A taxonomical outline of the Gymnosomata (Mollusca)

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INTRODUCTION

This outline is composed to honour Dr. C.O. van Regteren Altena, who, over a long period, has stimulated the author with advice and assistance in his taxonomical studies.

Sixty-two valid taxa on species level or lower and eighteen genera, are recognized in the order Gymnosomata at the moment. In 1774 the first species was described, and in 1850 only seven species were known. At the end of the nineteenth century the knowledge of Gymnosomata had increased considerably and in 1900 already twenty-four species were known. The large scientific expeditions from around 1900 contributed much to the knowledge of oceanic plankton and pelagic molluscs. Between 1900 and 1920 another twenty-four species were described, but between 1920 and 1930 only nine taxa were added. The number of taxa recognized as new to science decreased rapidly; in the period 1930-1940 only four new ones were found and after 1950 only one valid taxon new to science was published. This means that, statistically, now only one or two unknown taxa are still expected to exist among the Gymnosomata. New theories and new methods still to be introduced may alter this estimated number. But at the moment we know, in my opinion, enough to establish a revised system for the group. This system is given below with brief references and comments.

The author is indebted to Dr. J. Knudsen who assisted him in consulting the Boas collections and Dana material on which the papers of Boas (1886), Pruvot-Fol (1942), and Tesch (1950) were based.

Order Gymnosomata (s.l.) Blainville, 1824

Suborder Gymnosomata (s.s.)

Family Pneumodermatidae Gray, 1840
(emend. Dall, 1870)

I Genus *Pneumodermopsis* (s.l.) Keferstein, 1862 (= *Dexiobranchaea,* Boas, 1885). Subgenus *Pneumodermopsis* (s.s.) Keferstein, 1862 (note 1).

I.a *P.(P.) ciliata* (Gegenbaur, 1885). – *Pneumodermon ciliatum* Gegenbaur, 1885; *Pneumoderma peroni* (non Lamarck, 1819, non Verrill, 1885) Locard, 1886. Type species of the genus and subgenus.

I.b *P.(P.) minuta* (Pelseneer, 1887). – *Dexiobranchaea minuta* Pelseneer, 1887.

I.c *P.(P.) simplex* (Boas, 1886). – *Dexiobranchaea simplex* Boas, 1886.

I.d *P.(P.) polycotyla* (Boas, 1886). – *Dexiobranchaea polycotyla* Boas, 1886.

I.e *P.(P.) oligocotyla* Massy, 1917. – *Pneumodermopsis oligocotyla* Massy, 1917 (note 2).

I.f *P.(P.) paucidens* (Boas, 1886) forma *paucidens* (Boas, 1886). – *Dexiobranchaea paucidens* Boas, 1886 (note 3).

I.g *P.(P.) paucidens* (Boas, 1886) forma *pulex* Pruvot-Fol, 1926 (note 4). – *Pneumodermopsis paucidens* var. *pulex* Pruvot-Fol, 1926.

I.h *P.(P.) canephora* Pruvot-Fol, 1924. – *Pneumodermopsis canephora* Pruvot-Fol, 1924.

I.i *P.(P.) pupula* Pruvot-Fol, 1926. – *Pneumodermopsis pupula* Pruvot-Fol, 1926.

Subgenus *Crucibranchaea* Pruvot-Fol, 1942 (note 5).

I.j *P.(C.) macrochira* Meisenheimer, 1905. – *Pneumodermopsis macrochira* Meisenheimer, 1905. Type species of the subgenus.

I.k *P.(C.) michaelsársi* Bonnevie, 1913 (note 6). – *Pneumodermopsis michaelsarsi* Bonnevie, 1913.

II Genus *Spongiobranchaea* d'Orbigny, 1835 (= *Cliodita* (part) Quoy & Gaimard, 1824; ? *Trichocyclus* (non Costa, 1865) (part) Eschscholtz, 1825) (note 7).

II.a *S. australis* d'Orbigny, 1835. – ?*Cliodita caduceus* Quoy & Gaimard, 1824; ?*Trichocyclus dumerilii* Eschscholtz, 1825; *Spongiobranchaea australis* d'Orbigny, 1835. Type species

of the genus.

II.b *S. intermedia* Pruvot-Fol, 1926 (note 8). – *Spongiobranchaea intermedia* Pruvot-Fol, 1926.

III Genus *Schizobrachium* Meisenheimer, 1903 (note 9).

III.a *S. polycotylum* Meisenheimer, 1903. – *Schizobrachium polycotylum* Meisenheimer, 1903; *Spongiobranchaea polycotyla* Massy, 1917 (= *Spongiobranchaea oligocotyla* Pruvot-Fol, 1926, err. typ.). Type species of the genus.

IV Genus *Pneumoderma* Peron & Lesueur, 1810 (= *Pneumodermis* Oken, 1815; *Aegle* Oken, 1815; *Pneumodermon* Cuvier, 1817; *Pneumonoderma* Agassiz, 1846; *Cirrifer* Pfeffer, 1879). Type genus of the family (note 10).

IV.a *P. atlanticum* (Oken, 1815) subsp. *atlanticum* (Oken, 1815) forma *atlanticum* (Oken, 1815) (note 11). – *Pneumodermis atlantica* Oken, 1815; *Pneumodermon violaceum* d'Orbigny, 1846; ?*Pneumodermon cucullatum* Gray, 1850; *Pneumodermon audebardii* (non Locard, 1886) Rang, 1852; *Cirrifer paradoxus* Pfeffer, 1879. Type species of the genus.

IV.b *P. atlanticum* (Oken, 1815) subsp. *atlanticum* (Oken, 1815) forma *eurycotylum* Meisenheimer, 1905. – *Pneumoderma eurycotylum* Meisenheimer, 1905.

IV.c *P. atlanticum* (Oken, 1815) subsp. *atlanticum* (Oken, 1815) forma *pygmaeum* (Tesch, 1903). – *Pneumonoderma pygmaeum* Tesch, 1903.

IV.d *P. atlanticum* (Oken, 1815) subsp. *atlanticum* (Oken, 1815) forma **bonnevii** nom. nov. (note 12). – *Pneumoderma atlantica* (non Oken, 1815) Bonnevie, 1913.

IV.e *P. atlanticum* (Oken, 1815) subsp. *souleyeti* (Pelseneer, 1887). – *Pneumonoderma souleyeti* Pelseneer, 1887.

IV.f *P. atlanticum* (Oken, 1815) subsp. *boasi* (Pelseneer, 1887). – *Pneumodermon violaceum* (part) Boas, 1886; *Pneumonoderma boasi* Pelseneer, 1887.

IV.g *P. atlanticum* (Oken, 1815) subsp. *pacificum* (Dall, 1871). – *Pneumodermon pacificum* Dall, 1871.

IV.h *P. peroni* (Lamarck, 1819) forma *peroni* (Lamarck, 1819) note 13). – *Pneumodermon peronii* (non Verrill, 1885, non Locard, 1886) Lamarck, 1819; ?*Pneumodermon ruber* Souleyet, 1852.

IV.i *P. peroni* (Lamarck, 1819) forma *heterocotylum* (Tesch, 1903) (note 14). – *Pneumonoderma heterocotylum* Tesch, 1903.

IV.j *P. meisenheimeri* Pruvot-Fol, 1926. – *Pneumoderma meisenheimeri* Pruvot-Fol, 1926.

IV.k *P. mediterraneum* (van Beneden, 1838) (note 15). – *Pneumoderme capuchonne* Peron & Lesueur, 1810; *Pneumodermon mediterraneum* van Beneden, 1838; *Pneumodermon macrocotylum* Boas, 1886.

Family Notobranchidae Pelseneer, 1886

V Genus *Notobranchaea* Pelseneer, 1886. Type genus of the family (note 16).

V.a *N. macdonaldi* Pelseneer, 1886 morpha *macdonaldi* Pelseneer, 1886. – "Trigonal tailed *Clio*" Macdonald, 1864; *Clione longicaudata* (non Souleyet, 1852) Verrill, 1884; *Notobranchaea macdonaldi* Pelseneer, 1886. Type species of the genus (note 17).

V.b *N. macdonaldi* Pelseneer, 1886 morpha *pelseneeri* Pruvot-Fol, 1942 (note 18). – *Notobranchaea macdonaldi* var. *pelseneeri* Pruvot-Fol, 1942.

V.c *N. grandis* Pruvot-Fol, 1942. – *Notobranchaea grandis* Pruvot-Fol, 1942.

V.d *N. inopinata* Pelseneer, 1887. – *Notobranchaea inopinata* Pelseneer, 1887.

VI Genus *Prionoglossa* Tesch, 1950 (= *Notobranchaea* (part) Pelseneer, 1886; *Microdonta* Bonnevie, 1913; *Fowlerina* (part) Bonnevie, 1913) (note 19).

VI.a *P. tetrabranchiata* (Bonnevie, 1913). – *Notobranchaea tetrabranchiata* Bonnevie, 1913. Type species of the genus.

VI.b *P. valdiviae* (Meisenheimer, 1905). – *Notobranchaea valdiviae* Meisenheimer, 1905.

VI.c *P. longicollis* (Bonnevie, 1913) (note 20). – *Microdonta longicollis* Bonnevie, 1913.

VI.d *P. hjorti* (Bonnevie, 1913) – *Fowlerina hjortii* Bonnevie, 1913; *F. hiurti* Pruvot-Fol, 1942, err. typ.

Family Cliopsidae Costa, 1873
(emend. Dall, 1889)

VII Genus *Cliopsis* Troschel, 1854 (= *Trichocyclus* (non Eschscholtz, 1825) (part) Costa, 1869; *Clionopsis* Keferstein, 1862). Type genus of the family (note 21).

VII.a *C. krohni* Troschel, 1854 morpha *krohni* Troschel, 1854;

(note 22). – *Cliopsis krohnii* Troschel, 1854; *Clio mediterranea* Gegenbaur, 1855; *Trichocyclus mediterraneus* Costa, 1869; *Clionopsis microcephalus* Tesch, 1903. Type species of the genus.

VII.b *C. krohni* Troschel, 1854 morpha *grandis* Boas, 1886. *Pneumodermon peronii* (non Lamarck, 1819, non Locard, 1886) Verrill, 1885; *Cliopsis grandis* Boas, 1886.

VII.c *C. krohni* Troschel, 1854 morpha *modesta* (Pelseneer, 1887). – *Clionopsis modesta* Pelseneer, 1887.

VIII Genus *Pruvotella* Pruvot-Fol, 1932 (= *Pneumodermon* Quoy & Gaimard, 1824) (note 23).

VIII.a *P. pellucida* (Quoy & Gaimard, 1824). – *Pneumodermon pellucidus* Quoy & Gaimard, 1824; *Pneumodermon ruber* Quoy & Gaimard, 1832. Type species of the genus.

VIII.b *P. danae* Pruvot-Fol, 1942. – *Pruvotella danae* Pruvot-Fol, 1942.

Family Clionidae Gray, 1840 (note 24)
Subfamily Thliptodontinae Kwietniewski, 1902
(emend. Pruvot-Fol, 1926)

IX Genus *Thliptodon* Boas, 1886 (= *Pelagia* Quoy & Gaimard, 1832; ?*Pteropelagia* Keferstein, 1862; *Pteroceanis* Meisenheimer, 1902) (note 25). Type genus of the subfamily.

IX.a *T. diaphanus* (Meisenheimer, 1902) (note 26). – *Pteroceanis diaphana* Meisenheimer, 1902.

IX.b *T. gegenbauri* Boas, 1886 (note 26). – ?*Pelagia alba* Quoy & Gaimard, 1832; ?*Pteropelagia alba* Keferstein, 1862; *Thliptodon gegenbauri* Boas, 1886; *Thliptodon atlanticus* Massy, 1917. Type species of the genus.

IX.c *T. antarcticus* Meisenheimer, 1906 (notes 26, 27). – *Thliptodon antarcticus* Meisenheimer, 1906; *Thliptodon rotundatus* Massy, 1917.

IX.d *T. akatukai* Tokioka, 1950. – *Thliptodon akatukai* Tokioka, 1950.

IX.e *T. schmidti* Pruvot-Fol, 1942. – *Thliptodon schmidti* Pruvot-Fol, 1942.

X Genus *Massya* Pruvot-Fol, 1924 (= *Clionopsis* (part) Massy, 1917) (note 28).

X.a *M. longicirrata* (Massy, 1917) (note 29). – *Clionopsis longicirrata* Massy, 1917. Type species of the genus.

XI Genus *Cephalobrachia* Bonnevie, 1913 (note 30).

XI.a *C. macrochaeta* Bonnevie, 1913. – *Cephalobrachia macrochaeta* Bonnevie, 1913. Type species of the genus.

XI.b *C. bonnevii* Massy, 1917. – *Cephalobrachia bonnevii* Massy, 1917.

Subfamily Clioninae Pruvot-Fol, 1926

XII Genus *Fowlerina* Pelseneer, 1906 (= *Clione* (part) Tesch, 1903) (note 31).

XII.a *F. zetezios* Pelseneer, 1906. – *Fowlerina zetezios* Pelseneer, 1906. Type species of the genus.

XII.b *F. punctata* (Tesch, 1903) (note 32). – *Clione punctata* Tesch, 1903.

XIII Genus *Thalassopterus* Kwietniewski, 1910 (note 33).

XIII.a *T. zancleus* Kwietniewski, 1910. – *Thalassopterus zancleus* Kwietniewski, 1910. Type species of the genus.

XIV Genus *Paedoclione* Danforth, 1907 (note 34).

XIV.a *P. doliiformis* Danforth, 1907. – *Paedoclione doliiformis* Danforth, 1907. Type species of the genus.

XV Genus *Paraclione* Tesch, 1903 (= *Cliodita* (part) Quoy & Gaimard, 1824; *Spongiobranchaea* (part) d'Orbigny, 1835); *Clione* (part) Gray, 1850; *Clio* (part) Souleyet, 1852) (note 35).

XV.a *P. pelseneeri* Tesch, 1903. – *Paraclione pelseneeri* Tesch, 1903. Type species of the genus.

XV.b *P. longicaudata* (Souleyet, 1852). – ?*Cliodita fusiformis* Quoy & Gaimard, 1824; ?*Spongiobranchea elongata* d'Orbigny, 1835; ?*Clione caudata* Gray, 1850; ?*Clio limacella* Rang, 1852; *Clio longicaudatus* Souleyet, 1852; *Clione longicaudatus* (non Verrill, 1884) Souleyet, 1852; *Paraclione caudata* Pelseneer, 1906; *Clionina longicaudata* Pruvot-Fol, 1924.

XV.c *P. flavescens* (Gegenbaur, 1855). – *Clio flavescens* Gegenbaur, 1855; *Clio aurantiaca* Fol, 1875.

XVI Genus *Clione* Pallas, 1774 (= *Clio* (non Linné, 1767) (part) Phipps, 1774; *Trichocyclus* (part) Agersborg, 1923) (note 36). Type genus of the family and subfamily.

XVI.a *C. limacina* (Phipps, 1774) subsp. *limacina* (Phipps, 1774) forma *limacina* (Phipps, 1774) (note 37). – *Clio limacina* Phipps, 1774; *Clione borealis* Pallas, 1774; *Clio retusa* (non Linné, 1767) Müller, 1776; *Clio miquelonensis* Rang, 1825; *Clione papilionacea* Jeffreys, 1869; *Clione dalli* Krause,

1885; *Clione kincaidi* Agersborg, 1923; *Trichocyclus hansineensis* Agersborg, 1923; various authors: "northern form", "larger form". Type species of the genus.

XVI.b *C. limacina* (Phipps, 1774) subsp. *limacina* (Phipps, 1774) forma *minuta* Pruvot-Fol, 1926 (note 37). – *Clione minuta* Pruvot-Fol, 1926; various authors: "southern form", "smaller form", "dwarf form".

XVI.c *C. limacina* (Phipps, 1774) subsp. *limacina* (Phipps, 1774) forma *elegantissima* Dall, 1870 (note 37). – *Clione elegantissima* Dall, 1870.

XVI.d *C. limacina* (Phipps, 1774) subsp. *limacina* (Phipps, 1774) forma *gracilis* Massy, 1909 (note 37). – *Clione gracilis* Massy, 1909.

XVI.e *C. limacina* (Phipps, 1774) subsp. *limacina* (Phipps, 1774) forma *filifera* Pruvot-Fol, 1926 (notes 37, 38). – *Clione filifera* Pruvot-Fol, 1926.

XVI.f *C. limacina* (Phipps, 1774) subsp. *limacina* (Phipps, 1774) forma *meridionalis* Pruvot-Fol, 1926 – *Clione limacina* var. *meridionalis* Pruvot-Fol, 1926 (note 37).

XVI.g *C. limacina* (Phipps, 1774) subsp. *antarctica* Smith, 1902 (note 37). – nom.nov. pro *Clio australis* Bruguière, 1789; *Clione australis* Adams, 1853; *Clione antarctica* Smith, 1902.

Suborder Gymnoptera (note 39)

Family Hydromylidae Pruvot-Fol, 1942

XVII Genus *Hydromyles* Gistel, 1848 (= *Psyche* (non Linné, 1758) Rang, 1825; *Cymodocea* d'Orbigny, 1840; *Anopsia* Gistel, 1848; *Philopseudes* Gistel, 1848; *Eurybia* Souleyet, 1852; *Halopsyche* Keferstein, 1857; *Theceurybia* Keferstein, 1862; *Verrillopsyche* Cossman, 1900) (note 40). Type genus of the family.

XVII.a *H. globulosa* (Rang, 1825) (note 41). – *Psyche globulosa* Rang, 1825; ?*Eurybia hemispherica* Rang, 1827; *Cymbulia norfolkensis* Quoy & Gaimard, 1832; *Hydromyles globulosa* Gistel, 1848; *Euribia gaudichaudii* Souleyet, 1852; *Euribia norfolkensis* Souleyet, 1852; *Euribia globulosa* Souleyet, 1852; *Theceurybia gaudichaudii* Keferstein, 1862; *Theceurybia norfolkensis* Lankester, 1883; *Halopsyche gaudichaudii* Boas, 1886; *Anopsia gaudichaudi* Meisenheimer, 1905. Type species of the genus.

Family Laginiopsidae Pruvot-Fol, 1922

XVIII Genus *Laginiopsis* Pruvot-Fol, 1922. Type genus of the family.

XVIII.a *L. trilobata* Pruvot-Fol, 1922. – *Laginiopsis trilobata* Pruvot-Fol, 1922. Type species of the genus.

COMMENTS AND NOTES

The classification is based on the ideas of Meisenheimer (1905) who stated that the Gymnosomata consist of different phylogenetic branches. The six families, given above, represent these phylogenetic branches (see also Van der Spoel, 1967, and note 24).

1 – The genus *Pneumodermopsis* is characterized by the presence of one median sucker arm and two lateral sucker arms or by three such groups of suckers, a lateral gill, and sometimes a posterior gill. *Pneumodermopsis* has been subdivided into two subgenera of which *Crucibranchaea* is characterized by the absence of a lateral gill, while *Pneumodermopsis* s.s. always has such a gill. Lalli (1970) found a distinct lateral gill in *P.(C.) macrochira,* while *P.(P.) pupula* has no lateral gill. The best discriminating character is consequently the existence of a median sucker arm in *Pneumodermopsis* s.s. and the absence of this arm in *Crucibranchaea.* This also indicates the intermediate character of the latter subgenus. Among the species of *Pneumodermopsis* s.s. two groups may be recognized. The first group has free lateral sucker arms (species: I.a, e, h and i), the second group has the lateral suckers implanted on the buccal wall (species: I.b, c, d, f and g). In both groups a gradual reduction of the suckers is seen; for the first group, this line ends in *P.(P.) canephora* and for the second group in *P.(P.) simplex.*

2 – The description of this species is incomplete; it may be a synonym of *P.(P.) canephora.* When it is proved that this is not the case it is a valid species and as such it is considered here.

3 – A subdivision of this species in the formae *paucidens* and *pulex* is proposed, as *pulex* may represent a west Mediterranean stock of smaller specimens with a life cycle slightly different from that of the populations in the open ocean. As no sharp boundary between the populations and no clear taxonomical differences between the formae exist, they cannot be considered subspecies.

4 – The forma *pulex* is not based on immature specimens or merely smaller specimens, but on full-grown individuals. The radula has more laterals than in mature specimens of the forma *paucidens.*

5 – As mentioned before, Lalli (1970) described a lateral gill in the subgenus *Crucibranchaea.* This description differs in one more point from the original description of *P.(C.) macrochira* as the large subterminal suckers are not present. For the remainder the specimens of Lalli resemble *Crucibranchaea* so much that it does not change our opinion on the status of this subgenus (see also notes 1 and 6).
6 – This species is placed in this subgenus, as radula and sucker arms resemble those of the preceding species very closely. Specimens investigated by the present author were so damaged that nothing could be added to the original description, but very probably this is a rare but valid species.
7 – The value of this genus becomes dubious after the discussion on the previous subgenus, but the circular shape of the posterior gill, the shape of the median radula plates, with a strong median and two or four cusps on their lateral corners and the absence of any trace of a group of median suckers induced me to follow classical nomenclature.
8 – This species differs from *S. australis* by the larger number of suckers. *Spongiobranchaea polycotyla* Massy, 1917 is transferred to the next genus as a synonym because the number of suckers is too large (cf. Tesch, 1950). The radula is of the *Spongiobranchaea* type and a trace of a posterior gill is present (see also note 9).
9 – The branched sucker arms with numerous subequal suckers are the only really typical characteristics of this genus. Like in *Sp. polycotyla* the posterior gill for *Sch. polycotyla* is described by Meisenheimer (1905) as consisting of two minute simple crests on the ventral side. As a consequence discrimination between the two species is impossible, which explains the synonyms given.
10 – In this genus four species are described with a wide distribution; *P. mediterraneum, P. peroni,* and *P. meisenheimeri* show a distribution resembling Tethyan dispersal, *P. atlanticum* is a cosmopolitan warm water species as far as could be concluded from the scarce records. The genus is characterized by two lateral sucker arms, and a well developed lateral and posterior gill.
11 – This species is subdivided into four subspecies and four formae. The subspecies IV.a, IV.e, IV.f and IV.g are allopatric, occurring in warm water, cold N. Atlantic and N. Pacific, cold S. Pacific and cold N. Pacific respectively. The four formae are found within the range of the first subspecies and probably represent formae in the terminology of Van der Spoel (1971). The name *peronii* occurs so frequently as a junior synonym of different species, that only the

most important references are given in this paper.
12 – *P. atlantica* Bonnevie, 1913 is considered indeed a new taxon not synonymous with *P. atlanticum* (Oken, 1815) as there are fewer suckers in mature specimens than in the latter species and because these suckers are implanted on the buccal wall. The name *bonnevii* is proposed in honour to Dr. Kr. Bonnevie.
13 – This species is subdivided into formae for the same reason as those distinguished in the preceding species; the forma *heterocotylum* can be considered a local group of populations in the Indo-Malayan Archipelago in which differentiation has started (Van der Spoel, 1971).
14 – The forma *heterocotylum* belongs to this species as it has a high number of suckers; this and the forma *peroni* are the two taxa in the genus with nearly twice as many suckers as in the other taxa. I have to admit that differences between the two formae of this species may very well be due to contraction after fixation. The fact that there are minor differences in the radula prevents me from synonymizing them.
15 – This species and *P. atlanticum* are the only valid species in the opinion of Tesch (1950). All other names are placed in synonymy by him in which he agrees with Pruvot-Fol (1942). The argument that variability in the genus is chiefly due to age differences is incorrect because small "species" which they considered to be young, sometimes show "adult" characters, while large ones, considered to be adult, may show "juvenile" structures. Though a number of these "species" are known only from very few records it is incorrect to conclude that they are not valid because they have not yet been completely described.
16 – This genus is characterized by a triradiate posterior gill, two pairs of buccal cones and a unicuspid median radula plate.
17 – In the opinion of Tesch (1950) the genus is only represented by *N. macdonaldi*. In my opinion two more species are to be recognized, viz., *N. inopinata* with distinct footlobes, and *N. grandis* differing from the type species. Tesch (1950) stated: "I cannot discover any really fundamental differences from *N. macdonaldi*", when dealing with *N. grandis*. The holotype shows, however, that the pigmented areas are unique structures of a special ephithelium and chromatophores and the "épron énigmatique à la partie antérieure du pied" (Pruvot-Fol, 1942) is indeed distinct and of taxonomical value, the more so because the parts of the foot are of great importance for the taxonomy in this genus.
18 – The morpha *pelseneeri* is no longer considered a variety or

subspecies for in my opinion we are dealing with dwarf specimens occurring in the same population as the real *macdonaldi* specimens. Neoteny may be the cause of this phenomenon.

19 – This genus should comprise species with saw-like median radula plate, and without buccal cones. The difference in gill crests between this and the preceding genus mentioned by Tesch (1950) does not hold as Pruvot-Fol described *N. macdonaldi* var. *pelseneeri* having three to four gill rays, but these animals always have a unicuspid median plate (cf. note 16). The radula is thus characteristic for this genus.

20 – Species based on one specimen, or represented by only a few records and incompletely described cannot be considered junior synonyms without a detailed explanation. This is one of the reasons that four separate species are still recognized in this genus. *P. hjorti* and *P. longicollis* belong to this genus as they have saw-shaped median plates.

21 – This genus is represented by one species with a tetraradiate, hexagonal posterior gill, no lateral gill, well developed proboscis and showing no buccal cones.

22 – This species is subdivided into morphae, as together in the same populations, different forms of adults may occur which show different development; these groups are of no taxonomical importance. As the relative abundance of the different morphs seems to vary in different geographic regions they are dealt with separately. Strong differences in development indicate that a type of neoteny occurs in this genus; cf. *Paraclione.*

23 – This genus differs from the preceding one by the presence of a lateral gill.

24 – This family differs from that proposed by Pruvot-Fol (1942) as the Notobranchidae which possess gills are not included here. The present classification is perhaps better because it results in a family with gills and with suckers (Pneumodermatidae), one with gills and buccal cones (Notobranchidae), one with or without gills but without buccal cones (Cliopsidae) and one without gills and usually with buccal cones (Clionidae). The Clionidae consist of two subfamilies, one with real buccal cones (Clioninae) and one without buccal cones (Thliptodontinae). The latter forms a subfamily intermediate with the Cliopsidae as is, among others, shown by the gullet-bladders in *Thliptodon. Thalassopterus* is not referred to this subfamily as opposed to the proposals by Pruvot-Fol (1926). To avoid confusion, the family-group name Clionae proposed by Van der Spoel (1967)

for a group of Thecosomata should by substituted by the correct name Clioinae.
25 – The intermediate radula teeth, gullet-bladders and rather small hooksacs are typical for this genus.
26 – The differences between these three species are small and many so-called discriminating characters are due to contraction after fixation. Most reliable taxonomic characters are provided by the radula.
27 – *Thliptodon rotundatus* Massy, 1917, was always considered to be the correct name for this species, but nothing is against accepting *Th. antarcticus* Meisenheimer, 1906, which name has priority over the other. Pruvot-Fol (1926, 1942) and Tesch (1913, 1950) did not refer to this name which may explain why it is usually neglected.
28 – This genus is placed in the present subfamily but the head appendages may not be interpreted as buccal cones though their function may be the same as that of these cones. Pruvot-Fol (1926) described a posterior gill but this does not agree with the studies of Tesch and of Massy (1917) and my own results so that nothing prevents us to use the proposed classification.
29 – The spelling *longicirrata* is also used by Massy (1917), and though this name was considered incorrect and replaced by *longecirrata* by the same author, page priority and correct latin spelling makes the name given here the correct one.
30 – This genus is characterized by the absence of intermediate radula plates, and the presence of very muscular and large hooksacs.
31 – The existence of only one pair of buccal cones is typical for this genus.
32 – This species is referred to the present genus according the opinion of Tesch (1950).
33 – This genus is characterized by the absence of hooksacs and two pairs of rudimentary buccal cones.
34 – This genus is characterized by two buccal cones at the right and one at the left side.
35 – This genus is characterized by two pairs of buccal cones and well developed hooksacs. *Paraclione* and *Clionina* are not separated as the discriminating characters proposed by Pruvot-Fol (1924) do not hold good.
36 – *Clione* is the only genus with three pairs of well-developed buccal cones.
37 – The single species in the present genus shows a remarkable variation comparable to that described for *Limacina helicina* and *Clio pyramidata* by Van der Spoel (1967). In northern cold and temperate waters a subspecies has developed and the same has

occurred on the southern hemisphere. The northern subspecies is subdivided into formae according the theory given by Van der Spoel (1971).

38 – In my opinion this forma is based on specimens showing a unique type of contraction after fixation, and it should be easy to synonymize this forma with the preceding one if the buccal cones did not show a kind of bifurcation. This bifurcation may also be the result of contraction as the filaments proved to have a muscle system. On the other hand, specimens with bifurcating filaments, seen by the present author, did not show special features of contraction in other body parts.

39 – This suborder is separated from the Gymnosomata s.l. as the two species in this group differ too much in the anatomy of the parts of the foot, the digestive system, tentacles, and buccal organs to regard them as real Gymnosomata.

40 – The complicated synonymy of the present genus and species is discussed sufficiently by Pruvot-Fol (1942) and Tesch (1950).

41 – The only problem left in the synonymy of this species is the question whether *Psyche globulosa* and *Eurybia hemispherica*, described by Rang in 1825 and 1827 respectively, are identical. In my opinion Rang had two animals belonging to different species because the original figures and descriptions are completely different. It would indeed be better to consider *Eurybia hemispherica* as a dubious, and possibly very rare, species, but the intricate synonymy does prevent me to do so at the moment.

LITERATURE

BOAS, J.E.V., 1886. Spolia Atlantica, bidrag til Pteropodernes morfologi og systematik samt til kundskaben om deres geografiske udbredelse. Vidensk. Selsk. Skr. 6 Raekke, Naturv. Mathem. Afd. IV, I: 1-231.

LALLI, C.M., 1970. Morphology of Crucibranchaea macrochira (Meisenheimer), a gymnosomatous pteropod. Proc. Malac. Soc. London 39: 1-14.

MASSY, A.L., 1917. The gymnosomatous Pteropoda of the coast of Ireland. Sci. Proc. Roy. Soc. Dublin N.S. 15: 223-224.

MEISENHEIMER, J., 1905. Pteropoda. Wiss. Ergebn. Dtsch. Tiefsee-Exp. Valdivia 1: 1-314.

PRUVOT-FOL, A., 1924. Etude de quelques gymnosomes méditer-

ranéens des pêches de l' "Orvet" en 1921 et 1922. Arch. Zool. Exp. Gén. 62: 345-400.

———— , 1926. Mollusques ptéropodes gymnosomes provenant des campagnes du Prince Albert Ier de Monaco. Rés. Camp. Sci. Monaco 70: 1-60.

———— , 1942. Les gymnosomes. I. Dana Rep. 4: 1-54.

SPOEL, S. VAN DER, 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda): 1-375. Gorinchem.

———— , 1971. Some problems in infraspecific classification of holoplanktonic animals. Zeitschr. Zool. Syst. Evol. 9: 107-138.

TESCH, J.J., 1913. Pteropoda. Das Tierreich 36: I-XVI, 1-154. Berlin.

———— , 1950. The Gymnosomata. II. Dana Rep. 6 (36): 1-55.