THE PALEOBIOGEOGRAPHY OF EARLY TETRAPODS AS REFLECTED IN THE TETRAPOD DATABASE

Glenn Simonelli
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INTRODUCTION

Tetrapods are vertebrates, usually with four leg-like appendages. All amphibians, reptiles, birds and mammals are descendants of the first tetrapods.

The oldest known occurrences of tetrapods in the fossil record are in late Devonian-age rocks. Early specimens have been in found in North America, China, Russia and Latvia, (Benton, 2005), but the most complete late Devonian fossil specimens, those of genera Acanthostega and Icthyostega, were discovered in eastern Greenland. (Carroll, 1992) These earliest tetrapods appear to be related to the osteolepform fish Eusthenopteron (Godfrey, 1997, Benton, 2005), although other types of fish have been proposed as the closest relative (see for example, Hensen, 1996). Unfortunately, extensive gaps in the fossil record obscure the connection between osteolepiform fish and the earliest tetrapods. Additionally, there is a 30-million-year gap in the tetrapod fossil record between the late Devonian and the early Mississippian epochs. This gap, called "Romer's Gap" in honor of Alfred Romer, an early pioneer in the study of the evolution of tetrapods who first recognized and described the gap, blurs the transition between these early tetrapods and the later, diverse taxa of the Mississippian period. Therefore, there is no distinct taxonomic relationship between Devonian and Mississippian, although some recent discoveries are beginning to fill in a few of the gaps (Clack, 2002).

METHODOLOGY

The Data Set

The tetrapod "database" is actually an Excel spreadsheet containing entries of tetrapod fossils from the Devonian through the Permian assembled from online databases. It is available online at: http://mypage.iu.edu/~gsimonel/Library/Tetrapod_Database.xls.

Data were collected from the University of California Museum of Paleontology, (http://fossils.valdosta.edu/), the Yale Peabody Museum Vertebrate Collection, (http://www.peabody.yale.edu/collections/vp/) the Berkeley Natural History Museums (http://bnhm.berkeley.edu/) and the Valdosta State University Virtual Museum (http://fossils.valdosta.edu/). Originally, the use of data from additional collections was planned, the four collections currently comprising the database were simply the first four online collections accessed. However, after including the data from these four collections close to 400 individual entries were obtained and, in consideration of time limitations, it was decided that the data assembly process of this project be completed. Ultimately, it would be beneficial to expand the database by including records from other large collections.

The spreadsheet includes information about the class, order, family and taxon of the tetrapod fossils in the four collections. There are entries representing both amphibia and reptilia—plus three additional entries identified only as “tetrapoda”—including entries for 15 different identified orders, 64 identified families and 147 identified genera. Also included were data about the period, epoch, stage and formation of the stratigraphic layer in which the fossils were recovered. The location at which the fossil was found, including the specific locality, county, state or province, country, and continent, is included, along with the latitude and longitude of the site. Entries are included from Asia, Africa, Europe, North America and South America, representing 14 different counties, 30 states or provinces (including 11 different US states) and 132 different localities. There is also information entered about the collection(s) in which the specimen resides, literature in which the specimen is referenced, and other additional notes, such as previous taxonomic assignments. Not every entry in the database has information about each of the data points. For example, some entries may list the class and order but no other taxonomic information. Some entries list the state in which the specimen was found but no more specific location information.

There are 383 different entries in the database. Each entry is a unique combination of taxonomy and locality and has been assigned a unique catalog number. When multiple specimens of a species recovered from the same location were listed in the collections, only one entry was made. However, different species found at the same location are listed separately, as well as entries for the same species found at different locations. Indeterminate species are treated as distinct from determinate, so a single location may have listings for, e.g., both *Aerosaurus wellesi* (#312) and *Aerosaurus sp* (#311), but this is not common. For simplicity, the entries were arranged alphabetically according to class, order, family and taxon (genus and species) and numbered beginning with the number 1. This will require continual renumbering of the entries as the database expands. However, since any citation of an entry in the database will most likely reference the original catalogue number assigned by the museum housing the specimen, this should not pose a problem. The numbers assigned by this author are simply for his convenience, and only scholastic reference to the numbers will be in this paper.

Of the 383 entries in the database, 381 provided enough location information to be included on a paleomap. Latitude and longitude were determined by several different methods. In many cases the precise latitude and longitude of the discovery location were included with the data provided by the collection. In other cases it was determined by searching online for the latitude and longitude of the county of recovery. Online searches were conducted by entering the search terms “latitude, longitude [location]” into Google (www.google.com). In both cases these entries are listed in the database as using a political unit as the basis for their coordinates. It should be noted that the spatial resolution of these political units may vary according to the location information included with the specimen. Entry #309, for example, which is listed as being found “1.5 Mi. S of Norman (Hennessey Beds), Logan County, OK” is a more precise location description than that for entry #277, which is listed simply as “Young County, TX,” and thus, potentially improving the spatial resolution of that entry. Some entries, however, did not give precise enough information to pinpoint a specific county, listing mere a state or country as the locality. In this case the basis of coordination was listed as “geographical estimate,” and one of two different methods was used to assign latitude and longitude values. If many other similar specimens were listed in the database and all these specimens were found in a relatively contiguous area, such as in 5 different counties all in the southern part of a state, the known localities were plotted on a state or country map and a point approximately in the middle of the area defined by the points was selected. The latitude and longitude of this point was then determined by online search. In situations where there was no definable area where similar specimens were discovered then a point in the approximate geographical center of the state or county was selected and the latitude or longitude of that point was used. In both cases the basis of coordinates was listed as “geographical estimate” in the database. A few entries included latitude and longitude and listed canyons, riverbeds or other topographic features as the locality. In these cases “topographic unit” was listed as the basis of coordinates.

Limitations of the Data Set

All four of the collections from which the database was complied are housed in museums in the United States. It is possible that the specimens recorded may be heavily skewed in favor of those found in the United States. Specimens from other parts of the world may be underrepresented.

Also, the collections were limited to fossil remains, so no tetrapod tracks are included in the database, even though these obviously provide evidence of tetrapod activity at a specific location during a particular time period. Thus, despite the recovery of Pennsylvanian era tetrapod tracks from southern Indiana known to this author, there are no entries in the database of fossils from Indiana. In interpreting the paleomaps included with this paper, it must be recognized that the database may not reflect the complete range of Paleozoic tetrapods, only the range of recovered Paleozoic tetrapod fossils.

Paleomaps

The paleomaps used for the range reconstructions were developed by Christopher Scotese as part of the Paleomap project (http://www.scotese.com/Default.htm). Other paleomaps are available, including those of Ron Blakey, (see http://jan.ucc.nau.edu/~rcb7/globaltext2.html), but the maps from the Paleomap Project were chosen because of their somewhat greater facility in comparison to modern maps. Additionally, maps from the Paleomap Project are finding wide acceptance and increasing use in the research literature, (e.g., Golonka, 2002). However, it should be noted that the maps of Scotese are different from those of Blakey in some respects. In particular, Blakey's maps tend to show the area that today comprises Southeast Asia as further south then Scotese's. Fortunately, the land masses that today make up North America, South America, Europe and Africa—which is where the overwhelming majority of the fossils in the database were recovered—are shown at approximately the same latitude on both Scotese's and Blakely's maps.

Maps showing the geographic range of the fossil discoveries were constructed by the author. Separate spreadsheets were created for different subgroups of the database, i.e. spreadsheets for each period, class or order. The maps were created by importing the latitude and longitude of individual entries into PanMap, a shareware map generating program available at http://www.pangaea.de/Software/PanMap/ . The program translated each set of coordinates into a single point and plotted it on a current world map. This map was then copied into Photoshop where the countries were cut apart, re-sized and rotated, copied and pasted over the appropriate area of the appropriate paleogeographic plate reconstruction map, or paleomap, of the world during the time period represented by the fossils. After removing the background and boundary markings of the pasted PanMap segments, only the plotted data points remained, superimposed over the paleomap at a point corresponding to their relative position in the world during the time period represented by the paleomap.

RESULTS

Periodic Distributions

Figure 1 shows the distribution of tetrapod fossils during the Devonian period. A caution is in order when interpreting this map: the tetrapod fossils plotted on the map date from the Late Devonian epoch. Unfortunately, no Late Devonian maps were available to this author during the life of this project, so a map from the Middle Devonian was used. Since the continents on which the fossils were discovered were drifting northward at the time, at the time of deposition the tetrapods were likely living approximately 5º-10º closer to the equator.

Included on this map are three Devonian tetrapod fossils (red diamonds) and two Devonian fossils of *Eusthenopteron sp*, (blue diamonds) an osteolepiform fish that many consider one of the nearest known relatives of the tetrapods. (Carroll, 2001)

Immediately, several problems arise when interpreting this map. The earliest known tetrapod fossils were found very far from any of those of their fish-like cousins. Moreover, the fossils of the tetrapods—the first of which were assumed to have evolved from fish trapped in anoxic waters (Carroll, 2001)—were discovered mid-continent and at relatively high elevation. This is confusing since one would expect to find the earliest fossils near the paleoshorelines close to the waters from which they had recently emerged. Clearly, there are major gaps in the fossil record, and this makes the complete evolution from fish to tetrapod impossible to trace at the present.

Figure 2 plots the distribution of Mississippian period tetrapod fossils. Several patterns are discernable. First, dispersal and speciation has increased. There are four identified genera represented on this map, compared to two for the Devonian. The fossils were found near coastlines, more in keeping with expectations since all the tetrapods represented on this map were amphibious. Notably absent, however, are any fossil discoveries in the areas between the coastlines and the higher elevation areas in which the

Devonian fossils were discovered. What this illustrates is a second gap in the fossil record. This is, in fact, Romer's Gap, which was discussed briefly earlier.

Figure 3 shows the distribution of Pennsylvanian fossils. Notable on this map is the wider geographic dispersal of the tetrapods and the spread from the coastlines into the continental interiors. However, the fossils are still located close to the paleoequator. Little latitudinal distribution is seen. Speciation has increased greatly. Seven different orders—5 of amphibia and 2 of reptilia—are represented, comprising 66 different identified families (62 amphibian and 4 reptilian).

On Figure 4 it becomes apparent that the geographic distribution of tetrapods has become widespread during the Permian period. Amphibia (red diamonds) increased their lateral distribution but remain restricted near the paleoequator, with the exception of a single specimen reported far to the south in what is today part of India. The fact that this is a single specimen found over half a hemisphere away leads one to suspect that the specimen may be misidentified, either taxonomically or temporally. Reptiles (green diamonds), however, have clearly dispersed over much of the southern paleocontinent. In fact, the southern reptile fossils raise some questions. It is notable that there is no geographic connection between the reptile fossils found near the paleoequator and those found in the southern half of the southern hemisphere. Is this disconnect because of the limited size of the database, preservation issues, sampling bias, or is there a different explanation?

Issues of Taxonomy

Taxonomic uncertainties, in fact, cloud the interpretation of these paleobiogeographic maps. There are many major uncertainties and disagreements about the correct taxonomic classification of early tetrapod fossils. One reason for this is the major gaps in the fossil record, including the 30-million-year Romer's Gap. Another problem is that the taxonomic interpretation of the record is influenced by the characteristics examined and the classification approach taken. Different researchers frequently assign different groups of tetrapods to different clades or taxonomic levels, and historically the taxonomy has been frequently revised. The use of subclasses, superorders and/or suborders is not always consistent, and different taxonomic names tend to gain and lose favor with researchers over time. Some researchers use terms such as lepospondyli and labyrinthodontia to describe a superorders or subclasses (Benton, 2005), while others use them to describe orders (Carroll, 1992; see also Warren and Turner, 2004 for a completely different interpretation based on cladistic assignments).

This can make examination of the paleobiogeographic distribution of different taxa problematic, because it is not always clear which specimens to include in a specific taxon, and the inclusion or omission of different specimens can greatly affect the geographic patterns revealed. For this project, it was realized that taxonomic uncertainties and small sample sizes could lead to inaccurate depictions of distribution patterns if examined at the species, generic or familial level, so it was decided to plot and examine the paleobiogeography of tetrapods only at the level of the order. Additionally the taxonomic assignments of the four museum collections, which were generally in agreement as to which terms describe an order, which describe a family, and so on, were used for the taxonomic hierarchies. Superorder, subfamily, etc., terms were not used.

Thus, terms like "labyrinthodontia," "lepospondyli," "lissamphibia" and "amniota" do not appear in the database. While these decisions did not eliminate the problems discussed above, they did provide a consistent reference point against which the information presented and the inferences drawn could be evaluated.

Geographic Distribution of Orders

Tetrapods were grouped at the order level in accordance with the classification scheme used by the museum housing the collection containing the specimen. Occasionally the classification at the order level was supplied by this author when that information was missing from the notes accompanying the specimen or in conflict with general consensus. The following section will briefly discuss the different tetrapod orders plotted on paleomaps and will offer observations gleaned from these maps.

<u>Aistopoda.</u> Aistopods were completely limbless. They have elongated backbones consisting of up to 230 vertebrae. (Earth Science Club of Northern Illinois, 1989) They were amphibious and most likely aquatic. Today, their fossils are usually found in coal swamp locations. (Carroll, 1992) Figure 5 shows the paleodistribution of aistopods during the Pennsylvanian (red diamonds) and Permian (blue diamonds) periods. The geographic dispersal of this order appears to be rather slow and unidirectional. Their distribution is restricted to paleoequatorial regions. Although the map does show a slight southward advance during the Permian, it must be remembered that the continents drifted northward during this time period and that the apparent southward advance is more accurately interpreted to reflect continued aistopod presence along the paleoequatorial

region during the northward advance of the continents. Considering the slow physical dispersal of the order, it is perhaps not surprising that speciation is also relatively slow, with just two different families and two different genera identified from the fossils of the time period represented.

<u>Anthracosauria.</u> Anthracosaurs were also amphibious. Many researchers consider them the ancestors of the amniotes and, by extension, the reptiles (but see Sumida and Modesto, 2001). As Figure 6 shows, they appear early in the fossil record, first showing up during the Mississippian period (yellow diamonds) and continuing through the Pennsylvanian (red diamonds) and Permian (blue diamonds) periods. Their dispersal appears bidirectional, spreading laterally in the paleoequatorial region. They show a higher degree of speciation, with 10 distinct families and 25 different genera identified, but this is expected, perhaps, for an order represented in the fossil record for such a great length of time.

<u>Captorhinida.</u> Captorhinida are the earliest reptiles represented in the fossil record. (Modesto and Smith, 2001) They are notable for their large, bulky bodies and their strong limbs. Figure 7 shows the distribution of their fossils. Once again, the apparent southward migration displayed on the map is actually a result of the northward drift of the continent from the Pennsylvanian (red diamonds) to the Permian (blue diamonds) period. The presence of a Captorhinida fossil in modern day South Africa is notable, and suggests either widespread dispersal, with a large geographic gap in the fossil record possibly due to preservational issues or sampling biases, or taxonomic or temporal misidentification.

Cotylosauria. Cotylosaurs (Figure 8) are problematic to this database in that their taxonomic treatment varies in the research literature. They have been variously treated as a separate order from (Laurin, 2004), a superorder of (Warren, 1961) and as a synonym for Captorhinida. (e.g., see Biognomen, Brock Filer at: http://webpages.charter.net/teefile/biognomen/Cotylosauria.html) For this reason, Figure 9 combines the distribution of both orders on one map. If this is a reasonable representation, then it shows an interesting paleobiogeographic pattern, as the Captorhinida disperse laterally during the Mississippian period (red diamonds) and then split off during the Permian, with one group (blue diamonds) continuing its lateral movement and remaining relatively taxonomically stable, and another group (yellow diamonds) moving northward and undergoing greater evolutionary changes perhaps through vacariance or simple divergence. While this interpretation is open to question, the fact that the Cotylosauria do not appear in this database until the Permian period undermines the justification for treating them as a superorder, that is, a group from which the Captorhinida branched off.

Mesosauria. Mesosaurs were the first reptiles to return to water. They are noted for their broad tails, long hind legs and fine teeth that some researchers assert were used for straining plankton and small crustaceans (Carroll, 1982). As seen on Figure 10, mesosaurs were able to move away from the paleoequatorial regions well into the southern latitudes. They have been found only in what is present day South America and Africa. In fact, the presence of mesosaur fossils on both continents was taken as early evidence in support of the theory of continental drift. Despite their wide dispersal, mesosaurs evince surprisingly low diversity. They are, in fact, monophyletic, with only one family and one genus represented in the database. Also surprising is the fact that, despite their compete return to aquatic environments, their only appearances on the map are in the middle of the southern continent.

Microsauria. The amphibious microsaurs include the modern salamanders as their descendants. They are generally small and diverse, ranging from fully aquatic to terrestrial and lizard-like in appearance, which in the past has caused some taxonomic confusion. (Henson, 1996) Their fossils distribution is shown on Figure 11. As can be seen, they experienced only limited lateral dispersal during the Pennsylvanian (red diamonds) and Permian (blue diamonds) periods, which makes their broad diversity (5 families recorded, with 10 identified genera) somewhat surprising. Their small size may be a partial explanation for this. Even though the range of the order is limited, the size of the range relative to the size of an individual is large. The distance needed to separate one population from the closest nearby population was probably not very great, and the dispersal range illustrated on the map may represent a very high number of isolated populations that thus led to the high diversity reflected in the fossil record.

Nectridea. Like the microsaurs, the nectrideans were generally very small and amphibious. They were usually aquatic and often display large, boomerang-shaped heads. Figure 12 plots the location of Pennsylvanian (red diamonds) and Permian (blue diamonds) period nectridean fossils discoveries and shows that nectrideans also had relatively wide lateral dispersal but remained close to the paleoequator. Large geographic gaps are also revealed, which may reflect the difficulty of finding fossils of such a typically small tetrapod. Comparing Figures 11 and 12 shows that the ranges of both orders were very similar and may have overlapped in areas. Nectrideans do not show quite as much diversity as the microsaurs, however. They are represented in the database by just 3 families and 7 identified genera.

Pelycosauria. Pelycosaurs are taxonomically problematic, largely because of their morphological diversity (Hanson, 1996). They are often grouped as a suborder of the reptilian synapsida. Others treat them as a distinct order and treat synapsida as a superorder or subclass (Hansen, 1996). Still others avoid the use of the term synapsida altogether (Foreman and Martin, 1988). The collections included in the database treat pelycosaurs as a distinct order, so that is the approach taken here, and the term synapsida is not used. Pelycosaurs were not amphibious, but their classification as reptilian is also tenuous. They are considered the ancestors of the earliest mammals (Reisz, 1988), and there is speculation that they may have developed a primitive endothermia (McNab, 1978). Their geographic distribution, as shown in Figure 13, is slightly farther north of the paleoequator than most of the other orders examined, although their position during the Pennsylvanian period was much closer to the paleoequator and appears northern here due to continental drift. Despite their possible endothermia, their distribution is primarily lateral; there is only very limited latitudinal distribution. Pelycosaurs show a broad diversity considering their somewhat limited distribution, with 7 families and 15 identified genera represented in the database. This suggests the possibility that, even though they were not widely dispersed geographically, they may have had adaptations (such as endothermia) that enabled them to move into a wider range of environments and/or elevations that may have ultimately led to separation of different populations.

Temnospondyli. Temnospondyls are the amphibious ancestors of modern frogs and toads. (Carroll, 2001) They were usually semi-terrestrial and are noted for their large heads relative to their body size. Figure 14 shows their distribution plotted on a map showing the positions of the continents during the Pennsylvanian period. The temnospondyls appeared early in the fossil record and remained for the duration of the Paleozoic era. As might be expected because of the longevity of the order, they are very diverse, with 16 different families and 40 different genera identified from the specimens. With one exception, discussed below, their distribution is mostly lateral across the paleoequatorial region.

The appearance on the map of a specimen in a glaciated area (lower southern hemisphere) seems unlikely. However, as the key indicates, this specimen dates from the Permian period. During much of the Permian period that part of the globe was warmer and the glaciers had retreated. However, there is still a significant geographic gap between that specimen and all other recorded specimens. While it is possible that this gap is due to lack of preservation or sampling bias, it is also possible that this specimen has been misidentified.

Therapsida. Therapsids are closely related to the pelycosaurs. They are often grouped with or referred to as synapsids. Although considered reptiles, many of their skeletal features were mammal-like. They were well designed for land travel, and during the Permian period they were the dominant land animal, dispersing far from the paleoequator and spreading throughout most of Gondwana and even into Kanzakhstania despite their relatively late appearance in the fossil record. (See Figure 15.) This wide dispersal may have been responsible for the wide taxonomic diversity reported, with 11 identified families and 19 identified genera represented in the collections examined. Once again, large geographic gaps are visible on the paleomap.

CONCLUSIONS

Gaps in the fossil record, both temporal and geographic, clearly hinder attempts to draw paleogeographic inferences from the paleomaps about the radiation and speciation of tetrapods. Despite this limitation, some patterns are observable. Most of the orders, including all of the amphibians, with the exception of the one possibly misidentified temnospondyl discussed earlier, were restricted to a narrow paleoequatorial region. The two exceptions were the therapsids and the mesosaurs. These “pioneer” orders apparently developed an evolutionary advantage that allowed them to leave the tropical regions for temperate climates. For the mesosaurs, returning to an aquatic environment may have enabled them to increase their range since the marine environments may have dampened temperature fluctuations. The therapsids were land-based, however, and the expansion of their range into temperate zones raises intriguing possibilities. One is that some of them were endothermic. Another possibility is that they may have developed the ability to hibernate during the colder seasons.

A few observations about species diversity are possible. In general, the diversity of an order increases the longer that order appears in the fossil record, e.g. anthracosauria and temnospondyli. Range also plays an apparent role, e.g., therapsida, but the correlation of range size with species diversity is not simply linearly proportional. Rather, the range of an entire order relative to the range of an individual member of that order appears to be a factor, as with the microsauria.

LIMITATIONS

As mentioned earlier, all four collections used for this project were from museums in the United States. The distribution of tetrapods represented in the database may be biased in favor of fossils discovered in North America due to the choice of collections incorporated into the data set. Many of the geographic gaps observed in the reptiles made be due to this sampling bias, and the author's suggestions of misidentified fossils that are inspired by the gaps may be unjustified.

The spatial resolution of the paleomaps and the inconsistent precision in pinpointing the location of the fossil recovery sites limits the ability to draw inferences about the local environmental conditions of the specimen's original habitat. This restricts the possibility of identifying refugia, geographical barriers, or other physical characteristics that might aid in identifying instances of radiation, vicariance and/or allopatric or sympatric speciation. The lack of precise temporal resolution also hinders attempts to identify extinction patterns and identify features posing extinction risk factors.

Finally, taxonomic uncertainties and disagreements impact the paleobiogeographic representations of the paleomaps. Whether or not a particular specimen or group of specimens is included with a taxon can have a large impact on the geographic distributional pattern revealed. Therefore, all interpretations of these patterns should be considered tentative.

IMPLICATIONS FOR FUTURE RESEARCH

It is hoped that the data set included in this database will expand. Increasing the number of entries can help increase the spatial and temporal resolution. It may also help fill in some of the geographic and taxonomic gaps. Increasing the geographic distribution of collections incorporated to include collections from outside the United States may help to ameliorate the possible North American bias in the discovery locations.

Increasing the number of entries might increase spatial resolution enough to allow the examination of distributional patterns at the familial or generic level. A corresponding increase in temporal resolution could allow the researcher to examine extinction patterns through the Paleozoic era.

Finally, including entries from the early Mesozoic era could yield clues about survival patterns across the Permian/Triassic boundary. A greater understanding of which species managed to survive this mass extinction and the geographical distribution of those species may yield additional clues about the sequence of events that contributed to this greatest of all mass extinctions. Assembling this information into a single database can facilitate the examination of the early history of tetrapods from many different perspectives using many different criteria.

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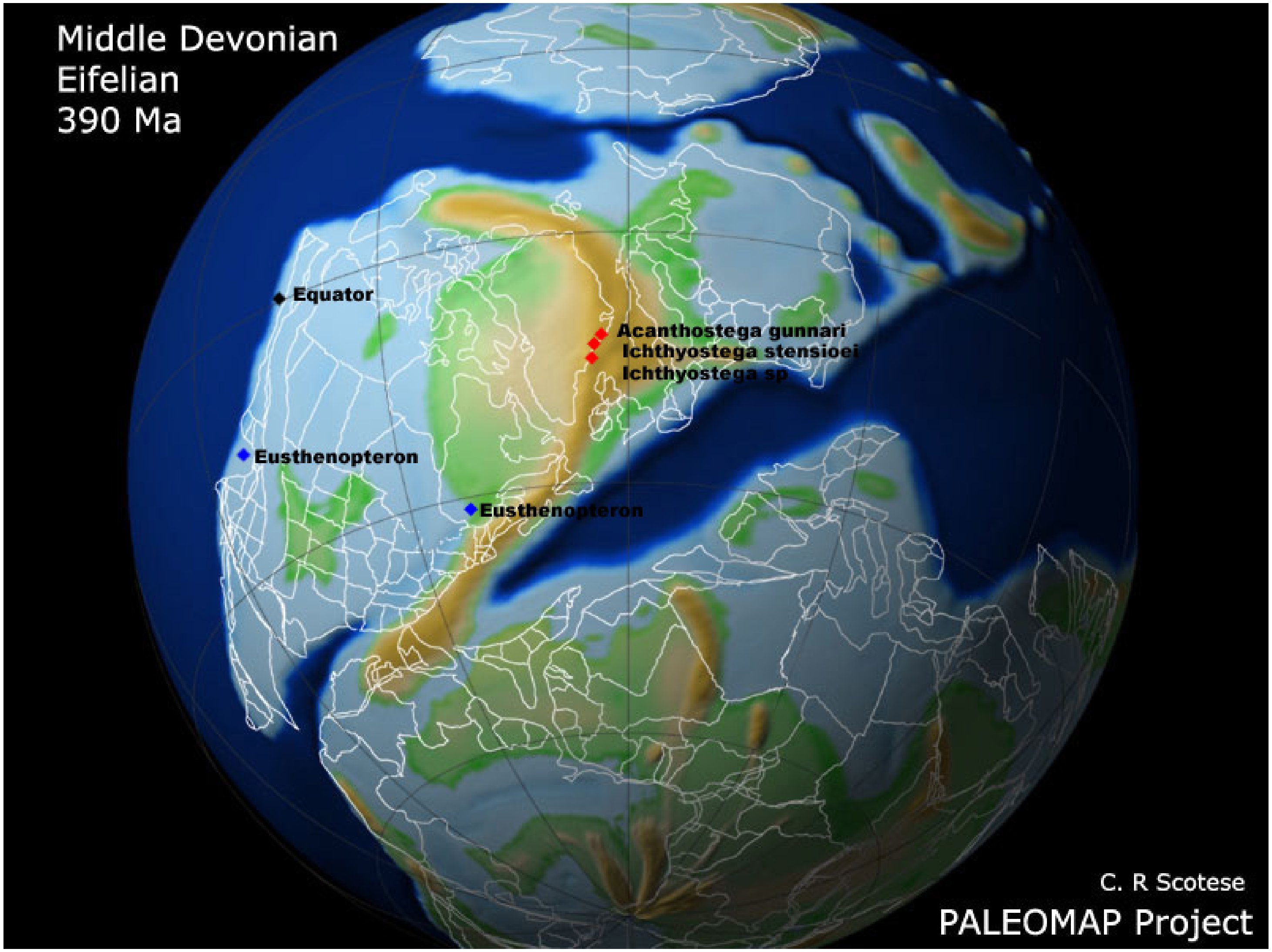

Figure 1: The Devonian period.

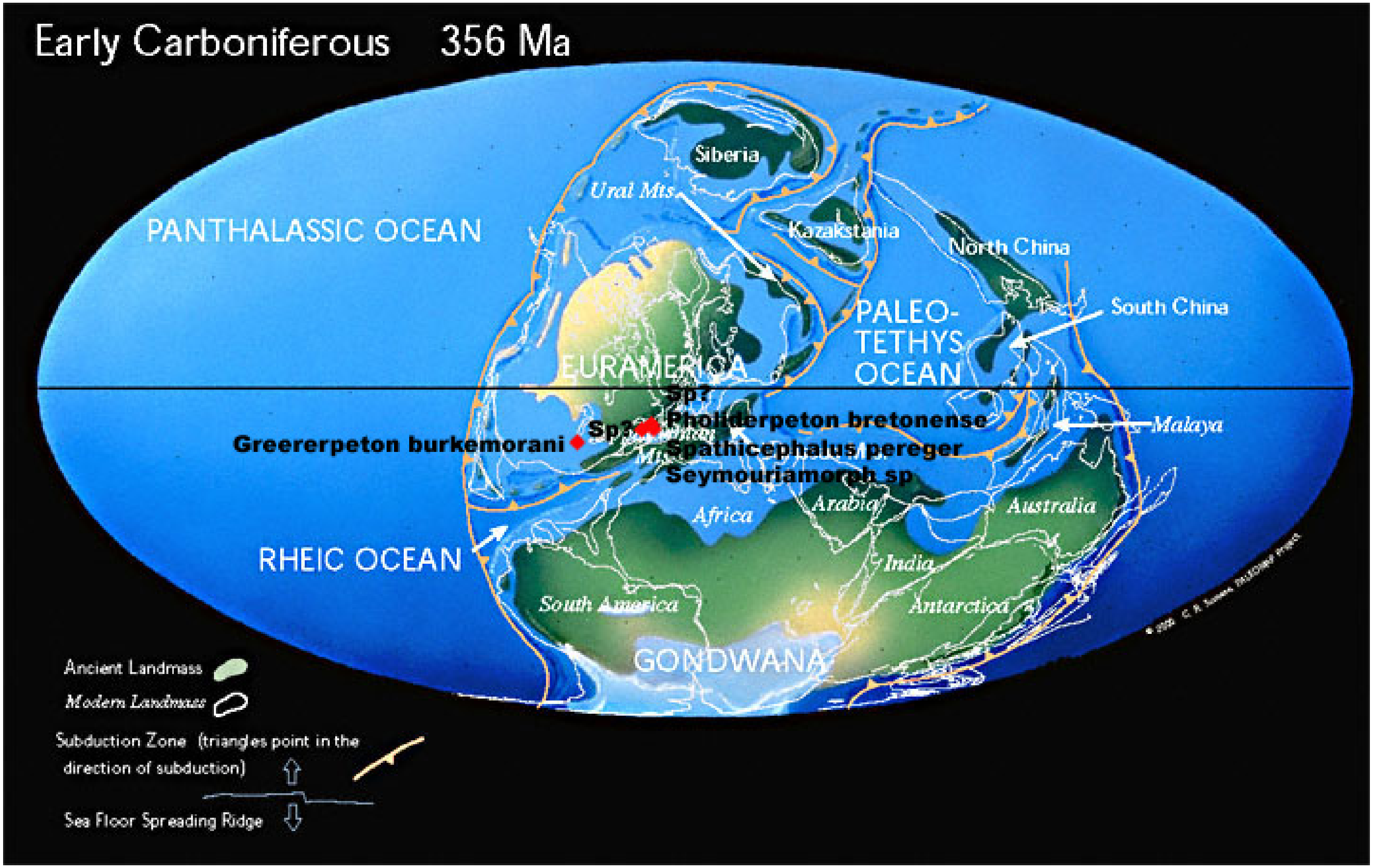

Figure 2: Mississippian period tetrapod fossils.

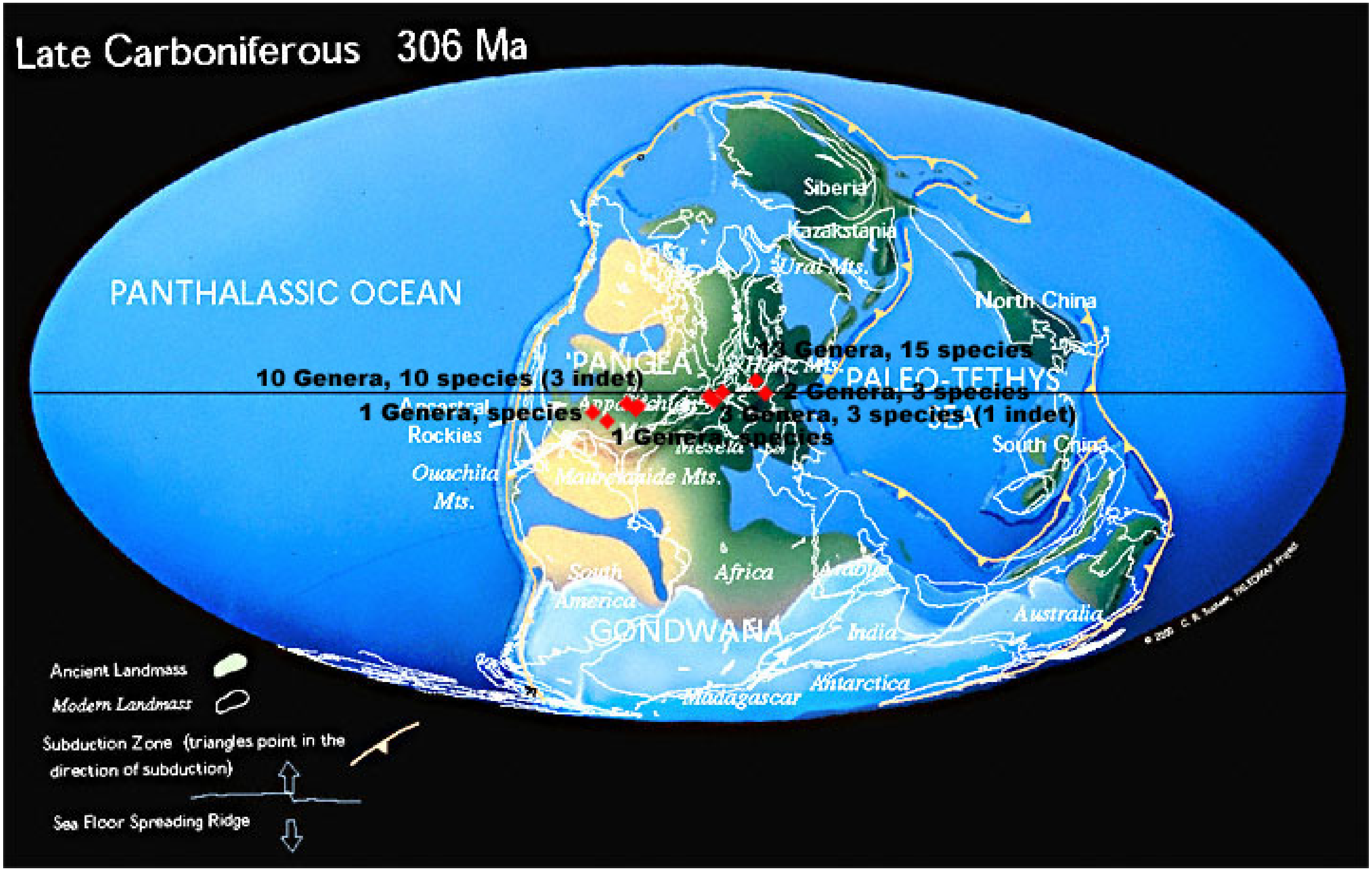

Figure 3: Pennsylvanian period tetrapod fossils.

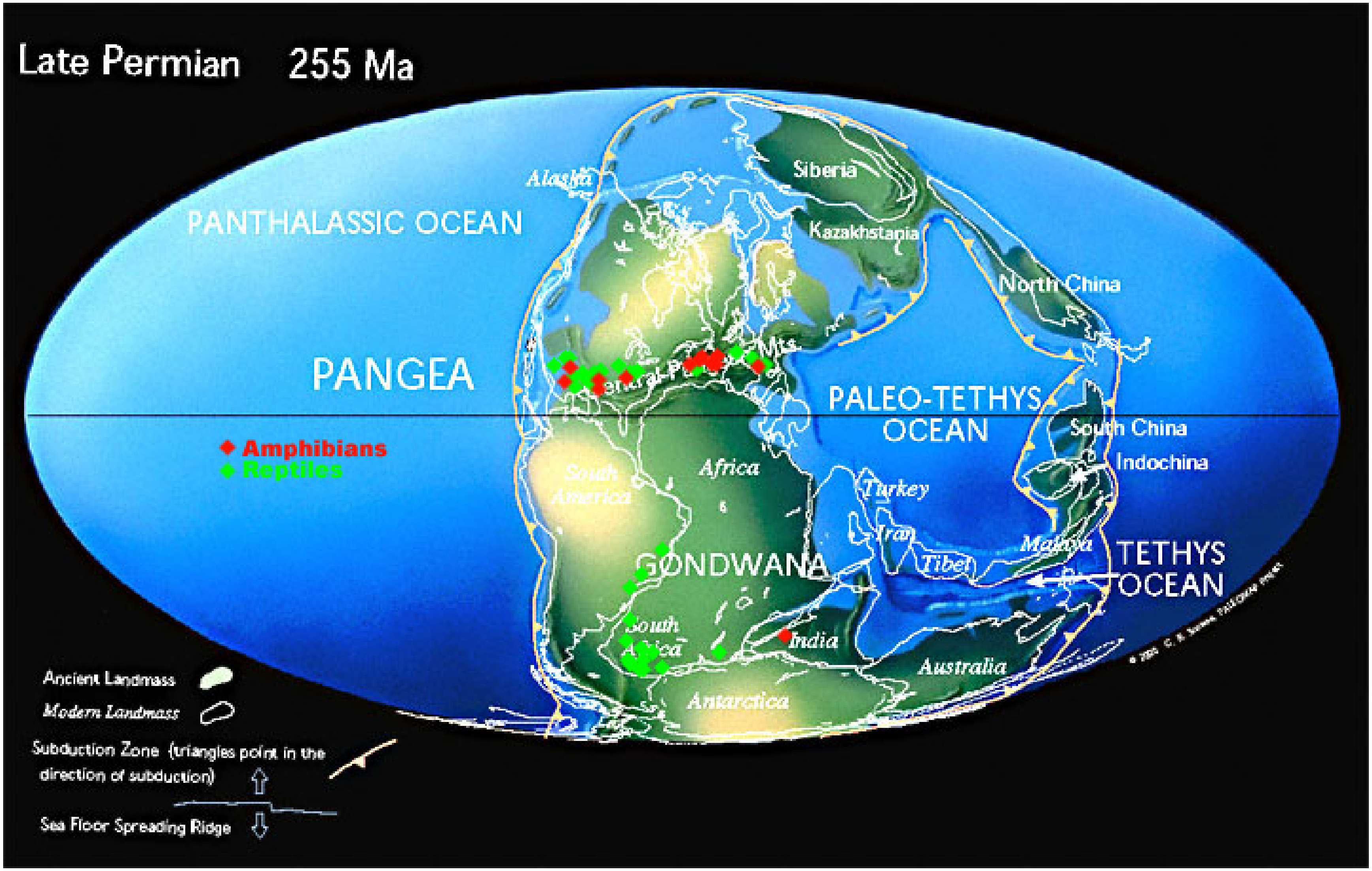

Figure 4: Permian period tetrapod fossils.

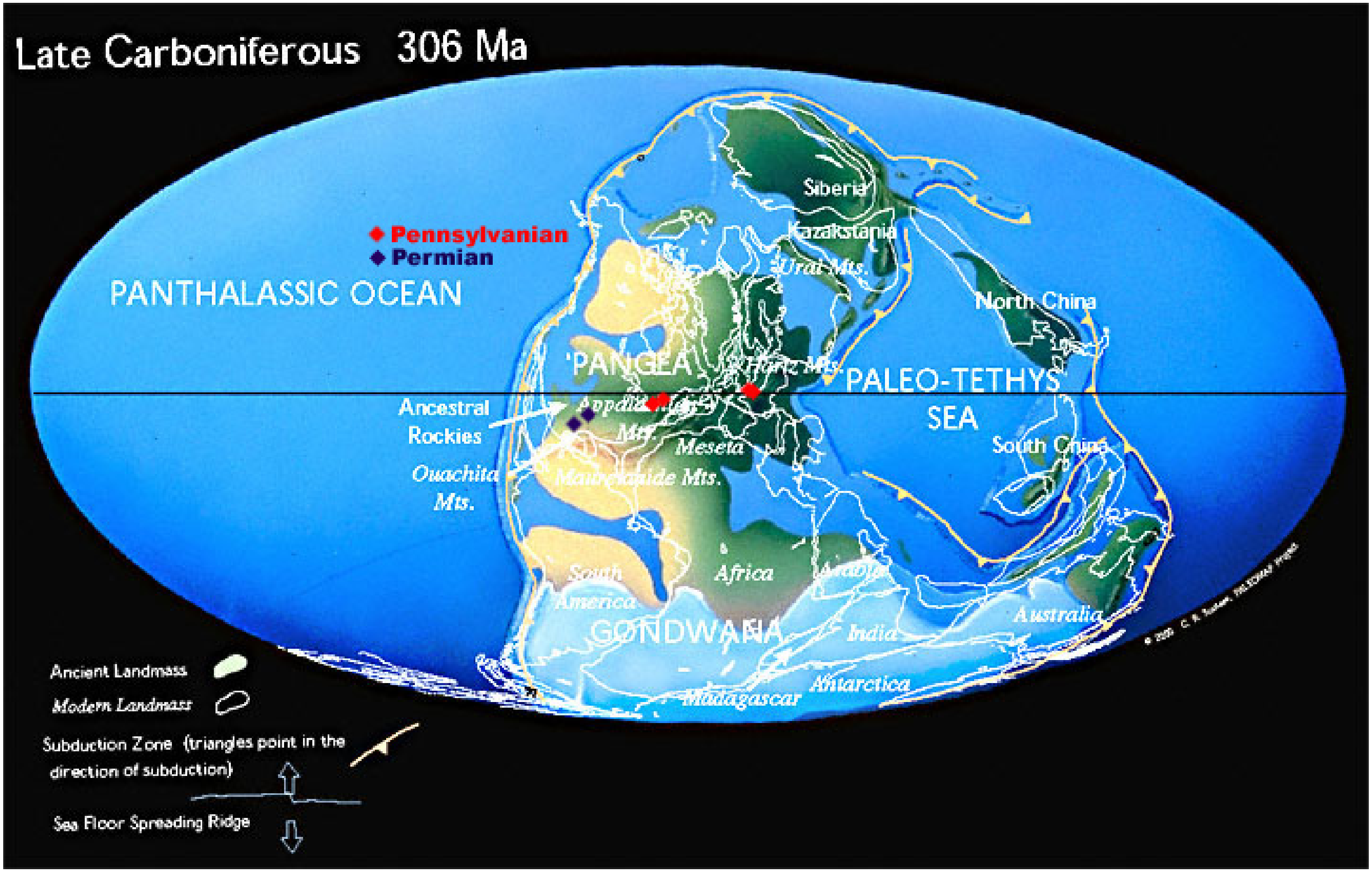

Figure 5: Distribution of Aistopoda.

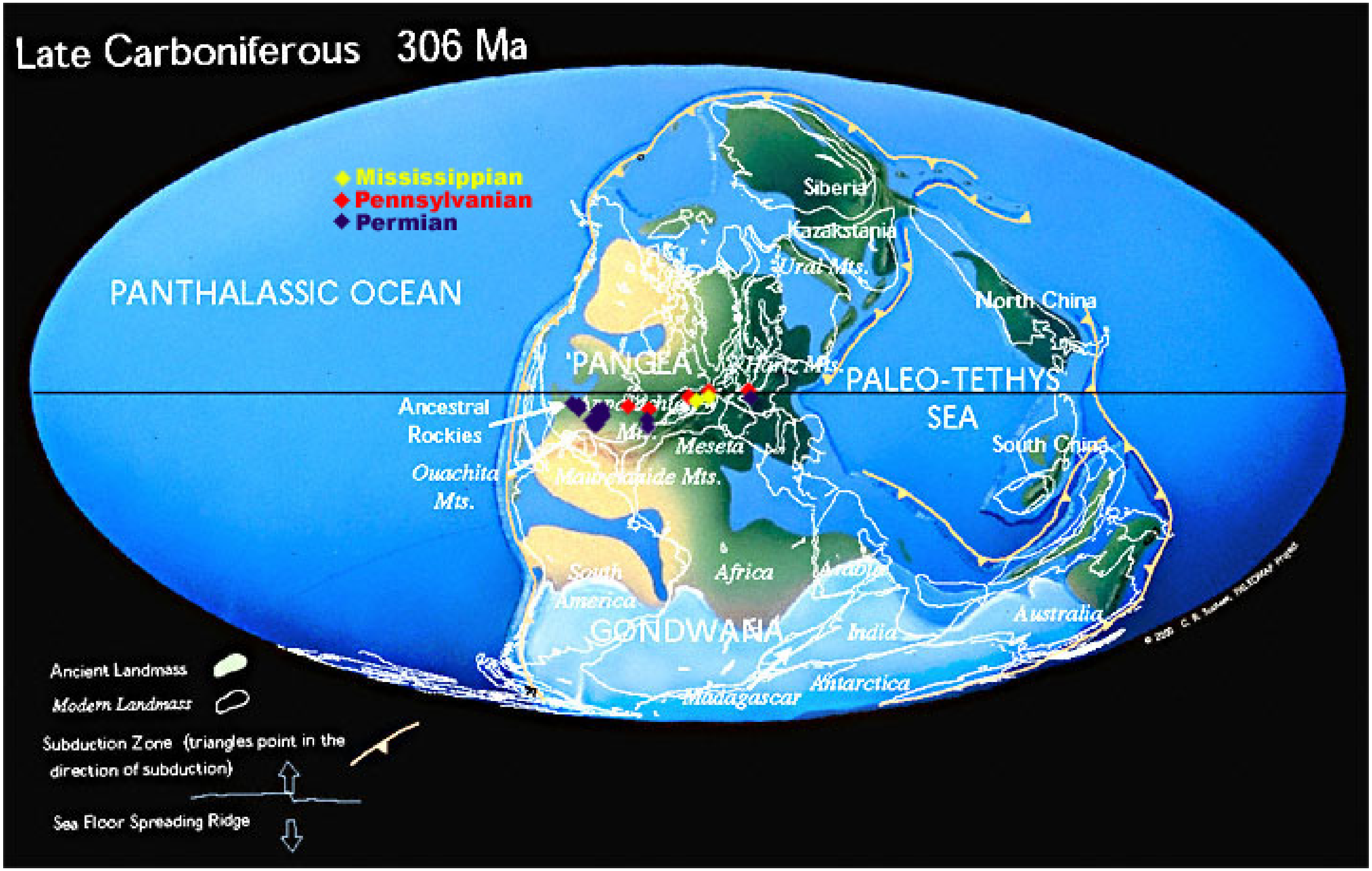

Figure 6: Distribution of Anthracosauria.

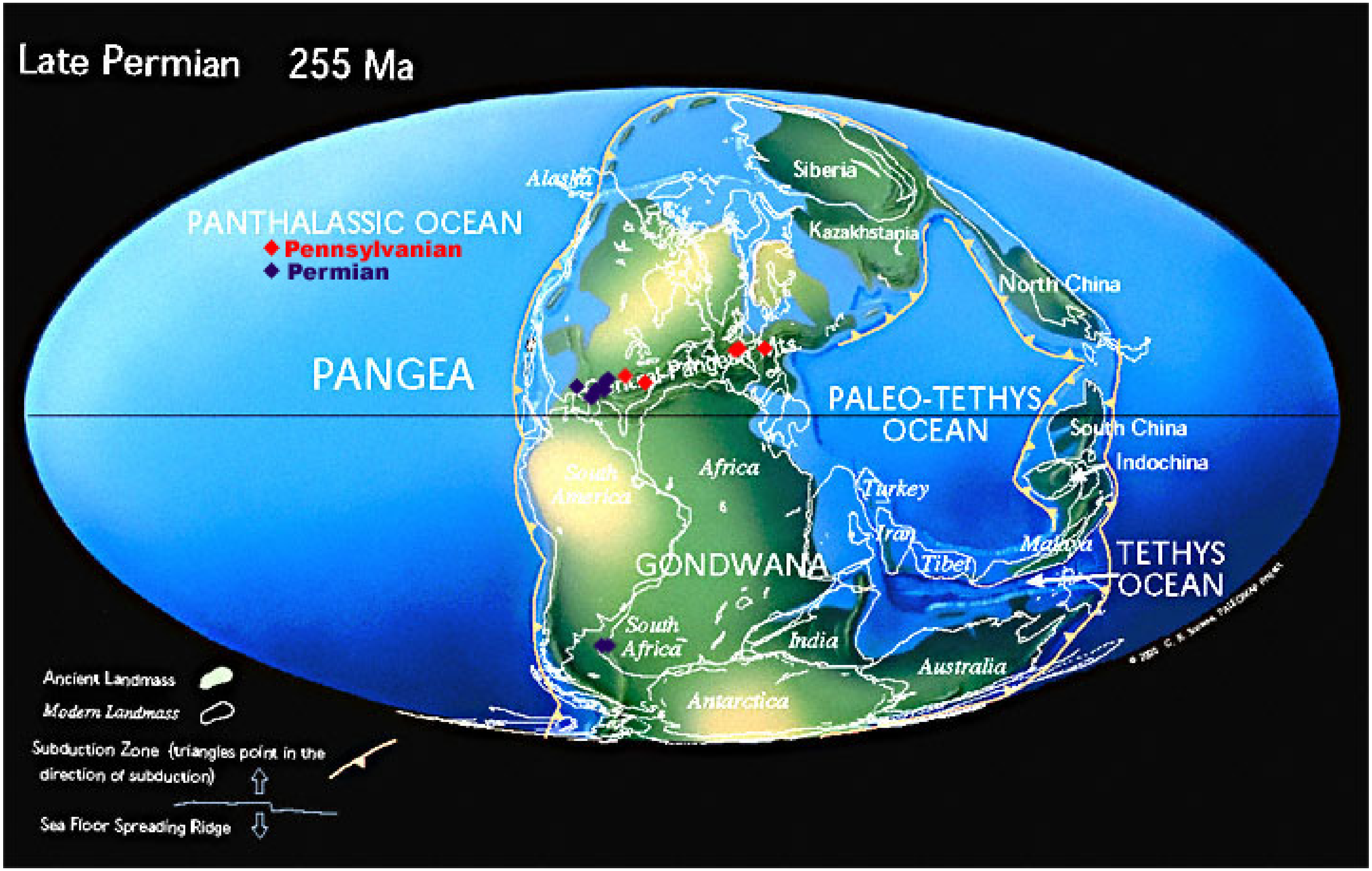

Figure 7: Distribution of Captorhinida.

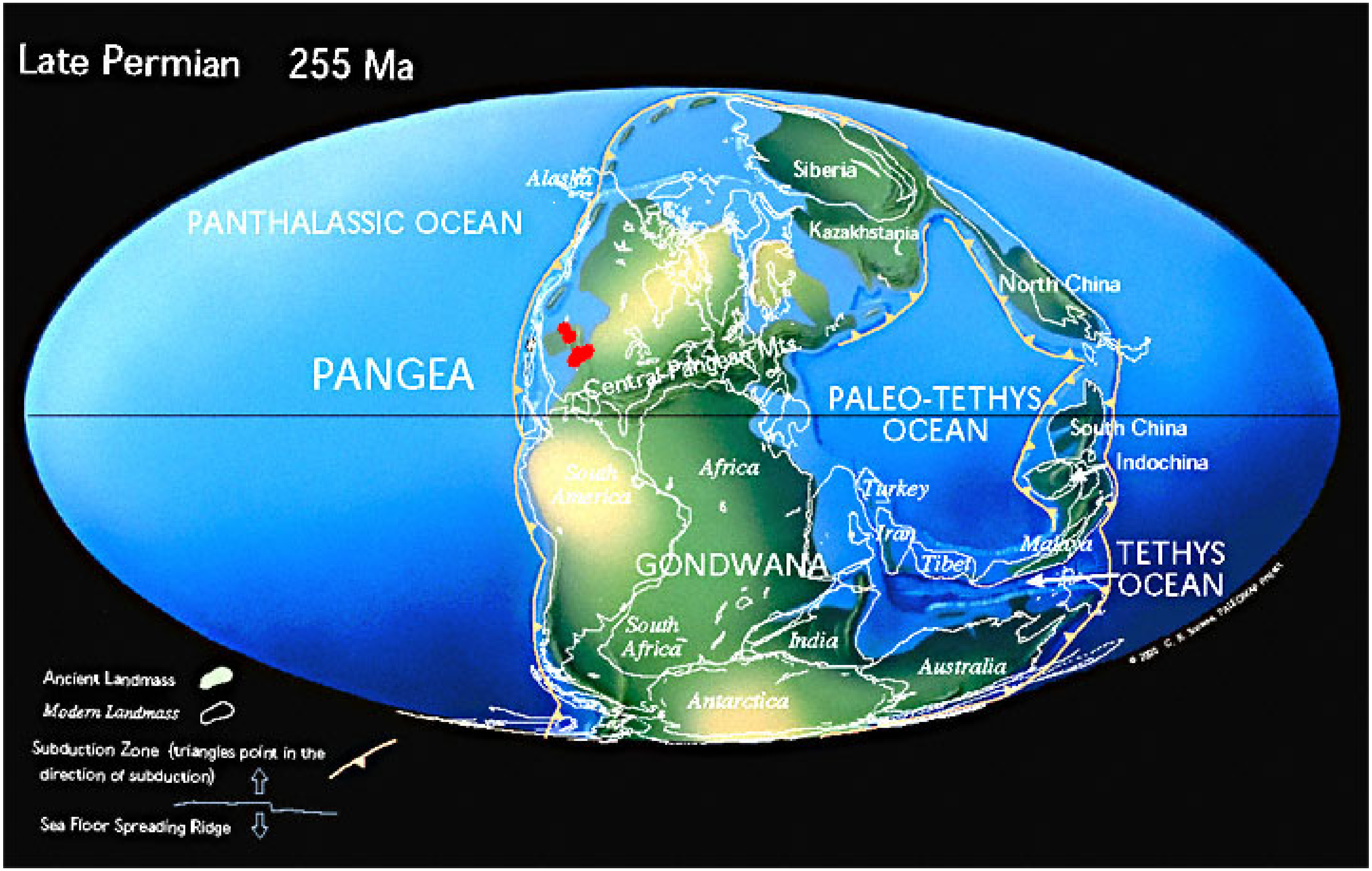

Figure 8: Distribution of Cotylosauria.

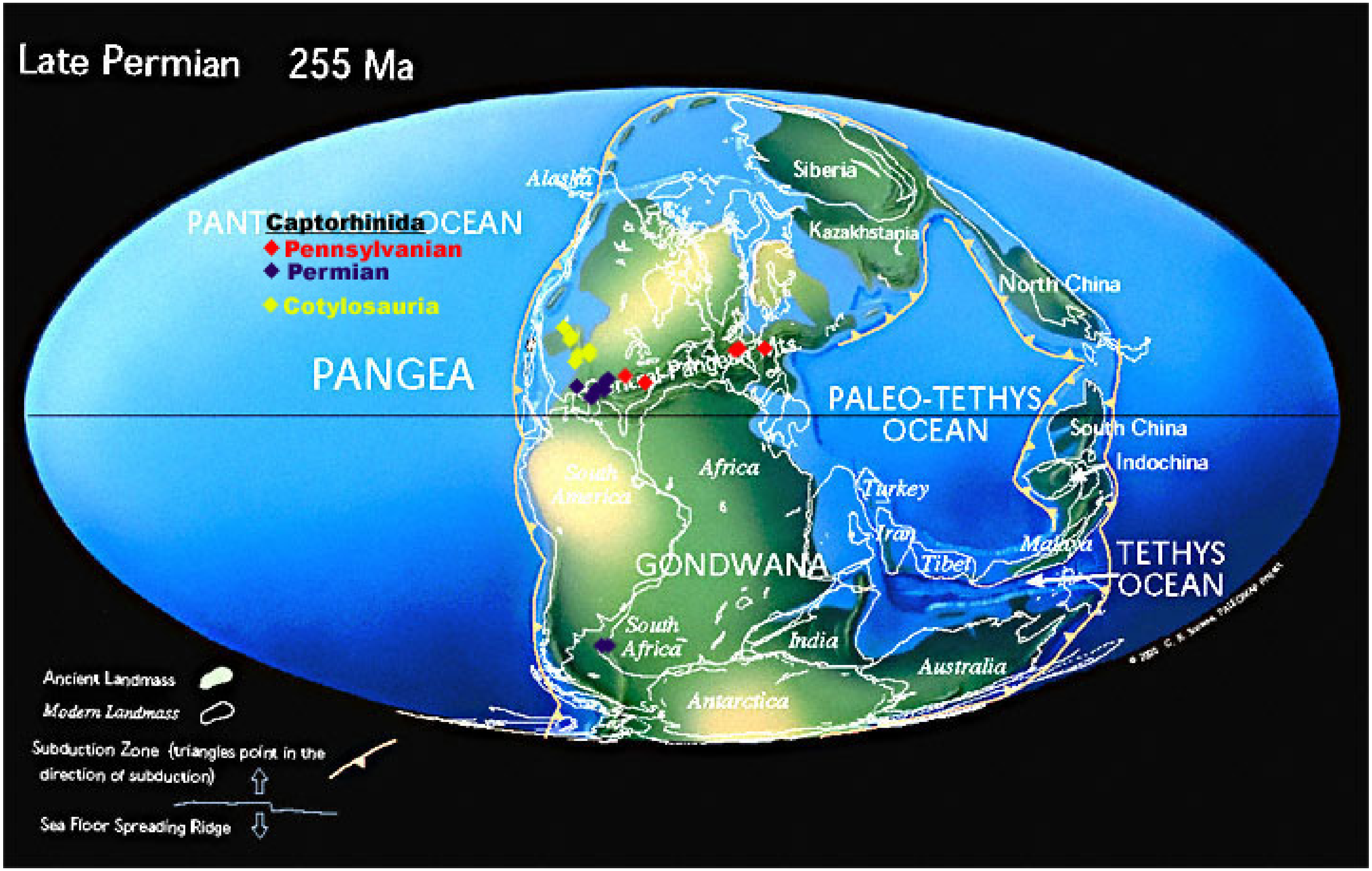

Figure 9: The distributions of Captorhinida and Cotylosauria.

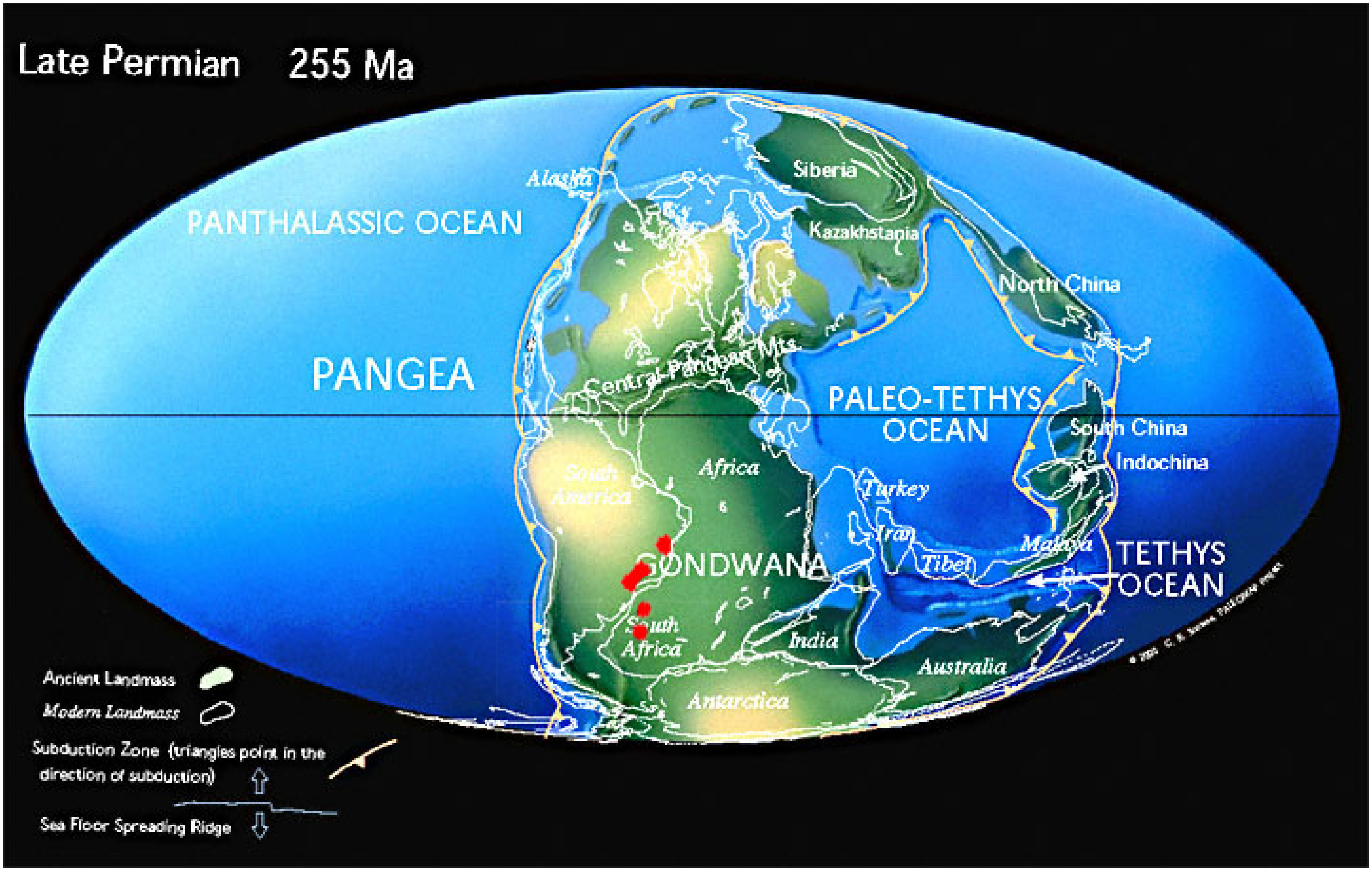

Figure 10: Distribution of Mesosauria.

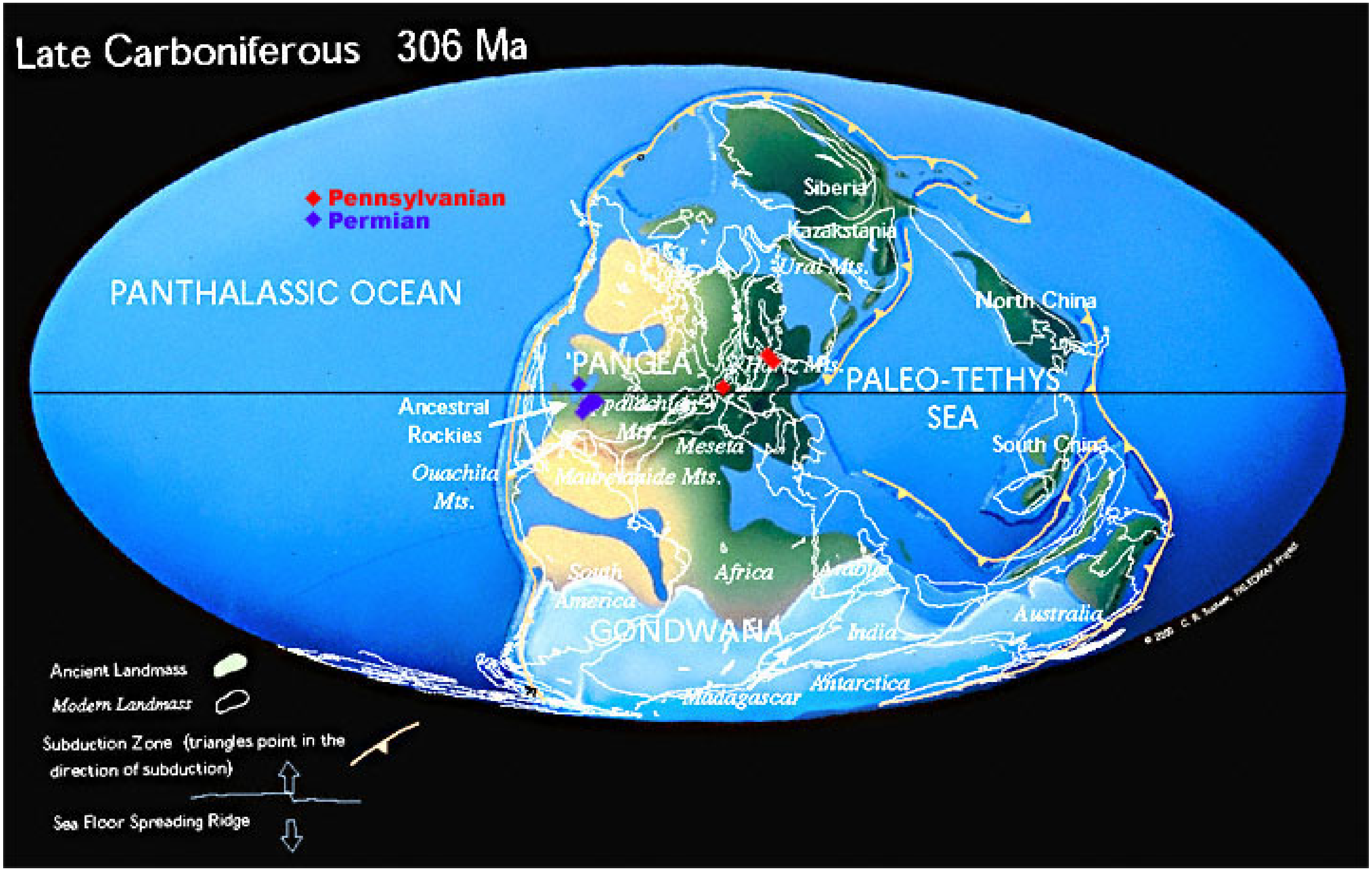

Figure 11: Distribution of Microsauria.

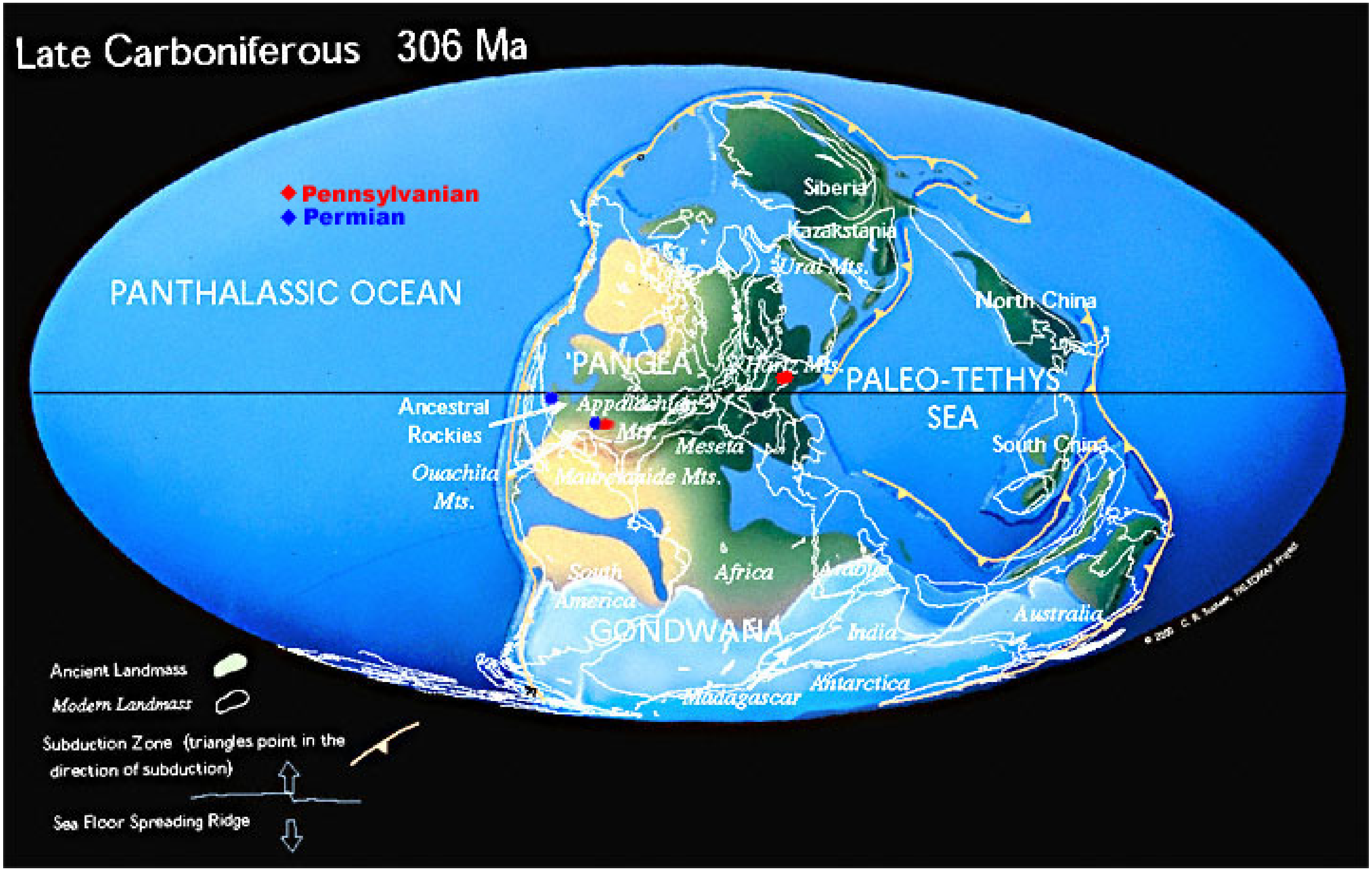

Figure 12: Distribution of Nectridea.

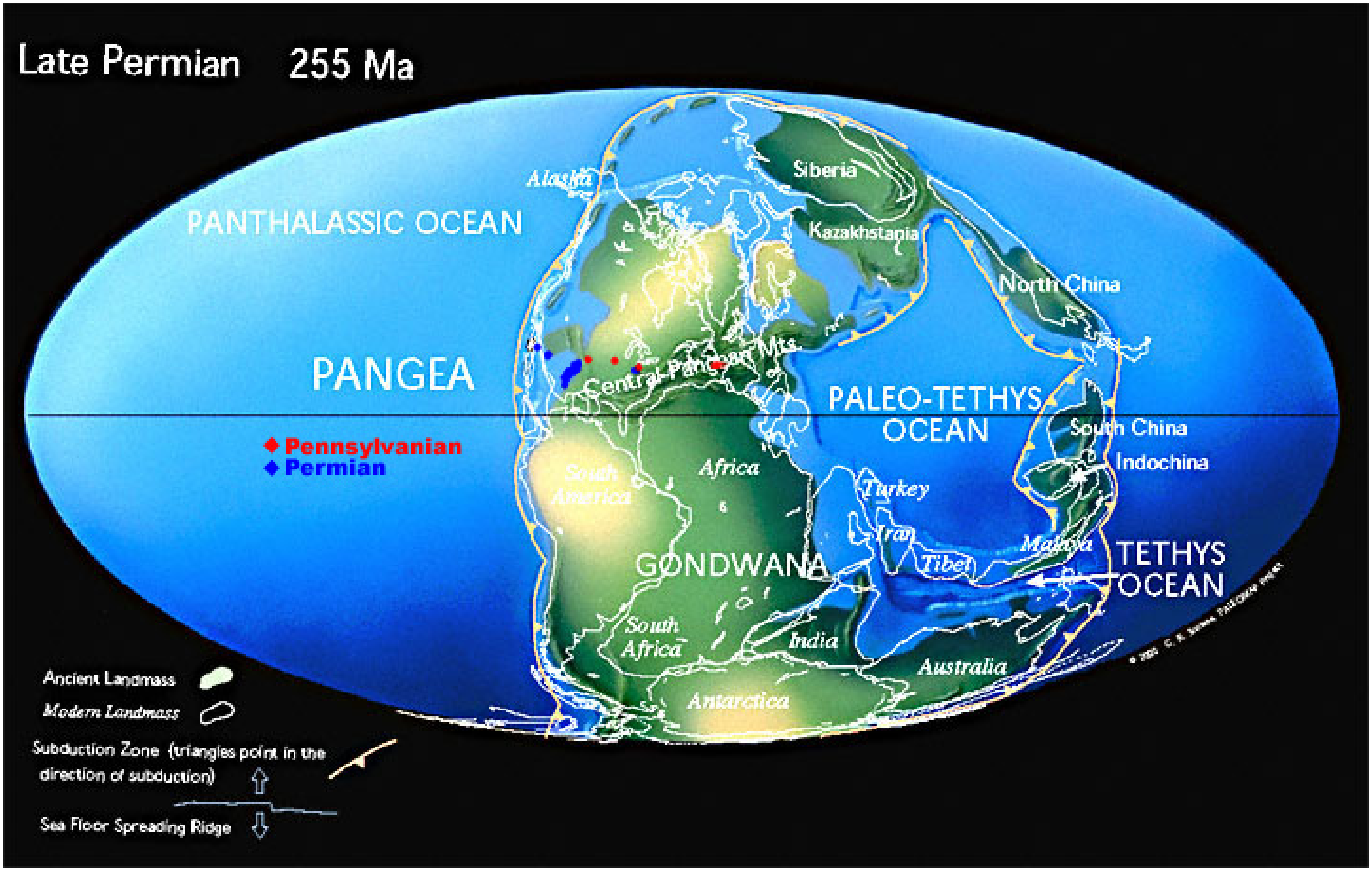

Figure 13: Distribution of Pelycosauria.

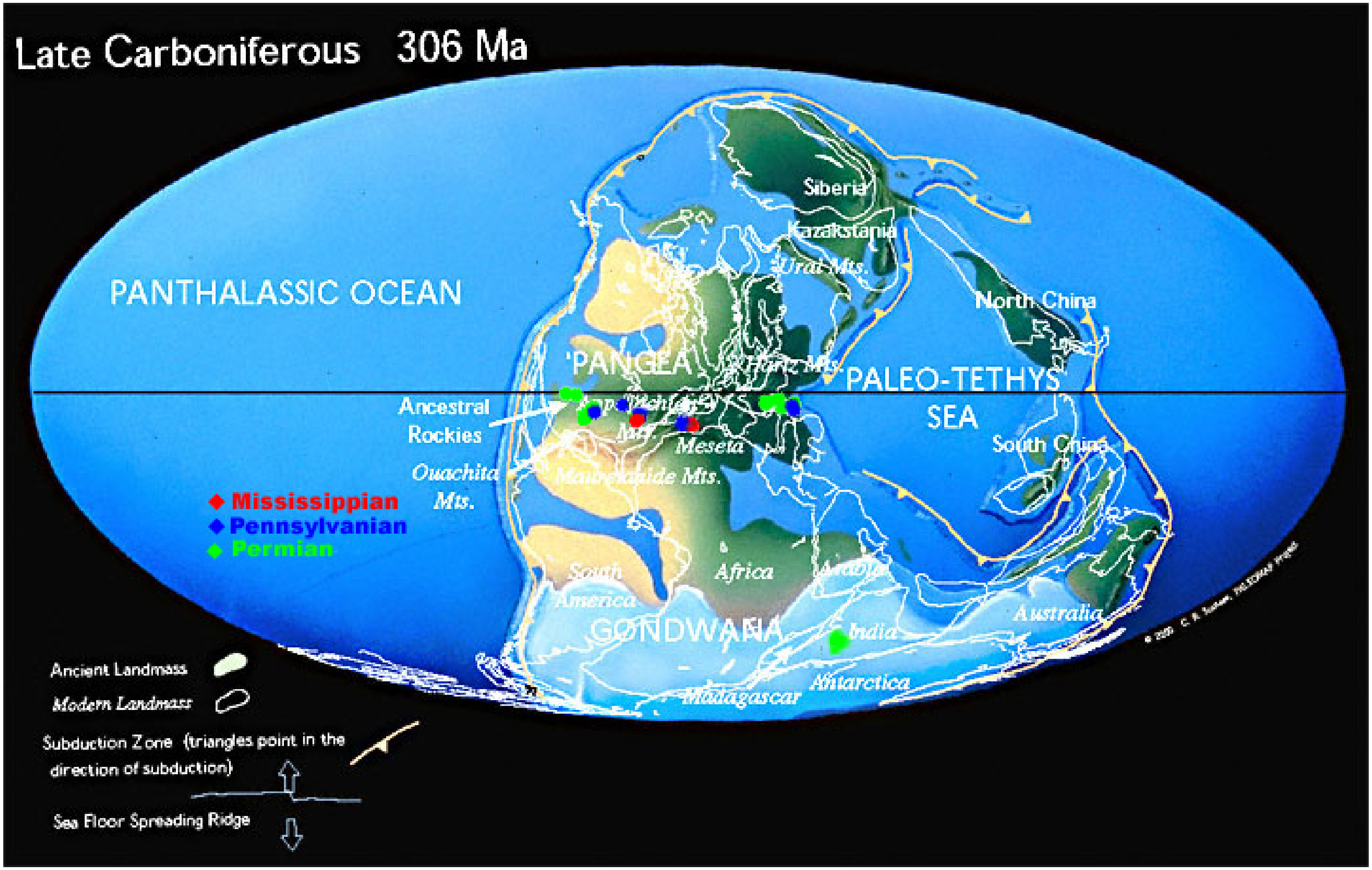

Figure 14: Distribution of Temnospondyli, plotted on a Pennsylvanian period paleomap. The glaciation of the southern hemisphere had disappeared by the middle of the Permian period.

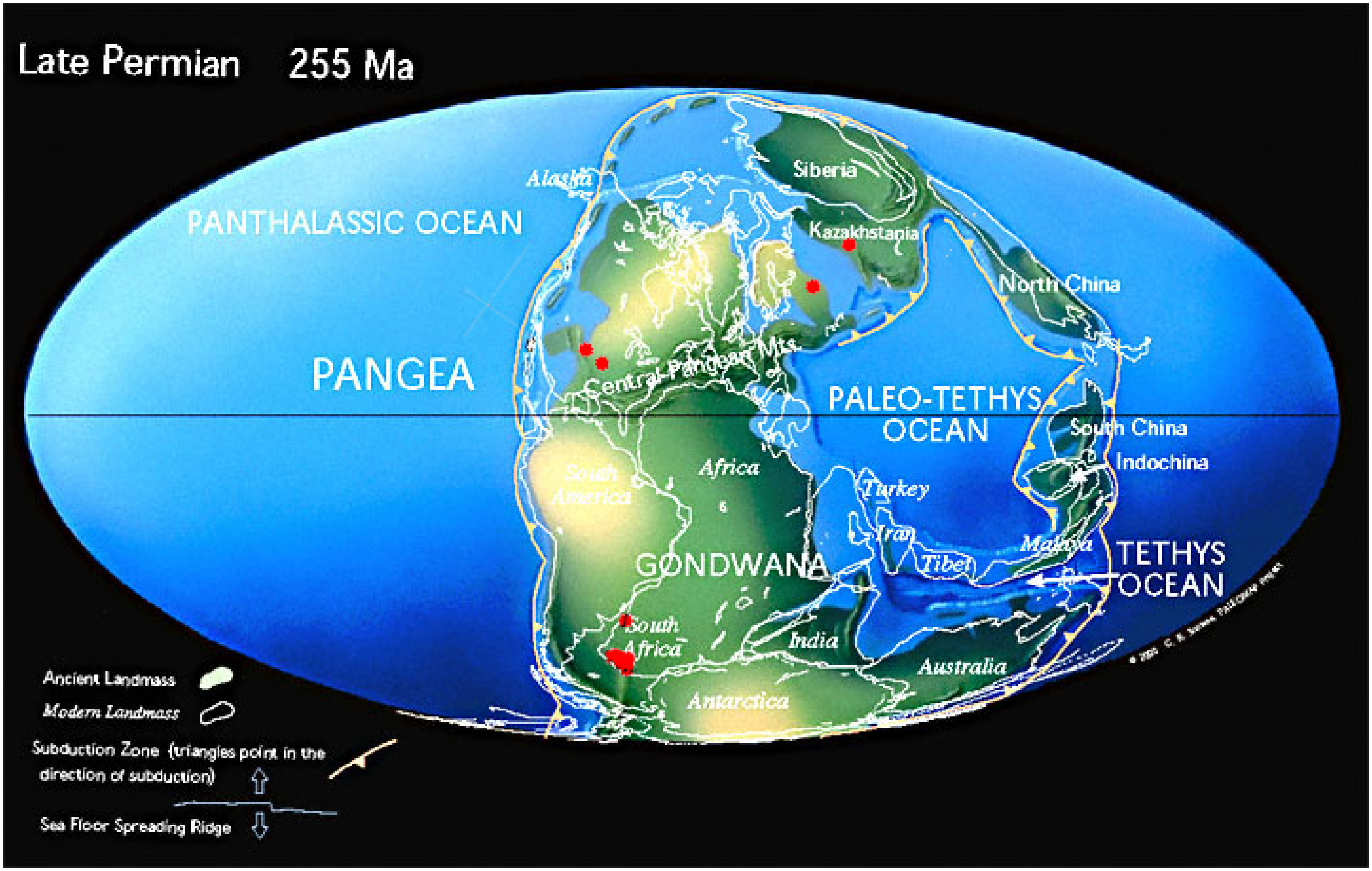

Figure 15: Distribution of Therapsida.