

Report on genital studies of European Clausiliidae for taxonomic and phylogenetic work

Hartmut Nordsieck (XII. 2020)

I. General remarks, Material and methods

Like in other stylommatophoran families the genitalia of the species of Clausiliidae, especially the copulatory organs, are of high taxonomic importance and thus of interest for phylogenetic studies. Therefore, for a book on European Clausiliidae I studied the genitalia of 302 species of all subfamilies by describing and measuring the 487 preparations, which I had made from alcohol material of these species (1-2, in part more specimens prepared). The material used and the preparations are stored in the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Forschungsinstitut Senckenberg Frankfurt am Main (SMF).

In this article my former papers on genital morphology are cited by the publication years.

The material comprises the following genera (in brackets number of examined species):

Phaedusinae:

Former Serrulininae:

Pontophaedusa (1), *Pontophaedusella* (1), *Laeviphaedusa* (1), *Caspiophaedusa* (1), *Pravispira* (1), *Dobatia* (1), *Serrulina* (2).

Laminiferinae:

Neniatlanta (1).

Alopiinae:

For the tribe system see article on DNA studies.

Alopiini (sensu lato):

Cariniger (15), *Isabellaria* (4), *Albinaria* (14), *Inchoatia* (3), *Cristataria* (6), *Medora* (7), *Agathylla* (8), *Lampedusa* (1), *Muticaria* (1), *Leucostigma* (1), *Strigilodelima* (1), *Montenegrina* (7), *Protoherilla* (1), *Herilla* (7), *Triloba* (2), *Alopi* (20).

Cochlodinini:

Cochlodina (14).

Delimini:

Charpentieria (5), *Siciliaria* (17), *Papillifera* (2), *Delima* (16), *Dilatataria* (3), *Barcania* (1).

Macedonicini:

Macedonica (13).

Clausiliinae:

Former Mentissoideinae + *Graciliaria*:

Boettgeria (6), *Euxinella* (1), *Olympicola* (1), *Filosa* (1), *Scrobifera* (1), *Strigileuxina* (2), *Sumelia* (2), *Akramowskia* (1), *Acrotoma* (2), *Roseniella* (2), *Armenica* (5), *Inobseratella* (2), *Phrygica* (2), *Sprattia* (3), *Euxina* (8), *Elia* (7), *Euxinastra* (2), *Galeata* (3), *Mentissoidea* (1), *Idyla* (3), *Graciliaria* (1), *Micridyla* (1).

Clausiliini:

Ruthenica (1), *Pseudofusulus* (1), *Erjavecica* (1), *Julica* (1), *Macrogastra* (10), *Clausilia* (10), *Fusulus* (2).

Baleini:

Quadriplicata (2), *Mucronaria* (3), *Micropontica* (1), *Mentissa* (1), *Mentissella* (1), *Laciniaria* (3), *Alinda* (4), *Pseudalinda* (4), *Strigillaria* (12), *Vestia* (4), *Pavlovicia* (2), *Balea* (4).

For definitions and terms of the parts of the copulatory organs see 2007a (: chapter I: 9-11, 16, appendix 2: 178-180). The terms proximal and distal are used as seen from the gonad.

The measurements were made as exactly as possible making use of an ocular micrometer (accuracy ± 0.1 mm).

Before measuring the preparations were stretched as far as possible without tearing and fixed by micropins without piercing. It is important for measurements to know about the limitation of the parts (see Fig. 1). The limitation of the female parts are given by the branchings. The limitation of the male parts are more difficult to make out, especially in groups in which they are more or less modified (former Serrulininae, Clausiliini, Baleini). They are located by changes of the lumen and the wall structure.

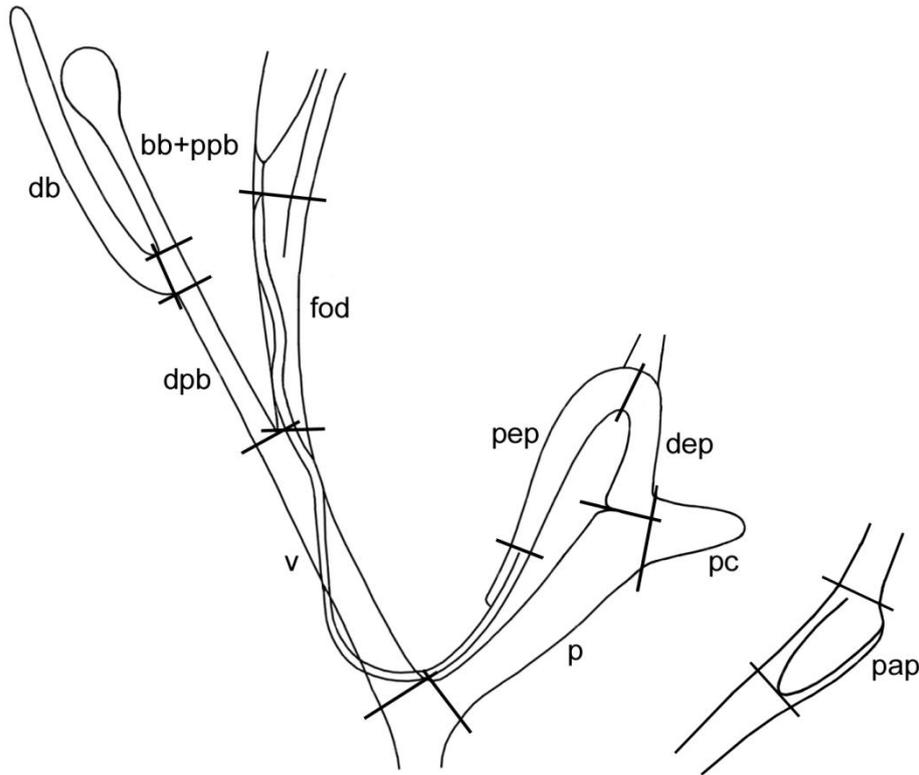


Fig. 1. End genitalia of Clausiliidae (scheme for explanation of measurements).

Abbreviations used: bb+ppb = bursa + proximal part of pedunculus, db = diverticulum, dep = distal part of epiphallus, dpb = distal part of pedunculus, fod = free oviduct, p = penis, pap = penial papilla, pc = penial caecum, pep = proximal part of epiphallus, v = vagina.

From these studies I elaborated diagnoses of the genus and family taxa (subgenera, genera, tribes) and compared the measurements by calculating the length ratios of the copulatory organs.

II. Results

As examples for the results four tables of length ratios are given: 1. Alopiini (sensu lato) (Alopiinae), 2. *Cochlodina* (Alopiinae), 3. Clausiliini (Clausiliinae), 4. Baleini (Clausiliinae). The importance of the values for phylogenetic work is discussed.

1. Alopiini (sensu lato)

Table 1: Length ratios of end genitalia of Alopini (sensu lato).

For the copulatory organs of Alopini see 2007a (: chapter I: fig. 7).

Species numbers in brackets.

Extreme values of species or values of subgroups in brackets.

Albinaria group including the genera *Carinigera*, *Isabellaria*, *Albinaria*, *Inchoatia*, and *Cristataria*.

Abbreviations used: bb+ppb = bursa + proximal part of pedunculus, dpb = distal part of pedunculus, db = diverticulum, dep = distal part of epiphallus, ep = epiphallus, p = penis, pc = penial caecum, pep = proximal part of epiphallus, v = vagina.

	db/bb+ppb	dpb/v	p/v	pc/p	ep/p	pep/dep
<i>Albinaria</i> group (38)	0.6-1.9	0.2-1.2 (-1.5)	0.4-1.3	0-1.9	(0.9-) 1.2- 3.2 (-4.8)	0.9-2.1
<i>Medora</i> (7)	0.6-1.0	0.4-0.9	0.4-0.9	0.4-1.1	0.8-1.5	1.2-2.9
<i>Agathylla</i> (8)	0.5-1.1	0.3-0.6	0.4-0.7	0.2-1.4	0.8-1.6 (- 2.3)	1.2-2.4
<i>Lampedusa</i> , <i>Muticaria</i> (2), <i>Leucostigma</i> (1)	0.3, 0.4, 0.5-0.7	0.4, 0.6, 0.7-0.9	1.1, 0.7, 0.7-0.9	0.4, 0.3, 0.1-0.2	0.9, 1.2, 1.1-1.6	0.8, 1.2, 1.0-1.3
<i>Strigilodelima</i> (1)	1.2, 1.3	0.5, 1.5	0.8, 1.2	0.1	1.3	2.1, 2.2

<i>Montenegrina</i> group (8) (<i>Protoherilla</i>)	0.9-1.9 (2.1)	0.1-0.4	0.4-0.7	0	1.2-2.0	0.7-1.3
<i>Herilla</i> group (9) (<i>Triloba</i>)	0.7-1.3	0.2-0.6	0.5-1.0	0.2-1.3 (0.1, 0.3)	1.0-2.8 (0.7, 0.8)	0.8-2.8
<i>Alopi</i> (20) (<i>Kimakowiczia</i> group)	0.6-1.3 (1.7, 1.9)	0.4-1.0	0.5-1.4 (2.1, 2.2)	0.1-1.2 (nearly 0)	1.1-2.2	0.5-2.0

As is shown in the table the length ratios of the subgroups of the Aloiini (sensu lato) do not much differ.

The diverticulum is shorter or longer than the proximal pedunculus, with all transitions of ratio.

Distal pedunculus and penis are mostly shorter than the vagina. In the *Albinaria* group and *Strigilodelima* the vagina is in part shortened. In *Alopi* (*Kimakowiczia*) the penis is lengthened.

In the *Albinaria* group (except of *Albinaria* itself), *Medora* and *Agathylla* the penial caecum is on average longer. In some *Albinaria* species, *Leucostigma*, *Strigilodelima* and some *Alopi* species (including *Kimakowiczia*) the caecum is reduced. In the *Montenegrina* group and two groups of the *Albinaria* group the caecum is missing; instead a penial papilla is present. These groups exhibit also a vaginal retractor originated from the vaginal connection of connective tissue.

As a rule, in the subgroups of Aloiini (sensu lato) the epiphallus is longer than the penis. In *Medora* and *Agathylla* it is in part equally long, in *Lampedusa* and the *Herilla durmitoris* group it is equally long, in *Triloba* it is shorter.

The proximal part of epiphallus (parts delimited by the insertion point of the penial retractor) is in most subgroups longer than the distal part. In several species of *Montenegrina* and *Alopi* it is equally long or shorter. Also in the *Herilla durmitoris* group and *Triloba* both epiphallus parts are about equally long.

Thus, in several subgroups of Aloiini (sensu lato) apomorphic character states evolved in parallel. The examination of end genitalia does not reveal evolutionary lineages which are defined by synapomorphies (except of the *Montenegrina* group, see above).

2. *Cochlodina*

Table 2: Length ratios of end genitalia of *Cochlodina* species.

For the copulatory organs of *Cochlodina* see 1969a.

Sample numbers are given in brackets.

Extreme values of *C. laminata* with shortened vagina (2007b) in brackets.

For abbreviations see table 1.

	db/bb+ppb	dpb/v	p/v	ep/p	pep/dep
<i>laminata</i> (6)	0.47-0.64	0.59-0.93 (- 1.68)	1.01-1.20 (- 1.82)	0.71-1.00	1.10-1.64
<i>inaequalis</i> (2)	0.57, 0.62	0.64, 0.69	0.98, 1.02	0.97, 1.07	1.00, 1.27
<i>dubiosa</i> (4)	0.54-0.64	0.64-0.92	0.93-1.07	1.14-1.28	0.87-1.13
<i>liburnica</i> (2)	0.58, 0.75	0.67, 0.70	1.14, 1.30	1.12, 1.18	0.61, 0.64
<i>fimbriata</i> (4)	0.62-0.65	1.29-1.50	1.76-2.33	0.84-1.20	0.56-0.80
<i>triloba</i> (4)	0.45-0.73	0.56-0.73	1.07-1.33	0.94-1.06	0.55-0.91
<i>costata</i> (10)	0.51-0.73	0.88-1.78	0.50-1.01	1.39-3.55	0.85-1.35
<i>incisa</i> (1)	0.64	0.41	0.85	0.93	1.28
<i>kuesteri</i> (1)	0.79	0.58	0.92	1.09	0.94
<i>meisneriana</i> (1)	1.04	0.73	0.79	1.45	0.97
<i>comensis</i> (1)	0.62	0.44	0.99	0.95	1.33
<i>orthostoma</i> (4)	1.17-1.55	0.58-0.96	1.00-1.19	1.00-1.26	1.67-1.89
<i>cerata</i> (2)	1.63, 1.57	0.81, 0.88	0.67, 0.75	2.28, 2.80	1.16, 1.34
<i>marisi</i> (1)	1.71	1.13	1.27	1.04	1.78

In the table the high diversity of the end genitalia of *Cochlodina* is shown.

Two main subgroups of *Cochlodina*, which are defined by their diverticulum length, are recognized: *C.*

(*Paracochlodina*), with diverticulum longer than bursa + proximal pedunculus, and the *C. (Cochlodina)* group, with diverticulum shorter. The latter has been divided into the subgenera *C. (Cochlodina)*, *C. (Procochlodina)* and *C. (Cochlodinastra)*, defined by shell and non-measurable genital characters (1969b, 1977). Within *C.*

(*Cochlodina*) in the table the *C. costata* subgroup and the *C. fimbriata* subgroup (*C. liburnica*, *C. fimbriata*, *C. triloba*) are recognizable by measurable apomorphies: *C. costata* subgroup by the penis reduced in size and *C. fimbriata* subgroup by the lengthened distal part of epiphallus. The two subgroups differ from the *C. laminata* subgroup also by the presence of a penial papilla. Within *C. (Paracochlodina)* *C. cerata* exhibits a penis reduced in size like *C. costata*, a striking case of parallel evolution.

Because of the high diversity within the genus *Cochlodina* non-measurable and measurable genital characters make possible the recognition of evolutionary lineages. This is an exception within the Aloiinae.

3. Clausiliini

Table 3: Length ratios of end genitalia of Clausiliini.

For the special male copulatory organs of Clausiliini see 2007a (: chapter I: fig. 9).

Species numbers are given in brackets.

Extreme value of *Clausilia rugosa* in brackets.

Abbreviations used: bb+pd = bursa + pedunculus, fod = free oviduct, p = penis, pa = parepiphallus, v = vagina.

	fod/v	bb+pd/v	p/v	pa/p
<i>Ruthenica</i> (1)	1.8	3.3	1.3	0.6
<i>Pseudofusulus</i> (1)	1.8	4.3	0.6	2.0
<i>Julica</i> (1)	1.4	3.3	0.4	1.5
<i>Macrogastera</i> (<i>Pyrostoma</i>) (1)	2.0	3.4	0.7	0.9
<i>Macrogastera</i> (other subgenera) (8)	2.1-3.8	3.9-5.1	0.5-0.9	0.2-0.8
<i>Erjavecica</i> (1)	2.1	4.0	0.5	0.7
<i>Clausilia</i> (<i>C.</i>) (5)	0.9-1.7	2.2-3.4	0.4-0.6 (1.2)	0.5-1.1
<i>Clausilia</i> (other subgenera) (4)	0.8-1.1	2.2-3.8	0.3-0.4	0.7-1.4
<i>Fusulus</i> (<i>F.</i>) (1)	3.5	6.9	1.4	0.3
<i>Fusulus</i> (<i>Erjavecicella</i>) (1)	4.9	9.0	1.3	0.4

In the table considerable differences in the length ratios between the genera of the Clausiliini are recognizable. The free oviduct is longer than the vagina in *Ruthenica*, *Pseudofusulus*, the *Macrogastera* group (*Julica*, *Macrogastera*) and *Erjavecica*, about as long as the vagina in *Clausilia* (with exceptions) and much longer in *Fusulus*.

The bursa copulatrix (bursa + pedunculus) is in all genera longer than the vagina, in *Fusulus* much longer.

The penis is longer than the vagina in *Ruthenica*, in the other genera shorter (exception: *Clausilia rugosa*), in *Fusulus* longer.

The parepiphallus is longer than the penis in *Pseudofusulus* and *Julica*, in the other genera shorter, in *Clausilia* in part longer.

In the values of penis and parepiphallus again the directed evolution of the male copulatory organs to a shortening of their length with a reduction of the penis (1963, 1966, article on DNA studies) is visible. The exceptional development of the end genitalia in *Fusulus* is also recognizable.

The copulatory organs of the Clausiliini provide a classic example for the reconstruction of phylogeny with the help of genital morphology.

4 Baleini

Table 4: Length ratios of end genitalia of Baleini.

For the special copulatory organs of Baleini see 2007a (: chapter I: fig. 10).

Species numbers are given in brackets.

For abbreviations see table 3.

	fod/v	bb+pd/v	p/v	pa/p
Caucasian genera (6)	2.0-2.3	2.9-5.3	1.0-1.5	0.3-0.6
<i>Laciniaria</i> (3)	0.8-2.2	2.0-4.6	0.6-0.8	0.3-0.6
<i>Alinda</i> (4)	1.0-1.6	2.4-3.2	0.6-1.0	0.4-0.6
<i>Pseudalinda</i> (4)	0.7-1.2	2.1-3.2	0.6-0.9	0.5-0.7
<i>Strigillaria</i> (10)	0.9-4.1	1.9-8.9	0.6-2.6	0.2-0.6
<i>Vestia</i> (4)	1.3--3.2	2.9-8.5	0.8-1.4	0.2-0.4
<i>Pavlovicia</i> (2)	1.0, 1.7	2.6, 3.7	0.6, 0.9	0.3, 0.4
<i>Balea</i> (4)	1.3-1.8	1.9-3.4	0.6-1.1	0.5-0.7

As demonstrated by the values given in the table the length ratios of the genera of Baleini do not much differ. This is a remarkable difference to the related Clausiliini.

Some species of *Strigillaria* exhibit a shorter vagina and longer penis than the others. In *Vestia* the vagina is on average shorter; the values of the related genus *Pavlovicia*, however, are like those of the other genera. The relative lengths of the vagina of the Caucasian genera are similar to that of *Vestia*.

The male copulatory organs of the Baleini exhibit non-measurable characters (1973, 1977), which are probably autapomorphies of evolutionary lineages, e. g., the absence of a delimited proximal part of penis in *Strigillaria* and the presence of a penial papilla in *Balea* (see Fig. 2).

In the Baleini non-measurable characters of the copulatory organs are more useful to recognize evolutionary lineages than measurable ones.

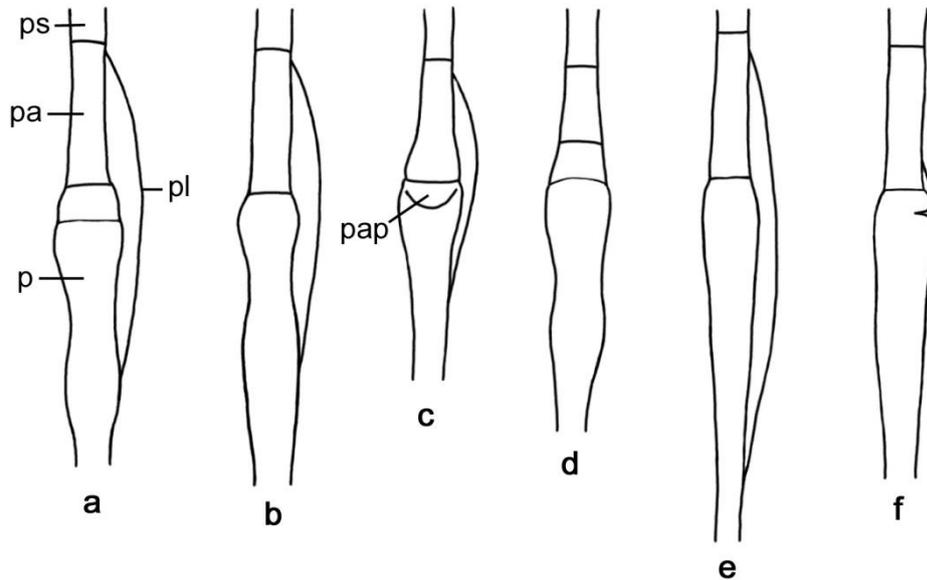


Fig. 2. Male copulatory organs of Baleini genera (schematized).

a *Alinda*.

b *Laciniaria*.

c *Balea*.

d *Vestia* (V.).

e *Strigillaria* (S.).

f *Strigillaria* (Bulgarica).

Abbreviations used: p = penis, pa = parepiphallus, pap = penial papilla, pl = penial ligament(s), ps = pseudoeipiphallus.

References

(1963): Zur Anatomie und Systematik der Clausilien, I. – Archiv für Molluskenkunde, **92** (3/4): 81-115.

(1966): Zur Anatomie und Systematik der Clausilien, III. *Clausilia whateliana* und ihre Beziehungen zu den übrigen *Clausilia*-Arten, besonders zum Subgenus *Neostyriaca*. – Archiv für Molluskenkunde, **95** (1/2): 19-47.

(1969a): Zur Anatomie und Systematik der Clausilien, V. Genitalsystem und Systematik des Genus *Cochlodina*. – Archiv für Molluskenkunde, **99** (3/4): 107-132.

(1969b): Zur Anatomie und Systematik der Clausilien, VI. Genitalsystem und Systematik der Clausiliidae, besonders der Unterfamilie Aloiinae. – Archiv für Molluskenkunde, **99** (5/6): 247-265.

(1973): Zur Anatomie und Systematik der Clausilien, XIII. Neue Balkan-Formen der Mentissoideinae und Baleinae (mit taxonomischer Revision der zugehörigen Gruppen). – Archiv für Molluskenkunde, **103** (4/6): 179-208, pls. 6-7, 7a.

(1977): Zur Anatomie und Systematik der Clausilien, XVIII. Neue Taxa rezenter Clausilien. – Archiv für Molluskenkunde, **108** (1/3): 73-107, pls. 3-5.

(2007a): Worldwide Door Snails (Clausiliidae), recent and fossil. – 214 pp., 20 pls. Hackenheim (ConchBooks).

(2007b): *Cochlodina laminata* (MONTAGU 1803) – polytypic in genital morphology (Gastropoda: Stylommatophora: Clausiliidae). – Mitteilungen der deutschen malakozoologischen Gesellschaft, **77/78**: 23-25.