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AN ESSAY TO ASSESS THE AGE OF THE FRESHWATER INTERSTITIAL OSTRACODS OF EUROPE

by

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ABSTRACT

The freshwater ostracods living exclusively in interstitial and/or interstitial and cavernous habitats belong to the Candoninae, Pseudolimnocytherinae, Timiriaseviinae, Kliellinae and Darwinulidae. An assessment of the antiquity of several interstitial ostracod groups has been attempted using direct evidence from the phylogenetical affinities between living hypogean and fossil ostracod species, and indirect evidence from the morphological characters of the subterranean ostracods and from the bio- and paleobiogeographical distribution of the different ostracod groups.

CONTENTS

> "What we firmly believe, if it is not true, is called error. What we firmly believe, if it is neither knowledge nor error, and also what we believe hesitatingly, because it is, or is derived from, something which has not the highest degree of self evidence, may be called probable opinion. Thus the greater part of what could commonly pass as knowledge is more or less probable opinion."
>
> Bertrand Russell (1912: 139-140)

> "Finalement ce jeu énigmatique que Platon me laisse ici le soin de mener comme je pourrai, me fait connaître ou tout au moins soupçonner que l'idée est toujours hors d'elle même, et que penser c'est se dépasser en cette réflexion, toujours cherchant l'idée de l'idée, ce qui est ne point se prendre à la chose ni se laisser tromper à la chose..."
>
> Alain (1967: 26-27)

I. INTRODUCTION

a. *Preamble*

The ostracods are widely distributed in various aquatic (seldom in terrestrial) habitats. Because these crustaceans have a calcareous (seldom a phosphatic) carapace, they fossilize well. Therefore the Ostracoda, as a subclass, is one of the best documented groups within the animal kingdom. The most archaic ostracods, viz. the Bradoriida, are known from the Cambrian. Müller (1979) achieved to recover and to describe the appendages of several ostracods of the suborder Phosphatocopina, which have been fossilized in Upper Cambrian sediments in Sweden.

An important radiation of the Ostracoda took place in the Paleozoic (McKenzie, 1972; Pokorny, 1978). Representatives of all the ostracod orders, viz. Bradoriida, Leperditocopida, Beyrichicopida, Myodocopida and Podocopida, are documented already in the Ordovician (fig. 1). At the end of the Permian and during the Triassic many of the flourishing paleozoic ostracod taxa got extinct (e.g. the bradoriids, the leperditocopids, the beyrichicopids) and in the marine environment new ostracod groups, mainly belonging to the order Podocopida, radiated (Sylvester-Bradley, 1962).

Freshwater ostracods are known since the Devonian (McKenzie, 1971). They exclusively belong to the suborder Podocopina (table I).

The freshwater subterranean milieu has been inhabited only by a few number of podocopine ostracod groups, viz. representatives of the superfamilies Cypridacea, Cytheracea and Darwinulacea

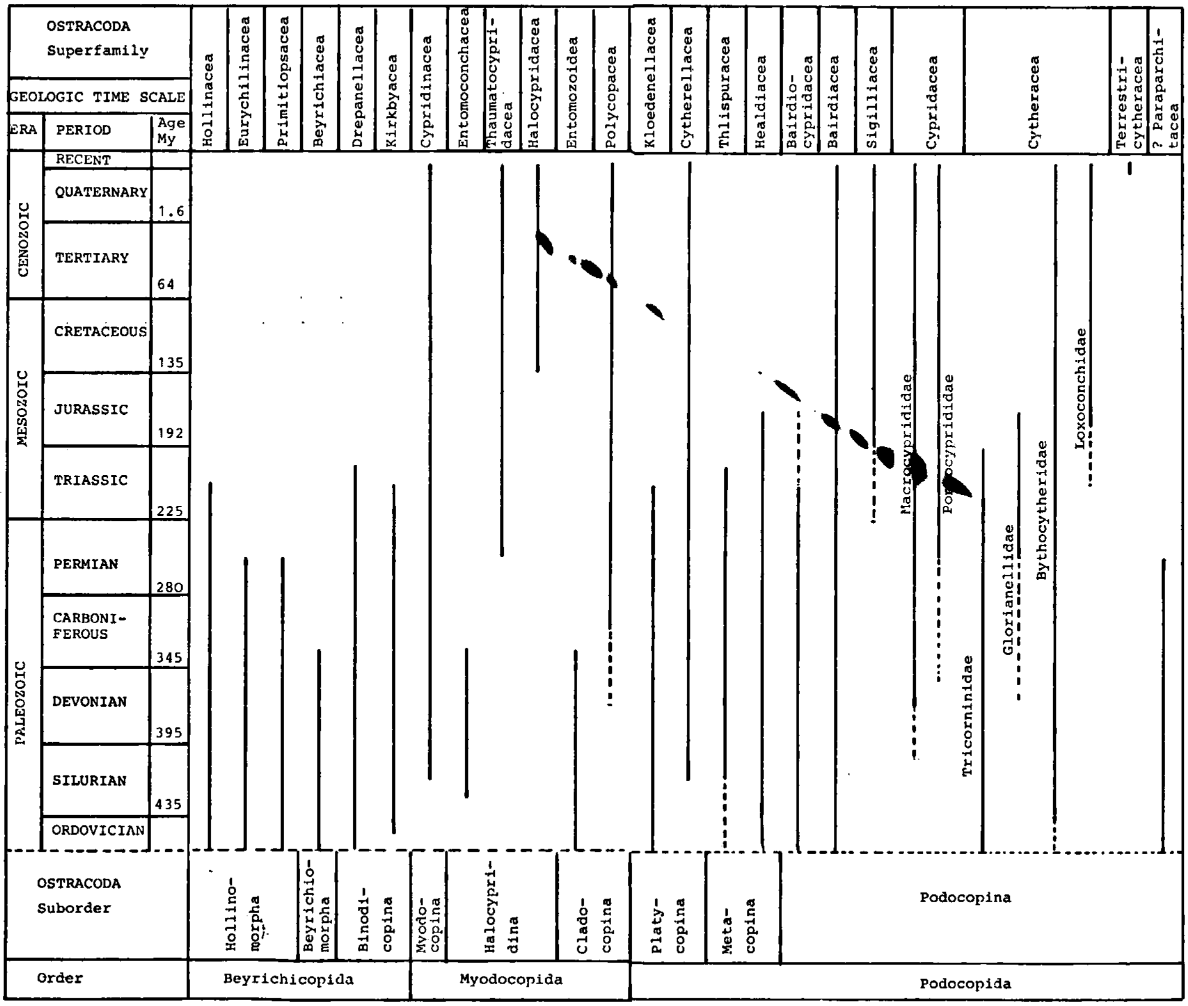

Fig. 1. The stratigraphic distribution of some of the major post-Cambrian marine ostracod groups of the orders Beyrichicopida, Podocopida and Myodocopida (data from Moore, 1961; Sylvester-Bradley, 1962; Danielopol, 1972 a & b; Kornicker & Sohn, 1976; Grundel, 1978 a & b; Pokorny, 1978).

TABLE I

The main ostracod groups of the suborder Podocopina and the suprageneric taxa with subterranean freshwater dwellers (M = marine environment; F = freshwater environment; T = terrestrial environment; S = suprageneric taxa with freshwater subterranean dwellers). Data from Hartmann & Puri (1974) and Danielopol (1972b, 1978).

Suborder	Superfamily	Family	Subfamily (S)
Podocopina	Bairdiacea (M)		
	Sigilliacea (M)		
	Terrestricytheracea (T)		
	Cytheracea (M, F)	Limnocytheridae	Timiriaseviinae
		Loxoconchidae	Pseudolimnocytherinae
		Entocytheridae	Entocytherinae
			Sphaeromiculinae
		Kliellidae	Kliellinae
	Cypridacea (M, F)	Cyprididae	Cypridinae
			Cyclocypridinae
			Candoninae
	Darwinulacea (F)	Darwinulidae	Darwinulinae

(table I). An important part of the information on hypogean ostracods comes from investigations in Europe (Danielopol, 1978).

b. *The freshwater interstitial ostracods of Europe and the problem of their antiquity*

The first truly interstitial ostracod, blind and unpigmented, i.e. *Pseudocandona eremita* (a candonine) was described about 100 years ago (Vejdovski, 1882). Later Paris (1920) studied several cave ostracods collected by Racovitza and his colleagues in southern Europe. Between 1925 and 1950 W. Klie intensively studied the systematics of the groundwater ostracods of Europe (see the list of his publications in Danielopol, 1978). Significant contributions to our knowledge of the freshwater subterranean ostracods of Europe have been made by Schäfer (1945), Löffler (1960-1964), Petkovski (1962, 1966, 1969) and Sywula (1976).

Between 1964 and 1976 I collected a rich fauna of interstitial ostracods mainly in Romania but also in France, Austria, Yugoslavia, and Greece. Many colleagues allowed me to study their collections of subterranean ostracods from Europe. I also had the chance to study the type material of some of the subterranean and surface ostracods described by W. Klie now housed in the Zoological Institute and Museum of the University of Hamburg. From this material I described several new species and I attempted a revision of the groups to which the new subterranean ostracods belonged (see Danielopol, 1978).

Table II shows the "true interstitial" ostracods living in Europe. I considered (1977, 1978) "true interstitial" ostracods to be species found in interstitial and/or cavernous aquatic habitats, which show eye reduction and/or long antennal aesthetascs "Y". In cases where data on these characteristics are not available, species recorded exclusively from the above-mentioned habitats are referred to as "true interstitial" forms as well. These species are likewise called hypogean species or troglobites. For a definition of these terms see also Danielopol, 1978 and 1980c.

Table II shows that most interstitial ostracods, living exclusively in freshwater habitats of Europe belong to the subfamily Candoninae (see, for a review, Danielopol, 1971a, 1977 and 1978). This group is also abundantly represented in surface freshwater habitats of Europe (Löffler & Danielopol, 1978). The superfamily Cytheracea, the most abundant and diversified marine recent ostracod group, is represented in freshwater interstitial habitats by a small number of species, viz. four species of Timiriaseviinae (Colin & Danielopol, 1980; Danielopol, 1970b), two species of Pseudolimnocytherinae (Danielopol, 1979), and two species of Kliellidae (Schäfer, 1945). Of these three cytherid groups, the Timiriaseviinae is a group

TABLE II

The freshwater interstitial ostracods recorded in Europe (i = interstitial habitat; k = karstic habitat). Data from: (1) Danielopol, 1970b, 1976a; (2) Danielopol, 1970a; (3) Danielopol, 1978; (4) Sywula, 1976; (5) Klie, 1938a; (6) Danielopol, 1980d; (7) Danielopol & Cvetkov, 1979; (8) present paper; (9) Schäfer, 1945.

Taxa	Habitat	Reference
Superfamily CYPRIDACEA		
Family CYPRIDIDAE		
Subfamily CANDONINAE		
Pseudocandona		
eremita (Vejdovski, 1880) s.l.	i + k	3,6
zschokkei (Wolf, 1919)	i	3
puteana (Klie, 1931)	i	3
schellenbergi (Klie, 1934)	i + k	3
triquetra (Klie, 1936)	i + k	3
belgica (Klie, 1937)	i	3
hertzogi (Klie, 1938)	i	3
brisiaca (Klie, 1938)	i	3
insueta (Klie, 1938)	i	3
bilobata (Klie, 1938)	i	3
spelaea (Klie, 1941)	i + k	3
dichtliae (Brehm, 1953)	i	3
szoecsi (Farkas, 1957)	i	3
bilobatoides (Löffler, 1961)	i	3
pseudoparallela (Löffler, 1961)	i	3
profundicola (Löffler, 1960)	i	3
tyrolensis (Löffler, 1963)	i	3
altoalpina (Löffler, 1963)	i	3
rouchi Danielopol, 1978	i + k	3
delamarei Danielopol, 1978	i	3
serbani Danielopol, 1980	i	3,6
mira Sywula, 1976	i	4
Cryptocandona		
phreaticola (Klie, 1927)	i	3
leruthi (Klie, 1936)	i	3
kieferi (Klie, 1938)	i	3
juvavi (Brehm, 1953)	i	3
matris Sywula, 1976	i	4
Cryptocandona sp.aff. *matris*	i	8
Fabaeformiscandona		
latens (Klie, 1940)	i	3
wegelini Petkovski, 1962	i	3
Candonopsis		
boui Danielopol, 1978	i	3
Phreatocandona		
motasi Danielopol, 1978	i	3
Mixtacandona		
laisi (Klie, 1938)	i	3
stammeri (Klie, 1938)	i + k	3
chappuisi (Klie, 1943)	i	3
transleithanica (Löffler, 1960)	i	3
loeffleri (Danielopol, 1978)	i	3
botosaneanui Danielopol, 1978	i	3
petrosanii Danielopol & Cvetkov, 1978	i	3
elegans Danielopol & Cvetkov, 1978	i	7
Mixtacandona n.sp.	i	7
Mixtacandona sp.aff. *chappuisi*	i	3
pseudocrenulata Schäfer, 1945	i + k?	3,8
cottarellii Danielopol, 1980	i	6
Nannocandona		
stygia Sywula, 1976	i	4
Superfamily CYTHERACEA		
Family LIMNOCYTHERIDAE		
Subfamily TIMIRIASEVIINAE		
Kovalevskiella		
phreaticola (Danielopol, 1965)	i	1
cvetkovi (Danielopol, 1969)	i	1
bulgarica (Danielopol, 1970)	i	1
Kovalevskiella sp.	i	1,8
Family LOXOCONCHIDAE		
Subfamily PSEUDOLIMNOCYTHERINAE		
Pseudolimnocythere		
hypogea (Klie, 1938)	i + k	5
hartmanni Danielopol, 1979	i	8
Family KLIELLIDAE		
Kliella		
hyaloderma Schäfer, 1945	i? + k?	9
Nannokliella		
dictyoconcha Schäfer, 1945	i? + k?	9
Superfamily DARWINULACEA		
Darwinula		
boteai Danielopol, 1970	i	2

which diversified widely in surface freshwater habitats during the Mesozoic (Colin & Danielopol, 1980). Finally, one has to mention the presence in Europe of an interstitial species of *Darwinula*. The Darwinulidae is a cosmopolitan freshwater group having only few species in Europe (Danielopol, 1968, 1970a).

Hartmann (1974) suggested that the Kliellidae found in a karstic area usually live in an interstitial habitat. This was inferred from the reduced size of the carapace, the reduced number of setae on antennal and thoracic limbs, similar to the situation found in marine interstitial cytherids. Moreover, the crustacean association in the wells where the two kliellids were found contained typical interstitial dwellers, viz. isopods of the genus *Microcharon* and harpacticoids of the genus *Parastenocaris* (Schäfer, 1945). I pointed out (1978) that several ostracod species recorded from karstic habitats could also live in interstitial habitats but this has not yet been documented (e.g. *Mixtacandona peliaca* Schäfer, 1945, *M. pseudocrenulata* Schäfer, 1945, *Mixtacandona* aff. *riongessa, M. hvarensis* Danielopol, 1969, *M. tabacarui* Danielopol & Cvetkov, 1978, *Candonopsis thienemani* Schäfer, 1945, *C. trichota* Schäfer, 1945, and *Cryptocandona dudichi* Klie, 1930). During new investigations in Greece (Euboea Island), *M. pseudocrenulata* was discovered in sandy gravel sediments (Danielopol, 1980b), thus confirming my suppositions.

During my studies on subterranean ostracods I have searched for some clues as to their history and evolution; for example why (in the sense of "how come" of Mayr, 1961) did the Candoninae more than other cypridid groups colonize the freshwater interstitial habitats? I have provided an answer to this question in two recent contributions (1977, 1978). The Candoninae with exclusively crawling representatives live often on sand and gravel substrates. These ostracods are predisposed to move within the substrate. As compared to the other freshwater ostracod groups with crawling representatives, the Candoninae have greater evolutionary plasticity allowing a higher rate of diversification.

I have been asked several times what is the antiquity of the interstitial freshwater Ostracoda of Europe (see the question of Oertli, in the discussion which followed my lecture delivered at the Saalfelden Symposium; Danielopol, 1977). Even though there is an impressive amount of information concerning the age and the antiquity of subterranean animals (Thienemann's, 1950, and Vandel's, 1965, monographs provide detailed reviews), there is little information on the subterranean ostracods (Danielopol, 1970b, 1971a, 1977, 1978). The problem of the age of an animal group is interesting in order to better understand its evolution. "Everything is time-bound and space-bound" writes Mayr (1961: 1501), and Jacob in "La logique du vivant" (1970: 147) notes: "Tout organisme, quel qu'il soit, se trouve alors indissolublement lié, non seulement à l'espace qui l'entoure mais encore au temps qui l'a conduit là et lui donne une quatrième dimension."

In the present contribution I shall try to assess the age of several interstitial ostracod groups living in freshwater habitats of Europe using some of the well-known methods, viz. the study of fossils and their phylogenetic affinities with living ostracods, the study of the morphology and the ecological distribution of the Recent ostracod fauna, and the use of biogeographic models. I want to demonstrate two things:

(1) that the ostracods provide realistic data for those interested in the general problem of the age of the subterranean fauna;

(2) that some of the tests to assess the antiquity of subterranean faunas, when applied to ostracod data, prove to be unsatisfactory.

c. *The three different meanings of the age of the subterranean fauna*

As mentioned above, one can find in the literature a large amount of information on the age of hypogean animals. For different authors the concept of age means at least three things:

(1) The phylogenetic age of an animal group at a supraspecific level, i.e. how old is a group since its first appearance in the animal kingdom. This can be inferred from direct evidence produced by fossils, or, indirectly, from morphological studies of living animals. Vandel (1967) showed, for instance, that the degree of morphological regression can give an idea of the phylogenetic age of an animal group. Very old animal groups have, for example, a high number of regressive characters. The phylogenetic age of an animal group plays an important role in the explanation of the origin of the subterranean fauna in the theories of the partisans of oriented evolution through orthogenesis. Jeannel (1928, 1950) considers that the representatives of phylogenetically old animal groups, faced to a phase of evolutionary senility, take refuge in subterranean habitats where they continue to evolve following their orthogenetic trends. Information on the phylogenetic age of the Candoninae and other related Cypridacea (Macrocyprididae, Pontocyprididae, Cypridinae, Ilyocypridinae, Notodomadinae, Cyclocypridinae) as inferred from the degree of their morphological specialization, can be found in Danielopol, 1978. For the Timiriaseviinae and Darwinulacea there is direct evidence of their phylogenetic age due to the exist-

ence of fossil records (Danielopol, 1968, Colin & Danielopol, 1980, and see the next sections below). I showed (1977, 1978) that the subfamily Candoninae which has the highest number of subterranean species is neither a primitive nor a hyperspecialized group as compared to the other main cypridacean groups mentioned above. The Candoninae do not appear to have a greater phylogenetic age than the Macrocyprididae, Pontocyprididae, Cypridinae or Cyclocypridinae. To date there is no evidence in any of the ostracod groups that the phylogenetic age influences the evolution of subterranean dwellers. Therefore, this aspect of the age concept will not be discussed in the present paper.

(2) The age of a subterranean animal group as the time spent by a group in the hypogean realm. In other words this is the time since the representatives of an animal group penetrated and started to adapt to the underground environment. This is an important factor allowing us to understand the different processes in the evolution of subterranean animals. The present paper deals with this problem.

(3) The age of a subterranean animal as the time spent in a specific geographic area. Many aquatic interstitial animals have the possibility of migrating actively and colonizing new territories. For example Magniez (1978b) showed that some populations of stenasellids (Isopoda) colonized alluvial sediments of the mountain valleys in the Pyrenean area from the lowland groundwater habitats during postglacial times. But the penetration by stenasellids of the subterranean realm happened most probably during the Tertiary or even earlier (Magniez, 1974, 1978a). At present we have too little information on the geographical distribution of subterranean ostracods from which we could infer the age of the different local populations of a subterranean species. So this aspect of the age of subterranean ostracods will not be discussed here.

d. *Some paradigms pertinent to the problem of the antiquity of the subterranean fauna*

The concept of paradigm has been introduced by Kuhn. It means, as its author noted recently (1970: 175) two things: "On the one hand, it stands for the entire constellations of beliefs, values, techniques, and so on shared by the members of a given community. On the other, it denotes one sort of element in that constellation, the concrete puzzle-solutions which, employed as models or examples, can replace explicit rules as a basis for the solution of the remaining puzzles of normal science."

The interest in the study of the subterranean fauna developed considerably since the second part of the past century. Many naturalists have been impressed by the morphological specialization of the cave fauna. Darwin in "The origin of species" (the fourth chapter) shows that the conservative habitats, exerting a low selective pressure, harbour many archaic animals or "living fossils". In considering such types of habitats, Darwin discussed also the case of caves (see the fifth chapter). He expected that cave faunas would be richer in "living fossils" than actually known at the time.

At the beginning of this century, Racovitza synthesized the bulk of information on the underground environment and its biotas. His "Essai sur les problèmes biospéologiques" published in 1907 represented the basis of what has become "modern biospeleology".

As Racovitza remarked later (1926), his decision to investigate the subterranean fauna came from his interest in the study of evolutionary processes. He thought that cave habitats were rather simple in structure, and that many environmental factors would vary to a lesser extent there than in surface habitats. Moreover, it was known that cave habitats harbour "living fossils", a very important tool for phylogenetical reconstructions. The effects of Racovitza's "Essai" were incredibly great (Codreanu, 1970; Orghidan, 1970) and during the following decades, subterranean investigations developed all around the world. Many discoveries confirmed the ideas put up by Racovitza and his students and became classic paradigms.

Here I shall give several examples of paradigms pertinent to the "age problem".

1. The subterranean realm is very rich in relict animals and "living fossils". Racovitza (1926) summarized this situation very well: "The discovery of a geologic stratum full of varied and

well-preserved fossils is a remarkable and important scientific event. But a more fortunate and important event is the discovery of the subterranean realm as a 'stratum' crowded with numerous and varied relicts, which are better preserved, as they are 'living fossils' ".[1])

2. The aquatic subterranean habitats developed in clastic rocks are very old. In these types of habitats some animal groups could persist through several geological epochs (even from Paleozoic to Recent). An expression of this paradigm can be found in Noodt (1968: 472): "Solange Erosion auf der Erde wirksam ist, hat es neben zerklüftetem Fels Sedimente und damit auch Grundwasser in ihnen gegeben. Das Biotop Stygon ist demnach uralt." Noodt shows that the crustacean group Bathynellacea could have existed in this type of habitat since the Paleozoic. Similar ideas can be found in Leruth (1939), Delamare Deboutteville (1960) and Delamare Deboutteville & Botosaneanu (1970).
3. Many epigean animals, relicts of old faunas, took refuge in the subterranean realm during different geologic epochs as a result of climatic deteriorations. A quotation from Banarescu (1975: 135, 136) exemplifies this point: "In general, the hypogean habitat is refugial, being populated by archaic groups of animals... Withdrawal into the hypogean habitat was partly due to some climatic changes: the Quarternary cooling (for some relatively thermophile animal groups it was easier to survive in subterranean, permanently cool, environments where the temperature was nevertheless constant, than on the surface, exposed to the winter frosts),..."
4. The possibilities of certain animal groups being able to spread through the subterranean habitats are limited. The present geographical distribution of these animal groups when superimposed on paleogeographical maps can provide information on the time when they penetrated into the hypogean realm. Vandel (1962: 32) gives a clear statement of this paradigm: "Les cavernicoles ont été fixés en place par la vie souterraine d'une façon aussi immuable que des fossiles. Leur répartition ne correspond plus à l'état présent du globe, mais à celui dans lequel se trouvait la terre au moment où les cavernicoles ont gagné les profondeurs de la terre" and "The geographical distribution of cavernicoles is sometimes capable of being superimposed onto paleogeographical maps. This allows an estimate of the date of the period of their expansion to be made." (Vandel, 1965: 466.)

These four paradigms show us that in the literature the origin and the age of subterranean faunas is presented in a very clear way but, unfortunately, without mentioning the initial assumptions and the implicit limits of the hypotheses. In this contribution I shall show that some paradigms are confirmed by the ostracod data, others are not corroborated and subsequently need to be further improved. In my argumentation I shall use some of the epistemological methods proposed by Popper (1934).

II. DO REPRESENTATIVES OF PALEOZOIC AND MESOZOIC OSTRACOD GROUPS STILL LIVE IN FRESHWATER INTERSTITIAL HABITATS OF EUROPE?

a. *Preamble*

I have already shown that it is widely accepted that certain biotas could have lived in subterranean habitats for very long periods of geological time. Very elegant demonstrations of this hypothesis have been presented for several groups of Crustacea: E.g. by Schminke (1973) for the Bathynellacea, by Stock (1976b, 1979) for the amphipod ingolfiellids, by Holsinger (1974) for the amphipods of the *Crangonyx* group, and by Magniez (1974, 1978b) for the isopod stenasellids. Schminke (1973, 1974) pointed out that a related group of the Bathynellacea, the Paleocarida, is represented in marine Paleozoic deposits. Because the Paleocarida possess more apomorphic characteristics than the Bathynellacea, Schminke inferred that the origin of the present subterranean bathynellids should be sought in a paleozoic marine group which invaded the subterranean freshwater

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[1]) Translated from the Romanian by D.L.D.

environment during the Carboniferous. For the ingolfiellids, the phylogenetic affinities between subterranean species living in Europe and those of South and Central America (all representatives of the subgenus *Gevgeliella*) led Stock (1976b) to the idea that this group spread on a unique landmass, Pangea, during the Mesozoic or earlier.

Holsinger (1974) discussed the geographical distribution and phylogenetic affinities of the amphipod genus *Stygobromus*. He suggests two concurrent hypotheses which could give an idea of the origin and the age of this genus and related groups of North American genera:

(1) a marine ancestor colonized southern North America during a regressive phase in the late Cretaceous or possibly early Tertiary;

(2) the ancestors of the North American subterranean amphipods invaded freshwater habitats before the breakup of the Laurasian landmass, perhaps in the late Paleozoic. As Holsinger noticed (1974: 59), this alternative is attractive because "it diminishes the importance of the lack of an extant group of potential marine ancestors and makes the widespread, Holarctic, distribution of the entire *Crangonyx* group easier to comprehend."

In these examples the actual evidence of a Mesozoic and/or Paleozoic age of subterranean animals is inferred from the phylogeny of groups without fossils and from bio- and paleobiogeographical data. The hypotheses concerning the age of subterranean animals presented here are difficult to corroborate or to refute and in the case of a concurrent hypothesis it is difficult to find a falsifier able to eliminate one of them. In the following I shall present the possibilities and the limits of the use of fossils to infer the age of presently living interstitial ostracod groups.

b. *The main marine ostracod groups occurring in the Paleozoic and early Mesozoic. Could they colonize the inland interstitial habitats?*

The ostracods are known from the Upper Cambrian onward. During the Paleozoic the marine environment was inhabited by a rich and diversified ostracod fauna (fig. 1) belonging to the orders Bradoriida (= Archeocopida), Leperditocopida, Beyrichicopida, Myodocopida, and Podocopida (Adamczak, 1968; McKenzie, 1972; Pokorny, 1978; Müller, 1979). The Bradoriida became extinct during the Ordovician, the Leperditocopida during the Devonian, most of the Beyrichicopida during the Triassic, although two genera persist until today. Some of the Paleozoic myodocopids and podocopids disappeared during the Carboniferous, the Permian and Triassic (McKenzie, 1972; Pokorny, 1978). During this last period the podocopids with the Bairdiidae and the metacopids with the Healdiidae dominated the marine habitats (Bolz, 1971; Gramm, 1972; Von Krömmelbein, 1974; Kristan-Tollmann, 1977). During the Jurassic the importance of the bairdiids and healdiids diminished in the marine environments, and we notice an explosion of the podocopid Cytheracea, a benthic group which continued to diversify through geologic time until the present day (see for details Whatley & Stephens, 1976). Two benthic groups of the order Myodocopida (Thaumatocypridacea and Polycopacea) have at present interstitial and cavernicolous representatives. These groups occur as early as the Permian ²) (Kornicker & Sohn, 1976) and it seems that they never attained a high diversity during the Paleozoic and Mesozoic (Scott & Sylvester-Bradley in Moore, 1961).

The representatives of the five ostracod orders found in Paleozoic and early Mesozoic sediments can be identified using the carapace shape and structure, the shape of the ventral margin, the type of the carapace dimorphism, the pattern of the central adductor muscle scars, the nature of the radial pore canals, the ornamentation and the hinge structure (Van Morkhoven, 1962; Henningsmoen, 1965; Adamczak, 1968; Gramm, 1972; Schornikov & Gramm, 1974).

Regarding the most ancient ostracod orders, i.e. Bradoriida (= Archeocopida) and Leperditocopida, Pokorny (1978: 129) writes: "There is a wide agreement among recent authors that the archeocopids are ancestral to all post-Cambrian ostracodes... After studying leperditocopids in thin section Levinson (1951) considered it possible that they were not Ostracoda, as we know them today, but rather an early specialized branch."

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²) Pokorny (1978) considers that the cladocopins (Polycopacea) could occur also in the Devonian.

The representatives of the order Beyrichicopida are strongly ornate and females have a complicated brood pouch (Henningsmoen, 1965; Pokorny, 1978). The carapace shape seems to make them unsuited for life in an interstitial habitat. As Hartmann (1974) and Maddocks (1976) showed, the carapace of the Recent marine interstitial ostracods is generally of small size, the shape is elongated or rounded, the calcareous valves are thin and the external ornamentation is poorly developed.

During the Cambrian, Ordovician and Silurian the continental climate was very arid and less suitable for the existence of continental freshwater habitats (Termier & Termier, 1968). Freshwater ostracods first appeared in the Devonian during which lacustrine and swamp habitats came to development. Well-diversified freshwater ostracod faunas are found in the Carboniferous (McKenzie, 1971).

The dominant group in the inland waters during the Carboniferous, Permian and the Lower Triassic appears to be the Darwinulacea (Bushmina, 1959; Neustrueva, 1970, 1977; Sohn, 1976). During the middle of the Mesozoic and then in the Cenozoic we witness an explosion of the Cypridacea in the freshwater habitats of all continents (Sylvester-Bradley, 1962; McKenzie, 1971). To a lesser but notable extent the Cytheracea diversified in continental waters (McKenzie, 1971).

Adamczak (1969) showed that the fossil paleozoic platycopids could have been filter feeding like the present cytherellids. Myodocopids are also filter feeders. This last group has many species which live in marine interstitial habitats, viz. the Polycopacea (Hartmann, 1974). All the interstitial ostracods living in freshwater habitats are deposit feeders. However, filter feeding is also a common feature among entomostracans living in the freshwater environment. It seems a priori that this is not a limiting factor. The bairdiids which are deposit feeders have one group containing marine interstitial species, viz. the pusselids (Maddocks, 1976; Danielopol, 1976d). The most serious limiting factor seems to be the limited euryhalinity of the marine Paleozoic and Mesozoic ostracod groups discussed here, viz. the Leperditocopida, Beyrichicopida, Myodocopida, some suborders of the Podocopida (Metacopina, Platycopina), and the bairdiids within the Podocopina; all these groups are known only from marine environments. They have no species, living or fossil, inhabiting surface oligohaline or freshwater habitats. Conversely, the cytherid group which has representatives in subterranean freshwater habitats, i.e. the Loxoconchidae (with the hypogean Pseudolimnocytherinae, see details in the next chapter) shows marked euryhalinity, e.g. *Loxoconcha galilea* lives in Lake Tiberias in salinities of 0.5-0.6 ‰ (Lerner-Seggev, 1968). *Loxoconcha gauthieri* can live at salinities varying from 2 to 40 ‰ (Schornikov, 1969). The marine interstitial *Tuberoloxoconcha* lives in euhaline mediterranean waters as well as in the Black and Azov Seas in oligo- and mesohaline waters (Schornikov, 1969). *Danielopolina orghidani* (Thaumatocypridacea) is the only representative of the Myodocopina found in an inland subterranean habitat, viz. in Cuban waters of 22 ‰ salinity (Danielopol, 1976c; Juberthie et al., 1977).

c. *The hypogean* Kovalevskiella *are "living fossils"*

In 1970 I showed that the interstitial ostracods of the genus *Kovalevskiella* (= syn. *Cordocythere*) belong to a group with one surface species widely distributed in Europe (*Metacypris cordata* Brady & Robertson) and several species distributed in southern and central America. I hypothesized that the interstitial species which now live in eastern, central and southern Europe are the thermophilous relicts of an ostracod group which lived in surface waters during the Tertiary. Most of the species disappeared from the surface waters in Europe at the end of the Tertiary. The revision of the ostracod species related to the subterranean *Kovalevskiella* (Colin & Danielopol, 1978; 1980) allows to present a more subtle and complicated picture of the history and evolution of this group. *Kovalevskiella* is a limnocytherid belonging to the subfamily *Timiriaseviinae* Mandelstam, 1947. Within it Colin & Danielopol (1978, 1980) recognized four groups of genera, viz. 1, *Timiriasevia-Metacypris*; 2, *Kovalevskiella*; 3, *Theriosynoecum*; 4, *Afrocythere-Elpidium*.

The first group of genera has many fossil spe-

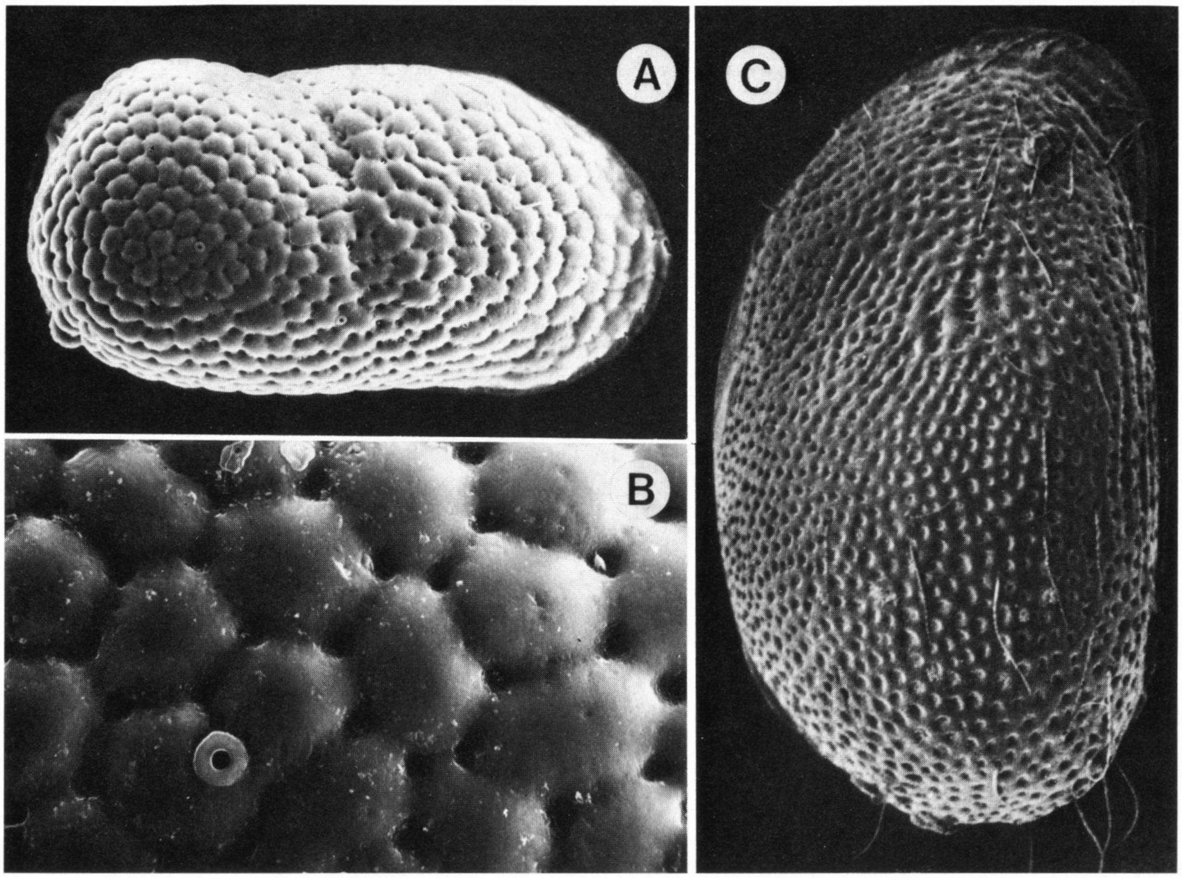

Fig. 2. A-B, *Kovalevskiella* sp., ♀ (Lobau, Vienna): A, right valve (× 215); B, detail of the external ornamentation (× 1075).
C, *Metacypris cordata,* ♀ (Caldarusani, Bucharest) (× 195).

cies known from Europe and Asia whereas only one species still lives in European surface waters, i.e. *Metacypris cordata* Brady & Robertson (figs. 2C, 3A). *Theriosynoecum* has no living species although it was a very successful genus during the Jurassic and Cretaceous periods (Colin & Danielopol, 1980). *Afrocythere-Elpidium* are known only as Recent species which live in the surface waters of West Africa and America (see the geographical distribution in fig. 3A). The group of genera *Kovalevskiella* Klein, 1963 (= syn. *Cordocythere* Danielopol, 1965) includes also *Rosacythere* Colin (in Colin & Danielopol, 1980) and *Frambocythere* Colin (in Colin & Danielopol, 1980). The morphological characteristics of this group of genera are: carapace of reduced size (about 0.5 mm length); posterior side inflated into a brood pouch; both valves having one or two transversal dorsolateral sulci (figs. 2A, 4F); carapace surface covered with small foveolae in a rosette shape (fig. 2B); hinge of lophodont type with the cardinal teeth in the left valve; the right valve larger than the left. The carapace ornamentation of the *Timiriasevia-Metacypris* group differs from that of the *Kovalevskiella* group in that the foveolae are in long concentric lines (fig. 2C). In *Timiriasevia* there is a tendency to build concentric microridges.

The genus *Kovalevskiella* Klein differs from *Rosacythere* Colin and *Frambocythere* Colin in having a carapace with only one straight and deep dorsolateral sulcus and rounded foveolae. *Rosacythere* has a large and atenuated sulcus; the foveolae are triangular in shape. *Frambocythere* has two sulci and rounded foveolae.

The living species of *Kovalevskiella* are distributed throughout central and southeastern Europe, and in Anatolia, Turkey (fig. 3A). *K. phreaticola*

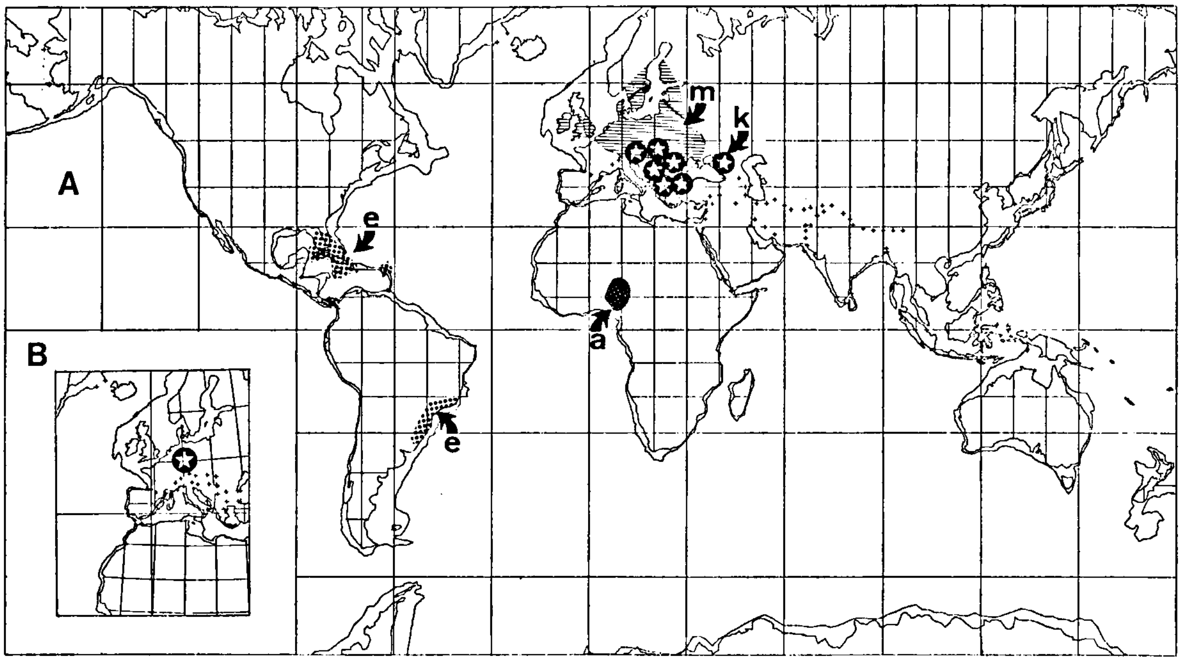

Fig. 3. A, The geographical distribution of the Recent ostracod Timiriaseviinae: m = *Metacypris*; e = *Elpidium*; a = *Afrocythere;* k (white stars) = *Kovalevskiella.*
B (inset), The distribution of *Kovalevskiella* in the Lower Oligocene (40 million years ago). Geographical maps from Smith & Briden, 1977.

(Danielopol) is widely distributed in Romania, *K. cvetkovi* (Danielopol) occurs in southeastern Bulgaria, and *K. bulgarica* (Danielopol) in western Bulgaria (Danielopol, 1970b). Representatives of the genus *Kovalevskiella,* whose specific status is not yet determined, are known from southwestern Romania, from the upper Danube Valley in Lower Austria near Vienna, from the Kiref Valley in northern Euboea Island (Danielopol, 1976a), from northern Italy (Colin & Danielopol, 1980), from southern Yugoslavia and from the Eregli cave in southern Anatolia (Petkovski, pers. comm.). Two species have been found in karstic areas, viz. *K. rudjakovi* (Danielopol) in Transcaucasia and *Kovalevskiella* n. sp. in Dobrodjea, Romania (Danielopol, 1970b).

Several fossil *Kovalevskiella* species have been described. *K. prima* (Carbonnel & Ritzkovsky, 1969) has been found near Kassel in northern Germany in Lower Oligocene lacustrine beds of oligohaline origin. *K. caudata* (Lutz, 1965) has been found in Upper Miocene (Tortonian) lacustrine sediments in southern Germany near Regensburg. *Kovalevskiella* sp. (figs. 5E, F) has been discovered in Upper Miocene (Lower Pontian) strata in Bolgrad (Soviet Union).[3] *K. turianensis* Klein has been found in Lower Meotian, Pontian, Kuyalnikian and Gurian in Georgia and Abkazia and Apsheronian, Lower Pleistocene, in Azerbaidjan (Soviet Union) (for more details see Klein, 1963; Popkhadze, 1975; Vekua, 1975; Colin & Danielopol, 1980).

One has to note that the oldest species, *K. prima* and *K. caudata,* occur at the northern and western margins of the geographical area occupied by Recent living *Kovalevskiella* (fig. 3B).

The fossil species of *Rosacythere* occur in the Lower Cretaceous (Albian and Albo-Aptian) of Europe and those of *Frambocythere* in the Upper Cretaceous and Paleocene of Europe (Colin & Danielopol, 1980).

From these data we can infer that the epigean *Kovalevskiella* could have penetrated into the subterranean realm between the Lower Oligocene and the Lower Pleistocene. There is no other evidence

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[3] One carapace collected by S. Gillet has been deposited in the Senckenberg Museum (SMFXe 6603; carapace length 0.39 mm).

which can be used to date the migration of the Timiriaseviinae into the hypogean habitat more precisely. The recent subterranean *Kovalevskiella* are the "living fossils" of the group *Rosacythere-Frambocythere-Kovalevskiella* which range from the Lower Cretaceous, i.e. a group which is documented to have existed for a little more than 100 million years.[4]

d. *The* Darwinula pagliolii *and the* Candonopsis kingsleii *groups with living interstitial and fossil species in Europe*

The Darwinulidae are represented in the subterranean freshwater habitats of Europe by at least one species, *Darwinula boteai* Danielopol (Danielopol, 1970a). This species has been found in the alluvial sediments of the river Mraconia, southwestern Romania (fig. 9). The family Darwinulidae is primarily a freshwater group which achieved an acme of diversification during the Upper Paleozoic, more precisely during the Carboniferous and Permian epochs (Bushmina, 1959; Neustrueva, 1977; Sohn, 1976). After the Triassic the number of darwinulid species diminished conspicuously (McKenzie, 1971). The group continued to exist through the Mesozoic and Cenozoic. A small number of species is at present distributed in freshwater habitats all over the world (Danielopol, 1968).

Darwinula boteai Danielopol has close affinities with the following living species: *D. malayica* Menzel, 1920 (see further details in Klie, 1935 and Pinto & Kotzian, 1961), *D. cuneata* Klie, 1939, *D. pagliolii* Pinto & Kotzian, 1961, *D. lundi* Neale & Victor, 1978, *Darwinula* sp.A from Cuba (figs. 8A, B) and *Darwinula* sp.B from Tunisia (figs. 8C, D). All these species have in common: the carapace length varying between 0.4 and 0.62 mm; the left valve overlapping the right; the antennal exopodite with one long and one short seta (figs. 8E, F); the furcae well developed, with one distal seta; the posterodistal process of the body elongated (fig. 8G). The darwinulids mentioned above form a group of species that I shall call the *Darwinula pagliolii* group.[5]

The right valve of *Darwinula boteai* Danielopol has a small posteroventral ridge (figs. 4G, 6B) on its outer side, the left valve has a small tubercle within the anterior third of the ventral side (figs. 6A, B). An outer ridge on the right valve has been noticed in *D. pagliolii* (see Pinto & Kotzian, 1961), *Darwinula* sp.A from Cuba (fig. 8B) and *Darwinula* sp.B from Tunisia (figs. 8C, D). An inner tubercle on the left valve can also be found in *Darwinula* sp.A (fig. 8B).

At the Senckenberg Museum (Frankfurt am Main) there are kept two fossil *Darwinula* species found in Pliocene deposits (Upper Dacian) at Valea Budureasca (near Calugareni, Jud. Prahova, Romania; see also fig. 9). *Darwinula* sp.1 (fig. 5D) from Valea Budureasca (catalogue collection in Senckenberg Museum: no. Fa 413) has a length of 0.67 mm. *Darwinula* sp.2 (figs. 5A-C), found at the same locality has a carapace length of 0.50 mm and the left valve larger than the right (catalogue no. of this specimen SMFXe - 6606); the left valve has a small inner ridge on the anteroventral side (fig. 5B); the right valve (length 0.47 mm for the specimen SMFXe - 6607) has a small outer posteroventral ridge similar to that of *D. boteai*. The shape of the left valve (fig. 5B)

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[4] Danielopol (1972a) showed that the fossil "*Candona*" *procera* Straub, 1952, from Lower Miocene (Aquitanian) deposits near Ehringen in the southern part of the Federal Republic of Germany could belong to the genus *Mixtacandona*. This was inferred from a comparative study of the Recent interstitial species, *Mixtacandona* sp.aff. *chappuisi* from Romania and fossil specimens of *Candona procera* from Germany (material deposited by Straub at the Senckenberg Museum) and from Italy (Pleistocene specimens from the Liri Valley described by Devoto, 1965).

Unless this hypothesis is invalidated by it being demonstrated that *Candona procera* resembles *Mixtacandona* because of homeomorphy in carapace shape, or even unless the fossil material represents already interstitial animals (this could be the case for the Pleistocene *C. procera* from Italy), we have to admit that the presently subterranean *Mixtacandona* species are another example of "living fossils". This group therefore has existed in Europe for at least 20 million years (using the radiometric scale and stratigraphic correlations of Rögl et al., 1978).

[5] For this group of species I chose the name of *D. pagliolii* instead of *D. malayica*, the oldest species known of this group, as Pinto & Kotzian (1961) presented for the former species a remarkably complete description, whereas only a poor description exists for *D. malayica*. A supplementary argument was also the fact that I was able to study specimens of *D. pagliolii* kindly supplied by Professor Pinto. The material of *Darwinula* sp.A and sp.B, from Cuba and Tunisia, respectively, discussed in this paper is deposited at the Limnological Institute, Vienna.

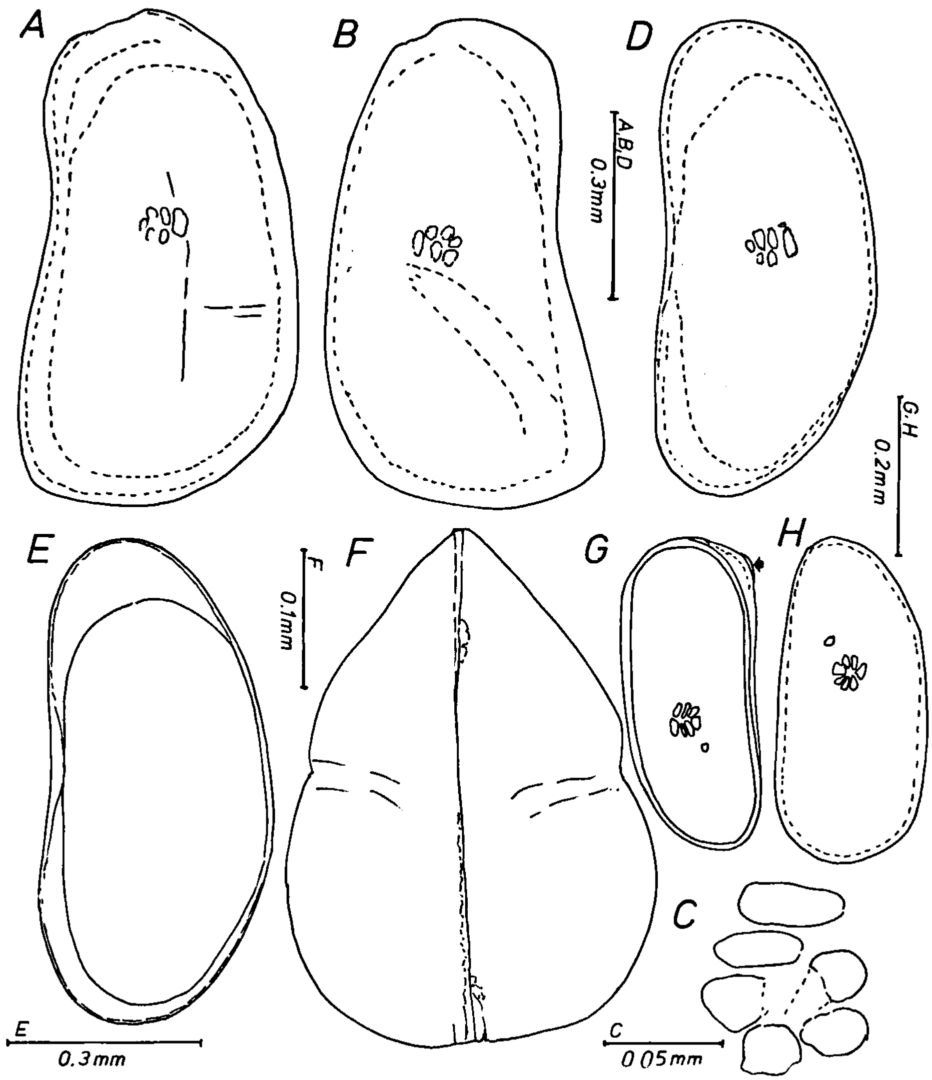

Fig. 4. A-C, *Candona altanulaensis* Szczechura & Blaszyk (Campanian), Nemegt Basin, Mongolia: A, left valve; B, right valve; C, central adductor muscle scars.
D, *Candonopsis boui* Danielopol, Albi, ♀, left valve.
E, *Candonopsis* cf. *arida*, right valve (after Malz & Moayedpour, 1973).
F, *Kovalevskiella bulgarica* Danielopol, Simitli, ♀, carapace, dorsal view.
G-H, *Darwinula boteai* Danielopol, Mraconia Valley, ♀ (after Danielopol, 1970b): G, right valve (arrow = outer ridge); H, left valve.

is very similar to that of *D. boteai* (fig. 4H) and *D. pagliolii*. In my opinion, the Pliocene species *Darwinula* sp.2 from Valea Budureasca belongs to the *D. pagliolii* group. We can infer from these data that a *Darwinula* species of this group could have inhabited the groundwater, in Europe, at least since the Pliocene (Upper Dacian), i.e. for about 4 million years using the radiometric scale and the biostratigraphic correlations of Steininger & Papp (1979).

As mentioned above, the darwinulids range from the Paleozoic. Therefore it is possible that other fossil *Darwinula*, older than the Tertiary species described here could refute the present state of our knowledge on the "maximum potential age" of the subterranean species of this group.

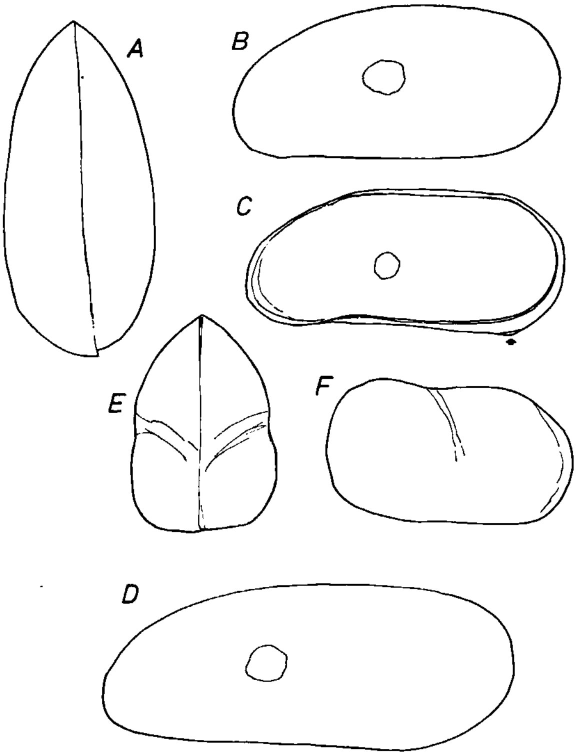

Fig. 5. A-D, Fossil *Darwinula* species, ♀♀, from the Upper Dacian from Valea Budureasca, Romania: A, *Darwinula* sp. 2, carapace, dorsal view; B, *Darwinula* sp. 2, carapace, lateral view; C, *Darwinula* sp. 2, right valve; D, *Darwinula* sp. 1, left valve.
E-F, Fossil *Kovalevskiella* sp., ♀, Pontian, from Bolgrad, carapace: E, dorsal view; F, lateral view.

Fossil Candoninae which could belong to groups with Recent representatives are known from lacustrine Cretaceous sediments in China (Yun Sian et al., 1978) and Mongolia (Szczechura, 1978). Such species as *Candona scopulosa* Furtos (sensu Yun Sian et al.) and *Candona* cf. *fabaeformis* (Fischer) (sensu Szczechura) recall those of the Recent living representatives of the genus *Fabaeformiscandona* Krstic. As an example the Cretaceous candonine *Candona altanulaensis* Szczechura & Blaszik, 1970, is illustrated here (figs. 4A-C), from the Upper Cretaceous (Campanian) of the Nemegt Basin, Mongolia. An evolutionary burst in the diversification of the Candoninae is recorded in the Paratethys Basin during the Upper Miocene and Pliocene (Mandelstam & Schneider, 1963; Stancheva, 1966; Krstic, 1972; Sokac, 1972; Marinescu & Olteanu, 1975). The Candoninae are presently widely distributed in the Holarctic realm; among the European ostracod groups it is the richest in species (Löffler & Danielopol, 1978).

Because of frequent parallel evolution in the form of the carapace, many homeomorphic Candoninae exist, both fossil and Recent species. This makes it difficult to identify and follow all the phylogenetic lineages which exist in this very diversified group of ostracods.

The representatives of the genus *Candonopsis* are distributed on the main continents, with the exception of Australia (see the list of species and their geographical distribution in Danielopol, 1980a). Klie (1932) divided the genus *Candonopsis* into three groups of species using the peculiarities of the furcal claws. The European species of *Candonopsis* have in common furcal claws without conspicuous central teeth. One can divide the six European *Candonopsis* species into two groups:
(1) *C. kingsleii* group (*C. kingsleii* (Brady & Norman), *C. parva* Sywula, 1967, *C. stammeri* Nüchterlein, 1969, *C. boui* Danielopol, 1978) and
(2) *C. trichota* group (*C. trichota* Schäfer, 1945, *C. thienemanni* Schäfer, 1945).

The *C. kingsleii* group has an elongated carapace, very narrow in dorsal view (maximum width less than 1/3rd of the carapace length), the dorsal and the ventral margins slightly curved, the anterior and posterior margins largely rounded. The male clasping organs of the maxillar palp are short. *Candonopsis boui* Danielopol, 1978 (see for a detailed description Danielopol, 1980a) has been found in the alluvial sediments of the river Tarn near Albi in southern France (fig. 7). This is a blind species with a rather short aesthetasc "Y" (see table III) and an elongated, slightly triangular carapace.

The fossil species *Candonopsis arida* Sieber, 1905, has been found in Miocene lacustrine sediments in the Steinheimer Basin near Ulm in the Federal Republic of Germany (see details in Lutz, 1965). *Candonopsis* cf. *arida* Sieber has recently been described by Malz & Moayedpour (1973) from the Miocene sediments (post-Aquitanian) of Theobaldshof, near Tann-Rhön, south of Kassel,

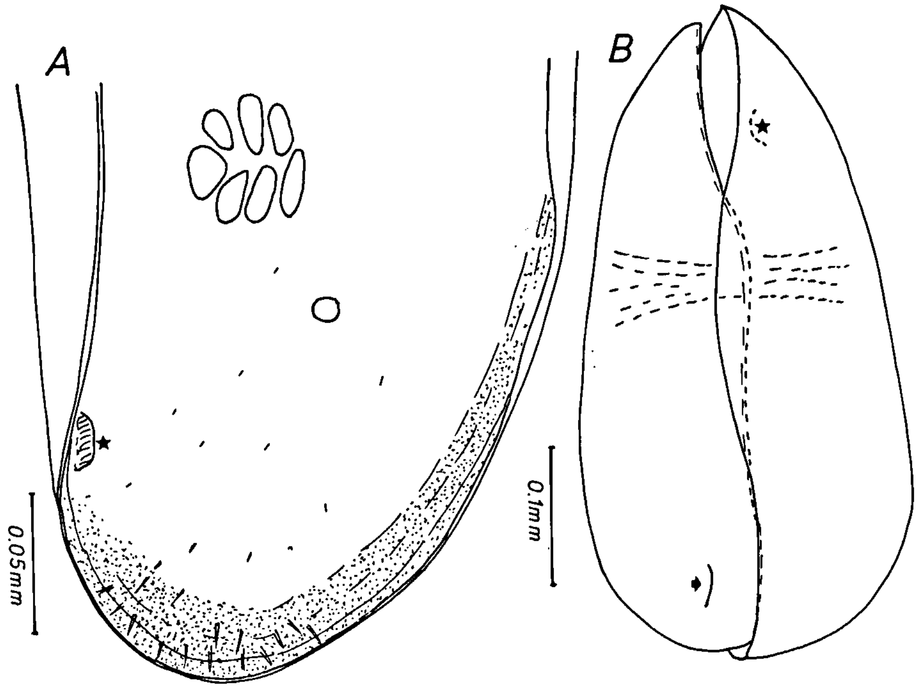

Fig. 6. A, *Darwinula* sp. A, ♀, (Cueve del Aqua, Cuba), left valve inner view (star = inner ridge). B, *Darwinula boteai,* ♀ (Mraconia Valley), carapace, ventral view (star = inner ridge; arrow = outer ridge).

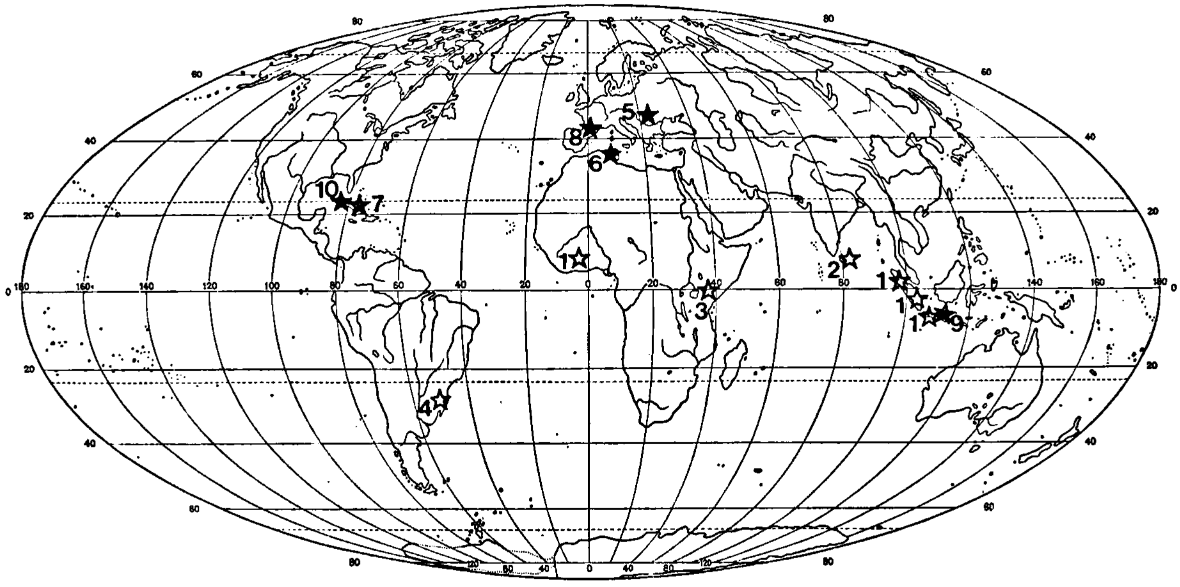

Fig. 7. The geographical distribution of the *Darwinula* of the group *pagliolii* and of the hypogean species of the genus *Candonopsis*: 1, *Darwinula malayica*; 2, *Darwinula lundi*; 3, *Darwinula cuneata*; 4, *Darwinula pagliolii*; 5, *Darwinula boteai*; 6, *Darwinula* sp. B; 7, *Darwinula* sp. A; 8, *Candonopsis boui;* 9, *Candonopsis putealis*; 10, *Candonopsis cubensis* (black stars = hypogean species; white stars = epigean species).

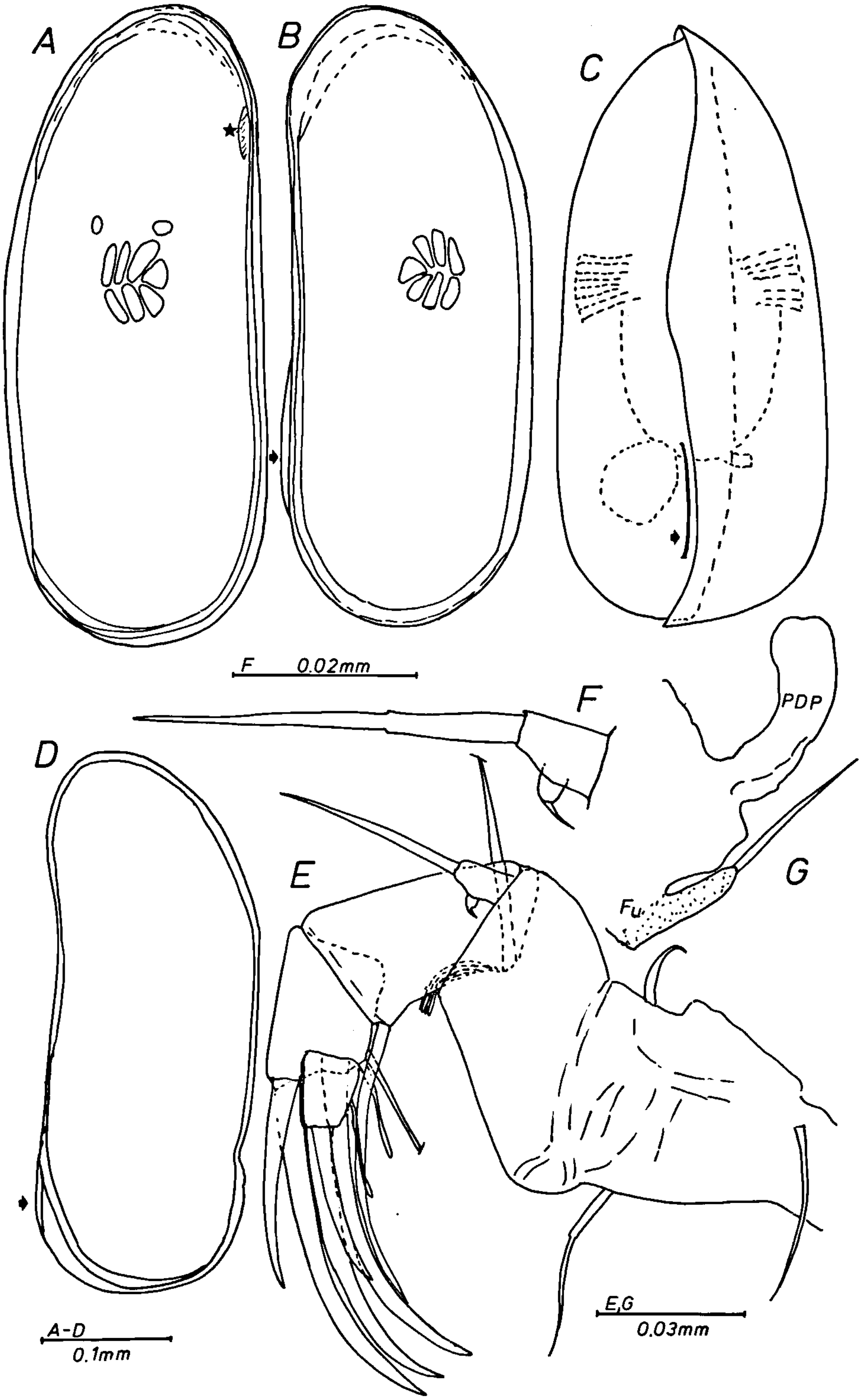

Fig. 8. *Darwinula* of the group *pagliolii*. A-B, *Darwinula* sp. A, ♀, from Cueva del Aqua, Cuba: A, left valve; B, right valve.

C-G, *Darwinula* sp. B, ♀, from Oued Lebga, Tunisia: C, carapace, ventral view; D, right valve, posterodorsal side folded due to the decalcification of the lamellar wall; E, antenna, general view; F, antennal exopodite; G, posterodorsal process of the body (PDP) and furca (Fu).

The arrows indicate the external ridge and the star the inner ridge of the valves.

in the Federal Republic of Germany.6) The carapace shape of *Candonopsis boui* is similar to that of *Candonopsis* cf. *arida* (figs. 4D, E). The length is about 0.8 mm, the maximum height does not exceed 1/2 of the carapace length. The posterior margin is very rounded. From these data one can infer that the *Candonopsis* species could have inhabited the groundwaters since about the Lower Miocene. The "maximum potential age" of a subterranean *Candonopsis* could be more than 20 million years (using the radiometric scale and stratigraphic correlations of Rögl et al., 1978). These data will probably be modified by the eventual description of a new *Candonopsis* species occurring in the Upper Oligocene deposits of Rhein-Hessen (unpublished material deposited in the Senckenberg Museum, Frankfurt am Main).

e. *Discussion*

From these data I would suggest that there is little chance of finding in the freshwater interstitial habitats of Europe, representatives of some of the dominant marine ostracod groups which flourished during the Paleozoic and early Mesozoic. Theoretically one could expect to find in Europe representatives of some of the dominant Mesozoic freshwater groups, viz. the cypridids of the group Cyprideinae and the Timiriaseviinae of the groups *Timiriasevia-Metacypris* and *Theriosynoecum* (see for details concerning these groups Sylvester-Bradley, 1962, and Colin & Danielopol, 1980).

The data presented here show that in the case of the freshwater interstitial ostracods there is no evidence of any group which could colonize the hypogean realm prior to the Lower Oligocene. This means that we do not know of the existence of interstitial ostracod groups of more than 30-40 million years old (using the radiometric time scale published by Berggren & Van Couvering, 1974, fig. 1).

The fossil ostracods are potential falsifiers of the present statement, and future investigation on Recent interstitial ostracods in Europe could produce new evidence of "living fossils" closely related to Paleozoic and Mesozoic ostracod groups now extinct in surface waters. This situation is, amongst the Crustacea, virtually unique to the Ostracoda, since they are the only group to enjoy a good fossil record and are thus able to provide valuable information concerning the problem of the antiquity of the European interstitial fauna.

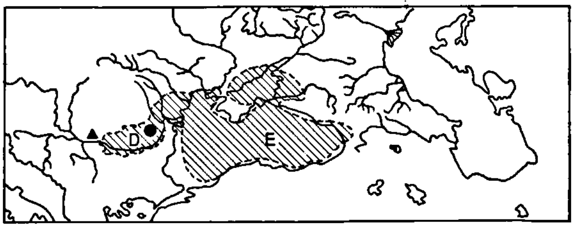

Fig. 9. The distribution of *Darwinula boteai* (triangle) and *Darwinula* sp. 2 (dot) and the paleogeography of the Euxinic (E) and Dacian (D) basins in the Upper Dacian, Pliocene (after Gillet, 1961).

III. THE MARINE REGRESSION MODEL

a. *Preamble*

It has been known since the early stages of the development of biospeleology that present freshwater animals living in hypogean habitats originated from surface marine forms. Viré (1899) was among the first to notice that the cave sphaeromids in southeastern France are distributed in the vicinity of the shores of a Tertiary sea. Further investigations by Racovitza (1910), Hubault (1938) and Chappuis (1943) corroborated the idea that the actual distribution of many freshwater subterranean animals superimposed on paleogeographical maps can give us clues to the antiquity of these animal groups.

In describing *Microcharon acherontis*, Chappuis (1943: 231) explains clearly how the age of this isopod, found in Transylvania, can be evaluated through the reconstruction of the paleogeography of central Europe: "*Microcharon* ist, wie aus seiner Verwandtschaft unzweifelhaft hervorgeht, marinen Ursprungs. Die Art lebte wahrscheinlich in dem Sande der sarmatischen Meere, die einen großen Teil Mitteleuropas bedeckten. Zu Anfang des Pliozäns verschwanden diese Meere oder süß-

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6) The *Candonopsis* aff. *kingsleii* mentioned by Lienenklaus (1905: 21) in the *Hydrobia obtusa* beds (Lower Miocene) near Wachenbuchen (Hessen, F.R.G.) has closer affinities with *C. arida* than with *C. kingsleii* (Malz & Moayedpour, 1973, and Malz, pers. comm.).

ten aus. *Microcharon* wurde dadurch Süßwasserbewohner, und als die Seen, die die ungarische Tiefebene und einen großen Teil der Balkan-Halbinsel bedeckten, verschwanden, blieb die Art in den Sand- und Schottermassen der einmündenden Täler."

The geographical distribution of *Troglochaetus beranecki* (Archiannelida), of *Chappuisius* (Harpacticoida), of *Desmoscolex aquaedulcis* (Nematoda), of amphipods belonging to the genera *Ingolfiella* and *Bogidiella*, of isopods, microparasellids, stenasellids, cirolanids, in inland areas which have been once Tertiary seas, have often been mentioned as examples of archaic subterranean animals in textbooks (Thienemann, 1950; Delamare Deboutteville, 1960; Vandel, 1965) or in reviews (Chappuis, 1956; Vandel, 1962; Husmann, 1962, 1978; Noodt, 1968).

Stock, in a series of papers (1976-1979), produced new evidence for the correlation between the present distribution of subterranean Crustacea and old paleogeographical configurations of landmasses. He showed that in the case of the Thermosbaenacea, Microparasellidae, some cirolanids, mysids, and atyids, the present distribution fits in well with the distribution of the landmasses existing during Tertiary regressive periods (commonly those of the Miocene). He called (1977b: 8) this biogeographical pattern of distribution the Regression Model ("During the various regressions, several marine littoral species 'stranded', were uplifted, and got adapted to mixohaline or limnic conditions. This way of origin of certain inhabitants of the inland waters may be called the Regression Model.").

b. *Initial assumptions*

To fit present geographical distributions of inland subterranean animals with a marine origin to past configurations of the landmasses, one has to admit as an initial assumption the low mobility of the animal groups involved (see for a discussion Sneath & McKenzie, 1973; Banarescu & Boscaiu, 1978).

Ruffo, who recently reviewed the data on the geographical and ecological distribution of the amphipod bogidiellids, remarked (1973: 75) that one can distinguish between two groups of interstitial species: one group "localized in regions corresponding to Tertiary seas far from the actual coastal lines . . ." which colonized the subterranean inland waters before the Quaternary period and a second group which is presently distributed in supra-litoral interstitial habitats. Tilzer (1968, 1973) and Magniez (1974, 1978b) showed that representatives of the genera *Troglochaetus* (Archiannelida) and *Stenasellus* (Isopoda) are distributed in areas which were glaciated during the Quaternary (the Alps and the Pyrenees). This implies that the freshwater interstitial fauna spread actively in these areas during the Late Pleistocene and Holocene. Some *Bathynella* (Syncarida) and *Parastenocaris* (Harpacticoida) species (Husmann, 1973, 1975; Enckell, 1969) display a similar biogeographical pattern.

This proves that the mobility of some of the subterranean animals is much higher than is commonly accepted. This difficulty was also encountered by Birstein & Ljovuschkin (1965: 318, 319) when they tried to find the antiquity of the aquatic fauna of some Central Asiatic caves ("Geological data do not permit one to consider this fauna as a relict of any of the Tertiary seas . . . We can either admit a far greater antiquity of this fauna or an ability of its components to disperse very widely beyond the boundaries of marine transgressions.")

c. *The active migration model - an alternative to the regression model*

An alternative model can be opposed to the regression model in order to explain the mechanism of colonization of inland groundwater by marine animals. This is the active migration model according to which interstitial marine animals with a higher degree of salinity tolerance could have colonized the inland groundwater by and by as a normal process of occupation of a free niche. This means that the migration process is not restricted to a definite period of time and that it is not related to the uplift of the coastal shore followed by the isolation of the marine fauna in brackish and later in freshened aquatic habitats.

Ruffo (1973: 75) gives such an example for the coastal interstitial bogidiellids (". . . as a matter

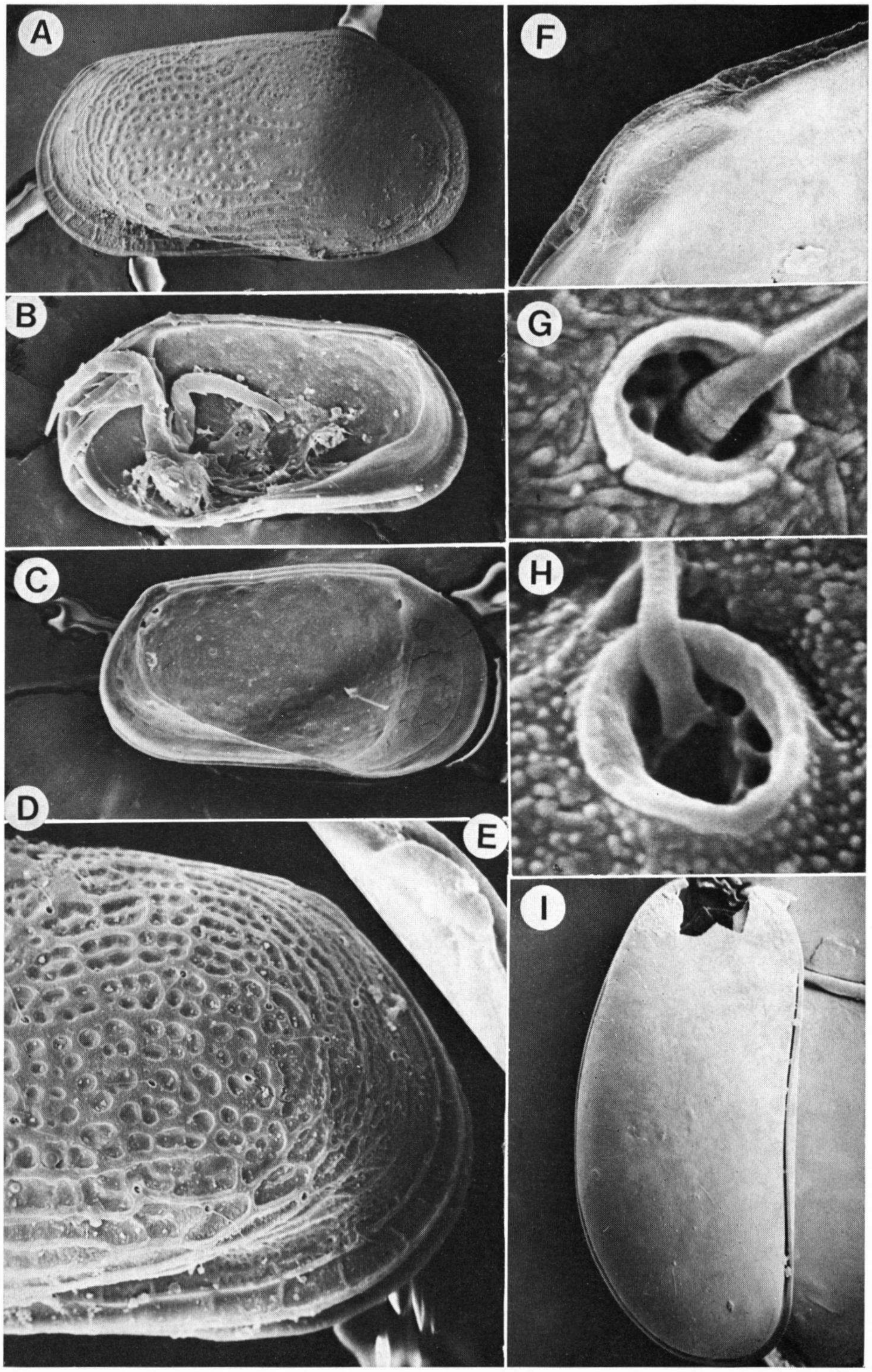

Fig. 10. A-H, *Pseudolimnocythere hartmanni* Danielopol, Aghios Georghios, Euboea, carapace structure: A, right valve, general view, outer side (X 208); B, right valve, general view, inner side (X 200); C, left valve, inner side (X 200); D, left valve, outer posterior side (X 400); E, right valve, posterior cardinal tooth (X 10,400); F, left valve, posterior cardinal socket (X 2400); G, H, left valve, two sieve pores (X 10,400).
I, *Mixtacandona pseudocrenulata* (Schäfer), Aghios Georghios, carapace (X 160).

of fact it is possible to find, even today, littoral interstitial species moving to the freshwater ...") and Stock (1979: 83) discussing the dispersal capacities of the ingolfiellids in the Carribean, states: "I have no doubt, that certain members of this group are still in the process of invading the continental waters via the mixohaline interstitial waters of sandy beaches ...". Petrova (1974) presented new arguments for this model using the limnohalacarids from Bulgaria. Kosswig and his students showed experimentally that major changes in the genotype of species which became troglobites occurred after the break of the gene-flow between the original populations and the subterranean ones (Kosswig, 1960; Peters & Peters, 1973). Based on this observation, it seems to me that the regression model could better explain the origin of many groundwater animals of marine origin which now live in freshwater habitats, than can the active dispersion model. But once again one has to notice that we need more information about the animals which are in the first stages of specialization to life in inland groundwater.

In the following I shall present two concurrent hypotheses using the regression model from which one could infer the antiquity of the cytherid ostracods belonging to the genus *Pseudolimnocythere*. I shall also propose several possibilities by which additional information could be obtained which might invalidate one or the other of these hypotheses.

d. *The interstitial ostracods of the genus* Pseudolimnocythere *Klie - morphology and systematics*

Klie (1938a) erected the genus *Pseudolimnocythere* for a species (*Ps. hypogea*) found in groundwater in southern Italy (wells in Bari, Murge area, and two caves near Lecce in the southern Puglia area, fig. 12). The origin and affinities of this genus remained obscure for a long time. Klie (1938a), Hartmann & Puri (1974), and Hartmann (1975) showed that this form of cytheracean could have affinities either with the marine Cytheridae and Loxoconchidae or with the freshwater Limnocytheridae. The discovery of two other species of *Pseudolimnocythere*, one in a well fed by fresh water on the northwestern coast of Euboea Island, Village Aghios Georghios, Greece (figs. 12, 13, 14), and the other one in the Skuljica Cave, on Krk Island, Yugoslavia (fig. 12), as well as the investigation of marine interstitial cytherids having close affinities with *Pseudolimnocythere* allow me to present the following data.

The genus *Pseudolimnocythere* is closely related to the marine interstitial group of *Tuberoloxoconcha* Hartmann, 1974. Both have carapaces with a rectangular shape, small sieve pores, the external face of the carapace being ornated with fossae and the hinge is smooth henodont (figs. 10, 11, 20G). The antenna has two distal claws (fig. 21C), the maxillular respiratory plate with one marginal aberrant seta (fig. 21E). The furca has 2 (3) distal setae (fig. 21G). In this complex of characteristics, the representatives of these two genera belong to the Loxoconchidae (superfamily Cytheracea). Within this family they form a definite phylogenetic lineage called the subfamily Pseudolimnocytherinae (Hartmann & Puri, 1974).

The Loxoconchidae are a marine cytherid group having about 150 Recent and 300+ fossil species divided into 15 genera (Hartmann, 1975). Representatives of this family are known since the Triassic. During the Upper Cretaceous a large number of species occurred (Whatley & Stephens, 1976). The radiation continued during the Tertiary. This group lived in littoral and sublittoral habitats. A *Loxoconcha* species (*L. helgolandica* Klie, 1929) is known from a brackish-water interstitial habitat on the Island of Helgoland (Klie, 1929). The Pseudolimnocytherinae are loxoconchids adapted to life in interstitial habitats. The carapace has thin calcareous valves, the hinge is reduced to a central smooth bar and a posterior tooth. The eye tubercles on the carapace are missing and no pigmented eyes have been noticed. The length of the carapace is reduced to 0.3-0.4 mm. The surface littoral and sublittoral Loxoconchidae have mainly strong amphidont, merodont, or gongylodont hinges, heavy calcareous and ornated carapaces with the eyes and eye tubercles well developed. The length of the carapace is generally medium large, 0.5-0.7 mm (Hartmann, 1975).

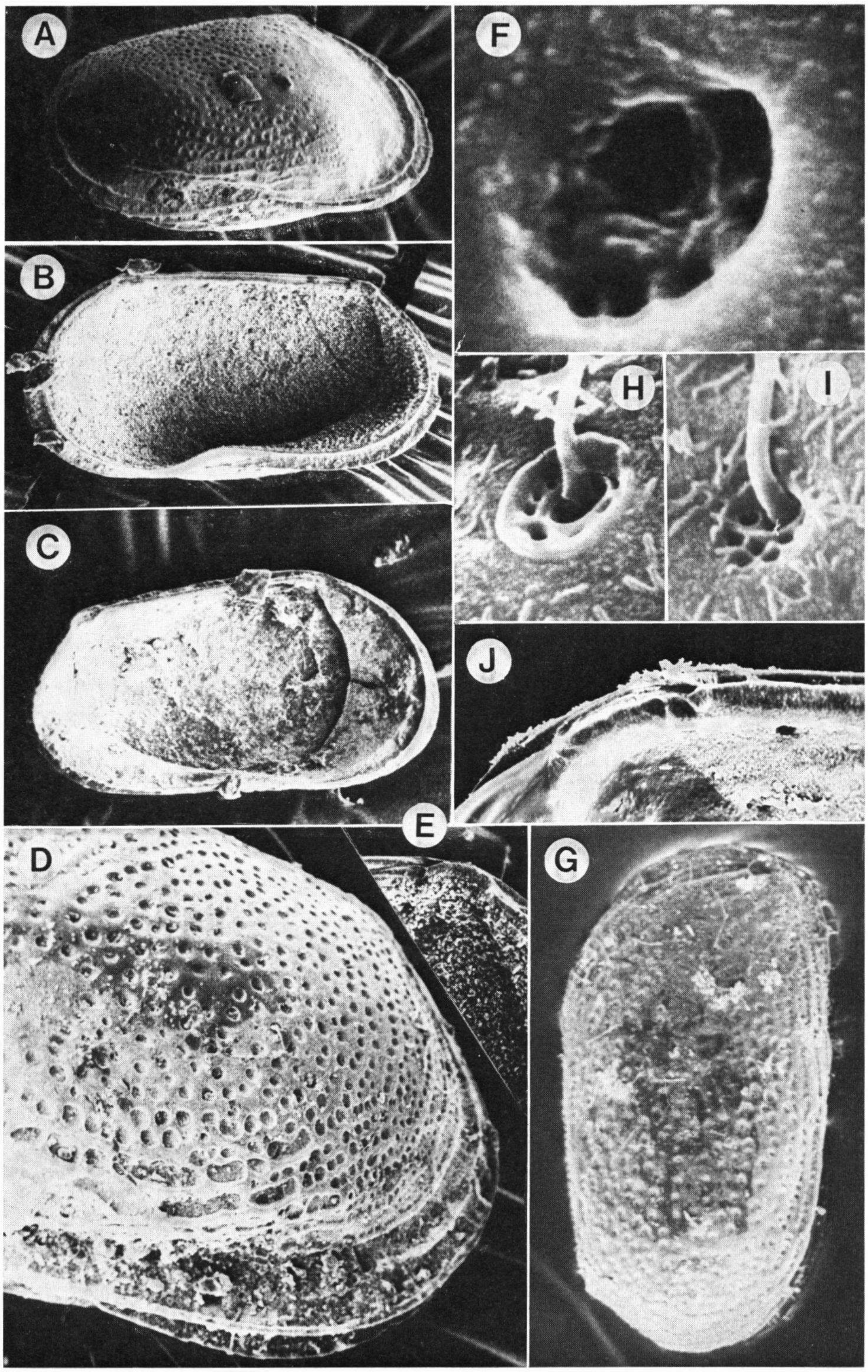

Fig. 11. A-F, *Pseudolimnocythere* sp., Skuljica cave, Krk Island: A, carapace, right side (X 176); B, right valve, general view, inner side (X 176); C, left valve, inner side (X 176); D, left valve, outer posterior side (X 440); E, right valve, posterior cardinal tooth (X 440); F, left valve, sieve pore (X 17,600).
G-J, *Tuberoloxoconcha* n. sp., Marina di Orosei, Sardinia, right valve: G, outer side (X 240); H, I, two sieve pores (X 4400); J, posterior cardinal socket (X 880).

The genus *Tuberoloxoconcha* has only marine interstitial representatives. *T. tuberosa* (Hartmann, 1953) is spread in the supralittoral interstitial habitats in the South of France and Italy as well as in the littoral of the northern Adriatic coast (Uffenorde, 1972).

T. nana Marinov, 1962, lives in marine interstitial habitats of the Black Sea, Bulgarian and Romanian coasts (Caraion, 1967) and in the Azov Sea (Schornikov, 1969). Two undescribed species belonging to this genus exist: one on the Atlantic coast of North America, Nahant, Massachusetts (Hartmann, unpublished) and a second in the Mediterranean in a lagoon near Marina d'Orosei, eastern coast of Sardinia.7)

The species of the genus *Pseudolimnocythere* which I have investigated differ from those of *Tuberoloxoconcha* in the following: The sieve pores of *Ps. hartmanni* Danielopol (figs. 10G, H) and *Pseudolimnocythere* sp. (fig. 11F) are situated in a small groove instead of on the outer ring or directly on the carapace surface (*Tuberoloxoconcha tuberosa, Tuberoloxoconcha* n. sp. from Sardinia — figs. 11H, I); the posterior hinge tooth and socket are larger than in *T. tuberosa* and the two undescribed *Tuberoloxoconcha* species (see figs. 10B, C, F, and 11B, C, E, J); the 6th antennular segment (the distal one) is longer than the 2nd and also than the 3rd + the 4th segment in *Ps. hypogea* and *Ps. hartmanni* (fig. 21A) as compared to those of *T. tuberosa, T. nana* and the two undescribed *Tuberoloxoconcha* species (fig. 22H). In *Ps. hartmanni* Danielopol the inner sclerified framework which sustains the walking legs (fig. 21G) is formed by simple distal bars joined to a complex proximal bar system. The anterior cell is open. The two undescribed *Tuberoloxoconcha* species that I investigated have a closed anterior cell between the proximal bars (fig. 22I).

e. *First hypothesis*

The *Pseudolimnocythere* species penetrated into the inland subterranean waters during a Pleistocene regressive phase.

The species of the genus *Pseudolimnocythere* are located near the present shore lines of the Mediterranean. *Ps. hypogea* has been found in the Grotta Abisso cave which opens to the sea, *Pseu-*

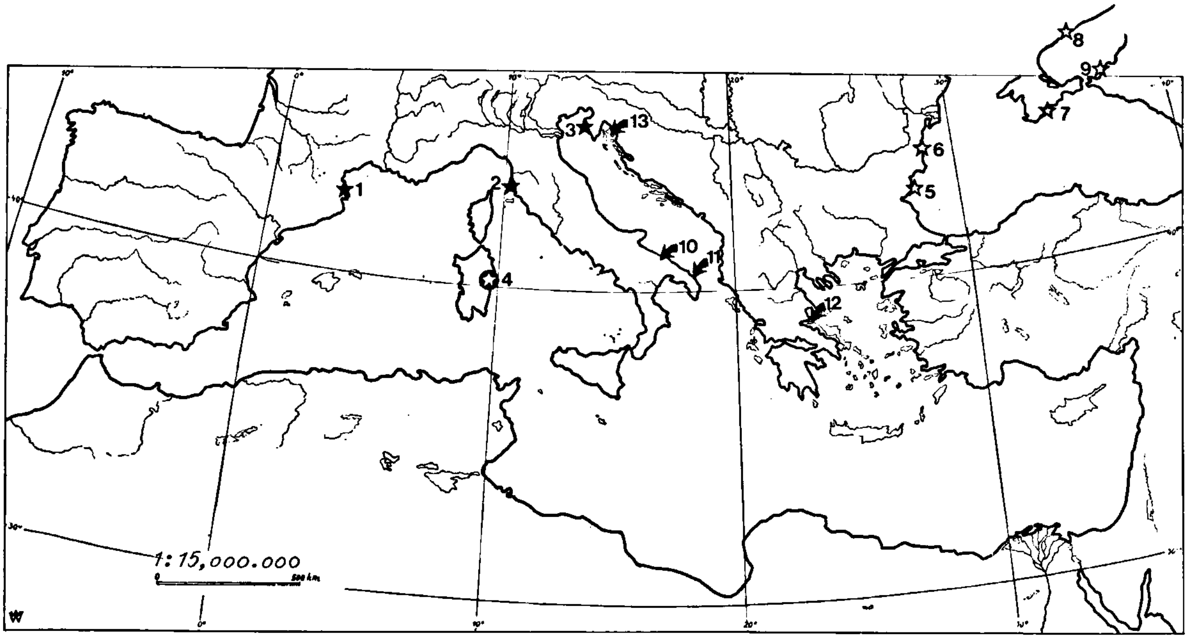

Fig. 12. The geographical distribution of representatives of the Pseudolimnocytherinae in Europe: 1-3, *Tuberoloxoconcha tuberosa*; 4, *Tuberoloxoconcha* n. sp.; 5-9, *Tuberoloxoconcha nana*; 10-11, *Pseudolimnocythere hypogea*; 12, *Pseudolimnocythere hartmanni*; 13, *Pseudolimnocythere* sp. (see also details in text).

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7) The material of *Tuberoloxoconcha* n. sp. from Sardinia has been deposited with the whole collection N. Coineau in the Biological Station of Naples.

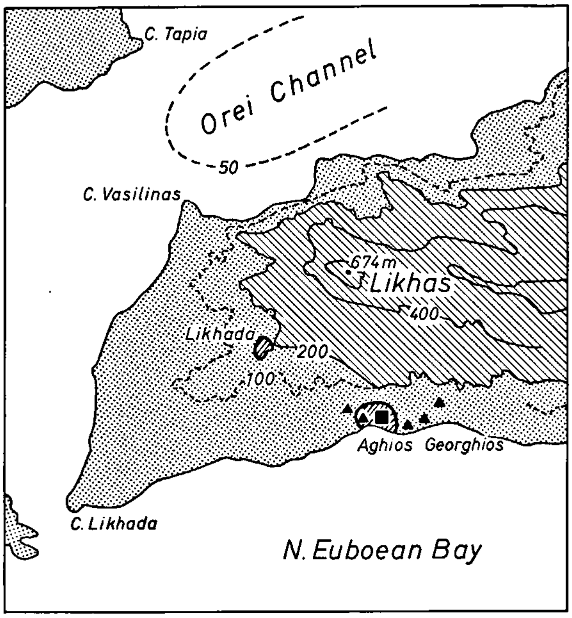

Fig. 13. The northwestern part of Euboea Island and the location of the wells where *Mixtacandona pseudocrenulata* (triangle) and *Pseudolimnocythere hartmanni* (square) have been found.

dolimnocythere sp.[8]) in the Skuljica cave, in the upper part of a 30 m cavity which opens to the northern Adriatic, on Krk Island, and *Ps. hartmanni* in a well located at 19 m from the sea shore on Euboea Island (fig. 13). As during the Pleistocene several regressive and transgressive phases took place (Pomerol, 1973), one should hypothesize that *Pseudolimnocythere* became adapted to the coastal freshwater habitats during one of the Pleistocene regressive phases.

The extension and the shape of the Euboean coasts (fig. 13) varied during the Pleistocene. In the Villafranchian, for instance, the northwestern coast of Euboea was connected with the mainland (Psarianos & Thenius, 1953). Later this area was most probably flooded as marine Quaternary sediments are registered in the Zarka Valley on the eastern coast of Euboea at about 10 m altitude (Guernet, 1971). Lüttig & Steffens (1976: 47) noticed that during the Pleistocene "the most radical changes in the Aegean area occurred during Tyrrhenian. Large regions in the Central and Northern parts foundered and were flooded by the sea." After this period a new regressive phase occurred.

f. *Second hypothesis*
The *Pseudolimnocythere* species penetrated into the inland subterranean waters during the Upper Miocene - Lower Pliocene regressive phase.

The Recent freshwater *Pseudolimnocythere* could have originated from the marine interstitial Pseudolimnocytherinae which lived in the Tethys or the Paratethys before the Pleistocene. The marine "*Pseudolimnocythere*" could have colonized the oligohaline and freshwater habitats during the Upper Miocene (the Messinian) when a strong marine regression (fig. 14) occurred in the Mediterranean area (Hsü et al., 1977). This means that the freshwater *Pseudolimnocythere* could be not older than 5-6 million years. The marine interstitial "*Pseudolimnocythere*" disappeared during the Messinian salinity crisis in the Mediterranean realm and the present *Tuberoloxoconcha* species in the Mediterranean might belong to an ostracod group which penetrated from the Atlantic Ocean after the reopening of the Iberian Portal in the Pliocene (see more details in Benson, 1975, for the Neogene history of the "mediterranean" ostracods).

A variant of this hypothesis would be that the marine ancestor of the current *Pseudolimnocythere* lived in the Paratethys during the Miocene-Pliocene. Hsü (1978a, 1978c) postulated that the Paratethys during the Messinian flowed in the desiccated Mediterranean through one or several channels that existed in the Balkan area (fig. 15), e.g. through the Morava-Vardar Valleys. The regression of the Paratethys and the subsequent

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[8]) The material is deposited at the Limnological Institute, Vienna. Dr. Moog found repeatedly (1977, 1978) only carapaces and valves (no living specimens) in two pools in the last part of the cave which is fed with fresh water from the upper part of the karstic system. In the samples collected in 1978, Moog found beside *Pseudolimnocythere* sp. also a valve of *Limnocythere* sp. (det. D. L. Danielopol) and several specimens of the amphipod *Niphargus* sp. (gr. *tauri*) (det. B. Sket, Ljubljana). In the first part of the cave which opens to the sea only a marine fauna (foraminiferans and polychaetes) has been found. These data suggest that the living *Pseudolimnocythere* should be located somewhere deep in the karstic system of Krk Island which is fed by fresh water. Its presence in the Skuljica cave near the sea coast is obviously due to a drift effect most probably during the rain periods and high waters in karst.

severance of its marine connection with the Mediterranean during the Lower Pliocene could have determined the penetration of Pseudolimnocytherinae species into freshwater subterranean habitats. Such a mechanism has often been postulated for the Recent hypogean fauna living in the Balkans and central Europe (Codreanu & Balcescu, 1970; Straškraba, 1972; Botosaneanu, 1978; Hsü, 1978).

g. *Discussion*

If we are to accept the first hypothesis, a Pleistocene age of the *Pseudolimnocythere* group and the subsequent initial assumption that the marine immigrants remained located near the Mediterranean, one should also expect to find strong morphological similarities between the *Pseudolimnocythere* and the *Tuberoloxoconcha* species. In fact we have seen that there are notable differences (see for instance the differences referring to the length of the antennular segments, to the sieve plate shape of the carapace pores, to the shape of the posterior hinge tooth).

An opposite situation applies to the Mediterranean and the Black Sea *Tuberoloxoconcha* species. *Tuberoloxoconcha nana* from the Black Sea shows close affinities with the Mediterranean species (*T. tuberosa*), see the shape of the hemipenis and the length of the antennular segments in Hartmann (1953), Marinov (1962), Caraion (1967), and Schornikov (1969).

It is highly probable that *T. nana* penetrated into the Black Sea during the Late Pliocene or early Pleistocene when the connection with the Mediterranean opened in the Bosphorus (Gillet, 1961; De Lattin, 1967). The colonization of the Sea of Azov by *T. nana* could have only occurred after the Würm glacial period. During the Würmian the Black Sea suffered a strong regressive phase which desiccated the Azov basin (see the paleogeographical situation in De Lattin, 1967, fig. 48).

An alternative situation could be that the presence of *Pseudolimnocythere* species in coastal inland waters (fig. 12) is conjectural as these species also live in deep inland or could represent a secondary colonization of the coastal areas in later time (e.g. post-Pliocene) from some "Hinterland" area. This seems to be for instance the case in the ostracod *Mixtacandona pseudocrenulata* (Schäfer) in Greece. This species has been recorded (Schäfer, 1945) from several wells near Larisa about 40 km remote from the sea on the mainland (fig. 14) and I found it (Danielopol, 1980b) in five wells around the village Aghios Georghios on the northern coast of Euboea Island (fig. 13) at less than 200 m from the seashore. This part of the Euboean lowland (less than 10 m altitude) was most probably flooded during the Pleistocene, as discussed above; so we have to accept that the recolonization of the northern coast of the island occurred in recent times.⁹)

The discovery of *Pseudolimnocythere* species far inland would corroborate the idea that this ostracod group could periodically migrate into coastal groundwater habitats. This implies that the initial assumptions would be contradicted and that the Pleistocene hypothesis should be revised.

Sket (1977) showed that the amphipods belonging to the genus *Niphargus* found in mixohaline waters along the Adriatic coast can survive there because of their salinity tolerance. Their presence in the coastal brackish groundwater is the result of recent geological events. Such species as *Niphargus hebereri* and *N. hvarensis* are widely distributed in Dalmatia, on the mainland and island coasts. This distribution does not reflect a recent migration from the sea but the fragmentation of a primitive continental area due to the present marine transgressive phase of the Mediterranean.

From these data we can conclude that there are not enough arguments to accept or to reject a Pleistocene age of the continental *Pseudolimnocythere* species.

There are several arguments for the second hypothesis, too:

(1) the morphological differences between the *Pseudolimnocythere* and the *Tuberoloxoconcha* species mentioned above,

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⁹) A similar pattern could apply to the interstitial amphipods *Ingolfiella* (*Gevgeliella*) *petkovskii* and *Bogidiella skoplensis* which are known from Yugoslavia (near Skopje) and southwestern Bulgaria and which occur also in the coastal area of Euboea (Bou, 1975; Danielopol, 1980b).

(2) the paleogeography of the Tethys and Paratethys during the Upper Miocene and Lower Pliocene,
(3) a *Tuberoloxoconcha* species lives today on the western coast of the Atlantic Ocean,
(4) during the Messinian salinity crisis an obvious change is recorded in the ostracod faunal associations (Benson, 1975).

In the following I shall develop these arguments:

Through the closing of the communication with the Atlantic, the proto-Mediterranean area underwent in the Upper Miocene a strong regressive phase with strongly evaporative conditions (Hsü et al., 1977). The sea level dropped by more than 1 000 m, as compared with the present sea level (Ryan, 1976; Ryan & Cita, 1978). In the non-desiccated part of the basin, lagoons remained where evaporites were deposited. During this period (the event occurred about 5.5 million years ago, according to Berggren & Van Couvering, 1974) many representatives of the Miocene ostracod groups disappeared (Sissingh, 1972; Benson, 1976). It is possible that due to the evaporative conditions (deposition of gypsum, anhydrites, carbonates or hypersaline waters) the supra- and sublittoral interstitial habitats were adversally affected and their ostracod fauna destroyed. Bate (1971) showed that in the Abu-Dhabi lagoon with similar evaporative conditions no interstitial ostracod could be found. It is, therefore, not unplausible that some pseudolimnocytherids could on the one hand survive in the outlet of springs, in the interstitial habitats of deltaic areas as well as in the inland coastal groundwater, on the other hand became extinct in the hypersaline environment like Sabkha.

Guernet (1971 and pers. comm.) presumes that during the Upper Miocene in the Central Aegean area, for short periods of time a marine arm occurred, which could be called the pre-Aegean Sea (fig. 14).

The colonization of the continental area near Euboea Island could have happened during the regression of the pre-Aegean Sea. If one accepts such an event, the present distribution of *Ps. hartmanni* near Aghios Georghios will be the result of an active dispersion through the continental groundwater (see fig. 14) just as this could be the case for *Mixtacandona pseudocrenulata,* mentioned above. A new invasion of ostracods in the Mediterranean happened during the Pliocene when a new connection from this basin opened to the Atlantic. Ruggieri (1971) showed that several psychrophilous cytherids penetrated into the Mediterranean from the Atlantic during the Pleistocene.

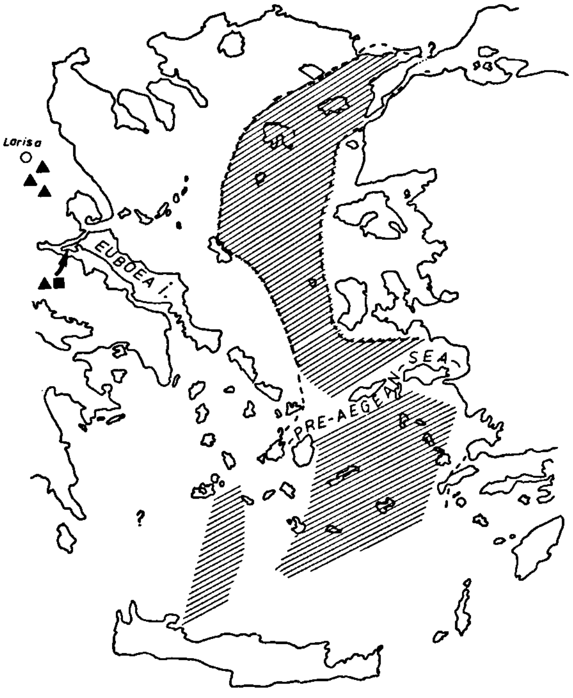

Fig. 14. The eastern part of the Mediterranean area with the pre-Aegean Sea in the Upper Miocene (after Guernet, 1971). Present geographical distribution of *Mixtacandona pseudocrenulata* (triangle) and *Pseudolimnocythere hartmanni* (square).

Coineau (1971) showed that the marine interstitial isopod *Microcharon marinus* differs morphologically from those members of the same genus living in inland fresh water of Europe. *Microcharon marinus* is distributed along the Atlantic coast of Portugal and in the Mediterranean on the coasts of Morocco, France, Italy, Corsica, and Sardinia.

At present there is no evidence that freshwater *Pseudolimnocythere* could be derived from a Paratethys interstitial form. This hypothesis, however, could be verified by trying to find pseudolimnocytherids in the areas occupied by the Paratethys in the Miocene and Pliocene (fig. 15). The dis-

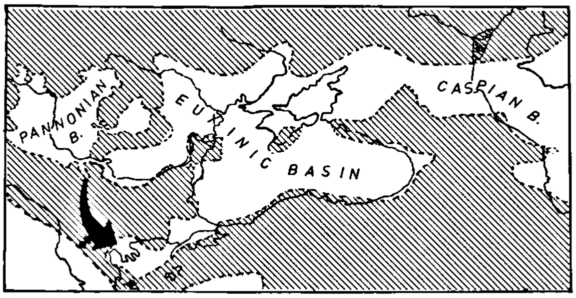

Fig. 15. The paleogeography of the Paratethys in the Upper Miocene - Lower Pliocene (after Seneş & Marinescu, 1971; Steininger et al., 1976; Steininger & Papp, 1979). The arrows indicate hypothetical connections to the Mediterranean (after Hsü, 1978c).

covery of pseudolimnocytherids in the Balkan area and in central and/or eastern Europe around the central and eastern Paratethys and around the Morava-Vardar hypothetical connecting channel between the Paratethys and the Mediterranean (fig. 15) would be an argument for the Mio-Pliocene antiquity of the freshwater interstitial ostracods of this group but will not necessarily prove that they originate from the Paratethys unless one can demonstrate morphological affinities with some ostracod groups that existed exclusively in this area.[10])

Cvetkov (1975) who recently analyzed those elements of the groundwater fauna of Bulgaria with marine origin, could not find any example of paratethyan species which could survive in the freshwater subterranean habitats. Sket (1970) showed that the geographical distribution of isopods of the genus *Monolistra* in Slovenia is not related to the present-day drainage systems. Their distribution is related to the Pliocene watersheds. For Sket the presence of this originally marine group in deep inland areas of Yugoslavia is an argument that they are old, ante-Pleistocene, immigrants coming from surface freshwater basins.

For the ostracods of the genus *Pseudolimnocythere* the discovery of fossils will be of invaluable help in solving the antiquity problem.

New investigations should be done in central and southeastern Europe in order to find other freshwater *Pseudolimnocythere* and on the eastern Atlantic coast, to find marine *Tuberoloxoconcha*. Only in this way we could corroborate one of the two concurrent hypotheses and thus strengthen the regression model.

IV. THE CLIMATIC REFUGIUM MODEL

a. *Preamble*

Racovitza (1907) suggested that many of the Recent subterranean animals are relicts of ante-Quaternary faunas. Stammer (1936: 1055) gave a clear definition of the climate refugium hypothesis: "Wir finden in den Höhlengewässern Mittel- und Südeuropas, sowie des ganzen Mediterrangebietes außerordentlich zahlreiche Tierarten, die wir als Relikte einer tertiären Süßwasserfauna betrachten müssen. Teils sind es wirkliche Süßwasserbewohner, zum großen Teil handelt es sich um marine Einwanderer, denen das tropische Klima des Alttertiärs eine Einwanderung in das Süßwasser ermöglichte. Sie alle zogen sich bei der Verschlechterung der Lebensbedingungen gegen Mitte oder Ende des Jungtertiärs in die Höhlengewässer mit ihren gleichmäßigen Lebensbedingungen zurück und blieben uns so hier erhalten."

Considering the aquatic animals, Chappuis (1927, 1933) showed that the representatives of the copepod genera *Speocyclops*, *Graeteriella*[11]), and *Elaphoidella* are found in Europe mainly in groundwater habitats. In the tropical countries, there are related species which live only in epigean habitats. This pattern suggested to Chappuis that

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[10]) The fossil *Darwinula* and *Kovalevskiella* species from the Miocene and the Pliocene of the Paratethys which show similarities with the Recent subterranean dwellers of these groups (see previous sections) do not prove that the Recent hypogean living species *D. boteai* Danielopol and various *Kovalevskiella* originate from the Paratethys. This is due to the fact that representatives of these two groups live also in surface freshwater habitats, as documented by fossil and living material.

We have seen that *Kovalevskiella caudata* Lutz occurred in a lacustrine habitat (Lutz, 1965) during the Miocene and all the *Darwinula* species of the group *pagliolii* are freshwater dwellers. Therefore it is also possible that the *Darwinula* and *Kovalevskiella* species penetrated the hypogean realm from a freshwater surface habitat like running waters (for a discussion see also Danielopol, 1977).

[11]) Chappuis (1927) discussed the affinities of the troglobites *Cyclops unisetiger* and *Cyclops troglodytes*. These species nowadays are included in the genera *Graeteriella* and *Speocyclops*.

the representatives of these groups were widely distributed in European surface waters during the Tertiary, but that they took refuge in groundwater habitats at the end of the Pliocene, due to the drastic deterioration of the climate. Other similar examples can be found in Fage (1931), Jeannel (1943), Orghidan (1955), Chappuis (1956), Borutskii (1964), Vandel (1965), Codreanu & Balcescu (1970), Delamare Deboutteville & Botosaneanu (1970), etc.

b. *Initial assumptions*

The climatic refugium model can be used for the determination of the age of a subterranean group only if one accepts two initial premises:

(1) that any species of a given group did not inhabit subterranean habitats during mild climatic periods,

(2) that species of a group should be specialized within narrow limits to their niche, therefore making difficult a further adaption to the drastic climatic changes in Europe during the Late Neogene, so that they took refuge in the groundwater.

c. *The* Darwinula *of the group* pagliolii *(fig. 7)*

In the previous chapter I defined this group of species morphologically. I shall now present the ecological distribution of the seven Recent and one fossil *Darwinula* species and I shall try to check if there is any evidence to say that the presently interstitial species *Darwinula boteai* Danielopol originates from an epigean *Darwinula* which sought refuge in groundwater due to the climatic deterioration which occurred at the end of the Pliocene and/or during the Pleistocene in Europe (see details on the climate evolution during the Late Neogene and Quaternary in Berggren & Van Couvering, 1974; Frakes, 1979).

Darwinula malayica Menzel, 1920, occurs in Tjipanas, Java, in Lake Ranau and Lake Bedali, Sumatra (Klie, 1932). In West Africa (Ivory Coast) it has been found in the algae covering crevices of the stony bottom of a stream near Touba (Klie, 1935). *D. lundi* Neale & Victor, 1978, has been collected from a sandy river bank with coarse gravel in the province Sabaragamuwa in southern Sri Lanka (Neale & Victor, 1978). *D. cuneata* Klie, 1939, occurs in mosses of a spring near Nairobi, Kenya (water temperature 29 °C) and in the swamps of the Athi River (Klie, 1939). *D. pagliolii* Pinto & Kotzian occurs near Porto Alegre, Brasil, "in the ponds along the border of a stream linking two lagoons and frequently flooding it" (Pinto & Kotzian, 1961). From fig. 7 one can see that these four epigean species occur in tropical and subtropical areas. *D. malayica* of Java and Sumatra and *D. lundi* of Sri Lanka inhabit a wet equatorial area with rain at all seasons.[12]) *D. cuneata* and *D. malayica* in Africa, occur in areas with a tropical wet-dry climate (tropical rain savanna climate, with dry season). *D. pagliolii* lives in a humid subtropical area.

Darwinula sp.A from Cuba was collected in a cave in the province of Camaguey, named Cueva del Aqua (Botosaneanu, 1970). A great number of females and juveniles live in a "lago phreatico" (water temperature 22.4 °C). The Cuban climate is of the tropical wet-dry type. Another *Darwinula,* sp.B, belonging to the group *pagliolii* was found in subsurface waters of alluvial sediments of the Oued el Lebga and the Oued Delma in northwestern Tunisia, Medjerda catchment area, near Ain Draham. The climate is of the mediterranean type with dry summers and wet winters (Berthélemy, pers.comm.). *Darwinula boteai* Danielopol was found by Botea in 1968 in alluvial sediments of the Mraconia stream near its confluence with the Danube (Jud. Caraş-Severin), southwestern Romania (fig. 9). I collected this species one year later in the same area, which suggests that this darwinulid permanently lives in groundwater (Danielopol, 1970a). The climate in this area is of the humid continental type.

The fossil species *Darwinula* sp.2 from Valea Budureasca was found in Pliocene (Upper Dacian) sediments of the Paratethys (fig. 9). This species has not been found by Hanganu (in Hanganu & Papaianopol, 1977) who studied the Upper Dacian ostracods from this locality. From the paleogeographical maps of Seneş & Marinescu,

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[12]) Cf. "The distribution of the climates in the modern world" by Strahler, 1971, reprinted in Raup & Stanley, 1978, fig. 12-7.

1971, it would appear that the waters of the Dacian basin in the Prahova area suffered a reduction in salinity during the Pliocene. The ostracod association described by Hanganu is of the euxini-brackish type, i.e. mesohaline to oligohaline salinity (see also Seneş & Marinescu, 1971). The *Darwinula* species are not typical Paratethyan elements like the Candoninae of the group *Caspiolla, Bakunella, Pontoniella,* etc. or like some cytherids of the genera *Loxoconcha, Cyprideis* and *Leptocythere,* mentioned by Hanganu.

The presence of darwinulids in oligohaline and mesohaline waters has been recorded several times. For instance, Keyser (1977) showed that *Darwinula stevensoni* Brady & Robertson and *D. furcabdominis* Keyser in S.W. Florida are most abundant in beta-oligohaline waters (0.5-3 ‰ salinity) but they also occur in waters with higher salinities (up to 12 ‰).

The evolution of the climate in the eastern Paratethys and in the southern Carpathians area where *Darwinula* sp.2 and *Darwinula boteai* have been recorded seems to have followed the general trend of cooling which was recorded all over Europe during the Late Pliocene (Berggren & Van Couvering, 1974; Frakes, 1979). For the western Carpathians of Slowakia, Planderova (1974) showed that in the Late Pliocene the climate was "mild-warm", in contrast to the Early Pleistocene which was "mild-cool". For the southwestern part of the Black Sea, sites 380 and 381 of the Deep-Sea Drilling Project, Hsü (1978b) showed that during the Pliocene there was a permanent climatic change from warm conditions to cooler ones. The glacial conditions as indicated by the "Steppe indices" occur for the first time in the Lower Pleistocene sediments (the glacial stage alpha).

d. *Discussion*

From the data presented above we may obviously not infer that *Darwinula boteai* originates from an epigean *Darwinula* which took refuge in groundwater due to the climate changes which took place in the Late Pliocene and during the Pleistocene. The presence of *Darwinula* sp.A in a subterranean habitat in the tropical conditions of Cuba contradicts the basic assumptions of the climatic refugium model; it shows us that the cooling trend of the climate is not a prerequisite for the presence of *Darwinula* in groundwaters.

Another *Darwinula* species is known to occur in tropical subterranean waters, i.e. *D. protracta* Rome from the Tsebahu Cave in Zaire (Rome, 1953). The ecological distribution of *D. malayica, D. lundi,* and *D. cuneata* is interesting because it shows a trend in these darwinulids to live in running waters with close connections to interstitial habitats, viz. sandy bottoms, mosses, stony crevices.

From these observations one can speculate that the colonization of European groundwater habitats by darwinulids might also have occurred prior to the deterioration of the Plio- and Pleistocene climate.

Is low temperature really the master factor which determined the refugial migration, in this case? We have no idea about the lower limits of the temperature tolerance of the *Darwinula* of the group *pagliolii.* An alternative climatic factor could be increasing aridity during warm stages. This explains, for instance, the presence of *Darwinula* sp.B in the alluvial sediments in the Aim-Draham area, northwestern Tunisia, where the summers are very dry. During the Late Miocene (Upper Pontian) in central Europe, around the Paratethys there was a change of climate from wet-temperate to dry-temperate (Steininger & Papp, 1979). During such a dry phase an epigean *Darwinula* theoretically could easily migrate to an interstitial habitat when the surface running waters desiccated. Finally, one has to note that unless a causal answer to the question of the limiting factors of the *Darwinula* of the group *pagliolii* can be found, we cannot fulfil the second assumption of the climatic refugium model stated above.

From these data I will conclude that the climatic refugium model as it was presented by Stammer or Chappuis is an unsatisfactory tool to determine the age of the subterranean ostracod *D. boteai.* Is this an exceptional case? I suspect that it is not. For instance, Petkovski (1973) described several new *Elaphoidella* species from tropical caves in Cuba. This means that, even in the classic example of Chappuis, we find a similar weakness of the hypothesis as mentioned above for *Darwinula.* We obviously need supplementary information to strengthen or refute the climatic refugium model. For instance, we need data about the first stage in the specialization of the ostracods to subterranean life. How and when does an epigean species become a troglophile and eventually a troglobite?

V. RACOVITZA'S RULES

a. *Preamble*

In his "Essai sur les problèmes biospéologiques", Racovitza (1907) shows that subterranean biotas are very heterogeneous, each taxon having its own history. Subsequently the age of cavernicoles (as indicated by the time spent by a taxon in subterranean habitats) is highly different. Racovitza proposes four rules to approximate the relative age of cavernicoles, viz.:

1. Organisms living indifferently in caves and surface habitats are "young" hypogeans.
2. Cavernicoles strictly inhabiting cave habitats, but having close relatives in surface habitats, are relatively "young" hypogeans.
3. Troglobites having a wider geographic range than their closest epigean relatives, are "old" hypogeans.
4. Troglobites whose closest relatives live in a different type of habitat are also "old" hypogeans.

Jeannel (1943) called the "young hypogeans" neotroglobites and the old ones paleotroglobites. A similar classification has been proposed by Motaş (1962) for interstitial water mites; by analogy the younger immigrants are called neophreatobites and the older paleophreatobites. The first two rules are also used by Vandel (1965) to estimate the age of cavernicoles.

The 1st rule of Racovitza will not be considered here as it refers to epigeans or troglophiles. Elsewhere (1980c) I showed that at present it is difficult or even impossible to identify a troglophile ostracod with incipient morphological and biological specializations to subterranean life. Considering the 2nd rule, the ostracods of the genera *Pseudocandona* and *Candonopsis* could probably fit in, but more investigations are necessary; see for discussion Danielopol (1980c). The 4th rule applies to an ostracod genus, *Danielopolina* Kornicker & Sohn (Thaumatocypridacea), where a species lives in a cave in Cuba (Danielopol, 1976c) and the closest relative *D. carolynae* is a deep-sea dweller (Kornicker & Sohn, 1976). There are no such examples among the European ostracods with freshwater interstitial representatives. In the following, I shall discuss only Racovitza's 3rd rule because one ostracod group, the genus *Cryptocandona* (Candoninae) could fit in with it.

b. *Initial assumptions*

Racovitza (1907) seems to have adopted for his 3rd rule, as an initial premise, the existence of a direct relationship between the age of a group and the range of its geographical distribution; older groups theoretically spread over larger areas than younger groups. Furthermore, these older groups became extinct in surface habitats but continued to live in the subterranean environment over larger areas. The first part of this premise recalls the concept of "age and area" (Willis, 1922). Cox, Healey & Moore (1976) critisized this concept showing that the spreading of an organism depends on a complex of physical and biological factors, and, therefore, it is practically impossible to identify a direct relationship between the age and the area variables. However, recent investigation on subterranean Crustacea with a world-wide distribution like the Bathynellacea (Schminke, 1973, 1974) and the ingolfiellid amphipods (Stock, 1976b, 1979) support partly Willis' rule. Schminke (1974), for instance, demonstrated that there are close phylogenetical relationships between the Madagascar-African and the South American parabathynellids of the group *Ceniobathynella*. There is a trend from the more plesiomorphic Madagascan species to the most apomorphic species of South America. These data suggested to Schminke that the representatives of this group spread on Gondwanaland from East to West prior to the different major splittings of this landmass, viz. the Triassic splitting off of Madagascar from Africa and the Cretaceous separation of Africa and South America.

c. *The ostracods of the genus* Cryptocandona *Kaufmann*

The genus *Cryptocandona* was proposed by Kaufmann (1900) for a parthenogenetic Candoninae (*C. vavrai*) having an elongated and laterally compressed carapace, a maxillar exopodite with 3 setae, a cleaning leg with 4 endopodal segments, each with at least 1 seta. The distal segment of the 2nd thoracic leg bears 3 long setae, the shortest being longer than the 4th endopodal segment, the furca has a short posterior seta (see also figs. 16A-E). The discovery of amphigonic *Cryptocandona* (e.g. *C. vavrai* Kaufmann, *C. reducta* Alm, *C. kieferi* Klie) (see for details Klie, 1938c) allowed the generic diagnosis to be supplemented. The male clasping organ is asymmetric, the right one being larger than the left one. The hemipenis has a peniferum with a large lateral lobe (figs. 16F-H).

There are at present five epigean and seven hypogean *Cryptocandona* species (fig. 17) known from Europe (Löffler & Danielopol, 1978; Sywula, 1976) and one cavernicolous species living in Japan (Klie, 1934).[13])

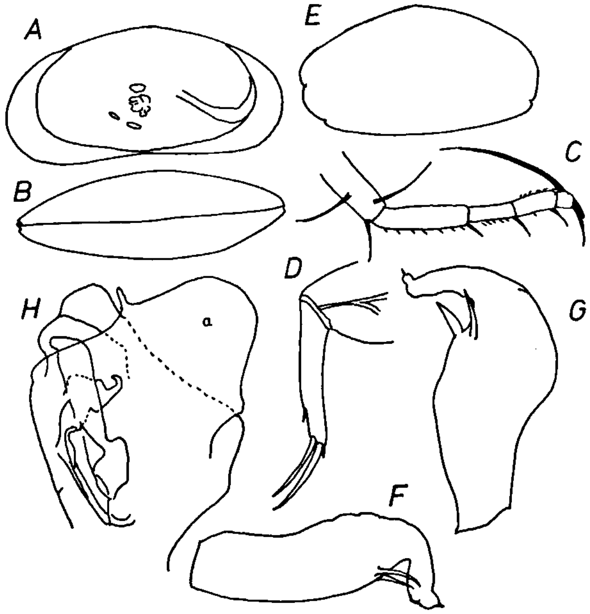

Fig. 16. A-D, *Cryptocandona brehmi* (Klie), ♀ (after Klie, 1934): A, left valve; B, carapace; C, 2nd thoracopod; D, furca.
E, *Cryptocandona angustissima* Ekmann, ♀ (after Alm, 1915), left valve.
F-H, *Cryptocandona matris* (Sywula), ♂ (after Sywula, 1976): F, G, left and right clasping organs; H, hemipenis (a = lateral process of the peniferum).

Cryptocandona vavrai lives in surface habitats in northern Italy near Pallanza (Munro-Fox, 1966) throughout central Europe and in Scandinavia (Löffler & Danielopol, 1978). In eastern Europe it has been found in southern Romania (Danielopol, unpubl.). This species lives also in the groundwater of river sediments in central Europe (Löffler, 1961) and southern France (Gourbault, 1972).

C. longipes (Ekman, 1908), has been found in surface waters in northern Sweden, in the Torne-Träsk area (Alm, 1915).

C. reducta (Alm, 1914) is an epigean species, which occurs in northern and central Europe (Löffler & Danielopol, 1978).

C. pygmaea (Ekman, 1908) has been found in swamps and pools in northern Sweden, in the same area as *C. longipes* (Alm, 1915).

C. angustissima (Ekman, 1908) occurs in Berga Småland, Sweden.

C. phreaticola (Klie, 1927) is an interstitial species found in a well in Tekovske Luzany and several springs, all in southern Slovakia (Kiefer & Klie, 1927; Petkovski, 1966).

C. leruthi (Klie, 1936) has been described from a well in Hermalle, Belgium (Klie, 1936).

C. kieferi (Klie, 1938) is widely distributed in the Rhine and Danube drainage systems (Löffler, 1963).

C. juvavi (Brehm, 1953) has been found in wells in the Salzburg area in Austria (Löffler, 1963).

C. matris Sywula, 1976, has been found in alluvial sediments of different valleys in the Carpathian Mountains in southern Poland. I collected *Cryptocandona* sp.aff. *matris* in several wells from the Iza Valley in northern Romania (Maramures).

C. dudichi (Klie, 1930) has been found in a cave basin in Hungary (Klie, 1930).

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[13]) Klie (1936) erroneously attributed *Eucandona cyproides* Von Daday, 1905, from South America, to the genus *Cryptocandona*. Von Daday (1905) clearly stated in his description that this candonine has a maxillar exopodite with two setae. By this peculiarity *E. cyproides* has affinities with the species of the genera *Candona, Fabaeformiscandona* and *Pseudocandona*.

C. brehmi (Klie) has been described from a sample coming from Hirogawara cave, about 120 km northwest of Tokyo in the Province of Shinamo (Klie, 1934).

Mandelstam & Schneider (1963) designated several Neogene Candoninae from the Soviet Union as belonging to the genus *Cryptocandona*. All these species have a "highly triangular" carapace very similar to that of the cave species *Mixtacandona riongessa* (Bronstein, 1947). This last species was originally included in the genus *Cryptocandona*. However, Danielopol & Cvetkov (1979) showed that *C. riongessa* belongs to the genus *Mixtacandona* and is the type of the "*riongessa*" species group.

Krstic (1972) described two fossil *Cryptocandona* species from the Lower and Middle Pannonian of the Paratethys, viz. *C. dolici* Krstic and *C. nocens* Krstic. The elongated and slightly triangular shape of the carapace of *C. nocens* recalls that of *C. matris* Sywula, 1976, but also that of *Mixtacandona pietrosanii* Danielopol & Cvetkov (see fig. 51B in Danielopol, 1978). Krstic (1972) considers that *C. dolici* has a carapace shape re-

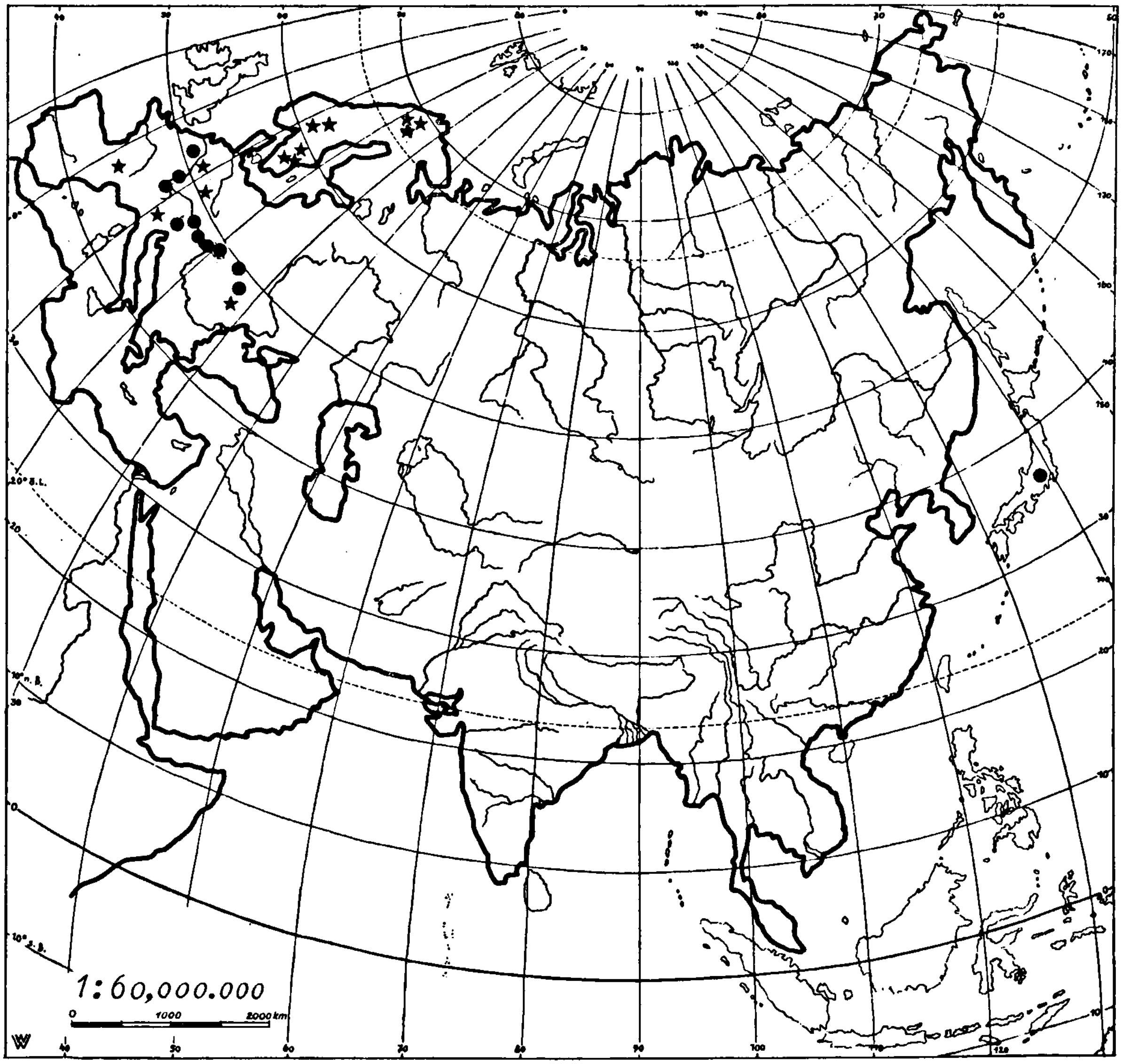

Fig. 17. The geographical distribution of *Cryptocandona* species (star = epigean species; dot = hypogean species).

sembling that of *Cryptocandona reducta* Alm, *C. kieferi* Klie and *Mixtacandona riongessa* (Bronstein). From these data it is obvious that for none of the fossil *"Cryptocandona"* discussed above it is definitely possible to make a clear statement on the phylogenetical affinities with living *Cryptocandona*. Therefore, we cannot use them with any certainty to infer the antiquity of *Cryptocandona*.

d. *Discussion*

Fig. 17 summarizes the geographic distribution of living surface and subterranean *Cryptocandona* species. It is noticeable that the subterranean species are spread over a larger area than that occupied by the surface species. This fits the 3rd rule of Racovitza. Unfortunately, we cannot infer from these data that the subterranean species are older than the surface ones because we do not actually know whether *Cryptocandona brehmi* Klie is closely related to the European subterranean species. Only females of this species have been found.

The interstitial species of Europe, *C. phreaticola, C. leruthi, C. kieferi,* and *C. matris* have a male copulatory organ with a conspicuous lateral lobe on the peniferum which is most similar to that of the epigean species *C. vavrai* and *C. reducta* (see figures in Klie, 1938b). This suggests that the subterranean European species are related to some of the European *Cryptocandona* now living in surface waters. On the other hand, the shape of the carapace and of the 2nd thoracic leg and the furca of *C. brehmi* (figs. 16A, C, D) resembles that of *C. angustissima* (fig. 16E), an epigean species from Sweden. If a direct phylogenetic link can be established between these last two species by using other morphological characteristics as well, and if a significant morphological gap between the subterranean *Cryptocandona* living in Europe and in Japan can be proved, in this case the hypothesis of Racovitza will be invalidated so that this rule cannot be used as a tool to identify the age of the hypogean *Cryptocandona* species.

From this discussion we may conclude that additional morphological and biogeographical data are needed to accept or to reject the 3rd rule of Racovitza in our attempt to infer the antiquity of the hypogean *Cryptocandona* species.

VI. THE DEGREE OF MORPHOLOGICAL AND/OR BIOLOGICAL SPECIALIZATION TO SUBTERRANEAN LIFE AS AN INDICATION OF THE ANTIQUITY OF A HYPOGEAN ANIMAL GROUP

a. *Preamble*

The morphological and biological specializations achieved by some animals living in the subterranean environment were an attraction for many generations of biologists. Delamare Deboutteville (1960, Poulson (1964), Vandel (1965), Ax (1966), Barr (1968), Poulson & White (1969), Juberthie (1975) inter alia presented reviews on this topic.

As the morphological and/or biological specializations are the result of an evolutionary process, they are necessarily time-dependent. It was thought that the age of a subterranean animal group, i.e. the time spent by this group in a subterranean habitat, could be roughly inferred from the degree of morphological and/or biological specialization of these animals.

Jeannel (1943: 38) wrote: "... il est certain que la foule des troglobies est hétérogène, formée d'espèces qui ont peuplé les grottes à des époques différentes. Il est naturel que les cavernicoles les plus anciens aient leurs organes visuels plus réduits et c'est ce qu'on observe en effet."

Vandel (1965: 465) proposes two rules to state the relative antiquity of troglobites:

1. "Recent cavernicoles are usually united to surface types by intermediate forms, while ancient cavernicoles remain very isolated in the present world.
2. The degree of physiological specialization ... allows a division of cavernicoles into Recent and ancient types ..."

b. *Initial assumptions*

The model of the degree of morphological and/or biological specialization to subterranean life as an indication of the antiquity of hypogean animals supposes, when one compares different species, at least two initial conditions:

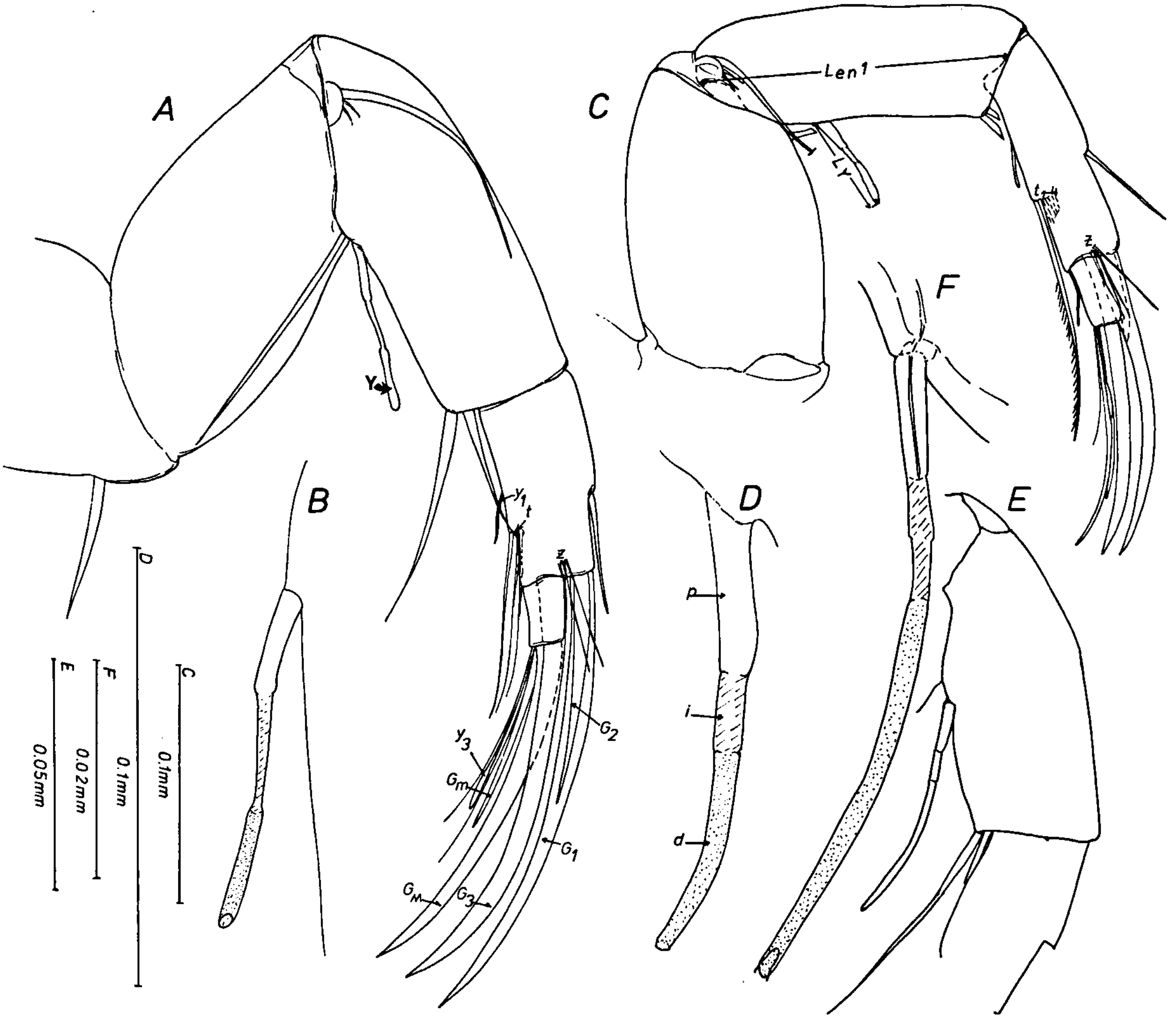

Fig. 18. Second antenna and the aesthetasc "Y". A-B, *Pseudocandona bilobata* (Klie), ♀ (Grosswaldstadt): A, second antenna, general view; B, aesthetasc "Y".

C-D, *Pseudocandona compressa* (Koch), ♀ (Lake Mogosoaia, Bucharest): C, second antenna, general view; D, aesthetasc "Y".

E, *Mixtacandona stammeri* (Klie), ♀ (Castelcevita), aesthetasc "Y".

F, *Mixtacandona chappuisi* (Klie), ♀ (Vallea Draganului), aesthetasc "Y".

Abbreviations: Len 1 = length of the 1st endopodal segment; Ly = length of the aesthetasc y; y, y_1, y_2, y_3 = antennal aesthetascs; t_1-t_4, z = antennal setae of the 2nd and 3rd endopodal segment; G_1-G_3, G_m, G_M = distal antennal claws; p, i, d = proximal, intermediary and distal parts of the aesthetasc "Y".

1. The selective pressures, acting on the species to be compared, should be similar.
2. The evolutionary potentialities and furthermore the evolutionary rates of change of the species under investigation should also be similar.

Wilkens (1973 a & b) tested this model using several cave fishes and a shrimp from caves of Yucatan, in Mexico. He studied the degree of eye regression in these freshwater animals and correlated this with precisely dated geological events which had occurred in Yucatan. The genetic processes which were involved in the eye regression in the cave animals were thoroughly studied by Kosswig and his students (see for a review Peters & Peters, 1973). They found that in the cavernicolous fishes they studied, the degenerative evolutionary processes occur by genetic drift, selection playing an insignificant role. Considering this premise, Wilkens (1973a) showed that in closely related animal species like those of the teleost fishes of Yucatan the rates of evolution are similar, and, therefore, the differences in the eye structure are the result of the different time spans during which the degenerative processes took place.

c. *The length of the antennal aesthetasc "Y" in epigean and hypogean Candoninae*

In the following I shall try to trace if by using the morphological criteria in conjunction with the phylogenetic relationships and geographical distribution of several freshwater ostracod species belonging to the subfamiliy Candoninae, one can assess their antiquity as subterranean dwellers.

As mentioned above, the Candoninae represent the most important freshwater ostracod group (in terms of specific diversity) in interstitial habitats of Europe. One can divide the subterranean Candoninae into 3 groups based on the degree of colonization of the subterranean realm. In group 1 there are no exclusively hypogean species. This is the case of the genus *Candona.* In group 2 there are epigean and hypogean species (the case of the genera *Fabaeformiscandona* Krstic, *Pseudocandona* (Kaufmann) and *Candonopsis* Vavra). Finally, group 3 consists of hypogean dwellers only (the genera *Phreatocandona* Danielopol and *Mixtacandona* Klie). The shape and the length of the sensorial organ, aesthetasc "Y" in several epigean and hypogean Candoninae was studied by Danielopol (1973).

The aesthetasc "Y" (Danielopol, 1971b) is a modified seta on the posterior side of the 1st endopodal segment of the 2nd antenna (fig. 18). This organ in the Cyprididae is presumed to be a chemoreceptor (Rome, 1947; Anderson, 1975). Externally this organ consists of three different parts (fig. 18D): a proximal part inserted on the endopod segment, an intermediary one (both with smooth surfaces), and a distal one, the last having a complicated ornamentation (Danielopol, 1971b, 1973; Anderson, 1975). The distal part carries a large receptor cavity and several cilia of the sensory cells which lie within the antenna (fig. 18F). Anderson (1975) showed that the surface membrane of the central part of the aesthetasc "Y" allows penetration of compounds of low molecular weight, while the distal part allows penetration of compounds of higher molecular weight.

The ratio between the total length of the aesthetasc "Y" and the length of the 1st endopodal segment of the antenna (fig. 18C) shows marked differences between surface and hypogean Cando-

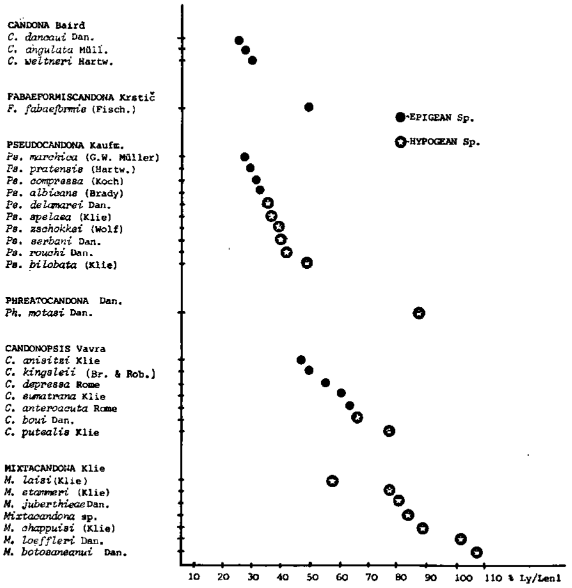

Fig. 19. The ratio of the lengths of the aesthetasc "Y" and the 1st endopodal segment of the antenna in epigean and hypogean Candoninae species expressed as a percentage.

TABLE III

The ratio between the length of the aesthetasc "Y" and the length of the first endopodal segment as a percentage in several Candoninae (see also fig. 19, data from Danielopol, 1973).

Taxa	Ly/Len 1
Candona	
dancaui Dan.	26.66
angulata Müll.	27.77
weltneri Hartw.	30.76
Fabaeformiscandona	
fabaeformis (Fisch.)	51.66
Pseudocandona	
marchica (G. W. Müll.)	28.76
pratensis (Hartw.)	29.33
compressa (Koch)	31.18
albicans (Brady)	31.0
delamarei Dan.	35.78
spelaea (Klie)	38.88
zschokkei (Wolf)	40.0
serbani Dan.	40.27
rouchi Dan.	42.59
bilobata (Klie)	50.0
Phreatocandona	
motasi Dan.	90.0
Candonopsis	
anisitzi Klie	47.0
kingsleii (Br. & Rob.)	51.56
depressa Rome	58.10
sumatrana Klie	62.96
anteroacuta Rome	65.0
boui Dan.	66.66
putealis Klie	80.0
Mixtacandona	
laisi (Klie)	60.18
stammeri (Klie)	76.92
juberthieae Dan.	79.10
Mixtacandona sp.	83.72
chappuisi (Klie)	87.50
loeffleri Dan.	101.72
botosaneanui Dan.	107.35

ninae species (Danielopol, 1973). Fig. 19 and table III show that the Candoninae of the genus *Candona* (group 1) have the shortest aesthetascs. The species of *Fabaeformiscandona, Pseudocandona* and *Candonopsis* (group 2) have intermediate lengths. The most elongated aesthetascs are those of *Mixtacandona* (figs. 18E, F) and *Phreatocandona* species (group 3).

Within the genera of group 2 one can see (fig. 19) that the interstitial Candoninae (exclusively hypogean) always have longer aesthetascs than the epigean species. One can speculate that in the hypogean-dwelling Candoninae the elongation of the aesthetasc is a specialization to the subterranean environment; it allows a better sensorial reception and it compensates for lack of vision. All the hypogean Candoninae I investigated have no noticeable eye structure in living specimens, in marked contrast to the epigean ones (Danielopol, 1978).

d. *Discussion*

Using the aesthetasc as a morphological index, one can state that the representatives of the genera *Mixtacandona* and *Phreatocandona* are the oldest representatives in subterranean waters and that those of *Candonopsis* and *Pseudocandona* are younger. Several qualifications must be made, however, to this too simplistic statement:

1. Within the genus *Candonopsis, C. boui* Danielopol is an interstitial species from southern Europe and *C. putealis* Klie is a hypogean species (interstitial) from Java in Indonesia.[14]) The differences in the aesthetasc length of these two species could also be attributed to different selective pressures in tropical and temperate countries, respectively. Mitchell (1969: 82) made a similar observation discussing the characteristics of temperate and tropical cave habitats: "Between the caves of major geographical areas, one could hardly expect selection pressures to be comparable..." (See also Elliott & Mitchell, 1973.)
2. The degree of development of an organ is also dependent on the internal characteristics of the genome (see Fryer, 1976 and Riedl, 1978, for discussion).

Vandel (1965) supposes that the evolutionary rates of subterranean animals are independent on external factors, being influenced only by internal factors. This author considers that subterranean animals are representatives of senile phyletic lines. Considering the Candoninae, I demonstrated

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[14]) *Candonopsis cubensis* Danielopol, 1978, is a hypogean species which has been found in a cave in Cuba (Danielopol, 1980a). The value of the ratio: aesthetasc "Y"/endopod segment is similar to that in *C. putealis* (Danielopol, 1973). The length of the aesthetasc of the other European and hypogean *Candonopsis*, viz. *C. thienemanni* Schäfer and *C. trichota* Schäfer, is, judging by the figures of Schäfer (1945), intermediate between that of *C. boui* Danielopol and that of *C. putealis* Klie and *C. cubensis* Danielopol.

(1977, 1978) that this subfamily is neither a primitive nor a senile phyletic lineage. Within the larger group Cypridacea, the Candoninae have a great evolutionary plasticity, and large possibilities for speciation. Grant (1977), following Simpson (1944, 1953), showed that different animal groups display different rates of evolution. De Lattin (1939), Kosswig (1960) and Sket (1969) arrived to the same conclusion for cave organisms. Considering the ostracods, Gramm (1976: 291, 292) showed that the evolutionary rate of carapace development differs markedly within the different phylogenetic lineages of the Podocopa: "As a result, the historical destinies of various groups proved to be unequal. Some remained conservative although widely distributed (Bairdiacea, Darwinulacea). The others - Cypridacea and especially Cytheracea - have undergone significant evolutionary changes..." In the case of the aesthetasc "Y" of the Candoninae, actually it is not possible to evaluate the rate of evolution of this organ within the groups mentioned above, viz. the genera *Candona, Fabaeformiscandona, Pseudocandona, Candonopsis*, etc.

From this discussion I must conclude that in the case of the interstitial Candoninae, the test of this morphological and/or biological index to assess the age of a subterranean group is unsatisfactory as none of the initial premises could be validated. It seems to me that at present for any subterranean animal group it would be difficult to fulfil such initial assumptions as stated above. Sket (1969) developed similar arguments using examples from cave animals of the Dinaric Alps. For the ostracods we obviously need more information on the genetics, phylogeny and zoogeography of different groups in order to strengthen the model, to make it more restrictive and more precise.

VII. FINAL DISCUSSION

As mentioned above, the "Essai sur les problèmes biospéologiques" published by Racovitza in 1907, from the beginning has been accepted by biospeleologists and considered as a scientific revolution. In a critical review of Racovitza's "Essai", Botosaneanu & Decou (1973: 518, 519) present the following "hommage" to this work: "Il est en effet rare qu'un ouvrage scientifique s'érige d'emblée en tant qu'acte de naissance d'une discipline, qu'il reste pendant de longues périodes source d'inspiration et de réflexion pour les spécialistes, qu'il puisse supporter la comparaison avec une monture en métal précieux, permettant qu'on y enchasse harmonieusement les pierres des acquisitions, au fur et à mesure de leur découverte." A similar "hommage" is presented by Orghidan (1978). This author notes that normally a new discovery in biospeleology confirms the ideas of Racovitza formulated in 1907.[15])

In the present essay I have attempted to assess the age of several interstitial ostracod groups inhabiting groundwater using some of the classical methods: the study of fossils and their phylogenetical affinities with living ostracods, the study of the morphology and the ecological distribution of the Recent ostracod fauna, and the use of bio- and paleobiogeographical models. Using Ostracoda, I examined some classical biospeleological paradigms: Many of the subterranean animals are "living fossils"; some animal groups lived since Paleozoic and Mesozoic times in the subterranean aquatic milieu; many epigean animals took refuge in the subterranean realm as a result of climatic deteriorations; the possibilities for some animal groups to spread through the subterranean habitats are limited.

The ostracods with their large number of fossils provided realistic data to discuss the antiquity of different living interstitial ostracod groups. Phylogenetical affinities between Tertiary (fossil) species and Recent subterranean forms could be proved in the case of the Timiriaseviinae, Candoninae and Darwinulidae. They gave us positive information (empirically proved) on the existence of "living fossil" groups (e.g. *Kovalevskiella*) which existed during the Tertiary in surface waters and which are now present in groundwater habitats only. For some groups, viz. *Kovalevskiella, Candonopsis* gr. *kingsleii, Darwinula* gr. *pagliolii*, the affinities between Tertiary fossils and Recent interstitial species allow us to approximate the maxi-

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[15]) Orghidan (1970: 110) also wrote: "... la biospéologie que Racovitza avait présentée dans son Essai ressemble d'une façon saisissante à la biospéologie actuelle."

mum potential time of an animal's occupation of the groundwater. The study of the ecological requirements of the main marine ostracod groups which flourished during the Paleozoic and the beginning of the Mesozoic suggests that there is little chance of finding them in the freshwater subterranean habitats of Europe, due to their limited tolerance of low salinities.

These data are important for the general problem of the antiquity of subterranean animals because in most of the other subterranean biotas the age of an animal group is inferred from indirect evidence, either by logical extrapolations or by comparisons with groups where direct empirical data have been found.

The deduction of the antiquity using morphological bio- and paleobiogeographical models failed to give satisfactory results. The data presented above are far from the optimistic situation drawn by Botosaneanu & Decou (1973) and from those of Orghidan (1978).

The age of the subterranean *Cryptocandona* could not be established as we still have too little information on the phylogenetic affinities between the surface and subterranean species living in Europe and Japan. The degree of morphological and/or biological specialization to subterranean life as an indication of the antiquity of a hypogean animal group is an unsatisfactory method when comparing different species, as the initial assumptions on which the model is based can hardly be fulfilled. The Candoninae do not seem to be an exception as I found the same difficulty occurring in other animal groups. In order to improve this situation I showed that we need more research into the genetics and the evolutionary rates of the different ostracod groups with subterranean representatives.

The test of the climatic refugium model proved to be unsatisfactory, too, when used with darwinulids. The ecological and geographical distribution of the *Darwinula* of the group *pagliolii* contradicts the initial assumptions of the model. It appears that the climatic refugium hypothesis, as it was stated by Stammer, Chappuis, Borutskii and others, is an oversimplified model. In order to improve it we need information on the causal mechanisms which determine the colonization of subterranean habitats by an epigean animal. We have to understand how an animal became a troglophile and then a troglobite. Now it seems that, after a long period of intensive study of troglobites, the time has arrived in which the epigean animals that normally colonize subterranean waters (sometimes called troglophiles) should also be studied intensively because they could yield important information on the problem of the initial phases of "troglobization" (Rouch, 1974, made a a similar remark).

Considering the antiquity of the freshwater interstitial ostracods of the subfamily Pseudolimnocytherinae, I showed using the test of the regression model, that their age could be Miocene-Pliocene or Pleistocene. In the ostracod case this model appeared too general as it accepts two concurrent hypotheses. Neither of them could be refuted using additional biological and paleogeographical information. In order to make the model more precise I suggest continuation of the faunistic investigations in southern, southeastern and central Europe as well as the eastern Atlantic coast to find additional interstitial *Tuberoloxoconcha* and *Pseudolimnocythere*. A further effort should be made to find fossil loxoconchids which could have morphological affinities with Recent Pseudolimnocytherinae.

If this study of ostracods confirmed that the subterranean habitats harbour "living fossils", some of them old relicts, it did not, however, corroborate that these "living fossils" are Paleozoic or Mesozoic subterranean dwellers. The paradigms of the climatic refugium and of the slow movement of aquatic animals through the subterranean realm could not be corroborated with the existing ostracod data. Moreover, I gave examples from other animal groups where these two biological "rules" are simply contradicted. Therefore, one should ask what is the degree of generality of these "rules"? In which case are they valid?

In a discussion on the necessity to state the limits of a scientific hypothesis, Toulmin (1953: 15) noted: "Even a real key is of little use if we do not know what rooms it will let us into." This phrase applies obviously also to the usefulness of the models discussed above.

The ostracod examples presented here show a more complicated picture of the "antiquity" problem than those stressed by the paradigms found in textbooks and reviews mentioned in the previous sections. Despite other opinions I consider that biospeleological problems as seen in the light of modern studies are more complex than those stated by Racovitza in 1907. Faced with this new situation one needs new methods, new hypotheses and new conceptual models. Some of them have been already proposed. See for instance the new concept of the karstic ecosystem of Rouch (1977). By emphasizing the limits of certain models and suggesting solutions to improve these models I hope to honour E. G. Racovitza. Certainly I did not propose here a new set of paradigms but I hope that I have been sufficiently persuasive to stimulate other students to intensify their studies of ostracods and thereby to contribute to the scientific revolution that is impending in biospeleology. "What is more satisfying for a scientist than to be challenged by scientific problems and to work in a field that continually poses new ones?" notes Mayr (1976: 408), and this is certainly true also for the problem of the antiquity of the subterranean ostracods discussed in this essay.

VIII. ACKNOWLEDGEMENTS

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IX. APPENDIX

Description of **Pseudolimnocythere hartmanni** Danielopol, 1979

Carapace and valves (figs. 10A-H, 20A-G): The form is elongated, subrectangular, laterally compressed. The anterior extremity is slightly more pointed than the posterior. The maximum width, about 1/4 of the length, is situated in the central third. The maximum height is about 1/2 of the length and is situated in the anterior third. The anterior margin is largely bent and higher than the posterior. The dorsal margin is straight and has a slightly oblique position as compared to the ventral margin. The latter is slightly concave in the mouth area. The asymmetry of the valves is not markedly distinct. The right valve is slightly larger than the left on the anterior and posteroventral sides. The cardinal angles are well defined. The flange is well developed on the outer and posteroventral margins. An outer ridge extends parallel to the outer and posteroventral margins. The external ornamentation of the carapace is better devel-

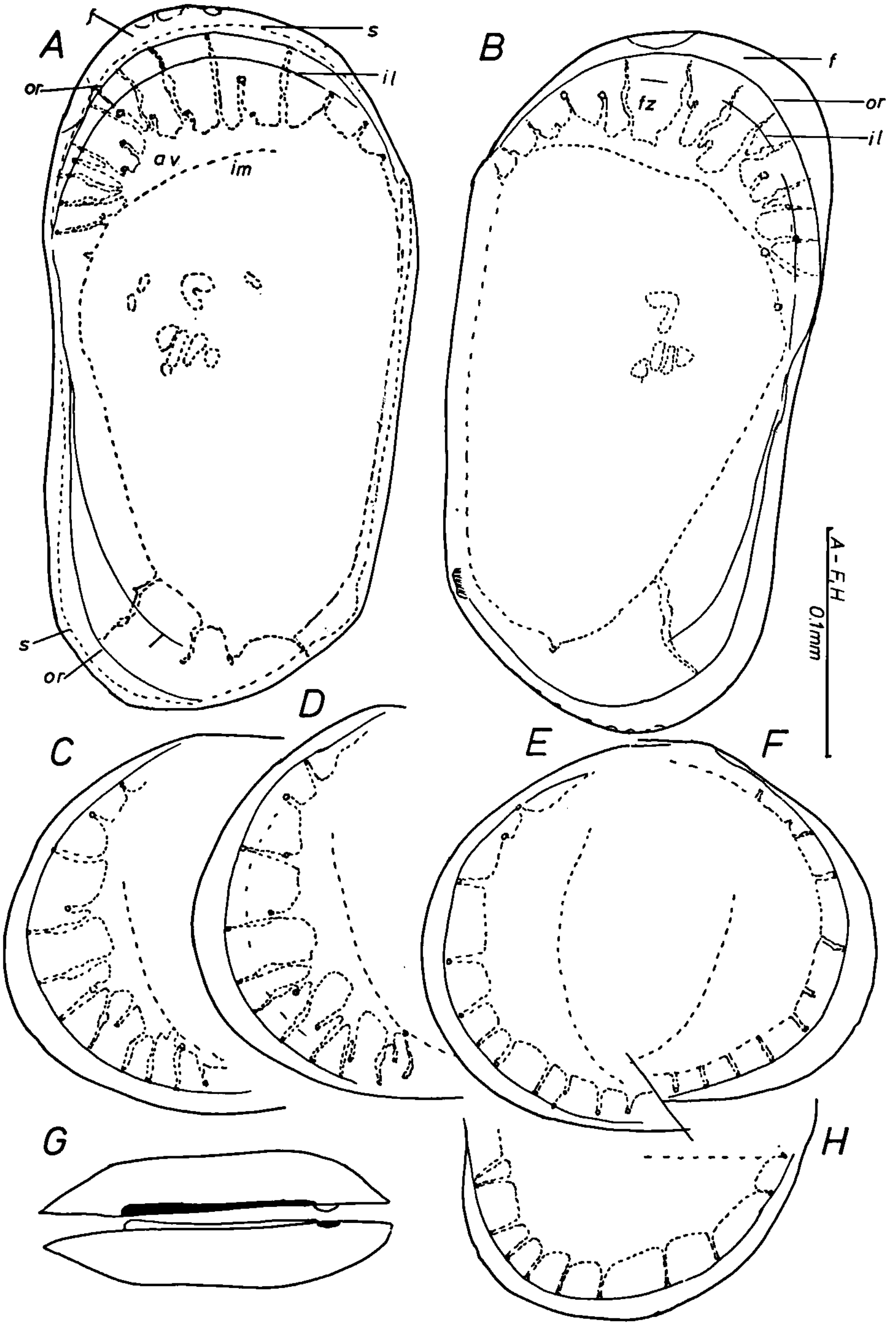

Fig. 20. A-G, *Pseudolimnocythere hartmanni* (Aghios Georghios, Euboea Island; A-C, E, male; D, F, female): A, B, left and right valves, general view; C-E, left valve, details of the anterior third (note the variability of the marginal canals); F, do., right valve; G, dorsal view of the hinge.

H, *Tuberoloxoconcha* n. sp., ♂ (Marina di Orosei, Sardinia), detail of the anterior third of the right valve.

Abbreviations: s = selvage; f = flange; or = outer ridge; il = inflexion line (area); fz = fused zone; av = anterior vestibule; im = inner margin.

oped in the posterior half than in the anterior. Round pits (large foveolae or fossae), are dispersed in slightly parallel lines. There is a trend to enlargement of the foveolae and to fusion in larger fossae on one side and to strengthening of dorsal and ventral muri forming longitudinal carinae which extend in more or less parallel lines, especially on the ventral side. In the anterior third the foveolae become less well developed and the outer wall becomes smooth. The normal pores are rimmed and have a sieve plate with 6-8 holes disposed in one row, deep at the bottom of the funnel. The central seta is simple. Posteriorly the pores are situated on the ridges (intramural pores).

The hinge is smooth henodont i.e. the right valve has a well-developed posterior cardinal tooth and an inter-cardinal groove which is larger near the anterior cardinal angle; the left valve has an open socket and an inter-cardinal smooth bar which is rounded on the anterior side. Selvage well developed on both valves. The left has a selvage which runs parallel to the outer margin and the flange. The right valve has on the anterior and posteroventral sides a smaller selvage than the left valve (figs. 10B, C). The inner margin is straight on the anterior and ventral sides; it forms an angle at the anteroventral junction and is largely bent posteriorly. On the ventral side the inner margin has an oblique position. The marginal radial pore canals can be simple or ramified. Their shape is variable as can be seen in the figures. The anterior and posteroventral vestibulae also vary widely due to the differences in the extension of the fused zone. The number of anterior marginal pore canals varies between 8 and 12 and posteriorly between 2 and 5. The central adductor muscle scars are formed by a row of 4 longitudinal scars and a U-shaped anterior scar. Frontal and mandibular scars are also visible. Carapace length 0.30-0.34 mm.

The carapace does not display sexual dimorphism.

Antennula (fig. 21A): Five segments (the 4th fused with the 5th). The length ratios of the last 4 segments are 4.2 : 2 : 4 : 5. Chaetotaxy[16]: II = P-1m; A-0. III = A-1l; P-0. IV+V = A-1l, 3l; P-1l, 1l. VI = 1m+y_a, 1l.

Antenna (figs. 21B, C): With 3 endopod segments (the 2nd fused with the 3rd). Endopodal chaetotaxy: I = A-0; P-1s. II+III = A-2c; P-2s, y, 1s. IV = 2C. The length of the aesthetasc "Y" slightly exceeds the distal margin of the 2nd + 3rd endopod segments. The distal endopod segment bears 2 pointed claws: the posterior is shorter than the anterior (length ratio 3.3 : 4).

Mandible (fig. 21D): Mandibular palp with 4 segments. The chaetotaxy is: I = I-2l; E-0. II = I-4l; E-1l. III = I-1l (2?); E-4l (5-6?). IV = 2l. The 2 setae of the 1st mandibular segment exceed shortly the length of the next segments. All the other setae are longer than these 2 bristles. Mandibular gnathobasis with 7 teeth and 1 seta. Epipodite with 1-3 setae.

Maxillule (fig. 21E): Respiratory plate with about 16 normal (plumose) setae and one long "aberrant" (smooth) seta (as). Maxillular palp 2-segmented. The proximal segment has 1 seta on the inner margin and 3 setae on the outer margin. The distal segment bears 2 setae.

Rake-like organ (fig. 21F): No teeth on the distal transversal branch (ro).

Thoracopod 1 (fig. 22A): Protopodite with 4 anterior and posterior setae. The 1st endopodal segment has one anterior small seta. The length ratios of the endopod segments and the distal claws are 4.5 : 2.7 : 3.6 : 5.7.

Thoracopod 2 (fig. 22B): Protopodite with 3 anterior and posterior setae. The 1st endopod segment has one anterior seta. The length ratios of the endopod segments and the distal claws are 5.9 : 3.0 : 4.0 : 5.9.

Thoracopod 3 (fig. 22C): Chaetotaxy similar to that of the previous thoracopod except the endopodal seta of the 1st segment which is larger. The length ratios of the endopod segments and the distal claws are 6.7 : 2.7 : 3.9 : 7.2. The 3rd thoracopod is longer than the previous two due to the elongation of the 1st endopodal segment and of the distal claw.

Furca (fig. 22D): With a rounded process and 2 (-3?) small setae. The posterodorsal process of the body (fig. 21G) is rounded, covered with tiny bristles.

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[16] I, II, III, IV, V, VI = segment's number; A = anterior; P = posterior; I = interior; E = exterior; ya = antennular aesthetasc; C = claw; 0, 1, 2, 3 = number of setae/claws; l, m, s refers to the length of the setae, i.e. long, medium, short.

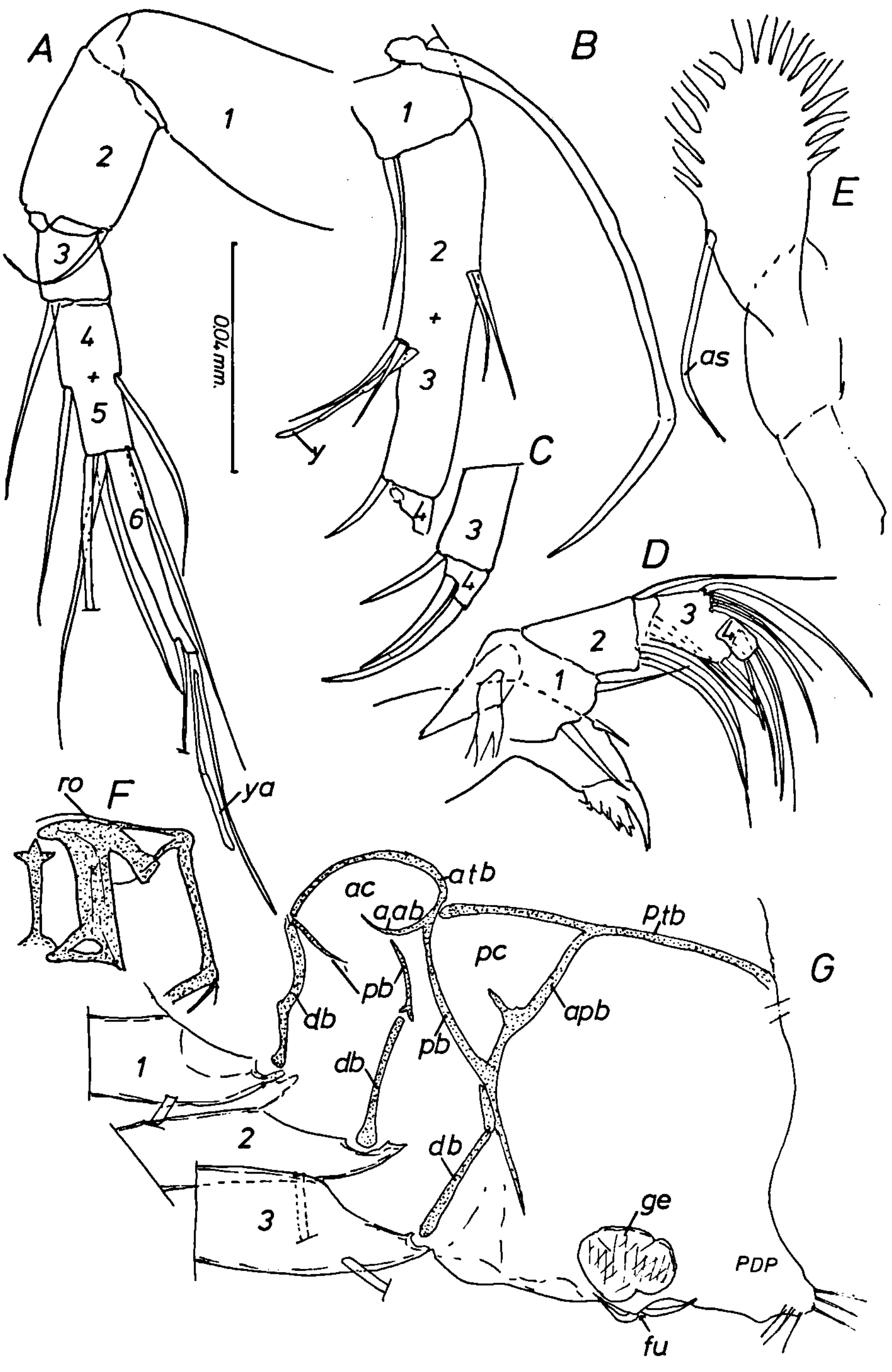

Fig. 21. *Pseudolimnocythere hartmanni* (Aghios Georghios, Euboea Island; A-C, F, G, female; D, E, male): A, antennula; B, C, antenna; D, mandible; E, maxillula; F, rake-like organ; G, posterior part of the body.
Abbreviations: as = aberrant seta; ya = antennular aesthetasc; y = antennal aesthetasc; pb = proximal bar; db = distal bar; tb = transversal bar; apb = accessory posterior bar; ac = anterior cell; pc = posterior cell; fu = furca; ge = genital area; ro = distal branch of the rake-like organ; PDP = posterodorsal process of the body.

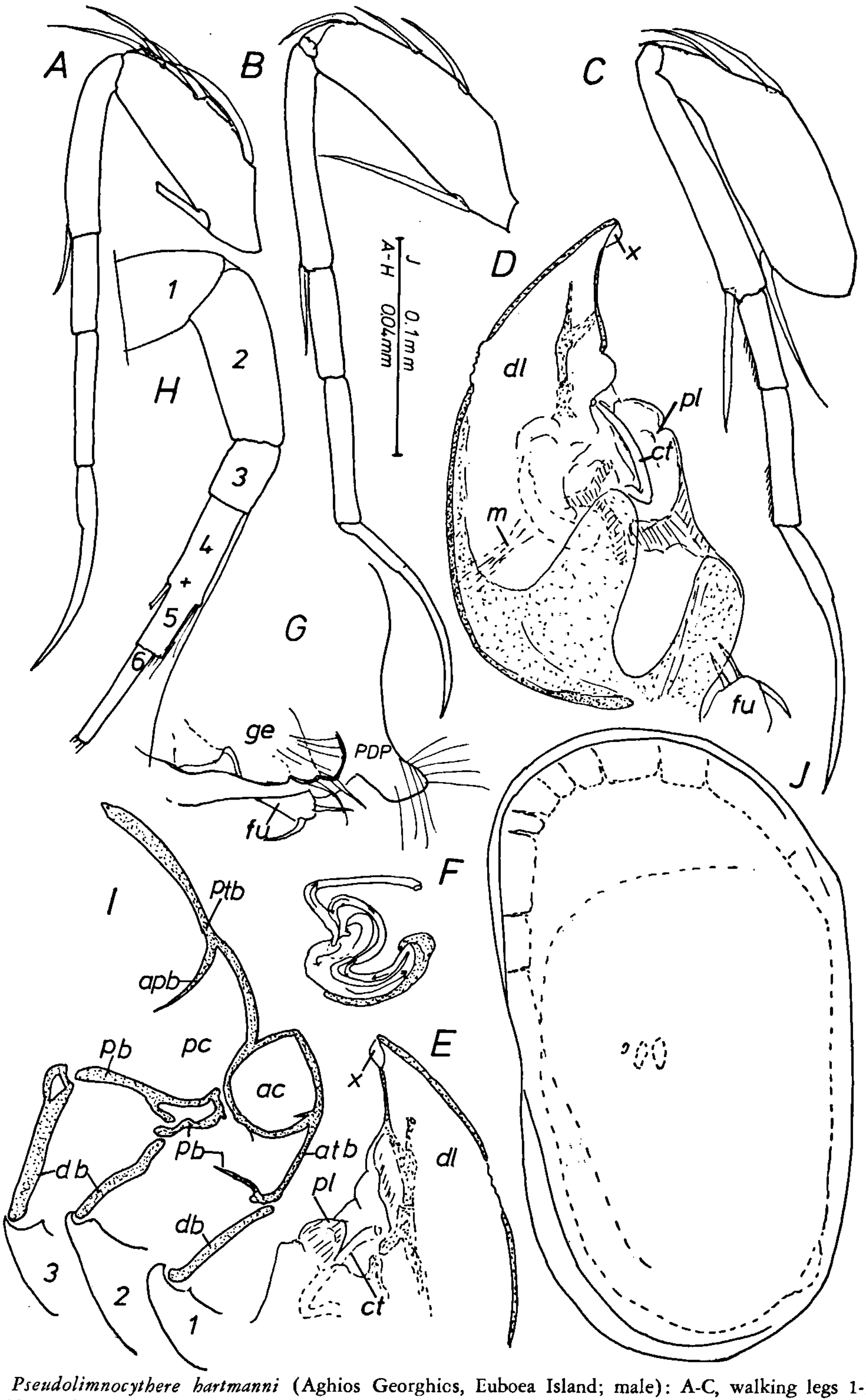

Fig. 22. A-F, *Pseudolimnocythere hartmanni* (Aghios Georghios, Euboea Island; male): A-C, walking legs 1-3; D, hemipenis, lateral side; E, hemipenis, medial side; F, copulatory tube, detail.

G-J, *Tuberoloxoconcha* n. sp. (Marina di Orosei, Sardinia; G, female; H-J, male): G, extremity of the body; H, antennula; I, inner sclerified frame; J, left valve.

Abbreviations: x = hyaline area; ct = copulatory tube; dl = distal lobe; pl = proximal lobe; pb = proximal bar; db = distal bar; atb and ptb = anterior and posterior transversal bars; apb = accessory posterior bar; ac = anterior cell; pc = posterior cell; fu = furca; ge = genital area; m = muscle; PDP = posterodorsal process of the body.

Inner sclerified framework (fig. 21G): Represented by an anterior transversal bar bent dorsally and posteriorly. It forms an open anterior cell, which also participates in the proximal bar of the 1st thoracopod. The distal bar of the 1st thoracopod is articulated to the anterior extremity of the anterotransversal bar. The 2nd thoracopod has simple proximal and distal bars. A long posterotransversal bar participates partly to build the posterior cell. This has a triangular shape and is formed also from the proximal bar of the 3rd thoracopod and an additional proximal bar. The distal bar of the third thoracopod points to this posterior cell.

Female genital opercule (figs. 21G, 22F): Rounded, sclerified.

Hemipenis (figs. 22D-F): With a triangular distal lobe, which has a subapical hyaline area (x). The dorsal margin is largely rounded; the lobe is fused to the peniferum on its proximal margin. A short proximal lobe covers the copulatory tube. The latter is coiled in the peniferum.

Discussion. — *Ps. hypogea* Klie, 1938, differs from *Ps. hartmanni* Danielopol in having a longer antennal aesthetasc "Y", its extremity reaching the distal margin of the distal endopod segment. The mandibular palp has 3 setae on the inner margin of the 2nd segment. Male copulatory organ with a distal triangular lobe which is folded on the dorsal margin.

Pseudolimnocythere sp. from the Skuljica cave, Krk, has a carapace which is slightly larger (0.34-0.36 mm) than that of *Ps. hartmanni* Danielopol. The external ornamentation of the former species is less well developed; especially the fossae are smaller and more numerous on the posteroventral side and the carinae (figs. 11A, D) are not so prominent as in the species from Euboea Island.

X. SUMMARY

1. Realistic data concerning the antiquity of several interstitial ostracod groups have been obtained in those cases where phylogenetical affinities with fossil ostracods (mainly Tertiary species) could be established, viz. the genera *Kovalevskiella, Candonopsis,* and *Darwinula.* The study of the main marine Paleozoic and Early Mesozoic ostracod groups, except for the cytherids, suggests that they could not inhabit the freshwater subterranean milieu because of their low salinity tolerance.
2. Considering the freshwater interstitial ostracods of the subfamily Pseudolimnocytherinae it is hypothesized, using the test of the marine regression model, that marine representatives of this group could have penetrated into the freshwater subterranean realm either during the Upper Miocene - Lower Pliocene, or during the Pleistocene. None of the two concurrent hypotheses could be refuted.
3. The age of *Darwinula boteai,* the unique interstitial species in Europe belonging to the *Darwinula pagliolii* group, has been tested with the climatic refugium model. The test failed as the ecological and geographical distribution of some of the *Darwinula* gr. *pagliolii* contradicted the initial assumption, i.e. that no species of a given group should inhabit the groundwater in areas with a mild climate.
4. For the representatives of the genus *Cryptocandona* the 3rd rule of Racovitza, stating that the troglobites which have a wider geographical range than their closest epigean relatives are more or less old immigrants to the subterranean realm, could not give any conclusive answer. This is due to the fact that we do not know well enough the true phylogenetical relationships between the European and the Japanese *Cryptocandona* species.
5. The inference of the "antiquity" of the subterranean ostracod groups using the morphological index of the length of the antennal aesthetasc "Y", by comparing several epigean and hypogean Candoninae failed to give a satisfactory answer as the two initial assumptions could not be fulfilled, i.e. the selective pressures acting on the different species compared and the evolutionary rates of these species should be similar.
6. In all the ostracod cases I have studied here, I have tried to strengthen the hypotheses to make them more restrictive and better testable. In this way it is considered that this essay is

written in honour of E. G. Racovitza who developed modern biospeleology at the beginning of the century.

7. A detailed description of *Pseudolimnocythere hartmanni* Danielopol, 1979, is presented in an appendix.

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