



MIOCENE LAND SNAILS FROM BĘŁCHATÓW (CENTRAL POLAND). IV: PUPILLOIDEA (GASTROPODA PULMONATA). SYSTEMATIC, BIOSTRATIGRAPHIC AND PALAEOECOLOGICAL STUDIES

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ABSTRACT: Twenty five species of Pupilloidea of 10 genera have been found in the Miocene brown coal deposits of the open-cast mine Bełchatów. Four genera: *Gastrocopta*, *Strobilops*, *Nesopupa* and *Negulus* became extinct in Europe before the first major glaciation. Another one – *Planogyra* – is now represented by one extant species in southern Europe only. Three malacofauna-bearing horizons: Beł-C, Beł-B and Beł-A are correlated with biozones MN 4, MN 5 and MN 9, respectively. Analysis of ecological requirements of extant pupilloid snails, particularly of the taxa extinct in Europe and found in the Bełchatów mine, combined with palaeobotanical data, provide some palaeoecological and palaeoclimatic cues. Stratigraphic significance of some pupilloid species is discussed. A new combination, *Nesopupa minor* (Boettger, 1870), is proposed.

KEY WORDS: Pupilloidea, Miocene, Bełchatów, Poland, systematics, biostratigraphy, palaeoecology

INTRODUCTION

Pupilloidea underwent the most spectacular changes during the Neogene, resulting in extinction in Europe of some genera, which today have representatives in remote regions of the world. Twenty five species of Pupilloidea of 10 genera have been identified in the Miocene deposits of the Bełchatów brown coal mine. Of these, four genera, namely *Gastrocopta*, *Strobilops*, *Nesopupa* and *Negulus*, became extinct in Europe before the first major glaciation. Another genus, *Planogyra*, is now represented in Europe by only one extant species; its occurrence is limited to the western parts of the Balkan Peninsula and Italy (GITTENBERGER 1972). Apart from Pupilloidea, land Prosobranchia (STWORZEWICZ 1995, STWORZEWICZ & SOŁTYS 1996), Carychiinae (STWORZEWICZ in press), one species of *Helicodiscus* (STWORZEWICZ & PRISYAZHNYUK 1997) and other representatives of Endodontidae, Clausiliidae, Subulinidae, Vitrinidae, Zonitidae and Helicidae have been found. Freshwater

gastropods and bivalves have been dealt with by PIECHOCKI (1997).

The brown coal mine Bełchatów (51°15'N, 19°20'E) is one of the largest open-cast mines in Central Europe. The thickness of the brown coal deposits reaches ca. 60 m (locally 250 m). According to the lithostratigraphic scheme of the Tertiary deposits in the Bełchatów basin (cf. STWORZEWICZ & SZYNKIEWICZ 1989, STUCHLIK & SZYNKIEWICZ 1998) lacustrine limestones with molluscan and mammalian remains were found in the coal unit W – in the upper part of the main coal seam (Beł-C) and above xylitic brown coal seam B (Beł-B), as well as in the mid part of clayey-coal unit I-W consisting of clays and small xylitic-clayey coal layers with lacustrine limestone intercalations (Beł-A) (Fig. 1). Within the Neogene sequence, exposed in the Bełchatów mine escarpments, there are several tuffitic intercalations that enable dating. Zircons extracted from two of them yielded

fission-track ages of 18.1 ± 1.7 My and 16.5 ± 1.3 My (BURCHART et al. 1988). These dates suggest that the part of the sediment was deposited between the Upper Eggenburgian and the Mid Badenian. One more tephra layer has been lately sampled for subsequent radiometric dating.

Based on mammalian remains (KOWALSKI 1993a, b, KOWALSKI & KUBIAK 1993), the three fauna-bearing horizons: Beł-C, Beł-B and Beł-A have been correlated with MAIN's biozones MN 4, MN 5/6 and MN 9, respectively. However, taking into account the above fission-track dates, it is more probable that horizons Beł-B and Beł-C are somewhat older: Beł-B should rather be correlated with MN 5 and Beł-C with MN 3/4 or even MN 3 (SZYNKIEWICZ pers. com.). The Lower and Mid Miocene age of the deposits was also confirmed by pollen and leaf flora analyses (STUCHLIK et al. 1990, WOROBIEC 1995, STUCHLIK & SZYNKIEWICZ 1998). Due to the continuous exploitation of the coal bed, two upper fauna-bearing horizons (Beł-A and Beł-B) have been covered with an overlay and their further palaeontological examination is impossible, whereas the lowermost horizon Beł-C is still regularly sampled.

The material collected hitherto in Bełchatów provides an exceptional opportunity to study the changes of malacofauna during almost ten million years.

Specimens of land snails from Bełchatów are stored at the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, under catalogue numbers given in the text.

The following abbreviations of the museum collections have been used in the text:

BSP – Bayerische Staatssammlung für Paläontologie und Historische Geologie (Munich)

IGS – Institute of Geological Sciences (Kiev)

ISEA PAS – Institute of Systematics and Evolution of Animals, Polish Academy of Sciences (Cracow)

Fig. 1. Lithostratigraphic scheme of the Tertiary brown coal deposits of the open-cast mine Bełchatów and correlation of the malacofauna-bearing horizons: 1 – erosion border of the Tertiary and Quaternary (Q) deposits, 2 – sands, 3 – coaled sands with plant detritus, 4 – clayey sands, 5 – peat, 6 – clays, 7 – coaled clays, 8 – sapropelic coals, 9 – xylite-sapropelic brown coals with clay, 10 – xylite brown coals, 11 – bituminous-pyropissite brown coals, 12 – lacustrine limestones, 13 – weathered Mesozoic rocks with silica or ferruginous cement, 14 – silicated sands or quartzitic sandstones, 15 – kaolinized volcanic tuff (paratonstein), 16 – distinct erosion borders and discordance, 17 – range of palaeontological profiles with continental mammals and malacofauna (Beł-A, Beł-B, Beł-C – profile numbers, MN 4, MN 5, MN 9 – continental Neogene Mammalian zone number) (according to STWORZEWICZ & SZYNKIEWICZ 1989 and STUCHLIK & SZYNKIEWICZ 1998).



MAFI – Magyar Állami Földtani Intézet (Hungarian Geological Survey – Budapest)

MHN – Muséum d'Histoire Naturelle (Toulouse)

MNHN – Muséum National d'Histoire Naturelle (Paris)

NHML – The Natural History Museum (London)

NMP – Narodni Muzeum (Prague)

NMW – Naturhistorisches Museum (Vienna)

PIM – Paleontological Institute of Russian Academy of Sciences (Moscow)

SMF – Senckenberg Museum (Frankfurt/Main).

Unfortunately, holotypes of most species discussed in this paper were destroyed during the Second World War (cf. LUEGER 1981). Remarks on the remaining types (those that could be located) are given in the text.

All measurements (in mm) were taken with Nikon measurescope MM-11, accuracy 0.01 mm; whorls were counted according to EHRMANN'S (1933) method.

SEM photos of gold-coated shells were taken with Jeol JCF-35 at the laboratory of Collegium Medicum, Jagiellonian University.

SYSTEMATIC REVIEW

Family: Pupillidae Turton, 1831

Genus: *Argna* Cossmann, 1889

***Argna oppoliensis* (Andreae, 1902)**

Figs 2–5

1902 *Coryna oppoliensis* ANDREAE: 16, Fig. 8a.

1902 *Coryna oppoliensis* var. *turrita* ANDREAE: 16, Fig. 8b.

1956 *Agardhia sümegehyi* BARTHA: 519, Pl. 4: Figs 3–4, 7–8.

1976 *Argna oppoliensis* – SCHLICKUM: 10, Pl. 2: Fig. 28.

Material examined: Bełchatów: Beł-B – 8 specimens MI/990/98, 2 specimens MI/991/98 with damaged aperture, 33 damaged specimens without aperture MI/992/98; Opole (Astaracian, MN 7+8) – 1987/43/1 (NMW), 152511/2 (SMF), 1954 XV/1 and 1966 XXVI (BSP).

Measurements of 8 adult shells from Bełchatów and one from Opole:

	Shell		Aperture		Body whorl	Number of whorls	H/W ratio
	H	W	h	w	H		
Beł-B	2.59	1.15	0.94	0.76	1.45	6.0	2.25
	2.80	1.19	1.02	0.78	1.53	6.0	2.35
	2.80	1.12	1.03	0.79	1.55	6.0	2.50
	2.82	1.15	1.02	0.71	1.53	6.0	2.45
	2.83	1.14	0.99	0.72	1.59	6.0	2.48
	2.86	1.16	1.01	0.80	1.51	6.0	2.46
	3.08	1.23	1.09	0.73	1.60	6.5	2.50
	3.29	1.15	0.92	0.75	1.54	7.0	2.86
Opole	2.70	1.04	0.90	0.67	1.54	6.0	2.59

Comparative remarks: Specimens from Bełchatów vary in the height of whorls and in the general shape of their shells which is cylindrical or claviform, whereas their aperture shape and apertural barriers are only slightly variable. They were referred to *A. oppoliensis*, but the systematic position of the species

and its description by ANDREAE (1902) require a comment. Neither ANDREAE nor subsequent authors took into consideration all of the apertural barriers that are actually present in this species. A close examination of over a dozen specimens of *A. oppoliensis* from Opole (ex coll. BSP, NMW and SMF) and those from Bełchatów indicates that, besides one parietal, one columellar and two palatal lamellate teeth (noted by ANDREAE 1902) there are very often two small, short-lamellate or knob-shaped additional barriers: supraparietal (spiralis) and infracolumellar teeth, located deep inside the aperture, hardly visible in a direct front view, and a rudimentary basal tooth situated at a distance from the aperture margin, often missing (Fig. 4). Two of the specimens from Bełchatów have also a rudimentary suprapalatal tooth. This type of apertural barriers makes *A. oppoliensis* similar to recent *A. biplicata* (Michaud, 1831), and particularly to *A. biplicata excessiva* (Gredler, 1856) and to *A. bielzi* (Rossmässler, 1859). However, the shells of the fossil species are nearly by half smaller than those of the latter two and they have fewer whorls (by 3–4). Besides, in recent *A. bielzi* there is a distinct callus between the apertural margin and the palatal teeth, but there is no trace of small knob-shaped surface tooth (sensu SHILEYKO 1984) on the palatal margin, the tooth being rather well visible in most specimens of *A. oppoliensis* from Opole (Fig. 5) and less distinct (looking like a convexity rather than a tooth) in the shells of ANDREAE'S (1902) var. *turrita* and in specimens from Bełchatów (Fig. 3). The shell surface of *A. oppoliensis* is very weakly and rather irregularly striated or nearly smooth, similar to that of *A. biplicata*, whereas *A. bielzi* differs from both in having its surface sculpture composed of regular, rib-like striae. Nevertheless, *A. oppoliensis* can be undoubtedly regarded as an ancestor of the mentioned living species.

Examination of almost two hundred shells of *A. bielzi* from a valley in the Tatra Mts (W Carpathian Mts, coll. ISEA PAS) revealed a great variability in the shell shape, number of whorls and their convexity, as



well as in the position and degree of development of palatal teeth. This induced me to regard some forms of *Argna* known from Miocene and Pliocene as conspecific.

Figs 2–5. *Argna oppoliensis* (Andreae): 2 – specimen from Belchatów, front view, H = 2.72 mm; 3 – aperture with some teeth visible (lower palatal weakly developed), 100×; 4 – aperture with palatal wall broken, all teeth visible; 5 – aperture of specimen from Opole (lower palatal tooth strongly developed), 100×

According to ANDREAE (1902) the shells of *A. oppoliensis* var. *turrita* are higher (3.5 mm) than those of *A. oppoliensis* (2.5–3 mm) and have a higher number of whorls (7 instead of 5–6), while such a variability range is a normal phenomenon in *A. bielzi*, even within one population. Among the specimens from Bełchatów there are also some with higher shells (above 3 mm) and a higher number of whorls (6.5–7). Hence, in my opinion ANDREAE'S (1902) var. *turrita* (treated as a subspecies by subsequent authors) should not be regarded as a separate form on subspecific level, but as a morphotype at most.

In the light of the above facts, the systematic distinction of *A. suemeghyi* (Bartha, 1956) and *A. reyi* Schlickum, 1978 also seems to be questionable. Disregarding the overlapping shell shape and the number of whorls of all the mentioned forms/species, the only clear difference between *A. oppoliensis* from Bełchatów on one hand and *A. oppoliensis* from Opole and *A. suemeghyi* from Tab (ex coll. MAFI No. Pl. 116) on the other, is a weakly or strongly developed lower palatal tooth (Figs 3, 5). However, both such a variability of palatal teeth and the presence of a more or less distinct surface tooth are characteristic of *A. biplicata* (PILSBRY 1922–1926).

A. reyi was described on the basis of one specimen only, and its similarity to *A. oppoliensis* is so close that its specific distinctness is rather questionable.

Finding *A. oppoliensis* in the mid horizon (Beł-B) of the Bełchatów mine shifts the stratigraphic range of this species to the Lower/Mid Miocene limit and thus it is the oldest known trace of *Argna* in the Neogene.

Family: Vertiginidae Fitzinger, 1833

Genus: *Vertigo* O. F. Müller, 1774

Subgenus: *Vertigo* s. str.

Vertigo callosa (Reuss, 1849)

Figs 6–7

- 1849 *Pupa callosa* REUSS: 30, Pl. 3: Fig. 7.
1858 *Pupa (Vertigo) alloeodus* SANDBERGER: 58, Pl. 35: Fig. 10.
1860 *Pupa callosa* – REUSS: 72, Pl. 2: Figs 6–7.
1914 *Vertigo (Alaea) callosa* – FISCHER & WENZ: 99, Pl. 6: Fig. 23.
1923 *Vertigo (Vertigo) callosa alloeodus* – WENZ: 984.
1966 *Vertigo (Vertigo) antivertigo callosa* – STEKLOV: 145, Pl. 3: Figs 49–50.
1981 *Vertigo (Vertigo) callosa* – LUEGER: 20, Pl. 2: Figs 3–5.
1998 *Vertigo callosa* – FINGER: 18, Pl. 9: Figs A, B, C.

Material examined: Bełchatów: Beł-B – 58 specimens Ml/993/98; Wiesbaden (Agenian, MN 2) – 31A/40 (BMNH); Frankfurt a. M.: Corbiculathonen (Lower Miocene, MN 2b) – 31A/40 (NHML);

Tuchořice (Orleanian, MN 3) – 1196 (NMP), 1966 XXVI (BSP), 1909.I.77 (NMW), 31A/40 (BMNH), 1390 (MNHN); Öcs (Vallesian, MN 10) – Pl. 197, 374, 393 (MAFI); Varpalota (Turolian) – Pl. 627, 658, 808, 856 (MAFI); Ciscaucasia (Sarmatian) – 1872/265–268 (PIM).

Measurements of 30 specimens from Bełchatów; shell: H = 1.72–2.30, W = 1.11–1.48; aperture: h = 0.61–0.80, w = 0.64–0.83; H of body whorl = 1.06–1.35; number of whorls: 4.5–5.5.

Comparative remarks: Shells of *V. callosa* from Bełchatów are very variable in their size and shape – from ovate to tapering ovate. Poorly convex whorls separated by a rather shallow suture are covered with very weak and irregular striae. The umbilicus is deep, open but very narrow. A distinctly heart-shaped aperture has a deep incision at the level of the upper palatal tooth. On the outer surface of the palatal wall there is usually a weakly developed crest and two more or less visible depressions corresponding in position to the two palatal teeth.

Out of 58 specimens having 6 teeth, 13 had an additional vestigial suprapalatal tooth and only one specimen had a small tubercular infraparietal tooth. Because of all the above mentioned characters, the specimens from Bełchatów are the most similar to the typical form of the species known from Tuchořice and to the form described as *V. alloeodus* (Sandberger, 1858) [= *V. callosa alloeodus* sensu Wenz].

V. callosa is one of the commonest vertiginid snails in the European Neogene, the most variable (cf. BOETTGER 1889, WENZ 1923, STEKLOV 1966) and widespread. Several forms were described, starting with the Upper Oligocene, with five, six and more teeth and some of them were later regarded as subspecies or even separate species; WENZ (1923) listed as many as six subspecies of *V. callosa* from one locality – Steinheim am Albuch! However, it is necessary to take into account that most of those forms were described on the basis of very scanty material, in some cases single specimens only, so intraspecific variability was not known. Examination of a large series of recent *V. antivertigo* (Draparnaud, 1801) from one locality has shown that even intrapopulation variability of the species is conspicuous. In the light of recent knowledge (POKRYSZKO 1990), some shell characters of the vertiginids, e.g. number of teeth, vary considerably not only between but also within populations.

From among extant vertiginids, *V. antivertigo* and North American *V. ovata* Say, 1822 were considered to be the closest related to *V. callosa*. STEKLOV (1966: 145) regarded the latter species even as a subspecies of *V. antivertigo*. On the other hand, BOETTGER (1889: 311) proposed a phyletic lineage starting with forms of *V. callosa* and leading to the recent *V. antivertigo*.

In my opinion *V. antivertigo* differs significantly from *V. callosa* in the position of angular tooth which

Figs 6–7. *Vertigo callosa* (Reuss): 6 – shell, front view, H = 2.2 mm; 7 – aperture with well visible parietal and angular teeth, 100×

in the latter species is located high (closer to the parietal callus margin) and short – its inner end only very slightly overlaps with the outer end of the parietal tooth (Fig. 7). Besides, the short lamellate columellar tooth in *V. callosa* is moderately developed and subhorizontal whereas in *V. antivertigo* it is larger and more or less ascending inward. Moreover, the umbilicus in *V. callosa*, being somewhat narrow, is always open.

It seems probable that *V. callosa* became extinct not leaving any direct descendant, and a more likely ancestor for *V. antivertigo* is *V. diversidens*.

Vertigo diversidens (Sandberger, 1874)

Fig. 8

- 1874 *Pupa (Vertigo) diversidens* SANDBERGER: 549, Pl. 29: Fig. 23.
 1919 *Vertigo (Alaea) callosa diversidens* – GOTTSCHICK & WENZ: 15, Pl. 1: Fig. 31.
 1919 *Vertigo (Alaea) callosa steinheimensis* GOTTSCHICK & WENZ: 15, Pl. 1: Figs 32–33.
 1919 *Vertigo (Alaea) callosa perarmata* GOTTSCHICK & WENZ: 15, Pl. 1: Figs 34–35.

1998 *Vertigo callosa steinheimensis* – FINGER: 44, Pl. 9: Fig. D.

1998 *Vertigo callosa diversidens* – FINGER: 44, Pl. 9: Fig. E.

1998 *Vertigo callosa perarmata* – FINGER: 44, Pl. 9: Fig. F.

Material examined: Bełchatów: Beł-B – 12 specimens M1/994/98; Sansan (Astaracian, MN 6) – 3 specimens B 30057 and 30 B 30053 (MNHN).

Measurements of 12 specimens from Bełchatów; shell: H = 1.57–2.04, W = 1.06–1.23; aperture: h = 0.58–0.80, w = 0.58–0.75; H of body whorl = 1–1.23; number of whorls: 4.25–5.25.

Comparative remarks: A comparison of specimens from Bełchatów with *V. diversidens* from the type locality (Sansan) has revealed no significant differences. The shells from both localities are very similar in their outline, size, surface sculpture of whorls, shape of aperture and in having rather strongly developed crest and two depressions corresponding to the palatal teeth on the outer surface of the palatal wall. Their apertural barriers: columellar, basal, parietal, angular, lower and upper palatal and suprapalatal (more often present) are essentially also similar, but the other secondary teeth (infraparietal and infrapalatal) in the specimens from Bełchatów are more frequent. The number of



teeth seems to be the only difference between the forms described by GOTTSCHICK & WENZ (1919).

A conspicuous character of *V. diversidens* is the position and degree of development of parietal and angu-

- Fig. 8. *Vertigo diversidens* (Sandberger) – shell, front view, H = 1.9 mm
Fig. 9. *Vertigo protracta* (Sandberger) – shell, front view, H = 1.65 mm
Fig. 10. *Vertigo* sp. – shell, front view, H = 1.85 mm

lar teeth. The lamellate parietal tooth is more or less arcuate in top view. Its outer end only slightly overlaps with the inner end of angular tooth which is much shorter and thinner. Both these teeth are often distinctly divergent. Besides, the angular is situated very high (closer to parietal margin of aperture, like in *V. callosa*) and, in combination with the very solid upper palatal tooth and the incision of palatal margin of aperture, results in an almost circular sinulus (called "kleeblattförmig Mündung" by BOETTGER 1889, GOTTSCHICK & WENZ 1919 and others). This character is unknown among recent vertiginid snails in Europe.

Because of the shell shape and size, very convex whorls and the suture deeper than in *V. callosa*, surface sculpture of very weak and irregular, poorly visible striae and as a rule more than 6 teeth (7–9, only exceptionally 6), *V. diversidens* seems to be closer to *V. antivertigo* than *V. callosa*, as was thought before.

The oldest fossil record of *V. diversidens* is that from Bełchatów (Beł-B), but a very similar species – *V. kochi* – was described by BOETTGER (1889) from Upper Oligocene deposits in Hochheim; however, BOETTGER'S specimens which I have examined (SMF N° 152150/5) did not conform to his description (1889: 304). Two successive findings of *V. diversidens* come from Sansan (MN 6) and Steinheim (MN 7). PRISYAZHNYUK (in: GOZHIK & PRISYAZHNYUK 1978) listed some findings of *V. (Vertigo) antivertigo callosa* from the Upper Miocene of Ukraine and Ciscaucasia, but emphasized that there were two forms of the subspecies. Judging from PRISYAZHNYUK'S (1978) descriptions and figures it seems likely that the author had among his materials both *V. callosa* and *V. diversidens*.

Vertigo protracta (Sandberger, 1874)

Fig. 9

- 1874 *Pupa protracta* SANDBERGER: 400.
 1889 *Vertigo (Alaea) protracta* – BOETTGER: 300, Pl. 7: Fig. 5.
 1919 *Vertigo (Alaea) protracta suevica* GOTTSCHICK & WENZ: 21, Pl. 1: Figs 40–41.
 1973 *Vertigo (Vertigo) protracta* – PRISYAZHNYUK: 67, Pl. 2: Fig. 9.
 1998 *Vertigo protracta* – FINGER: 44, Pl. 9: Fig. I.

Material examined: Bełchatów: Beł-B – 6 specimens MI/996/98; Hochheim (Upper Oligocene) – 152192/2 (SMF); 1966 XXVI (BSP); Steinheim (Astaracian, MN 7) – specimens 1953 XXXVII (BSP, as *V. suevica* Gott. et Wenz); Bogdanowski Karier (Ukraine) and Goyani (Moldavia) (both Mid Sarmatian) – ex. coll. IGS; Eichkogel (Turolian, MN 11) – 2 specimens (NMW).

Measurements of specimens from Bełchatów; shell: H = 1.50–1.68, W = 1.03–1.08; aperture: h =

0.55–0.60, w = 0.52–0.56; H of body whorl = 0.95–1.08; number of whorls: 4.5–5.

Comparative remarks: There are no distinct differences in shell characters between the specimens from Bełchatów and those from other localities. BOETTGER (1889) considered the smaller size and the lack of basal tooth as main characters to distinguish *V. protracta* from *V. callosa*. However, some of the examined specimens have a small convexity or even a clearly visible knob in place of basal tooth. In my opinion *V. protracta* differs from *V. callosa* in several other important characters, apart from the smaller size: 1 – position of angular tooth; contrary to the latter species, in *V. protracta* the outer end of angular tooth is situated in line with the outer end of parietal tooth (i.e. angular is not displaced towards aperture margin) and they are parallel, 2 – aperture is rounded-triangular rather than heart-shaped, with no distinct palatal incision, 3 – upper palatal tooth is situated deeper inside the body whorl, 4 – shape is ovate but more or less elongated.

The differences between *V. protracta* and *V. protracta suevica* – the form described by GOTTSCHICK & WENZ (1919) from Steinheim – do not justify their separation. Although BOETTGER (1889), in his complement to SANDBERGER'S (1874) very cursory description, noted that *V. protracta* from Hochheim (locus typicus) had always 5 teeth (basal tooth absent), the specimens from his collection, stored at the Senckenberg Museum, have a distinctly visible basal tooth. On the other hand, LUEGER (1981) noted "5–6 Zähne, angedeutetes Basalzahnchen kann fehlen" in *V. protracta suevica*.

V. protracta is known from several localities since the Upper Oligocene to the Upper Miocene, but everywhere is rather rare.

Vertigo sp.

Fig. 10

Material examined: Bełchatów: Beł-B – 6 specimens MI/997/98.

Comparative remarks: Six shells from horizon Beł-B are similar in outline to *V. protracta* but somewhat bigger (H = 1.85–2.05 mm), with somewhat heart-shaped apertures and, most of all, with very distinctly striated whorls. They are tentatively called *Vertigo* sp. since they are not comparable with any known member of the genus. Such specimens are also kept in the collection from Opole stored in the Bayerische Staatssammlung in Munich, labelled as *V. cf. callosa*.

Vertigo ovatula (Sandberger, 1874)

Figs 11–13

1874 *Pupa ovatula* SANDBERGER: 400.



Figs 11–13. *Vertigo ovatula* (Sandberger): 11 – shell, front view, H = 1.45 mm; 12 – a more inflated specimen, front view, H = 1.4 mm; 13 – aperture with spoon-like lower palatal tooth, 110×

1884 *Vertigo (Alaea) ovatula* Sandb. var. *miliiformis*
BOETTGER: 270, Pl. 4: Figs 9a–c.

1889 *Vertigo (Alaea) ovatula* – BOETTGER: 301, Pl. 7:
Figs 6–8.

1914 *Vertigo (Alaea) ovatula* – FISCHER & WENZ: 101,
Pl. 6: Fig. 25.

1914 *Vertigo (Alaea) trolli* WENZ: 102, Pl. 7: Fig. 27.

1921 *Vertigo (Vertigo) ovatula trolli* Wenz – WENZ: 28.

1966 *Vertigo (Vertigo) ovatula* – STEKLOV: 144, Fig. 50 and Pl. 3: Fig. 54.

Material examined: Bełchatów: Beł-C – 9 specimens MI/998/98 + 8 fragments with aperture MI/999/98; Hochheim (Upper Oligocene) – 152162/~ (SMF); Budenheim (MN 2) – 152166/1 (SMF); Frankfurt a. M.: Corbicularschichten (Lower Miocene, MN 2b) as *V. ovatula miliiformis* Boettger – 152167/1 (labelled as “Typus”) and 152170/3 (SMF); Opole (Astaracian, MN 7+8) as *V. ovatula trolli* Wenz – 152175/2 and 152176/7 (SMF), as *V. trolli* Wenz – 274198/9 (SMF); Dniepropetrovskaya Oblast (Lower Sarmatian) – 1872/261–264 (PIM).

Measurements of specimens from Bełchatów; shell: H = 1.27–1.43, W = 0.85–0.90; aperture: h = 0.47–0.53, w = 0.48–0.54; H of body whorl = 0.81–0.85; number of whorls: 4.5–4.8.

Comparative remarks: Specimens from Bełchatów correspond very well to those from Ukraine, Opole and Frankfurt a. M., but particularly well to those from Ciscaucasia. STEKLOV (1966) gave a comprehensive description of the species based on 20 specimens from Dniepropetrovskaya Oblast and he was the first to note the presence of the longitudinal groove along the upper surface of a thick and wide lower palatal tooth. Only two specimens from Bełchatów have that tooth very wide, with the groove strongly marked (Fig. 13); in some other shells the tooth is narrow and flattened – LUEGER (1981) termed it “kantig” – being “normal” in the remaining ones. Furthermore, LUEGER mentioned an arcuate columellar tooth with its inner end turned downward. A similar columellar tooth, more or less deflected downward, was observed in the specimens from Bełchatów. The angular tooth in *V. ovatula* is situated much higher than the parietal (like in *V. callosa* and *V. diversidens*); it is somewhat arcuate and seems to be connected with the aperture margin, resulting in an almost circular sinulus.

The specimens from Bełchatów and Ciscaucasia have 7 teeth (infrapalatal always present) whereas those from other localities are as a rule 6-toothed (infrapalatal lacking), and rarely 7-toothed. Unfortunately, the specimens from older collections very often have their apertures filled with sediment, frequently obliterating the teeth; this pertains particularly to the knob-shaped infrapalatal.

V. ovatula was considered to be closely related to recent American *V. ovata* Say, 1822 (SANDBERGER 1874) and *V. milium* (Gould, 1840) (BOETTGER 1884) as well as to European *V. substriata* (Jeffreys, 1833) (LUEGER 1981). PILSBRY (in: PILSBRY & COOKE 1918–1920: 146), having not examined BOETTGER'S materials, rejected this view, based on the imprecise illustration of the columellar lamella presented by BOETTGER (1884). However, a recent examination of the specimens provides evidence that BOETTGER'S view is the most justified. Among the European Mio-

cene vertiginids also some other species, besides *V. ovatula*, have columellar lamella more or less deflected downward.

V. ovatula is known from over a dozen localities (mainly in Germany) since the Upper Oligocene to the Upper Miocene, including two sites in Poland: Opole and Bełchatów (only Beł-C). Furthermore, it seems possible (based on figures, since the description is only in Chinese) that *V. (Vertigo) mostrata* described by LI YUNTONG (date unknown) from the Pliocene of Ertemte (northern China) is conspecific with *V. ovatula*.

Subgenus: *Vertilla* Moquin-Tandon, 1855

Vertigo oecensis (Halaváts, 1911)

Figs 14–16

1911 *Pupa öcsensis* HALAVÁTS: 60, Pl. 3: Fig. 10.

1923 *Vertigo (Vertilla) angustior öcsensis* – WENZ: 1007.

1956 *Vertigo angustior öcsensis* – BARTHA: 518, Pl. 3: Fig. 20–21.

1966 *Vertigo (Vertilla) angustior* Jeffreys – STEKLOV: 148 [partim], Pl. 3: Fig. 58 (non 59).

1978 *Vertigo (Vertilla) angustior* – GOZHNIK & PRISYAZHNYUK: 99, Pl. 15: Fig. 2.

1981 *Vertigo angustior* – STWORZEWICZ: 49.

1989 *Vertigo oecensis* – STOJASPAL: 653, 659.

1996 *Vertigo (Vertilla) oecensis* – FORDINAL: 7, Pl. 1: Fig. 6.

Material examined: Bełchatów: Beł-A – 12 specimens MI/1000/98 + 5 damaged MI/1001/98; Öcs (Vallesian, MN 10) – holotype Pl. 100 + 13 specimens Pl. 515, 237 and 241 (MAFI), 152146/3 (SMF); Orešany (Upper Pannonian) – 1 damaged specimen MI/1002/98 (ISEA, ex coll. K. FORDINAL, Slovak Republic); Eichkogel (Turolian, MN 11) – 1966 XXV (BSP), 274215/~ (SMF).

Measurements of 10 specimens from Bełchatów and (in brackets) *V. angustior* (after POKRYSZKO 1990); shell: H = 1.33–1.49 (1.50–1.90), W = 0.81–0.88 (0.90–1.00); aperture: h = 0.45–0.52 (0.40–0.53), w = 0.43–0.48 (0.45–0.63); H of body whorl = 0.79–0.86 (0.85–1.00); number of whorls: 4.75–5 (4.5–5.1); H/W ratio = 1.58–1.82 (1.61–1.90).

Comparative remarks: Until quite recently *V. oecensis* was regarded as a subspecies of *V. angustior* Jeffreys, 1830 (e.g. WENZ 1923 and LUEGER 1981) or as its older, Lower Sarmatian form (STEKLOV 1966). STEKLOV drew attention to the differences in the shape of columellar tooth between both these forms but he considered the older populations to have the columellar tooth less solid, lower palatal tooth lacking and shell of a smaller size. On the other hand, STOJASPAL (1989) elevated the form *oecensis* to the species rank but without any explanation.



Figs 14–16. *Vertigo oecensis* (Halaváts): 14 – shell, front view, H = 1.45 mm; 15 – side view of palatal wall with gutter-like depression in the outer surface; 16 – H = 1.37 mm, knob-shaped columellar tooth exposed
Fig. 17. *Vertigo angustior* Jeffreys – H = 1.56 mm, lamellate columellar tooth exposed

Based on the fossil material examined and on recent specimens of *V. angustior*, I regard the differences in the shape of columellar tooth – lamellate and subvertical in *V. angustior* (Fig. 17) and knob-shaped in *V. oecsisensis* (Fig. 16) – together with some other characters (callus on the palatal wall absent, shell of a smaller size, with very slightly striated whorls), as sufficient to justify their specific status. A very long upper palatal tooth and a long, gutter-like depression in the outer surface of palatal wall (Fig. 15) are characteristic of all the members of the subgenus *Vertilla*.

V. oecsisensis was described from the Upper Pannonian of Hungary. In Bełchatów it was found in the horizon Beł-A and it is the oldest known finding of the species.

Vertigo angulifera O. Boettger, 1884

Fig. 18

1884 *Vertigo (Alaea) angulifera* O. BOETTGER: 271, Pl. 4: Fig. 10a–c.

1919 *Vertigo (Alaea) angulifera milleri* GOTTSCHICK & WENZ: 21, Pl. 1: Figs 38–39.

1985 *Vertigo (Vertilla) angulifera angulifera* – ČEJCHAN: 176, Figs 1–2, Tab. 1 Figs 1–5, Pl. 2: Figs 1–3.

Material examined: Bełchatów: Beł-B – 14 specimens MI/1003/98; Frankfurt a. M.: Corbículaschichten (Lower Miocene, MN 2b) – holotype 152127/1 (SMF), 1966 XXVI i 1953 XXXVII (BSP); Dniepropetrovskaya Oblast (Lower Sarmatian) – 1872/272-279 (PIM); Steinheim (Astaracian, MN 7) – 274247/48, 274248/5; Hollabrunn (Astaracian, MN 8) – 190014 (SMF); Voronovka (Upper Sarmatian) – II/152-160 (IGS).

Measurements of specimens from Bełchatów; shell: H = 1.25–1.65, W = 0.80–0.93; aperture: h = 0.45–0.53, w = 0.45–0.55; H of body whorl = 0.75–0.85; number of whorls: 4.5–5.2.

Comparative remarks: *V. angulifera* is another species of *Vertilla* with a knob-shaped columellar tooth, similar to that in *V. oecsisensis*. STEKLOV (1966) and ČEJCHAN (1985) gave comprehensive descriptions of the species based on new materials from Ukraine (the youngest localities) and former Czechoslovakia, respectively. Both STEKLOV'S and ČEJCHAN'S specimens are ovate, more or less elongate and correspond to the type series from Frankfurt a. M. GOTTSCHICK & WENZ (1919) described subspecies *V. a. milleri* from Steinheim, characterized by cylindrical shape and somewhat more convex and weakly striated whorls. Among specimens from Bełchatów there is one shell quite cylindrical in outline, but having the remaining characters of “*angulifera*” type. All the specimens from Bełchatów have a very long lamellate palatal tooth,

Fig. 18. *Vertigo angulifera* Boettger: shell, front view, H = 1.46 mm

lowered moderately in the middle of its length but not divided in two parts (cf. ČEJCHAN 1985).

V. angulifera is common in the whole Miocene deposits (from MN 2 to MN 7 zones) but in Bełchatów it was found only in the middle horizon – Beł-B.

Genus: *Nesopupa* Pilsbry, 1900

Nesopupa minor (Boettger, 1870) comb. nov.

Figs 19–22

1870 *Vertigo callosa* var. *minor* BOETTGER: 296, Pl. 13: Fig. 7a–b.

1889 *Vertigo (Alaea) minor* – BOETTGER: 305.

1923 *Vertigo (Vertigo) minor* – WENZ: 906.

Material examined: Bełchatów: Beł-B – 2 specimens MI/1004/98 + 8 fragments with aperture MI/1005/98; Tuchořice (Orleanian, MN 3) – XII 1714a (labelled as “Typus”), XII 1714b (SMF) and ca. 60 specimens I199 (NMP).

Measurements of specimens from Bełchatów; shell: H = 1.50–1.60, W = 0.97–1.04; aperture: h = 0.54–0.60, w = 0.53–0.60; H of body whorl = 0.90–1.02; number of whorls: 4.3–4.5.

Comparative remarks: Specimens from Bełchatów correspond very well to those from Tuchořice, al-



Figs 19–22. *Nesopupa minor* (Boettger). 19–20 – specimens from Bełchatów: 19 – H of last two whorls = 1.2 mm; 20 – side view of palatal wall with gutter-like depression in the outer surface; 21–22 – specimens from Tuchořice: 21 – details of aperture; 22 – shell in front view, phot. P. ČEJCHAN

though the description of *N. minor* and its systematic status require some comments. Two shells from Bełchatów are ovate but those from Tuchořice range from ovate to globosely ovate. Examination of the specimens from Tuchořice and Bełchatów in SEM revealed a very minute puncturation on the embryonic whorls (1.75) and a combination of a distinct pitted-granulose sculpture with closely spaced, more or less regular striae on the surface of the definitive whorls (Figs 19–20). Such a surface sculpture is characteristic of most members of *Nesopupa* (PILSBRY & COOKE 1918–1920), while it has never been noted in *Vertigo*. The aperture of *N. minor* is irregularly triangular with broadly rounded angles and with slightly marked lip. The body whorl ascends somewhat near the aperture. The columellar margin of aperture is slightly reflexed, whereas the palatal and basal parts are slightly contracted. The contraction passes into a low swelling parallel to the aperture margin, looking like a slight crest of *Vertigo*. Beyond the swelling there is a depression with two grooves corresponding in position to the palatal teeth. The aperture is armed with 7–8 teeth. Out of three teeth on the parietal wall, the middle one – arcuate and deeply entering parietal tooth – is the largest. The infraparietal is moderately developed and deepest set. The angular is most variable – from a very short plica, not extending to the aperture margin (specimens from Bełchatów) to a well developed lamella, almost joining the aperture margin (specimens from Tuchořice) (Figs 21–22). The columellar tooth is rather strong, somewhat ascending in front, but its inner end is slightly deflected downward. There are two (specimens from Bełchatów) or three (a knob-shaped suprapalatal present in specimens from Tuchořice), deeply seated palatal teeth, slightly converging backwards. A high lamellate upper palatal has the highest rise in its middle part. The lower palatal is much more solid but low. The basal tooth is either fairly big (specimens from Tuchořice) or only slightly marked, sometimes absent. The umbilicus is hardly open, slit-like.

BOETTGER (1870) placed the species in *Vertigo*, ignoring the pitted-granulose surface sculpture and the peculiar features of aperture (though the angular tooth not fully joins the aperture margin), and both PILSBRY & COOKE (1918–1920) and WENZ (1923) shared his view. However, I am inclined to place the form *minor* in *Nesopupa*, though a different combination of other characters makes it difficult to specify which nesopupine group could be the closest related (cf. PILSBRY & COOKE 1918–1920: 275). In terms of the pitted-granulose surface sculpture of typical *Nesopupa*, *N. minor* seems to be the closest to the Oriental and, particularly, Ethiopian group of species, some of which have both pitted surface sculpture and weakly developed angular tooth (ADAM 1954, 1957). On the other hand, a very short angular tooth, not

reaching the margin of the aperture (like in specimens from Bełchatów) is frequent in Hawaiian species having, however, the shell surface mostly ribbed-striate and covered with very minute wrinkles, visible under high magnification.

Fossil species of *Nesopupa* – *N. blumi* (Boettger, 1884), *N. trigonostoma* (Sandberger, 1863) and *N. minor* – are known in Europe from the Upper Oligocene to the Lower and Mid Miocene limit and, according to PILSBRY (in PILSBRY & COOKE 1918–1920) they appear to be the closest related to *Indopupa* group (Oriental Region). Their weakly developed angular tooth is only slightly (if at all) connected with the peristome by a callus. SOLEM (1988), studying nesopupines from Australia, remarked that “the reduced angular tooth recurs in peripheral parts of the genus range”. It seems probable that during the Neogene the present area of Europe could be just a peripheral part of the then range of *Nesopupa*.

Genus: *Negulus* O. Boettger, 1889

Negulus suturalis (Sandberger, 1858)

Figs 23–25

- 1843 *Bulimus lineolatus* A. BRAUN: 149 (nomen nudum).
 1858 *Pupa suturalis* SANDBERGER: 54, Pl. 5: Fig. 13, Pl. 6: Fig. 1–1a.
 1889 *Negulus lineolatus* (Al. Br.) – BOETTGER: 269, Pl. 6: Fig. 8.
 1914 *Negulus suturalis* – FISCHER & WENZ: 92, Pl. 5: Fig. 13.
 1919 *Negulus suturalis gracilis* GOTTSCHICK & WENZ: 9, Pl. 1: Fig. 12–13.
 1919 *Negulus suturalis francofurtanus* GOTTSCHICK & WENZ: 10.
 1989 *Negulus gracilis* – STOJASPAL: 659.
 1996 *Negulus gracilis* – FORDINAL: 6, Pl. 1: Fig. 3–4.

Material examined: Bełchatów: Beł-C – 10 specimens + 5 damaged MI/1006/98; Beł-B – 27 specimens MI/1007/98 and 10 damaged specimens with aperture MI/1008/98; Hochheim (Chattian, Upper Oligocene) – 151990 (SMF), 1966 XXVI (BSP), specimens labelled as *N. lineolatus* and *N. suturalis* (NHML); Ulm (Agenian, MN 2) – 273737/20 (SMF); Tuchořice (Orleanian, MN 3) – 1909.I.71 (NMW); Zwiefaltendorf (MN 5–6) – 273738/1 and 241670/1 (SMF); Frankfurt a. M.: Landschneckenmergel (MN 5–6) – 152008/3 (SMF) as *N. suturalis francofurtanus*; Opole (Astaracian, MN 7+8) – 1987/43/2 and 2b (NMW), 152005/1 (SMF), two specimens from BSP; Steinheim (Astaracian, MN 7+8) – 152006/1 (SMF) as *N. suturalis gracilis*.

Measurements. 10 specimens from Beł-C; shell: H = 1.54–1.91, W = 0.78–0.86; aperture: h = 0.57–0.68, w = 0.47–0.57; H of body whorl = 0.95–1.17; number of



whorls: 4–4.5. 27 specimens from Beł-B; shell: H = 1.45–1.77, W = 0.69–0.85; aperture: h = 0.55–0.66, w = 0.45–0.54; H of body whorl = 0.92–1.09; number of whorls: 4–4.5. The number of ribs on the penultimate

whorl (16–20) in specimens from Beł-C and in those from Beł-B is similar.

Comparative remarks: The systematic position of *N. suturalis* is rather intricate since several varieties of

the species were described from the Neogene of Europe. However, these descriptions were based on a very scanty material including only few specimens from the type locality, hence the range of shell variation was not considered. The type specimen could not be located, and the description by SANDBERGER (1858) does not quite correspond to the figures of the species by this author. He wrote (1858: 54): "Anfractus sex convexi..." while in his figure at most 5 whorls can be seen. Another few specimens from the type locality (Hochheim), stored in SMF (No. 151 990) and BSP (1966 XXVI), are similar to those from Bełchatów with respect to their number of whorls.

A detailed comparison of the material from Bełchatów and from some collections (SFM, BSP, NMW) reveals that the shells of *N. suturalis* vary considerably in their size and shape (Fig. 25) as well as in the degree of development and the number of sparse ribs on the shell surface. Finely wrinkled-granulose embryonic whorls (Fig. 24) and very fine striation of definitive whorls are similar in all the specimens. Shells of the Bełchatów specimens are mostly nearly cylindrical (like those from Ulm and Zwiefaltendorf), whereas those from Tuchořice, Hochheim and Opole have both cylindrical and somewhat tapering shells; specimens with tapering shells were described by BOETTGER (1889: 270) as var. *sublineolata*, the name later placed among synonyms by WENZ (1923: 1025). The number of whorls in the specimens from Bełchatów is rather constant, most often 4.25; the whorls are extremely convex and often shouldered, the suture is deep or very deep, and the umbilicus is slit-like. The aperture margin is more or less reflexed but not thickened.

The measurements have revealed that the subspecies *N. suturalis gracilis* and *N. suturalis francofurtanus* are well within the variability range of *N. suturalis* from Bełchatów, and thus are not justified.

N. suturalis was a widespread species in the area of the present Europe from the Upper Oligocene throughout the whole Miocene. Earlier authors referred it to the extant African species *N. reinhardti* (Jickeli, 1874), but none of the four living *Negulus* species have surface sculpture similar to that of *N. suturalis* (cf. PILSBRY 1920–1921). The resemblance to the American *Pupoides* (*Ischnopupoides*) *hordaceus* (Gabb, 1866) dis-

cussed by BOETTGER (1889: 269) seems not to be so close since the latter species – in contrast to *N. suturalis* – has a smooth shell surface between widely spaced ribs. On the other hand, PILSBRY (1922–1926: 253) indicated another species with sculpture similar to that of *N. suturalis*, living in Australia – *Glyptopupoides egregia* (Hedley et Musson, 1891) [= *Pupoides hedleyi* Pilsbry, 1926]; however, the latter species has a prominent spiral striation between rather widely separated radial ribs (SOLEM 1988).

Family: Valloniidae Morse, 1864

Genus: Vallonia Risso, 1826

Vallonia subcyclophorella (Gottschick, 1911)

Fig. 26

1911 *Helix* (*Vallonia*) *subcyclophorella* GOTTSCHICK: 503, Pl. 7: fig. 2.

1996 *Vallonia subcyclophorella* – GERBER: 147, Figs 3w, x; 56b-e; 59; 60; 61a-c.

Material examined: Bełchatów: Beł-B – 1 specimen M1/1009/98 + 1 specimen in GERBER'S coll.; Reisperbach bei Stein (Upper Miocene) – 275345/2 (SMF); Ukraine (Lower Sarmatian) – 275348/12 (SMF).

Measurements of one specimen from Bełchatów and (in brackets) extremes of variability range of *V. subcyclophorella* after GERBER (1996); shell: H = 0.85 (0.87–1.13), W = 2.02 (1.70–2.36); aperture: h = 0.77 (0.74–0.94), w = 0.80 (0.77–1.04); number of whorls: 3 (2.63–3.25).

Comparative remarks: Two specimens from Bełchatów conform very well to GERBER'S description of the species in his comprehensive account of

Fig. 26. *Vallonia subcyclophorella* (Gottschick): shell, front view, W = 2.02 mm

Vallonia (GERBER 1996). On the other hand, GERBER'S data on the age of sediments with *V. subcyclophorella* from Bełchatów are not quite correct, since the species was found only in the middle horizon (Beł-B) correlated to biozone MN 5.

V. subcyclophorella is very frequent in the Miocene deposits beginning from the Lower/Mid Miocene limit (MN 5) to the Upper Miocene (MN 10) (for details, see GERBER 1996).

Genus: *Acanthinula* Beck, 1847

Acanthinula trochulus (Sandberger, 1874)

Figs 27–29

1874 *Pupa (Modicella) trochulus* SANDBERGER: 601, Pl. 29: Fig. 25a-b.

1902 *Modicella* cf. *trochulus* – ANDREAE: 15.

1916 *Acanthinula trochulus* – GOTTSCHICK & WENZ: 67.

Material examined: Bełchatów: Beł-C – 3 specimens MI/1010/98; Beł-B – 2 specimens + 3 fragments with aperture MI/1011/98; Undorf (Orleanian, MN 5) – 241676/1 (SMF), 1967 XI (BSP); Mörsingen (Orleanian, MN 5) – 1966 XXVI (BSP); Opole (Astaracian, MN 7+8) – as *Acanthinula tuchoricensis* (Klika, 1891) (NMW).

Measurements of all specimens from Bełchatów (* – juv.):

	Shell		Aperture		Body whorl	Number of whorls
	H	W	h	w	H	
Beł-C	2.16	1.78	0.98	0.90	1.49	4.00
	2.20	1.86	1.17	1.00	1.67	4.00
	2.43	2.07	1.10	1.00	1.65	4.25
Beł-B	2.01*	1.62	0.80	0.77	1.33	3.75
	2.66	1.98	1.09	0.97	1.69	5.00

Comparative remarks: *A. trochulus* is very distinct in its regularly conical shape, whereas other Neogene *Acanthinula* have a more or less dome-like conical form. The only adult specimen from Beł-B distinctly differs from three specimens from the older horizon (Beł-C) in having a more elongate shell (like that figured by SANDBERGER 1874). Several highly conical specimens, similar to those from Beł-B, were found in one of the samples from Opole stored at the Vienna Museum of Natural History and labelled as *A. tuchoricensis* (Klika, 1891). All the specimens from Bełchatów have their embryonic whorls (1.5) spirally sculptured (Fig. 28). The remaining whorls are covered with combined fine, irregular, radial striae and rather distinct spiral lines. Apart from the microsculpture, there are widely spaced, finely marked ribs. The aperture ranges from broadly ellip-

tical to almost circular, except for the parietal incision. A more or less reflexed aperture margin has a very slightly thickened lip, in contrast to *A. tuchoricensis* having it unexpanded and simple. The umbilicus of *A. trochulus* (Fig. 29) is distinctly wider than that of *A. tuchoricensis*.

A. trochulus is a rare species in Miocene deposits; the present study extends its stratigraphic range to the Lower Miocene. The upper limit of its occurrence is determined by the finding in Opole (MN 7+8), although LUEGER (1981) reports *A. trochulus* from deposits of two Upper Miocene localities in Austria. However, his specimens are not in a condition sufficient to make detailed comparisons with other species, hence the data are uncertain.

Genus: *Spermodea* Westerlund, 1902

Spermodea cf. *candida* Falkner, 1974

Figs 30–31

1974 *Spermodea candida* FALKNER: 231, Pl. 10: Figs 1–2, Pl. 11: Figs 5–6.

Material examined: Bełchatów: Beł-B – 2 damaged specimens MI/1012/98; Undorf (Orleanian, MN 5) – holotype 1967 XI 25, paratype 1967 XI 26 (BSP).

Comparative remarks: Both specimens from Bełchatów are damaged, thus precluding complete measurements. One specimen, of 4.75 whorls, is not quite adult, hence its deep and narrow umbilicus is still quite open. The second specimen, of almost 5 whorls (the first three whorls are somewhat pressed into the lower two), has its umbilicus partly covered with a reflexed columellar margin of semilunar aperture. In the second specimen, there is a very weak but visible knob on the columella (Fig. 31), somewhat similar to that described by FALKNER and considered to be a vestigial columellar lamellate tooth. A comprehensive discussion of the Neogene *Spermodea* and *Acanthinulinae* as well as their relationships with recent species has been presented by FALKNER (1974) and SCHLICKUM & TRUC (1972).

Genus: *Planogyra* Morse, 1864

Planogyra nana (A. Braun, 1851)

Figs 32–33

1851 *Helix nana* A. BRAUN in: WALCHNER: 1140.

1874 *Patula (Acanthinula) nana* – SANDBERGER: 374, Pl. 22: Figs 4a-c.

1923 *Acanthinula nana* – WENZ: 972.

1974 *Planogyra nana* – FALKNER: 240, Pl. 10; Fig. 4, Pl. 11: Figs 9–10.

Material examined: Bełchatów: Beł-B – 6 specimens + 4 juv. MI/1013/98; Tuchořice (Orleanian, MN 3) –



Figs 27–29. *Acanthinula trochulus* (Sandberger): 27 – shell with reflexed peristome partly broken, front view, H = 2.25 mm; 28 – microsculpture of first three whorls, 130×; 29 – shell, umbilical view

275433/10 (SMF); Opole (Astaracian, MN 7+8) – 275435/5 and 238829/4 (SMF), 1966 XXVI 3 (BSP).

Measurements of specimens from Bełchatów:

Shell		Aperture		Number of whorls
H	W	h	w	
0.83	1.17	0.42	0.48	3.3
0.90	1.22	0.39	0.50	3.4
0.79	1.23	0.37	0.46	3.4
0.80	1.24	0.40	0.47	3.5
0.86	1.27	0.37	0.49	3.5

Comparative remarks: Specimens from Bełchatów do not differ from those from Tuchořice and Opole. Examination of materials from the mentioned localities indicates that variation among and within fossil

populations of *P. nana* is insignificant. All of them have a rather low spire (although higher than in three recent species of *Planogyra*) and distinct, rounded keel on the body whorl, above the periphery. The surface sculpture is similar to that of *A. trochulus*, except for embryonic whorls which are distinctly pitted-granulose. The aperture is broadly semilunar, simple, oblique in side view. In the moderately broad, circular umbilicus all the whorls are visible.

The generic membership of the species has remained unclear until quite lately. On the basis of the granulose microsculpture of embryonic whorls FALKNER (1974) placed it in *Planogyra*. He also listed all localities of *P. nana* known from the Upper Oligocene (Hochheim) to the Mid Miocene (Opole).



Figs 30–31. *Spermodea* cf. *candida* Falkner: 30 – shell, front view, H = 2.3 mm; 31 – shell with body whorl partly broken to show a small knob on the columella
Figs 32–33. *Planogyra nana* (A. Braun): 32 – shell, front view, W = 1.22 mm; 33 – microsculpture of first two whorls, 320×

Family: Strobilopsidae Pilsbry, 1918**Genus: *Strobilops* Pilsbry, 1892****Subgenus: *Strobilops* s. str.*****Strobilops costata* (Clessin, 1877)****Figs 34–37**1877 *Strobilus costatus* CLESSIN: 37.1915 *Strobilops costata* – WENZ: 79, Textfig. 7, Pl. 4:
Figs 15–16.

Material examined: Bełchatów: Beł-C – 20 + 16 damaged specimens MI/1014/98, Beł-B – ca. 1500 + 45 damaged specimens MI/1015/98; Undorf (Orleanian, MN 5) – 275453/5 (SMF); Opole (Astaracian, MN 7+8) – 151122 (SMF), 1967 XI and 1966 XXVI (BSP); Ciscaucasia (Upper Miocene) – 1872/31-33, 1872/43 (PIM); Zamiehov (Lower Sarmatian) – *S. costata govorkaensis* Prisyazhnyuk, 1978: holotype II/8 + 20 specimens (IGS).

Measurements. All specimens from Beł-C; shell: H = 1.23–1.52, W = 1.97–2.15; W/H ratio = 1.41–1.64; number of whorls: 4.5–5. 30 specimens from Beł-B; shell: H = 1.32–1.58, W = 1.98–2.26; W/H ratio = 1.37–1.58; number of whorls: 4.7–5.2.

Comparative remarks: Examination of a large series of *S. costata*, the most abundant species of the Bełchatów deposits, provides comprehensive data on its variability. Specimens from the older horizon (Beł-C) differ somewhat from those of Beł-B horizon in having smaller and less elevated shells, whereas the variability of other characters is similar. The embryonic whorls (ca. 1.5) of *S. costata* are finely granulose and the definitive whorls are distinctly ribbed. The number of ribs on the body whorl varies considerably (40–60), and the sculpture of its base is also variable, from hardly striated to distinctly ribbed. The periphery of the shell is more or less obtusely subangular. All the specimens have a generally similar umbilicus: very narrow and deep, but the last half whorl deflects rapidly and considerably from the shell axis (Fig. 36). The aperture is semilunar with expanded and thick peristome and distinct parietal callus.

The apertural barriers of *S. costata* and other strobilopsids are generally lamellate in shape (only exceptionally very short lamellate, almost knob-like) and their evolution differs from that in other Pupilloidea (PILSBRY 1948). Hence, in my opinion, it seems more appropriate to call them all lamellae: columellar, parietal, infraparietal, interparietal, palatal and basal (instead of lamellae and plicae or folds).

There are two or three lamellae on the parietal wall, but only two are visible in the aperture. The parietal lamella is somewhat elevated before reaching the margin of the distinct parietal callus, its inner edge being provided with regular, thin but well marked nodules (Fig. 37). The infraparietal lamella is lower

and poorly nodulose, its anterior part ends just before the callus margin. Between their inner parts there is occasionally a very short interparietal lamella, not visible in the aperture. The columellar lamella of *S. costata* is very variable; from well developed in specimens from Bełchatów (Fig. 35) and Podolia (*S. costata govorkaensis* Prisyazhnyuk, 1978) to weakly marked (“eben angedeutet” – WENZ 1915) in specimens from Undorf and absent in those from Podolia and Ciscaucasia (STEKLOV 1966). There are as a rule two basal lamellae, rarely three or one, and only exceptionally four, positioned as follows: the shorter one near the columella, the middle one – the most massive and always present, and the peripheral – thin and the most variable, varying from very long to very short or absent.

S. costata has been hitherto found in the Mid and Upper Miocene deposits, therefore the finding of the species in Bełchatów considerably shifts its stratigraphic range in the Miocene.

Strobilops tiarula* (Sandberger, 1886)*Figs 38–40**1886 *Strobilus tiarula* SANDBERGER: 331.1915 *Strobilops tiarula* – WENZ: 81, Pl. 4: Fig. 13.

Material examined: Bełchatów: Beł-B – 117 + 20 damaged specimens MI/1016/98, Beł-A – 1 + 4 damaged specimens MI/1017/98; Leobersdorf (Vallesian, MN 10) – 151134/1 (SMF), 1958 XI (BSP); Öcs (Vallesian, MN 10) – 248372 (SMF), Pl. 193, 305, 337, 369, 380 (MAFI).

Measurements of 30 specimens from Beł-B; shell: H = 1.50–1.71, W = 2.02–2.25; W/H ratio = 1.29–1.42; number of whorls: 5–5.5.

Comparative remarks: The shells of *S. tiarula* from Bełchatów are similar to those from the type locality (Leobersdorf) and differ from specimens from Öcs in having a less thickened peristome. LUEGER (1981) examined about two hundred specimens from Leobersdorf (his search for the holotype failed) and his description is compatible with my observations. STEKLOV (1966) described *S. ukrainica* as a new species from Ciscaucasia; it is strikingly similar to *S. tiarula* but somewhat bigger (“nieskolko krupnyj” – STEKLOV 1966: 171): H = 1.45–1.65, W = 1.95–2.1. Only one specimen is 1.45 high and one is 1.95 wide, whereas the remaining ones are 1.50–1.65 x 2–2.1, and thus fit well within the size range of *S. tiarula*. Moreover, W/H ratio is also similar – 1.25–1.37 for *S. ukrainica*. A closer examination of STEKLOV'S material is needed to synonymise both species.

The shells of *S. tiarula* differ at first glance from those of *S. costata* in having a more elevated spire (W/H ratio is lower), a very narrow and deep umbili-



Figs 34–37. *Strobilops costata* (Clessin): 34 – shell, front view, $W = 1.45$ mm; 35 – top view of lamellae inside the body whorl; 36 – umbilical view; 37 – side view of broken shell with two parietal and one of the basal lamellae visible

cus, partly covered with reflexed peristome (Fig. 40) and a more flattened base. The ribbing seems to be more distinct than that of *S. costata*.

The parietal and infraparietal lamellae are similar to those of *S. costata*, except the nodules on their

inner edges which in *S. tiarula* are much weaker and closer spaced. The interparietal lamella is almost always present. The columellar lamella is weakly marked. There are as a rule three basal lamellae, arranged in a sequence, from the shortest one being



Figs 38–40. *Strobilops tiarula* (Sandberger): 38 – shell, front view, $W = 1.65$ mm; 39 – top view of lamellae inside the body whorl; 40 – umbilical view

located near the columella, to the longest. The middle one is the most massive and the highest. It seems that *S. tiarula* is much more constant, both in its proportions and in apertural barriers, than *S. costata*.

S. tiarula was hitherto regarded as an Upper Miocene element, then the occurrence of the species in Beł-B horizon shifted its stratigraphic range to the Lower/Mid Miocene limit.

***Strobilops cf. joossi* (Gottschick, 1911)**

Figs 41–43

1911 *Strobilus joossi* GOTTSCHICK: 502, Pl. 7: Fig. 16.

1915 *Strobilops joossi* – WENZ: 80, Textfig. 9, Pl. 4: Fig. 14.

Material examined: Bełchatów: Beł-B – 23 + 10 damaged specimens M1/1018/98; Steinheim (Astaracian, MN 7+8) – 151132/1 and 246439/1, syntypes (SMF).



Figs 41–43. *Strobilops* cf. *joossi* (Gottschick): 41 – shell, front view, W = 2.17 mm; 42 – top view of lamellae inside the body whorl; 43 – umbilical view

Measurements of specimens from Beł-B; shell: H = 1.35–1.67, W = 1.95–2.20; W/H ratio = 1.27–1.43; number of whorls: 4.8–5.25.

Comparative remarks: Although *S. joossi* is at first glance very similar to *S. tiarula* in general proportions of the shell, it differs in having umbilicus of *S. costata* type – the last half whorl deflects rapidly from the shell axis, but not so distinctly as in *costata*. STEKLOV (1966) noted that with respect to the umbilicus, *S. joossi* was intermediate between *S. costata* and *S. tiarula*. Another specific character of *S. joossi* from

Bełchatów is its very distinct ribbing (36–42 ribs on the body whorl), which is also strongly marked on the base. The lamellae inside the body whorl are actually similar to those of *S. tiarula*, but the inner end edges of parietal and infraparietal lamellae are only weakly folded, rather than nodulose.

The specimens from Bełchatów have been compared with only two specimens from Steinheim, hence the identification, despite the general similarity, is uncertain.

S. joosi was hitherto known only from Steinheim (Mid Miocene), and the locality is stratigraphically placed between Beł-A and Beł-B.

Subgenus: *Discostrobilops* Pilsbry, 1927

Strobilops uniplicata (A. Braun, 1851)

Figs 44–45

1851 *Helix uniplicata* A. BRAUN in: WALCHNER: 1138.

1858 *Helix uniplicata* – SANDBERGER: 35, Pl. 3: Fig. 7.

1874 *Strobilus uniplicatus* – SANDBERGER: 406, Pl. 23: Fig. 24.

1923 *Strobilops (Strobilops) uniplicata uniplicata* – WENZ: 1057.

1923 *Strobilops (Strobilops) uniplicata plana* (Clessin) – WENZ: 1059.

1923 *Strobilops (Strobilops) uniplicata sesquiplicata* (Boettger) – WENZ: 1060.

1948 *Strobilops (Discostrobilops) uniplicata* (Sandberger) – PILSBRY: 865, Fig. 468 (10–13).

Material examined: Bełchatów: Beł-B – 2 + 3 damaged specimens M1/1019/98; Hochheim (Upper Oligocene) – 151136/5 (SMF), 1950 XXXIV (BSP);

Budenheim (Agenian, MN 2a) – 151143/17 (SMF); Niederrad/Frankfurt (Lower Miocene, MN 2b) – XII 3014a/1, labelled as *S. uniplicata sesquiplicata*, Typus (SMF); Tuchořice (Orleanian, MN 3) – 151147/3 (SMF), 3 specimens in KLIKA'S coll. (NMP), 31A/40 (NHML); Undorf (Orleanian, MN 5) – 238825/1, labelled as *S. uniplicata plana*, Topotyp (SMF); Zwiefaltendorf (Orleanian/Astaracian, MN 5–6) – 275490/1 (SMF).

Measurements of two adult specimens from Bełchatów; shell: H = 1.07–1.10, W = 2.25–2.44; umbilicus: max. W = 0.68–0.70, min. W = 0.50–0.58; number of whorls: 4.4.

Comparative remarks: *S. uniplicata* is the only fossil species of *Discostrobilops*, the subgenus distinguished by having a depressed shell with a large umbilicus, exhibiting all the whorls. The shell surface of *S. uniplicata* is covered with rather regular, closely spaced, fine ribs, with the exception of 1.5 embryonic whorls which are finely granulose. The ribs on the base of the shell are weak and irregular. The shape of the umbilicus changes with the increasing number of whorls; initially it is circular but the last half whorl deflects rapidly from the shell axis, so that the umbilicus gets oval. The aperture is rounded semilunate, with moderately expanded peristome, well thickened within.

Of two adult specimens from Bełchatów only one has its apertural barriers well preserved. The parietal lamella, ca. 1/4 whorl long, is somewhat elevated before reaching the edge of the distinct parietal callus. The infraparietal lamella is very low, inconspicuous in its anterior part and shorter than the parietal (not reaching the edge of the callus). Between their inner ends there is a very short, thread-like interparietal lamella. Three basal lamellae of various length are situated inside the aperture, within the last ca. 1/3 body whorl. The columellar lamella is absent; although WENZ (1915: 76) reports that in *S. uniplicata* columellar lamella is “schwache, tiefsitzende Falte”, neither PILSBRY'S (1948) nor my observations confirm it. Particular lamellae are also well visible in the other, damaged shells from Bełchatów.

The subspecific distinction of *S. uniplicata sesquiplicata* (Boettger, 1884) and *S. uniplicata plana* (Clessin, 1885) presented by WENZ (1915, 1923) seems not to be well justified. Both forms occur together with typical *S. uniplicata* in most localities, and the differences between them – infraparietal lamella reaching the parietal callus edge in the former subspecies and more depressed shell in the latter – seem to be, in my opinion, only infraspecific variations. A similar variation of infraparietal lamella was observed by PILSBRY (1948) in extant American *S. hubbardi* (Brown, 1861). Moreover, PILSBRY stated that *S. uniplicata* “in all of its characters ... agrees so com-

Figs 44–45. *Strobilops uniplicata* (A. Braun): 44 – shell, front view, W = 2.44 mm; 45 – umbilical view

pletely with the living *S. hubbardi* that the relationship appears to be well established”.

S. uniplicata has been recorded from over ten localities in Europe, dated from the Upper Oligocene to the Mid Miocene (WENZ 1915, 1923), but the first record of the species from Poland is Bełchatów.

Subgenus: *Eostrobilops* Pilsbry, 1927

Strobilops boettgeri (Andreae, 1902)

Figs 46–47

1902 *Strobilus böttgeri* ANDREAE: 10, Textfig. 5.

1915 *Strobilops boettgeri* – WENZ: 80, Textfig. 8, Pl. 4: Fig. 4.

Material examined: Bełchatów: Beł-C – 30 + 20 damaged specimens MI/1020/98, Beł-B – 2 specimens ML/1021/98, Beł-A – 6 specimens MI/1022/98; Opole (Astaracian, MN 7+8) – 151115/1, 151117/7, 151118/14 (SMF), 1954 XV and 1966 XXVI (BSP), 1987/43/5 (NMW).

Measurements of 30 specimens from Beł-C; shell: H = 1.10–1.27, W = 1.82–2.05; number of whorls: 4.1–4.5.

Comparative remarks: Specimens of *S. boettgeri* from the three horizons of Bełchatów do not differ from each other; they are also similar to those from Opole. Specimens from both Bełchatów and Opole have a rather low conical spire, covered with more or less visible closely spaced striae, whereas the base is only very weakly striated, almost smooth. The body whorl is rounded at the periphery. The umbilicus is very deep and narrow, however the last ca. 1/3 whorl deflects somewhat from the shell axis (Fig. 47) and a more or less reflexed peristome partly covers it.

The description of apertural barriers by ANDREAE (1902) is rather cursory and it concerns only lamellae on the parietal wall. Both parietal and infraparietal lamellae reach the callus margin. They have their inner ends with nodulose edges, but in contrast to *Strobilops* s. str. the nodules are very weak and closer spaced. On the other hand, the incisions between them are deeper (like in the other species of *Eostrobilops* from Bełchatów, Fig. 50). There is no interparietal lamella. The columellar lamella is weakly marked, and of three basal lamellae the middle one is the most massive and always present. The peripheral basal lamella is much variable, from long and thin to very short, or is absent. Among the specimens examined there was even one with only one basal lamella – a similar phenomenon was described by MANGANELLI et al. (1989) as a specific character of their newly described *Eostrobilops aloisii*.

S. boettgeri was hitherto known only from Opole, hence its occurrence in all horizons of Bełchatów significantly extends its stratigraphic range in the Miocene.

Figs 46–47. *Strobilops boettgeri* (Andreae): 46 – shell, front view, W = 1.85 mm; 47 – umbilical view

Strobilops fischeri Wenz, 1914

Figs 48–50

1914 *Strobilops fischeri* WENZ in: FISCHER & WENZ: 107.

1915 *Strobilops fischeri* – WENZ: 78, Textfig. 6, Pl. 4: Fig. 5.

Material examined: Bełchatów: Beł-C – 58 + 25 damaged specimens MI/1023/98, Beł-B – 3 specimens ML/1024/98, Beł-A – 2 specimens MI/1025/98; Tuchořice (Orleanian, MN 3) – 151131/1 “Cotypus”, 275462/1 (SMF), 1971 XXVII (BSP).

Measurements of 30 specimens from Beł-C; shell: H = 1.30–1.47, W = 2.30–2.56; number of whorls: 4.5–5.

Comparative remarks: Specimens of *S. fischeri* from Bełchatów correspond very well to WENZ’S



Figs 48–50. *Strobilops fischeri* Wenz: 48 – shell, front view, W = 2.63 mm; 49 – umbilical view; 50 – top view of lamellae inside the body whorl

(1915) description, with exception of the number of basal lamellae. In several of the examined specimens there are two or three basal lamellae instead of only two recorded by WENZ (1915: 79, Textfig. 6). The apertural barriers of *S. fischeri* are essentially similar to those of *S. boettgeri* (WENZ'S figures are not quite precise). Nonetheless, both species differ clearly; *S. fischeri* has a bigger and more flattened shell, its umbilicus quickly expands (the last half whorl deflects rapidly from the shell axis) and, first of all, the body whorl is distinctly angled at the periphery and narrowed toward the base (Fig. 48).

STEKLOV (1966) described *S. caucasica*, very similar to *S. fischeri*, from the Upper Miocene of Ciscaucasia,

and noted that the former species differed in being bigger and having three basal lamellae. However, the measurements of only five out of 34 well preserved specimens of *S. caucasica* given by STEKLOV (1966) are similar to those of the biggest specimens of *S. fischeri* from Bełchatów. The basal lamellae of both species are similar. On the other hand, STEKLOV'S (1966: Pl. 5: Fig. 96) figure of the umbilical view of *S. caucasica* is hardly legible, thus precluding a detailed comparison of umbilicus of both these species.

S. fischeri was recorded only from the Lower Miocene deposits of Tuchořice and the investigation of the Bełchatów deposits significantly extends its stratigraphic range in the Miocene.



Family: Chondrinidae Steenberg, 1925
Subfamily: Gastrocoptinae Pilsbry, 1918
Genus: Gastrocopta Wollaston, 1878

***Gastrocopta turgida* (Reuss, 1849)**

Figs 51–54

- 1849 *Vertigo turgida* REUSS: 30, Pl. 3: Fig. 8.
1858 *Pupa lamellidens* SANDBERGER: 55, Pl. 5: Fig. 8a–c.
1860 *Pupa (Pupilla) turgida* – REUSS: 71.
1870 *Pupa (Leucochila) lamellidens* Sandb. = *Pupa turgida* Rss. – BOETTGER: 295.
1889 *Leucochilus quadriplicatus* var. *lamellidens* – BOETTGER: 280.
1891 *Leucochilus quadriplicatus* var. *lamellidens* – KLIKA: 88, Textfig. 87.
1916 *Leucochila turgida* – GOTTSCHICK & WENZ: 63.
1923 *Gastrocopta (Albinula) turgida turgida* – WENZ: 922.

Material examined: Bełchatów: Beł-C – 35 specimens mostly damaged ML/1026/98, Beł-B – ~ 200 specimens mostly with broken lip ML/1027/98; Hochheim (Upper Oligocene) – 152406/3 (BSP); Tuchořice (Orleanian, MN 3) – some specimens No. 1190 from KLIKA'S coll. (NMP), XII 1712a (SMF, BOETTGER'S coll.), 1971 XXVII (BSP), 1909.I.73 (NMW), some specimens labelled *G. quadriplicata* var. *lamellidens* (NHML).

Measurements. 5 specimens from Beł-C; shell: H = 2.60–3.09, W = 1.65–1.79; aperture: h = 1.05–1.30, w = 1.03–1.13; H of body whorl = 1.56–1.80; number of whorls: 5.2–5.5. 20 specimens from Beł-B; shell: H = 2.25–2.60, W = 1.44–1.58; aperture: h = 0.94–1.16, w = 0.83–0.96; H of body whorl = 1.40–1.56; number of whorls: 4.8–5.3.

Comparative remarks: Specimens from Bełchatów are ovate to short ovate, rarely elongatedly ovate, with moderately convex whorls covered with very fine, irregular striae. The aperture is rounded triangular with reflexed lip, almost occluded by large teeth. The edge of the parietal callus is distinctly raised across the parietal wall. Inside the body whorl a distinct palatal-basal callus runs obliquely from the sinulus region to the columella (hence it is deeply situated) and is also visible on the outer surface of the whorl. There are 5, rarely 4 teeth. The inner end of the very solid parieto-angular tooth is deflected towards the periphery. The columellar tooth is large, ear-shaped (Fig. 53), very deeply placed. Two knob-shaped palatal teeth, of which the lower one is distinctly thicker and somewhat flattened (Fig. 54), are situated on the palatal-basal callus, similarly to the rather small basal tooth; rarely the basal tooth is absent. None of these teeth extends beyond the callus. The umbilicus is open, deep and slit-like.

Specimens from two horizons of Bełchatów (B and C) differ somewhat. First of all, those from the older

horizon (Beł-C) are slightly larger and somewhat more elongated.

The original description of *G. turgida* from Tuchořice (type locality of *Vertigo turgida*) by REUSS (1849) is very poor. Later REUSS (1860) complemented it on the basis of very well preserved specimens of the same species from Lipno, a site located near Tuchořice. On the other hand, SANDBERGER (1858) described *Pupa lamellidens* from Hochheim and referred it to *Pupa contracta* Say, 1822, extant in America. Unfortunately, it is now impossible to locate the type specimens of both forms, and I am forced to base my conclusions on other, very scanty, material and literature data. In his revision of the Bohemian Tertiary mollusc fauna, BOETTGER (1870: 295) wrote: “Ich besitze über 20 Exemplare von Tuchořic, die in nichts von den mir direct verglichenen Hochheimer Formen unterschieden sind...”. Thus he was the first to regard both forms as conspecific and referred *Pupa lamellidens* Sandb. = *Pupa turgida* Rss. to *Leucochila* (for status of *Leucochila* Martens and *Leucochilus* Boettger see PILSBRY 1916–1918: 8). However, he did not take into account that REUSS'S *turgida* was a senior name and thus should be valid (the problem was explained later by GOTTSCHICK & WENZ 1916: 63). In his next paper BOETTGER (1889: 280) changed his previous opinion and assigned *Pupa lamellidens* [= *Pupa turgida*] as a variety to *Pupa quadriplicata* described by SANDBERGER (1958) from Wiesbaden, but remarked that those two forms differed in the shape and position of the columellar tooth. KLIKA'S (1891) opinion is similar. In *Pupa lamellidens* the columellar tooth is deeply and more obliquely located. According to BOETTGER (1889), also palatal teeth are deeply situated and more solid in the latter species. Those characters are very well visible in a big series of specimens of the species from Bełchatów.

WENZ (1923) recorded *G. turgida* from some Upper Oligocene and Lower Miocene localities in France, besides those from Hochheim and Tuchořice, as well as from Opole. Specimens from Tuchořice, seen by me in some collections, are very similar to those from Bełchatów (Figs 51 and 52), contrary to specimens from Hochheim stored at the Senckenberg-Museum, which are in a very bad condition making a comparison difficult. Specimens from Opole kept in Munich (1954 XV 7, BSP) have turned out to be *G. edlaueri*.

***Gastrocopta edlaueri* (Wenz, 1921)**

Fig. 55

- 1921 *Leucochylus* (sic!) *edlaueri* WENZ: 30, Textfig. 3.
1923 *Gastrocopta (Albinula) edlaueri* – WENZ: 922.
1973 *Gastrocopta (Albinula) steklovi* PRISYAZHNYUK: 64, Pl. 2: Fig. 2.



Figs 51–54. *Gastrocopta turgida* (Reuss): 51 – specimen from Bełchatów with broken peristome, H = 2.45 mm; 52 – specimen from Tuchořice, phot. P. ČEJCHAN; 53 – side view of columellar and parieto-angular teeth; 54 – top view of palatal wall fragment with palatal teeth (lower palatal is the most massive)

figure it looks horizontal, since he probably missed its inner part) like in *G. turgida*, but it is rather short and only slightly arched. There is a distinct difference between the palatal teeth, the lower being always solid and hooked, and the upper very thin, knob-like. On the outer surface of the body whorl, a deep gutter-like concavity (corresponding to the lower palatal tooth) perpendicular to the crest is marked. On the inner lip, in basal position, a small but distinct swelling is marked instead of basal tooth. The umbilicus is deep and very narrow but circular.

A close comparison of specimens from Belchatów with four shells of *G. steklovi* indicates that they are conspecific. The only difference is a somewhat more distinct microsculpture (striation) on the shell surface of *G. steklovi*.

G. edlaueri was regarded as a species of younger periods of Miocene and the finding in the mid horizon of Belchatów distinctly changes its stratigraphic range.

Gastrocopta acuminata (Klein, 1846)

Fig. 56–58

1846 *Pupa acuminata* KLEIN: 75, Pl. 1: Fig. 19.

1853 *Pupa quadridentata* KLEIN: 216, Pl. 5: Fig. 13.

1889 *Leucochilus quadriplicatum* mut. *quadridentata* – BOETTGER: 278.

1900 *Pupa (Leucochilus) quadridentata* – MILLER: 399, Tab. 7 Fig. 17.

1916 *Leucochila acuminata* – GOTTSCHICK & WENZ: 62.

1923 *Gastrocopta (Albinula) acuminata acuminata* – WENZ: 916.

1923 *Gastrocopta (Albinula) acuminata larteti* (Dupuy) – WENZ: 919.

1923 *Gastrocopta (Albinula) acuminata wenziana* Pilsbry – WENZ: 921

Material examined: Belchatów: Beł-B – 20 specimens MI/1029/98 + ~ 300 specimens mostly with broken lip MI/1030/98; Undorf (Orleanian, MN 5): 152395/2, 152397/3 (SMF); Zwiefaltendorf (MN 5–6): 274519/3 (SMF); Ciscaucasia (Upper Miocene): 1872/95–96, 1872/325–326 (PIM); Ukraine: Bogdanovsky Karier and Michailovsky Karier (Upper Miocene): 9 specimens (IGS).

Measurements of 20 specimens with relatively well preserved lip; shell: H = 2.56–3.24, W = 1.53–1.93; aperture: h = 1.09–1.30, w = 1–1.16; H of body whorl = 1.50–1.84; number of whorls: 5–5.75.

Comparative remarks: *G. acuminata* is one of the most abundant pupilloid snails in Belchatów and one of the most variable. Such a big series makes it possible to recognize the variability range of some characters, which is significant for ascertaining the taxonomic status of some forms described within *G. acuminata* group.

Fig. 55. *Gastrocopta edlaueri* (Wenz): shell, front view, H = 2 mm

Material examined: Belchatów: Beł-B – 18 specimens + 2 damaged MI/1028/98; Opole (Astaracian, MN 7+8): 152404/5 (SMF), 1966 XXVI (BSP); Leobersdorf (Vallesian, MN 9): two paratypes from coll. EDLAUER (NMW); Oberdorf/Wies (Upper Miocene): 274533/2 (SMF); Zamechov and Letitshev (Upper Miocene): (IGS).

Measurements of 18 specimens from Beł-B and (in brackets) 4 specimens from Letitshev; shell: H = 1.83–2.20 (1.84–2.10), W = 1.17–1.28 (1.17–1.27); aperture: h = 0.68–0.88 (0.64–0.78), w = 0.68–0.80 (0.60–0.72); H of body whorl = 1.15–1.27 (1.06–1.21); number of whorls: 4.5–5 (4.5–5).

Comparative remarks: Specimens of *G. edlaueri* from Belchatów are somewhat smaller than those from Leobersdorf and Oberdorf – LUEGER (1981) gave the size: H = ca. 2.5 mm, W = ca. 1.4 mm – but do not differ in other characters. They are all conical rather than ovate-conical, with tapered spire and moderately convex whorls, more or less distinctly striated. The aperture is rounded triangular with poorly reflexed lip. There are 4 teeth: the angular part of parieto-angular tooth is short and somewhat bent toward the palatal wall; the columellar is rather deeply situated, oblique in front view (although in WENZ'S



Figs 56–58. *Gastrocopta acuminata* (Klein): 56 – shell, front view, H = 3.1 mm; 57 – side view of columellar and parieto-angular teeth; 58 – top view of palatal wall fragment with palatal teeth (lower palatal is the longest)

1. Shell shape. In his description of *Pupa acuminata* KLEIN (1846) stated: “testa ... acuminato-ovata”, and his remark is correct, also for specimens from Bełchatów, with an addition: more or less elongated. There are no other details useful for the identification of the species in KLEIN'S (1846) paper (for explanation of the problem of KLEIN'S material – see GOTTSCHICK & WENZ 1916, STEKLOV 1966). Further characters were discussed by MILLER (1900) on the basis of Steinheim specimens assigned to *Pupa (Leucochilus) quadridentata*,

described later by WENZ (1923) as *G. acuminata procera* [= *G. acuminata wenziana* Pilsbry, 1921]. Unfortunately, I have failed to locate the type material of the subspecies. The only specimens labelled as *G. acuminata wenziana* from Steinheim that I have examined (1966 XXVI BSP) did not correspond to GOTTSCHICK & WENZ'S (1916) description. On the other hand, figures of the subspecies presented by those authors in two papers (1916: Pl. 1: Fig. 5 and 1919: Pl. 1: Figs 18–19) show two somewhat different forms – more and less ova-



te-elongated. Both forms, as well as some other of various degree of "inflation" (with exception of those regarded as *larteti*), are found among the specimens of *G. acuminata* from Bełchatów. Another different, more elongated form, was presented by MILLER (1900: Pl. 7: Fig. 17) although in his description it has fewer whorls than that in the figure. With respect to the shell shape and size, *G. acuminata* is somewhat similar to specimens of *G. turgida* from Bełchatów C, but differs in apertural barriers.

2. Aperture shape. The aperture of *G. acuminata* is most often semi-oval or rather horseshoe-shaped according to the previous authors, and it is, in my opinion, one of the differences between that species and *G. turgida* from Bełchatów, which has a rounded triangular aperture.
3. Umbilicus. The umbilicus is open but narrow, deep, partly covered with the body whorl, clearly wider than that in *G. turgida*.
4. Parieto-angular tooth. The parieto-angular tooth is the most constant both in *G. acuminata* and in *G. turgida*. Its angular part in the former species is generally somewhat more arched, hence its inner end seems to be "detached" from the parietal part in front view.
5. Columellar tooth. The columellar tooth is the most variable tooth in *G. acuminata* (Fig. 57). In specimens from Bełchatów all types of columellar tooth described by various authors are found. Generally it is large and lamellate, its anterior part is horizontal and extends to the peristome, whereas the posterior part is more or less bent towards the base. Sometimes the anterior part is somewhat folded and then it may be visible in front view as an oblique tooth. The posterior part, not always well visible in front view, in some specimens is much bent, so that it comes to resemble the ear-like columellar tooth in *G. turgida*.
6. Palatal teeth. There are 2–4 palatal teeth, most often 2. Only a few out of over 300 specimens have a very small interpalatal tooth and only a few have a barely marked suprapalatal tooth. The teeth are placed on not very well marked callus and it is one of the distinct differences between this species and *G. turgida*. The second difference, in my opinion, is the shape of the lower palatal tooth which in *G. acuminata* is lamellate and clearly emerging toward the aperture margin (Fig. 58) whereas in *G. turgida* it is knob-shaped and "sitting" on the callus (Fig. 54).
7. Basal tooth. Almost all specimens have a more or less developed knob-shaped basal tooth, only exceptionally it is absent.

G. acuminata is one of the most frequent gastrocoptine snails in European Neogene, known from the biozone MN 5 to the end of Pliocene and

even to the younger horizons of Early Pleistocene. It was also recorded from Poland on the basis of only one specimen from a Plio/Pleistocene site in Kielniki (STWORZEWICZ 1981, 1989 as *G. turgida quadruplicata*).

Gastrocopta nouletiana (Dupuy, 1850)

Figs 59–61

1850 *Pupa Nouletiana* DUPUY: 309, Pl. 15: Fig. 6.

1875 *Pupa (Leucochila) nouletiana* – SANDBERGER: 549, Pl. 29: Fig. 22.

1875 *Pupa gracilidens* SANDBERGER: 600.

1923 *Gastrocopta (Sinalbinula) nouletiana nouletiana* – WENZ: 930.

1923 *Gastrocopta (Sinalbinula) nouletiana gracilidens* – WENZ: 930.

1966 *Gastrocopta (Sinalbinula) nouletiana* – STEKLOV: 140, Textfig. 48, Pl. 2: Figs 40–42.

1966 *Gastrocopta (Sinalbinula) gracilidens* – STEKLOV: 141, Pl. 2: Figs 43.

1998 *Gastrocopta nouletiana* – FINGER: 19, Pl. 8: Figs A-C.

Material examined: Bełchatów: Beł-B – 200 specimens mostly with broken lip MI/1031/98, Beł-A – 20 damaged specimens ML/1032/98; Undorf (Orleanian, MN 5): 152367/5 (SMF); Sansan (Astaracian, MN 6): 5 specimens (MHN), 8 specimens (MNHN), 6 specimens 274734/7 (SMF); Frankfurt (Upper Miocene): 152326/1 (SMF), 31A/40 (NHML); Ciscaucasia (Upper Miocene): 1872/352-358 as *G. nouletiana*, 1872/359-364 as *G. gracilidens* (PIM); Ukraine: Bogdanovsky Karier (Upper Miocene): 32 specimens (IGS); Öcs (Vallesian, MN 10): Pl. 203, 209, 215, 230, 259, 297, 481 (MAFI).

Measurements: 20 specimens of *nouletiana*-type; shell: H = 1.90–2.45, W = 1.05–1.32; aperture: h = 0.71–0.95, w = 0.68–0.85; H of body whorl = 1.15–1.48; number of whorls: 4.75–5.25. 20 specimens of *gracilidens*-type; shell: H = 1.85–2.53, W = 1.16–1.36; aperture: h = 0.75–0.98, w = 0.71–0.87; H of body whorl = 1.15–1.53; number of whorls: 4.5–5.25.

Comparative remarks: *G. nouletiana* is one of the most variable Miocene gastrocoptines, of the group regarded by some authors as subgenus *Sinalbinula*. In Bełchatów there are two forms of the species – *nouletiana* and *gracilidens*, earlier having a status of subspecies or even distinct species (see synonyms). They differ mainly in their shell shape and the number of palatal teeth. One (*nouletiana*) is as a rule ovate, with three palatal teeth (Fig. 59), whereas the other (*gracilidens*) is more elongate, sometimes strongly elongate, with four palatal teeth (interpalatal tooth present) (Fig. 60). Both forms were found together in most of the known localities including Sansan – type locality of the species, although DUPUY (1850) based his description of *Pupa Nouletiana* on elongate ovate specimens with three palatal teeth (Fig. 61).

Figs 59–61. *Gastrocopta nouletiana* (Dupuy): 59 – specimen with three palatal teeth, H = 2.23 mm; 60 – specimen with four palatal teeth, H = 2.3 mm; 61 – specimen from Sansan (ex coll. MHN), H = 2.32 mm, E. STWORZEWICZ del.

Some other taxa similar to *G. nouletiana* were described from younger Neogene horizons, but the taxonomic status of *G. nouletiana* has never been precisely determined. A review of the forms of *G. nouletiana*, as well as of closely related species, with an analysis of their variability will be published separately (in preparation).

G. nouletiana is common in the deposits of European Neogene since the Mid Miocene (Bełchatów B is one of the oldest sites where the species was found), and widespread from France to the Caucasus.

Gastrocopta suevica (Sandberger, 1875)

Fig. 62

1875 *Pupa (Vertigo) suevica* SANDBERGER: 654.

1900 *Pupa (Leucochilus) suevica* – MILLER: 398, Pl. 7: Fig. 16.

1919 *Leucochila suevica* – GOTTSCHICK & WENZ: 13, Pl. 1: Figs 24–25.

1923 *Gastrocopta (Sinialbinula) suevica* – WENZ: 937.

1998 *Gastrocopta suevica* – FINGER: 19, Pl. 8: Figs D-F.

Material examined: Bełchatów: Beł-B – 20 specimens MI/1033/98; Steinheim (Astaracian, MN 7+8) – 152387/3, 217604 (SMF), 1966 (BSP), 10815 (MNHN).

Measurements of 20 specimens; shell: H = 1.90–2.17, W = 1.02–1.09; aperture: h = 0.71–0.80, w = 0.66–0.77; H of body whorl = 1.08–1.25; number of whorls: 4.8–5.5.

Comparative remarks: Specimens from Bełchatów have been compared with those from Steinheim and from Öcs. Of them, only specimens from Steinheim correspond to SANDBERGER'S (1875) very laconic description; none of the 10 specimens from Öcs stored at the Senckenberg Museum (274610/10) is similar to those from Steinheim. On the other hand, there is a great similarity between the specimens from Bełchatów and from Steinheim, particularly those figured by FINGER (1998: 42, Pl. 8: Figs D-F).

According to SANDBERGER (1875: 654) *G. suevica* is somewhat similar to form *gracilidens* of *G. nouletiana*, however he did not mention differences between them. In my opinion those two species have apertural barriers of similar type (with exception of somewhat more united parieto-angular tooth in *G. suevica*) but they differ very clearly and consistently in their shell shape. The angular and parietal in *G. suevica* are united into a continuous bifid tooth, the angular part being somewhat shorter and only slightly, if at all, bent to the palatal margin. The columellar tooth is horizontal, short lamellate, and basal – knob-shaped. There are, as a rule, 3 palatal teeth, but specimens with 2 teeth were also, though rarely, found. The parietal callosity in *G. suevica* is very distinctly marked and makes the aperture almost regularly circular. In *G. nouletiana* the parietal aperture margin is distorted by the parietal callosity which is weak and “sunken” into the body whorl.

G. suevica differs from *G. nouletiana* at first glance in its slim shape. In contrast to the latter species, *G. suevica* has a smooth surface of the body whorl, with-



Fig. 62 – *Gastrocopta suevica* (Sandberger), shell, front view, H = 2.14 mm

out a crest or incision on the palatal wall, corresponding to the lower palatal.

LUEGER (1981) placed *G. suevica* among synonyms of *G. serotina* Ložek, 1964, but his decision seems to be unjustified, particularly on the ground of different shape of parieto-angular tooth in both species.

The older and the only certain finding of *G. suevica* was that in Steinheim, but its occurrence in Beł-B horizon shifts the stratigraphic range of the species to the Lower/Mid Miocene limit.

Gastrocopta cf. ferdinandi (Andreae, 1902)

Fig. 63

1902 *Leucochilus ferdinandi* ANDREAE: 18, Textfig. 9.

1923 *Gastrocopta (Sinalbinula) ferdinandi* – WENZ: 929.

Material examined: Bełchatów: Beł-B – 160 + 50 damaged specimens MI/1034/98; Opole (Astaracian, MN 7+8) – 1966 XXVI (BSP), 1987/43/3 (NMW).

Measurements of 30 specimens; shell: H = 1.83–2.40, W = 1.06–1.13; aperture: h = 0.68–0.78, w = 0.66–1.0; H of body whorl = 1.09–1.30; number of whorls: 5–5.6.

Comparative remarks: Specimens from Bełchatów are referred to *G. ferdinandi* with some doubts because the material from Opole, the type locality of the spe-

Fig. 63 *Gastrocopta cf. ferdinandi* (Andreae), shell, front view, H = 2.32 mm

cies, stored at the museums in Vienna and in Munich, does not correspond with ANDREAE'S (1902) description; neither is there any information about type specimen(s) (see: LUEGER 1981: 26).

In his description of *G. ferdinandi* ANDREAE (1902) pointed out that the species was characterized by having very convex whorls and a deep suture, whereas both these characters are quite different in specimens from the mentioned collections. The specimens from Bełchatów are turret-shaped, like that figured by ANDREAE (1902: Fig. 9), and have very convex whorls and a deep suture. The size of the Bełchatów shells and the number of their whorls also correspond to ANDREAE'S *G. ferdinandi*. However, there are some differences in the apertural barriers between the latter specimens and the shells from Bełchatów. ANDREAE (1902) noted that the parieto-angular tooth was bifid in its outer part, whereas in the specimens from Bełchatów the angular and parietal parts of the tooth are almost separate and slightly arcuately bent outward. He compared *G. ferdinandi* to *G. fissidens* (SANDBERGER, 1858) and stressed that the latter species had all the teeth more distinct than the former. Thus the apertural barriers of the specimens from Bełchatów would be similar to those of *G. fissidens*, but the shape is clearly different, *G. fissidens* being cylindrical.

BIOSTRATIGRAPHY

Because of being mostly long-lived, terrestrial snail species only rarely provide a basis for stratigraphic conclusions. However, some of older species, known since the Oligocene, have survived only till the Lower Miocene and as such they are indicative of horizons of comparatively early age. Some other species appeared as late as the Upper Miocene and also provide information about the horizon age. Both these groups are rather poorly represented among the Bełchatów pupilloids.

The occurrence of pupilloid species in the three horizons of the Bełchatów deposits is presented in Table 1.

Of the three horizons in Bełchatów, the older two: B and C, are not very remote in age, whereas Beł-A is considerably younger. In consequence, the malacofauna of the former two horizons can not be expected to differ significantly. Nonetheless, a certain tendency to size variability is observed in some species. Shells of both *Negulus suturalis* and *Gastrocopta turgida* are clearly bigger in the oldest horizon (Beł-C), whereas *Strobilops costata* shows a reverse tendency – specimens from Beł-C are smaller and more flattened than those from Beł-B.

In contrast, the morphological similarity of some European Miocene species and those living now in America is so close that it is difficult to find a difference, e.g. *Strobilops uniplicata* from Tuchořice and Bełchatów and recent *S. hubbardi* from America (cf. p. 156 and STWORZEWICZ & PRISYAZHNYUK 1997).

The lowermost horizon of the Bełchatów deposits (Beł-C) contains only seven species, only one of them – *Vertigo ovatula* – being limited to that horizon. The species, described from the Upper Oligocene, has survived only till the Mid Miocene. Likewise, another species known from the Upper Oligocene – *Gastrocopta turgida* – has not been found in horizons younger than the Lower/Mid Miocene (Beł-B).

The next horizon, Beł-B, is the richest in pupilloid species (23). Of these, *Strobilops tiarula* and *Gastrocopta nouletiana* continue throughout the Mid and till the Upper Miocene. Two species occur throughout the three horizons. The remaining species, though absent from the youngest horizon (Beł-A), have been found at other localities of the Mid Miocene. Stratigraphically, the horizon can be correlated with the locality in Undorf (CLESSIN 1877).

Both of the above fauna-bearing horizons can be placed between the locality in Tuchořice (KLIKA 1891) on one hand and those in Sansan and Opole (DUPUY 1850, ANDREAE 1902, 1904) on the other. The malacofauna of Beł-C and Beł-B is particularly close to that of Tuchořice in having quite many species in common. These are: *Vertigo callosa*, *V. angulifera*, *Nesopupa minor*, *Negulus suturalis*, *Planogyra*

nana, *Strobilops uniplicata*, *S. fischeri* and *Gastrocopta turgida*. Somewhat fewer species are shared with the older, Upper Oligocene locality in Hochheim

Table 1. Pupilloids in the three horizons of the Bełchatów deposits

Species	Horizons of Bełchatów		
	Beł-C MN 4	Beł-B MN 5	Beł-A MN 9
<i>Argna oppoliensis</i> (Andreae)		+	
<i>Vertigo</i> (s. str.) <i>callosa</i> (Reuss)		+	
<i>V. diversidens</i> (Sandberger)		+	
<i>V. protracta</i> (Sandberger)		+	
<i>V. ovatula</i> (Sandberger)	+		
<i>V. (Vertilla) oecensis</i> (Halaváts)			+
<i>V. angulifera</i> Boettger		+	
<i>Nesopupa minor</i> (Boettger)		+	
<i>Negulus suturalis</i> (Sandberger)	+	+	
<i>Vallonia subcyclophorella</i> (Gottschick)		+	
<i>Acanthinula trochulus</i> (Sandberger)	+	+	
<i>Spermodea</i> cf. <i>candida</i> Falkner		+	
<i>Planogyra nana</i> (A. Braun)		+	
<i>Strobilops</i> (s. str.) <i>costata</i> (Clessin)	+	+	
<i>S. tiarula</i> (Sandberger)		+	+
<i>S. cf. joossi</i> (Gottschick)		+	
<i>S. (Discostrobilops) uniplicata</i> (Sandberger)		+	
<i>S. (Eostrobilops) boettgeri</i> (Boettger)	+	+	+
<i>S. fischeri</i> Wenz	+	+	+
<i>Gastrocopta turgida</i> (Reuss)	+	+	
<i>G. edlaueri</i> (Wenz)		+	
<i>G. acuminata</i> (Klein)		+	
<i>G. nouletiana</i> (Dupuy)		+	+
<i>G. suevica</i> (Sandberger)		+	
<i>G. cf. ferdinandi</i> (Andreae)		+	



(FISCHER & WENZ 1914): *Vertigo protracta*, *V. ovatula*, *Negulus suturalis* and *Gastrocopta turgida*.

A comparison of the Bełchatów fauna with that from not very remote (ca. 100 km) site in Opole is not surprising. They share as many as 10 pupilloid species, besides those of other taxa (STWORZEWICZ 1995, STWORZEWICZ & SOŁTYS 1996, STWORZEWICZ & PRISYAZHNYUK 1997). The common pupilloids are: *Argna oppoliensis*, *Vertigo callosa*, *V. ovatula*, *Negulus suturalis*, *Planogyra nana*, *Strobilops costata*, *S. boettgeri*, *Acanthinula trochulus*, *Gastrocopta edlaueri* and *G. ferdinandi*.

Only two species described from Sansan have been found in Bełchatów: *Vertigo diversidens* and *Gastrocopta nouletiana*.

The uppermost horizon, Beł-A, contains only five pupilloid species, only one of which – *Vertigo oecensis* – may be regarded as an Upper Miocene element. It is known also from other Upper Miocene deposits: Öcs,

Eichkogel and Ořesany (HALAVÁTS 1911, LUEGER 1981, FORDINAL 1996). In the light of recent studies, specimens from the Plio/Pleistocene deposits in Kielniki, recorded as *Vertigo angustior* (STWORZEWICZ 1981), seem to be closer to *V. oecensis*, and may represent this species or a very similar form. In this case the stratigraphic range of the species would be slightly wider.

Among the Bełchatów pupilloids there are some extremely long-lived species. The Bełchatów records of *Strobilops boettgeri*, previously known only from Opole (MN 7+8; ANDREAE 1902), extend its stratigraphic range to ca. 9 My. Likewise, *S. fischeri*, previously known only from the Lower Miocene in Tuchořice (KLIKA 1891), has turned out to occur also in the Upper Miocene. They provide an example of species which, as far as it can be judged from shell characters, have remained unchanged for almost 10 My.

PALAEOECOLOGICAL ANALYSIS

Ecological requirements of extant pupilloid snails, particularly of the groups extinct in Europe and found in Bełchatów, as well as palaeobotanical data allow, in general, for inferring about the habitat, which existed in the present Central Poland over a dozen million years ago. A palaeobiogeographic analysis of the Miocene land snails from Poland, including Pupilloidea, has been presented elsewhere (STWORZEWICZ 1993).

Some of the ten pupilloid genera represented in the Bełchatów deposits are still extant in Europe, and constitute the most numerous group. Pupillidae are represented by *Argna oppoliensis*, a species described from Opole. The recent range of the genus *Argna* is restricted to the mountain forests of Central Europe, mainly the Alps and the Carpathians. In the Tertiary the genus appeared not earlier than the Miocene.

Vertigo is at present a widespread genus of humid habitats or regions, chiefly in the Northern Hemisphere and rather well known. In Poland it is represented by 10 species (POKRYSZKO 1990). Members of *Vertigo* occur both in subarctic woodland of Norway and, much more rarely, in American tropics; hence the group is not very useful for palaeoecological considerations.

Another vertiginid genus, *Negulus*, is represented in Bełchatów by one species only – *N. suturalis*. The four extant members of *Negulus* are restricted to the Afrotropical region, not exceeding 20° latitude either north or south. A revision of the genus by VAN BRUGGEN (1994) provides some data on the ecology of this taxon. Members of *Negulus* are mountain-dwellers living in evergreen forest litter, between

800 and 4,000 m a.s.l. Almost twice as many species are known from the Tertiary of Europe, from the Lower Oligocene to the end of Pliocene.

Nesopupa minor, similarly to the other members of *Nesopupa* known from the Neogene of Europe, since the Upper Oligocene till Pliocene, seems to be the closest related to the Oriental and Ethiopian groups. According to the very scanty information on the ecological requirements of this group, Ethiopian (and African) *Nesopupa* are also (like *Negulus*) mainly mountain snails, living under rotten leaves, wood and stones (PILSBRY & COOKE 1918–1920) between 750 and 4,300 m a.s.l. (ADAM 1957).

Strobilopsids are at present known from humid eastern part of North America, south of ca. 52° N, Central America and northern South America, as well as Far East and New Guinea. They live in moderately humid deciduous and mixed forests, in leaf-litter and under decaying logs. In Europe the group was very speciose (over 30 species) and greatly diversified since the Mid Eocene to the Upper Pliocene. Comprehensive information on recent and fossil Strobilopsidae was summarized by MANGANELLI et al. (1989).

Gastrocoptinae in Bełchatów are represented by the genus *Gastrocopta*, which is at present very widely distributed in tropical and temperate zones of nearly all continents with exception of Europe: in America – south of 53°N and in Far East – south of 45°N. In general, members of *Gastrocopta* live in habitats similar to those of *Strobilops*. In the Tertiary of Europe gastrocoptines, like *Strobilops*, were very numerous and greatly diversified. Six species of

Gastrocopta from Bełchatów distinctly fall in two groups: one refers to American species, such as *G. armifera* (Say, 1821) or *G. contracta* (Say, 1822) which, according to PILSBRY (1916–1918), form the subgenus *Albinula*. It includes *G. turgida*, *G. acuminata* and *G. edlaueri*. It is noteworthy that in Bełchatów those species are very abundantly represented in older horizons (Beł-C and Beł-B), whereas another group, referring to Far-Eastern *Gastrocopta* and regarded by PILSBRY (1916–1918) as the subgenus *Sinalbinula*, is particularly numerous in the mid horizon Beł-B, being less so in the upper horizon Beł-A. The second group includes *G. nouletiana*, *G. suevica* and *G. cf. ferdinandi*.

Palaeobotanical research in the open cast mine Bełchatów has been based on pollen assemblages and macroscopic plant remains (STUCHLIK et al. 1990, WOROBIEC 1995). In general it may be inferred that the development of vegetation varied from open landscape, through swamp forest to forest of dry habitats. The swamp forest facies is more or less similar in all horizons. There are *Taxodiaceae-Cupressaceae* forests with an admixture of *Nyssa*, *Alnus* and others. The facies of drier habitats are differentiated and represent several types of forests.

The lowermost fauna-bearing horizon (Beł-C) contains only a few species of *Gastrocopta*, *Strobilops* and *Vertigo*. There is only one taxon of Pupilloidea characteristic of that level – *V. ovatula*. The composition of the flora with the prevalence of *Rhus* and *Engelhardtia* and the high percentage of *Quercoidites henrici* and *microhenrici*, older *Myrica* types, as well as some palms indicates a warm and humid subtropical or even paratropical climate. The age of this flora could be determined as Oligocene and this is also confirmed by radiometric dating of volcanic tuffites which yielded a date of 18.1 ± 1.7 MA. It should be added that teeth of a fruit-eating bat, a member of Megachiroptera (probably *Rousettus*) were also found in the same horizon, and it is the northernmost locality of Megachiroptera in the world (KOWALSKI 1995).

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The mid horizon (Beł-B) contains the most diversified fauna with particularly numerous species of *Gastrocopta*, *Strobilops*, *Vertigo*, *Nesopupa*, *Negulus*, *Acanthinula*, *Vallonia* and *Argna*. Some of them are shared with Beł-C horizon. The main vegetation complex is represented by *Taxodiaceae-Cupressaceae* forests with an admixture of *Nyssa* and *Alnus*, whereas the facies of drier habitats is represented by mixed forests with *Pinus* and some leafed trees like *Celtis*, *Carya*, *Ulmus* or *Quercus*. The flora was recognized as Karpatian, and the dating of overlying tuffites gave a date of 16.2 ± 1.3 MA.

The upper horizon (Beł-A) includes, apart from some species of *Gastrocopta* and *Strobilops* found already in older horizons, the species known only from the Upper Miocene deposits – *Vertigo oecensis*. The floristic composition is characterized by a group of Arcto-Tertiary elements. The main vegetation complex is represented by temperate forests with the predominance of *Pinus*, *Ulmus*, *Alnus*, *Fagus*, *Quercus*, *Carpinus* and others. A small admixture of Tertiary elements, such as *Carya*, *Ilex*, *Pterocarya*, *Liquidambar*, *Castanea* and *Taxodiaceae*, determines the flora as still of the Neogene age.

A comparison of the map of vegetation zones and recent distribution of *Gastrocopta* and *Strobilops* shows that contemporary ranges of these groups overlap with the zone of subtropical mixed mesophytic forests and swamp forest. They are essentially evergreen, associated with a warm and humid climate, but with distinct changes of temperature during a year. Rainfall is periodically very rich, associated with the occurrence of monsoon and trade-winds, which carry along much humidity from over the sea. At present mixed mesophytic forests occur in south-eastern Asia, and swamp forests resembling the fossil ones grow in the south-eastern states of the USA, mainly in Florida and Mississippi Delta. In Europe, such a type of forest was common in the Tertiary. Its remnants are found today in the Caucasus, where *Gastrocopta* is still living and, partly, at higher altitudes in the Canary Islands.

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