

Mitt. Geol.-Paläont. Inst. Univ. Hamburg	Heft 84	S. 131-208	Hamburg, September 2000
---	---------	------------	-------------------------

Speciation among the Melanopsidae (Caenogastropoda)

Special emphasis to the Melanopsidae of the Pannonian Lake at Pontian time
(Late Miocene) and the Pleistocene and Recent of Jordan

KLAUS BANDEL, HAMBURG *)

With 176 figures

Contents

Abstract	131
Zusammenfassung	132
I. Introduction	133
II. The history of Lake Pannon at late Miocene and of Jordan since late Pliocene	134
III. Systematics	137
III.a. Introduction to the genera considered to belong to the Melanopsidae	137
III.b. The <i>Melanopsis impressa</i> group	141
III.c. The <i>Melanopsis praemorsa</i> group	151
III.d. The <i>Melanopsis bouei</i> group	159
III.e. The <i>Melanopsis costata</i> group	166
III.f. The <i>Melanopsis fuchsi</i> - <i>Esperiana esperi</i> group	186
III.g. The <i>Melanopsis tihanyensis</i> group	187
III.h. The <i>Melanptychia-Boistelia</i> group	189
III.i. The <i>Melanosteira</i> group of Greece and the genus <i>Amphimelania</i>	190
IV. Reconstruction of the evolutionary history	192
IV.a. The modern <i>Melanopsis</i> in the Mediterranean region	192
IV.b. The Pliocene and early Pleistocene developments	193
IV.c. The Pontian assemblage	194
IV.d. The Pannonian <i>Melanopsis</i>	195
IV.e. Pre Miocene development	196
V. Hypothesis regarding the evolutionary processes in the <i>Melanopsis</i> lineage	197
VI. Results	199
Acknowledgements	201
References	201

*) Author's address: Prof. Dr. Klaus BANDEL, Geologisch-Paläontologisches Institut und Museum der
Universität Hamburg, Bundesstraße 55, D-20146 Hamburg. e-mail: bandel@geowiss.uni-hamburg.de

Abstract

Melanopsis and the Melanopsidae can be traced to the Santonian (Cretaceous). Their closest relation among the Cerithioidea is with the Potamididae which remained in the coastal swamps, while Melanopsidae entered the fresh water. For ribbed *Melanopsis* like modern *M. costata* and smooth species like modern *M. buccinoidea* record can be traced to the Cretaceous. Alongside with unidirectional evolutionary change from one to the next species through an unknown amount of time the process of sudden and local hybridization plays a major role in the appearance of new species within the Melanopsidae. Hybrids occur in modern populations of *Melanopsis* living in the Jordan catchment and may be present among those that live in the Maghreb and Spain. Hybrids between the smooth species like *Melanopsis buccinoidea praemorsa* and the axially ribbed species like *M. costata tingitana* and, in the western populations, also the spirally keeled *M. dufouri* may locally be common. A member of the *M. dufouri* group was still present in the late Pliocene of the Orontes-Jordan area, but is no longer in existence here.

During late Miocene in Lake Pannon of the Paratethys basin even more species were involved in the hybridization process than today. *Melanopsis impressa*, *M. bouei*, and *M. kleini* are known from the earlier Miocene. But also species regarded to represent members of other genera like *Esperiana* without posterior callus pad on the inner lip and record to the Cretaceous and *Melanoptychia* with a plication on the columella and unknown fossil record apparently mixed their genes with those of the obvious members of the genus *Melanopsis* within the vicinity of Lake Pannon.

The seven groups involved in hybridisation recognised at Lake Pannon belong to the large sized *Melanopsis impressa* with angulated whorls, and the smaller smooth *M. kleini*, the tuberculous *M. bouei*, the ribbed *M. oxyacantha*, the small *M. fuchsi* with slender *Esperiana*-like shell, the keeled *M. tihanyensis/brusinae*, and the *Melanoptychia* group with columellar plicae. The taxonomic treatment of melanopsids encountered in such meeting and hybridization places of two or more species resulted in many morphologically more or less distinct forms and, thus, numerous species names. Hybridization in differently mixed populations occurred at different times and places, sometimes with similar results regarding shell morphology, in other cases resulting in quite unique morphologies. Even though taxonomy is difficult, it is still evident that at different time slices since the Santonian the general shell characters within the melanopsids changed. For example Campanian, Eocene, late Miocene, Pliocene, Pleistocene and Recent melanopsids differ, even though some species appear very similar. The large lakes of the late Miocene Paratethys show a high diversity and display different characters than are noted today, even though quite a number of relict species are still living. The latest large shift seems to have occurred in connection to the Messinian drying up of much of the Mediterranean Sea and, thus, the meeting of the catchment areas of rivers within the Mediterranean Basin. In its process two of the six groups from the Lake Pannon disappeared, while a few were greatly successful and developed several new hybridisation centres.

The oldest known ribbed *Melanopsis* is described as *M. trempensis* from the Campanian, and the genus *Stilospirula* from the Eocene is characterized. New species described are *M. pseudobesa*, *M. sharhabili*, *M. barthai*, and *M. papkesiensis*.

Zusammenfassung

Melanopsis und die Melanopsidae können bis ins Santon (Kreide) zurück verfolgt werden. Ihre nächsten Verwandten unter den Cerithioidea stellen die Potamididae dar, die im Milieu des Küstensumpfes verblieben sind, während die Melanopsidae ins Süßwasser vordrangen. Sowohl berippte Arten, wie die heutige *M. costata*, als auch glattschalige Arten, wie die *M. buccinoidea* können bis in die Kreide hinein belegt werden.

Neben geradliniger Evolution von einer zur nächsten Art während des Ablaufs einer unbekannten Zeit spielte auch die kurzzeitige und lokale Hybridbildung bei der Herausbildung von Arten der Melanopsiden eine große Rolle. Hybride sind aus den heutigen Populationen von *Melanopsis* im Einzugsbereich des Jordan nachgewiesen und für die Arten des Magreb und SE Spaniens wahrschein-

lich. So bilden die glattschaligen *Melanopsis buccinoidea* und *M. praemorsa* mit den berippten *M. costata/tingitana* lokal Hybride, und in der westlichen Provinz tritt noch die *M. dufouri* mit Spiralkiel hinzu. Eine solche gekielte Form der *M. dufouri* war während des späten Pliozäns im Orontes/Jordan Gebiet noch mit beteiligt, lebt dort heute aber nicht mehr.

Während des späten Miozäns waren im Pannensee der Zentralen Paratethys sogar noch mehr Arten an der Hybridbildung beteiligt. Unter diesen sind *Melanopsis impressa*, *M. bouei* und *M. kleini* schon aus dem früheren Miozän bekannt. Aber auch Arten aus anderen Gattungen, wie *Esperiana* ohne Kallusverdickung der hinteren Innenlippe der Apertur sind schon seit der Kreide bekannt. Auch hat eine *Melanoptychia* mit Kolumellarfalten sich mit den Arten der Gattung *Melanopsis* im Bereich des Pannonses eingemischt. Zu den sieben Gruppen, die sich bei der Hybridbildung am Pannensee beteiligten, gehören die großwüchsigen Vertreter der *Melanopsis impressa* Gruppe mit eckigen Windungen, die kleinere und glatte *M. kleini*, die bedornte *M. bouei*, die axial-berippte *M. oxyacantha*, die kleine *M. fuchsi* mit schlanker *Esperiana*-artiger Schale, die mit Kiel versehene *M. brusinai/tihanyensis* und schließlich Vertreter der *Melanoptychia* Gruppe mit Kolumellafalte.

Die taxonomische Einordnung der Arten und Formen der Melanopsiden an solchen Orten der Hybridbildung, an denen zwei oder mehr Arten beteiligt sind, führte zu zahlreichen Taxa mit der mehr oder weniger gut faßbaren Gestalten. Zudem traten Hybride zu verschiedenen Zeiten und an verschiedenen Orten auf, manchmal mit sehr ähnlichen Ergebnissen, manchmal aber auch mit eigentümlichen Resultaten. Auch wenn diese taxonomischen Probleme bestehen, wird doch deutlich, daß während verschiedener Zeitscheiben seit dem Santon der generelle Charakter innerhalb der Gestalt der Melanopsiden sich veränderte. So können zum Beispiel für die campanen, die eozänen, späten miozänen, pliozänen, pleistozänen und für die heutigen Melanopsiden Unterschiede belegt werden, obwohl einige Arten fast unverändert erscheinen. Die Arten der großen Seen des späten Miozäns im Raum der Paratethys zeigten eine hohe Diversität und eine Anzahl von Charakteristika, die sich von heutigen unterscheiden, obwohl eine ganze Reihe der damaligen Arten noch heute fast unverändert existieren. Die letzte große Veränderung scheint mit der messinischen Austrocknung des Mittelmeeres einherzugehen, bei der sich die Einzugsbereiche verschiedener Flüsse trafen. Während dieses Prozesses verschwanden zwei der sechs Gruppen der Pannensee-Melanopsiden vollständig, und einige Gruppen waren danach sehr erfolgreich und bildeten eine Reihe neuer Zentren.

I. Introduction

According to THIELE (1929) and WENZ (1938) the Melanopsinae (Cerithioidea, Caenogastropoda) hold the genera *Fagotia* (= *Esperiana*), *Melanopsis*, and *Faunus* along with a few fossil genera of doubtful status. The Melanopsidae with the genera *Melanopsis* and *Esperiana* have been present since Santonian times (TAUSCH 1886, OPPENHEIM 1892, BANDEL & RIEDEL 1994). They lived next to the Tethys Ocean in fresh water, in rivers and creeks from the springs to the estuary, near the shore in freshwater lakes. They also entered brackish seas marginally, and they still live in thermal and mineral springs. A transitional species living part of its life in the sea and part of its life in the estuary and fresh water still exists with *Zemelanopsis trifasciata* in New Zealand, which has marine planktotrophic larvae and freshwater preferring benthic adults (BROT 1874, BILGIN 1973). We know a similar case from the Maastrichtian of northern Spain (KOWALKE & BANDEL 1996) where *Melanopsis serchensis* VIDAL, 1874 had a planktotrophic veliger.

In Ajka just north of Lake Balaton the slender *Melanopsis ajkaensis* TAUSCH, 1886 and the wider *M. pauli* BANDEL & RIEDEL, 1994 lived during the Santonian. They resemble smooth representatives of the modern Mediterranean *M. praemorsa*, *M. buccinoidea* as well as their relation from New Caledonia with *Melanopsis mariae* CROSSE, 1869 and *M. frustulum* MORELET, 1856 (STARMÜHLNER 1970, 1973). Of similar Santonian or Campanian age

is *Melanopsis laevis* (STOLICZKA, 1860) from the Brandenberg Gosau in the northern Alps (KOWALKE & BANDEL 1996). From the Campanian of northern Spain we also know a *Melanopsis* that is axially ribbed (described below as *M. trempensis*). It lived alongside with species having a smooth shell like the Maastrichtian *Melanopsis crastina* VIDAL, 1874 of the same region of the modern Tremp Basin. *Esperiana obeloides* (TAUSCH, 1886) from the Santonian of Ajka has a shell that is rather similar with *Esperiana acicularis* that lives in the river Danube. Its protoconch is like that of lecithotrophic *Melanopsis* and the aperture with short anterior siphon has the inner lip forming callus like *Esperiana*, but unlike that of *Melanopsis* with its characteristic posterior callus pad (BANDEL & RIEDEL 1994, Pl.12).

A *Melanopsis americana* WHITE is known from the Cretaceous of Northern Colorado, but according to TAYLOR (1968) freshwater Neritidae, Melanopsidae and Pyrguliferidae had disappeared in the western USA when the Tertiary began. During the Oligocene *Melanopsis pomahaka* (HUTTON, 1873) lived in New Zealand (BEU & MAXWELL 1990) with elongate ovate shell and looked quite similar to the European *Melanopsis impressa* that lived at about the same time in Europe (see below).

Preliminary data based on DNA analysis carried out by Ralf BISCHOFF (ongoing research) revealed that the Melanopsidae with *Melanopsis* and *Esperiana* are close to each other and can be grouped with the Potamididae and Pachymelaniidae among the Cerithioidea. DNA indicates a closer relation of *Melanopsis* from New Caledonia with *Melanopsis* from Jordan and Spain than to *Esperiana* from SE Europe. Melanopsidae on the other hand are separated from the Tanganyika cerithioideans like *Lavigeria* and *Spekia* (BANDEL 1998) as well as the Thiariidae s.s. with *Thiara* and *Melanoides* and the *Pleuroceras/Potadoma* relation. Melanopsidae, Pachymelaniidae and Potamididae represent Cerithioidea which even though related have developed away from each other and independently since late Cretaceous times (BANDEL & KIEL 2000). The two later have remained within the coastal swamp environment (BANDEL & KOWALKE 1999), while the first have settled the fresh water.

Melanopsis and *Esperiana* deposit their eggs surrounded by a capsule with usually sticky cover in the sediment, rarely to hard substrates (ANKEL 1928). After about two weeks of development one crawling young hatches from each capsule. We have described the embryonic shells from the species of the Santonian of Ajka in Hungary (RIEDEL 1983, BANDEL & RIEDEL 1994) and they closely resemble those of the living species, for example the protoconchs of Spanish *Melanopsis* (PUJANTE et al. 1990). The mode of ontogenetic development of the *Melanopsis* species of Lake Pannon can, thus, be reconstructed from the shape and size of their protoconch. All protoconchs are relatively large and resemble those of *Melanopsis* living around the Mediterranean Sea, including those that have been cultured in the aquarium in Hamburg, coming from Jordan and from Spain.

II. The history of Lake Pannon at late Miocene and of Jordan since late Pliocene

During late Miocene time the large Lake Pannon occupied much of the Hungarian plains. It formed in the Carpathian/Pannonian basin representing the central portion of the Paratethys (RÖGL & STEININGER 1983, ROYDEN & HOVATH 1988, STEININGER & RÖGL, 1984). Before the establishment of Lake Pannon, the area was occupied by the sea. During Badenian time this sea was still connected to the world oceans and had basically normal marine salinity, while by Sarmatian time it was more isolated from the ocean, but extended from the Vienna Basin to the Caspian Basin and here the region of the Aral lake. The fauna of this

Sarmatian sea disappeared when Lake Pannon was established about 11 million years ago (PAPP 1985).

Lake Pannon had a large volume and extended to the west into the Vienna Basin and in the east into Romania, to the south into Croatia and Serbia. In the Vienna area deposits of near shore derival are exposed at Brunn-Vösendorf (PAPP 1951) and their molluscs were described in detail by PAPP (1953a). The beach of Lake Pannon was also close to Tinnye situated between Budapest and Esztergom not far from the Danube. Here LÖRENTHEY (1911) described a fauna that is similar to that of Löbendorf near Vienna (HANDMANN 1887). A shore fauna is also represented by that of Soceni in Romania which was very well described by (JEKELIUS 1944). It has quite a number of interesting differences with the fauna in the west. A distinctive character can also be stated regarding the fauna found in Serbia (PAVLOVIC 1929) and in Markusevec in Croatia (BRUSINA 1874, 1892).

At about 8,8 million years ago this Lake Pannon had been filled with sediment in its western part (up to 1200 m according to PAPP 1985) and the shore had moved eastward. At this time it is found near the modern Lake Balaton. In the far east also brackish lakes established which with the begin of the Pontian period came into contact with Lake Pannon (RÖGL & STEININGER 1984, STEININGER & RÖGL 1984). The migration of species from the east into the Lake Pannon along the shores initiated also a change in the composition of the melanopsids living here. But species could also have come with the early Danube river that was flowing to the east and into Lake Pannon, and obviously there were also contacts to the south-east in the area of Greece and Turkey as is documented by the fauna that was described by WILLMANN (1980, 1981) and RUST (1997).

Near the modern Lake Balaton, that does not represent a relict of ancient Lake Pannon, but has formed since its disappearance, fossiliferous deposits of the Pontian stage of Lake Pannon occur. Of these the fauna of the outcrops near Varpalota, Tihany, Papkesi/Balatonfűzö, Fonyod/Balatonszentszörgy, and Tab are analysed, all of which formed during Pontian time. They are deposits of two biozones recognized by MÜLLER & MAGYAR (1992) with the aid of bivalves. These belong to a late phase of perhaps the last two Million years in the history of Lake Pannon that lasted to about 5,4 million years ago and included the Messinian stage of the Mediterranean area. CSATO (1993) noted a lake level change near the Tortonian-Messinian boundary, that is during the time of the Messinian salinity crisis of the Mediterranean area, and it is thought that the lake disappeared by being filled with sediment during or after the Messinian. Afterwards Lake Pannon in Hungary had filled with sediment and ceased in its existence.

The actual deep lake lay to the south of the Balaton area. The region now taken by modern Lake Balaton at Pontian time lay at an about 300 km long NE trending shore line of Lake Pannon. Here interconnected delta systems deposited their sediment load towards the S-SE (MÜLLER & MAGYAR 1992). It is within the zone of the shore line that the faunas containing the discussed melanopsids of Papakesi on the eastern shore of Lake Balaton and Fonyod on the south-western shore of that same lake lived. The salinity of the Lake Pannon is debated somewhat, but apparently it varied between 5 and 16 g/kg salinity with some changes possible (KORECZ 1985, KORPAS-HODI 1983, PAPP 1985, MÜLLER & MAGYAR 1992, MÁTYÁS et al. 1996). GEARY et al. (1989) suggested from their data an abrupt salinity drop in the early Pontian, but MÁTYÁS et al. (1996) interpreted similar data differently relating them to a change in climate instead of salinity. Climatic changes were also noted by LUEGER (1978) to have occurred with begin of the Pontian by evidence of land snails.

During more humid phases of the Pleistocene in Jordan lakes formed within the catchment area of the Dead Sea and Jordan Rift. It is thought that the fresh water region of this area on and off was in contact with the catchment of the Orontes to the North. The European glacial and cold times have been interpreted by HOROWITZ (1979) to have resulted in a pluvial climate in Palestine/Israel and Jordan, characterized by higher rainfall. Lakes covered the area of the modern Jordan Valley or different parts of it. The interglacial periods resulted in dry climate resulting in an aridity which sometimes may have been beyond that of the present time. During these periods the Jordan Valley lakes shrank to become playas or peat forming marshes. The lacustrine beds are intercalated with deposits of rivers coming from the surrounding mountains (HOROWITZ 1979).

There was an intermediate lake at the present Dead Sea Region, the Ghor al Qatar Lake (BENDER 1968) interpreted to have existed during the early Pleistocene. It could have existed at the same time during which south of the modern Lake Kinnereth (Lake Tiberias) there was a lake with fresh water that deposited its calcareous and muddy sediments now exposed at the Ghor canal just SW of Abu Habil in Jordan. These deposits overlies in part pisolitic gravels corresponding to times when extensive portions of the Jordanian highlands were covered with calcareous caliche. At the same time valleys were not as deeply eroded as now so that pisolites were washed from the surface and placed as gravel in the depression of the Jordan rift intercalated by pebble layers from eroded Paleogene and Cretaceous rocks. In this lake a rich fresh water fauna is present with the oldest species of *Melanopsis* which have been recognized in Jordan. They resemble Pliocene forms as are known from Rhodos (BUKOWSKI 1895), and are described below as Ghor Canal fauna (III.e.2.). The fossils were extracted from beds which are steeply inclined, in part projecting above the last formed sediments of the Lisan Lake.

Most of the other sediments exposed in the central Jordan Valley containing a *Melanopsis* bearing fauna still are in horizontal position at an elevation of approximately 200 m below sea level and below. They are usually found stratigraphically below the laminated marly deposits of the salinal Lisan lake. The rift valley containing them is bordered by steep escarpments to the east and west. The bottom sediments are cut by the modern Jordan and the northern part is occupied by Lake Tiberias, 212 m below sea level.

HUCKRIEDE (1966) noted that pisolitic limestones of the Abu Habil Series in Jordan found exposed extensively near Abu Habil contain Oldowan pebble tools and could thus be placed in the Middle Pleistocene. They may be similar in age as the Erk el-Ahmar Formation that is described from an outcrop in the Jordan Valley located some 10 km south-west of Lake Tiberias (HOROWITZ, 1979). This fauna had been noted by BLANKENHORN & OPPENHEIM (1927), and they called it "*Melanopsis* Stufe". TCHERNOV (1975b) noted 18 species of molluscs within the sediments, among these a *Melanopsis doriae*. The depositional environment was interpreted to have been a freshwater lake) that existed during Günz glaciation at about 1,8 to 1,5 million years ago and contained a pollen flora of pluvial character (HOROWITZ 1979). It was suggested to be time equivalent to the lower Abu Habil Series in Jordan, and it was also interpreted to have had contact with the catchment of the Orontes (HOROWITZ 1979). From fluvial sands well below the well bedded Lisan Formation on the Jordan road west of Mashara and Wadi Rihan a fauna was extracted that may belong here.

During Mindel time 1,2 to 0,6 million years ago, in the the Central Jordan Valley the Ubeidiya Lake was present, corresponding to the upper Abu Habil Series of BENDER (1968) according to HOROWITZ (1979). The area of Ubeidiya lies 3 km southwest of Lake Tiberias. According to TCHERNOV (1973) *Melanopsis praemorsa* (= *buccinoidea*) lived here along

with unionids. The malakofauna of the Ubeidiya is therefore interpreted to be quite modern in contrast to that of the Erk el-Ahmar. This contrasts somewhat to the results of a study by PICARD (1934). Yarmouk Basalt overlies the Ubeidiya (HOROWITZ 1979) so that the formation is older than 700000 years and also Lisan Formations follows above. It is quite possible that the fauna extracted from fluvial sands below the Lisan marls on the eastern side of the Jordan between Mashara and Deir Alla is time equivalent to Ubeidiya deposits.

The Würmian Lisan Formation is underlain by beds rich with *Melanopsis* with quite modern appearance. Lisan Formation covers the central and southern Jordan Valley, down to about 40 km south of the present Dead Sea. The Lisan Formation has been named from Lisan Peninsula, later called "Lisanmergel" by BLANCKENHORN (1914). Its time of formation lies between 80000 to 11000 years ago and it consists of laminated deposits of a brackish water lake in which no *Melanopsis* lived. But in the creeks, springs and rivers that issued into it from the Jordanian height *Melanopsis buccinoidea* was abundant. The Lisan lake reached an uppermost level of about -180 m (NEEV & EMERY 1967). In the Wadi-al-Hammeh near Mashara about 30 km S of Lake Tiberias a perennial warm mineral spring Hammet Abu Dabli about 3 km upstream joins the creek. Here *Melanopsis* occurs below extensive gravel and sinter beds (Knob Limestones) at about - 184 m, or just about at the uppermost level reached by Lake Lisan. MACUMBER & HEAD (1991) determined the age of the calcareous bands by radiocarbon analysis and found the ones intercalated with the beach deposits to be 15000 years old and the upstream most occurrence on the plateau about 32000 years old. *Melanopsis* of the same type but better preservation was collected just a few kilometers to the south near Tell Abu Aluba in Wadi En Heir east of Al Marazeh representing the southern most portion of the town Mashara. Here marly deposits left by an ancient spring next to beach gravels of the Lisan lake at its highest stand contain *Melanopsis*, which are clearly of Lisan age.

The extensive Lisan lake existed during most of the time of last glaciation between 70000 and 11500 years ago and since that time has shrunk to form the Dead Sea. The rivers and springs coming from the Jordanian escarpment all join the Jordan River to the north of the Dead Sea. The creeks and rivers from the escarpment along the Dead Sea, including the Mujib River, end in the salinal waters of the Dead Sea and are not connected to each other. Also Azraq Oasis that lies about 100 km to the east of Amman in the Jordanian desert has no modern connection with any other *Melanopsis* bearing stream in Jordan. *Melanopsis* is found in springs and streams from the Yarmouk in the North of Jordan to the last ones in the south that issue in the Dead Sea (Wadi Chanisira).

III. Systematics

III.a. Introduction to the genera considered to belong to the Melanopsidae

Superfamily Cerithioidea

Family Melanopsidae H. & A. ADAMS, 1854

Members of the genera *Melanopsis* and *Esperiana* have lived in Europe since the Santonian. In well documented continuous succession they have occurred since the Miocene. The genera *Holandriana*, *Amphimelania*, and *Microcolpia* can be included under *Esperiana* or *Melanopsis*. Even the dividing line between *Esperiana* and *Melanopsis* is not easy to draw, especially regarding fossil species, as is shown below. *Melanoptychia* and *Boistelia* represent *Melanopsis*-like species differing from the others by having a columella fold. *Stilospirula* with slender early teleoconch existed in the Paleogene. Whether

Genus *Amphimelania* FISCHER, 1885

(Subfamily Amphimelaniinae) = *Holandriana* BOURGUIGNAT, 1877

Description: The shell measures 7-19 mm in height and 5-12 mm in width. The shell shows some variability, is pointed egg-shaped and either smooth or with a pattern of spiral and axial lirae. The type is *Melania holandri* FERUSSAC, 1823 (= *M. holandri* C. PFEIFFER, 1828) from Slovenia to Albania and in Lake Ochrid.

Remarks: Two species exist of which both live in southern Austria and Croatia, the ornamented *H. holandri* and the smooth *H. parvula* (SCHMIDT, 1854), have been described by WILLMANN & PIEPER (1978). The subfamily Amphimelaniinae had been proposed by TROSCHER (1856-63), accepted by THIELE (1929) and WENZ (1938). *Amphimelania gayi* BRUSINA, 1902 (WENZ 1938, Fig. 2021) (= *Melanopsis mitzopoulozi* PAPP, 1955) from the Pliocene of Croatia and Greece has a stronger ornament of spiral ribs, but otherwise closely resembles the two living species of *Amphimelania*. OPPENHEIM (1891b, Pl. 27, Figs. 1-8) and PAPP (1955a,b, Pl. 20, Figs. 1-19) documented its gradation into *Melanopsis* (= *Melanosteira*) *aetolica* NEUMAYR, 1880 in the Pliocene of Greece and to *Melanopsis clavigera* that is close to *M. oxyacantha* (chapter III.i.). The genus *Amphimelania* may thus be expensible, as is the subfamily Amphimelaniinae.

Genus *Melanoptychia* NEUMAYR, 1880

Description: The shell is axially ribbed or not, and characteristically the columellar lip bears a fold (with smooth shell it would be *Boistelia*). The type is *Melanoptychia bittneri* NEUMAYR, 1880 from the Pliocene of Bosnia.

Differences: According to JEKELIUS (1944) the most important character that distinguishes *Melanoptychia* from *Melanopsis* is the presence of one or two columellar folds. But he also noted that there are species in *Melanoptychia* which have exact counterparts in the genus *Melanopsis* with the only difference of the presence of a columellar fold, which even may be quite variable (chapter III.h.). The subgenus *Boistelia* COSSMANN, 1909 represents a smooth variety. But JEKELIUS noted that *Boistelia* is difficult to distinguish from *Melanoptychia* and that mixed forms exist between these.

Genus *Stilospirula* (ROVERETO, 1899)

Description: The juvenile shell is slender and turritiform and bears an ornament of spiral elements, while the later teleoconch is fusiform resembling the ordinary smooth *Melanopsis* in shape. Here the inner lip bears a callus pad. The type is *Melanopsis (Stilospirula)* ROVERETO, 1899 is *Melanopsis proboscidea* DESHAYES, 1824 from the Sables de Beauchamp of the Eocene in the Paris Basin.

Differences: *Stilospirula* differs from *Melanopsis* s.s. by having a slender and extended spire that is ornamented. Regarding the later teleoconch it resembles that of *Melanopsis*.

Stilospirula doroghensis (OPPENHEIM, 1892)

(figs. 13 - 16)

Description: The shell in its early portion is slender turritelliform, and only later, in the 9th or 10th whorl whorl-diameter increases and a melanopoid shape is acquired. Nine whorls are turritiform with convex angulated whorls ornamented with one spiral rib that lies in more anterior position with a flattened posterior shoulder. The aperture of the juvenile shell is simple with an evenly rounded thin outer lip that extends into the narrow siphon and a straight inner lip and columellar lip that has a slight sinistral twist into the siphonal end. In the tenth whorl the shell expands and the posterior callus pad of the inner lip of the aperture appears. The protoconch consists of a little more than one whorl of about 0.2 mm in diameter and is distinguished from the early teleoconch by insertion of sinuous growth lines. Fully grown shells from the fresh water limestones of the Eocene of Gant in Hungary are up to 15 mm high and 7 mm wide. The holotype is from the Eocene of the Dorog area near Esztergom in Hungary.

Differences: Whether *Stilospirula doroghensis* differs from *Stilospirula ancillaroides* is not clear, but the shape and ornament of the juvenile shell and the late allometric growth pattern distinguishes from *Melanopsis impressa* or *M. kleini* of the Miocene.

Remarks: *S. doroghensis* was described by OPPENHEIM (1891a, 1892, Pl.33, Figs.7-11), SZÖTS (1953, Pl.2, Figs.58-61) and KECSKEMETI-KÖRMENDY (1972, Pl.2, Figs.8-10) from the Doroger Basin with the synonymy presented by Szöts (1953) and STRAUSZ (1966). The juvenile portions of *S. doroghensis* were regarded to represent a different species called *Pleurotoma pygmaea* by PAPP. Among the Paleogene melanopsids *Melanopsis ancillaroides* DESHAYES, 1824 as described by AZPETTIA MOROS (1929, Pl.14, Figs.326, 327) resembles *S. doroghensis* in having an allometric growth pattern and very pointed spire, but it comes from Paleocene deposits in the Paris Basin, and its early shell portion appears to be unknown.

Genus *Zemelanopsis* FINLAY, 1927

Description: This *Melanopsis* has the first whorl of the teleoconch enlarged in posterior direction covering most of the spire including the larval shell. The characteristic feature of the genus is the presence of a larval shell (PILKINGTON 1976).

Remarks: *Zemelanopsis* with the only species *Melanopsis trifasciata* GRAY, 1843 from estuarine areas in New Zealand produces spawn consisting of meandering egg ribbon that is attached to hard substrates (BILGIN 1973). Each egg is contained within a round egg capsule and these are aligned in a tube which is enwrapped in jelly substance. Own observations 1987 and 1988 revealed that one egg mass may release 1000 to 2000 planktotrophic veligers. In case that the egg mass develops in fresh water, ontogeny is arrested after the first cleavages have occurred. This was observed from spawn collected at Orongorongo estuary in the south of the northern island of New Zealand. When this spawn was brought into contact with sea water development proceeded. In this case the stunted development continued and within 10 days the young hatched with a shell measuring about 0.2 mm in width. It has a strong larval hook on its outer lip and is covered with a fine ridge and groove pattern.

Genus *Faunus* MONTFORT, 1810

Description: *Faunus ater* has a smooth turritiform black shell consisting of up to 20 whorls. Juvenile whorls are weakly inflated and later whorls are flattened. A weak ornament is formed by a subsutural band formed by concave plicae and collabral axial growth lines. The embryonic shell is unknown, as is the mode of reproduction. The shell may reach a size of 9 cm in height. The aperture is ovoid in shape, amounts to about one fifth in shell height and has a deep sinus anteriorly and a large anal notch posteriorly. *F. ater* lives widespread in estuarine environment in the Indo-Pacific region occurring from southern India through SE Asia to the New Hebrides and Solomon Islands (BENTHEMJUTTING 1956, BRANDT 1974, STARMÜHLNER 1979). According to the revision by HOUBRICK (1991) the genus *Faunus* with only one living species that represents the type species *Faunus ater* (LINNEUS, 1758) lives in estuaries in SE Asia.

Differences: The deep apertural sinuses distinguish *Faunus* quite well from the similar *Stemomelania* and *Melanoides* which may co-occur in the same environment. This feature also distinguishes from *Melanopsis*. In juvenile shells differences are more difficult to note. Shell shape resembles that of *Melanatria* but radula shape distinguishes that from *Faunus* (TROSCHEL 1856-63). COSSMANN (1906) recognized several fossil species from the Eocene of the Paris Basin.

Remarks: SUNDERBRINK (1929) observed that the nervous system of *Faunus* differs more from that of *Melanopsis* than from that of *Cerithium*, which would actually indicate not such a close relation to the Melanopsidae, but HOUBRICK (1991) repeated anatomic inspection and preferred a place of *Faunus* within the Melanopsidae. He also suggested the presence of a planktotrophic veliger during ontogeny. BRANDT (1974) preferred a relationship of *Faunus* with the Potamididae ADAMS & ADAMS, 1854.

III.b. The *Melanopsis impressa* group

The group around *Melanopsis impressa* holds species with relatively large (larger than 15 mm in height) shells which in their last whorls have an angulation or keel below an inclined flattened posterior portion, while more juvenile shell portions have evenly rounded elongate whorl shape. The aperture usually has an inner lip callus with thickened pad near its posterior end.

corner of the outer lip. Characteristic *M. caryota*, in contrast, have a more smoothly rounded outer lip and oval body-whorl. There is an overlap in shape to *M. vindobonensis* (JEKELIUS 1944).

Remarks: Much variation among individuals of one population in regard to adult ornament is noted in literature. The fully grown shell measures around 20 to 30 mm in height (PAPP 1953a, STALEY, 1992) or may even be larger (JEKELIUS 1944). The presence of the lateral angulation in the outer lip differs with whorl number among individuals and forms. Transitions between *M. impressa* and *M. fossilis* (= *martiniana*) were noted to occur in the fauna of Tinnye by LÖRENTHEY (1902) who connected *M. fossilis* with *M. matheroni* MAYER, 1888 from southern France. LÖRENTHEY noted that specimen from Tinnye in Hungary were large and had a colour pattern of orange axial ribbons preserved.

PAPP (1953a) suggested several subspecies of *M. fossilis* such as *M. fossilis coaequata* HANDMANN, 1887. Here the increase in shell width in the juvenile shell is more rapid than in the typical *M. fossilis* while later whorls are similar (PAPP, 1953a, Pl.10, Figs.9-12). The shell, thus, appear shorter in the early spire of the teleoconch. In the subspecies *M. fossilis rugosa* HANDMANN, 1887 the shell has strong rugosities. In *M. fossilis coaequata* the shell has the same increase in shell width in the juvenile shell but differs from variety *rugosa* in having a less rugose growth ornament (PAPP 1953a, Pl.10, Figs.13-16).

PAPP (1953a) considered *M. rugosa* to represent an independent species. It is more probable that it represents individuals of *M. fossilis* that are provided with uneven and strong growth interruptions. In case of *Melanopsis rugosa* illustrated by PAVLOVIC (1928, Pl.12, Figs.3-12) from Karagac near Beograd the up to 35 mm high shell actually has real axial ribs which are not just pronounced growth increments. According to JEKELIUS (1944) *Melanopsis rugosa* is a rare variety of *M. fossilis* in Soceni, while it is the most common variety in the Serbian locality and here represents most occurring specimens. *M. fossilis* is an extremely variable species in Soceni with overlap in shape to *M. vindobonensis*.

The subspecies *M. fossilis constricta* HANDMANN, 1887 is characterized by a shell like that of normal *M. fossilis* but of larger size (PAPP 1953a, Pl.11, Figs.1-4). The height of the fully grown shell

Fig. 1. *Melanopsis buccinoidea* FÉRUSAC, 1807 from a fresh water spring about 2 km to the east of the northern Dead Sea and near Wadi Mukheiris. The shell is 17 mm high.

Fig. 2. *Melanopsis praemorsa* (LINNÉ, 1758) from the river of Todhra Gorge in Morocco, the shell is 14 mm high. Seen from the back and same as in fig.3.

Fig. 3. *Melanopsis praemorsa* seen from the front, same as in fig.2.

Fig. 4. *Melanopsis impressa* KRAUSS, 1852 from the late Miocene of SE- Spain, Arenas del Rey with 16 mm high juvenile shell that appears more slender than later growth stages (figs.5-7) which are from the same locality.

Fig. 5. *Melanopsis impressa* of the same shell as in fig. 6 with apertural view and 28 mm high shell.

Fig. 6. *Melanopsis impressa* seen from behind of the same as in fig.5.

Fig. 7. *Melanopsis impressa* with almost fully grown shell of 31 mm in height with characteristic body whorl-angulation.

Fig. 8. *Esperiana esperi* (FÉRUSAC, 1823) from the thermal spring in Bad Vöslau, Austria in apertural view with 12mm high shell.

Fig. 9. *Esperiana esperi* (FÉRUSAC, 1823), the same as in fig. 9 seen from the back.

Fig. 10. *Esperiana acicularis* (FÉRUSAC, 1823) from the river Danube about 100km upstream of Budapest. The shell is 20 mm high.

Fig. 11. *Esperiana acicularis* from the same locality as fig.10, with 21 mm height.

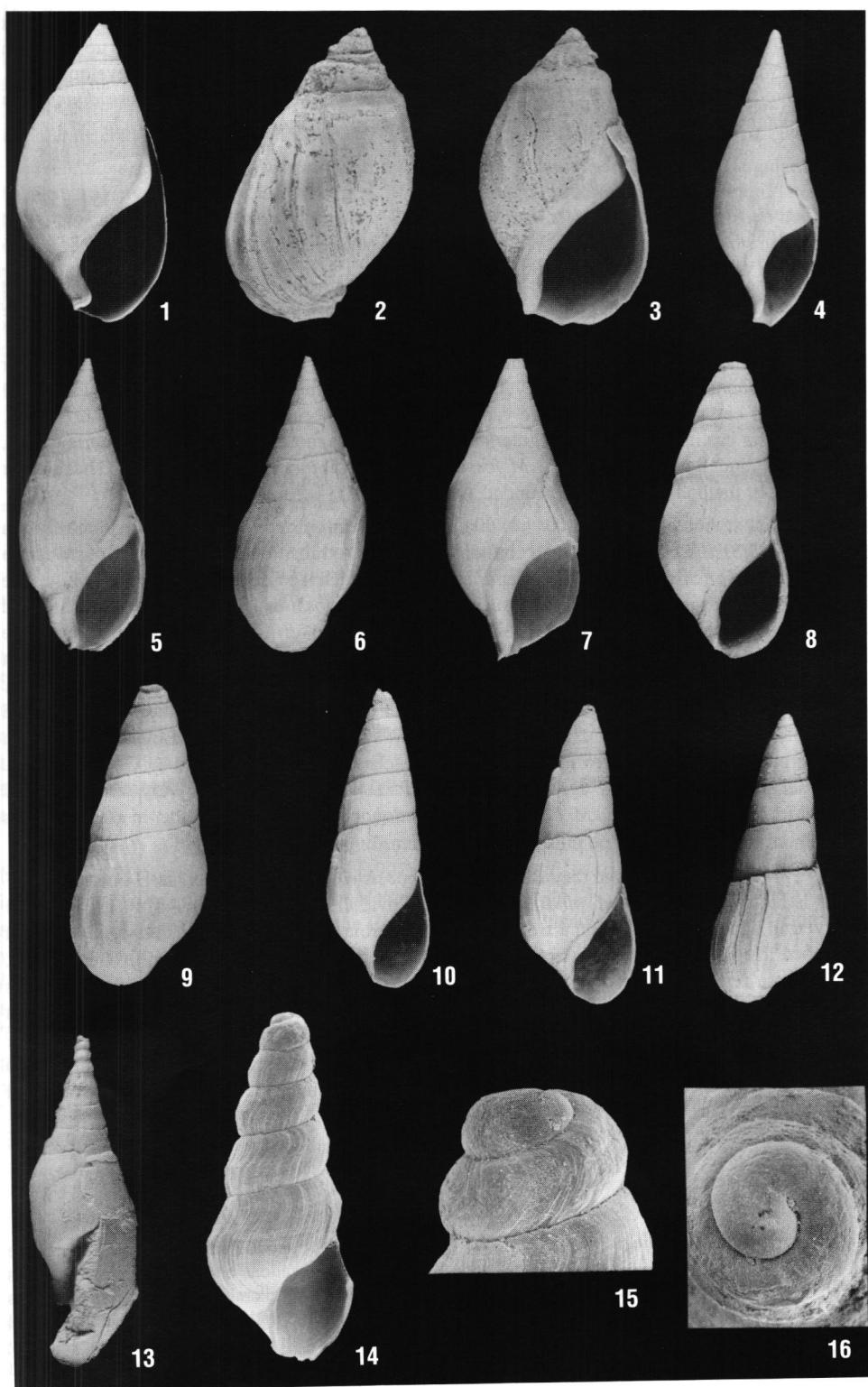
Fig. 12. *Esperiana acicularis* with the same shell as in fig. 11 seen from behind.

Fig. 13. *Stilospirula doroghensis* (OPPENHEIM, 1892) from the Eocene of Gant in Hungary with 16 mm high shell. Same locality in figs.14-16.

Fig. 14. *Stilospirula doroghensis* with 2 mm high juvenile shell that forms a keel within the third whorl.

Fig. 15. *Stilospirula doroghensis* with the transition from the embryonic whorl to the early teleoconch with growth lines indicating time of hatching. Same shell as in figs. 14 and 16.

Fig. 16. *Stilospirula doroghensis* with the embryonic whorl that measures 0,2 mm in diameter and was a little more than one whorl when hatching.



Remarks: There are all transitions from *M. dufouri* to *Melanopsis tricarinata* BOURGUIGNAT, 1884 with strong spiral elements (PUJANTE et al. 1990). This species or form of *M. dufouri* according to AZPEITIA MOROS (1929, Pl.10, Figs. 226-235) has a slender, up to 4 cm high, conical shell with flattened sides and up to three spiral keels. They form a keel on the edge of the shoulder, a depression on the side below it, and the corner to the elongate and rounded base. Colour patterns may be axial colour bands.

Melanopsis tricarinata (BRUGUIERE 1789) has a slender shell and no axial ribs which differs from *M. cariosa*. Smaller varieties of *M. tricarinata* have been named *M. spirata* CHENU, 1859 and *M. acutespira* BOURGUIGNAT, 1884. *Melanopsis isseli* BOURGUIGNAT, 1884 represents a transition between the strongly keeled *M. tricarinata* and *M. dufouri* in Spain (AZPEITIA MOROS 1929, Pl.10, Figs.241-245), while the very similar *M. subgraellsiana* BOURGUIGNAT, 1884 from Algeria is the African representative of this form (AZPEITIA MOROS 1929, Pl.10, Figs.246-250). GASULL (1971, 1981) found a total transition in shell shapes to exist between *M. dufouri* and *M. tricarinata* in the surroundings of Valencia. During the Spanish Pleistocene *Melanopsis dufouri* as well as *M. tricarinata* (= *M. graellsii* VILLA, 1845) have been in existence in similar shape as today (MADURGA MARCO 1973, Pl.2, Figs.1-4). The *M. dufouri* from the Pleistocene of Granada looks extremely similar to *M. delessei* from the late Neogene of Greece. PUJANTE et al. (1990) described the protoconch of *M. dufouri* which is like that generally found among the Mediterranean *Melanopsis* and that of the Cretaceous species in Ajka in Hungary (BANDEL & RIEDEL 1994). They also noted a total transition from *M. dufouri* to the axially ribbed *M. sevilensis* in the populations noted in the rivers and springs of eastern Andalusia.

Melanopsis stricturata BRUSINA, 1892

Description: The shell is 10 to 11 mm high and 4 to 5 mm wide and bears two angulations on the upper and lower corner of the whorl and a weak concavity between them. It consists of 8 whorls of which the first three are rounded and with the fourth whorl the sides become flattened. Whorl diameter increases more rapidly with the 7th and 8th whorl. Here a rounded rim forms at the posterior shoulder, a wide depression on the side and another ridge at the corner to the rounded base.

Differences: When the illustrations of JEKELIUS (1944, Pl.47, Figs.3-11) of Pannonian *M. stricturata* are compared with those of PERES (1939, Pl.5, Figs.1-29) of *M. dufouri* (= *scalaris*) from springs and creeks in Morocco it becomes quite evident, that differences do not exist. *M. stricturata* is smaller than most species of the *M. impressa* clade, and it has a lower ridge on the edge to the base in addition to an upper one. JEKELIUS noted that *M. varicosa* HANDMANN from the Vienna Basin and *M. pavlovici* BRUSINA from Croatia represent the same or at least very similar species that lived in the vicinity of Lake Pannon from north-west to the east and south. *M. stricturata* does not resemble *Melanopsis pygmaea* of the same size, since the latter has rounded sides.

Remarks: LÖRENTHEY (1902) described this species from the Pannonian of Tinnye near Budapest. BRUSINA (1902a, Pl.5, Figs.48-50) noted it in the fauna of the Croatian Markusevec, and JEKELIUS (1944, Pl.47, Figs.3-11) from Soceni in Romania. According to GEARY (1990) *Melanopsis stricturata* is predominantly found in the eastern part of the Lake Pannon during mid Pannonian time, which would not agree with JEKELIUS (1944). Geary's observation may be related to the fact that *M. stricturata* has a variety called *Boistelia stricturata* by JEKELIUS (1944, Pl.55, Figs.1-14) and *Boistelia substricturata* (JEKELIUS 1944, Pl.55, Figs.15-19) which is of the same shell shape but has one or two columellar folds. Such columellar folds are present in several quite different branches of the *Melanopsis* clade of the Late Miocene, and apparently best developed in the Soceni locality (see chapter III.h).

Melanopsis vineta BLANCKENHORN, 1897 from the late Pliocene of the mid-Orontes area in Syria according to BLANCKENHORN (1897, Pl.9, Figs.6,7) grew to about 14 mm in height with about 8 whorls. The first five whorls are smooth and afterwards the stair-like spire develops by the formation of a cornered shoulder. A groove below the shoulder forms and there is, thus, also an angulation to the rounded base. The inner lip has a thick posterior callus pad. BLANCKENHORN's *M. vineta* is a *M. dufouri* that is more slender than the *M. dufouri* from the Jordan valley (see chapter III.e.2.). As in the later form *M. vineta* produced hybrids with members of the *M. costata* group (chapter III.e.2.).

III.b.2. Remarks to the group of *Melanopsis impressa* and *M. dufouri*

A subgenus *Lyrcaea* H. & A. ADAMS, 1854 has been suggested to include *Melanopsis* resembling *M. dufouri*. As SCHÜTT (1988c) remarked, this subgenus could also be implied to the *M. impressa* relation. While there appears to be no direct survivor of the *M. impressa* proper, the species of the *M. dufouri* group could well have been the outcome of interbreeding of the members of the *M. impressa* group with forms of other groups. While there is quite some variety and there are species both in southern Spain and in western North Africa, members of the *M. dufouri* group have ceased to exist in the East since the Pliocene or early Pleistocene (see chapters III.e.3 and III.i). CIANFANELLI et al. (1991) suggested that *Melanopsis affinis* and *M. etrusca* with variants which are spirally lirated or keeled have evolved from *M. impressa*-like ancestors (chapter III.c.2.).

Key to the species of the *M. impressa/dufourii* groups

Melanopsis impressa KRAUSS, 1852: Shell spindle-shaped, last whorl three times higher than the spire; angulation in the posterior third of the outer lip; first whorls rounded; size up to 30 mm.

Subspecies *Melanopsis impressa carinatissima* SACCO, 1889 is wider.

Subspecies *Melanopsis impressa pseudonarzolina* PAPP, 1953: With groove between angulation and suture.

Subspecies *Melanopsis narzolina dodderleini* PANTANELLI, 1886: Smaller than *M. impressa pseudonarzolina*.

Subspecies *Melanopsis impressa posterior* PAPP, 1953: With concave upper side of the whorls. Transitional to *Melanopsis fossilis* and *Melanopsis caryota*.

Melanopsis fossilis (Gmelin, 1790) (= *M. martiniana* Hoernes, 1856): Last three whorls of shell with concavity above the angulation, short spire.

Subspecies *Melanopsis fossilis coaequata* Handmann, 1887: With more rapid increase in shells width.

Subspecies *Melanopsis fossilis rugosa* Handmann, 1887: With strong rugosities.

Subspecies *Melanopsis fossilis constricta* Handmann, 1887: Large sized.

Subspecies *Melanopsis fossilis pseudoimpressa* PAPP, 1953: Up to 60 mm, early whorls like *M. impressa bonelli* and later shape like *M. caryota* and *M. cylindrica*.

Melanopsis bonelli Manzoni, 1871: Shell 25-45 mm high and pronounced keel.

Melanopsis vindobonensis Fuchs, 1870: Last whorls almost spherical, spire short.

Subspecies *Melanopsis vindobonensis contigua* Handmann, 1887: Large size.

Subspecies *Melanopsis vindobonensis karagacensis* Pavlovic 1928: Spinous.

Melanopsis caryota Brusina, 1902: Conical shape; up to 6 cm high.

Subspecies *M. impressa posterior* PAPP, 1953: More slender.

Subspecies *M. fossilis pseudoimpressa* PAPP, 1953: More angular shape.

Subspecies *Melanopsis impressa posterior* PAPP, 1953: More concave sides, transitions to *Melanopsis fossilis*.

Melanopsis cylindrica Stoliczka, 1862: Cylindrical last whorl, short spire. More or less identical with *Melanopsis delessei* Tournouer, 1875; *Melanopsis narzolina* Archiac, *Melanopsis matheroni* Mayer, 1888, *Melanopsis pachecoi* Royo Gomez, 1922.

Melanopsis stricturata Brusina, 1892: Small, otherwise like *M. cylindrica*. Other names: *Melanopsis varicosa* Handmann and *M. pavlovici* Brusina.

Melanopsis dufouri Ferussac, 1823: Conical shell with up to three spirals, one on posterior edge, second whorl, third on corner to base.

Remarks: *Melanopsis impressa* appears to have been living basically unchanged in European areas for more than 10 million years at least to the end of the Messinian. It discontinued existence with the end of the Tertiary, but may well continue in the spirally keeled forms still found in Spain, like *Melanopsis dufouri*, as was suggested by Royo Gomez (1922). *Melanopsis stricturata* could be regarded a transitional form from the *M. impressa* group. Both *M. impressa* and *M. dufouri*-like species lived side by side since Pannonian time. Relatives to the *M. impressa*-clan older than middle Miocene are not known, but it can be imagined that there exists a relation to the slender *Melanopsis* (*Stilospirula*)

Remarks: According to the definition of AZPEITIA MOROS (1929, Pl.7, Figs.171-175), *M. maroccana* has an up to 35 mm high shell and is based on individuals living in Morocco which are smooth, dark and quite of the same shape as found in *M. buccinoidea* (= *M. praemorsa ferussaci* ROTH, 1839). The latter species is based on individuals living in the Levant. Under the name *M. buccinoidea* the common normal smooth form in Israel is treated (HELLER et al. 1999, Fig.4 A).

Melanopsis algerica PALLARY, 1904 represents a more slender form of *M. maroccana*, and according to AZPEITIA MOROS (1929 Pl.8, Figs.178, 186-191, 196) also lives in southern Spain, some varieties having different names. These are for example *Melanopsis laevigata* LAMARCK, 1822 and *Melanopsis obesa* GASSIES, 1856. BLANKENHORN (1897) called smooth *Melanopsis* from Syria also *M. laevigata*. This species has also been noted from the Pleistocene of SE Spain near Granada (MADURGA MARCO 1973, Pl.3, Figs.1,2) and looks like a normal *M. buccinoidea*, but also like *M. kleini* as illustrated by JODOT (1958) from the Sarmatian of SE Spain near Murcia. The species PERES (1939) described as *M. praemorsa* from a lake near Fes in Morocco has an up to 3 cm high shell with the same shape and ornamentation as found among the shells of *M. buccinoidea* from Pella in Jordan, and it is the same or very similar to *M. maroccana*.

SCHÜTT (1983) interpreted *M. buccinoidea* to represent a variety of *Melanopsis praemorsa* that is distributed all over the eastern Mediterranean region and the Mesopotamian basin with several subspecies in Mesopotamia and the Levant (KINZELBACH 1987). In his study of the *Melanopsis* species of the Orontes catchment SCHÜTT (1983) the subspecies *M. praemorsa ferussaci* ROTH, 1839 was usually applied to smooth forms as in *M. buccinoidea*. They live in coastal rivers which drain into the Mediterranean Sea and not the Orontes catchment (KINZELBACH 1987). Very solid representatives of *M. buccinoidea* were called *M. praemorsa olivieri* BOURGUIGNAT, 1884 in Syria (Basin of Aleppo) and the mountains of Lebanon (SCHÜTT 1988a).

Melanopsis doriae ISSEL, 1866

(figs. 25 - 29)

Description: In Jordan a form with conical shape and flat sides is recognized from the hydrogensulfide rich water of the Hemma spring next to the Yarmouk River. It is characteristically more conical and less rounded than *M. buccinoidea* and also has a higher spire (about half of shell height) than *M. praemorsa*.

Fig. 17. *Melanopsis cylindrica* STOLICZKA, 1862 from the Pontian at Fonyod near Lake Balaton with fully grown shell of 32 mm in height. The specimen in figs. 18 and 19 are from the same locality.

Fig. 18. *Melanopsis cylindrica* with 27 mm high shell is more rounded.

Fig. 19. *Melanopsis cylindrica* with 26 mm high shell.

Fig. 20. *Melanopsis buccinoidea* FÉRUSAC, 1823 from a thermal spring in the base of Wadi Mukheiris just east of the northern shore of the Dead Sea in Jordan. The shell is 22 mm high.

Fig. 21. *Melanopsis buccinoidea* from the same locality as in fig.20, with 27 mm high shell.

Fig. 22. *Melanopsis buccinoidea* from Pleistocene marly sands found just below the Lisan lake deposits on the cliffs of Jordan River west of Abu Habil, Jordan. The shell is 25 mm high.

Fig. 23. *Melanopsis buccinoidea* from the spring next to Sharhabil Ibn Hassana mosque near Wadi Raiyan, Jordan Valley. The shell is 29 mm high.

Fig. 24. *Melanopsis buccinoidea* from the spring Ain el Trap between Um Qais and Irbid in northern Jordan. The shell is 20 mm high.

Fig. 25. *Melanopsis doriae* ISSEL, 1866 from the H₂S rich waters of the thermal spring at Hemma in the Yarmouk valley, North Jordan. The shell is 16 mm high. The specimen in figs. 26-29 are from the same locality and with exception of 29 were MgO coated before photographed.

Fig. 26. *Melanopsis doriae* with 12 mm high shell.

Fig. 27. *Melanopsis doriae* with 15 mm high shell.

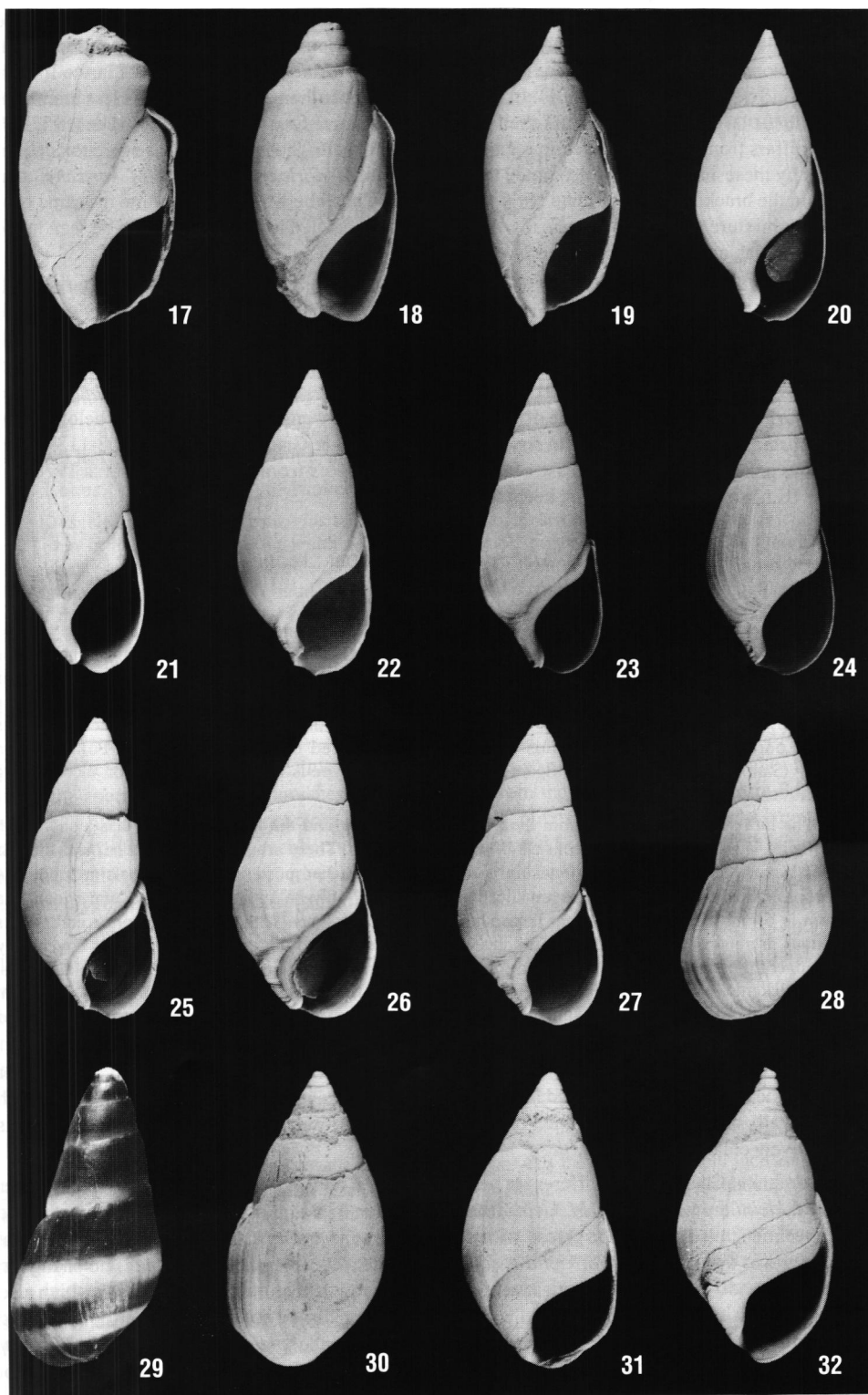
Fig. 28. *Melanopsis doriae* with 14 mm high shell.

Fig. 29. *Melanopsis doriae* as in fig. 28, but showing a colour banding of white and dark brown.

Fig. 30. *Melanopsis kleini* KURR, 1856 from the Pontian of Fonyod near Lake Balaton in Hungary with the same shell as in fig. 31.

Fig. 31. *Melanopsis kleini* with 14 mm high shell.

Fig. 32. *Melanopsis kleini* from the same locality as fig. 30 with 13 mm high shell.



shoulder (JEKELIUS 1944, Pl.53), but young stages of both these forms from the Pannonian are rather similar to each other.

Remarks: This species has been described as *Melanopsis avellana* FUCHS, 1873 and *Melanopsis textilis* HANDMANN, 1887 from Tinnye (LÖRENTHEY 1902, Pl.12, Figs.15-20), and it occurs as well in Markusevec in Croatia and in Loebersdorf in the Vienna Basin (PAPP, 1953a, Pl.9, Figs.24-27). *M. inermis* connects to the *M. impressa* group, since it is very close in shape to *M. vindobonensis*, which again connects up with *M. fossilis*. Within the *M. praemorsa* group, or the *M. bouei* group there is no angulation on the whorl as noted in *M. inermis*. The increase in whorl diameter during growth of the fifth whorl would place it close to member of the *M. bouei* clan. The aperture of *M. inermis* is rather similar to that of *M. pseudobesaa*. According to JEKELIUS (1944, Pl.49, Figs.11-17) *Melanopsis pseudopygmaea* JEKELIUS, 1944 is similar, with also a zigzag colour pattern, but also some low rounded tubercles on the body whorl. JEKELIUS also noted a *M. inermis* with a *Boistelia* character, that is a columellar thickening represented by a weak columellar fold (see chapter III.h.). Thus, *M. inermis* appears to unite the characters of most of the groups that lived in the Lake Pannon proper.

Melanopsis sharhabili n. sp.

(figs. 119-123)

Diagnosis: The five to six first whorls are like those of *M. buccinoidea*, and in the next whorl the shell becomes wider and an ornament of distinct spiral liration is developed.

Holotype: The specimen in figs. 121, 122 represents the holotype, Coll. Geological-Palaeontological Institute and Museum University of Hamburg, no.4267.

Locus typicus and derivatio nominis: Spring and creek next to the Wadi Raiyan Plantation in the Jordan Valley near the town of Wadi Raiyan and close to the mosque of the grave of Sharhabil Ibn Hassana, one of the leaders of the Islamic conquest of the Byzantine Empire after whom the species is named.

Description: The shell consists of 9 whorls and is up to 18 mm high and 9 mm wide. The first five to six whorls are of a fusiform shell with conical spire and regular increase in shell width. In the next whorl the shell increases in width more rapidly, whorl height in relation to shell height increases, so that it is two thirds of total shell height. With increasing diameter of the whorls an ornament of somewhat irregular

Fig. 33. *Melanopsis pseudobesa* n. sp. with same shell as in fig. 34 seen from the back.

Fig. 34. *Melanopsis pseudobesa* n. sp. representing the holotype of the species from the Pontian of Papkesi, near Lake Balaton, Hungary. The shell is 11 mm high.

Fig. 35. *Melanopsis pseudobesa* with 10 mm high shell from the same locality as in fig. 34.

Fig. 36. *Melanopsis pseudobesa* with the backside of the shell in fig. 35

Fig. 37. *Melanopsis bouei* FERUSSAC, 1823 from the Pontian of Papkesi, near Lake Balaton, Hungary. All individuals shown in figs.38 to 42 and 45 are from the same species and the same locality. The shell is 9 mm high.

Fig. 38. *Melanopsis bouei* of the same shell as in fig. 37 seen from behind.

Fig. 39. *Melanopsis bouei* with 12 mm high shell.

Fig. 40. *Melanopsis bouei* of the same shell as in fig. 39 seen from behind.

Fig. 41. *Melanopsis bouei* of a 4,2 mm high juvenile shell with 5 smooth whorls and tubercles and increase in diameter in the sixth whorl

Fig. 42. *Melanopsis bouei* with smooth shell portion measuring about 2 mm in height and consisting of five whorls.

Fig. 43. *Melanopsis barthai* n. sp. from the Pontian of Papkesi, near Lake Balaton, Hungary. Holotype, with 14 mm high shell. The individuals in figs. 45-51 are from the same locality.

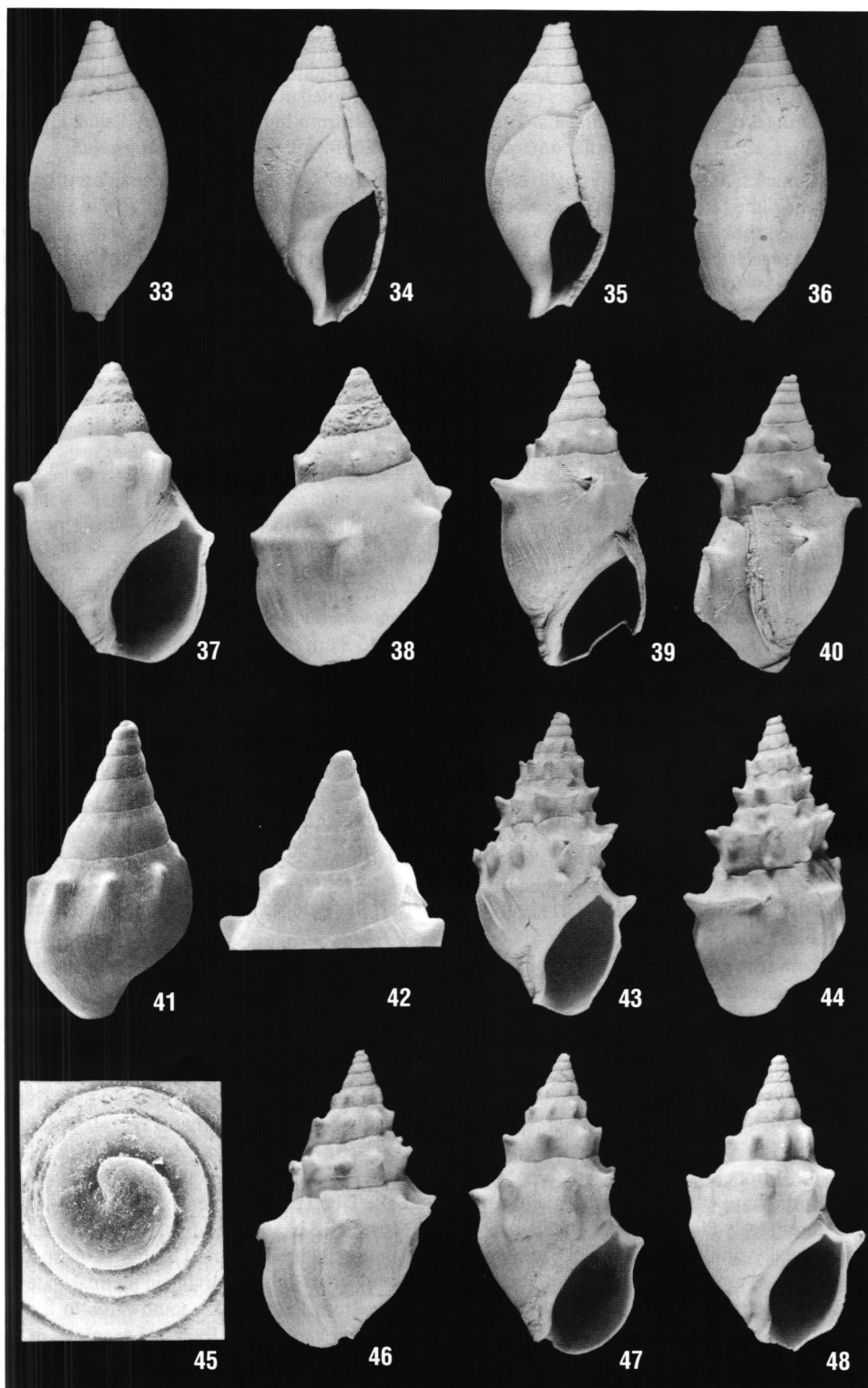
Fig. 44. *Melanopsis barthai* with the backside of fig. 43.

Fig. 45. *Melanopsis bouei* with the embryonic and first whorl measuring 0,37 mm across and first growth lines in the 1,5 whorl indicating hatching.

Fig. 46. *Melanopsis barthai* with same shell as in fig.47 seen from behind.

Fig. 47. *Melanopsis barthai* with 12 mm high shell.

Fig. 48. *Melanopsis barthai* with 17 mm high shell.



The two spines in the ornamental row distinguish *Melanopsis rarispina* from *Melanopsis affinis* in LÖRENTHEY'S (1902) terminology. PAPP (1953a, Pl.12, Figs.9-11) selected only the more slender shell forms in *Melanopsis bouei affinis* HANDMANN, 1887, while stubbier ones would be with *Melanopsis bouei bouei*. In this he followed JEKELIUS (1944, Pl.48, Figs.14-17). *M. bouei rarispina* occurs in the Pannonian of the Vienna Basin (HOERNES 1856; PAPP 1953a), also in Tinnye near Budapest, and in Soceni in Romania (JEKELIUS 1944). According to PAPP (1953a) *M. bouei affinis* is very common in all Pannonian deposits with *Melanopsis* in the Vienna Basin, and he related differences in the number of thorns per whorl to the coarseness of the sediment. In more sandy sediment rib number is smaller than in more clay-rich sediment. The subspecies *Melanopsis bouei multicostata* HANDMANN, 1887 is also slender, but has a double row of tubercles or spines as ornament (JEKELIUS 1944, Pl. 48, Figs.18-22; PAPP 1953a, Pl.12, Figs.12-14).

Melanopsis barthai n. sp.

(figs. 43, 44, 46 - 51)

Diagnosis: The early whorls are smooth up to the fifth where the diameter of the whorls increases more rapidly and where axial ribs insert as ornament. After featuring one or two whorls (fifth and sixth) axial ribs change into a single or double row of nodes, tubercles, or spines and growth ends with the 8th or 9th whorl.

Holotype: The individual figured in figs. 43, 44 represents the holotype, Coll.Geological-Palaeontological Institute and Museum University of Hamburg no.4268.

Description: According to BARTHA (1956, Pl.1, Figs.2,3) the shell of what he called *M. bouei sturi* consists of 8-9 whorls and measures between 11 and 18 mm in height and between 5 and 9 mm in width with average value of 14 and 7 mm. Only the individual figured by BARTHA (1956, Pl.1, Fig.2) is considered this new species *M. barthai*. (The specimen from Papkesi that would fit into the frame of this species is 11 x 6 mm). The individuals from Papkesi have an embryonic whorl with a rounded initial cup that measures 0.14 mm in width and a first whorl with about 0.35 mm in diameter. First growth lines along with a fine spiral striation appear after 1.25 whorls. Whorls are smooth up to the fifth one when about 10 axial ribs appear. Here the apical angle changes from about 40° to about 45-50°. After featuring one or two whorls the axial ribs change into a double row of nodes or tubercles of which the upper one on the peripheral edge is the stronger and the lower one on the corner to the rounded base is weaker and may disappear on the last whorls. Shells may grow to a size of 14 mm and usually measure only half of that in width or a little less. The inner lip of the aperture is not thickened posteriorly, but a slit-like posterior notch may be well developed.

Fig. 49. *Melanopsis barthai* with 10 mm high shell that shows the color pattern of brown dots.

Fig. 50. *Melanopsis barthai* with 11 mm high shell that shows the color pattern of brown dots.

Fig. 51. *Melanopsis barthai* with 10 mm high shell that shows the color pattern of brown dots.

Fig. 52. *Melanopsis papkesiensis* n. sp. with 11 mm high shell that shows the color pattern of brown dots. The specimen in figs. 53 - 58 belong to the same species, all from the Pontian of Papkesi near Lake Balaton in Hungary.

Fig. 53. *Melanopsis papkesiensis* n. sp. with frontal view of the holotype and 15 mm high shell.

Fig. 54. *Melanopsis papkesiensis* with the same shell as in fig.53 seen from behind.

Fig. 55. *Melanopsis papkesiensis* with 12 mm high shell.

Fig. 56. *Melanopsis papkesiensis* with same shell as in fig. 55.

Fig. 57. *Melanopsis papkesiensis* with first whorl of 0,3 mm in width representing most of the protoconch with hatching time indicated by first growth lines with about 1,5 whorls.

Fig. 58. *Melanopsis papkesiensis* with 2,5 mm high juvenile shell with ornament of axial ribs initiating in the fifth whorl and becoming obsolete two whorls later.

Fig. 59. *Melanopsis eulimopsis* BRUSINA, 1902 from the Pontian of Papkesi near Lake Balaton in Hungary with 13 mm high shell. All individuals in figs. 60-70 belong to this species and come from the same locality.

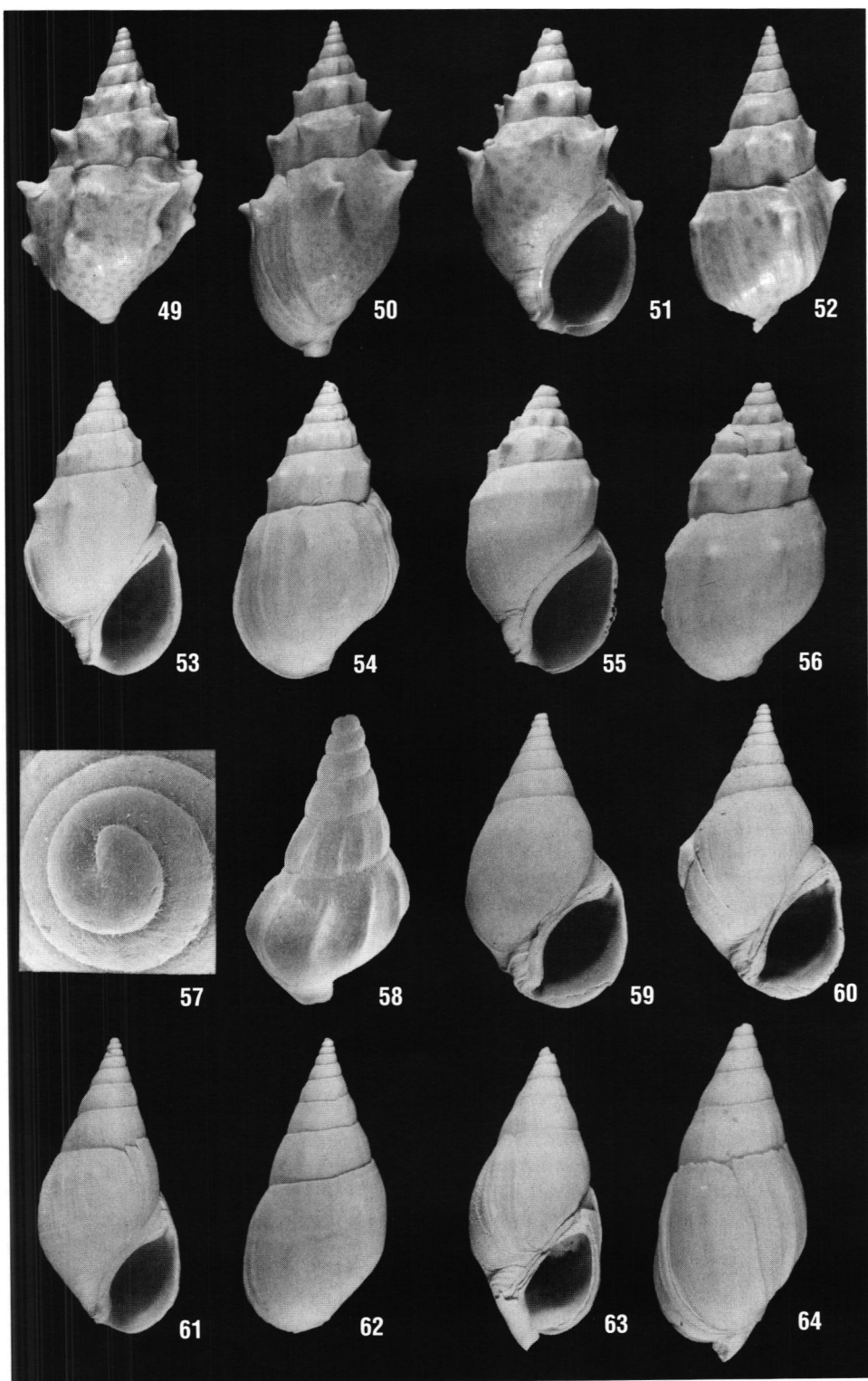
Fig. 60. *Melanopsis eulimopsis* with 13 mm high shell.

Fig. 61. *Melanopsis eulimopsis* with 13 mm high shell.

Fig. 62. *Melanopsis eulimopsis* of the same shell as in fig. 61 from behind.

Fig. 63. *Melanopsis eulimopsis* with 14 mm high shell.

Fig. 64. *Melanopsis eulimopsis* of the same shell as in fig. 63 from behind.



Derivatio nominis and type locality: The species is named after the Hungarian palaeontologist Ferenc BARTHA who described these forms first. The shells are from the sand pit near Papkesi in Pontian strata.

Differences: *Melanopsis barthai* has axial ribs as first ornament, in contrast to *M. bouei* with nodes as first ornament. The ornament is present also on the last whorls, of which *M. barthai* has at least one more than *M. bouei*. Also the shell is more slender. But in the fauna of Papkesi transitional forms exist which mediate between these two and the more slender and smooth *M. papkesiensis*. In contrast to *M. papkesiensis*, *M. barthai* has the shell ornamented to the last whorl. *M. oxyacantha* has no allometric growth in the fifth whorl and is more regularly ribbed. *M. eulimopsis* is totally smooth, but of similar shell shape.

Remarks: Unlike the illustrations and descriptions of JEKELIUS (1944, Pl.17, Figs.1-17) and GEARY (1988) of *M. bouei* and *M. sturii* the ornament of *M. barthai* begins with axial ribs. It is possible that *Melanopsis minotauri* WILLMANN, 1980 is the same as *M. barthai*. According to WILLMANN (1980, Fig.11 a,b,c) this axially ribbed *Melanopsis* has an ornament of two rows of tubercles which may or may not be connected by axial ribs. The up to 14 mm high and 8 mm wide shell has a colouration of brown dots. Its early whorls are not known so that it can not be decided whether it should be regarded closer to *M. sturii* with ten whorls in the adult, *M. bouei* with fewer whorls, both with early ornament of nodes or *M. barthai* with early ornament of axial ribs.

Melanopsis papkesiensis n. sp.

(figs. 52 - 85)

Diagnosis: Like in *Melanopsis barthai* the first ornament consists of axial ribs. In difference the shell is more slender, and ornament is less developed, in late whorls often missing.

Holotype: The specimen in figs. 53-54 represents the holotype; Coll. Geological-Palaeontological Institute and Museum University of Hamburg no.4269.

Derivatio nominis and type locality: This species is called according to the village that lies closest to the sand pit of the type locality in the Pontian deposits near the eastern margin of Lake Balaton.

Description: In this species from Papkesi the shell consists of eight whorls and is about 11 mm high and 6 mm wide. The protoconch consists of about 1.5 whorls without growth lines. Its initial cup is of 1.2 to 1.5 mm in width, a first whorl measures 0.25 mm in width and has a total size of about 0.33 mm. At the fifth whorl there is a slight increase in apical angle from about 45° to 50°, and in this whorl axial ribs appear. There may be 10 to 12 in the sixth whorl and less or more in the seventh. But in other individuals ribs in the seventh whorl are shorter or consist only of tubercles. In the eighth and last whorl ribs may disappear, there may only be an angulation or a few low nodes. The aperture is oval with strongly convex inner lip that has no posterior callus pad, but a narrow notch here. Preserved colour patterns consist of brown dots which are arranged in indistinct spirals.

Differences: In the fifth whorl axial ribs appear in *M. papkesiensis*, just as in case of *M. oxyacantha*, but in contrast to the latter they disappear again in later whorls. Regarding colour pattern and number of whorls *M. papkesiensis* resembles *M. eulimopsis*, but the latter is totally smooth. *M. bouei* has spines or nodes as first ornament, and not axial ribs as are found in *M. papkesiensis*. *M. barthai* has more ornament up to the last whorl and is usually less slender.

Remarks: PAPP (1953a) named a similar species from the Pannonian of the Vienna Basin *M. bouei sturii* recognizing that there is not really a difference between *M. sturi* and *M. bouei* in former descriptions like that of JEKELIUS (1944), but according to his illustrations it is the same as *M. sturii* of LÖRENTHEY (1902) from the Budapest area. Regarding transitions to the *M. bouei* proper, *M. bouei multicostata* is similar in ornament, but differs regarding the more rapid increases in whorl diameter (PAPP 1953a, Pl.12, Figs.12-14). *Melanopsis pseudopygmaea* JEKELIUS, 1944 has orange dots and zigzag patterns and shallow nodes on the last whorl. It can represent *M. papkesiensis*, perhaps a variety that is more characteristic to the Soceni locality (JEKELIUS 1944, Pl.49, Figs.11-17).

Melanopsis eulimopsis BRUSINA, 1902

(figs. 59 - 70)

Description: The protoconch and teleoconch are smooth. From the fifth whorl onward whorl diameter increases a bit faster than in the whorls before. The colouration consists of brown dots. The shell is of ovoid shape. There is a callus pad, but only a minute posterior notch.

The shell consists of about 8 whorls and is 12 mm high and 5-6 mm wide with a 6 mm high aperture of drop like shape. Other more slender smooth adult shell measure 11-13 mm in height and 6-7 mm in width with 7 to 7.5 whorls. The aperture is about 5 mm high and of tear-like shape with the inner lip thickened and forming an evenly thickened posterior pad and a slit-like posterior furrow between outer lip and callus pad. The outer lip is evenly curving. The first four to five whorls have a regular increase in whorl diameter, while later whorls increase in diameter a little more or remain similar. In general contour the whole shell has straight or slightly concave sides. The protoconch consists of about 1.5 rounded whorls and these grade into the teleoconch without change in whorl shape. The gradational transition may be noted in the appearance of some collabral growth lines. Whorl curvature remains of similar convexity throughout. When colouration is preserved it consists of brown dots (fig. 174).

Differences: The missing posterior callus pad of the inner lip connects *Melanopsis eulimopsis* with the members of the *Esperiana* group. *M. eulimopsis* closely resembles *Melanopsis pygmaea* HOERNES, 1856, but has smooth whorls without a subsutural groove. In shape of the shell it resembles *Melanopsis fuchsi*, but has no juvenile shell ornament, usually has fewer whorls, a more rapid increase in shell diameter in juvenile whorls, and a pattern of brown dots instead of axial stripes. While *M. eulimopsis* is smooth, most of the other forms of the *Melanopsis bouei* group have ornament on some of their teleoconch whorls.

Remarks: BARTHA (1955, Pl.1, Fig.5) illustrated *M. eulimopsis* as *M. fuchsi* together with a real *M. fuchsi* (Pl.1, Fig.13), which according to his description should have juvenile ornament. Both species are very common in Papkesi. But while *M. eulimopsis* shows transitions into *M. bouei*, *M. barthai* and *M. papkesiensis*, *Melanopsis fuchsi* has no such intermediate forms. Three somewhat worn individuals are from Balatonszentgyöry. They have probably been transported here from upstream, but have lived contemporary with *M. caryota* and *M. cylindrica*. The modern *Esperiana* (= *Fagotia*) *esperi* from a river at Jubiljana (Croatia) has not only a similar shell shape and size to *M. eulimopsis*, but also a colour pattern of brown dots (JAECKEL et al. 1958; SCHÜTT 1965). BARTHA (1956) also compared individuals from Tab with *Fagotia*. *Melanopsis pseudopigmea* MAGROGRASSI, 1928 from the Pliocene of Kos (WILLMANN, 1981, Pl.8, Figs.17-18) may be the same species as found in Papkesi. Like *M. eulimopsis* it has rounded whorl sides and a pattern of brown dots.

Melanopsis pygmaea HOERNES, 1856

Description: The shell with 6-8 whorls is smooth, and the last whorl has half the height of the total shell. The whorl has right below the suture a recess so there appears to be a narrow ridge right next to the suture. The colouration consists of alternating rows of elongate spots (PAPP 1953a, Pl.12, Figs.28-30, 33,34).

Differences: The subsutural furrow and low ridge distinguishes from the similar *Melanopsis eulimopsis* from the Pontian of Papkesi, which is also more slender.

Remarks: PAPP (1953a) included *Melanopsis eulimopsis* in his subspecies *Melanopsis pygmaea mucronata* HANDMANN, 1887 from the Pannonian of Löbersdorf. But this only documents, that a rather similar *Melanopsis* to that of the Pontian *M. eulimopsis* existed already in Pannonian time. A less slender form without the subsutural furrow was called *M. handmanni* BRUSINA, 1892 (PAPP 1953a, Pl.12, Figs.35-37). GEARY (1988) suggested that *M. pygmaea* is a development of a *M. bouei* - *sturi* that became mature before spines could evolve in the ornament. Thus, it was interpreted as heterochoneous transition of the adults retaining the smooth shape of the juvenil. GEARY (1988) assumed and not really observed in continuous stratigraphic transition from ornamented *M. bouei* to smooth *M. pygmaea*. This is not such a miracle, since these forms of the *Melanopsis bouei* group have lived side by side from the Pannonian to the end of the Pontian, and therefore the process is not heterochoneous but rather synchronous.

Melanopsis minotauri WILLMANN, 1980

Description: The shell is in shape like that of *Melanopsis bouei rarispina* of JEKELIUS (1944) and has a row of spines below the shoulder connected to axial ribs of which 10 are present on the last whorl (WILLMANN 1980, Fig.11 A). Colour pattern is by brown dots.

Remarks: WILLMANN (1980) noted the large variety of shell forms which connect his typical *M. minotauri* with morphs that are more slender and also such with ribs having two nodes. He, thus, noted a connection of forms like *Melanopsis bouei rarispina* to such like *Melanopsis bouei multicostata* in the terminology of PAPP (1953a, Pl.12, Figs.7,8,12-14), but WILLMANN did not discuss this obvious similarity. PAPP (1953a) had documented these forms from the Pannonian of the Vienna basin, while according to LÖRENTHEY (1902, Pl.17, Figs.1-32) the three shells of the *M. minotauri* group from Crete illustrated by WILLMANN could be placed in the species *M. sturii*, *M. affinis*. The holotype of *M. minotauri* would fit with *M. rarispina*, all of which occur together in the Tinnye locality near Budapest of Pannonian age. JEKELIUS (1944) found the interconnections between the species of *M. bouei* in the fauna he studied from Romania, and, thus, changed the concept of different species to different subspecies. But JEKELIUS did not state the differences of the *M. bouei* clade from that of the *M. sturii* clade, the latter of which has also varieties resembling those of *M. minotauri*.

Melanopsis inermis HANDMANN, 1882

Description: The smooth small sized shell is rounded with rapid increase in shell width after the fourth whorl. Ornamental colour patterns are axial zigzag-lines (JEKELIUS 1944, Pl.54, Figs.1-20; PAPP 1953a, Pl.9, Figs.24-27). PAPP (1953a) described *M. inermis* from the Pannonian of the Vienna Basin (Leobersdorf) which represents the area of its original description. It was also described in detail by JEKELIUS (1944) from the middle Pannonian Turislav Valley in Romania.

Differences: *M. inermis* is clearly distinct from the core species of the *M. impressa* group by its small size and the short barrel-like shell shape (see chapter III.b.). It resembles members of the *M. bouei* group by having their allometric growth. But it is also similar to members of the *M. impressa* group, especially *M. vindobonensis* in having by a totally smooth shell with a distinct posterior corner and relatively broad last whorl. It is also similar to *M. stricturata* by also having a corner with the base, but differs from it by having a much shorter spire.

Remarks: *M. inermis* could rather well represent the result of mixing between a member of the *M. bouei* group with short spire and a member of the *M. impressa/stricturata* group with cornered margins of the whorl.

III.d.1. Remarks about the *Melanopsis bouei* group

Key

Melanopsis sturi FUCHS, 1873: Ornament inserts with tubercles within the fifth whorl, later 10 axial ribs, on last whorl row of double nodes; increase in width in 5th whorl; body whorl same size as spire; colour of yellow dots. Distinction from *M. bouei* unclear.

Melanopsis bouei FERUSSAC, 1823: Ornament inserts with tubercles, increase in width in 4th or 5th whorl; ornament of tubercles or spines continues to last whorl.

Subspecies *Melanopsis bouei rarispina* LÖRENTHEY, 1902: With double row of spines. Like *M. minotauri* of WILLMANN (1980), row of spines connected to axial ribs, colour of brown dots.

Subspecies *Melanopsis bouei bouei*: With single row of spines, stubby shell form.

Subspecies *Melanopsis bouei affinis* HANDMANN, 1887: With slender shell forms.

Subspecies *Melanopsis bouei multicostata* HANDMANN, 1887: With slender shell and double row of spines.

Melanopsis barthai n. sp.: Ornament first axial ribs, on last whorl row of double nodes; increase in width in 5th whorl; body whorl same size as spire; colour of yellow dots, callus pad present; colour of brown dots. *Melanopsis bouei sturii* is the same.

Melanopsis papkesiensis n. sp.: Ornament first like *M. barthai* with axial ribs, shell more slender, less ornament.

Melanopsis eulimopsis BRUSINA, 1902: Shell smooth, increase in whorl width in 5th whorl; colour

of brown dots; no posterior callus pad and notch. Probably the same as *Melanopsis pseudopigmea* from Kos. ? *Melanopsis pygmaea mucronata* HANDMANN, 1887

Melanopsis pygmaea HOERNES, 1856: Shell smooth and subsutural groove; body whorl half of shell height.

Melanopsis senatoria JEKELIUS, 1944: Smooth *M. bouei*.

Melanopsis inermis HANDMANN, 1882: Smooth with increased width after 4th whorl; cornered sides, colour of zigzag-lines

Remarks: The *M. bouei* clade is well represented by different forms in the fauna of Papkesi. These can be differentiated by the mode of insertion of ornament and here several forms could be recognized. A first *M. barthai* would have straight axial ribs inserting and also present in the next whorl before they grade into a row of tubercles. A second also has one or two whorls with such ribs before they grade into tubercles (*M. papkesiensis*) which later usually disappear. The third has weaker and more inclined axial ribs in the first whorl (unnamed hybrid). A fourth begins its ornament with tubercles (*M. bouei*) and a fifth has only few such tubercles (unnamed hybrid) while the sixth is smooth (*M. eulimopsis*).

These different forms could be related to species and subspecies or forms as recognized by LÖRENTHEY (1902) and PAPP (1953a) from the Pannonian. LÖRENTHEY (1902) had recognized that *Melanopsis bouei* with its varieties and related species is present in the Hungarian Tinnye as well as in the Croatian Markusevec and the Austrian Löbersdorf. The insertion of ornament on the first ornamented whorls of the teleoconch is usually not well described for the Pannonian forms of the *M. bouei* group and, therefore, it is difficult to set them into relation with the many forms present in the Pontian of Papkesi. Apparently most individuals of the members of the *M. bouei*-group from the Pontian begin their ornamental pattern with axial ribs which in later whorls become nodes, while *M. bouei* from the Pannonian begin ornament with a row of nodes. The species *M. bouei* is, thus, diagnosed as having nodes as first ornament. This character is used to distinguish others which are initially ribbed like *M. barthai* and *M. papkesiensis*. Their shell is between 7 and 12 mm high and consists of only 5 to 7 whorls. While apertural features are as in *M. sturii*.

According to GEARY (1990) the *M. bouei* or *M. sturii* from the Pannonian develops its nodal ornament between the fifth and the seventh whorl and the shell becomes more inflated in these whorls as well. The shell height does not exceed 19 mm with an average approximately 12 mm. Obviously *Melanopsis bouei* and/or *Melanopsis sturii* were present with begin of the fresh water environment within the lake proper of Lake Pannon in the lowest beds of the Pannonian in the Vienna Basin (PAPP 1953a) and in the Sarmatian of the Romanian Soceni (JEKELIUS 1944). The small variety called *M. bouei affinis* was clearly ribbed and from it transitions to regularly ribbed species such as present in Papkesi with *Melanopsis oxyacantha* as well as to spiny forms such as *Melanopsis bouei* as well as to smooth species like *M. eulimoides* appear to be present throughout the existence of Lake Pannon from the north to the south (JEKELIUS 1944). A special development from *M. bouei* to a smooth species by heterochrony as assumed by GEARY (1988) may have happened or not and is difficult to check when melanopsids with such shapes lived side by side from the origin of the lake at the Sarmatian to its end several million years later in the Messinian.

According to GEARY (1990) members of the *M. bouei* clade formed most species in the Pannonian basin. She identified 7 species from the Pannonian, of which 5 belong to that clade. This coincides more or less closely with the interpretation of PAPP (1951) who distinguished 5 subspecies of *M. bouei*, most of which can also be recognized in the Pontian. The assumption can be offered that the spiny *Melanopsis impressa* and *M. vindobonensis* from Serbia described by PAVLOVIC (1928) may actually be the result of hybridization with ornamented forms, perhaps those of the *M. bouei* clan. The hybridization with representatives of the ribbed *M. oxyacantha* is quite probable and noted in the fauna from Papkesi. *M. inermis* can also be interpreted as originated by hybridization of members of the *M. bouei*-group and members of the *M. impressa* - group.

III.e. The *Melanopsis costata* group

The members of this group, which had been included in an own subgenus *Canthidomus* SWAINSON, 1840 are characterized by axial ribs as ornament. Since it can be shown in fossil and living faunas that members of the *Melanopsis costata* group form hybrids with members of the smooth subgenus *Melanopsis* and also with members of the subgenus *Lyrcaea* with stair-like spire, and also did so in the past, the taxon *Canthidomus* is of no use in a phylogenetic sense. The *M. costata*- group includes species with the typical *Melanopsis* shape provided with the posterior callus pad of the inner lip of the aperture, but also such of *Esperia* shape without such a callus pad as for example *M. oxyacantha*. To include species of the *M. costata* group as subspecies within the species *M. praemorsa*, as has repeatedly been suggested, is also of little use, since there is recent and fossil evidence of large populations of ribbed *Melanopsis* that live and lived without smooth relatives next to them (for example BUKOWSKI 1895, HELLER et al. 1999). There is also evidence for smooth and ribbed forms to live side by side without mixing (see chapter III.e.1.), as there is evidence of intense hybridization occurring or having occurred in other locations.

Melanopsis costata OLIVIER, 1804

(figs. 72 - 75)

Description: According to HELLER et al. (1999, Fig.4B) the main feature of *M. costata* is the presence of an ornament of 9-14 axial ribs on each flattened whorl and an usually slender relatively large shell (around 2,5-3 cm high) with rounded upper whorl side. More than 9 whorls compose the shell, and the straight ribs are usually continuous onto the base. Ribs may have a weak posterior swelling subsuturally that may be accompanied by a shallow furrow on the whorl side anterior of it. BLANCKENHORN (1897) discovered that the type locality of the species is the middle Orontes region in Syria and it was here collected in a canal for irrigation. The shape of the shell is taken as that illustrated by HELLER et al. (1999) without stair-like spire, and not as in the illustration of OLIVIER as given by AZPEITIA MOROS (1929, Pl.14, Fig.340). This differs from that presented by WENZ (1938, Fig.1986a,b), but resembles his Fig. 1986c. The figure by AZPEITIA MOROS as well as those by WENZ shows a species with more strongly shouldered shell. It is more likely that the originally described *M. costata* representing a living form when it was collected, has a shape like the shell from near Homs in Syria named *M. praemorsa costata* (OLIVIER, 1804) by SCHÜTT (1988a, Pl.1, Fig.4). The same is described in chapter III.e.1 from the Azraq oasis.

Fig. 65. *Melanopsis eulimopsis* with 10 mm high shell, see fig. 59 for location.

Fig. 66. *Melanopsis eulimopsis* with 10 mm high shell.

Fig. 67. *Melanopsis eulimopsis* with 12 mm high shell and colour pattern of orange dots.

Fig. 68. *Melanopsis eulimopsis* with 12 mm high shell and colour pattern of orange dots.

Fig. 69. *Melanopsis eulimopsis* with protoconch having a 0, 4 mm wide first whorl.

Fig. 70. *Melanopsis eulimopsis* with 2,5 mm high juvenile shell with increase in diameter more rapid with the fifth whorl.

Fig. 71. *Melanopsis buccinoidea* from a pond at Azraq Druz in the Jordanian Desert. The shell is 25 mm high.

Fig. 72. *Melanopsis costata* OLIVIER, 1804 from a pond at Azraq Druz of Azraq Oasis in the Jordanian Desert. The shell is 24 mm high. The individuals of figs. 73-75 are from the same locality.

Fig. 73. *Melanopsis costata* with 22 mm high shell.

Fig. 74. *Melanopsis costata* with 24 mm high shell.

Fig. 75. *Melanopsis costata* with 28 mm high shell.

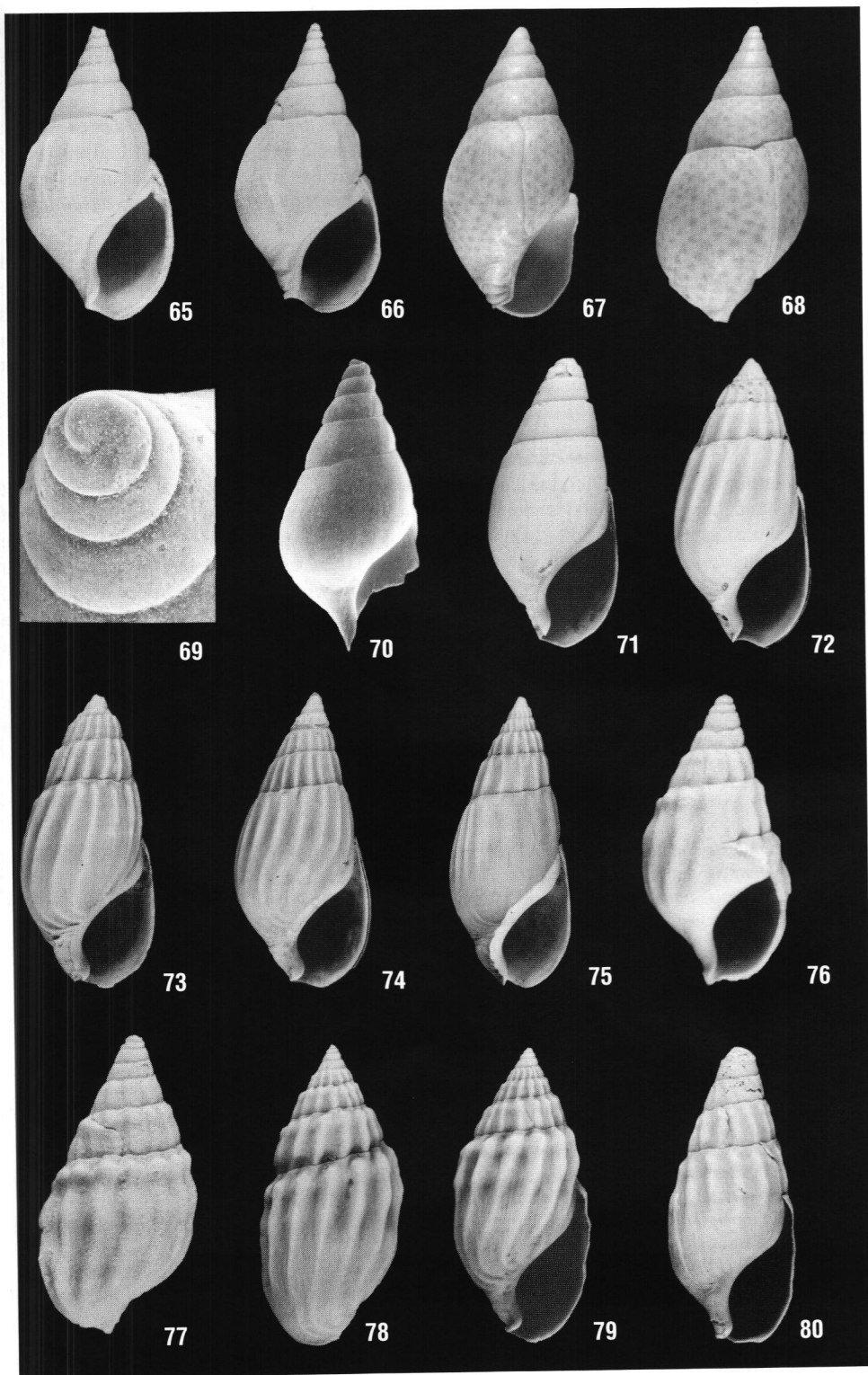
Fig. 76. *Melanopsis saulcyi* with juvenile shell of 8 mm in height from the Pleistocene marly sand just below the Lisan lake deposits exposed from the cliffs of the Jordan at the creek coming from Pella springs, west of Mashara.

Fig. 77. *Melanopsis saulcyi* with the same shell as in fig. 76 seen from behind.

Fig. 78. *Melanopsis saulcyi* BOURGUIGNAT, 1853 from pond and creek next to Tell Murashed to the west of Mashara, Jordan Valley, Jordan. The shell is 13 mm high.

Fig. 79. *Melanopsis saulcyi* with same shell as in fig. 78 in frontal view.

Fig. 80. *Melanopsis bandeli* with 13 mm in height from the springs and creek of Pella in Jordan.



Differences: *M. costata* differs from *M. saulcyi* by a more elongate, *M. buccinoidea*-like shell, larger size and less developed subsutural row of nodes and following depression on the side of the whorl. It differs from the Pleistocene *M. noetlingi* by more widely spaced axial ribs and higher last whorl. *M. sevilensis* from the western Mediterranean area is of more fusiform shape. *M. oxyacantha* is more slender without a callus pad on the inner lip and *M. trempensis* has also a strong spiral ornament along with more rounded shell shape. The other species recognized from fossil and recent occurrences in Jordan described below are difficult to distinguish in detail since hybrids among *M. costata* and *M. saulcyi* as well as with other species of the *M. dufouri* and the *M. buccinoidea/praemorsa* groups occur.

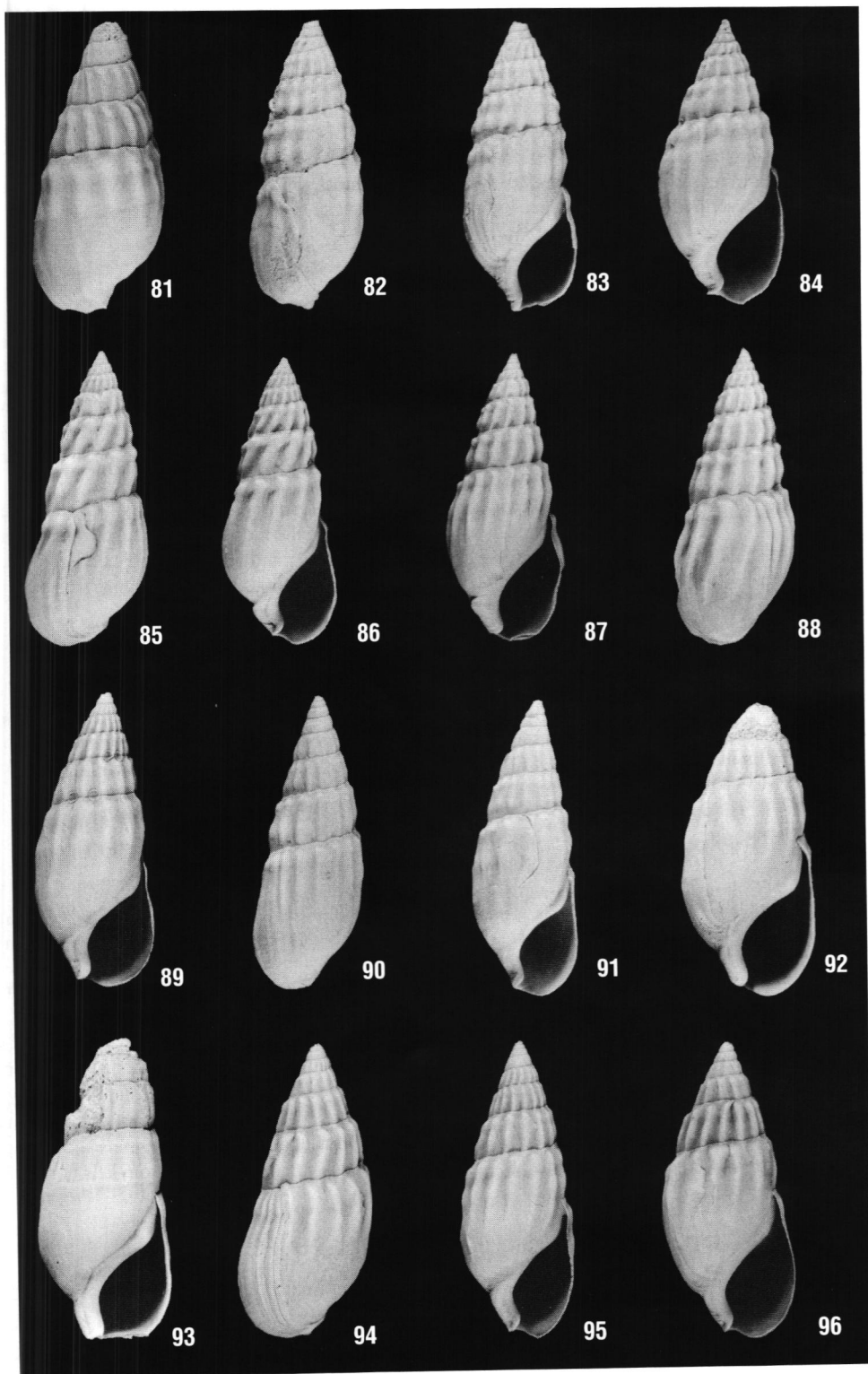
Remarks: BILGIN (1973) noticed differences regarding the radula morphology of *M. costata* and *M. praemorsa*. But this observation needs not to reflect true relations and may just be a chance variation (see GLAUBRECHT 1996). *M. costata* and similar forms are very common in the eastern areas of the Mediterranean realm, actually from the Iranian mountains to Greece and in an outlier in western Romania (thermal springs near Oradea). Members of the *M. costata* group are present in the Near East to Central Jordan.

Melanopsis parreyssi MÜHLFELD, 1847

According to KORMOS (1905) the elongate shell consists of 7-8 whorls (probably juveniles not counted), has a stair-like spire, and is about 20 mm long and 9 mm wide. In fully grown shells the last whorl is almost as high as the spire, while it is higher than the spire in more juvenile shells. The ornament consists of a variable number of ribs which form a nodule at the periphery and are sigmoidal in their lower course, which is later covered by the succeeding whorl. There may be one to four spiral lirae, or none. The aperture is oval elongated with a siphonal notch and thickened callus pad on the inner lip. Its only occurrences is in western Romania (Oradea) in the pond and creek formed by a thermal spring.

Differences: *Melanopsis parreyssi* due to its variable shell shape fits more or less well into shell shapes as found in the *M. costata*, but appears to be a bit shorter in general. The stair-like spire

-
- Fig. 81. *Melanopsis bandeli* of the individual in fig. 80 seen from behind.
 Fig. 82. *Melanopsis bandeli* of the individual in fig. 83 seen from the back.
 Fig. 83. *Melanopsis bandeli* (SCHÜTT, 1988) from marly sands below the Lisan lake deposits in the cliff of the Jordan next to the creek from Pella/ Mashara, Jordan. The shell is 18 mm high.
 Fig. 84. *Melanopsis saulcyi* from pond and creek next to Tell Murashed to the west of Mashara, Jordan Valley, Jordan. The shell is 13 mm high.
 Fig. 85. *Melanopsis bandeli* of the individual in fig. 86 seen from the back.
 Fig. 86. *Melanopsis bandeli* (SCHÜTT, 1988) from pond and creek next to Tell Murashed to the west of Mashara, Jordan Valley, Jordan. The shell is 19 mm high.
 Fig. 87. *Melanopsis bandeli* with 17 mm high shell from the same locality as in fig. 86.
 Fig. 88. *Melanopsis bandeli* of the individual in fig. 87 seen from the back.
 Fig. 89. *Melanopsis bandeli* with 19 mm high shell from the spring and creek next to the Sharhabil Ibn Hassana mosque near Wadi Raiyan in the Jordan Valley.
 Fig. 90. *Melanopsis bandeli* of the individual in fig. 91 seen from the back.
 Fig. 91. *Melanopsis bandeli* from marly sands below the Lissan lake deposits in the cliff of the Jordan next to the road west of Abu Habil, Jordan Valley. The shell is 19 mm high.
 Fig. 92. *Melanopsis bandeli* from the thermal spring in the base of Wadi Mukheiris close to the NE shore of the Dead Sea, Jordan. The shell is 14 mm high.
 Fig. 93. *Melanopsis bandeli* from the same thermal spring as fig. 92 with 18 mm high shell.
 Fig. 94. Hybrid of *Melanopsis bandeli* and *M. saulcyi* from the spring and creek next to the Sharhabil Ibn Hassana mosq near Wadi Raiyan in the Jordan Valley. Same shell as in fig. 96 seen from the back.
 Fig. 95. *Melanopsis bandeli* with 20 mm high shell from the same locality as fig. 94.
 Fig. 96. Hybrid of *Melanopsis bandeli* and *M. saulcyi* of the same individual as in fig. 94 with 19 mm high shell.



resembles that of the Pleistocene representatives of the group like *M. noetlingi* and *M. blanckenhorni*, which would usually be a little more slender.

Remarks: KORMOS (1903) distinguishes two species of *Melanopsis* from Oradea, *M. parreyssi* living in the warm water of the spring and *M. hungarica* living further away from it in cooler water. But according to SCHÜTT (1988b) only *M. parreyssi* is living in Bischofsbad= Püspökördő= Oradea. He considered it to be related to *Melanopsis costata* from the Middle East. According to BRUSINA (1902b) the living form represents the direct relatives of fossil ancestors which also lived in the vicinity of the springs. He described 7 new fossil species and distinguished 23 forms.

Melanopsis saulcyi BOURGUIGNAT, 1853

(figs. 78 - 79, 84)

Description: Below the more or less well developed corner of the posterior shoulder of the spire the axial ribs insert with a spiral row of tubercles accompanied by a depression anterior to it. The shell in addition to axial ribs is, therefore, also ornamented by some spiral elements, and is usually smaller (about 15 mm high) than that of *M. costata*. The type was described from the Near East and can not be well distinguished from *M. costata* (PERES 1945). Here shells like that of *Melanopsis praemorsa obsoleta* DAUTZENBERG, 1894 as illustrated by SCHÜTT (1988a, Pl.1, Fig.6) are placed and other names to the species have been assembled by PERES (1945).

Remarks: HELLER et al. (1999, Fig.4 F,G) placed with *M. saulcyi* two forms which are here considered to represent *M. saulcyi* and *M. bandeli*. This is due to the fact that in Jordan they occur in several independent populations that are very rich in individuals and are geographically isolated. These can, in addition, be traced back in their existence for at least 50,000 years (chapter III.e.1.)

Melanopsis sevilensis GRATELOUP, 1840

(figs. 149 - 150)

Description: The fusiform shell with relatively short spire and relatively large last whorl is ornamented by axial ribs that end in a spiral row of tubercles near the posterior shoulder of each whorl. The type is from SE Spain, but has very similar forms in the Maghreb area which may be called *M. tingitana*.

Melanopsis aegaea TOURNOUER, 1875

(figs. 129 - 132)

Description: This species from a Neogene lake of Kos differs from the others of this *M. costata* group in having well rounded whorl sides and strong and evenly developed axial ribs. Apparently such forms are characteristic to Kos (WILLMANN 1981, Pl.9, Figs.11,12, and here extended synonymy). WILLMANN also observed a transition to normal members of the *M. costata* group with shouldered shells to occur in stratigraphically younger deposits. Rather round short forms occur as well as more slender ones.

Remarks: OPPENHEIM (1891b) described a similar form with more ribs on each whorl as in *M. aegaea* as *M. eleis* from the Pliocene of Greece which is rather similar in shell shape and also similar to *Melanopsis eleis posterior* SCHÜTT, 1986 that differs from *Melanopsis eleis* OPPENHEIM, 1891 by having a less thickened last whorl and shallower sutures (SCHÜTT 1986). *M. eleis posterior* comes from lake deposits of the late Pliocene of Greece exposed not far from lake Lysimachia. *M. eleis* according to OPPENHEIM (1891b, Pl.26., Fig.5) the about 24 mm high and 12 mm wide shell from Elis north of Pyrgos in Greece.

III.e.1. The *M. costata* group in the Jordanian Pleistocene and in the Recent

It has been recognized that the Jordan Valley contains a variable number of ribbed *Melanopsis* species or forms belonging to the two species *M. costata* and *M. saulcyi*. HELLER et al. (1999) found *M. costata* to be basically of similar size as *M. buccinoidea*, while *M. saulcyi* is smaller. They distinguished the subspecies *costata costata*, *costata jordanica*,

and *costata noetlingi* which all have an ornament of 9-10 axial ribs on each whorl. HELLER et al. (1999) suggested that the three species (*M. buccinoidea*, *M. costata*, *M. saulcyi*) from the Jordan catchment are generally isolated from each other, but where they meet they may form hybrids. Hybridisation has since been recognized in more detail (HELLER, pers.com.). The subspecies of HELLER et al. (1999) are here considered as species, even though it is realized that they form hybrids. But since there is also hybridisation with *M. buccinoidea* in Jordan (see chapter III.c.) observed by HELLER et al. (1999) in Israel as well, varieties forming large uniform population locally are best described as species. Coloration of Jordanian members of the *M. costata*-group is by brown spiral bands as is the case in *M. buccinoidea*.

Among the Pleistocene to Recent *Melanopsis* it is, thus, of no major consequence to either regard different recognizable forms as species, subspecies or varieties. BLANCKENHORN (1927) treated them as species, SCHÜTT (1983, 1984, 1988a, SCHÜTT & ORTAL 1993) as subspecies of *M. praemorsa*, and HELLER et al. (1999) as partly species and partly subspecies. The later authors demonstrated that all have the possibility to form fertile hybrids with each other, even though they commonly do not mix their genes when meeting. Hybridisation resulting in a species mix should be noted in the field, either in the waters where they live together or in layers of sediment where they occur together. As is shown below such species mix occurs in Jordan at Azraq oasis in the eastern desert (now no longer observable), in the spring and creek near Wadi Riyan in the Jordan Valley, and in a creek and pond next to Tell Murashad in the Jordan Valley, in each case with different partners involved in the process. HELLER et al. (1999) had documented hybrids to occur in the area of creeks ending in Lake Tiberias.

The following 6 species can be recognized from recent and Pleistocene fossil *Melanopsis* in Jordan according to the morphology of their shell.

Melanopsis costata OLIVIER, 1804

(figs. 72 - 75)

Description: The slender fusiform shell with up to ten whorls reaches a size of up to 3.3 cm in height. Shell shape is that of a slender *M. buccinoidea*, with which it forms hybrids. But ribbed individuals of this species are by far the more common ones in the population of Azraq Druz pond 1995, and now extinct. The ornament consists of 12 to 15 rounded ribs which are continuous across the whorl forming an even curve pointing forwards in the rounded transition of the whorl sides into the base. Ribs are usually continuous onto the base but may become less distinct here. Transitional individuals to *M. buccinoidea* have weak ribs present only in the juvenile shell or irregular ribbing up to the end whorl. The species comes from Azraq Druz pool and resembles that from the southern pool illustrated by SCHÜTT (1988a) and considered to belong to *M. costata*. In the warm spring in Wadi Mukheiris similar forms occur, but are not quite the same due to the presence of spiral liration and generally weaker axial ribs near the base of the shell. The later are here placed with *M. bandeli*.

The species that lives next to Lake Tiberia and in the Jordan north of it closely resembles the species that lived up to 1995 in the ponds of Azraq oasis in Jordan, and is here considered to present *Melanopsis costata*.

Differences: The spire of *M. saulcyi* is shorter, the ribbing in *M. noetlingi* is more pronounced, and the stair-like whorl shape from the fifth whorl onwards distinguishes *M. blanckenhorni* and *M. orientalis*.

Melanopsis noetlingi BOURGUIGNAT, 1886

(figs. 105, 106)

Description: According to BLANCKENHORN & OPPENHEIM (1927) this species from its original locality in fluvial sands below the Yarmouk basalt has an about 25 mm high shell that is 10 mm wide and an aperture that is less than half shell height. The spire is conical and with pronounced suture, but not stair-

like. There are about 14 ribs on the last whorl, and these are about as wide as the interspaces, they are a little widened near the suture, and they continue onto the base. This species has been recognized with several typical individuals from two distinct localities from fluvial sands of the cliff next to the road on the Jordan, one west of Abu Habil and the other west of Deir Alla. Both locations are in their position well below the Lisan marls.

Differences: The fossil *M. noetlingi* differs from the recent *M. costata* by an ornament of more narrow and pronounced axial ribs. The also fossil *M. orientalis* and *M. blanckenhorni* have a stair-like instead of a conical spire.

Remarks: PICARD (1934) noted that his *M. obediensis* had more curving ribs than *M. noetlingi* (and his *M. costata* which here is considered to represent *M. blanckenhorni*). *M. noetlingi* is a species of the *M. costata* group with strong ribs and weakly rounded whorl sides. PICARD (1934) also noted close similarity with *M. biliotti* from the Pliocene of Rhodes as described by BUKOWSKI (1893, Pl.3, Fig.15, Pl.4, Figs.1-4).

Melanopsis blanckenhorni SCHÜTT, 1988

(figs. 97 - 103)

Description: According to SCHÜTT (1988b, Pl.3, Figs.18-20) the shell is ornamented by about 12 strong ribs, is of more or less slender shape and has a staircase-like spire. Strong ribs that continue from suture to base distinguish this species that is found in Jordan only as fossil. BLANCKENHORN (1897, Pl.10, Figs.9,10) called such forms *M. costata*. The type locality is from the banks of the middle Orontes in Syria (SCHÜTT 1988b).

Differences: *M. blanckenhorni* resembles *M. orientalis* that is found in the oldest fauna with *Melanopsis* in Jordan from the Ghor canal (chapter III.e.2.). It is common in all limnic and fluvial faunas collected from sands older than the base of the Lisan marls and from the beds of the upper Jordan Valley which are basically not inclined. PICARD (1934) included such forms in *M. noetlingi*. It differs from modern forms with straight ribs, similarly as is shown by HELLER et al. (1999 Fig.4B) in *M. costata* by having a distinctly stair-like spire. *M. orientalis* is very similar, but has a more stout and cylindrical body whorl and an even more angular stair-like spire. *M. turiformis* PICARD, 1934 from Ubeidiya could be included in the *M. multiformis* complex of BLANCKENHORN (1897) and differs by having a more slender shell, more ribs in each whorl and a less stair-like spire.

Fig. 97. *Melanopsis blanckenhorni* SCHÜTT, 1988 with 19 mm high shell from the Pleistocene fluvial sands and gravel of the Jordan cliff well below Lisan marls to the west of Abu Habil next to the Jordan river road.

Fig. 98. *Melanopsis blanckenhorni* with 20 mm high shell from the Pleistocene river sands of the Jordan River cliff SW of Mashara, Jordan.

Fig. 99. *Melanopsis blanckenhorni* with 14 mm high shell from the same sands as fig. 98, well below the Lisan marls.

Fig. 100. *Melanopsis blanckenhorni* with 24 mm high shell from the same locality as in fig. 97.

Fig. 101. *Melanopsis blanckenhorni* of the same individual as in fig. 100 seen from behind.

Fig. 102. *Melanopsis blanckenhorni* of the same individual as in fig. 97 seen from the back.

Fig. 103. *Melanopsis blanckenhorni* SCHÜTT, 1988 with 28 mm high shell from the Pleistocene of the same locality as in fig. 97.

Fig. 104. *Melanopsis orientalis* BUKOWSKI, 1895 with 29 mm high shell from the late Pliocene lake deposits exposed next to the Ghor Canal just west of Abu Habil, Jordan Valley.

Fig. 105. *Melanopsis noetlingi* BOURGUIGNAT, 1886 from Pleistocene fluvial sands well below the Lisan marls of the cliff next to the road on the Jordan, one west of Abu Habil. The shell is 22 mm high.

Fig. 106. *Melanopsis noetlingi* BOURGUIGNAT, 1886 of the same individual as in fig. 105 seen from behind.

Fig. 107. *Melanopsis orientalis* of the same locality as in fig. 104 with 26 mm high shell.

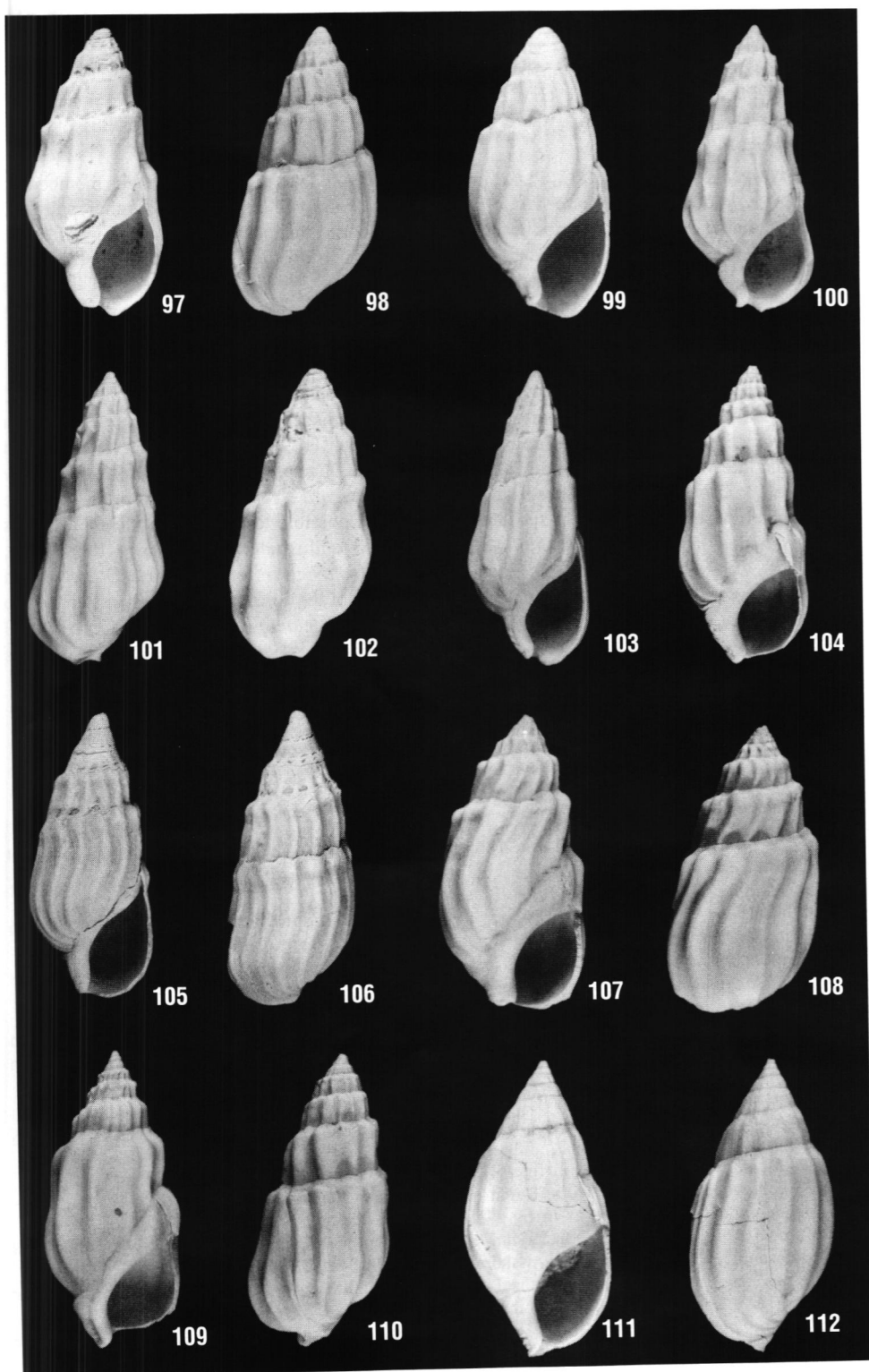
Fig. 108. *Melanopsis orientalis* of the same individual as in fig. 107 seen from behind.

Fig. 109. *Melanopsis orientalis* of the same locality as in fig. 104 with 29 mm high shell.

Fig. 110. *Melanopsis orientalis* of the same individual as in fig. 104 seen from behind.

Fig. 111. *Melanopsis vandeveldi* BUKOWSKI, 1895 from the late Pliocene deposits next to the Ghor Canal just west of Abu Habil, Jordan Valley. The shell is 24 mm high.

Fig. 112. *Melanopsis vandeveldi* with the same shell as in fig. 111 seen from behind.



Remarks: Species from the others of the *M. costata* group still living in Jordan have no stair-like spire. There is little difference to *M. multiformis* BLANCKENHORN, 1897 from the Pliocene of the mid Orontes area regarding shell shape. Also *Melanopsis obediensis* PICARD, 1934 from the Pleistocene deposits of Obedieh (Ubeidiya), just SW of Lake Tiberias, is similar (PICARD 1934, Pl.7, Figs.30-44). But its ribs are more curving and there is a median lobe in the outer lip which is absent in *M. blanckenhorni*.

BUKOWSKI (1893, Pl.3, Fig.15, Pl.4, Figs.1-4) noted from lake deposits of Rhodos members of the *M. costata* group which he named *M. orientalis* for elongate shells with stair-like short spire, *M. biliottii* for similar ones but noded ribs near the peripheral corner and posteriorly concave whorl sides. A pair of ribbed *M. costata* from lake deposits of Rhodos with more fusiform shell shape were named by BUKOWSKI (1893) as *M. vandevelde* (slender variety) and *M. phanesina* with shorter shell. These are similar to the *M. blanckenhorni* of the Jordan valley. The forms of the *M. costata* group in Rhodos described by BUKOWSKI occurred in populations that contained no smooth shelled *Melanopsis* species, unlike the Pleistocene populations in Jordan where there is always also *M. buccinoidea* to be found.

PAPP (1953a, Pl.23, Figs.1-8) described a very similar species from the Pliocene of Greece as *M. costatiformis*, which would include morphologies as distinguished in the four species of BUKOWSKI (1893). Even though PAPP (1953a) noted, as had BUKOWSKI (1893) that *Melanopsis* formed and ornamented like *M. costatiformis* was widely present in the Pliocene of SE Europe and also closely related to *M. coatica* of Croatia (BRUSINA 1874) and *M. clavigera* NEUMAYR, 1875 from Slavonia, he distinguished these as independent species. It is also not possible to distinguish the shell of this species from that of *Melanopsis orientalis* BUKOWSKI, 1893 as illustrated by WILLMANN (1981, Pl.10, Figs.18-20). OPPENHEIM (1891b, Pl.26, Fig.4) illustrated *M. clavigera* from Megara in Greece which also closely resembles *M. blanckenhorni* in the Pleistocene of the Jordan river deposits. This is also the case with *M. inexpectata* WILLMANN, 1981 from Rhodos and *Melanopsis heldreichi* NEUMAYR, 1880 or *M. gorceixi reducta* WILLMANN, 1981 both from Kos (WILLMANN 1981, Pl.9, Figs.17-20, Pl.10, Figs.12-17).

Fig. 113. *Melanopsis ammonis* TRISTRAM, 1865 with 17 mm high shell from the Wadi Mujib near its mouth into the Dead Sea.

Fig. 114. *Melanopsis ammonis* as in fig. 113 seen from behind.

Fig. 115. *Melanopsis ammonis* with 17 mm high shell from a spring in Hashemiye in the Ajlun, northern Jordan. The individuals shown in figs. 116 and 117 are from the same locality.

Fig. 116. *Melanopsis ammonis* as in fig. 115 seen from behind.

Fig. 117. *Melanopsis ammonis* with 15 mm high shell.

Fig. 118. *Melanopsis ammonis* with 16 mm high shell from Wadi Mujib as in fig. 113.

Fig. 119. *Melanopsis sharhabili* n. sp. from the spring and creek next to the Wadi Raiyan Plantation in the Jordan Valley near the town of Wadi Raiyan and close to the mosque of the grave of Sharhabil Ibn Hassana. The shell is 14 mm high.

Fig. 120. *Melanopsis sharhabili* as in fig. 119 seen from behind.

Fig. 121. *Melanopsis sharhabili* n. sp. with 16 mm high shell from the same locality as fig. 119, represents the holotype.

Fig. 122. *Melanopsis sharhabili* as in fig. 121 seen from behind.

Fig. 123. *Melanopsis sharhabili* with 18 mm high shell from the same locality as fig. 119.

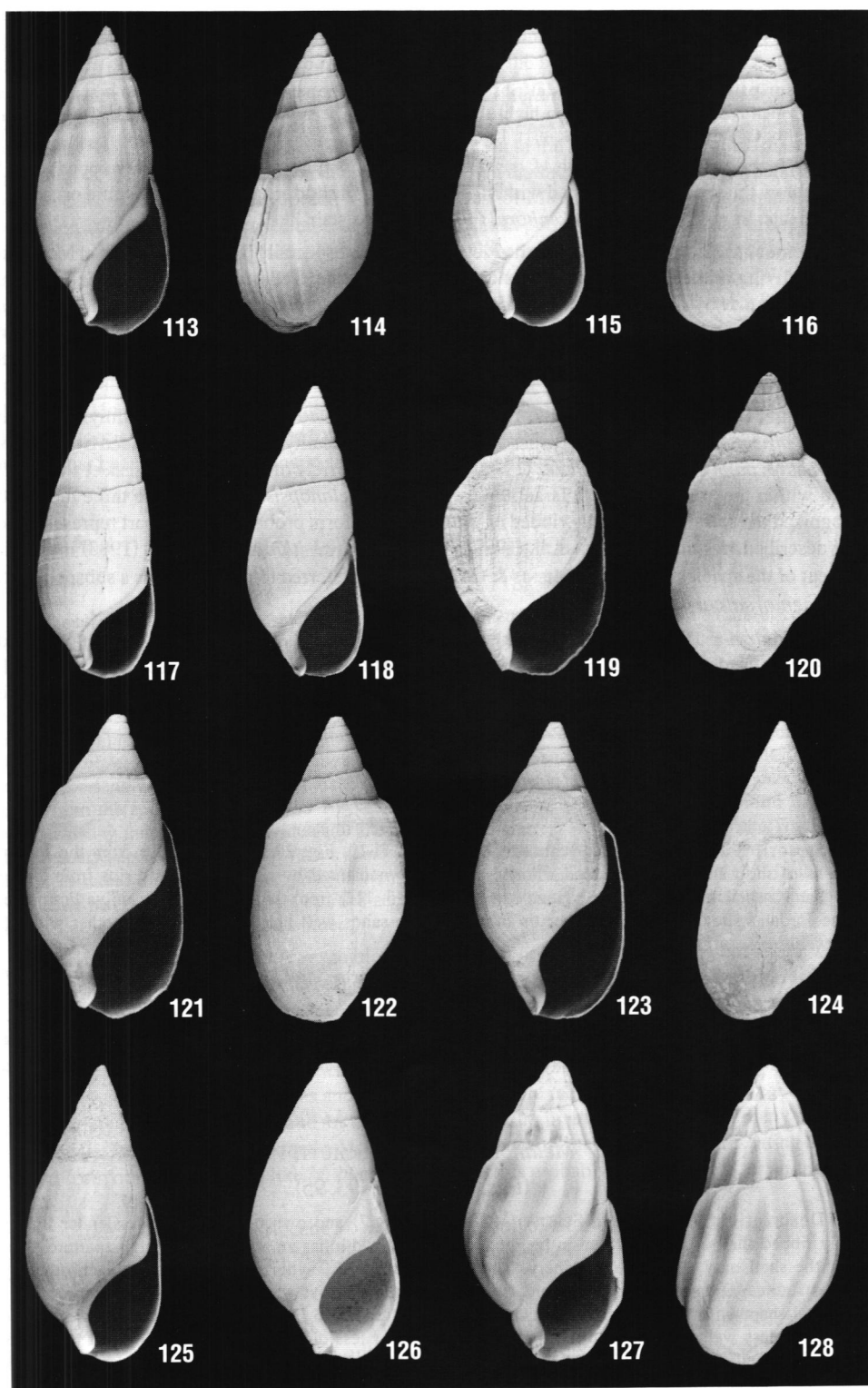
Fig. 124. *Melanopsis buccinoidea* as in fig. 125 seen from behind.

Fig. 125. *Melanopsis buccinoidea* with 19 mm high shell from the thermal spring in the Wadi Mukheiris east of Möwenpick Hotel at the northern shore of the Dead Sea, Jordan.

Fig. 126. *Melanopsis buccinoidea* from the Pleistocene fluvial sands and gravel of the Jordan river cliff west of Abu Habil. The shell is 24 mm high.

Fig. 127. *Melanopsis jordanica* (ROTH, 1839) with 20 mm high shell from the Pleistocene fluvial sands and gravels of the Jordan River cliff SW of Mashara, Jordan.

Fig. 128. *Melanopsis jordanica* of the same as in fig. 127, seen from the back.



modern *M. tingitana* but has some peculiarities, so it is called here according to a fossil species from Greece which is closer in shape, *M. vandevelde*. Both of these have disappeared in the general area during the Pleistocene but survived in the western Mediterranean realm. The third is just like *M. buccinoidea*, and the fourth resembles *M. blanckenhorni* as found in the Pleistocene of the Region, but is closer to *M. orientalis* from the Pliocene of Greece. This mix resembles, but is not identical to the case described by BLANCKENHORN (1897) from fossil lake deposits in the central Orontes valley that according to BLANCKENHORN is of Pleistocene age and according to SCHÜTT (1988b) is of late Pliocene age.

BLANCKENHORN (1897, Pl.9) reconstructed two assemblages that can be recognized in his populations from the Orontes. In the older of these a smooth species of the *M. dufouri* type was called *M. vincta* BLANCKENHORN, 1897 with keeled ornament. *M. vincta* can not be distinguished from a slender individual of a modern *M. dufouri* as live now in Morocco (PERES 1939). This smooth species in the Syrian lake lived together with a *Melanopsis multiformis* BLANCKENHORN, 1897, which represent a mixture of forms as in *M. costata* with strong simple ribs, *M. saulcyi* with subsutural spiral rib, and a species with more stair-like spire that was later named *M. blanckenhorni* by SCHÜTT (1988b). While the ribbed *M. multiformis* and *M. blanckenhorni*, a smooth *M. buccinoidea* and the keeled *M. dufouri* *vincta* in a lower layer of the lake deposits have been noted to occur without transitions into each other, in a layer above they mix. This probably represents a hybridisation that results in *M. bicincta* BLANCKENHORN, 1897, *M. unicincta* BLANCKENHORN, 1897 and *M. binodosa* BLANCKENHORN, 1897 with more or less strongly developed nodes and keels.

Melanopsis bicincta as illustrated by BLANCKENHORN (1897, Pl.9, Figs.37-40) resembles modern *M. tricarinata* as illustrated by AZPÉTTIA MOROS (1929, Pl.10, Figs.226-235), MADURGA MARCO (1973), PUJANTE et al. (1990, Fig.2). *Melanopsis binodosa* as figured by BLANCKENHORN (1897, Pl.9, Figs.20-34) has similar spiral keels but these are tuberculated. There is no modern counterpart to this morph which apparently resulted from hybridization between *M. dufouri*

Fig. 129. *Melanopsis aegaea* TOURNOUER, 1875 with 25 mm high shell from the Early Pliocene Kos Formation, Island of Kos. Slender form.

Fig. 130: *Melanopsis aegaea* of the same individual as in fig. 129 seen from behind.

Fig. 131. *Melanopsis aegaea* with 21 mm high shell from the same locality as in fig. 129. Broad form.

Fig. 132. *Melanopsis aegaea* of the same individual as in fig. 131 seen from behind.

Fig. 133. *Melanopsis buccinoidea* from the late Pliocene deposits next to the Ghor Canal just west of Abu Habil, Jordan valley. The shell is 25 mm high.

Fig. 134. *Melanopsis buccinoidea* of the same individual as in fig. 133 seen from behind.

Fig. 135. Hybrid between *Melanopsis buccinoidea* and *M. dufouri* from the late Pliocene deposits next to the Ghor Canal just west of Abu Habil, Jordan Valley. The shell is 20 mm high.

Fig. 136. Hybrid between *Melanopsis buccinoidea* and *M. dufouri* with 20 mm high shell from the same locality as in fig. 135.

Fig. 137. Hybrid between *Melanopsis buccinoidea* and *M. dufouri* with 19 mm high shell from the same locality as in fig. 135.

Fig. 138. Hybrid between *Melanopsis buccinoidea* and *M. dufouri* of the same individual as in fig. 137 seen from behind.

Fig. 139. *Melanopsis dufouri* FERUSSAC, 1823 with 17 mm high shell from the late Pliocene deposits next to the Ghor Canal just west of Abu Habil, Jordan Valley.

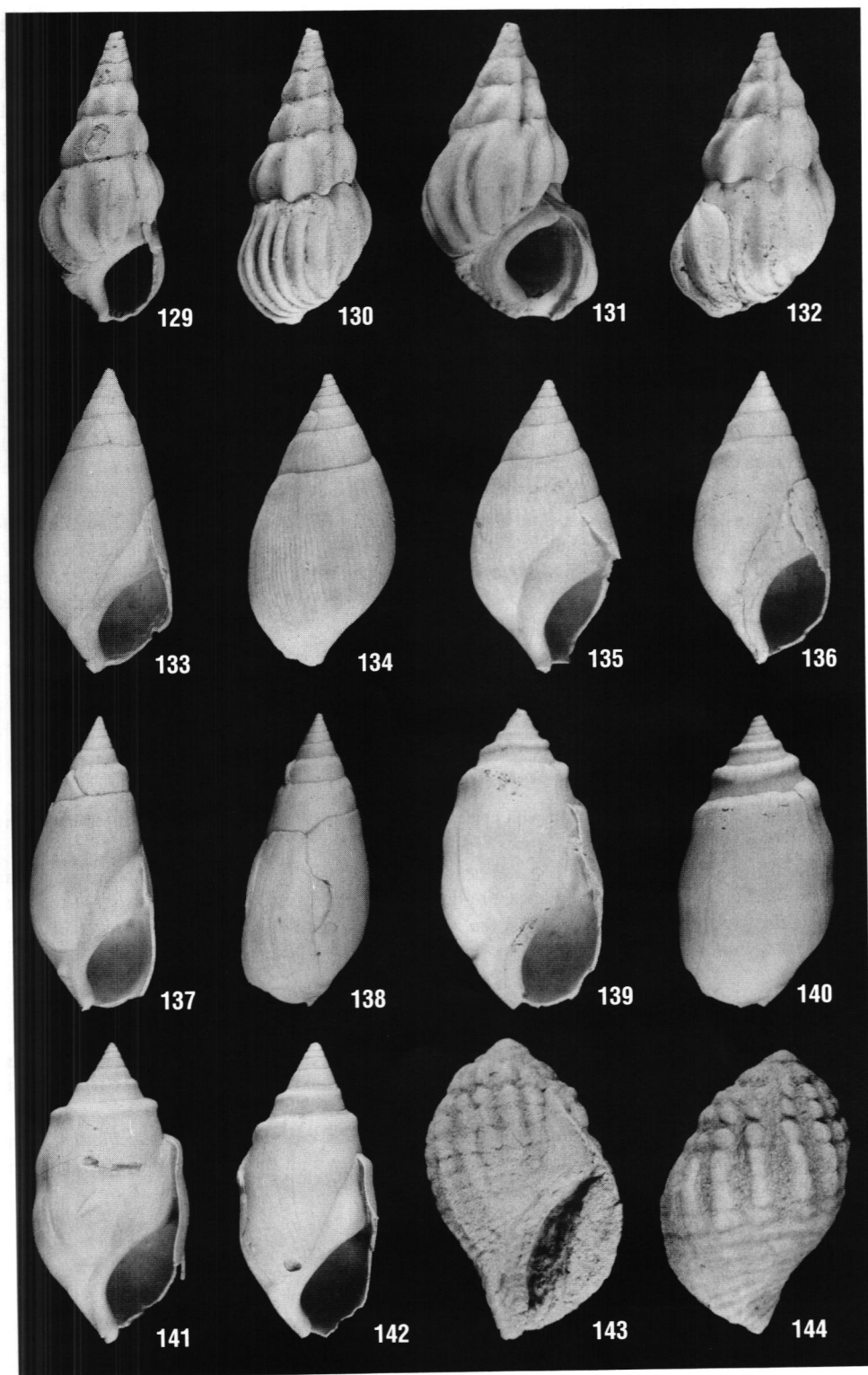
Fig. 140. *Melanopsis dufouri* of the same individual as in fig. 139 seen from behind.

Fig. 141. *Melanopsis dufouri* with 15 mm high shell from the same locality as in fig. 139.

Fig. 142. *Melanopsis dufouri* with 15 mm high shell from the same locality as in fig. 139.

Fig. 143. *Melanopsis trempensis* n. sp. from the Pumanous slump exposed near Torallola in the Tremp Basin in northern Spain within Campanian Valcarga Formation. The holotype is 11 mm high.

Fig. 144. *Melanopsis trempensis* of the same individual as in fig. 143 seen from behind.



vincta and *Melanopsis costata/multiformis*. But very similar shells to *M. binodosa* from the Orontes locality were described by PAPP (1953b, Pl.23) from the Pliocene of Greece as *M. scalaritesta* and *M. macrosculpturata*. In this fauna from Elis in the Peloponnese there is a *Melanopsis narzolina* that resembles *M. dufouri*, and a *M. costatiformis* PAPP, 1953 that resembles *M. blanckenhorni/M. orientalis*. These when hybridising would have come to the same result in a lake in Greece as they did in another lake in Syria at about the same time. PAPP (1953b) regarded the morphological transition in the tradition of FUCHS (1872) as a chaotic polymorphism, but suggested that it could be useful to stratigraphy.

Melanopsis dufouri (= *M. hammamensis* GASSIES, 1901)

(figs. 139 - 142)

Description: The cylindrical shell has a stair-like spire. Whorl sides are smooth or slightly concave or convex with two low ridges and grooves. The shoulder, thus, is accompanied by a rounded ridge, a slightly concave area follows succeeded by a swelling that forms the greatest shell width, a further shallow groove and a swelling that forms the rounded transition to the base. The shell with 15 mm in height and 8 mm in width consists of between 8 and 9 whorls of which the first 5 are conical with flattened sides and the sixth develops a shoulder. A more slender shell with 17 mm in height measures only 7 mm in width. The aperture has a curving inner lip with concave frontal portion and a thick callus pad in its posterior part.

Differences: The spire is a little shorter than that of *M. stricturata* from the Pannonian of Soceni (JEKELIUS 1944), and the shell is a little more stout and cylindrical than most of the *M. dufouri* illustrated by PERES (1939) living in Morocco. *M. tricarinata* from Spain is more slender, and the three spiral elements are more pronounced (AZPEITIA MOROS 1929, Pl.10,11). *M. delessei* from the Pliocene of Kos is identical (WILLMANN 1981, Pl.8, Figs.19-21).

Remarks: *M. dufouri* from Jordan probably formed hybrids with *M. buccinoidea* and with *M. orientalis* with which it lived together in the same lake.

Melanopsis buccinoidea

(figs. 133 - 136)

Description: The fusiform shell with conical spire consists of about 10 whorls when 25 mm high and 11 mm wide.

Remarks: Hybridisation with *M. dufouri* can be observed (figs. 137, 138) and may result in a fine axial liration as is also observed in case of the Spanish Late Messinian *M. impressa* (see chapter III.b.). It also produced a small recess near the suture in other individuals.

Melanopsis vandevelde BUKOWSKI, 1895

(figs. 111 - 112)

Description: According to BUKOWSKI (1895, Pl.4, figs.5-11) the shell is fusiform and consists of at least eight whorls. These form a conical spire with distinct sutures but not stair-like spire. The type is from Pliocene deposits of Rhodos.

Remarks: This species can well represent a hybrid of *M. orientalis* and *M. buccinoidea* with ribs but without the stair-like spire. There is some similarity with the modern *M. tingitana* from Morocco.

Melanopsis orientalis BUKOWSKI, 1895

(figs. 104, 107 - 110)

Description: According to BUKOWSKI (1895) the early whorls of the shell are smooth and of conical shape before an angular shoulder is developed that features at least the three last whorls. Ornament is by 11-13 axial ribs on each of the last whorls. The inner lip of the aperture is curving and bears a thickened

posterior callus pad. The Jordanian form is with 27 mm in height and 12 mm in width composed of about 10 whorls of which only the first three are smooth. The number of ribs in the fifth whorl is about the same as in the last whorl.

The type is from lacustrine deposits of the Pliocene of Rhodes.

Differences: *M. orientalis* from the Pliocene of the Ghor Canal at Abu Habil is very close to *M. blanckenhorni* that occurs in later fluviatile sands of the Pleistocene Jordan before Lisan time. In difference *M. orientalis* has a stronger stair-like appearance of the spire and a more cylindrical body whorl. The hybridization with *M. buccinoidea* led to rounded types which resemble *M. vandevelde*.

III.e.3. Western relation to the *M. costata* group

(figs. 146 - 148, 149 - 150)

In the southern Spanish region and the North African zone of Algeria and Morocco several species of forms of the *M. costata* group have been recognized as fossils and are still living. A *Melanopsis costata* FÉRUSAC, 1823 was determined by ROYO GOMEZ (1922, Fig.27) from the Pontian of Valencia as a 14 mm high shell with 9-10 whorls having 14-18 axial ribs on the last whorl. These ribs are straight, more or less continuous onto the base and have a row of tubercles on their subsutural portion accompanied by a furrow. This species resembles some forms still living in the modern fauna of Jordan and here described as *M. saulcyi*. PERES (1945) included in the *M. costata* group a *Melanopsis costellata* FÉRUSAC, 1823. According to the original description FÉRUSAC (1823) determined such a fusiform shell with relatively short spire and relatively large last whorl that is ornamented by axial ribs that end in a spiral row of tubercles near the posterior shoulder of each whorl. PERES (1945, Fig.5) noted that the relative size difference of spire and last whorl resulted in the creation of numerous species, among which *M. sevilensis* GRATELOUP, 1840 with intermediate spire length and *M. cariosa* with large spire also live in Spain. The Spanish species *Melanopsis penchinati* BOURGUIGNAT, 1868 has a shell shape like that of *Melanopsis praemorsa* but is axially ornamented and it resembles *M. sevilensis* which is less slender (PUJANTE et al. 1988b). According to these authors *M. penchinati* has quite a number of different shapes in the warm springs of Alhama de Aragon, which had been given different names by AZPEITIA MOROS (1929, Pl.3). The up to 16 mm high and 7 mm wide shell is sculptured by rounded axial ribs.

M. sevilensis of Spain (Figs. 149, 150) is the same or quite similar to *Melanopsis tingitana* MORELET, 1864 (Figs. 146-148) of the Maghreb by having a slender conical shell with flattened whorl sides and aperture less than half of total shell height with ornament of axial ribs (PERES 1939), but which just below the suture may also be noded (AZPEITIA MOROS 1929, Pl.6, Figs.141-150). A well ribbed form was described from the Pleistocene of Spain by MADURGA MARCO (1973, Pl.1, Figs.3,4) as *M. costata*, but it has the characteristically short spire of the Spanish and Moroccan forms and can be placed better with *Melanopsis tingitana* as known from northern Africa. It is quite similar in shape to the Spanish *Melanopsis turrita* ROSSMÄSSLER, 1880 which appears to be less strongly ribbed. But this form from thermal springs in SE Spain may represent a hybrid with the smooth *M. praemorsa*.

The forms around *Melanopsis cariosa* (LINNE, 1767) have the shell flattened to even slightly concave on the whorl sides and an ornament of axial ribs. Below the suture there is a depression and a narrow shoulder (AZPEITIA MOROS 1929, Pl.12 with variations). Without the axial ribs it is *Melanopsis dufouri*, studied in detail by PUJANTE et al. (1988a). A similar form, that would be determined as *M. sevilensis* by PUJANTE & GALLARDO (1990, Fig.3) has lived and multiplied in the aquarium in Hamburg for 6 years (originally collected by M.

GLAUBRECHT in eastern Andalusia) (figs. 149, 150). Here the early ontogenetic shell up to the fifth whorl has a regular increase in shell width and no ornament with exception of growth lines. Sutures are quite well developed, and whorls are rounded. Just anterior of the suture there is a groove that begins on the third whorl and on the fourth whorl develops into a flattened depression, which is present on all further whorls. With the fifth whorl diameter of the shell increases more rapidly and axial collabral folds develop. Also clearly visible are fine spiral lirae on the whorls surface. The aperture in small individuals of three or four whorls demonstrated a small rudimentary callus pad, which in the fifth whorl becomes a thickened posterior callus pad as is characteristic to the species. The size of the aperture in relation of the shell increases in such a way that in the adult it composes up almost two thirds of total shell height. In this last whorl there are about 15 collabral and rounded ribs that extend from the suture to the columella not ending on the base until they reach the callus of the inner lip. The aperture is drop shaped with an evenly rounded posterior callus pad of the inner lip that forms a posterior slit with the outer lip. Above the callus the outer lip is straight or even weakly concave and anterior of this zone it is evenly rounded. Interestingly with the fourth or fifth whorl a colour pattern develops that consists of axial brown ribbons which later become irregular by brown spiral bands that can be added and by a general black colour of the last whorl in other individuals. Very similar shells to *M. sevilensis* are found in species of *Melanopsis ovula* BOURGUIGNAT, 1884, *Melanopsis pleuroplagia* BOURGUIGNAT, 1884, *Melanopsis harpa* (WESTERLUND, 1882), and *Melanopsis huidobroi* AZPEITIA, 1929. The group around *Melanopsis costellata* FERUSSAC; 1823 has more ribs on each whorl (AZPEITIA MOROS 1929, Pl.12, Figs.278-282), but this was not seen as species difference by PERES (1945). *Melanopsis sevilensis* (probably = *M. cariosa*) was observed by PUJANTE & GALLARDO (1990) to represent one of the two species of *Melanopsis* that live in Andalusia usually in separated populations. The other is *M. dufouri* with spiral ribs and no axial ones.

III.e.4. *Melanopsis trempensis* from the Campanian of northern Spain

Melanopsis trempensis n. sp.

(figs. 143 - 145)

Diagnosis: The stubby shell with short spire and last whorl encompassing much of the former whorls is ornamented by axial and spiral ribs forming a cancellate pattern. The aperture has an inner lip callus that forms a thick posterior callus pad.

Holotype: The specimen illustrated on figs. 43 - 44 represents the holotype; Coll. Geological-Palaeontological Institute and Museum University of Hamburg no. 4270; five further specimens have been studied..

Description: The shell is a little less than double as high as wide and consists of more than five whorls. These cover each other to a large extent so that the spire is short. This spire is worn, so that the exact number of whorls can not be recognized. The shape of the shell is drop-like with well rounded base. The aperture is ovoid in shape extending into a short anterior siphonal notch. A narrow posterior furrow between the massive callus pad is developed high up on the inner lip callus and between it on the outer lip, which is not thickened. The body whorl is ornamented with about 15 rounded spiral ribs separated from each other by incised narrow grooves. These spiral elements are crossed by about 13 axial ribs on the last whorl. These are rounded, separated from each other by grooves and become weaker on the base. Only one row of spirally arranged nodes remains uncovered by the succeeding whorl. The fully grown shell appears to be about 14 mm high and almost 8 mm wide. The spire is corroded but probably was not higher than 5 mm.

Differences: The short and rounded *Melanopsis trempensis* differs from all known other Cretaceous members of the genus *Melanopsis* by its reticulate ornament of axial ribs and spiral furrows. The axially ribbed species of later times are usually more slender in shape and spiral ornament

is much more delicate or restricted to the posterior whorl. *Melanopsis* with smooth shell that lived at the same time and location are short and fusiform, but are clearly distinguished by having no trace of axial ornament. They resemble *M. pauli* BANDEL & RIEDEL, 1994 from the Cretaceous of Hungary (BANDEL & RIEDEL 1994, Pl. 12, Figs. 2, 3).

Derival of name and locus typicus: *M. trempensis* is from the Tremp basin in the southern Pyrenees and called according to the town of Tremp. It comes from the Pumanous slump exposed near Torallola within Valcarga Formation which washed shallow water gastropods from the shore and near it into the basin during Campanian time (ROSSELL SANUY et al. 1972).

III.e.5. Only *M. oxyacantha* belongs to the *M. costata* group in the Pannon Lake

Melanopsis oxyacantha BRUSINA, 1902

(figs. 151 - 158)

Description: The shell is axially ribbed with ornament inserting in the fifth whorl. Whorls are shouldered and convex and the inner lip of the aperture has no posterior callus pad and the posterior narrow notch is very short. The fully grown shell consists of about 10 whorls, 5 of which bear about 10 axial ribs each. These may alternate somewhat in their position in consecutive whorls. The shell is about 18 mm high and 7 mm wide with the aperture being 6,5 mm high. The protoconch consists of about two whorls with pointed cup-like initial portion of about 0,15 mm in width. The embryonic shell measures approx. 0,25 mm with about 1,5 whorls in diameter of the first whorl and is set off from the juvenile shell by the insertion of growth lines. It grades indistinctly into the first whorls of the teleoconch. Only in the fifth whorl about 8 axial ribs appear. In the sixth whorl they have increased to about 10 and this number remains stable in the following four whorls. These ribs end on the shoulder before they reach the suture in posterior direction. Ribs end on the rounded base following the pattern of the apertural outline here and curve towards the columella. But this anterior sinus in each rib is covered by the succeeding whorl. Ribs are highest at their posterior end and here they commonly form a tubercle. Rather indistinct spiral liration is present, but on some specimen it is more expressed and results in an undulating surface of the ribs. Mostly ribs are straight but in some individuals may also be bend regularly or irregularly forwards. The outer lip of the aperture is slightly angulated at the shoulder. The inner lip is evenly callus covered and forms a short narrow posterior notch with the outer lip. The columella is a little folded near the anterior short siphonal notch. Where there are colour patterns preserved they show irregular brown spiral lines and spiral dots.

Differences: In general shell shape and number of whorls *M. oxyacantha* resembles *M. barthai*, but is distinguished from it by the ornament of ribs and by a more regular increase in shell diameter. In its transition of the protoconch into the smooth early ontogenetic shell *M. oxyacantha* resembles *M. bouei*, *M. barthai*, *M. papkesiensis*, but differs from the later by having more whorls, a pattern of ribs throughout the last 5 whorls, continuous diameter increase of the whorls, and no callus pad in the aperture. This absence of a callus pad on the inner lip distinguishes *M. oxyacantha* from most of the other members of the *M. costata*-group. From *M. tihanyensis* the transition of protoconch into teleoconch clearly distinguishes and the absence of a keel. *Melanopsis austriaca* is close in shape and ornament, but has a more conical shell shape since its whorls are more flattened and less shouldered (JEKELIUS 1944, Pl. 49, Figs. 1-4).

Remarks: From the Pannonian of the Vienna Basin PAPP (1953a) distinguished a *Melanopsis brusinai* group with *Melanopsis austriaca* HANDMANN, 1882 and *Melanopsis scalariformis* PAPP, 1953. *M. austriaca* actually resembles *M. oxyacantha* but has better developed spiral elements in its ornament, is of more conical shape and less slender (LÖRENTHEY 1902, Pl. 18, Fig. 1). *M. austriaca* with about 10 mm high shell occurs in the Pannonian beds at Tinnye, Marksevec, Loebersdorf, and Soceni. *Fagotia (Fagotia) sangarica* SCHÜTT & BILGIN, 1974 from the spring of Sakarya river 160 km WSW of Ankara in Anatolia in all essential features of its shell resembles *M. austriaca* from the Pannonian of Soceni. Typical are the indistinct sutures in the conical shell, straight axial ribs that form nodes with the rounded spiral ribbon present just anterior of the suture (compare SCHÜTT & BILGIN 1974, Fig. 4 and JEKELIUS 1944, Pl. 49, Figs. 1-4). While the fossil shells represent juvenile individuals with the early whorls well preserved, the shell of the living species is corroded apically with only the last three whorls well preserved. SCHÜTT & BILGIN (1974) interpreted this recent *Melanopsis austriaca* to be

closely related to *Fagotia* (= *Esperiana*) because of anatomical similarities with *Esperiana esperi* and *E. acicularis*, without stating what these similarities may actually be.

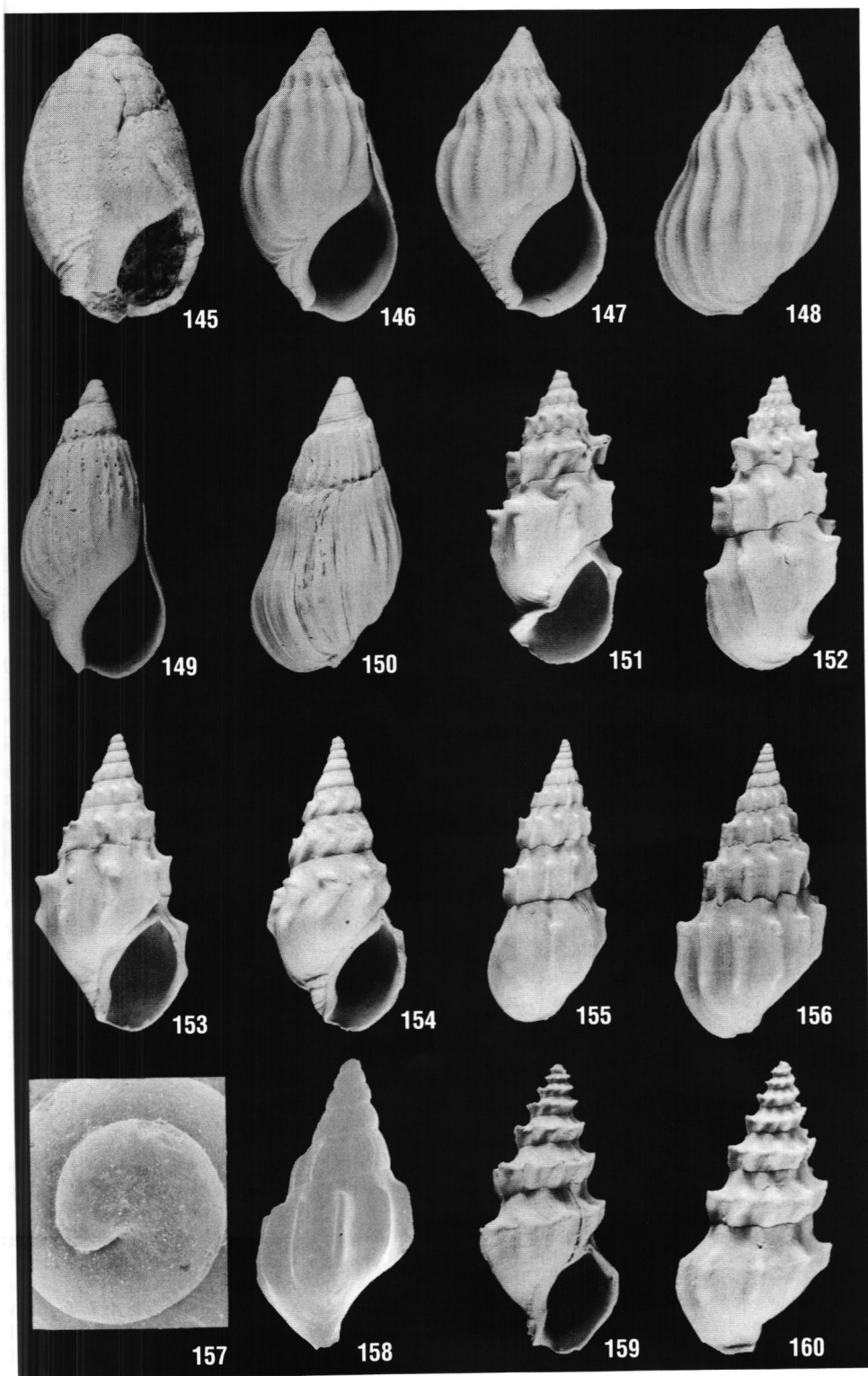
III.e.6. Remarks to the *Melanopsis costata* group

Melanopsis trempensis from the Campanian of northern Spain demonstrates that axially ribbed species have been present among early species of the *Melanopsis* relation. Even though *M. trempensis* is not a close relative to *M. costata*, it demonstrates that ribbed species did not only develop during the late Miocene as was assumed by WILLMANN (1981) on material from Greece and repeated by GLAUBRECHT (1993, 1996, 2000), even though WENZ (1938) noted their occurrence since the Paleocene.

The Pontian *Melanopsis oxyacantha* is more slender and has less flattened whorls than *Melanopsis austriaca*, but otherwise both appear to be related to each other. Amazingly *M. austriaca* survived in *Esperiana sangarica* in NW Anatolia under that name. *M. oxyacantha* obviously formed hybrids with members of the *M. bouei* group with *M. barthai* and *M. papkesiensis* representing such species that could have evolved during this process. Perhaps hybrids with larger *Melanopsis* species, like those of the *M. impressa* group, changed the relatively small *M. oxyacantha/austriaca* (shell height usually below 20 mm) into larger forms (shell height commonly above 20 mm) as present with *M. orientalis* in the late Neogene (BUKOWSKI 1893, 1895). But such a transition has not been documented up to date, or not been recognized.

Melanopsis orientalis BUKOWSKI, 1893 from Rhodos (BUKOWSKI 1893, Pl.3, Figs.5-14, WILLMANN 1981, Pl.10, Figs 18-20) resembles in shape and ornament *Melanopsis costata* from the Jordan (HELLER et al.1999, Fig.4 B,C). If one disregards the theory that similar looking *M. costata* group members from Croatia, Slavonia, Greece, Rhodos and Kos because of geographical distance and phylogenetic hypothesis should not be placed in the same closely related species or species group (as phrased by BUKOWSKI 1893 and later again by WILLMANN 1981) it is quite evident, that members of the *M. costata*-group lived from Spain to the lakes of the Paratethys and from there to the Aegean area during the Pliocene.

-
- Fig. 145. *Melanopsis trempensis* n. sp. from the same locality as in fig. 143, with shell height of 14 mm.
Fig. 146. *Melanopsis tingitana* MORETLET, 1864 from Paradise valley Morocco with 17 mm high shell.
Fig. 147. *Melanopsis tingitana* from Morocco with 16 mm high shell, creek in Paradise Valley.
Fig. 148. *Melanopsis tingitana* of the same individual as in fig. 147 seen from behind.
Fig. 149. *Melanopsis sevillensis* GRATELOUP, 1840 from the aquarium population in Hamburg originating from animals that were collected in SE Spain. The shell is 17 mm high.
Fig. 150. *Melanopsis sevillensis* of the same individual as in fig. 149 seen from behind.
Fig. 151. *Melanopsis oxyacantha* BRUSINA, 1902 with 17 mm high shell from the Pontian sands near Papkesi, next to Lake Balaton in Hungary. The specimen illustrated in figs. 152-158 are from the same locality.
Fig. 152. *Melanopsis oxyacantha* of the same individual as in fig. 151 seen from behind.
Fig. 153. *Melanopsis oxyacantha* with 15 mm high shell.
Fig. 154. *Melanopsis oxyacantha* with 16 mm high shell.
Fig. 155. *Melanopsis oxyacantha* with 17 mm high shell.
Fig. 156. *Melanopsis oxyacantha* with 16 mm high shell.
Fig. 157. *Melanopsis oxyacantha* with first whorl of the protoconch measuring 0,25 mm in diameter.
Fig. 158. *Melanopsis oxyacantha* with 5 mm high juvenile shell which for the first four whorls are smooth.
Fig. 159. *Melanopsis tihanyensis* WENZ, 1928 with 12 mm high shell from the Pontian sands near Papkesi, next to Lake Balaton in Hungary. The specimen illustrated in figs. 160- 167 are from the same locality.
Fig. 160. *Melanopsis tihanyensis* of the same individual as in fig. 159 seen from behind.



BUKOWSKI (1893) noted populations that consist purely of members of this *M. costata*-group in the lake deposits of Rhodos, while WILLMANN (1981) had mixed populations with members of the *M. praemorsa* group in the late Miocene and Pliocene of Kos. Among these *Melanopsis inexpectata* WILLMANN, 1981, *M. heldenreichi* NEUMAYR, 1880, *M. broti* NEUMAYR, 1880 could be placed within the *M. multiformis* group recognized by BLANKENHORN (1897) from late Pliocene lake deposits in Syria. But there is also a clear difference of this Kos fauna to that of the *M. costata*-group known from the Orontes/Jordan area noted in *Melanopsis aegaea* TOURNOUER, 1875 which has no counterpart in the east, but in the west with *Melanopsis tingitana* living in Morocco (compare figs. 131, 132 and 146-148).

WILLMANN (1981) preferred because of theoretical reasons to relate all members of the *M. costata*-group from the Neogene of Kos to the one species *Melanopsis gorceixi* TOURNOUER, 1875 regarding them as subspecies, similarly as was done by SCHÜTT (1983, 1988a,b) in regard to the Pleistocene and recent forms of this group from the catchment of the Orontes and Jordan, but he considered them as subspecies to *M. praemorsa*.

III.f. The *Melanopsis fuchsi* - *Esperiana esperi* group

Esperiana acicularis (FERUSSAC, 1823)

(figs. 10 - 12)

Description: The conical slender shell with about 9 whorls measures about 25 mm in height and 8 mm in width with the last whorl about as high as the spire. Sutures are shallow, and the whorl sides are flattened to weakly convex. The ornament consists only of fine collabral growth lines and a very delicate and fine spiral liration and appears smooth. The illustrated shell is from the Danube near Komárom, Hungary.

Remarks: The species *Fagotia* (= *Esperiana*) *esperi* (FERUSSAC, 1923) and *Fagotia* (= *Esperiana*) *acicularis* (= *Melanopsis acicularis* FERUSSAC, 1823 = *Microcolpia* BOURGUIGNAT, 1884) live in the northern Balkan area (Eastern Alps to Black Sea) JAECKEL et al. (1958), and Turkey. SCHÜTT & BILGIN (1974) noted their occurrence from the mouths of the rivers Dnjester, Bug, and Dnjepr, NW Anatolia across the Balkan to Slovenia. There exist transitional forms between *E. esperi* and *M. acicularis* which make a taxonomic evaluation difficult, but may also be the result of hybridisation. LUEGER (1980, Pl.2, Fig.5) described *Fagotia* (= *Esperiana*) *acicularis* from Pannonian river deposits in the Vienna Basin. It is in all details of the shell exactly like the modern forms of this species that live in the Danube about 100 km upstream of Budapest (figs. 10-12). *Esperiana* cf. *acicularis* as described by RUST (1997, Pl.9, Figs.2-4,6) from the Neogene of Greece according to this author is very close in shape to *Esperiana* (= *Microcolpia*) *acicularis* from a warm spring of Vöslau in Austria. But actually the latter is a bit more pupoid in shape (figs. 8, 9) and here placed in *Esperiana esperi*. What has been described as *Esperiana sangarica* (SCHÜTT & BILGIN, 1974) from a spring in NW Anatolia closely resembles *Melanopsis austriaca* HANDMANN, 1882 from the Pannonian of Romania (JEKELIUS 1944, Pl.49, Figs.1-4), which is similar to *Melanopsis oxyacantha* from Papkesi in Hungary (chapter III.e.5.).

Melanopsis fuchsi HANDMANN, 1852

(figs. 168 - 173, 175 - 176)

Description: Characteristic to the species is that the early teleoconch is ornamented by short ribs while later whorls are smooth. Also the colour pattern consists of brown collabral stripes that may be straight or somewhat zigzag patterned.

The slender shell consists of about 10 whorls with the last three ones of smooth evenly convex shape ornamented only by sinuous collabral growth lines. Coloration here is by 15 to 20 brown collabral bands. The smooth protoconch with almost 0.5 mm wide first whorl ends after about 1.5 whorls and is succeeded by two round whorls with only very delicate spiral liration. After these 3 to 4 whorls follow that have an ornament 12-14 short axial ribs best developed in the anterior two thirds of the whorl and connected to a weak angulation near its centre. The second of these ornamented whorls has 10-12 ribs and the third about 10 ribs. Afterwards ribs disappear and the following three whorls are smooth. The shell is

between 10 and 15 mm high when fully grown. A 15 mm high shell measures about 6 mm in width with a 7 mm high aperture. The aperture of the body whorl is thickened in fully grown specimen and there may be a weak posterior callus thickening or just an acute end of the tear like aperture. Anteriorly there is a broad and short siphonal notch.

Differences: The very similar *Melanopsis eulimopsis* has a colour pattern of dots and not of radial stripes, the early teleoconch is smooth and not ornamented by short ribs as in *M. fuchsi*, and the shell is usually shorter with less whorls. Also the callus of the inner lip is more simple in *M. fuchsi*. A similar ornament present on juvenile shells was documented by PAVLOVIC (1928, Pl.7, Figs.9,10) on shells named *Melanopsis (Melanosteira) striatula* PAVLOVIC, 1928 from the vicinity of Beograd (Karagac). But this species is based only on juvenile shells. In contrast to *Melanopsis oxyacantha* the juvenile ornament does not continue onto the last three whorls. In *M. tihanyensis* the ornament inserts earlier succeeding directly the protoconch. *Melanopsis soceni* JEKELIUS, 1944 is more slender and also has an angulation in the fourth and fifth whorl which disappears in succeeding whorls. But in contrast to *M. fuchsi* the early ornament is only a spiral corner, and not composed of short axial ribs and the shell is more slender (JEKELIUS 1944, Pl.16, Figs.14-17). *Esperiana acicularis* is more slender than *M. fuchsi* and has no ornament on its early whorls and also a relatively smaller aperture.

Remarks: PAPP (1953a, Pl.12, Figs.38-40) included here an indistinctly ribbed form from the Pannonian of the Vienna Basin. It is described as dotted and he compared it with *Esperiana*. The dots indicate a probable relation to the *M. eulimopsis* group rather than to the *M. fuchsi* with axial colour stripes. *Melanopsis entzi* BRUSINA, 1894 as illustrated by PAVLOVIC (1928, Pl.7, Figs.12-15) resembles *M. striatula* PAVLOVIC, 1928 which is based on ornamented early ontogenetic shells (PAVLOVIC 1928, Pl.7, Figs.9-10). These may very well represent *M. fuchsi* from Papkesi. *Melanopsis soceni* from the Sarmatian is more slender but could be related to *M. fuchsi*. JEKELIUS (1944) noted a great similarity that exists when young individuals of *M. impressa* are compared with fully grown ones of *M. soceni*. This similarity is not present in *M. fuchsi* since early ornament here includes axial ribs which are never seen in *M. impressa*, and the last whorls are shorter and more rounded as would be the case in *M. impressa*.

BARTHA (1956) discussed *M. fuchsi* as it occurs in Tab, but he did not describe the ornament or the early whorls of the teleoconch since his specimen were corroded. From Varpalota BARTHA (1955) suggested that *M. fuchsi* and *M. entzi* represent the same species as had also been suspected by PAPP (1953a). BARTHA repeated the original description of HANDMANN (1852) according to which whorls are convex and there is an indistinct ornament of ribs that may be somewhat tuberculated. Only later HANDMANN (1887) illustrated his species, but without mentioning an ornament of the early whorls of the teleoconch but coloration of the shell with orange dots. This indicates that the two similar species *M. eulimopsis* and *M. fuchsi* noted from Varpalota and Papkesi have become mixed up with each other. BARTHA (1956) therefore concluded that *M. fuchsi* represents a late Pannonian *Melanopsis acicularis* variety and that *Fagotia esperi* and *F. acicularis* do not represent independent species but are actually subspecies of *Melanopsis fuchsi* that developed at different time levels, which can not be supported here.

III.f.1. Remarks to the *Esperiana* group

Melanopsis fuchsi resembles *Esperiana* (PAPP 1953a, SCHRETER 1978). It may be that this species is related to ancestors of some modern *Esperiana* (= *Microcolpia*). KROLOPP (1977) suggested such a connection from *M. fuchsi* from the Late Pannonian of the Vienna Basin to both *Fagotia* and *Microcolpia*. On the other hand modern *Esperiana acicularis* lived practically without the slightest difference in the Pannonian Danube, as it lives there now (LUEGER 1980). SCHRETER (1978) had the opinion that BARTHA (1956) had not correctly connected the modern *M. acicularis* and *M. esperi* with the fossil *M. fuchsi*. A species resembling *M. fuchsi* was noted by WILLMANN (1981, Pl.13, Figs. 3-4) in the about 12 mm high smooth shells of *Melanopsis gersondei* WILLMANN, 1981 from the Pliocene of Kos. It also has axial colour bands. RUST (1997) determined from the late Miocene of Tessonike in

Greece *Fagotia* cf. *acicularis*. It has 9 whorls, measures more than 17 mm in height and almost 7 mm in width, is smooth and has a pattern of spirally arranged brown dots. The inner lip of the aperture has no callus pad. This species is a *M. eulimoides*. According to RUST (1997) it is very similar to *Esperiana acicularis* from Bad Vöslau in Austria, but this is not so (compare figs. 8, 9 and 174). BARTHA (1955) called shells with similar shape and brown dots *Melanopsis pygmaea subaudebardi* according to its similarity with *Fagotia audebardi* Prévost from thermal springs in eastern Hungary. All these data indicate that among the modern species of *Esperiana* there are several different lineages, one related to *Esperiana acicularis*, the other to *M. eulimoides*, and perhaps a third one to *M. fuchsi*.

III.g. The *Melanopsis tihanyensis* group

The group around *Melanopsis brusinai* and *M. tihanyensis* is characterized by an early insertion of ornament consisting of spiral keels as well as axial ribs. This ornament remains on the shell, which is usually about 1 cm in height up to the last whorl. The aperture has no posterior callus pad on the inner lip.

Melanopsis tihanyensis WENZ, 1928 (= *M. gradata* FUCHS, 1870) (figs. 159 - 167)

Description: The whorls of the shell have a characteristic keel and in addition an ornament by short axial ribs. This keel begins with the onset of the teleoconch onto the protoconch within the second whorl. The shell consists of 9.5 whorls and is about 13 mm high and 7 mm wide with 7 mm high aperture. BARTHA (1956) found an average height of 11 mm, noted differences in the apical angle to occur among individuals of the same population, and noted that the early teleoconch is ornamented by a keel which on later whorls changes into a row of nodes. Own observations document that the protoconch consists of only 2 rounded whorls which increase only little in width. The embryonic portion without growth lines is rather wide, measuring almost 0.4 mm in diameter. First growth lines insert after three fourth of a whorl and there is one further whorl with simple rounded shape. In the end of the second whorl first ornament inserts with a median keel. In the end of the third whorl short axial ribs with collabral inclination appear forming about 12-14 pointed projections with the keel. The keel in successive whorls remains of about the same size and in the last two whorl delimits their peripheral corner. The tubercles increase in size, but not in number in successive whorls. The aperture has an indistinct posterior and short distinct anterior notch and a simple inner lip which is evenly curving and may be covered by a thick callus, but without the posterior callus pad that is characteristic to most *Melanopsis* species. The outer lip is angulated at the position of the keel and spines. The anterior siphon is short but distinct, while a posterior notch is not developed or rather short and indistinct.

Differences: The rapid appearance of a keel on the early teleoconch along with a very large initial whorl distinguishes *M. tihanyensis* from most of the other species present in the Pontian of the Lake Balaton area, especially from the ornamented and more slender *M. oxyacantha*. *Melanopsis brusinai* LÖRENTHEY, 1902 from Tinnye near Budapest is very similar but differs regarding the median keel and the size of the last whorl, which is larger than the spire. *M. scalariformis* from the Pannonian is as slender as *M. tihanyensis*, but has the keel as ornament up to the last whorl (PAPP 1953a, Pl. 3, Figs. 27, 28). *Melanopsis moesiensis* JEKELIUS, 1944 closely resembles *M. brusinai* and is more slender than *M. tihanyensis*. *Melanopsis banatica* JEKELIUS, 1944 has a later insertion of ornament (within the fourth whorl nodes appear), but otherwise the shell is extremely similar to *M. tihanyensis* (JEKELIUS 1944, Pl. 50, Figs. 3-8, 12-14). *Melanoptychia brusinai* JEKELIUS, 1944 differs only by having a columellar fold (JEKELIUS 1944, Pl. 56), which is not present in *M. tihanyensis*.

Remarks: BARTHA (1955, Pl. 1, Figs. 1, 4, 8) described *M. tihanyensis* from Varpalota, where it occurs commonly. WENZ (1938) had changed the name of *M. gradata* FUCHS, 1870 into *M. tihanyensis* because it was preoccupied. While STRAUZ (1942) suggested that this species shows transitions to other species, BARTHA (1955) noted no such cases in Varpalota. This later observation is confirmed also for the fauna of Papkesi. *Melanopsis brusinai* LÖRENTHEY, 1902 is described to have 7-8 whorls

with rapid increase in whorl width and last whorl larger than the spire. A keel inserts after 2,5 smooth initial whorls and is a dominant feature up to the last whorl. The inner lip of the aperture shows a posterior callus pad. As had been noted by LÖRENTHEY (1902, Pl.16, Fig.7, Pl.18, Figs.3-6) the *Melanopsis gradata* (= *tihanyensis*) from Tihany is very similar but *Melanopsis brusinai* differs in having a larger last whorl and a more pronounced keel on the late whorls. In order to confirm the close relation of *M. brusinai* with *M. tihanyensis* the initiation of ornament following the protoconch should be known which is quite characteristic in the latter.

PAPP (1953a) distinguished an own evolutionary group of *Melanopsis* from the Pannonian Basin based on *Melanopsis brusinai*. From the Pannonian of the Vienna Basin he considered *Melanopsis austriaca* HANDMANN, 1882 and *M. scalariformis*, both occurring in Loebersdorf, to belong here. *M. scalariformis* is more slender than *M. brusinai*, but has a keel continuous into the last whorl as the latter. *Melanopsis austriaca*, in contrast, more properly belongs in the group of *M. costata*, connected to *M. oxyacantha* (see chapter III.e.4). A transition from smooth ancestral species resembling *Esperiana acicularis* to a keeled species was observed in case of *Melanopsis doboi* SCHRÉTER, 1978. Here the elongate turritiform shell with about 7 whorls and less than 15 mm in height and 6 mm in width is ornamented by one or two spiral keels. The spire is stair-like and the aperture is oval with rounded posterior end and channelled anterior end. The callus of the inner lip is uniform. SCHRÉTER (1978) observed transition within the waters of a thermal spring at Eger (Hungary) that was active during the early Pleistocene. *M. doboi* usually has a keel in central position on each whorl. It was not checked though in which whorl this keel inserts.

Melanopsis doboi is of similar size and shape as *Melanopsis tihanyensis* with which it clearly is not directly related. In case of *M. doboi* the origin of the species related to warm mineral springs is demonstrated. Spirally ornamented forms have also been noted in the Italian *M. etrusca* BROT, 1862 (chapter III.c.1.), as well as with morphs in the Oradea assemblage of *M. parreyssi* relation from Romania (chapter III.e.)

III.h. The *Melanptychia-Boistelia* group

JEKELIUS (1944) described from the Pannonian of Soceni in Romania several species which closely resemble a species of *Melanopsis*, but differ from it by having a columellar fold or plication. Such forms had been placed into separate genera such as *Melanoptychia* NEUMAYR, 1880 and *Boistelia* COSSMANN, 1909, the first having shell ornament, the second with smooth shell. JEKELIUS (1944) noted that *Melanopsis brusinai*, *M. stricturata*, and *M. turrita* have such counterparts in the genus *Melanoptychia*.

Melanoptychia brusinai JEKELIUS, 1944 has the characteristic two rounded initial whorls and develops on the third whorl a tuberculated keel. These tubercles become more prominent in later whorls while the keel loses prominence in the last, eighth or ninth whorl (JEKELIUS 1944, Pl.56, Figs.1-23). This species is very similar to *Melanopsis brusinai* and also to *M. gradata* (= *tihanyensis*) with exception of the columellar fold, which is never found in the later two. Thus, *Melanoptychia brusinai* closely resembles *M. tihanyensis* from Papkesi in size as well as in ornament.

A very similar pair of species has also been described by JEKELIUS (1944 Pl.50, Figs.3-8, 12-14) as *Melanoptychia banatica* and *Melanopsis banatica*. A comparable case exists also with *Melanoptychia turrita* JEKELIUS, 1944 that has a 12 mm high and 6 mm wide shell that consists of 10 whorls. This shell in size, shape and ornament resembles *Melanopsis turrita* HANDMANN representing a variety of *Melanopsis sturi*, but has a columellar fold (JEKELIUS 1944, Pl.57, Figs.1-21). The juvenile shell of the species from Soceni is very close to that of *Melanopsis bouei* from Papkesi, but the latter never has a columellar fold.

Boistelia stricturata JEKELIUS, 1944, *Boistelia substricturata* JEKELIUS, 1944, and *Boistelia inermis* JEKELIUS, 1944 with small shells resemble *Melanopsis stricturata* BRUSINA,

1892 and *Melanopsis inermis* when they are not fully grown, but in contrast to the latter have one or even two columellar folds.

There is only one species from Soceni that differs from all other *Melanopsis* species present here as well, and that is *Melanoptychia moensiensis* JEKELIUS, 1944. This only 5 mm high shell is 1,5 to 2 mm wide and consists of 8 whorls. Together with tuberculation an angulation occurs with first ornament of the teleoconch. This difference with the others is connected to a strong fold on the columella. Perhaps this species represent the one that hybridised with the other species living next to and in Lake Pannon or a neighbouring lake in the position of the Soceni locality and could have introduced the columellar fold here, that is absent in other localities of the same Lake Pannon at that time.

This scenario should be rechecked. It appears as if a species with columellar fold formed hybrids with quite a number of other species of quite different relation. One would be of the *M. brusinai*, *M. tihanyensis* relation. Another one could be with the *Melanopsis fuchsi* relation that has on ornament of a spiral keel crossed by short ribs on the juvenile shell, while the later shell is smooth. Here *Boistelia inermis* would be the hybrid. *Melanoptychia turrita* would have arisen of hybridization between the unknown species with columellar fold and a slender variety from the ornamented *M. bouei* clan.

III.i. The *Melanosteira* group of Greece and the genus *Amphimelania*

The type to *Amphimelania* is *Melania holandri* FERUSSAC, 1823 (= *M. holandri* C. PFEIFFER, 1828) that lives from Slovenia to Albania and in Lake Ochrid (WILLMANN & PIEPER 1978). It resembles *Amphimelania gayi* BRUSINA, 1902 (WENZ 1938, Fig.2021) (= *Melanopsis mitzopoulopsi* PAPP, 1955) from the Pliocene of Croatia and Greece which has a stronger ornament of spiral ribs. *A. gayi* (= *M. mitzopoulopsi*) is close in shape to a juvenile *M. aetolica* NEUMAYR, 1880. OPPENHEIM (1891a, Pl.27, Figs.1-8) and PAPP (1955a, Pl.20, Figs.1-19) documented the gradation of shells as present in *Amphimelania* into those of *Melanopsis* (= *Melanosteira*) *aetolica* in the Pliocene of Greece. The genus *Amphimelania* may thus be expensible, as well as the whole subfamily Amphimelaniinae.

Fig. 161. *Melanopsis tihanyensis* with 11 mm high shell, locality see fig.159.

Fig. 162. *Melanopsis tihanyensis* of the same individual as in fig. 163 seen from behind.

Fig. 163. *Melanopsis tihanyensis* with 11 mm high shell.

Fig. 164. *Melanopsis tihanyensis* with 2,5 mm high juvenile shell that shows the early insertion of the keel.

Fig. 165. *Melanopsis tihanyensis* with protoconch in which the first whorl measures 0,3 mm across.

Fig. 166. *Melanopsis tihanyensis* protoconch with 0,3 mm wide first whorl.

Fig. 167. *Melanopsis tihanyensis* with the 9 mm high shell demonstrating the orange-brown spots.

Fig. 168. *Melanopsis fuchsi* HANDMANN, 1852 with 15 mm high shell that is coated and shows the early ornament and later smooth surface. Same locality as in fig. 169.

Fig. 169. *Melanopsis fuchsi* with 11 mm high shell from the Pontian sands near Papkesi, next to Lake Balaton in Hungary. The specimen illustrated in figs. 170- 173, and 175, 176 are from the same locality.

Fig. 170. *Melanopsis fuchsi* of the same individual as in fig. 169 seen from behind.

Fig. 171. *Melanopsis fuchsi* with 16 mm high shell and colour pattern of brown stripes.

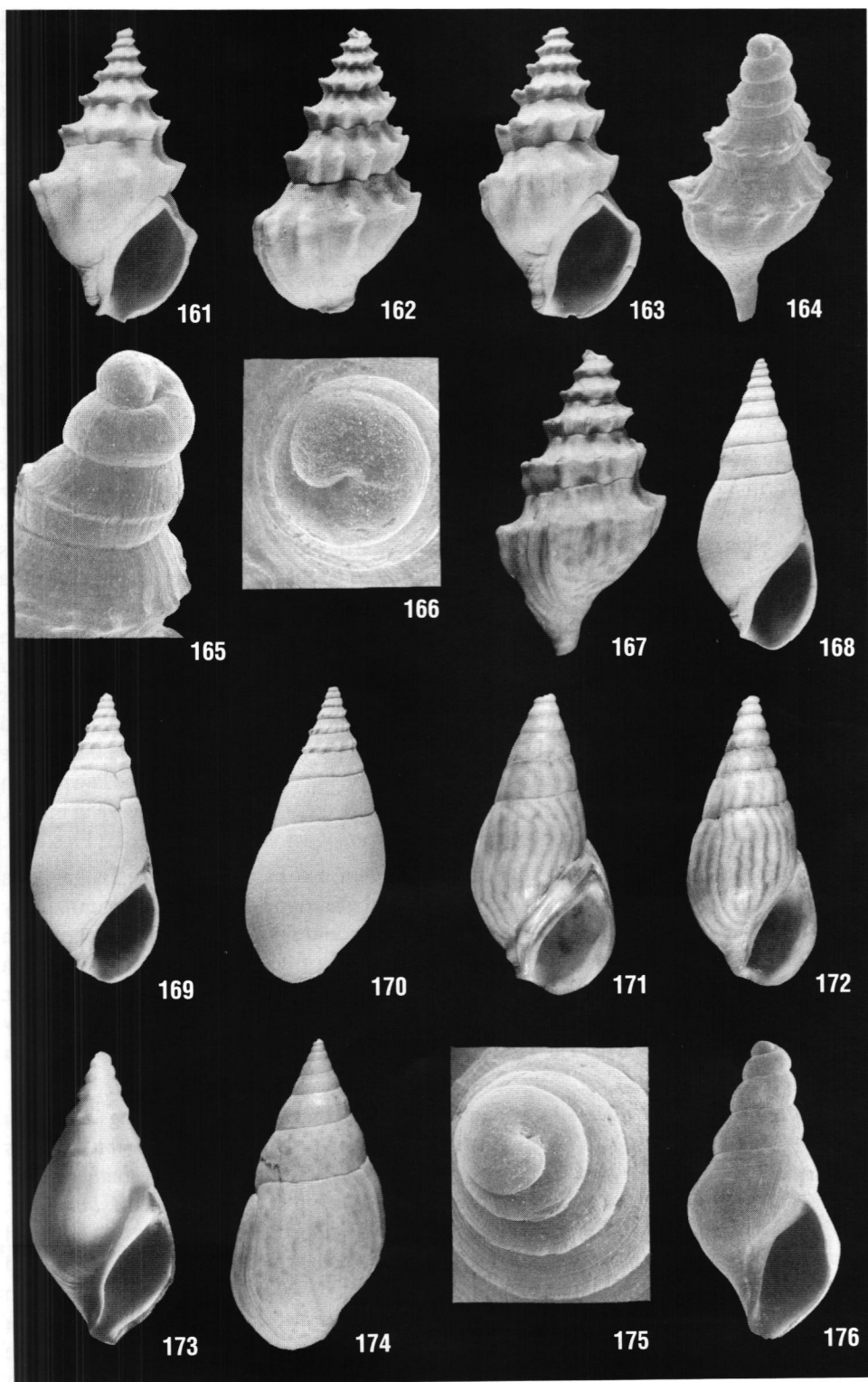
Fig. 172. *Melanopsis fuchsi* with 11 mm high shell and striped colour pattern.

Fig. 173. *Melanopsis fuchsi* with 5 mm high juvenile shell demonstrating the transition from the early ornamented whorls to the smooth later whorls.

Fig. 174. *Melanopsis eulimopsis* with 12 mm high shell and a quite different ornament of orange to brown dots and smooth early whorls. Same locality as *M. fuchsi*.

Fig. 175. *Melanopsis fuchsi* with first whorl measuring 0,5 mm in diameter.

Fig. 176. *Melanopsis fuchsi* with 4 mm high juvenile shell that shows initial whorls without ornament.



A mixture of axially ribbed *M. costata*-type species resembling *M. oxyacantha* from the Pannonian and called *Melanopsis conemenosiana* OPPENHEIM, 1891 from the Pliocene of Greece obviously formed hybrids with keeled forms of the *M. doufour* (= *M. delessei*) type which in the Pliocene of Greece was *Melanopsis aetolica* NEUMAYR, 1880. This species differs from the living *M. doufour* and also from the Pannonian *M. stricturata* by having a more flattened base (OPPENHEIM 1891b, PAPP 1955b, Pl.20, Figs.1-5; and PAPP & PSARONIOS 1955). It was suggested that *Melanopsis clavigera* NEUMAYR, 1875 as illustrated by OPPENHEIM (1891b, Pl.26, Fig.4) from Megara in Greece was involved in this evolutionary process. *M. clavigera* had axial ribs with a row of nodes on their posterior, peripheral part and, in addition, at the corner to the base and on the base. OPPENHEIM (1891b) suggested that such forms with flattened whorl flanks and two rows of nodes in the axial ribs evolved into *Melanopsis aetolica* NEUMAYR, 1880 forming the begin of the "*Melanosteira*"-group. But it may be suggested that ribbed species like *M. oxyacantha* (chapter III.e.5.) hybridised with conical species that had evolved from *M. stricturata* branch in this Pliocene environment between Croatia and the Peloponnes.

In the typical *Melanopsis aetolica* (OPPENHEIM 1891b, Pl.27, Figs.3,4) the sides of the whorls form a concavity and only the early teleoconch has axial ribs. According to PAPP (1955a, Pl.10, Figs.1-5) *M. aetolica* has 7 whorls without keel but only with noded axial ribs, and in the eighth and ninth whorl lateral keels become the dominant ornament and axial ribs disappear. OPPENHEIM (1891b, Pl.27, Figs.1,2) suggested that the starting point here was a *Melanopsis bouei* that evolved into what he called *Melanopsis carinatocostata* OPPENHEIM, 1891 in which the latest whorl has either weak ribs or only the spiral elements united to form keels. In that Pliocene fauna in question with *M. aetolica* in it no member of the *M. bouei* group has been recognized so that this assumption is not very likely to be true. In *Melanopsis stamnana* OPPENHEIM, 1891 the juvenile shell is ornamented like *M. carinatocostata* and later whorls have only the two spiral ribs on the periphery and the edge to the base (PAPP 1955a, Pl.20, Figs.1-5). A form with similar shell shape, but axial ribs also in the late portion of the shell was named *Melanopsis conemenosiana* OPPENHEIM, 1891 from Preveza in Epiros, and *Melanopsis lanceolata* NEUMAYR, 1880 from Megara (OPPENHEIM 1891b, Pl.27, Figs.7-8).

The interesting result of this hybridisation event that happened in the Balkan area during the Pliocene is the formation of a low conical gastropod that looks quite unlike any of the usual *Melanopsis*. In a way this strange evolution resembles what had happened in the Steinheim lake during Miocene time where a trochiform solid shell had evolved from a normal planispiral planorbid ancestor (HILGENDORF 1867, MENSINK 1987, NÜTZEL & BANDEL 1993, FINGER 1998). But in contrast to that later case the outcome of this Pliocene evolutionary event appears to have survived and is still about in the Balkan region with *Amphimelania hollandri* (chapter III.a).

A similar species to that of the Balkanian *Melanopsis clavigera* resembling *M. costata* or *M. saulcyi* from the modern Near East was involved in the appearance of *M. multiformis* of BLANKENHORN (1897) from the Pliocene of the Orontes. Here the spirally ornamented *M. vincata* was involved in the transition from *M. multiformis* to *M. bicincta* and *M. binodosa*. And a rather similar sequence can also be noted in the ribbed forms present in Abu Habil layers next to the Ghor canal in the Jordan Valley. Here slender ribbed *M. orientalis* hybridized with *M. doufour*-like forms having a stair like spire, and with *M. buccinoidea*-like forms with smooth shell (chapter III.e.3.). It can be learned from the transition observed by OPPENHEIM (1891b) and to some extent by NEUMAYR (1880a,b) in comparison with the mix seen in the late Pliocene or early Pleistocene of Jordan and the late Pliocene of the mid Orontes area that

similar mixtures will result in more or less comparable morphs but with local character. It can also be learned, that the outcome of such hybridisation events may later have their independent evolutionary history or they may also disappear from the scene.

IV. Reconstruction of the evolutionary history

IV.a. The modern *Melanopsis* in the Mediterranean region

Three different faunal provinces can be recognized in regard to *Melanopsis*, and its relation such as *Esperiana* and *Amphimelania* in the Mediterranean region. The Western Province of the Maghreb including portions of Algeria, Tunisia and Morocco, and SE Spain is nowadays isolated from the other two provinces. The region east of Tunisia all the way to the northern Sinai bears no Melanopsidae. To the north of Andalusia to Slovenia/ eastern Austria no melanopsids can be encountered, with an exception of enclaves in Italy. The Western Province consists of two regions the North African Maghreb being one and southern Spain the other separated from each other by the Strait of Gibraltar since the end of the Messinian. The northern Province is centred around the Balkan and is connected by Anatolia with the Eastern Province that consists of the Near East including Iran.

On the southern portion of the Iberian Peninsula, on the Balears and Africa north of the Sahara from Algeria to Morocco similar species had been noted by PALLARY (1924, 1926) and PERES (1939, 1945). The Spanish species of the Western Province were well documented by AZPEITIA MOROS (1929), but according to PUJANTE et al. (1988a,b) to many varieties of *M. penchinati* had been considered to represent independent species and actually belong to *M. sevilensis*. This Spanish species resembles *Melanopsis tingitana* of the Maghreb. *Melanopsis cariosa* is considered to be the same as *M. sevilensis* by PUJANTE & GALLARDO (1990), but could also represent the result of mixing with the other group around *M. dufouri/tricarinata* with spiral ribs and no axial ones. *M. praemorsa* without ornament represents a third group. AZPEITIA MOROS (1929) recognized 5 or 6 groups all of which are connected to each other by intermediates. But more likely *Melanopsis* of the Western Province when interpreted without inclusion of the small faunal elements which are largely known from single thermal springs appear to consist, thus, of three main species. One is *Melanopsis praemorsa* with smooth shell and short, conical spire, the second is *M. tingitana/sevilensis* with similar shell shape but ornament of axial ribs, and the third is *M. dufouri/tricarinata* with stair like spire and three spiral elements on its body whorl. While these appear to form the populations in SE Spain, the Maghreb also holds with *M. maroccana* a species that is close to the fusiform *M. buccinoidea*.

Today *Melanopsis* in the east occurs in the Aegean Islands, Sicily, Greek Islands, Rhodos and Cyprus, in the Ponto-Aralo-Caspian province, Turkey, southern Caucasus, Mesopotamia, Palestine. In this Eastern Province *Melanopsis* consists basically only of two elements, one around *Melanopsis buccinoidea*, including the more conical *M. doriae*, and the other around *M. costata*, including the shorter *M. saulcyi*, the more elongate *M. bandeli* and the forms intermediate between *M. buccinoidea* and *M. costata* like *M. ammonis* and *M. sharhabili*. *M. costata* may have an isolated outlier with *M. parreyssi* in Romania in which more ancient trends of the Eastern province may have become preserved, while *M. buccinoidea* today reaches as far west as Greece (PAGET 1976).

The Northern Province is characterized by *Esperiana* and *Amphimelania*, both of which still represent problematic forms regarding the relation of the species included within

them. *Melanopsis parreyssi* from the thermal ponds of Oradea may represent a relict of the fauna of the Eastern Province that extended here not long ago. It needs to be determined whether the Italian *M. etrusca* is an isolated relict of the past or connected to the West or East Province. *Esperiana acicularis* is clearly old and has lived in the Balkan since the Miocene. But whether *Fagotia* (= *Esperiana*) *esperiana* living also from the Eastern Alps to Black Sea is related is still quite unknown. There appear to exist transitional forms between these, but whether they can be interpreted as result of hybridisation or evolutionary history from different ancestors is impossible to judge with the available data. The modern *Esperiana* with coloration by dots could be descendent of *M. eulimopsis* while the other or some of the others could be related to striped *M. fuchsi*, both species from Pontian Lake Pannon.

IV.b. The Pliocene and early Pleistocene developments

The arising of the modern melanopsid fauna has been interpreted to have occurred in the time following the Messinian salinity crisis of the Mediterranean Basin. But actually the Pliocene fauna differs quite considerably both from that of the Late Miocene on one side and the modern one on the other. But connections from the Miocene to the Pliocene are very evident, as is the transition from the later to the Recent.

Basically unchanged into the Pliocene and from there into the modern fauna members of the *Melanopsis praemorsa* and *M. buccinoidea* group appear to continue. But within this morphological group differences are difficult to state even if they would exist, due to the simplicity of the shell that has not changed much from Cretaceous onwards. Regarding *Esperiana acicularis* there is also no change visible, but it can be expected that within that group of *Esperiana* and *Microcolpia* some of the Miocene developments are hidden that connect smooth species like *M. fuchsi* and *M. eulimopsis* with species living in different regions of the Northern Province today. Such potential survivors can be detected much better when the shell has a characteristic ornament, as is the case in *M. austriaca* from the Miocene that may still live on in *Fagotia sangarica* from an Anatolian river.

Groups coming from the Miocene and ending in the Pliocene or just before its begin are that of *M. impressa* and that of *M. bouei*. But relations of these like in the first case represented by *M. stricturata* (fossil) and *M. dufouri* (living) are more unclear and the smooth varieties of the second case (*M. bouei*) live or may live within the *Esperia* group

It is evident, that the *M. costata* group with large shells and prominent callus pad appear in the early Pliocene within the Balkan region. But they spread well since AZPEITIA MOROS (1929) reported a ribbed form from the Pliocene of Huescar, province of Granada. A *Melanopsis costata* was determined by ROYO GOMEZ (1922, Fig.27) even from the Pontian of Valencia resembling modern *M. saulcyi*. Apparently members of the *M. costata* group occurred within the region of the modern Western Province as well as within the other two Provinces and it is quite likely that these provinces were not well differentiated at these times. On the other hand the origination of modern *Amphimelania* as is documented from the Balkan within the *Melanosteira* group (OPPENHEIM 1891b) gave rise to species that apparently did not leave that region.

Members of the *M. costata* group in Pliocene time commonly had a prominently stair-like spire which has become lost in the Eastern Province together with the whole *M. dufouri* clan. Surviving axially ribbed species in the shape of their spire more reflect that of *M. buccinoidea* with which they locally produce hybrids, and most probably have done so for a long time. In the Western Province and here its Spanish extension among the smooth *Melanopsis* only those with short spire have survived in *M. praemorsa*. Here and in Northern

Africa *M. dufouri* continued and hybridised both with *M. praemorsa* and members of the *M. costata* group. The ribbed species, thus, acquired their own character now seen in *M. sevilensis* and *M. tingitana*. *M. laevigata* has been noted from the Pleistocene of SE Spain near Granada (MADURGA MARCO 1973, Pl.3, Figs.1,2), and it resembles a modern *M. buccinoidea*, but is also like *M. kleini* as illustrated by JODOT (1958) from the Sarmatian of SE Spain near Murcia. Such forms, nowadays, appear to still live in the north African portion of the Western Province in *M. maroccana*.

IV.c. The Pontian assemblage

Among the Pontian species found at Papkesi the most common species are the ribbed *Melanopsis oxyacantha*, the keeled *M. tihanyensis*, the basically smooth and axially striped *M. fuchsi*, and the members of the *M. bouei* group with spiny *M. bouei*, the similarly shaped but smooth *M. eulimopsis*, and *M. barthai* and *M. papkesiensis* with axial ribs as early ornament. The later two obviously represent transitional forms from *M. bouei* to *M. oxyacantha* and more such forms could easily be recognized. It also represents hybrids between species like *M. oxyacantha* without thickened callus pad on the inner lip of the aperture and, thus, if it were living now, a member of the genus *Esperiana* and *M. bouei* with callus pad and thus, if connected to modern forms a member of the genus *Melanopsis*. A more rare species in this environment of the swampy shore region is *M. pseudobesa* from the *M. praemorsa* group. At more or less the same time in probably more estuarine environment of Fonyod *M. impressa* formed gradation into *M. cylindrica*, and *M. kleini* occurred rarely here as well.

All 12 species found in Papkesi and Fonyod appear to have lived close to each other and more or less at the same time. The accompanying fauna is that of fresh and brackish water. The later environment was the living place of the bivalves *Congeria* and *Limnocardium*, while *Sphaerium* and unionids are from the fresh water. A number of lymnaeid and planorbid basommatophorans are present and there are bithyniids as well as valvatids of fresh water derival and hydrobiids possibly of brackish water influence. *M. tihanyensis* formed no transitional specimen with the other five species. *M. fuchsi* and *M. oxyacantha* in their majority are of uniform shape and ornament as well. *M. pseudobesa* is rare, but also of characteristic grain shape with thick inner lip pad. The number of species encountered in Papkesi and near Fonyod seems to be pretty much the same as can be noted from the Pannonian time, and it could be extended if more hybrid varieties would be treated as species.

IV.d. The Pannonian *Melanopsis*

Pannonian Melanopsidae from Lake Pannon and surrounding water bodies that extended from the area of Vienna, to eastern Croatia, northern Hungary, western Romania and the region near Belgrad in Serbia have been the topic of many studies of which that of HOERNES (1856), LÖRENTHEY (1902), JEKELIUS (1944) and PAPP (1953a) are well illustrated. The main groups involved in hybridisation here are those of the large sized *Melanopsis impressa* with angulated whorls, and the smaller and tuberculous *M. bouei*. Present were also *Melanopsis austriaca* resembling the Pontian *M. oxyacantha*, the slender *Esperiana acicularis* in fluvial deposits nearby the lake, the keeled *M. brusinai*, in the eastern regions of the lake the *Melanoptychia* group with columellar plicae, and *M. handmanni* (= *kleini*) of the simple smooth *M. praemorsa* group.

PAPP (1953a) distinguishes three groups from the western part of Lake Pannon. The two characterized by *M. impressa* and *M. bouei* were here already during Sarmatian time (PAPP 1954). A similar starting condition to the Pannonian fauna had also been noted by JEKELIUS (1944) on the eastern side of the lake. But he called *M. bouei* from Sarmatian deposits *M. sturi* and he noted in addition to *M. impressa* a slender form in *M. soceni*. It resembles a juvenile *M. impressa*, but has grown to have more whorls without much increase in width. The interpretation of GEARY (1988, 1990, 1992) according to which *Melanopsis* evolution in the Pannonian Lake Pannon had originated within one and the same group can, thus, not be accepted. GEARY (1990) assumed that in the vicinity of Lake Pannon and surrounding lowlands at least 7 new species of *Melanopsis* evolved, most appearing first in a middle Pannonian burst when the lake level rose. It has also to be taken into consideration that members of the *Melanopsis praemorsa* group lived nearby next to the foredeep of the Alps in southern Germany with *Melanopsis kleini*. Also *Esperiana acicularis* was present (LUEGER 1980), and in his detailed account of the fauna in Soceni in Romania from Sarmatian and Pannonian time by JEKELIUS (1944) suggests that also a group of small forms with columellar fold became involved.

LÖRENTHEY (1902) subdivided *Melanopsis* from the Pannonian of Tinnye near Budapest into 16 species and some more varieties or subspecies amounting to a total of 22. In the deposits of a single Pannonian beach in the Vienna Basin PAPP & THENIUS (1954) noticed 12 species of *Melanopsis*. Disregarding subspecies or forms it would still be 7 species. PAPP (1953a) recognized 17 species from the Pannonian of the Vienna Basin and 15 subspecies, thus a total of 32 taxa within *Melanopsis*. JEKELIUS (1944) recognized 18 species from Soceni in the Turislav Valley of Romania.

GEARY (1988a,b, 1990, 1992) and STALEY, (1992) repeated and reviewed some of the data that had been assembled by JEKELIUS (1944) and PAPP (1953) and utilized part of them to prove some aspects of evolutionary theories and interpret them anew. But JEKELIUS (1944) had documented the total transition that exists between *M. impressa*, *M. fossilis*, *M. rugosa*, *M. vindobonensis* and *M. inermis* in the lake deposits of Pannonian time at Soceni. *Melanopsis stricturata* from the Pannonian in Soceni (JEKELIUS 1944) represents the earliest known member of the *M. dufouri* group, and it was not recognized in the fauna of the Pontian here analysed. *M. banatica* and *M. moesiensis* recognized by JEKELIUS (1944) from the Pannonian are close to *M. brusinai* of LÖRENTHEY (1902) and all three represent relatives to *M. tihanyensis* from the Pontian.

IV.e. Pre Miocene development

The preliminary data by Ralf BISCHOFF indicate that the distance seen in DNA composition between *Melanopsis buccinoidea* and *M. bandeli* in Jordan is low, and between these and *Melanopsis sevilensis* from Spain and *M. lirata* from New Caledonia as a group the distance is less than to *Esperiana* from the spring in Vöslau. All these again form a group that is distinct from *Esperiana acicularis* from the Danube. But melanopsids as a whole are clearly set off from other Cerithioideans of the coastal swamps and fresh water. This pattern is not detailed enough to allow great interpretations, but it is in accordance with paleontological evidence. The species from Jordan are still hybridising, those from Spain are and, thus, the Western Province, are distinct from those of the Eastern Province since begin of the Ice ages and colder climatic conditions connected to that event. *E. acicularis* appears to have been living unchanged in the rivers of south-eastern Europe since Miocene time. Amazing is only the small distance to *Melanopsis* from New Caledonia.

According to MORRISON (1954), the Melanopsidae settled the margins of the former Tethys Ocean and produced fresh water species in the area of the Paratethys and Mediterranean Sea. One branch of these in the New Zealand-New Caledonian area demonstrate the complex history of this group. STEVENS (1994) stated that continuous land links between New Zealand, Australia and Antarctica had virtually disappeared during Campanian-Maastrichtian times ca. 85 Ma, shallow water links persisted for perhaps another 25-30 Ma, in the early and middle Paleocene, before finally severed by the continuance of sea floor spreading in the developing Southern Ocean. *Zemelanopsis* with its planktonic larval development in the open sea could represent the only relict of the original melanopsids that had entered the coastal swamps, as recognized in *M. serchensis* from the Maastrichtian of Spain.

Substantial links between Australia and Asia began to appear in the early Neogene. As Australia moved northwards the fringes of island arcs, depositional troughs and allochthonous terranes along its northern boundary began to interact with the southern edge of the Indonesian arc as Indonesia and south-east Asia moved southwards in response to the opening and continued expansion of the South China Sea. The land areas produced as a result of this interaction provided routes for the interchange of terrestrial flora and fauna between Australia and south-east Asia. DNA analysis of New Caledonian *Melanopsis* indicates that it was probably part of that relatively late interchange. Whether *Melanopsis pomahakensis* HUTTON, 1873 from the late Oligocene of southern New Zealand (BEU & MAXWELL 1990) belongs to that migration event or to that possibly earlier one of *Zemelanopsis* is still unknown. The detailed history of pre-Miocene *Melanopsis* is still quite mysterious. It can be hypothesized that *Stilospirula* evolved into *M. impressa*-like forms, but it would certainly be better to have some more data available for analysis.

V. Hypothesis regarding the evolutionary processes in the *Melanopsis* lineage

It is quite comprehensible why literature data on late Miocene and Pliocene melanopsids since the times of HOERNES (1856) were used only sparsely and selectively by most authors discussing the evolutionary history of the Melanopsidae or certain subgroups. The amount of species that has been described is overwhelming. In addition faunal composition in one stratigraphical horizon of only Lake Pannon differs considerable when geographically separated localities are concerned, such as the surroundings of Vienna (HANDMANN 1887, FUCHS 1870a,b, 1872, HOERNES 1856, PAPP 1954, 1985, GEARY 1992), the area of eastern Croatia (BRUSINA 1874, 1884, 1892, 1902a), near Beograd (PAVLOVIC 1927), near Budapest (LÖRENTHEY 1902, 1911), and in Soceni of western Romania (JEKELIUS 1944). A similar picture arises when the fauna extracted from Pliocene localities, mainly from the Balkan and Syria are considered (BUKOWSKI 1893, PAPP 1953b, 1955a,b, BLANCKENHORN 1897, BRUSINA 1902a, OPPENHEIM 1891, NEUMAYR & Paul 1875, WILLMANN 1981). But most confusing is the status of the recent species in existence in the different provinces, which is apparent when studies of FERUSSAC (1823), PALLARY (1911, 1924, 1925, 1939), PERES (1939, 1945), BOURGUIGNAT (1884), AZPEITIA MOROS (1929) and others are consulted.

Literature contains quite a lot of different species names and not all taxa had been introduced with good description and illustration. To find a way through the resulting confusion is not easy. But by avoiding this task assumptions have been made which cause erroneous statements, as for example that of WILLMANN (1980) that ribbed *Melanopsis* appears first in very late Miocene or early Pliocene in Greece, while actually it is older. Also

the statement of GEARY (1990a,b, 1992) that *Melanopsis impressa* is the most ancient melanopsid in the Pannonian basin and from it as founder species a number of species of the Paratethys evolved that lived during the late Miocene. This scenario appears to be to simplistic and at least members of axially ribbed, spiny and smooth species of the *M. costata*, *M. bouei*, *M. praemorsa* and *Esperiana* groups lived here as well. GEARY (1988) thought that *M. sturii* has a paedomorphic descendant in *M. pygmaea*. This model was connected to the hypothesis that the early slender shell of *M. sturii* remained so during the whole life in *M. pygmaea*, which, therefore, constructed the shell according to the juvenile style of *M. sturii*. In the *M. sturii*, *M. pygmaea* sequence GEARY (1988) interpreted that ornament and shape were affected by paedomorphosis. GEARY did not find a good stratigraphic control to her idea. But it can be shown that both types of *Melanopsis*, one with a regular shell growth, the other with allometric growth and more rapid whorl diameter growth after the fifth whorl have lived in the surroundings of Lake Pannon for more than 4 Million years side by side. GEARY (1990) assumed that evolutionary radiation of *Melanopsis* in the Pannonian basin occurred in an isolated area. She thought that all up to 120 species evolved by cladogenesis sometimes slowly and sometimes rapidly from one or two founder species.

TCHERNOV (1975) suggested that *Melanopsis praemorsa* represents one highly variable species that lives around the Mediterranean Sea and in neighbouring areas. It is thought to have a high degree of intraspecific polymorphism and to have vast number of ecotypes all belonging to that same species with the name *M. praemorsa*. All these have been interpreted to belong to the same "Superspecies" (GLAUBRECHT 1993, 1996, 2000). But unfortunately it was not reproducibly explained what such a taxon may be, and the scenario was reconstructed based on the assumption that the Messinian stage of the Mediterranean Sea somehow induced new appearances for example of ribbed forms among the *Melanopsis* as had been suggested prior by WILLMANN (1981). GLAUBRECHT did not take into consideration a large part of the literature that deals with the fossil occurrences of *Melanopsis*, especially that related to the Pannonian Basin from eastern Austria to western Romania (even though cited 1996). Otherwise it would have been quite evident, that not only smooth species of the *Melanopsis* relation lived before the Messinian time.

In the discussion on modes of evolution and in the confirmation of evolutionary theories and hypothesis *Melanopsis* and relation has commonly served as an example. In early studies of *Melanopsis* it had been recognized that species with very wide range of morphologies or a mixture of species occurred (FUCHS 1872). BLANCKENHORN (1897) described faunal sequences from Pleistocene deposits next to the Orontes in Syria, compared his data with those from similar deposits in Slavonia studied by NEUMAYR & PAUL (1875) and central Greece by OPPENHEIM (1891b) and noted that the melanopsids found here are difficult to interpret by purely Darwinian methods of descent according to selectional forces.

The theory of origination of species as worked out by HENNIG (1966) and in detail by AX (1984) guided WILLMANN (1981, 1983, 1985a,b) in his interpretation of speciation mainly based on Greek late Neogene faunas. He suggested that ribbed forms even though resembling each other in great detail still evolved independently at least four times only within the Dodekanes area (Greece). This hypothesis was based on the assumption that ribbed species could not have migrated to the spot where they now appear in the sediments, but that they evolved here. According to his hypothesis, thus, smooth forms have evolved four times into strongly ribbed ones and these again back into smooth ones. It also helped that WILLMANN (1981) assumed that smooth shelled *Melanopsis* are the long lived (plesiomorphic) forms and all ribbed forms are short lived. Based on that assumption WILLMANN (1981)

corrected all the "erroneous" remarks in the literature, according to which ribbed *Melanopsis* from geographically separate localities may be directly related to each other. With the theory of phylogenetic evolution in mind he suggested that smooth species living at different times and different locations should be interpreted to represent different taxa. But this only needs to be the case (even when using the "laws" of that theory) if the assumption is correct that in their lineage ribbed forms actually occurred. Also bottlenecks of evolution were made responsible for changes (WILLMANN 1979, 1985a), speeding up speciation events.

The fauna of hot springs also boosted the amount of species. BRUSINA (1902b) noted 23 forms or species of the thermal springs at Oradea, but also indicated that they could represent varieties of the one species *M. parreyssi*. He then expressed his opinion that this large variation in morphology represents a good example of the theory of descent that had been presented by Charles DARWIN a few decades before. KORMOS (1905) described a geological section from the area of the warm spring of Oradea and distinguished several more subfossil species and suggested the relation of the group to the fossil *M. lanceolata* NEUMAYR from Slawonia. AZPEITIA MOROS (1929) separated in a similar way quite a number of species from a thermal spring and pond in southern Spain.

VI. Results

The history of *Melanopsis* and relation is traced to the Santonian (Ajka and Gosau) from which we know smooth forms of the *Melanopsis* and the *Esperiana* type (BANDEL & RIEDEL 1994). From the Campanian of the Tremp basin of northern Spain smooth *Melanopsis* as well as the axially and spirally ornamented *Melanopsis trempensis* are documented. In the Maastrichtian of the Isona Formation in the same general area of the Tremp basin a *Melanopsis* of the type as is still living in *Zemelanopsis* of New Zealand is noted in the species *M. serchensis* that had a planktotrophic larva. Melanopsids, thus, during the late Cretaceous lived in coastal swamps and fresh water lakes and had basically all features of the morphology of the shell and the same types of ontogeny that still characterizes the group nowadays. It can be resumed that since Cretaceous times their mode of life has not changed much.

About the melanopsids from the Paleogene there is not enough information available to understand their history and evolution. Species of *Stilospirula* with their characteristic juvenile shell present evidence for their independence and distinct character in comparison to older and younger relation. The presence of a single corner connected to a keel on the whorls of the juvenile shell of *Stilospirula doroghenensis* from fresh water lakes next to the warm Tethys Ocean in Hungary could indicate a relationship with the *M. impressa* group. Like the juveniles of *M. impressa* the juveniles of *Stilospirula* are very slender, but in contrast the initiation of the cornered whorl is within the juvenile shell in the species from the Eocene, while it occurs only after the fifth whorl has been formed in the species from the Miocene. But there could also be connections to *Melanopsis fuchsi* with similar juvenile ornament, but different adult shell.

For the late Miocene the Central Paratethys is the main source of information regarding the history of *Melanopsis*. At the begin of a well documented evolution of quite a number of species and their varieties five different species or species groups existed, the large and slender *M. impressa*, the short and spinous *M. sturii/bouei*, the river dwelling *Esperiana acicularis* related perhaps to *M. fuchsi*, the fusiform *M. kleini* and the axially ribbed *M. austriaca/oxyacantha*. Of these only *M. impressa* and *M. sturii* were common in the estuaries

of the Sarmatian Sea. This sea was almost land locked and extended from the Vienna area to the east of the Caspian Sea, probably connecting here with the ocean (JONES & SIMMONS (1996).

With the observations on hybridisation of modern species in Israel (HELLER et al. 1999) and Jordan in mind the succeeding development along the shores of brackish Lake Pannon during Pannonian and Pontian time can be interpreted. Species meeting in a certain locality may or may not form hybrids. Why this is so is not known, but that it is a fact has been proven in the modern examples in Israel. In Jordan it was possible to observe morphological transitions in some localities, while they apparently do not happen in other places nearby. This observation confirms the results from nearby Israel. They also document that hybridisation produces different morphs, depending on the partners involved in it.

The process of hybridization between species of *Melanopsis* on the shores of Lake Pannon may have played a similar role to that observed to occur nowadays around the modern Lake Tiberias in Israel, and along the Jordan and its tributaries. Hybridization as source of great shell variety was suggested in fossil occurrences by FUCHS (1872) and modern faunas by PERES (1945). Locally around that large Lake Pannon characteristic hybridisation zones have been present, each of which has a distinctive touch to it. For example, in the Papkesi area of Hungary the coastal swamps provided an environment for the intermixture of the slender ribbed *M. oxyacantha* with its smooth inner lip with the spinous, short *M. bouei* with allometric growth and callus pad during Pontian time. In the Romanian locality at Soceni at Pannonian time, for example, a species of *Melanoptychia* with columellar plicae was involved that hybridized with several quite distinct species like the smooth cylindrical *Melanopsis inermis*, the keeled *M. brusinai* and a species that resembles *M. fuchsi* called *M. turrita* (JEKELIUS 1944, Pls.55-57). Hybridisation can also be made responsible for transitions from *M. impressa* to *M. fossilis*, *M. caryota*, *M. vindobonensis* during Pannonian time and from *M. impressa* to *M. cylindrica* during Pontian time, which, therefore, would not be a good model to study evolution from one to the next species by different processes of heterochrony such as paedomorphosis etc. Even if these processes had actually occurred, hybridisation would obscure this process quite strongly and prevent an interpretation.

Hybridisation of similar species produced identical or nearly identical results in localities which were quite distant from each other as in case of the Pliocene faunal assemblages in Greece (PAPP 1953,b) and in the Orontes area in Syria (BLANCKENHORN 1897). It can also look very similar when it occurs at different times within one and the same locality as is the case in faunal assemblages of Kos (WILLMANN 1981). Actually the results of hybridization as was noted from the Pliocene fresh water in Rhodos and Kos are rather similar to those that have been documented from Syria and Jordan to have occurred about the same time, indicating that pretty much the same species were involved in these processes.

Pannonian and Pontian melanopsids demonstrate quite a number of differences, that indicate that in the species involved were not the same when they formed hybrids. The hybrids in the *M. bouei* group for example in Pannonian time had only the ornament of tubercles and spines, while those with otherwise rather similar shell shape in the Pontian time had an early ornament of axial ribs as well, due to the influence of a new partner, *M. oxyacantha* who jointed in the process. In case of the *M. impressa* group the hybridisation with unknown partner in the Pannonian resulted in *M. fossilis*, while a similar process in the Pontian produced *M. cylindrica*. In the Pliocene a change in partners was even more pronounced. The results of hybridisation processes as that observed in the *Melanosteira*

group described by OPPENHEIM (1891bv) and PAPP (1955a,b) resulted in completely different shell types like that of *Amphimelania*, which afterwards was apparently a stable new group still living in the general area of its origin.

In the case of the living *Melanopsis* of Israel HELLER et al. (1999) suggested that three distinct species are involved. Similarly from Sarmatian time to the Recent, that is for at least the last 10 million years, the species of *Melanopsis* locally hybridise. If we compare the Miocene *Melanopsis* with the Pliocene and Recent one, there is clearly a change to be observed. But evolution producing this change did not proceed in a purely "Hennigian" way by bifurcation only from one to the next species, but also by recombination of quite distinct and sometimes probably quite distant partners with each other. The outcome of such mixing processes sometimes resulted in apparently stable species, that can be recognized as genera if they have many characters distinct from that of *Melanopsis* as is case in *Amphimelania*. From a morphological point of view the mixing event also sometimes produces results which are not between the two partners regarding their shape but have rather a unique shape. An example of this may be seen in *M. sharhabili* from the Jordan valley that shows allometric growth as is found in neither of the hybridising partners of the *M. buccinoidea* and the *M. costata* groups involved. The similar appearance of new morphological characters due to hybridising of species that are closely related but have a long history of independent evolution was documented by CHIBA (1997) from land snails on the Japanese Bonin Islands.

The latest Miocene or early Pliocene lake deposits in Greece and further north on the Balkan area appear to represent the localities where the origination of the species of the *Melanopsis costata* group as found in the Pleistocene of Jordan and as is still living has occurred. Slender small species like *M. ocyacantha* could have hybridized with more round and larger forms of the *M. impressa*/*M. dufouri* group as in *M. delessei*. The transitions to the species now characterizing the Eastern Province and the Western Province has occurred since, in case of the region of the Near East apparently during the Pleistocene. The resulting fauna is quite characteristic on one side and has a rather local expression on the other side.

Apparently a mix of hybrid formation and chance biogeographic meeting of populations with more or less extended independent development for the last 100 Million years formed the species of the Melanopsidae as we can observe them now. The history of this group of gastropods can not be reconstructed by a cladogram with simple bifurcate branching, but we have to adopt methods known to the botanists, for example when dealing with the reconstruction of the phylogeny of the orchids. Naturally the here presented scenario can be doubted, but it should be testable for example with the study of the composition of the genetic material (analysis of DNA) present in the surviving species.

Acknowledgment

In the collection of the gastropods Ute GEBHARDT, Thorsten KOWALKE, Steffen KIEL and Carolin HARLOS (Hamburg) helped in Hungary and in Spain, Rafie SHINAQ and Abdalla ABUHAMAD (Irbid) joined in collecting in Jordan. The discussion with JOSEPH HELLER (Jerusalem) was very helpful. The text was improved by Marlies BECKER, the photos taken and plates assembled by Eva VINX (both Hamburg). Financial support came from two projects of the DFG, one centred around the Central Paratethys (Ba675/18) and the other around the geology of Jordan (Ba 675/25). I like to thank all these persons and institutions, especially also for the hospitality of Yarmouk University in Jordan.

References

- ANKEL, W.E. (1928): Beobachtungen über Eiablage und Entwicklung von *Fagotia esperi* (Ferussac). - Arch. Moll., **60**: 251-256. Frankfurt a. Main.
- AZPEITIA MOROS, F. (1929): Monografía de las *Melanopsis* vivientes y fosiles de España. - Memorias del Instituto Geologico y Minero de Espana, 402p, Madrid.
- AX, P. (1984): Das Phylogenetische System.- Gustav Fischer Verlag, 349 p., Stuttgart.
- BANDEL, K. (1976): Observations on spawn, embryonic development and ecology of some Caribbean lower Mesogastropoda.- The Veliger **18**: 249-271.
- BANDEL, K. (1998): Evolutionary history of East African fresh water gastropods interpreted from the fauna of Lake Tanganyika and Lake Malawi. Zbl. Geol. Paläont. Teil 1: 233-292.
- BANDEL, K. & KIEL, S. (2000): Earliest known (Campanian) members of the Vermetidae, Provannidae and Litiopidae (Cerithioidea, Mollusca) and a discussion of their possible relationships. This volume.
- BANDEL, K. & KOWALKE, T. (1999): Gastropod fauna of the Cameroon coast. - Helgoland Marine Research **53**: 129-140.
- BANDEL, K., REICHERTER, K. DYRSSEN, U. & REISS, S (2000): Late Neogene lacustrine sedimentary facies and gastropod assemblages (Granada Basin, southern Spain). This volume.
- BANDEL, K. & RIEDEL, F. (1994): The Late Cretaceous gastropod fauna from Ajka (Bakony Mountains, Hungary): a revision.- Ann. Naturhist. Mus. Wien. **96A**, S. 1-65, 1994.
- BANDEL, K. & SALAMEH, E. (1981): Hydrochemical and hydrobiological research of the pollution of the waters of the Amman Zerka area (Jordan). - Schr. Dtsch. Ges. Techn. Zusammenar.GTZ, **94**: 1-60. Eschborn.
- BARTHA, F. (1955): Untersuchungen zur Biostratigraphie der pliozänen Molluskenfauna von Varpalota.- Jb. Ungar. geol. Anst. Budapest **43**: 275-359.
- BARTHA, F. (1956): Die pannonischen Fava von Tab. - Jb. Ungar. geol. Anst. Budapest **45**: 479-584.
- BENDER, F. (1968): Geologie von Jordanien. Beiträge zur Regionalen Geologie der Erde, 7. - Gebr. Bornträger; Berlin.
- BENTHEN JUTTING, W.S.S. van (1956): Systematic studies on the nonmarine Mollusca of the Indo-Australian archipelago. 5. Critical revision of the Javanese freshwater gastropods. - Treubia, **23(2)**: 259-477. Bogor.
- BEU, A.G. & MAXWELL, P.A. (1990): Cenozoic mollusca of New Zealand. - New Zealand Geol. Surv. Paleon. Bull., **58**: 1-518. Lower Hutt.
- BILGIN, F.H. (1973): Studies on the functional anatomy of *Melanopsis praemorsa* (L.) and *Zemelanopsis trifasciata* (GRAY). - Proceedings of the Malacological Society of London, **40**: 379-393.
- BLANCKENHORN, M. (1897): Zur Kenntnis der Süßwasserablagerungen und Mollusken Syriens.- Palaeontographica, **44**: 71-144. Stuttgart.
- BLANCKENHORN, M. (1914): Syrien, Arabien, Mesopotamien. - Handbuch regionaler Geologie, Abt. **5(4)**: 1-154, Heidelberg.
- BLANCKENHORN, M. & OPPENHEIM, P. (1927): Neue Beiträge zur Kenntnis des Neogens in Syrien und Palästina. - Geol. Palaeont. Anh., N.F **15(4)**: 321-356. Jena.
- BOURGUIGNAT, J.R. (1884): Histoire des Méléniens du Système Européen.- Ann. Malacol., **2**: 1-168. Paris.
- BRANDT, R.A.M. (1974): The non-marine aquatic Mollusca of Thailand. - Archiv für Molluskenskunde, **105(1/4)**: 1-423. Frankfurt a.M.
- BROT (1862): Brot, A. (1874): Die Melaniaceen (Melanidae) in Abbildungen nach der Natur mit Beschreibungen. - In: MARTINI, F.H.W. & CHEMNITZ, J.H. (eds.), Systematisches Conchylien-Cabinet, Bd. 1, Abt. **24**: 488 pp. Nürnberg (BAUER & RASPE).
- BRUSINA, S. (1874): Fossile Binnenmollusken aus Dalmatien, Kroatien und Slavonien. - Abhandl. d. südsl. Aka. d. Wissensch., **28**, 138 pp., Agram.
- BRUSINA, S. (1884): Fauna der Congerienschichten von Agram in Kroatien. - Beitr. Paläontol. Österreich-Ungarns, Orient **3**: 125-187, Wien.
- BRUSINA, S. (1892): Fauna fossile tertiaria di Markusevec in Croatia. - Glas. hrvat.nara. Drusteva, : 113-210.
- BRUSINA, S. (1902a): Iconographia molluscorum fossilium in tellure Tertiaria Hungariae, Croatiae, Slavoniae, Dalmatiae, Bosniae, Herzegovinae et Bulgariae inventorum. - Agram (Zagreb).
- BRUSINA, S. (1902b): Eine subtropische Oasis in Ungarn.- Mitt. naturw. Ver. Steiermark, **39**: 101-121. Graz.

- BUKOWSKI, G. (1893): Die levantinische Molluskenfauna der Insel Rhodus. I. Teil. - Denkschr. K. Akad. Wiss. Wien, math.-nat. Cl., **60**: 265-306. Wien.
- BUKOWSKI, G. (1895): Die levantinische Molluskenfauna der Insel Rhodus. II. Teil. - Denkschr. K. Akad. Wiss. Wien, math.-nat. Cl., **63**: 1-70. Wien.
- CHIBA, S. (1997): Novel colour polymorphism in a hybrid zone of *Mandarina* (Gastropoda: Pulmonata). - Biological Journey of the Linnean Society **61**: 369-384.
- CIANFANELLI, S., TALENTI, E. & CALCAGNO, M. (1989): Le stazioni di *Melanopsis dufouri* FERUSSAC, 1823 (Gastropoda Prosobranchia) in Italia. - Quad. Mus. di Storia Nat. Livorno, **10**: 59-76. Livorno.
- COSSMANN, M. (1906): Essais de paleoconchologie comparée. - Presses Universitaires de France, **7**: 1-261. Paris.
- CSATO, I. (1993): Neogene sequences in the Pannonian basin, Hungary. - Tectonophysics **226**: 377-400.
- ESU, D. (1980): Neogene freshwater gastropods and their evolution in the western Mediterranean area. - Geol. Romana, **19**: 231-249. Rom.
- ESU, D. & GIROTTI, O. (1975): La malacofauna continentale del Plio-Pleistocene dell'Italia centrale. 1. Paleontologia. - Geol. Romana, **13** [1974]: 203-293, Rom.
- FALINOWSKI & HELLER in press
- FERUSSAC, M. (1823): Monographie des espèces vivantes et fossiles du genre *Mélanopsid*, *Melanopsis*. - Mem. Mus. nat. Hist. natur., **1**: 132-164. Paris.
- FINGER, I. (1998): Gastropoden der *kleini*- Schichten des Steinheimer Beckens (Miozän, Süddeutschland). - Stuttgarter Beiträge zur Naturkunde, Ser. B, Nr. **259**, 51 p., Stuttgart.
- FUCHS, Th. (1870a): Die Fauna der Congerienschichten von Radmanest im Banat. - Jahrbuch k. k. geol. Reichsanst., **20** (3): 343-364, Wien.
- FUCHS, Th. (1870b): Die Fauna der Congerienschichten von Tihany am Plattensee und Kup bei Pápa in Ungarn. - Jahrb. geol. Reichsanst., **20**. Wien.
- FUCHS, Th. (1872): Über den sogenannten "chaotischen Polymorphismus" und einige fossile *Melanopsiden*-Arten. - Verh. d. zool.-botan. Ges. Wien, **22**.
- GASULL, L. (1971): Fauna malacológica de las aguas continentales dulces y salobres del Sureste Ibérico. - Bol. R. Soc. Hist. Nat. Baleares, **16**: 23-94.
- GASULL, L. (1981): Fauna malacológica terrestre y de agua dulce de la provincia de Castellón de la Plana. - Bol. R. Soc. Hist. Nat. Baleares, **25**: 55-102.
- GEARY, D.H. (1988): Heterochrony in gastropods: a paleontological view. - In: McKINNEY, M.L. (ed.), Heterochrony in evolution: a multidisciplinary approach, pp. 183-196. New York (Plenum Press).
- GEARY, D.H. (1990): Patterns of evolutionary tempo and mode in the radiation of *Melanopsis* (Gastropoda: Melanopsidae). - Paleobiology, **16**(4): 492-511. Jacksonville.
- GEARY, D.H. (1990): Exploring the roles of intrinsic and extrinsic factors in the evolutionary relations of *Melanopsis*. - In: ROSS, R.B. & ALLMON, W. A. (eds.) Causes of Evolution. A paleontological perspective. - p. 305-321, The University of Chicago Press, Chicago.
- GEARY, D.H. (1992): An unusual patterns of divergence between two fossil gastropods: ecophenotypy, dimorphism, or hybridization. - Paleobiology, **18**(1): 93-109, Jacksonville.
- GEARY, D.H.; RICH, J.; VALLEY, J.W. & BAKER, K. (1989): Stable isotopic evidence of salinity change: influence on the evolution of melanopsid gastropods in the late Miocene Pannonian basin. - Geology, **17**: 981-985.
- GLAUBRECHT, M. (1993): Mapping the diversity: Geographical distribution of the freshwater snail *Melanopsis* (Gastropoda: Cerithioidea: Melanopsidae) with focus on its systematics in the Mediterranean Basin. - Mitt. Hamb. Zool. Mus. Inst., **90**: 41-97.
- GLAUBRECHT, M. (1996): Evolutionsökologie und Systematik am Beispiel von Süß- und Brackwasserschnecken (Mollusca: Caenogastropoda: Cerithioidea): Ontogenese-Strategien, paläontologische Befunde und historische Zoogeographie. - Backhuys Publishers, Leiden. 544 pp.
- GLAUBRECHT, M. (2000): A look back in time- Toward a historical biogeography as a synthesis of systematic and geological patterns outlined with limnic gastropods. - Zoology **102**: 127-147, Stuttgart.
- HANDMANN, R. (1887): Die fossile Conchylienfauna von Leobersdorf im Tertiärbecken von Wien. Münster.

- HELLER, J., SIVAN, N. & MOTRO, U. (1999): Systematics, distribution and hybridization of *Melanopsis* from the Jordan Valley (Gastropoda: Prosobranchia). - Journal of Conchology, 36: 49-81.
- HENNIG, W. (1966): Phylogenetic systematics. - 263 p., Univ. Illinois Press, Urbana, Chicago, London.
- HILGENDORF, F. (1867): Über *Planorbis multiformis* im Steinheimer Süßwasserkalk. - Monatsbericht der königlich Preussischen Akademie der Wissenschaften, Berlin 1866: 474-501.
- HÖRNES, M. (1856): Die fossilen Mollusken des Tertiärbeckens von Wien - Univalven. - Abhandlungen der kaiserlich-königlichen Geologischen Reichsanstalt, 3:1-430, Wien.
- HOUBRICK, R.S. (1991): Anatomy and systematic placement of *Faunus* MONTFORT, 1810 (Prosobranchia: Melanopsinae). - Malacol. Review, 24: 35-54. Ann Arbor.
- HOROWITZ, A. (1979): The Quaternary of Israel. - Academic Press, New-York, 394 p.
- HUCKRIEDE, R. (1966): Das Quartär des Arabischen Jordan-Tales und Beobachtungen über Pebble Culture und Prauringac. Eiszeitalter und Gegenwart. Vol. 17, pp. 211-212.
- (1966):
- JAECKEL, S.G., KLEMM, W. & MEISE, W. (1958): Die Land- und Süßwassermollusken der nördlichen Balkanhalbinsel. - Abh. Ber. Staatl. Mus. Tierkunde, Dresden, 23:141-246, Dresden.
- JEKELIUS, E. (1944): Sarmat und Pont von Soceni (Banat). - Memorie Institutului al Romaniei 5: 1-167. Imprimeria Nationala; Bucharest.
- JODOT, P. (1958): Les faunes des mollusques continentaux reparties dans le sud-est de l'Espagne entre le Miocene Supérieur et le Quaternaire. - Mem. Comun. Inst. Geologica, Barcelona 17: 134 p.
- JONES, R.W. & SIMMONS, M.D. (1996): A review of the stratigraphy of Eastern Paratethys (Oligocene - Holocene). - Bull. Nat. Hist. Mus. Lond. (Geol.) 52: 25-49.
- KECSKEMÉTI-KÖRMENDI, A. (1972): A Dorogi-Medencei Eocén Mollusca Fauna. - Annales Instituti Geologici Publici Hungarici 55:147-377, Budapest.
- KINZELBACH, R. (1987): Faunal history of some freshwater invertebrates of the Northern Levant (Mollusca, Crustacea). - In: KRUPP, F., SCHNEIDER, W. & KINZELBACH, R. (eds.), Proc. Symp. the fauna and zoogeography of the Middle East, Mainz; Beih. TAVO, A 28: 41-61. Wiesbaden (REICHERT).
- KOBELTY (1904): Die geographische Verbreitung der Mollusken in dem palaearktischen Gebiet. - In: ROSSMAESSLER, E.A. (ed.), Iconographie der Land- und Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten, N.F. 11118-120, Wiesbaden.
- KORECZ, A. (1985): Die Ostracodenfauna des Zsambeker Beckens. - Chronostratigraphie und Neostatotypen. Miozän der Zentralen Paratethys, 7: 173-176, Akademiai Kiado, Budapest.
- KORMOS, T. (1903): Beiträge zur Kenntnis der *Melanopsis*-Arten aus den Thermen von Püspökfürdő bei Nagyvárad. - Földt. Közlöny, 33(1-4): 496-503. Budapest.
- KORMOS, T. (1905): Über den Ursprung der Thermenfauna von Püspökfürdő. - Földt. Közlöny, 35(8-9): 421-452. Budapest.
- KORPÁS-HÓDI, M. (1983): Palaeoecology and biostratigraphy of the pannonian Mollusca fauna in the northern forland of the Transdanubian central range. - Ann. Inst. Geol. Pub. Hung., 66: 1-163. Budapest.
- KOWALKE, T. & BANDEL, K. (1996): Systematik und Paläoökologie der Küstenschnecken der nord-alpinen Brandenburg-Gosau (Oberconiac/Untersanton) mit einem Vergleich zur Gastropodenfauna des Maastrichts des Tremeckens (Südpyrenäen, Spanien). - Mitt. Bayer. Staatsslg. Paläont. hist. Geol., München, 15-71, 5 Pl., 10 Tab.
- KROLOPP, E. (1977): Angaben zur Entfaltung der mitteleuropäischen fluviatilen Molluskenfauna. - Malacologia, 16(1): 149-153. Ann Arbor.
- LOCARD, A. (1883): Malacologie des lacs de Tibériade, d'Antioche et d'Horns. - HENRI GEORG, Lyon, 99 pp.
- LÖRÉNTHEY, E. (1902): Die Pannonische Fauna von Budapest. - Palaeontogr., 48: 137-296. Stuttgart.
- LÖRÉNTHEY, E. (1911): Beiträge zur Kenntniss der Fauna der Pannonischen Schichten in der Umgebung des Balatonsees. - In: Resultate der wissenschaftlichen Erforschung des Balatonsees 1/1, Paläontologischer Anhang 4/3: 1-215. Budapest.
- LUEGER, J.P. (1978): Klimaentwicklung im Pannon und Pont des Wiener Beckens aufgrund von Landschneckenfaunen. - Anz. Österr. Akad. Naturwiss. Math. - Naturwiss. Kl. v. : 127-149, Wien.
- LUEGER, J. (1980): Rezente Flußmollusken im Pannon (o. Miozän) des Wiener Beckens (Österreich). Sitzungsber. Österr. Akad. Wiss., math.-naturw. Kl. 6. Wien.

- MACUMBER P.G. & HEAD H.J. (1991): Implications of the Wadi al-Hammeh sequences for the terminal drying of Lake Lisan, Jordan. - *Palaeogeography, Palaeoclimatology, Palaeoecology* **84**, 163-173
- MADURGA MARCO, C. 1973: Los gasteropodos dulceacuicolas y terrestres del Cuaternario espanol. - *Boletin de la Real Sociedad Espaniola de Historia Natural (Geol.)*, **71**: 43-165, Madrid.
- MARTINEZ-LOPEZ, F., ALFONSO, S. & PUJANTE, A. (1988): La malacofauna de la cuenca del Rio Mijares (Castellon, Espana): distribucion y aspectos ecologicos. - *Iberus*, **8**(2): 65-70. Sevilla.
- MÁTYÁS, J.; BURNS, S.J.; MÜLLER, P. & MAGYAR, I. (1996): What can stable isotopes say about salinity? An example from the late miocene pannonian lake. - *Research Reports*, **11**:31-39. Palaios.
- MENSINK, H. (1984): Die Entwicklung der Gastropoden im miozänen See des Steinheimer Beckens (Süddeutschland). - *Palaeontographica*, **A**, **183**:1-63, Stuttgart.
- MIENIS, H. (1983): A preliminary checklist of the freshwater molluscs of Israel and administered areas. - *Levantina* **47**: 543-550.
- MORRISON, J.P.E (1954): The relationship of Old and New World melanians. - *Proc. U.S.Nat.Mus.*, **103**:357-394, Washington.
- MOUHADIS, A., IDAGHDOUR, M., GHAMIZI, M. & MONÉ, H. (1995): Preliminary results on the reproductive strategy of *Melanopsis praemorsa* (Prosobranchia: Thiaridae). - *Abstr. 12th Int. Malaol. Congr. Vigo*: 37, Viego.
- MÜLLER, P. & MAGYAR, I. (1992): Continuous record of the evolution of lacustrine cardiid bivalves in the late Miocene Pannonian Lake. - *Acta Palaeontologica Polonica*, **36**:353-372.
- NEEV, D. & EMERY, K.O. (1967): The Dead Sea, depositional processes and environments of evaporites. - *Geol. Surv. Isr. Bull* **41**:147 pp.
- NEUMAYR, M. (1880): Über den geologischen Bau der Insel Kos und über die Gliederung der Jungtertiären Binnenablagerungen des Archipels. - *Denkschr. k. Akad. Wiss.*, **40**: 213-314. Wien.
- NEUMAYR, M. (1880): Die Mittelmeer-Conchylien und ihre jungtertiären Verwandten. - *Jahrbuch der deutschen malakologischen Gesellschaft*, **7**:201-224, Frankfurt a.M.
- NEUMAYR, M. & PAUL, M.C. (1875): Die Congerien- u. Paludinenschichten Slavoniens und deren Faunen. - *Abhandlungen der geologischen Reichsanstalt*, **7**, Wien.
- NÜTZEL, A. & BANDEL, K. (1993): Studies on the side-branch planorbids (Mollusca, Gastropoda) of the Miocene carter lake of Steinheim am Albuch (Southern Germany). - *Scripta Geol., Spec. Issue* **2**: 313-313, Leiden.
- OPPENHEIM, P. (1891a): Die Brackwasserfauna des Eozän im nordwestlichen Ungarn. - *Z. dtsh. geol. Ges.*, **43**: 801-814. Berlin
- OPPENHEIM, P. (1891b): Beiträge zur Kenntnis des Neogen in Griechenland. - *Z. dt. geol. Ges.*, **43**: 420-487. Berlin.
- OPPENHEIM, P. (1892): Über einige Brackwasser- und Binnenmollusken aus der Kreide und dem Eozän Ungarns. - *Z. dtsh. geol. Ges.*, **44**: 697-818. Berlin.
- PAGET, O.E. (1976): Die Molluskenausbeute der Insel Rhodos. - *Ann. Naturhist. Mus. Wien*, **80**: 681-780, Wien.
- PALLARY, P. (1911): Description de quelques *Melanopsis* nouveaux ou peu connus du Maroc. - *Bull. Soc. hist. nat. Afrique du Nord*, **3**(8): 1-8. Algier.
- PALLARY, P. (1924): Revision des *Mélanopsis* de l'Espagne. - *Bull. Soc.Hist. Nat. Afrique du Nord*, **15**: 240-254. Algier.
- PALLARY, P. (1926): Répertoire des *Mélanopsis* fossiles et vivants connus en 1925. - *Bull. Soc. hist. nat. Afrique du Nord*, **17**: 73-93, 126-136. Algier.
- PALLARY, P. (1939): Deuxième addition a la faune malacologique de la Syrie. - *Mémoires de l'Institut d'Egypte*, **39**: 1-141. Cairo.
- PAPP, A. (1944): Brack- und Süßwasserfaunen Griechenlands. 2. Brack- und Süßwasserarten von Kythera. - *Ann. Géol. Pays Hellén.* **1**: 112-119, Athen.
- PAPP, A. (1951): Das Pannon des Wiener Beckens. - *Mitt. Geol. Ges.*, **39**-41. Wien.
- PAPP, A. (1953a): Die Molluskenfauna des Pannon im Wiener Becken. - *Mitt. geol. Ges. Wien.*, **44** [1951]: 85-222. Wien.
- PAPP, A. (1953b): Brack- und Süßwasserfaunen Griechenlands. IV. Süßwassermollusken aus dem Pliozän von Elis (Peloponnes). - *Ann. Géol. Pays Hellén.*, **5**: 107-113, Athen.

- PAPP, A. (1954): Die Molluskenfauna im Sarmat des Wiener Beckens. - Mitt. geol. Ges. Wien **45**: 1-112.
- PAPP, A. (1955a): Über einige Süßwassergastropoden aus pliozänen Ablagerungen Griechenlands. - Ann. Géol. Pays Hellén., **6**: 145-160. Athen.
- PAPP, A. (1955b): Brack- u. Süßwasserfaunen Griechenlands. V. Bemerkungen über Melanopsiden der Untergattung *Melanosteira* OPPENHEIM 1891. - Ann. Géol. Pays Hellén., **6**: 122-132, Athen.
- PAPP, A. (1985): Die Mollusken-Fauna des Pannonien der zentralen Paratethys. pp. 274-339, in PAPP, A., JÁMBOR & STEININGER (eds.): Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys 7, M 6 Pannonien. - Akadémiai Kiadó. Budapest.
- PAPP, A. & THENIUS, E. (1954): Vösendorf - ein Lebensbild aus dem Pannon des Wiener Beckens. - Mitt. Geol. Ges. Wien, **46**. Wien.
- PAPP, A. & PSARONIUS (1955): Über einige Süßwassergastropoden aus pliozänen Ablagerungen Griechenlands. - Ann. Géol. Pays Hellén., **6**: 145-150, Athen.
- PAVLOVIC, P. (1928): Les mollusques du Pontien inférieur des environs de Beograd. - Ann. Geol. Balk. **9**.
- PERES, J.M. (1939): Contribution à l'étude de *Melanopsis* du Maroc. - J. Conchyl., **83**: 129-162. Paris.
- PERES, J.M. (1945): Contribution à l'étude de *Melanopsis*. - J. Conchyl., **86**: 109-174. Paris.
- PICARD, L. (1934): Mollusken der levantinischen Stufe Nordpalästinas (Jordanal). - Archiv für Molluskenkunde, **66**: 105-139. Frankfurt a. M.
- PILKINGTON, M.C. (1976): Description of veliger larvae of montocardian gastropods occurring in Otago plankton hauls. - Journal of Molluscan Studies, **42**: 337-360.
- PUJANTE, A. & GALLARDO, A. (1990): Distribucion del genero *Melanopsis* Ferussac, 1807 en algunos rios de Andalucía occidental (España). - Iberus, **9**(1-2): 439-447. Sevilla.
- PUJANTE, A., MARTINEZ-LOPEZ, F. & SALVADOR, A. (1988a): Aportaciones al conocimiento de la anatomia interna de *Melanopsis dufouri* Fer., 1823. - Iberus, **8**(2): 59-64. Sevilla.
- PUJANTE, A., MARTINEZ-LOPEZ, F. & SALVADOR, A. (1988b): Estudio comparado de dos poblaciones de *Melanopsis* FER., 1807 de Alhama de Aragon y Jaraba (Zaragoza, España). - Iberus, **8**(2): 65-70. Sevilla.
- PUJANTE, A., MARTINEZ-LOPEZ, F. & TAPIA, G. (1990): Analisis mediante el meb de la protoconcha de *Melanopsis dufouri* FERUSSAC, 1823. - Iberus, **9**(1-2): 461-466. Sevilla.
- RIEDEL, F. (1993): Early ontogenetic shell formation in some freshwater gastropods and taxonomic implications of the protoconch. - Limnologica, **23**(4): 349-368. Jena.
- RÖGL, F. & STEININGER, F.F. (1983): Vom Zerfall der Tethys zu Mediterran und Paratethys. Die neogene Paläogeographie und Palinspastik der zirkum-mediterranen Raumes. - Ann. Naturhist. Mus. Wien, **85/A**: 135-163. Wien.
- RÖGL, F. & STEININGER, F.F. (1984): Neogene Paratethys, Mediterranean and Indo-Pacific Seaways. Implications for the paleobiogeography of marine and terrestrial biotas. - Fossils and Climate **171-200**.
- ROYDEN & HORVÁTH, F. (1988): The Pannonian Basin: A study in Basin evolution. - American Association of Petroleum Geologists Memoir, **45**: Tulsa 394 pp.
- ROYO GÓMEZ, J. R. (1922): El Mioceno continental Ibérico y su fauna Malacologica. - Comision de Investigaciones Paleontologicas y Prehistoricas, Madrid. 215 pp.
- RUST, J. (1997): Evolution, Systematik, Paläoökologie und stratigraphischer Nutzen neogener Süß- und Brackwasser- Gastropoden im Nord- Ägais- Raum. - Palaeontog. Abt.A, **243**: 37-180, Stuttgart.
- SANDERBERG, C.L.F. (1870-1877): Die Land- und Süßwasser-Cochylien der Vorwelt. - **VIII**: 1000, Wiesbaden.
- SCHRÉTER, Z. (1978): Studien über Melanopsiden aus dem Unterpleistozän der Ungarischen Volksrepublik. - Schriftenr. geol. Wiss. Berlin, **10**: 87-111. Berlin.
- SCHÜTT, H. (1965): Zur Systematik und Ökologie türkischer Süßwasserprosobranchier. - Zoologische Mededelingen, Leiden, **41**: 43-73. Leiden.
- SCHÜTT, H. (1983): Die Molluskenfauna der Süßgewässer im Einzugsgebiet des Orontes unter Berücksichtigung benachbarter Flußsysteme. - Archiv für Molluskenkunde, **113**: 1-91. Frankfurt a.M.
- SCHÜTT, H. (1984): Die bisher aus Jordanien bekannten süßwasser- und landbewohnenden Mollusken anhand der Aufsammlungen von Dr. BANDEL 1978. - Natur und Mensch, 1983: 49-64. Nürnberg.
- SCHÜTT, H. (1986): Mollusken aus jungpliozänen Seesedimenten von Antirrhion in Akarnanien. - Ann.Géol.Pays Helléniques, **33**: 339-361, Athen.

- SCHÜTT, H. (1987): The molluscs of the oasis Palmyra.- In: Krupp, F., SCHNEIDER, W. & KINZELBACH, R. (eds.), Proc. Symposium on the fauna and zoogeography of the Middle East, Mainz; Beihefte zum TAVO, A 28: 62-72. Wiesbaden (Reichert).
- SCHÜTT, H. (1988a): Über eine relikthäre *Melanopsis* aus Jordanien. Ein Beitrag zur Kenntnis der Rassenbildung durch geographische Isolation.- Annalen des Naturhistorischen Museums in Wien, 90: 215-219. Wien.
- SCHÜTT, H. (1988b): Ergänzungen zur Kenntnis der Molluskenfauna oberpliozäner Süßwasserkonglomerate Syriens. - Archiv für Molluskenkunde, 118:129-143. Frankfurt a. M.
- SCHÜTT, H. (1988c): Mollusken aus den tertiären Brackwasserschichten von Githion in Lakonia (Griechenland).- Geologica et Palaeontologica, 22: 145-155. Marburg.
- SCHÜTT, H. & BILGIN, F.H. (1974): Recent *Melanopsines* of the Aegean.- Archiv für Molluskenkunde, 104: 59-64. Frankfurt a.M..
- STALEY, A.W. (1992): Patterns of morphologic change and iterative evolution in the gastropod genus *Melanopsis* from the Late Miocene Pannonian Basin. Unpublished Masters Thesis; University of Wisconsin, Madison.
- STARMÜHLNER, F. (1961): Eine kleine Molluskenausbeute aus Nord- und Ostiran. - Sitz. Ber. Österr. Akad. Wiss. Wien, math.-nat. Kl. (I), 170(3/4): 89-99. Wien.
- STARMÜHLNER, F. (1970): Etudes hydrobiologiques en Nouvelle-Calédonie. Die Mollusken der Neukaledonischen Binnengewässer. - Cah. ORSTOM, sér. Hydrobiol., 4(3/4): 3-127. Paris.
- STARMÜHLNER, F. (1973): Die Gattung *Melanopsis* FERUSSAC 1807 auf Neukaledonien.- Malacologia, 14: 242-243. Ann Arbor.
- STARMÜHLNER, F. (1979): Distribution of freshwater molluscs in mountain streams of tropical Indo-Pacific islands (Madagascar, Ceylon, New Caledonia). - Malacologia, 18(1): 245-255. Ann Arbor.
- STARMÜHLNER, F. & EDLauer, A. (1957): Ergebnisse der Österreichischen Iran-Expedition 1949/50: Beiträge zur Kenntnis der Molluskenfauna des Iran.- Sitz. Ber. Österr. Akad. Wiss., math.-nat. Kl. (I), 166(9/10): 435-494. Wien.
- STEININGER, F.F. & RÖGL, F. (1984): Paleogeography and palinspastic reconstruction of the Neogene of the Mediterranean and Paratethys. - In: DIXON, J.E. & ROBERTSON, A.H.F. (eds.), The geological evolution of the Eastern Mediterranean. Spec. Publ. Geol. Soc. London, 17: 659-668. Oxford, London (Blackwell Scient. Publ.).
- STEVENS, G.R. 1994: Developing trends in western Pacific biogeography in Late Mesozoic and Cenozoic times. - Palaeopelagos, special publication, 1: 397-420.
- STRAUSZ, L. (1942): Das Pannon des mittleren Westungarns. - Annales Historico- Nat. Mus. Nat. Hun., pars Min., Geol. et Palaeont., 5: 1-102, Budapest.
- STRAUSZ, L. (1955): Zur Fauna des Mittelmiozäns von Várpalota. - Földtani Közl. 85(2): 198-210. Budapest.
- SUNDERBRINK, O. (1929): Zur Frage der Verwandtschaft zwischen Melaniiden und Cerithiiden. - Zeit. Morph. Ökol. Tiere, 14: 261-337. Jena.
- SZÖTS, E. (1953): Magyarorszag eocen puhatestűi. I. Gantkörnyeki eocen puhatestűek.- Geologica Hungarica, Series Palaeontologica,, 22:1-270, Budapest.
- TAUSCH, L. (1886): Über die Fauna der nicht-marinen Ablagerungen der Oberen Kreide des Csongerthales bei Ajka im Bakony (Ungarn) und über einige Conchylien der Gosauermegel von Aigen bei Salzburg.- Abh. Geol. Reichsanstalt, 12(1): 1-32. Wien.
- TAYLOR, D.W. (1968): Summary of North American Blancan nonmarine molluscs. - Malacologia 4: 1-172.
- TCHERNOV, E. (1973): On the Pleistocene molluscs of the Jordan valley. - Israel Academy of Science and Humanities, 1973: 1-50. Jerusalem.
- TCHERNOV, E. (1975a): The Molluscs of the Sea of Galilee.- Malacologia, 15: 147-184. Ann Arbor.
- TCHERNOV, E. (1975b): The early Pleistocene molluscs of 'Erq el-Ahmar.- Israel Academy of Science and Humanities, 1975: 7-36. Jerusalem.
- THIELE, J. (1929): Handbuch der Systematischen Weichtierkunde. Teil 1. 376 pp. Jena (Fischer).
- TRISTRAM, H.B. (1865): Report on the terrestrial and fluviatile Mollusca of Palestine. - Proceedings of the Zoological Society of London, 530-545.
- TROSCHEL (1856-63): TROSCHEL, F.H. (1856-1863): Das Gebiss der Schnecken zur Begründung einer natürlichen Classification. Bd. 1: 252 pp. Berlin (Nicolaische Verlagsbuchhandlung).
- TRUC, G. (1971): Gastéropods continaux néogènes du Bassin Rhodanien. - Docum. Lab. Géol. Univ. Lyon (H.S.), 49: 79-129.

- WENZ, W. (1938). Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. - In : SCHINDEWOLF O.H. (ed.), Handbuch der Paläozoologie, **6 (1)**, 1639 pp., Berlin (Borntraeger).
- WILLMANN, R. (1979): Erhöhung der Evolutionsgeschwindigkeit bei Verringerung der Populationsgröße. - Umschau, **79(14)**: 451-453.
- WILLMANN, R. (1980): Die neogenen Süßwassergastropoden von Chersonisos (Kreta). - N. Jb. Geol. Paläont. Abh., **159**: 273-295. Stuttgart.
- WILLMANN, R. (1981): Evolution, Systematik und stratigraphische Bedeutung der neogenen Süßwassergastropoden von Rhodos und Kos/Ägäis. - Palaeontographica, Abt. A., **174**: 10-235. Stuttgart.
- WILLMANN, R. (1983): Die Schnecken von Kos. - Spektrum der Wissenschaft, Februar 1983: 64-76.
- WILLMANN, R. (1985a): Responses of the Plio-Pleistocene freshwater gastropods of Kos (Greece, Aegean Sea) to environmental changes. - In: BAYER, U. & SEILACHER, A. (eds.), Sedimentary and Evolutionary Cycles, pp. 295-321. Berlin, Heidelberg (Springer).
- WILLMANN, R. (1985b): Die Art in Raum und Zeit. Das Artkonzept in der Biologie und Paläontologie. - Parey. Berlin, Hamburg: 207 pp.
- WILLMANN, R. & PIEPER, H. (1978): Gastropoda. - In: ILLIES, J. (ed.), Limnofauna Europaea, pp. 118-134. 2. Aufl. Stuttgart (Fischer).