Fol. Hist.-nat. Mus. Matr. 9. 1984.

*Patterns of distribution of some freshwater molluscs of the Levant region**

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ABSTRACT: The evolutionary and dispersal history of the following freshwater mollusc species of the northern Levant has been reconstructed as an example by using new records and an analysis of the subspecific arrangement: *Unio elongatulus, Unio terminalis, Corbicula fluminalis, Leguminaia saulcyi, Leguminaia wheatleyi, Potomida littoralis, Margaritifera homsensis* (Bivalivia), *Theodoxus jordani, Melanopsis praemorsa* (Gastropoda). The patterns of distribution confirm and complement the general geological and paleogeographical theories concerning the Levant region.

INTRODUCTION

The Levant, situated at the intersection of several faunal regions, deserves, also in malacological, view, a particular attention. BOURGUIGNAT (1825), LEA (1863, 1864), ROLLE et KOBELT (1895—1897), BLANCKENHORN (1897), TCHERNOV (1973, 1975 a, b), SCHÜTT (1982) stand for the large number of authors who worked in this field. Above all recent specialists pointed out clearly the still existing gaps in our knowledge, chiefly regarding the colonizationary and evolutionary history of this region. Filling them up will lead to results of general interest.

As a basis of further research in this field collecting travels to the Levantine rift valley and its surroundings were carried out by KINZELBACH and his students during the years 1975—83, supported by Stiftung Volkswagenwerk and Deutsche Forschungsgemeinschaft. SCHÜTT (1982) already revised to some extent the 60 species of freshwater molluscs collected so far.

Great importance was attached to the requirement, that the collecting sites cover the freshwater systems in question as densely as possible. Additionally the subspecific arrangement of the species collected was investigated. From this procedure we expect information about the establishment of isolates and pathways of dispersal.

In the following patterns of distribution of some selected bivalve and gastropod species will be presented and discussed.

* Results of the travels of R. Kinzelbach to the countries of the Middle East, no. 70.

PATTERNS OF DISTRIBUTION OF SOME SELECTED SPECIES

1. *Unio elongatulus eucirrus* (BOURGUIGNAT, 1857) (Fig. 1).

Middle Eastern subspecies of *Unio elognatulus* C. PFEIFFER, 1825, formerly *Unio mancus* (LAMARCK), which is known from the western Mediterranean since the Pliocene and which spread eastward through southern Greece (e. g. Lake of Kopias) and Anatolia (e. g. Lake Suğla near Konya) as far as Iran. Starting from the Çukurova region this species colonized many of the Levantine coastal rivers down to Palestine but was unable to invade the Levantine rift valley. Further south it reached the Nile, where it is represented by the subspecies *dembeae* SOWERBY (MODELL 1951).
Its occurence in the lower course of the Orontes river indicates, that this part of the Orontes was a coastal river in the past. The rivers Quwaiq and Sagūr were colonized by this mussel from the Euphrates system, after their being separated from the Orontes.

2. *Unio terminalis terminalis* (BOURGUIGNAT, 1852) (Fig. 2).

According to MODELL (1951) *Unio terminalis* originated from the Lower Danube and reached the Levant region through the Vardar depression and the Levant region throught the Vardar depression and the Egean lakes. As an easily distinguishable subspecies, *U. t. terminalis*, it appeared within the Antakya basin (Amik Gölü) and the Gāb rift valley during the Pliocene and disappeared from there during the Pleistocene. In the southern Levantine rift valley this subspecies still exists; it invaded the Nahal Quišon, using the Yisrce'l plain as a pathway.

3. *Unio terminalis delicatus* (LEA, 1863) (Fig. 2).

After the extinction of *U. t. terminalis* in the northern Levantine rift valley the region was colonized by *U. t. delicatus* from southern Anatolia. At this time there were no connections from the Orontes to the Quwaiq nor to the Euphrates. A short termed connection between the upper Orontes and the Mediterranean Sea via the Gate of Homs during the late Pleistocene allowed *U. t. delicatus* to penetrate into the Nahr al-Kabīr (S) and several temporarily connected rivulets north of its mouth. An isolated occurence in the Lake of Muzairib was caused by recent introduction, maybe by fishes of the genus *Tilapia* from fish-hatcheries of the Gāb. The two taxa listed here as subspecies are possibly already isolated at the specific level.

4. *Corbicula fluminalis* (O. F. MÜLLER, 1774) (Fig. 3).

Within the Levant this species, which already during the Tertiary was widely spread in Africa and the Middle East, was originally restricted to the entire Levantine rift valley. Apparently, it invaded this area coming from the Euphrates system. During the Pleistocene it dispersed into the

coastal rivers of Palestine, the Nahr al-Kabîr (S) through the Gate of Homs and finally into the lower courses of the Orontes and the Ceyhan rivers.

5. *Leguminaia saulcyi* (BOURGUIGNAT, 1852) (Fig. 4).

The pathway of dispersal of this species, which represents a Pliocene immigrant from the Euphrates system, cannot yet be reconstructed accurately. On its way along the coast it spread as fas as southern Palestine down to Jaffa (MODELL 1951). During the Pleistocene it lived for a short period of time within the Jordan valley (= *L.chantrei* according to TCHERNOV 1973), which it probably reached through the Yisrce'l plain.

6. *Leguminaia wheatleyi* (LEA, 1862) (Fig. 4).

This species dispersed from the Euphrates system towards the southwest into the Orontes river. By invading the lower Orontes and the Nahr al-Kabir (S) it reached areas already colonized by its neighbouring species *L. saulcyi*. Both taxa coexist there without hybridizing.

7. *Potomida littoralis delesserti* (BOURGUIGNAT, 1852) (Fig. 5).

According to MODELL (1951) *Potomida littoralis* came from the Lower Danube region to southern Anatolia during the Pliocene by way of the Vardar depression and the Egean lakes. In that region the subspecies *P. l. tracheae* (KOBELT, 1895) occurs down to Iskenderun. It is only slightly different from the subspecies *delesserti*, which lives in the rivers of the coastal plain between the lower course of the Orontes and Haifa.

8. *Potomida littoralis semirugata* (LAMARCK, 1819) (Fig. 5).

Still during the Pliocene *Potomida littoralis* invaded the Levantine rift valley and further the Ğabbül basin. Here a particular subspecies, *semirugata*, developed. As the result of the Pleistocene fusion of the central Orontes with its present lower course *semirugata* reached the Amik Gölü. It immigrated further through the Gate of Homs into the Nahr al-Kabīr (S), which was already occupied by *P. l. delesserti*. The existence of shells with intermediate characters in both of these areas confirms their subspecific status.

9. *Margaritifera homsensis* (LEA, 1864) (Fig. 6).

1864 *Unio homsensis* LEA, Proc. Acad. nat. Sci. Philad. *8:* 285.
1865 *Unio episcopalis* TRISTRAM, Proc. Zool. Soc. London *1865:* 544.
1893 *Unio barroisi* DROUËT, Rev. Biol. Nord France *5:* 285, F. 1; J. de Conch. *41:* 36.
1929 *Margaritana syriaca* PALLARY, Mém. Inst. Egypte *12:* 34.
1951 *Potomida littoralis homsensis*, — MODELL, Rev. Fac. Sci. Instanbul (B) 16: 357, 361.
1964 *Margaritifera* cf. *auricularia*, — MODELL, Arch. Moll. *83:* 97.

A very large mussel (up to 15 cm in length) is found in the Orontes river mainly at the same localities as *P. l. semirugata*. It is absent from the Qu-

waiq river and the Gabbūl basin. Fossil records from the Jordan area are still to be confirmed. Until present the mussel in question was considered to be a subspecies of *Potomida littoralis*, namely *Potomida littoralis homsensis*. According to MODELL (1964), however, this taxon belangs to the genus *Margaritifera;* it is therefore considered here as a valid species, *Margaritifera homsensis*. During the Pliocene it spread from the lower Danube through the Vardar depression and the Egean lakes into the Orontes system. The closely related *Margaritifera auricularia* occurs in southwest and central European rivers.
Because of its thick pink nacreous layers this shell served as jewelry since lang ago. A piece of shell was found near Polmyra.

10. *Theodoxus jordani* (SOWERBY, 1832) (Fig. 7).

Coming from the north, the Ponto-Caspian area, the ancestors of the widespread, quite polymorphic snail *Theodoxus jordani* penetrated into Middle East, where they are known to occur since the Pliocene (TCHERNOV, 1973). It has not yet been possible to establish clearly distinct subspecies. However, comparative studies on the radula teeth indicate a genetic heterogeneousness between different geographical units (ROTH, 1983), namely

a) the southern part of the Levantine rift valley, where one out of two possible morphological types of the first lateral tooth, the „J-form" predominates (with exception of the springs arround the Dead Sea),
b) the coastal rivers except for the Nahr al-Kabīr (N), where solely the second type, the „A-form" occurs, and
a) the southern part of the Levantine rift valley, where one out of two gether.

It is not very easy to explain this varying but orderly distribution of radula types within the populations. Probably the A-form represents a generally distributed original state. On the other hand, the J-form may have developed in an isolated population, most likely in the area of the Jordan valley, and later invaded the Orontes system and the Euphrates. This would at least help to explain its absence from the coastal rivers.

11. *Melanopsis praemorsa* (L., 1758) (Fig. 8).

In this context only a few principal features of the subspecific arrangement of the snail *Melanopsis praemorsa* can be outlined. The basic pattern of distribution, which is exhibited by the mussels, applies in this case as well despite quite different means of dispersal.

1. The first group consists of mainly smooth shelled or, rarely finely ribbed specimens without shouldered whorls. It is distributed in Anatolia, in the tributaries to the upper Euphrates and the coastal rivers of the Levant region. It reaches the Quwaiq river and Gabūl basin, the Damascus basin, the Biqāc plain and parts of the Jordan system. It may be subdivided into the chiefly black *Melanopsis praemorsa ferussaci* (ROTH, 1839) of the Levantine coast and Palestine and the yellowish or ochre coloured *M. pr. olivieri* (BOURGUIGNAT, 1884) of eastern Anatolia.

2. A second group are the mainly costated or, rarely smooth shelled specimens which always possess a stepped outline. They occur in the Orontes river incl. Krasu and Afrin, the Quwaiq river, the Jordan river incl. Nahr az-Zarqã and at isolated localities of the Syrian Plateau. It is named *M. pr. costata* (OLIVIER, 1804); another distinct subspecies of the water boides of Palmyra is *M. pr. obsoleta* (DAUTZENBERG, 1894).
3. The third group comprises individuals of the Euphrates river, probably representatives of a species of its own, *Melanopsis nodosa* FÉRUSSAC, 1823. Specimens of similar morphology are known from Pleistocene sites in the Orontes and Jordan valleys.

These groups do apparently not represent local varieties or morphs but true genetic units, the status of which will have to be clarified in the future. The natural limis of distribution are frequently broken through by former or recent displacement.

PALEOGOGRAPHICAL CONCLUSIONS

The patterns of distribution even of he few species discussed here show principal agreement, hus their evolution may be explained by the same paleogeographical situations.
These are in detail:

1. A north-south junction along the Levantine coast during the Pliocene or earlier, which allowed the spreading of *Unio elongatulus eucirrus, Leguminaia saulcyi, Potomida littoralis delesserti* and *Unio tigridis* (not treated here); the latter and *Unio elongatulus* reached the Nile.
2. The particular development of the Levantine rift valley with the endemic species *Dreissena bourguignati* and *Viviparus apameae,* which are not treated here as well as the subspecies *Potomida littoralis semirugata* and *Unio terminalis terminalis.*
3. A clear cut separation of the northern and southern part of the Levantine rift valley; connections existed only for a short period of time by way of the Biqãc plain (which was used as a pathway by *Corbicula fluminalis)* and the Damascus basin; *Margaritifera homsensis* and *Unio terminalis delicatus* for instance are forms restricted to the northern part.
4. A connection between the northern Levantine rift valley and the Euphrates by way of the Quwaiq river and the Gabbūl basin during the Pliocene and perhaps even later; possibly also the Amik Gölü basin and the upper courses of Afrin and Karasu rivers discharged to the east; this was used by the genera *Leguminaia, Potomida* and *Corbicula.*
5. The present lower Orontes was formerly a short and unimportant river of the Mediterranean coastal plain which shares till now serveral faunal elements such as *Potomida littoralis delesserti, Leguminaia saulcyi, Unio elongatulus eucirrus* with the other coastal rivers.
6. The close junction between the lower course of the Orontes and the Ceyhan river during a period of marine regression during the Pleistocene, which led to a faunal exchange: *Corbicula fluminalis* and *Melanopsis praemorsa ferussaci* invaded the Ceyhan, the reverse way was used by *Unio terminalis delicatus.*

7. A passage to the Nahr al-Kabīr (S) in the area of the Gate of Homs, which was blacked again later by basaltic extrusions; this way was used by *Potomida littoralis semirugata, Margaritifera homsensis, Corbicula fluminalis, Leguminaia wheatleyi, Unio terminalis delicatus.*

These findings support the geological theories of the Levant (WEULERSSE 1940, VAUMAS 1957, 1961, HOROWITZ 1979) and add beyond that some details. They may be confirmed and differenciated by considering all mollusc species and also species of other taxonomical units.

DISCUSSION

At present only relative dating of the above mentioned paleogeographical events is possible. It is our intention to establish an absolute chronology by consulting exactly dated fossil sites, thus allowing to date evolutionary events. Therefore additional materials from the dried-up lake basins of the Syrian Plateau and from right tributaries of the Euphrates are necessary.

Because of occasional displacement, routes of dispersal of the one or the other species might be misleading, but in connection with the results obtained in other species this may easily be revognized.

A better knowledge of the subspecific division may be achieved mainly in gastropods by using additional anatomical and serological characters.

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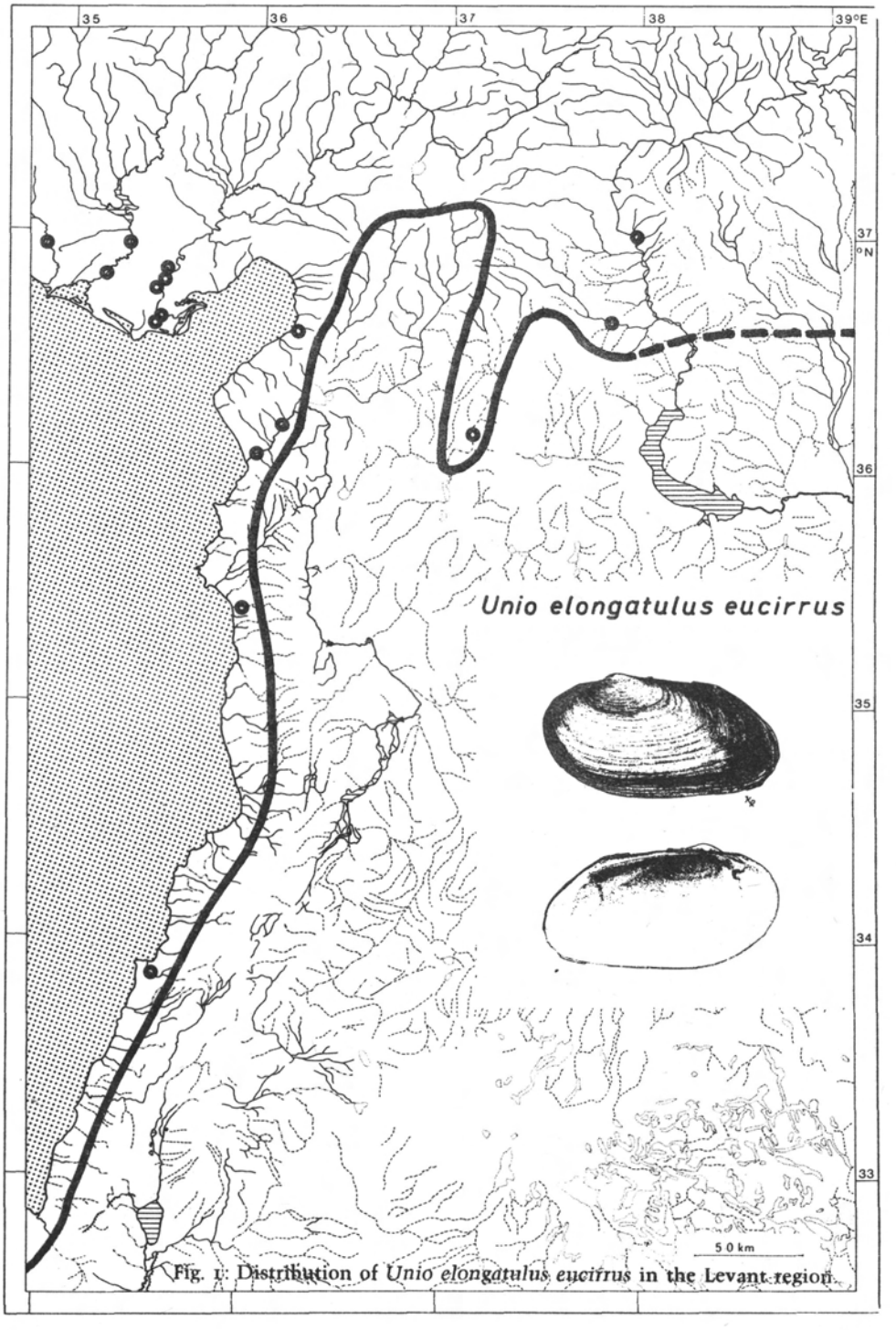

Fig. 1: Distribution of *Unio elongatulus eucirrus* in the Levant region.

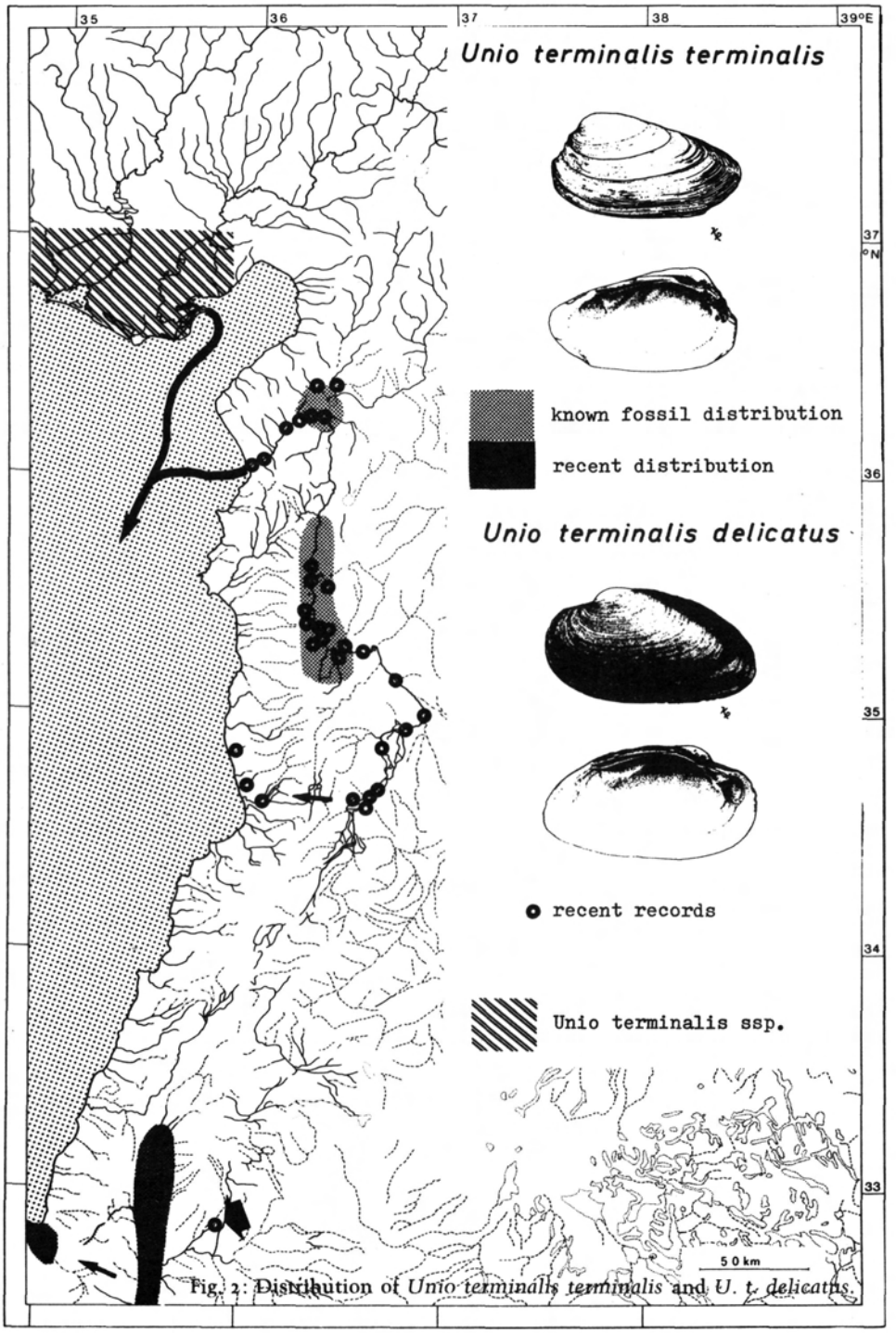

Fig. 2: Distribution of *Unio terminalis terminalis* and *U. t. delicatus*.

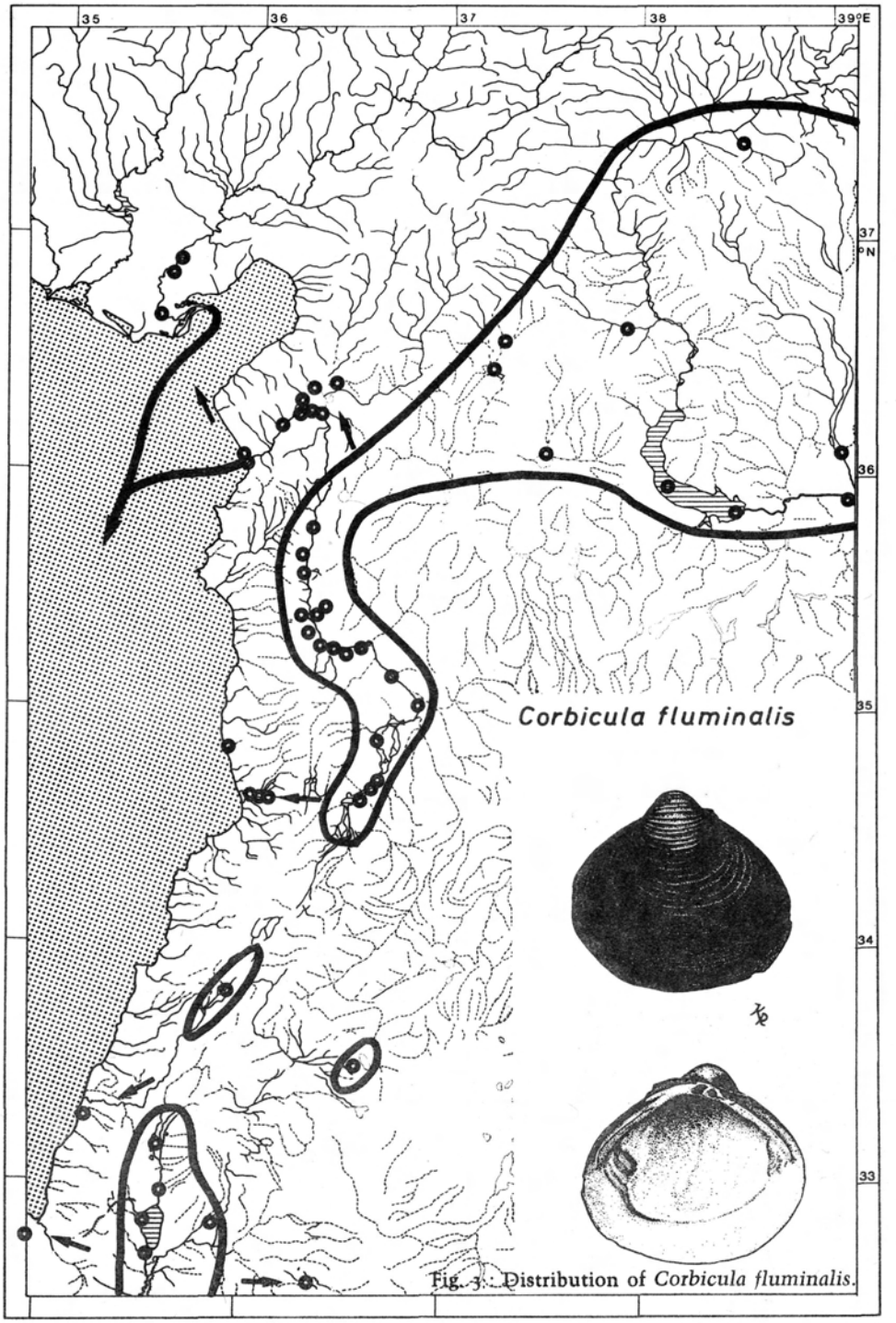

Fig. 3. Distribution of *Corbicula fluminalis*.

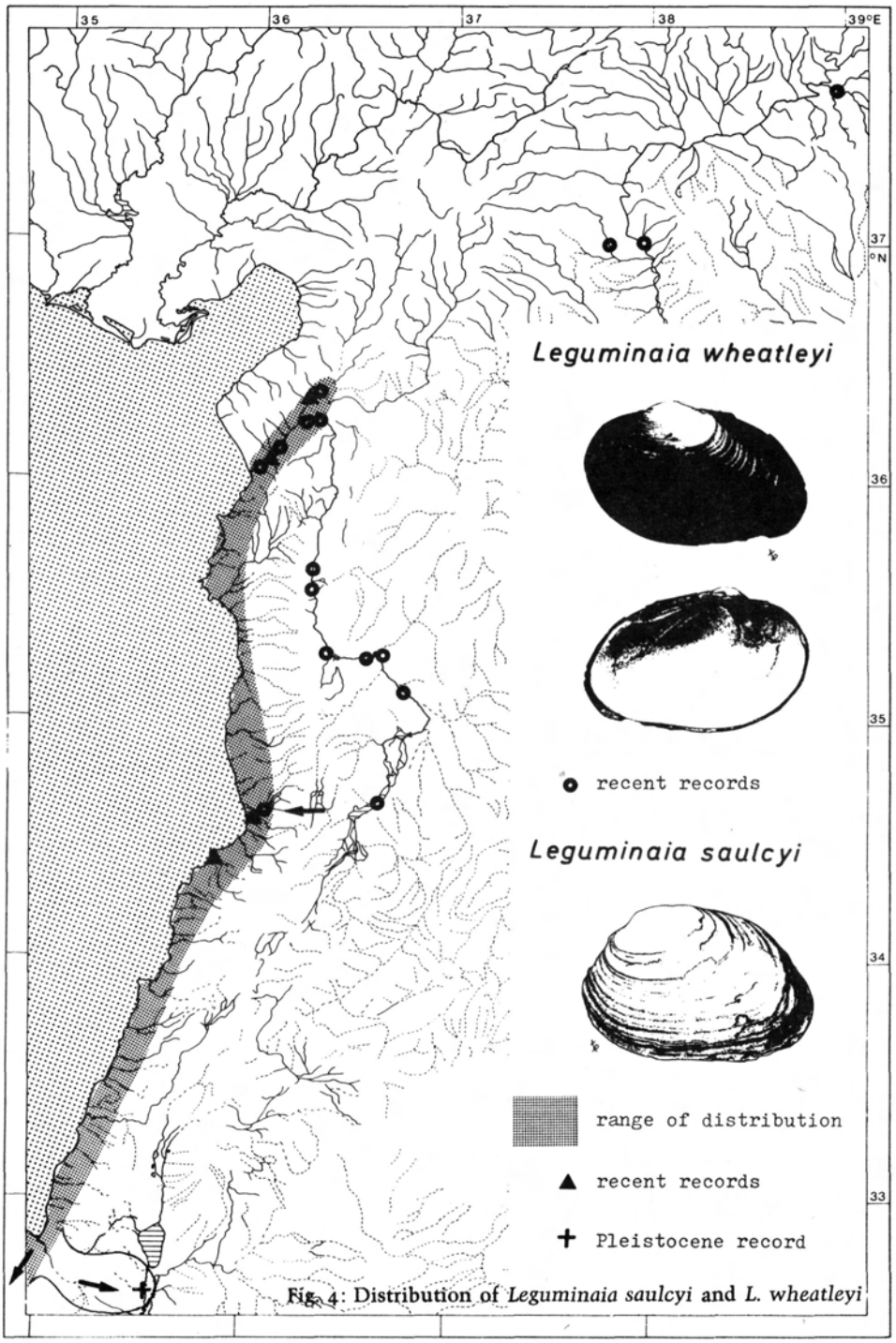

Fig. 4: Distribution of *Leguminaia saulcyi* and *L. wheatleyi*

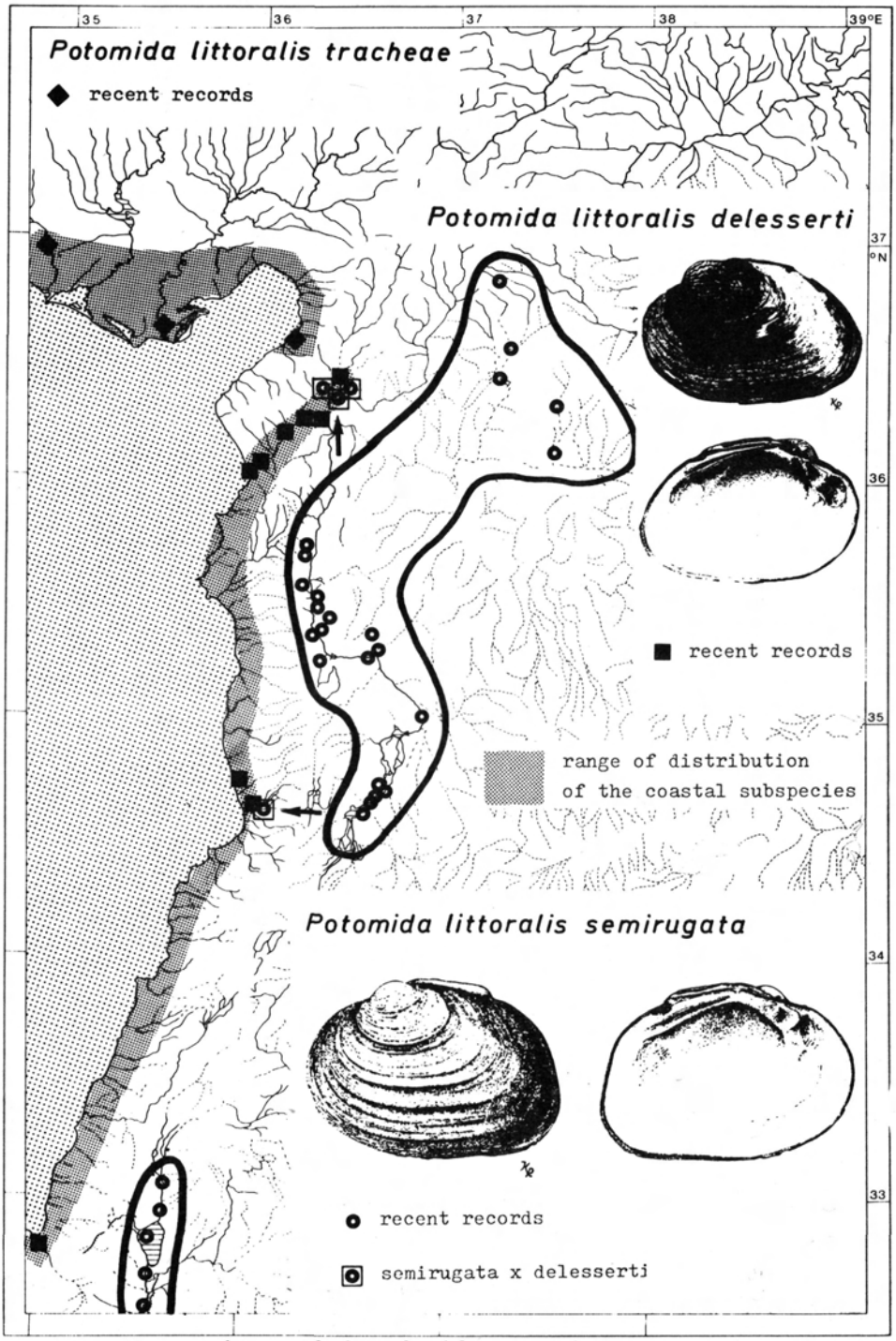

Fig. 5: Distribution of *Potomida littoralis delesserti*. *P. l. semirugata* and *P. l. tracheae*.

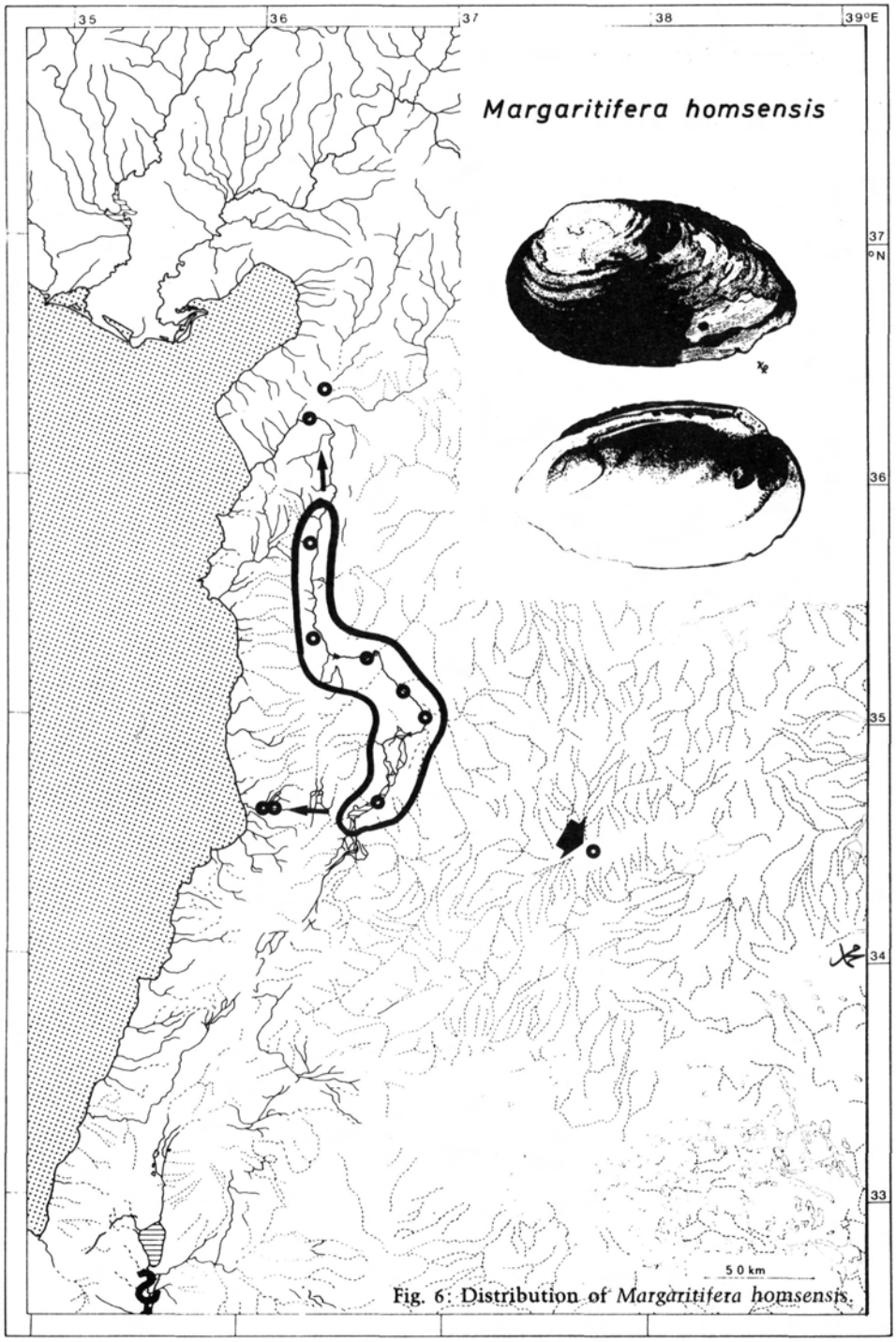

Fig. 6: Distribution of *Margaritifera homsensis*.

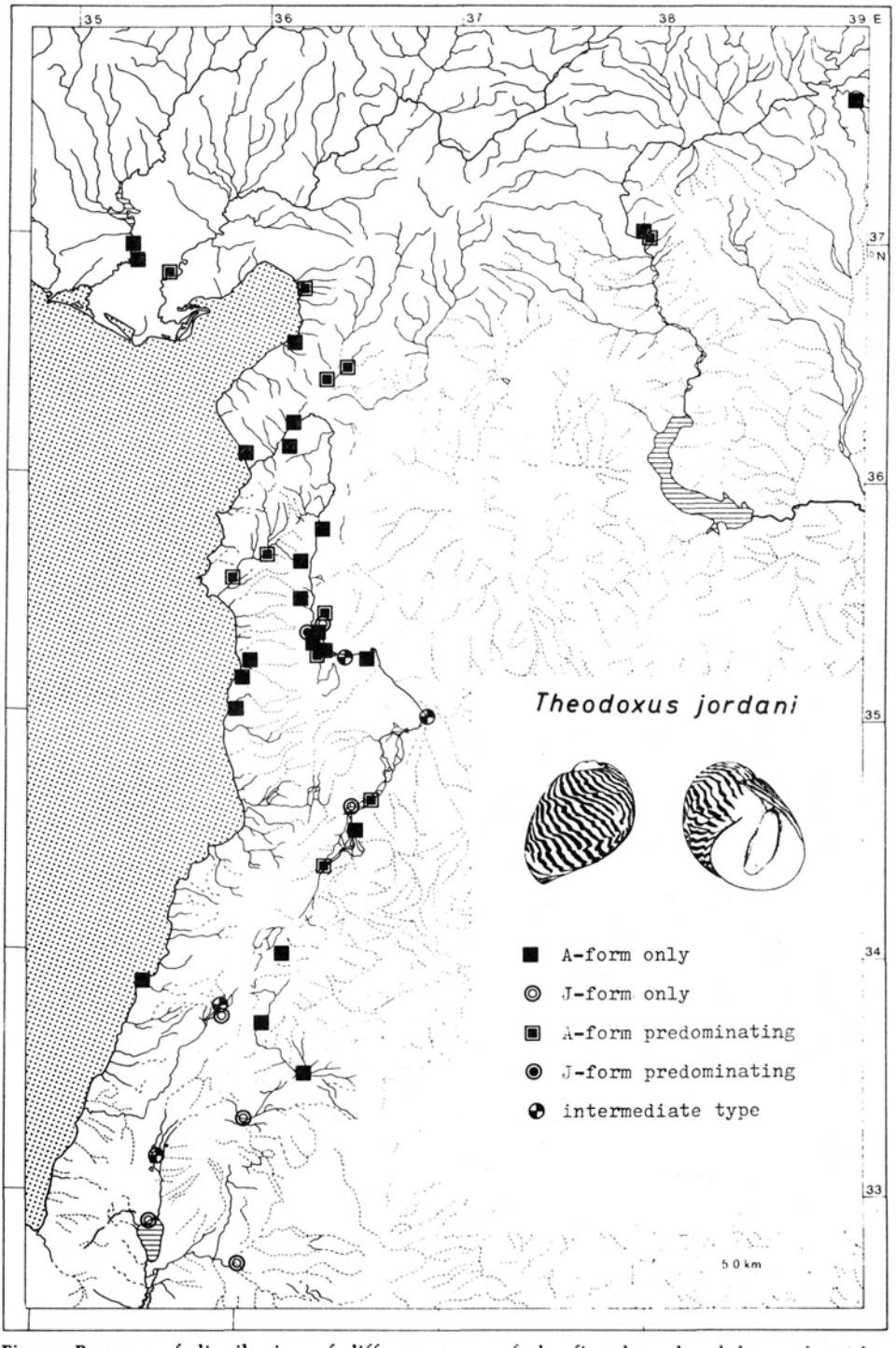

Fig. 7: Patterns of distribution of different types of the first lateral radula tooth within the populations of *Theodoxus jordani*.

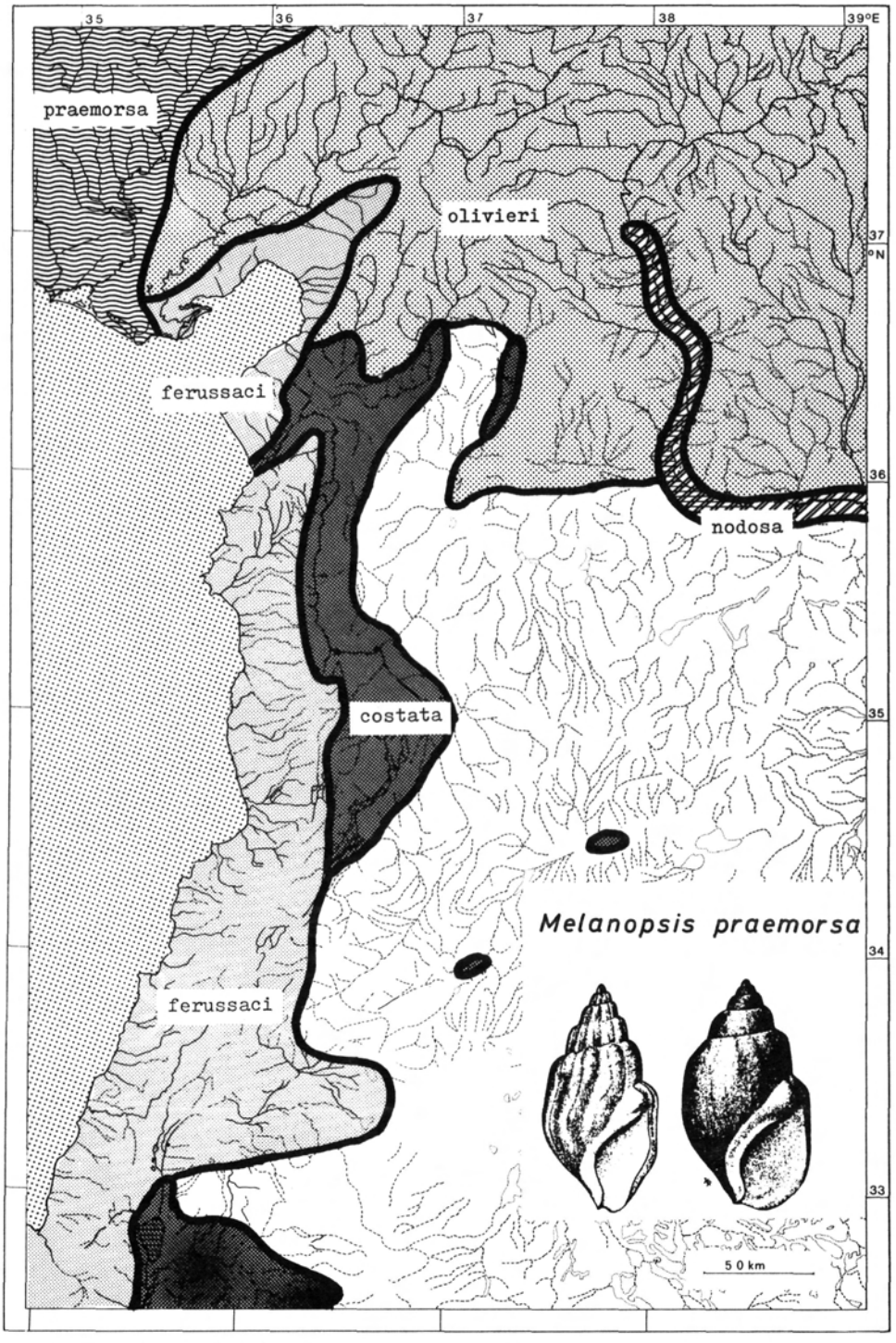

Fig. 8: Distribution of the subspecies of *Melanopsis praemorsa* in the Levant region.