On the Taxonomy of the Family Tritoniidae

(Mollusca : Opisthobranchia)

BY

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Since my systematic survey of the "Nudibranchia Dendronotacea" was published in 1936, a great many taxonomic novelties have appeared. It is necessary to undertake some revision of this part of the opisthobranch mollusks: above all, the family Tritoniidae seems to be in urgent need of revision. In 1936 I used for this family the name Duvaucceliidae, following the opinion of IREDALE & O'DONOGHUE (1923). These authors claimed priority for the genus name *Duvaucelia* RISSO, 1826 (not RISSO 1818, as given by some authors) over *Tritonia* CUVIER, 1797, an opinion that must be changed (*cf.* PRUVOT-FOL, 1931; 1954, p. 346). Most importantly, it has seemed necessary to restore the genus names to their respective types. In some instances, too, changes of nomenclature and relations have to be adopted. Thus it may be remarked here that BERGH established in 1907 a genus *Tritonidoxa* which was omitted - while awaiting additional material or reports - from my work of 1936. In 1926, however, I did mention this genus and said about it (ODHNER, 1926 b, p. 32):

> "Freilich ist die Anwesenheit von Kiemen eine für Duvaucceliidae mit Ausnahme von *Tritoniella* charakteristische Regel, ohne Ausnahmen ist sie jedoch nicht. So beschreibt BERGH 1884 (Malac. Unters. XV, S. 726) ein Exemplar von *Tritoniopsis tetraquetra,* von dem er sagt: 'Am Rückenrand fehlten Kiemen fast ganz (abgerieben?), und DALL behauptet, aber kaum richtig, dass solche auch im Leben fehlen.' (In der Regel hat diese Art aber Kiemen, vgl. O'DONOGHUE 1922.) Dies zeigt, dass es kaum berechtigt ist, wenn BERGH 1907 die Abwesenheit von Kiemen in *T. capensis* für einen hinreichenden Grund hält, für diese Art eine besondere Gattung, *Tritonidoxa,* zu schaffen. Dieser negative Charakter ist umsomehr hinfällig, als alle positiven Charaktere der Art *Tritonia*-artig sind, so vor allem Kiefer und Radula, und ich füge daher die Art in jene Gattung ein." *Tritonidoxa,* however, may be a distinct subgenus characterized by a flagelloid penis, as BERGH himself stated in the description of the species.

In my work of 1939, however, I revived, following PRUVOT-FOL (1931) and WINCKWORTH (1932), the genus name *Tritonia* for the large species *T. hombergi* CUVIER, 1797 (type) and *T. griegi* ODHNER, 1922 - further described and figured, as to morphology of genital organs, by me in 1926 [a], when it turned out that *T. griegi* belongs to the subgenus *Tritonidoxa* because of a flagelliform male organ. I also pointed out that the large forms of *Tritonia* differ in anatomy and even in external characters from the small ones to which the genus name *Duvaucelia* should be restricted, inasmuch as *Tritonia,* just as also *Tritoniella* and *Tritoniopsis,* has the site of the anus in or behind the middle of the body, while in *Duvaucelia* the anus is situated much farther towards the front on the right side [b].

Some other differences between *Tritonia* and *Duvaucelia* are found in the number of radular teeth, which is smaller in the small species (*Duvaucelia*); but in general appearance of the teeth the two genera agree. The just mentioned two genera *Tritonia* and *Duvaucelia* are examples of the two trends of development followed by the members of the family Tritoniidae, namely the one pointed out by me in 1936 as starting from the already begun detorsion in the large species of opisthobranchs. I said in that work (ODHNER, 1936, p. 1075):

> "The primitive condition in the nudibranchs is, as mentioned above, that the liver originates at the larval stage as two distinct masses, one on each side of the stomach. In their phylogeny, however, the nudibranchs are supposed to have passed a process of detorsion. This, of course, was preceded by the torsion common to all gastropods. We may assume that the liver was made the subject of these processes in such a way that its original bipartition was obliterated by the earlier torsion, which made these portions fuse intimately with each other, whereas the detorsion activated the tendency to separate them anew. Where the detorsion

[a] Detailed descriptions of these organs given by THOMPSON (1961).

[b] In 1932 I referred *Tritoniopsis plebeia* to *Duvaucelia,* but its position is more correct in *Tritonia* and it forms, indeed, a subgenus of its own, *Candiella,* to which it has now been restored. *Candellista,* on the other hand, is a synonym of *Tritonia* (in its restricted sense, *cf.* below).

has not been completed, as in the primitive opisthobranchs and even the Pleurobranchacea, the root of the nudibranchs, the liver still keeps this unity. According to this view we have to consider those forms of Duvauceliidae as the primitive ones, in which the liver remains a single mass composed by the fused right and left portions. To this section all genera belong except *Marionia* which shows a complete bipartition, inasmuch as its right liver is a distinct mass of its own. Just its position proves that the detorsion is less perfect, because in *Marionia* the right liver lies at the right side of the stomach, below the intestine, and debouches in the anterior stomach wall, whereas in *Duvaucelia* its position is to the left, on the upper side of the stomach and its mouth more medially; so in *Tritoniella,* too (*cf.* Odhner 1934, figs. 58 [the designations of the liver portions in the figure have been reversed: l_1 is the right liver, l_2 the left posterior one] and 63.) *Marionia* has also another secondary character of organization, namely its stomachal plates. These thin, elevated, easily loosened laminae do not occur in the more primitive genera *Duvaucelia* and *Tritoniella* but have originated from the pyloric folds in these forms by means of their increase and strong cuticularization."

There are, besides, other characteristics to take into consideration when judging the interrelations of the genera of the family Tritoniidae, such as a continuous decrease of the body size in some of the genera combined with a displacement of the anus towards the front end. In the large species, the anus is situated as a rule in or behind the middle of the right side, while in the small species its position is decidedly more anterior, and this is especially evident in *Duvaucelia* as compared with *Tritonia.* It seems that in this combined evolution the diminishing size of the body contrasts with the tendency of the detorsion, since this latter tends to a displacement of the anus backwards. We should note, however, that a reduction of the body size has also a relation to the earlier stages of ontogeny, which in such a case can reappear in the adult stage. Therefore the conclusion seems justified that the small species constituting the genus *Duvaucelia* may have originated from larger forms and can be derived from Tritonias, in such a retrograde evolution, expressing itself in the more or less anterior displacement of the anal and genital openings. There are, together with these gradual modifications and other kinds of differentiation, good specific characters in colour or ornamentation in external appearance. We find further that there is probably a parallel evolution starting out from *Marionia,* inasmuch as in *Paratritonia* described by Baba in 1949, a reduced body size is combined with a similar anterior position of the same orifices as in *Duvaucelia* but also combined with the presence of stomachal plates, though smaller than in *Marionia. Paratritonia* therefore seems to be derived in the same way as *Duvaucelia* and by means of parallel evolution, but from the distinct genus *Marionia.*

A still dubious genus, probably derived by means of a similar reduction from unknown source, is represented by a small form described by Pruvot-Fol in 1945 as *Tritonidoxa cincta.* This species shares the reduced external habitus of the genera *Duvaucelia* and *Paratritonia* and even shows further reduction in possessing only two pairs of gills and only two simple velar papillae; it therefore could belong to a distinct genus akin to *Paratritonia.* Pruvot-Fol (1954, p. 349, figure explanation) suggests *Tritonidoxa.* The first lateral tooth (in *Tritonidoxa ingolfiana* and *T. griegi*) is more regularly hook-shaped than it is in *Tritonia,* but it shows in *Tritonidoxa cincta* a still better agreement with that of *Paratritonia,* as does also the median tooth. Pruvot-Fol's careful observations thus enable us to expect where the next allies of this enigmatical species may be sought.

We may take this occasion also for a revision of some species named and described by me in 1936 as belonging to the new genus *Marioniopsis,* which in external habitus is very similar to *Marionia* but differs in the anatomy in having the two liver portions fused and not distinctly separated as in the last mentioned genus.

In 1936 I described, though only preliminarily and because of lack of material, a species that had been referred by Baba in 1933 to Bergh's *Tritonia irrorata;* I renamed it *Marioniopsis babai* (Odhner, 1936, *loc. cit.,* page 1087). In 1937 the same species was described by Baba as new under the name *Marionia obscura.* That it is identical with Baba's *T. irrorata* (and different from Bergh's species of the same name) is, however, not communicated by Baba in his description, but he has stated this fact in a letter to me dated February 9th, 1936: "Your kind letter dated Jan. 16 and 17 reached me this morning. I have (been) engaged in the monographic work of the Japanese opisthobranchs, containing more than 160 species — both known and unknown, and the manuscript has just (been) finished. In this Ms. I have made correction of the previous mistakes into which I fell: *Duvaucelia irrorata* is altered to *Marionia ornata* nov. sp. with the following description '— *Marionia ornata* nov. sp. *Duvaucelia irrorata* Baba, Annot. Zool. Japon., Vol. 14, no. 2, 1933, pp. 274-275, fig. 1. Tomioka.' " Dr. Baba also kindly sent me two specimens (under a provisional name) both of which I could identify as his *Marionia obscura* and even could state as belonging to *Marioniopsis* for they show the two liver portions fused below the stomach. In fact, therefore, Baba's *Marionia obscura* of 1937 is the same species as my *Marioniopsis babai* of 1936, though no convincing literary data have been given to this identity. Because of the priority the name of 1936 should be the valid one.

A further parallel evolution seems to have taken place in the forms which I included (1936) in the genus *Tritoniopsilla* PRUVOT-FOL, 1933 (= *Tritoniopsis* ELIOT, 1905). First it should be remarked that a change of ELIOT's denomination is unjustifiable, because that name was not preoccupied by CARPENTER, since his similar genus name was *Tritonopsis* (*cf.* NEAVE, 1939-1940); the name *Tritoniopsis* ELIOT, 1905 therefore remained valid. The most primitive form of the three species which I included in that genus is no doubt *Tritoniopsis tetraquctra* (PALLAS, 1788), which has, in its general shape (relatively broad body and marked back margin) a greater agreement with *Tritonia* than with the smaller and more typical species of *Tritoniopsis;* even the remarkable position of the anus behind the middle of the body was striking to BERGH; further, its radula is broad as in *Tritonia,* with the sum of the lateral and marginal teeth numbering about 250 on each side of the unicuspid median tooth. In the typical species of *Tritoniopsis,* on the other hand, the anus is situated more towards the front than in the middle of the body, and the number of radular teeth is at most about 30 on each side of the radula. A still smaller number of teeth is stated to occur in *T. elegans* (radular formula: 7-9.1.7-9, *cf.* ODHNER, 1936) and in *T. alba* BABA, 1949 (5-6.1.5-6) in which latter species, as in *T. elcgans,* the laterals bear a series of faint denticles, while they are smooth in the typical *T. brucei* ELIOT, 1905.

The differences just mentioned in the species of *Tritoniopsis* indicate clearly that the large and evidently more primitive members mentioned should be considered as nearer the original source than the smaller species and thus to form a distinct genus, separate both from the genus *Tritoniopsis* (in characters mentioned) and from *Tritonia* (in the shape of the median radular tooth). I propose for this genus the name *Tochuina* ODHNER, gen. nov. with *Limax tctraquetra* PALLAS, 1788 (= *Tritonia gigantea* BERGH, 1904, = *Tritoniopsis tetraquetra* in ODHNER, 1936) as type species. The name *Tochuina* is derived from the vernacular name Tochui, which, according to BERGH, 1879, p. 154, note, was the name of this animal in the Kurile Islands where, according to PALLAS, it was generally used as food in a raw or cooked state [c].

Lastly, some dubious species may also be mentioned. The small green coloured black-marbled *Sphaerostoma flemingi* POWELL, 1937, from Auckland, New Zealand, with a length of only 6 mm and with 5 gills on each side; its buccal veil has only two sharply conical lobes; rhinophore-sheaths entire edged. Only the left side is figured and nothing is said about the position of the openings on the right side. It may be a *Duvaucelia.*

In every case the genus *Duvaucelia* RISSO, 1826, should be held apart (as PRUVOT-FOL did in 1954) from *Tritonia* because of its more slender body shape and the more anterior site of anus and genital pore. The anus is situated well in front of the middle of the body and the genital pore below or even in front of the first branchial tuft, quite as is the case in *Duvaucelia cincta* PRUVOT-FOL, 1945 (*cf.* PRUVOT-FOL, 1954, fig. on p. 349).

But it is especially in the external colouration that the differentiation of the small *Duvaucelia* forms has become specialized; and therefore these species can be recognized from external characteristics as to the descriptions given in the diagnoses by PRUVOT-FOL, 1954.

Some changes must also be made in the two closely related genera *Marionia* VAYSSIÈRE, 1877, and *Marioniopsis* ODHNER, 1936. The difference between them was stated in my latter paper; the chief character is of an anatomical nature and therefore somewhat difficult to find because observable only by means of dissection. Whereas in *Marionia* the two parts of the liver (one large left-sided and a smaller right-sided one) are separate, this is not the case in *Marioniopsis* where the two liver parts are fused, as in all Tritoniids. In comparing the two figures 14 and 16 in my paper of 1936 we find that the two liver parts are divided in *Marionia pustulosa* (fig. 16) because the left one leaves the stomach uncovered, the right, on the contrary, has its mass concentrated as a small ball to the right side. In *Marioniopsis cyanobranchiata* (fig. 14) the left liver extends in length up to gill 3, and in the intestine curves above the left liver to which the right one is fused; but in *Marionia pustulosa* (fig. 16) the intestine does not curve to the left side at all. All these differences seem, however, to be of secondary importance in comparison with the fact that a separation or a fusion of the two parts of the liver is to be clearly noted, though, of course, with some difficulty.

In "*Marionia*" *olivacea* BABA, 1937, a still stronger curve of the intestine towards the left side is observed (*loc. cit.* p. 118, textfig. 2). "The liver consists of a small anterior and a large posterior lobe," says BABA (*loc. cit.* p. 120). I found these to be not separated as in *Marionia* but fused as in *Marioniopsis.* I observed this fact in two specimens of the present species kindly sent to me by Dr. Baba in February 1936. In his "Opisthobranchia of Japan (II)" of 1937, BABA also accepts the name *babai* ODHNER, 1936 as valid for his *Duvaucelia irrorata* (which is not that of BERGH, 1905).

Considering the species of the genus *Tritonia s. s.,* and especially the small ones, we have not as yet any possibility to arrange them all systematically. I refer the reader for confirmation of this difficulty to the statement by MARCUS (1961, p. 32), where he says about the Cali-

[c] BERGH cites the name (incorrectly) "Tochni", but PALLAS in 1788 writes "Tochui" and I follow his orthography.

fornia *Tritonia palmeri* Cooper, 1862, that it "cannot be assigned to any of the subgenera at this time," because specimens from different localities differ too much in the stated characters of external as well as internal morphology.

SYNOPSIS OF GENERA AND SUBGENERA OF THE FAMILY TRITONIIDAE

1. Branchial gills replaced by simple processes in lateral dorsal margins. Back surface with blunt keels. Anus in the middle of the right body side. Radula with simple or tripartite median tooth. No stomachal plates. Jaws with smooth margins. Liver in a single mass. *Tritoniella* Eliot, 1907
   (type by subsequent designation
   T. belli, Eliot, 1907)
— Branchial gills ramose in lateral dorsal margins (rarely absent), of uniform or alternating size 2
2. Liver in two masses; left liver leaving stomach uncovered, right liver distinctly marked off, debouching into frontal wall of stomach. Gills branched, of uniform - not alternating - size. Stomach plates present. Anus in the middle length of the body. Genital opening below second or third gill. Velar papillae compound. Jaws with 3 to 6 series of fine denticles. Radula as in *Tritonia* (median tooth tricuspidate; first lateral differentiated).
   Marionia Vayssière, 1877
   (type by subsequent monotypy
   M. berghi Vayssière, 1877
   = *Tritonia blainvillea* Risso, 1818)
— Liver fused into a single mass, covering upper and left sides of stomach, right liver thus indistinctly marked off, with its own duct 3
3. Strong stomachal plates. Genital opening below second or third gill. Jaws with a single series of strong denticles 4
— No stomachal plates 5
4. Radula as in *Tritonia* (median tooth with 3 to 5 cusps), first lateral differentiated
   Marioniopsis Odhner, 1934
   (type by original designation
Tritonia cyanobranchiata Rüppell & Leuckart, 1828)
— Median tooth unicuspidate, first lateral undifferentiated. Anus in front of mid-body length. Gills and velar papillae few in number. Genital opening below first gill. *Paratritonia* Baba, 1949
   (type by original designation
   Paratritonia lutea Baba, 1949)
5. Median tooth of radula unicuspidate; first lateral tooth undifferentiated (similar to subsequent laterals); a narrow continuous posterior margin distinct. Jaws smooth. 6
— Median tooth of radula tricuspidate. First lateral tooth differentiated (dissimilar to subsequent laterals) 7
6. Body clumsy; anus behind mid-body length; radula broad with about 250 elongate smooth teeth on each side of the median tooth; penis flagelliform; colour of living animal reddish
   Tochuina Odhner, gen. nov.
   (type *Limax tetraquetra* Pallas, 1788)
— Body relatively slender; anus at about mid-body; radula narrow, with maximum 30 teeth on each side of the median tooth; color whitish or marbled
   Tritoniopsis Eliot, 1905
   (type by original designation
   Tritoniopsis brucei Eliot, 1905 [*Tritoniopsilla* Pruvot-Fol 1933 is an unnecessary replacement])
7. Body clumsy. Gills numerous, of uniform or alternating size. Anus about in the middle of the body. Genital opening behind the foremost end of dense branchial series. *Tritonia* Cuvier, 1798 8
   (type *Tritonia hombergi* Cuvier, 1802, (?)
   [under consideration by the ICZN])
   (*Candellista* Iredale & O'Donoghue, 1923
   according to Thompson, 1961)
— Body slender. Gills at most five to eight on each side. Anus decidedly in front of mid-body. Genital opening below or in front of foremost gill tuft. Velar papillae only two to six [a]
   Duvaucelia Risso, 1826, *ex* Leach MS
   (type by monotypy
   Tritonia gracilis Risso, 1826)
8. Velum bilobed, with numerous simple papillae 9
— Velum rounded, with at most eight to ten papillae. Genital opening below the foremost one to two papillae of the more distant branchial series.
   subgenus *Candiella* Gray, 1850
   (type by monotypy
   Tritonia plebeia Johnston, 1828)
9. Back surface smooth or pustulose. Penis short and broad, with a low crest in front and behind.
   Tritonia s. s.
— Back surface smooth. Penis flagelliform.
   subgenus *Tritonidoxa* Bergh, 1907
   (type by monotypy
   Tritonidoxa capensis Bergh, 1907)
— Back surface porous. Penis elongate conic.
   subgenus *Myrella* Odhner, *nom. nov.*
   (*pro Microlophus* Rochebrune & Mabille, 1889 [Mission Sci. Cap Horn, 6 (2), Moll., p. 11] *non Microlophus* Duméril & Bibron, 1837 [Reptilia])

[a] A new species of *Duvaucelia* with 6 velar papillae, from the west coast of France, will be described by Mr. J. Tardy.

(type by monotypy
Microlophus poirieri ROCHEBRUNE & MABILLE, 1889)

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