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How many hydrozoan species are there?

P. Schuchert

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P. Schuchert, Natural History Museum, Dept. of Invertebrates, PO Box 6434, CH-1211 Geneva 6, Switzerland. e-mail: schuchert@ubaclu.unibas.ch.

Key words: Biodiversity; Hydrozoa; species number; future trends; Athecata; Thecata; Narcomedusae; Trachymedusae; Siphonophora.
A list of all living hydrozoan species was compiled and analysed. The number of supposedly valid species was found to be around 3200. Considerable uncertainties exist due to the possibly high number of invalid nominal species. The total number of existing hydrozoan species cannot be estimated because the accumulation curve for new species shows no sign of convergence. Only in the Thecata, Narcomedusae and Trachymedusae is an estimate of the maximal number feasible. However, application of new methods, notably a molecular systematic approach, could drastically alter these predictions.

Introduction

In recent years, biodiversity studies have seen a remarkable increase in public awareness (Randall, 1991; Barrowclough, 1992), inspired - but not solely - by the United Nations Conference on Environment and Development (the Earth Summit), held in Rio de Janeiro, in June 1992. Although being only one aspect of biodiversity, speculation on species numbers has therefore become popular. The current number of scientifically described animal species is about 1 million. However, estimates of the total number of existing animals vary drastically from 3 to 30 million (May, 1988; 1992; Wilson, 1992; May & Nee, 1995).

These discussions prompted me to estimate the number of described hydrozoans as well as the possible total number of hydrozoan species. The number of described hydrozoan species is not precisely known, and may never be so due to a large number of dubious and invalid species and high number of invalid nominal species (see below and May & Nee, 1995). Werner (1984) gives an estimate of about 3000 species, but it is not clear how this number was derived. Thus, a more detailed analysis was needed.

Results and Discussion

The Hydrozoa is a monophyletic group (Schuchert, 1993), but there exists no modern catalogue for all hydrozoan species and the synopsis of Kramp (1961) is restricted to medusae only. Bedot (1901-1925) compiled all citations for nominal hydroid and hydromedusan species up to 1910. Although Bedot's work is invaluable for taxonomic research, a very large proportion of the listed names are either synonyms or doubtful. Additionally, many genus names have changed since Bedot's time. In order to assemble a new catalogue of all hydrozoan species, I began to compile valid species names using Bouillon (1985) as a taxonomic framework of the genera. Species names were taken from Kramp (1961; 1968), Totton (1965), Zoological Record (1977 to 1996), Arai & Brinckmann-Voss (1980), Boero & Bouillon (1993), Bouillon (1971 to 1985), Bouillon et al. (1988 to 1991), Brinckmann-Voss (1970), Cairns (1991), Calder (1988; 1990), Cornelius (1995), Hirohito (1988, 1995), Kirkpatrick & Pugh (1984), Medel & Vervoort (1995), Millard (1975), Naumov (1969), Namikawa (1991), Pagès et al. (1992), Petersen (1990), Ramil & Vervoort (1992), Rees & Vervoort (1987); Schuchert (1996; 1997), Segonzac & Vervoort (1995), Svoboda & Cornelius (1991), Vervoort (1993), Watson (1978 to 1994), and Wedler & Larson (1986). After this, I was fortunate enough to receive from Prof. Wim Vervoort a more complete list of all hydrozoans except the Siphonophora. This list also was integrated into the catalogue. Obviously doubtful or unidentifiable species (according to the above cited studies) were set aside and will not show up in the following treatment. The work on this catalogue will continue and I intend to provide for each species a list of synonyms and references that allow a proper identification. Fig. 1 gives an idea how this catalogue will look. The catalogue in its present state is available from the author on diskette in a variety of formats and it is hoped that in the near future it will be available on the internet (see also Expert Center for Taxonomic Identification (ETI), University of Amsterdam, the Netherlands; UNESCO-IOC Register of Marine Organisms, at http://wwweti.eti.bio.uva.nl; this internet server will provide the list of nominal species compiled by W. Vervoort).

Table 1. The most prolific authors and the approximate number of hydrozoan species names introduced by them.

Author	species
Fraser	222
Allman	154
Nutting	121
Stechow	101
Cairns	92
Billard	89
Bale	82
Kramp	70
Millard	61
Bouillon	59
Totton	56
Haeckel	50
Bigelow	48
Hartlaub	45
Naumov	45
Jäderholm	43
Browne	42
Mayer	38
Watson	35
Linnaeus	35
Kirchenpauer	34
Vervoort	33
Torrey	32
Hirohito	31

Although it may never be possible to have a complete catalogue, my estimate is that at present it includes at least 90% of the available species names and it is thus representative for the following analyses. The catalogue was used to extract a species list by means of the Microsoft® Office Software package and it was converted to an MS-Access database. This enabled condensing and plotting the data.

The total number of putatively valid species described up to January 1997 is about 3260, which comes close to Werner's (1984) estimate of 3000. The contributions of the 24 most prolific authors are given in table 1. On top of this list is clearly Fraser, followed by Allman, Nutting and Stechow. However, Stechow and Fraser are notorious for their unreliability and I presume that in the future many of their species will be invalidated.

The 24 authors in table 1 described 1614 species, which account for almost exactly 50% of all known species. Some authors, notably Vervoort, have actually contributed more new descriptions than given in table 1, because species with multiple authors were scored separatedly. Including the co-authored publications, Vervoort's tally would rise to at least 53.

Research effort can roughly be estimated by counting the publications per year.

Genus *Solanderia* Duchassaing & Michelin, 1846

***Solanderia dendritica* (Fraser, 1938)**
Eugemmaria dendritica Fraser, 1938: 14, pl. 2 fig. 7.
Solanderia dendritica - Bouillon, Wouters & Boero 1992: 7, pl. 1.
TYPE LOCALITY: White Friars Islands and Navidad Head, Mexico Pacific Ocean.

***Solanderia fusca* (Gray, 1868)**
Ceratella fusca Gray, 1868: 579, fig. 2; Bale 1884: 48.
Dehitella atrorubens Gray, 1868: 579; Bale 1884: 48.
Solanderia atrorubens - Millard 1975: 61, 63.
Solanderia fusca - Watson 1982: 83, pl. 8 fig. 1; Bouillon, Wouters & Boero 1992: pls 2-3.
TYPE LOCALITY: Bondi Bay, Australia.

***Solanderia ericopsis* (Carter, 1873)**
Chitina ericopsis Carter, 1873: 13; Bouillon & Cornelius 1988: 1551, figs 1-5, 7.
Solanderia misakinensis - Wineera 1968: 2, figs 1-2, pl. 1-3.
Solanderia ericopsis - Schuchert 1996: 139, fig. 84a-g, frontispiece.
TYPE LOCALITY: New Zealand.

***Solanderia gracilis* Duchassaing & Michelin, 1846**
Solanderia gracilis Duchassaing & Michelin, 1864: 219; Wedler & Larson 1986: 81, fig. 4A, a, b; Bouillon, Wouters & Boero 1992: 8, pl. 4.
TYPE LOCALITY: Guadeloupe.

***Solanderia misakinensis* (Inaba, 1892)**
Dendrocoryne misakinensis Inaba, 1892: 96 figs 106-110.
Solanderia misakinenesis - Bouillon & Cornelius 1988: 1553, fig. 8; Bouillon, Wouters & Boero 1992: 10, fig. 1, pl. 7.
Solanderia misakiensis - Hirohito 1988: 47, fig. 14.
TYPE LOCALITY: Misaki, Japan.

***Solanderia proumbens* (Carter, 1873)**
Ceratella procumbens Carter, 1873: 10.
Ceratella spinosa Carter, 1873: 12.
Solanderia atrorubens - Marshall, 1892: 12 pl. 5, pl. 7 figs 2-4.
Solanderia procumbens - Millard 1975: 59, fig. 22; Bouillon, Wouters & Boero 1992: 11, pls 8-9.
TYPE LOCALITY: Natal.

***Solanderia secunda* (Inaba, 1892)**
Dendrocoryne secunda Inaba, 1892: 98, figs 111-113.
Solanderia rufescens Jäderholm, 1896: 5, pl. 1 figs 1-2.
Ceratella minima Hickson, 1903: 114, pl. 13; Wasin, East Africa.
Solanderia secunda - Hirohito 1988: 49, fig. 15.
Solanderia minima - Vervoort 1967: 25, fig. 2, pl. 3 figs 3-4; Millard 1975: 59, fig. 21C-E; Bouillon, Wouters & Boero 1992: 12 pls 5-6, 10-12.
Ceratella crosslandi Thornely, 1908: 85.
TYPE LOCALITY: Misaki, Japan.

Doubtful or unrecognisable *Solanderia* species (Bouillon, Wouters & Boero 1992):
Solanderia labyrintica (Hyatt, 1877); ***Solanderia leuckarti*** Marshall, 1892; ***Solanderia rugosa*** Marshall, 1892

Fig. 1. Part of the catalogue. Literature indicated in this table is not included in the present reference list, but can be found in Bouillon et al. (1992) and Schuchert (1996).

Since the volume and species numbers of systematic publications can vary drastically, the number of publications per decade (e.g. 1981 to 1990) is given in fig. 2. This will hopefully equalise the influence of single, voluminous publications. The graph in fig. 2 has some minor uncertainties, because all publications of the same author within one year had to be treated as one publication only. However, only a small minority of authors is thus concerned, and the difference will not be discernible in the figure. Fig. 2 shows a steady increase of the number of publications from 1820 to 1880. The depression of publication numbers in the twenties to forties can be attributed safely to World War I, the following economic crisis, and finally World War II. The consistently high numbers of publications during the last three decades proves that interest in hydrozoan taxonomy is not waning.

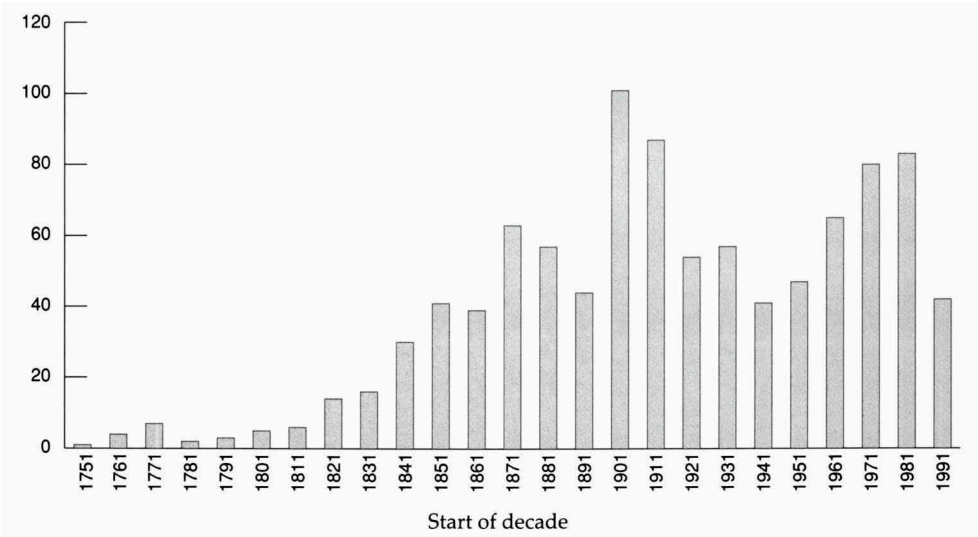

Fig. 2. Numbers of publications per decade.

Fig. 3 shows the total number of known hydrozoan species for each year starting with 1758. It is clear that species numbers initially accumulated only slowly, but after 1850 the curve becomes much steeper. The increase of new species can be explained mainly by the increase of studies (fig. 2). A secondary factor might be the availability and use of improved compound microscopes, allowing to study more distinctive micro-anatomical traits, especially in the Thecata. It is obvious that the curve (fig. 3) does not lend itself to making any prediction of future trends. The slope of the curve appears to be constant since 1900 and it might be expected to continue like that for a while or to level off.

The plot for the Athecata-Anthomedusae (also included here are the Laingiomedusae Bouillon, 1978b) looks rather similar, and no extrapolation for a maximal number can be made (fig. 4). About 1000 athecate hydroids and anthomedusae are known to date. During recent years, an astonishingly large number of Stylasteridae have been described, mainly by S.D. Cairns (see table 1, and Cairns, 1986 to 1991). Omitting the Stylasteridae from fig. 4, however, does not change the slope of the curve significantly (figure not shown).

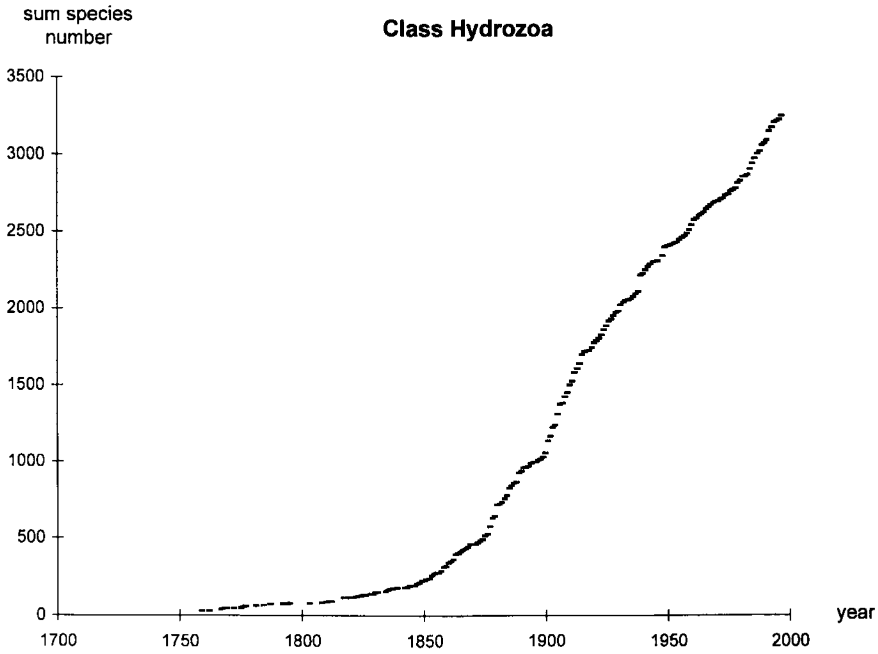

Fig. 3. Accumulation of hydrozoan species numbers since 1758.

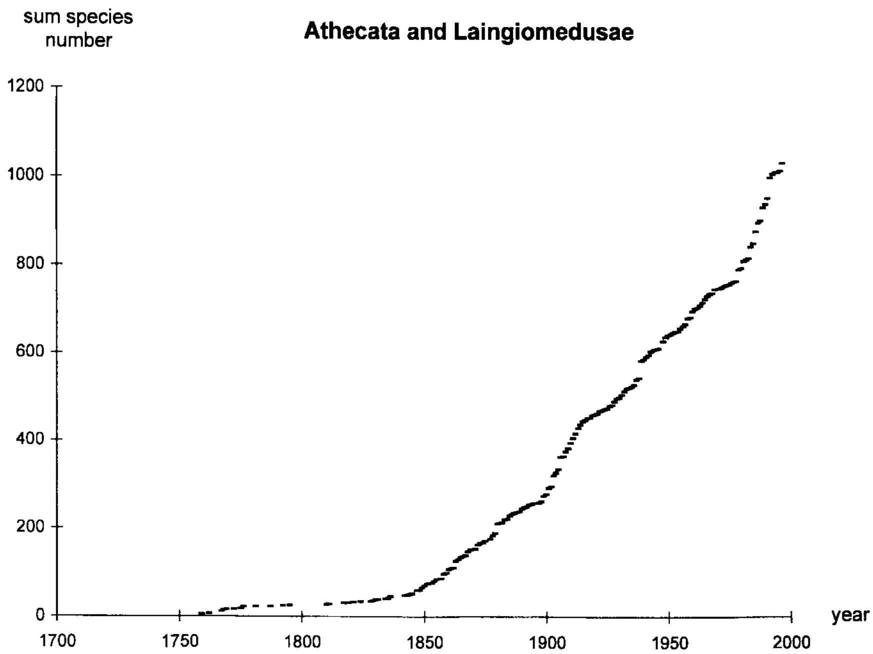

Fig. 4. Accumulation of species numbers for the Athecata and Laingiomedusae.

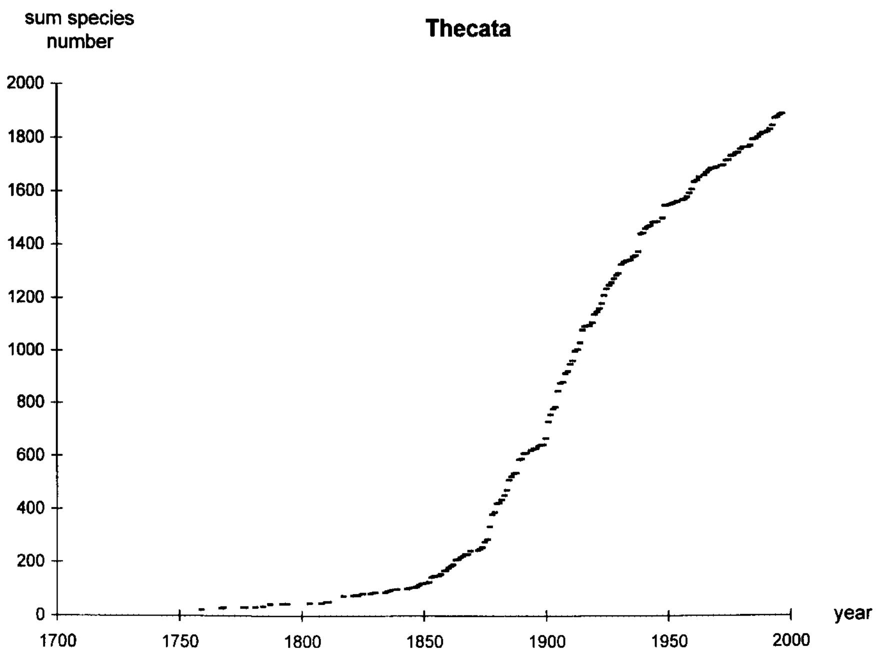

Fig. 5. Accumulation of species numbers for the Thecata-Leptomedusae.

The curve of the Thecata-Leptomedusae alone (fig. 5), suggests that the number of species will not increase so much as it did in the first part of this century. Extrapolating roughly, the number of Thecata will probably level off around 2500 species. However, this projection is valid only if the present intensity of research and the present methods will prevail. New methods may result in an increased rate of new species descriptions (see below).

The curve for the Trachymedusae (fig. 6) differs conspicuously from the previous ones. Although it also shows an accelerated accumulation of species after 1850, the curve bends sharply after 1920 and subsequently reflects moderate growth only. It thus appears that the number of the rather well investigated Trachymedusae will not exceed about 100 species.

The Narcomedusae (fig. 7) show a trend comparable with that of the Trachymedusae: their curve sharply bends after 1900 and species numbers have not increased very much since. The total number will thus probably amount to about 60 species.

The likewise mostly holopelagic Siphonophora (fig. 8), however, show a completely different curve again. Here we have a rather constant growth since 1800 and the curve shows no sign of convergence in the near future. Thus, the number of siphonophores will probably increase constantly over the coming years.

However, these extrapolations rely on the assumption that neither methods nor research effort will change. But for the former this may not be the case. Molecular techniques are being used more and more (see Hillis & Moritz, 1996). Unfortunately,

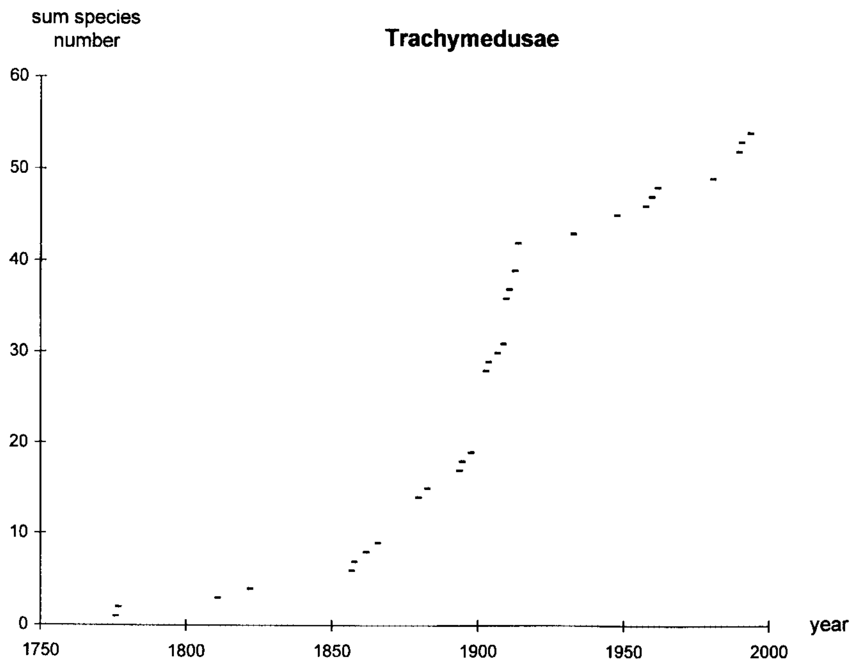

Fig. 6. Accumulation of species numbers for the Trachymedusae.

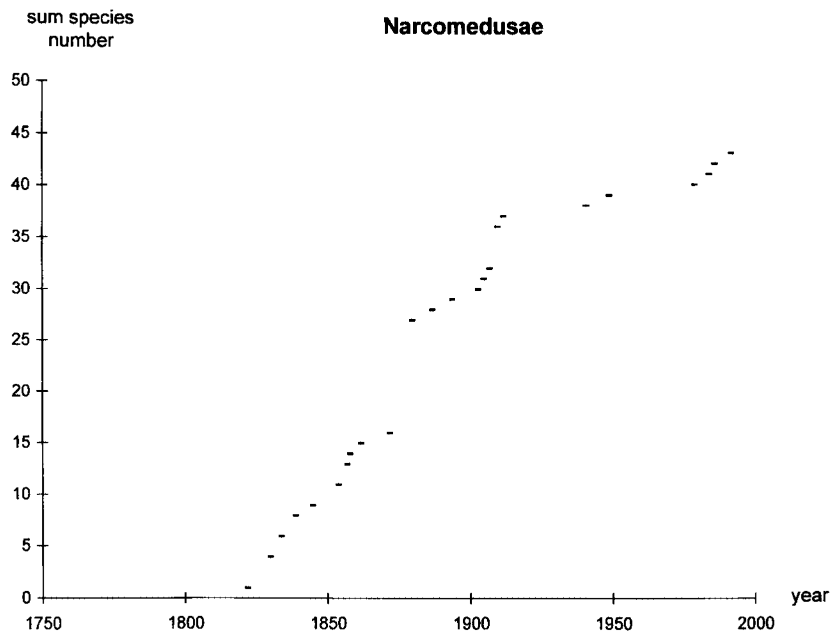

Fig. 7. Accumulation of species numbers for the Narcomedusae.

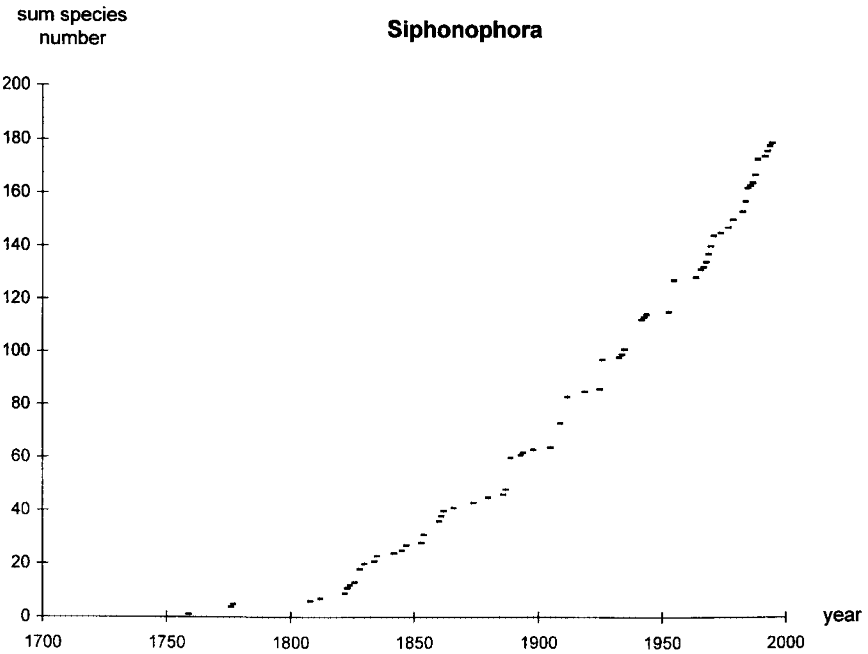

Fig. 8. Accumulation of species numbers for the Siphonophora.

genetic methods have been applied only rarely to systematic problems concerning hydrozoans. But the studies of Buss & Yund (1989) and Thorpe et al. (1992) elegantly demonstrate the power of these methods. Population genetic methods have also demonstrated the existence of sibling species in other marine cnidarians (Knowlton et al., 1992; McFadden et al., 1997), and it must be assumed that numerous hydrozoan species will turn out to represent species complexes (cf. Palumbi 1994). Thus, application of molecular systematic methods will definitely reveal a number of hidden species. However, a number of nominal species must be acknowledged to be unrecognisable and future morphological and molecular studies could invalidate a considerable fraction of the nominal species described so far. May & Nee (1995) estimated that about 20 % of all described species names are actually synonyms. This number also seems a good estimate in the Hydrozoans (pers. unpublished data). An illustration to the possible extent of invalid nominal hydrozoan species can be found in the genus *Obelia*. Cornelius (1975) reduced about 120 nominal *Obelia* species to three valid ones, which he later changed to four (Cornelius 1990; 1995). This is certainly an extreme case, but underlines the need for further revisions in other genera and families. Thus, although molecular techniques will probably enable us to distinguish new sibling species, this increase in total number will certainly be compensated by invalidations in other genera.

Concluding, the data and arguments presented above demonstrate that species level taxonomy in the Hydrozoa is still rewarding and that many interesting findings can be expected in the future.

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