

Heike Wägele (*)

NEW RESULTS ON THE SYSTEMATICS OF NUDIBRANCHIA
(OPISTHOBRANCHIA, GASTROPODA)
FROM THE SOUTHERN POLAR SEAS (**)

KEY WORDS: Antarctica, Nudibranchs, Opisthobranchs

Summary

The difficulties when working on Antarctic Nudibranchia are demonstrated with the help of the genus *Austrodoris* Odhner, 1926, and new results are presented. A list of the recently revised nudibranchs genera of the South Polar Sea, with synonyms, and a list with those species collected and described only once or twice from that area, is given.

Riassunto

Lo studio della sistematica dei Molluschi Nudibranchi antartici pone, ancor oggi, notevoli problemi sia per la difficoltà di ottenere esemplari, sia per la copiosa letteratura esistente che, tuttavia, non essendo sempre stata curata da specialisti, è spesso di difficile interpretazione. Ne è un esempio il genere *Austrodoris* Odhner, 1926 che viene qui discusso.

Viene inoltre presentata una lista ragionata delle specie di Nudibranchi oggi considerate valide per l'Oceano Polare Antartico con i relativi sinonimi.

Introduction

The first nudibranchs from Antarctic and Subantarctic waters were already described by BERGH (1884). Since then new species have been described continuously (BERGH, 1898; VAYSSIÈRE, 1906; 1917; ELIOT, 1905; 1907; THIELE, 1912; ODHNER, 1926; 1934; 1944; MINICHEV, 1969; 1972; EV. MARCUS, 1985; CATTANEO-VIETTI, 1991). But it is amazing that, with only few exceptions, they have been described new species. Mainly in the last 20 to 30 years specimens newly collected from the Southern Polar Seas have been assigned to existing species. But very often it is quite difficult to understand the reasons for the assignment to a particular species (VICENTE, 1974; VICENTE & ARNAUD, 1974).

In 1985, when the author started studying Antarctic nudibranchs, 64 nominal species belonging to 24 genera had been described from the southern continent. This is a very small number compared to the large area studied. Many of the early descriptions of Antarctic nudibranch species gave more or less, or exclusively, external features (e.g. *Bathydoris clavigera* Thiele, 1912). Thorough descriptions of the anatomical features are rather exceptional.

(*) Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Postfach 33501, 4800 Bielefeld 1, Germany.

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Some authors justified this practice by saying that they did not want to dissect, and therefore destroy, the most valuable type material (THIELE, 1912).

Therefore it is no wonder that all who have studied Antarctic nudibranchs consider the assignment of newly collected specimens as extremely difficult, or even as impossible.

The author was confronted with these difficulties, when she tried to assign the material she had collected to existing species. Over 600 specimens had been collected, and after each year's new cruise by the German-Antarctic Research Vessel «Polarstern», augmented the number considerably.

Between 1987 and the present the author revised several of the most common taxa of Antarctic nudibranchs (WÄGELE, 1987; 1989b; 1989c; 1990a; 1990b; 1991) (tab. 1).

The purpose of this present paper is to demonstrate the difficulties confronting anyone had, or still has, to cope with, when he is working on Antarctic nudibranchs. This is shown with the help of the genus *Austrodoris* Odhner, 1926. In this connection new results are also presented. A list of Antarctic and Subantarctic Nudibranchia, partly with new synonyms, is given (tab. 1).

Results and discussion

To demonstrate the difficulties in identifying newly collected specimens, the methods of clarifying possible synonymies are described. As an example, the species *Austrodoris* Odhner, 1926 is chosen, since this genus is the oldest known from the Antarctic waters and 14 nominal species have been included in the past.

All the nominal species have had a rather limited distribution: e.g. *Austrodoris rubescens* (Bergh, 1898) was known only from the Atlantic sector of the Subantarctic waters. Many species were described from only one locality (some only based on one specimen), and never rediscovered subsequently (e.g. *A. mishu* Marcus, 1985; *A. michaelsoni* Odhner, 1926; *A. grandis* Minichev, 1972). The distribution of *Austrodoris kerguelenensis*, described by BERGH (1884) under the generic name *Archidoris*, seemed to be restricted to Subantarctic waters (Kerguelen Islands, Herd Islands, Macquarie Islands and Patagonia).

The distinction of the species mainly based on external features (ODHNER, 1926; 1934; EV. MARCUS, 1985; VICENTE, 1974; VICENTE & ARNAUD, 1974): the shape of the body (oval, roundish or elongate); the shape of the tubercles (digitiform, conical or clubshaped); the number of gills (8, 10, or 12); the relation between the length of the body compared to the length of the peribranchial room (the room between the gill's sheath and the caudal margin of the notum: 1/6, 1/8, etc.).

Observations of living animals in special temperature controlled containers showed that many of the external characters, which were thought to be species specific, in fact varied within one and the same individual. Fig. 1 shows the same specimen some days after collection and several weeks later.

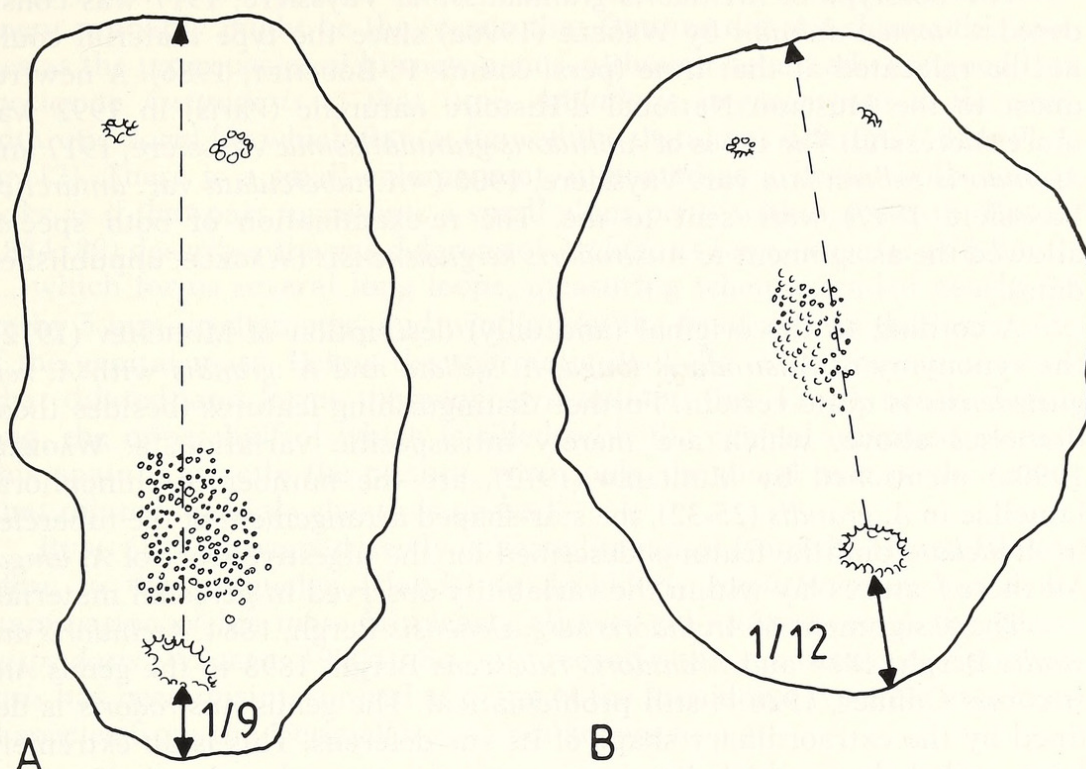


Fig. 1. *Austrodoris kerguelensis* (Bergh, 1884). Redrawn from a photograph taken on the day of collection (A), and 5 months later (B).

The external features of about 100 specimens of *Austrodoris* were investigated and nearly 50 specimens were partly or completely dissected. Some specimens were also examined by histological means (Wägele, 1989a; 1990a). All organ systems (digestive tract, nervous system, genital tract, excretory system and glands) were taken into account. Specimens from one haul (therefore probably from the same population) of similar size and external features, and of quite different external features were compared with specimens from completely different localities (South Georgia, Antarctic Peninsula, Weddell Sea).

Specimens, which were fixed directly after the haul were compared with others that had been kept in aquaria for several weeks or months.

Re-examination of available type specimens and other material stored in different museums also revealed some new results on the variability of features, a variability that was often overlooked in the past.

A comparison of this museum material with personally collected material led the author (Wägele, 1990a) to the conclusion that at least 9 of the 14 nominal species are synonymous with *Austrodoris kerguelensis* (Bergh, 1884). Some specimens, which were subsequently assigned to different species (*A. rubescens*: det. Odhner 1926; *A. granulatissima*: det. Odhner 1934; *Archidoris kerguelensis*: det. Burn 1973), could also be assigned to *Austrodoris kerguelensis*.

The holotype of *Archidoris granulatissima* Vayssi re, 1917 was considered a *nomen dubium* by W GELE (1990a) since the type material could not be relocated at that time (pers. comm. P. BOUCHET, 1986). A new request to the Mus um National d'Histoire naturelle (Paris) in 1992 was more successful. The types of *Archidoris granulatissima* Vayssi re, 1917 and *Archidoris tuberculata* var. Vayssi re, 1906 (= *A. tuberculata* var. *antarctica* Vayssi re 1917) were sent to me. The re-examination of both species allowed the assignment to *Austrodoris kerguelenensis* (W GELE, unpublished data).

According to the original (and only) description of MINICHEV (1972), the synonymy of *Austrodoris longa*, *A. stellata* and *A. grandis* with *A. kerguelenensis* is quite certain. Further distinguishing features (besides those discussed above, which are merely intraspecific variation, s. W GELE, 1990a) mentioned by MINICHEV (1972), are the number of rhinophoral lamellae in *A. grandis* (25-32), the star-shaped arrangement of the tubercles in *A. stellata* and the features described for the digestive tract of *A. longa*. All these features lay within the variability observed in personal material.

The assignment of *Archidoris kerguelenensis* Bergh, 1884, *Archidoris australis* Bergh, 1884 and *Archidoris rubescens* Bergh, 1898 to the genus *Austrodoris* Odhner, 1926 is still problematical. The genus *Austrodoris* is defined by the extraordinary shape of its vas deferens. This is an extremely long, coiled duct, which lies in a very long, muscular sheath (ODHNER, 1926; W GELE, 1989a; 1990a). A glans penis is absent. ODHNER designed *Archidoris rubescens* Bergh, 1898 as the type species of the genus *Austrodoris*. He had re-examined the holotype of *A. rubescens*, but he mentioned that the genital organs were missing in the type material.

ODHNER had material from the type locality of *Archidoris rubescens* (Punta Arenas) and from the Burdwood Bank, Shag Rock Bank, Falkland Islands and South Georgia. Since that time no other archidorid species were collected in that area.

BERGH's descriptions and (when present) the figures of the genital system are not precise enough.

At Bergh's time (and probably still now) special interest was taken in the shape of the distal vas deferens, the form of the penis and other penial structures, and presence or absence of a prostate gland. But the shape of the vas deferens, which usually has no special features, might have been easily overlooked, before ODHNER recognized its peculiarity. In the genus *Archidoris* a glans penis within a penial bulb is present (BERGH, 1878; ODHNER, 1934; SCHMEKEL, 1968). For *Archidoris rubescens*, BERGH writes (1898: 503): «Der Samenleiter ohne prostatistische Abtheilung, kaum 2 cm lang, vorn in den wenig weiteren ungef hr 2 mm langen Penissack (Vorhaut)  bergehend; die kleine Glans Penis am Boden des Penissackes unbewaffnet».

This is typical, when observing the vas deferens without opening the sheath in its complete length. Very often, there is a small enlargement of the sheath just before entering the notal tissue (W GELE, 1990a). This gives the false impression of a small, but separate penial bulb.

The same holds true for *Archidoris kerguelenensis*, which was described 14 years earlier by BERGH (1884) from the Kerguelen Islands. The type

locality just at the opposite side of the Atlantic sector of the Antarctic continent probably might be the reason that ODHNER did not choose this species as the type species of his new genus, although he already assigned this species to *Austrodoris* at that time. *Archidoris kerguelenensis* is the only Antarctic dorid for which BERGH figured the distal vas deferens (1884: Pl. I, fig. 12). There is a small enlargement, indicated as a penial bulb, and it looks as if that part represents a small glans penis within a sheath. BERGH (1884: 89) describes the vas deferens of *Archidoris kerguelenensis* as follows: «... which forms several long loops, measuring when extended nearly 3,3 cm by 5 mm, in diameter, and winding on the front and on the inner side of the genital mass. Below the spermatic duct (fig. 12, a) becomes somewhat dilated, and forms the penis (*praeputium*) (fig. 12, b), nearly 2 mm long, the upper half of which is filled with the conical unarmed glans». This again is exactly the picture, when only the distal part of the somewhat dilated «penial» sheath is opened.

BURN (1973) assigned newly collected material from the Heard Islands (close to the Kerguelen Islands) to *Archidoris kerguelenensis*, but a re-examination of his material clearly allowed an assignment to the genus *Austrodoris* (WÄGELE, 1990a). So only recently the vas deferens of *Austrodoris* has been misinterpreted as being of the archidorid type. No archidorid species from the Kerguelen zone are known to me.

Although the type material of BERGH's species seems to be lost (s. WÄGELE, 1990a; K. JENSEN, pers. comm., 1992), the interpretation of the figures and the descriptions, and the fact of the absence of other archidorids in the Antarctic and Subantartict waters, allow to conclude that BERGH's species belong to the genus *Austrodoris* Odhner, 1926.

ODHNER (1926) also mentioned the similarity of *Doris antarctica* Hedley, 1916 to the austrodorid species. According to the figure 102 (plate 9) the protruded vas deferens is very long and also has no separate penis. A protruded vas deferens of a similar length was also observed several times in own material. The assignment of HEDLEY's two specimens to the genus *Austrodoris* therefore seem to be correct. But since nothing is known about the anatomy (except for the radula), it is impossible to clarify the status of the species.

HEDLEY (1916) also assigned four specimens to *Doris nivalis* (Thiele, 1912), without giving any reasons for doing so. WÄGELE (1990a) considered the name *Archidoris nivalis* Thiele, 1912 as *nomen dubium*, since the description does not allow a re-identification, and the holotype, except for the radula, is lost. Whether Hedley's specimens also belong to *Austrodoris kerguelenensis*, has to be affirmed by examination of his material.

WÄGELE (1990a) already synonymized nine austrodorid species with *Austrodoris kerguelensis*. The number of synonymous nominal taxa is now extended to 14 (Tab. 1).

Besides revising the genus *Austrodoris*, several other quite common genera of Antarctic nudibranchs were studied by the author (WÄGELE, 1987; 1989b; 1989c; 1990b; 1991). In some of them a rather high degree of intraspecific variation in several features could be observed. A good example is the monotypic genus *Tritoniella* Eliot, 1907 which shows great varia-

tion in external morphology as well as in the structure of the rachidian teeth in the radula (WÄGELE, 1989b). In other genera (e.g. *Bathydoris* Bergh, 1884, *Notaeolidia* Eliot, 1905) the organ systems are relatively consistent in their shape (WÄGELE, 1989c; 1990b).

ODHNER (1934: 233) united the genera *Bathydoris* Bergh, 1884 and *Doridoxa* Bergh, 1900 under the name Gnathodoridacea: «.... these two types have one character in common which separates them from all other Doridacea, viz. the possession of very homogeneous mandibles in the pharynx». WÄGELE (1989e) showed, that there exists no synapomorphy for the two genera. She removed *Doridoxa* from the Gnathodoridacea and considered the latter as the sister taxon of the Doridacea. The name «Gnathodoridacea» is inadmissible because it is not based on an existing genus (R.C. WILLAN, pers. comm., 1993). According to the rules of the International Code of Zoological Nomenclature, (Art. 36: Principle of Coordination) the name Bathydoridoidea Bergh, 1891 has to be established, since Bergh described the family Bathydorididae for the first time in 1891.

Although many nations have contributed to our knowledge of the Antarctic benthos, there are still many species that remain known from Antarctic or Subantarctic waters by only one or a few specimens and which have been seldomly re-collected (e.g. *Doto antarctica* Eliot, 1907; *Armodoris antarctica* Minichev, 1972; *Prodoridunculus gaussianus* Thiele, 1912, tab. 1). Nevertheless it can be assumed that ecologists, taxonomists, or other interested people wishing to identify Antarctic nudibranchs will find it much easier now to assign their material to the known nudibranchs species from the south polar seas.

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Table 1: List of species from the southern polar seas, with synonyms.

NUDIBRANCHIA

ANTHOBRANCHIA

DORIDOIDEA

Aegires albus Thiele, 1912; Hedley 1916; Odhner 1926; 1934: Wägele 1987
= *Aegires protectus* Odhner, 1934

Armodoris antarctica Minichev, 1972

Austrodoris kerguelenensis (Bergh, 1884); Odhner 1926; 1934; Wägele 1990a

= *Austrodoris kerguelensis* Cattaneo-Vietti 1991

= *Archidoris kerguelenensis* Bergh, 1884; Bergh 1898

= *Archidoris kerguelensis* Bergh 1894

= *Archidoris australis* Bergh, 1884

= *Austrodoris australis* (Bergh): Odhner 1934

= *Archidoris rubescens* Bergh, 1898

= *Austrodoris rubescens* (Bergh): Odhner 1926

= *Archidoris tuberculata* var. Vayssière, 1906; new synonym

= *Archidoris tuberculata* var. *antarctica* Vayssière, 1917; new synonym

= *Archidoris granulatissima* Vayssière, 1917; new synonym

= *Austrodoris granulatissima* (Vayssière): Odhner 1934; ? Vicente & Arnaud 1977; ? Ev. Marcus 1985

= *Austrodoris crenulata* Odhner, 1926

= *Austrodoris michaelsoni* Odhner, 1926

= *Austrodoris macmurdensis* Odhner, 1934; ? Bouchet 1977

= *Austrodoris nivium* Odhner, 1934; Minichev 1972; Vicente 1974

= *Austrodoris tomentosa* Odhner, 1934; Vicente 1977

= *Austrodoris grandis* Minichev, 1972; new synonym

= *Austrodoris stellata* Minichev, 1972; new synonym

= *Austrodoris longa* Minichev, 1972; new synonym

= *Archidoris kerguelenensis* Bergh: Burn 1973; ? Merilees & Burn 1969

= *Austrodoris mishu* Ev. Marcus, 1985

= *Austrodoris vicentei* Ev. Marcus, 1985

? *Austrodoris antarctica* (Hedley, 1916)

Cadlina affinis Odhner, 1934

Cadlina falklandica Odhner, 1926

Doris falklandica (Eliot, 1907)

Prodoridunculus gaussianus Thiele, 1912

BATHYDORIDOIDEA

Bathydoris clavigera Thiele, 1912; Wägele 1989c; 1989d

= *B. obliquata* Odhner, 1934; Minichev 1972

= *B. argentina* Kaiser, 1980

Bathydoris hodgsoni Eliot, 1907; Hedley 1916; Wägele 1989c

= *B. inflata* Eliot, 1907

= *B. brownii* Evans, 1914

Bathydoris vitjazi Minichev, 1969

Bathydoris patagonica Kaiser, 1980

SUBORDER CLADOBRANCHIA
SUPERFAMILY DENDRONOTOIDEA

Doto sp. Thiele, 1912

Doto antarctica Eliot, 1907

Marionia cucullata Vicente & Arnaud, 1974; non *M. cucullata* (Gould, 1852): Ev. Marcus 1983

Tritonia australis Bergh, 1898; Ev. & Er. Marcus 1969; Ev. Marcus 1983
= *T. poirieri* Odhner, 1926 (non Rochebrune & Mabilie, 1891;

Tritonia appendiculata Eliot, 1905

Tritonia challengeriana Eliot, 1907; Odhner 1926; Minichev, 1972
= *T. antarctica* Pfeffer in Pfeffer & Martens, 1886

Tritonia vorax (Odhner, 1926: as *Duvaucelia*)

Tritoniella belli Eliot, 1907; Odhner 1934; Minichev 1972; Vicente & Arnaud 1974; Wägele 1989b; Cattaneo-Vietti 1991
= *T. sinuata* Eliot, 1907; Hedley 1916; Odhner 1926; 1934; Vicente & Arnaud 1974

ARMINOIDEA

Charcotia granulosa Vayssière, 1906

Pseudotritonia quadrangularis Thiele, 1912; Cattaneo-Vietti 1991; Wägele, 1991

Pseudotritonia gracilidens Odhner, 1944; Cattaneo-Vietti 1991; Wägele 1991

Pseudotritonia antarctica (Odhner, 1934): Cattaneo-Vietti 1991;
= *Telarma antarctica* Odhner, 1934; Wägele 1991;

AEOLIDOIDEA

Coryphella falklandica Eliot, 1907; Odhner 1926; 1944

Cuthona antarctica (Pfeffer, 1884; as *Aeolis*); Martens & Pfeffer 1886;
Odhner 1926

Cuthona claviformes Vicente & Arnaud, 1974

Cuthona crinita Minichev, 1972

Cuthona georgiana (Pfeffer, 1884; as *Aeolis*); Martens & Pfeffer 1886;
Odhner 1926; 1944; Cattaneo-Vietti 1991

Cuthona georgiana longipapillata: Minichev, 1972

Cuthona paucicirra Minichev, 1972

Cuthona schraderi (Pfeffer, 1884: as *Aeolis*); Martens & Pfeffer 1886

Cuthona schraderi bouvetensis Odhner, 1944

Cuthona arnaudi (Vicente, 1974: as *Eubbranchus*); Cattaneo-Vietti 1991

Cuthona macquariensis (Burn, 1973: as *Trinchesia*)

Cuthona modesta (Eliot, 1907: as *Cuthonella*)

Cuthona elioti Odhner, 1944: nom. nov. for *Cuthonella antarctica* Eliot, 1907

Cuthona paradoxa (Eliot, 1907: as *Cuthonella*); Odhner 1944

Eubbranchus sp. Vicente & Arnaud, 1974

Eubbranchus adarensis Odhner, 1934; Vicente & Arnaud 1974

Eubbranchus falklandicus (Eliot, 1907: as *Galvina*)

Galvinella antarctica Eliot, 1907

Galvinella glacialis Thiele, 1912

Guyvalvoria francaisi Vayssière, 1906
Notaeolidia depressa Eliot, 1905; Hedley 1916; Wägele 1990b
 = *N. rufopicta* Thiele, 1912
 = *N. robsoni* Odhner, 1934; Vicente & Arnaud 1974
 = *N. subgigas* Odhner, 1944
 = *N. alutacea* Minichev, 1972
 = *N. flava* Minichev, 1972
Notaeolidia gigas Eliot, 1905; Wägele 1990b
 = *N. purpurea* Eliot, 1905
 = *N. subgigas*: Wägele, 1988, non *N. subgigas* Odhner, 1944
Notaeolidia schmekelae Wägele, 1990
Tergipes antarcticus Pelseneer, 1903
Tergipes valentini (Eliot, 1907: as *Cratena*); Cattaneo-Vietti 1991

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