BASTERIA, 54: 17-62, 1990

A revision of Obscurella Clessin, 1889 (Gastropoda Prosobranchia: Cyclophoridae)

J. G. M. RAVEN

84 Mortlake Road, Kew, Surrey, TW9 4AS, United Kingdom

A review is presented of the eight recent species of *Obscurella*, one of which, *O. asturicum* spec. nov. is new to science. The subdivision in species is supported by sympatric occurrence without intermediate forms. A key is given and the shell, soft parts, ecology and distribution of the species are described. Sexual dimorphism is evident in the shells of all species. Micropenises have been found occasionally in males of five species; in *O. oscitans* (Gofas, 1989) all male specimens have a micropenis. Based on differences in shell and preferred habitat, three subgenera are distinguished within *Obscurella*, viz. *Obscurella, Cantabrica* subgen. nov. and *Canestrinia* subgen. nov.

RESUMEN

Se presenta une revisión de las ocho especies recientes de *Obscurella*, una de las cuales, *Obscurella asturicum* spec. nov., es nueva para la ciencia. La subdivisión en especies es corroborada por la ocurriencia simpátrica sin formas intermedias. Se ofrece una tabulación de identificación y se describen la concha, las partes blandas, la ecología y la distribución de las especies. En las conchas de todas las especies es evidente un dimorfismo sexual. En los especimenes machos de cinco especies se han encontrado ocasionalmente micropenes; en *O. oscitans* (Gofas, 1989) todos los machos tienen un micropene. Diferencias en concha y biotopo preferido son la base para distinguir tres subgeneros de *Obscurella*, viz. *Obscurella, Cantabrica* subgen. nov. y *Canestrinia* subgen. nov.

Key words: Gastropoda, Prosobranchia, Cyclophoridae, *Cochlostoma, Obscurella*, taxonomy, sexual dimorphism, micropenis, distribution, Spain, France, Italy.

INTRODUCTION

Species of the genus *Cochlostoma* Jan, 1830, have slender, conical shells, usually with fine ribs and a roundish aperture, generally with a thick, reflected lip. The animal has a short proboscis and two conical tentacles with eyes at their base. The sole is undivided. The shell can be closed with a horny multispiral operculum.

Several subdivisions into subgenera have been proposed, all based on shell characters. The latest classification is that used by Zilch (1958), who distinguished *Cochlostoma* s.s. Jan, 1830, *Obscurella* Clessin, 1889, *Personatus* Westerlund, 1883, *Turritus* Westerlund, 1883, *Holcopoma* Kobelt & Möllendorff, 1899, *Apollonia* Brandt, 1958, and *Auritus* Westerlund, 1883. *Obscurella* (syn. *Rhabdotakra* Wagner, 1897 and *Anotus* Westerlund, 1883), with the type species *Cyclostoma obscurum* Draparnaud, 1805, consists of species which have relatively large and broad, conical shells with 6.5 to 11 rather flat whorls, often with a slight carina at the base of the last whorl, a sculpture of numerous riblets, an open umbilicus, a round or slightly drop-shaped aperture and a strongly reflected, thick lip. Wenz (1938: 488) indicated *Cyclostoma apricum* Mousson,

1847, as type of what he considered the monotypical subgenus *Obscurella*. Indeed, Clessin (1889: 591, 599) only described *O. apricum*, which is the only species occurring in the area covered by his publication. Also he does not mention a type species of *Obscurella*. However, on p. 600 he compares *O. apricum* with *O. obscurum*: "Die Art die zwar dem *P. obscurus* Drap. nahe steht..". The name *Obscurella* suggests that he meant to designate the latter species as type species. Although the names of both the subgenus and the nominal taxon are not absolutely identical, I suggest that article 68e of the ICZN can be applied. In the present paper *Obscurella* is considered a separate genus (see below).

Giusti (1971) studied several species of different subgroups of the genus *Cochlostoma* and concluded that the generally accepted subdivision into subgenera should be rejected. Based on shell characters *Cyclostoma striolatum* Porro, 1840, was generally included in the subgenus *Obscurella*, but Giusti found that female specimens have a seminal receptacle, which is absent in other species classified in the genus *Cochlostoma*, whereas male specimens have a sulcus in the penis instead of an internal vas deferens. Since he found these characters only in *C. striolatum* he erected a new genus for this species: *Toffolettia*. Because Giusti did not study all the species of *Cochlostoma* s.l., it is not known what taxonomical value should be given to these characters. Giusti (1971) recorded an internal vas deferens in *O. canestrinii* (Adami, 1876), *O. apricum* (Mousson, 1847) and *O. hidalgoi* (Crosse, 1864). I found the same character in *O. oscitans* (Gofas, 1989), *O. asturicum* spec. nov., *O. obscurum* (Draparnaud, 1805), *O. nouleti* (Dupuy, 1851) and *O. bicostulatum* (Gofas, 1989). This character, thus, occurs in all species of *Obscurella*.

Based on shell characters, it is possible to distinguish three groups of species within *Obscurella*, viz. 1) *O. obscurum, O. apricum, O. nouleti* and *O. bicostulatum*, all with a pale yellowish shell which has reddish-brown spots or bands; 2) *O. hidalgoi, O. asturicum* and *O. oscitans*, all with a greyish-brown shell without a strong deflection in the peristome; 3) *O. canestrinii*, a decollating species with a greyish-brown shell which has a strong deflection in the peristome.

Members of these groups prefer different habitats. The species of the first group live preferentially at vegetated and shaded localities with a humid microclimate, mainly on the northern and western sides of mountain chains. They are not only known from calcareous rocks but also from trees in forests. The species of the second, and probably also the third, group prefer unshaded bare rock (they were never found on trees) and occur in more varied microclimates. The greatest part of the ranges of these groups is at the sunnier, drier and less vegetated southern sides of mountain ranges.

The colour of the shells may be adaptive: the pale, yellowish shells with darker spots of the first group are less well visible between vegetation and the greyish-brown shells of the second and third groups are well-adapted to the colour of the limestone rock faces on which they generally live. Where species of the different groups live sympatrically, each prefers the part of the environment typical for its group.

The ranges of the different taxa of each group and the shell characteristics indicate that each group is a monophyletic entity. They may be evolutionary entities, in each of which the most widespread species is supposedly the most similar to the ancestral species. These monophyletic groups no longer vicariate. Due to their extension, the ranges of two of the groups now have a secondary overlap.

These groups are herein described as subgenera, thus elevating *Obscurella* to genus level. The genus *Cochlostoma* has many species within a large number of well defined

subgenera. After the distinction of *Toffolettia* and *Obscurella* as separate genera, other subgenera within *Cochlostoma* may also be raised to genus status.

In the eighteenth century many species of '*Pomatias*' were described from southern France and northern Spain, mostly from the Pyrenees. The authors generally belonged to the French "Nouvelle École". Bourguignat and Fagot in particular introduced many names. Most alleged species were based on material from one locality only, often with vague descriptions such as "more ribs than..." "broader than...", referring to other badly defined taxa. Illustrations are rarely given. In this way over fifty nominal taxa were introduced. Most authors (e.g. Westerlund, 1885, Locard, 1894, Kobelt, 1902) mention all these "species" without any critical evaluation. Some, however, tried to reduce the enormous number of names. Wagner (1897) considered many nominal taxa varieties (forms) or synonyms. Unfortunately, his revision was based on material from few localities only. In their work on regional faunas Haas (1929), Germain (1931) and Altimira (1963) lumped many of the taxa, but a revision of the entire *Obscurella* group was never attempted.

In particular during the last years Dutch and Spanish malacologists have collected much new material, most of it from northwestern Spain, an area from where very few samples were hitherto available. During numerous field trips from 1976 onwards, I studied the living animals and their habitat and collected many samples. In this way in particular the Cantabrian mountains were studied intensively. I distinguish the western Cantabrian mountains consisting of the predominantly Palaeozoic rocks west of Pico Tres Mares and the eastern Cantabrian mountains consisting of mainly Mesozoic rocks which extend to the Pyrenees. The descriptions of the species living in other areas are mainly based on material collected by others.

The available samples were compared and subdivided into different species which were then compared with the literature data and, if possible, with type material. It proved impossible to track down and borrow all the type material, but this shortcoming was compensated by the large number of other samples available. In particular from *O. obscurum* few types were seen but a large number of samples was available from the entire range of the species, many of which are from type localities, and none of these samples has two or more forms without intermediate specimens. Only the studied types and topotypes are mentioned in the list of synonyms in the systematic part. A species from the Cantabrian mountains proved to be new to science.

The preparation of this paper commenced in 1980. In 1983 much material from the Universidad del Pais Vasco (Bilbao, province of Vizcaya, Spain) was identified and undescribed species were indicated as such. While the paper was in press two of the three species that would be introduced were published by Gofas (1989), who collected material with help of scientists from the Universidad del Pais Vasco. The present author is disappointed that no cooperation was sought for a more complete, joint publication.

In this paper the following abbreviations will be used for the collections from which material was studied: A, Dr. M.T. Aparicio, Museo Nacional de Ciencias Naturales, Madrid; Ba, R.A. Bank, Haarlem; B, Dr. H.D. Boeters, Münich; D, N. Dekker, Venlo; E, J.C.A. Eikenboom, Hellevoetsluis; M, W.J.M. Maassen, Amsterdam; Me, Ir. H.P.M.G. Menkhorst, Krimpen aan de IJssel; N, W.N. Neuteboom, Heemskerk; R, Raven, London; RGM, Rijksmuseum van Geologie en Mineralogie, Leiden; Ri, Th.E.J. Ripken, Delft; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SMF, Senckenberg Museum, Frankfurt; UPV, Universidad del Pais Vasco, Bilbao;

V, Drs. J.J. Vermeulen, Leiden; W, Ir. A.J. de Winter, Wageningen. Other abbreviations used are: MHNG, Muséum d'Histoire Naturelle, Geneva; MNCN, Museo Nacional de Ciencias Naturales, Madrid; MNHN, Muséum National d'Histoire Naturelle, Paris; MZB, Museo de Zoología, Barcelona; NMW, Naturhistorisches Museum Wien, Vienna; in descriptions of shells: H, height; W, width.

GENERAL CHARACTERS

The animals are of separate sex and shells of male and those of female specimens are clearly distinct. Female specimens have relatively high and slender shells, with a gradual change in colour from top to aperture. Male specimens have broader shells, with fewer whorls and, except the yellowish-white embryonal whorls, the upper part of the shell is bluish-violet, gradually passing into the yellowish or brown colour of the lower part. These differences occur in all the *Obscurella* species and also in species belonging to *Cochlostoma* and *Toffolettia* (e.g. Varga, 1984, and own observations). In some populations the differences are more marked than in others. As an example, the shells of males and females from some populations were measured (with a marking gauge); the results are given in fig. 1.

The intraspecific conchological variation is a result of both the sexual dimorphism within a population and large differences between the populations. In particular the size, the number of ribs and the development of the ribs vary between the populations. Since the ribs have a lighter colour than the ground colour of the shell, shells with weakly developed ribs and smooth shells appear to be darker than those with well-developed ribs. The extremes have often been considered separate species. The smooth form of *O. hidalgoi* was described as *O. alopioides* (Fagot, 1905) (figs. 30, 34, 35) and that of *O. apricum* as *O. sabaudinus* (Bourguignat, 1864). Also in *Cochlostoma* such smooth and dark forms have been found (Bank, 1988). In the description of most species an indication of the spacing of the ribs is given, which was always measured at the apertural side of the penultimate whorl.

There are no populations of *O. h. hidalgoi* known in which both the smooth and ribbed form occur, always all specimens have either smooth or ribbed shells. At the only locality from which smooth specimens of the subspecies *O. hidalgoi martorelli* (Bourguignat in Servain, 1880) are known, however, there is a gradual change from populations with ribbed shells only, through mixed populations to those with smooth shells only (field observations by the author). The carbonate content of the rocks on which the animals live and the humidity of the environment apparently play no role in the formation of the ribs, in contrast to what was supposed by Haas (1929: 397). Smooth and ribbed forms both prefer limestone rock and both may occur in drier or more humid environments. In *O. hidalgoi* shells of the smooth form occur in several unconnected populations and are always large with flat whorls. This suggests that these characters may be genetically combined and do not represent an ecophenotypic variation.

Since the external penis cannot be retracted, the sex can be determined easily. The length and shape of the penis vary considerably and in some cases this can be used to distinguish between species (fig. 2). For example the penis of *O. hidalgoi* is very long (fig. 2f, g), whereas those of the closely related species *O. oscitans* (fig. 2j, k) and *O. asturicum* (fig. 2h, i), which live in small areas within the range of *O. hidalgoi*, are

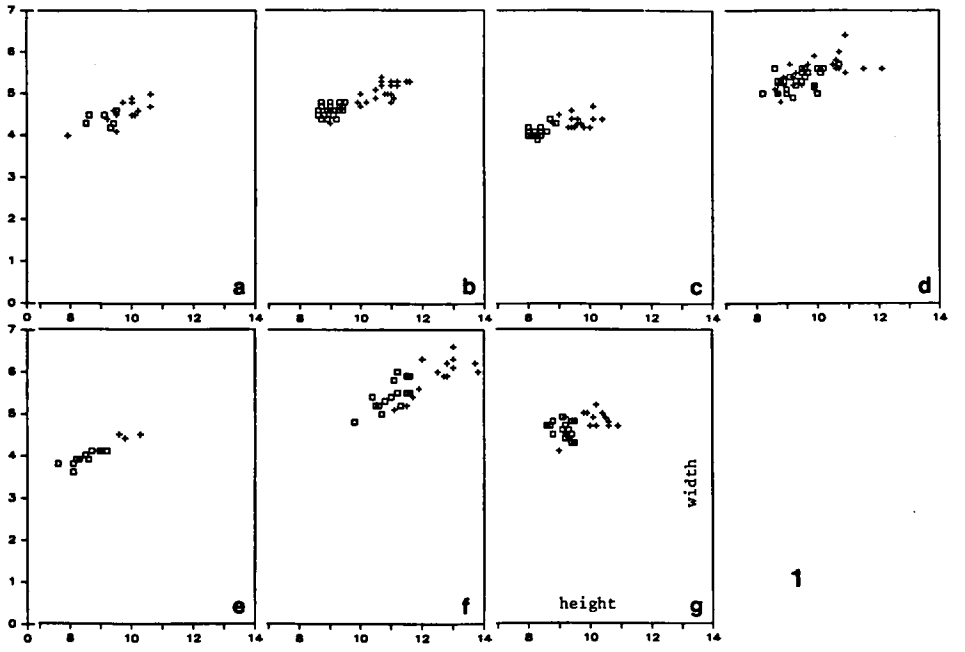


Fig. 1. Relation between height and width (in mm) of the shells of several *Obscurella* species. The height is indicated on the horizontal axes and the width of the vertical ones. Measurements on male individuals are indicated by open squares, female individuals by crosses. Except for figure 1c, the sex of all specimens was anatomically checked. a, *Obscurella (O.) bicostulatum* (Gofas, 1989), 2.5 km SW. of Argame (Asturias) Spain, TN6397 (J.G.M. Raven leg.); b, c. *O. (O.) obscurum* (Draparnaud, 1805); b, Arrayoz (Navarra) Spain, XN1577 (J.G.M. Raven leg.); c, Parque Nacional de Ordesa (Huesca) Spain, YN32/34 (J.G.M. Raven leg.); e, *O. (O.) apricum* (Mousson, 1847), Gorges du Guiers Mort, SE. of St. Laurent-du-Pont (Isère) France, GL13 (E. Gittenberger leg.); d, *O. (Cantabrica) oscitans* (Gofas, 1989), Cascadas del Asón (Santander) Spain, VN5283/5284 (J.G.M. Raven leg.); f, *O. (C.) h. hidalgoi* (Crosse, 1864), between Puerto de San Isidro and Felechosa (Asturias) Spain, UN0271 (J.G.M. Raven leg.); g, *O. (C.) asturicum* spec. nov., Lago de la Ercina, 8 km SE. of Covadonga (Asturias) Spain, UN3992 (J.G.M. Raven leg.).

generally much shorter. There is a dimorphism in penis shape and size. Few specimens of *O. obscurum, O. bicostulatum, O. apricum* (fig. 2e) and *O. asturicum* (figs. 2h, i, 3) have an exceptionally short penis. Varga (1984) found few specimens with such exceptionally short penises in several species of *Cochlostoma* and introduced the term 'micropenis'. All specimens of *O. oscitans* are considered to have such a micropenis.

Generally the body of *Obscurella* species is grey, with a darker proboscis and tentacles; the sole is white. On the lowermost part of the tentacles there is a lighter grey ring. Although the pigmentation of animals of each species is quite variable, the species have different pigmentation patterns (fig. 4) which are described for each species in the systematic part of this paper.

The radulae of the studied species are all long (4-11 mm), but only 0.1 mm broad. They consist of a central (C), a lateral (L), and two marginal rows of teeth (M1 and

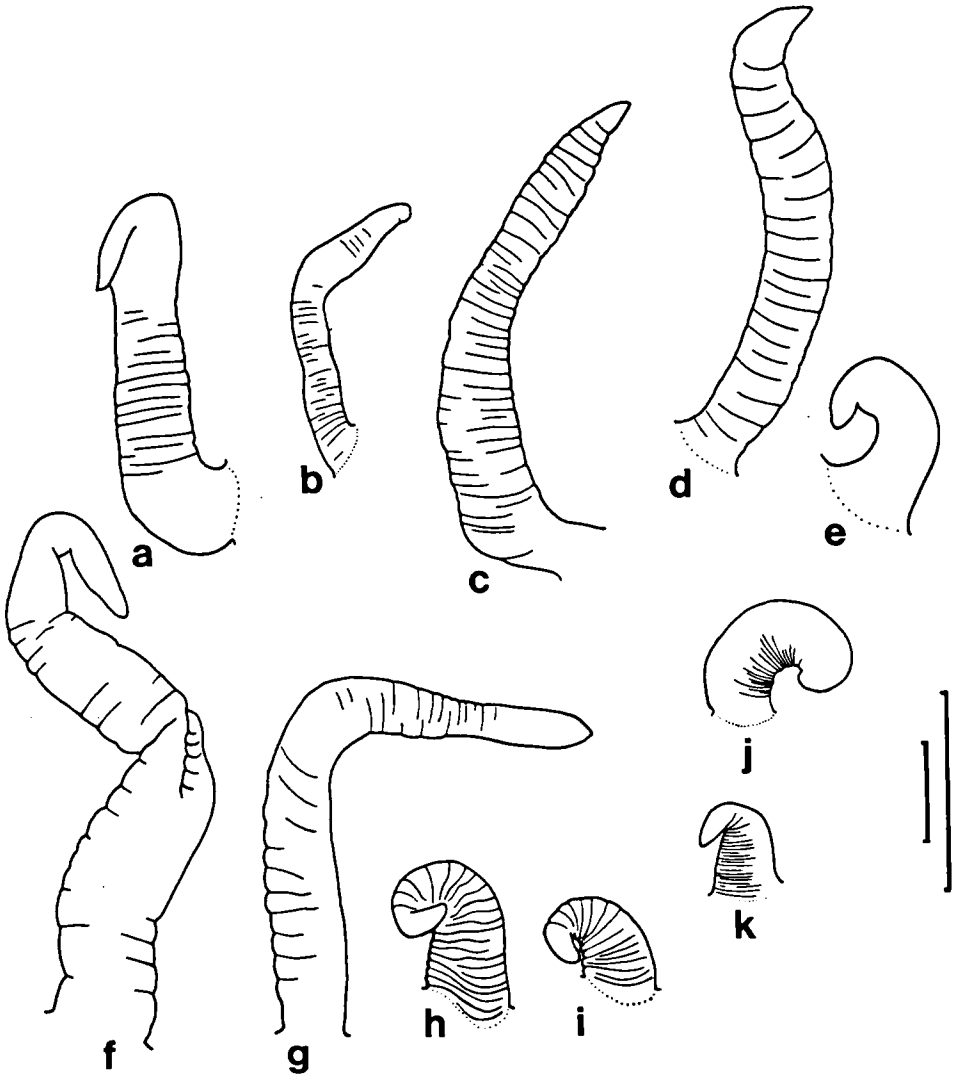


Fig. 2. Penises of different *Obscurella* species. a, b, *Obscurella (O.) bicostulatum* (Gofas, 1989), 2.5 km SW. of Argame (Asturias) Spain, TN6397 (J.G.M. Raven leg.); c, *O. (O.) obscurum* (Draparnaud, 1805), N of Escaroz (Navarra) Spain, XN5550 (J.G.M. Raven leg.); d (penis) and e (micropenis), *O. (O.) apricum* (Mousson, 1847), Gorges du Guiers Mort, SE. of St. Laurent-du-Pont (Isère) France, GL13 (E. Gittenberger leg.); f, g, *O. (Cantabrica) h. hidalgoi* (Crosse, 1864), 1.5 km N. of Lebeña (Santander) Spain, UN7187 (J.G.M. Raven leg.); h, i, (micropenises) *O. (C.) asturicum* spec. nov., Lago de la Ercina, 8 km SE. of Covadonga (Asturias) Spain, UN3992 (J.G.M. Raven leg.); j, k, *O. (C.) oscitans* (Gofas, 1989), Cascadas del Asón (Santander) Spain, VN5283/5284 (J.G.M. Raven leg.). Scale 1 mm; the larger scale only applies to figs. 2 j-k.

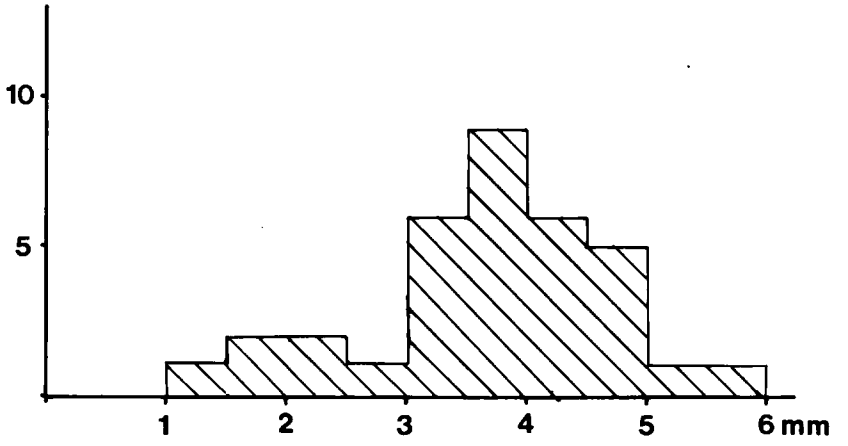


Fig. 3. Frequency of penis lengths in *Obscurella (Cantabrica) astricum* spec. nov. from Puente Angoyo, Desfiladero de los Beyos, border between León and Asturias, Spain, UN3180 (J.G.M. Raven leg.). Penises which are less than 2.5 mm long are considered to be 'micropenises'.

M2), one of which with rudimentary teeth (M2). The basal part of the teeth is curved but the protruding end is straight. Since the radulae appear very different when seen from different angles (fig. 5), it is necessary to compare photographs taken under the same angle. S.E.M. photographs indicate that the differences between the radulae of different species are very small. Since only few specimens were studied, the descriptions are provisional. The general shape of the teeth varies; e.g. in *O. obscurum* the teeth are quadrangular and they all have the same width (fig. 5a, g), whereas e.g. in *O. hidalgoi* all teeth are much more rounded (fig. 5i). The length of the radula as a whole varies also. More specimens should be studied, however, before final conclusions can be drawn.

The animals are generally restricted to calcareous habitats, they occur on bare limestone hard rock faces, in fissures, below loose blocks in scree, on calcareous sandstones or between and on vegetation on such rocks. Mostly they are very numerous (fig. 6) and therefore it is easy to collect large samples. In the western Cantabrian mountains there are very few places with the proper habitat where the genus is not represented. This even applies to new exposures of limestone rock, artificially created, e.g. for the construction of roads. Where such roads cause much pollution, however, *Obscurella* does not occur, as is the case with the road between Mieres and Oviedo in Asturias, Spain, constructed in the 1960's (observation 2.I.1989). Specimens were never found where water flows regularly along the rock face and travertine is deposited.

The animals are inactive during dry periods. Then the shell is attached to the rock or plant with mucus, the apex pointing downwards (fig. 6). Since solar and thermal radiation can be very high on unshaded rock faces, the animals must be very well attached to prevent desiccation. The broad, reflected peristome increases the contact surface. As soon as humidity is high enough, either due to dew, fog or rain, the

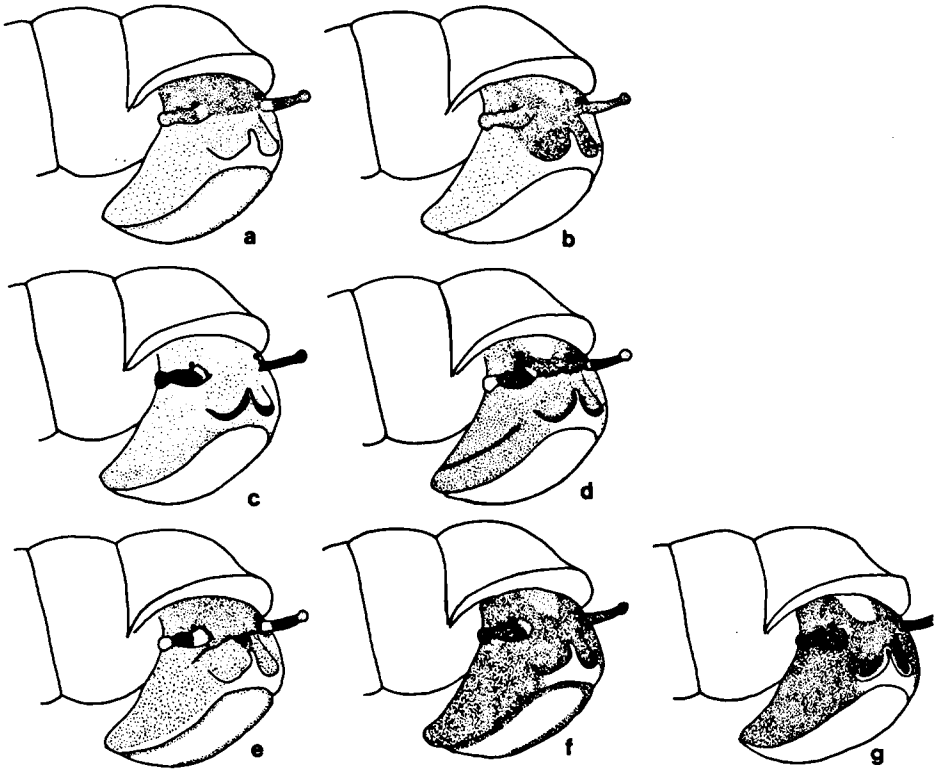


Fig. 4. Colour patterns on the soft parts of *Obscurella* species. The drawings are generalisations based upon colour patterns of several specimens from each species. a, *Obscurella (O.) nouleti* (Dupuy, 1851); b, *O. (O.) apricum* (Mousson, 1847); c, *O. (O.) obscurum* (Draparnaud, 1805); d, *O. (O.) bicostulatum* (Gofas, 1989); e, *O. (Cantabrica) h. hidalgoi* (Crosse, 1864); f, *O. (C.) asturicum* spec. nov.; g, *O. (C.) oscitans* (Gofas, 1989).

animals become active, those on the most hidden places (in fissures, below overhanging rock) the last.

Probably the animals mainly feed on lichens (and algae?), as can be concluded from the common observation of specimens occurring on rock faces with no other vegetation. They produce oval faecal pellets of about 1 mm long and 0.5 mm in diameter.

The eggs of *O. obscurum* are round, 1-1.5 mm in diameter, grey, and provided with a slightly calcareous shell. The animals are born after 20-25 days (Dupuy, 1851: 511). The eggs of *O. hidalgoi* were found to be more or less round, 1.5-2 mm in diameter, cream coloured, soft and slightly sticky. The eggs deform easily and shrink when they dry. They stick to plants but may also stick to birds or mammals which can explain the large area of most species.

The distribution of the species is given on maps (figs. 18, 27, 44, 49 and 52), which are based on personally checked material only. The literature data are generally unclear and do not provide much additional information. Generally not more than a

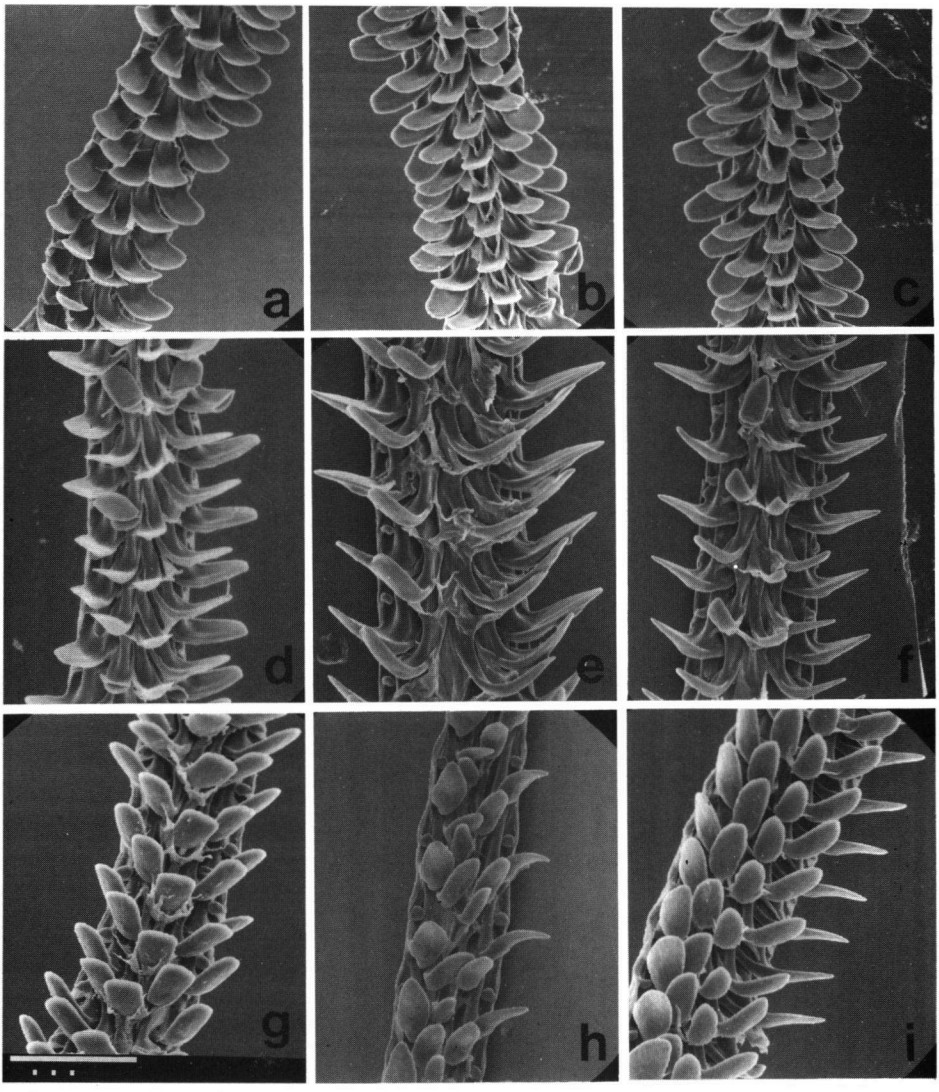


Fig. 5. Radulae of *Obscurella* species. a-c, inclined view from top of radula; d-f, vertical view; g-i, inclined view from base of radula. a, g, *Obscurella (O.) obscurum* (Draparnaud, 1805), Tolosa (Guipúzcoa) Spain, WN7475 (J.G.M. Raven leg.); b, d, h, *O. (O.) bicostulatum* (Gofas, 1989); b, d, 2.5 km W. of Argame (Asturias) Spain, TN6397 (J.G.M. Raven leg.); h, Lago Enol, 7 km SE. of Covadonga (Asturias) Spain, UN3793 (J.G.M. Raven leg.); c, f, *O. (Cantabrica) h. hidalgoi* (Crosse, 1864), between Posada de Valdeón and Cain (León) Spain, UN4583/4585 (J.G.M. Raven leg.); e, *O. (C.) oscitans* (Gofas, 1989), Cascadas del Asón (Santander) Spain, VN5283/5284 (J.G.M. Raven leg.); i, *O. (C.) hidalgoi martorelli* (Bourguignat in Servain, 1880), Merli (Huesca) Spain, BG9291 (J.G.M. Raven leg.). Scale 0.1 mm.

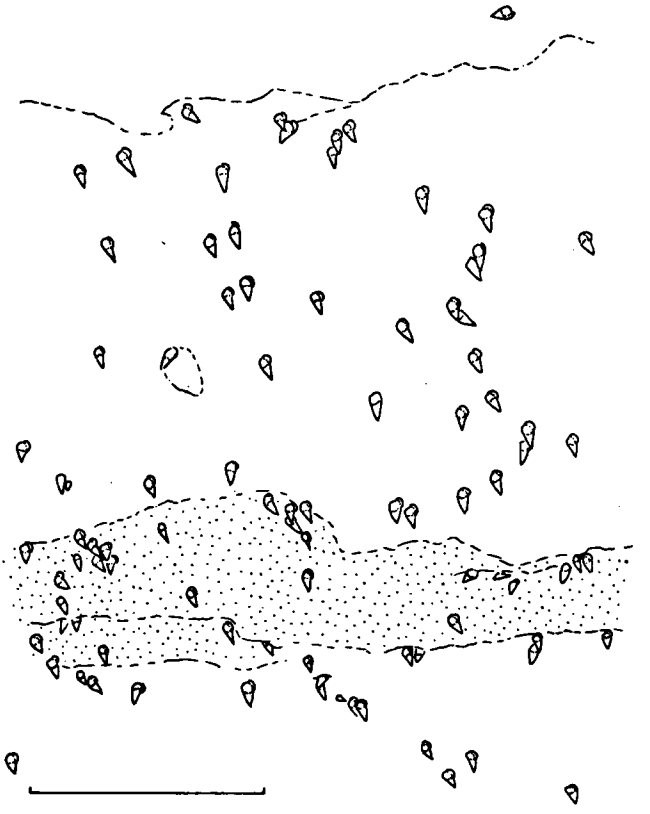


Fig. 6. *Obscurella (Cantabrica) h. hidalgoi* (Crosse, 1864) and *O. (C.) asturicum* spec. nov. completely mixed in rest position attached to a limestone rock face next to Puente Angoyo, Desfiladero de los Beyos, at the border between León and Asturias, Spain, UTM UN3180, July 1978. The upper interrupted line marks the sharp transition between the top of the limestone bed and the vertical front end; the dotted zone marks where the rock reclines, thus protecting the top part of the vertical rock face just below it. Note that there are almost no molluscs on the top of the limestone and that most occur below the overhanging part where they are protected from being washed away by rain and where they are less exposed to solar radiation. The density (several hundreds of individuals per square metre) is high but not exceptional. Nearly all shells have their apex pointing downward. Most are adult specimens, juvenile animals generally form a small minority. Scale 10 cm (sketched from a photograph by the author).

single species was found per locality. In the Pyrenees only at two localities two species were found together, viz. *O. obscurum* and *O. nouleti* at the SW. edge of St. Béat and E. of Boutx (Haute-Garonne, observations by J.J. Vermeulen). Also Germain (1931: 577-578) mentions both species from one locality: Cierp (Haute-Garonne) where they probably occur sympatrically. In the Cantabrian mountains often two, and rarely three or even four, species were found together: *O. hidalgoi hidalgoi, O. obscurum* and *O. bicostulatum* at Peña Ranero (Vizcaya, observation by C.E. Prieto) and Ramales de

la Victoria (Santander); *O. hidalgoi hidalgoi, O. oscitans* and *O. bicostulatum* at Nacimiento del Gándara (Santander) and *O. hidalgoi hidalgoi, O. bicostulatum* and *O. asturicum* at Covadonga, Lago Enol and Lago de la Ercina (all in Asturias). At these localities animals belonging to the various species live partly very close to each other, in slightly different habitats or totally mixed. At Cascadas del Asón (Santander) even four species were found together, on bare rock in the shade behind the cascade they were found completely mixed within less than one square metre: *O. hidalgo hidalgoi, C. bicostulatum, O. obscurum* and *O. oscitans.* At Seldesuto, near Matienzo (Santander) Gofas (1989) observed the same four species living closely together. Since there are no intermediate forms at any of these localities the taxa are clearly distinct biological species.

In Spain the genus is restricted to the northernmost part of the country, which has a humid climate with moderate temperatures. Further extension to the south is obstructed by the absence of hard limestone rocks and the dry climate in the Duero and Ebro valleys. In the west the acid granitic and metamorphic rocks of Galicia obstruct further extension. Also in the central part of the eastern Pyrenees the subgenus is absent due to acid granitic and metamorphic rocks. The factors influencing the distribution in France and northern Italy are less evident, due to the scarcity of data. In France *O. obscurum* is not just restricted to rock faces, it also occurs in forests and therefore has a wide distribution, even in lowland areas in the northeastern part of the country.

IDENTIFICATION TABLE

Since the intraspecific variation may be considerable, at least several specimens should be considered. Data on the shell and aperture size and the number of whorls measured on several species are summarized in table 1.

1. — The width of the shell is less than half its height 2
   — The width of the shell is more than half its height. The shell is brown with brown-grey, narrowly spaced, regular ribs. Two darker brown bands may be present. The penis is short (1.6-2.6 mm) and thick . *O. oscitans* (Gofas, 1989)
2. — Between major lamellar ribs up to five distinctly finer riblets occur (fig. 7) 3
   — All the ribs are more or less equal in prominence 4
3. — The translucent shell is pale brown to greenish. The lamellae are irregular. The peristome is broad and the aperture is narrow .. *O. bicostulatum* (Gofas, 1989)
   — The shell is corneous brown with two bands below the periphery and sometimes irregular spots below the suture. The sculpture consists of regular, straight lamellar ribs and a low number of riblets ..... *O. nouleti* (Dupuy, 1851)
4. — The shell is yellow to pale corneous brown with a dark band or row of dark spots below the suture and two dark bands below the periphery 5
   — The shell is brown with sharply defined light coloured ribs 6
5. — The shell is small and slender (H: 7-10.3; W: 3-4.5 mm), covered with very fine riblets or smooth; the peristome is only slightly reflected and thin .... *O. apricum* (Mousson, 1847)
   — The shell is small and slender to large and broad (H: 8.1-12.6 mm; W: 4-6 mm), covered with fine, closely to rather widely spaced ribs. The peristome is strongly reflected and thick ..... *O. obscurum* (Draparnaud, 1805)
6. — The shell is large with rather flat, finely ribbed whorls. Near the umbilicus there

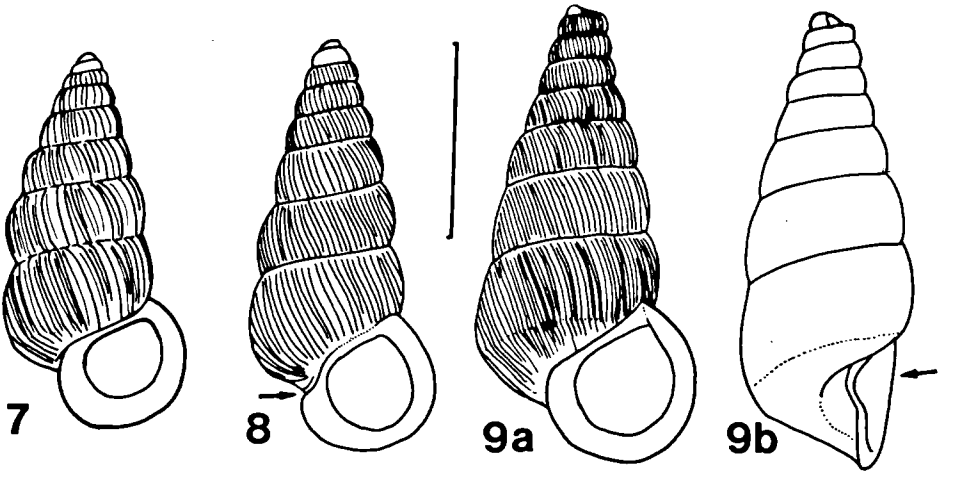
species		shell H	shell W	shell H/W	aperture H	aperture W	aperture H/W	number of whorls
	min	8.3	4.1		2.6	2.7		
nouleti	max	11.1	4.8		3.1	3.2		
(10/1)	mean	9.6	4.6	2.10	2.9	2.9	0.99	7.7
	min	7.9	3.9		2.8	2.7		
bicostulatum	max	12.9	5.1		4.1	3.7		
(46/7)	mean	9.8	4.6	2.12	3.1	3.2	0.98	7.8
	min	7.9	3.7		2.6	3.2		
apricum	max	9.6	4.5		2.5	2.9		
(15/1)	mean	8.8	3.9	2.24	2.8	2.7	1.03	7.4
	min	8.3	4.1		2.8	2.9		
obscurum	max	11.3	5.2		4.0	3.7		
(28/3)	mean	10.0	4.8	2.09	3.4	3.2	1.09	7.9
	min	8.3	4.2		2.8	3.0		
hidalgoi	max	14.0	6.8		4.8	4.8		
(49/5)	mean	11.0	5.2	2.14	3.6	3.8	0.95	8.0
	min	8.8	4.2		2.9	3.0		
asturicum	max	11.8	5.4		4.0	4.0		
(20/2)	mean	10.1	4.8	2.12	3.4	3.5	1.02	7.7
	min	8.4	4.8		3.1	3.2		
oscitans	max	11.6	6.1		4.2	4.2		
(38/2)	mean	9.7	5.3	1.90	3.7	3.6	1.02	7.1

Table 1. Shell and aperture sizes for representative samples from one to three populations of most *Obscurella* species; for *C. hidalgoi* only specimens of the subspecies *hidalgoi* are included. Below the species name, the number of measured specimens and the number of populations from which specimens were measured are indicated. The shell shapes are very close, in particular those of *C. nouleti*, *C. bicostulatum* and *C. asturicum*. *C. oscitans* has a broad shell with few whorls; the aperture of *C. obscurum* is higher than broad. *C. hidalgoi hidalgoi* is the most variable.

is a typical deflection (notch) in the lip (fig. 9). Generally the upper whorls have broken off ..... *O. canestrinii* (Adami, 1876)

— The ribs are closely spaced, irregular, white lamellae. The whorls are convex and are generally not angular below the periphery. The animal is dark grey to black, the penis may be lighter coloured, only the sole is white. The penis is short (1.3-5.5 mm, generally about 3.5 mm) and thick *O. asturicum* spec. nov.

— The shell may be smooth or provided with widely spaced ribs which vary from fine lines to lamellar ribs. The whorls are rather flat and are angular near the base. The animal is dark grey, the area near the penis is lighter coloured and



Figs. 7-9. Some shell characteristics of assistance in the identification of *Obscurella* species. 7, Alternating irregular lamellar ribs and finer riblets in *O. (O.) bicostulatum* (Gofas, 1989), female, El Mazo, 5 km E. of Panes (Asturias) Spain, UN7498 (J.G.M. Raven leg.; R); 8, protrusion (arrow) at the columellar side of the peristome in *O. (Cantabrica) hidalgoi martorelli* (Bourguignat in Servain, 1880), syntype of *Pomatias esseranus* Fagot, 1888, Desfiladero de Campo (Huesca) Spain, BG89 (P. Fagot leg.; SMF); 9, deflection (or notch, arrow) in the peristome and broken off upper whorls in *O. (Canestrinia) canestrinii* (Adami, 1876), syntype of *Pomatias insubricum* Pini, 1877, male, Valle di Scalvi (Bergamo) Italy (N. Pini leg.; SMF. Scale 5 mm.

the sole is dark grey. The penis is long (4.5-8.5 mm) 7

7. — The thick, reflected peristome has a protrusion at the columellar side (fig. 8). The shell has a pattern of darker and lighter bands and spots (not necessarily all specimens) and the ribs are generally closely spaced .... *O. hidalgoi martorelli* (Bourguignat in Servain, 1880)

— The thick, reflected lip has no protrusion at the columellar side. The shell is uniformly coloured and the ribs are widely spaced .... *O. hidalgoi hidalgoi* (Crosse, 1864)

Subgenus *Obscurella* Clessin, 1889

Obscurella Clessin, 1889: 559. Type species: *Cyclostoma obscurum* Draparnaud, 1805. See p. 18.
Anotus Westerlund, 1883.
Rhabdotakra Wagner, 1897: 583.

Redescription. — The shell has rather flat to convex whorls, separated by a shallow suture. The peristome is slightly to strongly reflected. The shell has a pale yellowish colour with reddish-brown spots or bands, the peristome is white.

Ecology. — The species of this subgenus live preferentially at vegetated and shaded localities with a humid microclimate, mainly on the north and west sides of mountain chains. They are not only known from calcareous rocks but also from trees in forests.

Obscurella (Obscurella) obscurum (Draparnaud, 1805)

Cyclostoma obscurum Draparnaud, 1805: 39-40, pl. 1 fig. 13. Locus typicus: northern France. Types lost (see Locard, 1896: 41-42); neotype: NMW.

Cyclostoma partioti De Saint-Simon, 1848: 36. Locus typicus: Gavarnie, Hautes-Pyrénées, France Topotypes: Me.

Cyclostoma obscurum var. *albinos* Partiot, 1848. Locus typicus: Saint-Saveur, Hautes-Pyrénées, France.

Cyclostoma obscurum var. *minus* Partiot, 1848. Locus typicus: Gavarnie, Hautes-Pyrénées, France. Topotypes: Me.

Pomatias crassilabrum Dupuy, 1849: no. 255. Description without a type locality being mentioned, probably surroundings of Lourdes, Hautes-Pyrénées, France (Dupuy, 1851).

Cyclostoma obscurum var. *cinerascens* Moquin-Tandon, 1855: 499. Locus typicus: Barèges, Hautes-Pyrénées, France.

Cyclostoma obscurum var. *truncatulum* Moquin-Tandon, 1855: 499. pl. 37 figs. 28-29. Locus typicus: Pyrénées-Orientales, France.

Cyclostoma partioti var. *ornatum* Moquin-Tandon, 1855: 501. Locus typicus: valleys of Gavarnie and Héas, the foot of the Vignemale and near the lakes Gaube and Estom, Hautes-Pyrénées, France.

Pomatias rayianum Bourguignat, 1860: 28-29, pl. 4 figs. 7-9. Locus typicus: Aube, France (Bourguignat is not sure whether the specimens were collected at Bar-sur-Seine, des Riceys or Clairvaux).

Pomatias partioti var. *crossei* De Saint-Simon, 1867: 11. Locus typicus: Cirque de Gavarnie and Pas-de-Echelle, Hautes-Pyrénées, France. Topotypes: Me.

Pomatias mabillianus De Saint-Simon, 1869: 7-8. Locus typicus: Vallée du Pic du Gers near Eaux-Bonnes, Pyrénées-Atlantiques, France.

Pomatias frossardi Bourguignat in Frossard, 1870: 18. Locus typicus: Grotte d'Aurensan near Bagnères-de-Bigorre, Hautes-Pyrénées, France.

Pomatias spelaeus Fagot, 1876: 62. Locus typicus: lower cave of Bédat near Bagnères-de-Bigorre, Hautes-Pyrénées, France.

Pomatias hidalgoi var. *laburdensis* Folin & Bérillon, 1877: 202-203. Locus typicus: Sarre (= Sare), Cambo, Hendaye, all in Pyrénées-Atlantiques, France. Topotypes: R.

Pomatias crassilabrum var. *iratyensis* Folin & Bérillon, 1877: 206-207. Locus typicus: forest house at the border of the Hourbelcha, Forêt d'Iraty, Pyrénées-Atlantiques, France.

Pomatias berilloni Fagot, 1880a: 17. Locus typicus: near St. Jean-de-Luz, Pyrénées-Atlantiques, France. New name and status for *P. hidalgoi* var. *laburdensis* Folin & Bérillon. Topotypes: R.

Pomatias lapurdensis Fagot, 1880a: 21. Locus typicus: interior of the Grotte des Espélugues near Lourdes, Hautes-Pyrénées, France. Syntypes: SMF 159909/5.

Pomatias fagoti Bourguignat in Fagot, 1880b: 291-292, fig. 5. Locus typicus: Cascade d'Arse along the road of Castelminier near Aulus, Ariège, France.

?Pomatias hueti Kobelt, 1882: 121-122. Locus typicus: Constantinople (Istanbul), Turkey.

Pomatias isoicus Fagot, 1889: 11. Locus typicus: Iso, Navarra, Spain.

Pomatias isabanus Fagot, 1889: 11-12. Locus typicus: Isaba, Navarra, Spain. Topotypes: R.

Pomatias filicium Fagot, 1889: 12. Locus typicus: Puerto de Larrau, Navarra, Spain.

Pomatias subobscurus Fagot, 1891: 290. Locus typicus: central and western Pyrénées. Nomen nudum.

Pomatias neglectus Fagot, 1891: 291. Locus typicus: Lourdes, Hautes-Pyrénées, France. Topotypes: N.

Pomatias harlei Fagot, 1891: 293. Locus typicus: Loyola, Guipúzcoa, Spain. Nomen nudum.

Pomatias bearnicus Bourguignat in Fagot, 1891: 293. Locus typicus: valley of Eaux-Chaudes, Pyrénées-Atlantiques, France. Topotypes: RMNH.

Pomatias saulcyi Bourguignat in Fagot, 1891: 293. Locus typicus: entrance of the Gorge des Eaux-Chaudes, Pyrénées-Atlantiques, France. Syntypes: SMF 160916/6.

Pomatias daralli Bourguignat in Locard, 1894: 344. Locus typicus: valley of the Pic-du-Gave near Eaux-Bonnes, Pyrénées-Atlantiques, France.

Pomatias angustus Bourguignat in Locard, 1894: 345. Locus typicus: Eaux-Chaudes, Pyrénées-Atlantiques, France. Topotypes: RMNH.

Pomatias (Rhabdotakra) obscurum var. *jetschini* Wagner, 1897: 586, pl. 3 fig. 29. Locus typicus: Gerde, Hautes-

Pyrénées, France. Lectotype: SMF 159927; paratypes: SMF 159928/9 and SMF 159929/1; topotypes: M.

Pomatias (Rhabdotakra) berilloni var. *kobelti* Wagner, 1897: 588, pl. 3 fig. 34. Locus typicus: Bilbao, Vizcaya, Spain. Lectotype: SMF 160056; paratypes: SMF 160057-8/10 and SMF 160061-2/9,8.

Cochlostoma (Obscurella) löbbeckei Kobelt, 1902: 50. Locus typicus: Lourdes, Hautes-Pyrénées, France (nom nov. for *P. lapurdensis* Fagot). Syntypes: SMF 159911/2.

Shell (figs. 1b,c, 10-17, 31, 38). — The shell has 7-8.5 slightly to rather convex whorls which are separated by a shallow suture. Shells of male specimens are smaller and have less whorls than those of females. Near the aperture the last whorl rises slightly. The peristome is strongly reflected, in particular in male specimens. At the apertural side of the penultimate whorl the ribs are generally rather widely spaced (about 5/mm), but in some specimens or populations they are very close (8-9/mm). They are even closer on the last whorl, except near the aperture. The ribs are rather regular but the number of ribs is very variable. On the penultimate whorl their number varies from 51 to 151. In some populations there are thin riblets in between these ribs.

Height 8.1-15.5 mm; width 4.0-6.4 mm.

The shell has a yellow to pale corneous brown colour; the peristome and part of the last whorl are white. The ribs have a pale corneous colour. Below the suture and on the lower part of the whorls, respectively, there are generally one and two bands, which may be uniformly brown or consisting of irregular whitish and brown spots; sometimes there is a light coloured band in between the two lower bands. The bands may be so broad that the shell is brown with only two lighter bands. Some specimens have broad, irregular vertical spots. In male specimens the upper whorls are violet, except the uppermost, embryonic, whorls which both in male and female specimens are pale yellow. In general, the colours are more vivid in male specimens.

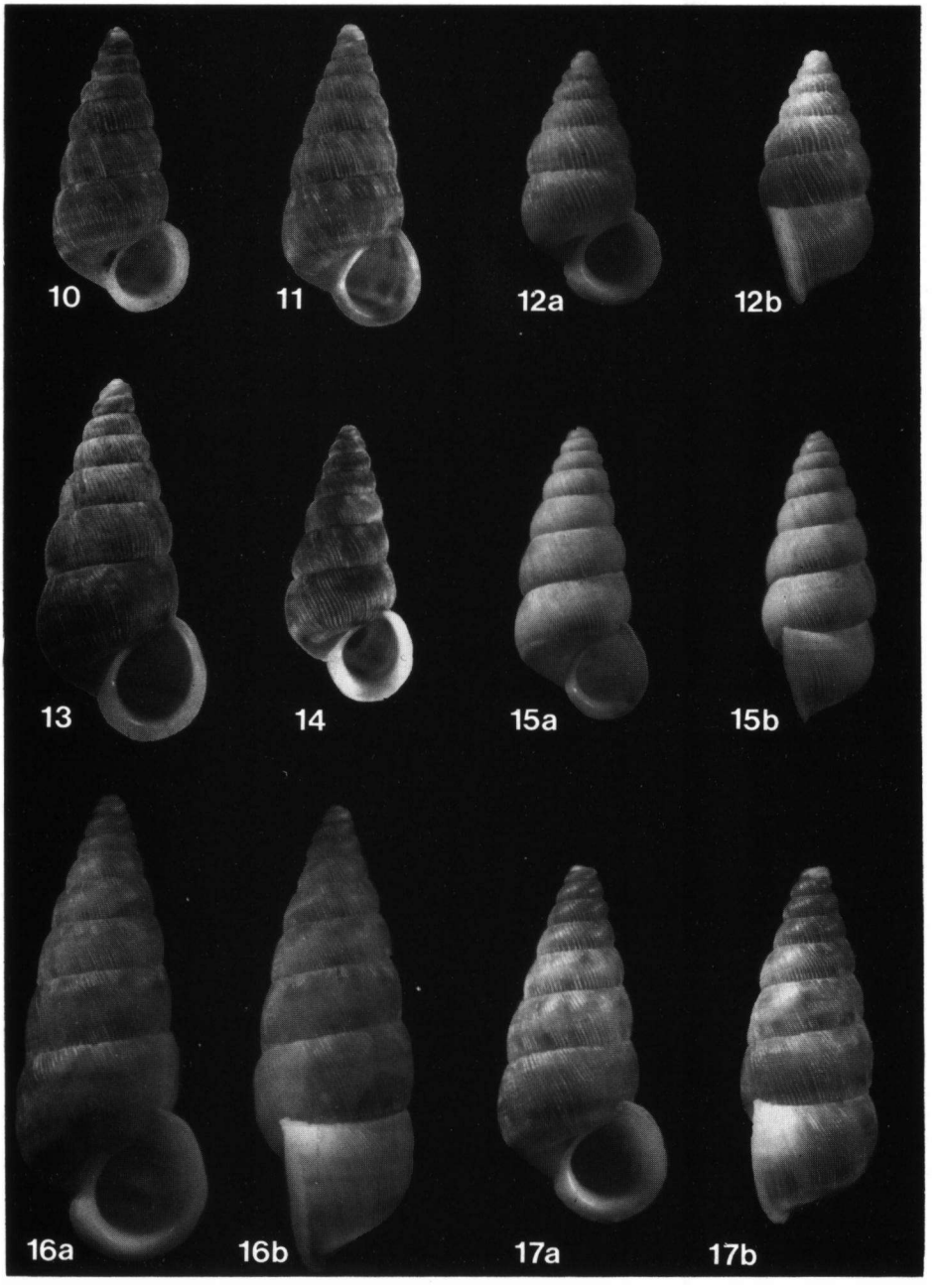
In this variable species two extreme forms can be distinguished, viz. a large and broad type with flat whorls, rather widely spaced ribs and a large aperture (figs. 16-17), and a small and narrow type with convex whorls, closely spaced ribs and a small aperture (figs. 14-15). The first form is most common in the lower areas along the northern slope of the Pyrenees and the second form is most common in higher mountainous areas in the central Pyrenees and in Spain. Both forms, however, may occur within a single population, connected by intermediate forms.

Animal (fig. 4c). — The animal is light grey, rarely blackish specimens occur. The sole is white, sometimes with a darker band along the edge. The anterior part of the proboscis is occasionally darker or lighter than the body and often the tentacles are darker grey with a pale ring near the base.

Genitalia (fig. 2c). — The penis is generally rather short (3-6 mm) and slender (0.5-0.8 mm) but occasionally about 1 mm thick specimens are found. Micropenises may be only 1 mm long. Sometimes marked constrictions occur. The penis is yellowish white with a greyish tip.

Radula (fig. 5a, g). — The radula is much shorter than it is in the other species, viz. 4-5 mm instead of 7-10 mm. The teeth have a quadrangular shape and central, lateral and marginal (M1) teeth are all 0.27-0.30 mm broad.

Designation of a neotype. — *O. (O.) obscurum* is the type species of *Obscurella*. All syntypes have disappeared from Draparnaud's collection (Locard, 1896: 41-42). The last person who mentions the types is Wagner (1897: 525) but they are not in his collection in the Zoological Museum of Warsaw (pers. comm. Dr. A. Riedel, Warsaw).


10
11
12a
12b
13
14
15a
15b
16a
16b
17a
17b

There may be confusion about the identity of the species: the original description is not sufficiently detailed to distinguish it from the other species of the subgenus and Draparnaud described the species from 'northern France' without mentioning a specific locality. Therefore it is necessary to designate a neotype, for which I select a specimen from 'northern' France: Arcy-sur-Cure, Yonne, UTM EN57 (fig. 10). The sample was collected by J.G.J. Kuiper (Paris) in 1950 and was preserved in RMNH; the neotype is donated to the NMW (Vienna) where the Draparnaud collection is kept.

Ecology. — The animals live on sheltered, humid, densely overgrown carbonate rocks, often below blocks. Locally they live on trees or between litter in forests in calcareous areas (e.g. in the Ordesa national park in the province of Huesca, Spain). In the western part of its range *O. obscurum* was found sympatric with *O. hidalgoi hidalgoi, O. bicostulatum*, and *O. oscitans*. At the SW. edge of St. Béat and E. of Boutx (Haute-Garonne) the species was found together with *O. nouleti*.

According to Dupuy (1851: 511): "Aux environs d'Auch, dès les premiers beaux jours du printemps, ce Mollusque monte sur les arbres où on le trouve en très grande quantité sur les chênes des bosquets rocailleux. Il est facile alors, en quelques heures, d'en recueillir plusiers milliers."

Distribution (figs. 18, 52a). — The species lives in the eastern Cantabrian mountains and the Pyrenees (except the southeastern part) and is further known from scattered localities in northeastern France (Côte-d'Or, Yonne, Aube). Probably it occurs also in the intermediate departments: Germain (1931: 576) mentioned it as common in northern and central France and Kerney & Cameron (1979, map 2) indicate it in most of southern and eastern France. The species was mentioned from Constantinople (now Istanbul), Turkey (as *P. hueti* Kobelt, 1882), where it was probably introduced with plants (Wagner, 1897).

Material. — Neotype: FRANCE, YONNE: Arcy-sur-Cure, EN57 (NMW). Other samples: FRANCE, YONNE: Vézelay, EN55 (RMNH); Arcy-sur-Cure, EN57 (RMNH). COTE D'OR: NE. of Montbard, FN07 (RMNH). PYRENEES-ATLANTIQUES: Bayonne, XP21 (M, N, R, RMNH, V); Lahonce, XP3016 (M); Cambó-les-Bains, XP30 (M, Me); Isturits, E. of Hasparren, XP40 (RMNH); Suhare (UPV); 1.5 km N. of Urdós, XN38 (M); between Labastide and Villefrance, XP51 (Me); SE. of Mendive near St. Jean-Pied-de-Port, XN5576 (R); Muskuldi, XN6584 (UPV); near Grottes de Sare, 5 km S. of Sare, XN1691 (R); Maule, XN7187 (UPV); Atherei, XN7371 (UPV); Gorges de Kakouetta, XN7561 (UPV); Sainte Engrâce and surroundings, XN7762/8262 (UPV); 1 km E. of Montory, XN77 (Me); Barkoxe, XN8184 (UPV); near Lac d'Orbiette and in Bois de Bresne, Gave d'Aspe/Cirque de Lescun, XN85

Figs. 10-17. Shells of *Obscurella (O.) obscurum* (Draparnaud, 1805). 10, neotype, male, Arcy-sur-Cure (Yonne) France, EN57 (J.G.J. Kuiper leg., originally RMNH, now NMW), H. 9.6 mm; 11, female, Bayonne (Pyrénées-Atlantiques) France, XP21 (J.G.M. Raven leg., R), H. 10.2 mm; 12, female, forma *kobelti* (Wagner, 1897), typical for high parts of eastern Cantabrian mountains, 4.4 km N. of Puerto de Orduña (Alava) Spain, VN9857 (Th. Ripken leg., RMNH), H. 8.3 mm; 13, 14, 5 km N. of Col de Soulor (Hautes-Pyrénées) France, YN26 (H.P.M.G. Menkhorst leg., R); 13, female, H. 11.9 mm; 14, male, H. 9.1 mm; 15, female, slender specimen of forma *partioti* (De Saint-Simon, 1848), typical for high of parts of the Pyrenees, Bosque de las Hayas, Parque Nacional de Ordesa (Huesca) Spain, XN4324 (J.G.M. Raven leg., RMNH), H. 9.6 mm; 16, 17, large specimens with a rich colour pattern, typical for low parts of Pyrenees, St. Béat (Haute-Garonne) France, CH15 (J.C.A. Eikenboom leg., R); 16, female, H. 15.5 mm; 17, male, H. 11.9 mm. Enlargement approximately 4.0 x.

(RMNH); 0.2 km NE. of Féas, XN88 (Me); Borce, 8 km SSE. of Accous, XN95 (RMNH); Lescun, XN95 (D, RMNH); between Urdos and Etsaut, XN95 (N); N. of Etsaut, XN95 (D); Sarrance, XN96 (N); between Bedous and Sarrance, XN96 (N, RMNH); Osse, 2 km W. of Bedous, XN96 (RMNH); between Bedous and Aydius, XN96/YN06 (RMNH); between Sarrance and Escot, XN96 (N, RMNH); Accous, XN96 (RMNH); Pont d'Esquit, 1 km SW. of Accous, XN96 (RMNH); between Accous and Eygun, XN95/96 (N, RMNH); between Cette and Eygun, XN95 (N, RMNH); Escot, XN97 (N, RMNH); Pont d'Escot, XN97 (N, RMNH); Défilé d'Escot, XN97 (N, RMNH); La Pène d'Escot, XN97 (RMNH); Lurbe, near Escot, XN97 (N, RMNH); between Issor and Lourdios, XN97 (N); Lourdios, 8 km NW. of Bedous, XN97 (N, RMNH); Oloron, XN98 (RMNH); 3 km N. of Col du Portalet, YN14 (Ri); around Fort du Portalet, YN14 (N, RMNH, V); between Gabas and Bious-Artigues, YN05/06 (RMNH); Les Eaux-Chaudes, YN05 (RMNH, SMF); Col du Somport, S. of Pau, YN04 (M, N); Laruns, YN06 (D, RMNH); between Laruns and Les Eaux-Chaudes, YN07 (RMNH); Izeste, YN07 (RMNH); Castet, YN17 (RMNH); Bruges, YN17 (D); between Castet and Louvie-Juzon, YN17 (N, RMNH); between Les Eaux-Chaudes and Gabas, YN16 (RMNH); Col d'Aubisque, YN16 (E, RMNH); 2.7 km E. of Col d'Aubisque, YN16 (Ri); Gourette, YN16 (RMNH); between Gourette and Les Eaux-Bonnes, YN16 (N, RMNH); between Les Eaux-Bonnes and Assouste, YN16 (RMNH); between Laruns and Aste, YN16 (RMNH); between Aste and Béon, YN16 (RMNH); Pau, YN19 (N, RMNH). HAUTES-PYRENEES: about 5 km N. of Col de Soulor, YN26 (Me); La Herrère, N. of Col de Soulor, YN2368 (V); 2 km W. of Col de Soulor, YN25 (Ri); between Aucun and Col d'Aubisque, YN26 (M); Gave de Cauberets near Port d'Esdenrorats, YN35 (M, Me); Gavarnie, in direction of Cirque de Gavarnie, YN43 (E, Me); Gorge de Luz, between Pierrefitte and Luz, YN45 (Ri); Lourdes, YN37/47 (N); Donjon d'Aigles, SE. of Beaucens, YN36/46 (Me); in Grotte des Espélugues near Lourdes, YN37 (SMF); W. of La Mongie, BH65 (M); Beaudéan, S. of Bagnères-de-Bigorre, BH66 (RMNH); Gerde, near Bagnères-de-Bigorre, BH67 (M, SMF); Val d'Aure, BH74 (M): Gripp, NE. of Col du Tourmalet, BH75 (N); Grézian, BH85 (M); 5 km W. of Col d'Aspin, BH85 (RMNH). HAUTE-GARONNE: Luchon, CH04 (RMNH); N. of Bagnères-de-Luchon, CH05 (M); Superbagnères, CH03 (N); St. Béat, CH15 (R, V); E of Boutx, 2 km E. of St. Béat, CH15 (V). ARIEGE: near Cognetz, valley of the Salat, CH53 (RMNH); Le Mas d'Azil, CH6671 (M); between Foix and Vernajoul, CH85 (RMNH); Col Labouche, CH86 (RMNH).

SPAIN, SANTANDER: Puerto Palombera, UN9573 (UPV); W. of Anero, VP40 (N); 3 km S. of Arredondo, VN5088 (Ri); Cascadas del Asón, VN5283/5284 (R); near Cueva la Coventosa, Asón, VN58 (W); Arredondo, VN5189 (W); Regules, VN5983 (E, Me); near Incedo, N. of Portilla de la Sia, VN6284 (E, Me); Ramales de la Victoria, VN6289/6290 (E, Me, N); La Gándara, VN8288 (RMNH); Ontón, E. of Castro Urdiales, VP8601 (M). BURGOS: Villabasil, VN7764 (UPV). ALAVA: Txarllazo, Pico del Fraile, Orduña, VN9650 (UPV); Angosto, VN9445 (UPV); 2-5 km N. of Puerto de Orduña, VN9856/9857 (Me, N, R, Ri); Delica, WN0157 (UPV); N. of Embalse del Gorbea, WN2161 (R); Puerto de Opacua, 6 km S. of Salvatierra, WN5540 (Me); Santa Cruz de Campezo, WN5624 (UPV). VIZCAYA: Peña Ranero, along Carranza river, VN6991 (UPV); outside Cueva de los Cuervos, Galdanes, VN9289 (UPV); Traslaviña, VN8288 (Ri, RMNH); Lendoño de Arriba, VN9562 (UPV); Bilbao, WN08/09 (SMF); Baracaldo, WN0092 (UPV); along Padrobaso river, Peña Gorbea, WN16 (UPV); below Atxas, Gorbea, WN16 (UPV); Aldamiñape, Peña Gorbea, WN1865 (UPV); Arimekorta, Peña Gorbea, WN1866 (UPV); Atxuri, Peña Gorbea, WN2065 (UPV); Cueva de Otxas, Urkizu, WN1981 (UPV); Laga, WP2706 (UPV); just S. of Durango, WN2987 (Me); Untzillaitz, Durango, WN2975 (UPV); Orduña, VN96 (SMF). GUIPUZCOA: E. of Urbia, Sierra de Aitzgorri, WN55 (W); 8 km W. of Zumaya, WN5692 (Me); 5 km S. of Deva, WN5191 (Me); Ataún, WN6762 (RMNH, UPV); Vidania, W. of Tolosa, WN6877 (N); Tolosa, WN7475 (R); Ausa Gaztelu, Sierra de Aralar, WN7163 (UPV); Orio, WN7191 (Ri); Alto de Lizarrusti, 13 km SE. of Beasain, WN75 (W); San Sebastián, WN8197/8297 (Ri, UPV). NAVARRA: between Bernedo and Santa Cruz de Campezo, WN42 (W); N. side of Sierra de Urbasa, 3 km S. of Alsasua, WN64 (W); Alsasua, WN6849 (RMNH); between Lizarra and Atallo, WN8169 (Ri); Satrústegui, Beriain, WN8349 (UPV); near Huarte Araquil, WN8453 (M, UPV); Altxueta, Sierra de Aralar, WN8456 (UPV); 10 km N. of Lecumberri, WN86 (M); Sima de Leregalde, Lecumberri, WN8959 (W); Lecumberri, WN9062 (M); 1 km N. of Puerto de Usateguieta, WN9171 (Me, R, RMNH); near Cueva Akelar, Allí, WN9060 (UPV); Paso de Dos Hermanas, N. of Irurzún, WN9272 (E, R, V); Puerto de Zuarrarrate, between Lecumberri and Irurzún, WN95 (V); Oricaín near Pamplona, XN1345 (M); Vera de Bidasoa,

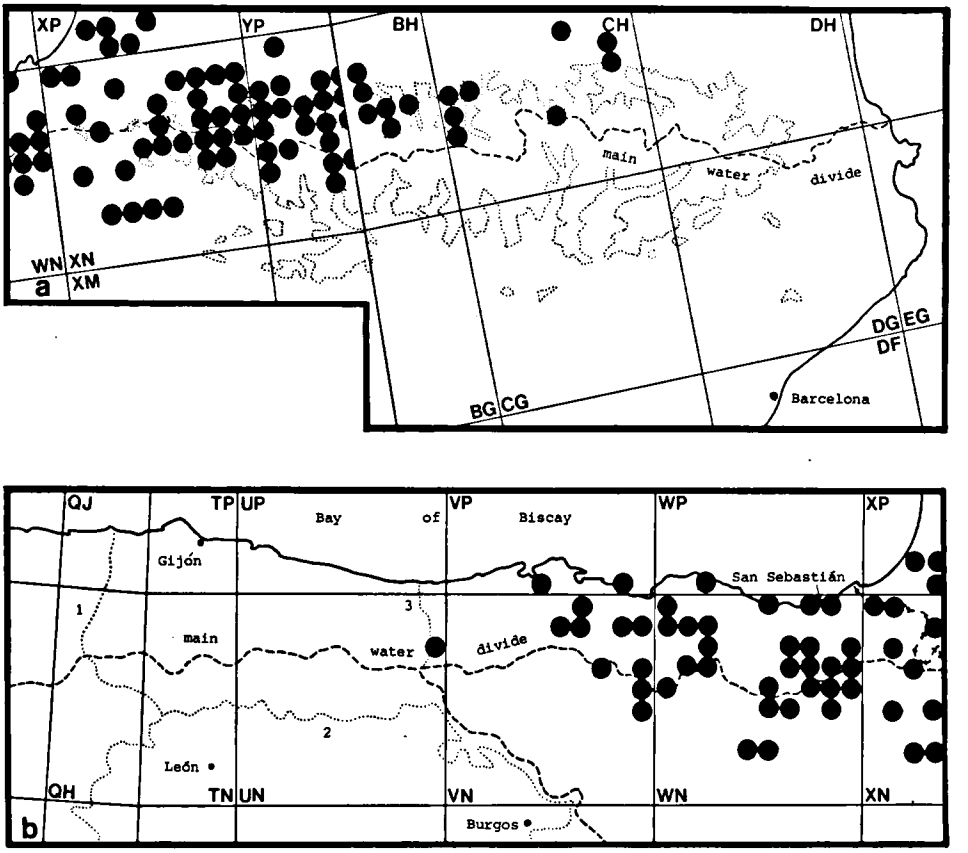


Fig. 18. Confirmed records of *Obscurella (O.) obscurum* (Draparnaud, 1805), indicated on UTM 10 km square maps; the thick, interrupted lines indicate the main water sheds, which constitute important zoogeographical border lines; in figure 18b the dotted lines stand for other zoogeographical boundaries: (1) the boundary between non-calcareous rocks in the West and calcareous rocks in the East, (2) the limitation of the Castilian uplands, and (3) the boundary running from Comillas to the Pico Tres Mares; for the Pyrenees in figure 18a, where such zoogeographical boundaries have not yet been investigated, the 1200 m altitude line is indicated by a dotted line.

XN0693 (UPV); Arrayóz, XN1577 (E, Me, R, V); Monreal, Elomendi, XN2229 (UPV); Cilveti, XN2560 (UPV); Nagore, N. of Aoiz, XN3343/3246 (RMNH, UPV); Lumbier, XN3923 (UPV); N. of Arive, 8 km SE of Burguete, XN4257 (R); Orbaiceta, XN4459 (UPV); Usún, XN4625 (UPV); Foz de Arbayún, 11 km NE. of Lumbier, XN4827/4928 (R, UPV); Birgüezal, XN5127 (UPV); N of Escaroz, XN5550 (R, UPV); Irati, XN5561 (R, UPV); 1.2 km SE. of Uztárroz, N. of Isaba, XN6950 (R); 1 km W. of road from Isaba to Arette, XN7557 (W). HUESCA: Zuriza, Vall d'Ansó, XN74 (E, RMNH); between Hecho and Ansó, XN74/84 (E); Bosque de Oza, Valle de Hecho, XN84 (RMNH); Canfranc and surroundings, YN03 (N, RMNH); Arañones, YN03 (RMNH); Candanchú, YN0039 (UPV); Faldas del Tobazo, Candanchú, YN03 (RMNH); Broto, YN32 (RMNH); Torla, YN32 (RMNH); numerous localities in the Parque Nacional de Ordesa, YN32 to 34 (E, M, N, R, RMNH).

Remarks. — A sinistral specimen was collected by H.P.M.G. Menkhorst at 1 km N. of Puerto de Usategui eta, Navarra, Spain, WP9171 (Me) (fig. 38).

This species was described by Draparnaud in 1805, not 1801. Locard (1882: 213, 1896: 41-42) and Germain (1931: 576) regarded *Turbo conicus* Vallot, 1801, as a synonym. Although the description of *T. conicus* is very vague, it might concern the same species indeed. The name *T. conicus* was introduced before *O. obscurum* but because it has always been considered a junior synonym, it has never been used after its original introduction. Therefore I will propose to add *Turbo conicus* Vallot, 1801, to the 'Official index of rejected and invalid specific names in zoology'.

Many different names were introduced for this variable species, of which a few are still commonly used, viz. *O. obscurum* mainly for specimens from France beyond the Pyrenees (figs. 10, 11), *'O. partioti'* for specimens from the central Pyrenees (fig. 15), *'O. crassilabrum'* for specimens from the northern Pyrenees and *'O. berilloni'* for those from the extreme west of the Pyrenees and from the eastern Cantabrian mountains (figs. 12, 31). While comparing samples from all these areas, including types of many nominal taxa, and taking the distribution pattern into consideration, it became evident that although the material is very variable, no distinct species or subspecies can be distinguished. There is not a single population where two of these alleged species occur without intermediate forms. For example, in several populations only the slender form (*'O. partioti'*) occurs (e.g. at Lourdes and Gavarnie in the Hautes-Pyrénées and at the Parque Nacional de Ordesa in Huesca; fig. 15), but elsewhere this form occurs together with the typical form, connected by intermediates (e.g. at Bedous in the Pyrénées-Atlantiques; fig. 14). Already Wagner (1897: 585) considered *partioti* a variety (form) and *crassilabrum* a synonym of *O. obscurum*. He introduced two new varieties (forms), viz. *kobelti* from the eastern Cantabrian mountains (fig. 12), which is slightly smaller than the commonest form, and *jetschini* from the central Pyrenees, which is also a somewhat shorter form. All these forms cannot be clearly separated since they grade into each other. Gofas (1989) distinguished the subspecies *laburdensis* (Folin & Bérillon, 1877). The topotypes collected near Sare (Pyrénées-Atlantiques) are similar to shells of the populations of the Spanish Basque provinces (*'O. berilloni'*), which grade into other forms. Therefore I see no reason to distinguish this taxon as a subspecies.

Obscurella (Obscurella) apricum (Mousson, 1847)

Cyclostoma obscurum Gras, 1846 (non Gray, non Draparnaud): 55, pl. 4 fig. 28. Locus typicus: Sassenage, Grande Chartreuse, Isère, France. Homonym of *C. obscurum* Draparnaud.

Cyclostoma apricum Mousson, 1847: 47. Locus typicus: Dent-du-Chat near Aix-les-Bains, Savoie, France Topotypes: SMF.

Pomatias carthusianum Dupuy, 1849: No. 254 (nomen nudum).

Pomatias carthusianum Dupuy, 1851: 516-518, pl. 26 fig. 14. Locus typicus: Alps around La Grande Chartreuse, Isère, France. Syntype: SMF 160049/1.

Pomatias sabaudinus Bourguignat, 1864: 64-66, pl. 2 figs. 11-14. Locus typicus: Between Col de la Dent-du Chat and La Vacherie, Savoie, France.

Shell (figs. 1e, 23, 24). — The shell is relatively small and slender, consisting of about eight, slightly convex whorls with a shallow suture. The ribs (about 9-10/mm) are fine, smooth and very regular, thus giving the shell a silky lustre. The aperture

is small with a thin, slightly reflected lip, which is broad on the columellar side but narrow on the parietal side.

Height 7.0-10.3 mm; width 3.0-4.5 mm.

The shell is pale corneous with three continuous or interrupted reddish-brown bands: one near the suture and two near the base. Between the two latter bands the shell mostly has a lighter colour. The peristome is whitish.

Male shells have dark top whorls (except for the whitish embryonic whorls) and are smaller and more slender than those of female specimens (fig. 1e).

Animal (fig. 4b; Giusti, 1971: fig. 4). — The head and the warty proboscis are dark grey. The tentacles are lighter grey, sometimes with whitish rings near the base. The body is also light grey and the sole is white.

Genitalia (fig. 2d, e; Giusti, 1971: fig. 4). — The penis is long (3-6 mm) and rather thick (0.6-0.8 mm) compared to the relatively small size of the animal. It has marked constrictions as well as an internal vas deferens. Some specimens have a micropenis (fig. 2e).

Ecology. — The species occurs on rocks and scree, also in forests, mainly in the mountains (Kerney & Cameron, 1979).

Distribution (fig. 52a). — The species is extremely common in a small area in the western Alps, in the French departments of Isère, Savoie and Haute-Savoie, between 425 and 1900 m altitude, and in SW-Switzerland (Clessin, 1889: 599).

The species was mentioned from the Alpes-Maritimes (e.g. Germain, 1931: 581), but Caziot (1910: 447) doubts the occurrence in that area. Specimens in a sample supposedly collected at Triest (province of Trieste, Italy) were described as *Pomatias obscurum* var. *fimbriatum* Held by Pfeiffer (1846: 187, pl. 26 figs. 31-33), but were identified by Wagner (1897: 586-587) as belonging to two separate species: *O. apricum* and *Cocholostoma (C.) scalarinum* (A. & J.B. Villa, 1841). Although later on several collectors searched for *O. apricum* near Triest nobody ever found any specimen (Wagner, 1897). Therefore that record is considered erroneous.

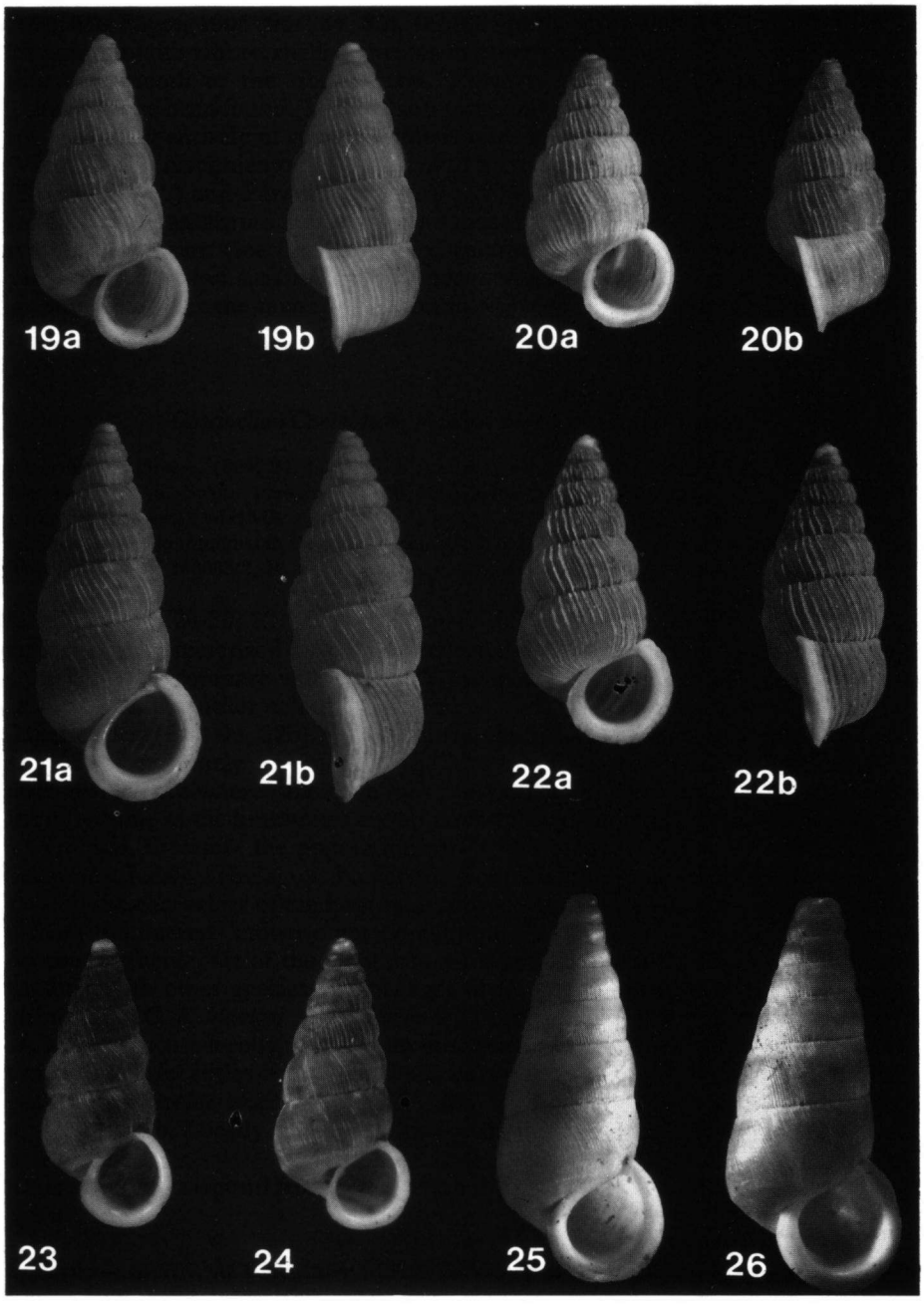
Material. — FRANCE, SAVOIE: Abbaye de Hautecombe, GL27 (RMNH). ISERE: Les Vialles, Grande Chartreuse, GL (RMNH); St. Pierre-de-Chartreuse, GL (RMNH); 4 km W. of St. Pierre-de-Chartreuse, GL12 (RMNH); Grande Chartreuse, GL (SMF); Gorges du Guiers Mort, SE. of St. Laurent-du-Pont, GL13 (R, RMNH); Gorges du Guiers Vif, between St. Pierre d'Entremont and Les Echelles, GL13/GL23 (RMNH); Pont-St. Bernard, Massif de la Chartreuse, GL22 (RMNH); between Charmant and Sous, Massif de la Chartreuse, GL12 (RMNH).

Remarks. — The shell of *O. apricum* has the same shape as slender specimens of *O. obscurum* (forma *partioti*, figs. 14, 15) from which it can be distinguished by its thin, only partially reflected lip, its fine and smooth ribs, the generally darker colour and the lower position of the angle in the columellar side of the lip.

Completely smooth shells were described by Bourguignat (1864: 64-66, pl. 2 figs. 11-14) as *Pomatias sabaudinus* and may be referred to as forma *sabaudinus*. This form is known from the Col de la Dent du Chat, Savoie, France and probably occurs also elsewhere in separate populations (compare *O. hidalgoi* forma *alopioides*, below).

Obscurella (Obscurella) nouleti (Dupuy, 1851)

Pomatias nouleti Dupuy, 1851: 351, pl. 26 fig. 12. Locus typicus: Axat, Aude, France. Topotypes: W. *Cyclostoma nouleti* var. *crosseana* De Grateloup & Raulin, 1855.


19a
19b
20a
20b
21a
21b
22a
22b
23
24
25
26

Pomatias arriensis De Saint-Simon, 1867: 16. Locus typicus: Montagne d'Arri between Saint-Béat and Marignac and surroundings of Cierp and Bertreu, Haute-Garonne, France. Topotypes: V.
Pomatias arriacus Bourguignat in Mabille, 1875: 150. Nomen nudum.
Pomatias marquetianus De Saint-Simon, 1876: 24. New name for *P. arriensis* and *P. arriacus*, thus a synonym.

Shell (figs. 19, 20). — The shell has 7-9.5 slightly convex whorls, which may be angled below the periphery. The suture is rather deep; over a short distance it rises slightly towards the aperture. The white, reflected and flat peristome is not thick. The uppermost three whorls are covered with fine, regular ribs. The lower whorls have irregular ribs: sharp lamellae alternate with zero to four finer ribs. Where those riblets are present the lamellae are more widely spaced. There are generally no riblets on the last whorls where the lamellae are closely spaced. Male specimens are smaller and more slender.

Height: 8.3-12.1 mm; width: 4.1-5.3 mm.

The shell is corneous brown to grey, in many specimens with two darker bands below the periphery and in few specimens also with two dark spots below the suture. Further there may be a pattern of broad, irregular vertical bands. In male specimens the initial whorls have a dark violet colour, except for the yellow first whorl. The ribs are lighter coloured than the shell.

Animal (fig. 4a). — The animal is pale grey with dark grey tentacles and head. Near the base of the tentacles there is a broad, white ring and upwards along the tentacle the colour changes from dark to pale grey. The proboscis is pale grey but changes to white or yellow along the edge. The white sole may also have a pale grey edge.

Genitalia — The few specimens studied have a rather long (5-6 mm) and thick (1 mm) penis, nearly without constrictions.

Ecology. — The species lives on trees and on moss-covered rocks and scree in mountainous areas (A.J. de Winter, personal communication).

Distribution (figs. 44, 52a). — The species occurs in the northeastern Pyrenees (departments of Haute-Garonne, Ariège, Aude, Pyrénées-Orientales). It occurs between 400 and 1600 m altitude, mostly in river valleys. The range coincides partly with that of *O. obscurum*. The two species were found sympatrically at the SW. edge of St. Béat and E. of Boutx (Haute-Garonne).

Material. — FRANCE, HAUTE-GARONNE: SW. edge of St. Béat, NE. of Bagnères de Luchon, CH15 (V); E. of Boutx, 2 km E. of St. Béat, CH15 (V); ARIEGE: Quié, CH84 (RMNH), between Quié and Genat, CH84 (RMNH); between Capoulet and Niaux, CH84 (RMNH); Rabat, W. of Tarascón, CH8246 (E); between Rabat and Carniés, CH74/84 (RMNH); between Foix and Labouche, CH85/86 (RMNH); AUDE: Défilé de Joucou, DH24 (E, R, RMNH); Défilé d'Adouxes, DH1536 (E); Forêt de

Figs. 19-26. Shells of *Obscurella* species. 19, 20, *O. (O.) nouleti* (Dupuy, 1851), Défilé de Joucou (Aude) France, UTM DH24 (J.C.A. Eikenboom leg., RMNH); 19, female, H. 9.6 mm; 20, male, H. 8.2 mm; 21, 22, *O. (O.) bicostulatum* (Gofas, 1989); 21, male, El Mazo, 5 km E. of Panes (Asturias) Spain, UN7498 (J.G.M. Raven leg., RMNH56142), H. 9.4 mm; 22, female, with colour pattern best visible below suture, Cueva de Ventalaperra, SE. of Gibaja (Santander) Spain, VN6998 (B.J. Gómez & C.E. Prieto leg., RMNH56163), H. 11.2 mm; 23, 24, *O. (O.) apricum* (Mousson, 1847), Gorges du Guiers Mort, SE. of St. Laurent-du-Pont (Isère) France, GL13 (E. Gittenberger leg., R); 23, female, H. 8.8 mm; 24, male, H. 8.7 mm; 25, 26, *O. (Canestrinia) canestrinii* (Adami, 1876), syntypes, Monte Presolano (Bergamo) Italy (G.B. Adami leg. (?), SMF158335/2); 25, H. 11.6 mm; 26, H. 11.8 mm. Enlargement approximately 4.5 x.

Bac/Estable, 1.2 km SE. of Axat, DH32 (W); Gorges de St. Georges, S. of Axat, DH32 (N, RMNH, W); Forêt des Fanges, between Quillan and Axat, DH33 (W); valley of the Rebenty, near the Aude, DH34 (RMNH); Défilé de Pierre/Lys, SE. of Quillan, DH34 (N, RMNH); Trou du Curé, SE. of Quillan, DH34 (Mc, RMNH); above the châlet Cachar, Quillan, DH34 (RMNH); between Quillan and Gignoler, DH35 (W); PYRENEES-ORIENTALES: between Caudiès and Fonevillet, DH31 (RMNH); between Caudiès and Col St. Louis, DH31 (RMNH).

Remarks. — Conchologically this species resembles *O. bicostulatum*; in both species the shells have alternating coarser and finer ribs. The shell is corneous brown to grey, with darker spots and bands in *O. nouleti* and greenish corneous brown without spots or bands in *O. bicostulatum*. In *O. nouleti* the ribs are not serrated, the aperture is smaller and the mouth-edge is less broadly reflected. Both species have clearly different ranges.

Pomatias arriensis De Saint-Simon, 1867, is described as more strongly angled below the periphery, nearly forming a carina. The ribs are less prominent. This taxon is reported from the Montagne d'Arri near Marignac, Cierp and the surroundings of Boussens, all in the department of Haute-Garonne (Saint-Simon, 1867, cited in Germain, 1931: 578). Germain considers *O. arriensis* a variety (forma) of *O. nouleti*. I saw only few specimens of *O. nouleti* from this area (see section Material) but the angle below the periphery is not very strong and the ribs are as prominent as in other areas. Therefore I see no reason to distinguish a separate entity.

Obscurella (Obscurella) bicostulatum (Gofas, 1989)

Cochlostoma bicostulatum Gofas, 1989: 45-46, fig. 6-9. Locus typicus: Saldesuto, near Matienzo, Santander, Spain. Types (not seen): holotype, paratypes: MNHN; paratypes: MNCN, MZB, UPV.

Shell (figs. 1a, 7, 21, 22 and 39). — Relatively small, with 7-9 quite convex whorls and a deep suture. The ribs are straight, slightly serrated, rather sharp lamellae. The distance between the ribs is very variable and in between the ribs there may be up to four weaker riblets. There may be a slight incision in the ribs, at about half a mm below the suture, all together forming a characteristic line. The aperture is roundish with a thick, reflected peristome.

Height: 7.0-12.9 mm; width: 3.9-5.1 mm.

The shell is corneous brown, often with a green tint. The lamellar ribs are slightly lighter in colour. The peristome is whitish, the inside of the aperture is pale to dark brown. Only in few populations, amongst others those collected near the Ventalaperra cave in the province of Vizcaya and at Levinco and Desfiladero de las Xanas in Asturias, just behind the aperture, a row of faint pale and dark spots occurs below the suture, as well as a pale band near the base of the whorls with dark spots above and below it.

Animal (fig. 4d). — Moderately to dark grey, in some specimens with a dark line above the sole. The proboscis and tentacles are darker, although the tips of the tentacles may be lighter grey. Near the base of the tentacles (about 1/10 to 1/5 of the tentacle length above it) there is a light ring. A sharp line between the tentacles divides the light grey lower part of the head and the upper part which is darker grey with a light coloured area in the middle. The sole is white.

Genitalia (fig. 2a, b). — The pale grey to whitish penis is 5-7 mm long or only 2-4 mm (micropenis) and is 1 mm thick with rather widely spaced constrictions.

Radula (fig. 5b, d, h). — The radula is long (about 7-8 mm). The teeth all have an acute tip, the central teeth are slender (0.13-0.21 mm), the lateral teeth are slightly broader (0.21-0.24 mm) and the marginal teeth (M1) are the broadest (0.24-0.27 mm).

Ecology. — The species prefers rather humid, shaded, overgrown limestone rocks on which it occurs together with *O. hidalgoi*. Whereas *O. bicostulatum* is most abundant on the vegetated rocks, *O. hidalgoi* prefers the bare parts. Some animals were found very close to the sea, even on rocks protruding above the sea. Although *O. bicostulatum* does not live high in the mountains, in deep river valleys it may geographically approach the water divide of the Cantabrian mountains. This suggests that the species prefers areas with a temperate climate, a high humidity and few days of frost. At various localities the species occurs sympatric with *O. hidalgoi, O. asturicum, O. oscitans* or *O. obscurum*.

Distribution (figs. 27, 52a). — The species is restricted to the northern slope of the Cantabrian mountains (Spain), where it has been found between 10 and 700 m altitude.

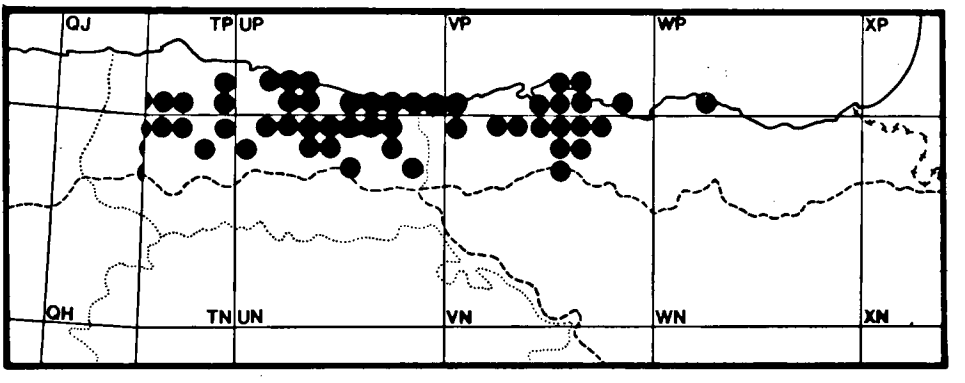


Fig. 27. Records of *Obscurella (O.) bicostulatum* (Goías, 1989), indicated on UTM 10 km square maps; for further explanation see fig. 18).

Material. — SPAIN, ASTURIAS: 1.5 km NNW. of Páramo, QH4077 (R); Desfiladero de Peñas Juntas, QJ4191 (R); E. of Caranga de Arriba, QH4187 (R); N. of Tuñon, TN5798 (R); Desfiladero de las Xanas, N. of Villanueva, TN5796 (R); 2.5 km W. of Argame, TN6397 (R); 3 km NNW. of Trubia, TP6806 (R); Palomar, TN6399 (R); Peña Avis, E. of Caldas de Oviedo, TN6399/TP6300 (R); SE. side of Monte Naranco, Oviedo, TP6807 (R); Santa Eulalia de Morcin, TN6595 (R); Parteayer, 1 km NE. of Santa Eulalia de Morcin, TN6796 (R); SE. of La Roza, TN6595 (R); El Collado, Monsacro, TN6694 (R); Olloniego, TN7198 (R); Pico Arnea, 1 km W. of Manzaneda, TN6999/7099 (R); 1 km E. of Tudela-Veguin, TP7501 (R); 3 km N. of San Román, TP9711 (R); Levinco, TN8980/8881 (R); E. of Muñera, TN9690 (R); E. of Condado, TN9890 (R); E. of Rioseco, UN0189 (R); 0.5 km N. of Buspriz, UN0683 (R); 2 km W. of Campo de Caso, UN0884 (R); S. of Las Cuevas, UN0691 (R); Fuensanta, E. of Nava, TP9802 (R); N. of Loroñe, Reserva de Sueve, UP1816 (N); 2 km S. of Caravia, 10 km W. of Ribadesella, UP2213 (R); La Torre, 5 km W. of Ribadesella, UP2715 (R); Corao, UP3201 (B, M, RMNH56153/alc.9238); Ribadesella, UP3214 (Me, UPV); near Frias, 4 km SSW. of Ribadesella, UP3210 (W); Santillán, UN2693 (Me); near Central de Dobrá between Precendí and Cien, UN2990/3089 (Me, R); Beyos,

Desfiladero de los Beyos, UN3085/7 (Me, R); Covadonga, UN3396 (N, R); 1 km SE. of Covadonga, UN39 (W); 4.5 km SE. of Covadonga, UN3596 (N, UPV); 2.1 km W. of Mirador de la Reina, SE. of Covadonga, UN3597 (Ri); Mirador de la Reina, UN3895 (N); Lago Enol, UN3793 (B, N, R, Ri, RMNH56155, UPV); Lago de la Ercina, UN3992 (R, Ri, W); near spring Tremar de Canal, 3 km SSE. of Lago de la Ercina, UN49 (W); Vega de Ario, some 6 km SSE. of Lago de la Ercina, UN49 (N); Ortiguero, UN4598 (N); Cueva El Covaron, La Pereda, UP5607 (W); near entrance of Cueva La Boriza, 1 km E. of El Mazuco, UP5004 (W); Arenas de Cabrales, UN 5295 (N, RMNH56143); 2.7 km S. of Arenas de Cabrales, UN5294 (Ri); Puente Poncebos, S. of Arenas de Cabrales, UN59 (RMNH56150); 3 km W. of Tielve, UN5391 (R); near Tielve, UN5691/2 (UPV, W); Llanes, UP5708 (RMNH56147); 2 km E. of San Roque, UP6106 (UPV); Mier, UN6497 (N); Purón, UP6501 (A); N. of Pendueles, UP6706 (R); 5 km SSW. of Panes, UN6894 (R); Estragüeña, 7 km SW. of Panes, UN6994 (M, N, R, RMNH56146, V); along road to Tresviso, UN6691 (W); Robriguero, 4 km SW. of Panes, UN6997 (M, RGM227091); Puentelles, 3.5 km SSW. of Panes, UN7095 (E, Me, N, R); La Franca, UP72505 (R, UPV); El Mazo, 5 km E. of Panes, UN7498 (E, Me, N, R, RMNH56142, V); Buelles, UN7599 (E, Me); 3 km NW. of Unquera, UP7506 (R). LEON: Desfiladero de los Beyos, UN3180 (Ri); between Cordiñanes and Cain, UN4583/5 (R). SANTANDER: Fuente Dé, UN5278 (N); SE. of La Hermida, UN69 (Ri); 1.5 km NW. of La Hermida, UN6891 (R); 1.5 km N. of Lebeña, UN7187 (R); between Puentenansa and Pesués, UP7900 (V); Pechón, UP7905 (RMNH56145); 2 km E. of Pesués, UP8103 (R); La Lastra, 2 km N. of Pantano de la Cohilla, UN8878 (V); near entrance of the Cueva de Tijeras, SE. of Hacer, UP90 (W); 2 km E. of Revilla, UP9004 (N); Comillas, UP9504 (B, M, N, RMNH56152/alc.9236, RGM227094); Canales, 2 km N. of Cabezón, UP9700 (M, RGM227093); between Cobreces and Sierra, W. of Santillana del Mar, VP004 (R); 10 km E. of San Vicente de la Barquera, VP0100 (E, Me); between Golbardo and Barcenaciones, VN0699 (W); Novales, 8 km W. of Santillana del Mar, VP0403 (B, Me, R, RMNH56162); Caranceja, VN0599 (E, Me); E. of Orena, VP0805 (N); near Cueva de Altamira, S. of Santillana del Mar, VP0903 (N); near Cueva El Castillo, Puente Viesgo, VN2194 (Me); between Hoz de Anero and Praves, VP40 (Me); W. of Anero, VP40 (N); 5 km E. of Santander, along the river Miera, VP40 (M); La Encina, VN5189 (W); 2 km N. of Puerto de las Alisas, 5 km NW. of Arredondon, VN49 (W); Arredondo, VN5189 (W); 3 km S. of Arredondo, VN5088 (Ri); 3 km NW. of Portilla de la Sia, VN5280 (Me, R); Nacimiento del Gándara, VN5282/5382 (R, RMNH56149, W); Cascadas del Asón, VN5283/4 (R); near Cueva del Patatal, Matienzo, VN5196 (W); 2 km W. of Beranga, some 5 km W. of Laredo, VP5106 (Me); Isla, VP5315 (E, Me); between Isla and Noja, VP5514 (E, Me); between Castillo and Noja, VP5613 (R, V); Noja, VP5814 (M); near Cueva la Coventosa, Asón, VN58 (W); Portilla de la Sia, VN5378 (E); Argoños near Santoña, VP6010 (M); Santoña, VP6310/6312/6412 (M, Ri); Castro Urdiales, VP8104 (B, E, Me, R, RMNH56151, UPV); Ontón, E. of Castro Uridales, VP8601 (M); Mioño, VP8401 (Mi, R); Ramales de la Victoria, VN6289 (N, Ri, RMNH56146); S. of Ramales de la Victoria, VN6682 (W); between La Pesquera and Laredo, VP6406 (E, Me). VIZCAYA: Peña Ranero, VN6991 (UPV); Cueva de Ventalaperra, SE. of Gibaja, VN6998 (R, RMNH56163; UPV); Trucios, VN7990 (UPV); Ibarranguelua, WP2705 (UPV).

Gofas (1989) mentions the following localities: SPAIN, SANTANDER: Seldesuto, near Matienzo, VN495953 (MNCN, MNHN, MZB, UPV); Oriñon/Iseca; Suances, VP10; VIZCAYA: Peñas de Ranero, VN69; Ispazter; ASTURIAS: Desfiladero de los Beyos, UN38 (MZB).

Remarks. — A sinistral specimen was collected by J.C.A. Eikenboom at Puentelles, 3.5 km SSW. of Panes, Asturias, Spain, UTM UN7095 (E, fig. 39).

In the collection of the late C. Altimira (in RMNH) there are some samples of this species labelled '*Cochlostoma azpeitianum* Ortiz de Zárate', which implies that Ortiz recognized the material as representing a separate species, although he never published a description. A sample from Lago Enol, Asturias, Spain, consists entirely of specimens of *O. bicostulatum*. On the other hand, a sample from Covadonga, Asturias, Spain, collected and identified by Ortiz, consists of another species, described herein as *O. asturicum*. A sample from Arenas de Cabrales, Asturias, contains *O. bicostulatum*, but most specimens are *O. hidalgoi*.

Subgenus **Cantabrica** subgen. nov.

Type species: *Pomatias hidalgoi* Crosse, 1864.

Diagnosis. — The shell has rather flat to slightly convex whorls, separated by a shallow suture. The peristome is strongly reflected, without a flexure. The shell is greyish-brown and has a white peristome.

Ecology. — The species of this subgenus prefer unshaded, bare rock (they were never found on trees).

Discussion. — Bofill (1890) already distinguished a 'Hidalgoi' group within the genus *Pomatias* for all the "species" which in the present publication are included in the two subspecies of *O. (C.) hidalgoi* (Crosse, 1864). The newly described taxa *O. (C.) oscitans* (Gofas, 1989) and *O. (C.) asturica* spec. nov. clearly belong to this same group. The subgenus is named after the Cantabrian mountains in which all species occur.

Obscurella (Cantabrica) hidalgoi (Crosse, 1864)

Shell (figs. 1f, 8, 28-30, 32-37, 40-43). — The shell is medium-sized to large, with 7-9 rather flat whorls and a shallow suture, mostly with an angle below the periphery. The ribs are generally rather far apart, 5-7 ribs/mm. The aperture is large, surrounded by a broad, reflected peristome. The shell colour varies from bluish grey or grey to brown, with a white peristome.

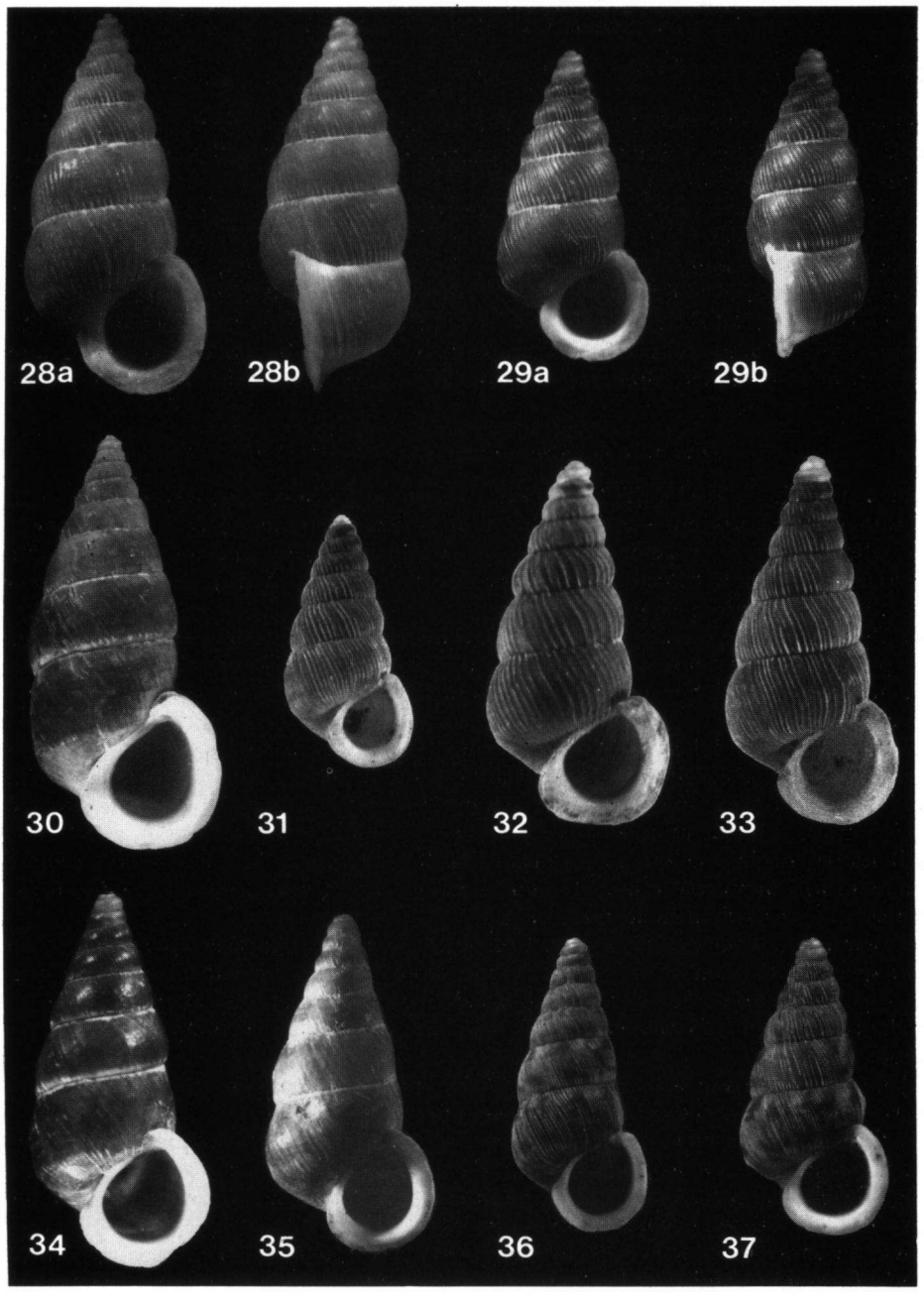
In this species the shell is very variable, some characters are well-developed in certain populations and not in others, but the extremes are always connected through intermediate forms. The variation within and between populations may concern various characters.

1) Size (H: 8.5-15.1 mm, W: 4.2-6.8 mm). Some populations consist entirely of large specimens (e.g. Mirador de la Reina, Asturias: H, 12.5-15.1 mm; W, 5.7-6.8 mm [fig. 30]) or small specimens (e.g. Bellmunt/Vidrá, Gerona: H, 9.1-11.0 mm; W: 4.5-5.5 mm), whereas in other populations the size is very variable (e.g. near Cueva del Bollo, W. of Campo de Caso, Asturias: H, 8.9-12.5 mm; W, 4.5-5.7 mm). Female specimens are larger and relatively more slender, with a larger aperture and a higher number of whorls than male specimens.

2) Number and shape of the ribs. Generally the ribs are further apart than in the other species, 5 ribs/mm (e.g. fig. 32), but populations occur with up to 7/mm (fig. 37). Also nearly to completely smooth specimens occur (figs. 30, 34, 35). If ribs are developed, they vary from very fine riblets to lamellar ribs. The embryonic whorls are smooth.

3) Convexity of the whorls. As a rule the smaller specimens have rather convex whorls whereas larger specimens may have very flat whorls.

4) Colour of the shell. The colour varies with the strength of the ribs: smooth specimens have a dark brown colour and those with prominent ribs are grey or bluish grey. The shell may have a uniform colour (figs. 28, 29) or a pattern of darker bands (figs. 36, 37). The embryonic whorls are yellow. The inside of the shell is generally brown, in some specimens with a light band, corresponding with the angle in the whorl. This light band may be visible on the outside of the whorl. The peristome is white. Male specimens are darker, in particular the upper part of the teleoconch which is dark brown with dark blue or violet.


28a
28b
29a
29b
30
31
32
33
34
35
36
37

5) Angle below the periphery. Generally there is a well-developed angle (fig. 34), but sometimes the whorl is smoothly curved (fig. 35).

Animal (fig. 4e). — The animal is light to dark grey. There is a dark line between the tentacles and the proboscis. The tentacles are dark grey, becoming darker near the base, with a broad, lighter coloured ring just above the base (at about 1/5-1/4 of the tentacle length). The sole is white, in some specimens becoming darker near the edge.

Genitalia (fig. 2f, g). — I found the penis generally long (3.5-8.3 mm), with rather widely spaced constrictions. The upper side is grey and the lower side is yellowish white. Micropenises have not (yet) been found in this species. A description of the female reproductive organ is given in Giusti (1971: fig. 6).

Radula (fig. 5c, f; Giusti, 1971: pl. 69 figs. 1-2). — The radula is long (6.5-11 mm). All teeth have a rounded tip. The teeth of the central row are rather narrow (0.18 mm), the lateral and marginal (M1) teeth are broader (0.24-0.30 mm) and asymmetrical.

Ecology. — This species prefers bare, shaded or unshaded limestone rock. It may also occur under limestone blocks or near or between vegetation on the rocks. At various localities the species occurs sympatric with *O. obscurum, O. bicostulatum, O. oscitans* and *O. asturicum.*

Remarks. — Due to the variability of this species, a large number of names was proposed, mainly for local forms from the Pyrenees. Even four different names were proposed for specimens from Montserrat in the province of Barcelona. Large collections demonstrate that all names concern only one species, because intermediate forms connect the various described extremes. Wagner (1897) and Haas (1929) also regarded most nominal taxa from the southeastern Pyrenees as synonyms, but they included all in *O. obscurum* as subspecies *esseranum.*

Some combinations of shell characters of *O. hidalgoi* are geographically limited, therefore two subspecies can be distinguished, viz. *O. hidalgoi hidalgoi* and *O. hidalgoi martorelli.* The ranges of these subspecies are separated by a 100 km broad zone where *O. hidalgoi* has not (yet) been found (fig. 44).

In the Congost d'Organyá in the Segre valley, province of Lérida, Spain, animals occur which have large and dark brown shells with smooth, flat whorls, described as

Figs. 28-37. Shells of *Obscurella (Cantabrica) hidalgoi* (Crosse, 1864) and *O. (O.) obscurum* (Draparnaud, 1805). 28-30, 32, *O. (C.) hidalgoi hidalgoi* (Crosse, 1864); 28, 29, Desfiladero de la Paraya-Llananzanes (Asturias) Spain, TN9071 (J.G.M. Raven leg., RMNH); 28, female, H. 13.0 mm; 29, male, H. 10.5 mm; 30, forma *alopioides* Fagot, 1905, 2.1 km W. of Mirador de la Reina, SE. of Covadonga, UN3597 (Th.E.J. Ripken leg., R), H. 14.8 mm; 31, Paso de Dos Hermanas near Irurzún (Navarra) Spain, WN9554 (J.G.M. Raven leg., R), H. 12.3 mm; 33-37, *O. (C.) hidalgoi martorelli* (Bourguignat in Servain, 1880); 33, male specimen from western part of areal, showing transition towards the nominate subspecies (compare Figure 32), note the virtual absence of a colour pattern, 1.2 km E. of Merli (Huesca) Spain, BG9490 (J.G.M. Raven leg., R), H. 10.8 mm; 34, 35, forma *alopioides* Fagot, 1905, Congost d'Organyá (Lérida) Spain, CG67; 34, topotype (J.J. Vermeulen leg., R), H. 13.3 mm; 35, syntype, note the absence of the protrusion in the peristome and the angle below the periphery (P. Fagot leg. (?), SMF 3935/2), H. 14.4 mm; 36, 37, topotypes, 0.5 km E. of the church of Montserrat (Barcelona) Spain, DG0305 (J.G.M. Raven leg., R); 36, female, H. 12.8 mm; 37, male, H. 10.3 mm; 31, *O. (O.) obscurum* (Draparnaud, 1805), typical form for the western Pyrenees and eastern Cantabrian mountains in Spain, male, Arrayóz (Navarra) Spain, XN1577 (J.G.M. Raven leg., R), H. 8.7 mm. Enlargement approximately 4.0 x.

P. alopioides Fagot, 1905 (figs. 34, 35). In some parts of the cleft they occur fully mixed with animals with ribbed shells, whereas in other parts populations consist entirely of either the smooth or the ribbed form. Nowhere else in the Pyrenees comparable specimens have been found. In the Cantabrian mountains, on the other hand, populations consisting entirely of such specimens were found amongst others at Ramales de la Victoria and Nacimiento del Gándara in Santander and at Lago Enol, Mirador de la Reina (fig. 30) and Páramo in Asturias. The only difference between the populations from the Cantabrian mountains and those from Organyá is that the former never have the protrusion (see fig. 9b) in the columellar part of the peristome, which is typical for *O. hidalgoi martorelli*. Most specimens from Organyá have this protrusion (fig. 34). I consider the taxon as the forma *alopioides* which occurs in both subspecies of *O. hidalgoi*.

Obscurella (Cantabrica) hidalgoi hidalgoi (Crosse, 1864)

Pomatias hidalgoi Crosse, 1864: 24, pl. 2 fig. 3. Locus typicus: Igurinao and Pico de Altamira, Peña de Gorbea, Vizcaya, Spain. Paratypes: SMF 160069/4; holotype and paratypes (not seen): MNHN; paratypes (not seen): MHNG.

Pomatias hispanicus Bourguignat in De Saint-Simon, 1869: 6-7. Locus typicus: near Oviedo, Asturias, Spain Topotypes: SMF 160083/2, R; paratypes (not seen): MHNG.

Shell (figs. 1f, 28-30, 32, 40-43); Wagner, 1897: pl. 4 figs. 35-39). — The nominate subspecies is characterized by a thick, reflected peristome without a protrusion in the columellar part (compare with fig. 8). Most specimens have broadly spaced ribs and lack a pattern of darker coloured bands.

Distribution (figs. 44, 52b). — The subspecies is widely distributed in northwestern Spain. It is extremely common in the western Cantabrian mountains, occurring nearly everywhere where limestone rock is exposed. In the eastern Cantabrian mountains only some of the limestones are apparently hard enough to be a good substratum for *Obscurella*, therefore the populations are wider apart. A single specimen from the easternmost locality (Belagua, Navarra), from the only population in the Pyrenees, shows all the characters of the nominate subspecies although it was collected about 80 km from the nearest known other population.

In the northern part of the Cantabrian mountains the subspecies was found to be sympatric with other species. The ranges of *O. asturicum* and *O. oscitans* are entirely within that of *O. h. hidalgoi*. All three species prefer bare limestone rock and therefore *O. h. hidalgoi* occurs locally together, in the same habitat, with one of the other species. At many more localities the subspecies occurs with *O. bicostulatum* or *O. obscurum*, but these species prefer shaded, humid parts with vegetation, also occurring below limestone blocks. Locally the subspecies occurs completely mixed with several of these species.

O. h. hidalgoi was found from sea-level up to 2000 m altitude. It is less common near the sea.

Material. — SPAIN, ASTURIAS: 1.5 km S. of Valle de Lago, QH2771 (R); 3 km N. of Pola de Somiedo, QH2377 (R); Agüera, QH2288 (R); 1 km E. of Grullos, 5 km N. of Grado, QJ3813 (R); near entrance of Cueva de Huertas, Fresnedo, QH3979 (W); 1.5 km NNW. of Páramo, QH4077 (R); 3 km NNE. of La Plaza de Teverga, QH3784 (R); near Lago Cueva, 13 km SE. of Pola de Somiedo, QH3670

(R); 500 m S. of Santiago la Barca, QJ3107 (R); Desfiladero de Peñas Juntas, QJ4191 (R); E. of Caranga de Arriba, QH4187 (R); N. of Tuñon, TN5798 (R); Desfiladero de las Xanas, N. of Villanueva, TN5796 (R); El Torno, 9 km SW. of Grado, QJ3102 (R); N. of Coallajú, 5 km SSE, of Grado, QJ3903 (R); Palomar, TN6399 (R); Peña Avís, E. of Caldas de Oviedo, TN6399/TP6300 (R); SE. side of Monte Naranco, Oviedo, TP6807 (R); Parteayer, 1 km NE. of Santa Eulalia de Morcín, TN6796 (R); SE. of La Roza, TN6595 (R); El Collado, Monsacro, TN6694 (R); 0.8 km W. of Riospaso, TN6567 (R); Puerto de la Cubilla, TN6363 (R); Puerto del Aramo, 2 km WNW. of Armada, TN6684 (R); Villar, 2 km NW. of Pajares, TN76 (Me); Pico Arnea, 1 km W. of Manzaneda, TN6999/7099 (R); 1 km E. of Tudela-Veguín, TP7501 (R); N. of San Antonio de la Foz, TN6693 (R); Villar, 2 km N. of Pajares, TN76 (Me); Levinco, TN8980/8881 (R); Entrepeñas, TN9080 (R); Viobes, N. of Nava, TP9607 (R); E. of Muñera, TN9690 (R); E. of Condado, TN9890 (R); E. of Rioseco, UN0189 (R); 0.5 km N. of Buspriz, UN0683 (R); 2 km W. of Campo de Caso, UN0884 (R); 2 km NW. of Soto de Caso, UN1282 (R); La Colladona, TN8784 (R); Desfiladero de la Paraya/Llananzanes, TN9071 (R); 4 km W. of Puerto de San Isidro, UN0271 (R); N. of Collado de Arnicio, UN0790 (R); N. of Loroñe, Reserva de Sueve, UP1816 (N); 2.4 km S. of Amandi, UP0213 (N); 2 km S. of Caravia, 10 km W. of Ribadesella, UP2213 (R); La Torre, 5 km W. of Ribadesella, UP2715 (R); Corao, UP3201 (B, RMNH); Ribadesella, UP3214 (Me, R, UPV); near Frias, 4 km SSW. of Ribadesella, UP3210 (W); Balneario de Mestas, NW. of Beleño, UN2286 (R); Santillàn, UN2693 (Me); Tornin, S. of Cangas de Onís, UN2798 (Me); near Central de Dobrá between Precendí and Cien, UN2990-3089 (Me, N, R); Desfiladero de los Beyos, UN3085-3087 (Me, R, Ri, RMNH); Desfiladero de los Beyos, UN2693 (Ri); 0.5 km E. of Arriondas, UP2307 (R); Covadonga, UN3396 (N, R, Ri, RMNH); Vega la Piedra, Covadonga, UN39 (UPV); 5 km SE. of Covadonga, UN39 (UPV); 2.1 km W. of Mirador de la Reina, SE. of Covadonga, UN3597 (R, Ri); Lago Enol, 7 km SE. of Covadonga, UN3793 (B, M, R, RMNH, UPV); Lago de la Ercina, 8 km SE. of Covadonga, UN3992 (N, R, Ri, UPV, W); near spring Tremar del Canal, 3 km SSE. of Lago de la Ercina, UN49 (W); NE of Puerto del Ponton, UN3674 (Me); Ortiguero, UN4598 (N); Desfiladero del Cares, UN48-49 (UPV); Arenas de Cabrales, UN5295 (N); S. of Arenas de Cabrales, UN5194-5293 (R, Ri); Puente Poncebos, S. of Arenas de Cabrales, UN59 (RMNH); 3 km W. of Tielve, UN5391 (R); Bulnes, UN5288 (A); Mier, UN6497 (N); 5 km SSW. of Panes, UN6894 (R); Estragüeña, 7 km SW. of Panes, UN6994 (M, N, R, RMNH, V); along road to Tresviso, UN6691 (W); Robriguero, 4 km SW. of Panes, UN6997 (M, RGM 227.090); Puentelles, 3.5 km SSW. of Panes, UN7095 (E, Me, N, R); between Unquera and Panes, UN79 (N); El Mazo, 5 km E. of Panes, UN7498 (N); Buelles, UN7599 (Me); S. of Unquera, UN7599 (R). SANTANDER: Mirador del Cable, N. of Fuente Dé, UN5379 (R); Fuente Dé, UN5278 (N); W. of Cosgaya, UN5974 (E, Me, N, R); 3 km SW. of Camaleño, UN6076 (N); 1 km NW. of Cillorigo-Castro, UN7184 (N, R); Lebeña, UN7185 (RMNH); 1.5 km N. of Lebeña, UN7187 (R); 3.5 km SSE. of La Hermida, UN7288 (Ri); La Hermida, UN6990/1 (M, N, R, Ri); Pechón, UP7905 (RMNH); La Lastra, 2 km N. of Pantano de la Cohilla, UN8878 (V); 2 km S. of Celis, UN8493 (V); Canales, 2 km N. of Cabezon, UP9700 (M, RGM227.092); W. of Abanillas, UP7900 (V); Caranceja, W. of Torrelavega, VN0599 (E, Me); between Golbardo and Barcenaciones, VN0699 (W); Puente Viesgo, VN2194 (M, N); 1 km S. of Mirones, VN4393 (Me); Puerto de las Alisas, VN4894 (M, N, R, Ri); 2 km N. of Puerto de las Alisas, VN49 (W); Arredondo, VN5189 (W); near Cueva la Coventosa, Asón, VN5 (W); 3 km S. of Arredondo, VN5088 (Ri); S. of Asón, VN5186 (Ri, RMNH); Cascadas del Asón, VN5283/4 (R, RMNH); Nacimiento del Gándara, VN5282 (R, Ri, RMNH); 3 km NW. of Portilla de la Sia, VN5180 (Me, R); Portilla de la Sia, VN5378 (E); near Cueva del Patatal, Matienzo, VN5196 (W); Ramales de la Victoria, VN6289 (Me, N, Ri); S. of Ramales de la Victoria, VN6682 (W); Mioño, VP8301 (M); Ontón, VP8601 (M). VIZCAYA: Cueva de Ventalaperra, SE. of Gibaja, VN6889 (UPV); Peña Ranero, VN6991 (UPV); Peña Gorbea, WN16 (RMNH); Arreba, Peña Gorbea, WN1666 (UPV); below the Atxas, Peña Gorbea, WN1569 (UPV); Cueva de Otxas, Urkizu, WN1981 (UPV); Atxuri, Peña Gorbea, WN2065 (UPV); Rio Padrobaso, Peña Gorbea, WN2164 (UPV); Untzillaitz, Durango, WN2975 (UPV); just S. of Durango, WN2978 (Me); Cueva Ezkutua, SW. side of Anboto, WN3270 (UPV). LEON: Puente Angoyo, Desfiladero de los Beyos, UN3180 (M, N, R, Ri, RMNH); Ribota, UN3378 (Me); Oseja de Sajambre, UN3380 (R); between Cordiñanes and Cain, UN4583/5 (R); Lumajo, 7 km NE. of Villablino, QH2362/3-QH2462/3 (R); Caldas de Luna, TN6558 (R); 2 km NNE. of Barrios de Luna, TN6749 (R); Geras, TN7451/5 (R); Piedrasecha, TN7245 (R); Los Barrios de Gordón, TN7848 (R); Beberino, TN8150 (R); Los Llanos, E. of Pola de Gor-

dón, TN8248 (R); 0.5 km NE. of Pendilla, TN8068 (R); 1.2 km N. of Piedrafita, TN8866 (R); Matallana estación, TN9457 (R); Las Hoces de Vegacervera, TN9254 (R, RMNH); Coladilla, TN9151 (RMNH); Nocedo de Curueño, UN0452 (R); 2.5 km SE. of Genicera, TN9856 (R); Las Hoces de Valdeteja, UN0455 (R); Puerto de Vegarada, TN9868 (R); E. of Embalse del Porma, 8 km N. of Boñar, UN1555 (M, R, RMNH); Pico Grande, 7 km N. of Boñar, UN1155/1255 (R); E. of Valdecastillo, UN1153 (R); San Adrián, UN1145 (R); S. of La Herrera, 2 km W. of Sabero, UN2243 (M, R, V); SE. of Sahelices de Sabero, UN2344 (R, RMNH); SE. of Alejico, UN2645 (M, R); 2 km NW. of Cistierna, UN2442 (M, R); E. of Cistierna, UN2641 (M, R); 2 km SSE. of Fuentes de Peñacorada, UN3043 (R); NW. of Robledo de Guzpeña, UN3342 (R); Santa Olaja de la Varga, UN2745/2846 (M, R); 1.5 km NE. of Oceja de la Peña, UN3049 (R); 1 km NE. of Aleje, UN2747/8 (M, R); Valdoré, UN2349 (M, R, RMNH); Pico Aguasalio, E. of Crémenes, UN2553 (R); 1 km N. of Crémenes, UN2553 (M, Me, R); 1 km SE. of Argovejo, UN2851 (M, R); 3 km ESE. of Argovejo, UN3051 (R); NE. of Sabero, UN3645 (R); S. of Remolina, UN3152 (RMNH); 1.3 km W. of Acevedo, UN2467 (R); 1.5 km WSW. of Maraña, UN2168 (R); 0.7 km W. of Pico Mampodre, UN2066 (R); Valle de Valdosin, 3 km NW. of La Uña, UN2472 (R); SE. of Riaño, UN3359 (N); N. of Portilla de la Reina, UN4969 (R); Cobarcil, UN3279 (N); N. of Puerto del Pontón, UN37 (N). PALENCIA: between Cardaño de Abajo and Cardaño de Arriba, UN5656 (R); Peña de Santa Lucia, W. of Santibañez de Resoba, UN6753 (V); between San Martin de los Herreros and Rebanal de las Llantas, UN65 (RMNH); 1 km SSW. of San Martin de los Herreros, UN6949 (R, RMNH); Pico de los Pilones, SW. of Cervera de Pisuerga, UN7445 (V); Arroyo de Tosande, 4 km SW. of Cervera de Pisuerga, UN7544 (V); Ruesga, UN7447 (V); 1 km S. of Piedrasluengas, UN8165 (V); between Piedrasluengas and Camasobres, UN86 (N). BURGOS: Hoz de Arreba, VN3753 (UPV); 1 km S. of cave near Cueva de Ojo Guareña, 11 km WSW. of Espinosa de los Monteneros, VN46 (W); Montes Machorras, VN5176 (UPV); Las Machorras, VN5273/4 (Me); Valdenoceda, VN5145 (UPV); Tartales de los Montes, VN6041 (UPV); Cereceda, VN6136 (R, UPV); between Villasante de Montija and Colina, VN6268 (UPV); La Horadada, VN6535 (UPV); Villabasil, VN7764 (UPV); El Portillo, San Zadornil, VN8774 (UPV). ALAVA: Sobrón, artificial lake, VN93 (UPV); Pico del Fraile, Txarlazo, Puerto de Orduña, VN9658 (UPV); 2 km N. of Puerto de Orduña, VN9856 (Me, R, Ri); Laguna de Arreo, WN0136 (UPV); Puerto de la Herrera, WN2616 (UPV); Peñacerrada, WN2419 (UPV); Santa Cruz de Campezo, WN5624 (R, UPV). LOGROÑO: Leiva, VN9605 (UPV). GUIPUZCOA: near Santuario de Aránzazu, 10 km S. of Oñate, WN4959 (Me); Ausa Gaztelu, Sierra de Aralar, WN7163 (UPV); Alto de Lizarrusti, 13 km SE. of Beasain, WN75 (W); E. of Urbia, Sierra de Aitzgorri, WN55 (W). NAVARRA: between Bernedo and Santa Cruz de Campezo, WN42 (W); Satrústegui, Beriain, WN8349 (UPV); Altxueta, Sierra de Aralar, WN8456 (UPV); San Miguel de Aralar, WN8554/5 (M, UPV); Peña de Echauri, WN9539 (UPV); Paso de Dos Hermanas, N. of Irurzún, WN9554 (M, N, R, Ri, RMNH); Belagua, XN7756 (UPV).

Remarks. — Sinistral specimens from: Lago Enol, 7 km SE. of Covadonga, Asturias, UN3793 (R, fig. 40), and Caranceja, W. of Torrelavega, Santander, VN0599 (Me, fig. 41).

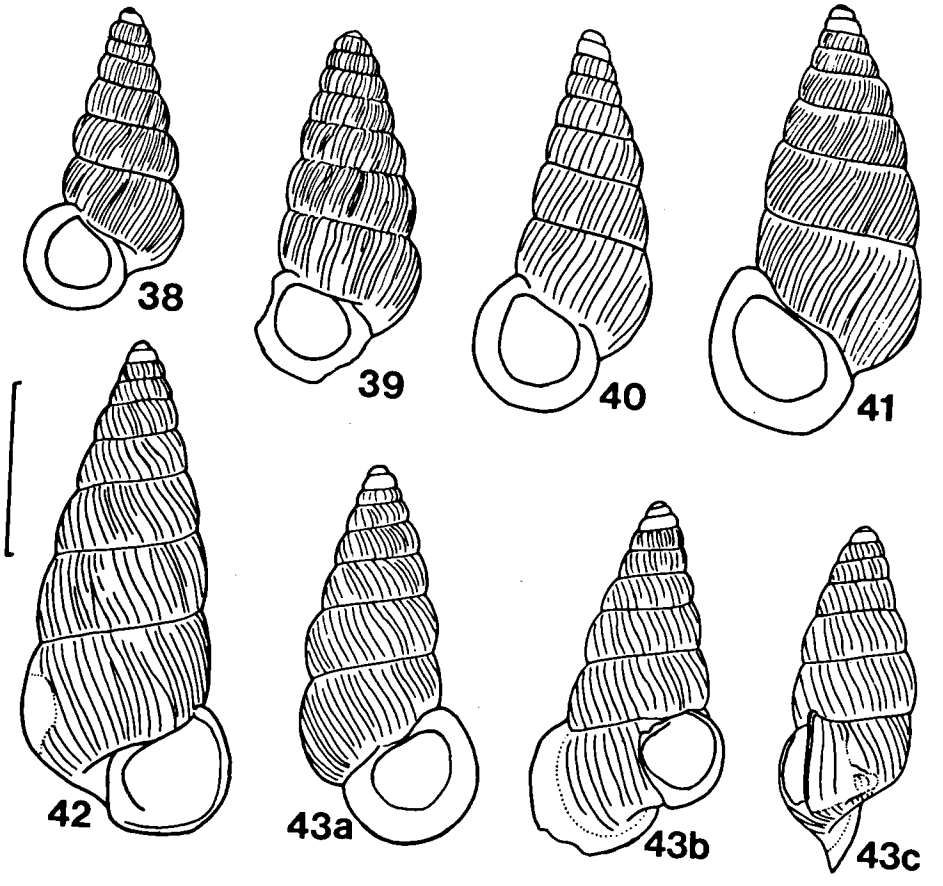
The specimens from the southern slopes of the Cantabrian mountains are generally corneous brown with regularly spaced, rounded ribs. In that area the variation is very limited. At the northern slopes of the mountains the variation is much greater, in that area the forma *alopioides* is common.

Obscurella (Cantabrica) hidalgoi martorelli (Bourguignat in Servain, 1880)

Pomatias martorelli Bourguignat in Servain, 1880: 144-145. Locus typicus: Montserrat, Barcelona, Spain Topotypes: M, N, R, RMNH, SMF 160025/1.

Pomatias lapurdensis var. *labrosa* Westerlund, 1883: 10. Locus typicus: Montserrat, Barcelona, Spain Topotypes: M, N, R, RMNH, SMF 160025/1.

Pomatias labrosus Westerlund, 1885: 117. Locus typicus: Montserrat, Barcelona, Spain. Topotypes: M, N, R, RMNH, SMF 160025/1.



Figs. 38-43. Some deformations in shells of *Obscurella* species. 38, *O. (O.) obscurum* (Draparnaud, 1805), sinistral, male, 1 km N. of Puerto de Usategueta (Navarra) Spain, WP9171 (H.P.M.G. Menkhorst leg., Me); 39, *O. (O.) bicostulatum* (Gofas, 1989), sinistral, female, along the N634, 100 m E. of sideroad to Roiz, 10 km E. of San Vicente de la Barquera (Santander) Spain, VP0100 (H.P.M.G. Menkhorst leg., Me); 40-43, *O. (C.) hidalgoi hidalgoi* (Crosse, 1864); 40, forma *alopioides* Fagot, 1905, sinistral, female, Lago Enol, 7 km SE. of Covadongo (Asturias) Spain, UN3793 (J.G.M. Raven leg., R); 41, sinistral, female, along the N634 near sideroad to Novales, 10 km W. of Torrelavega (Santander) Spain, VN0599 (H.P.M.G. Menkhorst leg., Me); 42, abnormally high shell, female, Cereceda (Burgos) Spain, VN6136 (UPV leg., R); 43, specimen with a second aperture formed after the shell was damaged, Paso de Dos Hermanas near Irurzún (Navarra) Spain, WN9554 (J.G.M. Raven leg., R). Scale 5 mm.

Pomatias bolosianum Salvaña, 1888: 118. Locus typicus: Olot region, Gerona, Spain. Syntypes: SMF 159931/3, SMF 3936/4

Pomatias esseranus, Fagot, 1888: 197: Locus typicus: Desfiladero de Campo, Huesca, Spain. Syntypes: SMF 3932/2.

Pomatias montsicci Fagot, 1888: 198. Nomen nudum.

Pomatias rudicosta Fagot, 1888: 198. Nomen nudum.

Pomatias noguerae Fagot, 1888: 198. Nomen nudum.
Pomatias rudicosta Bofill, 1890: 277. Locus typicus: Can Tinquilla de la Serra (= Ca'n Quinquilla de la Serra), Lérida, Spain. Syntypes: SMF 160000.
Pomatias montsiccianus Bofill, 1890: 277. Locus typicus: Montreveig between Pont de Montanyana and Portell del Montsech, Lérida, Spain. Syntypes: SMF 3939/12, SMF 3942/5, SMF 15999/8.
Pomatias montserraticus Fagot, 1891: 287-288. Locus typicus: Montserrat, Barcelona, Spain. Topotypes: M, N, R, RMNH, SMF 160025/1.
Pomatias mouganicus Fagot, 1891: 288. Locus typicus: Mouga farm at the boundary of Gerona, Spain and Pyrénées-Orientales, France.
Pomatias bofilli Fagot, 1891: 290. Locus typicus: Castellar-de-Nudi (= Castellar de Nuch), Barcelona, Spain Syntypes: SMF 3933/15, SMF 159932/6.
Pomatias noguerae Fagot, 1891: 290-291. Locus typicus: valley of the Noguera Pallaresa, Lérida, Spain Topotypes: RMNH.
Pomatias ripacurcicus Fagot, 1891: 291. Locus typicus: Escalas de Sopeira, Huesca-Lérida, Spain. Syntypes SMF 3934/6; topotypes: RMNH.
Pomatias alopioides Fagot, 1905: 143. Locus typicus: Congost d'Organyá, Lérida, Spain. Syntypes: SMF 3935/2; topotypes: M, N, R, RMNH, V, W.
Pomatias organiacus Fagot, 1905: 143. Locus typicus: between Coll de Nargó and Congost d'Organyá, Lérida, Spain. Syntypes: SMF 3937/2, SMF 159930/7; topotypes: RMNH.
Pomatias sanctilaurentii Bofill, 1917. Locus typicus: El Farell near Caldas de Montbui, Barcelona, Spain Nomen nudum.
Pomatias monserraticus var. *major* Bofill, 1971. Locus typicus: Montserrat, Barcelona, Spain and Montsech, Huesca, Spain. Nomen nudum.

Shell (figs. 8, 33-37; Bofill & Haas, 1920: pl. 2 figs. 32-42, pl. 3 figs. 1-2). — This subspecies is characterized by a protrusion (see fig. 9b) of a part of the columellar side of the lip (fig. 8). Most specimens have closely spaced, fine to coarse ribs and a colour pattern formed by three dark brown bands which may be interrupted: one below the suture and two near the base of the whorl (figs. 36, 37).

Distribution (figs. 44, 52b). — The subspecies is widely distributed in the SE. Pyrenees, occurring from close to the Mediterranean to high in the mountains, between about 200 and 1700 m altitude. It is remarkable that the subspecies is common in valleys and on mountains at the southern border of the Pyrenees (e.g. Montserrat) but is completely lacking in the central part of the Pyrenees. Probably the acid rocks of the axial zone obstruct a further extension towards the North. The subspecies was recorded from the surroundings of Vilanova de Prades, Sierra de la Llana, Tarragona, UTM CF28 by Vilella (1967) and from Chodos, Castellón, UTM BE35 by Gasull (1981). Although there is no doubt that these are valid records of the subspecies they are not included in the distribution maps because I received these data at a too late stage during the preparation of this paper. The subspecies was nowhere found together with other *Obscurella* species.

Material. — SPAIN, HUESCA: Desfiladero de Campo, BG89 (SMF); 1.5 km NW. of Merli, BG9192 (R); 0.6 km WNW. of Merli, BG9291 (M, R); 1.2 km E. of Merli, BG9490/1 (R); 0.5 km N. of Carrasquero, BG9688 (R). LERIDA: Escalas de Sopeira, CG18 (RMNH); Portell dels Terradets, N. of Embalse de Camarasa, CG15/25 (RMNH); N. tip of Embalse de Camarasa, CG25 (RMNH); 5 km S. of Senterrada, CG28 (RMNH); Desfiladero de Collegats, NE. of Pobla de Segur, CG38 (RMNH); 1 km N. of Gerri de la Sal, S. of Sort, CG4088 (V); S. of Castellnou de Basella, CG55 (N); weir of Embalse de Oliana, CG56 (N, R); Oliana, CG65 (RMNH); between Oliana and Coll de Nargó, CG56/57 (N, RMNH); between Coll de Nargó and Valldarques, CG56 (RMNH); 2 km NE. of Coll de Nargó, CG67 (N, RMNH); Congost d'Espluvins, between Oliana and Organyá, CG56/57/67 (RMNH); Congost d'Organyá, CG67 (M, N, R,

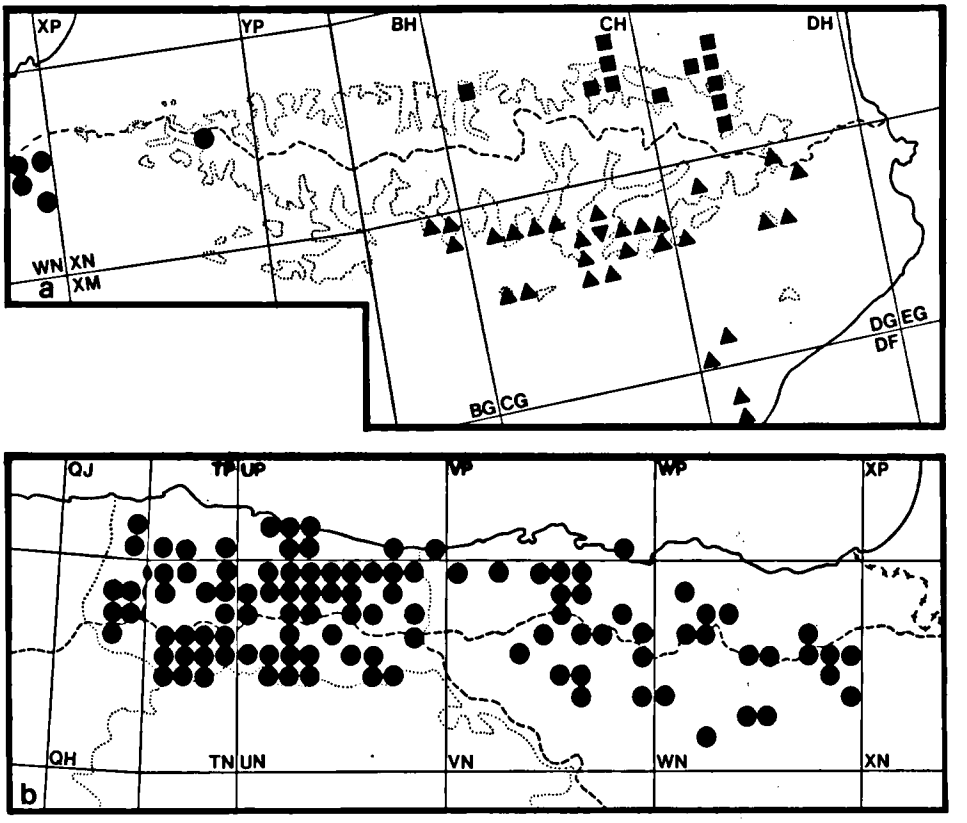


Fig. 44. Confirmed records of *Obscurella (O.) nouleti* (Dupuy, 1851) (squares), *O. (Cantabrica) h. hidalgoi* (Crosse, 1864) (circles) and *O. (C.) hidalgoi martorelli* (Bourguignat in Servain, 1880) (triangles, the triangle pointing down indicates forma *alopioides* Fagot, 1905), indicated on UTM 10 km square maps; for further explanation see figure 18.

RMNH, SMF, V, W); between Congost d'Organyá and Hostal Novi, CG67 (RMNH); between Hostal Novi and Montant, CG67 (RMNH); Montant, CG67 (RMNH); Odén, CG76 (RMNH); between Castella and Hostalets, CG68 (N, RMNH); between Hostalets and Tost, CG68 (N, RMNH); between Hostalets and Plá de Sant Tirs, CG68 (N); Saldes, Pedraforca, Sierra del Cadi, CG97 (RMNH); 0.3 km N. of Fornols, CG7779 (W); 1 km SE. of Fornols, CG7878 (W); 1.5 km NW. of Tuxent, CG8077 (W); 1 km S. of Tuxent, CG8175 (W); 3 km NE. of Tuxent, CG8478 (W); 1.8 km SW. of Josa del Cadi, CG8478 (W). BARCELONA: near hostal La Cantina, km 17 on road Berga/San Lorenzo de Morúnys, CG9363 (V); between Sot de l'Infern and Gavá, DF17 (RMNH); Plá d'Ardenya, between Villarana and Begas, DF18 (RMNH); Montserrat, DG00 (M, N, R, RMNH); Canal dels Monjes/Sant Llorens del Munt, DG11 (RMNH); Santuario de Guerali, Berga, DG06 (M); Le Nou de Bergueda, N. of Berga, DG06 (V); source of the river Llobregat, Castellar de Nuch, DG18 (SMF); Sant Llorens del Ribens (SMF). GERONA: between Bellmunt and Vidrá, DG46 (RMNH); Puig de Bassagoda, DG68 (SMF); Sant Privat de Bas, Olot, DG56 (SMF).

FRANCE, PYRENEES ORIENTALES: La Preste, DG59 (M, RMNH, W).

Remarks. — The shells from the westernmost localities (province of Huesca) are close to those of *O. h. hidalgoi* (compare fig. 33 with figs. 32 and 37). Specimens from the Segre valley, province of Lérida, with a smooth colour and widely spaced ribs were described as *P. organiacus* Fagot, 1905. These connect the forma *alopioides* (see above and figs. 34, 35) with other populations of *O. hidalgoi martorelli* which have the characteristic closely spaced ribs and the colour pattern with darker bands (figs. 36, 37). All these forms pass gradually into each other (for example see Bofill & Haas, 1920: pl. 2 figs. 32-42). Except for some specimens of the forma *alopioides*, which is apparently restricted to the surroundings of the Congost d'Organyá, all shells have the characteristic constriction in the peristome (fig. 8). There is no good explanation for the occurrence of specimens intermediate between *O. hidalgoi hidalgoi* and *O. hidalgoi martorelli* in the centre of the range of the latter. Maybe specimens from the Cantabrian mountains somehow have reached this location. This can have occurred through birds transporting eggs, or man transporting eggs or shells, for example with plants.

Obscurella (Cantabrica) asturicum spec. nov.

Diagnosis. — A species of *Cantabrica* with a dark body and a violet brown, slender shell with convex whorls and white, sharp, well-defined ribs.

Shell (figs. 1g, 45, 46). — Small, with 7-8 convex whorls, separated by a deep suture. Near the aperture the suture rises over about 1/3 of the penultimate whorl. The ribs are sharp lamellae, mostly with a tortuous crest.

Height 8.8-10.6 mm; width 4.2-4.9 mm.

The peristome is strongly reflected, broad and white, passing via yellow into reddish brown at the inside of the aperture. The shell is dark violet brown, the ribs give it a greyish bloom.

Animal (fig. 4f). — Dark grey with black tentacles which have a broad, lighter coloured ring near the base. Behind the tentacles there may be a small lighter coloured area on the body. The sole is yellowish to pale grey. The penis is white to pale grey.

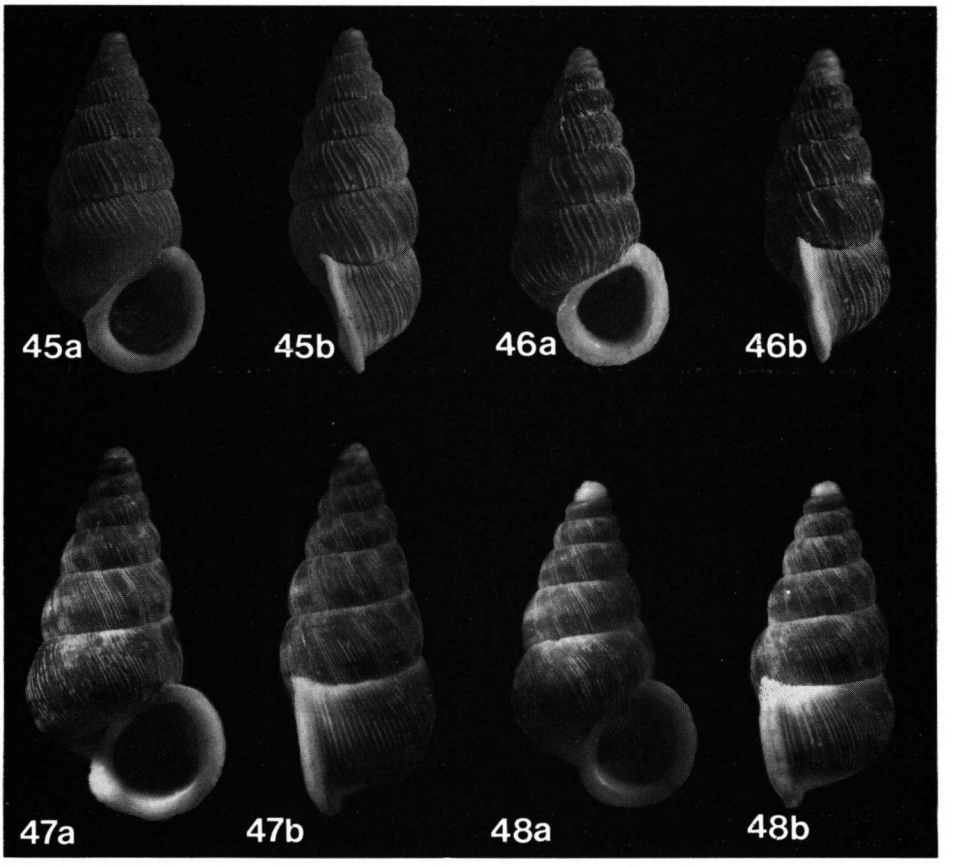
Genitalia (figs. 2h, 2i, 3). — The penis is short (2.6-5.5 mm, mean c. 4 mm) and broad, with closely spaced constrictions, which are not as close as in *O. oscitans*. The tip of the penis is smooth. Specimens with a micropenis are rather common, such a micropenis is 1.3-2.5 mm long (fig. 3).

Radula. — The radula is short (about 5 mm). The teeth of the central row are slender and rectangular, the lateral teeth are much broader and the marginal teeth are diamond shaped.

Ecology. — The animals live on limestone rock, on bare rock as well as below blocks. The species was found sympatric with *O. hidalgoi hidalgoi* and *O. bicostulatum*.

Distribution (figs. 49, 52b). — The species is restricted to a small area in eastern Asturias (on the north side of the western Cantabrian mountains): part of the Beyos valley and the area around and southeast of Covadonga, between 400 and 1500 m altitude.

Material. — Holotype: SPAIN, ASTURIAS, Lago de la Ercina, 8 km SE. of Covadonga, UN3992 (RMNH56141). Paratypes. SPAIN, ASTURIAS: Lago de la Ercina, 8 km SE. of Covadonga, UN3992 (N, R, RMNH56140, Ri); Lago Enol, 7 km SE. of Covadonga, UN3793 (N, R, Ri, RMNH56138, UPV); Vega de Ario, 6 km SE. of Lago de la Ercina, UN49 (W); Vega la Piedra, near Covadonga, UN39 (UPV); 1 km SE. of Covadonga, UN39 (W); Covadonga, UN3396 (N, R, Ri, RMNH56136); Beyos, Desfiladero



Figs. 45-48. 45-46, shells of *Obscurella (Cantabrica) asturicum* spec. nov., Lago de la Ercina, 8 km SE. of Covadonga (Asturias) Spain, UN3992 (J.G.M. Raven leg., RMNH); 45, paratype, female (RMNH56140), H. 10.2 mm; 46, holotype, male (RMNH56141), 9.6 mm; 47-48, shells of *O. (C.) oscitans* (Gofas, 1989), Cascadas del Asón (Santander) Spain, VN5283-52484 (J.G.M. Raven leg., RMNH); 47, female, 10.7 mm; 48, male, H. 9.5 mm. Enlargement approximately 4.5 x.

de los Beyos, UN3087 (Me); 1 km SSE. of Beyos, UN3085 (Ri, RMNH56139). ASTURIAS/LEON: Puente Angoyo, Desfiladero de los Beyos, at both sides of the province boundary, UN3180 (A, M, R, Ri, RMNH56137/alc.9117).

Remarks. — Derivatio nominis: The species is called after the Spanish Principality of Asturias.

Where the species occurs together with *O. hidalgoi hidalgoi* forma *alopioides*, which has large shells with unribbed, flat whorls (fig. 30, e.g. at Lago Enol in Asturias), it is easy to distinguish both species. Where it is sympatric with the smaller, ribbed form of *O. h. hidalgoi* (figs. 32, 43, e.g. at Covadonga and in the Desfiladero de los Beyos), it can

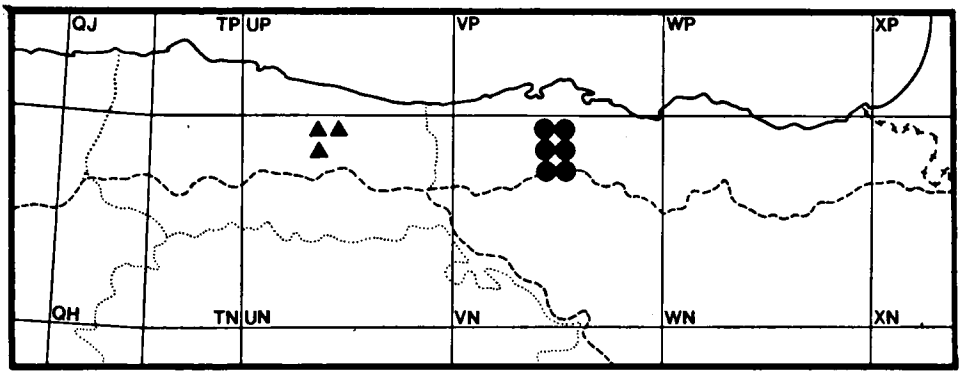


Fig. 49. Records of *Obscurella (Cantabrica) asturicum* spec. nov. (triangles) and *O. (C.) oscitans* (Gofas, 1989) (dots), indicated on UTM 10 km square maps; for further explanation see fig. 18.

be distinguished by its darker shell with convex whorls which have no angle below the periphery, by its narrower and rounder aperture with a broader peristome, by the closer, sharper ribs, the darker body colour of the animal and often by a shorter penis.

Obscurella (Cantabrica) oscitans (Gofas, 1989)

Cochlostoma oscitans Gofas, 1989: 46-47, figs. 13-15. Locus typicus: Seldesuto, near Matienzo, Santander, Spain. Types (not studied): holotype, paratypes: MNHN; paratypes: MNCN, MZB, UPV.

Shell (figs. 1d, 47, 48). — Relatively short and broad, with 6 1/2-8 comparatively flat whorls, separated by a deep suture. Due to the peristome, at the very end of the last whorl the suture rises to 1/4 or 1/3 of the height of the penultimate whorl. The aperture is large and rather round with a slightly reflected peristome. The first, embryonic, whorl is smooth or has small granulae. The second whorl has fine growth lines. The other whorls have numerous, very regular ribs which are narrowly spaced (6-10/mm).

Height 8.1-11.4 mm; width 4.8-5.5 mm.

The shell is chocolate brown with a grey bloom. The ribs are white with brown; the brown parts are arranged into two broad bands, one just below the suture and the other near the periphery. The first whorl is yellow. The peristome is white and the inside of the aperture is pale brown.

The shells of female specimens are brownish whereas those of male specimens are bluish grey with violet top whorls (except the embryonic whorls). The shells of male specimens are also more slender.

Animal (fig. 4g). — Dark grey, darkest are the proboscis and tentacles. Near their base the tentacles have a narrow, light ring. The sole is white to pale yellow.

Genitalia (fig. 2j, k). — The penis is extremely short (1.6-2.6 mm) and has closely spaced constrictions. It ends in a smooth, pointed tip. The penis may be dark grey, yellowish white or provided with a spotted pattern.

Radula (fig. 5e). — Long (about 7-8 mm), with slender central teeth and broader lateral and marginal teeth, which all have a rounded tip.

Ecology. — The animals occur mainly on bare limestone rock, further they are found below large blocks and in scree. *O. oscitans* occurs sympatric with *O. hidalgoi, O. bicostulatum* and *O. obscurum.*

Distribution (figs. 49, 52b). — The species is known from only a very small area SE. of Santander (in the eastern Cantabrian mountains), between 200 and 800 m altitude. It is most common north of the water divide of the Cantabrian mountains; only one population has been recorded just south of it.

Material. — SPAIN, SANTANDER: Cascadas del Asón, VN5283/4 (R, RMNH); Nacimiento del Gándara, VN5282 (R, RMNH56164/56165); 3 km S. of Arredondo, VN5088 (Ri); Socueva, S. of Arredondo, VN5190 (R); Puerto de las Alisas, between La Cavada and Arredondo, VN4894 (N, Ri); 2 km S. of San Roque de Riomiera, VN4288 (E, Me, Ri); about 2 km N. of Puerto de las Alisas, VN49 (W); 1 km S. of Mirones, VN4393 (Me); Puerto de las Estacas de Trueba, at the boundary of Santander and Burgos, VN4275 (Me). BURGOS: Las Machorras, VN5273/4 (E, Me).

Remarks. — In the collection of the late C. Altimira (in RMNH) there are some samples labeled *C. hidalgoi español* Altimira. However, Altimira never published this new subspecies.

Subgenus **Canestrinia** subgen. nov.

Type species: *Pomatias canestrinii* Adami, 1876.

Diagnosis. — The dark corneous brown shell has rather flat whorls, slightly angular at the periphery, and is generally decollate. The thick, reflected lip has a typical flexure near the umbilicus (fig. 9).

Discussion. — Based on, amongst others, the shape of the peristome and the common decollation, Wagner (1897: 584) already classified this species within a separate group ('Formenkreis') of his subgenus *Rhabdotakra.*

Obscurella (Canestrinia) canestrinii (Adami, 1876)

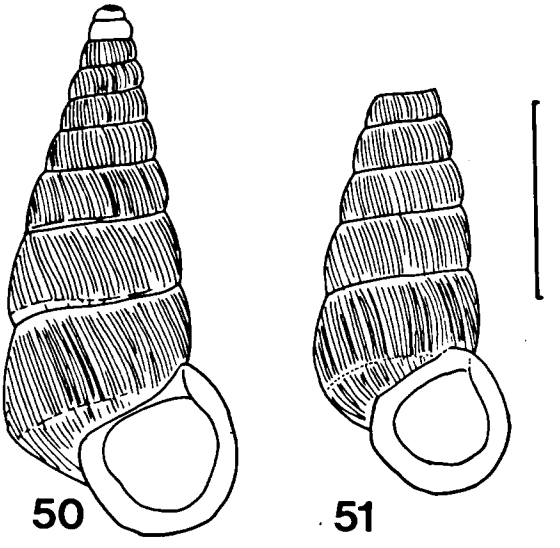
Pomatias canestrinii Adami, 1876: 79, figs. 17-18. Locus typicus: Monte Presolano, Bergamo, Italy, 1800-2350 m altitude. Syntypes: SMF 158335/2.

Pomatias insubricum Pini, 1877: 496. Locus typicus: Valle di Scalve, Bergamo, Italy. Syntypes: SMF 158339/2.

Shell (figs. 9, 25, 26, 50, 51). — The large shell consists of 9-11 rather flat whorls which are slightly angular below the periphery. Just behind the aperture the suture rises slightly. The aperture is large and has a thick, reflected lip with a typical flexure near the umbilicus (fig. 9). The whorls have numerous (7-10/mm) very fine riblets which are regularly spaced and rounded, thus giving the shell a silky lustre. Generally one or more (up to four) of the top whorls have broken off (figs. 9, 25, 26, 51).

Height: 10.8-16.0 mm; width: 4.6-5.8 mm.

The shell is dark corneous brown with slightly lighter coloured top whorls. There is a light band along the angle below the periphery. The peristome is white. Male specimens have violet top whorls (except the embryonic whorls).



Figs. 50-51. Shells of *Obscurella (Canastrinia) canestrinii* (Adami, 1876). 50, specimen with all whorls preserved, female, (Bergamo) Italy, (H. Nolle leg., SMF); 51, specimen which lost about four whorls, male, west side of Monte Presolano (Bergamo) Italy, (K.L. Pfeiffer leg., SMF). Scale 5 mm.

Animal. — See Giusti (1971: fig. 3).

Genitalia (Giusti, 1971: figs. 3, 7). — The penis is long and broad.

Radula (Giusti, 1971: pl. 67 figs. 1, 2). — The radula has central teeth with on both sides one lateral and two marginal teeth. The M2 are very small. The radula closely resembles that of *O. hidalgoi* but has more obtuse teeth.

Ecology. — The species occurs on limestone rocks in mountainous areas.

Distribution (fig. 52a). — The species is only known from part of the Bergamask Alps, Lombardia, Italy. It occurs on some high mountains, above 1500 m, along the Valle di Scalve and Valle Seriana (Pini, 1877).

Material. — ITALY, BERGAMO: Monte Presolano (SMF); Valle di Scalve (SMF); Bergamo (probably reference is made to the province in general and not to its capital) (SMF).

Remarks. — This species is represented in very few collections. This is probably due to the relative isolation of the area where it occurs and the great altitude at which it lives (the limestone rock in the area is restricted to the uppermost parts of the mountains, J.C.A. Eikenboom pers. comm.).

It is unknown why some specimens preserve all whorls whereas nearly all specimens have lost their (up to four) top whorls. In one specimen the top of the shell was closed about one whorl below the break-off point, but generally the shell is closed where it is damaged. Pini (1877: 496) supposes that the upper whorls are generally lost when the animal falls from the dolomitic limestone rock on which it lives, but this is no good explanation since the other *Obscurella* species only rarely lose their top whorls, whereas

they also live on rock faces. Hochpöchler & Kothbauer (1975) studied the mechanism of decollation in *Rumina decollata* (Linné, 1758). They found that the animal prepares the break-off point by removing calcium from part of the top whorls. The same might be true for all decollating gastropods, supposedly also for *O. canestrinii*. The general absence of the top whorls seems to be characteristic for the subgenus.

DISCUSSION

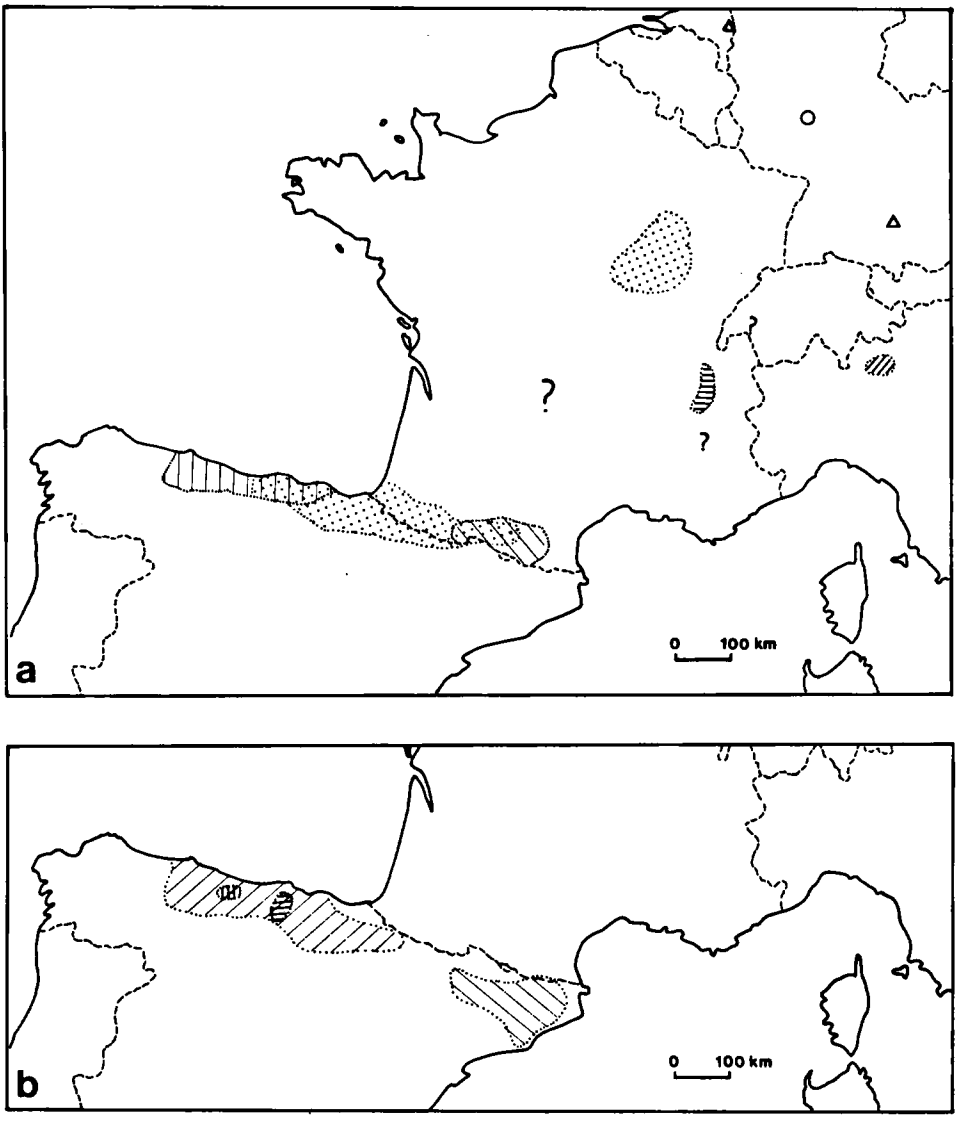
In *Obscurella* s.s. and *Cantabrica*, respectively, *O. (O.) obscurum* and *O. (C.) hidalgoi* have the most variable shells. These species also have the largest and most central ranges. The other species of each subgenus have much smaller and more peripheral ranges, which partly or entirely overlap that of the type species (fig. 52). They might have evolved by allopatric speciation from (peripherally) isolated small populations.

Cantabrica occurs in the Cantabrian mountains, on the southern slope of the Pyrenees and in the Catalonian coastal mountains (figs. 44, 52b). *O. hidalgoi hidalgoi* has the greatest variation in shell size, shape and ornamentation on the northern slope of the Cantabrian mountains (Asturias, Santander, Vizcaya). This area has a large variety in habitats and microclimates. Actually many terrestrial molluscs in this area have very variable shells and there are many endemic taxa. The two species of the subgenus which are endemic to this area have very restricted ranges: *O. asturicum* and *O. oscitans*, the latter of which always has a micropenis. They are considered "young" species. On the other side of the watershed in León and Palencia the mountains only slope to the Castilian uplands, thus giving less varied biotopes and the continental climate results in often harsh conditions. There, only *O. h. hidalgoi* occurs with relatively homogeneous populations.

Obscurella s.s. occurs locally in eastern central France, the westernmost Alps, the northern and southwestern part of the Pyrenees, the eastern Cantabrian mountains and the northern slopes of the western Cantabrian mountains (fig. 52). It is remarkable that near the southwestern and southeastern limits of the range of *O. obscurum*, species have developed which have shells with alternating ribs and riblets, viz. *O. bicostulatum* and *O. nouleti*. In the Alps another species has developed, viz. *O. apricum*.

The range of *O. obscurum* is not fully known. The species is abundant in the eastern Cantabrian mountains and the Pyrenees (fig. 18) but very few samples are available from lowland areas in other parts of France, although many authors cite the species from the eastern and northern parts of that country. It is uncertain whether the distribution in France is really patchy, as one would conclude from the studied material. If so, it is unknown whether the northern populations are vanguard populations or indicative of a once more continuous range. The scarce fossil material suggests the latter (see below). The occurrence in lowland areas is remarkable since all other species of the genus occur only on limestone rock in mountainous ranges.

Only very little is known about fossil *Obscurella*. The records prove that the subgenus has occurred farther North than its actual range. *O. salomoni* (Geyer, 1914) is a species described from lower pleistocene river deposits along the Nagelfluh near Illertissen, south of Ulm (Baden-Württemberg, Federal Republic of Germany). Judging from the photographs in Geyer's paper, this species is closely related to *O. obscurum* and may even be conspecific. Geyer's collection was stored in the Stuttgart Museum which was totally destroyed during the Second World War (Dance, 1966: 287). Meijer (1987) identified a fragment from the Tiglian (lowermost Pleistocene) of the Egypte quarry



Figs. 52. Overview of the distribution of recent and fossil *Obscurella*. 52a, distribution of the species of *Obscurella* s.s. and *Canestrinia* and localities of the fossils *O. labellum* (Thomae, 1845) (circle) and *O. salomi* (Geyer, 1914) (triangles). *Obscurella* s.s. occurs in northermost Spain and in France: *O. (O.) obscurum* (Draparnaud, 1805) (dots) probably has a disjunct range, *O. (O.) bicostulatum* (Gofas, 1989) (vertical hatching), *O. (O.) nouleti* (Dupuy, 1851) (left-inclined hatching) and *O. (O.) apricum* (Mousson, 1817) (horizontal hatching), which may occur in a larger range than the one indicated, which is based on confirmed localities only. *Canestrinia* has only one species, *C. (O.) canestrinii* (Adami, 1876) (right inclined hatching) which is restricted to a small area in Italy. 52b, distribution of the species of *Cantabrica*: *O. (C.) h. hidalgoi* (Crosse, 1864) (right-inclined hatching), [also collected at two localities further to the southwest], *O. (C.) hidalgoi martorelli* (Bourguignat in Servain, 1880) (left-inclined hatching), *O. (C.) asturicum* spec. nov. (vertical hatching) and *O. (C.) oscitans* (Gofas, 1989) (horizontal hatching).

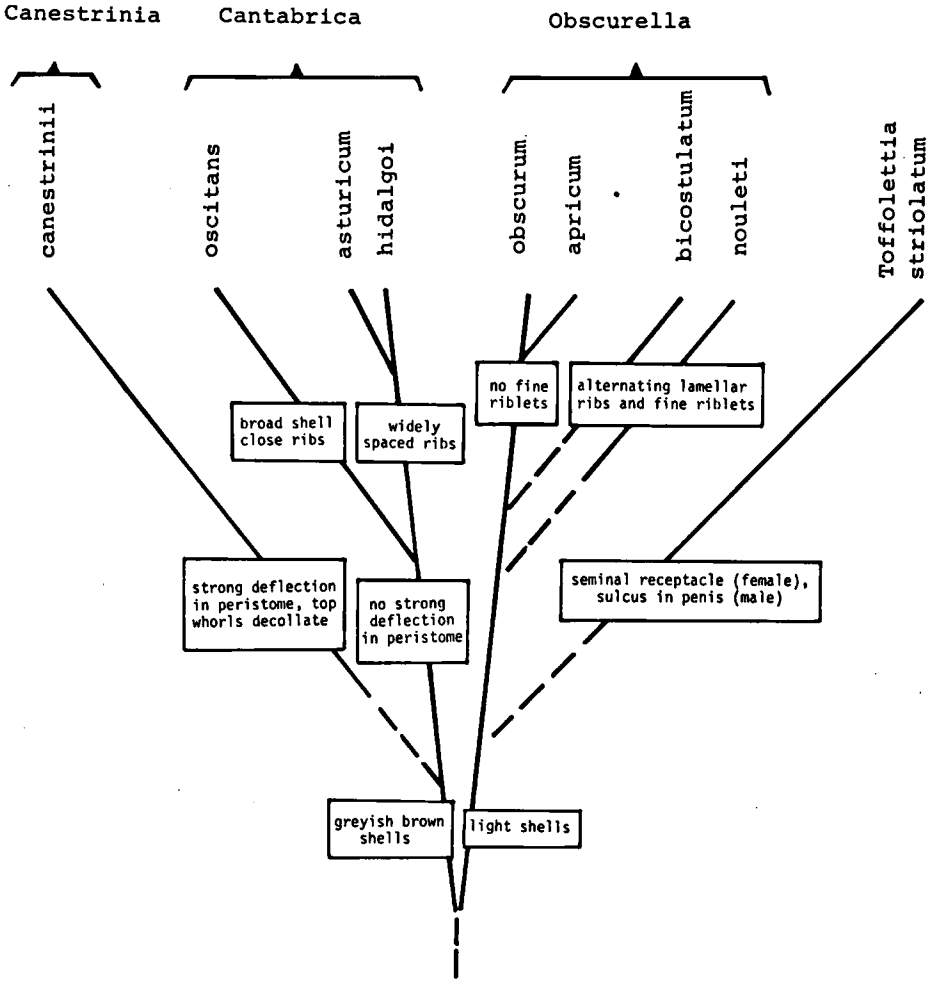


Fig. 53. Evolutionary scheme of the taxa discussed in this paper. The vertical axis is a measure of time, the horizontal axis a measure of difference between the taxa and the inclination of the line is a measure of velocity of change.

near Tegelen (Limburg, Netherlands) as *O.* cf. *salomoni*, whereas fragments of several species of *Cochlostoma* s.l. from Waalian (Lower Pleistocene) deposits in the Netherlands could not be identified with certainty yet.

The only extinct species which can certainly be attributed to *Obscurella* is *O. labellum* (Thomae, 1845) from the Chattian (Upper Oligocene) of the Mainz basin (Hessen, Federal Republic of Germany). I studied a sample from Hochheim (RGM: St 59290). The shells are very close to those of *O. asturicum* but are sculptured with finer and closer

riblets and at the columellar side the reflected peristome has a protrusion as in *O. hidalgoi martorelli*.

Thus no fossils are known from the present range. Fossil material is scarce and comes from lowland areas north of the recent area of *Obscurella*. Although rivers may have transported part of this material over short distances, all these animals must have lived north of the present range. The preservation potential for fossils which lived in these northern lowland areas is much higher than for those that lived on rock faces and in rock debris in the southern mountainous areas. Therefore the fossil material indicates that in the past the range of the genus extended into more northern areas, but it does not provide evidence for a southward shift of the whole range.

Based on overall similarity, some conclusions can be drawn on the degree of affinity between the recent species. This is summarized in a speculative evolutionary scheme (fig. 53).

ACKNOWLEDGEMENTS

This study commenced following discussions with my friends Mr. J.C.A. Eikenboom (Hellevoetsluis) and Ir. H.P.M.G. Menkhorst (Krimpen aan de IJssel). The discussions with Prof. Dr. E. Gittenberger (RMNH, Leiden) were very valuable and he assisted also in several other ways, amongst others by critically reading earlier versions of this manuscript and by permitting me to study the collections at the RMNH. Dr. H.D. Boeters (Munich) independently concluded that *O. bicostulatum* was new to science. Mr. J.H.W. Krom (RMNH, Leiden) took the SEM photographs of the radulas. The shells were photographed by Mr. A.G. van der Sman (Amsterdam) and by Prof. Dr. E. Gittenberger (RMNH). Dr. R. Janssen (SMF, Frankfurt) permitted me to study many type specimens from the collections of the Senckenberg Museum. Mr. C.E. Prieto (UPV, Bilbao) sent me numerous samples from the Spanish Basque provinces. Several others put their collections at my disposal. I am very grateful for all this help without which this study would not have been possible.

REFERENCES

ADAMI, G.B., 1876. Molluschi terrestri e fluviatili viventi nella valle dell'Oglio ossia nelle valli Camonica, di Scalve e di Borlezza, spettanti alle provincie di Brescia e Bergamo. — Atti Soc. ven.-trent. Sci. 5: 7-95.

ALTIMIRA, C., 1963. Notas malacológicas. — Miscelánea Zool. 1 (5): 15-26.

BANK, R.A., 1988. Revision der nordostitalienischen Arten und Unterarten der Gattung Cochlostoma Jan, 1830 (Gastropoda, Prosobranchia: Cyclophoridae). — Basteria 52: 151-174.

BOFILL, A., 1890. Contributions à la faune malacologique de la Catalogne IV. Description de trois espèces nouvelles du Montsech. — Bull. Soc. malac. Fr. 7: 274-279.

——, 1917. Moluscos ingressats en el museu desde el mes de juny de 1916. — Publ. Junta Cienc. nat. Barcelona (Mus. barcin. Scient. nat. Op.) 2: 533-549.

BOFILL, A., & F. HAAS, 1920. Estudi sobre la malacologia de les valls pirenaiques XII. Vall del Segre i Andorra. — Treballs Mus. Cienc. nat. Barcelona (Mus. barcin. Scient. nat. Op.) 3: 225-375.

BOURGUIGNAT, J.R., 1860. Aménités malacologiques 2: i-vii, 1-216. Paris.

——, 1864. Malacologie d'Aix-les-Bains: 1-86. Paris.

CAZIOT, E., 1910. Etude sur les mollusques terrestres et fluviatiles de la Principauté de Monaco et du département des Alpes-Maritimes: 1-559. Monaco.

CLESSIN, S., 1887-1890. Die Molluskenfauna Oesterreich-Ungarns und der Schweiz. Die Mollusken-Fauna Mitteleuropa's 2: 1-858. Nürnberg.

CROSSE, H., 1864. Catalogue des espèces appartenant au genre Pomatias, et description d'une espèce nouvelle. — J. Conch. Paris 12: 23-33.

DANCE, S.P., 1966. Shell collecting. An illustrated history: 1-344. Berkeley, Los Angeles.

DRAPARNAUD, J.P.R., 1801. Tableau des mollusques terrestres et fluviatiles de la France: 1-116. Montpellier, Paris.

——, 1805. Histoire naturelle des mollusques terrestres et fluviatiles de la France: i-viij, 1-160. Paris, Montpellier.

DUPUY, D., 1849. Catalogus extramarinorum Galliae testaceorum in opere cui titulis histoire naturelle des mollusques terrestres et d'eau douce qui vivent en France, descriptorum: 1-4. Paris, Auch.

——, 1851. Histoire naturelle des mollusques terrestres et d'eau douce qui vivent en France 5: 459-594. Paris.

FAGOT, P., 1876. Description de deux espèces de Pomatias des environs de Bagnères-de-Bigorre. — Bull. Soc. Ramond 11: 62-64.

——, 1880a. Histoire malacologique des Pyrénées françaises VI: Basses-Pyrénées. — Bull. Soc. Hist. nat. Toulouse 21: 3-24.

——, 1880b. Mollusques terrestres, et d'eau douce de la vallée d'Aulus (Ariège). — Bull. Soc. Agric. scient. litt. Pyrén.-Orient. 24: 265-293.

——, 1888. Contribuciones a la fauna malacológica de Aragón. Catálogo razonado de los moluscos del valle del Essera 3. — Crónica cient. Barcelona 11: 31-39.

——, 1889. Contribuciones a la fauna malacológica de Aragón y de Navarra Oriental. Catálogo razonado de los moluscos de los valles de los rios Ezca, de la Sierra de Leire y Salazar. — Crónica cient. Barcelona 12: 274-282, 297-300.

——, 1891. Histoire malacologique des Pyrénées Françaises et Espagnoles. — Bull. Soc. Ramond 26: 277-296.

——, 1905. Contributions à la faune malacologique de la Catalogne. — Butll. Inst. catal. Hist. nat. 5: 122-124, 138-143.

FOLIN, L. DE, & F. BÉRILLON, 1877. Contributions à la faune malacologique de la région extrême S.-O. de la France I-VIII. — Bull. Soc. Borda 2 (1): 199-210.

FROSSARD, E., 1870. Note sur une grotte renfermant des restes humains de l'époque paléolithique, découvert à Bagnères-de-Bigorre. — Bull. Soc. Ramond 5: 18-19.

GASULL, L., 1981. Fauna malacológica terrestre y de agua dulce de la provincia de Castellón de la Plana. — Boll. Soc. Hist. nat. Balears 25: 55-102.

GERMAIN, L., 1931. Mollusqes terrestres et fluviatiles 2. — Faune de France 22: 479-897, ix-xiv Paris.

GEYER, D., 1914. Über diluviale Schotter Schwabens und ihre Molluskenreste 5. Die Molluskenreste der diluviales Nagelfluh von Buch bei Illertissen. — Jber. Mitt. oberrhein. geol. Ver. (N.F.) 4: 136-138.

GIUSTI, F., 1971. Primo contributo alla revisione del genere Cochlostoma Jan e descrizione di Toffelettia n. gen. (Gastropoda Prosobranchia Cyclophoridae). — Atti Soc. ital. Sci. nat. 112: 353-380.

GOFAS, S., 1989. Descripción preliminar de dos nuevos Cochlostoma (Gastropoda, Prosobranchia) del Cantabrico. — Publções ocas. Soc. port. Malac. 14: 43-48.

GRAS, A., 1846. Description des mollusques fluviatiles et terrestres de la France et particulièrement du département de l'Isère: 1-82, 1-27. Grenoble.

GRATELOUP, J.P.S. DE, & V. RAULIN, 1855. Catalogue des mollusques terrestres et fluviatiles, vivants et fossiles, de la France continentale et insulaire: 1-65. Bordeaux.

HAAS, F., 1929. Fauna malacológica terrestre y de agua dulce de Cataluña. — Trabajos Mus. Cienc. nat. Barcelona 13: 1-491.

HOCHPÖCHLER, F., & H. KOTZBAUER, 1975. Der Mechanismus der Dekollation bei Rumina decollata (L.) (Gastropoda, Stylommatophora). — Arch. Molluskenk. 106: 119-121.

KERNEY, M.P., & R.A.D. CAMERON, 1979. A field guide to the land snails of Britain and North-West Europe: 1-228. London, Glasgow.

KOBELT, W., 1882. Diagnosen neuer Arten. — NachrBl. dt. malakozool. Ges. 14: 121-123.

——, 1902. Cyclophoridae. — Das Tierreich 16: i-xxxix, 1-662. Berlin.

KOBELT, W., & O.F. MÖLLENDORFF, 1898-1899. Catalog der gegenwärtig bekannten Pneumopomen. — NachrBl. dt. malakozool. Ges. 30: 129-160.

LOCARD, A., 1882. Catalogue général des mollusques vivants de France: i-vi, 1-462. Lyon, Paris.
——, 1894. Les coquilles terrestres de France. Description des familles, genres et espèces: 1-370. Paris.
——, 1896. Ipsa Draparnaudi conchylia. Etudes critiques sur la collection Draparnaud du Musée Royal et Impérial de Vienne: 1-190. Paris.
MABILLE, J., 1875. Des espèces françaises de la famille des Cyclostomatidae. Revue Mag. Zool. (3) 3: 145-156.
MEIJER, T., 1987. De molluskenfauna van het Waalien in Nederland. — Corresp Blad ned. Malac. Veren. 237: 276-279, 288-297.
MOQUIN-TANDON, A., 1855-1856. Histoire naturelle des mollusques terrestres et fluviatiles de France. I: i-viii, 1-416; II: 1-646. Paris.
MOUSSON, A., 1847. Bemerkungen über die natürlichen Verhältnisse der Termen von Aix in Savoyen. — Neue Denkschr. Allg. schweiz. Ges. Naturw. 8: 1-48.
PARTIOT, L., 1848. Mémoire sur les Cyclostomes: 1-72. Toulouse.
PFEIFFER, L., 1846. Die gedeckelten Lungenschnecken (Helicinacea et Cyclostomacea). In: Martini & Chemnitz, Syst. Conchylien-Kabinett I (19): 1-228. Nürnberg.
PINI, N., 1877. Notizie malacologiche relative alla fauna Lombarda. — Atti Soc. ital. Sci. nat. 19: 493-499.
SAINT-SIMON, A. DE, 1848. Miscellanées malacologiques I: 1-41. Toulouse.
——, 1867. Observations anatomiques sur quelques Pomatias du midi de la France: 1-16. Toulouse.
——, 1869. Description d'espèces nouvelles du genre Pomatias suivies d'un aperçu synonymique sur les espèces de ce genre. — Revue Mag. Zool. 2: 3-28.
——, 1876. Mollusques des Pyrénées de la Haute-Garonne. — Bull. Soc. Hist. nat. Toulouse 10: 122-145.
SALVAÑÁ, J.M., 1888. Contribución a la fauna malacológica de los Pirineos Catalanes o sea Descripción de la Comarca de Olot en relación con la faunula malacológica local y monografia de los moluscos terrestres y fluviatiles de aquel territorio. — An. Soc. esp. Hist. nat. 17: 1-58.
SERVAIN, G., 1880. Etude sur les mollusques récueillis en Espagne et en Portugal: 1-172. Saint-Germain.
VALLOT, J.N., 1801. Exercise sur l'histoire naturelle: 1-8. Dijon.
VILELLA, M., 1967. Notas malacológicas. IV. Nuevas citas de dispersión. — Miscelánea Zool. 2: 17-21
WAGNER, A.J., 1897. Monographie der Gattung Pomatias Studer. — Denkschr. Akad. Wiss. Wien 64: 565-632.
WENZ, W., 1938. Gastropoda Teil I; Allgemeiner Teil und Prosobranchia. In: O.H. Schindewolf (ed.), Handbuch der Paläozoologie 6: 1-1639. Berlin.
WESTERLUND, C.A., 1883. Malakologische Miscellen I. Descriptiones 2. Conspectus formarum in regione palaeoarctica viventium generis Pomatias Studer. — Jb. dt. malakozool. Ges. 10: 51-72.
——, 1885. Fauna der in der Paläarctischen Region (...) lebenden Binnenconchylien V. Fam. Succineidae, Auriculidae, Limnaeidae, Cyclostomidae & Hydrocenidae: 1-135, 1-14. Berlin, Lund.
ZILCH, A., 1958. Die Typen und Typoide des Natur-Museums Senckenberg 21: Mollusca, Cyclophoridae, Craspedopominae-Cochlostominae. — Arch. Molluskenk. 87: 53-76.