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ON THE SUBGENERIC CLASSIFICATION OF *VERTIGO* O. F. MÜLLER, 1774 (GASTROPODA: PULMONATA: VERTIGINIDAE)

BEATA M. POKRYSZKO[1], EWA STWORZEWICZ[2]

[1]Museum of Natural History, Wrocław University, Sienkiewicza 21, 50-335 Wrocław, Poland (e-mail: bepok@culex.biol.uni.wroc.pl)

[2]Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland (e-mail: stworzewicz@isez.pan.krakow.pl)

ABSTRACT: The following subgeneric names are synonymized: *Vertigo* s. str. O. F. Müller, 1774 = *Isthmia* Gray, 1821 = *Alaea* Jeffreys, 1830 = *Angustula* Sterki, 1888 **syn. n.** = *Vertillaria* Pilsbry, 1919 **syn. n.** = *Ungulidenta* Popova et Shileyko, 1981 **syn. n.**; *Vertilla* Moquin-Tandon, 1855 = *Alloptyx* Pilsbry, 1953 **syn. n.** = *Angustella* Steklov, 1967 **syn. n.** Of the two resulting subgenera *Vertilla* Moquin-Tandon, with the type species *V. angustior* Jeffreys, includes also *V. angulifera* O. Boettger, *V. oecsensis* (Halaváts), *V. bicolumellata* Steklov and *V. hinkleyi* Pilsbry; *Vertigo* s. str., with the type species *V. pusilla* O. F. Müller, includes all the remaining members of the genus.

KEY WORDS: terrestrial snails, systematics, *Vertigo*, subgenera

INTRODUCTION

The genus *Vertigo* O. F. Müller – very widely distributed, speciose and well-represented also in fossil record – has not been subject to a modern revision on a world-wide basis. The ever-increasing number of described and named species is accomodated by a subgeneric classification which is partly a heritage of the malacological past, and partly a result of addition of further subgenera without, however, any attempt at treating the already existing system as a reference point. Bringing the subgeneric system to modern taxonomic standards seems at present even more important than a thorough specific-level revision.

Vertigo O. F. Müller is one of the best defined genera within the pupilloids. Characterized by unique synapomorphies of the genital organs (cf. POKRYSZKO 1990), it is monophyletic beyond any reasonable doubt. Its structural uniformity, both with respect to the rather plesiomorphic shell and the much derived reproductive system, makes it possible to define the genus, and at the same time renders attempts at its subgeneric classification extremely difficult. *Vertigo* O. F. Müller seems to comprise mostly species that are characterized mainly by generic synapomorphies on one hand and by autapomorphies on the other.

Of several subgenera proposed by earlier authors within *Vertigo* O. F. Müller, 1774 (GRAY 1821, 1847, JEFFREYS 1830, MOQUIN-TANDON 1855, STERKI 1888, PILSBRY 1919 in PILSBRY & COOKE 1918–1920, PILSBRY 1948, 1953; see also ZILCH 1959–1960), some were later abandoned or synonymized, while some other are still uncritically accepted at least in European literature, sometimes being even elevated to the generic rank (e.g. SHILEYKO 1984). The situation is further complicated by contemporary palaeomalacologists who, besides using the old subgeneric names, often propose further subgenera in order to emphasize the purportedly isolated position of their newly discovered fossil members of *Vertigo* (cf. STEKLOV in STEKLOV & TSYTOVICH 1967, POPOVA & SHILEYKO 1981). The result is a classification with several rather poorly defined subgenera, each – except *Vertigo* s. str. – including only very few species. Recent data on the evolution and polarity of characters in the whole superfamily Pupilloidea (POKRYSZKO 1990,

1994, 1997a, b) and the increasing information on fossil record (STEKLOV 1966, STWORZEWICZ 1999 and literature contained therein) provide a good basis for re-considering the subgeneric classification of *Vertigo*.

EXISTING SUBGENERA – DIAGNOSES AND TYPE SPECIES

The following subgenera were distinguished within *Vertigo* O. F. Müller, 1774: *Vertigo* s. str., *Isthmia* Gray, 1821, *Alaea* Jeffreys, 1830, *Vertilla* Moquin-Tandon, 1855, *Angustula* Sterki, 1888, *Vertillaria* Pilsbry, 1919, *Alloptyx* Pilsbry, 1953, *Angustella* Steklov, 1967 and *Ungulidenta* Popova et Shileyko, 1981.

Isthmia Gray, 1821

Isthmia Gray, 1821 was originally based on chirality; its type species *Helix* (*Isthmia*) *cylindrica* Gray [= *Vertigo pygmaea* (Draparnaud)] was dextral, contrary to the type species of the genus *Vertigo* and subgenus *Vertigo* s. str. – *V. pusilla* O. F. Müller. Consequently, the name was interpreted by some authors (e. g. MOQUIN-TANDON 1855) as referring to all dextral *Vertigo*. Though no distinctive characters except chirality were given by GRAY (1821: 237: "shell dextral"), some of the later authors (e. g. SHILEYKO 1984) applied the name to species of *Vertigo* with 0–1 teeth on the parietal wall. An additional complication was the fact that in the previous century *Isthmia* referred also to members of *Truncatellina* R. T. Lowe, 1852 (see e.g. WESTERLUND 1887). The subgenus has often been questioned or simply omitted from classifications (e.g. PILSBRY 1948, ZILCH 1959–1960, POKRYSZKO 1990).

Alaea Jeffreys, 1830

JEFFREYS's (1830: 357) diagnosis of *Alaea* was: "Testa vere cylindrica. Apertura extus plerumque marginata, et intus denticulis sive lamellis incontinuis munita, marginibus subaequalibus: peristomio simplici", with a comment "From *Pupa* it differs in the shell being always of a more cylindrical form, and in having the aperture generally thickened by an exterior rib, and never reflexed. The teeth too, when present, are never laminar or continued on the penultimate whorl". JEFFREYS separated it from *Vertigo* because its shell was dextral which follows from his (JEFFREYS 1830: 357) comment "I have separated this form from the genus *Vertigo* as established by Férussac, for the reasons stated in my remarks on *Clausilia*" (again contrary to the type species of the genus *Vertigo* and subgenus *Vertigo* s. str. – *V. pusilla* O. F. Müller). He included there several dextral species, among others *Alaea palustris* Leach, in Turton [= *V. antivertigo* (Draparnaud)]. In 1847 (p. 176) GRAY selected the latter species as type. Later the name was applied to all dextral members of *Vertigo* (CLESSIN 1887: 272: "rechtsgewunden, gezähnt oder ohne Zähne" [dextral, with or without teeth], or CAZIOT & MARGIER 1909, without any diagnose), and used more or less constantly since GRAY's (1847) publication till WESTERLUND's (1887) "Fauna". DALL (1905) removed some species from JEFFREYS's (1830) list of members of *Alaea* (not, however, formulating any diagnostic features of the subgenus in this new sense) and designated as its type *V. minutissima* Hartmann [= *Truncatellina cylindrica* Férussac] – an unwarranted act from both the viewpoint of the stability of nomenclature and of the taxonomic soundness, quite rightly criticized by PILSBRY (1905). Like the preceding subgenus, in more recent literature it has often been questioned or omitted (ZILCH 1959–1960, SHILEYKO 1984, POKRYSZKO 1990).

Vertilla Moquin-Tandon, 1855

Vertilla was introduced by MOQUIN-TANDON (1855) to accomodate two species: *V. plicata* A. Müller [= *V. angustior* Jeffreys] and *V. pusilla* O. F. Müller. No type species was originally designated, and the diagnose was "Coquille sénestre" [shell sinistral] (MOQUIN-TANDON 1855: 408), later followed by e.g. CLESSIN (1887: 280: "linksgewunden" [sinistral] or CAZIOT & MARGIER 1909, without any diagnose). In 1900 PILSBRY & VANATTA (p. 597) removed *V. pusilla* O. F. Müller from *Vertilla* Moquin-Tandon "leaving *V. plicata* [= *venetzii* = *angustior*] the type of *Vertilla*". In 1919 (pp. 210–213 in PILSBRY & COOKE 1918–1920) PILSBRY again designated *V. plicata* A. Müller as its type species, at the same time including there *V. callista* Westerlund [= *angustior* Jeffreys], and giving the following diagnose: "Angular and parietal lamellae well developed, the angular not connected with the peristome, parietal long; columellar lamella subvertical, spirally entering above. Upper palatal fold very long, its inner end curving down; the lower palatal short or wanting". ZILCH (1959–1960: 149) diagnosed the subgenus: "Gehäuse meist links-, seltener rechts-gewunden (wie die fossile *V.* (*V.*) *angulifera* O. Boettger); Columellarlamelle im Inneren ansteigend; Angulare und Parietallamelle kräftig; Parietallamelle lang; obere Palatalfalte lang, tief eindringend, untere kurz oder fehlend. [...] O. Miözan → Europa. Wenige Arten. → Rezent. Europa. Wenige Arten." [Shell mostly sinistral, less often dextral (like in fossil *V.* (*V.*) *angulifera* O. Boettger); columellar lamella inwards ascending; angular and parietal lamellae robust; parietal lamella long; upper palatal fold long, deep

entering, lower short or absent. [...] Upper Miocene → Europe. Few species. → Recent. Europe. Few species.]. He included there "few" species, but listed only two.

SHILEYKO (1984: 213) diagnosed *Vertilla*, which he elevated to the generic rank, as follows: "Rakovina levozavita. Kolumelarnaya plastinka dlinnaya, pochti vertikalnaya. Verkhnaya palatalnaya skladka ochen' dlinnaya, zadniy konets yeë skvoz uste ne viden" [Shell sinistral. Columellar tooth long, nearly vertical. Upper palatal tooth very long, its posterior end not visible in the aperture], with a range including Europe and Caucasus and with 1–2 species. He stated that in fossil state it was known since the Mid Miocene (Europe, Ciscaucasia) but did not mention any species besides *V. angustior* Jeffreys. In his Table 4 (1984: 85) SHILEYKO included *Vertilla* as known since the Upper Miocene, but again he did not specify which species, besides *V. angustior*, were included. As data source for the table he quotes STEKLOV (1966) and ZILCH (1959–1960); both these authors mention only *V. angustior* Jeffreys and *V. angulifera* O. Boettger, the latter from the Mid Miocene of Germany and Upper Miocene of Germany and Ukraine (STEKLOV 1966: 148).

In a monograph dealing exclusively with recent species, POKRYSZKO (1990: 211) diagnosed *Vertilla* as having "Shell spindle-shaped. Columellar tooth in the shape of a lamella parallel to the aperture plane", including only *V. angustior* Jeffreys, the type species.

It follows from the above that *Vertilla* was variously and often imprecisely diagnosed, and basically (except MOQUIN-TANDON 1855, ZILCH 1959–1960, STEKLOV 1966 and PILSBRY 1919 in PILSBRY & COOKE 1918–1920) its only member specified by name was *V. angustior* Jeffreys.

Angustula Sterki, 1888

V. angustior Jeffreys, the type species of *Vertilla* Moquin-Tandon, was initially included in one more subgenus, viz. *Angustula*, that was introduced by STERKI (1888: 378) for *V. milium* (Gould) and *V. venetzii* Charpentier [= *V. angustior* Jeffreys], without type species designation. STERKI (1888: 378) diagnosed it as follows: "the main distinguishing features [...] are: 1. the narrowed ultimate whorl, with deep constriction; 2. the long gular lamella, connected with one of the outer primary teeth; 3. the position of the columellar lamella along the pillar; 4. the small lamella D [= lower palatal] on the peristome"; the diagnose in some points disagreeing with the actual appearance of the species (cf. lower palatal in Fig. 509 in PILSBRY 1948). In 1900 PILSBRY & VANATTA (p. 597) stated that "*Vertilla* must replace *Angustula* as a subgeneric name for *V. milium* and *venetzii*, the latter species being the type". Almost fifty years later PILSBRY (1948), changing his mind, designated *V. milium* (Gould) as the type species of *Angustula*, not referring to the earlier synonymization and including besides *V. bermudensis* Pilsbry and a Pliocene *V. hibbardi* F. C. Baker. He diagnosed the subgenus (PILSBRY 1948: 944): "Angular, parietal and columellar lamellae are strongly developed, the parietal long, columellar crescentic, its inner end curving downward. Palatal folds strong, the lower entering to the dorsal side, its inner end curving downward", in a way suggesting exclusion of *V. venetzii* Charpentier [= *V. angustior* Jeffreys] from STERKI's (1888) subgenus. Though he did not exclude it explicitly, some years before (PILSBRY & VANATTA 1900, PILSBRY 1919 in PILSBRY & COOKE 1918–1920) he designated it as the type species of *Vertilla* Moquin-Tandon.

Vertillaria Pilsbry, 1919

Vertillaria, described by PILSBRY (1919 in PILSBRY & COOKE 1918–1920: 144), with its only member – North American *V. oscariana* Sterki – was diagnosed "Shell oblong, with the columellar lamella in form of a blunt vertical plate, other teeth short; outer lip biarcuate. In the type species there is no angular lamella or basal fold, and the upper-palatal fold is minute or wanting". Besides the vertically oriented columellar the type species has rather poorly and quite typically developed apertural barriers (cf. also PILSBRY 1948: Fig. 510: 8, 10, 11), with only lower palatal and parietal present.

Alloptyx Pilsbry, 1953

The monotypic subgenus *Alloptyx* was erected by PILSBRY (1953: 164) for North American *V. hinkleyi* Pilsbry and diagnosed: "*Vertigo*, having a long, deeply entering upper-palatal fold; the lower-palatal fold much shorter and deeply immersed; the parietal and columellar lamellae being arranged as in *Vertigo* s. str." The type species is characterized by a very long upper palatal accompanied by a corresponding gutter in the outer surface of the body whorl (Fig. 1), and by a short, reduced lower palatal; the characters shared among others with *V. angustior* Jeffreys. PILSBRY (1953: 164) recognised its similarity to *Vertilla* but pointed to the structure of columellar tooth that "differs widely".

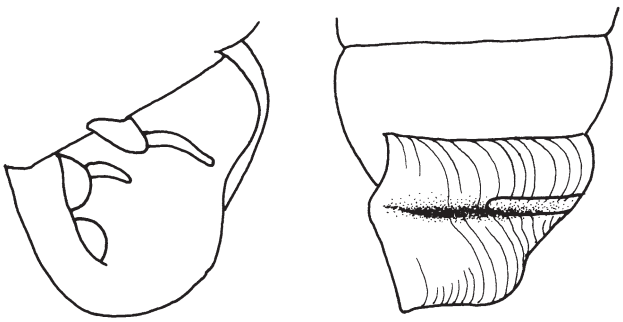

Fig. 1. Type of *Vertigo hinkleyi* Pilsbry. Diagrammatic, modified from PILSBRY's (1948) Figures 12 and 14

Angustella Steklov, 1967

STEKLOV (in STEKLOV & TSYTOVICH 1967: 115–116) diagnosed *Angustella* as follows: "Rakovina pravozavernuta, yaytsevidnaya, kompaktnaya, s serdtsevidno vdavlennym s palatanoy storony ustem. Verkhnaya palatalnaya skladka vysokaya, dlinnaya; nizhnaya – boleye korotkaya, izognutaya, lezhit ochen' gluboko w uste. Vnutrenneye okonchaniye kolumellarnoy plastinki nakloneno knizu. Imeyetsa, krome togo, yavstvennaya subkolumellarnaya plastinka" [Shell dextral, ovate, compact, with palatally heart-like incised aperture. Upper palatal fold high, long; lower shorter, bent, located very deep in aperture. Inner end of columellar lamella bent downward. Besides, distinct subcolumellar present]. Its type species, by original designation, is *V. bicolumellata* Steklov from Miocene deposits of Central Kazakhstan. In his notes on the systematic position of *Angustella*, STEKLOV (in STEKLOV & TSYTOVICH 1967) states that the columellar in most members of *Vertigo* is either horizontal (*Vertigo* s. str.) or subvertical (*Vertilla* and *Vertillaria*), only in American *Angustula* it has its inner end deflected downwards; hence his opinion that the new subgenus is related to the latter taxon, which it resembles also in the structure of palatals. It differs, however, in the presence of subcolumellar and in the upper (not lower) palatal being the longest, like in *Angustula*. From STEKLOV's figure of the type species (STEKLOV & TSYTOVICH 1967: Fig. 9), though very diagrammatic (Fig. 2), it is clear that the upper palatal is much like that in *V. angustior* and also accompanied by a gutter in the outer wall of the body whorl, while the lower palatal is deeper situated and very small.

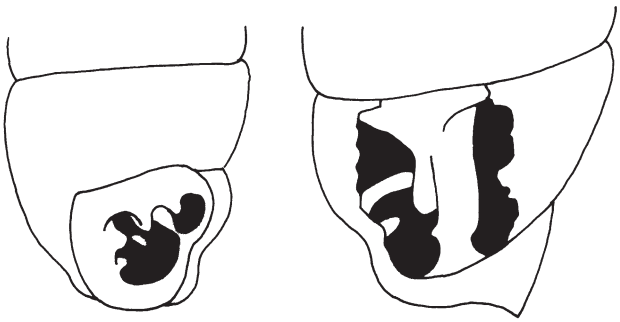

Fig. 2. Paratype of *Vertigo bicolumellata* Steklov. Diagrammatic, modified from STEKLOV & TSYTOVICH's (1967) Figure 9 b, v

Ungulidenta Popova et Shileyko, 1981

The subgenus, with the type species *V. olchonica* Popova et Shileyko (Pliocene deposits of the Olkhon island on the lake Baikal), by original designation, was diagnosed (POPOVA & SHILEYKO 1981: 113) as having "Rakovina malenkaya, ot ovalnoy do ovalnotsylindricheskoy. Paryetalnykh plastinok dve, kolumellarnaya odna, v vide prituplennogo bugorka. Bazalnyi zub raspolozhen vplotnuyu k kolumelarnomy krayu. Na kraye palatalnoy stenki imeyetsa 1–2 skladki; krome togo, na palatalnoy stenke, otstupya ot ustego kraya, mezhdu bazalnym zubom i palatalnoy skladkoy, raspologaetsya podkovovidnaya skladka, koncy kotoroy napravleny knaruzhi; uchastok stenki zazhatyi mezhdu vetvami etoy skladki slegka pripodnyat" [Shell small, from oval to oval-cylindrical. Two parietal lamellae, one columellar tooth, in the form of a blunted tubercle. Basal located just next to columellar wall. One-two palatal teeth on the margin of palatal wall. Between basal and palatal, at a distance from aperture margin, a horshoe-shaped lamella, directed with its ends outward, the inside of the horseshoe somewhat thickened]. Besides the type species, it includes Neogene *V. uncata* Steklov, with a similarly shaped lamella.

TAXONOMIC VALUE OF CHARACTERS

The characters used to distinguish the subgenera: chirality, number of teeth on the parietal wall and degree of their development, form and degree of development of the columellar, presence/absence of basal and/or subcolumellar, length and degree of development of the palatals and the form of the lower palatal, are by no means of equal value and need a thorough discussion.

CHIRALITY

Like in many other snail taxa, chirality in *Vertigo* seems to be merely a specific attribute, especially that the sinistral *V. pusilla* O. F. Müller, the type species of the genus, in its other characters seems to be closer to the dextral *V. antivertigo* (Draparnaud) and *V. substriata* (Jeffreys), whereas another sinistral species, viz. *V. angustior* Jeffreys, is very close to e. g. dextral fossil *V. angulifera* O. Boettger (see also below). The use of this character to distinguish genera or subgenera is at present of historical rather than systematic significance.

APERTURAL BARRIERS

The mere presence of at least five basic well developed teeth in the aperture, viz. columellar, parietal, angular, upper and lower palatal, is plesiomorphic not only within *Vertigo*, but within the whole superfamily Pupilloidea (cf. POKRYSZKO 1990,

1994, 1997a, b). In many pupilloid families and genera, otherwise well defined by unique synapomorphies, there is a parallel tendency to reduce apertural barriers, and the reduction nearly always proceeds according to a common pattern (POKRYSZKO 1990, 1994, 1997a).

Parietal wall teeth

The presence of 2–3 teeth on the parietal wall is plesiomorphic within the family and thus provides no good basis for a subgeneric division. Their reduction or loss could possibly be regarded as apomorphic, but applying this criterion to *Vertigo* would encounter serious difficulties implied in polarization of polymorphic characters. Such species as *V. pygmaea* (Draparnaud) or *V. moulinsiana* (Dupuy), of a very wide variability range of apertural barriers, could be differently classified, depending on an individual examined. The angular tooth, obligatory in e.g. *V. antivertigo* (Draparnaud), appears fairly often in *V. moulinsiana* (Dupuy), less often and only as a vestige in *V. pygmaea* (Draparnaud), and only exceptionally in e.g. *V. alpestris* Alder (POKRYSZKO 1990). In all such variable species the degree of development of the teeth just named varies individually. In view of the fact that the mere presence of 2–3 teeth on the parietal wall is plesiomorphic, and that the number of teeth may vary individually in some species, it seems groundless to establish subgenera on this basis.

Only one character of parietal wall teeth seems to have evolved separately and once only. In most members of *Vertigo* with more than one tooth on the parietal wall, the parietal is the largest i.e. the highest and the longest, while the angular is much smaller and among the first teeth to get reduced; the situation is similar in many other pupilloid taxa, e.g. *Lyropupa* Pilsbry (POKRYSZKO 1997b) or Chondrinidae (GITTENBERGER 1973). Only in very few members of *Vertigo* (*angustior* Jeffreys, *angulifera* O. Boettger, *oecsensis* (Halaváts), *bicolumellata* Steklov) the angular is developed equally well as or better than the parietal. All these species consistently display other unique characters of apertural barriers (see below) which they share with V. *hinkleyi* Pilsbry, though the latter has no angular tooth at all.

Columellar

Both the variation and the possibility of parallel evolution pertain also to the columellar. In its most ancestral form the tooth originates on the border between the embryonic and definitive whorls and grows with the shell, while its older, i.e. deeper situated part is gradually resorbed (POKRYSZKO 1994). In some species it is formed during sexual maturation, but still

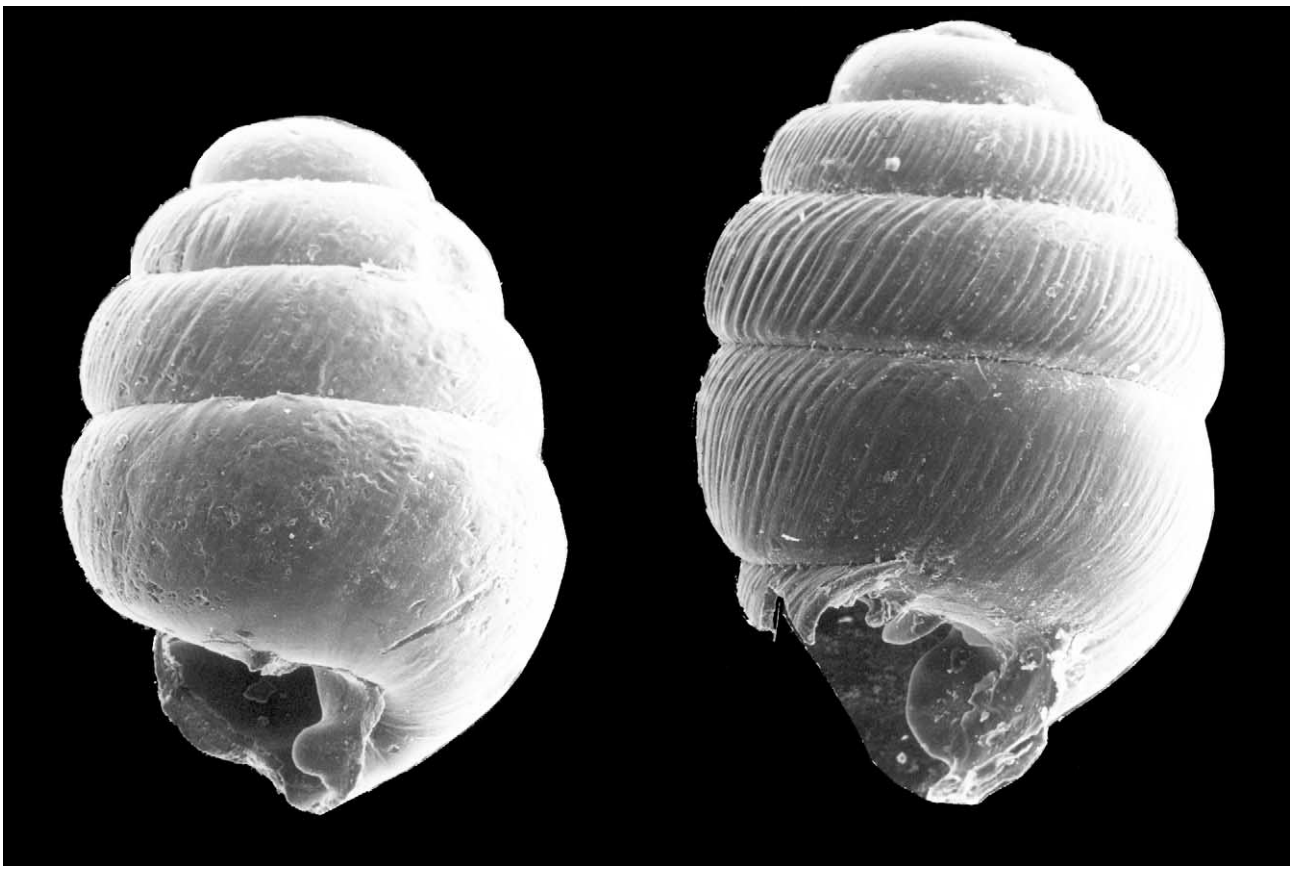

Fig. 3. Columellar tooth in *Vertigo oecsensis* (Halaváts) from the Miocene of Bełchatów (left, shell height 1.37 mm) and recent *Vertigo angustior* Jeffreys (right, shell height 1.56 mm)

preserves its characteristic shape of a fairly sharp lamella ascending the columella for ca. 0.5 whorl and terminating with a nodule in the aperture. A further stage of its evolution is a mere nodule, e.g. in most *Vertigo* (cf. POKRYSZKO 1990), but in some members of e.g. *Vertigo*, *Lyropupa*, *Nesopupa*, *Gastrocopta* (cf. POKRYSZKO 1990, 1996, 1997a, b) it assumes various shapes: of a horizontal or crescentic lamella, a vertical plate, a "spoon" etc. Besides, it is much variable individually and within groups of very closely related species (Fig. 3) and, though in some instances useful as an accessory character, it should not be adopted as the only or the main taxonomic criterion.

The value of the presence of subcolumellar [= infracolumellar] is also questionable. The tooth is present, but only rarely obligatory, in species of many various pupilloid taxa, such as e.g. *Gastrocopta* Wollaston, *Leiostyla* R. T. Lowe or various members of Chondrininae (for review of characters see e.g. PILSBRY 1916–1918, GITTENBERGER 1973, SHILEYKO 1984). It is also present in many members of *Vertigo*, in which it is often reduced or absent (cf. PILSBRY & COOKE 1918–1920 and PILSBRY 1948) and thus in itself provides no justification to distinguish *V. bicolumellata* Steklov in a separate subgenus *Angustella*.

Palatal teeth

In more plesiomorphic pupilloids which have retained the whole set of apertural barriers, the upper of the two palatals is always smaller, whereas the lower is sometimes very long and usually high. The lower palatal is often accompanied by a depression in the outer surface of the palatal wall. Only a very shallow and short depression may sometimes accompany the upper palatal. Reduction of the palatal teeth nearly always starts with the upper. The loss of this tooth took place parallelly and independently in some members of e.g. *Vertigo* O. F. Müller, *Truncatellina* R. T. Lowe, *Gastrocopta* Wollaston, various Chondrininae etc. (for review of characters of apertural barriers see PILSBRY & COOKE 1918–1920, GITTENBERGER 1973, SHILEYKO 1984, POKRYSZKO 1990, 1996, 1997a).

The lower palatal undergoes a wide variation, both inter- and intraspecific, in various pupilloid taxa, e.g. *Vertigo* O. F. Müller, *Gastrocopta* Wollaston, *Lyropupa* Pilsbry (for review of characters see e.g. PILSBRY 1916–1918, POKRYSZKO 1997b). The "horshoe-shaped lamella" found in *V. olchonica* Popova et Shileyko and *V. uncata* Steklov is the lower palatal – very robust (cf. POPOVA & SHILEYKO 1981: Figs 1, 2), with a concavity that actually makes it spoon- rather than horseshoe-shaped. A similar form of the lower palatal was found in some (but not all!) specimens of *V. ovatula* (Sandberger) (STWORZEWICZ 1999: Fig. 13) (Fig. 4). Though STEKLOV (1967) and POPOVA & SHILEYKO (1981) based their descriptions on 32 and 50 specimens, respectively, they did not mention any variation; the character may represent an intraspecific variation, like in *V. ovatula* (Sandberger) or be species-specific, but does not appear to justify the existence of *Ungulidenta* Popova et Shileyko.

The reduction or loss of the lower palatal, not preceded or accompanied by any reduction of the upper, seems to be unique among the pupilloids. In those species in which it takes place, the upper palatal becomes prolonged so that its inner end is no longer visible in the aperture in front view, and the outer sur-

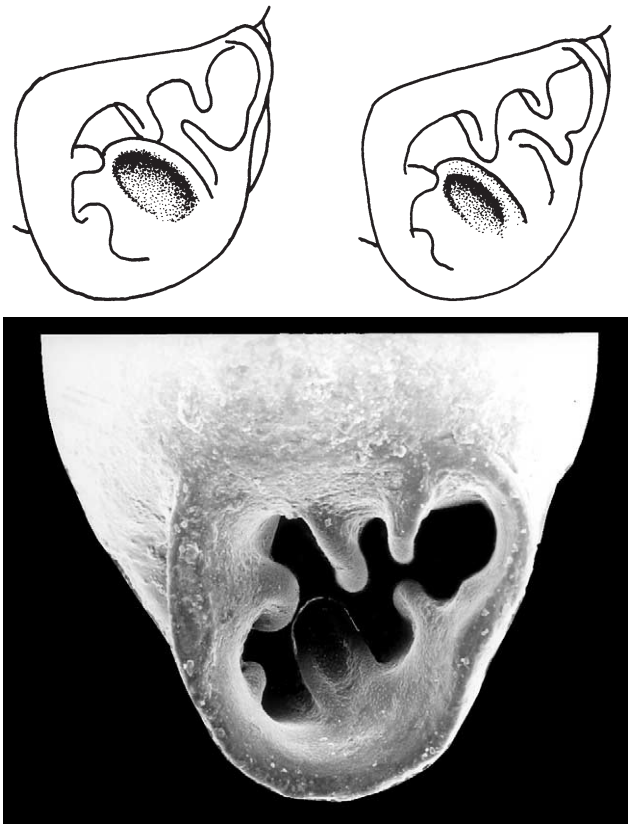

Fig. 4. Holotype of *Vertigo olchonica* Popova et Shileyko (top left), semidiagrammatic, modified from Figure 1 in POPOVA & SHILEYKO (1981), paratype of *Vertigo uncata* Steklov (top right), modified from Figure 2 in POPOVA & SHILEYKO (1981), and a specimen of *Vertigo ovatula* (Sandberger) from the Miocene deposits of Bełchatów (bottom), of aperture height 0.52 mm

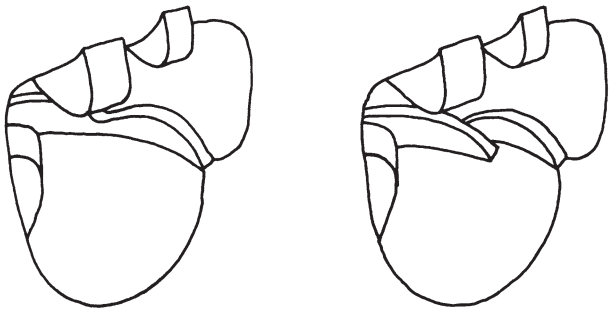

Fig. 5. Apertural barriers of *Vertigo angulifera* O. Boettger from the Miocene deposits of Dolnice, Czech Republic, with undivided (left) and divided (right) upper palatal. Diagrammatic, modified from ČEJCHAN's (1985) Figure 2

face of the palatal wall acquires a corresponding deep and narrow gutter. Such a situation is found only in a few members of *Vertigo: angustior* Jeffreys, *angulifera* O. Boettger, *oecsensis* (Halaváts), *bicolumellata* Steklov, and *hinkleyi* Pilsbry. In some fossil forms (*V. angulifera* O. Boettger) the prolonged upper palatal may be divided in two parts, situated almost in line, but partly overlapping (Fig. 5). The situation is, however, found only in some specimens and thus represents an intraspecific variation.

All the forms related to *V. angustior* Jeffreys require a specific- and infraspecific-level revision based on a more detailed study of their variation; this will be published elsewhere (POKRYSZKO & STWORZEWICZ in prep.).

CONCLUSION

Vertigo s. str. in the present sense would certainly be a sister group to *Vertilla* with which it shares the generic apomorphies. Except for the tendency to reduce apertural barriers, mainly the palatals, it can not be characterized by any apomorphies and thus in cladistic sense constitutes a typical "non-A" group (ELDREDGE & CRACRAFT 1980). If cladistic principles were to be followed strictly, the genus *Vertigo* should not be subdivided, but then the obvious monophyly and close relationships of the five members of *Vertilla*, with their possible zoogeographic and palaeobiological implications, would not be retrievable from the system. For this reason we are in favour of splitting *Vertigo* in two subgenera.

The new diagnoses of the genus and its subgenera, and a list of species included in *Vertilla*, are presented below.

Genus: *Vertigo* O. F. Müller, 1774

Vertigo O. F. MÜLLER 1774: 124. Type species: *Vertigo pusilla* O. F. Müller, 1774, by monotypy.

Diagnose: Shell less than 3 mm long, of 4–5.6 whorls, most often dextral, rarely sinistral, ovate or ovate-cylindrical; surface sculpture radial. Apertural barriers formed at the time of sexual maturation, originally complete, with a tendency to get reduced or (rarely) further complicated. Male genitalia with no accessory organs. Prostate gland reduced to a few processes, penis bi-partite, constricted, penial retractor undivided, vas deferens outlet apical, free oviduct long, spermoviduct short.

Subgenus: *Vertigo* s. str.

Type species: *Vertigo pusilla* O. F. Müller, 1774, by monotypy.

Isthmia GRAY 1821: 239. Type species: *Helix* (*Isthmia*) *cylindrica* Gray, 1821 [= *Vertigo pygmaea* (Draparnaud, 1801)], by monotypy.

Alaea JEFFREYS 1830: 357. Type species: *Alaea palustris* Leach, in Turton, 1831 [= *Vertigo antivertigo* (Draparnaud, 1801)], designated by GRAY 1847: 176.

Angustula STERKI 1888: 378. Type species: *Vertigo milium* (Gould, 1840), designated by PILSBRY 1948: 944. **Syn. n.**

Vertillaria PILSBRY 1919, in PILSBRY & COOKE 1918–1920: 144. Type species: *Vertigo oscariana* Sterki, 1890, by original designation. **Syn. n.**

Ungulidenta POPOVA & SHILEYKO 1981: 113. Type species: *Vertigo olchonica* Popova et Shileyko, 1981, by original designation. **Syn. n.**

Diagnose: Apertural barriers originally complete, with a tendency to get reduced in a sequence: basal and/or angular → lower palatal → upper palatal → parietal and/or columellar; very rarely further complicated by addition of small accessory teeth.

The subgenus includes most i.e. over 100 fossil and extant members of the genus.

Subgenus: *Vertilla* Moquin-Tandon, 1855

Vertilla MOQUIN-TANDON 1855: 408. Type species: *Vertigo plicata* A. Müller, 1838 [= *Vertigo angustior* Jeffreys, 1830], designated by PILSBRY 1919 in PILSBRY & COOKE 1918–1920: 210.

Alloptyx PILSBRY 1953: 164. Type species: *Vertigo hinkleyi* Pilsbry, 1921, by original designation. **Syn. n.**

Angustella STEKLOV in STEKLOV & TSYTOVICH 1967: 115–116, Type species: *Vertigo bicolumellata* Steklov, 1967, by original designation. **Syn. n.**

Diagnose: Upper palatal very long, so that its inner end is invisible in front view, and accompanied by a corresponding long gutter in the outer surface of the palatal wall; lower palatal reduced or absent; angular from nearly as large as parietal to larger; only exceptionally absent; columellar tending to assume a shape of a horizontal/oblique or vertical plate. Five species.

List of species:

Vertigo angustior Jeffreys, 1830: European recent (POKRYSZKO 1990: 115–122)

Vertigo angulifera O. Boettger, 1884: European Miocene (ČEJCHAN 1985: Fig. 1b, STWORZEWICZ 1999: Fig. 18)

Vertigo oecsensis (Halaváts, 1911): European Miocene (STWORZEWICZ 1999: Figs 14–16, for comparison with *V. angustior* Jeffreys see also Fig. 17 in STWORZEWICZ 1999 and Fig. 3 in this paper)

Vertigo hinkleyi Pilsbry, 1921: North American recent (PILSBRY 1948: Fig. 542: 12–16)

Vertigo bicolumellata Steklov, 1967: Asian Miocene (STEKLOV & TSYTOVICH 1967: Fig. 9)

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