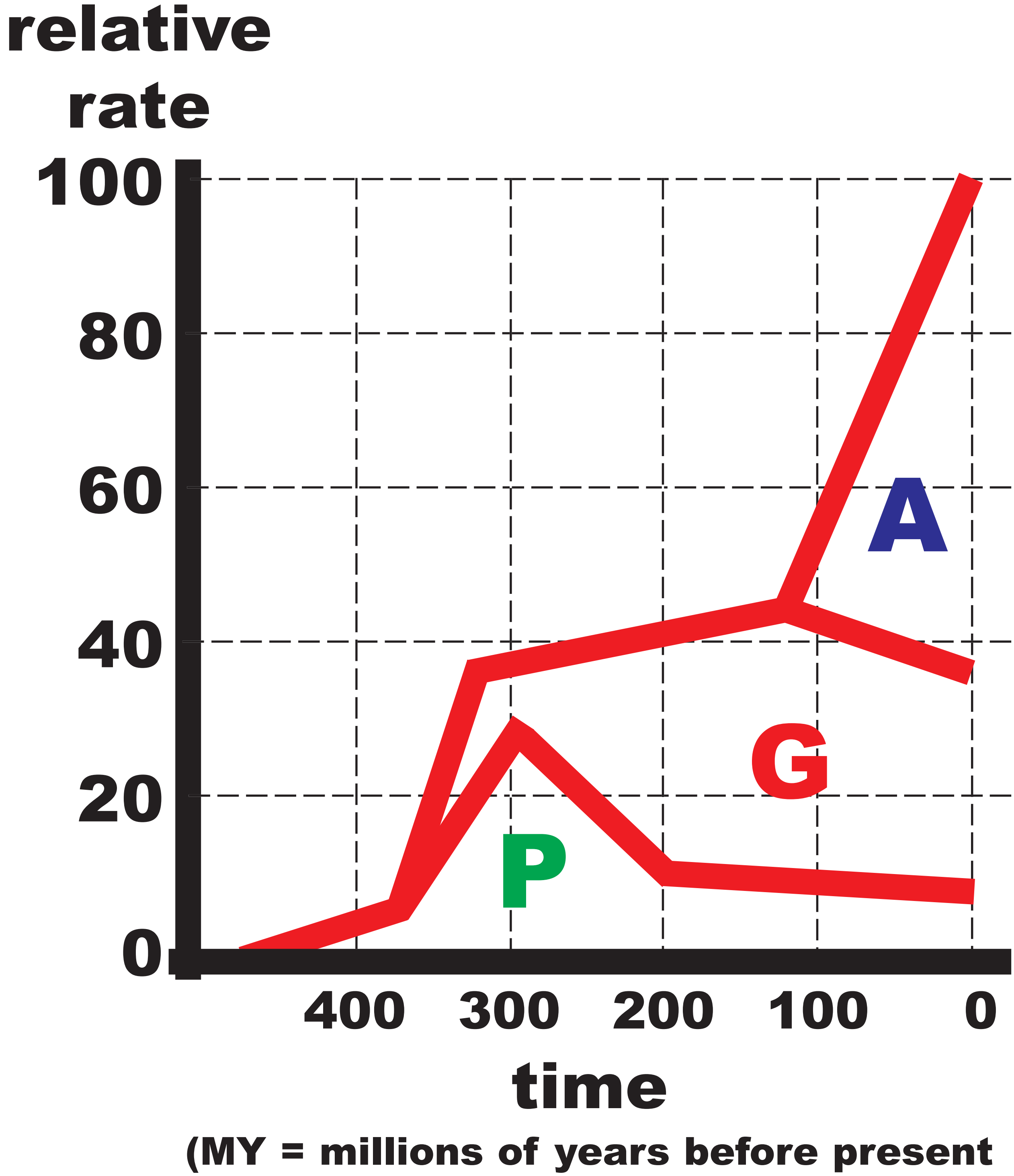


Figure 35: Species diversity and vascular land plant type over the last 450 million years.

P = primatives; G = gymnosperms; A = angiosperms.

(derived from Kenrick & Davis 2004; Niklas 1997; Willis & McElwain 2002)

tree species	incept date	tree species	incept date
witchhazel	(127MY)	elm	(80MY)
sycamore	(127MY)	palms	(75MY)
sweetgum	(127MY)	sandalwood	(71MY)
magnolia	(120MY)	screwpines	
boxwood	(112MY)	(pandans)	(71MY)
oaks	(100MY)	olives	(71MY)
willows	(95MY)	dogwoods	(71MY)
maples	(95MY)	Bombaceae	(71MY)
Ericaceae	(95MY)	Symplocaceae	(71MY)
holly	(95MY)	Rhamnaceae	(71MY)
hackberry	(95MY)	Clethraceae	(71MY)
buckeyes	(89MY)	aralia	(71MY)
chestnut	(87MY)	legumes	(69MY)
alder	(87MY)	bamboo	(60MY)
waxmyrtle	(85MY)	eucalyptus	(55MY)
walnut	(83MY)	acacia	(38MY)
birch	(80MY)		

Figure 36: Example list of current trees and their first evolutionary inception time in millions of years before present (MY). These species groups will continue to diversify and form new species.

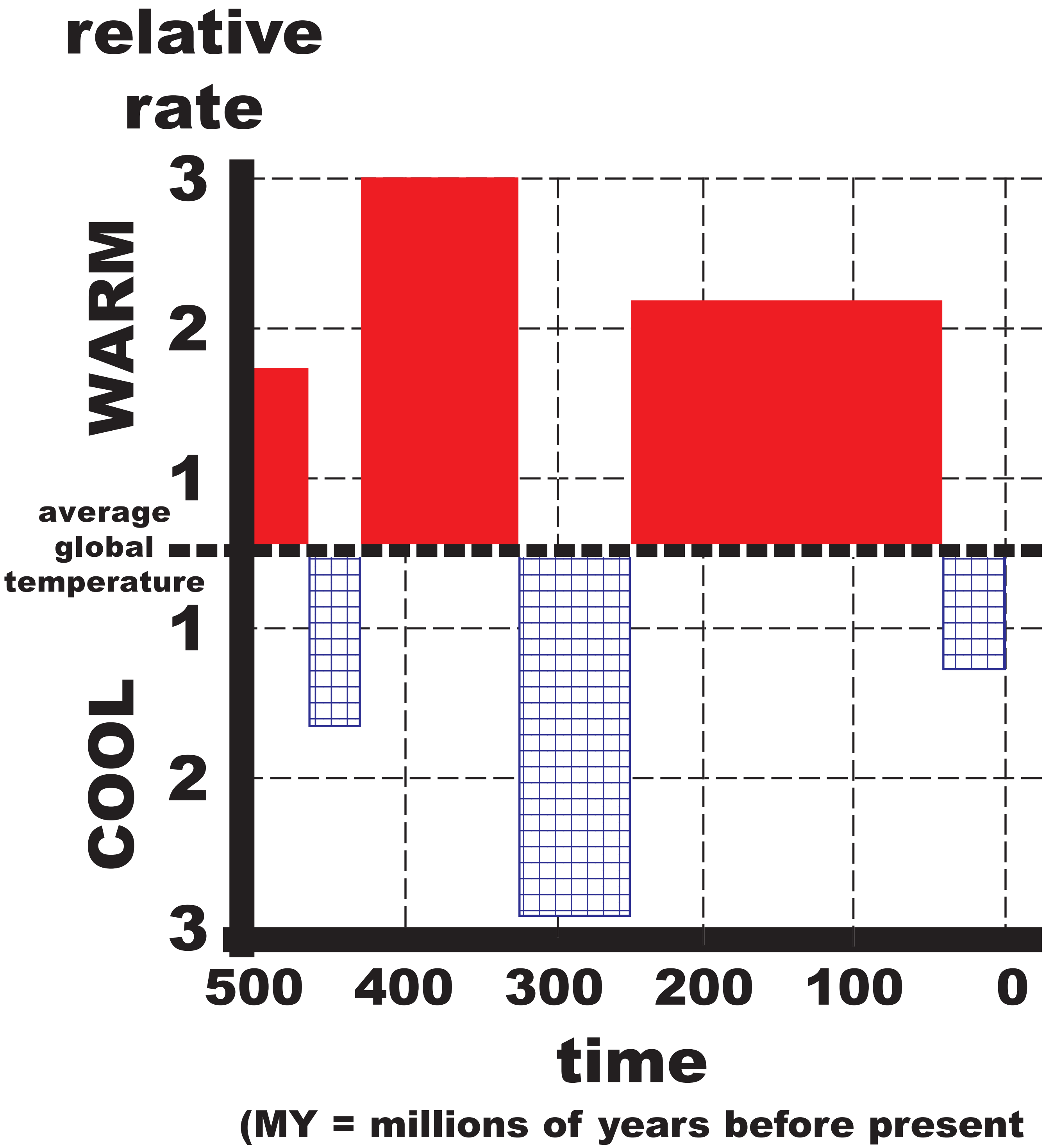


Figure 37: Average global temperatures with intensity and extent of cool and warm periods given.
(derived from Martin 1995; Willis & McElwain 2002)

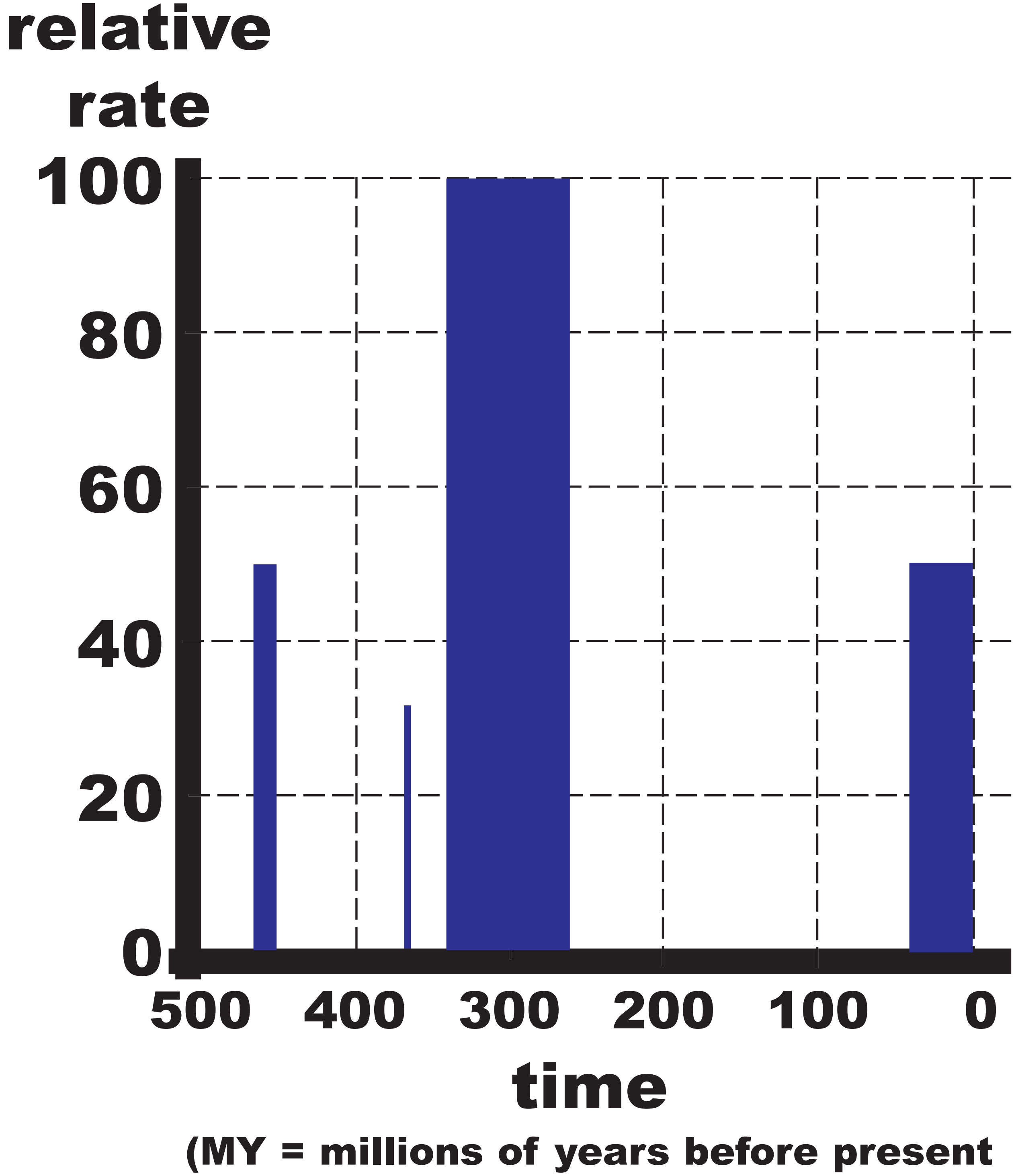


Figure 38: Four major glaciation periods intensity and extent since 500my.
(derived from Willis & McElwain 2002)

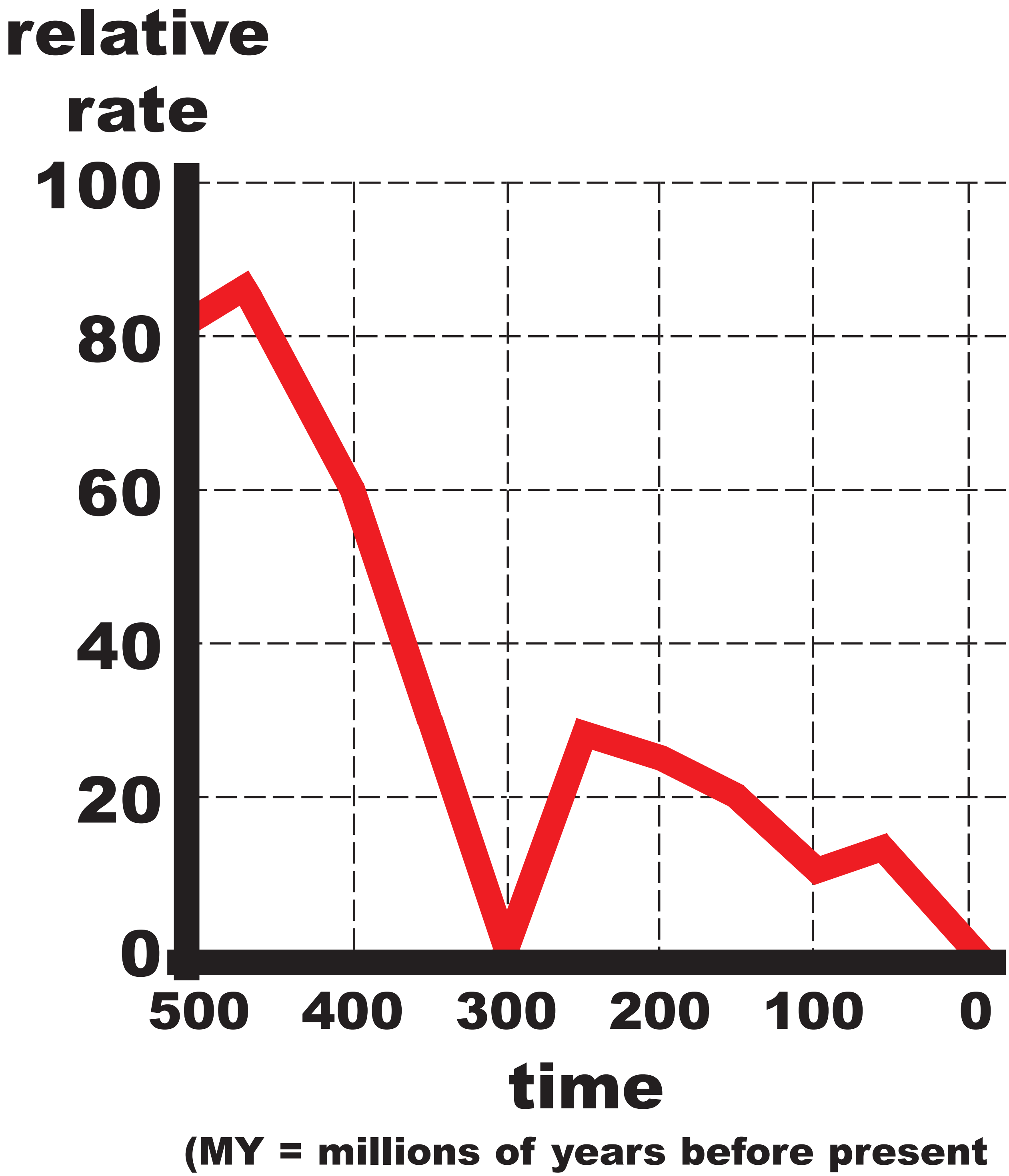


Figure 39: Relative carbon-dioxide (CO2) atmospheric concentration above present day concentration values. (range from high of 17 times current CO2 levels) (derived from Berner 1990)

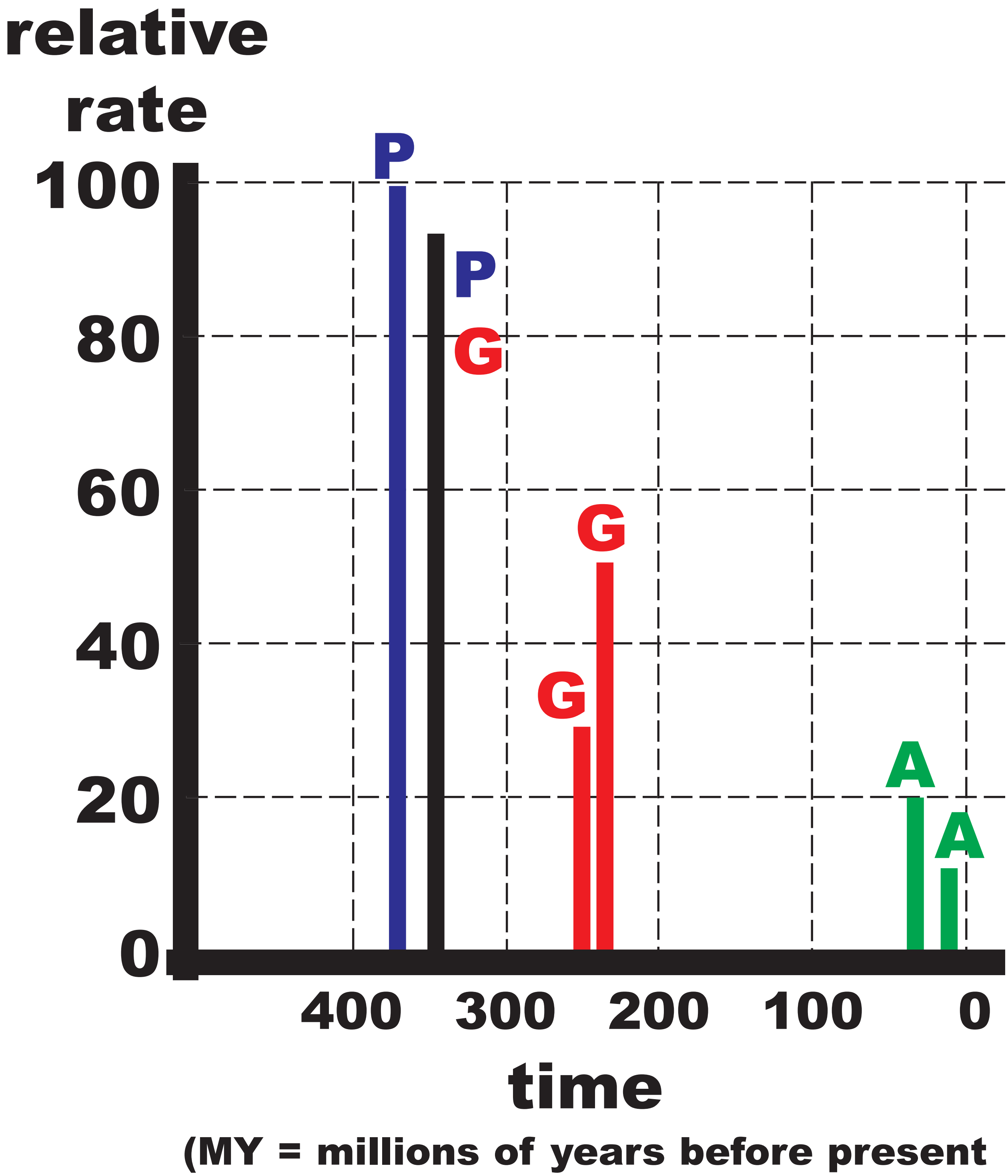


Figure 40: Six major vascular land plant species formation peaks.
P = primatives; G = gymnosperms; A = angiosperms.
(derived from Niklas 1997; Willis & McElwain 2002)

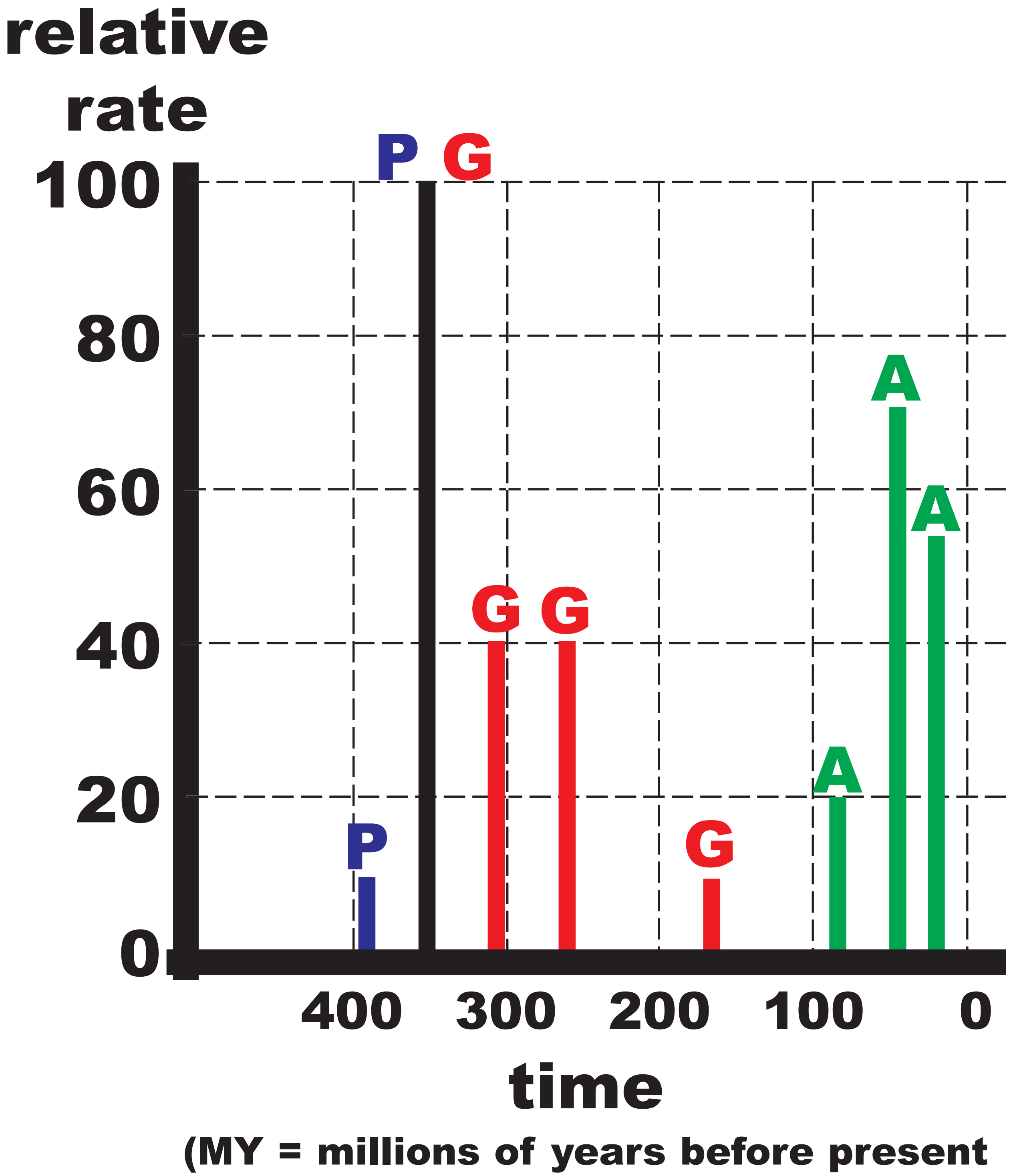


Figure 41: Primary vascular land plant species development and diversification peaks.
P = primatives; G = gymnosperms; A = angiosperms.
(derived from Niklas 1997; Willis & McElwain 2002)

Tertiary

16.3MY	gymnosperm loss
29.3MY	MAJOR loss of gymnosperms & some angiosperms

Cretaceous

131.8MY	angiosperms & gymnosperms loss

Jurassic

152.1MY-154.7MY	MAJOR loss of pteridophytes & gymnosperms

Triassic

240MY-241MY	MAJOR loss of pteridophytes & some gymnosperms

Carboniferous (Pennsylvanian)

290MY	many pteridophytes & some gymnosperms loss

Devonian

362.5	pteridophytes loss
377.5	MAJOR loss of pteridophytes
390.6	pteridophytes loss

Figure 42: Land plant extinction periods. (Niklas 1997)

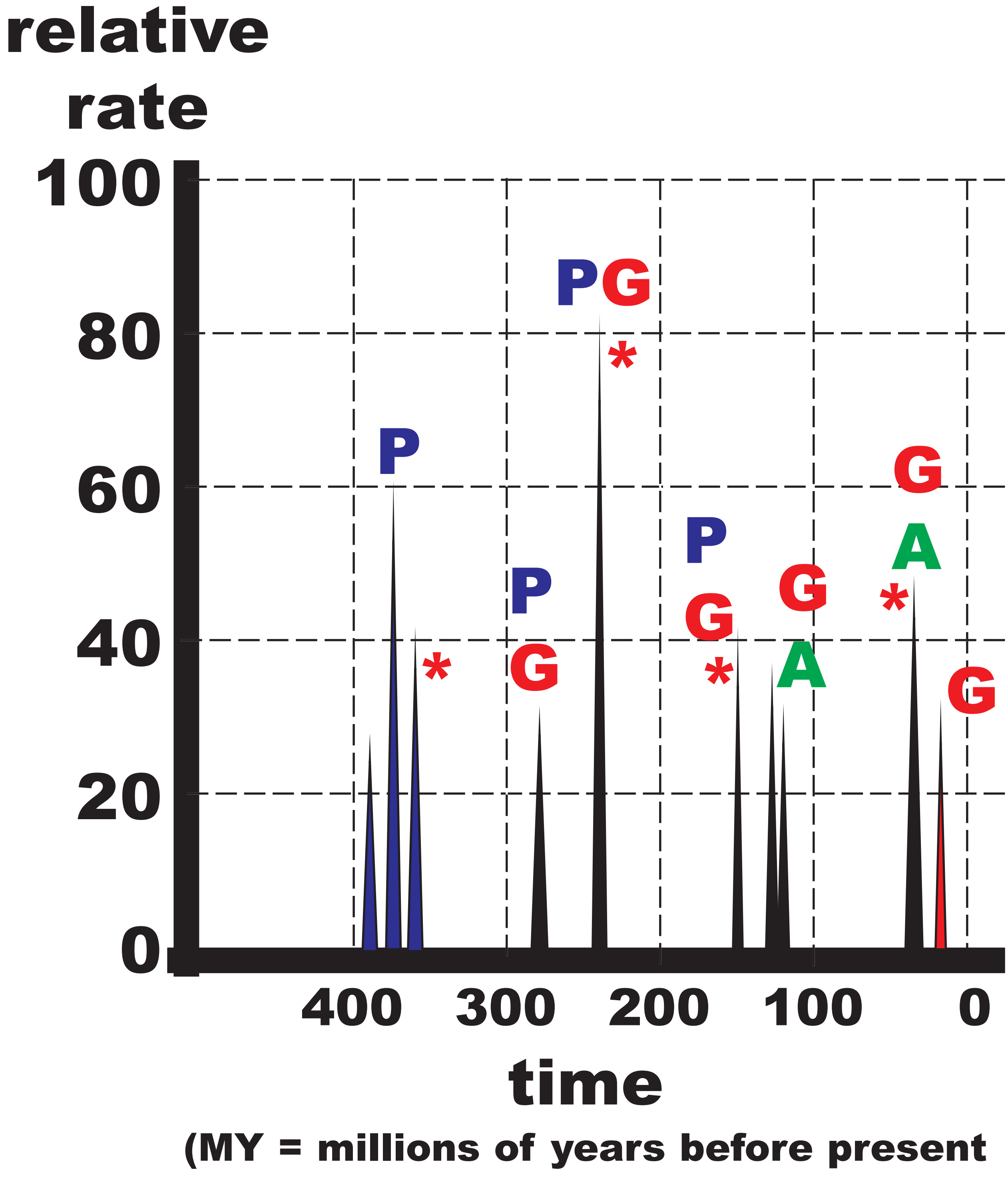


Figure 43: Primary extinction periods for vascular land plants. Ten periods of loss with only four (designated by *) associated with significant animal extinction periods.
P = primatives; G = gymnosperms; A = angiosperms.
(derived from Niklas 1997)

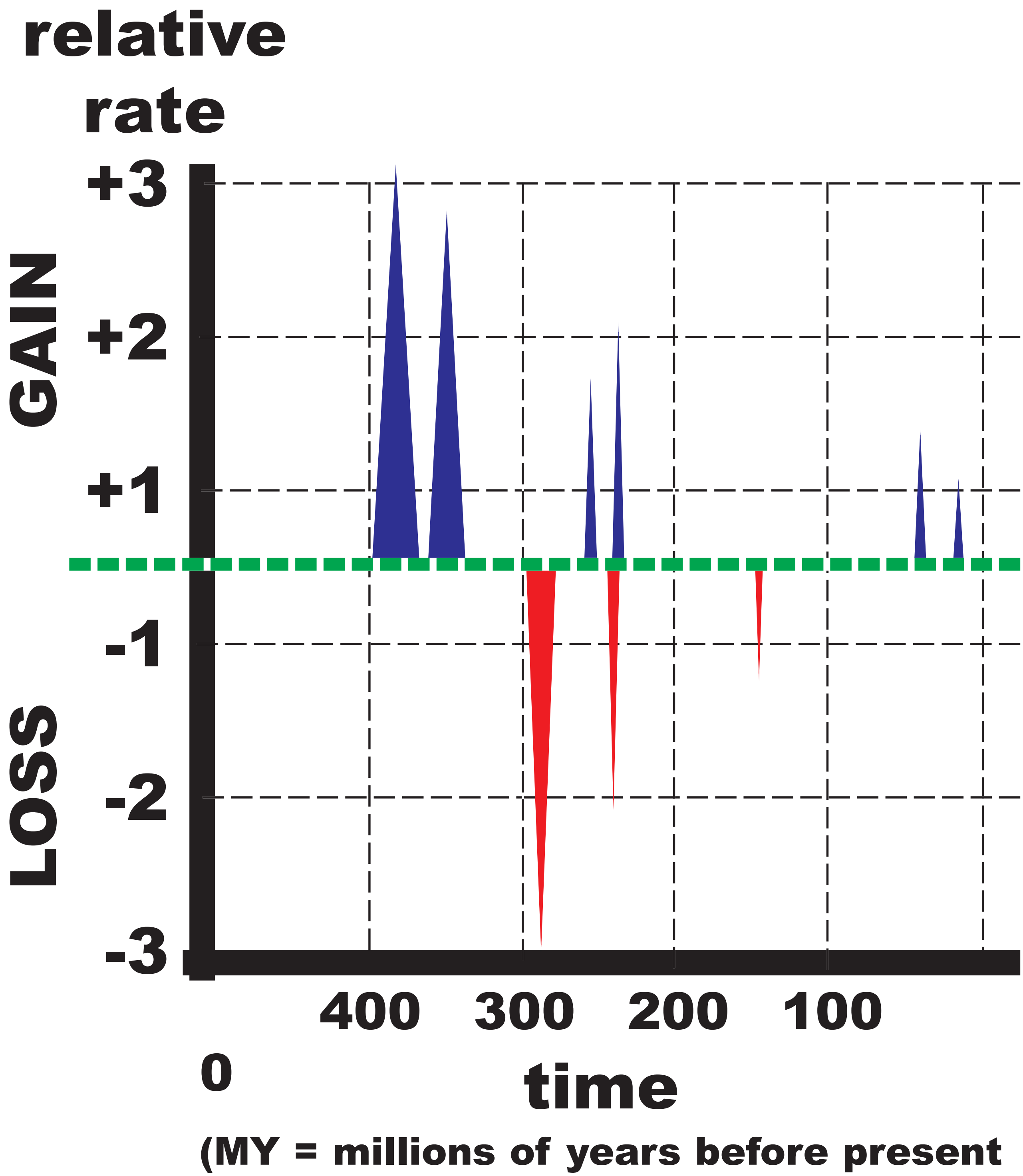


Figure 44: Major shifts in terrestrial vascular plant species numbers. High speciation rates occurred in 6 periods with the first two periods lasting longer than later events. Three major extinction periods occurred.
(derived from Niklas 1997)

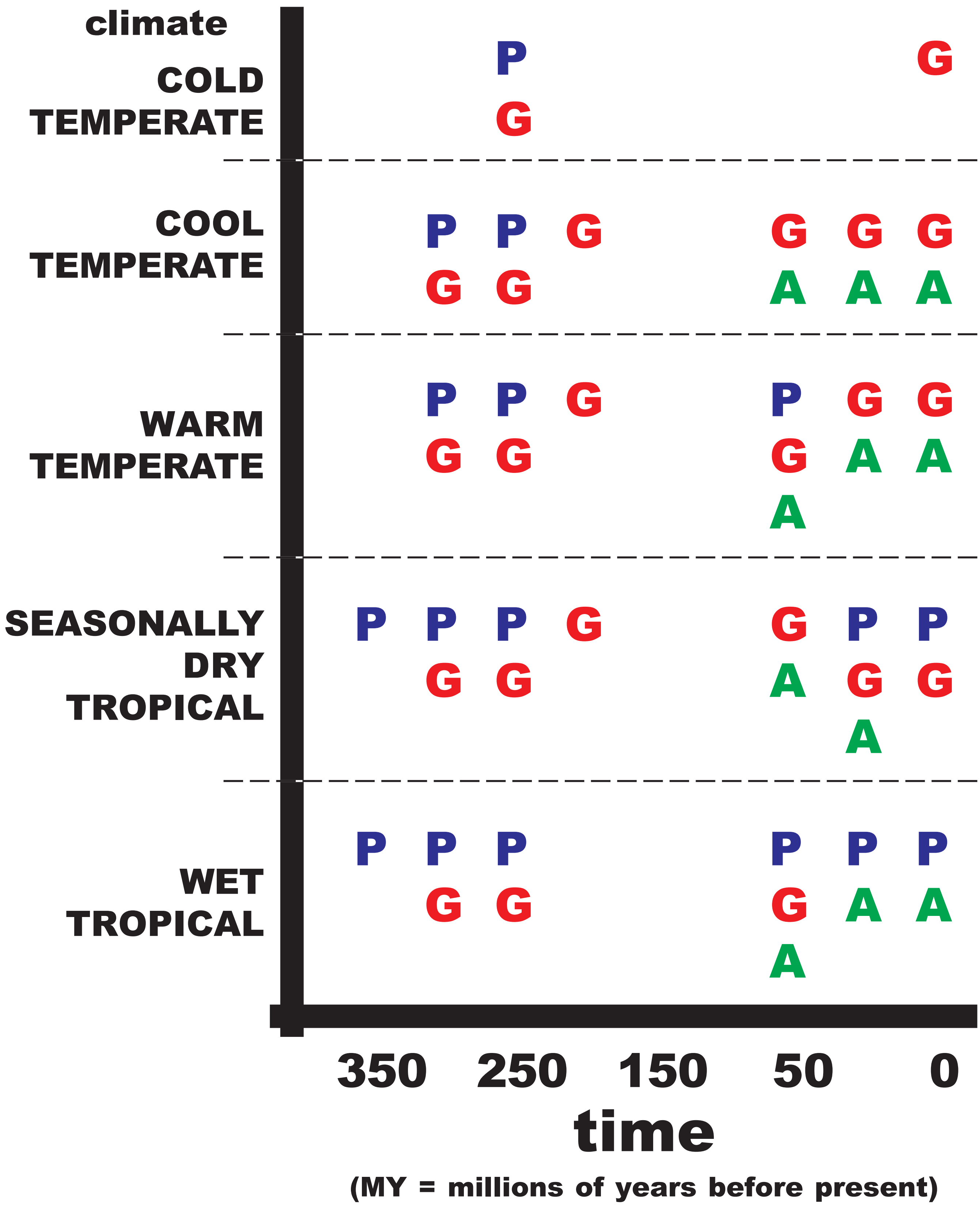


Figure 45: Tree types by global climatic zones over time.
P = primatives; G = gymnosperms; A = angiosperm.

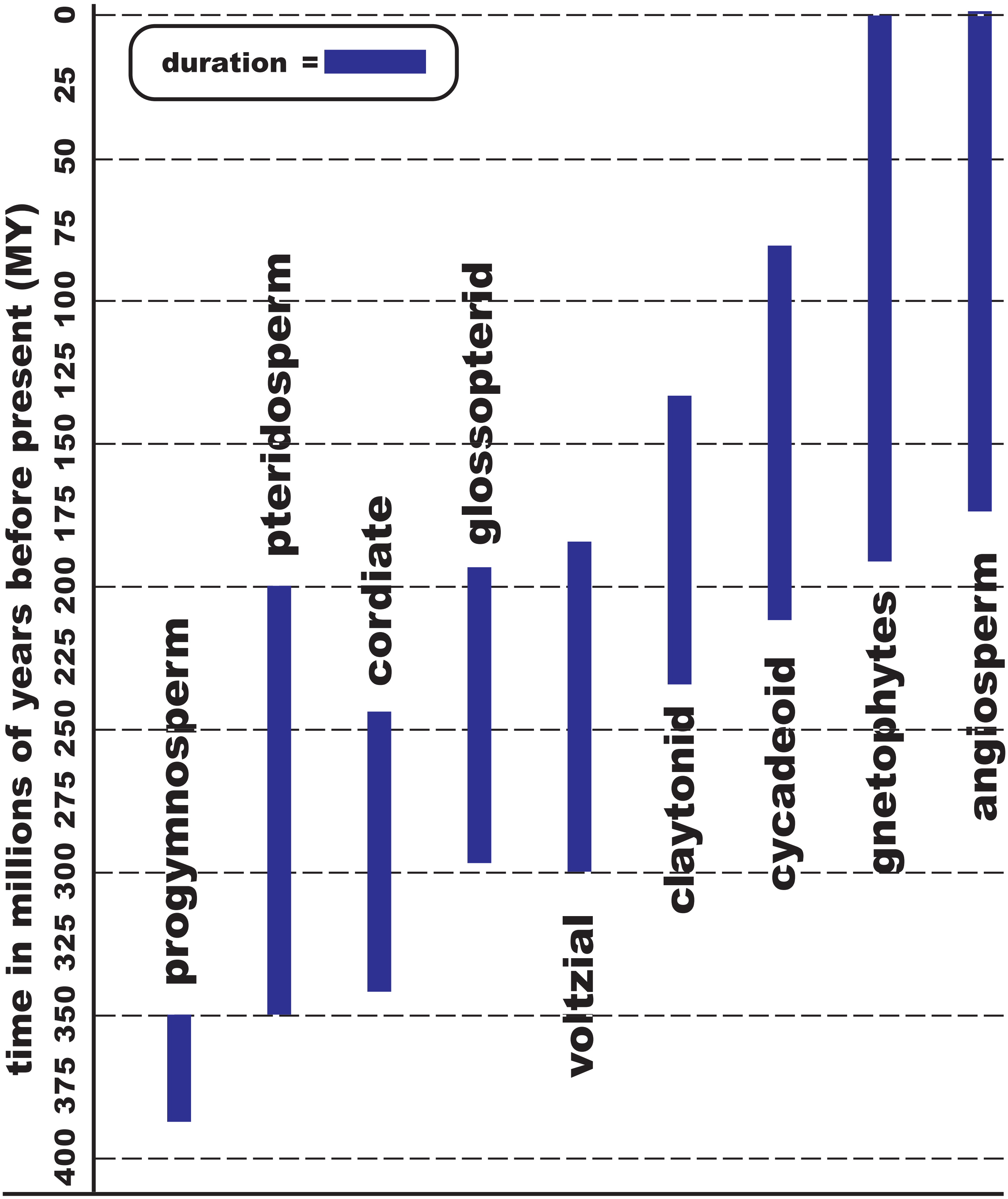


Figure 46: Progression summary of gymnosperm tree form development to angiosperms.
(Stewart & Rothwell 2009; Niklas et.al. 1985)

Angiosperm Tree Forms

The third wave of tree development, of which we are currently in the middle of, is the flowering trees of angiosperms (150my). Somewhere around 220my there was an ancestral split from a seed fern gymnosperm (like an entre leaf gigantopterid) that would eventually develop into the first angiosperm. Historically, a huge diversification explosion in angiosperms occurred around 100my. Angiosperm tree forms began to dominate the world's forests over gymnosperms by 70my. Figure 47 shows relationships among modern angiosperms. Figure 48 breaks out modern eudicot relationships.

The dates for angiosperm development is quite confusing because of a multitude of authors using a number of tools and technique to determine dates. One author defines the beginning of angiosperms at 192my while other authors provide a range between 200my and 125my. From the fossil record there is angiosperm pollen present by 130my, and macrofossil of angiosperm plants by 125my.

Angiosperms are a complex group to keep track of and assign to specific subdivisions, partially because of the shear numbers of species. Angiosperms currently have approximately 415 families and anywhere from 265,000-400,000 species. Of all these species, about 75% are eudicots, 23% are monocots, 2% are magnoliids, with a remainder of about 0.1 % additional plant species. The largest three current families of angiosperms are the daisy family with about 23,600 species (edicts), orchids with 22,075, and legumes (eudicots) with 19,400. Figure 49 shows the duration time for angiosperms. Peak times remain to be seen.

Most Primitive Angios

The angiosperm groups Amborellales, Nymphaeales, and Austrobaileyales represent the earliest of the angiosperms. First among these primitive angiosperms was Amborella trichopoda from New Caledonia. This species represents the characteristics of the first angiosperm. Amborella was a divergence on the genetic line generating angiosperms at about (170my). Amborella is a small tree growing to 25 feet in height with simple evergreen leaves. It has a dioecious sexual system generating small creamy white, inconspicuous flowers in terminal inflorescence in the axils of leaves. The fruit is a red drupe with one seed.

The second most ancient angiosperm group is the Nymphaeales which includes about 80 species of water lilies and other aquatic plants divided into 3 families and 75 species. The third eldest angiosperm group is the Austrobialeyales, which is a diverse group of 100 species of woody plants divided into three families: Austrobaileyaceae with 2 species, Schisandraceae (includes Illiciaceae) with 24 species, and Trimeniaceae with 6 species. A notable member of these groups is the spice star anise.

Mes-angios

The largest grouping of flowering plants are the mesangiosperms. This group houses more than 350,000 species representing greater than 99% of all flowering plants. There are five divisions among the mesangiosperms: magnoliids; Chloranthales; monocots; Ceratophyllales; and, eudicots. All of these groups appear to have broken away from each other within as little as four million years around 150my.

Magnoliids & Chloranths

Magnoliids are considered primitive angiosperms with large, showy, animal-pollinated flowers and cone-like spirally arranged fruits (i.e. yellowpoplar, magnolias, and laurels). The magnoliids represent more than 9,000 species across 20 families. The four major groups are: Magnoliales (families are Annonoaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, and Myristicaceae); Laurales (families are

Atherospermataceae, Calycanthaceae, Gomortegaceae, Hernandiaceae, Lauraceae, Monimiaceae, and Siparunaceae); Piperales (families are Aristolochiaceae, Hydnoraceae, Lactoridaceae, Piperaceae, and Saururaceae); and, Canellales (families are Canellaceae and Winteraceae). These groups represent common trees and products such as magnolia, yellow-poplar, and laurel trees, black pepper, avocados, bay leaves, nutmeg, cinnamon, and camphor. Within these groups, magnolias and laurels groups are considered closely related as are the Piperales and Canellales groups.

A related group to the magnoliids is the Chloranthaceae, with 4 genera and 24 species. All species are evergreen, and highly aromatic with inconspicuous flowers, and a single seeded drupe fruit.

Monocots & Ceratophyles

Monocots house approximately 65,000 species. Monocots probably began at the same time as eudicots as an aquatic plant (150my). Usually monocots are not considered trees, but there are a number tree forms within this group. For example, palms (Arecaceae), banana (Musaceae), screwpines (Pandanaceae), yucca, aloe, dracaena, and cordyline. It is suspected monocots were derived from an aquatic plant source.

Palms are usually considered the eldest tree form among monocots (90my or less). Tree-form palms have a single apical meristem (single terminal bud) with a crown of leaves (fronds) clustered at the top of a long stem. Leaf bases wrap around and support the stem. Vascular tissue and fiber bundles are interwoven among other living and dead tissues. Vascular bundles are more heavily concentated around the outside of the stem. Palm stems are stiff and hard, with these attributes increasing toward the base. Palm stems are resistant (in tension) to lateral wind forces.

Ceratophyllum are not monocots but share ecological backgrounds. Ceratophyllum contain six species of wetland flowering plants commonly called hornworts. They grow submerged with stems 3-10 feet long. Usually they are most commonly seen in fish aquarium.

Eudicots

Eudicots are a large and complex grouping of many diverse plants. Eudicots comprise more than 70% of all angiosperm plant species (>175,000 species). Eudicots are divided into many groups, the most simplest form of dividing species is provided here. Eudicots are divided into primitive and core groups. The base or more primitive eudicots are collectively called Eudicotinae composed of Buxales, Proteales, Ranunculales, Sabiales, and Trochodendrales.

The core eudicots are collectively called the Rosinae. Core eudicots are subdivided into the Gunnerales and Pentapetalae. The Pentapetalae are further subdivided into Dilleniales, Superasteridae, and Superrosidae. Each super subgroup is further divided: Superasteridae is broken up into Asterids (lamiides & campanulids), Bereridopsidales, Caryophyllales, and Santalales; Superrosidae is broken up into Rosids (fabids & malvids), Saxifragales,and Vitales.

Figure 50 provides an expanded view of current tree angiosperms.

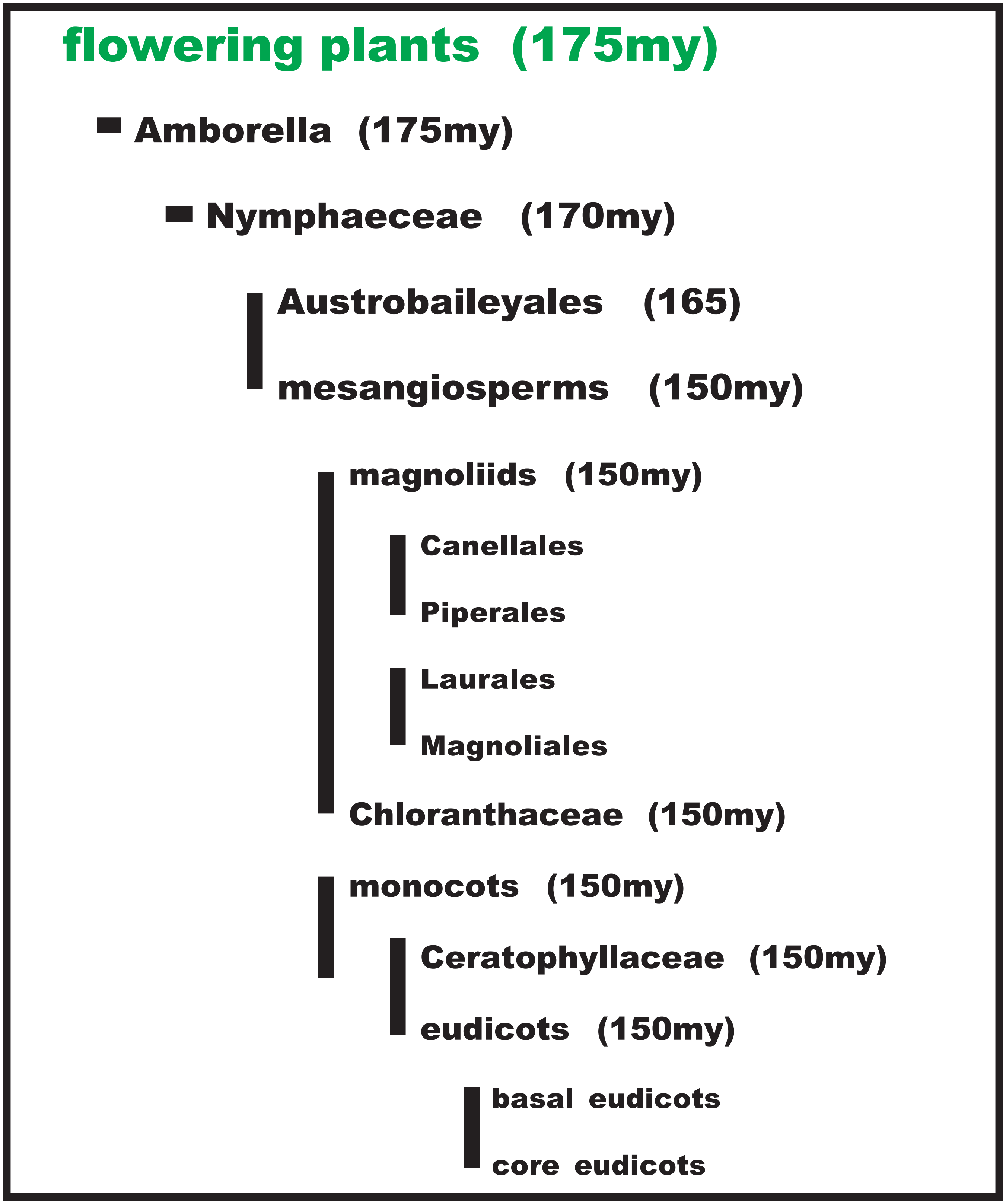


Figure 47: Relationships among angiosperm trees.

Eudicots **(>70% of angiosperm species)**

- **Basal eudicots (Eudicotinae)**
  - **Ranunculales**
  - **Sabiales**
  - **Proteales**
  - **Trochodendrales**
  - **Buxales**
- **Core eudicots (Rosinae)**
  - **Gunnerales**
  - **Pentapetalae**
    - **Dilleniales**
    - **Superasteridae**
      - **Bereridopsidales**
      - **Caryophyllales**
      - **Santalales**
      - **Asterids**
    - **Superrosidae**
      - **Saxifragales**
      - **Vitales**
      - **Rosids**

Figure 48: Current eudicot groupings.

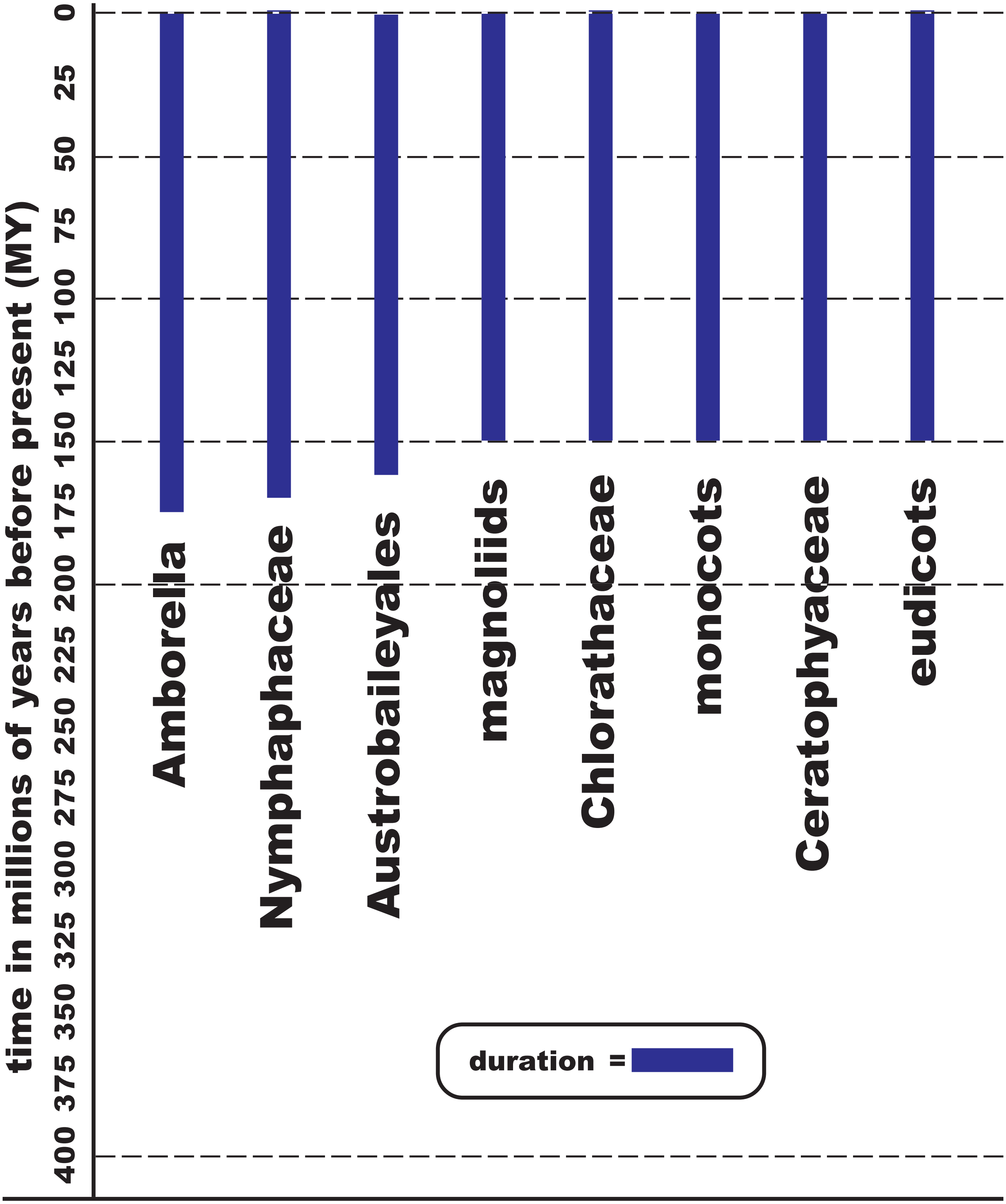


Figure 49: Duration times of angiosperms.

Angiosperms

Derived from a single ancestor around 175MY.
First angiosperm a shrub, second a water lilly.

Primitive Angiosperms

most primative

Illicium anisetree

Magnoliids

magnolia, custard apples, nutmeg, laurel, sweetbay, red bay, greenheart

Eudicots

Primitive Eudicots

macadamea, sycamore, boxwood

Core Eudicots

Madagascar thorny trees, cactus, sandalwood

Rose Group
- **Primitive Rosids**
  - **witch-hazel, swetgum, kaysura**
- **Core Rosids**
  - **creosote bush, lignum vitae, euonymous, mangrove, willow, poplar, legumes, apples, plums, elms, figs, myrtles, eucalypts, linden, cacao, baobabs, frankincense, myrrh, citrus, maples, mahogany oaks, beech, birch, hazels, walnuts**

Aster Group
- **Primitive Asterids**
  - **Earliest Primitive Asterids**
    - **dogwood, tupelo**
  - **Late Primitive Asterids**
    - **persimmon, tea, brazil nuts**
- **Core Asterids**
  - **coffee, olive, ash, teak, holly**

Monocots

Joshua tree, screw pines, palm-forms, palms, traveler’s palm herb trees (bamboo, bananas), yucca, grass trees

Figure 50: Select example list of modern angiosperm tree forms.

Mix In Humans !

Tree time has passed. Figure 51 shows the walk of time from timid attcks on beaches to today's trees. Note again the plant ages listed which trees survived. Roughly 12,000 years ago (0.012MY) the Pleistocene ended and the Holocene -- the age of humans – began. Glacial ice sheets retreated. Men were beginning to impact trees and forests around them.

Forests of Eastern North America after the last glacier could be summarized as:

1. deciduous forest (10,000 years) of oak, hickory, beech, and chestnut (which has been dominated by oak in the last 4,000 years);

2. prairie / forest mix (10,000 years) whose interface has moved East and West several times in the last 10,000 years replacing oak, elm, and ash with grass; and,

3. mixed hardwood / conifer forest (7,000 years) composed of species which had not overlapped in the past, especially the widespread presence of spruce.

Family Tree

The history of trees spans more than 400 million years depending upon your definition of a tree. Figure 52 presents the three massive tree form waves of species development Earth has sustained. What minor species today will spawn the fourth wave of plant or tree developement?

Today we work with and see only "tree winners" in a long development process. Figure 53. Trees we see today have been ecologically tuned for Earth at this moment in time (broadscale ecological time). Many trials and errors have come before, and most tree species which ever existed have become extinct. Tree forms continue to decline in today's world, and projections suggest within another 50 million years, only a few residual trees will exist, if humans do not further push trees to extinction. Figure 54.

Blessed

Today's trees and forests visually and genetically represent the past vulgarities of Earth changes, now coupled with recent changes wrought by humans. We are blessed with successful and lucky trees who survived through genetic and climatic engineering within an environment trying to kill them, and neighbors trying to steal their resources. Trees are awe inspiring for their tenacity and longevity. But tree forms are on their way out, as new plants which are more efficient arise and dominate Earth (with help from meddling humans). We need to better care for these most ancient of lives, the trees, and by doing so, enrich ourselves and our communities.

Phanerozoic Eon

Paleophytic Era		(295my duration)	
Cambrian		6.3 TT	543 MY
Ordovician		6.2 TT	490 MY
Silurian		6.1 TT	443 MY
Devonian	[tree birth]	6.0 TT	417 MY
Carboniferous			
Mississippian		5.9 TT	354 MY
Pennsylvanian		5.8 TT	323 MY
Permian		5.7 TT	290 MY
Mesophytic Era		(183my duration)	
Triassic		5.5 TT	248 MY
Jurassic		5.3 TT	206 MY
Cretaceous		5.0 TT	142 MY
Cenophytic Era		(65my duration)	
	[tree boom]		
Tertiary			
Paleocene		4.2 TT	65 MY
Eocene		4.0 TT	55 MY
Oligocene		3.5 TT	34 MY
Miocene		3.2 TT	24 MY
Pliocene		1.7 TT	5.4 MY
Quaternary	[tree burr]		
Pleistocene		0.6 TT	1.8 MY
Holocene			(12,000 ybp)

Figure 51: Breakdown of Phanerozoic Eon by eras and sub-eras in Coder tree time units (TT) and millions of years ago (MY). (ybp = years before present)

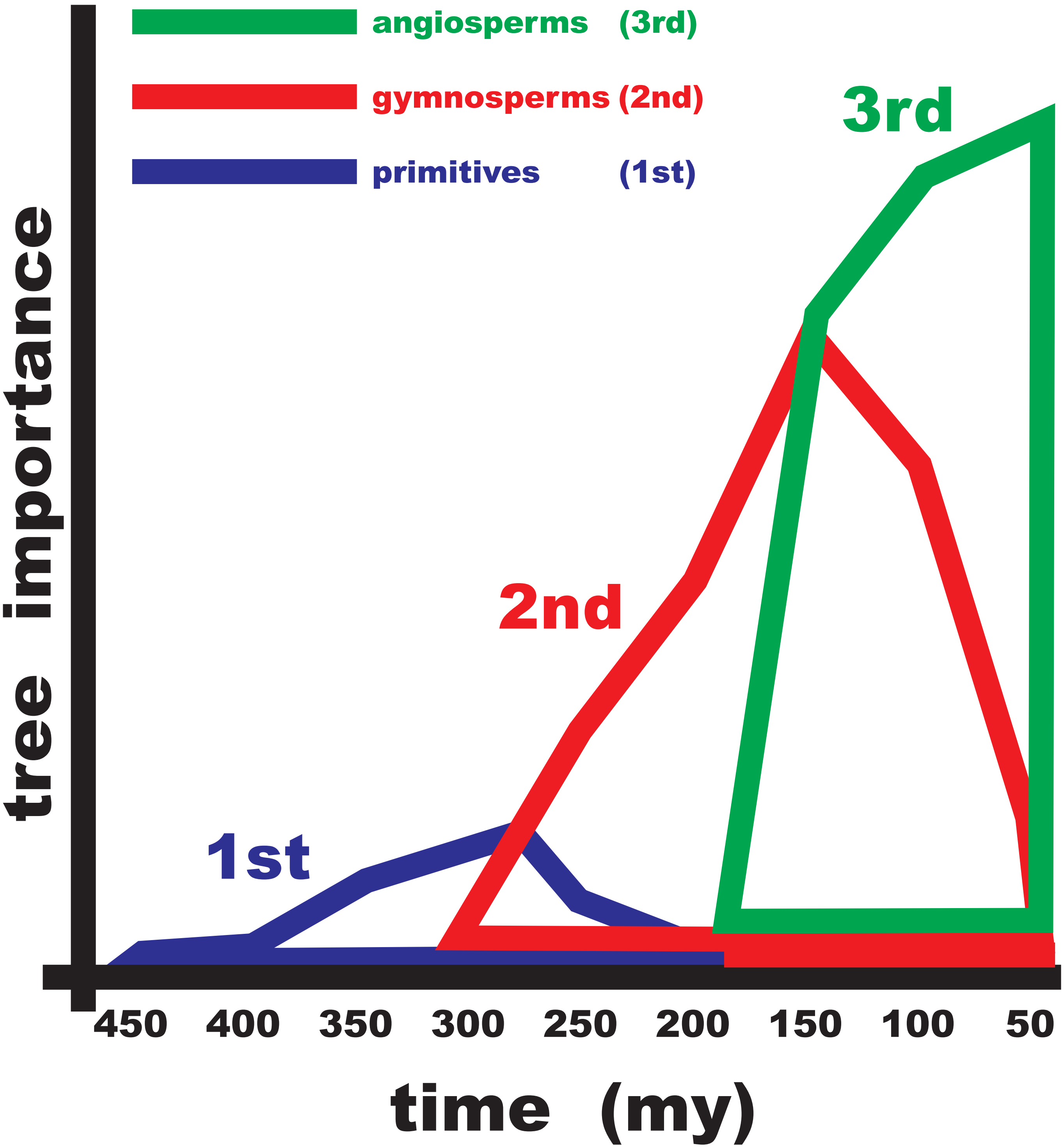


Figure 52: Three waves of tree-form development.
(derived from: Kenrick & Davis 2004; Niklas 1997; Niklas et.al. 1985)

425my-365my	rhyniopsids
380my-350my	trimerophytopsids
380my-350my	progymnosperms
400my-355my	zosterophylls
365my-280my	lycopods
360my-325my	horsetails (archaeocalamites)
350my-265my	horsetails (calamites)
355my-240my	tree seed ferns (pteridosperms)
325my-240my	cordaites
290my-200my	tree seed ferns (glossopterids)
295my-185my	voltziates
270my-	ginkgo
230my-135my	tree seed ferns (claytonids)
230my-	cycads
220my-	pinophytes
210my-70my	cycadoids
150my-	eudicots
150my-	monocots
150my-	magnoliids

Figure 53: General order of tree form development across time to generate modern trees.

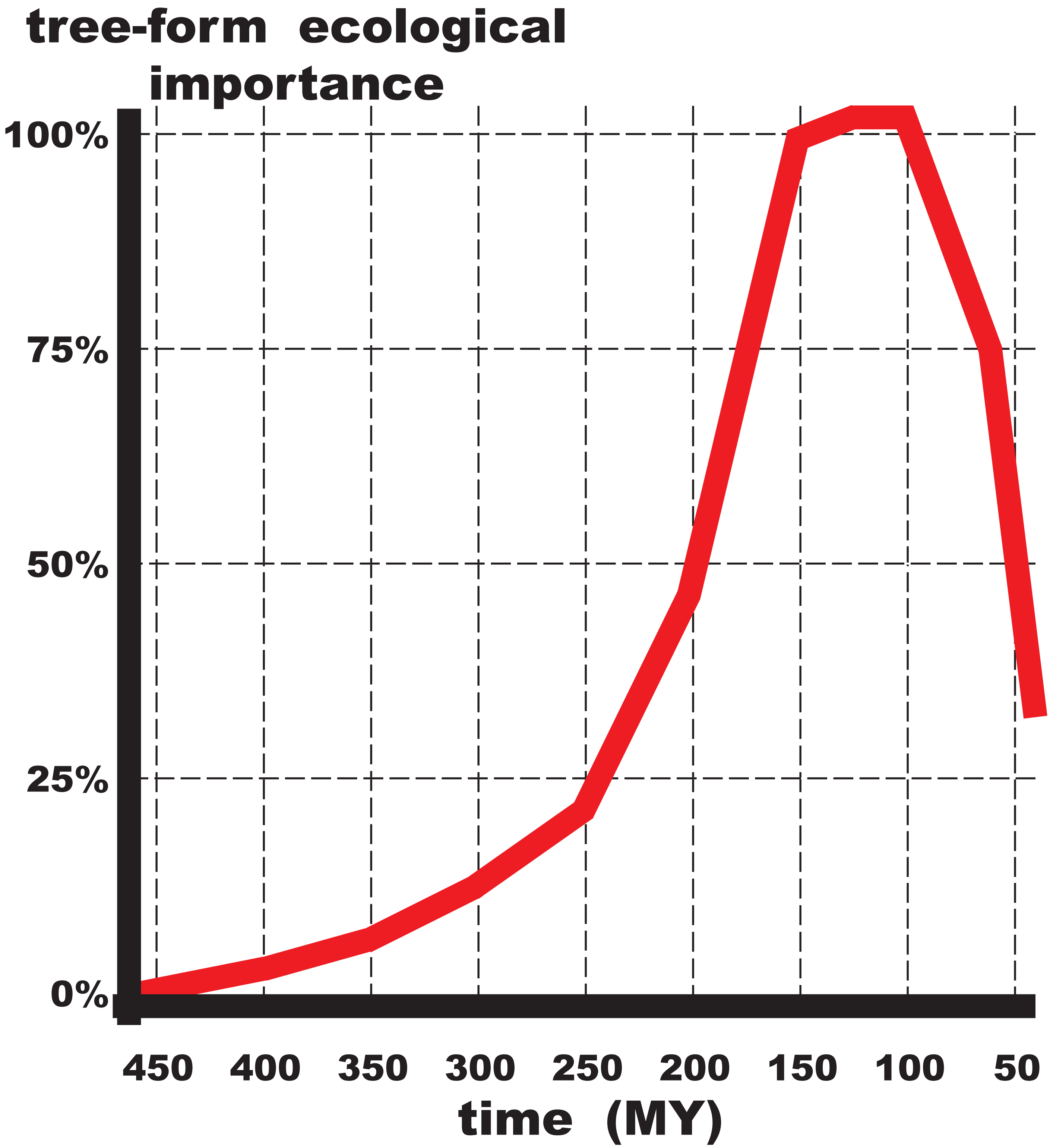


Figure 54: Relative ecological importance of tree-forms on Earth over 500 million years compared with other land plants.

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