

ZOOLOGISCHE MEDEDELINGEN

UITGEGEVEN DOOR HET

RIJKSMUSEUM VAN NATUURLIJKE HISTORIE TE LEIDEN
(MINISTERIE VAN WELZIJN, VOLKSGEZONDHEID EN CULTUUR)

Deel 62 no. 3

25 mei 1988

ISSN 0024-0672

MEDUSIVOROUS FISHES, A REVIEW

by

R.M.L. ATES

Ates, R.M.L.: Medusivorous fishes, a review.

Zool. Med. Leiden 62 (3), 25-v-1988: 29-42, tables 1-2. — ISSN 0024-0672.

Key words: Hydromedusae; Scyphozoa; Ctenophora; jellyfish; fishes; prey.

A preliminary review is presented of fish species having consumed pelagic Cnidaria (Scyphozoa and Hydrozoa) as well as Ctenophora. Quantitative data are scarce. Knowledge of morphological and physiological adaptations of fishes foraging on gelatinous plankton is almost non-existent. Many fish species consume medusae and some reasons to suspect that there are even more that do so, are discussed.

R.M.L. Ates, Govert Flinckstraat 19, 1506 LL Zaandam, The Netherlands.

INTRODUCTION

In Indonesia, Japan, China and the Philippines some species of medusae are highly praised (Kishinouye, 1899; Ates, 1987). However, in the western world medusae have since long been despised for human consumption. Possibly for psychological reasons, the refusal of jellyfish as a food source in Europe went so far that it was regarded most unlikely that they could serve other animals as such. So, Günther (1882), speculating in respect of *Schedophilus medusophagus*, stated: "The idea expressed by the specific name of our fish, viz. that it follows Medusae in order to feed on them could not be correct as the fish could draw but little nourishment from those animals . . .".

Jellyfishes as predators of fish and fish larvae have received much attention. Their impact on fish stocks is considerable (Möller, 1984). Their role as prey for other organisms, however, is neglected. Gudger (1934) reviewed fish eating jellyfishes and remarked: „Jellyfishes do eat fishes, and in turn some of the fishes eat medusae . . .". From the literature it does not appear that Gudger (1934) ever reviewed jellyfish-eating fishes, and later Mansueti (1955:2) stated in respect of jellyfish: ". . . as far as is known, the adults do not serve as food for other species . . .". Mansueti (1963:68) reviewed three

species of fish feeding upon jellyfishes calling them spectacular examples. A review by Von Salvini-Plawen (1972) demonstrated that Cnidaria are a vast source of food for marine invertebrates; the nematocysts contained by this type of prey are apparently no barrier for many predators and parasites contrary to a widely held belief. Von Salvini-Plawen (1972:387) also made allusion to a few fishes eating jellyfish and Siphonophora. Oviatt & Kremer (1977) mentioned four fish species consuming "such unlikely food sources as ctenophores, jellyfish . . .". Black & Low (1983) put forward that a jellyfish diet of fishes, in their case a ctenophore diet of two salmonids, may be more important than hitherto realized. Runge et al. (1987) confirmed *Scomber scombrus* to consume medusae, if available in the laboratory, and also stressed that such a diet may be important to this fish. Scattered in the literature many more incidental references, often somewhat obscured, are to be found of fishes preying upon pelagic Cnidaria and Ctenophora (cf. table 1 and 2).

Table 1. Review of medusivorous fishes as found in the literature, systematically arranged according to Nelson (1984).

Identification of predator and prey organisms has not been checked. Some authors did not, or could not distinguish between certain prey items (/ = and/or; * = aquarium observation; ** see discussion; # = more references are available).

predator	prey	locality	source
Callorhynchidae <i>Callorhynchus milii</i> (Bory de St. Vincent)	Scyphozoa	New Zealand	Graham, 1939
Squalidae <i>Etmopterus spinax</i> (L.)	medusae	north Atlantic	Mauchline & Gordon, 1983a
<i>Centroscyllium fabricii</i> (Reinhardt)	medusae	north Atlantic	Bigelow & Schroeder, 1953
<i>Centroscymnus coelolepis</i> Bocage & Capella <i>Somniosus microcephalus</i> (Schneider)	medusae (<i>Atolla</i>)	north Atlantic	Mauchline & Gordon, 1983a
<i>Squalus acanthias</i> L.	Pleurobrachia Ctenophora Ctenophora	north Atlantic Danish waters Gulf of Maine	Bigelow & Schroeder, 1953
	<i>Beroe</i> jellyfish	North Sea North Sea	Mortensen, 1912 Blegvad, 1916 Holden, 1966
			Bigelow & Schroeder, 1953 Rae, 1967
Elopidae <i>Megalops atlanticus</i> Cuvier & Valenciennes	Ctenophora	Florida waters	Randall, 1967
Clupeidae <i>Sardinops melanostictus</i>	jellyfish-larva	Japanese waters	Yasuda, 1960

(Temminck & Schlegel)			
<i>Opisthonema oglinum</i> (LeSueur)	Siphonophora	Caribbean	Randall, 1967
Argentinidae			
<i>Argentina silus</i> (As-canius)	Salpidae/Ctenophora	north Atlantic	Mauchline & Gordon, 1983b
Bathyagidae			
<i>Bathyagus euryops</i> Goode & Bean	Salpidae/Ctenophora	north Atlantic	Mauchline & Gordon, 1983b
Alepocephalidae			
<i>Alepocephalus bairdii</i> Goode & Bean	Ctenophora & medusae <i>Periphylla hyacinthina</i> Streenstrup <i>Atolla</i> medusae	central & east Atlantic north Atlantic north Atlantic	Golovan & Pakhorukov, 1975 Du Buit, 1978
	medusae	north Atlantic	Wheeler, 1978 Mauchline & Gordon, 1983b Glukhov et al., 1983
Salmonidae			
<i>Salmo salar</i> L.	Ctenophora	North Sea	Krumbach, 1928
<i>Oncorhynchus keta</i> (Walbaum)	Ctenophora	Japanese waters	Suyehiro, 1942
<i>Oncorhynchus tshawytscha</i> (Walbaum)	Ctenophora	Br. Columbian waters	Black & Low, 1983
		Br. Columbian waters	Black & Low, 1983
Sternoptychidae			
<i>Argyropelecus aculeatus</i> Valenciennes	Siphonophora	eastern north Atlantic	Merrett & Roe, 1974
Myctophidae			
<i>Ceratoscopelus warmingi</i> (Lütken)	Siphonophora	central Pacific	Clarke, 1980
Gadidae			
<i>Gadus morrhua</i> L.	<i>Pleurobrachia</i> <i>Beroe</i> & <i>Bolina</i>	Danish waters Greenland waters	Poulsen, 1931 Jensen & Hansen, 1931
	<i>Pleurobrachia</i> , <i>Beroe</i> & <i>Bolina</i> , <i>Mertensia</i>	Greenland waters	Hansen, 1949
	<i>Pleurobrachia</i>	Gulf of Maine	Bigelow & Schroeder, 1953
<i>Melanogrammus aeglefinus</i> (L.)	<i>Beroe</i>	Barentsz Sea	Kamshilov, 1960
<i>Merlangius merlangus</i> L.	<i>Cyanea</i>	North Sea	Scheuring, 1915*
<i>Pollachius virens</i> (L.)	<i>Cyanea</i> Ctenophora	North Sea Gulf of Maine	Dahl, 1961* Bigelow & Schroeder, 1953
	<i>Pleurobrachia</i> medusae	north Atlantic North Sea	Lie, 1961 Robb & Hislop, 1980

Macrouridae			
<i>Coryphaenoides rupestris</i> Gunnerus	Ctenophora/Salpidae medusae	north Atlantic north Atlantic	Mauchline & Gordon, 1984 Du Buit, 1978
Scorpaenidae			
<i>Sebastes flavidus</i> (Ayres)	Siphonophora/ Ctenophora/Cnidaria	northeastern Pacific	Brodeur & Pearcy, 1984
Hexagrammidae			
<i>Hexagrammos superciliosus</i> (Pallas)	jellyfish	north Pacific	Grossman, 1986
Cyclopteridae			
<i>Aptocyclus ventricosus</i> (Pallas)	medusae/ Ctenophores	Bering Sea	Yoshida & Yamaguchi, 1985 see Ates, 1987#
<i>Cyclopiterus lumpus</i> L.	Scyphozoa/ Ctenophora	north Atlantic	
<i>Paraliparis calidus</i> Cohen	Cnidaria/Ctenophora/ Salpidae	north Atlantic	Wenner, 1979
<i>Paraliparis copei</i> Goode & Bean	Cnidaria/Ctenophora/ Salpidae	north Atlantic	Wenner, 1979
Carangidae			
<i>Trachurus trachurus</i> (L.)	<i>Cyanea</i>	North Sea	Malm, 1852
	<i>Cyanea</i>	North Sea	Scheuring, 1915
<i>Caranx fuscus</i> Geoffroy de St. Hilaire	Siphonophora	Caribbean	Randall, 1967
Coryphaenidae			
<i>Coryphaena hippurus</i> L.	medusae	Mediterranean	Bannister, 1976
Emmelichthyidae			
<i>Inermia vittata</i> Poey	Siphonophora	Caribbean	Randall, 1967
Lutjanidae			
<i>Ocyurus chrysurus</i> (Bloch)	Siphonophora, Ctenophora	Caribbean	Randall, 1967
Sparidae			
<i>Chrysophrrys auratus</i> L.	scyphomedusae/hydromedusae	New Zealand waters	Godfriaux, 1969
<i>Pagrosomus major</i> (= <i>Pagrus major</i> (Temminck & Schlegel))	certain jellyfishes	Japanese waters	Suyehiro, 1942
Sciaenidae			
<i>Sciaenops ocellata</i> (L.)	Ctenophora	Gulf of Mexico	Bass & Avault, 1975
Pomacentridae			
<i>Chromis cyanea</i> Poey	Siphonophora	Caribbean	Randall, 1967
<i>Chromis multilineata</i> (Guichenot)	Siphonophora	Caribbean	Randall, 1967
<i>Chromis vanderbilti</i> (Fowler)	Siphonophora	Hawaiian waters	Hobson, 1974
<i>Chromis verater</i>	Siphonophora	Hawaiian waters	Hobson, 1974

(Fowler)			
<i>Pomacentrus fuscus</i> (Cuvier & Valen- ciennes)	Scyphozoans	Caribbean	Randall, 1967
Labridae			
<i>Clepticus parrae</i> (Bloch & Schneider)	Siphonophora	Caribbean	Randall, 1967
Pholididae			
<i>Pholis gunnellus</i> (L.)	<i>Pleurobrachia</i>	North Sea	Greve, 1972*
Anarhichadidae			
<i>Anarhichas latifrons</i> Steenstrup	Quallen	north Atlantic	Künne, 1950**
Nototheniidae			
<i>Notothenia larseni</i> Lönnberg	Coelenterata/ Ctenophora	Antarctica	Daniels, 1982
<i>Notothenia neglecta</i> Nybelin	Coelenterata/ Ctenophora	Antarctica	Daniels, 1982
Opistognathidae			
<i>Opistognathus au- rifrons</i> Jordan & Thompson	Siphonophora	Caribbean	Randall, 1967
Acanthuridae			
<i>Acanthurus thompsoni</i> (Fowler)	Siphonophora	Hawaiian waters	Hobson, 1974
<i>Naso hexacanthus</i> (Bleeker)	Siphonophora	Hawaiian waters	Hobson, 1974
Scombridae			
<i>Scomber japonicus</i> Houttuyn	jellyfish-larva	Japanese waters	Yasuda, 1960
<i>Scomber scombrus</i> L.	<i>Vevelia</i>	northwestern Pacific	Hart, 1974
	Quallen	Baltic	Möbius & Heincke, 1883
	jellyfish	western north Atlan- tic	Baird, 1889
	<i>Pleurobrachia</i>	Irish Sea	Scott, 1920, 1924
	Medusen und	North Sea	Künne, 1950
	Ctenophora		
	<i>Aglantha digitale</i> (O.F. Müller)	Canadian waters	Runge et al, 1987*
Luvaridae			
<i>Luvarus imperialis</i> Rafinesque	Scyphozoa & Ctenophora	eastern north Atlantic	Gotshall & Fitch, 1968
Centrolophidae			
<i>Centrolophus niger</i> (Gmelin)	<i>Rhizostoma</i>	Mediterranean	Lo Bianco, 1909*
	Siphonophora		
<i>Hyperoglyphe percifor- mis</i> (Mitchill)	jellyfishes	central Atlantic	Collett, 1896
	Ctenophora	north Atlantic	Wheeler, 1978
		Gulf of Maine	Bigelow & Schroeder, 1953

<i>Icichthys lockingtoni</i>	Siphonophora	north Pacific	Haedrich, 1966
<i>Jordan & Gilbert</i>			
<i>Psenopsis anomala</i> (Temminck & Schlegel)	jellyfish	Japanese waters	Suyehiro, 1942
<i>Schedophilus</i> <i>medusophagus</i> Cocco	medusae	north Atlantic	Haedrich, 1967
<i>Schedophilus pemarco</i> Poll	<i>Atolla</i> jellyfish	north Atlantic	Wheeler, 1978
		north Atlantic	Haedrich & Cervigon, 1969
Nameidae			
<i>Nameus gronovii</i> (Gmelin)	<i>Physalia</i>	Japanese waters	Kato, 1933
	<i>Physalia</i>	Florida waters	Jenkins, 1983*
Stromateidae			
<i>Pampus argenteus</i> (Eu- phrasen)	medusae Salpidae and hydromedusae	Japanese waters Arabian Sea	Suyehiro, 1942 Rege & Bal, 1963
	medusae	East China Sea	Higashikawa et al., 1981
<i>Pampus chinensis</i> (Eu- phrasen)	Ctenophora and medusae	Bay of Bengal	Pati, 1980
<i>Peprilus burti</i> Fowler	<i>Cyanea</i> jellyfish	Gulf of Mexico	Phillips et al., 1969
<i>Peprilus paru</i> (L.)	<i>Chrysaora</i>	Gulf of Mexico	Horn, 1970
	sea nettle	north Atlantic	Dunnington & Mansueti, 1955
	<i>Chrysaora</i> jellyfish	north Atlantic	Cargo & Schultz, 1966
<i>Peprilus triacanthus</i> (Peck)	Ctenophora	western Atlantic	Mansueti, 1963*
	<i>Chrysaora</i> jellyfish	north Atlantic	Horn, 1970
	<i>Mnemiopsis</i>	north Atlantic	Bigelow & Schroeder, 1953
		north Atlantic	Mansueti, 1963
		north Atlantic	Oviatt & Kremer, 1977
<i>Stromateus fiafola</i> L.	<i>Cotylorhiza</i>	Mediterranean	Lo Bianco, 1909*
Pleuronectidae			
<i>Pleuronectus platessa</i> L.	<i>Pleurobrachia</i>	North Sea	Greve, 1972*
Balistidae			
<i>Aluterus schoepfi</i> (Wal- baum)	<i>Chrysaora</i>	north Atlantic	Cargo & Schultz, 1966
<i>Aluterus scripta</i> (Os- beck)	<i>Physalia</i>	Arabian Sea	Chappgar, 1977*
<i>Canthidermis sufflamen</i> (Mitchill)	Siphonophora	Caribbean	Randall, 1967
<i>Melichthys niger</i> Bloch	Siphonophora	Caribbean	Randall, 1967
<i>Xanthichthys ringens</i> (L.) = <i>X. mento</i> Jor- dan & Gilbert	Siphonophora	Hawaiian waters	Hobson, 1974
Ostraciidae			
<i>Acanthostracion quad- ricornis</i> L.	Scyphozoa	Caribbean	Randall, 1967

Molidae

<i>Mola mola</i> (L.)	medusae jellyfishes jellyfish, Ctenophora	north Atlantic Japanese waters Gulf of Maine	Binney, 1842 Suyehiro, 1942 Bigelow & Schroeder, 1953
	jellyfish jellyfishes, comb- jellies	northeastern Pacific north Atlantic	Hart, 1974 Wheeler, 1978*
<i>Ranzania laevis</i> (Pen- nant)	medusae and combjellies	north Atlantic	Wheeler, 1978

Table 2. Fish species listed in table 1, reported to have their stomach(s) filled solely or for a considerable part with the remains of medusae [two references, however (indicated by asterisk), may relate to salps].

species	source
<i>Alepocephalus bairdii</i>	Golovan & Pakhorukov (1975)
<i>Aptocyclus ventricosus</i>	Yoshida & Yamaguchi (1985)
<i>Cyclopterus lumpus</i>	Ates (1987)
<i>Icichthys lockingtoni</i>	Haedrich (1966)
<i>Mola mola</i>	Bigelow & Schroeder (1953), Wheeler (1978)
<i>Pampus argenteus</i>	Suyehiro (1942)
<i>Paraliparis copei</i>	Wenner (1979)*
<i>Paraliparis calidis</i>	Wenner (1979)*
<i>Peprius paru</i>	Cargo & Schultz (1966)
<i>Peprius triacanthus</i>	Horn (1970), Oviatt & Kremer (1977)
<i>Peprius burti</i>	Phillips et al (1969)
<i>Psenopsis anomala</i>	Suyehiro (1942)
<i>Ranzania laevis</i>	Wheeler (1978)
<i>Schedophilus pemarco</i>	Haedrich & Cervigon (1969)
<i>Schedophilus medusophagus</i>	Wheeler (1978)

DISCUSSION

Larson (1986) suggested a high water content of gelatinous zooplankton to be an adaptation, a.o. to prevent these organisms from being consumed; a high water content would make "poor food for predators and parasites". However, many parasites of medusae are known (Thiel, 1976, Brandon & Cutress, 1985, Harbison et al., 1977 and Harbison et al., 1978 and others). In addition, the present paper reviews many fish species recorded to have consumed medusae, suggesting that medusae are a useful source of food instead.

Though the data are not overwhelming, it seems that the fishes listed in table 2 consume Cnidaria and Ctenophora indiscriminately. It is hard to

deduce from the information contained in tabel 1 if the non-specialized fishes distinguish between Cnidaria and Ctenophora.

Quantities of medusae found in the stomachs of non-specialized fishes sometimes are so small according to the records (often less than 1% of stomach contents), that including these fishes in table 1 may seem useless, but in point of fact it is quite likely that the amount of pelagic Cnidaria and Ctenophora consumed by various fish species is more significant than suggested:

a. Jellyfish prey presumably soon disintegrates after being consumed. Therefore, jellyfish remains may easily be overlooked in fish stomachs. Thus, only a small number of authors recognized the whitish mass in the stomachs of *Cyclopterus lampus* as such (Ates, 1987). Most of the methods to analyze fish stomach contents as reviewed by Hyslop (1980) do not seem to be suitable to establish the presence or absence of jellyfish remains. For this purpose, microscopical research will invariably be necessary. Only the microscope could clear up the origin of the unidentified jelly/mucous in the stomachs of *Xenodermichthys copei* (Gill) (Alepcephalidae) as quoted by Mauchline & Gordon (1983b). On the other hand, there is the example of *Tetragonurus cuvieri* Risso, for more than 150 years believed to be a jellyfish-eating specialist (Risso, 1826), but which, as a result of microscopical investigations (Janssen & Harbison, 1981) turned out to be a salp-eating specialist.

A method for stomach contents analysis in order to reveal the presence of remains of Cnidaria is described for sea turtles by Den Hartog (1980).

b. It seems from table 1 as if no special adaptations are involved for a fish to become a jellyfish predator. Considering the presumed fragility of their skins and sometimes the presumed unsuitability of their mouths, it is hard to imagine members of fish families such as Elopidae, Clupeidae, Argentinidae, Salmonidae, Sternopychidae, Gadidae, Macrouridae, Carangidae, Sparidae, Pomacentridae, Opistognathidae, and Scombridae to be predators of medusae if the records in table 1 would not prove that they are. It is clear from table 1 that jellyfish predation by fishes is a common phenomenon. In view of jellyfish abundance it seems reasonable to assume that in the future more planktonivorous fish species will be found to consume medusae if available.

c. Fisheries research started and is still mainly centered around the Atlantic. Most references concern fish species from the Atlantic and the references are disproportionately distributed among commercially important fish species. So it seems obvious that more jellyfish consuming fish species are to be discovered as soon as fisheries research develops elsewhere and in groups of non-commercial fish.

d. Many fishes belonging to the suborder Stromateoidei (families Amarripidae, Ariommataidae, Centrolophidae, Nomeidae and Stromateidae) show

similarities in dentition (Janssen & Harbison, 1981: 925, Bühler, 1930: 88 and others), stomach morphology (Bühler, 1930: 94 etc.) and ecology (Haedrich, 1967) and at least some of them share a similar feeding behaviour (Haedrich in Horn, 1977). The stomachs of some species of the Stromateoidei invariably contain "chunks of whitish or transparent, amorphous tissue" (Horn, 1970). In view of the foregoing it seems likely that more, perhaps most, fishes of this suborder are medusivorous specialists.

Incidentally, it is noted that many species of Stromateoidei maintain a symbiotic relationship with a jellyfish host (Mansueti, 1963). Most of the records of the symbiosis between members of the Stromateoidei and medusae do not include the identification of the host (Mansueti, 1963). The information available on some of them (for instance *Schedophilus medusophagus* together with *Phacellophora camtschatika* Brandt according to Bone & Brook, 1973) suggests that these relationships may be with a limited number of hosts or strictly specific. In consequence, it is tempting to speculate that the variations in dentition, gullet morphology etc., within the suborder Stromateoidei may be related to specialisation on certain jellyfish prey. As *Cyclopterus lumpus*, *Aptocyclus ventricosus* and (possibly) members of the genus *Paraliparis* are jellyfish predators to a large extent, it may be worth-while to investigate whether other members of the Cyclopteridae are jellyfish predators as well. More specialist medusivorous fishes may be found among other slow moving oceanic fishes like Alepocephalidae, Molidae and Balistidae (in respect of the latter, see Anon., 1985).

e. Another reason to assume that there are more fish species consuming medusae is the circumstance that certain species of jellyfish are used in Japan as bait to catch *Monacanthus* (Balistidae) and *Pagrus* (Sparidae) (Kishinouye, 1899). Similar information is quoted by Townsend (1929) according to Randall (1967) for *Chaetodipterus faber* (Broussonet) (Ephippidae) who states that fishermen in Trinidad catch this fish with pieces of *Physalia* as bait.

FURTHER NOTES

Anarhichas denticulatus as a jellyfish predator. — Künne (1950:75) asserts that the flesh of the jelly-cat, *Anarhichas denticulatus* Krøyer (= *A. latifrons* Steenstrup) becomes whitish and of low quality when it eats many jellyfishes. A stomach content analysis, however, does not seem to have been carried out. Therefore, the statement of Künne (1950) may be questioned. According to Wheeler (1978) the flesh of this species is weak and watery without exception, although its normal diet consists of hard-shelled benthic invertebrates like crustaceans, sea-urchins and brittle-stars.

Amphipod remains in fish stomachs. — Hyperiid amphipods in fish stomachs may originate from consumed jellyfishes, but not necessarily so. Many authors (a.o. Haedrich & Cervigon, 1969: 3; Glukhov et al., 1983; Mauchline & Gordon, 1983b: 69; Brodeur & Pearcy, 1984: 276, 277; and Ates, 1987) report the combined presence of remains of hyperiid amphipods and jellyfish in fish stomachs. However, some species of hyperiid amphipods regularly found with medusae, are also capable to lead a life separate from these hosts [see Von Westernhagen & Rosenthal, 1976, concerning *Hyperoche medusarum* (Krøyer) and note that it is unknown what happens to the countless numbers of *Hyperia* symbiotic with medusae such as *Aurelia* when the latter disappear from the plankton after a bloom]. This implies that the presence of hyperiid amphipod remains in fish stomachs should not be interpreted as an indication for the consumption of jellyfish, unless the presence of the latter is obvious. Thus, a high percentage of hyperiid remains, coinciding with significant amounts of unidentifiable matter in fish stomachs, as reported by Peterson et al. (1982:848) for salmon in the north Pacific, may result from the consumption of medusae. Although Peterson et al. do not consider this possibility, the studies by Black & Low (1983) strongly suggest so.

CONCLUSION

Many fish species have apparently adapted to live on medusae and it is obvious that there are many more that do so than those contained in table 1. It remains to be seen if jellyfish stocks are controlled by fishes as calculated to be possible by Oviatt & Kremer (1977) and by Runge et al. (1987) for certain pairs of predator/prey species.

ACKNOWLEDGEMENTS

I thank Mr. J.C. den Hartog, Prof. Dr. W. Vervoort (both RMNH, Leiden) and Dr. R.W.M. van Soest (I.T.Z., Amsterdam) for commenting on the manuscript. Their suggestions, and the discussions with J.C. den Hartog, greatly improved it. Thanks are also due to the library staffs of the National Institute for Fisheries Research (RIVO) and the Institute for Taxonomical Research (I.T.Z.) and the Artis-Bibliotheek (Zoological Museum, University of Amsterdam) for their hospitality.

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