Andrzej WIKTOR

Milacidae (Gastropoda, Pulmonata) — systematic monograph

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[With 225 text-figures and 15 maps]

Contents

Abstract .................................................. 154
Introduction .............................................. 155
I. General part .......................................... 156
   1. Morphology ........................................ 156
      Taxonomic suitability of morphological characters ........................................... 165
   2. Ecology and bionomics .......................... 165
   3. Distribution ........................................ 171
   4. Origin and relationships ...................... 171
   5. Methods of collection, preservation, raising, preparation .......................... 174
II. The key to Milacidae ............................. 177
III. Systematic part ..................................... 183
   Milacidae Ellis, 1926 ............................... 183
   Milax Gray, 1855 .................................. 184
   Milax aegaeicus Wiktor et Mylonas, 1986 ......................................................... 186
   Milax altenei Forcart, 1972 ...................... 190
   Milax ater (Collinge, 1895) ....................... 193
   Milax barypus Bourguignat, 1866 ............... 196
   Milax caucasicus (Simroth, 1912) .............. 200
   Milax gagates (Draparnaud, 1801) ............. 202
   Milax gasulli Altena, 1974 ....................... 206
   Milax monstruosus Wiktor, 1986 ............... 208
   „Palizzolia” monterosati Bourguignat, 1877 ...................................................... 211
   Milax nigricans (Schulz, 1836) ................. 211
   Milax parvulus Wiktor, 1968 ..................... 214
   Milax riedeli Wiktor, 1986 ....................... 215
   Milax verrucosus Wiktor, 1969 ................. 218
This is the first critical revision of the whole family *Milacidae*, and it discusses all basic problems of their systematics, taxonomy, phylogenesis, morphology, ecology, bionomies, distribution, and the research methods. There is a detailed presentation of all taxa whose status the author managed to find out on the basis of types, topotypes, ample museum material, and of his own twenty-year long experience. In all species synonymy is given, as well as original diagnoses and detailed descriptions of external morphology, anatomic characters, and the majority of spermatophores. Spermatophores were found to be particularly suitable in taxonomy. Data on bionomies and distribution were brought together and discussed. There is large illustrative material, made by the author, of all species, and
distribution maps. The monograph is supplied with a completely original identification key to species and contains a great number of suggestions, remarks and opinions on poorly studied taxa.

INTRODUCTION

*Milacidae* are one of the poorer studied groups of slugs, and they still make trouble for systematists. Their distribution range embraces many poorly studied regions, and many species occur locally in small mountainous territories, often difficult of access. Many species live in hidden places, sheltering deep inside rock crevices, and leave them only at night. All this has resulted in the fact that evidence material in museum collections is poor, incomplete, and it is rarely that large series of specimens from one locality can be found. There are still species known only from the original description, their types do not exist. The family has not been described comprehensively, nor revised so far. Most of the existing species names were gathered by *Hesse* (1926), this is a valuable guide that facilitates search for most descriptions. In many cases *Hesse* synonymized particular names, very often correctly. However, *Hesse* did not study *Milacidae* himself but depended on existing literature. Original descriptions of particular species are scattered in literature, they were written by numerous students. Certainly it is *Simroth* who has the greatest achievements. Also the Hungarian malacologist *Janosz (= Heinrich) Wagner* was particularly interested in *Milacidae*. He left not only descriptions of many species (esp. of Balkan ones) but also keys and zoogeographic information. After World War II the following were especially interested in *Milacidae*: *C. O. van Regteren Altena*, *A. Grossu*, *W. Rähle*, and *A. Wiktor*. The latest studies by those researchers made it possible to synonymize many names, and supplied many data on morphology and zoogeography. As a result of the studies, though new species are still being described, the number of species not only does not increase but, on the contrary, decreases. It has turned out that the family is far smaller than it could be judged from the number of the specific names in the literature. Unfortunately there is still little information on bionomics and physiology of the slugs. Many species were studied only when preserved and those students that collected them often lived in distant countries, so they could not undertake long-term field observations in the countries where the slugs live.

Poor museum materials are a serious impediment in studying *Milacidae*. The largest group of descriptive types and evidence material from the 19th c. and from the beginning of the 20th may be found in the Naturhistorisches Museum in Vienna. Other important collections, founded later, are in the Rijksmuseum van Natuurlijke Historie in Leiden, Muséum d'Histoire Naturelle „Grigorie Antipa” in Bucharest and in the Zoological Institute of Academy of Sciences in Leningrad. *Simroth* unfortunately did not have his own collection, only the material he borrowed has been preserved, after studying he returned it to proprietors. Also the *Wagner* collection, very valuable probably, was not preserved: it was burnt down with a part of the Budapest museum. To this day only one jar has been preserved, kept by his family. At present the most complete and numerous collection of *Milacidae* is that at the Museum of Natural History, Wroclaw University, assembled by me.

The basis for this study was the material collected to large extent by me, moreover all accessible museum collections and material collected for me by my colleagues were used. In this respect my thanks are due to Prof. Dr. A. Riedel (Warsaw), Dr. L. Pintér (Budapest), Dr. M. Mylonas (Athens) Mr. P. Subai (Aachen), Dr. B. Malkin (Warsaw), Mr. W. J. M. Maasen (Duivendrecht), Ing. L. J. M. Butot (Bilthoven) and Prof. Dr. E. Gittenberger (Leiden).
Search for types, and for collections, was often troublesome and work-consuming. I was helped by my colleagues from other museums, and I would like to extend my thanks to them on this occasion. They were: Dr. N. J. Evans (London), Prof. Dr. E. Gittenberger (Leiden), Prof. Dr. A. Grossu (Bucharest), Dr. R. Janssen (Frankfurt a/M.), Dr. R. Kilias (Berlin), Prof. Dr. I. M. Likharev (Leningrad), Dr. D. Lupu (Bucharest), Dr. O. Paget (Vienna), Dr. L. Pintér (Budapest) and Dr. E. Wawra (Vienna).

I have also the pleasure of expressing my sincere thanks to colleagues from the Museum of Natural History (Wroclaw): Mr. T. Piotrowski, M. A. and Dr. B. M. Pokryszko, for, respectively, translating and supervising the English terminology.

The figures are author's, notice own, if not indicated otherwise. If not otherwise marked, the scale in all figures denotes 1 mm.

I. GENERAL PART

1. Morphology

All Milacidae are slugs, i.e. the shell is completely hidden inside the mantle. The body is strongly elongate, fusiform, its posterior part is tapered and wedge-shaped (figs 1, 2). The mantle is situated in the anterior body part. Along the whole of back, except the mantle, a sharp edge runs, called the keel (in badly preserved slugs it may be partly invisible). The mantle surface, as if gritty, is covered by small mobile papillae. This sculpture is visible only in living individuals, after preservation it vanishes and the mantle becomes smooth. In the central part of the mantle there is a horseshoe-shaped or semi-circular groove, its opening towards the posterior. In some species both ends of the semi-circle are so close that it forms almost a full circle. The pneumostome (= spiraculum)
is on the right side of the mantle, near its edge, and almost postmedially, i.e. in its posterior half. Above the pneumostome in the mantle groove the anus and the excretory duct open. The head and its regions do not differ significantly from those of other pulmonates, esp. slugs, e.g. *Limacoidea*. The extra-mantle posterior body part is covered with elongate wrinkles, their number between the keel and the pneumostome being small, 8–15, exceptionally 22. The genital opening is on the right side of the body, always in front of the pneumostome. The sole is almost as wide as the whole body, divided by two longitudinal grooves into three zones. After preservation on the surface of the whole of the sole an ornament originates: crosswise smaller grooves like the letter V (fig. 3).

Body coloration may be uniform or darker dots may occur on lighter background. Dots most often form an irregular pattern, varying between individuals. Most often the darker pigment accumulates in skin grooves. A typical character of the whole family is occurrence of accumulations of darker pigment below the arms of the semicircular groove on the mantle of most species. They look like irregular streaks in contrast with the background. Another characteristic feature of the family is absence of coloured stripes. The back and mantle are darker as a rule, sides and the sole being lighter. Most often colours met are black, brown and various shades of creamy or reddish-brown.

Mucus is usually very thick, after being touched with a finger it draws in strands. Usually it is colourless or yellowish but transparent. Slugs slightly irritated secrete additionally thinner, opaque, milky-white or slightly coloured mucus. Probably it is used in defense.

The shell (figs 4–6) is situated inside a closed cavity in the posterior mantle part. It is very flat, lenticular, convex dorsally and slightly concave ventrally, oval and symmetrical. The embryonic part is in the posterior, symmetrically in relation to the long axis. During life it grows concentrically, though clearly faster anteriorly and laterally than posteriorly. The whole shell is white, when fresh it may be partly transparent. In fossils it is well-preserved. Differences
in shell appearance in particular species are slight, though there may be considerable differences among individuals.

Musculature is similarly reduced as in most slugs, and this especially concerns the main retractor, i.e. musculus columellaris (Likharev and Wiktor 1979, Wiktor 1984). Of the system so highly developed in snails only the system of head retractors is retained in Milacidae. This muscle is most often called the cephalic retractor. Posteriorly it inserts to the elastic membrane, which

Figs 4-6. Shell of Tandonia cretica. 4 — dorsal view, 5 — side view, 6 — ventral view. (Specimen from Karystos, Euboea Isl., Greece).

Fig. 7. System of retractor muscles — Tandonia cretica.
Figs 8–9. Fragments of radula. 8 — *Milax nigricans*: 8a — in the middle two central teeth, 8b — lateral teeth, 8c — marginal teeth, 8d — fragment of right-side radula, comprising lateral and marginal teeth. 9 — *Tandonia budapestensis*: 9a — fragment of radula comprising boundary between lateral and marginal teeth, 9b — marginal teeth, 9c — central tooth (on right), 9d — central teeth (second row on right) and lateral teeth, 9e — boundary between marginal and lateral teeth. (after Jungbluth, Likharev and Wikt 1981).
constitutes the lower wall of the shell cavity. The insertion is roughly on the line of the posterior shell margin and thus, of the posterior mantle edge. Anteriorly the muscle branches most often into two strands of which one, branching somewhat later, becomes the pharyngeal retractor, the other, also bifurcated, is the ommatophore retractor (fig. 7). The only exception is Milax verrucosus, in which, probably due to body elongation (an adaptation to subterranean life) both muscle strands have parted, inserting posteriorly separately one behind the other, moreover, behind the mantle and the shell (WIKTOR 1969, 1981). Genitalia have their own muscle system. Only one undivided retractor occurs, usually called musculus retractor penis, as its anterior insertion is almost always on the penis, though sometimes the insertion is in the epiphallus region. The posterior insertion is located in various places, on the membrane under the shell. This retractor is sometimes so thin that it is difficult to find it in preparation. In the anterior part of the genitalia, usually in the region of atrium or of the posterior penis section there are membraneous retentor muscles, attaching genitalia to the body walls. The foot musculature is a band of muscles which form the ventral body part. Musculature of body walls is very well-developed. The walls are thick, have numerous lacunas, which fill in with body fluids. The whole body can strongly contract.

The pedal gland is large, elongate and is situated in the anterior body part. After dissection of the slug it is well visible, as it differs in coloration and structure from the foot internal surface.

Radula is made of teeth, similar in shape to those in Limacoidea (figs 8–9), i.e. the central tooth is symmetrical, with a large mesocone and two lateral cones. Lateral teeth have large mesocones, the exocone being gradually reduced, later also endocones are reduced, and they are completely lacking on external teeth. The marginal teeth are long, sabre-formed, sometimes with a small exocone (JUNGBLUTH, LIKHAREV and WIKTOR 1981). In the radula there are no characters that would distinguish Milacidae from other related snails.

The intestine (fig. 10) coils in two loops, one loop being more posterior than the other (as in Agriolimacidae and Boettgerillidae, see LIKHAREV and WIKTOR 1980). Both loops are also convoluted around the long body axis. The rectal coecum is absent.

Fig. 10. Intestine in Milacidae.
Pallial complex. It occupies the posterior mantle part. The long axis of the heart is tilted rightwards in relation to the long body axis at c. 45°. The aorta is long and usually crosses the rectum (figs. 11–13). The network of the lung vessels, differently developed in various species, can be found only below the heart. The kidney, slightly elongate, surrounds the heart laterally and posteriorly. The main part of the kidney is in the dome of the mantle cavity, while in the lower part there is a large renal lobe (lobus), which in Milacidae takes almost a half of the kidney. The secondary urether is S-shaped. It begins at the posterior kidney part and extends parallelly to the rectum. The bladder is absent. The excretory opening is in the crevice above the pneumostome, near the anus. Diagnostic characters of Milacidae: rightwards tilting of the heart axis, elongation of the kidney and its larger lobe, and lack of the bladder (WIKTOR and LIKHAREV 1980).

The brain was studied only in several species and its suitability for taxonomy is not known. It is similar as in the majority of Palearctic slugs — commisures are very short, as are connectives. Particular ganglia fuse, so that

Fig. 14. Brain of Tandonia kusceri. A — cephalic aorta, P — ganglia buccalia, M — ganglia cerebralia, N — ganglia podalia. 1 — nervus opticus, 2 — nerve leading to ommatophore retractor, 3 — nerves leading to sole and foot, 4 — nerve leading to pallial complex, 5 — nerves leading to tentacles, 6 — nerve leading to the peristome region, 7 — nerve leading to genitalia, 8 — statocyst (after LIKHAREV and WIKTOR 1980).
most often it is difficult to establish a boundary between them. Ganglia cerebral have occasionally a membraneous flattening anteriorly, which gives an impression of growing together of nerve bases going out of the brain (fig. 14).

Genitalia (figs 15–16). Glandula hermaphroditica, usually lightly coloured, is of several lobes, and each is of numerous spherical acini. The gland size changes with the change of the sexual activity, yet the differences in size, when occur, are smaller than e.g. in Limacoidea. Ductus hermaphroditicus is long in comparison to other parts and usually very twisted in the anterior part.

Glandula albuminalis is elongate, tongue-like or almost cylindrical, usually bent. Spermoviductus is wide and thick-walled. The male part is usually different in coloration than the female one, i.e. yellow or orange. Vas deferens is long, runs anteriorly, bends, and runs posteriorly. It opens to the epiphallus apically, usually asymmetrically. The only exception, where vas deferens opens laterally, is Tandonia pageti (fig. 174). The epiphallus is longer than the penis, cylindrical, conical, or club-like, most often widened posteriorly. Its posterior end is often as if abruptly truncated and flat-ended. Inside it has a rich ornamentation of folds or of dense papillae. The epiphallus is separated from the penis by a constriction, where nearly always the musculus retractor penis is inserted. The penis has various shapes, and is sometimes divided by constrictions into several parts. Inside at the boundary with the epiphallus there is papilla penis, variously developed. The characters of papilla penis have not been used so far and we know little about individual variability of this organ. The oviduct is tubular and long. The spermatheca is of various shape, most often oval, sometimes tubular or spherical. The spermatheca duct is usually thick-walled. In various species it differs in length, may be very short, even hardly visible, in extreme cases may have the length of almost the whole genitalia. It always opens into the female channel, and, being united, it becomes the vagina. The vagina is a tubular channel of various length in different species. In Tandonia there may be distensions on the vagina, moreover in this region there are always outlets of accessory glands, opening by means of two or more thin canaliculi into the vagina. The glands are usually channel-like in structure and adhere to the vagina. In the genus Milax vaginal accessory glands and distinct distensions are lacking. The atrium in Tandonia is small (except T. kaleniczenkoi) and tubular, and always without accessory glands. The atrium in Milax is large, barrel-like, laterally a large single atrial accessory gland opens, lobular in structure. The secretion of the gland is usually drained off by numerous thin canaliculi. A single wide channel occurs only in M. verrucosus. Walls inside the Tandonia atrium are smooth or covered with folds, exceptionally with spikes. In Milax inside the atrium there is a stimulator (absent only in M. verrucosus). The organ may be everted.

Characteristic traits of Milacidae are presence of the epiphallus and papilla penis, union of the spermatheca duct with the female channel, accessory glands opening into the vagina or into the atrium.

Eggs are oval or spherical, their shells being opaque, hard, calcified. Their appearance is known only for several species. Coloration is whitish, pinky, or yellowish.

Spermatophores are structurally very complicated. It seems that they are produced by all species, though they have not been found in each so far. They are elongate, closed capsules of semi-transparent, probably conchiolinous substance, yellow, copper, or red in colour. Most often a cirrose section (fig. 138) may be distinguished in the spermatophore, this section being the
first to be inserted in the receiver’s atrium. The remaining part is wider, filled with sperm. In some species the cirrose section is lacking, and the spermatophore is like an elongate cone (fig. 101). On the spermatophore surface there are always hooked processes. They have various shape and dimensions but are always forked or dichotomically branched. Spines never cover the whole of spermatophore. They usually form regular rows, mainly situated in the anterior part, and surround it on all sides. The central part, widened, either has no spines or is covered by them on one side. On the posterior part there are usually few, though large, hooks.

Taxonomic suitability of morphological characters

Characters of the external appearance have little use in taxonomy, mainly because they are difficult to be described precisely and unambiguously, and differences, if there are any, are so subtle that a lot of experience is required to use them. Most suitable in this respect are characters of coloration, esp. the body pattern. The individual variability in coloration is most often small, at least smaller than in other Palearctic slugs. The radula characters have not much use, as the teeth shape is dependent on food specialization, Milacidae being undifferentiated in this respect. The appearance of the shell, intestine, musculature and pallial complex has not much suitability for intra-familiar taxonomy. Systematics is based mainly on characters of genitalia, precisely, of copulatory organs. Division into genera was based on the atrium characters and on the location of accessory glands. Systematics of the species level is mainly based on characters of male copulatory organs and on appearance of the spermatheca and accessory glands. Characters of spermatophores are introduced as a completely new character here. Although not all of the specimens are collected with spermatophores, the differences in this respect are so great that they rule out any possibility of mis-determination. They seem to be useful for verification of taxonomic value of the remaining morphological features. At present the variability range of spermatophores within a species is poorly known, yet it appears to be far smaller than inter-specific differences.

2. Ecology and bionomics

Milacidae are associated with the Mediterranean climate, i.e. one rather mild with small thermic amplitude. Most Milacidae should be included with xerophilous slugs. This is both evidenced by their geographic range and by the activity limited to warm year-seasons. In contrast to other palearctic slugs the majority of the species occur in xerothermic habitats, sometimes so dry that being inaccessible even to snails with well-developed shell. Several species occur in wet forests, though they are never found in humid biotopes, e.g. in swamps or near water bodies. They live on the ground and do not crawl
up the tree trunks, nor do they climb high on other plants. Most species occur in rocky areas with a number of loosely scattered boulders. Some species occur in stone clatter, or on talus fens in mountains (scree), where boulders are moveable and where there are no flowering plants. The remaining species are mostly inhabitants of leaf litter, esp. of layers of rotting leaves. Few species shelter deep in clayey soil, burrowing canals there, while Milax verrucosus probably spends most of its life under the ground. Like other slugs they are nocturnal, but when it rains, esp. when it is foggy, they are also active in the daytime. They shelter under boulders, in rock crevices, in the ground or in litter. In comparison to other slugs they are rather slow, which is probably due to their thick mucus, which provides good protection but impedes crawling. The mucus is used for lining the shelters in drought, several slugs often gather at one place then. Feeding biology is poorly known. The slugs seem to be poorly specialized in this respect. They feed on various parts of plants, mainly of dead ones, or even on detritus. They also eat animal food or faeces of vertebrates.

Copulation has been studied only partly in these slugs. The whole process was described only for Milax gagates and Tandonia rustica, T. budapestensis and T. sowerbyi (Gerhardt 1936). I watched copulation in several species, but always in the field, without being able to see the whole, from the beginning to the end.

Copulation takes place at night, sometimes in the morning. It is on the ground, usually horizontally, often in sheltered places, e.g. under a stone. Both partners approach, cling with their sexual openings, the bodies being curved. Tentacles are hidden, pneumostomes closed, opening from time to time. The slugs move very slowly, sometimes circling rightwards, around one point, or stay in one position for an hour. Sometimes the bodies are curved stronger, their anterior parts raise above the ground. It cannot be established when the courtship ends and the copulation proper starts, as there is no change in the behaviour in slugs during both processes. Copulatory organs may be quite invisible on the outside, or they can be seen as a small roll between two clinging bodies. In some (T. reuleauxi) not only does the atrium swell intensely but also the regions of the sexual opening. A large lobe is formed, which covers all the everted organs from above (fig. 17). Stimulators in Milax are probably inserted into the body of the partner. Anyhow, they are not everted and rubbed against each other, as in Deroceras (Agriolimacidae). After dissecting Tandonia slugs, which had been put into alcohol during copulation, I saw that both partners transmit their spermatophores simultaneously (fig. 18). They are inserted directly into the spermatheca duct. The whole of the atrium and the penis is everted. The mechanism of transmission of the spiny spermatophores is not known, probably it is done during co-ordinated movements of atria and other copulatory organs of both partners. The final insertion of a spermatophore is probably effected by the receiver itself, as after copulation slugs are often seen with the end of the spermatophore sticking out, it vanishes after
some time due to the movements of the atrium. On the outside of the everted genitalia there is occasionally a clot of mucus on the margin (fig. 17). The duration of the courtship and copulation depends probably on the properties of the species, and also on the temperature of the environment. In Milacidae the courtship is exceptionally long, lasting from 1.5 h to as long as around the clock or longer. Probably during this time spermatophore tunicles are produced and the spermatophore filled with sperm. In my studies I managed to find the spermatophore in the epiphallus only twice. Nearly always it could be found in spermatheca or in the atrium, i.e. in the receiver. Sometimes two spermatophores can be found in the spermatheca (Bett 1960), which proves that there were two copulations at short intervals. Probably spermatophore tunicles are dissolved very quickly, as undamaged spermatophores can be found nearly always in specimens killed during, or just after, copulation.

The life cycle was not studied in detail in any species. Great differences may be expected in life cycles of various species, also life cycle may differ within one species under various climatic conditions. This can be seen in phenery first of all, esp. where winter is mild and very short. Probably all Milacidae live more than a year. This statement can be supported by the fact that adults occur together with sub-adults at the same time. In some species a two-year cycle was found. Tandonia budapestensis in Great Britain, for instance, hatches from eggs in April or May, matures sexually next autumn, then it lays eggs (Hunter 1968). Most of the students have found that sexual acti-
Fig. 18. Diagram showing the simultaneous transmission of spermatophores in *Tandonia reuleauxi*. The drawing was made after dissecting specimens which in copula were put in alcohol, thus killed and preserved. A — atrium, Ga — glandula albuminalis, Ep — epiphallus, Gh — glandula hermaphroditica, So — spermoviductus, Sp — spermatophore, whose one part is in spermatheca and spermatheca duct, the other inside penis and epiphallus of the partner.
vity occurs at the close of summer and in autumn but it was also observed in spring, though less intensive. It follows, then, that adults, sub-adults, and probably eggs overwinter. Slugs copulate several times in life and several times lay from several to twenty-plus eggs. *Tandonia rustica* lives longer, i.e. to c. 3 years. It matures sexually between the 6th and the 9.5th month, and usually in its 8th month of life it lays eggs. Egg-laying is repeated many times in three various periods. At one time 8–27 eggs are laid, 260 in lifetime. The development of eggs until their hatching lasts more than a month, and at low temperature it may be even 131 days (*Künkel* 1916, *Frömming* 1954). Eggs laid late in autumn overwinter and young slugs hatch in spring of the following year. They lay their first eggs in autumn, then they overwinter and again lay eggs. They can also reproduce in their third year, but they die at its end (fig. 19). *Milax gagates* under laboratory conditions has two phases of reproduction (*Focardi* and *Quattrini* 1972). One begins in March and lasts until the end of May, the other starts in October and finishes in December (fig. 20). 15 to 30 days after egg-laying slugs die. First eggs are laid not sooner
than 4 days after copulation, usually between the 5th and the 15th day after the copulation. Egg-laying lasts one or one and a half month. At one time the slug lays about 15 eggs (some species repeat this several times). The total number of laid eggs does not exceed 100. Roughly one hour after an egg is laid its cleavage begins. Hatching, at room temperature, is between the 26th and the 30th day. Between the 4th and the 5th month of life slugs mature. The whole cycle lasts about 9 months in a laboratory. Single individuals raised in isolation were seen to lay eggs, from which young hatched. This is probably due to self-fertilization.

A specific character of bionomics and ecology of Milacidae, in comparison to other Palearctic slugs, is their excellent adaptation to xerothermic conditions. Among slugs they are exceptional in depending on mild Mediterranean climate, small mobility, clearly overground way of life and most often association with rocky areas. They copulate almost motionlessly.
3. Distribution

The range of Milacidae covers small areas of the south-western Palearctic (maps 1 and 5). In the west they reach to the Canary Islands, the Strait of Gibraltar, the Atlantic coasts of Europe and Ireland. Their southern limits comprise northern Morocco and Algeria, islands of Mediterranean Sea and sea territories of Turkey and Syria. In the north they reach Ireland, Great Britain, coasts of the Northern Sea and to Central Europe. In the east—beginning from Roumania—the range is broken and endemic species appear in small isolated areas of the Crimea, Transcaucasus, in Georgia and Azerbaijan (Lenkoran environs). The original range of the family is not known. The oldest concentrations of shells belonging probably to those slugs date back to the Oligocene, and perhaps even to the Eocene (Zilch 1959–1960) and were discovered in the area of their present distribution. At present the largest number of species can be found in the Balkans, yet it is difficult to say whether this area was the centre of their origin, or whether it is the centre of their most numerous distribution at present. Most of the species have small ranges or occur even locally. None of the species colonized the whole area of the range of the family. The largest range is that of Milax gagates (map 3).

Only few species undergo introduction, though some of them tolerate anthropopressure quite well, and may be even regarded as synanthropes of native origin (e.g. Tandonia kusceri, T. rustica). Two species tend particularly to be synanthropized and to be easily introduced: Tandonia budapestensis and esp. Milax gagates, which was introduced nearly in the whole of the world, and can be found in agrocenoses, greenhouses, etc., even on distant continents like America and Australia.

4. Origin and relationships

Slugs are a group of various origin, and their similarity results from parallelism of their evolution (Likharev and Wiktor 1979). In the past the similarity between Milacidae, Boettgerillidae, Agriolimacidae and Limacidae appeared so great that they were classified as one group. Detailed studies showed, however, that beside the similarities there are far more significant differences, which show that they are of various origin. So far reconstruction of evolution on the basis of fossil shells has not been successful. It can be, however, studied on contemporary slugs, and particular characters form a coherent picture, which allows us to follow the trends in specialization. Milacidae seem to be most closely related to Parmacellidae, Zonitidae, Daudebardiidae (Likharev and Wiktor 1980). The appearance of the shell points out to that. Probably the families had a common ancestor with a shell similar to primitive Zonitidae, i.e. flatly spirally convoluted. In contemporary Zonitidae the number of whorls is reduced, the last is widened, and the shell tends to be thin. Dauderbardiidae have specialized to be predators. And in what seems to be
regularity in such snails the anterior part of the cephalopodium is strongly developed, and the reduced shell shifts to the posterior, remaining externally visible (Li kharev and Wik tor 1979). Hence they are not slugs proper. Parmacellidae and Milacidae are non-specialized herbivores, or they could be even called omnivores. As in other slugs of this type they have an elongate posterior part of the cephalopodium, into which viscera lowered, with a very long and coiled intestine, the mantle remaining anterior. The whole shell lowers inside the flattened mantle (Wik tor and Likharev 1979, Likharev and Wik tor 1979, Wikt or 1984) (Fig. 21). Parmacellidae seem to be a transitory form between typical snails and slugs. In sub-adult stages, just after leaving the egg tunicles, they are typical snails, and they can draw the whole body inside a sufficiently large shell. When they grow the body grows faster than the shell, which remains on the outside for some time to immerse later wholly into the mantle, yet always a narrow gap posteriorly to the shell remains. Milacidae, on the other hand, hatch from eggs as slugs from the start, and the flat lens-like shell is devoid of the spiral coil, being wholly buried in a cavity closed on all sides. When compared, shells of the above four families may be arranged in one line, which can provide some explanation how the spirally coiled shell

Fig. 21. Diagram showing embedding of viscera in cephalopodium and origin of “slugginess” due to adaptation in predatory forms (right top), and in phytophagous forms (right bottom). Arrows point to the tendencies to change in shape and proportion in various body parts (after Likharev and Wik tor 1979).
of the Zonitidae type could transform into the flattened, lens-like but symmetrical shell of Milacidae (fig. 22). Both Parmacellidae and Milacidae have numerous adaptations to life in dry environments, capability to endure long droughts was acquired by the two families in various ways. Parmacellidae make use of the juvenile stage, when they have a large shell, to live through diapause, which falls in the dry season of the year (ZHADIN 1946, LIKHAREV and WIKTOR 1980). Milacidae, on the other hand, have thick mucus which efficiently protects their bodies from drying up both in the active life and in the shelter lined up by the mucus where they wait till the drought ends.

The singled out families have many common characters in their structure of soft body parts, esp. in alimentary tract and genitalia. This concerns first

Fig. 23. Genealogical tree representing relations of Zonitoidea.
of all the way the intestine coils and the shape of radula teeth. Still more visible is the similarity in genitalia appearance. In all there is a union of the spermatheca with the oviductus, i.e. the vagina can be found. In the region of the vagina and in the region of the atrium there are various accessory organs (glands, stimulators, etc.). The epiphallus occurs universally, and consequently the spermatophore is produced. The penis has papilla inside, while it lacks flagellum or the penial gland. All the mentioned characters seem to point out unambiguously to affinity between Zonitidae, Daudebardiidae, Parmacellidae and Milacidae. Also they show differences as compared with Boettgerillidae, Agriolimacidae and Limacidae. The families should be separated from Zonitoidea, therefore a superfamily Limacoidea is suggested (Likharev and Wiktor 1980). Previously not only all these slugs were united into one group, but also the names Zonitoidea and Limacoidea were used as equivalent. In the light of the present investigations the phylogenetic relations are probably as in fig. 23.

5. Methods of collection, preservation, raising, preparation

Milacidae are collected like other slugs. The most convenient season for the field work is spring and autumn, i.e. seasons of the largest rainfalls, when slugs are easier to find. They should be looked for under stones, in stone clatter, and forest species in litter. They are never found on trees, under the bark. Night catches by the light of a good torch are very effective. Collected individuals may be kept several hours in containers, they should have sufficient quantity of moisture by having several fresh or dead leaves. The leaves also give protection against accumulation of excessive quantities of mucus, which the slugs poorly bear. This provides protection against their hurting themselves with radulae as well — a normal sign of overdensity, which triggers off mutual aggression. Overheating of slugs should be prevented first of all. If they are in a cool, though even small, container, there is no danger of their stifling.

Before preservation the slugs should be killed when they are fully extended. Use can be made of common methods, i.e. of putting them in water with some drug, or drowning them in water. In order to drown the slugs should be put into a small vessel, water poured to the rims, and the vessel closed so that no air bubble remains. The slugs should be kept so until they die, i.e. when there is no reaction when the head is touched. At room temperature this lasts from several to a dozen of hours. Sometimes the time they are dead can be overlooked and decay starts. To prevent that some crystal or liquid menthol should be added to water. Menthol acts both diastolically and bacteriostatically, so it delays decay.

Prior to preservation dead slugs should be rinsed from mucus as carefully as possible and put into 70% ethyl alcohol. Large slugs can be injected with
alcohol by means of a syringe, the needle should be inserted through the sole. Alcohol in the container the slugs are kept in should be changed after several days. If it is still coloured or becomes opaque it has to be changed every several weeks until it is clear and transparent. Slugs preserved in this way can be dissected even after 150 years. In order to preserve coloration, slugs can be also kept in 4% formalin. After this sort of preservation they cannot be dissected. Formalin-preserved specimens can be sometimes used in preparation after being soaked in water and put into 70% alcohol. All preserved specimens should be kept in darkness, as they fade in light, after some time they even become white.

Raising, esp. short-termed, is not particularly difficult. Boxes of plastic, wood or glass, several cm high, are quite sufficient. A layer of soil (loose if possible) should be put on the bottom, soil ought to be wet and kept moist. Slugs should have a possibility to hide under pieces of flower-pots, or under stones. Overdensity should be avoided — a slug 2 cm long should have an area of at least 20 sq cm. At least every several days the mucus left on the container walls should be removed, or the soil changed. Decaying mucus causes restlessness of a slug first, then its death. Little is known about food preferences. Most species eat lettuce, sliced carrot, cottage cheese, yolks of boiled eggs. All slugs need calcium and if the substrate lacks it crushed egg-shells ought to be given.

Fig. 24. The best way of cutting body layers and dissection.
During dissection slugs should be immersed in fluid. If the specimens have not been preserved they should be dissected in physiological saline, or in 0.03 % NaCl water solution. Not preserved specimens are easier to dissect, their organs having different coloration and not being deformed. Preserved specimens should be dissected in the same fluid they were preserved in. Dissection should start from incising the body always leftwards (fig. 24). That enables one to expose all organs important for systematics without damaging them. Cutting with scissors should begin from the posterior, the cut should run somewhat above the foot margin to the head. Next skin should be cut across the head, just behind the tentacles. If necessary another crosswise cut should be made roughly at two-thirds of the body length. To cut the layers the scalpel or a bit of a razor blade can be used, though in this case the blade should go from the anterior to the posterior. The cut slug should be put on a dish with paraffin, the foot is to be fastened to the paraffin with pins, and the layers to be drawn rightwards with tweezers, and also fastened to the paraffin. A slug dissected in this way can be studied in detail, without the need to cut out particular organs. The organs can be moved only. After studying, the layers may be put again together, which gives protection against damage. Several slugs can be kept in one tube, and they can be studied many times after. The shell can be best dissected from the ventral side. After drawing aside the body wall and attaching it to paraffin, first the membrane of the kidney cavity should be incised archwise at the kidney posterior. After dissection the whole pallial complex may be studied. By another, somewhat deeper cut, also behind the kidney, the shell cavity can be opened. When the cut is wide enough it is possible to grip the posterior margin of the shell with tweezers and to take it out, without damaging the pallial complex or the outer mantle surface. To facilitate orientation in topography of the organs use can be made of the figure (fig. 25).

II. THE KEY TO MILACIDAE

Note. This key excludes the species that are still completely doubtful to me: Tandonia croatica, T. dalmatina and T. montenegrina. It also omits the taxa based on the shell morphology only: Amalia guebbardi and Palizzolia monterosati.

1. Vagina without accessory glands. From one side of atrium several or one duct connecting atrium to atrial accessory glands. Stimulator inside atrium (except M. verrucosus without stimulator) (fig. 15).

2. Vagina surrounded by vaginal accessory glands connected by numerous ducts. Atrium without stimulator, though folds may occur. No atrial accessory glands (fig. 16).

3. Atrial accessory gland connected with atrium by one duct (in subadults may be absent being undeveloped).
1. Atrial accessory gland connected with atrium at least by three ducts. The gland usually under pharynx.

2. Atrial accessory gland duct several times longer than gland. Inside atrium a small conical stimulator. Body thickset, ochrous or yellow with a darker pattern.

3. Atrial accessory gland duct shorter than the gland (note: both only in fully mature individuals). No stimulator. Body wormlike elongate, white or whitish without darker pattern.

4. Inside atrium flat, membraneous, very wide stimulator with fringed edges. Its inner surface with several spines. Body brownish covered by reticulate pattern.

5. Inside atrium three stimulators, one long tape-like and two others similar to each other like a cone cut lengthwise (fig. 76). Atrial accessory gland connected to atrium by three long ducts. Body brownish with darker pattern.

6. Inside atrium two stimulators, one long, coiled, the other several times smaller, claw-like hooked, located deeply near penis. Atrial accessory glands connected with atrium by numerous ducts, their other ends closely adhering to atrium (figs 27–28). Body ash-grey with darker pattern.

7. Stimulator tongue-like conical or elongate tape-like, sharp, claw-like ended. Its surface completely smooth.

8. Stimulator like a cone cut lengthwise or tongue-like, ended by one or several spines. Its inner surface covered by tubercles or by sharp spines.

9. Stimulator narrow tape-like coiled in several loops.

10. Stimulator different.

11. Stimulator very small, conical, at the base being surrounded by a roll.

12. Stimulator different.

13. Stimulator like a wide tongue or a cone, cut lengthwise with wide base. On the inner side, near the base, a round or spoon-like hollow. Darker pattern on mantle.

14. Stimulator like a strongly elongate tongue, its inner surface without hollows.
Milacidae — systematic monograph

(sometimes with small rounded papillae). Body unicolour, steel-grey, blackish or black) ........................................ 11.

11. On inner side of stimulator rounded papillae (in some specimens may be lacking). Free end of stimulator ended by conical spine.

.......................................................... Milax gagates (p. 202).

—. On outer stimulator side sharp spines or thorns. Free end in the shape of one or several spines, or may be flattened and partly membraneous .... 12.

12. Stimulator end membraneously flattened and ended by several processes.

.......................................................... Milax ater (p. 193).

—. Stimulator end conically ended or covered by several spines but not flattened ........................................ 13.

13. Body dark grey. Stimulator with several spines near the free end. Spermatoaphore with one end cut off, tubiform (fig. 74).

.......................................................... Milax gasulli (p. 206).

—. Body usually black. Stimulator covered by numerous spines. Spermatoaphore narrowed at both ends, one eclipsed by very dense and multiply forked processes (fig. 84).

.......................................................... Milax nigricans (p. 211).

14. Back and mantle uniformly dark, black or almost black ......... 15.

—. Back and mantle light, covered by dark pattern; if unicolour: not black nor blackish, can be grey ........................................ 27.

15. Spermatheca and spermatheca duct not separated and very long, 1.5 times longer than spermoviductus.

.......................................................... Tandonia jablanacensis (p. 251).

—. Spermatheca and spermatheca duct usually clearly separated, together at most equal in length to spermoviductus, usually several times shorter ........................................ 16.

16. Inside vagina or at its boundary with atrium hard, evertible lamellate structures of serrate or dentate edges (figs 202, 205).

.......................................................... Tandonia schleschi (p. 292).

—. Inside vagina no hard serrate lamellate structures, though papillae, conical spines, folds may occur ........................................ 17.

17. Inside vagina dense hard conically sharpened spines (fig. 169).

.......................................................... Tandonia nigra (p. 269).

—. Inner walls of vagina smooth, covered by elongate folds, or usually soft papillae ........................................ 18.

18. Large slugs, body length more than 60 mm ..................... 19.

—. Slugs distinctly smaller ........................................ 20.

19. Keel well arched, body wrinkles distinct, 12–15 of them between keel and pneumostome. Vaginal accessory glands like small rolls situated roughly transversely. Spermatheca duct almost as long as spermatheca.

.......................................................... Tandonia reuleauxi (p. 278).

—. Keel poorly arched, body wrinkles very delicate, 20–22 of them between the medial dorsal line and pneumostome. Vaginal accessory glands like

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short rolls along vagina and spermatheca duct. Spermatheca duct distinctly shorter than spermatheca.

........................................................................... Tandonia cretica (p. 236).

see also Tandonia strandi (p. 305).

20. Vagina long, several times longer than wide ............................................ 21.
—. Vagina short, not much longer than wide ................................................ 22.

21. Vaginal accessory glands like two long roll-like processes opening into vagina near atrium. Inner walls of vagina covered by dense small pointed papillae, similar structures inside penis and epiphallus.

........................................................................... Tandonia fejervaryi (p. 247).
—. Vaginal accessory gland in the shape of short crosswise rolls opening into vagina at the boundary of linking of spermatheca duct and oviduct. Inside vagina and penis elongate folds.

........................................................................... Tandonia baldensis (p. 225).

22. Atrium with lateral pocket (fig. 134), beside musculus retractor penis also musculus retractor epiphallus.

........................................................................... Tandonia ehrmanni (p. 246).
—. Atrium without lateral pocket, lack of retractor epiphallus .................... 23.

23. Very small slug, after preservation to 20 mm, at the boundary between vas deferens and its connection with epiphallus lateral coecum (fig. 182).

........................................................................... Tandonia piriniana (p. 276).
—. Slug distinctly larger, no coecum at the boundary between vas deferens and epiphallus ................................................ 24.

24. Inside atrium funnel-like formation like a stimulator (fig. 213).

........................................................................... Tandonia simrothi (p. 299).
—. Inside atrium no funnel-like structure .................................................... 25.

25. Papilla penis like a "mushroom", i.e. with disc-like ending and long thin stem (fig. 161). Epiphallus and penis distinctly elongate. (Note: besides black individuals there may be also ones of different coloration — see below).

........................................................................... Tandonia macedonica (p. 262).

26. Spermatophore on one end cigar-like narrowed, usually with a short cirrrose section, on the other end with large hooks. Considerable part of its walls smooth. Spermatheca strongly elongate and narrowed at the end. Spermatheca duct very thick and thick-walled (figs 97-98). (Note: besides black individuals there may be also ones of different coloration).

........................................................................... Tandonia albanica (p. 222).
—. A species very similar to the previous one. Spermatophore tapered on both ends, without large hooks, nearly all of its surface covered by small spines. Spermatheca oval, not tapered posteriorly. Spermatheca duct thinner, not thick-walled (fig. 165).

........................................................................... Tandonia melanica (p. 265).

27. Body creamy or ochrous creamy with a darker mantle and back. On body several black dots like India ink splashes (fig. 116). Large slug, more than 65 mm long. (Note: there happen individuals without the typical dots, identification then on the basis of genitalia. Characteristic features — fig.117:
epiphallus widened at the end, 3–4 times longer than penis, inside with elongate folds. Vaginal accessory glands very small).

—. Body of different coloration, and if covered by pattern, not by dots like India ink splashes. Genitalia of different structure than shown in the fig. 117

28. Slugs very large of body length more than 70 mm ...... 29.
—. Slugs small or medium, not more than 65 mm long ...... 31.

29. Epiphallus with coecum, as vas deferens opening to epiphallus laterally. On the prolongation of penis at its opening to atrium a tongue-like, ever-tible structure covered by microscopic needles.

—. Lack of coecum on epiphallus, vas deferens opening apically. Lack of tongue-like structure at the boundary of penis and atrium ...... 30.


—. Body ochrous, reddish-ochrous, back and mantle brown-violetish (genitalia unknown).

31. Body covered by black pattern so densely that only in few places lighter dots visible, keel light (fig. 178). Epiphallus conical clearly shorter than the irregular penis. Spermatheca oval, spermatheca duct longer than spermatheca, both 2–3 times longer than penis with epiphallus together. Body length to 52 mm.

—. Body of different coloration, and if coloration similar, then genitalia and body size different ...... 32.

32. Body uniformly coloured without clear pattern on mantle and back .. 33.
—. Body of various coloration covered by blackish or black pattern. On mantle two irregular lateral streaks, and the region outside mantle covered by dots, usually situated along skin grooves .......... 34.


34. Spermatheca and spermatheca duct indistinctly separated forming together a tube gradually widening, and together are about 2.5 times longer than penis with epiphallus.
Spermatheca more or less separated from spermatheca duct, together never as long (fig. 215) .................. 35.

35. Spermatheca very elongate, tubiform, posteriorly gently rounded (fig. 215). Penis and epiphallus with two retentors (fig. 215). Inside atrium at the boundary with vagina a plate-like thickening (fig. 216A). Keel very strongly arched, body in cross-section almost triangular (fig. 211). Body of various shades of brown, yellow or orange, covered by irregular dark pattern. Sole creamy or yellow-orange in living slugs. Length to 60 mm. Tandonia sowerbyi (p. 300).

—. Spermatheca egg-shaped or almost spherical. Lack of the above-mentioned retentors on penis or epiphallus. Inside atrium other structures or its walls smooth. Body in cross-section more rounded, keel poorer arched ...............................................................36.

36. Sole dark, blackish or brownish, more rarely orange-grey in living slugs, in preserved on its surface numerous black melanophores. Body very densely dotted by small spots, the emerging pattern almost invisible, back and mantle seem chocolate or blackish ........................................................37.

—. Sole white or creamy. Body pattern made of clear blackish dots, usually reticulate ............................................ 39.


—. Atrium small, tubiform, without barrel-like distension, internal walls smooth .......................................................... 38.

38. Epiphallus narrower than penis, cylindrical or mace-like, far longer than its own width. Accessory glands large, easily discernible (fig. 112). Body slender, mantle small, covering c. 1/4 of body length. Tandonia budapestensis (p. 230).

—. Epiphallus wider than penis, egg-shaped, its length not much exceeds its width. Accessory glands very small (fig. 200). Body more thickset, mantle somewhat larger. Tandonia samsunensis (p. 289).

39. Epiphallus several times longer than penis, coiled and convoluted. Its insertion with vas deferens like a gradual gentle widening (fig. 155). Spermatheca spherical. Body pattern very indistinct and diffuse. Length to 65 mm. Tandonia kusceri (p. 257).

—. Epiphallus short, never coiled, straight or at most twisted. Vas deferens clearly separated from the far wider epiphallus. Body pattern nearly always distinct or at least some dots well contrast with the background .......................................................... 40.

40. Spermatheca short, oval, or nearly spherical. Epiphallus nearly twice as long as penis. Penis with a very strong musculus retractor and membranous retentor inserted on both penis and atrium (fig. 209). Body pattern similar to T. kusceri, i.e. diffuse, moreover nearly always single black dots on body, as if splashes of India ink (fig. 208). Body length to 45 mm. Tandonia serbica (p. 295).

—. Spermatheca oval or sharpened, i.e. ended by an abrupt constriction and
pointed at the end. No retentor penis, if retentor occurs, inserted to atrium. Body pattern different ........................................ 41.

41. Spermatheca pointed, i.e. abruptly narrowed posteriorly ........ 42.
   — Spermatheca oval, posteriorly rounded ............................ 43.

42. Body light, whitish, creamy or light brown covered by dense small black dots clearly contrasting with background (fig. 196). Spermatheca duct short, shorter than spermatheca, soft. Papilla penis richly ornamented (fig. 199).

   ............................................................... Tandonia rustica (p. 286).
   — Body grey-brown-beige with blackish poorly contrasting pattern (Note: can be completely black). Spermatheca duct thick, thick-walled, longer than spermatheca. Papilla penis semi-spherical (fig. 99).

   ............................................................... Tandonia albanica (p. 222).

43. Body blackish-coffee with reticulate blackish pattern (very similar to T. albanica). Spermatheca duct longer than spermatheca. Papilla penis like a mushroom on a long stem (fig. 161).

   ............................................................... Tandonia macedonica (p. 262).
   — Body of different coloration. Spermatheca duct as long as spermatheca or shorter ........................................ 44.

44. Inside vagina at the boundary with atrium evertible to the outside hard lamellate structures of serrate or dentate edges (fig. 202). Vagina short.
   ............................................................... Tandonia schleschi (p. 292).
   — Inside vagina and atrium no hard lamellate structures, at most elongate folds occurring. Vagina long.

   ............................................................... Tandonia baldensis (p. 225).

III. SYSTEMATIC PART

Family Milacidae Ellis, 1926

Milacidae Ellis, 1926: 252.


Slugs long to 130 mm, after preservation to 95 mm. Body elongate, tapering posterad. Mantle in the anterior, covering less than 1/3 of the body length, mantle surface with small granular sculpture and with horse-shoe groove with the opening posterad. Pneumostome postmedial. Keel along the whole of back from the body end to the posterior mantle edge. Sole divided into three elongate zones, wrinkles on its surface forming the letter V.

Coloration uniform or body being spotted, never striped, though on mantle in most species two irregular darker streaks along the arms of the horse-shoe groove.

Mucus very thick, when irritated most species secrete opaque white or slightly coloured secretion.
Shell rudimentary oval, lens-like arched, covered by concentric lines of growth. Nucleus situated on the longitudinal axis, though clearly shifted backwards. The whole shell is in a closed cavity inside mantle.

Central and lateral radula teeth with three cusps. Marginal teeth knife-like sometimes with a small ectocone. Jaw oxygnatic. Alimentary canal forming two loops, the second being shifted backwards in relation to the first. Also right liver lobe shifted in relation to the left backwards.

Pedal glands on the internal foot surface (not in the muscles).

Pallial complex. Heart in the left anterior quarter of the complex, its axis being oblique in relation to the body axis rightwards at c. 54°. Aorta long. Lung in front of the kidney. Kidney elongate along the body axis, surrounding the heart on the right side, and has a large lobe. Secondary ureter bent like the letter S, separate from the posterior kidney end. No bladder, at most a small swelling at the end of the ureter. Main retractor insertion at the posterior edge of pallial complex.

Genitalia. Vas deferens opening to epiphallus, which is a large fleshy prolongation of the penis. In penis a papilla, lack of any external accessory organs on penis. Spermatheca duct joining with oviductus. Accessory glands occur, opening either into vagina or into atrium.

Sperm transmitted by means of spermatophore. Eggs surrounded by calcified sheath.

Ground slugs, not crawling up the trees or other plants. Most species thermophilous, xerothermic, or at least endure droughts well. Slugs living one or few years.

Inhabit mostly the Mediterranean and the coasts of the Black Sea, and adjacent regions of southern and western Europe, and Asia Minor and northern Africa.

The family is made of two genera with less than 50 species (separateness of some species is questionable).

Until recently the slugs belonging to the family were included with the Limacidae, usually in the sub-family Parmacellinae. After separating Parmacella and Boettgerilla as distinct families a family of Milacidae was formed, which, in the light of recent research is considered to be closer related to the Zonitidae than to the Limacoidea (Likharev and Wiktor 1980, Wiktor 1983).

**Genus Milax** Gray, 1855


*Palizzolia* Bourguignat, 1877: 15. Spec. typ.: *Palizzolia Monterosati Bourguignat*, 1877 (species described basing on the shell only).
Milacidae — systematic monograph

Sansania Bourguignat, 1881: 11. Spec. typ.: Limax Larteti Dupuy, 1870 (species described basing on the shell only).


Body length after preservation to c. 65 mm, usually far less than that. Body most often thickset, wedge-like tapering posterad, exceptionally vermiciform. Keel very strongly arched.

Accessory gland single, large, opening laterally to atrium. Atrium large with one, two or three stimulators inside (except *M. verrucosus*, without a stimulator).

12 species known.

Distribution (map 1): from the British Isles and the Canary Islands through the whole Mediterranean and Black Sea region to Transcaucasia. The greatest number of species is in the Mediterranean.

Map 1. Distribution of the genus *Milax*.

Notes. The genus was divided according to various systems (Simroth 1910a, Hesse 1926, Wagner 1930a,b). After a detailed analysis of the criteria the divisions were based on I have come to the conclusion that the di-
vision of the genus into numerous small taxa is groundless, some of the accepted characters existed only in the imagination of the authors. I have shown this in great detail in a paper written especially on this problem (WIKTOR 1981).

**Milax aegaeicus** WIKTOR et MYLONAS, 1986


Diagnosis. Slug of medium size, grey with unclear darker pattern on mantle and back and darker melanophores on external sole zones. Inside atrium two stimulators: one large band-like with smooth surface, the other several times smaller, like a flattened cone, with surface covered by small papillae. Atrial accessory glands connected to atrium in two ways: by a bundle

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Fig. 26. *Milax aegaeicus* — holotype (after WIKTOR and MYLONAS 1986).

Fig. 27. *Milax aegaeicus* — reproductive system of a specimen from Leukes (Amorgos Isl.) (after WIKTOR and MYLONAS 1986).
of thin ducts, the other end of the gland grows as a membrane around the atrium. Spermatophore strongly elongate and narrow with cirrose section covered by a few branched spines, the mid part being bare or with single spines. The posterior ending (approx. 1/3) with two rows of bifurcated spines on one side, a small section with small spines on all sides. On the posterior end a short tube ending in a trumpet-like swelling.

Description. Body length 40 mm, width 8.5, mantle length 12 mm. Keel well arched and distinct along the whole of back, the body in cross-section almost triangular. 12 wrinkles on skin between keel and pneumostome.

Coloration of living slugs not noted, preserved slugs being blackish-grey, covered by indistinct pattern of small darker dots (fig. 26). On mantle two indistinct darker streaks near the arms of the horse-shoe groove, and irregular accumulations of darker pigment. Also outside mantle the darker pigment in accumulations partly along the skin grooves, and occasionally forming small dark dots. Back darker than sides, keel always remaining light, creamy, without any accumulations of dark pigment. Sole creamy, yet in almost all specimens on its lateral zones, loosely scattered dark melanophores.

Mucus colour not noted.

Fig. 28. Milax aegaeicus — copulatory organs of holotype (after Wiktor and Mylonas 1986).
Genitalia (figs. 27–29, 31). In upper sections of genital system no distinguishing characters. Vas deferens thin, opening symmetrically and apically to epiphallus. Epiphallus cylindrically club-shaped: posteriorly somewhat wider, near its posterior ending small constriction separating the final section as a small cone. Boundary between penis and epiphallus in some individuals marked by a small constriction, in others being invisible (figs 27–28). Penis shorter than epiphallus, anteriorly swelled, posteriorly a wide cone (fig. 28). In some specimens barely discernible, closely adhering to atrium and with it surrounded by atrial accessory gland. Inside penis dense, small cross-wise located wrinkles, similar formations also inside epiphallus. Papilla penis was not found. Musculus retractor penis branched anteriorly. One branch, wider, inserting laterally on the boundary between penis and epiphallus, the other, thinner, to spermatheca duct. Oviduct longer than penis with epiphallus,

Fig. 29. *Milax aegaeicus* — anterior genitalia section with open atrium and visible stimulators (specimen from Prof. Ilias, Thira Isl.) (after Wiktor and Mylonas 1896).
roughly as long as spermoviduct, being a thick silky gleaming duct. Spermatheca oval with short, shorter than itself, spermatheca duct. Atrium also short, its shape difficult to describe, and surrounded by the membraneous part of accessory gland. The gland of peculiar structure: in most representatives of the genus *Milax* connected from one end by a bundle of ducts, the other end remaining free, at most connected to other organs by a thin membrane of mesenterium. In the species under description the gland also opening by a bundle of numerous ducts, opening at the base of the large stimulators. The ducts posteriorly abruptly widen, making a loose structure in the form of a ball, and direct anterad, uniting in one membraneous formation, which surrounds the atrium. Inside atrium stimulator very large, several times coiled, narrow, almost band-like with completely smooth surface. Its exterior surface somewhat convex, interior somewhat concave. At its base a small pocket-like cavity, near which penis inserts to atrium. Moreover between the openings of vagina and spermatheca duct on one side and of penis on the other, one more, several times smaller stimulator, covered on the whole surface by small papillae. The stimulator in the shape of a flattened cone (fig. 29), being so small and usually hidden, that it is easy to be overlooked, taken to be one of the atrium wall folds. Opening of both vagina and spermatheca duct similar to papillae. Inner atrium walls somewhat folded.

Spermatophore (fig. 30) strongly elongate and narrow. Anterior cirrose section gradually widening, being the widest roughly at $\frac{2}{3}$ of its length. The cirrose section covered by branched spines. The mid section bare, or at least single spines on the surface, on the posterior section, approx. at $\frac{1}{3}$ of the length, two rows of strongly branched spines as hooks. Both rows parallel, the other side being bare. Near the posterior spine, where it clearly narrows, very small spines surrounding the whole spermatophore. The ending narrows still more, being as if cut off, ending by a small trumpet-like widening with an opening inside.

**Distribution** (map 2). So far known only from the Cyclades, esp. in the southern islands. Probably an endemit of a narrow range.

**Notes.** The species is distinguished in the whole family by the following characters: two stimulators (large and small), bifurcated retractor penis and membranous part of the atrial accessory gland, surrounding atrium.

The most similar species are *Milax gagates*, *M. altenai* and *M. parvulus*. *Milax gagates* differs in uniform coloration (lack of colour pattern), lack of darker spots on sole, shorter stimulator, on which sometimes rounded papillae, spermatophore covered by spines along the whole length.

*M. altenai* of similar coloration though without darker melanophores on sole. A smaller slug. Its stimulator shorter and wide, only 2.5 times longer than wide. It has the shape of a flattened cone, on the interior side with oval hollow, similar to that in a spoon. The spermatophore is similar, differing only in details.
M. parvulus is far smaller. It has similar, but more intense body coloration. Its epiphallus looks as if it were abruptly cut off, so that the whole organ looks like a narrow cone, whose base is the posterior ending, to which the vas deferens opens (Wiktor 1968, 1983). The stimulator is similar but single.

**Milax altenai** Forcart, 1972


**Diagnosis.** Black pattern of fine spots on the mantle, grey back behind the mantle, gradually lightening on the sides. Short stimulator with deep oval hollow at the base, with a claw-like ending.

**Description.** Body length up to 29 mm, width up to 4.5, mantle length up to 8 mm. Slim body abruptly narrowed posteriorly. In preserved specimens the mantle covers less than $\frac{1}{2}$ of the body (figs 32–33). Pointed keel distinct along the whole body part behind the mantle. Between the middle of the back and the pneumostome 9–11 grooves.
Figs 32-33. *Milax alleni* — side and dorsal views. Specimen from Kalavarda (Rhodos Isl.).

Coloration of live slugs unknown. Preserved body cream with blackish back and sides lightening towards the bottom. Blackish pigment dispersed almost uniformly on the back, slightly darker in the skin grooves. Head almost black. On the mantle black pigment concentrated along the whole horse-shoe groove forming two irregular streaks on the sides. In the middle of the mantle irregular concentrations of pigment in partly fusing spots. Creamy sole.

Genitalia (figs 34–38). Thin vas deferens opens almost symmetrically and apically in epiphallus. Epiphallus broadening posteriorly, distinctly thinner than penis. Penis spherical. Spermatheca oval. Spermatheca duct fleshy, thick, its diameter and length being almost equal to those of spermatheca. Atrium indistinctly separated from penis and vagina. Free part of oviduct thin. Very big atrial accessory gland connected with atrium by 18 narrow tubules. Stimulator (figs 35–36) set upright in the shape of narrow triangle, in normal position bent hook-like. The tubules of accessory gland open to a separate oval hollow at its base. The free end of stimulator in cross-section is flat-convex and bent toward the flat wall. Penis papilla with ornamented glands like in figure 38. Vagina opens to atrium with a small papilla (fig. 38).

Spermatophore (figs 39–41). In one specimen I have found only a fragment of the cirrose part of spermatophore. On its surface two rows of hooks situated alternately.

*Biometrics:* unknown.

*Distribution* (map 2): Rhodos, Karpathos Isl. (Greece), Turkey.

Notes. Externally very similar to *Milax parvulus*. It differs in distinctly wider and shorter stimulator and oval hollow at its base.

**Milaceidae — systematic monograph**

*Milax ater* (Collinge, 1895)


**Diagnosis.** Body black, externally not differing from *M. nigricans*. Stimulator at loose end flattened, occasionally with small processes on its tip, its remaining sections without any papillae or processes.

**Description.** Holotype 34 mm in length, c. 7 mm in width, mantle 12 mm, other specimens attaining somewhat larger sizes, the biggest after preservation 34 mm, width 10 mm, mantle length 12 mm. In preserved specimens body thickset, keel well arched, visible at the whole length of back. Skin sculpture distinct, but grooves shallow. Between pneumostome and keel 13 grooves in holotype, in others 12-14.

**Coloration.** Back, mantle, head uniformly black. In some specimens head and sides downwards lighter. Sole dirty creamy or brownish-creamy. Mucus colour not known. Basing on external appearance cannot be distinguished from *M. nigricans* and some specimens of *M. gagates*.

**Genitalia** (figs 42-50). Copulatory organs very similar in appearance to *M. nigricans*, the only discernible difference being the shape of stimulator and arrangement of folds in the anterior penis section. Thin vas deferens opening clearly asymmetrically at the posterior flattened end of epiphallus. Inside epiphallus dense small papillae. Constriction at boundary of penis and epiphallus shallow, just behind it the insertion of the musculus retractor penis. Penis roughly equal in length to epiphallus, inside papilla penis of simple structure and complex folds of two types (fig. 50), by their appearance similar somewhat to those in *M. gagates*. Spermatheca thin-walled, without clear boundary between container and spermatheca duct, sometimes adhering to atrium. Atrial accessory gland usually very large in relation to body size. Atrium short slightly narrowed anteriorly. Stimulator oval (oval or circular in cross-section), clearly flattened at loose end, its surface smooth, i.e. without papillae, spines or tubercles, only at tip may be very delicately striped, ending with a sort of fan, or small processes. Stimulator, though variable, with the end so characteristic that the slug can be distinguished easily from other similar species (figs 45-49).

**Spermatophore**: unknown.

**Bionomics:** it is only known that it may occur synantropically and was collected on limestone in quite damp places, and may occur together with *M. nigricans*.

**Distribution** (map 2). So far found only in Algeria at Constantine, Gorges du Rhumel (where it was collected with *M. nigricans*) and at Tizi-Ougoulmime, Djurdjura Mts. Location of locus typicus unknown.

**Material examined:** 17 specimens, including holotype and one paratype.
Figs 42-44. *Milax ater* — genitalia. 42 — copulatory organs of the holotype, 43 — copulatory organs of a specimen from Constantine, Gorges du Rhumel (Algeria), 44 — penis and epiphallus of the holotype.
Figs 45–50. Milax ater. 45–46 — stimulator of the holotype, 47–49 — stimulator of specimens from Constantine, Gorges du Rhumel (Algeria), 50 — penis and epiphallus open, the internal structure marked, of a specimen from Constantine.

Notes. Slug very similar to M. nigricans and M. gasulli, also to very dark M. gagates. Describing material from Algeria (Wikt. 1983a) I thought that the small differences in the stimulator appearance, which distinguish this slug, were within the variability range of M. nigricans, M. gasulli and M. gagates (also similar to each other). After studying the types and restudying the other specimens (11 were collected with 6 specimens of M. nigricans at the same locality — Constantine) in which there were no intermediate stages in the stimulator appearance between M. ater and M. nigricans, and M. gagates, I decided that until new information was collected it would have to be treated as a distinct species. Apart from differences in the stimulator structure it is worth noting that there are differences in the appearance of folds in the anterior part of stimulator. They clearly differ from those in M. nigricans, resembling those in M. gagates. It seems also not to attain such great sizes as M. nigricans, yet this cannot be indisputably ascertained, as M. nigricans at Constantine and at other African localities attains far greater body size than e.g. in Italy.
It differs from *M. gasulli* in darker body coloration, appearance of papilla penis and stimulator (see p. 206).

*Milax barypus* BOURGUIGNAT, 1866

*Milax barypus* BOURGUIGNAT, 1866: 208, pl. 32 figs 7–10. Loc. typ.: vicinity of Nasareth (Israel). Type: no information.


*Amalia cypria* SIMROTH, 1906: 90. Terra typ.: Cyprus; SIMROTH 1909: 243, fig. 3. Type: no information.

*Amalia (Cypria) cypria*: SIMROTH 1910b: 158, pl. 21 figs 18–21.

*Milax (Micromilax) cyprius*: HESSE 1926: 114; WAGNER 1930a: 51.

*Milax (Micromilax) barypa*: SIMROTH 1906: 90; FORCART 1960: 111.

Diagnosis. Body colour ochrous or yellowish with darker, grey pattern. Atrium genitale with a side pocket. Inside the pocket a small claw-shaped stimulator. Atrial accessory gland opens with a very long duct.

Description. Dimensions of the examined specimens preserved in alcohol: body length 16 mm, width 4.5 mm, mantle length 5.75 mm. Body thickset, highly domed (figs 51–52). Mantle slightly narrowed in front, proportionally big, covering over $\frac{1}{3}$ of the body length (on SIMROTH’s drawings 1910b, pl. 21 fig. 18 it covers more or less $\frac{1}{3}$). Keel strongly arched. Between keel and
pneumostome 11 or 12 grooves (the specimen was poorly preserved so it is difficult to determine the number precisely).

Coloration unknown in live slugs, in preserved specimens olive-ochrous, yellowish with grey pattern, sometimes with violet undertone. Darker pigment concentrates mainly on the mantle, beside the horse-shoe groove, and on the back. Keel always lighter than its surroundings.

Genitalia (figs 56-58, 61-62). Vas deferens thin, long and partly coiled opening apically to epiphallus. Epiphallus in the shape of a slightly bent club, its wider end turned backwards. Papilla penis as in fig. 62. In the examined specimen almost pear-shaped, on Simroth's drawings (1910b) cylindrical. Oval spermatheca passes indistinctly into a very wide spermatheca duct. The width of oviductus almost equals that of vagina. Atrium consists of a small caniculated part, being an extention of vagina, and of an ample side pocket. Accessory gland pressed into uniform mass opens to atrium by means of a single duct. The examined duct was approximately equal to \( \frac{2}{3} \) of the length of the entire reproductive system. On Simroth's (1910b) drawings it is almost twice as long as the whole system. Inside the atrium pocket a small stimulator with a wide base and a claw-shaped somewhat bent pointed end (fig. 61).

Spermatophore unknown.
Pallial complex (fig. 55), the way of intestine coiling as well as cephalic muscle branching have no outstanding features (figs 54 and 60).

Biönomics: unknown.

Figs 54-60. *Milax barypus*, from Oranim near Haifa (Israel). 54 — cephalic retractors, 55 — pallial complex, 56 — glandula hermaphroditica and a part of ductus hermaphroditicus, 57 — reproductive system, on the left visible atrial accessory gland connected to atrium by a long single duct, 58 — copulatory organs in magnification, 59 — posterior penis end with a part of vas deferens, 60 — alimentary tract, glandula hermaphroditica site hatched.
Figs 61-62. *Milax barypus*, from Oranim near Haifa (Israel). 61 — stimulator visible in its pocket connected to atrium, on the left sexual opening, above cut-off penis, on the right vagina with oviductus and spermatheca cut off, at the opening of vagina a sort of papilla, 62 — papilla penis.

**Distribution (map 2):** Israel, Cyprus.

**Material examined:** Oranim near Haifa, Israel, leg. et det. ?, 27.11.1954, 1 spec. (Field Mus. Nat. Hist. Chicago, no. 51893).

**Notes.** Poorly studied species. The synonymization of the species name of *cypria* SIMR. with *barypus* BOURG. seems to be justified. Some minor differences (the shape of the penis and the length of the accessory gland canal) which I have found while comparing the SIMROTH's drawings of the specimen from Cyprus with the examined specimen from Israel, result probably from the abrupt preservation of the specimen. A separate subgenus was created for this species (*Cypria* = *Microlimax*, see WIKTOR 1981). It seems that it was not necessary and that the features distinguishing it from the remaining species (atrium pocket and the single accessory gland canal) are only a result of a high specialization. The single canal took over the function of draining off the entire gland secretion while other canals which still function in the remain-
ing species have been reduced. The monstrous dimensions of this single canal which — as the drawing shows — happens to be tightly coiled (the examined specimen had already been dissected) indicate the high level of specialization of this organ.

**Milax caucasicus** (Simroth, 1912)

*Amalia caucasia* Simroth, 1912: 52, pl. 3 fig. 48 (exterior), pl. 8 fig. 31 (genitalia). Loc. typ.: Borshom (= Borzhomi), Gruziya (USSR). Holotype: Zool. Inst. Academy of Sciences Leningrad.


Diagnosis. Intensively pigmented almost black body. Stimulator in the shape of short cone.

Description. Preserved body length up to 45 mm, width up to 6 mm, mantle length up to 15 mm. Body thickset, the mantle covers less than \( \frac{1}{3} \) of it. Mantle grooves and keel distinctly developed. 12 grooves on the skin between the keel and pneumostome.

Coloration (figs 63–64). I examined only the preserved specimens and in literature head is described as blackish with violet undertone. Body sides gradually lightening downwards to dirty creamy colour. Wide black streaks along the horse-shoe groove on the mantle. The intensity of black pigmentation varies between specimens. Due to this beside almost black specimens ones with grey-blackish backs occur. In some specimens, including the holo-

type, an organe spot occurs in the middle of the mantle. Keel cream coloured. Sole side zones covered with very small ochrous-yellow spots, middle zone is grey-blue. Apart from this, tiny spots of black pigment scattered all over the sole. Yellow-ochrous pigment gradually disappears in preservation, especially after long time, however, black spots remain. The trace of yellow or orange pigment originating from lipochrome pigment dissolving in alcohol indicates that the live slugs are probably brighter coloured than the preserved ones.

Genitalia (figs 65–66). Distinctly big albuminal gland. Spermoviduct weakly

glandular. Free section of oviduct and vas deferens long. Vas deferens opens apically and somewhat asymmetrically to epiphallus. The end of epiphallus a little widened or cylindrical, bent anterad. Penis in the shape of short cylinder, mostly 4 times wider than epiphallus. Before the connection with atrium it suddenly narrows. Musculus retractor penis wide. Spermatheca usually wide, oval and only in younger specimens narrowed at the end. Spermatheca duct short and thin. Vagina a little wider than oviduct and faintly separated from it. Atrium accessory gland big and lobular connected with atrium by 7–8 tubes. Atrium proportionally small. Inside there is also a small stimulator. It has the shape of a short cone surrounded at the base with an annular roll. Penis papilla (fig. 65) in the shape of short corrugated cylinder free of distinct ornamentation.

Spermatophore so far not described.

Bionomics: unknown.

Distribution (map 2): known in Gruziya and Talish Mts, so on the western and south-eastern side of Caucasus (USSR). The species should be expected also in other regions of Transcaucasia.

Material examined: 8 specimens from Leningrad collection including the holotype and specimens from Talish Mts.

Notes. Species much resembling M. altenai and M. parvulus. Similarity is mainly external. It differs in genitalia, especially in the structure of stimulator.

**Milax gagates** (Draparnaud, 1801)

**Limax gagates** Draparnaud, 1801: 100. Loc. typ.: presumably near Montpellier (France).


† **Milax scaptobius** Bourguignon, 1861: 43. Terra typ.: North Algeria (Bougie, Constantine).

**Limax pectinatus** Se lenka, 1865: 105. Loc. typ.: Sidney (Australia) (after Altena and Smith 1975).

**Milax atratus** Mabille, 1868: 144. Terra typ.: Portugal.


**Milax tasmanicus** Tate, 1881: 16. Terra typ.: Tasmania (Launceston and Hobart) (after Altena and Smith 1975).

**Milax nigricolus** Tate, 1881: 17. Loc. typ.: Adelaide area of South Australia (after Altena and Smith 1975).


**Amalia Babori** Collinge, 1897: 294, figs 4–6. Terra typ.: Hawaiian Isl. (Heleakala Maui and Olaa to Kilavea).

**Milax gagates**: Altena and Smith 1975: 65, fig. 2; Hesse 1926: 110; †Kuhna and Schnell 1963: 137, fig. 1; Likharev and Wiktor 1980: 362, figs 487–488; Pilsbry 1948: 563,

http://rcin.org.pl
Diagnosis. Body uniformly dark grey or blackish, spotless. Sole with blackish sides and lighter middle. Stimulator thin, tape-shaped, gradually narrowing towards its end, its inner walls smooth with several papillae at most.

Description. Body length 20–35 mm (according to Quick 1960 even up to 50 mm), width 6–8 mm, mantle length c. 13 mm. Body moderately thick-set, mantle proportionally big (fig. 67). Skin sculpture weak, keel and mantle grooves distinct. Between keel and pneumostome 16–17 grooves.

Coloration. Uniformly dark grey or blackish except somewhat lighter
sides, spotless. Sole with darker, grey or blackish, lateral zones and lighter medial zone.

Genitalia (figs 68–71). Vas deferens short, almost equal in length to epiphallus. Epiphallus claviform, slightly widened posteriorly, top being almost truncated. Vas deferens opens to this truncature asymmetrically. Penis of rounded but irregular shape almost half as long as epiphallus. Musculus retractor penis thin and long. Inside penis small papilla (fig. 70). Free section of oviductus, vagina and atrium form thick tube and are almost not separated. Spermatheca elongate, slightly narrowed at end. Spermatheca duct very short, indistinctly separated from spermatheca, opening laterally to vagina. Atrium short, not widened. Accessory atrial glands clustered into cream mass situated under pharynx. About 20 thin, short coiled tubules connect them with atrium. In atrium stimulator thin, gradually narrowing toward end, strongly flattened but on the end conical (fig. 71), mostly coiled, its inner surface being almost smooth having only a few irregularly scattered sharply pointed papillae near free end.

Spermatophore (fig. 72) — much elongate, posterior end somewhat wider, remaining in spermatheca duct of slug-receiver, the narrower part coils in spermatheca. Spines branching dichotomically yet quite irregularly. They

Fig. 72. *Milax gagates* — spermatophore of the specimen from Cagliari (Sardinia, Italy). On the left a single spine in great magnification.
cover one side of spermatophore, the other side being smooth, without processes and sculpture.

**Bionomics.** The species occurring preferably close to water. It hides under stones. It is liable to introduction and synanthropisation. It must display a great ecological tolerance as it is encountered in various climatic zones (as an introduced species). According to Quick (1960) during the copulation both slugs strongly cling together so that no everted copulatory organs can be noticed. The slugs copulate in spring, summer and autumn (data referring to Great Britain). For more information on life cycle see p. 169 and fig. 20. Eggs being $2 \times 1.5$ mm, transparent and thin-shelled. It feeds on plants including the roots, e.g. carrot and potato tubers. It may destroy crops.

**Distribution (map 3).** Probably, it occurs only in South-Western Europe and North-Western Africa as well as on the Canary Islands. Determining its range requires detailed investigations. In literature it was often mistaken for *Milax nigricans*. Its aptitude for synanthropisation impedes determining in which regions it is a native species and in which an introduced one. It is certainly introduced to West Germany (FRG), Finland, Australia, Tasmania, New Zealand, Polynesia, America, South Africa and numerous islands on the Atlantic and Pacific Oceans, including Japan and Bermudas.

**Material examined:** c. 50 spec. from Spain, Algeria, Morocco, Canary Islands, New Zealand.
Notes. The majority of authors made no distinction between *M. gagates* and *M. nigricans* treating them as one species. Only the data supplying the description of stimulator and its drawing can be accepted, all other should be checked. See notes to *M. nigricans* (p. 213), *M. ater* (p. 195) and *M. gasulli* (p. 207).

Collinge (1900) described a species *Amalia ponsonbyi* from South Africa. The similarity of this slug to *M. gagates* is significant. Collinge probably, however, had to do with a slug from the family *Arionidae*, belonging to the sub-family — recently described — *Ariopeltinae* Siegel, 1985, and the genus *Ariopelta* Siegel, 1985 (see Siegel 1985).

**Milax gasulli** **Altena, 1974**


**Diagnosis.** Body dark grey. Genitalia very similar to *Milax nigricans* and *M. ater*. Different from both in the stimulator with several papillae on its end. As compared with *M. nigricans* it has a larger and a bit different spermatophore.

**Description.** Holotype body length 49 mm, mantle length 15 mm, body width not measured when the species was being described, at present impossible to be measured on the dissected holotype. Body shape similar to that in *M. nigricans*, keel strongly arched. Between keel and pneumostome 13 wrinkles on skin.


Genitalia (fig. 73). Genitalia of holotype were not very well preserved and were partly destroyed in dissection. In appearance not very different from genitalia of *M. nigricans*. Thin vas deferens opening asymmetrically yet apically on a short, somewhat swelled epiphallus. Penis cylindrical, c. 1.5 times longer than epiphallus. Penis interior not studied. Between epiphallus and penis clear constriction to which musculus retractor inserts. Oviductus without swellings, tubular. Spermatic sheath was distended by spermophore and damaged in dissection: probably oval. Spermatic duct in holotype short but clearly separated from spermatic sheath (probably before being filled by spermophore spermatic duct is a bit longer). Vagina somewhat narrower than spermatic sheath duct. Atrium short, inside very large stimulator. Stimulator with surface almost entirely smooth, only near the loose end there are several sharp-pointed papillae. End of stimulator strongly narrowed and bent. On drawings by Altena (1974, figs 1–2) there are also sharp-pointed papillae on the whole inner side of the stimulator (as in *M. nigricans*). Drawings were

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\(^1\) In the paper Zaghuan — such name does not exist in lists of geographic names and on maps. Probably: Zaghuan.
probably made by the author from a paratype that I did not study. Accessory glands as a large double structure connected by numerous, very thin ducts.

Spermatophore (fig. 74). Only a part of it known. Covered on all sides by strongly bifurcated spines. Size of this fragment shows that the whole spermatophore has to be very large in comparison to the whole slug, its shape and spine shape being different from those in other species.

Bionomics unknown.

Distribution (map 2): known only from locus typicus.

Material examined: I studied only the holotype and know nothing of any other material of this species.

Notes. In the description and figures of ALTENA (1974) there are some inaccuracies. The spermatheca duct does exist, though it is short. There is no gland that he calls "vaginal gland". As I found in the studied specimen the gland is a part of detached ducts belonging to atrial accessory gland. In its external appearance the slug is very similar to *M. gagates*, *M. nigricans* and *M. ater*, occurring or expected in Tunisia. *M. gagates* differs in the stimulator without papillae and in a quite different spermatophore. It is very difficult to distinguish the species from *M. nigricans*. The structure of genitalia of this species is very variable, the size of the slug and its coloration are differ-
ent. But for the observed differences in the structure of spermatophore I would be inclined to assume *M. gasulli* to be a synonym of *M. nigricans*. Altena (1974) did not know the appearance of the *M. nigricans* spermatophore, and I studied the only spermatophore I could find. Nothing can be said about the variability of this structure, so important in systematics. Comparing spermatophore of both species it can be said that the part found in *M. gasulli* shows that its spermatophore is far bigger and, at least on one side, has a completely different ending (cf. figs 73 and 84). In both cases spines cover the spermatophore on all sides and in both cases they are very strongly forked. Their shape is similar but not identical.

*M. ater* is also very similar to *M. gasulli*, both in body size and in appearance of genitalia. In this case papillae also are at the end of stimulator, though look somewhat different (see figs 45–49). The morphological variability of this slug is also unknown, as is the appearance of its spermatophore. In short *M. gasulli* requires further studies, and the amount of knowledge about it justifies its treatment as a separate species.

**Milax monstruosus** Wiktor, 1986


**Diagnosis.** Slug lightly coloured with unclear brownish pattern. Inside atrium three stimulators. Two of them identical, short and tongue-like, the third narrow, longer than penis together with epiphallus.

**Description.** Holotype length 29 mm, width 10.5 mm, mantle length 7 mm. Body shape not particular. Keel well-discernible, as is skin sculpture. 11 wrinkles on skin between pneumostome and keel (fig. 75).

![Fig. 75. Milax monstruosus — side view of the holotype, losses of mantle and opening due to dissecting of genitalia hatched (after Wiktor 1986).](http://rcin.org.pl)
Fig. 76. *Milax monstruosus* — copulatory organs of holotype (after Wiktor 1986).

Fig. 77. *Milax monstruosus* — the whole reproductive system of holotype (after Wiktor 1986).
Coloration. Holotype as if faded, creamy, with unclear light brownish pattern. No information about coloration of living slugs or about mucus.

Genitalia (figs 76–77). The specimen under description fully mature. Glandula hermaphroditica small, lightly coloured. Vesicula seminalis white, well visible, i.e. probably filled with sperm. Glandula albuminalis large, hard. Vas deferens thin and long, surrounding as a loop the female parts of genitalia, opening apically and symmetrically to thin and club-like epiphallus (posteriorly widened). Penis thin tubular, without swellings and distensions, in the studied specimen probably partly everted, its anterior part invisible. I have not studied its interior. Musculus retractor penis in comparison to penis wide and short. The place of its insertion is the place of folding and boundary between penis and epiphallus. Spermatheca oval, ended posteriorly by a narrowing like a beak. Spermatheca duct somewhat longer than spermatheca, clearly separated (spermatheca of the studied specimen was filled by dissolved spermatophore). Oviductus tubular, thin and twisted, relatively long, roughly equal in length to penis together with epiphallus. The shape of atrium and its size could not be established, atrium being everted, three stimulators being outside the body. Two of them short, almost identical, in shape similar to triangle, surface smooth, their internal sides, i.e. those directed to the sexual opening furrowy indented. Towards the furrow they are hook-like bent. The third stimulator much longer and narrower, longer than penis with epiphallus, and twisted. At its base a spirally round ring covered by grooves. The other parts of its surface completely smooth. It is furrowy indented along the whole length. Atrial accessory gland as a single lobular white structure, connected with atrium by three very long and thin tubular ducts, white as in other species, with silky gloss.

Spermatophore unknown.

Bionomics unknown.

Distribution (map 2): known only from locus typicus.

Notes. I studied only one specimen, the only representative of the family known from Syria. The structure of its genitalia differs from those I know in as many as three stimulators, and the accessory gland connected to the atrium by three ducts. In all other species there is one or two stimulators, or it is lacking, and the accessory gland is connected by a dozen or more ducts, or by one. The structure of genitalia may suggest that they are a result of an anomaly. This has to be taken into account, as I had only one specimen to study. Yet it has to be pointed out that in the spermatheca there were the remains of the spermatophore, and the vesicula seminalis was also filled. This shows that the slug had already copulated, and with success. Though I had no possibility of checking whether the above characters can be found in other specimens, I have decided to describe the slug as a new species, and in future it will be seen whether there is such a species, or perhaps that it is a unique anomaly. Because of the strangeness of its anatomical structure I have named it monstruosus.
“Palizzolia” monterosati Bourguignat, 1877

Palizzolia Monterosati Bourguignat, 1877: 16. Loc. typ.: Calatafimi (Sicily, Italy).

Type: no information on its existence.

A name introduced when a shell of a genus distinguished by the student was being described. It refers to a slug from Sicily. Probably a shell of Milacidae representative was meant.

Milax nigricans (Schulz, 1836)

Pharmacella nigricans Schulz (in Philippi), 1836: 125, pl. 8 fig. 1. Terra typ.: Panormi (Palermo, Sicily).

Amalia (Pirainea) insularis Lessona et Pollonera, 1882: 57, pl. 1 figs 32-33, pl. 2 figs 6-7. Terra typ.: Sicily, Sardinia.

Amalia (Pirainea) ichnusae Lessona et Pollonera, 1882: 60, pl. 1 figs 26-27, pl. 2 fig. 4. Terra typ.: Sardinia.

† Amalia doderieini Lessona et Pollonera, 1882: 58, pl. 1 figs 22-25. Loc. typ.: Palermo (Sicily).


† Amalia gagates benoiti Lessona et Pollonera, 1882: 59, pl. 1 fig. 9. Loc. typ.: Messina (Sicily).

† Amalia cabiliana Pollonera, 1891: 4. Loc. typ.: El-Hammam nella Cabilia (= Kabylie, Camerano, Algeria).

† Amalia mediterranea Cockrell, 1891: 331. Terra typ.: Algeria. Syn. n.

† Amalia mediterranea f. similia Cockrell, 1891: 332. Loc. typ.: Catania (Sicily).


Milax insularis: Quick 1960: 156, figs 8D, H.

Milax nigricans nigricans: Giusti 1968: 289, fig. 9.

Diagnosis. Body blackish, uniformly black or with light markings breaking through. Stimulator massive, triangular, with several rows of big papillae or spines.

Description. Body length up to 65 mm, width to 13 mm, mantle length up to 17 mm. Body moderately thickset. Mantle relatively small (fig. 78). Skin sculpture conspicuous, grooves shallow. Between keel and pneumostome 14-15 grooves. Keel well arched. Mantle sinuate notched posteriorly, near keel. Mantle grooves shallow and indistinct.

Coloration. Body dark blackish or black. Sometimes black pigment unevenly scattered and on body sides where it is absent, lighter dirty cream irregular markings occur. Sole uniformly dirty cream.

Genitalia (figs 79-83). Vas deferens slightly longer than penis together with epiphallus, opening at apical end of epiphallus almost symmetrically medially or almost medially. Epiphallus claviform, posteriorly widened, its tip almost truncated. Penis oval, sometimes swelling at papilla site. Musculus retractor penis attached laterally on epiphallus or between penis and epiphallus. Papilla inside penis as in fig. 81. In anterior penis section folds. Oviductus
posteriorly thin, anteriorly widening into broad canal. Vagina and atrium of the same diameter are natural continuation of broader oviductus. Spermatheca oval, very big and thin-walled. Spermatheca duct very short, almost indistinct, opening laterally to vagina. Atrial accessory glands very big, usually placed under pharynx, connected with atrium by 16–18 or even more extremely thin tubules. Stimulator big fleshy, slightly bent, elongated triangular with wider base, its free end conical. Inside, several rows of papillae, mostly sharply ended, even spine-shaped, or (badly preserved specimens) spherically rounded. Most of them situated at stimulator base, and absent at its tip.
Spermatophore (fig. 84). The only item of spermatophore known to me is wholly preserved and has very characteristic features: strongly elongate, spindle-narrowed on both ends. Along its whole length and on all sides it is covered by multiply branched spines. The anterior ending, i.e. that by which it is inserted into the partner's body, covered by the largest and most dense spines, forming a sort of "pine cone". The only similar spermatophore among those I know is that of *Milax nigricans*, of which only fragment is known. It is bigger and distended on one end (see fig. 74).

**Bionomies unknown.**

**Distribution** (map 4). It requires examining as the majority of authors used to treat *M. nigricans* and *M. gagates* as one species. Undoubtedly, it occurs in Tunisia, Algeria, Morocco, Malta, Egypt, Sicily, Corsica, Majorca, Italy, France, Great Britain (Sussex), and probably in Spain.

**Material examined**: c. 60 specimens.

**Notes.** In young specimens penis and epiphallus are longer than in adult ones, stimulator having smaller papillae usually distinct at its base.

Species similar to *M. gagates* and often mistaken for it. It differs from *M. gagates* in its larger size, proportionally smaller mantle, darker coloration of its back and sides as well as lighter unicolour sole. The most reliable distinctive feature is the stimulator wider at its base together with its big papillae. It is worth remembering that here the papillae are at the base while in *M. gagates* they are at the tip. It is important for the identification of young specimens.

Another very similar species is *M. ater*, a bit smaller, so far little studied. It differs mainly in its stimulator appearance (see figs 45–49), which is almost
smooth, that is, without papillae and spines, while on the unattached end with several processes and with delicately striped surface. Both species (*nihricans-ater*) occur together in N. Africa.

The third similar species is *M. gasulli*, known only from descriptions of types. It is also smaller than *M. nigricans*, dark grey; the stimulator somewhat different, on its end papillae. Judging by the known fragment, it differs also in the spermatophore appearance (see figs 73–74 and notes by this species on p. 207).

The complex of species *M. nigricans, gagates, ater* and *gasulli* needs to be revised in detail on ample material in order to explain their mutual affinity or possible synonymy.

**Milax parvulus** WIKTOR, 1968


**Diagnosis.** In living slugs keel and sole orange, mantle brown-blackish with black pattern. Alcohol-preserved specimens grey with blackish pattern. Atrium barrel-shaped with long, tape-shaped, very gradually narrowing stimulator. No papillae in stimulator.

**Description.** Body size: preserved specimens — length up to 26 mm, breadth to 6 mm, mantle length 9 mm. Body posteriorly wedge-like narrowing. Keel prominent. Between keel and pneumostome 11–13 groves.

Coloration of living individuals: back dark, brown-blackish with distinct black or blackish pattern. On mantle orange blots, also keel and sole orange. Head and tentacles blackish. Preserved specimens (fig. 85) tend to lose the orange colour, also the brown vanishes; back, mantle, head, tentacles becoming ash-grey or bluish-grey with blackish pattern, keel, light blots on mantle and sole cream-white. Mantle-pattern of small spots, on sides concentrating in indistinct streaks. On posterior body end pigment concentrating mainly along grooves, hence a reticulate pattern on this body part.

Genitalia (figs 86–88). Penis and epiphallus indistinctly delimited. Both forming a well elongate conus, the posterior epiphallus end being widened. In this epiphallus part small papillae may occur on its exterior side. In natural position the penis and epiphallus hook-bent. Where musculus retractor penis inserts (limit between penis and epiphallus) there is no narrowing. Thin vas deferens opening approximately in the middle of the epiphallus, posterior side flattening. Inside penis small papilla (fig. 88). Spermatheca oval, spermatheca duct thick. Oviductus also thick, in its posterior part often a small lateral pocket (fig. 86). Vagina very strongly short-
ened, one may get an impression that oviductus and spermatheca duct open directly to atrium. Atrium broad, barrel-like, or irregular yet always broad. Atrial accessory gland like whitish, compact mass, connected to atrium by 9–13 thin, silk-glossy ducts. Inside atrium stimulator, very long, thin, gradually narrowing, in cross-section slightly crescent, exterior side completely smooth (without any papillae or sculpture). In natural position in atrium stimulator rolled (fig. 87).

Spermatophore unknown.

Bionomics. Nothing is known about the bionomics and ecology of this slug. I collected it on a calcareous (limestone) plateau with grassy plants, where it sheltered under stones.

Distribution (map 2): known only from several localities in Bulgaria. It may be expected in Yugoslavian Macedonia.

Material examined: 33 specimens, all from the Stara Planina Mts in Bulgaria.

**Milax riedeli** Wiktor, 1986

Diagnosis. Body covered by reticulate pattern. Inside atrium membranous wide stimulator covered with scarce spines.

Description. Holotype size — body length 28 mm, width 6 mm, mantle length 13 mm. Keel strongly arched. Skin sculpture distinct, between keel and pneumostome 13 wrinkles.

Coloration. What coloration was when the slug was alive is unknown. At present it is a bit faded. Mantle and back brown creamy, covered by blackish pattern. On mantle (fig. 89) pattern formed by a system of small diffuse dots quite evenly distributed. Lack of distinct darker lateral streaks, usually occurring in light Milacidae covered by a pattern. Back darkest, sides becoming gradually lighter downwards, the darker pattern accumulating in skin grooves producing a darker network. Keel light. Head blackish, sole creamy.

Colour of mucus unknown.

Genitalia (figs 90-91). Holotype fully grown-up, this being shown by large glandula albuminalis. Genitalia had been dissected before I could study the slug, they are somewhat damaged, the whole slug is hard and not very well preserved. Vas deferens opening apically and symmetrically. Epiphallus club-like, equal to penis in length. Penis with two swellings. Musculus retractor penis broken, the remaining part showing that it was a strong muscle. Spermatheca oval, elongate, clearly separated from spermatheca duct. Oviductus long and twisted. Atrium, despite the everted stimulator (i.e. atrium probably also partly everted) large, rounded in shape. Accessory gland much damaged, numerous ducts linking it to atrium preserved. Stimulator of appearance not encountered in other Milacidae: quite flat, leathery, full of folds, irregular in shape (fig. 91), its edges fringed. Also on the outer edge and in some places on internal side conical spines on surface with very delicate striations resembling fingerprints.
or stimulator surface in *Deroceras (Agriolimacidae)*. Surface of membranous part of stimulator fairly smooth. Stimulator in holotype was everted.

Spermatophore unknown.

Bionomics unknown.

Distribution (map 4): known only from locus typicus.

Notes. External appearance and general appearance of genitalia have no unambiguous diagnostic characters. The stimulator, however, is exception-

Figs 90-91. *Milax riedeli* — holotype. 90 — genitalia with everted stimulators, between it and a bunch of ducts the atrial accessory gland, right ommatophore removed with genitalia, 91 — stimulator everted, large magnification.
ally characteristic and unlike any other species. At the same time it is known that it is the stimulator that in the genus *Milax* is one of the most veritable specific features. This is why I have decided to describe this slug as a new species, though I had only one specimen.

**Milax verrucosus** Wiktor, 1969


**Diagnosis.** Body vermiform, mantle proportionally very small, covered with papillae visible with bare eye. Slug uniformly white or almost white. Vas deferens, epiphallus and penis indivisible. Accessory atrial gland connected to atrium with single short channel. No stimulator.

**Description.** Body strongly elongate, usually nearly vermiform (fig. 92). Length of crawling slugs to 35 mm, of preserved ones to 28 mm, breadth to 4 mm. Mantle in crawling slugs is \( \frac{1}{6} \) of the total body length. Keel poorly arched yet clearly reaches the anterior mantle edge. Body sculpture very distinct. On the mantle papillae clearly visible with bare eye, grooves on the anterior body section are narrow and long. When strongly contracted the slugs are quite covered with papillose sculpture.

Body unicolour, white, creamy-white, only in the largest specimens the mantle and back occasionally light ash-grey or blackish. Tentacles blackish.

Mucus very thick, colourless.

Genitalia (figs 93–95). Glandula hermaphroditica narrow and strongly elongate, ductus hermaphroditicus long as well. Glandula albuminalis very large in comparison to reproductive system, it makes approximately half of the system. Spermoviductus very short. The male section, especially vas deferens, is exceptionally short (a character not encountered in any other species of the family). Epiphallus not separated from the penis. The male section is a fleshy channel gradually widening anteriorly, to which very delicate musculus retractor penis is laterally inserted. Oviductus approximately equal to the male section, and also gradually widening anteriorly. Usually in its posterior section a small lateral pocket. In its natural position the oviductus and the male section coiled, together forming about one turn of a spiral (fig. 95). Spermatheca oval, small, set at the end of gradually widening anteriorly spermatheca duct. The channel length approximately equal to oviductus and the male section. Atrium not widened, its breadth approximately equal to that of joined male and female channels. Accessory atrium gland forms very late, when other genital parts are wholly developed. Originally it looks like a papilla or a pocket on lateral atrium wall (fig. 94), later when wholly developed it is
long, like a bird wing, connected with atrium by a short and thick channel (fig. 93). No stimulator.

Spermatophore unknown.

This slug in both its external appearance and internal structure clearly differs from other species of the family. Its specific character is an unusual structure of head retractors. There are two separate muscles, their posterior insertions lie on the medial body line beyond the mantle under the keel. The more anterior muscle is ommatophore retractor, the other pharynx retractor (fig. 96).

Bionomies. Collected in mountains above 1000 m a.s.l., in shaded valleys.
and fairly damp places, in deciduous and mixed forests with rich litter. It occurs mainly in litter, soil and under boulders, taken out of its hidden places it at once buries down or shelters under boulders, mainly occurs on calcareous rocks, it was met in caves.

**Distribution (map 4):** known only from the central part of the mountain range Stara Planina in Bulgaria.

**Material examined:** 33 specimens from the Stara Planina Mts.

Notes. Its external appearance and specific features in internal structure seem to result from its adaptation to living in soil or under the ground.

**Genus Tandonia Lessona et Pollonera, 1882**

*Tandonia Lessona et Pollonera, 1882: 54. Spec. typ.: Amalia marginata (Draparnaud, 1805) (= Limax marginatus Draparnaud, 1805 = Limax rusticus Millet, 1843, non Limax marginatus Müller, 1774).*

*Subamalia Pollonera, 1887: 5. Spec. typ.: Amalia robici Simroth, 1885.*

*Macrothylacus Wagner 1930a: 46 (as a subgenus of *Milax*). Spec. typ.: Milax jablanacensis Wagner, 1930.*

*Promilax Wagner 1930a: 50 (as a section of *Milax* s. str.). Spec. typ.: Milax (Milax) baldensis (Simroth, 1910) (= Amalia baldensis Simroth, 1910).*

**Aspidoporos:** Babor 1898: 33.

Body length after preservation to 95 mm. Body usually with sides almost parallel, abruptly tapered at the very end, rarely wedge-like. Keel along the whole of back, of various degree of arching.

Accessory glands of various shape, always more than one, opening into the female part of genitalia, i.e. to vagina at place somewhat lower than insertion of oviduct to spermatheca duct. Atrium without stimulator, at most with folds or fin-like swells.

About 36 species known.

Distribution (map 5): Black Sea area, eastern and central part of the Mediterranean region, south-eastern, partly western Europe. The largest number of species is in the Balkan Peninsula.

Map 5. Distribution of the genus Tandonia.

Notes. In earlier divisions of the family species of this genus were placed in different taxa. After detailed analysis of existing divisions I have come to the conclusion that the splitting of the family in many small taxa of a lower rank is ungrounded, or is based on misunderstanding. Problems related to this issue have been discussed in detail in a publication specially devoted to it (Wiktór 1981); see also p. 163–164.

In Milacidae many authors distinguished a separate genus Aspidoporus Fitzinger, 1833, with one species included Aspidoporus limax Fitzinger, 1833. The character distinguishing the species proved to be an artifact (opening in the mantle), and the types in the Naturhistorisches Museum in Vienna are young Tandonia. Other characters were ascribed to the genus by Babor
(1898) and result from errors and mistakes of the author (intestine with three loops, lack of accessory glands). The generic name *Aspidoporus* Fitz. and the specific one *Aspidoporus limax* Fitz. were considered nomina dubia, as at present it cannot be established what names they could be synonymized with. The whole problem was discussed in another paper (Wikt or 1979).

**Tandonia albanica** (Sóos, 1924)


Tandonia albanica: Wikt or 1982: 466, figs 1-5.

**Diagnosis.** Body similar to *T. melanica*, black or brown with darker pattern on mantle and back. Epiphallus cylindrical or conical, c. 1.5 times longer than penis. Papilla penis semispherical. Spermatheca oval, spermatheca duct long and thick-walled. Vaginal accessory glands large lobular. Spermatophore cigar-shaped, posteriorly with several large hooks, anteriorly covered by small bifurcated spines.

**Description.** Body length to c. 60 mm, mantle length to 18 mm, mantle width to 13 mm. Usually far smaller specimens can be met, less than 30 mm in length being fully mature. Keel poorly arched. Skin grooves shallow and indistinct, their number between keel and pneumostome 12–15.

Coloration of two kinds. On rocks and rock rubble usually quite black, with sides a bit lighter and sole creamy. On rivers and lakes grey-brown-beige with darker, almost black pattern on mantle and back. On mantle lateral streaks visible, the central mantle part most light. Keel usually lighter, darker pigment accumulating mainly in skin grooves. Apart from light individuals in the same biotopes also very dark ones can be met. I also watched copulation between an almost black and an almost beige individual.

Mucus colourless, on irritation also milky.

Genitalia (figs 97–98). Thin vas deferens opening a bit asymmetrically at the apical epiphallus end. Epiphallus cylindrical, sometimes somewhat tapered posterad, its posterior end smoothly rounded, usually with two protuberances or with two clear tubercles (fig. 98). Penis irregular in shape with several swellings, sometimes cylindric-spherical, somewhat shorter than epiphallus and always wider. Between penis and epiphallus a small constriction at which narrow musculus retractor penis inserts. Papilla penis semispherical, smooth or covered by several concentric wrinkles. Inside penis several swellings and wrinkles (fig. 99). Oviductus in comparison with other genitalia thin, tu-
bular. Spermatheca elongate oval usually tapered at the end. Spermatheca duct longer than spermatheca and thick-walled. Vagina short, as if a prolongation of spermatheca duct. Accessory glands lobular, multipartite and large, surrounding anterior sections of spermatheca duct and oviduct. Atrium short.

Figs 97-98. Tandonia albanica — copulatory organs. 97 — specimen from Trnica (Yugoslavia); 98 — specimen from Lukovo (Yugoslavia) (both after Wiktor 1982).

Spermatophore (fig. 101). Cigar-shaped, relatively short. Anterior part mildly narrowed and in undamaged spermatophores ended with a short cirrose process. The process most often cannot be dissected, or else it dissolves earlier in spermatheca and then anterior section tapers (like a cigar end) (see Soós 1924 and Wiktor 1982). Posterior part is wider, not narrowed, with variable irregular ending, where there are always several large hooked spines directed posteriorly or laterally. Anterior part, roughly to \( \frac{3}{5} \), covered by small branched spines directed anterad. The remaining spermatophore is smooth, only near the posterior end small areas, covered by very small and dense needles. Spermatophore straw-yellow or orange-yellow. It is only partly in spermatheca, its posterior end remaining in spermatheca duct.

Bionomics. In rocky areas overgrown with shrubs (less frequently with woods) and in rocky debris. Usually in numerous populations, after rain, e.g. on the Ohrid lake in some places several individuals in each square metre can be
met. Shelters under stones and in rock crevices. Often in river valleys, where I have met chiefly lighter individuals. Black form is less numerous, and can be met beside beige individuals covered with pattern. In mountains and in several places in the wood I have met only black ones. In exceptionally numerous individuals spermatophore in spermatheca can be encountered. They occur in individuals collected at the end of September and early in November. Several times I watched copulating slugs. They were motionless, both partners had the bodies arched. They adhered closely by their sides, between their mantles the everted atrium was visible like two whitish rolls. Copulating pairs were usually hidden under stones. The slugs copulate on warm wet days, particularly after rain. It follows from the literature that the species reaches considerable altitudes up to 2400 m. I collected them on smaller altitudes, i.e. between 600 and 2000 m.

Distribution (map 6). It probably occurs at a smaller area of Yugoslavian Macedonia and Albania and probably in frontier areas of Greece. The information I gave earlier about its occurrence in Greece (WIKTOR 1986a) referred to another species, new for the science: T. melanica.

Material examined: c. 130 specimens.

Notes. This species makes a lot of trouble as it is similar to two other ones:Externally it does not differ from T. macedonica, and black forms also from T. melanica, but it is clearly different from both in the appearance of the spermatophore. In the structure of genitalia it differs from T. macedonica in the short papilla penis and the shorter and wider epiphallus, and thick-walled spermatheca duct. From T. melanica it is different in thick-walled conical spermatheca duct and a more elongate and larger spermatheca, and larger, in comparison to body size, copulatory organs.

I dealt with the synonyms earlier (WIKTOR 1983). The types of this species, just as the synonymized T. adelpha, were destroyed in fire in the Budapest museum. Specimens studied by WAGNER (1931a) have been preserved; WAGNER uses both names. It is very probable that WAGNER had access to types of both species. Studying WAGNER’s specimens I found that they belong to one species.

See Tandonia melanica, p. 265.

Tandonia baldensis (SIMROTH, 1910)

Amalia baldensis SIMROTH, 1910a: 334 (? fig. 11 as Am. hessei n. sp. — see notes!). Terra typ.: N-Italy (Monte Baldo and Agordoschlucht). Type: probably does not exist — it is not in Frankfurt a/M, where it should be.

Milax (Milax) baldensis: WAGNER 1930a: 51.

Milax baldensis: ALTENA 1977: 65, fig. 1 A, B.

Tandonia baldensis: WIKTOR 1981: 151, fig. 7.

Diagnosis. Vagina very long. Its accessory glands invisible or poorly visible from outside, from inside visible as yellowish spots. On vagina inner wall an elongate fold.

Description. SIMROTH’s original description (1910a) has only a few details, which concern only one, probably sexually immature, specimen. The present description was based on individuals collected near the terra typica (see the material) on the opposite side of the lake Lago di Garda. These were the same specimens that ALTENA had studied and described (1977). It is not quite certain whether the slug SIMROTH described is the same as the below species.

Size of the largest alcohol preserved specimen: length 27 mm, width 7 mm, mantle length 8.5 mm. Keel well visible. Clear 11 grooves on mantle between keel and pneumostome.

Coloration. Young individuals: back and mantle uniformly black, sides getting gradually lighter downwards. The largest individual has black pattern
in body grooves, the whole body being somewhat lighter. Sole creamy in all specimens.

Genitalia (figs 102–105). All specimens I studied not wholly sexually mature (subadult), this being indicated by small glandula albuminalis. Ductus hermaphroditicus clearly widened medially, which may be a character or may depend on the sexual activity phase, for in some slugs the duct becomes widened when spermathozoa are intensively produced. Long, free sections of vas deferens and oviductus are characteristic, and a very long vagina. Epiphallus club-shaped, its length similar to that of penis. Penis cylindrical, clearly separated from epiphallus. Musculus retractor penis of moderate size. Papilla inside penis, structurally simple. Oviductus tubular. Vagina cylindrical, somewhat widened medially, inside it elongate folds. Accessory glands very small, situated more anteriorly than the linking of spermatheca duct to oviduct, in form of small tubercles, or short digitate processes around vagina (figs 103–104). Sper-
matheca oval, usually clearly separated from spermatheca duct. Spermatheca duct roughly equal in length to spermatheca. Atrium short, inserted to body walls with strands of retentor muscles.

Spermatophore — shape unknown. ALTENA (1977) in his paper has a drawing of its fragments (fig. 106).

Distribution (map 6). The specimens I studied come from a locality 20 km away from Monte Baldo, the locality being separated from the mountain by the lake Lago di Garda. The other type locality of SIMROTH's paper (he qualifies it with "?" in his paper) — Agordschlucht — about 125 km away from Belluno (ALTENA 1977). All the localities are in N-Italy.

Map 6. Distribution of different Tandonia species.


Notes. SIMROTH (1910a) did not describe the external appearance of the species. His description concerns only genitalia and few details. The text is accompanied by a schematic drawing of genitalia, with the caption "Am. hessei n. sp.". As far as I know SIMROTH had never described a species of this name (not to be confused with Amalia hessei BOETTGER, 1882 = sowerbyi). In the text there is a reference to the part of the drawing showing the interior of vagina (fig. 11A). This allows a suggestion that the other drawing, showing
genitalia, refers to *T. baldensis* as well, and the species name in the caption is an error (see also Hesse 1923, p. 195).

The description of *T. baldensis* given by Simroth (1910a), and the specimens I studied are very similar to *T. fejervaryi* (Wagner, 1929). The similarity is especially prominent in young *T. fejervaryi*, whose accessory glands have not wholly developed. The distance between known localities of *T. baldensis* and *T. fejervaryi*, occurring in Yugoslavia, is great, they are also separated by important zoogeographic boundaries. *T. baldensis* differs from *T. fejervaryi* in the internal structure of its penis, epiphallus and vagina, *T. baldensis* having longitudinal folds instead of papillae. It is too early to establish their possible synonymy, yet, if this should be so, the name *T. baldensis* should have priority.

**Tandonia bosnensis** Wiktor, 1986


Diagnosis. Body brownish with blackish back and blackish pattern on sides and mantle. Penis with epiphallus forming a mace-like elongate structure undivided by clear constrictions. Spermatheca not separated from spermatheca duct, strongly elongate, c. 2.5 times longer than penis with epiphallus.

Description. Body length in holotype 30 mm, the widest is the posterior body section, outside of the mantle, of 12 mm. Mantle length 8 mm. Paratypes are young, smaller than holotype. When alive the slug did not differ from other representatives of the genus with elongate slender body. The small mantle length was, however, prominent. After preservation a character previously not noticed was revealed (except in one paratype), i.e. that the widest body part is not the one covered by mantle, but the one outside it. It seems to be an artifact.

Coloration (fig. 107). Living slugs brownish-pink. Back and head blackish,
also blackish pattern on mantle and sides. Pattern of irregular dots on mantle, on sides dots diffuse, forming an irregular network. Keel pinkish. Sole creamy. After preservation pattern still blackish, the background becoming creamy. Mucus colourless, after irritation slug secretes also milky-whitish mucus. Genitalia (figs 108–109). Glandula albuminalis and spermoviductus strongly elongate. Copulatory organs in comparison to the size of other genitalia and to that of the whole body relatively small. Vas deferens clearly long, winding around penis, opening apically into epiphallus, somewhat asymmetrically. Epiphallus and penis not clearly separated, even at the place where very thin musculus retractor inserts without constriction. Both forming a club-like cylindrical structure, posteriorly somewhat widened and irregularly rounded. Inside epiphallus nodular structure. Papilla penis I failed to find. Probably at
the place it usually occurs there is only a narrowing of the internal diameter of penis. Oviductus as a twisted tube, somewhat narrower than penis and c. 1.5 times longer. Spermatheca and spermatheca duct form together a tube gradually widening and are not separated. Together they form an organ 2.5 times longer than penis and epiphallus together. Vagina very short, hard to discern. Into vagina lobular vaginal accessory glands opening. Atrium also very short. Sexual opening near lower mantle edge, roughly at $\frac{1}{3}$ of its length.

Spermatophore unknown.

Bionomics. All the specimens were collected on leaves, chiefly of beech (Fagus) at the bottom of low limestone rocks by the road.

Distribution: known only from locus typicus (map 6).

Material examined: 3 specimens (types).

Notes. This slug differs from all other known Milacidae, so that I have decided to describe it on the basis of only one adult specimen. The other young specimens have all the external characters noticed in the holotype. A character especially distinguishing is the very long spermatheca. A longer spermatheca was only described in T. jablanacensis. Both slugs differ both in their external appearance and in the structure of genitalia, moreover they occur in different regions of Yugoslavia.

**Tandonia budapestensis** (HAZAY, 1881)

**Limax gagates** MENEGAZZI, 1855: 64, pl. 2, figs 1-7 (! non gagates DRAPARNAUD, 1801) (after HESSE 1926).

**Limax gracilis** LEYDIG, 1876: 276, pl. 12 fig. 22. Terra typ.: environs of Tübingen (FRG) (! non gracilis RAPINESQUE, 1820).

**Amalia budapestensis** HAZAY, 1881: 37. Loc. typ.: Budapest (Hungary).

**Amalia Cibiniensis** KIMAKOWICZ, 1884: 103. Terra typ.: Transylvania.

**Milax gracilis valachicus** GROSSU et LUPU, 1961: 133. Loc. typ.: Bucharest (Roumania).


**Milax gracilis:** PHILIPS 1930: 65, figs 1-24a, pls 1-2 figs 1-17; PHILIPS and WATSON 1930: 65, figs 1, 4, 6, 8-11, 14, 17-19, pl. 1 figs 1-3, pl. 2 figs 1, 2, 5, 8-13.


**Tandonia budapestensis:** LIKHAREV and WIKTOR 1980: 376, figs 515-522; JUNGBLUTH, LIKHAREV and WIKTOR 1981: 19, fig. 38; WIKTOR 1983: 109, figs 23-25, map 9; WIKTOR and LIKHAREV 1980: 437, fig. 38.

**Milax (Milax) valachicus:** GROSSU 1983: 217, figs 130-134.

**Diagnosis.** Body narrow, slim, blackish-chocolate with dense darker pattern. Keel olive or dull orange, sole grey, ashen. Epiphallus approximately equal in length to penis, spermatheca elongate.

**Description.** Body length when crawling up to 70 mm, mantle covering less than $\frac{1}{3}$ of body. In preserved specimens body length up to 42 mm, breadth 5 mm, mantle length 11 mm. Body narrow (figs 110-111), nearly worm-
Milacidae — systematic monograph 231

-like, posteriorly very gradually narrowing, keel narrow. Keel well arched, always visible in its entire length, i.e. as far as the posterior mantle edge. Between keel and pneumostome 9–11 grooves.

Coloration. Body blackish-chocolate, at first appears unicolour, actually covered with a dense blending pattern of spots and dots on dull cream (or orange) background. Dorsum and mantle darker than sides. On mantle indis-

Distinct black side bands. Keel olive or dull orange without dark dots. Head and neck blackish. Sole dull orange, ashen or blackish. On its external zones dark melanophores visible. During preservation orange and brown hues fade, the

Figs 113–115. Tandonia budapestensis. 113 — papilla penis of a specimen from Bucharest (Roumania) (after Wiktort 1983), 114 — spermatophore of a specimen from Beograd (Yugoslavia), 115 — spine from the same spermatophore.
Milacidae — systematic monograph

slug taking blackish-ashen shade with light and dark dots. Within the same population individuals occur distinctly darker, even almost black, and lighter, even coffee.

Slime very thick, viscous, forming threads, orange or yellowish, transparent. Irritated slugs secrete, like other species, opaque milk-white defensive slime.

Genitalia (fig. 112). Vas deferens thin, clearly asymmetrically opening at the epiphallus posterior end. Epiphallus cylindrical or claviform, equal to, or slightly longer than, penis. Penis irregular, usually somewhat rounded, wider than epiphallus. Musculus retractor penis well developed. Inside the penis a small papilla of simple structure (fig. 113). Spermatheca oval, sometimes clearly narrowed posteriorly, or nearly cylindrical. Spermatheca duct usually fleshy, thick. Oviductus is a wide pipe, vagina very short, in cross-section approximately equal to oviductus. Vaginal accessory glands like two lobe-like whitish formations closely adhering to vagina and connected to it by several thin ducts. Atrium short, tubular.

Spermatophore (figs 114-115) thin, long, worm-like, about 16 mm long. Nearly all exterior surface covered with spines of two kinds (QUICK 1960).

Bionomics. An eurytopic species tending heavily to be synanthropic, shelters under stones and earth clods, in litter and detritus. Usually occurs in ruderal biotopes, shrubs, stone debris, graveyards, and on cultivated land, esp. in gardens. In Great Britain it copulates from November to January (QUICK 1960), in Czechoslovakia from April to autumn (HUDEC 1961). Courtship and

Map 7. Distribution of Tandonia budapestensis.
copulation last very long, usually begin at night and prolong to afternoon next
day, or even longer. Atria, penises and accessory glands get everted; the or-
gans are visible between the heads of both partners (Quick 1960) (see p. 166).

Distribution (map 7). Its original range has not been ascertained. It
probably occurred in the Southern Alps and the northern Balkans, and it spread
as a synanthropic species from there to other areas. Everywhere its occurrence
is insular. Now it is known from Austria, Italy, Germany, Switzerland, Hungary,
Roumania, and, clearly as introduced, from Turkey, Bulgaria, Yugoslavia, Cze-
choslovakia, Poland, Belgium, Great Britain, New Zealand and the Hebrides.

Material examined: several scores of specimens from Bulgaria, Yugoslavia, Poland,
Czechoslovakia, Italy, Great Britain.

**Tandonia cavicola** (Simroth, 1916)

*Amalia cavicola* Simroth, 1916: 4, figs 1-2. **Loc. t yp.:** Jama na Visokoj (Dalmacija, Yugo-
slavia). No information about preserved syntypes.

*Milax (Milax) cavicola:* Wagner 1930a: 50; 1931a: 65, fig. 11.


Diagnosis. Large slug, dull creamy, with some black spots like India
ink splashes. Penis short, epiphallus c. 3.5 times longer. Accessory glands very
small. Spermatheca duct thick and clearly separated from spermatheca con-
tainer.

Description. Largest size unknown. The largest specimen I know was
subadult, its body length after preservation was 65 mm, width 12 mm, mantle
length 12 mm. According to Simroth (1916) length up to 72 mm. Body thick-
set, skin thick, skin grooves delicate; 14 of them between keel and pneumostome.
Keel poorly arched, distinct only in posterior body section.

Coloration: Mantle and back creamy-white, dull creamy, ochrous-creamy,
darker on mantle than on sides. On this background large accumulations of
black spots, of various densities, like India ink splashes (fig. 116). Sometimes
without spots. Also in some individuals darker pigment in skin grooves, for-
mimg brownish reticulate pattern. Keel and its prolongation always without
spots and without the darker pattern. Head and tentacles grey or brownish.
Sole creamy-white.

Mucus not described till now.

Genitalia (figs 117-118). Simroth’s (1916) drawings are very simplistic
and careless. Probably no types. I based the genitalia description on specimens
which, I believe, belong to this species but come from other South Yugosla-
avian localities. Vas deferens longer than both penis and epiphallus, thin and
long. Epiphallus elongate, cylindrical, posteriorly club-like enlarged, inside
many elongate folds (fig. 118). Penis very short, cylindrically spherical, c.
3.5 times shorter than epiphallus and separated from it by shallow constric-
tion. Inside penis a small, structurally simple papilla (fig. 118) and the elongate
folds. Musculus retractor penis delicate, its insertion in the constriction se-
eparating penis from epiphallus. Oviductus nearly like a straight pipe. Sperm
matheca in specimens studied by me empty, posterior end sharpened. Accord-
ing to Simroth (1916) and also to Wagner (1931a) spermaphthea varies in
shape, container itself may be even spherical. Shape, as in other species, cer-
tainly depending on container having been filled in or not, or being filled with
spermatophore. Spermaphthea duct longer than spermaphthea, thick-walled, tu-

Figs 116-118. Tandonia caricola. 116 — side view, specimen from Zavala (Hercegovina,
Yugoslavia); 117 — copulatory organs (specimen from Šipan Isl., Yugoslavia), 118 — open
penis and epiphallus (specimen from Šipan Isl.) (all figs after Wiktór 1982).
bular. At its opening to atrium a small spherical papilla (fig. 118). Accessory glands small, foliaceous, adhering closely to vagina walls and spermatheca duct. Each gland with a separate thin canal draining off secretion, canals opening at boundary of vagina and atrium.

Spermatophore unknown until now.

Bionomics. According to SIMROTH (1916) the slug inhabits caves. My material does not confirm this. It is likely to be, like most other slugs, a trogloxen. No data available on its bionomics.

Distribution (map 6): all known localities are in Dalmatia, Herzegovina and Crna Gora, i.e. in SW Yugoslavia.

Material examined: 3 specimens described previously (WIKTOR 1982) and a specimen studied and described by WAGNER (1931a), being at Nat. Hist. Mus. Vienna (no. 36759), and 3 specimens from Stari Bar (S-Crna Gora). All specimens were either juvenile or subadult.

Notes. The very characteristic coloration is probably a sufficient diagnostic character to identify the species. WAGNER (1931a) overlooked the small accessory glands and pointed to their lack, in fact his specimen has the glands, which I found myself.

**Tandonia cretica** (SIMROTH, 1885)

*Amalia cretica* SIMROTH, 1885: 231, pl. 7 figs 20 XV, 22 XIXA, pl. 10 figs XIX 17B, 18C. 
Loc. typ.: Canea (= Khania = Chania, Crete, Greece). Type: probably does not exist.


*Milax* (Subamalia) *scyrius* WAGNER, 1931a: 75 — proposed conditionally for *Milax* (Subamalia) nov. spec. from Skyros (see above).


**Diagnosis.** Large blackish or black slug, in shape similar to *Limax*. Accessory glands as short rolls adhering to vagina, opening with very short and thin tubes, each separately.

**Description.** Body length of preserved specimens to 85 mm, breadth 15, mantle length to 22 mm. Body slender, in shape more like *Limax* than other *Tandonia* species. Keel poorly arched, but visible because of its lighter coloration. Skin sculpture very delicate, poorly standing out, fine. Between keel and pneustome 20–22 grooves (fig. 119).

Coloration very little variable, differing at most only in intensity. Head, mantle, back uniformly black (in living slugs with navy blue undertone) or
blackish. Sides downwards gradually lighter, foot edge being creamy-white. Keel also light, due to which along the middle of back to mantle a dirty creamy streak runs. Sole creamy-white.

![Figure 119: Tandonia cretica, from Potamia (Tinos Isl., Greece).](https://rcin.org.pl)

Mucus: colourless and transparent.

Genitalia (figs 120-125). Glandula hermaphroditica small and lightly coloured — coffee-creamy even in specimens laying eggs — usually divided into loose lobes. Ductus hermaphroditicus thin and long, convolute in anterior section. Glandula albuminalis as compared to other parts clearly small. Sperm-oviductus long, with well-developed glands, its male and female parts distinctly differing in appearance (fig. 120). Vas deferens thin and long, opening apically into epiphallus. Epiphallus cylindrical, narrowed posteriorly, on its external surface sometimes regular transverse rows of papillae (fig. 120), inside its posterior section complex structures (figs 121-122), in its thick walls a system of pits regularly arranged, in cross-section looking like a system of digital processes, in fact it is a system of narrow and deep pits. In anterior epiphallus section, walls somewhat thinner, and in its interior elongate folds. Penis also cylindrical with two distinct constrictions. Posterior constriction, just beside papilla, should be considered as boundary between penis and epiphallus. Between the constrictions in large penis cavity the papilla penis — strongly flattened cone-shaped, blunt, somewhat bent with asymmetrical opening. Anterior penis section almost smooth inside, if delicate folds not taken into account. Musculus retractor penis so delicate that usually escapes notice in preparation. Its insertion shifted slightly backwards at small constriction already at epiphallus (fig. 120), though being more posteriorly than the posterior limit of penis. On lateral wall of anterior penis section a membranous retentor. Epiphallus and penis joined to other genitalia parts by a system of membranes with numerous vessels (in figures this was not indi-
Figs 120–121. *Tandonia cretica* — genitalia. 120 — specimen from Potamia (Tinos Isl., Greece), 121 — penis dissected open with papilla visible (lectotype of *A. hellenica*).
cated). Oviductus: a short thick tube. Vagina is also a tube but shorter and at least twice as thick. Accessory glands as short rolls adhering to vagina, each opening separately with a short and thick tube. Interior vagina walls slightly longitudinally folded. Vaginal papilla situated somewhat anteriorly in relation to opening of accessory glands, shaped like a flattened disc with small central opening (fig. 122). Spermatheca with large, limp container, slightly sharpened posteriorly. Spermatheca duct shorter than container, sometimes with swellings. Atrium like a short tube.

Fig. 122. Tandonia cretica — copulatory organs with visible structures within vagina, penis and epiphallus, specimen from Tinos Isl., Potamia (Greece).

Spermatophore (figs 126–127) strongly elongate with two sections: thin cirrose, in recipient remaining inside spermatheca duct; and thicker being the container proper. All sides of cirrose section covered with spines. Spines small, first undivided, then somewhat bigger and bifurcated. Thicker spermatophore section covered with spines also on entire length yet on one side only, the other side being smooth. Spines on the thicker section first small
Figs 123–125. *Tandonia cretica* — copulatory organs. 123 — specimen being a lectotype of *A. hellenica*, 124 — holotype of *M. athenensis*, 125 — holotype of *M. scirius*.

Figs 126–127. Spermatophore of *Tandonia cretica*. 126 — from a specimen collected at Pétros, Parnon Mts (Greece), 127 — from a specimen being the lectotype of *A. hellenica*. 

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then increasing in size, branching dichotomously. Farther posteriorly the number of branchings diminishes, at the posterior end spines looking like unbranched hooks. Spine size, despite the reduction in branchings, little variable. Spermatophores from various slugs differ little in their shape, appearance and distribution of spines, though they may differ in size. Spermatophore tunicle golden-yellow or coppery-orange.

Bionomics. Occurring mainly on limestone, in maquis wood, open habitats and as a synanthrope. Shelters under stones. In mountains up to 1700 m a.s.l. I found spermatophores in specimens collected in autumn and winter (October to February).

Distribution (map 6). Known only from Greece. In south reaches Crete and Rhodos. In east to Samos, in north roughly to the line running between Pyrgos (= Pirgós), Parnassus Mts and Skyros (= Skiros) Isl. (WIKTOR 1986a).

Material examined: more than 140 specimens from the whole range of distribution.

Notes. Synonymization should not be doubtful because types have been preserved (see figs 123-127). I could not find only the type of Amalia cretica – probably not preserved, yet figures, description and material from Crete confirm that this is a slug widely distributed in Greece.

See also Tandonia strandi (WAGNER, 1934) — notes (p. 306) and Tandonia totevi (WIKTOR, 1975) — notes (p. 309).

Tandonia cristata (KALENICZENKO, 1851)

Krynikillus cristatus KALENICZENKO, 1851: 225, pl. 5 fig. 1a, b. Loc. typ.: Otuz (Crimea, USSR). Type: probably not existing. (Non Limax cristatus Leiblein, 1829).


Amalia cristata: SIMROTH 1901: 185, pl. 13 fig. 16.


Milax (Milax) cristatus nanus: URBAŃSKI and WIKTOR 1968: 80, fig. 14; GROSSU 1983: 226, figs 143-144.


Tandonia (Tandonia) cristata: LIKHAREV and WIKTOR 1980: 365, figs 489-496.

Diagnosis. Small, slim, grey slug. Accessory glands as two lobes adhering to vagina and discharging as two thin tubes.

Description. Body length to 30 mm, after preservation 25 mm, width 6 mm, mantle length c. 6 mm. Body slender, tapering posteriorly, when fully extended almost worm-like. Keel distinct along the whole back length, skin sculpture clear as well, number of grooves between keel and pneumostome 8–9, exceptionally 11 (fig. 128).

Coloration. In living slugs back, mantle and head ash-grey-greenish or ash-grey-yellowish. After preservation back and mantle pale-ash-grey or bluish-
-ash-grey, skin grooves darker — blackish, tentacles and head also blackish. Sole creamy.

Mucus thick, transparent, colourless or yellowish.

Genitalia (figs 129–132). Vas deferens distinctly thin, opening apically and symmetrically at epiphallus end. Epiphallus club-like, wider at posterior end, when contracted sometimes with swellings. Epiphallus roughly equal.

in length to penis or slightly shorter. At boundary of epiphallus and penis a deep constriction; retractor penis, wide and strong, inserting there. Penis oval, elongate or irregular, usually distinctly constricted. In penis anterior section a wide web-like musculus retentor. Penis interior almost smooth or with slight folds, laterally with a small oval plate (fig. 131). In penis two small semispherical papillae (fig. 132). Oviductus: a thick tube almost as long as penis with epiphallus, vagina very short. At boundary of vagina and oviductus and joining them spermatheca duct a clear distention, in contracted specimens even a large swelling. Accessory glands as two lobes adhering to vagina walls, each of lobes with one thin and short tube drawing secretion to vagina. Atrium short, tubular, with small retentor. Spermatheca in young specimens tubular, in older ones oval, posterior end sharpened, boundary between container and spermatheca remaining unclear. Atrium short, canali-form with small retentor.

Spermatophore (fig. 133): not divided distinctly into cirrous section and container. Broad cylindrical section being the container gradually tapering to thin cirrosse end. Spines only in middle section, bifurcated or singly bent, always hook-like. Spermatophore I found was not convoluted, only bent. This seems not incidental but conditioned by the shape of the structure.

Bionomics. Slug clearly selecting heavy clayey soils, sheltering under stones deeply in soil and probably also into deep soil cracks. Usually in deciduous and mixed woods, but also in bushes, gardens and even open biotopes.

Distribution (map 8). Nearly all of Bulgaria, (?) northern Turkey, SE-
Fig. 133. *Tandonia cristata* — spermatophore and one of the hooks (from a specimen from Ropotamo valley, Bulgaria) (after Wiktor 1983).

Roumania (Dobrudzha = Dobrudja), southern Ukraine (USSR — Odessa, Crimea, Uzhgorod), can be also expected in E-Yugoslavia.

In Bulgaria it is certainly native, probably also in Turkey and Roumania. It is unknown whether native in all its range in the Ukraine. Localities known from there are biotopes with heavy anthropogenic pressure and it is likely it was introduced there and lives as a synanthrope.

**Material examined**: more than 50 specimens, from Bulgaria, Turkey and Ukraine.

*? Milax croaticus* Wagner, 1929 (*? Tandonia*)

*Milax (Milax) croaticus* Wagner, 1929: 333, fig. 3. Loc. typ.: Mali Halan Mt. (=Mali Alan, Velebit Mts, N of Obrovac, Dalmacija, Yugoslavia — map 6). Holotype: probably burnt with the Budapest collection.


This slug is known only from Wagner’s description (1929). I enclose the following abbreviated description in translation, giving taxonomically useful characters: animal with back uniformly darkly grey-brown (graubraun). Sides downwards becoming gradually lighter to yellow. Body parts under mantle also light yellow. Mantle dark — coloured like back. Keel visible on the whole back from mantle to body, of the same colour as back. Sole divided by deep furrows (Furchen), its mid-band coffee-brown (kaffeebraun), lateral bands ochrous (ocker), of the same colour as lower side parts. The paper included a monochromous drawing of the slug. The author states that he had only one specimen, whose anatomy he did not study, and that the above characters
were sufficient to identify the slug as a distinct, i.e. new, species. Wagner also stated that the species was most closely related to *Milax dalmatinus* Simr. which, however, has light-red-ochrous (he uses "hellfleischig ockerig") body coloration, light keel, and dots on back, resembling splashes of India ink.

Notes. I have found that there is no holotype in the National Museum in Budapest. Thanks to the kindness of the family of J. Wagn er and Dr. L. Pintér from Budapest, I could study a small private collection of Wagner, where there is a very young specimen. It had never been anatomically studied, and I was the first to dissect it. The specimen was preserved with two labels written in ink, probably by Wagner. They read "Milax croaticus" and "Milax croaticus W.". In the test tube there is also a third label written in pencil by someone else "Conopac Gracac 1907 VI 7 Soós". It follows, then, that though the slug is from the close vicinity of the locus typicus it was collected 8 days later by the collector of the holotype. Wagner (1929) in his paper does not mention the specimen which he probably determined later.

During my field studies in Yugoslavia I collected slugs in the immediate vicinity of the locus typicus and yet I did not find slugs that would correspond to the description and could be regarded as topotypes. Characters mentioned by Wagner are of little diagnostic suitability, and basing on them, severa r quite distinct species could be determined, easy to distinguish basing on their anatomical characters. Thus at present I cannot say whether Wagner really had to do with a distinct species or with a slug known under another name. The specimen from Conopac is not a type, and is a slug with the genitalia not fully developed and externally it does not differ from *Tandonia robici* (Simroth, 1885), which may occur in this region.

**Tandonia dalmatina** (Simroth, 1900)

*Amalia dalmatina* Simroth, 1900: 106. Loc. typ.: Ragusa (= Dubrovnik, Dalmacija, Yugoslavia — map 8). Syntypes: I have no information on their existence, probably lost.

Species known only by description of Simroth (1900), no later reports of finding a similar slug. I collected slugs in this town and its environs but did not manage to find it. Below is its description after Simroth.

Body length to 47 mm, both individuals the author had were sexually immature. Body tapered only at the very posterior end (bis hinten gleichmässig dick).

Coloration: reddish-ochrous (hellfleischig ockerig), the younger individual on top slightly dully darkened. Keel outstanding by its light colour. Mantle unicolour. Back on top and laterally covered with small, sharply outlined many-sided (eckige) black spots (Spritzflecken). The spots bigger than in "*Amalia marginata*" (= *Tandonia rustica*), looking like fly specks, loosely scattered in grooves of skin sculpture, occurring only at $\frac{1}{4}$ of the length.

Genitalia, spermatophore, bionomics unknown.

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Notes. Simroth compares the slug to "Amalia marginata" (= Tandonia rustica), finding it to differ only in larger size, unicolor mantle without concentration of pigment in groove on mantle. Spots on mantle are bigger and fewer. This species may probably attain larger size than A. marginata. He compares it also to the unicolor ochrous form of "Amalia hellenica" (= Tandonia cretica), it has however lighter general coloration inclining to red (geht ins Rothe), and differing in dots which are lacking in "A. hellenica".

Map 8. Distribution of different Tandonia species.

*Tandonia ehrmanni* (Simroth, 1910)


Diagnosis. Black slug. Atrium with lateral pocket at the insertion with penis and with muscle attached to the pocket. Epiphallus with its retractor.

Description. I have never seen the slug, the only information available in literature is from Simroth (1910a).

Body black. Vas deferens thin and long opening at the widened and flattened distal end of epiphallus. Near it on edge of the flattening the musculus retractor epiphallus inserting. Penis roughly equal in length to epiphallus but far thicker, similar to smooth sac (glatter Sack). Oviductus — a long tube. Spermatheca oval, spermatheca duct very short and clearly separated. Vagina
relatively long with tubiform accessory glands gathered in two bundles. Atrium from the side of penis with a lateral process, to which retractor muscles attach (hat einen tiefen, mit besonderer Muskulatur versehnen Zipfel). According to SIMROTH this process (?pocket) is everted in copulation (fig. 134).

Fig. 134. Tandonia ehrmanni — copulatory organs (after SIMROTH 1910a).

No other information about this species. According to SIMROTH this is a high-mountain slug.

Distribution (map 8). So far known only from locus typicus.

Notes. The species requires redescriptions. It is distinguishable by two characters: presence of retractor inserted to posterior epiphallus end, and lateral atrium process. Very probably there is no retractor, a part of mesentery could be assumed to be retractor. It has to be also taken into account that the lateral atrium process could be an artifact due to a strong contraction of retentor during preservation, which resulted in distortion of the whole organ.

In order to explain the separateness of this species or its synonymy, the type (if it is found), or topotypes, should be compared to other black species expected in this region of the Alps, i.e. predominantly with Tandonia baldensis, T. robici, T. schleschi and T. simrothi.

Tandonia fejervaryi (WAGNER, 1929)


Description. Body size: preserved specimens — length up to 52 mm, breadth to 12 mm, mantle length up to 16 mm. Body nearly cylindrical, nar-
rowing abruptly anteriorly. Keel poorly arched, sometimes visible only in a part of back (especially in preserved specimens). Skin sculpture delicate, poorly standing out. Between keel and pneumostome 14 wrinkles (fig. 136).

Whole back (with mantle and head) deeply black, sides sometimes lighter. Sole whitish, creamy or lightly coffee-coloured.

Slime excreted while crawling colourless, irritated slugs secreting additionally lightly aquamarine, opaque, thick slime (probably for defence).

Genitalia (figs 135, 137, 139–140). Glandula hermaphroditica lightly coffee-coloured, or creamy. Ductus hermaphroditicus long and slender. Spermoviductus short, with well-developed glands. Prostate orange. Vas deferens slender and long. Epiphallus cylindrical, occasionally with small swellings, posterior end narrowing abruptly, vas deferens opening apically into the narrowed end. On epiphallus anterior section wall an insertion of very slender retractor (!). It is notable that retractor in almost all Milacidae joins posterior penis end or inserts at penis/epiphallus boundary. In T. fejervaryi insertion is situated more posteriorly on epiphallus, being vestigial at the same time. Interior walls of epiphallus covered with dense, sharp-pointed papillae. Penis elongate, cylindrical, inside no typical papilla penis, only at the boundary with

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Fig. 137–138. *Tandonia fejervaryi*. 137 — genitalia, 138 — spermatophore (both from Jablanac, Velebit Mts, Yugoslavia).

epiphallus distinct constriction of the lumen. Interior walls of penis, except small posterior section, covered with very dense, short, sharp-pointed papillae, like those in epiphallus. Spermatheca elongate tubular and thick-walled without clear division into container and spermatheca duct. Oviductus short tubular, usually partly connected by a membrane to anterior spermatheca section. Vagina very long and cylindrical, inside posterior section almost up to half of length longitudinal wrinkles, one somewhat thicker separating the interior into two sections: one leading to oviduct, the other to spermatheca (fig. 135). Anterior vagina section covered with dense sharp-pointed short papillae, like those in penis but larger. Accessory glands opening into vagina near its insertion to atrium, as thin filamentous tubes adhering closely to vagina walls. Atrium very short, almost invisible, but musculus retentor well-developed, inserted laterally at atrium.
Figs 139-140. Tandonia fejervaryi. 139 — genitalia (specimen designated as lectotype of Milax adensameri), 140 — copulatory organs (from specimen designated as lectotype of T. fejervaryi).

Spermatophore (fig. 138). Characteristic features being long anchoring spines in thin section and completely smooth walls of container. Orange-red in colour.

Bionomics. Till now collected sporadically. I collected it in extremely xerothermic biotopes, on limestone rocks, which were almost bare, covered only in places with scanty vegetation. Occurs at low altitudes up to 500 m in a small area under clear influence of Mediterranean climate. Very difficult to find its shelters in narrow rock crevices, it crawls out at dusk even on days with no dew or rain.

Distribution (map 6). All known localities in the region of Velebit (Obronac, Jablanac, Karlobag, Starigrad-Paklenica, Gračac).

Material examined: 45 specimens, including syntypes and topotypes.

Notes. See Tandonia baldensis.

"Amalia" guebhardi Pollonera, 1904


Species described on the basis of the shell alone. The slug has not been
seen by the author. The figure in the paper indicates that the shell was probably of a representative of *Milacidae*. Identifying the species on its basis is impossible now.

**Tandonia jablanacensis** (Wagner, 1930)

*Milax* (*Macrothylacus*) *jablanacensis*: Wagner, 1930a: 46, figs 1–3. Loc. typ.: Jablanac, Zivu bunari (Velebit, SW-Yugoslavia). Type: probably burnt down with the Budapest collection, where it was kept.

*Milax* (*Macrothylacus*) *jablanacensis*: Wagner 1930b: 105, figs 1–2, pl. 1 fig. 2; 1935: 191.

*Tandonia jablanacensis*: Wiktor 1981: 151, fig. 7.

This species is known to me only from Wagner’s descriptions (1930a, 1930b, 1935). In a preserved small own collection of Wagner this slug is lacking (see notes). My own studies, carried out in the region of Jablanac and other parts of Velebit, gave no result. As far as I know no one collected this species after description.

**Diagnosis.** Slug slender, dorsally black, laterally yellowish. A monstrous spermatheca, nearly two times longer than spermoviduct.

**Description** (based on Wagner). Body slender, up to 48 mm in length, breadth measured at mantle to 9.5 mm, mantle length to 13.5 mm. Keel well-developed and distinct along the whole of back (fig. 141).

**Coloration.** Mantle and back medially black. Outer mantle edges grey-yellow. Neck and parts covered by mantle ochrous, also body sides downwards gradually lighter, ochrous-coloured. Sole medially yellowish (blassgelb), its edges grey-yellow.

**Genitalia** (fig. 142). Glandula hermaphroditica, ductus hermaphroditicus and glandula albuminalis strongly elongate. Whitish-yellow spermoviduct gradually anteriorly tapering. Epiphallus cylindrical, longer than the twice wider penis, also cylindrical. Oviductus short tubular. Spermatheca monstrous, almost twice as longer as spermoviductus and wider, gradually widening posteriorly and ending with an oval distention. Yet clear distinction into container and spermatheca duct is lacking. Vagina tubular, long in comparison to other species. Accessory glands like small tubular processes. Atrium tube-shaped.

Spermatophore and bionomics unknown.

**Distribution** (map 9): known only from locus typicus.

**Notes.** Wagner in his description states that he had only two alcohol-preserved specimens. A total drawing in Wagner’s paper (1930b) shows an extended slug, as if crawling. The drawing seems not to be done by means of drawing apparatus but to be a reconstruction of a supposed body shape on the basis of the preserved specimen. Caution is then necessary in its interpretation. The drawing of the genitalia is very simplified, scale is lacking.
The characters of the genitalia show that they belonged to a slug that was still growing. Strong elongation of the genitalia and the body elongation, described by Wagner, could indicate that the slug lives underground. These are all speculations only, needing confirmation.

In the small private collection of H. Wagner, kept by his family in Budapest, I found a specimen with two labels, one read "Milax jablanacensis H. Wagn., Jablanac, leg. Paiewieth", the other "Milax reuleauxi", both written in the same hand, probably by Wagner. The slug with these labels has only primordial genitalia, and is probably Tandonia fejervaryi, its genitalia have not the characters typical of T. jablanacensis (!).
This species is species typica of the monotypic subgenus *Macrothylacus* Wagner, 1931. Basing on this description and drawings it can be said that it has all characters typical of *Tandonia* and the only character on which the subgenus was distinguished is the monstrous spermatheca. In my opinion there is no reason to distinguish a distinct supraspecific taxon (Wiktor 1981).

**Tandonia kaleniczenkoi** (Clessin, 1883)

*Amalia Retowskii* O. Boettger, 1882: 98 (nom. nud.) *Terra typ.*: Crimea.

*Amalia kalenzkoi* (nom. err.) Clessin, 1883: 39, pl. 2 fig. 11. *Loc. typ.*: Strateis (environs Yalta, Crimea, USSR). *Type*: probably does not exist.


*Tandonia (Tandonia) kaleniczenkoi*: Likharev and Wiktor 1980: 368, figs 497-504.


**Diagnosis.** Body covered with pattern of small blackish dots, so that the back is dark. Sole also dark. Spermatheca spherically oval. Atrium large, barrel-like, widened with folds inside.

**Description.** Body length after preservation to 27 mm, width to 7 mm, mantle length to 8.7 mm. Length of living specimens 60–80 mm (Svinkov in litt.). Body thickset, skin sculpture not very distinct, keel well-arched, distinct.
along the whole back. 9–11 grooves between pneumostome and keel (figs 143–144).

Coloration. The whole back and mantle covered with small, partly diffused blackish or black dots, scattered on the dirty creamy background. On the back dots more numerous, diffused, forming a dense net; sides downwards gradually lighter. Keel always without dots, dirty creamy. Mantle coloration like that of back, lack of clear dark streaks in the horse-shoe furrow. Head and neck blackish or completely black. Sole dark, blackish, in greater magnification numerous small melanophores visible. According to Shikov (in litt.) living young specimens whitish or yellowish with bluish tentacles. Adult creamy with dense dark small dots on the mantle and back, keel creamy.

Mucus colourless (Shikov in litt.).

Genitalia (figs 145–153). Gonads small, light grey, covered by liver lobes. Ductus hermaphroditicus long and thin. Glandula albuminalis large in relation to other organs, almost as long as spermoviductus. Epiphallus thick-walled, posteriorly widening and slightly rounded at loose end, club-like. Vas deferens opening into epiphallus apically, slightly asymmetrically. Penis roughly equal in length to epiphallus, also club-like, but is widening in the anterior section. Boundary between penis and epiphallus variable, marked by the well-developed musculus retractor penis. Papilla penis simple in structure (fig. 147), in posterior penis section longitudinal folds, anterior section with interior walls
almost smooth. Loose section of oviduct distinctly long, oviduct tube-shaped. Spermatheca almost cylindrical, clearly limited from long tubular spermatheca duct. Vagina short. Accessory glands as two lobes connected to vagina with short and thin canaliculi. Atrium exceptionally large (which is rare in *Tandonia*) and also barrel-like widened; inside large twisted elongate folds (figs 146, 153).

Spermatophore unknown.

**Bionomics:** unknown.
Figs 148-153. Tandonia kaleniczenkoi. 148 — copulatory organs, 149 — apical epiphallus end, 150 — papilla penis and diagram of penis longitudinal section, 151-152 junction of oviductus and spermatheca duct with small papilla and diagram of section through this region, 153 — atrium with visible structures inside [all figures from specimen from Zonguldak, N-Turkey identified as *Milax samsunensis* by Forcart (1953)].

**Distribution** (map 9). S-Crimea (USSR), Dobrudja (Roumania) and N-Turkey. Exact range unknown.

Material examined: 10 specimens from the Crimea, Mangalia (Roumania) (holotype and 1 paratype *M. dobrogicus*), Zonguldak (Turkey).

**Notes.** The species somewhat similar to *T. cristata*, differing greatly in its far darker coloration, dots on back and dark sole. A particularly distinctive feature is the large barrel-like atrium with characteristic folds inside, this in contradistinction to all other representatives of the genus.

This slug may be confused with *T. samsunensis*, a species known only by the holotype and two totopotypes and necessary to be studied on the basis of a larger number of specimens. Those preserved have darker dots on a dirty creamy background, in living specimens background is reddish (fleischfarben). Anatomical features distinguishing *T. samsunensis* require further studies,
and at present it is commendable to be cautious in identification of the slugs. The specimen from Zonguldak (Turkey) identified by its external appearance as *T. samsunensis* by FORCART (1953) belongs to *T. kaleniczenkoi* (figs 148–153).

**Tandonia kusceri** (WAGNER, 1931)


*Milax* (*Milax*) *Kuščeri*: WAGNER 1934a: 57, figs 11–12.

*Milax* (*Milax*) *kuščeri*: WAGNER 1934b: 90.

*Milax longipenis*: LUPU 1968: 34, figs 3 A–C.

*Milax longipenis bojanensis*: LUPU 1968: 35, figs 4A–B.

*Milax kusceri*: DAMJANOVIĆ and LIKHAREV 1975: 330, figs 261, 262; GROSSU 1983: 223, figs 139–141; HUDEC and VASÁTKO 1971: 19, fig. 8; OSANOVA 1972: 147, figs 1, 2; URBÁNSKI and WIKTOR 1968: 86, figs 18A–B, 19A, 20; WIKTOR 1977: 293.


**Diagnosis.** Body covered with darker delicate pattern. Distinguished by exceptionally long vas deferens and epiphallus, which is 5–6 times longer than penis, almost always spirally coiled or looped. Spermatheca rounded, its duct long, tubular.

**Description.** Living slugs when crawling stretching to c. 100 mm, mantle 1/4 of the total length. After preservation body length 55–65 mm, breadth 15 mm, mantle length c. 20 mm. Keel in living slugs distinct, always reaching to the posterior mantle edge. After preservation keel poorly arched, in specimens slightly macerated visible only in the posterior body part. Skin sculpture of poorly standing out, slightly flattened and strongly elongate wrinkles. 14–15 wrinkles between keel and pneumostome.

Coloration (fig. 154). Living specimens pink-brown or ash-grey-pink with many small blackish spots of diffuse edges. After preservation pink vanishing, the body becoming mucky yellow or brown. Blackish pattern becoming still more diffuse. The pattern of very small melanophores, of varying concentration. Spots not contrasting, with blurred edges. Darker pattern reticulate, as darker pigment accumulates mainly in the skin grooves. Keel always light (without the melanophores), yet back on sides of keel clearly darker than other.
body parts. Sides becoming lighter downwards. On mantle, especially anteriorly and laterally, irregular dark spots. Moreover along branches of the horse-shoe groove two distinct irregular lateral streaks, in many specimens also a darker streak, somewhat less distinct, along the middle of the mantle. Head and tentacles blackish. Sole mucky creamy. A large variability in coloration — even

within the same population some individuals clearly light, others, esp. young, darker, their pattern being less distinct, concentrations of melanophores higher.

Mucus colourless and thick. Irritated slugs secrete large quantities of thin, opaque, milky-white mucus: a defence reaction probably.
Genitalia (figs 155–156). The whole male part of genitalia very elongate and usually united by well-vascularized membrane, being a part of mesentereium. Vas deferens tubular and very thin, looping, occasionally 1.5 times longer than penis and epiphallus, opening symmetrically apically to cone-like narrowed posterior epiphallus end. Epiphallus tubular, somewhat widened in middle part, spirally coiled and intensely folded or looped, 5–6 times longer than penis; in no other species in the family is epiphallus so long in relation to other organs. Inside epiphallus complex small papillae and folds arranged concentrically. Shallow constriction being a boundary between epiphallus and penis; at this place very narrow musculus retractor penis inserts (in preparation can be easily overlooked and removed with mesenterium). Penis divided into two distinct sections: posterior cylindrical, only slightly wider than epiphallus, anterior almost spherically swollen. Inside posterior penis section ample folds similar to those in epiphallus. In anterior swollen section papilla penis, covered with folds, sharpened at the end (fig. 156). At the side of the swollen penis section a wide membraneous musculus retentor may be inserted, being a prolongation of similar muscle attached to atrium. Oviductus straight, tubel-shaped. Vagina very short, only slightly wider than oviductus. Spermatheca spherical or oval with long tubiform spermatheca duct. The duct diameter roughly equal to that of vagina. Accessory glands like two large creamy lobes of compressed ducts adhering to vagina, and partly to spermatheca duct and oviduct. Atrium very short and connected to body coats by numerous retentors. Spermatophore, despite studying a very ample material, was not found, and so far not observed.

Biology. Species of very high ecological tolerance, occurring in biotopes of various humidity, most often found in places of large quantity of loose stones, under which it shelters. Occurring in shrubs, woods, stone debris, and synanthropically. Usually in large numbers, especially on limestone, and in biotopes heavily destroyed by man (wasteland, dumps, ruins). In mountains only to c. 1250 m a.s.l. (in the Vitosha Mts, Bulgaria, OšANOVA 1972). Eggs laid in spring (April). Hatching of the young under laboratory conditions after 16–20 days. Eggs iridescent, oval (4.5 x 4) (OšANOVA 1972). Several generations probably overlap, as suggested by the size differences in simultaneously occurring specimens. Probably may be a pest on some vegetables.

Distribution (map 10). In west reaching roughly to the line Peć–Beograd (E-Yugoslavia), where there are, however, scattered isolated localities. Dense network of localities in S-Serbia (Yugoslavia) and Bulgaria. In Greece not found, but may be excepted in N-Macedonia and Trace, known from European Turkey and Roumanian Dobrudzha (= Dobrudja). Reported from Odessa (USSR) but probably introduced there.

Material examined: over 200 specimens from the whole range of occurrence (see above).
Notes. Slug very similar to *T. serbica*, both species often occurring together in a part of its range. Differing in larger body, lack of black spots on back, which occur in most individuals of *T. serbica*. Epiphallus far thinner and longer, penis smaller and different, musculus retractor penis smaller, different papilla penis.

Another similar species it can be confused with is *T. rustica*, which is different in lighter whitish body coloration, pattern of sharply delimited black dots, shorter epiphallus, which cannot be looped, different penis, stronger retractor penis, different papilla penis, spermatheca elongate, sharpened at the end.

In literature *T. kusceri* most often was confused with *T. rustica*.

**? Tandonia lagostoma (Wagner, 1940)**


Diagnosis. Slug large, brown-violetish on back, sides ochrous-reddish, darker grooves on skin.

Description. Description given after the only report by Wagner (1940). Body length to 70 mm, width to 17 mm, mantle length 22 mm, mantle breadth to 18 mm. Specimens were young, so they could be expected to attain larger sizes.
Coloration: reddish-ochrous (fleisch-ockerig), on back and mantle darker to brown-violetish. Darker pigment accumulating in the body grooves forming a network (similarly as in Deroceras reticulatum), the regions of horse-shoe groove on mantle being the most pigmented. Keel and sole edge light (fig. 158).

Figs 157-158. Tandonia lagostoma. 157 — genitalia, 158 — side view (both after Wagner 1940).


Spermatophore and bionomics unknown.

Distribution: known only from locus typicus (map 10).

Notes. I had no chance to see the type nor did I collect material on the Island Lagosta. Syntypes were so young that it is difficult to compare their characters with those of other species. I include this slug in Tandonia, though Wagner (1940) groups it with subgenus Milax s. str., basing on appearance of small atrium. Lack of the accessory glands makes it, however, difficult to include it in the genus with certainty.

Judging from Wagner’s description (1940) this slug may be similar or even the same as Tandonia toleri. The range of the latter is not known, but it is known that it tends to be synanthropic, and by this it may be expected practically anywhere.
**Tandonia macedonica** (Rähte, 1974)


**Diagnosis.** Slug of medium size, black and brown with dark pattern. Spermatheca duct longer than penis with epiphallus. Vagina very short. Inside penis a papilla in the shape of mushroom with long and thin stem.

**Description.** Body length after preservation to 35 mm, width to c. 10 mm, mantle length to 12 mm. Body moderately slender. Keel distinct along the whole of back, but low. On mantle a distinct groove, like the open letter V. Body wrinkles poorly standing out, 13–14 between keel and pneumostome.

Coloration varying, also within one population. Besides deeply black specimens with sides being slightly lighter and sole creamy, also blackish-coffee or coffee-coloured ones with lighter sides and sole creamy can be met. Not black specimens always with a darker, black or blackish pattern on mantle and back. Darker pigment most intense in the mantle groove (fig. 159). In some individuals on remaining mantle parts the background somewhat more reddish, on it a darker pattern of small irregular dots. Keel in black and in dark blackish individuals not different in hue from its immediate surroundings, while in light specimens, covered with darker pattern, keel distinctly lighter than surroundings, being creamy-coffee-coloured with no blackish pigment. In the extra-mantle body areas the darker pigment in skin wrinkles, producing a reticulate pattern. Living slugs coloured like the preserved ones, only some specimens being beige in hue or slightly reddish.

Mucus colourless, on irritation also whitish opaque (milky).

Genitalia (figs 160–163). Vas deferens opening apically and symmetrically on top of cylindrical or club-shaped epiphallus, which is slightly bent or straight. Epiphallus walls very thick, its inner diameter, esp. in the posterior section,
very small (fig. 161). Epiphallus internal surface not very regularly striated. Penis elongate, irregular, wider than epiphallus and separated from it by a clear constriction. Inside, on the boundary with epiphallus, a very characteristic papilla¹, distinguishing the slug from all other Milacidae, in the shape of a mushroom, with a very long stem (figs 161-163). In the centre of the mushroom "cap" a small depression. In posterior section of the "stem" just below the "cap" edge, a small opening of the papilla, through which the spermatoaphore goes out. Penis walls relatively thin, their internal surface smooth or covered with irregular cross-wise fibres. Musculus retractor well visible only in young still immature individuals, inserting to epiphallus walls approximately at its half. In grown-up specimens it most often cannot be found, the copulatory organs, on the other hand, being partly connected by a membrane with well-developed vessels. Free oviduct section tubular and long, usually longer than epiphallus. Vagina very short, oviductus and spermatheca being united almost at the atrium boundary. Spermatheca elongate, oval, tapering posterad. Spermatheca duct longer than penis and epiphallus together: a tube

¹ Rähle (1974) calls this organ Reizkörper, i.e. stimulator.
slightly widened anteriorly. Accessory glands as several (3–4) flattened lobes being connected with vagina by a separate thin canaliculus. Atrium genitale short, irregular, as if a prolongation of penis. Porus genitalis anteriorly, approximately at the anterior mantle edge.

Figs 161–164. *Tandonia macedonica*. 161 — epiphallus and penis, on one side visible cross sections of the places marked by the line (specimen from Trepka, S of Ohrid, Yugoslavia), 162 — papilla penis magnified, section showing its interior (the same specimen as in fig. 161), 163 — papilla penis (specimen from Gola Buka near Ohrid, Yugoslavia), 164 — spermatophore (from specimen from Galičica Mts, Yugoslavia).

Spermatophore (fig. 164) strongly elongate anteriorly, laterally covered only partly by small, adhering hooks, posteriorly with several thick branched (or else covered as if with knars) large processes-hooks. The whole goldish-yellow in colour.

**Bionomics.** Occurs in rocky areas, limestone, overgrown with shrubs or woods, shelters under stones. Spermatophore found in a specimen collected on May 19, and it should be judged to be copulating then. In mountains up to 1600 m a.s.l.

**Distribution** (map 9). So far known only from the Ohrid Lake region, esp. in the range Galicica (= Galičica, Makedonija, Yugoslavia) and is probably an endemit of a very small range.

**Material examined**: c. 90 young and adult specimens, partly collected by me.
Notes. Röhle (1974) distinguishes two forms, which he calls *Milax* sp. "dunkel Form", i.e. dark form, and *Milax* sp. "helle Form", i.e. light form. Similarly, I think there is no basis to distinguish the two colour forms as separate taxa, and they should be considered as forms of one species, i.e. of *T. macedonica*. The slug is very similar to *T. albanica*, with which it occurs in the same biotopes. The two slugs cannot be distinguished externally. In the structure of genitalia the differences are fairly clear. *T. albanica* has the epiphallus shorter and thicker, on it usually two tubercles occur posteriorly (fig. 98). Papilla penis has the shape of a semisphere. Vagina is longer, accessory glands are also bigger. Spermatophores are quite different in both: in *T. albanica* it has the shape of a conical cigar, anteriorly with dense spines, posteriorly with large hooks (fig. 101). Because *T. macedonica* has wide variability range and is externally similar also to several species it is necessary to identify it basing on several characters of which those of papilla penis and spermatophore are most diagnostic.

*Tandonia melanica* Wiktorr, 1986


Diagnosis. Black slug very similar to black specimens of *T. albanica*. Different in spermatophore, which is narrowed at one end, at the other cigar-like rounded, covered by small spines. Spermatheca not narrowed, at the end with thinner and with less developed muscles of spermatheca duct. Copulatory organs in comparison to body size smaller.

Description. Holotype size: length 42 mm, body width 9 mm, mantle length 12 mm, number of wrinkles on skin between pneumostome and middle of back 15. The largest paratype of 57 mm, width of body 9.5 mm, mantle length 15 mm. Skin sculpture delicate. After preservation keel discernible roughly along half of the back part behind the mantle, in living slugs well visible along the whole back to the mantle.

Coloration when alive black with dark violet tint. Sole creamy. After preservation deeply black with somewhat lighter sides. The parts of the neck usually covered by the mantle creamy. Sole whitish-creamy.

Mucus colourless. Irritated slugs were not noticed to secrete mucus of other colour.

Genitalia (figs 165-166). In comparison to body size copulatory organs relatively small. Thin vas deferens opening apically clearly asymmetrically on the flattened posterior epiphallus wall. Epiphallus as a short cone, its internal walls covered by small irregular papillae, separated from penis by shallow constriction, where thin musculus retractor penis inserts. Penis divided by constriction into two parts, both shaped like short cylinders, or with rounded, almost spherical, shape. Papilla penis of semispherical shape with the opening
Fig. 165. *Tandonia melanica* — copulatory organs (holotype) (after Wiktor 1986).

asymmetrically. Papilla penis at the place of penis constriction. In posterior part walls covered by elongate regular folds. In anterior part, beside more or less regular folds, also several larger irregular folds, probably functionally related to papilla. Spermatheca short oval with posterior end rounded. Spermatheca duct tubiform, somewhat longer than spermatheca. Oviductus tubiform, twisted. Vagina very short. Vaginal accessory glands large and lobular, in the usual position surrounding closely both the vagina and ⅔ of spermatheca duct and oviductus. Atrium very short. Regions of sexual opening in preserved specimens swelled in the shape of a well discernible mount (similarly as in T. reuleauxi).

Spermatophore (fig. 167). I could study two relatively well preserved spermatophores in paratype from Therakison. They are thin-walled structures of yellowish colour. One end — probably anterior — a bit cirroso narrowed, the other (probably posterior) gently cigar-shaped. The narrowed end is bare and strengthened by elongate ridges. More medially the spermatophore is covered by the largest asymmetrically branched spines. The remaining ⅔ of spermatophore covered by small branched or irregular small spines, scattered unevenly on the whole surface, without forming rows or lines.

Bionomics. I collected it on rocks and stone debris.

Distribution (map 11). So far known from Epir (N-Greece), probably more common in this region. In other regions (Tymfi, Pindos Mts, N-Greece)
I found many individuals of young Milacidae. Most probably this is the same species, but as there were no adults, I did not designate them as paratypes, in order not to confuse them with other similar species.

Notes. Slug very similar to T. albanica. At first I did not distinguish it myself and therefore in my paper on distribution of slugs in Greece (Wiktor 1986a) I gave the range of T. albanica as comprising also a part of Epir. The specimens from Epir turned out to be a new species. It was the appearance of the spermatophore that made me distinguish a new species. The spermatophore of T. melanica is of roughly the same size as the one in T. albanica, differing clearly in shape as it is more slender, one end being ended by a clearly longer cirrose section. The other end in T. albanica as if broken and wide, armed with powerful hooks. In T. melanica there are no such hooks, and the wider end gently cigar-like rounded. In contrast to T. albanica nearly all of the spermatophore (except the cirrose section) covered with small irregularly placed spines. As it is stated in the notes to T. albanica (p. 225) Soós (1924) described two black species from Albania, whose types were not preserved. One of the names I synonymized with T. albanica, even though I do not know what spermatophore it had. It seems impossible to establish whether it was more similar to T. albanica or T. melanica, therefore I think that a new name for the slug from Epir should be introduced.

? Tandonia montenegrina (Simroth, 1900)


The status of this taxon is not clear. From the imprecise description by Simroth (1900) the following can be deduced. Body length in the studied specimens did not exceed 42 mm. Coloration in specimens from various localities differed, though it was always dark: from uniformly dark through grey-black (grauschwartz) to dark dirty grey (dunkel schmutziggrau). Most specimens were subadult, those that were adult were only 30 mm long. From the genitalia description it follows that the epiphallus was cylindrical, straight or bent. Spermatheca large, in some narrowed posteriorly, in some elongate. In some specimens spermatheca duct separated from spermatheca. Accessory glands as two brown bundles resembling entomological pinheads (zwei ganz kleine braune Packete, kaum wie ein Insektennadelkopf), located symmetrically on both sides of spermatheca duct. No drawing in the description.

In later publications only Wagner (1931b) mentions that he studied the anatomy of the slugs from Italy and Yugoslavia. He gives neither description nor drawing.

Notes. Judging from Simroth's description (1900) it seems probable that Simroth had to do with juvenile individuals (perhaps of various species), in which genitalia could have been already developed, accessory glands being
yet underdeveloped. It is known that in many species the glands are the last to develop in the final development stage. The only decidedly distinguishing character singled out by Simroth, i.e. such glands, were seen by me in many juvenile slugs, never in adults. I myself collected material in all given localities, except Bazar, listed as terra typica, I also studied in detail ample material of my own and that at the Museum, from Yugoslavia, but I did not manage to find such a species. The quotation from Wagner (1931b) cannot be relied on as it is not supported by drawings or description. As it cannot be established authoritatively whether a slug of such characters as Simroth supplies exists I include this denomination in nomina dubia.

_Tandonia nigra_ (Pfeiffer, 1894)

_Amalia nigra_ C. Pfeiffer, 1894: 68. _Loc. typ._: On the top of Monte Generoso peak (1695 m) between Como and Lugano Lakes, Italy. _Holotype_: dry! Senckenberg Mus. Frankfurt, no. 107558/1 (information from dr. R. Janssen)

_Amalia nigra_: Simroth 1910: 331.

_Milax_ (Tandonia) niger: Mermod 1930: 46.

_Milax niger_: Forcart 1942: 114; Altena 1953: 43, figs 1-8.


**Diagnosis.** Mantle and back with keel and external sole edge black. Epi­phallus club-shaped, not much longer than penis, also club-shaped. Penis inside longitudinally striated. Accessory glands small, canal-like, in compact ball surrounding vagina. Vagina only slightly shorter than penis, inside covered by large conical papillae.

**Description.** Preserved specimens: length to 35 mm, width c. 7mm, mantle length c. 8-9 mm. Body slender. The groove on mantle poorly marked, body wrinkles delicate. Wrinkles difficult to count on the specimen I studied, probably 13 between keel and pneumostome. Keel well visible along the whole of back.

Coloration. Mantle at first sight uniformly black, in fact on its edges very dense black dots on dirty creamy background, visible however only in magnification. Back and keel black. Body sides becoming lighter downwards, the foot edges being surrounded by black. Head blackish, tentacles when con­tracted black. According to Altena (1953) they are covered with blackish dots on white background. Probably this character distinct only when ommatophores extended. Neck and sides of the anterior body part dirty creamy, sole of the same colour.

Mucus not described yet.

Genitalia (figs 168–169). Vas deferens thin, short, i.e. roughly equal in length to epiphallus and penis together, opening apically, slightly asymmetrical. Epiphallus club-shaped, posteriorly gently widened, posterior end somewhat flattened. In the specimen I studied on the external surface of epiphallus visible small papillae arranged in longitudinal rows. This character not
known to be stable. Epiphallus inside covered by small papillae. Penis anteriorly cylindrical, with spherical distension at its posterior end, inside clon­
gate wrinkles, occurring both in the spherical part and in the posterior sec­
tion of the cylindrical part. Papilla penis in the studied topotype did not occur,
only a clear constriction was visible and thickening of walls at the place it

occurs in other specimens. Musculus retractor penis thin, inserted laterally
to anterior epiphallus section. Oviductus thin, tubular, somewhat thinner
anteriorly. Spermatheca elongate, oval, narrowed posteriorly. Spermatheca
duct roughly twice shorter than the spermatheca. Vagina nearly equal in length
to penis and approximately of its width, anyhow it is thicker than oviductus
and spermatheca duct together. Anteriorly a small widening, later vagina again
narrows before it unites with atrium. Inside vagina dense large conical (i.e.
sharp-pointed) papillae. Vaginal accessory glands in the form of compact bun­
dle of ducts surrounding the transitional section between oviduct and vagina.
Atrium tubular, as if a prolongation of penis, approximately of the same width.
Inside small longitudinal striations. On the outside of atrium diffuse irregular
strands of muscles-retentors.

Spermatophore (fig. 170) was described by Altena (1953), who had an
incomplete specimen.

Bionomics. The few individuals known so far were collected in a very
small mountainous area, near the tops, at 1600 m a.s.l. A spermatophore found in an individual collected in July proves that the slug had to be copulating then (Altena 1953).

Distribution (map 11). Known only from locus typicus.

Material examined: 1 topotype, studied also by Altena, from the collection in Rijksmus. Leiden (no. 988).

Notes. A species requiring more detailed studies. Pfeiffer (1894) thought it can be a melanistic form of T. rustica. Altena (1953) excluded such a possibility, as the slug has a different anatomy. Externally T. nigra seems to be very similar to several other mountain species, esp. from Yugoslavia (T. albanica, T. jablanacensis, T. schleschi), also to the Alpine ones (T. robici, T. baldensis). All suggests, however, that it is different in the anatomical characters, esp. in internal sculpture of vagina and penis, and in the appearance of spermatophore. It is more similar in this respect to T. schleschi (see the remarks in the description of this species). It seems to be also an endemit of a very small range. As I know the secret way of life of mountain species, I know how difficult it is to find them. They most often crawl out at night and in rain. It can be expected, then, to be found in other sites in the Alps as well. In the Naturhistorisches Museum in Basel there is a specimen determined by Forcart (1959) as Milax simrothi, collected in Kaisergebirge (N-Tirol). The specimen is ill-preserved, almost certainly conspecific with the topotypes of T. nigra. It is also probable that the information of Gittenberger (1967) on T. simrothi from Karawanken Mts (Austria) also concern this species, T. nigra. However, I have not had an opportunity to study his materials.

See also T. simrothi p. 299.

Tandonia pageti (Forcart, 1972)


Diagnosis. Large slug, in shape resembling Limacidae. Keel poorly arched, wrinkles on skin fine. When alive, reddish-yellow, after preservation back and mantle blackish. Epiphallus with coecum at end, inside penis a fold covered with very fine needles.

Description. Body length to 73 mm, width 11.5 mm, mantle length to 24 mm. Individuals 60 mm in length already with developed copulatory organs, but glandula hermaphroditica and glandula albuminalis very small, not fully developed. In external appearance it resembles Limacidae because of poorly arched short keel, small skin sculpture and grooves poorly standing out, from 19 to 21 wrinkles between medial dorsal line and pneumostome. Groove on mantle shallow and poorly discernible. When alive the slug is reddish-yellow (Forcart 1972), after preservation mantle, back and head blackish-grey, covered with unequally diffused dark pigment (fig. 171). Sides, neck and sole

http://rcin.org.pl
dirty creamy. Lack of clearly delimited streaks on mantle. Keel of the same colour as the whole of back.

Mucus has not been described so far.

Fig. 171. *Tandonia pageti* — side view (specimen from Arif N of Finike, SW-Turkey).

Genitalia (figs 172–175). Vas deferens long, opening laterally to epiphallus. This is the only known case in *Milacidae* that vas deferens does not open apically but laterally. Epiphallus cylindrical, slightly bent posteriorly. Inside its walls are covered with irregular papillae, in posterior blind section also with elongate folds. Penis wider than epiphallus, cylindrical, somewhat constricted in the mid-section, and being as if a natural prolongation of atrium.

Inside a richly sculptured papilla (fig. 175), beside the opening to epiphallus, so papilla not patent. In posterior penis section, in front of papilla, there are also twisted folds, while more anteriorly, at the boundary with atrium or inside it, there is a tongue-like structure or fold covered with very fine needles. That structure is everted in the holotype, in other specimens it is partly visible in the sexual opening. (figs 174–175). Oviduct tubular. Vagina short but well visible as a duct twice wider than oviduct, inside with elongate wrinkles. Accessory glands lobular in holotype (fig. 173), in juvenile specimens poorly discernible as a swelling (fig. 174). Spermatheca oval. Spermatheca duct wide, anteriorly widening, thick-walled. Atrium cylindrical, not clearly separated from penis.

Spermatophore (fig. 176). Very characteristic in shape. Anterior section looks like a cigar on one side covered with multiple, dichotomically branched spines. Roughly at two third in length there is a section laterally covered with very small spines, their free ends directed anterad. Posterior section roughly equal to one third of length covered with two rows of strong hooks. The end itself is the largest hook.

Bionomics unknown.

Distribution (map 11). So far known from Rhodos Island and in SW-Turkey (Fethiye, Arif, Marmaris, Muğla — A. Riedel leg.).

Material examined: 11 specimens, but only one adult (holotype), the others have copulatory organs only partly developed.

Notes. Endemic species, probably restricted to SW-Turkey and adjacent
islands. It differs from the remaining species of the family in the structure of genitalia: coecum on epiphallus and the tongue-like structure, covered with needles, in the penis. Its spermatophore also differs in appearance from other species.

**Tandonia pinteri** (WIKTOR, 1975)


**Tandonia pinteri**: WIKTOR 1983: 118, figs 38–39, map 11.

**Diagnosis.** Slug so densely covered with dark spots that almost black. On mantle and body sides dirty creamy areas, also keel light. Epiphallus conical and small, penis irregular in shape. Papilla penis elongate. Spermatheca oval with spermatheca duct longer than its diameter.

**Description.** Body length to 52 mm (usually smaller), width to 8, mantle length to 12 mm. Body slender. Keel poorly arched, grooves on skin shallow. 11–12 grooves between keel and pneumostome.

Coloration varying in intensity, but the pattern, though irregular, characteristic. On dirty creamy or light coffee background a dark, usually deeply black, pattern, in living slugs dark blue-black (figs 177–178). On mantle wide
lateral streaks, being the darkest on the whole body, irregular in shape, crossed by a horse-shoe groove. Below streaks irregular dark spots, above them quite big elongate areas without dark pigment. Mantle centre darkened by diffuse dark pigment, producing also irregular spots. Back black or blackish, sides becoming gradually lighter downwards. Dark pigment, covering almost the whole back, yet some small areas may be light. Usually black pigment accumulating in grooves, going to skin wrinkles, in other places having the form of irregular network, independent of skin sculpture. Keel always light, dirty creamy or brownish. Head black or blackish. Sole dirty creamy.

Mucus not described so far.

Genitalia (figs 179–180). Vas deferens very thin and long, opening apically and symmetrically to a narrowed epiphallus end. Epiphallus, in comparison with all genitalia, very small, conical, usually bent, folded in two or twisted around its axis. Penis oval, pear-shaped or irregular, much wider than epiphallus, poorly delimited from atrium. Inside penis elongate papilla with a circular furbelow in the shape of collar (fig. 180). Musculus retractor penis thin and delicate, at its insertion no constriction, which most often occurs at the boundary of penis and epiphallus. Oviductus like a long twisted tube. Vagina very short. Accessory glands like several irregular bundles of ducts sticking together, the ducts opening by several thin tubes around vagina. Spermatheca oval or nearly spherical. Spermatheca duct long, usually twice longer
than the spermatheca itself. Atrium very short, closely adhering to body walls and inserted by numerous retentors. Sexual opening anteriorly of the line of mantle edge.

Spermatophore unknown so far.

Bionomics. Not studied. The slug occurs in damp biotopes at the bottom of mountain valleys reaching 1500 m of elevation. On lime substrate.

Distribution (map 12). Only in the Rodopi Mts in Bulgaria, only a few localities (Čudni Mostove'J Smolian, Deven).

Material examined: 35 specimens, most of them juvenile.

**Tandonia piriniana** Wiktor, 1983


Diagnosis. Small, dark green, almost black slug. On boundary between vas deferens and epiphallus lateral coecum. Epiphallus and penis very long.

Description. Body length to 20 mm, width to 4 mm, mantle length to 5 mm. Keel distinct, skin grooves distinct but shallow, 12–13 of them between keel and pneumostome (fig. 181).

Coloration. When alive slugs are very dark green, almost black. After preservation uniformly blackish, with skin grooves being slightly darker. Keel creamy. Sole blackish on edges, creamy centrally.

Mucus has not been described.

Genitalia (figs 182–183). Vas deferens long in anterior section, just near junction with epiphallus with a lateral pocket like process. This is a character not encountered in any other _Milacidae_ species. Its function is unknown, but it may be expected to be a gland. Epiphallus cylindric-conical, indistinctly.
Figs 181-183. *Tandonia piriniana*. 181 — side view (holotype), 182 — genitalia (holotype), 183 — section through epiphallus and penis with two papillae visible inside, on the right diagrams of cross sections through epiphallus and penis (paratype) (181-182 after Wiktór 1983).

separated from penis. Inside penis elongate folds. Penis roughly equal in length to epiphallus, cylindrical. Inside two chambers with elongate folds on walls (fig. 183) and two papillae, simple in structure. Musculus retractor penis inserting laterally near the posterior papilla. At insertion lack of clear constriction. Oviductus somewhat shorter than penis with epiphallus, tubular. Vagina short, slightly swelled. Accessory glands small, lobular, opening by few short ducts. Atrium short. Sexual opening well anteriorly, i.e. in the head region. Spermatophore unknown.

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Bionomics. Not numerous specimens were found under stone deeply squeezed into the ground, on a very dry locality, overgrown with shrubs. Distribution (map 12): known only from S-Pirin Mts (SW-Bulgaria). Material examined: only the types — 7 specimens.

**Tandonia reuleauxi** (Clessin, 1887)


*Amalia (Aspidoporus) limax*: Babor 1898: 33; Simroth 1909b: 604.

*Aspidoporus limax*: Wagner 1931a: 68, fig. 15; 1935: 212, fig. 36.

*Milax (Milax) Reuleauxi*: Wagner 1929: 335, fig. 6; 1930a: 40; 1930c: 104; 1931a: 61; 1935: 201, fig. 29.


Description. Body length of crawling slugs to c. 100 mm, in preserved slugs to c. 55 mm, breadth to 13 mm, mantle length to 20 mm. Keel distinct, occasionally almost crest-like, always visible along the whole back reaching
Mantle (fig. 184). Body wrinkles elongate and almost flat, grooves between them very shallow, 12–15 of them between keel and pneumostome. Groove on mantle shallow, forming an almost complete circle. Genital opening somewhat head­wards in relation to pneumostome. Its regions swelled, skin covered with fine sculpture of different appearance than on other body parts. Swelling like a plate, anteriorly and downwards forming a small fold in which genital opening is situated, visible in contracted adults, also in preserved slugs. This feature is very characteristic of this species.

Coloration uniform, i.e. without spots, darker colour on back gradually passing into lighter on sides. Most often the whole back with keel, head and mantle black, only sides downwards slightly lighter, blackish. Some specimens of chocolate hue. All specimens from Kotor where I also collected numerous individuals at various age were so coloured. In other parts of Yugoslavia I collected also individuals of blackish back and beige sides, and subadult ones completely beige but for somewhat darker back. Sole in darker and in lighter living specimens white-grey, in preserved specimens becoming beige-creamy. In black specimens occasionally outer sole edges blackish.

Mucus colourless, slugs when irritated also secreting somewhat thin milky or lightly aquamarine mucus.
Genitalia (figs 185–186). Glandula hermaphroditica partitioned. Ductus hermaphroditicus long. Vas deferens opening apically and asymmetrically. Posterior epiphallus part spherically rounded, anterior cylindrical. Boundary between epiphallus and penis indistinct, only occasionally a small constriction between the two occurring; at this place adhering very thin, almost piliform musculus retractor penis. Inside epiphallus small irregular elongate folds, smoothly running to posterior penis section, also cylindrical. The section look-
ing not dissimilar to epiphallus. Anterior penis section suddenly strongly distended in an irregular or sphericoid formation (fig. 186A). Papilla penis as in fig. 186A. In the distended penis section the inner diameter suddenly increasing, interior walls very finely striated. Free oviduct section long, thick tubular. Spermatheca elongate, oval. Spermatheca duct tubular, somewhat wider but shorter than oviductus. Its anterior section abruptly widened, at this place also the inner diameter increases (fig. 186B), and a structure occurs similar to papilla. Vagina very short, hardly visible, small accessory glands surrounding it. Atrium also very short, during preservation often everted, then in preparation difficult to be seen, and vagina accessory glands being in a deep fissure of the already everted section of atrium just by the genital opening.

Spermatophore (fig. 187). Anterior section narrowed, elongate slats on surface. Long bifurcated spines on all sides caudad. Central part gradually widening, the spines covering it only on one side, growing smaller caudad, and being increasingly bifurcated dichotomically, assuming shrubby form. More caudad a small constriction and spineless section. Posterior section cylindrical, on two sides covered with several rows of bifurcated shrubby processes and spines. Figure 187 shows the spermatophore partly inserted into the penis of one individual, partly being in the spermatheca of the other; it is undamaged and undigested at all. Tunicles transparent, golden.

Bioclimatology. Shelters under stones and in stone rubble. On limestone in mesophilous habitats in shade, preferably at the bottom of valleys or in canyons, protected by trees or herbs. I watched one copulating pair (figs 17–18), November 1, 1982, above the town Kotor, at 1 p.m. The slugs copulated under a loose boulder in shade but on exposed slope. Both had everted, intensely swollen atria and the regions of the genital opening, which both covered from above
the remaining everted genitalia and transmitted spermatophores. On the side of body, at the base of the everted organs in each there was a white clot of (?) mucus. In both specimens its location was different (fig. 17). Both slugs were put into alcohol, then dissected. It turned out that penises of both underwent eversion. Also spermatophores of both were being transmitted simultaneously, and it is they that entered into the partner (fig. 18), while the copulatory organs remained outside. Both spermatophores were completely formed and posteriorly closed. They were inserted by their posterior ends in epiphalluses, though anterior sections were already in spermathecas of partners. One spermatophore was somewhat deeper inserted into the partner than the other, the posterior part of epiphallus, where it was made, was already empty (fig. 18).

Distribution (map 13). Known only from S-Yugoslavia, i.e. from Crna Gora, Dalmatia and Hercegovina (Titograd, Kotor, Herceg Novi, and environs, & Niegos Mts, Nikšic, Trebinje, Mostar, Grabovica and Jablanica). Localities: Gračac and Jablanac (Wagner 1930c) need checking.

Material examined: 56 specimens from various localities in Yugoslavia.

Notes. Altena (1975) thought that the type T. reuleauxi did not exist and designated neotype. In my subsequent research I managed to find a shell of a syntype (Wiktor 1979).

As I proved earlier (Wiktor 1979), Babor (1898) on the basis of this spe-
cies described the anatomy of "Aspidoporus limax", committing mistakes in figures and descriptions on this occasion. He found that the slug had no accessory glands, and the intestine had 3 loops. I confirmed that by studying his evidence material preserved at the Naturhistorisches Museum, Vienna. Babor described the anatomy of specimens, which were not the types of Aspidoporus, basing only on slugs that he had identified as Aspidoporus.

The name Aspidoporus limax Fitzinger, 1833, has to be treated with regard to both genus and species as nomina dubia, as it is not certain what slug it refers to (Wiktor 1979). See also p. 221.

**Tandonia robici** (Simroth, 1885)

*Amalia Robici* Simroth, 1885: 230, pl. 7 figs 21 XVII A, B, pl. 10 figs 15 XVIIIIC and 16 XVIIID. Terra typ.: Kraina (= Krajina at present mainly Slovenija, Yugoslavia) „Suhadolnikthal” (probably in Grintovac Massiv NE of Kranj) and “Mokriea Alpe” (vicinity of Ljubljana)¹. Syntypes: probably do not exist.


*Amalia Robici*: Simroth 1910: 332, fig. 9.


**Diagnosis.** Body olive-beige, yellowish-green or reddish-beige. Epiphallus longer than penis. Penis internal walls covered with papillae, at partial contraction a large richly ornamented papilla originating. Vagina with internal walls covered by papillae.

**Description.** Length of alcohol-preserved specimens 28 mm, width 8.5 mm, mantle length 9 mm. Body rather thickset, especially after preservation. Keel poorly arched but visible along the whole length of back to the posterior mantle edge. Skin sculpture very delicate, between keel and pneumostome 8-13 wrinkles (fig. 188).

Coloration. Living slugs are green-olive or beige with darker back but without dots or clear pattern. Head blackish, tentacles black. Sole whitish. After preservation coloration shade changes, body becoming dirty yellowish, reddish in undertone, blackish-beige. Slugs, even preserved recently, look like faded.

Mucus yellow, transparent.

**Genitalia** (figs 189-191). Vas deferens thin, of medium length. Opening at an angle, as if tangently, at the apical epiphallus end. Epiphallus cylindric-conical, usually twisted, inside a large twisted fold (fig. 190). Penis rounded, often pear- or club-shaped, or irregular, far wider than epiphallus. Inside penis a spacious cavity. Papilla penis of various shape, depending on the degree of

¹ The localization of those sites could be established thanks to the kindness of Dr. Rähle.
contraction and perhaps also on ontogenetic advancement. In simplest cases like crater (fig. 190), and when penis evertion starts, a large, richly ornamented papilla penis arises, covered with "flounces", ruffs and spines (fig. 191). The ornamentation results from the fact that the inner penis walls are covered with small papillae. After evertion this papilliform sculpture changes into


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the ornamentation of the papilla penis. Musculus retractor penis poorly de-
veloped and inserted laterally on anterior epiphallus section. Spermatheca
elongate, with spermatheca duct slightly longer than penis, most often bound-
dary between container and spermatheca duct unclear. Oviductus somewhat
longer than vagina, which is very wide, c. 4 times wider than oviduct. Inside
vagina dense papillae. Sometimes, probably due to partial evertion, a papilli-
form structure is made, similar to the sunflower bottom (fig. 190). This is not
a stable character. Accessory glands like numerous digital, unbranched processes
surrounding the posterior vagina end. Atrium short, a natural prolongation of
vagina, i.e. is equal to it in width, slightly narrowing anteriorly.

Spermatophore (fig. 192) compared to body size exceptionally small. On
comparison with spermatophores of other species of that size it is nearly
twice smaller. The container with sperm without spines. Cirrus covered by
small, only partly forked hooks, on the thinnest section of the spermatophore
hooks adhere closely to its walls.

Bionomics. In litter and under stones. Most often in deciduous woods
and in shrubs, predominantly on lime substrate. In mountains up to 1300 m
elevation.

Distribution (map 13). Mainly in Yugoslavia and neighbouring regions.
From Triest through Istria to Bihać, in east to Delnice (Juliske Alpy Mts)
and to Karavanke Ridge (boundary of Yugoslavia and Austria) in north.

Material examined: 24 specimens from the whole area of distribution.

Notes. The synonymy of this species is complicated. I had the opportuni-
ty to exchange views in this matter with Dr. Rahle (Tübingen), and I owe
valuable suggestions to him, and appreciate being lent his material. T. robici
was described by SIMROTH (1885) very superficially, drawings are imprecise
(fig. 193), types probably do not exist. It was not possible to establish where
terra typica is (this regards concrete localities), it is known that it was the
former Kraina, i.e. present Slovenija. In 1910 SIMROTH again writes about
the slug, providing a drawing of the characteristic papilla penis. In this case,
he undoubtedly had to do with the species described above and with slugs
that RAHLE (1983) identified as T. robici (figs 194-195). WAGNER’s paper (1931c)
is about the same species. Wagner introduced a new specific name ploebsti.
That name was also used by me (WIKTOR 1982).

Tandonia rustica (MILLET, 1843)

Limax marginatus Draparnaud, 1805: 124, pl. 9 fig. 7. Terra typ.: probably France. Type:
probably does not exist. (Non Limax marginatus Müller, 1774).

Limax marginatus rusticus Millet, 1843: 1, pl. 63 fig. 1. Terra typ.: France. Type: pro-
ably does not exist.

Amalia marginata: SIMROTH 1885: 225, pl. 7 fig. 19 XIII, pl. 10 figs 1 XIII B, 3 XIII D.

Milax marginatus: GERMARDET 1940: 568, fig. 5; Frömming 1954: 227; HuDEC 1963: 149,
fig. 1, pl. 13 figs 1, 3; Lupu 1968: 31, figs 1, 2 AB; WIKTOR 1973: 51, figs 13-14, 87, 91,
103, 225, 245, 246.

**Diagnosis.** Body white or light creamy, densely covered with small black dots. Epiphallus cylindrical, clearly separated from vas deferens. Spermatheca elongate, posteriorly sharply narrowed.

**Description.** Extended living slugs: length to c. 100 mm. After preser-
vation to 45 mm, width c. 12 mm, mantle length c. 18 mm. Crawling slugs with body strongly elongate, sides being almost parallel, body narrowing only in the very posterior section (figs 196–197). Keel well arched and distinct, also in preserved specimens, along the whole of back. Between pneumostome and keel 18–19 wrinkles.

Coloration. Body most often whitish, light creamy or slightly brown, occasionally also pinky or violetish, somewhat darker on mantle and back. On this background numerous, black small dots with sharp boundaries, and, though irregular, they make the slug look like dotted. On mantle along the horse-shoe groove two irregular black or blackish streaks. The whole keel and sole uniformly creamy without dark dots. After preservation body somewhat darker, more straw-like, yellowish or brownish, dots not changing in colour.

Mucus colourless and very thick, when touched draws in long strands. Irritated slugs secrete additionally milky-white opaque mucus.

Genitalia (fig. 198–199). Thin vas deferens opening apically and symmetrically to epiphallus. Boundary between the two distinct, epiphallus being much wider. Epiphallus cylindrical, strongly elongate, with several small swellings. Its anterior boundary hard to establish unambiguously, boundary that would allow for separating it from penis. The place where well-developed musculus retractor inserts not constricted. Musculus inserted, according to some authors, laterally on epiphallus, others suggest its insertion at the boundary between penis and epiphallus. More anteriorly a clear swelling, belonging certainly to penis. Inside penis richly ornamented papilla penis (fig. 198). If the insertion of musculus retractor be assumed the boundary between penis and epiphallus, then epiphallus is 2–3 times longer than penis. Oviductus with few small swellings, most often twisted. Vagina not much wider than oviduct. Accessory glands like compact duct-like structures surrounding the vagina and opening to it at its boundary with atrium. Spermatheca always, i.e. in young and in

Fig. 199. Tandonia rustica — papilla penis (after Likharev and Wiktor 1980 — somewhat modified).
those that have already copulated, elongate and sharply ended (not rounded!). Spermatheca duct roughly equal to spermatheca or a bit shorter, centrally usually swollen. Atrium very short, tubiform.

Spermatophore — I have never seen it.

Bionomics. Forest species, also in shrubs, parks and graveyards. Prefers deciduous and mixed woods. The best habitats are places with numerous stones, or with rock rubble. In Central Europe almost always on limestone, the northern relict localities in Poland being related to limestone as a rule. In those sites it is the specific warm microclimate that makes it occur there. Very often encountered in ruins of medieval castles. Its life cycle discussed on p. 169.

Distribution (map 15). In west certainly reaching Central France, perhaps even to the Pyrenees. In south in France reaches the Mediterranean and Corsica, in Italy to Elba and the Central Apennines. Inhabits Switzerland, reaches Austria, widespread in Bohemia, where there is its eastern limit. Few known localities at the boundary with Hungary, known from central Roumania. In Slovakia probably does not occur. In Poland only relict localities in the Western Sudetes. The northern limit goes through southern areas in the GDR and reaches the northern areas of West Germany. Few scattered localities in Holland and Belgium, nowhere reaches the shores of the Northern Sea. Probably in parts of the mentioned areas is introduced and lives as a synanthrope; this remains to be studied in detail. Its homeland is probably southern-central Europe.

Notes. Previously it was confused with T. kuscerei and probably T. serbica, hence the erroneous reports on its occurrence in Bulgaria (WIKTOR 1983). From both species it differs in lighter body coloration, smaller dots, more contrasting with the background, narrowed spermatheca sharpened on end, epiphallus shape and papilla penis.

**Tandonia samsunensis** (FORCART, 1942)


Milax samsunensis: LIKAREV and WIKTOR 1980: 379, fig. 523.

Diagnosis. Small slug, similar to *T. kaleniczenkoi* and *T. budapestensis*. When alive, body reddish (meat-coloured) with very small dark dots on back and mantle. On sole black melanophores. Atrium very short. Accessory glands as small grape-like formation. Epiphallus wider than penis, nearly egg-shaped.

Description. So far only 3 specimens known: the holotype, described by FORCART (1942b) and two topotypes collected by A. RIEDEL in 1985. Holotype genitalia embedded in Canada balsam as a long-lasting preparation. FORCART made his drawing from it and based on it his description. A preparation like that is difficult to interpret, many details are indistinct. I had an
occasion to study all the specimens, yet, as this slug is very similar to other species, it is necessary to study further *T. samsunensis* to find its variability.

According to **Forcart (1942b)** holotype length is 20 mm, width 4.5, mantle length 6.2 mm. The larger of **Riedel**'s specimen is 23 mm long, 7 mm wide, mantle length 8 mm. Nine grooves between keel and pneumostome in all specimens.

**Forcart (1942b)** describes living slugs as meat-coloured (Fleischfarben) with darker dotting (Spenkelung) on back. Darker pigment is diffuse, so that back is blackish. Occasionally darker pigment in accumulations, forming dots and spots on back. Keel meat-coloured. On mantle blackish streaks in a horse-shoe groove. Sole meat-coloured, also with grey dots. Collecting the slugs **Riedel** did not note their coloration, he remembers, however, them being more brown than they are now after preservation. The alcohol-preserved specimens are blackish-grey (like *T. kaleniczenkoi*) at the first glance. Actually they are dirty creamy, with very dense blackish melanophores. The pigment cells accumulate particularly densely in skin wrinkles, on mantle making irregular accumulations. Sole of the same colour on all zones, dirty creamy. Also on all three zones loosely scattered melanophores occur, generally yet sole is lighter than other body parts. At present holotype is faded and is uniformly creamy.

Mucus has not been described.

Genitalia (fig. 200). The holotype drawing by **Forcart** is very detailed (see its reproduction, here fig. 200), but, as already mentioned, it was made from a permanent preparation, dehydrated and cleared. It lacks vaginal accessory glands and probably a part of atrium. As topotypes collected by **Riedel** seem to belong without doubt to that species, I described genitalia on their basis. Long vas deferens opening nearly symmetrically on somewhat flattened wide apical epiphallus section. Epiphallus wide, almost as wide as long, egg-shaped or cylindrical, shorter or almost as long as penis, with very thick walls, inside layered by dense papillae. Penis also short, cylindrical, medially as if surrounded by a wider roll. Inside penis asymmetrical, as if cut across, papilla. Inside the cutting, between two lobes of different size, an opening. Anterior penis section with small and irregular cross-wise foldings. Retractor penis, a very strong muscle, inserted at the boundary between epiphallus and penis. Spermatheca large, oval, anteriorly narrowed, set on a short but clearly separated spermatheca duct. In the holotype preparation spermatheca clearly larger in comparison to penis and epiphallus, the difference may be a result of fleshy walls of male copulatory organs being more dehydrated and contracted than flabby spermatheca. Unfastened end of oviduct tubular and long. Atrium and vagina very short, so that during dissection the insertion of penis, spermatheca duct and oviduct seems to be just by the wall. In that narrow gap between genitalia and body walls a small, probably single, grape-like structure, undoubtedly the vaginal accessory gland, whose apparent lack
Forcart noted. I could not find by how many ducts it is connected with female genitalia and where the ducts open (see fig. 200).

Spermatophore unknown.

Bionomics unknown.

Distribution: known only from locus typicus (map 12).

Material examined: Holotype and two specimens from Derbent, 5 km SE of Samsun, humid deciduous wood, among stones and in litter, leg. A. Riedel, 28 XI 1985.

Notes. Slug very similar externally to T. kaleniczenkoi, which is known from the Crimea and probably also occurring on the Turkish shore of the Black Sea. T. kaleniczenkoi has a large barrel-like atrium with elongate folds inside, also has large accessory glands (fig. 145). Judging on the basis of the preserved
specimens *T. kaleniczenkoi* is larger with body more thickset. In the Zoological Museum Amsterdam collection there is a specimen from Zonguldak (Turkey) identified by Forcart as *T. samsunensis* (see p. 256-257 and figs 148-153). I believe the slug is *T. kaleniczenkoi*.

The other, similar externally and anatomically, slug is *T. budapestensis*, with a darker sole, which after preservation is uniformly grey, with fewer melanophores on its surface. It also differs by a long, cylindrical or mace-like epiphallus and large easily discernible, lobular accessory glands (fig. 112). It should be noted that papilla penis in some *budapestensis* specimens is occasionally similar to *kaleniczenkoi*.

**Tandonia schleschi** (Wagner, 1930)

*Milax (Milax) Schleschi* Wagner, 1930 a: 48, figs 4-5. Terra typ.: “Krain” (now Slovenija, Yugoslavia); exact locality unknown. Syntypes: see notes. 

*Milax (Milax) Schleschi*: Wagner 1930b: 101, figs 3-4, pl. 1 fig. 1. 

† *Tandonia schleschi*: Wiktor 1982: 475, fig. 13. 
See also: *Tordonia nigra*, p. 271 and *Tandonia simrothi*, p. 299.

**Diagnosis.** Black or blackish slug. Epiphallus covered externally by small papillae. Spermatheca with spermatheca duct c. twice longer than penis with epiphallus. Inside atrium or vagina large radially situated spiny structures.

**Description.** After preservation body length to 45 mm, mantle length to 15, body width to 9 mm. Body slender, keel usually distinct along the whole of back or along \( \frac{2}{3} \) of its length. 11 grooves between keel and pneumostome (fig. 201).

![Fig. 201. *Tandonia schleschi* — side view of a specimen from Makarska (Yugoslavia).](http://rcin.org.pl)

Coloration uniform without dots. Head, mantle and back with keel most often deeply black. Neck and sides lighter. Sole edge blackish, the sole itself creamy. Some of the preserved specimens blackish-brown, even with reddish shade, as if faded, keel being lighter starting from back.

Mucus not described.

Genitalia (figs 202-207). Vas deferens thin, opening apically and symmetrically. Epiphallus very long, widened in the middle, its boundary with penis
indistinct because it is constricted in some places. On external surface of about \( \frac{2}{3} \) of it numerous small papillae, the anterior and the posterior epiphallus end lacking them. Inside dense small papillae. Penis, if it can be separated at all, somewhat wider, irregular, adhering laterally to atrium. Inside semi-spherical papilla (figs 205-206). Musculus retractor penis not found though

Fig. 202. *Tandonia schleschi* — copulatory organs (specimen from Makarska, Yugoslavia) (after Wiktor 1982).

Figs 203-204. *Tandonia schleschi* — copulatory organs. 203 — specimen from Knin (Yugoslavia), 204 — specimen from Carniolia (see notes).
many specimens have been dissected. Oviduct like a tube roughly equal in length to penis with epiphallus. Spermatheca, when container is not filled, small and elongate, spermatheca duct, however, being a thick-walled, thick, occasionally twisted duct. After being extended spermatheca still elongate (figs 203-204). Together spermatheca and spermatheca duct about twice as long as penis with epiphallus. Vagina and atrium not separated, producing an egg-shaped formation, many times wider than oviductus and spermatheca duct. Inside elongate lamellar structures (fig. 206), covered with flat dagger-like spines, the point being towards the sexual opening. In eversion of atrium the structures make a star-like formation resembling a flower covered with sharp spines (figs 205, 207). Accessory glands like small digital processes closely adhering to vagina.

Spermatophore unknown.

Bionomics. All specimens that I collected myself were deeply hidden in rock crevices, most often at the foot of a stone wall, where it was a bit more moist. I collected them only on limestone at small altitudes up to 600 m.

Distribution (map 12). It has to be studied. Certainly it occurs in Velebit Mts, Dalmatia. The locality Kamniška Alpe (N-Slovenija) that I wrote about in 1982 has to be checked (young slugs were there).

Material examined: 10 + 16 juv. specimens.

Notes. Wagner (1930a, b) states that the syntypes came from “Krain”

Figs 205-207. Tandonia schleschi. 205 — anterior body section with everted atrium and papilla closer to the mantle, 206 — spine from atrium, 207 — magnified part of everted atrium with radial spines — all from a specimen from Knin (Yugoslavia).
i.e. the area at present belonging in its great part to Slovenija. He did not know an exact locality. The drawings of the genitalia were probably based on a single specimen. The author states also that both syntypes were deposited in the National Museum in Budapest. It is known that the collection was destroyed in the fire. Due to Dr. Pinter's kindness some materials were found, kept by Wagner's family, and I was able to study them. One of the specimens has a label written in pencil "Milax (Milax) Schleschi H. Wagn., Carniolia. L. Kuscer" (i.e. from terra typica). The dimensions of the specimen agree with those of the syntype no. 1 (Wagner 1930a). The specimen had not been dissected and I dissected it (fig. 204). It is subadult. The genitalia differ slightly from those of Dalmatian specimens (compare figs 202-203). The penis is cylindrical, with longitudinal wrinkles inside. The retractor penis is quite large. The vagina is short, with only one longitudinal rib inside. The rib bears a few spines resembling structures characteristic of Dalmatian specimens. The spermatheca is shorter than penis and epiphallus together. I could not ascertain whether the specimen from Carniolia is one of the syntypes of T. schleschi (e.g. kept in Wagner's house) or another specimen, only determined by Wagner. In the latter case it cannot be regarded as authoritatively determined by the author of the species name. It had not been dissected and Wagner could not know its anatomical structure. Dealing with materials studied by this malacologist I found that he often determined erroneously undissected specimens even of species he described. The dissection and comparison with types or drawings and description allowed me to reveal his mistakes. Thus the case of T. schleschi is not quite clear and I doubt if it would ever be solved. Being unable to redescribe the species or describe topotypes I accept the name for the species which can be recognized as T. schleschi basing on Wagner's (1930a, b) short description and drawings.

**Tandonia serbica** (Wagner, 1931)

*Milax (Milax) serbicus* Wagner, 1931a: 63, figs 8-10. Loci typ.: Svetka Petka (= Sveta Petka) near Niš (Serbija, Yugoslavia). Syntypes: Naturhist. Mus. Vienna (I have not examined these specimens).


**Diagnosis.** Brownish, mucky creamy or pink-brown with blackish reticulate pattern. Epiphallus cylindrical, posteriorly abruptly narrowing, about twice as long as the oval penis. Spermatheca oval on long thick-walled spermatheca duct.

**Description.** Body length to 45 mm, width to 11, mantle length 15. Keel in living slugs distinct along the whole of back, in preserved ones at least along 2/3 of back length. Skin wrinkles not very distinct, 13 between keel and pneumostome.
Coloration very similar to *T. kusceri*. Body brownish, mucky creamy coloured with blackish reticulate pattern, which is formed by pigment in skin-grooves. A distinctive character in this species is occurrence in most specimens (but not in all) of larger, c. 1–2 mm in diameter, irregularly situated black dots, which look like India ink splashes, the dots occurring only on the posterior, outside mantle, body section (fig. 208). Head and mantle blackish or black. On mantle well-visible lateral streaks and reticulate irregular patterns. Keel light, without darker pigment, sole mucky creamy.

Mucus colourless, transparent.

Genitalia (figs 209–210). Vas deferens very thin, opening symmetrically, its boundary with epiphallus very clear. Epiphallus cylindrical, posteriorly abruptly conically narrowed, its lumen narrow, walls being densely covered with small papillae. Penis far wider than epiphallus, approximately twice as short, in shape oval or like a short club, anteriorly narrowed. Inside penis an ornamented papilla penis (figs 209–210), rather variable in shape. Musculus retractor penis is a wide strand, and, beside this, on penis sides numerous short membraneous muscles connecting it to body layers. Oviductus roughly equal to penis and epiphallus in length, tubular without swellings and distensions. Spermatheca when empty almost spherical, distended by spermatophore elongate oval. Spermatheca duct with thick walls, tubular, almost equal in length to epiphallus. Vagina very short. Atrium is as if a prolongation of penis and is about the same in width. Laterally it is fastened by strong retentor muscles. Accessory glands like adhering divided lobular formations surrounding vagina.

Spermatophore (fig. 211) very strongly elongate, coiling into a regular spiral inside spermatheca. I have studied several of the structures and they always have the same features, while they may differ in their size. The section inserted into the partner first somewhat wider. Along it two regular rows of twice dichotomically bifurcated spines. Sometimes one of rows may be broken along a short part. Roughly in the other half of the spermatophore spines not only become longer and longer but they also get branched dichotomically more, so that they have a score of endings each, being so strongly branched that they cover completely one side of spermatophore. Spermatophore coils spirally, its bare part inside. On external sides the spines form a structure which can be compared to trees whose tops have become united. The posterior section — i.e. that which leaves the donor of the spermatophore last is about \( \frac{1}{5} \) of the whole structure. It is straight, partly in the spermatheca duct of the receptor, covered by spines on all sides, arranged in 6 rows. The spines are forked or at most have four endings. The spines adhere to walls with their free endings being directed to the receptor.

Bionomics. Occurs in habitats with a large number of loose stones, in rock rubble, in shrubs. Usually in dry places, almost always on limy substrate. In mountains to 1200 m elevation. I have found spermatophore in specimens collected in June and October.

Distribution (map 13). Occurs in eastern Serbia (Yugoslavia) and in south-western Bulgaria. In Yugoslavia probably in a small area near Niš, while in Bulgaria in a large area, esp. in mountains. In north it reaches Prazhda and Vracanska Planina, in east to Shipka pass in the Stara Planina Mts and Kharmali. In south to Rila and the Pirin Mts. Should be expected in the Greek areas near the border.

Material examined: about 150 specimens.

Notes. T. serbica is very similar to T. kusceri (see p. 257), esp. in its external

http://rcin.org.pl
Fig. 211. *Tandonia serbica* — spermatophore (specimen from Shipka, Stara Planina, Bulgaria).
appearance and its ecological demands, as both species often occur together in the same biotopes. *T. serbica* is a slug slightly smaller, darker coloured and, if with dark splashes like that of India ink, easy to distinguish also by its external appearance (there are no such splashes in *T. kusceri*). In the structure of its genitalia it differs from *T. kusceri* in a thicker, many times shorter and never coiling epiphallus. Penis, in comparison to other organs, is far bigger and widens anterad. All muscles are much wider, esp. musculus retractor penis. Papilla usually differs in shape, but is variable and its taxonomic suitability is not exactly known. Both slugs often live together, yet *T. kusceri* seems to be more eurytopic and occurs more often and in larger populations. Bionomics of both species should be better studied and checked whether they do not cross. Their high similarity and mutual occurrence gives way to doubts. I have often found spermatophores in *T. serbica*, while never in *T. kusceri*, though I collected the latter species more often at the same time. Though I have not found intermediate forms, it cannot be excluded that the differences may result from sexual dimorphism related to the life cycle and *T. serbica*, whose epiphallus is wider and muscles of the male part of genitalia stronger, it is smaller and may be a form that functions as a male. These doubts I have not been able to explain, and they must be left to be solved in future.

**Tandonia simrothi** (Hesse, 1923)


A species requiring further study, particularly on the basis of topotypes. Its description is very short, and the drawings of Simroth point out to its strong similarity to other species.

The following description is after Simroth (1910).

Keel reaching or nearly reaching to the posterior mantle edge. Body black.

Genitalia (figs 212–213). Penis and epiphallus cylindrical. At the boundary between them a fold like a ring. Simroth states that in the anterior penis section there is a retractor — in fact, judging by the drawing, it is retentor, not retractor. Spermatheca without spermatheca duct, elongate oval in shape. Very short vagina and very short accessory glands surrounding it. Atrium short with strong bundle of retentor muscles. In atrium a funnel-like asymmetrical structure, like a stimulator, being a prolongation of vagina (!!).

Notes. A character distinguishing this species is the funnel-like structure in the atrium (fig. 213). Perhaps it was a part of the everted vagina; without study of the specimen it cannot be established without doubt. Judging by the short description and the appearance of genitalia on the figure the slug is very similar both to *Tandonia nigra* and *T. schleschi*. Both the species have, how-
ever, at the opening to vagina or inside it characteristic formations with hooks on end. It is not probable that Simroth, discriminating and experienced scientist, would not notice such structures when studying the inside of the atrium. This species is still unclear, especially that in the Alps there live several species of black colour. The preserved specimen of the species identified by Forcart (1959) as T. simrothi cannot be accepted as such because in the vagina it has structures typical of T. nigra (see p. 271).

*Tandonia sowerbyi* (Férussac, 1823)


*Limax carinatus* Risso, 1826: 56 (non Leach, 1847) (after Hesse 1926).

*Limax aegypticus* Gassies, 1866 (after Hesse 1926).

*Limax marginatus* Jeffrey, 1862 (non marginatus Draparnaud, 1805; nec marginatus Müller, 1774) (after Hesse 1926).

*Limax etruscus* Issel, 1888. Terra typ.: Toscana (Italy) (after Hesse 1926).

*Milax Barbarus* Mabille, 1869 (after Hesse 1926).

*Amalia marginata* var. fulva Paulucci, 1879: 22. Lec. typ.: S. Elia Mt. near Palmi, Calabria (Italy).


*Amalia pratensis* Torrez Miñuez, 1923 (after Hesse 1926, see Arch. Moll. 1924: 239).


*Amalia carinata pallidula* Cockerell, 1890: 286. Terra typ.: unknown, but probably South Europe. Syntypes: 2 young specimens, British Mus. (NH). No number on label.

*Amalia maculata* Collinge, 1895: 336, pl. 23 fig. 6. Terra typ.: Algeria. Type: no infor-
Milocidae — systematic monograph

Milax collingei HESE, 1926: 139 — a new name instead of preoccupied Amalia maculata COLLINGE, 1895.

Milax sowerbyi: HESE 1926: 113; QUICK 1960: 158, figs 8 B, F, I, 9B, pl. 2 fig. 26; many other authors use this transcription though the author of the species uses “sowerbii”.

In the literature numerous other names for “varietates” (see HESE 1926) can be found.

There are various colour forms, whose taxonomic status is unclear.

Diagnosis. Body brownish, covered with diffuse blackish pigment forming irregular accumulations. Penis with epiphallus without clear separation, cylindrical, posterad slightly narrowed. Beside retractor penis two membranous muscles connecting penis to body walls. Spermatheca strongly elongate, clearly separated from spermatheca duct, shorter than it.

Description. Its size varies among populations, in south seems a bit larger. Body length after preservation to c. 60 mm, width to 16 mm, mantle length to 18 mm. In comparison to other representatives of the genus: it has relatively small mantle and short head section. Posterior body section very slowly tapers. Keel very strongly arched like a ridge jutting out. In cross-section body almost triangular, esp. in the very posterior. Skin wrinkles flat (i.e. poorly standing out), 16 between keel and pneumostome (fig. 214).

Coloration. General coloration brownish-yellow of various hue, on this background diffuse blackish pigment producing more intense dots in some places. Sometimes the pattern like irregular reticulum, or else the slug seems dirty with something dark. Head and tentacles blackish. Mantle covered by irregular network, laterally indistinct streaks. Keel yellowish or orange when alive, after preservation dirty creamy. Sole on edges usually orange, after preservation also creamy. Numerous colour varieties known, e.g. body white, black with keel orange, blackish, etc.

Mucus yellowish, thick.

Genitalia (figs 215–216). Vas deferens thin, twisted, approximately twice as long as epiphallus, opening apically, clearly asymmetrically, almost laterally

Fig. 214. Tandonia sowerbyi, specimen from Apoikia (Andros Isl., Greece) — above left cross-section through body.
Boundary between epiphallus and penis difficult to find, both forming a cylinder narrowing posterad, in two places slightly constricted. Approximately at $\frac{1}{3}$ from the posterior very thick and short retractor penis inserting. At this place small constriction. Roughly at $\frac{2}{3}$ of length, also from the posterior, two opposite membranous muscles (retentors?) insert. Somewhat more anteriorly another deeper constriction. Inside the part situated caudally in relation to retractor penis small papillae covering internal walls. The section between constrictions, i.e. also between muscles, thick-walled, internal diameter being a very narrow duct which is terminated by a small flattened papilla penis (fig. 216). Papilla penis opening to quite large cavity, where thin walls (of penis) partly covered with small striations. Oviduct thin tubular, twisted, c. 1.5 times longer than penis with epiphallus. Spermatheca very elongate, like a cylinder with the posterior end slightly rounded, sometimes slightly widened in the anterior section. Spermatheca duct thin, tubular, several times thinner and 2–3 times shorter than spermatheca. Vagina short, indistinctly

Fig. 215. Tandonia sowerbyi — genitalia (specimen from Andros Isl., Greece).
Separated from atrium, also short. Inside the cavity common for both dense wrinkles, and a plate-like thickening, by many students (e.g. Quick 1960) called stimulator. Vaginal accessory glands like narrow lobes and ducts densely surrounding the anterior oviduct section.

Spermatophore (figs 217–219). Different in its appearance from all the remaining species. The end being inserted into the partner-receptor surrounded by fan-like widened membranous processes in four rows. The farther section, approximately equal to half of spermatophore, is a tube narrowed anteriorly with walls completely bare. The posterior section, i.e. the one that leaves the donor last, covered with short spines, adhering to walls, many times branched dichotomically.

**Bionomics.** Eurytopic species, mainly in open habitats, e.g. in meadows, grassy slopes of lower mountains and on wasteland, in shrubs, gardens and other synanthropic habitats. It shelters under stones and pieces of wood, in gardens may be a pest. According to QUICK (1960) it copulates in October and November in Great Britain. In Yugoslavia I collected slugs with spermatophore in September. Probably copulates also in other year seasons.

**Distribution** (map 14). It is difficult to establish the original range, because the slug tends very much to be synanthropic. It has probably accompa-
nied man for a long time, and in the Mediterranean region could have been introduced as early as in antiquity. It occurs in Greece, being very common there, and probably introduced, in Yugoslavia (isolated synanthropic localities), Austria (synanthropically), Italy, France, Belgium, the Netherlands, Spain, Great Britain and Ireland.Introduced also to S-America and New Zealand.

Material examined: several hundred specimens from Greece, Italy, Yugoslavia, the Netherlands.

Map 14. Distribution of Tandonia sowerbyi.

Notes. Easy to distinguish on the basis of the characteristic spermatheca, penis and epiphallus. In the literature it may have been confused with T. rustica.

Tandonia strandi (Wagner, 1934)

Milax (Subomalia) Strandi Wagner, 1934c: 331, figs 1-4. Terra typ: Turkey (Takir-Dagh and Istanbul). Syntypes: probably do not exist.

The description by Wagner (1934c) is little precise, the drawings being particularly careless. I have no information if the species was collected by someone after the description, and, in the material from Turkey that I had, there was no such slug to be found. The following short description is based on data of Wagner's description.

Dimensions of the preserved (?) specimens: length to 61 mm, width to 12 mm, mantle length to 18 mm. Keel poorly developed: in some specimens indiscernible.
Coloration. Back grey-brown or grey-violet (graubraun oder grauviolett). Sides downwards more and more light, at the foot edge grey-yellow (graugelb). Also neck, mantle edges, sole grey-yellow. Head dark. In some specimens keel light or at its place a light streak (Kiel-Linie).

Genitalia (figs 220–221). Epiphallus high, a very gradually tapering cone, on its top vas deferens symmetrically opening. Penis centrally swollen. No information on appearance of musculus retractor penis. Oviductus tubiform. Spermatheca in the shape of elongate oval, indistinctly separated from shorter but also narrow spermatheca duct. Vagina tubiform, roughly equal in length to spermatheca duct. Accessory glands like straight ducts surrounding vagina. No information about atrium, but it follows from the figure that it is tubiform.

Spermatophore (fig. 222) has a cirrose section, which, gradually widening, becomes a tubiform container. Spines, whose appearance not shown in magnification, along the whole length of spermatophore, though without covering its whole surface.

Bionomics unknown.

Distribution: known only from terra typica.

Notes. WAGNER compares the species to Milax creticus, Milax athenensis (=Tandonia cretica) and Milax hellenicus (=T. cretica). The characters distinguishing the species are, according to WAGNER, smaller size than hellenicus and athenensis and coloration. Judging from the description and from the genitalia figures, and from the spermatophore appearance, it seems that all the mentioned characters are within the range of variability of Tandonia cretica (see page 236). Preserved slugs, esp. slightly macerated have just the coloration that WAGNER states for T. strandi. Differences in size are not so great as to be

Figs 220–222. Tandonia strandi. 220–221 — copulatory organs, 222 — spermatophore (all from Skutari, after WAGNER 1934c).
doubtful. The figure of spermatophore is difficult to interpret because of little care in its making, but it seems to be very similar to the spermatophore of *T. cretica*. The difficulty in synonymization of the names *strandi* with *cretica* lies in: a) lack of types, and lack of topotypes, b) finding no *T. cretica* in the region. If it turns out that *T. cretica* occurs e.g. in the region of Istanbul, then the name *strandi* should be synonymized with it. At present existence of a species different from *T. cretica* should not be excluded in this region of Turkey, that is why the name *strandi* should be preserved.

**Tandonia totevi** (WIKTOR, 1975)


**Diagnosis.** Very large, to 95 mm, with external appearance very similar to *Limax*, as the keel is poorly arched and the horse-shoe groove very poorly visible on mantle. Back blackish-olive. Epiphallus cylindrical, c. twice as long as penis. Penis reel-like. Spermatheca and spermatheca duct indistinctly separated.

**Description.** Probably the largest species in the family. Preserved specimens: length to 95 mm, width to 15 mm, mantle length to 34 mm. Keel c. 10 mm long, distinct only in the posterior body section. Skin sculpture delicate, of very narrow elongate wrinkles, 20–21 wrinkles between the dorsal medial line and pneumostome.

Coloration blackish-olive or brownish-olive with lighter dots as if shining through (fig. 223). Keel and its prolongation as a clearly visible light dirty crea-

![Fig. 223. Tandonia totevi – specimen from Deven (Bulgaria) (after WIKTOR 1975).](http://rcin.org.pl)
my streak. Sides gradually lighter downwards until dirty creamy. Sole of the
same colour. Head and tentacles blackish.

Mucus not described.

Genitalia (figs 224–225). Vas deferens thin, twisted and long, opening api-
cally. Epiphallus like a long cylinder with several small swellings anteriorly and
posteriorly, caudally gradually narrowing. Depending on the degree of contrac-
tion its posterior ending either smoothly rounded or a short cone on top of
which vas deferens opening. Walls of epiphallus very thick, inside longitudinal
folds. Penis c. twice as wide as epiphallus and about 2–3 times shorter. Poste-
rior penis section reel-like, anteriorly penis narrowed, inside a small blunt-point-
ed (fig. 225) or slightly conical narrowed papilla penis with an opening on
top. Internal penis walls covered with longitudinal folds. Retractor penis very
delicate (usually difficult to find at all), inserting laterally to anterior epiphal-
lus section. Oviductus tubiform, roughly equal to epiphallus in length. Spermatheca without clear division into container and spermatheca duct, heavily
elongate, anteriorly tongue-like narrowing, longer than penis, with spermatophore inside it, may be even longer than penis with epiphallus. Vagina short,
at best as long as half of penis. Vaginal accessory glands closely adhering
to vagina walls like indistinct grape-like structures or irregular lump. Atrium
very short or difficult to find, inside and in vagina anterior section very small
longitudinal wrinkles (lack of large folds).

Spermatophore unknown.

Bionomics. Completely unknown. I collected it near gardens by the road
in the night (in locus typicus) where it occurred as a clear synanthrope.
Distribution (map 15). It is too early to discuss its distribution, particularly as it is unknown where its natural localities are, nor where it has been introduced. So far known from locus typicus in SE Bulgaria, I had also specimens collected by W. J. M. Maassen in ruins in Philippi (= Filippoi, Macedonia, Greece).

Material examined: 4 + 10 juv. specimens.

Notes. In external appearance sometimes so similar to large specimens of Limax flavus L. that it can be confused with it. It also resembles in its coloration and size T. pageti, but is clearly different in lack of the blind section of epiphallus and tongue-like structure in atrium. It also resembles T. cavicola, but the latter has dark spots loosely scattered on sides, spermatheca with spermatheca duct clearly separated and a different penis.

Lastly, it is also similar to very large specimens of Tandonia cretica, in both its external appearance and the structure of genitalia. T. cretica never has spotted body, it differs slightly in appearance of copulatory organs, especially their internal structure (see figures), and the most easily visible character is the appearance of vaginal accessory glands. In T. cretica they have a shape of parallely arranged short rolls, while in T. totevi the glands are of grape-like structure.
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Museum Przyrodnicze UWr.
Sienkiewicza 21, 50–335 Wrocław

STRESZCZENIE

[Tytuł: Milacidae (Gastropoda, Pulmonata) — monografia systematyczna]


W wyniku rewizji całej rodziny zsynonimizowano bardzo liczne nazwy, ostatecznie ustalając całkowitą listę znanych gatunków na 47, z czego odrębność przynajmniej czterech budzi poważne wątpliwości i należy oczekiwać, że w przyszłości mogą okazać się synonimami.

W spisie publikacji zestawiono piśmiennictwo z punktu widzenia taksonomii, morfologii i tylko częściowo zoogeografii. Nie uwzględniono całego piśmiennictwa faunistycznego, które nie zmienia istoty poglądu na zasięg geograficzny poszczególnych gatunków.

РЕЗЮМЕ

[Заглавие: Milacidae (Gastropoda, Pulmonata) — систематическая монография]

Это первая систематическая монография семейства Milacidae. Она составлена на основании двадцатилетних полевых исследований самого автора и обработки всех доступных музейских фондов и частных коллекций. Автор произвел ревизию всех типов, которые удалось найти и многочисленных топотипов, собранных позже. Общая часть подводит итог всех накопленных знаний о рассматриваемом семействе, касающихся вопросов, существенных для систематики. Особое внимание обращено на пригодность различных признаков для таксономического и филогенетического анализа. Приведена также характеристика семейства с точки зрения его экологии, биономии и зоогеографии. Даются также необходимые сведения по методике исследования этой группы. Монография содержит полностью оригинальный определитель видов. Во второй части автор рассматривает все таксоны, статус которых удалось установить. В ней приведены синонимы, данные относительно
типов и основной литературы. Обсужден габитус и строение половых органов, при этом указывается на многочисленные, не известные до настоящего времени признаки, особенно творов находящихся внутри гениталов. Например, папилла в пенисе или резьба внутренних стенок эпифаллюса и атриум. У большинства видов описан внешний вид сперматофоров, который имеет исключительное значение для таксономии, на что указывается впервые. Установлена также там, где это было возможно, шкала изменчивости отдельных признаков. Дополнением описаний являются замечания, предостерегающие перед возможными ошибками при идентификации сходных видов. Выражены тут также все сомнения и предположения автора.

В результате произведенной ревизии очень многие названия сведены в синонимы. Окончательный список известных видов составляет 47, из них систематическая принадлежность по крайней мере четырех видов вызывает серьезные сомнения и следует ожидать, что в будущем они могут оказаться синонимаами.

В списке литературы помещены публикации, касающиеся таксономии, морфологии и только частично распространения. Не принята во внимание вся фаунистическая литература, что не меняет существенным образом взглядов на географические ареалы отдельных видов.
INDEX OF GENERIC AND SPECIFIC LATIN NAMES

adelpha (us) 222, 225
Adensameri 247, 248 250
ageaeicus 178, 186, 196
agrilaceus 300
albanica (us) 180, 183, 222, 265, 268, 271
altenai 178, 189, 190, 196, 202
Amalia 184
antipodarum 202
Aspidoporus 220, 221, 222, 278, 283
ater 179, 193, 206, 208, 213, 214
athenensis 236, 240, 306
atratus 202
Babori 202
Balcanicus 257
baldensis 180, 183, 220, 225, 247, 250, 271, 292
Barbarus 300
barypa (us) 178, 185, 196
benoiti 211
bojanensis 257
boscensis 181, 228
budapestensis 159, 166, 167, 171, 182, 230, 289
cabiliiana 211
carinata (us) 257, 300
caucasica (us) 178, 196, 200
cavica 181, 234, 309
Cibinien8i8 230
clerxi 222
collingei 301
cretica 158, 180, 236, 246, 306, 307, 309
cristata (us) Kaleniczenko 181, 241, 256
cristatus Leiblein 241
croaticus 177, 244
Cypria 185, 196, 199
cypria (us) 185, 196, 199
dalmatina (us) 177, 245
dobrogicus 253, 256
doderleini 211
ehrmanni 180, 246
estrus 300
fejeraryt 180, 228, 247, 253
fulva 300
Gagates Draparnaud 166, 169, 170, 171, 179, 184, 185, 189, 193, 195, 202, 206, 207, 211, 213, 214, 230
Gagates Menegazzi 230
gasulli 179, 195, 196, 206, 213, 214
gracilis Leydig 230
grasili Rafinesque 230
Guebhardi 177, 250
ehlenica 236, 240, 246, 306
Hessei Boettgo. 227, 257, 300
hesseri Simr. 225, 227
Heustonii 202
ichnusae 211
insularis 211
jablanacensis 179, 220, 230, 251, 271
kaleniczenkoi 164, 182, 253, 289, 290, 291
Kalenzkoi 253
Kobelli Hesse 300
Kobelli Simr. 299
Krynickillus 241
kusceri (Kuščeri) 162, 171, 182, 257, 289, 296, 297, 299
lagostoma (us) 181, 260
Lallemantia 184
Larteti 185
limax 221, 222, 278, 283
longipenis 257
macedonica (us) 180, 183, 225, 262
Macrothylacus 220, 253
maculata 300, 301
Malinastrum 222
marginata (us) Drap. 220, 245, 246, 286, 300
marginatus JEFFR. 300
marginatus MÜLL. 200, 286, 300
maurus 202
mediterranea 211
melanica 180, 222, 225, 265, 267
Micromilax 185, 196, 199, 250
Milax 162, 164, 173, 177, 184, 185, 189, 196, 220, 265
Monginensis 300
montenegrina (us) 177, 267, 268
monstruosus 178, 196, 208
Monterosati 177, 184, 211

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