SOME ANATOMICAL, SYSTEMATICAL AND GEOGRAPHICAL DATA ON NENIINAE (GASTROPODA, CLAUSILIIDAE)

by

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(With 38 text-figures and 1 plate)

I. Introduction

Up to the moment more than one hundred species and subspecies of Neniinae are known from Central and South America. They are incorporated into 22 genera and subgenera, almost exclusively based on characters of the shells. Only little is known of the anatomy of the animals (Binney, 1871; Binney & Bland, 1871; Baker, 1961; Hesse, 1925; Scott, 1954; Loosjes, 1957; Pilsbry, 1926; Polinski, 1922; Zilch, 1953, 1959). These authors described the radula and/or the genital organs of one or several species. Thus from eleven species the radula has been described and from five the genital apparatus.

By the courtesy of Prof. Dr. W. Weyrauch we were able to study the anatomical features of a relatively large number (38) of Peruvian and Argentine Neniinae. We wish to express our most cordial thanks to him for his generosity and also to Dr. B. Hubendick, who provided us with a sample of *Nenia tridens* (Chemnitz) from Puerto Rico.

In Thiele's (1929/31) classification the American Neniinae are grouped into three genera, *Nenia, Peruinia* and *Temesa,* based on characters of the shells and of the radula. It turned out impossible to fit the information we found, into this system as it indicates the presence of many more units. In this survey we will follow Zilch's (1960) classification, which enumerates a number of genera and subgenera, based on conchological characters, although the order will be altered according to the results obtained (conf. chapter IV).

Thus conchological data of the genera or subgenera involved have to be studied in Zilch (1960), or eventually in Thiele (1929/31).

The American representatives of the subfamily Neniinae [1]) investigated,

1) Two Asiatic genera are provisionally incorporated into the subfamily.

all have the following characters of radula and genital apparatus.

Radula consisting of more than thirty rows of teeth, usually more than one hundred (the estimation of the total number is difficult, because many rows are at the same time in different stages of formation), each row has a central (c) or rhachidian tooth, and on each side lateral (l) and marginal (m) teeth; half a row consists of 9 to 46 elements. There is much variation in the radula, comparing the different genera. The central tooth may have one or three cusps, the laterals may have one and/or two cusps and the marginals three or more cusps. The form of the cusps may be more or less dagger- or crescent-shaped. Small differences in numbers of lateral or marginal teeth appear not to be of much importance, sometimes even the two sides of a row are not identical. It may also occur that the matrix of a certain tooth has a defect so that abnormal teeth are formed at that place in each row. We did not pay attention to these abnormalities.

Genital apparatus with a bisexual gland (consisting of groups of sac-like glands), spermoviduct leading via a vesicula seminalis into the ductus seminalis with prostate gland on the one side and into the oviduct with albuminous gland on the other. The seminal duct continues into the vas deferens which leads by way of the epiphallus, via the penis into the atrium. The oviduct passes into the clear oviduct, which continues as the vagina after the mouth of the duct of the receptaculum seminis; the vagina leads into the atrium. The vas deferens is distally often a bit wider than proximally, it runs along the clear oviduct and along the vagina, bends near the atrium and accompanies the penis until it passes into the epiphallus. A retractor penis is always present, as is the penis ligament. The duct of the receptaculum seminis (pedunculus) may have a distinct bulbus and a diverticulum, the latter ends either on the pedunculus itself, or, near or just at its mouth into the vagina. The diverticulum may be totally absent as well; but in some genera an appendix, often twisted, runs along the clear oviduct and ends distally from the place where the pedunculus enters the vagina. The retractor receptaculum seminis is usually well developed as is the retractor lateralis sinister. The retractor muscle of the left upper tentacle passes between penis and vagina. We never found an embryonic shell in a Nenian oviduct; such embryos are sometimes found in the uterus of viviparous Clausiliidae, for example in *Phaedusa corticina* (Pfr.).

In the following survey we do not repeat the above mentioned general information on the organs under study for each genus or species separately. We only give the special characteristics of the genera or of the species.

Genera and species of which we had no specimens available for dissection are not mentioned here. If no anatomical data are available of the type-

species of a genus (or subgenus) but there is anatomical information on other species of that genus, we still give anatomical characters for the genus but with the qualification "presumably the characters are . . .".

The specimens collected by Prof. Dr. W. Weyrauch are indicated with "W W", followed by his collection-number.

II. Descriptions of the genera, subgenera and species investigated

Nenia H. & A. Adams, 1855

Type-species: *Turbo tridens* Chemnitz, 1786.

Radula. $\frac{c}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The tooth-rows are almost rectilinear, with the central tooth somewhat advanced, the cusps are more or less dagger-shaped. The basal plates and the cusps are rather regularly diminishing in size from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has a diverticulum, the mouth of it divides the pedunculus into a distal and a proximal part.

Nenia tridens (Chemnitz, 1786) (fig. 1)

Binney (1871) and Binney & Bland (1871) published on the jaw and on the radula; Hesse (1925) described jaw, radula and genital organs; Baker (1961) figured the pallial complex and the penis.

The specimens investigated were collected on the island of Puerto Rico, El Yunque, on tree trunks in rain forest, leg. Dr. B. Hubendick.

The animals (alcohol specimens) are grey-brown, fading into white near the foot-sole, which is whitish grey.

Radula. $\frac{c}{1} + \frac{8-10\ 1}{2} + \frac{19\ m}{3-\infty}$. We found 8 to 10 lateral teeth (Hesse: 11 or 12) with 2 cusps and 19 marginal teeth (Hesse: 20 or 21) with 3 or more cusps.

Genital organs. Clear oviduct and vagina about equally long. The proximal part of the pedunculus (from the entrance in the oviduct to the mouth of the diverticulum) is a bit shorter than the distal part of it (from the mouth of the diverticulum to the end of the bulbus of the receptaculum). The bulbus is spatula-shaped and about twice as long as wide, its width is twice the width of the duct. Diverticulum strong, slightly wider and longer than the distal part of the pedunculus, both are built up in the same way, the one with strong, the other with rather weak longitudinal muscular strips internally. The epiphallus is internally provided with 4 longitudinal muscular strips, leaving a star-shaped lumen. The penis is provided with 6 or 7 similar strips. A definite penis papilla could not be found. The vas deferens is bound to the penis by the penis ligament over a rather long distance. These results are in accordance with Hesse's findings.

Ehrmanniella Zilch, 1949

Type-species: *Clausilia (Nenia) quadrata* O. Boettger, 1880.

Radula. $\frac{c}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The two sides of the tooth-rows form an angle of about 120° (60° with the axes), with the central tooth at the top, at the fifth tooth on both sides the rows regain a direction more vertical to the axis of the radula. Thus the central teeth and the first three lateral teeth have an advanced position compared with the other teeth of the row to which they belong; the central tooth is vertical to the axis about in line with the third lateral tooth of the previous row. The cusps are more or less dagger-shaped. The basal plates and cusps diminish rather regularly in size from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has a diverticulum, the mouth of it divides the pedunculus into a distal and a proximal part.

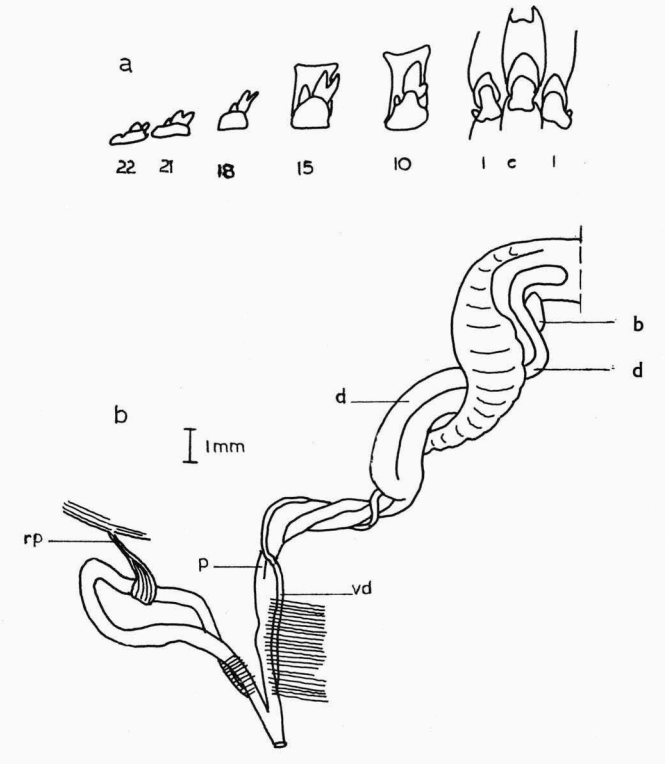

Fig. 1. *Nenia tridens* (Chemnitz). a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Ehrmanniella quadrata (O. Boettger, 1880) (fig. 2)

The specimens investigated were collected in central Peru, La Florida near Acobamba, Rio Tarma, 3000-3100 m (WW.265).

The animals (alcohol specimens) are greyish with a yellowish foot-sole.

Radula. $\frac{c}{1} + \frac{7\ 1}{2} + \frac{12\ m}{3-\infty}$. It is noteworthy that the third cusp of the first marginal tooth is not formed by splitting up of the main cusp, but of the small side cusp.

Genital organs. Clear oviduct short, about one tenth of the length of the vagina and less wide than the pedunculus. The proximal part of the pedun-

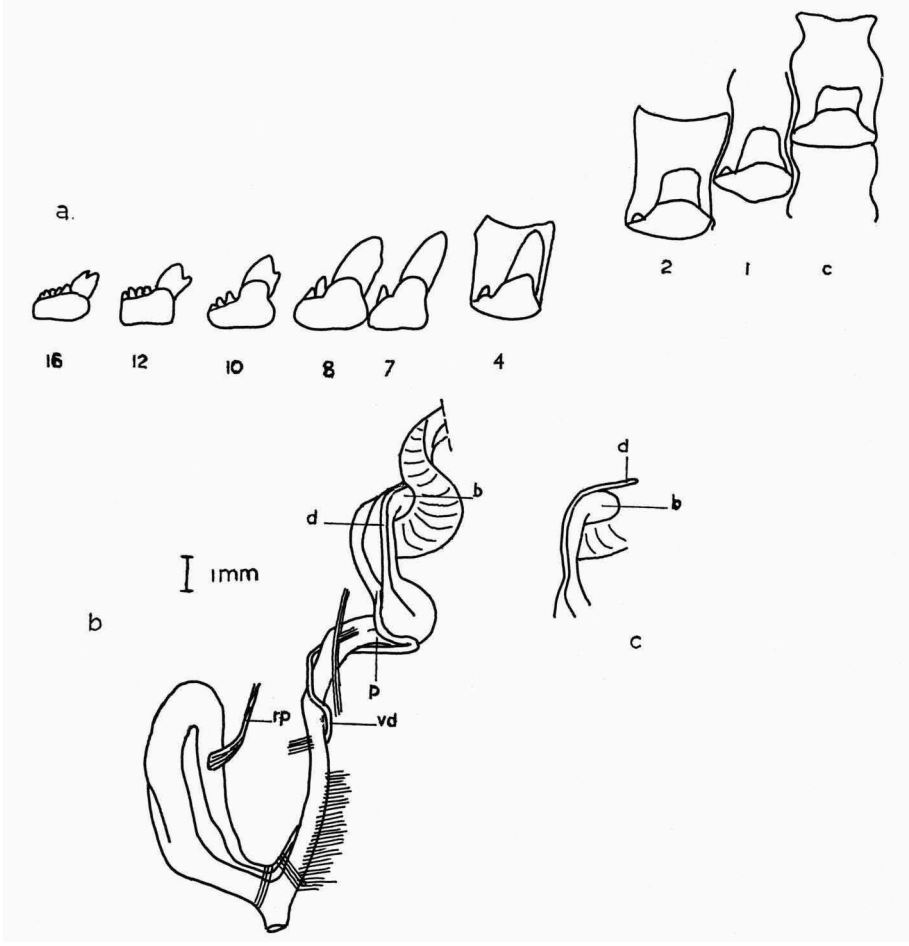

Fig. 2. *Ehrmanniella quadrata* (O. Boettger). a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

culus is short, about as short as the clear oviduct, and very wide; the distal part is short (about half as long as the vagina) and wide, with a distinct bulbus (1½ times as long as wide). The diverticulum is distally narrow, only the proximal end is wide, it is somewhat longer than the distal part of the pedunculus with the bulbus. The vagina is long, but not strikingly wide. The vas deferens passes into the epiphallus with an externally visible widening. The epiphallus is internally provided with about six muscular strips, regularly distributed over the inner side of the wall. Penis wide, internally provided with two very strong muscular strips, which run longitudinally close to one another, between them is an externally visible groove. The retractor penis is rather weak.

Ehrmanniella boettgeri (Pilsbry, 1945) (fig. 3)

The specimens investigated were collected in central Peru, Puente Iligyacu, Rio Tarma, 2200 m (W W.300).

The animals (alcohol specimens) are brownish-black, the foot-sole is whitish.

Radula. $\frac{c}{1} + \frac{11\,1}{2} + \frac{9\ m}{3-\infty}$. Here the main cusp and the small side cusp (of the laterals) both may split up in the same tooth, so that the marginals may begin already with teeth with four cusps.

Genital organs. Clear oviduct short, about one sixth of the length of the vagina and about as wide as the pedunculus. The proximal part of the pedunculus is short (about as long as the clear oviduct) and wide. The distal part is rather narrow, it has a distinct bulbus (1½ times as long as wide); together with the bulbus, it is more than half as long as the vagina. The diverticulum is narrow, only at its proximal end it becomes wider, it is somewhat longer than the distal part of the pedunculus with the bulbus. The vagina is neither very long nor very wide. The epiphallus is internally provided with about six weak muscular strips, regularly distributed over the inner wall, one of them may be a bit stronger than the others. The penis is wide and internally provided with two strong muscular strips, which run longitudinally close to one another; between them is an externally visible, groove. The retractor penis is rather weak.

Andiniella Weyrauch, 1958

Type-species: *Andinia (Ehrmanniella) flammulata* Loosjes, 1957.

Radula. $\frac{c}{1} + \frac{1}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The two sides of the rows form an angle of about 110° to 120°, with the central tooth at the top, at the fourth tooth the rows regain a direction more nearly vertical to the axis of the radula, thus

the central tooth and the first three lateral teeth have a very advanced position, compared with the other teeth of the row to which they belong; the central tooth is vertical to the axis about in line with the third lateral tooth of the previous row. The cusps are more or less dagger-shaped. The basal plates and cusps of the central tooth and of the first three lateral teeth are large in comparison with those of the next teeth of the rows; from the fourth lateral tooth the elements diminish rather regularly in size to the outermost marginal teeth. The number of elements in a row is comparatively small.

Genital organs. The pedunculus has a very narrow diverticulum, the mouth of it divides the pedunculus into a distal and a short proximal part.

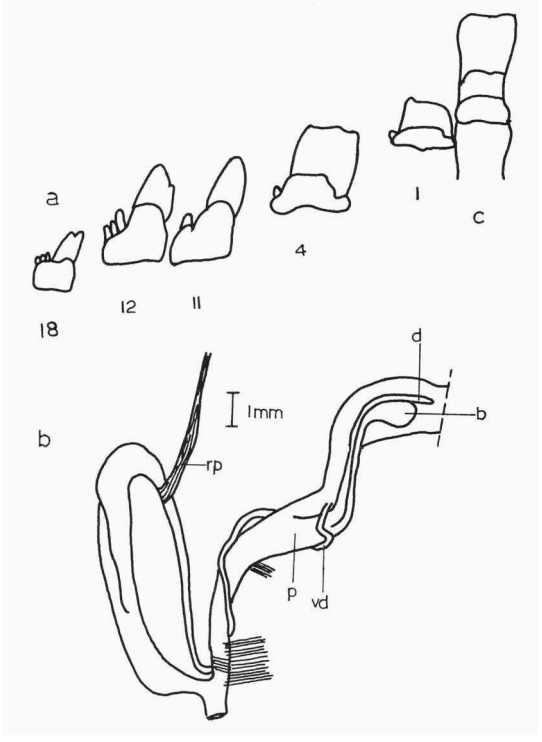

Fig. 3. *Ehrmanniella boettgeri* (Pilsbry). a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Andiniella flammulata (Loosjes, 1957) (fig. 4)

Loosjes (1957) described and figured elements of the radula and the genital apparatus.

The specimens investigated were collected in central Peru, Cerro Huilcashpata near Palca, Rio Tarma, 3100 m (W W.1310), paratypes.

The animals (alcohol specimens) are dark brownish-grey, with a whitish foot-sole.

Radula. $\frac{c}{1} + \frac{3—4\ 1}{1} + \frac{3—4\ 1}{2} + \frac{4—6m}{3—\infty}$. The central tooth is slightly smaller than the first three laterals.

Genital organs. Clear oviduct short, about one fifth of the length of the vagina and as wide as the pedunculus. The proximal part of the pedunculus is short, about as short as the clear oviduct, it is rather wide; the distal part is comparatively long, as long as the vagina or even longer, it has a distinct bulbus (1½ times as long as wide). The diverticulum is very narrow over its complete length and somewhat shorter than the distal part of the pedunculus. The vagina is not extremely long and rather wide. The vas deferens passes into the epiphallus with a distinct widening; the epiphallus internally has two large and one small muscular strip, forming a T-shaped lumen in cross-section, the penis is short and has a circular lumen, its inner wall is provided with many wrinkled muscular strips. The retractor penis is comparatively weak.

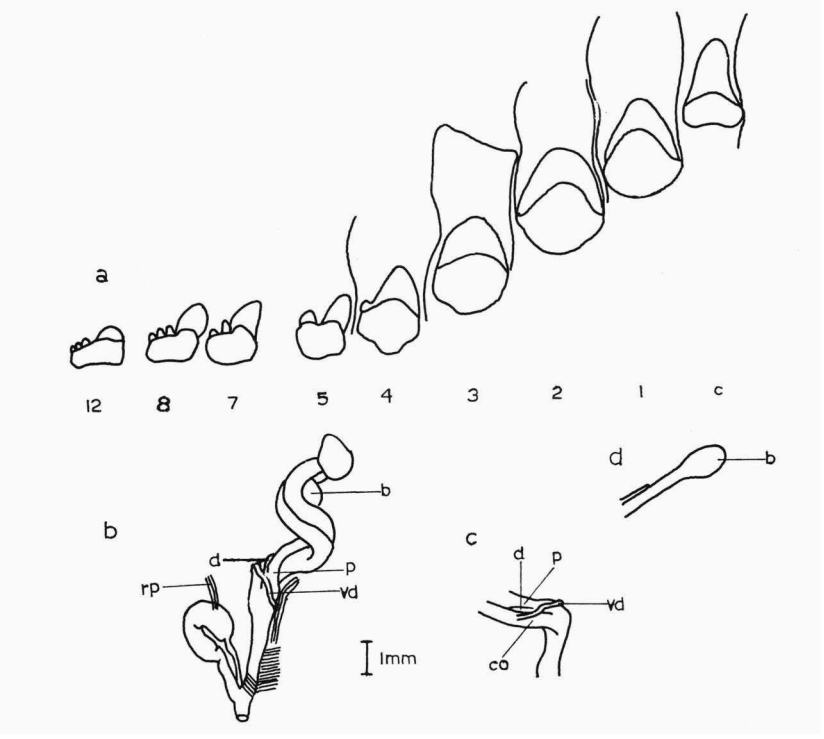

Fig. 4. *Andiniella flammulata* (Loosjes). a, some elements of the radula; b, c, d, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Andiniella sztolcmani (Polinski, 1922) (fig. 5)

Synonym: *Nenia acobambensis* Pilsbry, 1945.

The specimens investigated were collected in central Peru, La Florida near Acobamba, Rio Tarma, 3000-3100 m (W W.266).

The animals (alcohol specimens) are black, with a white foot-sole.

Radula. $\frac{c}{1} + \frac{5\,1}{1} + \frac{3\,1}{2} + \frac{5-6\ m}{3-\infty}$. The central tooth is slightly smaller than the first three laterals.

Genital organs. Clear oviduct short, about one sixth of the length of the vagina and as wide as the pedunculus. The proximal part of the pedunculus is still shorter than the clear oviduct, it is rather wide. The distal part is comparatively long, about as long as the vagina, it has a distinct bulbus (1½

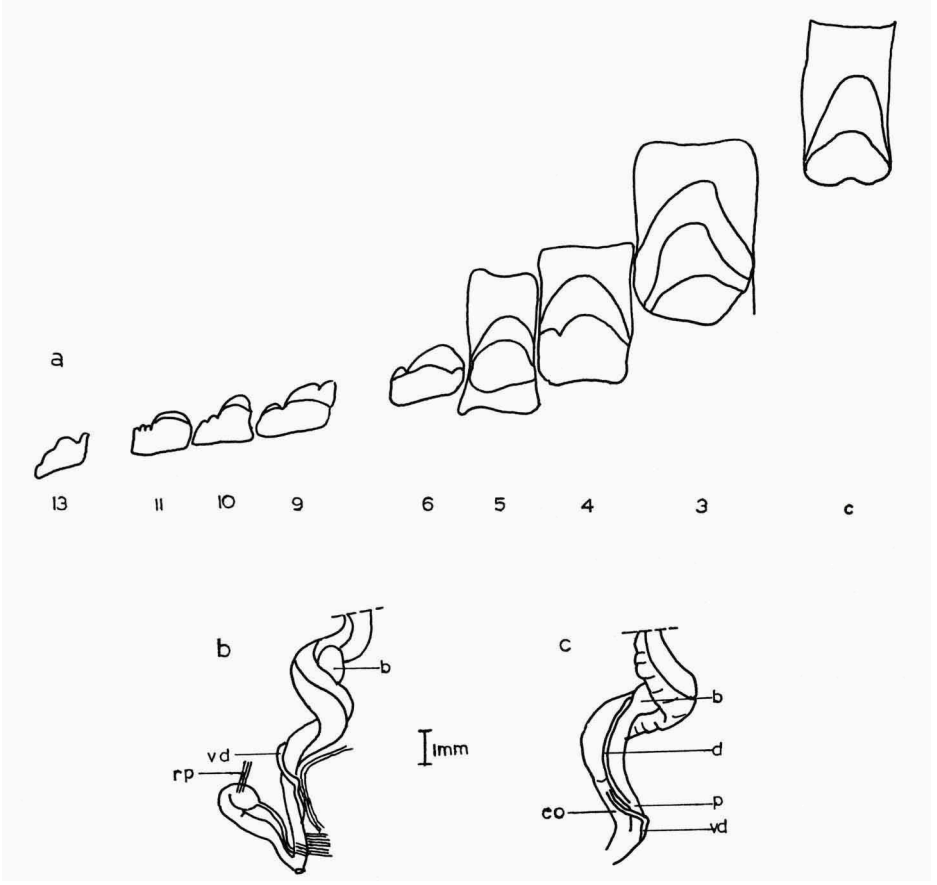

Fig. 5. *Andiniella sztolcmani* (Polinski). a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

times as long as wide). The diverticulum is very narrow over its complete length and as long as the distal part of the pedunculus, the bulbus excluded. The vagina is not extremely long and rather wide. The vas deferens passes into the epiphallus with an externally distinct widening; internally the epiphallus has two large and one small muscular strip, forming a T-shaped lumen. The penis is short and internally provided with many wrinkled muscular strips, giving a granulated appearance to the inner wall. The retractor penis is rather weak.

Peruinia Polinski, 1921

Type-species: *Clausilia peruana* Troschel, 1847.

Radula. $\frac{c}{1} + \frac{1}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The two sides of the rows form an angle of about 90°, with the central tooth at the top; at the fifth to seventh tooth the rows regain a direction more nearly vertical to the axis of the radula, thus the central tooth and the first five or six lateral teeth have a very advanced position compared with the other teeth of the row to which they belong; the central tooth is vertical to the axis about in line with the second lateral tooth of the previous row. The cusps are more or less crescent-shaped. The basal plates and cusps of the central tooth and of the first five lateral teeth are large in comparison with those of the next teeth of the rows; from the sixth or seventh lateral tooth the elements diminish rather regularly in size to the outermost marginal teeth. The number of elements in a row is comparatively small.

Genital organs. The pedunculus has a very narrow diverticulum, the mouth of it divides the pedunculus into a distal and a short proximal part.

Peruinia peruana peruana (Troschel, 1847) (fig. 6)

Polinski (1922) described and figured elements of the radula.

The specimen investigated was collected in central Peru, Pan de Azúcar, Rio Tarma, 1400 m (W W.285).

The animal (alcohol specimen) is grey and has a reddish foot-sole.

Radula. $\frac{c}{1} + \frac{6\,1}{1} + \frac{2\,1}{2} + \frac{5 \quad m}{-\infty}$.

Genital organs. Clear oviduct rather wide and about as long as the vagina. The pedunculus is very wide, wider than the clear oviduct. The proximal part is short, about one seventh of the distal part, which has a distinct bulbus (about 1½ times as long as wide). The diverticulum is very narrow over its complete length and distinctly longer than the distal part of the pedunculus with the bulbus, it enters the pedunculus at the side directed to the clear oviduct. The vagina is short and wide. The vas deferens passes into

the epiphallus with a distinct widening, the epiphallus has internally two large and some small longitudinal muscular strips, forming a tree-shaped lumen in a cross-section; the penis is short and very wide and has a rather complicated lumen and thick muscular walls over ¾ of its diameter, combined with strong papillae that penetrate far into the lumen.

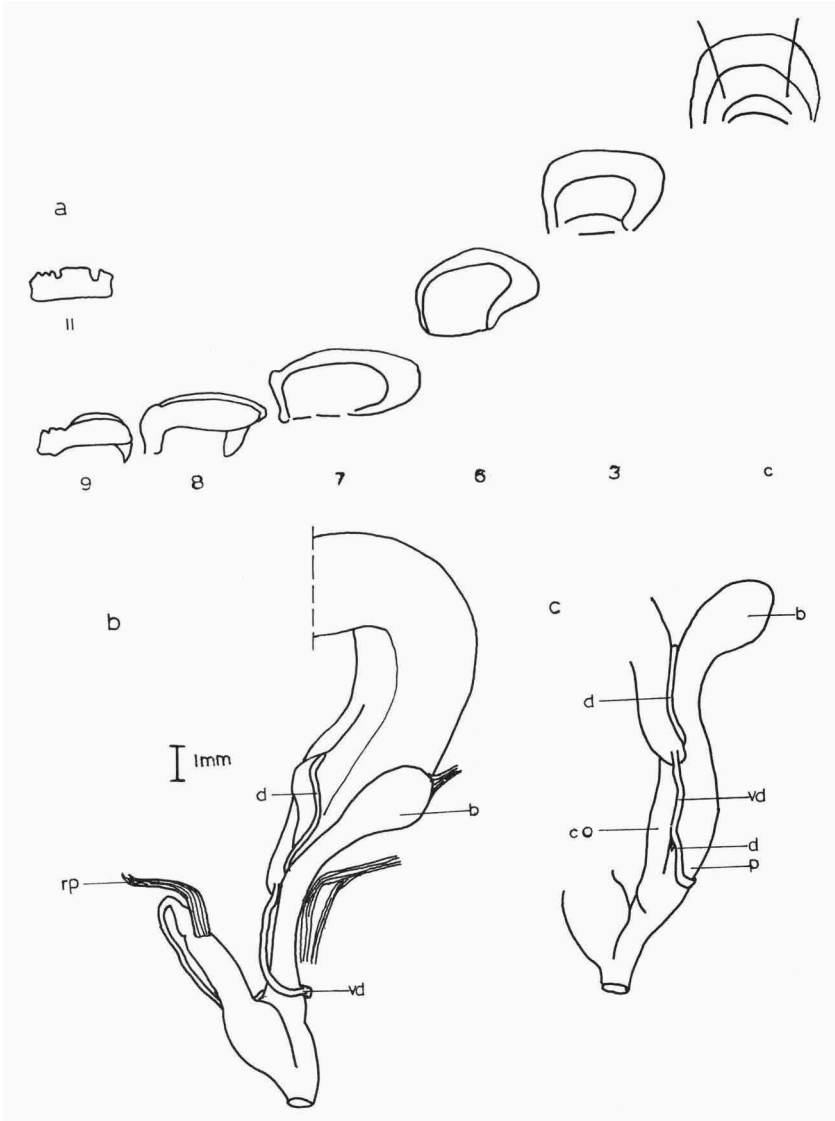

Fig. 6. *Peruinia peruana peruana* (Troschel). a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Peruinia peruana granulosa (Sykes, 1900) (fig. 7)

The specimens investigated were collected in central Peru, Valley of Chanchamayo, near the road from San Ramon to Pichita Calucha, 1200 m (W W.285-B).

The animals (alcohol specimens) are black with a whitish foot-sole.

Radula. $\frac{c}{1} + \frac{5\ 1}{1} + \frac{1\ 1}{2} + \frac{5\ m}{3-\infty}$.

Genital organs. Not different from those of the nominate subspecies.

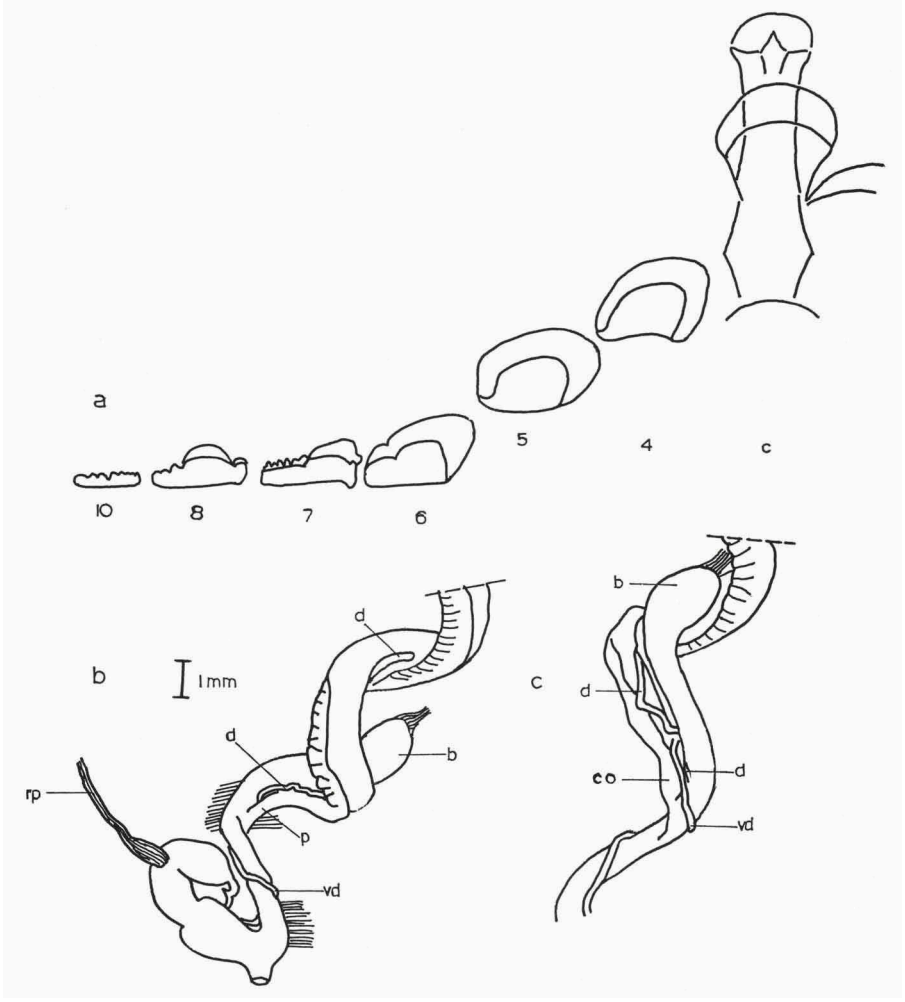

Fig. 7. *Peruinia peruana granulosa* (Sykes). a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Peruinia albicolor Weyrauch, 1957 (fig. 8)

The specimen investigated was collected in central Peru, 23 km N.E. from Tingo Maria, near the bridge across the Rio Tulumayo, on the road from Huanuco to Pucallpa, 670 m (W W.1818), paratype.

The animal (alcohol specimen) is grey, with a white foot-sole.

Radula. $\frac{c}{1} + \frac{4\ 1}{1} + \frac{2\ 1}{2} + \frac{5\ m}{3-\infty}$.

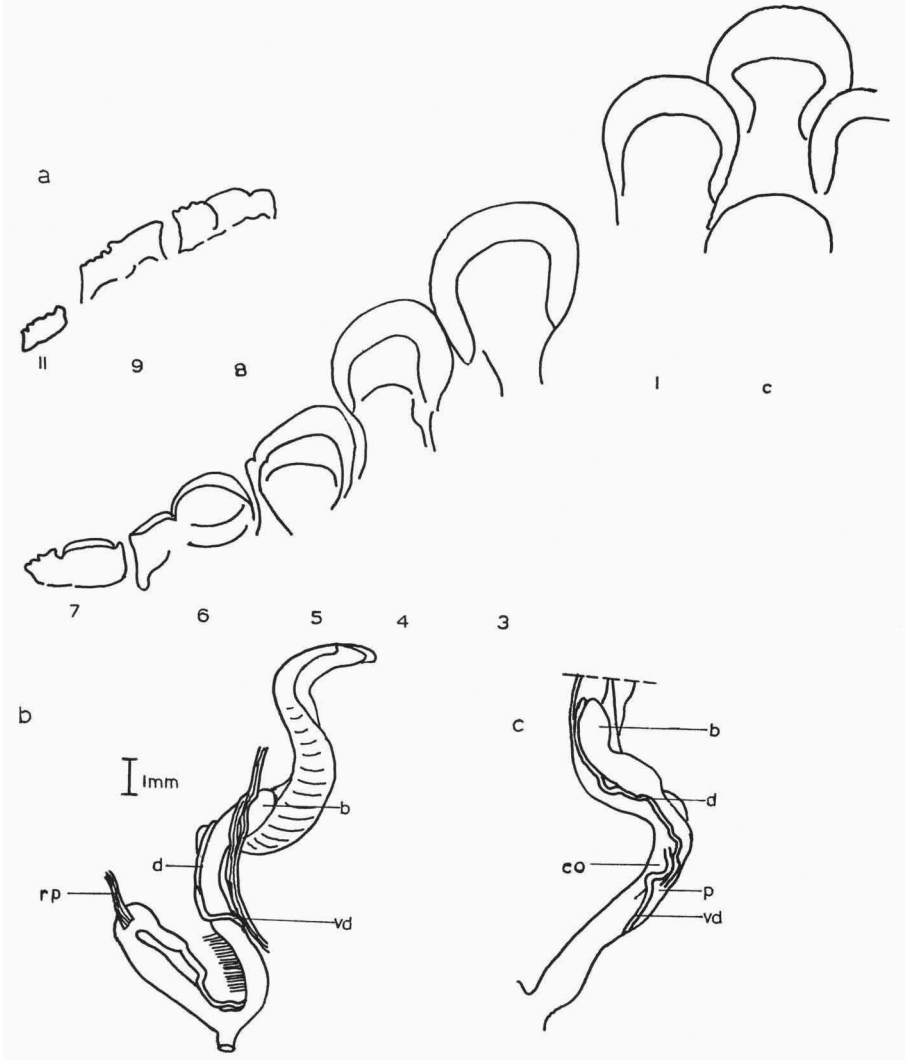

Fig. 8. *Peruinia albicolor* Weyrauch. a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Genital organs. Clear oviduct rather wide and about half as long as the vagina. The pedunculus is wide, slightly wider than the clear oviduct. The proximal part is short, about one seventh of the distal part, which has a distinct bulbus (about twice as long as wide). The diverticulum is very narrow over its complete length, it is about as long as the distal part of the pedunculus with the bulbus, it enters the pedunculus at the side directed to the clear oviduct. The vagina is rather short and wide. The vas deferens passes into the distinctly wider epiphallus, which is internally provided with one large and three small muscular strips, the lumen being cross-shaped in cross-section; the penis is short and as wide as the epiphallus, it has five longitudinal muscular strips.

Peruinia flachi superba Weyrauch, 1960 (fig. 9)

The specimen investigated was collected in central Peru near Pichita Caluga, in the area of the Rio Chanchamayo, 2200 m (W W.3092), paratype.

The animal (alcohol specimen) is black, with a light reddish foot-sole.

Radula. $\frac{c}{1} + \frac{6\,1}{1} + \frac{2\,1}{2} + \frac{6\quad m}{3-\infty}$.

Genital organs. Clear oviduct rather wide and as long as the vagina. The pedunculus is very wide, wider than the clear oviduct. The proximal part is short, about one ninth of the distal part, which has a distinct bulbus (about twice as long as wide). The diverticulum is very narrow over its complete length and distinctly longer than the distal part of the pedunculus with the bulbus; it enters the pedunculus at the side between the pedunculus and the clear oviduct. The vagina is short and wide. The vas deferens passes into the epiphallus with a distinct widening, the epiphallus is internally provided with two large and many small longitudinal muscular strips, forming a T-shaped lumen in cross-section. The penis is short and very wide, it has a rather complicated lumen and thick muscular walls over ¾ of its diameter, combined with strong papillae that penetrate far into the lumen.

Peruinia flachi tingamariae Pilsbry, 1922 (fig. 10)

The specimen investigated was collected in central Peru, Puente Cayumba, Rio Huallaga, 800 m (W W.506 A).

The animal (alcohol specimen) is light grey with a white foot-sole.

Radula. $\frac{c}{1} + \frac{4\,1}{1} + \frac{1\,1}{2} + \frac{7\quad m}{3-\infty}$.

Genital organs. Clear oviduct not very wide and about as long as the vagina. The pedunculus is very wide, about twice as wide as the clear oviduct. The proximal part is short, about one sixth of the distal part, which has a distinct bulbus (about 1½ times as long as wide). The diverticulum is very narrow over its complete length and about as long as the distal part of the

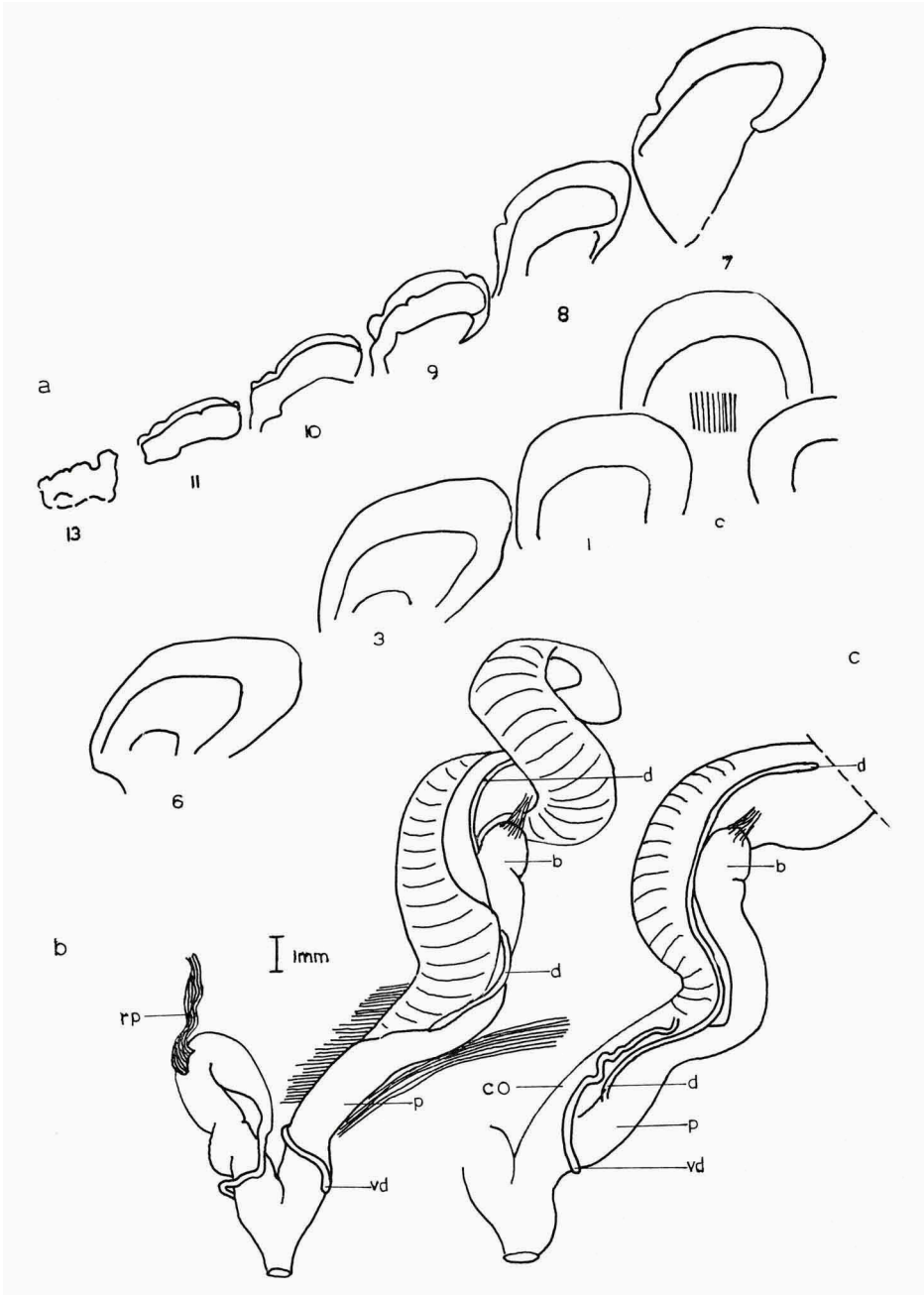

Fig. 9. *Peruinia flachi superba* Weyrauch. a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

pedunculus, it enters the pedunculus at the side between this and the clear oviduct. The vagina is wide and short. The vas deferens passes into the epiphallus with a distinct widening, the epiphallus is internally provided

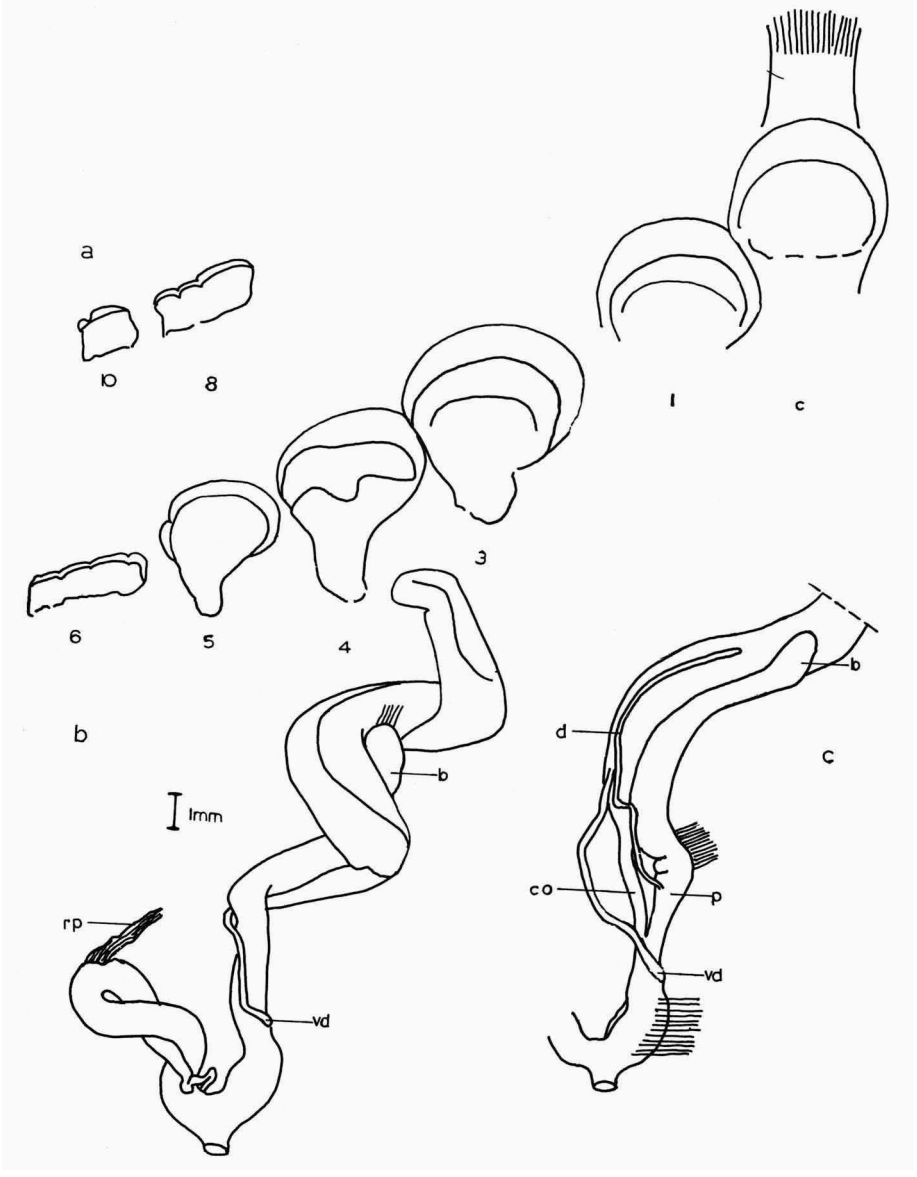

Fig. 10. *Peruinia flachi tingamariae* Pilsbry. a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

with one large and three smaller longitudinal muscular strips, forming a cross-shaped lumen in cross-section; the penis is wide, it has a rather complicated lumen and thick muscular walls over ¾ of its diameter, combined with strong papillae that penetrate far into the lumen.

Gracilinenia Polinski, 1921

Type-species: *Clausilia filocostulata* Lubomirski, 1879.

Radula. $\frac{c}{1} + \frac{1}{1} + \frac{m}{s-\infty}$. The two sides of the rows form an angle of about 120°, with the central tooth at the top; at the third tooth the rows regain a direction more nearly vertical to the axis of the radula, thus the central tooth and the first two lateral teeth have a very advanced position compared with the other teeth of the row to which they belong; the central tooth is vertical to the axis about in line with the third lateral tooth of the previous row. The cusps are more or less crescent-shaped. The basal plates and cusps of the central tooth and of the first two lateral teeth are large in comparison with those of the next teeth of the rows; from the third lateral tooth the elements diminish rather regularly in size to the outermost marginal teeth. The number of elements in a row is comparatively small.

Genital organs. The pedunculus has no diverticulum nor has the clear oviduct an appendix. The penis, however, has an appendix.

Gracilinenia filocostulata filocostulata (Lubomirski, 1879) (fig. 11)

The specimens investigated were collected in central Peru, Pan de Azúcar, Rio Tarma, 1400 m (W W. 286).

The animals (alcohol specimens) are dark grey, the foot-sole is whitish.

Radula. $\frac{c}{1} + \frac{s\,1}{1} + \frac{6-7\,m}{s-\infty}$.

Genital organs. Clear oviduct narrow, half as long as the vagina. Pedunculus wide, proximally about twice as wide as the clear oviduct. The bulbus of the receptaculum seminis is twice as wide as the duct itself. The vagina is rather short and narrow. The vas deferens passes into the epiphallus with a distinct widening, the epiphallus is internally provided with some small muscular strips, the lumen being a faintly curved line. The penis has a distinct appendix at its distal end, it is wider than the epiphallus and has internally two muscular strips, forming an m-shaped lumen in cross-section.

Gracilinenia filocostulata aequistriata Weyrauch, 1956 (fig. 12)

The specimens investigated were collected in central Peru, Valle de Chanchamayo, 1300 m (W W. 1531), paratypes.

The animals (alcohol specimens) are dark grey, almost black, with a reddish foot-sole.

Radula. $\frac{c}{1} + \frac{s\ l}{1} + \frac{6\ m}{s-\infty}$.

Genital organs. Clear oviduct narrow and about a quarter of the length of the vagina. Pedunculus wide, proximally about twice as wide as the clear oviduct. The bulbus of the receptaculum seminis is only a little wider than the duct itself. The vagina is rather short and narrow. The penis passes into the epiphallus with a distinct widening. The epiphallus is internally provided with some small muscular strips, the lumen is a faintly curved line in cross-section. The penis has the appendix at its distal end, it is rather wide and has a sickle-shaped lumen in cross-section, because of two thick muscular strips on the inner wall.

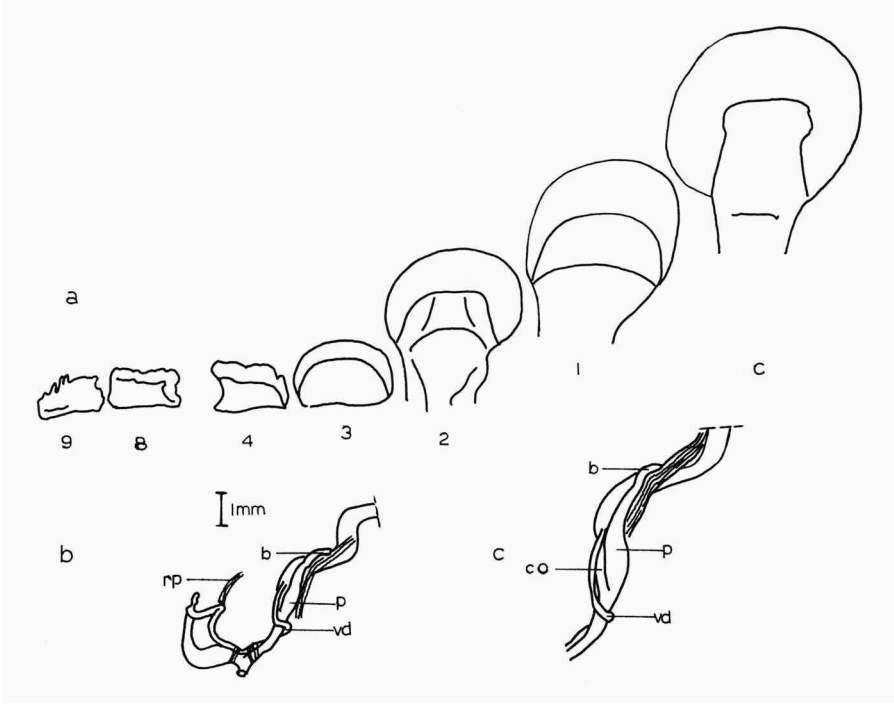

Fig. 11. *Gracilinenia f. filocostulata* (Lubomirski). a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; p, pedunculus; rp, retractor penis; vd, vas deferens).

Zilchiella Weyrauch, 1957

Type-species: *Z. grandiportus* Weyrauch, 1957.

Radula. $\frac{c}{1} + \frac{l}{1} + \frac{l}{2} + \frac{m}{s-\infty}$. The tooth-rows are almost rectilinear, with

the central tooth somewhat advanced. There are many small elements in one row, more than is usual in the Neniinae, the cusps are more or less dagger-shaped.

Genital organs. The pedunculus has a diverticulum which joins it just before it opens into the vagina, there is thus no "proximal part" of the pedunculus.

Fig. 12. *Gracilinenia filocostulata aequistriata* Weyrauch. a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; p, pedunculus; rp, retractor penis; vd, vas deferens).

Zilchiella grandiportus Weyrauch, 1957 (fig. 13)

The specimens investigated were collected in northern Peru, Peña Rota, 8 km N.E. of Bambamarca, left of Rio Llaucan, 2700 m (W W. 2005). paratypes.

The animals (alcohol specimens) are dark grey becoming black on the edge of the foot, sole whitish.

Radula. $\frac{c}{1} + \frac{28\ 1}{1} + \frac{5\ 1}{2} + \frac{13\ m}{3-\infty}$. The elements are strikingly small in comparison with the dimensions of the snail. The basal plates are elongate-rectangular; all the elements are of about the same size.

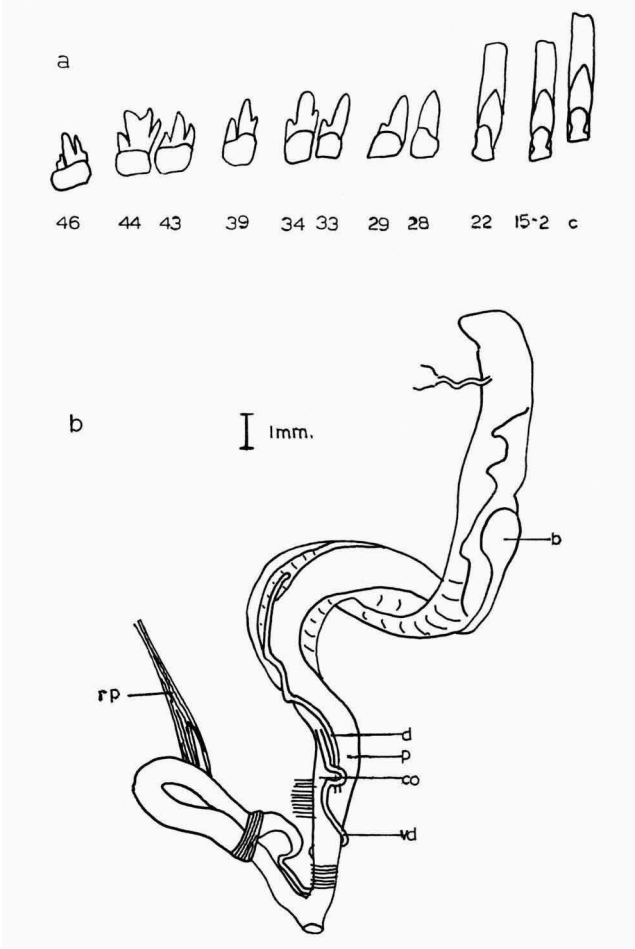

Fig. 13. *Zilchiella grandiportus* Weyrauch. a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Genital organs. Clear oviduct short, half the length of the short and wide vagina and about as wide as the pedunculus. The pedunculus is wide and long and has a large bulbus (twice as long as wide). The diverticulum is very narrow and about half as long as the pedunculus. The vas deferens passes gradually into the epiphallus, which has a hook-shaped lumen, the penis is moderately wide and has an S-shaped lumen. Retractor penis weak. The penis ligament is strong.

Pfeifferiella Weyrauch, 1957

Type-species: *Columbinia (Pfeifferiella) haasi* Weyrauch, 1957.

Radula. $\frac{c}{3} + \frac{1}{2} + \frac{m}{3-\infty}$. The tooth-rows are almost rectilinear with the central tooth somewhat advanced, the cusps are more or less dagger-shaped. The basal plates and the cusps diminish rather regularly in size from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has a glandular diverticulum which joins it just before it opens into the vagina, so there is no "proximal part" of the pedunculus.

Pfeifferiella haasi (Weyrauch, 1957) (fig. 14)

The specimens investigated were collected in northern Peru, Cerro Chunrun near Llama, 2350 m (W W. 2006), paratypes.

The animals (alcohol specimens) are brownish-black, with a whitish foot-sole.

Radula. $\frac{c}{3} + \frac{15\ 1}{2} + \frac{16\ m}{3-\infty}$.

Genital organs. Clear oviduct about as long as the vagina and as wide as the pedunculus. The latter is wide and long with hardly any widening to form a bulbus. The diverticulum opens into the pedunculus just at the mouth of this duct into the vagina, it is about half as long as the pedunculus. The distal half of the diverticulum is twisted and wider than the straight proximal end. The vas deferens passes into the epiphallus, visible by a distinct widening. The epiphallus is provided internally with one large muscular strip and many small wrinkled ones. The penis has distally an S-shaped lumen, proximally a line-like one. The retractor penis is rather short.

Pfeifferiella koepckei (Zilch, 1953)

Zilch (1953) described the radula (formula: $\frac{c}{3} + \frac{14\ 1}{2} + \frac{17\ m}{3-\infty}$) and gave a drawing of the genital organs, which agrees in its major features with that of *P. haasi* Weyrauch.

Temesa H. & A. Adams, 1855

Subgenus **Temesa** H. & A. Adams, 1855

Type-species: *Bulimus clausilioides* Reeve, 1849.

Presumably the characters of the radula and the genital organs of the genus are the following (based on the species investigated, the type-species is not known anatomically).

Radula. $\frac{c}{1} + \frac{1}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The tooth-rows are almost rectilinear, with the central tooth somewhat advanced, the cusps are more or less dagger-shaped. The often square basal plates and the cusps diminish rather regularly in size from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has a diverticulum which opens almost together with it into the vagina, so a "proximal part" of the pedunculus is

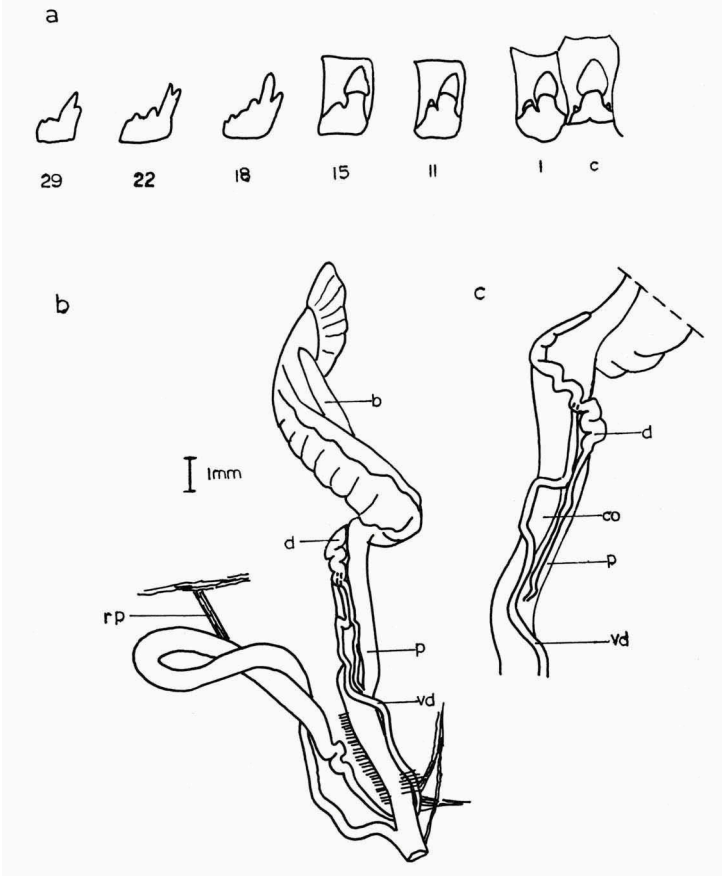

Fig. 14. *Pfeifferiella haasi* (Weyrauch). a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

not present. The rather long diverticulum is proximally wide, but its distal part is usually narrow.

Temesa (Temesa) albocostata albocostata Weyrauch, 1963 (fig. 15)

The specimens investigated were collected in central Peru, Alis, Rio Alis, side river of the Rio Cañete, 3300 m (W W. 3322), paratypes.

The animals (alcohol specimens) have the back black, sides and foot-sole grey.

Radula. $\frac{c}{1} + \frac{6\,1}{1} + \frac{2\,1}{2} + \frac{12\,m}{3-\infty}$. The basal plates are almost square.

Genital organs. Clear oviduct half as long as the vagina. Pedunculus proximally wider than the clear oviduct and the diverticulum together, about

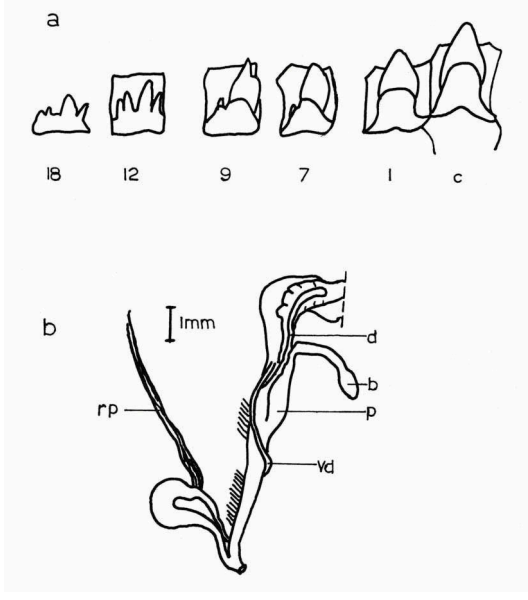

Fig. 15. *Temesa (Temesa) albocostata albocostata* Weyrauch. a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

as long as the vagina; the length of the bulbus is 1½ times its width. The diverticulum widens where the vas deferens and the oviduct separate, it is almost as long as the pedunculus. The epiphallus is internally provided with three muscular strips, which form a star-shaped lumen with three tips. The lumen of the penis is rather complicated by one large and some small muscular strips. The penis is distinctly broader than the epiphallus, a penis papilla is present there, accompanied by a small papilla, just beyond the retractor.

Temesa (Temesa) albocostata pygmaea Weyrauch, 1963

The specimens investigated were collected in central Peru, Quichao, 5 km from Laraos on the left bank of the Rio Mayo, sideriver of the Rio Cañete, 3500 m (W W. 3321), paratypes. The animals (alcohol specimens) are grey, the foot-sole is light grey.

We found no differences from the nominate subspecies.

Temesa (Temesa) andecola (Morelet, 1863) (fig. 16)

The specimens investigated were collected in central Peru, Tarmatambo near Tarma, 3500-3600 m (W W.277-A).

The animals (alcohol specimens) are brownish-grey, the foot-sole is reddish.

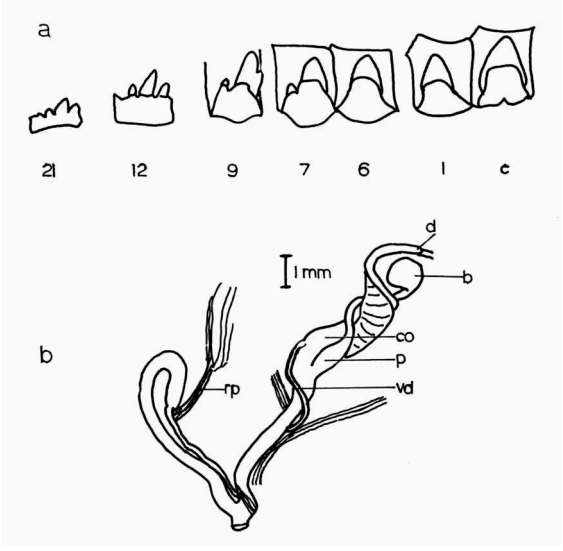

Fig. 16. *Temesa (Temesa) andecola* (Morelet). a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; co, clear oviduct; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Radula. $\frac{c}{1} + \frac{6\,1}{1} + \frac{2\,1}{2} + \frac{15\ m}{3-\infty}$. The radula-elements are rather small, the basal plates almost square.

Genital organs. Clear oviduct about one fifth of the length of the vagina and proximally as wide as the pedunculus and as the diverticulum. The pedunculus is as long as the vagina and has a true bulbus (1½ times as long as wide). The diverticulum is as long as the pedunculus (with the bulbus). The epiphallus is narrow, the lumen is slightly angle-shaped, it passes into the much wider penis; a penis papilla is present, just beyond the retractor.

Temesa (Temesa) balnearum (Crawford, 1939) (fig. 17)

The specimens investigated were collected in southern Peru, Tambo Machay, 6 km from Cuzco, Baño del Inca, 3500 m, leg. F. Carrasco.

The animals (alcohol specimens) are grey, the foot-sole is whitish.

The radula could not be studied.

Genital organs. Clear oviduct about one third of the length of the vagina. The pedunculus is twice as long as the vagina, and proximally as wide as the clear oviduct and the diverticulum together; the bulbus is about 1½ times as long as wide. The diverticulum is definitely longer than the pedunculus. The epiphallus is narrow, the lumen is slightly angle-shaped. A penis papilla is present, accompanied by one small additional papilla, just beyond the retractor; more proximally the penis lumen is circular.

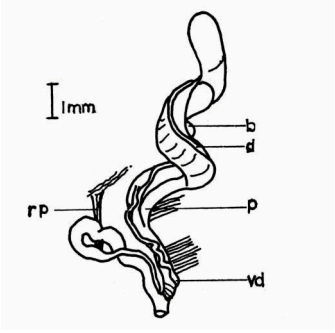

Fig. 17. *Temesa (Temesa) balnearum* (Crawford), genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Temesa (Temesa) decimvolvis crassicostata Weyrauch, 1958 (fig. 18)

The specimens investigated were collected in central Peru, Curicaca, Rio Mantaro, 3750 m (W W.3122), paratypes.

The animals (alcohol specimens) are grey, the foot-sole is white.

Radula. $\frac{c}{1} + \frac{7\ 1}{1} + \frac{4\ 1}{2} + \frac{17\ m}{3-\infty}$. The radula-elements are rather small, the basal plates almost square.

Genital organs. Clear oviduct about one fifth of the length of the vagina. Pedunculus proximally wider than the clear oviduct and the diverticulum together, and about as long as the vagina (the bulbus is not present, damaged). The diverticulum is as long as the pedunculus, it widens where the vas deferens and the oviduct separate. The epiphallus is narrow and has a more or less circular lumen excentrally situated. A penis papilla is present just beyond the attachment of the retractor, more proximally the penis is provided internally with many muscular strips, giving a complicated lumen.

Temesa (Temesa) incarum Pilsbry, 1926

Pilsbry (1926) gave some data on the radula and a drawing. According to him the radula formula is: $\frac{c}{1} + \frac{2\,1}{1} + \frac{6\,1}{2} + \frac{>16\,m}{3-\infty}$.

Temesa (Temesa) latestriata Weyrauch, 1958 (fig. 19)

The specimen investigated was collected in central Peru, above Acolla, along the road from Tarma to Jauja, 3700 m (W W.3121), paratype.

Radula. $\frac{c}{1} + \frac{5\,1}{1} + \frac{4\,1}{2} + \frac{18\,m}{3-\infty}$. The basal plates are almost square.

Genital organs. Clear oviduct about one fifth of the length of the vagina and half the width of the pedunculus. The distal parts of the latter duct and

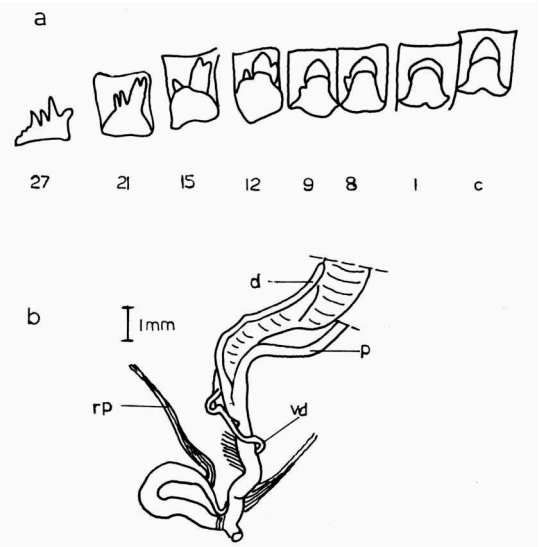

Fig. 18. *Temesa (Temesa) decimvolvis crassicostata* Weyrauch. a, some elements of the radula; b, genital apparatus (d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens; distal end of pedunculus damaged).

of the diverticulum could not be studied. The epiphallus is narrow. The penis widens rather abruptly and is provided with a penis papilla just beyond the attachment of the retractor; more proximally the penis has a more or less circular lumen, the inner wall is provided with rather weak muscular strips.

Temesa (Temesa) omissa Weyrauch, 1957 (fig. 20)

The specimens investigated were collected in central Peru, above Tarmatambo near Tarma, 3600 m (W W.277-B), paratypes.

The animals (alcohol specimens) are grey, the foot-sole is greyish.

Radula. $\frac{c}{1} + \frac{7\,1}{1} + \frac{2\,1}{2} + \frac{14\,m}{3-\infty}$. The radula elements are rather small, the basal plates almost square.

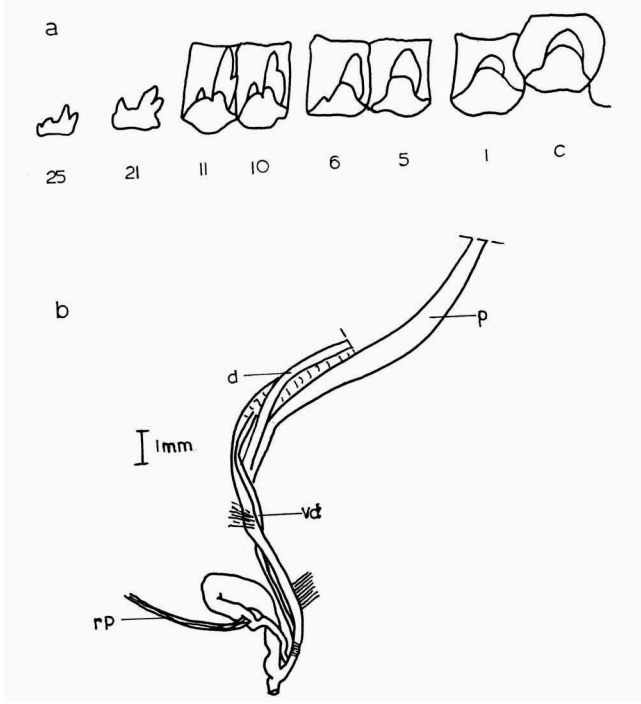

Fig. 19. *Temesa (Temesa) latestriata* Weyrauch. a, some elements of the radula; b, genital apparatus (d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens; distal ends of diverticulum and pedunculus damaged).

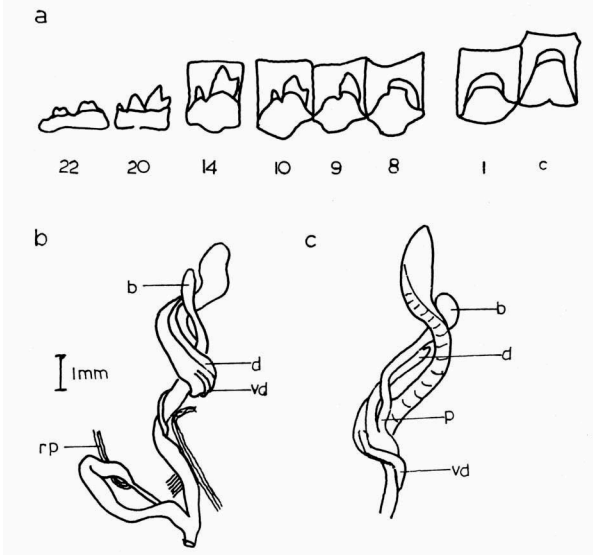

Fig. 20. *Temesa (Temesa) omissa* Weyrauch. a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Genital organs. Clear oviduct very short, about one tenth of the length of the vagina, it is as wide as the proximal part of the pedunculus and as the diverticulum. Pedunculus distinctly shorter than the vagina, and longer than the diverticulum. The bulbus is about 1½ times as long as wide. The epiphallus is narrow and has centrally a more or less circular lumen. A penis papilla is present shortly beyond the attachment of the retractor, more proximally the lumen of the penis is line-shaped.

Temesa (Temesa) peruviana peruviana (Pfeiffer, 1867) (fig. 21)

The specimens investigated were collected in southern Peru, Puno, 3900 m (W W.653).

The animals (alcohol specimens) are greyish-brown, the foot-sole is white.

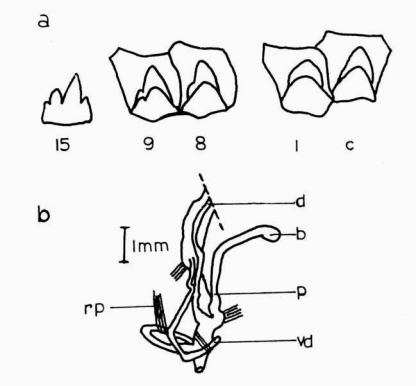

Fig. 21. *Temesa (Temesa) peruviana peruviana* (Pfeiffer). a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Radula. $\frac{c}{1} + \frac{8\,1}{1} + \frac{3\,1}{2} + \frac{13\,m}{3-\infty}$. The elements are rather small, the basal plates almost square.

Genital organs. Clear oviduct twice as long as the short vagina and as wide as the pedunculus and as the diverticulum. The bulbus is almost twice as long as wide. The penis has proximally four longitudinal muscular strips.

Temesa (Temesa) pilsbryi pilsbryi Weyrauch, 1956 (fig. 22)

The specimens investigated were collected in central Peru, El Infiernillo, on the right bank of Rio Rimac, 3360-3370 m (W W.3058), paratypes.

The animals (alcohol specimens) are light grey, with a white foot-sole.

Radula. $\frac{c}{1} + \frac{6\,1}{1} + \frac{2\,1}{2} + \frac{10\,m}{3-\infty}$. The elements are rather small, the basal plates rectangular.

Genital organs. Clear oviduct about one third of the length of the vagina.

The proximal part of the pedunculus is as wide as the clear oviduct and diverticulum together. This wide duct has a distinct bulbus (about twice as long as wide) and is about as long as the narrow diverticulum, more than twice as long as the vagina. The epiphallus is narrow and passes into the broader penis proximally to the attachment of the retractor; a penis papilla is present; more proximally three muscular strips protrude into the lumen of the penis.

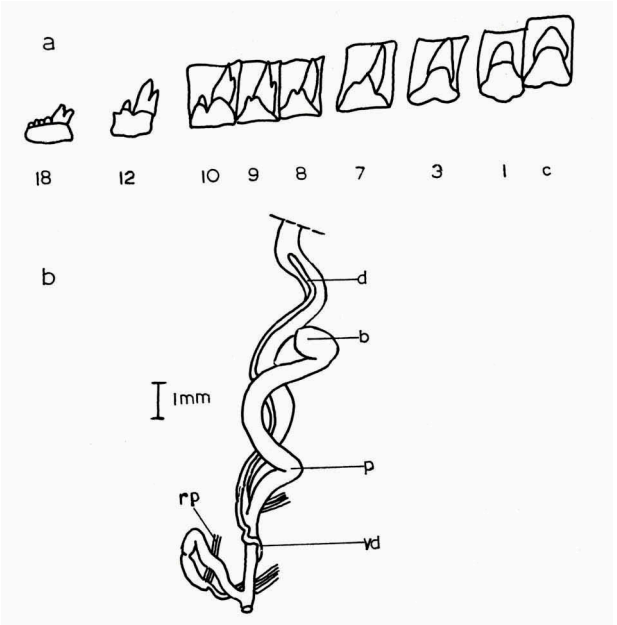

Fig. 22. *Temesa (Temesa) pilsbryi pilsbryi* Weyrauch. a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Temesa (Temesa) pilsbryi laraosensis Weyrauch, 1960 (fig. 23)

The specimens investigated were collected in central Peru, above Laraos, on the right bank of the Rio Shutco, 3750-3800 m (W W.3346-A), paratypes.

The animals (alcohol specimens) are dark grey and have a light grey foot-sole.

Radula. $\frac{c}{1} + \frac{4\ 1}{1} + \frac{3\ 1}{2} + \frac{14\ m}{3-\infty}$. The elements are rather small, the basal plates rectangular.

Genital organs. Clear oviduct about one eighth of the length of the vagina, in combination with the diverticulum it is wider than the proximal part of the pedunculus. The latter duct is narrow as is the diverticulum; the distal

parts of neither could be studied as the specimens were damaged. Epiphallus and penis as in the nominate subspecies. The penis is, as far as could be seen, proximally and internally not provided with conspicuous muscular strips.

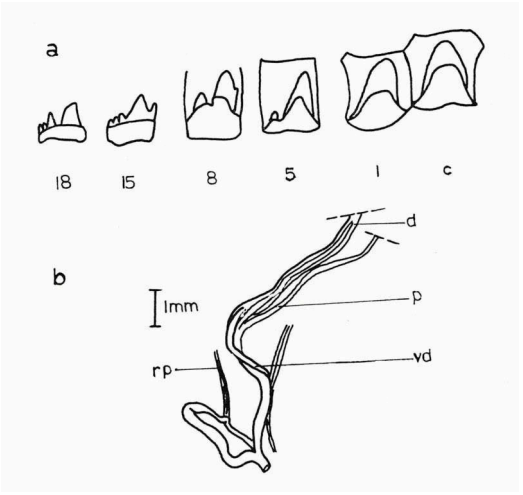

Fig. 23. *Temesa (Temesa) pilsbryi laraosensis* Weyrauch. a, some elements of the radula; b, genital apparatus (d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Temesa (Temesa) pilsbryi shutcoensis Weyrauch, 1960 (fig. 24)

The specimens investigated were collected in central Peru, above Laraos, on the left bank of the Rio Shutco, 3700 m (W W.3347), paratypes.

The animals (alcohol specimens) are dark grey and have a white foot-sole.

Radula. $\frac{c}{1} + \frac{4\,1}{1} + \frac{2\,1}{2} + \frac{17\,m}{3-\infty}$. The elements are rather small, the basal plates rectangular.

Genital organs. Clear oviduct about one fifth of the length of the vagina. The proximal part of the pedunculus is wider than clear oviduct and diverticulum together; it is about as long as the vagina and has a distinct bulbus (about 1½ times as long as wide). The diverticulum is definitely longer and narrower. Epiphallus and penis as in the nominate subspecies. The penis however is internally proximally not provided with conspicuous muscular strips.

Subgenus **Neniatracta** Pilsbry, 1926

Type-species: *Nenia belahubbardi* Pilsbry, 1922.

Presumably the characters of the radula and genital organs of the subgenus are the following (the type-species is not known anatomically).

Radula. $\frac{c}{3} + \frac{1}{2} + \frac{m}{3-\infty}$. The tooth-rows are rectilinear, or the two sides

of the rows meet at a slight angle, with the central tooth somewhat advanced, the cusps are more or less dagger-shaped. The basal plates and the cusps diminish rather regularly in size from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has a glandular diverticulum which opens almost together with it into the vagina, so there is no "proximal part" of the pedunculus.

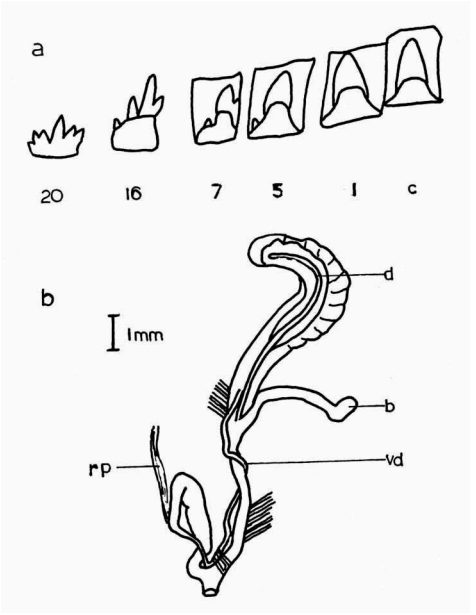

Fig. 24. *Temesa (Temesa) pilsbryi shutcoensis* Weyrauch. a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; rp, retractor penis; vd, vas deferens).

Temesa (Neniatracta) argentina (Hylton Scott, 1954) (fig. 25)

Scott (1954) described and figured the jaw, the radula and the genital apparatus.

The specimens investigated were collected in Argentina, Province of Salta, Camino de Corniza, between Salta and Jujuy, 1400 m, leg. W. Weyrauch.

The animals (alcohol specimens) are dark grey, with a white foot-sole.

Radula. $\frac{c}{3} + \frac{14\ 1}{2} + \frac{14\ m}{3-\infty}$ (Scott mentioned: $\frac{c}{3} + \frac{15\ 1}{2} + \frac{10\ m}{3-\infty}$). The rows are almost rectilinear, the basal plates and cusps comparatively small.

Genital organs. Clear oviduct short, about one fifth of the length of the vagina. The pedunculus is somewhat narrower than the clear oviduct; it is

rather short, about as long as the vagina and has a distinct bulbus (about 1½ times as long as wide). The diverticulum is short and narrow, it opens into the pedunculus just at its opening into the vagina, the most proximal part is distinctly twisted. The epiphallus is internally provided with a circular lumen, the penis has distally a star-like lumen with 3 tips and proximally a line-shaped lumen.

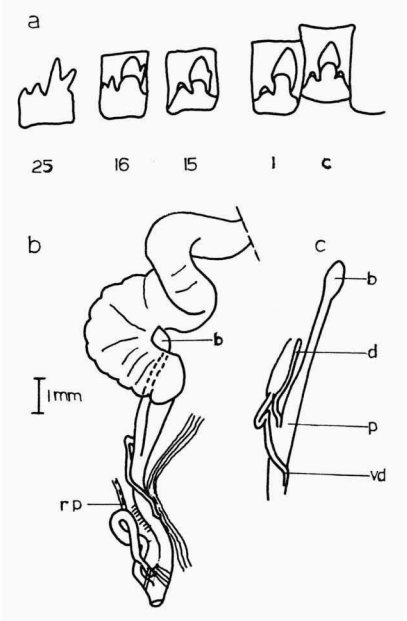

Fig. 25. *Temesa (Neniatracta) argentina* (Hylton Scott). a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Temesa (Neniatracta) bequaerti Weyrauch, 1957 (fig. 26)

The specimens investigated were collected in northern Peru at Cerro Machaipungo near Bambamarca, 3000 m (W W. 2010-A), paratypes.

The animals (alcohol specimens) are grey, with a whitish foot-sole.

Radula. $\frac{c}{3} + \frac{14\ 1}{2} + \frac{14\ m}{3-\infty}$. The rows are slightly angular, the basal plates and the cusps comparatively small.

Genital organs. Clear oviduct hardly present, at most one twelfth of the length of the vagina, and about as wide as the pedunculus. This duct is rather wide and long, it has a distinct bulbus, about 1½ times as long as wide. The short and twisting diverticulum is not longer than one third of the pedunculus, it opens into the latter duct just at its opening into the vagina. The epiphallus is internally provided with two strong muscular strips that

form a line-shaped lumen, its passage into the penis is externally visible by a distinct broadening within which the two strips become higher, with a smaller base; between the two bases are small wrinkled strips. Vas deferens bound to the penis over a rather long distance by the penis ligament.

Weyrauch (1964b) established a new genus, *Bequaertinenia*, for this species.

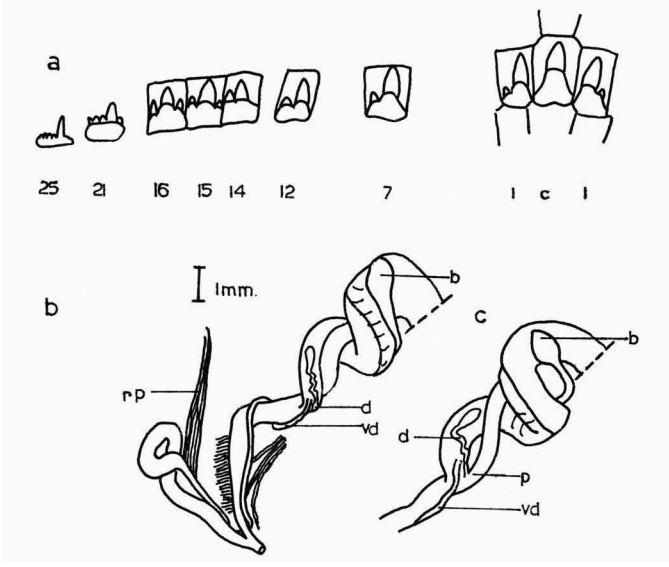

Fig. 26. *Temesa (Neniatracta) bequaerti* Weyrauch. a, some elements of the radula; b, c, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Temesa (Neniatracta) parcecostata Polinski, 1922 (fig. 27)

The specimens investigated were collected in central Peru, Cerro Huayuncayo near La Florida, Rio Tarma, 3050 m (W W.267-B).

The animals (alcohol specimens) are dark grey, with a light grey foot-sole.

Radula. $\frac{c}{3} + \frac{7\,1}{2} + \frac{21\ m}{3-\infty}$. The rows are almost rectilinear, the basal plates and cusps comparatively small.

Genital organs. Clear oviduct short, about one sixth of the length of the vagina. The pedunculus is narrower than both the clear oviduct and the proximal end of the diverticulum; it is a bit shorter than the vagina, and has a distinct bulbus (about 1½ times as long as wide). The diverticulum is proximally rather wide, distally narrow, it is longer than the pedunculus and about as long as the vagina. The diverticulum opens almost together with the said duct into the vagina. Both epiphallus and penis have, as far as can be seen, a circular lumen, the specimens are not in a good condition.

Andinia Polinski, 1922

Type-species: *Clausilia taczanowski* Lubomirski, 1879.

Radula. $\frac{c}{1} + \frac{1}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The rows are almost rectilinear, with the central tooth somewhat advanced. The cusps are more or less dagger-shaped, the basal plates square; the elements diminish rather regularly in size from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has no diverticulum, the clear oviduct however has a short and narrow appendix, which has a lumen distally but which ends without a lumen a short distance distally from the entrance of the pedunculus into the vagina.

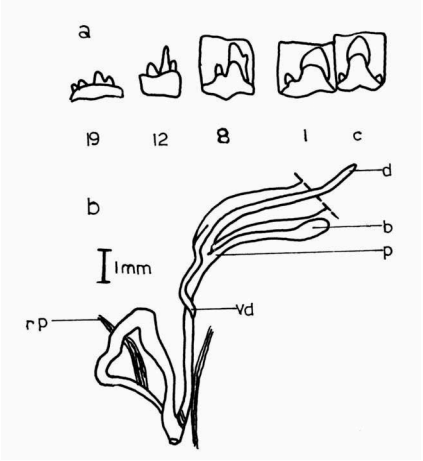

Fig. 27. *Temesa (Neniatracta) parcecostata* Polinski. a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; d, diverticulum; p, pedunculus; rp, retractor penis; vd, vas deferens).

Andinia taczanowski (Lubomirski, 1879) (fig. 28)

Polinski (1922) gave some data on the radula and figured some elements.

The specimens investigated were collected in northern Peru, Cerro Macheipungo, 4 km N.W. of Bambamarca, 3000 m (W W.655-A).

The animals (alcohol specimens) are black, the foot-sole is whitish.

Radula. $\frac{c}{1} + \frac{6-7\ 1}{1} + \frac{5-6\ 1}{2} + \frac{13\ m}{3-4}$.

Genital organs. Clear oviduct one fourth to one fifth of the length of the vagina and about as wide as the pedunculus; the latter is wide and long (as long as the vagina), the bulbus is hardly wider than the duct. The appendix to the clear oviduct is only slightly longer than the clear oviduct itself. The vagina is long and rather wide. The epiphallus is internally provided with two large and one small muscular strip, leaving a more or less T-shaped lumen. Penis

very wide, internally provided with about twelve rather strong muscular strips, forming a star-shaped lumen.

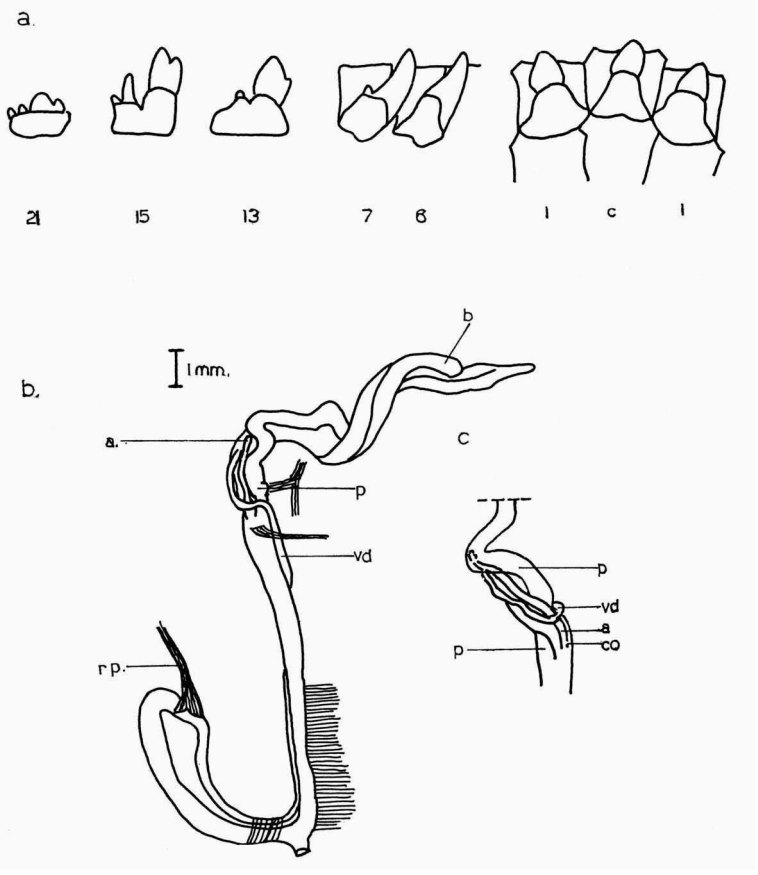

Fig. 28. *Andinia taczanowski* (Lubomirski). a, some elements of the radula; b, c, genital apparatus (a, appendix of clear oviduct; b, bulbus of receptaculum seminis; co, clear oviduct; p, pedunculus; rp, retractor penis; vd, vas deferens).

Steeriana Jousseaume, 1900

Subgenus **Steeriana** Jousseaume, 1900

Type-species: *Clausilia steeriana* Sykes, 1893.

Radula. $\frac{c}{1} + \frac{1}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The rows are almost rectilinear, with the central tooth somewhat advanced; the cusps are more or less dagger-shaped. The basal plates are almost square; the elements diminish rather regularly in size, from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has no diverticulum; the clear oviduct however has a short and narrow appendix, which has a lumen distally, but

which ends without a lumen a short distance distally from the entrance of the pedunculus into the vagina.

Steeriana (Steeriana) malleolata (Philippi, 1867) (fig. 29; pl. 1)

Synonym: *Clausilia steeriana* Sykes, 1893.

Pilsbry (1926) described and figured the radula.

The specimens investigated were collected in northern Peru, at the road from Cajamarca to Celendin, km stone 28, 3150 m (W W.122).

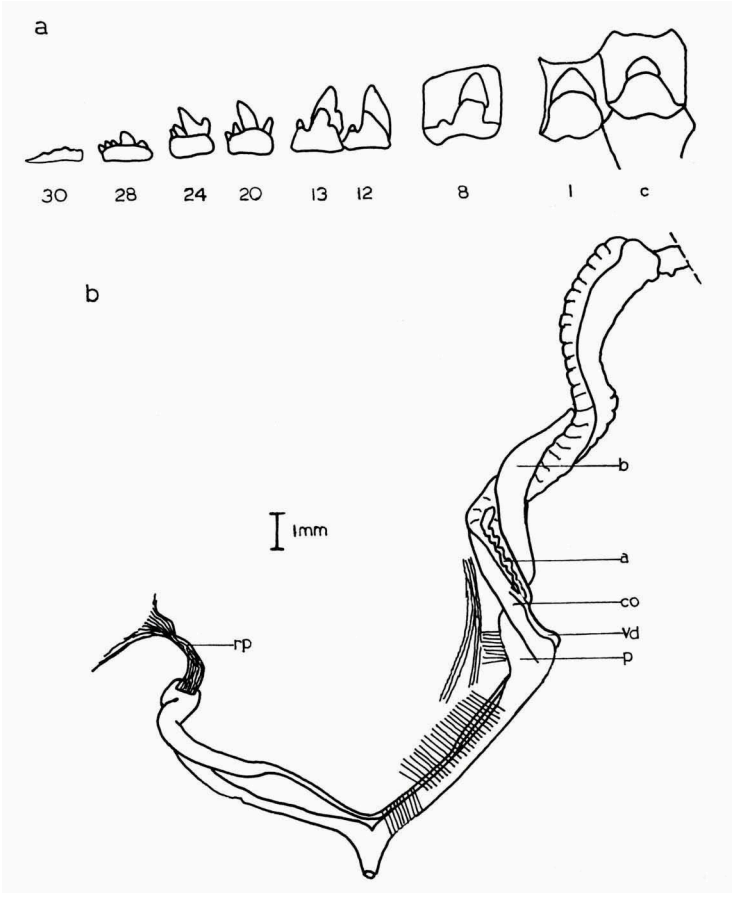

Fig. 29. *Steeriana (Steeriana) malleolata* (Philippi). a, some elements of the radula; b, genital apparatus (a, appendix of clear oviduct; b, bulbus of receptaculum seminis; co, clear oviduct; p, pedunculus; rp, retractor penis; vd, vas deferens).

The animals (alcohol specimens) are blackish-brown on the back, the colour fades downward, foot-sole whitish.

Radula. $\frac{c}{1} + \frac{7\ 1}{1} + \frac{5\ 1}{2} + \frac{18\ m}{3-\infty}$ (according to Pilsbry, 1926: $\frac{c}{1} + \frac{7\ 1}{1} + \frac{7\ 1}{2} + \frac{18-19\ m}{3-\infty}$).

Genital organs. Clear oviduct short, about one fourth of the length of the vagina and about as wide as the pedunculus. The latter is wide and has a long bulbus, about as long as the pedunculus itself. A diverticulum is not present; the appendix to the clear oviduct is distally wrinkled. The vagina is rather wide. The epiphallus is internally provided with two muscular strips, leaving a T-shaped lumen. Penis internally with many wrinkled muscular strips that give a granulated appearance to the inner surface, lumen circular.

Steeriana (Steeriana) cajamarcana Weyrauch & Zilch, 1954 (fig. 30)

The specimens investigated were collected in northern Peru, Hacienda Cochambul, 18 km from Cajamarca, on the road to San Marcos, 2850 m (W W.788), paratypes.

The animals (alcohol specimens) have black warts on back and sides, the foot-sole is whitish.

Radula. $\frac{c}{1} + \frac{5\ 1}{1} + \frac{5-7\ 1}{2} + \frac{11\ m}{3-\infty}$. The basal plates are less square than in the previous species.

Genital organs. Clear oviduct short, about one third of the length of the vagina and hardly as wide as the proximal end of the pedunculus. The latter is wide and has a distinct bulbus (1½ times as long as wide). A diverticulum is not present but the clear oviduct has a short, distally twisted appendix. The epiphallus is internally provided with two muscular strips, which

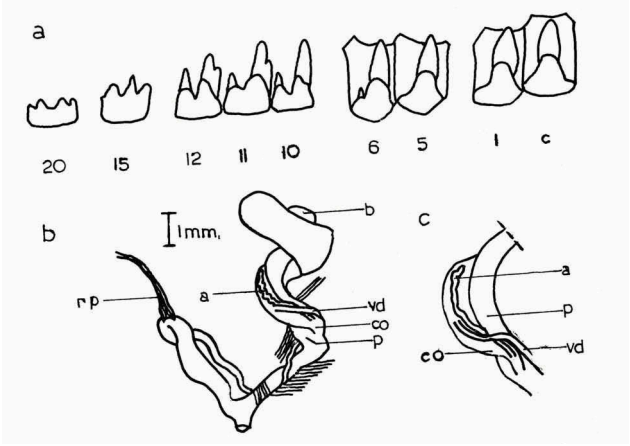

Fig. 30. *Steeriana (Steeriana) cajamarcana* Weyrauch & Zilch. a, some elements of the radula; b, c, genital apparatus (a, appendix of clear oviduct; b, bulbus of receptaculum seminis; co, clear oviduct; p, pedunculus; rp, retractor penis; vd, vas deferens).

leave a T-shaped lumen. Penis rather wide, internally with many wrinkled muscular strips that give a granulated appearance to the inner surface, lumen circular.

Specimens of another sample from northern Peru, 3 km N.W. from Cajabamba, 2780 m (W W.2133) agree with this description, except that the radula formula is $\frac{c}{1} + \frac{6\,1}{1} + \frac{3\,1}{2} + \frac{17\ m}{3-\infty}$.

Subgenus **Cylindronenia** Ehrmann, 1949

Type-species: *Clausilia maranhonensis* Albers, 1854.

Radula. $\frac{c}{1} + \frac{1}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The rows are almost rectilinear, with the central tooth only slightly advanced, the cusps are more or less dagger-shaped, the basal plates square; the elements diminish rather regularly in size, from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has no diverticulum, the clear oviduct however has a short and narrow appendix, which has a lumen distally, but which ends without a lumen a short distance distally from the entrance of the pedunculus into the vagina.

Steeriana (Cylindronenia) maranhonensis maranhonensis (Albers, 1854) (fig. 31)

The specimens investigated were collected in northern Peru, Sta. Rosa near Rio Chinchipe, at its confluence with Rio Marañon, 1400 m (W W.702).

The animals (alcohol specimens) are blackish, with a rather white foot-sole.

Radula. $\frac{c}{1} + \frac{6\,1}{1} + \frac{8\,1}{2} + \frac{6\ m}{3-\infty}$.

Genital organs. These were almost entirely degenerated and not fit for study.

Fig. 31. *Steeriana (Cylindronenia) maranhonensis maranhonensis* (Albers), some elements of the radula.

Steeriana (Cylindronenia) canescens (Polinski, 1921) (fig. 32)

The specimens investigated were collected in northern Peru, El Recodo, Rio Chamaya, at the road Olmos-Jaën, km stone 160, 700 m (W W.3366).

The animals (alcohol specimens) are light grey, both above and on the foot-sole.

Radula. $\frac{c}{1} + \frac{7-8\ 1}{1} + \frac{7\ 1}{2} + \frac{10-11\ m}{3-\infty}$.

Genital organs. Clear oviduct about half as long as the vagina and less wide than the pedunculus; the latter is rather narrow and only wide at its proximal end, the bulbus is long and wide (3 times as long as wide). The distal part of the appendix to the clear oviduct is definitely twisted and is slightly longer than the clear oviduct itself. The vagina is well developed and wide. The epiphallus has internally four distinct muscular strips, forming a cross-like lumen, the penis is very wide, the inner wall is provided with twelve strong muscular strips, the lumen is star-shaped.

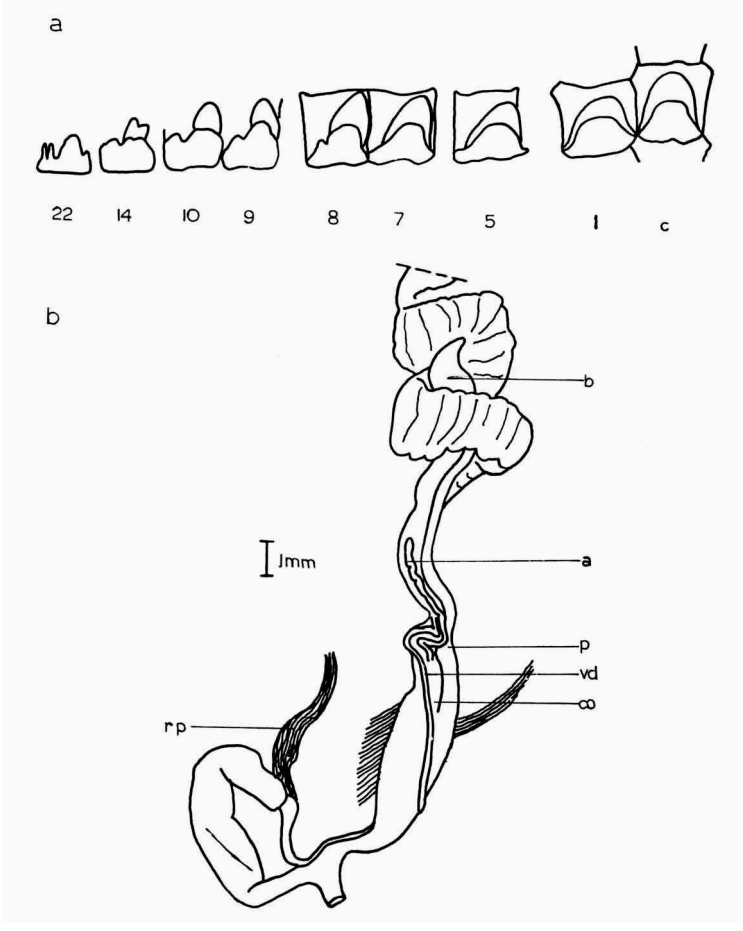

Fig. 32. *Steeriana (Cylindronenia) canescens* (Polinski). a, some elements of the radula; b, genital apparatus (a, appendix of clear oviduct; b, bulbus of receptaculum seminis; co, clear oviduct; p, pedunculus; rp, retractor penis; vd, vas deferens).

Steeriana (Cylindronenia) huarangoensis Zilch, 1949 (fig. 33)

The specimens investigated were collected in northern Peru, Huarango, near the confluence of the Rio Chinchipe and the Rio Marañon, 1600 m (W W.701).

The animals (alcohol specimens) are brown, with a greyish-white foot-sole.

Radula. $\frac{c}{1} + \frac{8\ 1}{1} + \frac{8\ 1}{2} + \frac{10\ m}{3-\infty}$.

Genital organs. Clear oviduct short, about one fifth of the length of the

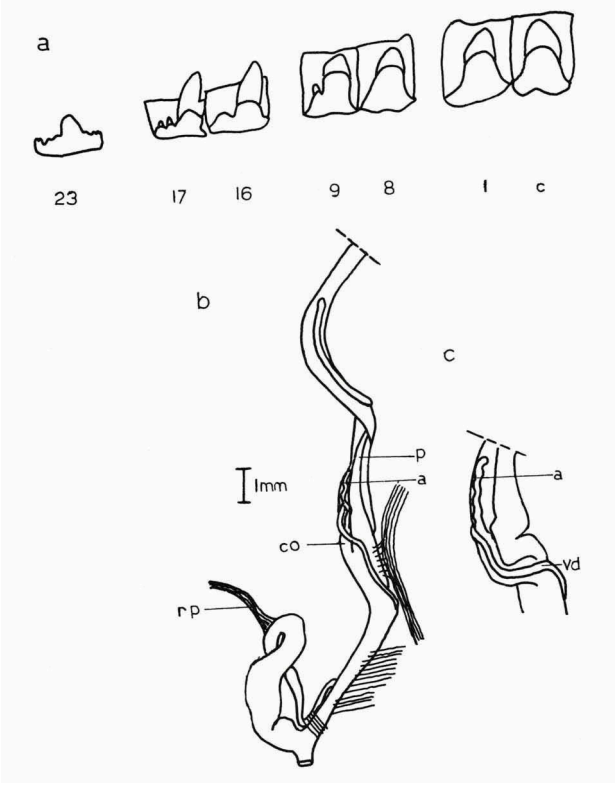

Fig. 33. *Steeriana (Cylindronenia) huarangoensis* Zilch. a, some elements of the radula; b, c, genital apparatus (a, appendix of clear oviduct; co, clear oviduct; p, pedunculus; rp, retractor penis; vd, vas deferens).

vagina and hardly as wide as the proximal end of the pedunculus, the latter is narrow and only wide at the proximal end, it has distally no definite bulbus. The twisted appendix to the clear oviduct is only slightly longer than the clear oviduct itself. The vagina is well developed. The epiphallus has internally two large muscular strips and between these at one

side one more small strip, the opposite side is devoid of strips. Penis very wide, with many wrinkled muscular strips that give a granulated appearance to the inner surface, the lumen is circular.

Hemicena Pilsbry, 1949

Type-species: *Nenia polinskiana* Pilsbry, 1949.

Radula. $\frac{c}{3} + \frac{1}{2} + \frac{m}{3-\infty}$. The rows are almost rectilinear, with the central tooth somewhat advanced, the cusps more or less dagger-shaped, the basal plates almost rectangular; the elements diminish rather regularly in size, from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has no diverticulum; the clear oviduct however has a short and narrow appendix, which has a lumen distally, but which ends without a lumen a short distance distally from the entrance of the pedunculus into the vagina.

Hemicena polinskiana polinskiana (Pilsbry, 1949) (fig. 34)

The specimens investigated were collected in central Peru, Tapacocha, Rio Fortaleza, 3200 m (W W.481-A).

The animals (alcohol specimens) are blackish-brown, with a whitish foot-sole.

Radula. $\frac{c}{3} + \frac{13\ 1}{2} + \frac{16\ m}{3-\infty}$.

Genital organs. Clear oviduct about half as long as the vagina and definitely wider than the pedunculus. The latter duct is rather narrow and has a bulbus which is about 3 times as long as wide. The narrow appendix to the clear oviduct has half the length of the pedunculus with the bulbus. The vagina is rather wide. The lumen of the epiphallus is rounded, like that of the penis. Both male organs are extremely small.

Hemicena polinskiana colcabambensis Zilch, 1959

Zilch (1959) described the radula and figured some teeth. Formula according to his data: $\frac{c}{1} + \frac{12\ 1}{2} + \frac{11\ m}{3-4}$. As the two side cusps of the central tooth in our *H. p. polinskiana* specimens are small and not always clearly visible (especially not in the first and last rows of the radula) we suppose that they have been overlooked. The genital apparatus shows for this subspecies a very twisted appendix to the clear oviduct.

Hemicena polinskiana cerrateae Weyrauch, 1958 (fig. 35)

The specimens investigated were collected in central Peru, Ainin, N. of Chiquián, Rio Pativilca, 3300 m (W W.1899-A), paratypes.

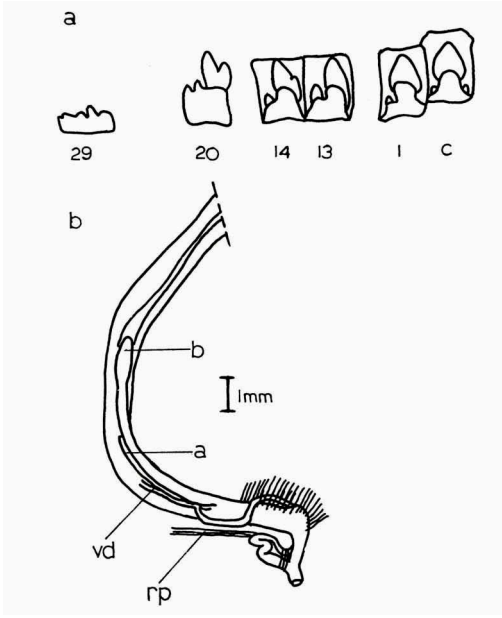

Fig. 34. *Hemicena polinskiana polinskiana* (Pilsbry). a, some elements of the radula; b, genital apparatus (a, appendix of clear oviduct; b, bulbus of receptaculum seminis; rp, retractor penis; vd, vas deferens).

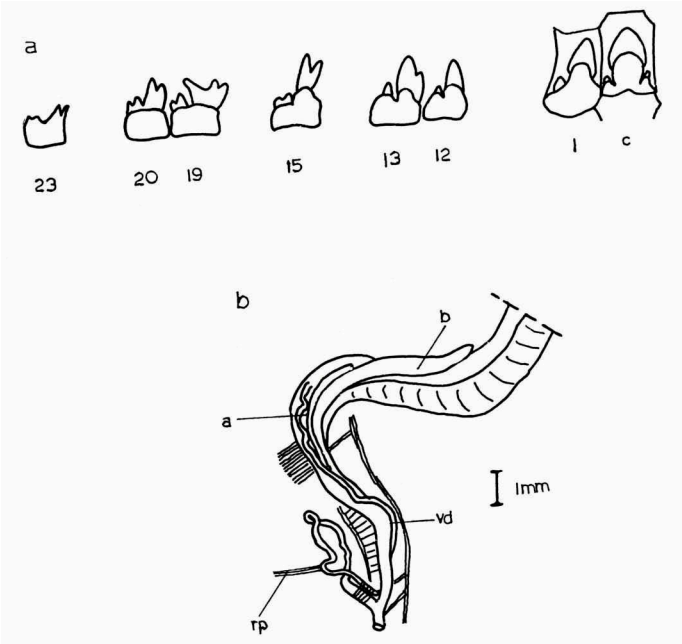

Fig. 35. *Hemicena polinskiana cerrateae* Weyrauch. a, some elements of the radula; b, genital apparatus (a, appendix of clear oviduct; b, bulbus of receptaculum seminis; rp, retractor penis; vd, vas deferens).

The animals (alcohol specimens) are blackish-brown on the back, black at the sides and have a white foot-sole.

Radula. $\frac{c}{3} + \frac{12\ l}{2} + \frac{13\ m}{3—\infty}$.

Genital organs. Clear oviduct less than half the length of the vagina and wider than the pedunculus. The latter has a definite bulbus which is 3 to 4 times as long as wide. The narrow appendix to the clear oviduct has half the length of the pedunculus with the bulbus. The vagina is rather wide. The epiphallus and penis are very small in comparison to the female tract.

Columbinia Polinski, 1924

Type-species: *Nenia columbiana* Polinski, 1924.

Presumably the characters of the radula and genital organs of the genus are the following (based on *C. bryantwalkeri* (Pilsbry); the type-species is not known anatomically).

Radula. $\frac{c}{3} + \frac{l}{2} + \frac{m}{3—\infty}$. The rows are almost rectilinear, with the central tooth somewhat advanced, the cusps are more or less dagger-shaped. The basal plates and the cusps diminish rather regularly in size from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has no diverticulum, an appendix to the clear oviduct is not present.

Columbinia bryantwalkeri (Pilsbry, 1922) (fig. 36)

The specimen investigated was collected in central Peru, Tingo Maria, Rio Huallaga, 670 m (W W.61).

Radula. $\frac{c}{3} + \frac{8\ l}{2} + \frac{15\ m}{3—\infty}$.

Genital organs. Clear oviduct almost twice as long as the vagina; it is only slightly wider than the pedunculus, which is thin and long, a bit less than twice as long as the clear oviduct. The pedunculus has no distinct bulbus, nor has it a diverticulum. The epiphallus passes into the penis with a distinct widening, internally a low penis papilla is present. The retractor penis is weak.

Columbinia cyclostoma (Pfeiffer, 1849)

Hesse (1925) described the radula, the formula is $\frac{c}{3} + \frac{11\ l}{2} + \frac{19\ m}{3—\infty}$.

Columbinia marshalli (Pilsbry, 1926)

Pilsbry (1926) gave some data on the radula: $\frac{c}{3} + \frac{l}{2} + \frac{m}{3—\infty}$, the basal plates are long, the cusps short.

Incania Polinski, 1921

Type-species: *Clausilia chacaensis* Lubomirski, 1879.

Presumably the characters of the radula and genital organs of the genus are the following (based on *I. trigonostoma* (Boettger); the type-species is not known anatomically).

Radula. $\frac{c}{1} + \frac{1}{2} + \frac{m}{3-\infty}$. The tooth-rows are almost rectilinear, with the central tooth somewhat advanced, the cusps are more or less dagger-shaped. The basal plates and the cusps diminish rather regularly in size.

Genital organs. The pedunculus has no diverticulum, an appendix to the clear oviduct is not present.

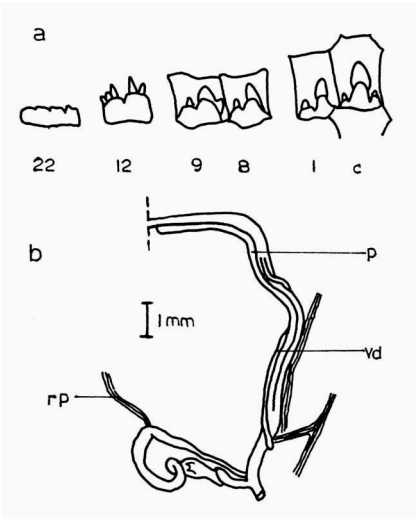

Fig. 36. *Columbinia bryantwalkeri* (Pilsbry). a, some elements of the radula; b, genital apparatus (p, pedunculus; rp, retractor penis; vd, vas deferens).

Incania jelskii (Polinski, 1921)

Polinski (1922) gave some data on the radula, the formula is $\frac{c}{1} + \frac{1}{2} + \frac{m}{3-4}$, the cusps are dagger-shaped.

Incania trigonostoma (O. Boettger, 1880) (fig. 37)

The specimen investigated was collected in central Peru, Pan de Azúcar, Rio Tarma, 1400 m (W W. 1371).

The animal (alcohol specimen) is whitish on the back, the sides are grey, fading into white near the foot-sole, which is almost white itself.

Radula. $\frac{c}{1} + \frac{13\ 1}{2} + \frac{25\ m}{3-\infty}$. The basal plates are comparatively small.

TABLE I

	radula			genital organs			
	I	II	III	IV	V	VI	VII
Nenia tridens (Chemnitz)	s	$\frac{c}{1}+\frac{8-10}{2}+\frac{19-21}{3-\infty}$	d	+	w		—
Ehrmanniella quadrata (O. Boettger)	a	$\frac{c}{1}+\frac{7}{2}+\frac{12}{3-\infty}$	d	+	w		—
boettgeri (Pilsbry)	a	$\frac{c}{1}+\frac{11}{2}+\frac{9}{3-\infty}$	d	+	w		—
Andiniella flammulata (Loosjes)	a	$\frac{c}{1}+\frac{3}{1}+\frac{3}{2}+\frac{6}{3-\infty}$	d	+	n		—
sztolcmani (Polinski)	a	$\frac{c}{1}+\frac{5}{1}+\frac{3}{2}+\frac{5-6}{3-\infty}$	d	+	n		—
Peruinia p. peruana (Troschel)	a	$\frac{c}{1}+\frac{6}{1}+\frac{2}{2}+\frac{5}{3-\infty}$	c	+	n		—
p. granulosa (Sykes)	a	$\frac{c}{1}+\frac{5}{1}+\frac{1}{2}+\frac{5}{3-\infty}$	c	+	n		—
albicolor Weyrauch	a	$\frac{c}{1}+\frac{4}{1}+\frac{2}{2}+\frac{5}{3-\infty}$	c	+	n		—
flachi superba Weyrauch	a	$\frac{c}{1}+\frac{6}{1}+\frac{2}{2}+\frac{6}{3-\infty}$	c	+	n		—
f. tingamariae Pilsbry	a	$\frac{c}{1}+\frac{4}{1}+\frac{1}{2}+\frac{7}{3-\infty}$	c	+	n		—
Gracilinenia f. filocostulata (Lubomirski)	a	$\frac{c}{1}+\frac{3}{1}+\frac{6}{3-\infty}$	c			—	+
f. aequistriata Weyrauch	a	$\frac{c}{1}+\frac{3}{1}+\frac{6}{3-\infty}$	c			—	+
Zilchiella grandiportus Weyrauch	s	$\frac{c}{1}+\frac{28}{1}+\frac{5}{2}+\frac{13}{3-\infty}$	d	—	n		—
Pfeifferiella haasi (Weyrauch)	s	$\frac{c}{3}+\frac{15}{2}+\frac{16}{3-\infty}$	d	—	n		—
koepckei (Zilch)	s	$\frac{c}{3}+\frac{14}{2}+\frac{17}{3-\infty}$	d	—	n		—
Temesa (Temesa) a. albocostata Weyrauch	s	$\frac{c}{1}+\frac{6}{1}+\frac{2}{2}+\frac{12}{3-\infty}$	d	—	w		—
andecola (Morelet)	s	$\frac{c}{1}+\frac{6}{1}+\frac{2}{2}+\frac{15}{3-\infty}$	d	—	w		—
balnearum (Crawford)	?	?	?	—	w		—
decimvolvis crassicostata Weyrauch	s	$\frac{c}{1}+\frac{7}{1}+\frac{4}{2}+\frac{17}{3-\infty}$	d	—	w		—
incarum Pilsbry	s	$\frac{c}{1}+\frac{2}{1}+\frac{6}{2}+\frac{16}{3-\infty}$	d	?	?	?	?
latestriata Weyrauch	s	$\frac{c}{1}+\frac{5}{1}+\frac{4}{2}+\frac{18}{3-\infty}$	d	—	w		—
omissa Weyrauch	s	$\frac{c}{1}+\frac{7}{1}+\frac{2}{2}+\frac{14}{3-\infty}$	d	—	w		—
p. peruviana (Pfeiffer)	s	$\frac{c}{1}+\frac{8}{1}+\frac{3}{2}+\frac{13}{3-\infty}$	d	—	w		—
pilsbryi pilsbryi Weyrauch	s	$\frac{c}{1}+\frac{6}{1}+\frac{2}{2}+\frac{10}{3-\infty}$	d	—	w		—
p. laraosensis Weyrauch	s	$\frac{c}{1}+\frac{4}{1}+\frac{3}{2}+\frac{14}{3-\infty}$	d	—	w		—
p. shutcoensis Weyrauch	s	$\frac{c}{1}+\frac{4}{1}+\frac{2}{2}+\frac{17}{3-\infty}$	d	—	w		—
Temesa (Neniatracta) argentina (Hylton Scott)	s	$\frac{c}{3}+\frac{14}{2}+\frac{14}{3-\infty}$	d	—	n		—
bequaerti Weyrauch	s	$\frac{c}{3}+\frac{14}{2}+\frac{14}{3-\infty}$	d	—	n		—
parcecostata Polinski	s	$\frac{c}{3}+\frac{7}{2}+\frac{21}{3-\infty}$	d	—	w		—
Andinia taczanowski (Lubomirski)	s	$\frac{c}{1}+\frac{6}{1}+\frac{6}{2}+\frac{13}{3-\infty}$	d			+	—
Steeriana (Steeriana) malleolata (Philippi)	s	$\frac{c}{1}+\frac{7}{1}+\frac{5}{2}+\frac{18}{3-\infty}$	d			+	—
cajamarcana Weyrauch & Zilch	s	$\frac{c}{1}+\frac{5}{1}+\frac{5}{2}+\frac{11}{3-\infty}$	d			+	—
Steeriana (Cylindronenia) m. maranhonensis (Albers)	s	$\frac{c}{1}+\frac{6}{1}+\frac{8}{2}+\frac{6}{3-\infty}$	d			?	?
canescens (Polinski)	s	$\frac{c}{1}+\frac{7-8}{1}+\frac{7}{2}+\frac{10-11}{3-\infty}$	d			+	—
huarangoensis Zilch	s	$\frac{c}{1}+\frac{8}{1}+\frac{8}{2}+\frac{10}{3-\infty}$	d			+	—
Hemicena p. polinskiana Pilsbry	s	$\frac{c}{3}+\frac{13}{2}+\frac{16}{3-\infty}$	d			+	—
p. colcabambensis Zilch	s	$\frac{c}{1}+\frac{12}{2}+\frac{11}{3-\infty}$	d			+	—
p. cerrateae Weyrauch	s	$\frac{c}{3}+\frac{12}{2}+\frac{13}{3-\infty}$	d			+	—
Columbinia bryantwalkeri (Pilsbry)		$\frac{c}{3}+\frac{8}{2}+\frac{15}{3-\infty}$	d			—	—
cyclostoma (Pfeiffer)	?	$\frac{c}{3}+\frac{11}{2}+\frac{19}{3-\infty}$	?			?	?
marshalli (Pilsbry)	s	$\frac{c}{3}+\frac{x}{2}+\frac{x}{3-\infty}$	d			?	?
Incania trigonostoma (O. Boettger)	s	$\frac{c}{1}+\frac{13}{2}+\frac{25}{3-\infty}$	d			—	—
Weyrauchiella huanucensis (Pilsbry)	s	$\frac{c}{3}+\frac{7}{2}+\frac{16}{3-\infty}$	d			—	+

I, radula, row a slightly curved line (s), or angular (a). II, radula formula. III, cusps of the radula dagger-shaped (d), or crescent-shaped (c). IV, diverticulum to the pedunculus present; proximal part of the pedunculus distinct (+), or almost absent (—). V, diverticulum to the pedunculus present and narrow (n), or at least partly wide (w). VI, diverticulum to the pedunculus absent; appendix to the clear oviduct present (+), or absent (—). VII, appendix to the penis present (+) or absent (—).

Genital organs. Clear oviduct about half as long as the vagina. The pedunculus is long (about 3 times as long as the clear oviduct) and rather narrow, it has a distinct spatula-shaped bulbus, which is twice as long as wide and twice as wide as the pedunculus. A diverticulum is not present. The epiphallus is wider than the vas deferens, the lumen is like a faintly curved line. The penis is internally provided with five or more wrinkled

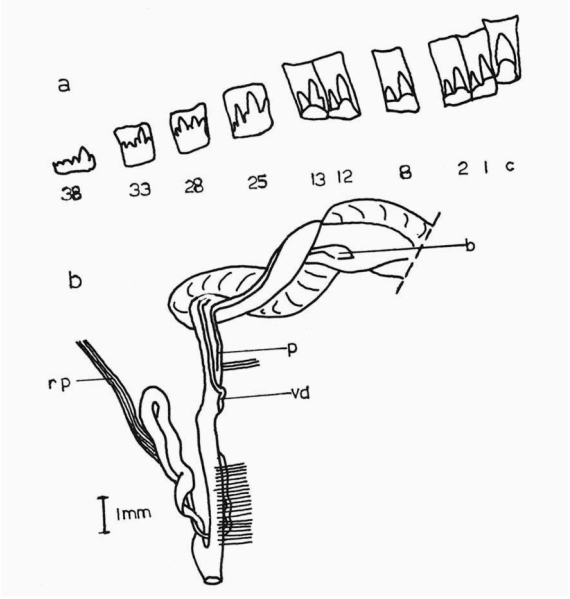

Fig. 37. *Incania trigonostoma* (O. Boettger). a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; p, pedunculus; rp, retractor penis; vd, vas deferens).

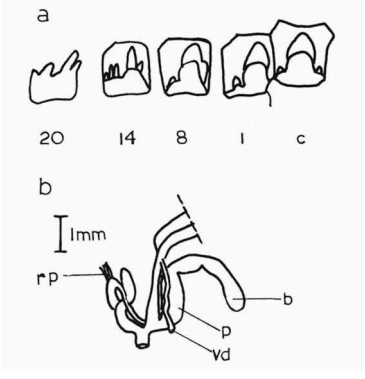

Fig. 38. *Weyrauchiella huanucensis* (Pilsbry). a, some elements of the radula; b, genital apparatus (b, bulbus of receptaculum seminis; p, pedunculus; rp, retractor penis; vd, vas deferens).

muscular strips leaving a circular lumen, a definite penis papilla could not be found. The retractor penis is rather strong.

It is almost certain that this species is closely related to *I. chacaensis* (Lubomirski) and thus that the principal characters described here are valid for the genus.

Weyrauchiella gen. nov.

Type-species: *Nenia angrandi huanucensis* Pilsbry, 1949.

Radula. $\frac{c}{3} + \frac{1}{2} + \frac{m}{3-\infty}$. The tooth-rows are almost rectilinear, with the central tooth somewhat advanced, the cusps are more or less dagger-shaped. The elements diminish rather regularly in size from the lateral teeth to the outermost marginal teeth.

Genital organs. The pedunculus has no diverticulum, nor has the clear oviduct an appendix. The penis is provided with an appendix.

Weyrauchiella huanucensis (Pilsbry, 1949) (fig. 38)

The specimens investigated were collected in southern Peru, Huanuco, 2000 m (W W. 45-A).

The animals (alcohol specimens) are black, the foot-sole is whitish.

Radula. $\frac{c}{3} + \frac{7\,1}{2} + \frac{16\,m}{3-\infty}$. The basal plates are almost square.

Genital organs. Clear oviduct about five times as long as the very short vagina and about half as wide as the pedunculus. The latter is almost three times longer than the clear oviduct. A bulbus is present as an indistinctly defined widening of the pedunculus. The vas deferens gradually passes into the epiphallus, which has a circular lumen. The penis has a rather long appendix and a lumen like a slightly curved line. The penis retractor is very well developed.

Our thanks are due to Dr. Tucker Abbott of the Academy of Natural Sciences of Philadelphia (U.S.A.) for sending on loan the holotype and some paratypes of this species.

III. Summary

A summary of the most important data on the radula and the genital organs enumerated in the foregoing descriptions, is given in table 1.

Of the following genera or subgenera no information on radula or genital organs is present at the moment: *Nenisca* Rehder, 1939; *Paranenia* Rehder, 1939; *Neniops* Pilsbry, 1926; *Gonionenia* Pilsbry, 1926; *Incaglaia* Pilsbry, 1949; *Steatonenia* Pilsbry, 1926 and *Gibbonenia* Zilch, 1954.

IV. Considerations

If we take into account that most Clausiliid species of European and Asiatic origin are known to have a diverticulum to the pedunculus of the receptaculum seminis and possess a radula with tooth-rows which form a slightly curved line, it seems acceptable to indicate a relative of *Nenia tridens*, that possesses both characters mentioned, as the possible ancestor of the South American Neniinae. Starting from this supposition and considering that the structure of the genital organs will be less dependent on external influences (by selection), than will be the structure of the radula and to a still greater degree that of the shells [2]), we believe that the genital structure is the most reliable base for taxonomy. On these grounds we have altered the arrangement of the genera and subgenera given by Zilch (1960).

However, it goes without saying that all groups of characters should be evaluated, only not all with the same weight.

First of all we recognize on the South American continent two series of genera which have a diverticulum to the receptaculum seminis and which thus can be traced back directly to *Nenia*.

The one (A) has a distinct proximal part of the pedunculus, corresponding at the same time with a peculiar angle-shaped radula (*Ehrmanniella, Andiniella, Peruinia*). The other series (B) has the diverticulum entering the pedunculus at its opening into the vagina, so that a proximal part of the pedunculus hardly exists. The radula of the genera of this series has the tooth-rows forming a slightly curved line (*Zilchiella, Pfeifferiella, Temesa, Neniatracta*). Further there is a number of genera that have no diverticulum. Some of them (C) show a narrow, often twisted and proximally closed appendix to the clear oviduct and have a radula with slightly curved tooth-rows (*Andinia, Steeriana, Cylindronenia, Hemicena*). The others do not have this appendix: they have a radula consisting of slightly curved tooth-rows (D) (*Columbinia, Incania, Weyrauchiella*) or the radula is angle-shaped (E) (*Gracilinenia*).

Considering these five groups the following observations may be made:

1. The obvious relationship between the radulae of groups A and E makes it plausible to bring them together and to suggest, that the diverticulum was lost in *Gracilinenia* independently of that in the genera of group D. Moreover it is striking that the genera of group A and E all are almost exclusively known from central Peru.

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2) Because of this, it will be clear that an arrangement based on the characters of the radula would resemble more one that is based on the shells, than an arrangement in accordance with the genital organs.

2. Group B seems, according to the characters of the shells, a rather heterogeneous community. The diverticulum of *Temesa* is proximally rather wide, that of the other three genera is narrow, with the exception of *Temesa* (*Neniatracta*) *parcecostata* which resembles *Neniatracta* because of its radula. According to the radula *Zilchiella* and *Temesa* agree, on the other hand *Pfeifferiella* and *Neniatracta* have much in common. However, both types of radulae occur also in other groups. The genera of this group occur mainly in northern and central Peru.

3. Group C combines three genera from northern Peru with corresponding radulae and one from central Peru with another, but still generally occurring type of radula (*Hemicena*). In our opinion these four genera are fairly closely related.

4. Group D. Two of the genera of this group (*Columbinia* and *Incania*) have a rather wide distribution, it seems likely that they originated independently a long time ago and had afterwards the time to spread along the Cordilleras. The radulae are rather uniform, only *Incania* has a central tooth with one cusp; in the other two the central tooth has three cusps.

We have as yet not the intention to attach more value to the above mentioned groups than as an indication of the possible relationships of the genera. In some cases, however, the similarities we have noted may be based on convergence, rather than on affinity and much more evidence is needed before we can be sure of the relationships of the South American Neniinae.

V. Distribution

The following is an enumeration of the species and subspecies of the subfamily Neniinae known from South and Central America (including the West Indies). The species of which anatomical data are known, are marked with an asterisk. The numbers behind the names refer to the bibliography; only the most important literature on the species concerned is mentioned.

West Indies

1. Puerto Rico

**Nenia (Nenia) tridens* (Chemnitz, 1786); 14, 16, 17, 25, 28, 31, 35, 40, 44, 50, 56, 66, 103, 104, 111, 135.

2. Haiti

Nenia (Nenisca) bartschi Rehder, 1939; 109.

South America

3. Venezuela

Nenia (Neniops) geayi Jousseaume, 1900; 25, 56.

Gonionenia dohrni (Pfeiffer, 1860) (according to O. Boettger, 1909 = *Clausilia perplexa* Sykes, 1893) [3]; 25, 86, 99, 104, 116, 135.
**Columbinia cyclostoma* (Pfeiffer, 1849); 25, 28, 38, 50, 56, 59, 77, 85.
Incertae sedis:
Nenia bequaerti Arias, 1953; 13.

4. Columbia

Nenia (Paranenia) perarata (Von Martens, 1873); 25, 58, 65, 71, 104, 109, 135.
Nenia (Neniops) bogotensis (O. Boettger, 1879); 21, 25, 117, 133, 135.
Nenia (Neniops) karsteniana karsteniana (Dohrn, 1859); 37, 58, 133.
Nenia (Neniops) karsteniana magistra (Sowerby, 1892); 99, 115, 117, 133, 135.
Gonionenia dohrni (Pfeiffer, 1860) (according to O. Boettger, 1909 = *Clausilia perplexa* Sykes, 1893) [3]; 25, 86, 99, 104, 116, 135.
Temesa (Temesa) funcki (Pfeiffer, 1847); 76, 99, 113, 117.
Columbinia bartletti (H. Adams, 1866) (according to Weyrauch, 1956 = *Nenia (Columbinia) obesa* Haas, 1949) [4]; 1, 25, 39, 56, 110, 117, 125.
Columbinia ? *blandiana* (Pfeiffer, 1855); 7, 56, 84.
Columbinia columbiana Polinski, 1924; 105, 135.
**Columbinia cyclostoma* (Pfeiffer, 1849); 25, 28, 38, 50, 56, 59, 77, 85.
Columbinia epistomium (Küster, 1847); 25, 26, 28, 59, 78, 105, 115.
Columbinia pseudepistomium (Bourguignat, 1876) (according to Sykes, 1896 = *Clausilia epistomium* Küster, 1847); 28, 117.
Columbinia smithiae (Pilsbry, 1902); 96.
Columbinia ? *stylina* (Ancey, 1887); 7.
Incertae sedis:
Nenia rochebrunei Jousseaume, 1900; 56.

5. Ecuador

Columbinia bourcieri (Pfeiffer, 1852); 73, 80, 92.
**Columbinia cyclostoma* (Pfeiffer, 1849); 25, 28, 38, 50, 56, 59, 77, 85.
Columbinia ? *femurina* (Jousseaume, 1900); 56.
Columbinia perezi (Jousseaume, 1887) (according to Jousseaume, 1900 = *Clausilia (Nenia) deyrollei* Ancey, 1895); 11, 25, 55, 56, 105, 133.
Columbinia reyrei (Jousseaume, 1887); 11, 55.
Incania crossei (Hidalgo, 1869); 8, 51, 52, 55, 56.
Incertae sedis:
Nenia archidona Jousseaume, 1900; 56.
Nenia auriculina Jousseaume, 1900; 56.
Clausilia (Nenia) buckleyi Higgins, 1872; 53.
Nenia cocaensis Jousseaume, 1900; 56.
Nenia cousini Jousseaume, 1900; 56.

6. Peru

**Ehrmanniella boettgeri* (Pilsbry, 1945); 100, 133, 136.
Ehrmanniella dedicata (Weyrauch & Zilch, 1954); 136.
**Ehrmanniella quadrata* (O. Boettger, 1880) (according to Pilsbry, 1949 and Zilch, 1954 = *Nenia lubomirskii* Polinski, 1921); 23, 100, 102, 103, 133.

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3) *G. dohrni* was described from Venezuela, *G. perplexa* from Columbia.
4) The species is known from Peru, only Jousseaume (56) and Sykes (117) mentioned it from Columbia.

5) According to Weyrauch (1957) the subgenera *Neniatracta* Pilsbry, 1926, and *Incaglaia* Pilsbry, 1949, are synonymous.

Temesa (Neniatracta) adusta olssoni (Pilsbry, 1949); 102, 126.
Temesa (Neniatracta) adusta tumens (Haas, 1955); 49, 126, 132.
Temesa (Neniatracta) angrandi angrandi (Morelet, 1863) (according to Weyrauch, 1964 = *Nenia angrandi urubambensis* Pilsbry, 1945); 70, 100, 102, 127.
Temesa (Neniatracta) angrandi pampasensis (Pilsbry, 1910); 36, 100, 102, 126, 132.
Temesa (Neniatracta) angrandi weyrauchi (Pilsbry, 1945); 49, 100, 102, 132.
Temesa (Neniatracta) belahubbardi (Pilsbry, 1922); 98, 99.
**Temesa (Neniatracta) bequaerti* Weyrauch, 1957; 126, 132.
**Temesa (Neniatracta) parcecostata* (Polinski, 1921) (according to Weyrauch, 1963 = *Nenia eka* Pilsbry, 1945 = *Nenia minuscula* Pilsbry, 1945); 100, 103, 126, 130.
**Andinia taczanowski* (Lubomirski, 1879); 62, 103, 104, 135.
**Steeriana (Steeriana) cajamarcana* Weyrauch & Zilch, 1954; 135, 136.
Steeriana (S.) celendinensis celendinensis Weyrauch & Zilch, 1954; 135, 136.
Steeriana (S.) celendinensis isidroensis Weyrauch & Zilch, 1954; 135, 136.
Steeriana (S.) celendinensis minor Weyrauch, 1958; 127.
**Steeriana (S.) malleolata* (Philippi, 1867) (according to Zilch, 1954 = *Clausilia steeriana* Sykes, 1893); 56, 94, 99, 102, 116, 126, 133, 135, 136.
**Steeriana (Cylindronenia) canescens* (Polinski, 1921); 103, 104, 133.
**Steeriana (Cylindronenia) huarangoensis* Zilch, 1949; 133, 135.
**Steeriana (Cylindronenia) maranhonensis maranhonensis* (Albers, 1854); 5, 25, 39, 41, 59, 133, 135.
Steeriana (Cylindronenia) maranhonensis terrestris Weyrauch, 1964; 132.
**Hemicena polinskiana polinskiana* Pilsbry, 1949; 102, 127, 130, 137.
**Hemicena polinskiana cerrateae* Weyrauch, 1958; 127, 130, 137.
**Hemicena polinskiana colcabambensis* Zilch, 1959; 137.
Hemicena polinskiana damianensis Zilch, 1959; 137.
Columbinia adamsiana (Pfeiffer, 1860); 26, 39, 63, 87.
Columbinia atracta Pilsbry, 1949; 102.
Columbinia bartletti (H. Adams, 1866) (according to Weyrauch, 1956 = *Nenia (Columbinia) obesa* Haas, 1949) [6]; 1, 25, 39, 56, 110, 117, 125.
Columbinia binkiae Pilsbry, 1949; 102.
**Columbinia bryantwalkeri* (Pilsbry, 1922); 98, 99.
Columbinia callangana Ehrmann, 1905; 26, 39, 135.
Columbinia columbiana Polinski, 1924; 105, 135.
Columbinia gracilis Pilsbry, 1949; 102.
Columbinia huancabambensis (Rolle, 1904); 39, 110, 135.
Columbinia juninensis (Smith, 1943); 102, 114.
**Columbinia marshalli* (Pilsbry, 1926); 48, 99.
Columbinia sublutea (O. Boettger, 1909); 25, 102, 135.
Steatonenia cooki (Pilsbry, 1919); 97, 99.
Incania chacaensis (Lubomirski, 1879) (according to O. Boettger, 1910 = *Clausilia (Nenia) chanchamayoensis* Preston, 1907); 26, 39, 62, 103, 104, 106, 119, 135.
Incania florezi Weyrauch, 1964; 131.
**Incania jelskii* Polinski, 1921; 47, 103, 104.
Incania mariae Zilch, 1954; 135, 136.
Incania pilsbryi (Sykes, 1901) (according to Ehrmann, 1905 = *Nenia macrotis* Ehrmann, 1905); 39, 119.
**Incania trigonostoma* (O. Boettger, 1880); 23, 47, 103, 104.

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6) The species is known from Peru, only Jousseaume (56) and Sykes (117) mentioned it from Columbia.

Incania warszewiczi Polinski, 1924; 49, 105.
**Weyrauchiella huanucensis* (Pilsbry, 1949); 102.

7. Bolivia

Temesa (Temesa) dichroa Haas, 1929; 34, 46, 135.
Temesa (T.) magnifica Sykes, 1901; 34, 46, 119.
**Temesa (T.) peruviana peruviana* (Pfeiffer, 1867); 28, 34, 89, 101, 124.
**Columbinia marshalli* (Pilsbry, 1926); 48, 99.
Columbinia ?orbignyi (Ancey, 1892); 8, 9, 10.
Columbinia zischkai Weyrauch, 1956; 125.
Incania boliviana (O. Boettger, 1893); 116, 135.

8. Argentina

**Temesa (Neniatracta) argentina* (Hylton Scott, 1954); 112, 126, 132.

9. Species from South America of which no further locality is known

Gibbonenia raimondi versicolor (Jousseaume, 1900); 56, 136.

Incertae sedis:

Nenia [subgen.?] *anoecia* Ehrmann, 1949; 41, 135.
Clausilia evae Sykes, 1896; 117.

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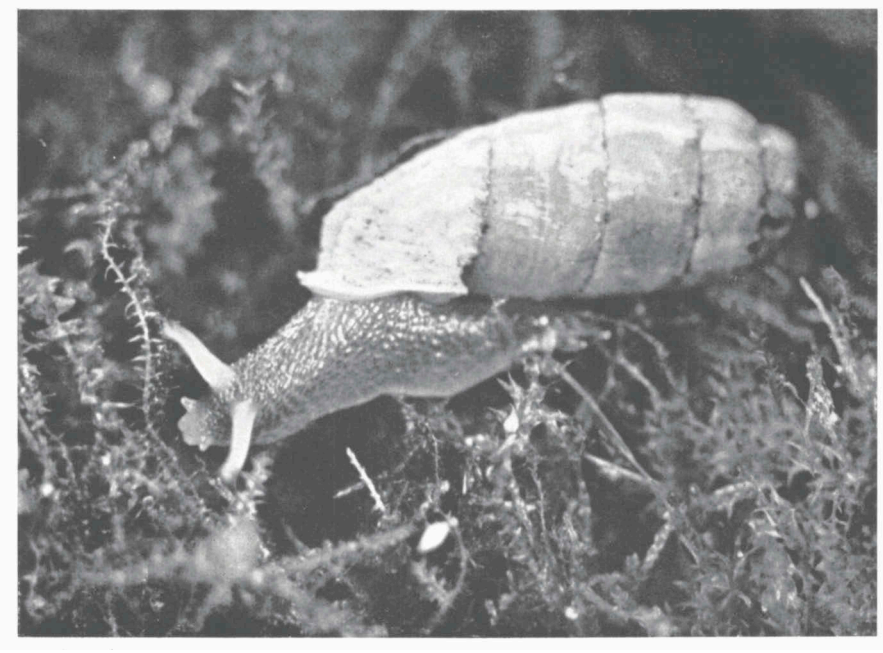

Steeriana (Steeriana) malleolata (Philippi), from Cajamarca-Celendin, Peru, alt. 3150 m, creeping.