Global diversity in the Thallassinidea (Decapoda): an update (1998-2004)

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Abstract

Within the past 6 years (1998-2004), the total number of known thalassinidean species has increased from 516 to 556, the number of genera from 80 to 96. The pattern of the latitudinal distribution changed markedly; the drop in species numbers between 10°N and 5°S is no longer present, mainly due to recent synonymisations and new collections. Thirty-six percent of the species are found in the Indo-West Pacific and 22 % in the Southwest Atlantic.

Key words: Thalassinidea, biodiversity, species numbers, latitudinal distribution

Introduction

Biodiversity as a field of scientific and common interest has rapidly become a catchword in the literature. One question raised in many papers on this topic is 'How many species are there?' (Diamond, 1985; May, 1988, 1990; Stork, 1993). Stork (1993) summarised five methods of obtaining an answer to this general question. These are based either on counting all species, extrapolations from known faunas and regions, extrapolations from samples, methods using ecological criteria, or censusing taxonomists' views.

Dworschak (2000) presented such a census of the known species within the Thalassinidea together with a survey on their latitudinal, regional and depth distribution.

The aim of this paper is to update this census and evaluate what has changed in the past six years.

Material and Methods

Data in figures 1-2 and Table I were derived from a database which held, per 31 December 1998, 3110, per 31 August 2004, 4115 records on Recent and fossil Thalassinidea. Known data on species numbers from the past (Fig. 1) were considered retrospectively, i.e. under current views of validity. The systematic arrangement of superfamilies and families follows that of Poore (1994) and Martin and Davis (2001). For practical reasons, the following families were pooled for figures on cumulative species numbers and latitudinal distribution: Ctenochelidae with the Callianassidae as Callianassidae s.l.; and Calocarididae, Micheleidae and Strahlaxiidae with the Axiidae as Axioidea. Due to low species numbers, the families Thomassiniidae, Laomediidae, Callianideidae and Thalassinidae are not shown separately in the graph on cumulative species numbers, but are included in the total Thalassinidea.

A particular species was considered valid when it was mentioned as such in several papers or - in case of single records - was never synonymised with any other taxon. In case of conflicting views of taxonomists in subsequent publications, the most recent opinion was adopted - with one exemption: *Nihonotrypaea japonica* and *N. harmandi* were considered different species following Wardiatno and Tamaki (2001) and Tamaki (2003) rather than Sakai (2001, 2004a).

Discovery curves and description rates were calculated using the methods outlined in May (1990) and Hammond (1992).

Latitudinal distribution of species was evaluated using 5° bands, assuming a continuous distribution between endpoints in cases of widely scattered records. For regional distribution, the geographic index of the Aquatic Science and Fisheries Abstracts (ASFA, Cambridge, UK) was used.

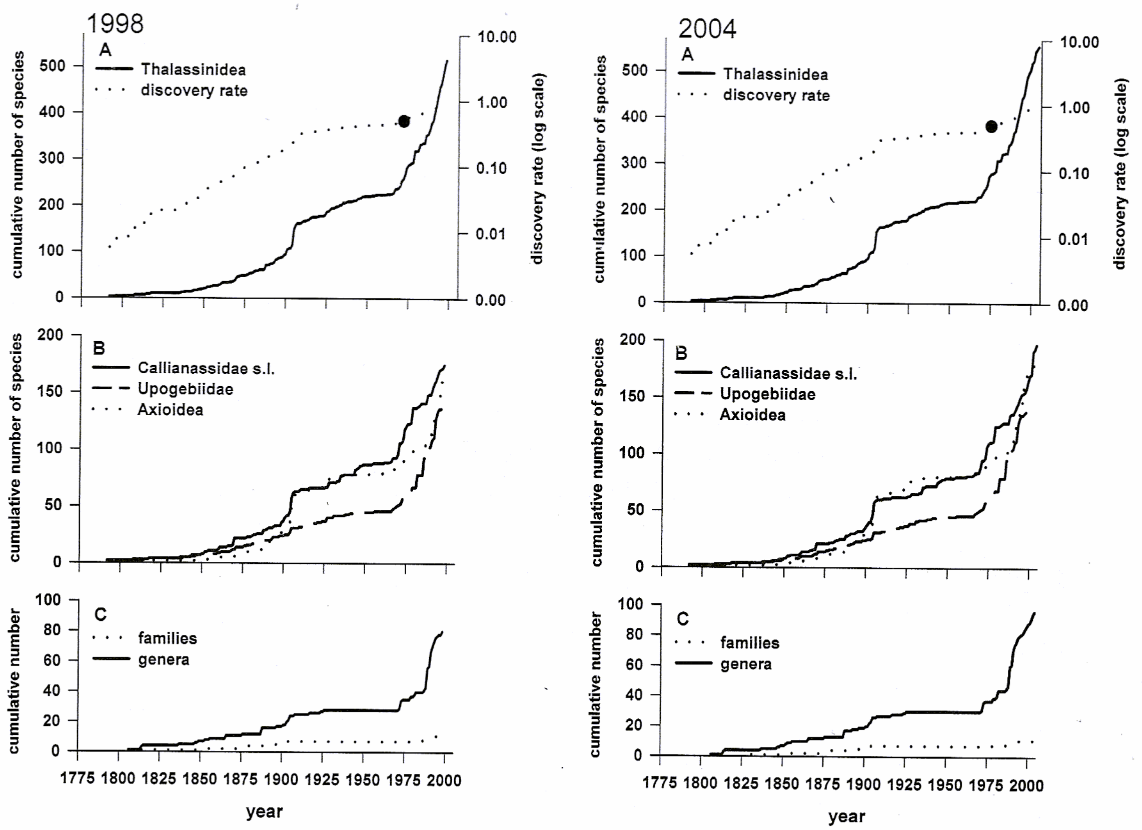

Figure 1: Time series for A: cumulative number of all thalassinidean species described up to 1998/2004 (solid line), cumulative number of known species expressed as a fraction of those known in 1998/2004 on a logarithmic scale (dotted line), the black circle indicates the point at which half of the 1998/2004 total was reached; B: cumulative numbers of species in major (super)families and C: cumulative numbers of genera and families within the Thalassinidea.

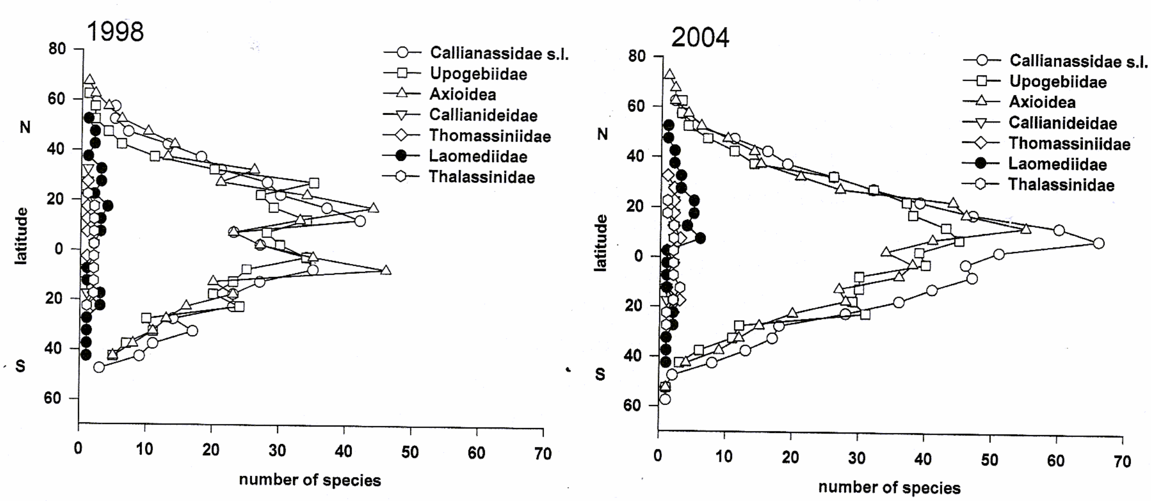

Figure 2: Latitudinal distribution of species numbers in the thalassinidean (super)families. Data of 1998 (left) and 2004 (right) for bands of 5° latitude.

Table I: Regional distribution of the Thalassinidea. Number of species recorded for each region (2004 data for families and net change from 1998-2004 for all). ANE: Atlantic Northeast; MED: Mediterranean; ASE: Atlantic Southeast; ANW: Atlantic Northwest; ASW: Atlantic Southwest; ISW: Indian Ocean; ISEW: Pacific Southwest; INW: Pacific Northwest; INE: Pacific Northeast; ISE: Pacific Southeast; PSE: Polar-Antarctic-Eastward; PSW: Polar-Antarctic-Westward. Ca: Callianassidae; Ct: Ctenochelidae; Up: Upogebiidae; Ax: Axiidae; Cc: Calocarididae; St: Strahlaxiidae; Cd: Callianideidae; To: Thomassiniidae; La: Laomediidae; Mi: Micheleidae; Ta: Thalassinidae. Sum of numbers may exceed that of total number of species because those species occurring in more than one region are added to each region separately.

Region	Ca	Ct	Up	Ax	Cc	St	Cd	To	La	Mi	Ta	all	change	%
ANE	4	1	4	2	3				1			15	+1	7.1
MED	8	1	7	3	1				1			21	+3	16.7
ASE	19	4	11	2	2				2			40	+10	33.3
ANW	3		1	3	1				1			9	0	0
ASW	37	6	25	22	8	1	1	2	7	11		120	+5	4.3
ISW	30	5	27	17	3	3	1	1	2	3	1	93	+12	14.8
ISEW	66	4	47	53	2	6	1	5	4	12	3	203	+40	24.5
INW	7	1	13	11	5							38	+2	5.5
INE	6	1	4	5	2							18	+2	12.5
ISE	14		19	11	2	2			4			53	-2	-3.9
PSE	9	2	5	7	1	1			2	1		30	+3	11.1
PSW	9		5	3	1					1		19	0	0
Total	172	25	143	121	26	9	2	8	21	26	3	556	+36	6.9

Results

Historical data on thalassinidean biodiversity

The first three species were described from the Mediterranean in 1792. From then on, the number of known species increased rapidly with doubling times between 23 and 24 years (Fig. 1). A very rapid increase in species numbers occurred between 1901 and 1906 with the major contributions of M. J. Rathbun, G. Nobili and especially J.G. de Man, who described numerous species collected during the Siboga Expedition 1899-1900. Between 1907 and 1950, species numbers increased only slowly and a plateau of around 220 species seemed to be reached in 1960. From that time on, species numbers again increased rapidly, doubling within 30 years and also continued after 1998. This pattern in the time series - with some deviations - is visible in the curves for the three species-rich (super)families. In the Callianassidae, the steep increase after 1900 is prominent compared to the weak one in the Upogebiidae. The time series of the number of families and genera also mirrors this pattern. A difference between the curves of the 1998 and the 2004 data is visible only for the Callianassidae s.l.; the increase in numbers is less steep up to 1975 in the latter, which is mainly due to synonymisations in the revision of this family by Sakai (1999). Currently, 11 families and 94 genera are recognised. Tudge & Cunningham (2002) presented data that support the retention of the family Axianassidae Schmitt, 1924 for the genus *Axianassa*. Here, however, this genus is included within the Laomediidae. Sakai (2004b) recently raised his subfamily Gourretiinae to family rank; here, this group is included within the Ctenochelidae following Tudge *et al.* (2000). In addition to the 80 genera considered in Dworschak (2000), the following genera were included in the counts: *Podocallichirus* Sakai, 1999; *Bathycalliax* Sakai & Türkay, 1999; *Grynaminna* Poore, 2000; *Pseudobiffarius* Heard & Manning, 2000; *Austinogebia* Ngoc-Ho, 2001; *Lipkecallianassa* Sakai, 2002; *Michaelcallianassa* Sakai, 2002; *Calliaxina* Ngoc-Ho, 2003; *Pestarella* Ngoc-Ho, 2003; *Manaxius* Kensley, 2003; *Laurentgourretia* Sakai, 2004; and *Paragourretia* Sakai, 2004. Not considered here is the synonymisation of 14 genera within the Callianassidae by Sakai (1999)(*Trypaea* Dana, 1852; *Cheramus* Bate, 1888; *Scallasis* Bate, 1888; *Biffarius* Manning & Felder, 1991; *Neotrypaea* Manning & Felder, 1991; *Notiax* Manning & Felder, 1991; *Gilvossius* Manning & Felder, 1992; *Poti* Rodrigues & Manning, 1992; *Nihonotrypaea* Manning & Tamaki, 1998; and *Necallianassa* Heard & Manning, 1998 with *Callianassa* Leach, 1914; *Corallianassa* Manning, 1987 and *Corallichirus* Manning, 1992 with *Glypturus* Stimpson, 1866; *Sergio* Manning & Lemaitre, 1994 with *Neocallichirus* Sakai, 1988, and *Eucalliax* Manning & Felder, 1991 with *Calliax* de Saint Laurent, 1973). Besides 556 valid taxa, 107 taxa are currently considered as junior synonyms. This represents a synonymisation rate of approximately 16%. Some 190+ names have been attributed to exclusively fossil Thalassinidea.

Latitudinal and regional distribution

The distribution of the Thalassinidea based on the 1998 data showed a clear latitudinal gradient with low species numbers in high and high species numbers in low latitudes (Fig. 2). For all three species-rich groups (Callianassidae s.l., Upogebiidae and Axioidea), two peaks were recognisable, one between 25 and 10°N and one between 0 and 15°S. The latter peak was more pronounced in the Axioidea than in the other two families. All three groups showed a drop in species number between 10°N and 5°S. The smaller families exhibited no clear pattern because of their low species numbers; the Thalassinidae occurred in low latitudes, whereas members of the Laomediidae are found only directly north and south of the equator.

The distribution based on the 2004 data also shows a clear latitudinal gradient. The drop in species numbers between 10°N and 5°S for the three species-rich groups, however, is no longer present.

The northernmost record (ca. 71° N) is still for the axiid *Calocarides coronatus* (Trybom, 1904) on the coast of Norway. The southernmost record was extended to 55°S by two new species from the Beagle Channel: *Notiax santarita* Thatje, 2000 and *Upogebia australis* Thatje and Gerdes, 2000 (Thatje, 2000; Thatje and Gerdes, 2000). The southernmost record in the Pacific is that of *Callianassa filholi* A. Milne-Edwards, 1878 from Stewart Island (ca. 47° S) (de Man, 1906). The widest north-south distribution is given for *Neotrypaea uncinata* (H. Milne Edwards, 1837) from 34°N to 47°S and for *Upogebia spinifrons* (Haswell, 1881) from 34°N to 34°S. Another species with a wide north-south range is *Callichirus major* (Say, 1818), which occurs from North Carolina (ca. 35°N) to southern Brazil (ca. 27° S). A wide circumtropical distribution has been attributed to *Axiopsis serratifrons* (A. Milne-Edwards, 1873)(Kensley, 1980).

The highest species numbers based on the 2004 data (36.5 %) are found in the Indo-West Pacific (ISEW in Table I) followed by the Atlantic Southwest with 21.6 %, where two-thirds of those occur in the Caribbean and Gulf of Mexico. In the Indian Ocean, species numbers (16.7%) are similar to those in the Caribbean. Only few species (1.6%) occur in the Atlantic Northwest compared to the Atlantic Northeast (2.7%) and the Mediterranean (3.8%). The Pacific Southeast is relatively species rich (9.5%) compared to the Pacific Northwest and Pacific Northeast, with 7% and 3.2 %, respectively.

The greatest increase in species numbers between 1998 and 2004 was observed in the Atlantic Southwest (+33%) followed by the Pacific Southwest (+24.5%) (Table I).

Depth distribution

Dworschak (2000) also presented an analysis of the depth distribution of thalassinidean species. A comparison of the 2004 with the 1998 data showed only slight changes of the depth distribution of the total Thalassinidea and that of most families. The Callianassidae are an exception. Here, the percentage of species found below 2 m increased, most pronouncedly between 20 and 200 m – from 23.9% to 33.1% of the total numbers. This was due to the numerous new species described by Sakai (2002, 2004b) which were sampled with grabs from deeper bottoms.

Discussion

The drop in species numbers between 10° N and 5° S in the latitudinal distribution of the Thalassinidea based on the 1998 data was explained by Dworschak (2000) as reflecting actual occurrence as well as collectors' activities. Evaluation of the 2004 data, however, shows that this gap was certainly due to collectors' and/or revisors' activities. New species described from formerly under-represented regions such as the Andaman Sea at 6-8°N (Sakai, 2002), Socotra (Sakai and Apel, 2002) and Guam (Kensley, 2003), together with the collection of already described species from these regions and the inclusion of new material in revisions (i.e. Sakai, 1999; Ngoc-Ho, 2003), led to an increase of species numbers between 10° N and 5° S. In addition, recent synonymisations resulted in wider distributions of single species compared to the limited distributions of two or more separate ones.

As mentioned earlier (Dworschak, 2000) this type of census approach is not suitable to predict actual species numbers. Comparison of the 1998 with the 2004 data show that species numbers continue to increase exponentially, that over the past 20 years the mean description rate has increased, and that the current description rate has slighly decreased (Table II).

Table II: Summary of species numbers in families and description rates for the 1998 and 2004 data. * one species of Thomassiniidae erroneously placed in Micheleidae in 1998. ** difference due to erroneous genus count - 73 in text versus 74 in keys - in Poore (1994) and 3 overlooked genera by Dworschak (2000).

Group		1998	new after 1998	2004	net change
Axioidea					
	Axiidae	113	10	121	+8
	Calocarididae	23	2	26	+3
	Strahlaxiidae	9	0	9	0
	Micheleidae	27	0	26	*-1
Callianassoidea					
	Callianassidae	155	35	173	+18
	Ctenochelidae	20	4	24	+4
	Callianideidae	2	0	2	0
	Laomediidae	19	1	21	+2
	Thomassiniidae	7	0	8	+1
	Upogebiidae	139	5	143	+4
Thalassinoidea					
	Thalassinidae	2		3	+1
	total species	516	57	556	+40
	families	11	0	11	0
	genera	80	12	96	**+16
	overall mean (species/year)	2.49		2.61	
	mean 1978(1984)-1998(2004)	10.62		11.05	
	growth rate per year from 1978/1984 on	2.06		1.99	
	50% of today's numbers reached in	1972		1975	

A census based on the taxonomists' views has several caveats and limitations. The database used for this census is based exclusively on published accounts. Thus, publications may have been overlooked, especially those in more local journals. Such incompleteness is probably less severe when it comes to species numbers, but may have a large influence on our knowledge of latitudinal and regional distribution patterns. In addition, more information is certainly present in "unpublished" accounts and in catalogues and inventories of natural history museums. This information is increasingly becoming available over the internet (Graham *et al.*, 2004). The species identifications in museum collections, however, are often outdated and need to be verified or revised (Wheeler, 2004).

Another general problem in counting species is the validity of the species and that of different species concepts, which may yield different counts when the same data are examined based on different taxonomies (Mallet, 2001). Even among taxonomists, who mainly use the typological concept, species delimination depends on whether they split or lump. Within the Thalassinidea, no controversial views on the validity of most species exist because only few researchers are currently active in this field. One exeption is *Nihonotrypaea japonica* versus *N. harmandi*: detailed studies on distribution, burrow morphology, behaviour, larval and adult morphology provided strong evidence that two very similar species occur in Japanese waters (Wardiatno and Tamaki, 2001; Tamaki, 2003 and references therein). This was denied by Sakai (2001) and ultimately reduced to a merely taxonomic and nomenclatural problem by Sakai (2004a).

Most thalassinidean species, however, are less well studied. Of the 556 species of Thalassinidea, 108 (or ca. 20%) are known only from a single specimen; 43 of those have not been found again since their description more than 50 years ago. It is very likely that many of the subsequently described species are identical with the already described ones but could not be attributed to them due to insufficient descriptions. This is especially critical within the Callianassidae, which have a pronounced sexual dimorphism and allometric growth in taxonomically important characters. Here, the probability that the male, the female and juveniles have been described as three separate species is very high.

The benefit of such a census is that it points to the gaps in our knowledge. Filling these gaps requires revisions using type material together with new collections from the type localities. Secondly, new collections with efficient techniques should be made. Yabby pumps should be employed in the intertidal (using SCUBA in the shallow subtidal), grab samples in deeper sublittoral sediments.

Acknowledgements

This paper is dedicated to the late Brian Kensley, the late Raymond B. Manning, the late Sergio de A. Rodrigues and the late Austin B. Williams, who contributed essentially to our knowledge of the Thalassinidea. My thanks are due to Fernando Mantelatto for inviting me to present this contribution at the 3rd Brazilian Crustacean Congress in Florianopolis, SC, Brazil.

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Received: 10th Mar 2005
Accepted: 13th May 2005