and South America provides the following percentages: North temperate 40%, Tropical or Sub-tropical 12%, New Zealand/ Antarctic 12%, South American 14%, Australian 9%, South African 5%, Cosmopolitan 8%.

The South African element has always been regarded as much less significant than the South American, but in this analysis both are about equally small.

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AGE OF THE ALPINE BIOTA

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The suggestion that the New Zealand alpine biota is geologically young is not new, but has recently been revived in the light of developing ideas on Tertiary and Pleistocene climatic and topographic history (Fleming 1962 b). Cockayne was aware of the problems raised by evidence of very warm Tertiary climates and minimal land relief, and he suggested that a nucleus of plastic species, descended from a Cretaceous mountain flora, survived until the growth of mountains and cooling climate in the Pliocene allowed them to exploit the alpine environment once more. A history back to the time of the Cretaceous mountains is, however, unlikely because the mountains formed in the Early Cretaceous Rangitata Orogeny were already dwindling by the time angiosperms were distributed in the Later Cretaceous, and because there is no evidence that climatic conditions in New Zealand were suitable for the alpine biota at that time.

The present pattern of altitudinal vegetation zones in New Zealand was shown by Zotov (1938) plotted on a base line showing mean midsummer-month temperature at sea level. In Figure 1 the snow-line and timberline which limit the Alpine Zone are plotted on a latitudinal base line and projected north to intersect the same boundaries at 15,400 ft. and between 11,000 and 12,000 ft. in New Guinea (from Reiner 1960, and Robbins 1961). Irregularities in these boundaries due to rainfall differences are not of sufficiently large order to affect the general picture. Also shown on Figure 1 are the altitudinal limits in New Guinea (Robbins 1961) and New Caledonia (Bader 1960) for *Nothofagus* of the *brassi* group (which formerly lived in Australia and New Zealand) with the optimum zone for beech forest distinctively shaded. From this it can be judged that these beeches could probably still live in New Zealand if they had been able to return after their Pleistocene extinction here.

In Figure 2, the climatic-vegetational zones have been lowered on the average 1200 meters to correspond with the geological evidence of snow-line position during the Last Glaciation (about 20,000 years ago) from data given by Willett (1950) for New Zealand and Reiner (1960) for New Guinea, and the *Nothofagus brassi* Zone correspondingly lowered. For simplicity the zone boundaries are shown as straight parallel lines, whereas the present boundaries seem to be slightly curved and not strictly parallel. The glacial-age sea level was probably about 119 meters lower than its present position (Curray 1961). Note that the upper limit for *brassi* beeches falls north of New Zealand confirming the suggestion of glacial age extinction.

Figure 3 attempts to show the same zones fitted to Pliocene (pre-glacial) topography and climate. Sea level temperatures are judged by evidence from Pliocene marine mollusca in New Zealand and Campbell Island; the Pliocene occurrence of *Dysoxylum* in Otago suggests the same order of warmth*. Geologists agree that the relief of

* Recorded from Middlemarch diatomite; the Pliocene age is, however, not certain.

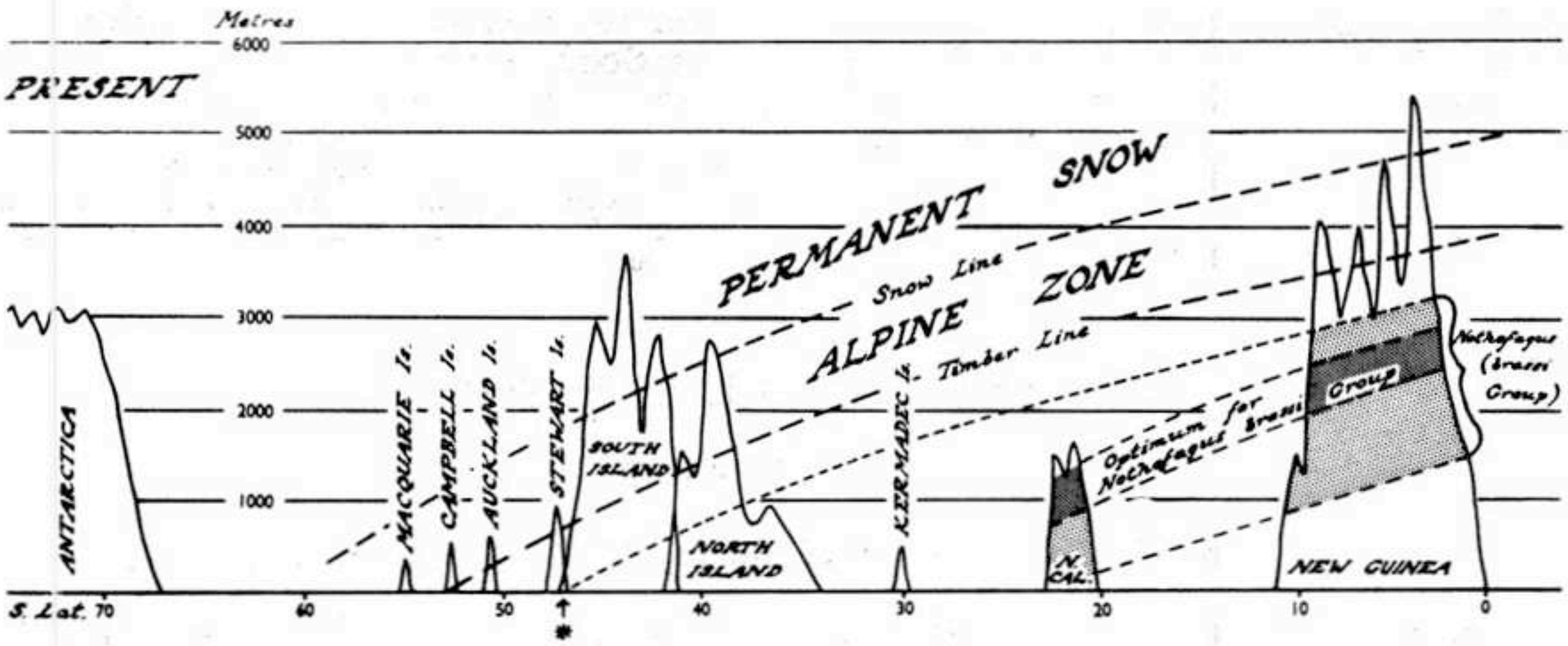

FIGURE 1. *Present altitudinal vegetation zones.*

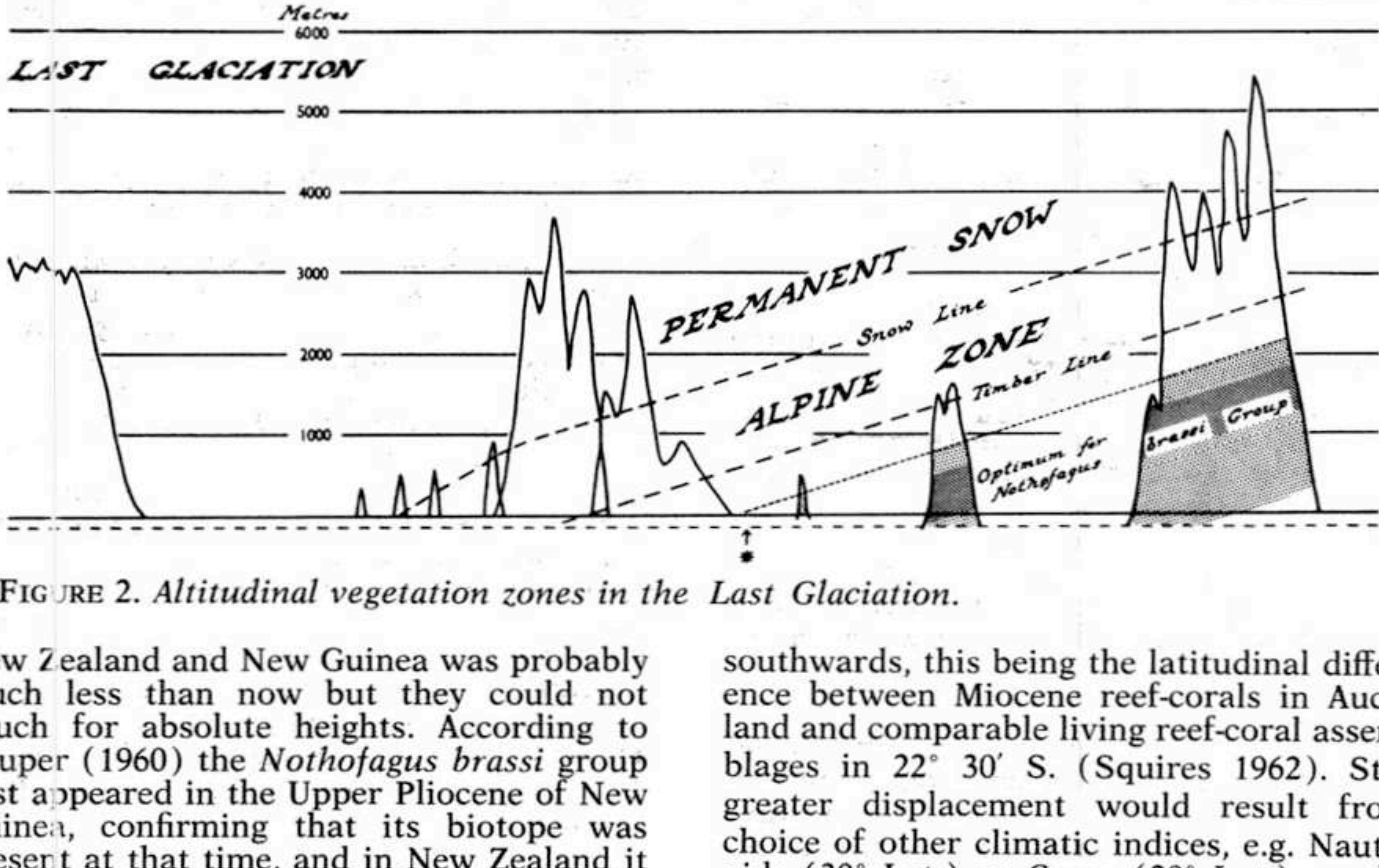

FIGURE 2. *Altitudinal vegetation zones in the Last Glaciation.*

New Zealand and New Guinea was probably much less than now but they could not vouch for absolute heights. According to Couper (1960) the *Nothofagus brassi* group first appeared in the Upper Pliocene of New Guinea, confirming that its biotope was present at that time, and in New Zealand it reached south to Otago (together with *Agathis*). No Alpine Zone was present in New Zealand, unless the mountains were higher than is judged likely, but it could have been widely developed in Antarctica.

Figure 4 shows the same type of reconstruction for the period of mid Tertiary warmth, with the zones at sea level displaced 15° Lat. southwards, this being the latitudinal difference between Miocene reef-corals in Auckland and comparable living reef-coral assemblages in 22° 30′ S. (Squires 1962). Still greater displacement would result from choice of other climatic indices, e.g. Nautiloids (30° Lat.) or *Cocos* (20° Lat.), so the diagram probably does not represent the period of maximum warmth, when podocarps and *Nothofagus* lived at Seymour Island (Lat. 64° 15′ S.) and shed pollen near McMurdo Sound (Cranwell 1959; Cranwell, Harrington & Speden 1960). It demonstrates, however, the conclusion that the Alpine Zone was most unlikely to have been present on land of such low relief as New

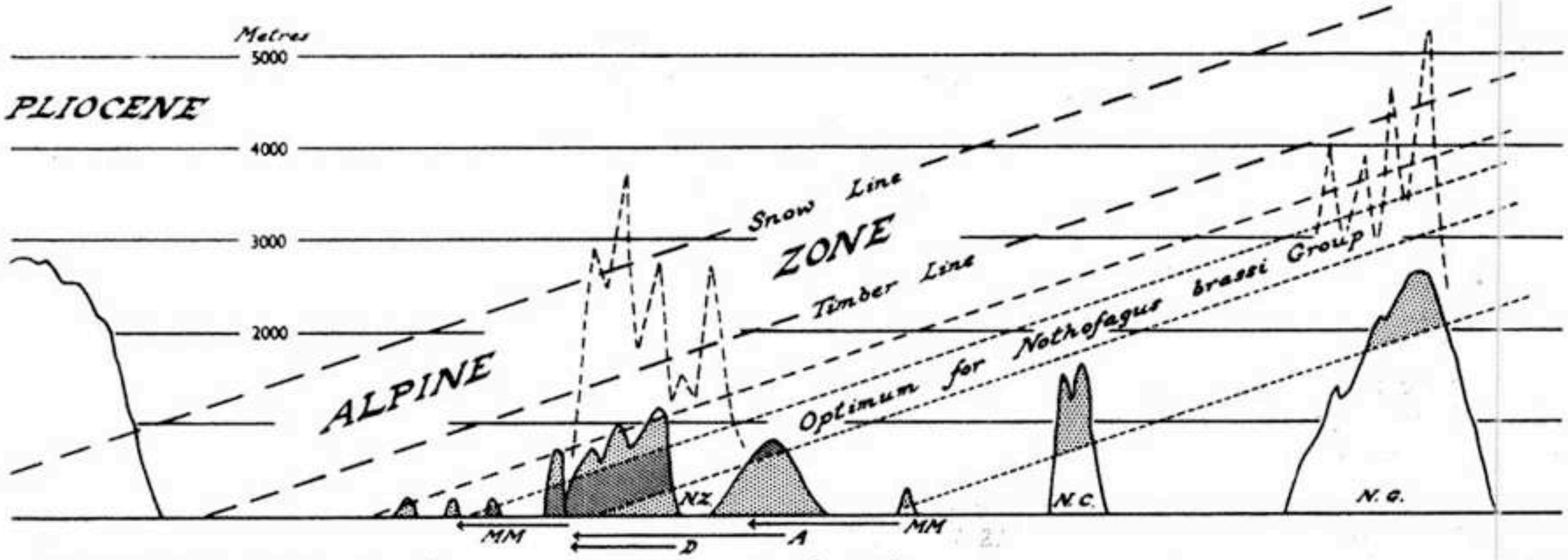

FIGURE 3. Altitudinal vegetation zones in the Pliocene.

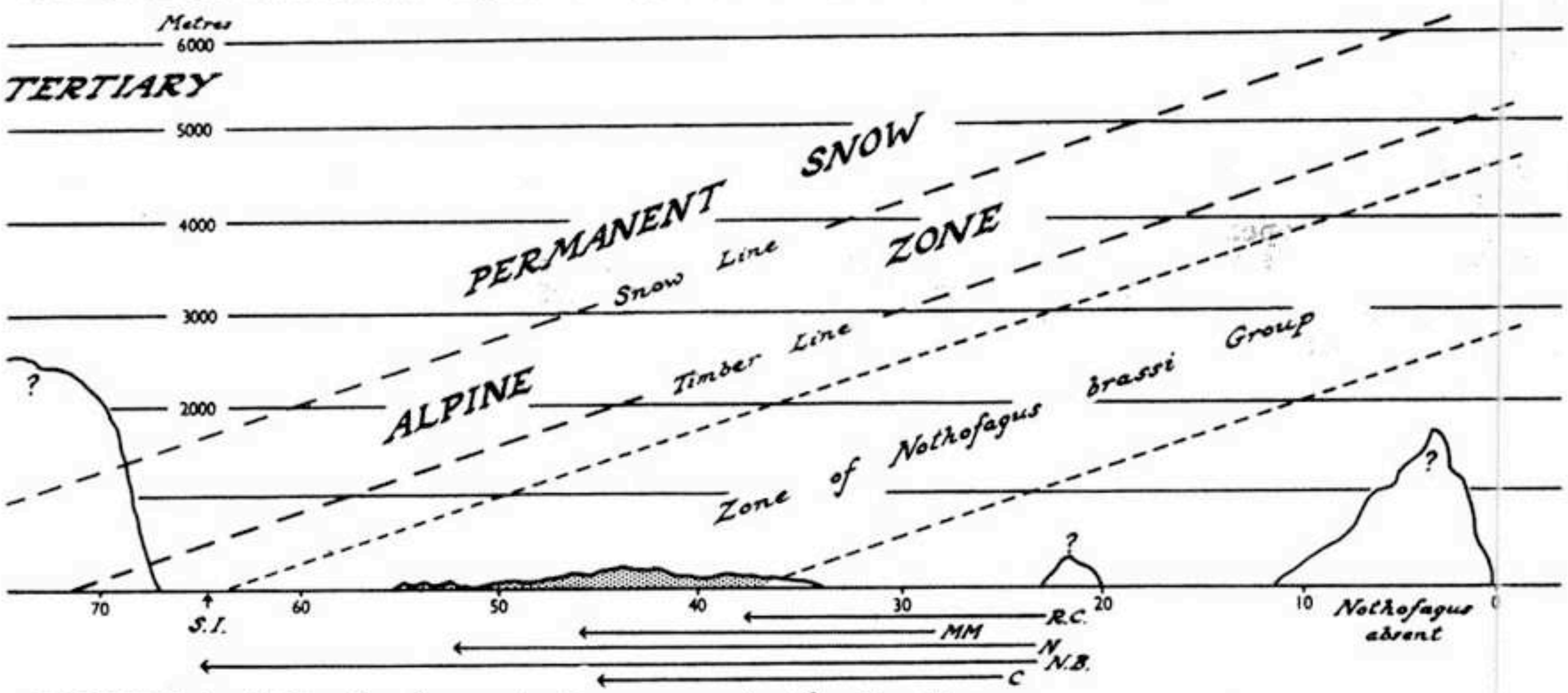

FIGURE 4. Altitudinal vegetation zones in the Tertiary.

Zealand was throughout early and mid Tertiary time. Nor does available evidence suggest that such a zone could have been present during the early history of Angiosperms in the later Cretaceous.

If, then, we may recapitulate the reconstructions in chronological order, the Alpine Zone was probably confined to Antarctica during the long period of Tertiary warmth (Fig. 4) lasting into Pliocene time (Fig. 3) and was established during the Pleistocene, when rising mountains first intersected the theoretical timber-line in its slow northward movement towards its fluctuating Ice Age position (Fig. 2). It is therefore suggested that New Zealand plants and animals now endemic to the Alpine Zone have only a short history as alpines in New Zealand. Some of the problems of the origin of New Zealand Alpine plants have been discussed by Dawson (1963). I would suggest that the alpine biota can be classed into several groups:

1. Old alpines with a long Tertiary history in the alpine zone of Antarctica that colonised New Zealand when the zone was first established in the Pleistocene.

2. Old alpines with a long history in the boreal region that crossed the equator when the alpine zone was first established on tropical mountains.

3. Facultative alpine organisms with a longer history in New Zealand that had wide

enough tolerance and plasticity to colonise the alpine zone; some have speciated within the zone to produce alpine-restricted forms.

Alpine animals doubtless include similar categories. The only ones I wish to mention are the two restricted alpine birds: the kea (*Nestor notabilis*) and rock-wren (*Xenicus longipes*). Both are derivatives of non-alpine genera with presumably long histories in New Zealand forest before the alpine zone arose, and thus fall in my Group 3. The fact that they are both well-defined species of forest inhabiting genera (*i.e.*, not alpine-endemic genera or merely subspecies) is in accord with the general thesis that full species of New Zealand birds are, on the whole, of Pleistocene origin (Fleming 1962a).

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