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Jurassic-Pliocene biogeography: testing a model with velvet worm (Onychophora) vicariance

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Abstract: Summary paleomaps of global continental vegetation from the Jurassic through the Pliocene were prepared (based on the literature) and used to define an area cladogram. Bouvier's natural classification of velvet worms (phylum Onychophora) was used to define a taxonomic/geographic cladogram of onychophorans for all regions where they are found today. Both cladograms show the same sequence of geographic vicariance. Thus, the paleogeographic model is supported by the taxonomic evidence. The paper includes a color atlas.

Key words: Onychophora, vicariance, retrovicariance, biogeography, cladistics, biogeography, Mesozoic, Cenozoic.

In the last decades, the availability of computers has resulted in a rapidly growing number of paleogeographic models that often differ among themselves (Scotese *et al.* 1988, Gyllenhaal *et al.* 1991, Patzkowsky *et al.* 1991) and normally use little or no biological information as a basis (Briggs 1989, Parrish 1993a).

This paper, which emphasizes the tropics and is addressed mainly to biogeographers, presents a summary of several paleogeographic reconstructions and includes brief descriptions of terrestrial ecosystems from a recent and comprehensive review (Behrensmeyer *et al.* 1992). The maps were used to produce an area cladogram that shows the sequence in which large landmasses separated from the Jurassic through the Pliocene, for comparison with independent evidence based on velvet worm taxonomy (phylum Onychophora).

Onychophorans, a group of scarce terrestrial worms, have long been considered appropriate biogeographic subjects because of their old age and low capacity to disperse (Sedgwick 1908, Vachon 1954, Monge-Nájera 1995). A review of the classification and keys of the phylum presented by Bouvier in 1905, showed that he intended them to present a natural classification (see Bouvier 1905: 7, 74-66). Thus, for this study, his classification was converted to graphic form by preparing a cladogram, which in this group is thought to reflect both the sequence of geographic isolation and of speciation (see Sedgwick 1905 and Ruhberg 1985).

This paper shows that when both cladograms are compared, they imply the same sequence of geographic isolation for the general areas where the phylum occurs today.

MATERIAL AND METHODS

Paleogeographic reconstructions are based on the projections presented by Briggs (1989), who takes into account biological evidence, and on a list of sources too long to repeat here but presented in Monge-Nájera (1995). Marine currents (Schopf 1980) and climatic data (Condie 80, Parrish 1993b) were added to the original maps. The hypotheses about overall vegetation types are based on the general associations between temperature, precipitation and plants in the modern world (Walter and Breckle 1986).

To convert the maps into the area cladogram, the sequence of separations was represented by a line that bifurcated whenever two areas separated. The same procedure was used for the onychophoran cladogram, by bifurcating the line whenever cladogenesis took place according to the classification and identification keys presented by Bouvier (1905). This is the standard procedure to make classifications into cladograms and assumes them to be natural rather than artificial (Brusca and Brusca 1990).

RESULTS

The paleogeographic maps appear in Figs. 1-11 and the area cladograms in Fig. 12.

Area relationships: There is important disagreement among authors regarding the position of India in the late Jurassic; it is thought to be closer to Australia, isolated, or connected with Antarctica according to fossil evidence from belemnites, dinosaurs and plants, respectively (Hallam 1973, 1994, Schuster 1983, Briggs 1989). The position presented in Fig. 3 and the following maps is the one that seems less conflictive with current evidence.

Despite the separation shown between Europe and Asia in the early Cretaceous (Fig. 4), plants and dinosaurs were relatively cosmopolitan in Laurasia and in Gondwana (Schuster 1976, Behrensmeyer *et al.* 1992). Similarly, North America may have actually been separated from Europe, in contrast with this reconstruction (Burden and Langille 1991). A possible connection of the Greater Antilles with Yucatan or Florida is debated (Coney 1982, Iturralde-Vinent 1988), and India was more to the south according to Barron (1987).

For the mid Cretaceous, reconstructions differ significantly about the position of India and the relationship between South America and Africa (Barron 1987, Dott and Batten 1988). In contrast with this map (Fig. 5), some authors believe that in the late Cretaceous Greenland was becoming an island and that the Antilles were more to the west, in the area where the early Central America is shown here (Alvarado 1988, Dott and Batten 1988). Again, there are other opinions about the position of India (Briggs 1989).

In the Paleocene, this map (Fig. 7) differs from those of Dott and Batten (1988), and Piccoli *et al.* (1991) because they place India to the south and Australia more separated from Antarctica. Also in disagreement with the map of Fig. 8, India may have been still an island in the Eocene (Scotese *et al.* 1988).

In the Oligocene (Fig. 9), South America could have been closer to Africa (Alvarado 1988), but for the more recent periods (Figs. 10 and 11) there are no significant disagreements between the consulted reconstructions.

Vegetation: This Jurassic reconstruction is consistent with Mojon and Mouchet (1992) and with Colorado data in Parrish (1993), but not with paleontological data which indicate moister conditions in NE North America (McDonald 1992), France (Thevenard 1993) and Denmark (Arndorff 1993).

There is a better fit for the Cretaceous (Antartic Peninsula, Chapman and Smellie 1992; Belgium, Bless *et al.* 1993; Nigeria, Edet and Nyong 1993; the Andes, Gayet *et al.* 1993 and Tibet, Xu and Mao 1992). Nevertheless, conifers grew in many parts of Laurasia that this map depicts as shrubland (Cevallos-Ferriz 1992, Millar 1993). Although no recent fossil data for the Paleocene were found, for the Eocene the fit was also satisfactory (Cuba, Siegle-Farkas *et al.* 1992; France, Kohler 1992; Argentina, Leguizamon *et al.* 1993) with the exception of parts of Saudi Arabia and France that had mangroves and humid forests, respectively, instead of savannas (Srivastava and Binoa 1991).

For the Oligocene there is full correspondence between the map and fossils for sites so separate as Antarctica and Europe (Alvinerie *et al.* 1992, Barron and Mahood 1993, Knobloch 1993).

A greater number of recent studies refer to the Miocene and are consistent with the map for Chile (Troncoso 1991), Hungary (Hably 1992), India (Prasad 1993) and Japan (Ina 1992, Sato 1992, Yamanoi 1993). The map

Fig. 1. Identification of continents in Pangaea. Use as basis to identify landmasses in following figures.

shows xeric vegetation in two places where moist–type fossil vegetation was found: Turkey (Gemici *et al.* 1993) and the Niger Delta (Morley and Richards 1993).

The Pliocene reconstruction is fully consistent with data from Antarctica (Marchant *et al.* 1993), North America (Watkins 1992) and Europe (Morley and Richards 1993).

Area cladograms: The area cladogram based on paleogeographic reconstructions (Fig. 12 A) shows a geologic time scale for the general fragmentation process, including first the latitudinal separation of two large landmasses, followed by separation of Indomalaysia from the Neotropica-Equatorial Africa complex. Australasia separated from the Chile-South Africa complex.

The second cladogram (Fig. 12 B) is fully independent of the first because it is based on taxonomic evidence. It shows how the onychophorans became geographically and genetically isolated. Genetical isolation resulted in an speciation process (*i.e.* cladogenesis), according to the taxonomic work done early in the century by Bouvier (1905). This cladogram shows first a large division into the equatorial and southern families (respectively: Peripatidae and Peripatopsidae). Bouvier's (1905) classification has no quantification of the taxonomic

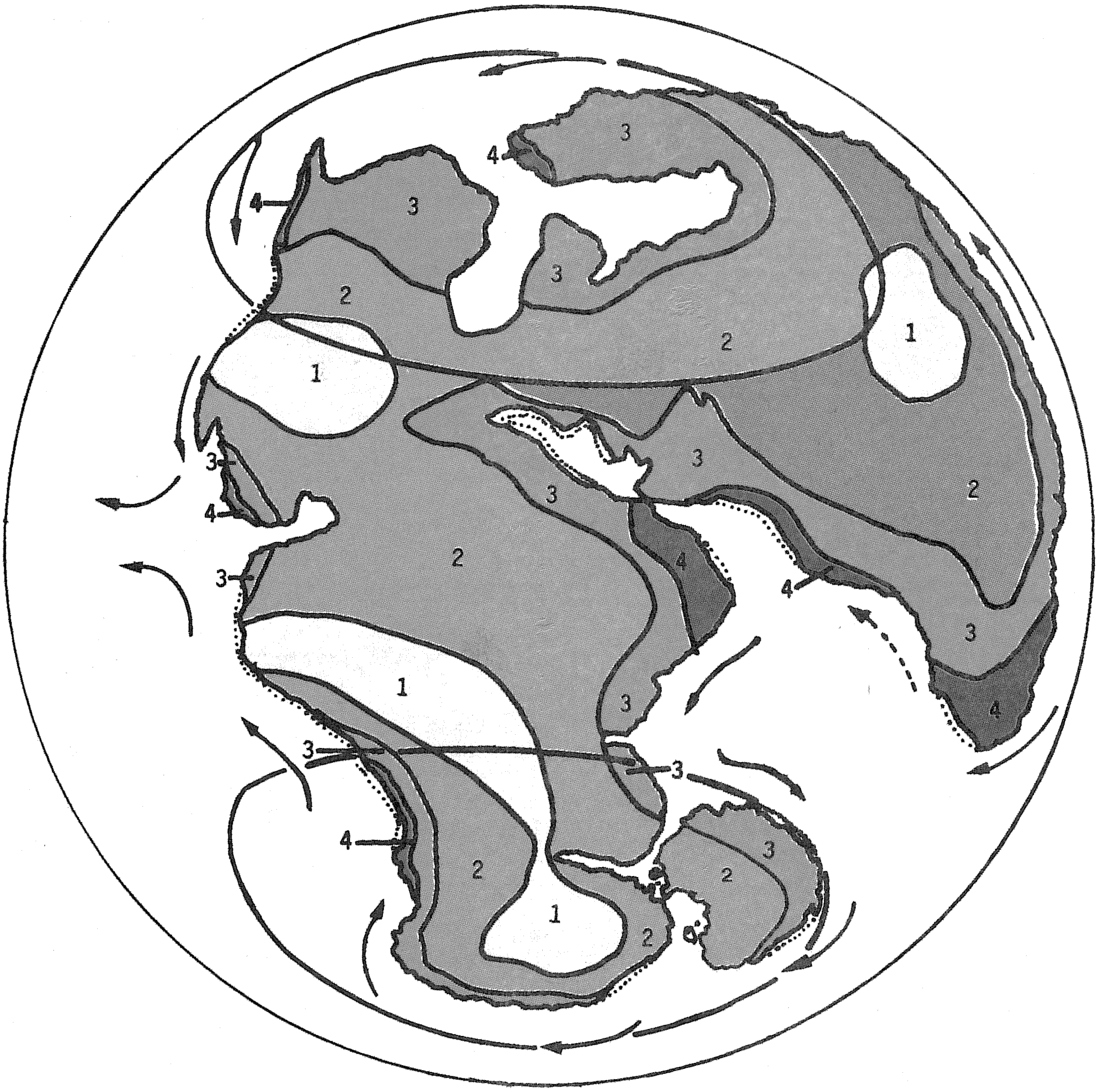

Fig. 2. Early Jurassic (180-165 million years before Present, mybP). Broken line: limit of submerged coastal areas (several authors show more or less flooded area than these reconstructions; the same applies to the following maps). Key to climates: 1 very dry, 2 dry, 3 moist and 4 very moist. The tropical-subtropical belt is marked by latitudinal lines. Key to hypothetical dominant vegetation types: **Tropical regions:** 1 Desert and semidesert, 2 Steppes and shrubby vegetation, 3 Savanna and 4 Rain forest. **Temperate regions:** 1 and 2 similar to tropical regions, 3 temperate forest and grassland, and 4 Coniferous forest and other types of temperate forest. Near the poles, only the drier areas had tundra and alpine vegetation.

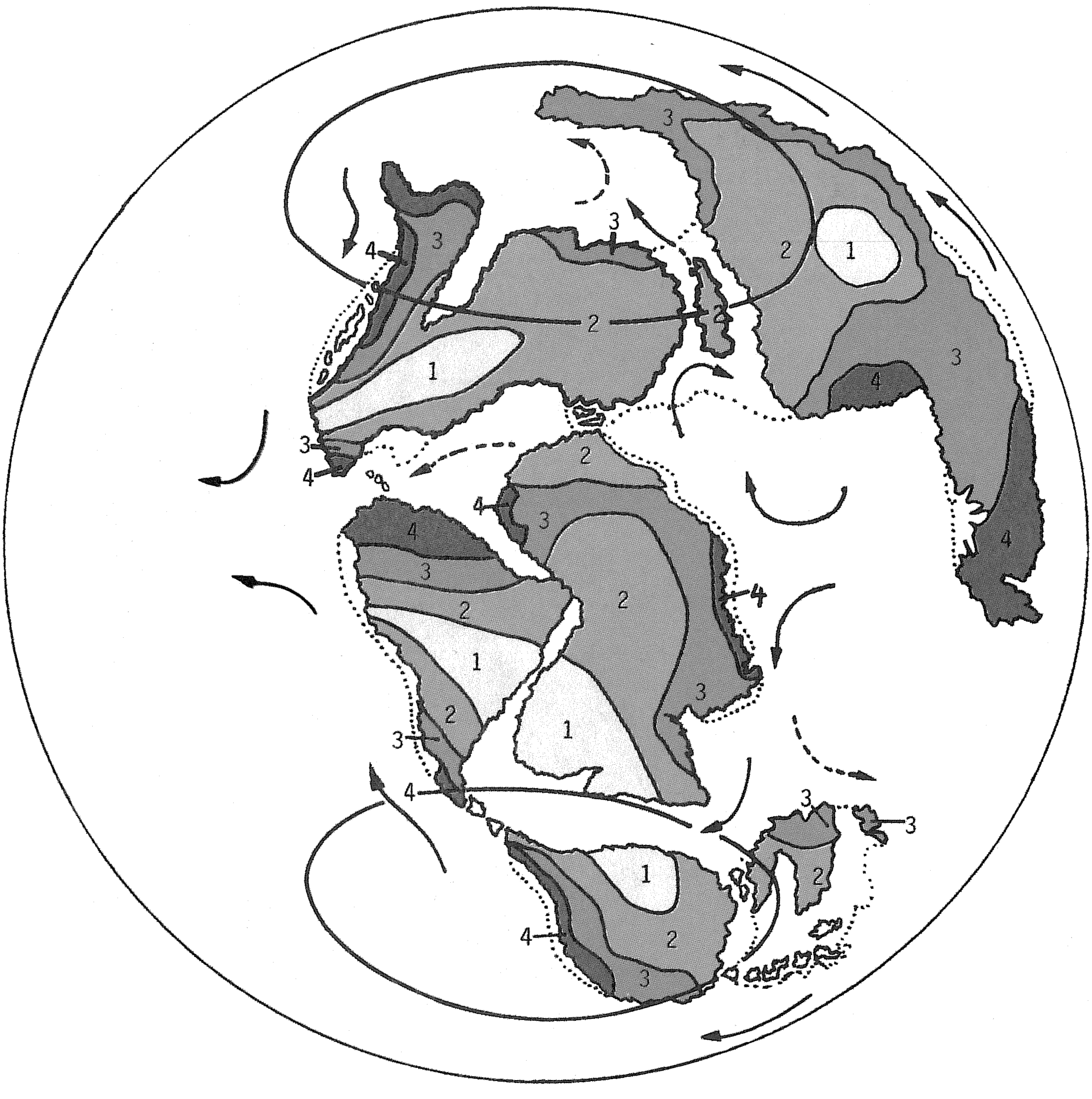

Fig. 3. Late Jurassic (160-135 mybP). Although not specifically showed in this and following maps, an important current is thought to have moved towards the west in the area between South and North America. Key to climate and vegetation as in Fig. 2. Summary of Jurassic ecology: **Climate and Flora:** Warm arid and seasonally arid areas, particularly near Tropic in W. Pangaea; moister in China and other high latitudes; breakdown of monsoonal system. No impassable barriers between continents, only minor N.-S. provincialism. At least in early Jurassic, angyosperms rare. Four defined floral provinces: N. Laurasia, S. Laurasia, N. Gondwana, S. Gondwana. Tropics: seasonally dry. Angyosperms more important near tropics. **Fauna:** Coleoptera very varied; first Thysanoptera. Large, high-browsing sauropods dominant; probably plants with more defenses and large re-growth capacity despite aridity. Some herbivores fed 10-12 m above ground.

Fig. 4. Early Cretaceous (135-110 mybP). Key to climate and vegetation as in Fig. 1.

Fig. 5. Mid Cretaceous (110-90 mybP). Key to climate and vegation as in Fig. 1.

Fig. 6. Late Cretaceous (89-65 mybP). Key to climate and vegetation as in Fig. 2. Summary of Cretaceous ecology. **Climate and flora:** Flowering plants appear with high diversity (specially riparian and burnt habitat) but were not important part of forest biomass. K/T boundary (Cretaceous / Tertiary): great extinction of large terrestrial vertebrates associated with plant devastation; less extinction apparent toward S. Pole. **Fauna:** Early period: Micropterigid lepidopterans; larvae fed on moss, liverworts and detritus: adults maybe ate polen. Late period: Lepidopteran miners, Orthoptera (Acridoidea); Hymenoptera (Cynipidae), aphids, Isoptera, ants. Laurasia: abundant high-browsing sauropods. Gondwana: sauropods dominant; mammals rare. Abundant small mammalian herbivores in Campanian-Mastrichtian (83-65). S. American mammals highly endemic. Hadrosaurid ornithopods and ceratopsid ceratopsicians important, oral food processing. Herd foraging? Coevolution with plants? Most feeding 1-3 m above ground.

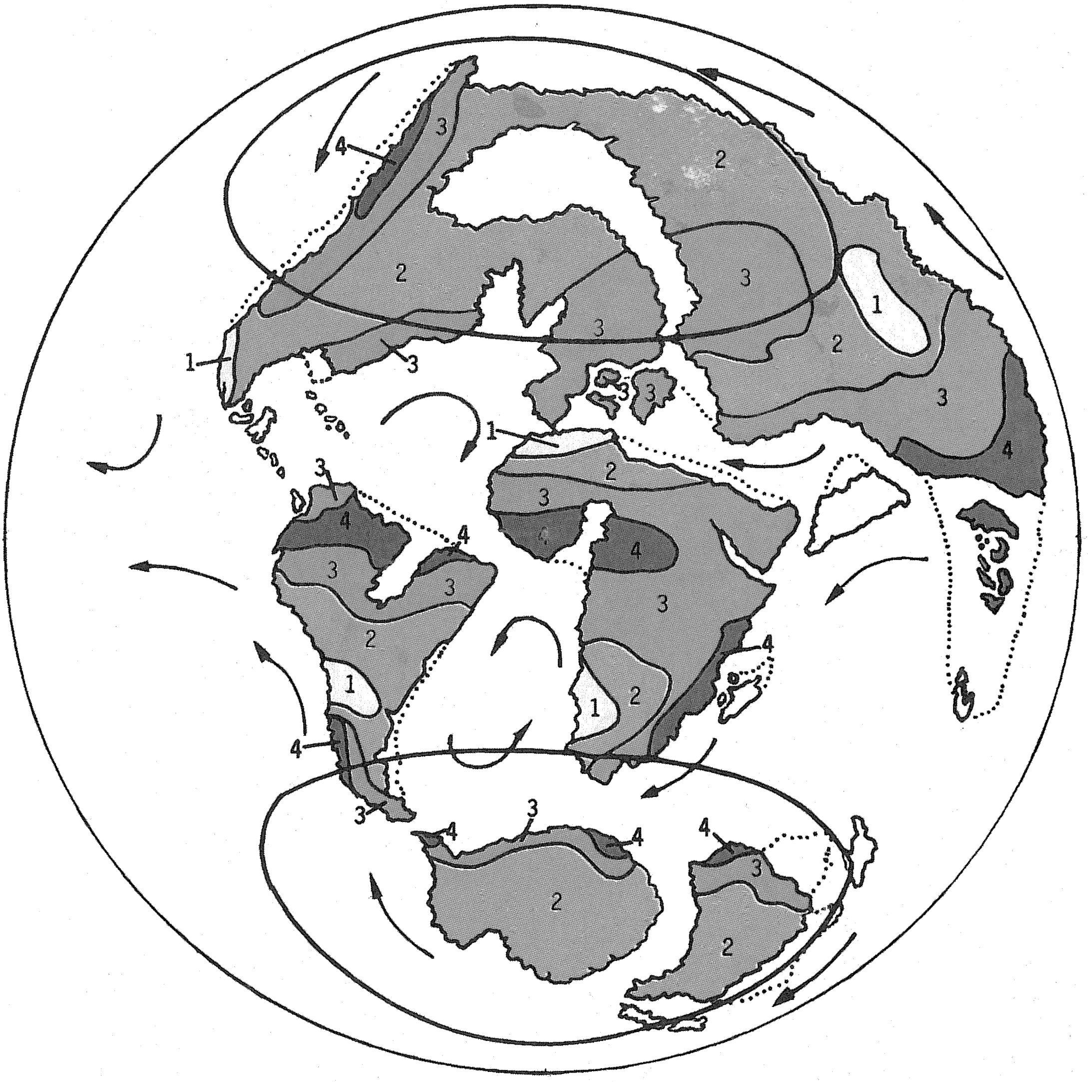

Fig. 7. Paleocene (65-54 mybP). Key to climate and vegetation as in Fig. 2. Summary of ecology. **Climate and Flora:** Colder climate? Probably angiosperms suffered great decimation (recovered near end of Paleocene) and were substituted by fern-dominated community. Deciduous conifer forest, but new Argentinan fossils indicate tropical and montane rain forest and savanna-sclerophyllous forest. **Fauna:** Rise of mammals, many consumers of fruit, seed and small prey; specialized browsers not important. Coevolution of plants and their mammal dispersers. Shift from browsers to fruits and seeds.

Fig. 8. Eocene (54-38 mybP). Key to climate and vegetation as in Fig. 2. Summary of ecology. **Climate and Flora:** Drier than Paleocene.; 33 mybP cooler, more seasonal toward end. Steep latitudinal thermal gradients. Final upwelling of Rocky Mountain rain-shadow: "Terminal Eocene event". Golden age of tropicality and angiosperm-dominated closed forest. Rainforest up to 30^{O}N, subtropical to 60^{O}N. Complexity of communities equal to highest today. Menispermaceae & Icacinaceae lianas. Australia: angiosperm dominated tropical and subtropical rainforest, *Eucalyptus*. Tasmania: cooler, subtropical, rainy. Argentina: moist with seasonal dryness. **Fauna:** Modern moths (Monotrysia) and butterflies (Ditrysia). Formicoid ant radiation. Contact of European and N. American mammals resulted in: (1) turnover, (2) homogenization; trend to larger size. Toward end: more open habitat fauna (more lophodonty and cursoriality; less arboreal forms), especially away from tropics. In Oligocene-Miocene (23 myb^{P}) partial return to browzing.

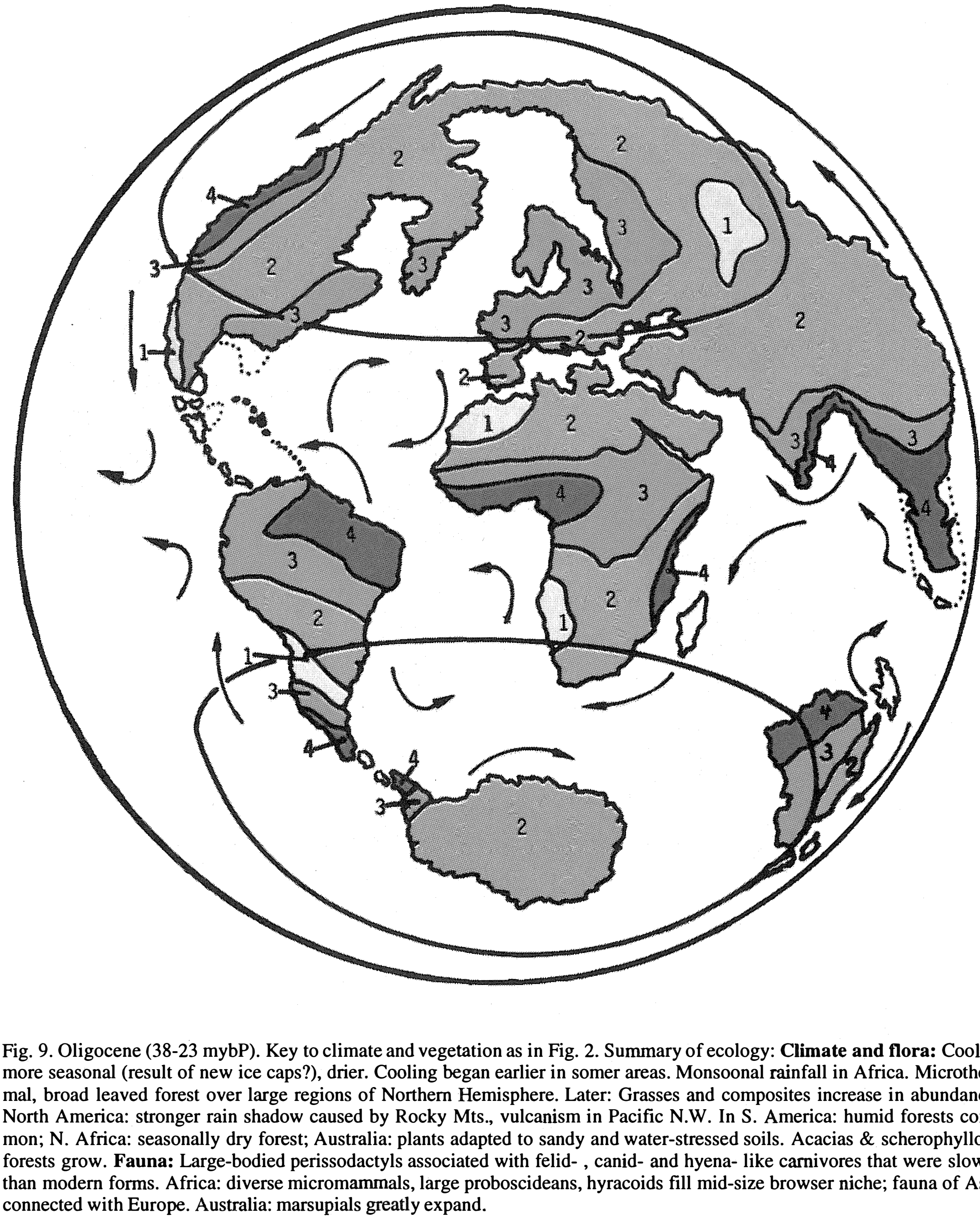

Fig. 9. Oligocene (38-23 mybP). Key to climate and vegetation as in Fig. 2. Summary of ecology: **Climate and flora:** Cooler, more seasonal (result of new ice caps?), drier. Cooling began earlier in somer areas. Monsoonal rainfall in Africa. Microthermal, broad leaved forest over large regions of Northern Hemisphere. Later: Grasses and composites increase in abundance. North America: stronger rain shadow caused by Rocky Mts., vulcanism in Pacific N.W. In S. America: humid forests common; N. Africa: seasonally dry forest; Australia: plants adapted to sandy and water-stressed soils. Acacias & scherophyllous forests grow. **Fauna:** Large-bodied perissodactyls associated with felid- , canid- and hyena- like carnivores that were slower than modern forms. Africa: diverse micromammals, large proboscideans, hyracoids fill mid-size browser niche; fauna of Asia connected with Europe. Australia: marsupials greatly expand.

Fig. 10. Miocene (23-5 mybP). Key to climate and vegetation as in Fig. 2. Summary of ecology: **Climate and flora:** Circum-Antartic marine current well established. Mid-Miocene global warming; Andes rise, causing rain-shadow; gradual cooling and drying in parts of America. Cool-warm cycles in S. America. 22 mybP: Africa, Arabia and Eurasia connected by intermitent bridges, less moisture from Thethys, more rain-shadow in E. Africa, more seasonal aridity (13 mybP); oscillations of cool and warm climate(9 mybP), drier Mediterranean. 18 mybP: Broad-leaved evergreen vegetation and coniferous forests expanded in northern hemisphere. Broad-leaved deciduous forest reduced. 13 mybP: Savannas and grasslands grow, forest replaced by woodlands in some areas. S. America: mixed forest and savanna as in Africa. Australia: wind & insect pollinated plants increase, rain forest replaced by dry forest and woodland. **Fauna:** Aprox. 12 mybP: diversification of small mammals (especially rodents), open-vegetation herbivores, large mammalian carnivores, and snakes. Second half of Miocene: diversification of large, soaring, carnivorous birds and other open-habitat birds, higher-crowned teeth in horses; increased cursoriality and body size, large head size; grazing, artiodactyls diversify. Biotic immigration Eurasia- N. America and exchange Eurasia-Africa. Australia: rain forests support large, slow moving browsers, flightless birds, lion and wolf-like carnivores.

Fig. 11. Pliocene (5-2 mybP). Key to climate and vegetation as in Fig. 2. Summary of ecology: **Climate and flora:** Himalayan uplift. Eurasia: hotter weather. 2.4 mybP: Periodic glaciation and build up of Northern Hemisphere ice sheets. Isthmus of Panama emerges. Retreat of paleotropical flora in N. hemisphere; expansion of temperate deciduous trees, grasses, composites. Australia drier, more wet-arid fluctuations. Conifers increase at high latitudes. Prairies, steppes and grasslands in N. America. Increased diversity (especially of rodents). **Fauna:** Further diversification of large, cursorial, grazing herbivores associated with evolution of larger, faster carnivores. Diversification of cryptic rodents, birds and small carnivores. Bipedal primates. Major invasion of S. America by N. American mammals; extinction of marsupial carnivores; Eurasia: more savanna fauna. Africa: more small carnivores, first large felids. Australia: open habitats inhabited by kangaroos; burrowing wombats.

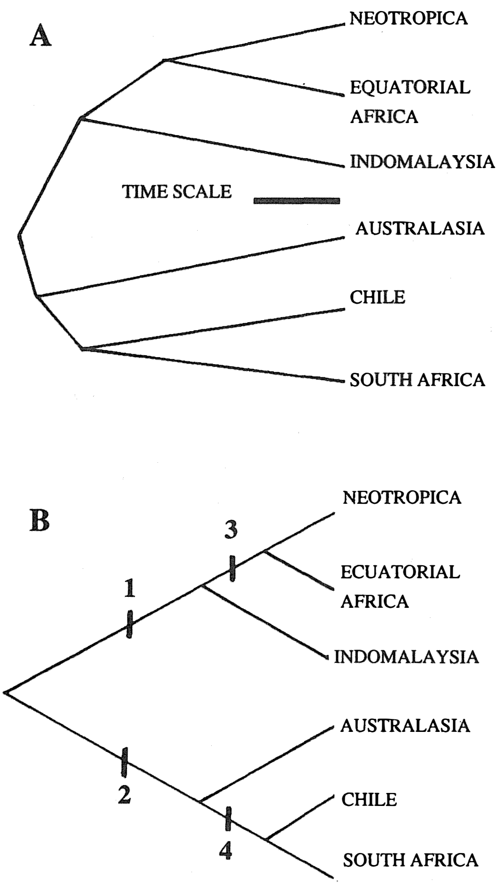

Fig. 12. Area cladograms produced from the reconstructions in Figs. 2-11 (A, scale bar: 50 million years) and from the systematics of velvet worms (B) according to Bouvier (1905). Both cladograms show the same sequence of geographic isolation. Cladogram characters: **1.** Sexual orifice between penultimate leg pair, brown reddish pigment soluble in preservation fluid, 14 regular dorsal folds per segment (rarely 22), variable number of foot-soles which are of subequal length, urinary pore of fourth and fifth leg pairs under the middle rear part of the third sole arch (or under it), inner mandible blade with a saw and a diastema; salivary reservoirs, seminal receptacles and ovular receptacles present. **2.** Sexual orifice amid the last leg pair or behind it, pigmentation often greenish blue not greatly altered by preservation fluids, very irregular dorsal folds of which there are 14-25 per segment, three-arched foot soles (middle ones much larger), urinary pore of fourth and fifth leg pairs amid the third arch, inner mandible blade without saw and without diastema, salivary reservoirs absent. **3.** At least three foot papillae, pores of male annal glands ventraly isolated in front of the anus, very small endogenous eggs, placented embryos. **4.** Very irregular dorsal folds, rudimentary seminal receptacle, eggs with very reduced reserves.

distance between groups, and for that reason the cladogram has the same distances between branch origins. Nevertheless, it does show that the species of Indomalaysia were the first to become isolated in the equatorial family and that the species of Neotropica separated more recently from those of Equatorial Africa. In the south, Australasian species were the first to separate and those of Chile were closely related with South African species until more recent times.

DISCUSSION

Although paleontological remains may provide more detailed paleoecological information than geophysical evidence, they are subject to important errors in identification, interpretation (Crame 1992, Varol 1992, Head 1993, Tanai 1993) and dating (Burnett *et al.* 1992, Rees 1993). The basic divergence in a comparison of the vegetation maps presented here (based on temperature and rainfall) with paleontological data is that fossils from moist habitats have been found in some areas where the maps indicate savannas or similar biomes. If the fossil data are more reliable than the climatic models, which seems probable, this may reflect the ocurrence of highlands not considered in this reconstruction, as well as the effects of lakes, rivers and seashores. Future maps could improve on this condition by including more topographic details. This paper emphasized differences because there is more disagreement among authors of paleogeographic reconstructions than is normally realized. Detailed local studies (*e.g.* Seyfried and Hellmann 1994) are also unveiling valuable new information.

The fit of area cladograms produced independently from the systematics of velvet worms and from tectonic analysis corrected with paleontological evidence, supports this reconstruction on a very general level. However, this fit should not be taken as support for every detail of the maps, which are only a rough representation of what must have been a much more complex paleogeographic history.

A previous attempt of relating paleomaps with onychophoran distribution (Monge-Nájera 1995), which lacked taxonomic and vegetation information, produced less clear results for the Indomalaysia-Australasia area and showed a different isolation sequence within the family

Peripatidae. The paleogeographic reconstruction presented here is consistent with the taxonomists' association of South African and Chilean species (Bouvier 1905, Ruhberg 1985), highlighting the importance of including vegetation in this type of study. A further advantage of this taxonomic-paleogeographic model is that it predicts more specific geologic times for the genetic isolation of onychophorans inhabiting different parts of the world. Such predictions are testable with the use of biochemical techniques that measure genetic distance (see Walker 1995). I hope that such studies will be undertaken by biochemical systematists in the future.

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RESUMEN

Con base en la literatura se hizo mapas resumidos de la vegetación continental desde el Jurásico hasta el Plioceno y se usaron para definir un cladograma de áreas. Independientemente, se usó la clasificación natural de los gusanos del filo Onychophora (elaborada por Bouvier) para preparar un cladograma taxonómico y geográfico de todas las regiones ocupadas por ellos en la actualidad. Ambos cladogramas muestran la misma secuencia de separación geográfica, por lo que el modelo paleogeográfico es apoyado por la evidencia taxonómica. El artículo incluye un atlas en color.

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