

Testacella haliotidea Draparnaud, 1801 in The Netherlands (Gastropoda Pulmonata, Testacellidae)

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This is the first formal report of the occurrence of a *Testacella* species in The Netherlands. In 2010 at least 20 specimens of *Testacella haliotidea* were discovered in a garden near Middelburg, Prov. of Zeeland, ranging from small juveniles to adults, indicating the presence of a reproducing population. In the collection of the Netherlands Centre for Biodiversity Naturalis, Leiden (RMNH) are also four samples from various parts of the country, collected between 1961 and 1988, which were never published. A single shell probably belonging to this species was found in the province of Limburg in 2009. *Testacella haliotidea* is probably an incidentally introduced species that can reproduce and establish temporary populations. However, it may be overlooked due to its subterranean habits. The external appearance, radula and genitalia of Dutch specimens are described. Genitalia of specimens attributed to *T. haliotidea* in the literature vary considerably, and suggest the presence of more than one species. Sequences ('barcodes') of the Cytochrome oxidase subunit 1 gene (CO1) are provided of three recently collected specimens.

Keywords: Gastropoda, Testacellidae, distribution, taxonomy, The Netherlands, genital anatomy, radula, CO1 barcode.

INTRODUCTION

Representatives of the earthworm-eating slug family Testacellidae are not often reported, undoubtedly due to their subterranean and nocturnal behaviour (Quick, 1960; Barker, 1979). On 28 September 2010 the second author discovered a slug in a garden in the village of Nieuw en Sint-Joosland near Middelburg (Province of Zeeland) which he had never seen before. It soon became clear that this concerned a species of *Testacella*, which seemed to constitute the first Dutch record of the land slug family Testacellidae. In the course of October and November additional specimens were found.

The first author tentatively identified the slug as *T. haliotidea* Draparnaud, 1801, on the basis of the external characters provided by Kerney & Cameron (1979). He had found an empty shell of a *Testacella* species a few years earlier and knew of additional Dutch samples of the same or a similar species in the collection of NCB Naturalis (formerly Rijksmuseum van Natuurlijke Historie, Leiden [RMNH]), which apparently had never been published. Specimens of various samples were dissected and all Dutch specimens appeared to belong to the same species. The genital morphology was compared to descriptions in the

literature, which more or less confirmed the external identification. However, study of the literature revealed considerable variability in genitalia of specimens attributed to *T. haliotidea*.

The morphology of Dutch specimens is concisely described, and the status of the species in the Dutch fauna is discussed. In addition, the remarkable variability of the genitalia reported for *T. haliotidea* in the literature is discussed. Since the possibility of cryptic species cannot be excluded, we decided to provide the base-pair sequence of the Cytochrome oxidase subunit 1 gene (CO1) as 'barcode'.

MATERIAL & METHODS

The following Dutch *Testacella* records are now known (Fig. 1):

- Prov. of Zeeland, Walcheren, Nieuw en Sint-Joosland near Middelburg, in garden; September-October 2010; F.A.D. van Nieulande leg. In the autumn of 2010 about 20 specimens were seen, ranging between ca. 12 and 55 mm in (extended) length; some animals were also spotted in a neighbouring garden. Specimens were again observed in February 2011. Apparently this concerns an established reproducing population. Specimens are deposited in the collection of NCB Naturalis in Leiden (RMNH.MOL.128804/3) and in the collection of the "Koninklijk Zeeuws Genootschap der Wetenschappen" (Middelburg KZGW coll. Nr. NHG04-1500); most captured specimens were released.
- Prov. of Limburg, a single shell probably belonging to *T. haliotidea* among debris close to a brook (Voer) near Withuis, Eijsden, S. of Maastricht; 29.viii.2009; A.J. de Winter leg. (RMNH. MOL.129113).
- Prov. of Zuid-Holland, Boskoop; November 1988; 1 specimen "imported with Bonsai trees from China". Plantenziektenkundige Dienst (PD) Wageningen leg. (RMNH. MOL.129113).
- Prov. of Noord-Holland, Aalsmeer; 28.i.1968; F.E. Loosjes leg.; 9 specimens "possibly from a greenhouse" (RMNH.MOL.8264).
- Prov. of Gelderland, Nijmegen, Oude Nonnendaalseweg; viii.1965; PD Wageningen leg.; 4 specimens (RMNH.MOL.6737).



Fig. 1. Distribution map of *Testacella haliotidea* in The Netherlands. Dots, live collected specimens; triangle, empty shell.

- Prov. of Zuid-Holland, Voorschoten, in greenhouse; ii.1961; C. Koudijs leg.; 2 adult specimens (RMNH.MOL.5387).

Of three specimens from Nieuw en Sint-Joosland foot tissue samples were used to extract DNA with the DNeasy Blood & Tissue Kit (Qiagen). Elution of the DNA was performed with 75 µl elution buffer instead of 200 µl as described in the protocol to increase the final DNA concentration. The primer sets published by Folmer et al. (1994) were used to amplify the mitochondrial barcoding marker CO-I. The PCR reaction mixtures contained: 2.5 µl PCR buffer, 0.5 µl DNTP's, 1.0 µl of each primer, 0.3 µl Taq and 18.7 µl MilliQ. To each reaction mixture 1 µl DNA extract

was added as template. Each PCR cycle consisted of 94°C for five seconds (denaturation), 50°C for one minute (annealing), and 72°C for one minute (extension). Each cycle was repeated 39 times. Sequencing was performed on an Automatic Sequencer 3730xl by MacroGen, Amsterdam. The raw sequence data were assembled and edited using Sequencher 4.2 (Gene Codes Corporation®) and aligned with ClustalX.

DESCRIPTION OF DUTCH SPECIMENS

External appearance (Figs 2A-D).— Live animals up to c. 55 mm when extended, and 40 mm in alc. 70%. Animals dirty-white or pale yellowish with brown or greyish blotches and dots. Sole whitish, occasionally with pale yellow blotches. Lateral grooves on the body are just separate at the junction with the shell.

Shell (Figs 3-4).— Shell of largest specimen ca. 6.4 × 4.2 mm, elongate triangular, with about one whorl.

Radula (Figs 5-7).— Radulae from two specimens (from Nieuw en Sint-Joosland and Voorschoten) were examined. There is no central tooth; in half a row there are 18 or 19 teeth gradually enlarging towards the outer edge of the row, but the last marginal tooth is clearly shorter than the penultimate one. In one specimen there is an even smaller, almost vestigial, outermost tooth (Figs 6-7).

Genitalia (Figs 8-11).— Six specimens from four Dutch localities were dissected. These vary in size and development of the genitalia, but all possess a long and slender, muscular flagellum on which apically a long, narrow penial retractor muscle inserts. The vas deferens enters the male organ proximally of a short penial caecum, leaving a distinct 'epiphallus' (see below). On cross-section, the 'epiphallus' can be seen to embrace two tubes within a common muscular envelope: the flagellum with its lumen invaginated by four major and three minor longitudinal ridges, and the oval

Fig. 2. *Testacella haliotideae* from Nieuw en Sint-Joosland. A, B, juvenile specimen (scale bar 10 mm); C, specimen attacking earthworm. Photographs Freddy van Nieulande.





Fig. 3. Different views of *Testacella haliotideae* shell found at Witmond (scale bar 1 mm).

14

vas deferens. All specimens possess a penial caecum, and show at least traces of a second widening at the same level opposite the penial caecum. The vagina is about as long as the penis, and about as long as the bursal duct. The bursal duct is wide and swollen, wider than the vagina. In mature specimens the bursa lies embedded in the bulky albumen gland. The vas deferens is relatively straight and follows the penio-vaginal angle attached by tissue strands; it is shorter (0.6-0.9 times) than the length of penis and flagellum together. The hermaphrodite duct is convoluted, but the tightness of coiling varies between specimens. The talon is not exposed.

Molecular data. — Tissue samples from three specimens from Nieuw en Sint-Joosland, yielded identical partial (688bp) COI sequences. The sequences are deposited in GenBank, accession numbers JF905694 — JF905696. A blast search revealed the specimens to best resemble the otherwise unrelated pulmonate gastropod *Partula*, but there was no close match.



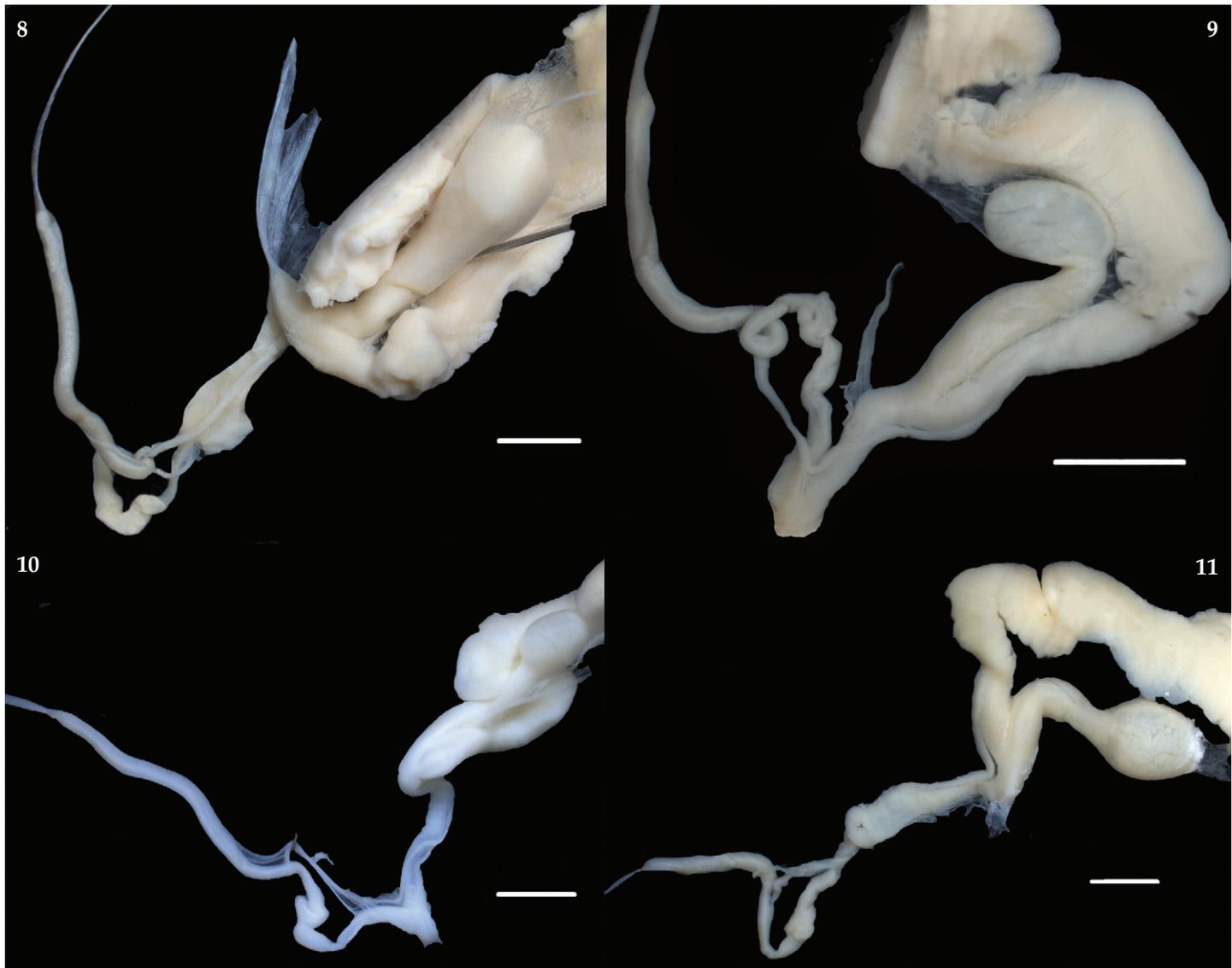
Fig. 4. Posterior portion of live specimen (Nieuw en Sint-Joosland). Photograph Freddy van Nieulande.



It is uncertain how many extant species the genus *Testacella* comprises. Three species are frequently recorded, *T. maugei* Férussac, 1819, *T. scutulium* Sowerby, 1820, and *T. haliotidea* Draparnaud, 1801 (Quick, 1960; Kerney & Cameron, 1979; Kerney et al., 1999). *Testacella maugei* can be easily distinguished externally. The other two species have been confused in the past, and even in the recent literature (Kerney, 1999) doubt was expressed as to their specific distinctiveness, although Quick (1960) had described diagnostic characters for each of the three British species. The status of *T. bisulcata* Risso, 1819, described from Nice (southern France), remains unclear. It was considered a valid species by authors like Plate (1891), Hoffmann (1925) and Falkner et al. (2002) but apparently not by Kerney et al. (1999). Giusti et al. (1995) suggested *T. bisulcata* to be a synonym of *T. scutulium*. Some distinctive species occur on Sardinia, on Malta and in Northwest Africa (Giusti et al., 1995), and there are many more nominal species (see e.g. Hoffmann, 1925; Rinaldi, 2003) which have mostly been considered synonyms of either *T. haliotidea* or *T. scutulium*, sometimes on the basis of little evidence.

Dutch specimens can be readily distinguished from *T. maugei* by the comparatively small, triangular shell. Based on Kerney & Cameron (1979), they differ from *T. scutulium* by the two lateral grooves on the body being separate at the junction with the shell (Fig. 2), leaving *T. haliotidea* as a likely identification. All Dutch specimens possess a long flagellum (Figs 8-11), which according to most literature sources is characteristic for *T. haliotidea* (Webb, 1897; Taylor, 1907; Hoffmann, 1925; Quick, 1960; Giusti et al., 1995), thus confirming the external identification.

Figs 5-7. Radulae of *Testacella haliotidea*. 5, specimen from Voorschoten, half a row, outermost marginals missing; 6-7, specimen from Nieuw en Sint-Joosland; 6, lateral and marginal teeth; 7, last marginals.



Figs 8-11. Distal genitalia of Dutch *Testacella haliotideae*. 8, Voorschoten; 9, Boskoop (allegedly imported from China); 10, semi-adult, Nieuw en Sint-Joosland; 11, Nijmegen. Scale bars 2 mm.

DISCUSSION

Faunal status.— The genus *Testacella* Cuvier, 1800, is known from the Canary Islands, Madeira and the Azores, southern

and western Europe (Portugal, Spain, France, Italy, various central and western Mediterranean islands, Great Britain and Ireland), and North-west Africa. Some records exist from Denmark, North and Central Germany, Belgium and

Switzerland (Gerber & Heins, 1991; Giusti et al., 1995; Turner et al., 1998; Rinaldi, 2003). Two *Testacella* species have been reported from outside their Palaearctic range: *T. maugei* from South Africa (Watson, 1915; Herbert, 2010) and North America (Quick, 1960), and *T. haliotidea* from the USA (California: Hanna, 1966; Mc Donnell et al, 2009), Canada (Forsyth, 2004), Australia (Smith, 1992) and New Zealand (Barker, 1979). Probably these species were transported with soil or pot plant material (Rinaldi, 2003). *Testacella* species have not been reported from The Netherlands before.

The status of *T. haliotidea* in Northwest-Europe is controversial. There is even discussion as to its indigenous status in the UK and Ireland where the species has been known since 1834 (Quick, 1960). According to Kerney (1999) all three *Testacella* species are probably introduced in Great Britain and Ireland, since their occurrence is largely confined to gardens and parks. Gerber & Heinz (1991) consider the German records as accidental introductions of a non-indigenous species. In Switzerland this species is almost exclusively known from man-made habitats (Turner et al., 1998). However, Rinaldi (2003) considers *T. haliotidea* as “probably autochthonous” in Belgium, Switzerland and France.

According to Rinaldi (2003) *T. haliotidea* is “certainly present” in Belgium, but proof of recent presence there as yet remains to be published. Taylor (1907, Fig. 19) provides a Belgian locality, “in gardens at Fonds-de Lefte, near Dinant”, and according to Van Goethem (1987) it is very likely that a *Testacella* species, possibly *T. haliotidea*, has been found in Belgium in the past. The locality where a fresh shell was found in 2008 (Withuis, Limburg) is close to the Belgian border.

Most Dutch material was collected by the Dutch Plant Protection Service (PD, Plantenziektenkundige Dienst, Wageningen). Some records are from greenhouses. Therefore the findings in the period 1961-1988 were probably considered accidental exotic introductions (e.g. the alleged import from China) or greenhouse aliens not worth publishing. However, the number of specimens and the large size variation in some samples suggest that these were actually reproducing populations, and this certainly holds for the population discovered in 2010 near Middelburg. As yet its

faunal status appears to be that of an incidentally introduced species that can reproduce and establish temporary populations (status 2c of the “Het Nederlands Soortenregister”, see <http://www.nederlandsesoorten.nl/nlsr/nlsr>). However, it cannot be ruled out that it is a more regularly occurring species (status 2b), overlooked due to its subterranean habits, as perhaps the recent finding of a shell suggests.

In view of its present non-autochthonous status, conservation measures are as yet not required, although records of *Testacella* species seem to be declining in the UK and Switzerland (Rinaldi, 2003 and references therein).

Comparison with descriptions in literature. — Dutch specimens seem to be smaller than described for *T. haliotidea* by e.g. Quick (1960) and Kerney & Cameron (1979), who characterize the species as a “large slug” with an extended length of 8-12 cm. Some reports (e.g. Gassies & Fischer, 1856; Hoffmann, 1925; Chemin, 1938) give smaller body sizes for adult specimens however, and the size indicated by Quick (1960) may be uncritically copied in later papers. The small size of Dutch specimens might also be due to recent introduction. Chemin (1939) described a specimen that hatched mid-July, and already produced eggs by the end of March in the next year before having attained its adult size (which according to Chemin, 1938 is at about 5 cm). *Testacella* species are known to be long-lived (six years, Heller, 1990), and growth probably continues after sexual maturity has been reached, like in some fully-shelled land snails, e.g. Achatinidae and Subulinidae.

The size at which animals become sexually mature seems to vary; some alcohol-preserved specimens of 25 mm already possess developed genitalia, whilst one of the recently collected larger specimens (c. 50 mm alive, 30 mm in alc. 70%) had very tiny, barely visible genitalia. The latter was killed in early December. A clearly smaller specimen from the same locality, but killed in February had its genitalia significantly more developed (Fig. 10), suggestive of a seasonal influence. According to Chemin (1939) there are distinct periods of egg-laying activity, one starting early spring, other in early summer (June), and probably a third early autumn.

The radulae examined differ slightly from those described by Taylor (1907) and Quick (1960). The last marginal tooth seems smaller, and one specimen had 19 teeth in half a row, instead of 18 found by Quick and Taylor. However, *Testacella* radulae are little studied and may be more variable than appears from the literature. For example, Crampton's (1975) thorough study reported a significantly larger number of teeth in *T. maugei* than indicated by Quick (1960).

The variability in the genitalia of dissected Dutch specimens is small, especially when all literature reports of

T. haliotideae (or to species later placed in the synonymy of *T. haliotideae*) are taken into account. Dutch specimens best resemble specimens described by Giusti et al. (1995, see Fig. 12A), Taylor (1907, see Fig. 12B) and Webb (1897, see Fig. 12D). Webb (1897) carefully described the anatomy of *T. haliotideae* based on dissection of "very many specimens", and he also noticed and discussed the variability reported in the literature of his days. Webb's paper seems to have been fallen in oblivion, although it represents one of the few accurate descriptions of the genital anatomy of *Testacella* species.

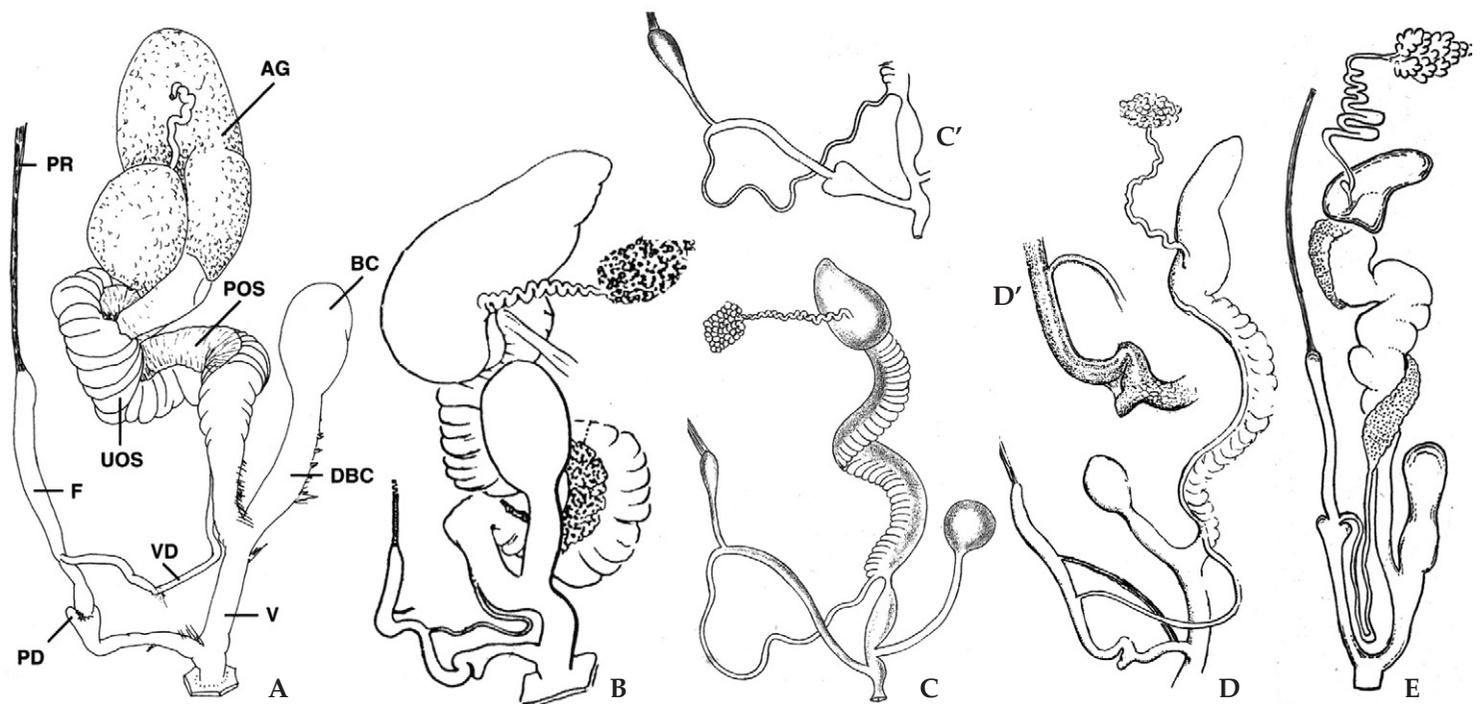
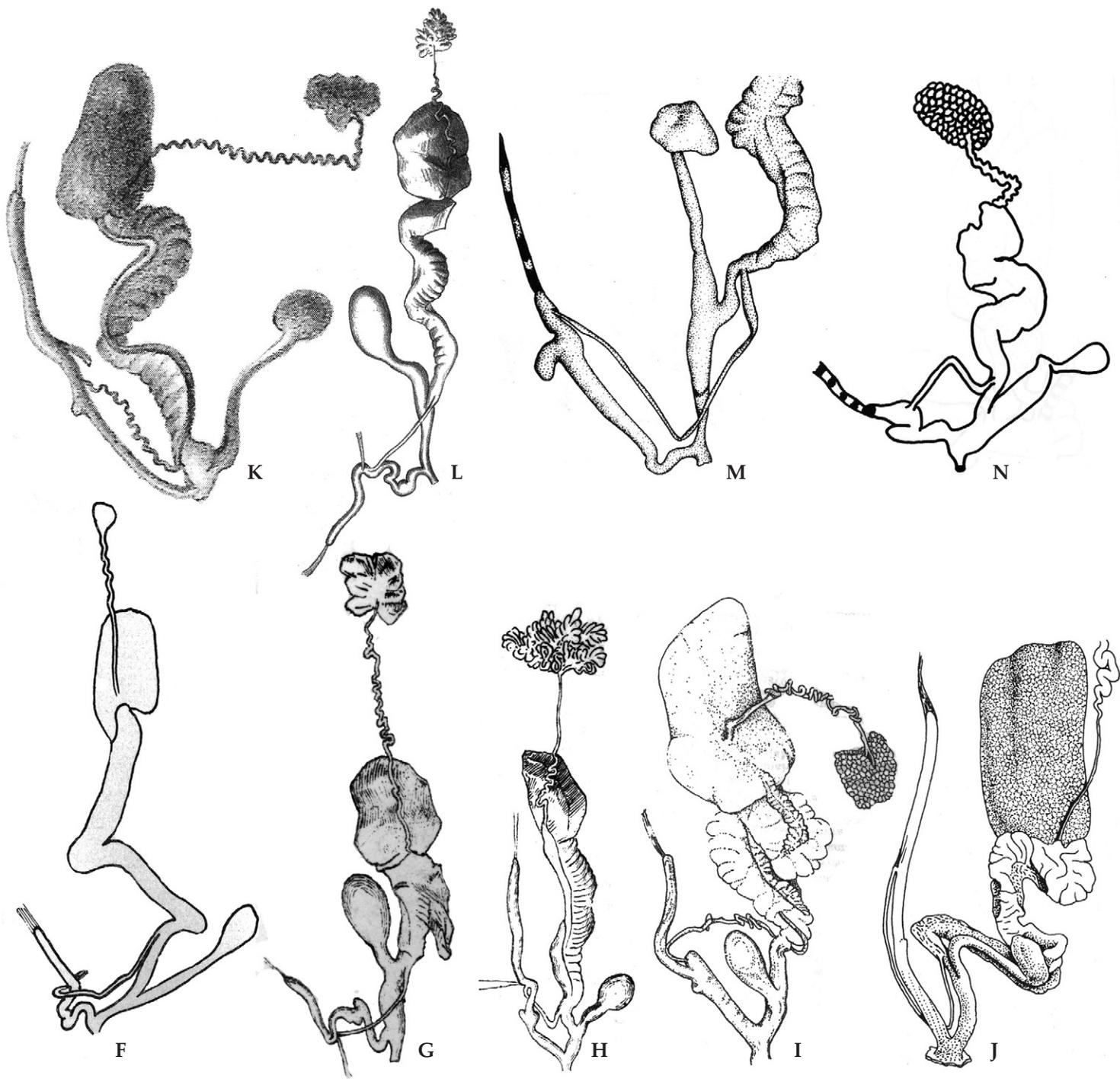


Fig. 12. A-N (above and right). Genitalia illustrations attributed to *Testacella haliotideae*. Orientation of some drawings has been rearranged to facilitate comparison. Illustrations are not comparable in size. **A**, modified from Giusti et al., 1995: Germany, Frankfurt am Main; abbreviations: AG, albumen gland; BC, bursa copulatrix; DBC, bursal duct; F, flagellum; POS, prostate; UOS, spermoviduct; P, penis; PD, penial caecum; PR, penial retractor muscle; V, vagina; VD, vas deferens. **B**, modified from Taylor, 1907: UK, Horsham. **C-C'**, modified from Collinge, 1893: UK. **D-D'**, modified from Webb, 1897: UK. **E**, modified from Quick, 1960: UK. **F**, modified from Hoffmann, 1925: NE Spain. **G**, modified from Pollonera, 1888: Italy, near Torino. **H**, modified from Pollonera, 1888: Italy, near Torino (type of *T. dubia* Pollonera). **I**, modified from Barker, 1979: New Zealand. **J**, modified from Schileyko, 2000: "Mediterranean" region. **K**, modified from Gassies & Fischer, 1856: France? (as *T. maugei*). **L**, modified from Pollonera, 1889: Spain, Barcelona (type of *T. barcinonensis* Pollonera). **M**, modified from Castillejo, 1998: (presumably) Spain. **N**, modified from Borreda et al., 1990: Spain, Valencia.



Most authors agree that *T. haliotidea* is characterized by a long, slender flagellum and a short penial caecum (e.g. Webb, 1897; Hoffmann, 1925, see Fig. 12F); Quick, 1960, see Fig. 12E; Giusti et al., 1995). All Dutch examined specimens exhibit these features. Some authors do not report a penial caecum, in particular Lacaze-Duthiers (1887, pl. 36, fig. 63) and Collinge (1893, see Fig. 12C). Both these authors also depict the flagellum with a swollen apex, as well as a spherical rather than oval bursa and a long, narrow bursa duct. Webb (1897) discussed these character states which were unknown to him, and cautiously concluded that “..there being a form of *Testacella* ..which differs from the more generally distributed *T. haliotidea* in some important particulars which may turn out to be of specific value”. The specimen illustrated by Schileyko (2000, see Fig. 12J) too has a long, slender bursa duct, but does seem to possess a minute penial caecum.

The variation reported in the flagellum length relative to other male organ parts is large. Quick (1960) and Castillego (1998) mentioned the presence of variation in this character, but it is unclear whether they only referred to reports by other authors. Two reports on Spanish specimens depict the flagellum as extremely short (Figs 12M, N). In some other populations (Figs 12B-D) the flagellum length seems to be proportionally short, but not nearly as extreme. According to Webb (1897, see Fig. 12D') the vas deferens runs from the point of entrance parallel and closely attached to the flagellum within a common envelope towards the upper penis opposite the caecum. Giusti et al. (1995) also appear to consider the portion between the penial caecum and the entrance of the vas deferens as part of the flagellum, whereas other authors used the term epiphallus for this section. The situation where the vas deferens enters at or very close to the penial apex has been reported in a few studies only (Quick, 1960; Barker, 1979, reproduced in Fig. 12I), and was apparently unknown to Webb (1897). As yet too few specimens have been studied to determine whether the entrance site of the vas deferens varies within or between populations. It might be the extreme of a continuous variation, or a polymorphy.

Related to this phenomenon is the presence of a distinct second dilatation at the upper penis junction in many speci-

mens (clearly present in Figs 8-11, 12C', E, H-I). According to Webb (1897, see Fig. 12D'), this swelling (“the elbow”) is caused by a sharp bend of the flagellum and the parallel vas deferens. Some studies indicate a weakly developed dilatation, or even complete absence (Fig. 12C, J).

There is also considerable variation in length and coiling of the vas deferens. In two reports (Gassies & Fischer, 1856; Barker, 1979) the vas deferens is convoluted, in most others it is relatively straight, like in the Dutch specimens. The variation in length correlates partly with significant variation in length of vagina and/or free oviduct.

For the time being we consider the Dutch specimens, as well as the ones illustrated by Quick (1960), Pollonera (1889), Hoffmann (1925), Giusti et al. (1995), Taylor (1907), and others with a long flagellum with apically a penial retractor and a penial caecum as a single variable species. The genitalia of Spanish specimens referred to as *T. haliotidea* by Castillego (1998, see Fig. 12M) and Borreda et al. (1990, see Fig. 12N) appear to deviate significantly and quite possibly belong to another species. Specimens of *T. haliotidea* with more typical genitalia also occur in Spain (Pollonera, 1888, 1889 [partly as *T. barcinonensis* and *T. dubia*, see Figs 12L and 12G, respectively]); Hoffmann, 1925; Bech, 1990). The status of the specimens described by Lacaze-Duthiers (1887) and Collinge (1893), of which the attribution to *T. haliotidea* was questioned by Webb (1897), remains unclear. An analysis of the genital morphology over a wider geographic range remains a desideratum, especially when combined with molecular data.

The genitalia of Dutch specimens are not very variable and especially resemble the German specimen illustrated by Giusti et al. (1995). Chemin (1939) described the incidence of self-fertilization in isolated *T. haliotidea*. This could be relevant in explaining the limited variability in morphological characters observed in some areas as well as the considerable between-population variability described. Single self-fertilizing specimens may be founders of populations of which genes coding for morphological traits are not freely exchanged with other populations, especially in areas where the species' presence depends on incidental introductions. Morphological characteristics of populations might then be signatures of their origin.

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REFERENCES

- BARKER, G. M., 1979. The introduced slugs of New Zealand (Gastropoda: Pulmonata). — *New Zealand Journal of Zoology* 6: 411-437.
- BECH, M., 1990. Fauna malacologica de Catalunya. Molluscs terrestres i d'aigua dolça. — *Treballs de la Institució Catalana d'Història Natural* 12: 1-229.
- BORREDA, V., COLLADO, M.A. & ROBLES, F., 1990. Pulmonados desnudos de la provincia de Valencia. — *Iberus* 9: 293-317.
- CASTILLEGU, J., 1998. Guia de las babosas Ibericas: 1-154. Real Academia Galega de Ciencias, Santiago de Compostela.
- CHEMIN, E., 1938. Observations sur la Testacelle: *Testacella europea* Roissy = *T. haliotidea* Drap. — *Travaux de la Station Zoologique de Wimereux* 13 (Volume Jubilaire dédiée a Maurice Caullery): 77-85, pl. II.
- CHEMIN, E., 1939. L'autofécondation chez *Testacella europea* Roissy = *T. haliotidea* Drap. — *Comptes Rendus des séances de la Société Biologie et de ses filiales Paris* 132 (24): 249-252.
- COLLINGE, W.E., 1893. The morphology of the generative system in the genus *Testacella*. — *Annals and Magazine of Natural History* (6) 12: 21-25, pl. 3.
- CRAMPTON, D.M. 1975. The anatomy and method of functioning of the buccal mass of *Testacella maugei* Férussac. — *Proceedings of the Malacological Society of London* 41: 549-570.
- FALKNER, G., RIPKEN, T.E.J. & FALKNER, M., 2002. Mollusques continentaux de France: Liste de référence annotée et bibliographie. — *Patri-moines naturels* 52: 1-350. Muséum National d'Histoire Naturelle, Paris.
- FOLMER, O., BLACK, M., HOEH, W., LUTZ, R. & VRIJENHOEK, R., 1994. DNA primers for amplification of mitochondrial cytochrome oxidase subunit I from diverse metazoan invertebrates. — *Molecular Marine Biology and Biotechnology* 3: 294-299.
- FORSYTH, R. G., 2004. Land snails of British Columbia: 1-188, Royal British Columbia Museum, Victoria.
- GASSIES, J.-B. & FISCHER, P., 1856. Monographie du genre Testacelle: 1-56, pl. 1. Paris.
- GIUSTI, F., MANGANELLI, G. & SCHEMBRI, P.J., 1995. The non-marine molluscs of the Maltese Islands. — *Monografie Museo Regionale di Scienze Naturali Torino* 15: 1-607.
- HANNA, G.D., 1966. Introduced mollusks of western North America. — *Occasional Papers of the California Academy of Sciences* 48: 35-66.
- HELLER, J., 1990. Longevity in molluscs. — *Malacologia* 31: 259-295.
- HERBERT, D.G., 2010. The introduced terrestrial Mollusca of South Africa. — *SANBI Biodiversity Series* 15: 1-108. Pretoria.
- HOFFMANN, H., 1925. Zur Kenntnis der Testacellen. — *Archiv für Molluskenkunde* 57: 171-211.
- KERNEY, M., 1999. Atlas to the land and freshwater molluscs of Britain and Ireland: 1-264. Harley Books, Colchester.
- KERNEY, M.P. & CAMERON, R.A.D., 1979. A field guide to the land snails of Britain and north-west Europe: 1-288. Collins, London.
- KERNEY, M.P. & CAMERON, R.A.D. & BERTRAND, A., 1999. Guide des escargots et limaces d'Europe: 1-370. Delachaux et Nestlé, Lausanne-Paris.
- LACAZE-DUTHIERS, H. DE, 1887. Histoire de la Testacelle. — *Archives de Zoologie Expérimentale et Générale* (2) 5: 459-596, pls 29-40.
- MC DONNELL, R.J., PAINE, T.D. & GORMALLY, M.J., 2009. A guide to the invasive and native slugs. — *Fauna of California Publication* 8336, available at <http://ucanr.org/freepubs/docs/8336.pdf>
- PLATE, L., 1891. Studien über opisthopneumone Lungenschnecken. I. Die Anatomie der Gattungen *Daudebardia* und *Testacella*. — *Zoologische Jahrbücher, Abtheilung für Anatomie und Ontogenie der Thiere* 4: 505-630, pls 32-35.
- POLLONERA, C., 1888. Appunti di malacologia I. Di alcune Testacelle raccolte presso Torino. — *Bolletino Musei di Zoologia ed Anatomia Comparata della R. Università di Torino* (3) 43: 1-10, pl. 2.
- POLLONERA, C., 1889. Osservazioni intorno ad alcune specie di *Testacella*. — *Bolletino Musei di Zoologia ed Anatomia Comparata della R. Università di Torino* (4) 57: 6 pp, 1 pl.
- QUICK, H.E., 1960. British slugs. — *Bulletin of the British Museum (Natural History) Zoology* 6 (3): 106-225, pls 1-2.
- RINALDI, A.C., 2003. Notes on *Testacella* Cuvier, 1800 (Gastropoda, Pulmonata, Testacellidae). — *La Conchiglia* 35 (309): 47-54.
- SCHILEYKO, A.A., 2000. Treatise on Recent terrestrial pulmonate molluscs. Part 6: Rhytididae, Chlamydephoridae, Systrophiiidae, Haplotrematidae, Streptaxidae, Spiraxidae, Oleacinidae, Testacellidae. — *Ruthenica Supplement* 2: 731-880.
- SMITH, B.J., 1992. Non-marine Mollusca. — *Zoological Catalogue of Aus-*

tralia 8: i-xi, 1-398.

- TAYLOR, J.W., 1907. Monograph of the land and freshwater Mollusca of the British isles. vol. 2. Testacellidae, Limacidae, Arionidae: 1-312. Leeds.
- TURNER, H, KUIPER, J.G.J., THEW, N., BERNASCONI, R., RÜETSCHI, J., WÜTRICH, M. & GOSTELI, M., 1998. Fauna Helvetica 2. Atlas der Mollusken der Schweiz und Lichtensteins: 1-527. Neuchâtel.
- VAN GOETHEM, J.L., 1987. Nieuwe naamlijst met aantekeningen van de recente niet-mariene weekdieren van België. — Studiedocumenten Koninklijk Belgisch Instituut voor Natuurwetenschappen 44: 1-65.
- WATSON, H., 1915. Studies on the carnivorous slugs of South Africa. — Annals of the Natal Museum 3 (2): 107-267.
- WEBB, W.M., 1893. The British species of *Testacella*. — The Journal of Malacology 6: 49-56, pl. 1.