

# ***Trochoidea geyeri* (Soós, 1926) (Pulmonata, Helicidae) in south-eastern France; ecology, biogeography and Quaternary history.**

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In southeastern France *Trochoidea geyeri* is mainly an upland open-ground species, which has a very discontinuous range. An altitudinal shift of *T. geyeri* in response to Quaternary climatic changes is described. The value of *T. geyeri* as a palaeoclimatic indicator species is discussed. Its distribution seems to be partly conditioned by competition with *Candidula unifasciata* (Poiret).

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## **Introduction**

Today in south-eastern France *Trochoidea geyeri* (Soós, 1926) characterises open upland environments. It is also an important element of lowland pleniglacial communities in the same region. This obvious altitudinal shift of *T. geyeri* in response to Quaternary climatic changes may lead us to regard it as a cold climate indicator. For this reason, it is important to discuss to what extent the use of such a simple palaeoecological model is justified.

## **Present-day ecology and biogeography**

Ecology — In southeastern France, *Trochoidea geyeri* today characterises open upland environments from about 900-1000 m above sea level (Magnin, 1989, 1991). *T. geyeri*, however, tolerates a wide range of temperatures, the annual mean temperature of the sites varying between 12°C for the warmest sites, and less than 4°C for the coldest. The vegetation cover of the sites is of several types: scrubland, grassland, or very sparse vegetation. *T. geyeri* is rarely found in open forests, as it prefers a tree layer cover of below 10%.

Biogeography — *Trochoidea geyeri* has a discontinuous range, limited to the main mountain tops which thus constitute a continental archipelago (Fig. 1). At lower alti-

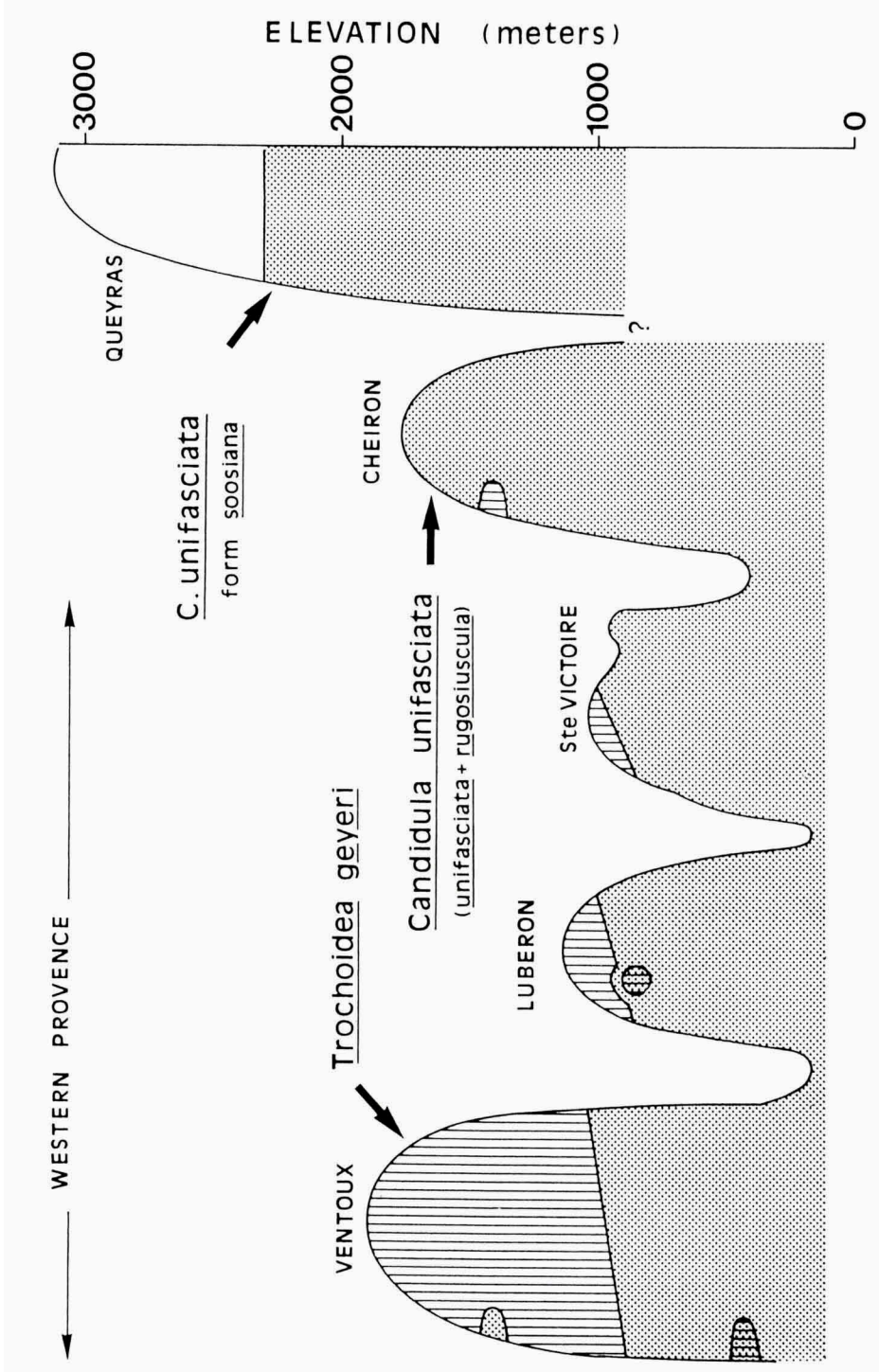


Fig. 1. Insular distribution of *Trochoidea geyeri*, and inter-island variation in altitudinal range of *Candidula unifasciata* in southeastern France.

tudes, *T. geyeri* is generally replaced by *Candidula unifasciata* (Poiret, 1801), another helicelline. However, we notice some anomalies in this pattern: *C. unifasciata* is found up to 2250 m in the eastern part of the area (Queyras) and, conversely, there are some isolated populations of *T. geyeri* as far down as 370 m (Mont Ventoux). These anomalies show that each of the two species can live in bioclimatic conditions which characterise the domain of the other species. Thus, competitive exclusion is a plausible hypothesis to explain the persistence of the patchy distribution of *T. geyeri*.

### Quaternary dynamics

The study of several Quaternary sequences in southeastern France enables us to reconstruct the dynamics of the population of *T. geyeri* in response to climatic changes (Magnin, 1989, 1991) (Fig. 2).

During glacial stages, *T. geyeri* constituted the main element of land snail communities which characterised dry open environments from the middle Rhône Valley to the Mediterranean coast. It was, however, excluded from the Nice area (Dubar, 1984).

During milder interstadial stages, an elevation of bioclimatic zones induced an upward shift of *T. geyeri*, the distributional limit between *T. geyeri* and *C. unifasciata* still being situated at low altitude (c. 200-300 m).

In the course of more intense warming (during interglacial stages), a much more obvious rise of bioclimatic zones favoured *C. unifasciata* at low altitudes, relegating *T. geyeri* to the upland refugia it occupies today. During the Holocene period, more specifically beginning with the Preboreal period, a continuous rise of bioclimatic zones (Borel et al., 1984) has resulted in the present insular distribution of *T. geyeri*.

To the north, as far as England, *T. geyeri* responds to climatic changes primarily by shifts in latitudinal distribution, without obvious altitudinal changes. In southeastern England, Normandy, Charente and Burgundy, *T. geyeri* is found in interstadial or transitional assemblages indicating a dry or very dry and moderately cold climate. In addition *T. geyeri* occurs in interglacial deposits in England (Preece, 1990; Sparks, 1953). In northeastern France, as in Central Europe, interstadial assemblages are characterised by *Helicopsis striata* (Müller, 1774), another more continental helicelline (Ložek, 1964; Puissegur, 1976).

### Conclusions

1) Historical factors, mainly climatic changes, are responsible for the present day patchy distribution of *T. geyeri* in southeastern France.

2) Current climates are not absolute limiting factors for these species: it only favours *T. geyeri* from c. 1000 m above sea-level when *T. geyeri* and *C. unifasciata* are found on the same altitudinal gradient.

3) Competitive interaction with *C. unifasciata* may possibly be the most important factor explaining the persistence of this insular pattern.

4) Quaternary climatic changes produced repeated altitudinal shifts of the contact zone between *T. geyeri* and *C. unifasciata*.

5) Palaeoclimatic reconstructions using these taxa must take into account historical factors and biotic interactions.

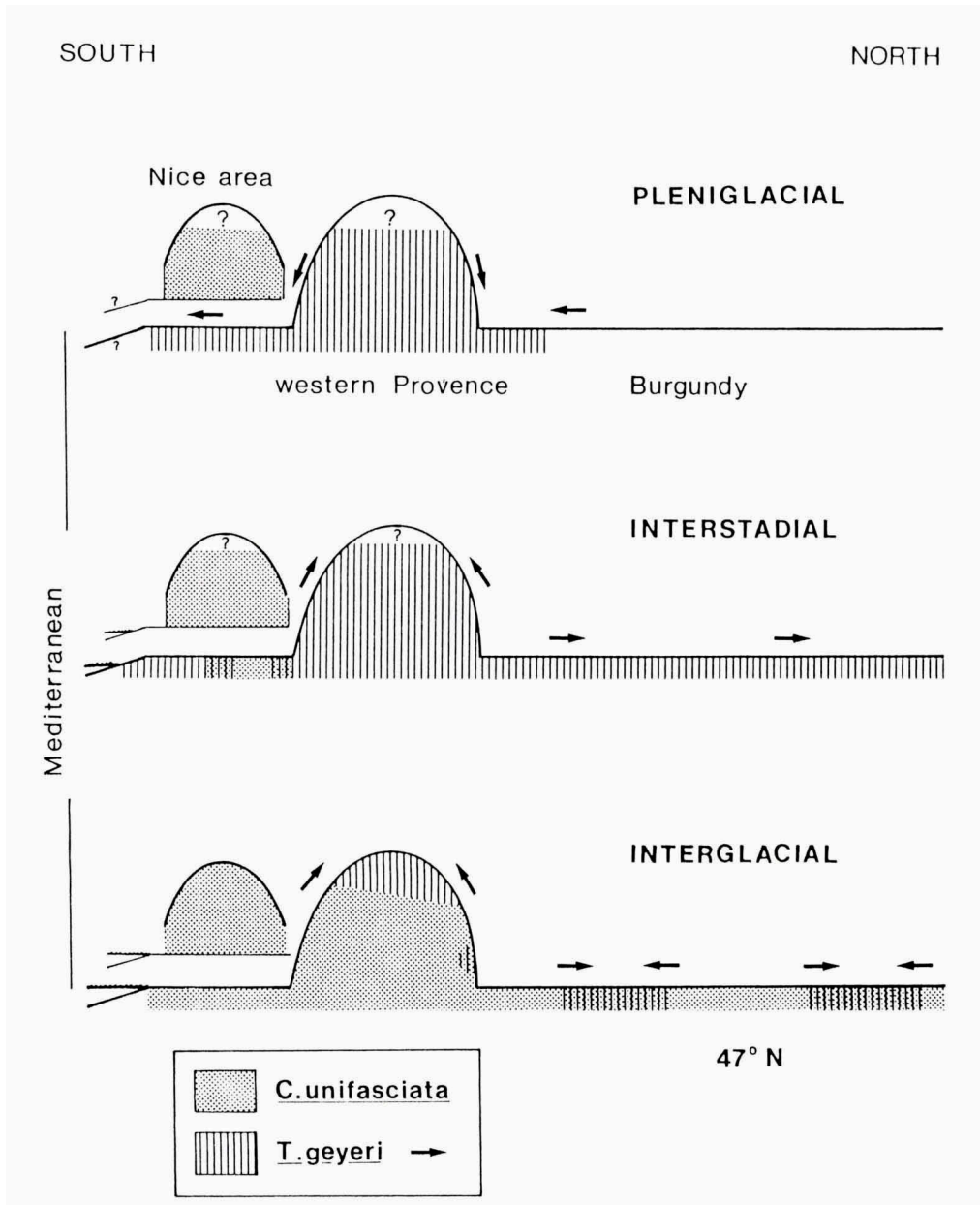


Fig. 2. Dynamics of *Trochoidea geyeri* and *Candidula unifasciata* in southeastern France in response to Quaternary climatic changes.

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