CNIDARIA AS FOOD-SOURCES FOR MARINE INVERTEBRATES

by

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Résumé

Les Cnidaires comme source d'alimentation pour les Invertébrés marins.

1. — Une revue des groupes d'animaux qui, comme prédateurs ou comme parasites, se nourrissent de Cnidaires, montre que les Coelentérés sont une très vaste source de nourriture et que, selon nos connaissances, l'existence de nématocystes urticants n'exerce aucune limitation anatomique ou écologique à son exploitation.

2. — Quand on compare tous ces animaux, on constate que l'effet urticant des capsules semble être évité, soit par une protection mécanique (cuticule du pharynx, etc.), soit par une action glandulaire (du tégument interne ou de l'intestin).

3. — Comme une hyperviscosité du milieu environnant empêche la décharge des nématocystes, la plupart des sécrétions muqueuses ou enzymatiques produisent un effet immunisant. La spécificité de la sécrétion du prédateur par rapport à la proie ne doit donc pas être nécessairement très stricte, ce qui expliquerait le nombre énorme des « cnidairivores ».

4. — Chez les Solénogastres, spécialement étudiés, aussi bien que chez les Turbellariés et les Gastropodes, plusieurs faits évidents et quelques preuves expérimentales viennent montrer qu'en réalité, des sécrétions de l'intestin stomodéal immunisent le tissu de la proie avant qu'elle ne soit dévorée.

Introduction

It is generally known that most aeolidiid Gastropods feed on Cnidaria, the nematocysts of which are stored in the cerata. On the other hand, little attention is usually paid to other cnidaria-vorous animal groups such as Turbellaria-Microstomidae, Pantopoda or Solenogastres, of which equal mention should be made with respect to biological relationships to various groups.

A revision of the aplacophorous Molluscs, in addition to other findings during recent years, has led to the surprising statement that the known diet of most species within the class Solenogastres (formerly Aplacophora-Neomeniamorpha, to be distinguished clearly from the mud-burrowing members of the class Caudofoveata, formerly Aplacophora-Chaetodermamorpha) consists of Cnidaria. This interesting fact, together with emphasis on acknowledgement of the significance of these animals which have been nearly ignored for over 50 years,

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has led to comparisons with other cnidariavorous invertebrates and thus to a general review.

Another aspect was initiated by man's increasing need to get high-value albuminous nutriment from the sea by raising the yield of fisheries. This demands not only exact knowledge of the biology of commercial fishes and other edible animals, but also of the sequence of whole food-chains. At first, it does not seem very obvious that the Cnidaria discussed here play a significant role within food-chains extending to commercially interesting animals; in fact, we do not know very much about this, but some essential relationships are evident and may shed light on other, lesser known, relationships:

a) Cnidaria (Scyphomedusae, Actiniaria) → Man (Saoma, Japan);

b) Cnidaria → Pisces $\begin{matrix}\text{Gadiformes}\\ \text{Anguilliformes}\\ \text{Pleuronectiformes}\end{matrix}$ → Man;

c) Cnidaria → Crustacea (Decapoda) → Man;

d) Cnidaria → Crustacea (Decapoda) → Cephalopoda → Man;

e) Cnidaria → $\begin{matrix}\text{Gastropoda}\\ \text{Ophiuroidea}\end{matrix}$ → Pisces $\begin{matrix}\text{Gadiformes}\\ \text{Pleuronectiformes}\end{matrix}$ → Man;

f) Cnidaria → $\begin{matrix}\text{Gastropoda}\\ \text{Ophiuroidea}\end{matrix}$ → Asteroidea → $\begin{matrix}\text{Pisces (Gadidae)} \rightarrow \text{Man;}\\ \text{Gastropoda (Streptoneura)}\end{matrix}$

g) pelagic Cnidaria → Pisces → Man ;

h) pelagic Cnidaria → diverse animals → $\begin{matrix}\text{squids}\\ \text{fish of prey}\\ \text{whales}\end{matrix}$ → Man;

i) Cnidaria → diverse animals: larve → plancton-eaters → Man;

The food-chains between Cnidaria and Man outlined here show that the Cnidaria, too, constitute an important factor in food-chains, as do other animal groups more evidently. Attention must be paid especially to all the cnidaria-vores producing free-swimming larvae (i) which, in this fashion, enter into pelagic life cycles.

Within these aspects, the animal group Cnidaria will be discussed with respect to its function as a food basis for other organisms. This review, however, does not claim to be a complete treatise; its purpose is to present a representative cross-section of the manifold animal organisms which depend on Cnidaria for nourishment, with a discussion about the manner of their feeding and how they protect themselves against the poisonous nematocysts.

CNIDARIA AS FOOD-SOURCE

The Cnidaria, systematically divided into the classes Anthozoa, Scyphozoa, and Hydrozoa, can be conveniently arranged ecologically as sedentary colonial forms (corals, Hydroidea), as solitary and/or errant forms (Actiniaria and Ceriantharia, scyphopolyps, numerous

Hydroidea) and as pelagic forms (jellyfish, Siphonophora). This division is only partially adequate and practical with regard to the Coelenterates as food sources. It shows that primarily the sedentary or colonial forms have come into consideration, for —according to our methods— these animals are relatively well investigated. The biology of the jellyfish and Siphonophora, however, due to their pelagic manner of life, cannot be subjected to such intensive study. Moreover, these pelagic forms seem to be captured (as far as we know) mainly by large vertebrates (whales: Cetacea-Mystaceti, seals: Carnivora-Pinnipedia, several fish as the Whiting *Gadus merlangus* L.); the Portuguese Man-of-War (*Physalia*) as an extreme example will be attacked by the Loggerhead Turtle (*Caretta caretta* L.), by the Marlin (*Makaira* sp., *Tetrapturus* sp.: Perciformes Scombrodei) and by the Portuguese Man-of-War Fish (*Nomeus gronovei* Gmelin: Perciformes - Stromateidae). But vertebrates, generally fishes (Gadiformes, Anguilliformes, Pleuronectiformes), are also principal enemies of Actiniaria and Ceriantharia, while the Parrot-fish (Perciformes-Scaridae) and representatives of other fish-families (Tetraodontidae, Balistodoi-Monacanthidae, Percoidei-Chaetodontidae, etc.; comp. Robertson 1970: 43, 50) have adapted themselves to feeding especially on corals which even sharks will consume (e.g. the nurse-shark *Nebrius concolor* Rüppel on *Stylophora*/Madreporaria, or other on Antipatharia).

We shall give our special attention, however, to the various invertebrate groups which are enemies of Cnidaria in general; according to eco-systematic principles they can be devided into isolated aberrant food specialists as well as into adapted groups of consumers.

I. Aberrant specialists

Numerous species, belonging to different related groups, have evolved characteristically but independently as specialists for certain Coelenterates. Generally, these forms may be of little importance for the Cnidaria as a whole, but they are all the more significant for the respective animal of prey therefore confronted with a specific enemy.

Some species of Protozoa feed on the tissue of certain Hydroidea, the stinging capsules of which are found as cleptocnids in an unexploded condition in the bodycell. The ciliate *Holophrya oblonga* Maupas and one *Kentrona*-species can be found on *Eudendrium* and *Hydra* respectively, whereas Suctoria-species as *Ophryodendron abietinum* Claparède & Lachmann and *O. sertulariea* (Wright) live on Thecaphora (e.g. *Campanularia*). In contrast, holotrichous Ciliates appear as parasites in Actiniaria, as *Foettingeria actiniarum* (Claparède) in *Actinia equina, Tealia felina, Anemonia sulcata,* etc., or *Eurychilum actiniae* André, in *Calliactis parasitica.*

Little is known about the Combjellies (Ctenophora) which prey regularly on jellyfish or, as *Beroe,* on Ctenophora themselves, or which with various Coeloplanidae nourish themselves frequently on the cenosarc of Octocorallia. (The problem whether *Euchlora* stores cleptocnids or produces nematocysts itself has not yet been cleared up; comp. footnote p. 395.

Only a few forms of the Nemathelminthes are known to be enemies of Coelenterates; as an example, the parasitic Rotifers (Rotatoria) of the genus *Proales* may be mentioned as living on Thecaphora. One can also include several parasitic worms such as the Trematodes which can be found in *Virgularia mirabilis* (Pennatularia) or in *Bunodactis* (Actiniaria).

Cnidaria-vorous Turbellaria and Mollusca will be discussed generally in the second section. However, we must pay attention to isolated specialists within the Gastropodas such as *Calliostoma ziziphinum* (L.) (= *Trochus conuloides*; Streptoneura-Diotocardia) which devours Hydroidea, as well as to the *Dupra-*(*Drupella-*)species which live and feed on corals (e.g. *D. ochrostoma* (Blainville); Stenoglossa-Muricidae; comp. Robertson 1970: 46/47). The pyramidellid *Turbonilla jeffreysi* (Forbes & Hanley) (Euthyneura-Cephalaspidea) sucks on thecaphoran Hydroids (e.g. *Halecium*), and hydras fall victim to the omnivorous freshwater snail *Lymnaea* (Basommatophora). The immature snail *Phyllirrhoe* (Nudibranchia-Dendronotacea) parasitizes on the Anthomedusa *Zanclea* (= *Mnestra*); the remains of the host are later carried on the foot-rudiment (comp. Ankel 1952). The pelagic adult animal continues to feed on Cnidaria by capturing and devouring smaller Scyphomedusae, Hydromedusae, and parts of Siphonophora, as do the related drifting *Scyllaea pelagica* (L.), and the Heteropoda (Streptoneura-Taenioglossa). The few *Glaucus* species which belong to the Aeolidiacea are also pelagic food specialists: like the Janthinidae (see p. 392) they nourish themselves on the disconanth jellyfish (*Velella, Porpita*) and on the Portuguese Man-of-War (*Physalia*) ; the pseudo-pelagic *Fiona pinnata* (Eschscholtz), likewise an Aeolidiacea, feeds on floating Cnidaria as well (comp. Bayer 1963).

Two aberrant representatives within the Molluscs should not be forgotten: The chemically boring mytilid Bivalve *Fungicava eilatensis* Soot-Ryen lives in *Fungia scutaria* and sucks its food out of the coelenteron by means of the siphon (comp. Goreau & al. 1969). The immature Octopode *Tremoctopus violaceus* Delle Chiaje injures *Physalia* by ripping off fragments of the tentacles; like the paper-boat (*Argonauta, A. hians* Solander) found attached to jellyfish (*Velella, Pelagia noctiluca* = *P. placenta*), the *Tremoctopus* is immune to the stinging nettle-poison and uses the fragments (attached to the rows of suckers of the four dorsal arms) as an offensive and defensive weapon against other organisms (comp. Jones 1963).

Among the Annelids many Bristleworms (Polychaeta) consume Cnidaria (comp. Ebbs 1966), e.g. some Syllidae, such as *Autolytus edwardsi* Saint-Joseph or *A. prolifer* Müller which suck out *Obelia*-species, the Amphinomid *Hermodice carunculata* (Pallas) which feeds on corals, or the well-known *Aphrodite aculeata* L. which crushes Hydroidea between jaws and pharynx cuticule.

Parasitic enemies among small Crustaceans are represented by several Copepoda and Amphipoda, such as *Hyperia latreillei* Guer. (Amphipoda) found in the brood-chamber of *Aurelia,* and as are numerous other Hyperina parasitizing in jellyfish (*Hyperoche medusarum* (Kröyer), *Hyperia* spp., etc.), *Metopa solsbergi* Schneider lives on the mucus of *Metridium senile,* and other Amphipoda are parasites on Pennatularia (e.g. *Echinoptilum*) and are even found in the gastrovascular cavity of Actinaria (comp. Stasek 1958).

Cyclopoid Copepodes are variously found as parasites (comp. Zulueta 1911, Humes 1967, Humes & Ho 1968) and especially numerous species of the family Lamippidae and of *Lichomolgus* spp. live in Gorgonaria (*Caligorgia, Chrysogorgia,* etc.), Pennatularia (*Renilla, Anthoptilum,* etc.) and Alcyonaria, whereas other Lichomolgidae parasitize in hexamerous Anthozoa (Madreporaria, Actinaria, Zoantharia). Even the Xarifiidae-species (in Madreporaria) and Vahiniidae (in Antipatharia) specialize as parasites on those corals; some of them, however, are predators such as *Xarifia maldivensis* Gerlach which crawls upon the Madreporarian *Pocillopora,* the tissue of which is torn by its sharp pointed claws. Malformations and protuberances are caused by *Staurosoma parasiticum* Will in *Anemonia sulcata,* by *Mesoglicola delagei* Quidor in *Corynactis viridis,* and by *Staurosoma caulleryi* Okada, *Anteacheres* sp., and other Copepodes in further Actinaria.

Mention must also be made of *Anchistrophus* (Cladocera) which attacks (fresh water) hydras, of the barnacle *Pyrgoma* (Cirripedia) associated with Madreporaria (comp. Ross & Newman 1969) as well as of the gall-forming crab *Hapalocarcinus marsupialis* Stimpson; the crab *Mithraculus sculptus* (Lam.), and *Trapezia* and *Tetralia* (comp. Knudsen 1967) prey on corals, whereas other decapode Crustacea often consume sea-anemones. Numerous species of the shrimp family Pontoniidae (*Vir, Periclimenes, Philarius, Platycaris, Ischnopontonia, Anapontonia, Pratypton, Fennera, Clavicheles, Jocaste, Coralliocaris, Harpiliopsis*; comp. Bruce 1969) depend mostly on acroporid, pocilloporid or oculinid Madreporaria for nourishment, or even (as *Metapontonia*) on Fungiidae; similarily *Propontonia pellucida* Bruce and *Periclimenes diversipes* Kemp live on Alcyonaria, and other species, "commensals" such as *Periclimenes* spp. for example, tear off tentacles of their sea-anemones.

Starfishes (Asteroidea) generally exist as "mussel-crackers", barnacle-eaters, etc., although some species do indeed attract attention by nourishing themselves on Anthozoans: *Acanthaster* grazes on coral polyps digesting them extraorally and only a bare strip marks the path of eating; the disastrous epidemic of the Crown-of-Thorns, *A. planci* (L.), on the Australian Great Barrier Reef recently received much publicity (comp. Chester 1969; Wickler & Seibt 1970). *Solaster* (e.g. *S. papposus* L.) devours *Calliactis parasitica* as well as further Actinaria and even Pennatularia.

Some serpent stars (Ophiuroidea) like *Asteronyx loveni* Müller & Troschel, *Ophiosoma* spp., and representatives of the Gorgonocephalidae live, similarly, partly from polyps of colonial Coelenterates, whereas both *Gorgonocephalus eucnemis* Müller & Troschel and *G. arcticus* Leach nourish themselves on the coenenchym of the Alcyonaria *Germesia glomerata* (=*Eunephta g.*). Further serpent stars which pluck off polyps are *Asteroceras* (on Alcyonaria), *Astroschema* and many Ophiotrichidae (all on Gorgonaria), whereas *Ophiocoma marmorata* (Lam.) of the same family can be considered a parasite on the 30 cm large Scyphomedusa *Rhipolema hispidum.*

Finally, Cnidaria themselves must be mentioned as aberrant food specialists: the larvae of *Peachia hastata* (Gosse) (Actinaria) live on jellyfish like *Eirene viridula* (Leptomedusae), while the adult animals devour small Hydromedusae and Combjellies in addition to other pelagic organisms. Early stages of development of the Narcomedusae *Cunina proboscidea* Metschnikoff and *C. octonaria* McCrady (= *Cunoctantha c.*, = *C. parasitica*) are parasites on other Hydromedusae such as *Geryona* or *Turritopsis*.

This abstract of those specialized forms which depend largely on specific Coelenterates as objects of prey or as host animals is by no means a complete review; its main purpose is to give an idea of the multiplicity of the various organisms which depend directly or primarily on Cnidaria. The degree of differentiation not only includes conquest of the habitat, but also demands a further adaptation to and an immunisation from nettle poison, an arrangement by which the nematocysts "are found in an unexploded condition in the tissue" (Martin 1914, p. 250). Of the above mentioned representatives, only the Asteroidea make clear use of this situation, in which enzymes of the digestional juices destroy any "resistance". Other forms have not yet been investigated, but some essential points might be transferred from the discussion made about the animals of the following groups.

2. Cnidaria-vorous groups

Not counting the already mentioned representatives of the Copepoda-Cyclopoida, the Amphipoda-Hyperina, the Decapoda-Pontoniidae, and the Ophiuroidea-Ophiotrichidae or Gorgonocephalidae which could perhaps be placed in this section, we know four animal classes, members of which form some phylogenetically conditional, largely cnidariavorous groups: Turbellaria, Solenogastres, Gastropoda, and Pantopoda.

Although the number of Turbellaria species to be treated is not especially large—fewer than thirty members (comp. Karling 1966)—, these animals are placed here at the very beginning, for the food specialization among related species can clearly be seen in twelve representatives of *Microstomum* (Macrostomida): this genus with its cnidaria-vorous species is native both to marine and to fresh water! Another group is formed by the six species of *Archimonocelis* (Proseriata), and a third by several forms within the Prolecitophora. Ordinarily, the prey consists of Hydroidea, whereby the fresh water animals *Microstomum lineare* (Müller), *M. caudatum* (Leidy), and *M. giganteum* Hallez feed on *Cordylophora caspia* and on *Hydra* (Hydrina), and the marine species nourish themselves on equivalent Hydroidea, e.g. *Microstomum rubromaculatum* Graff on *Obelia* and others.

There is little known about—certainly one reason why little attention is paid to—the numerous cnidaria-vorous species within the class Solenogastres (comp. p. 386). In contrast to the incomplete information given by Rees (1967, p. 224), about 40 p. 100 of all hitherto registered species are direct Cnidaria-eaters (Table 1 and Plate I, 1-4; comp. Salvini-Plawen 1967, 1968, 1969a, 1972). Until now, the majority of these representatives consist of epizoans living on Gorgonaria or Alcyonaria, and the species of *Strophomenia, Rhopalomenia,* and *Anamenia,* as well as several monotype genera, are characteristic examples. Among the free-living forms native to the

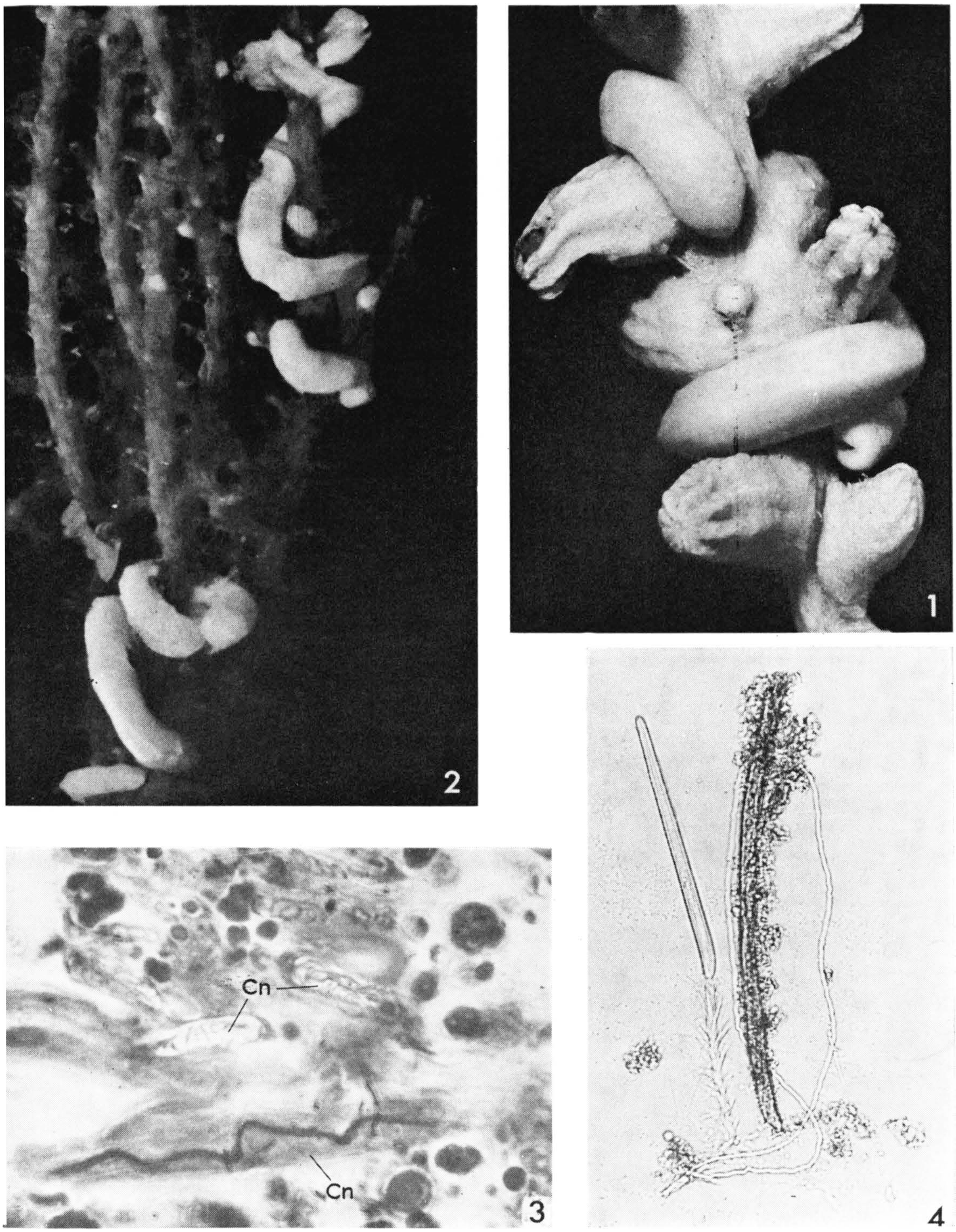

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Plate I

1: Solenogastres: *Proneomenia epibionta* coiled around a Chrysogorgiidae-stem (Gorgonaria). — 2: Solenogastres: two individuals of *Nematonemia banyulensis* (var. *norvegica* Odhner) on *Grammaria abietina* (Sars). — 3: Solenogastres: unexploded nematocysts (Cn) in the midgut-tissue of *Genitoconia* (from Salvini-Plawen 1967a). — 4: Solenogastres: Microbasic mastigophoran nematocysts from the midgut of *Genitoconia*, brought to ejection mechanically.

TABLE 1
List of all hitherto known cnidaria-vorous Solenogastres.

Species	Prey (or host)
Alexandromenia antarctica Salvini-Plawen	Cnidaria indet.
Alexandromenia grimaldii Leloup	hexamerous Anthozoa indet.
Anamenia agassizi (Heath)	*Acanthogorgia armata*
Anamenia farcimen (Heath)	*Acanthogorgia angustiflora*
Anamenia gorgonophila (Kowalevsky) (= *A. heathi* Leloup = *A. nierstraszi* (Stork)	Gorgonaria (Muriceidae)
Anamenia spinosa (Heath)	*Acanthogorgia japonica*
Anamenia triangularis (Heath)	*Calicogorgia* sp.
Dinomenia hubrechti Nierstrasz	Gorgonaria indet.
Dondersia annulata Nierstrasz	Gorgonaria indet.
Dondersia (?) *stylastericola* Salvini-Plawen	Stylasteridae
Drepanomenia(?)*tenuitecta* Salvini-Plawen	hexamerous Anthozoa indet.
Drepanomenia vampyrella (Heath)	*Epizoanthus* sp.
Driomenia pacifica Heath	*Sertularella* sp.
Eleutheromenia sierra (Pruvot)	*Lytocarpia myriophyllum, Nemertesia?*
Epimenia australis (Thiele)	Alcyonaria indet.
Epimenia verrucosa (Nierstrasz)	Alcyonaria, Gorgonaria, Hydroidea
Forcepimenia protecta Salvini-Plawen	Cnidaria indet.
Genitoconia atriolonga Salvini-Plawen	hexamerous Anthozoa indet.
Genitoconia rosea Salvini-Plawen	hexamerous Anthozoa indet.
Heathia porosa (Heath)	Pennatulidae
Hemimenia dorsosulcata Salvini-Plawen	hexamerous Anthozoa indet.
Lophomenia spiralis Heath	*Cryptolaria operculata*
Meromenia hirondellei Leloup	hexamerous Anthozoa indet.
Micromenia fodiens (Schwabl)	Cnidaria indet.
Micromenia simplex Leloup	Cnidaria indet.
Nematomenia banyulensis (Pruvot)	*Lafoea dumosa, Lytocarpia myriophyllum, Grammaria abietina*
Nematomenia coralliophila (Kowalevsky)	*Corallium rubrum*
Nematomenia flavens (Pruvot)	*Lafoea dumosa*
Nematonemia platypoda (Heath)	Campanulariidae
Ocheyoherpia lituifera Salvini-Plawen	Cnidaria indet.
Proneomenia epibionta Salvini-Plawen	Gorgonaria-Chrysogorgiidae
Proneomenia sluiteri Hubrecht	also *Alcyonium*
Proneomenia thulensis Thièle	Alcyonaria indet.
Pruvotia sopita (Pruvot)	*Sertularella polyzonas*
Pruvotina intermedia (Thièle)	Cnidaria indet.
Pruvotina longispinosa Salvini-Plawen	Cnidaria indet.
Pruvotina pallioglandulata Salvini-Plawen	Cnidaria indet.
Pruvotina providens Thiele	Cnidaria indet.
Pruvotina uniperata Salvini-Plawen	Cnidaria indet.
Rhopalomenia aglaopheniae (Kow. & Mar.)	*Lytocarpia myriophyllum*
Rhopalomenia atlantica (Leloup)	Lafoeidae (= « Perisiphonidae »)
Rhopalomenia carinata Salvini-Plawen	Syntheciidae
Rhopalomenia rhynchopharyngeata Salvini-Plawen	Cnidaria indet.
Rhopalomenia tricarinata Salvini-Plawen	Syntheciidae
Strophomenia debilis (Nierstrasz)	Gorgonaria indet.
Strophomenia indica (Nierstrasz)	*Paramuricea chamaeleon*
Strophomenia lacazei Pruvot	*Muricea* (*Paramuricea ?*) sp.
Strophomenia ophidiana Heath	*Acanthogorgia angustiflora*
Strophomenia regularis Heath	*Dendronephtya* sp.
Strophomenia scandens Heath	*Acanthogorgia armata*
Syngenoherpia intergenerica Salvini-Plawen	also Cnidaria indet.

mud-surface of predominantly deeper regions, more and more is being learned about representatives (*Micromenia, Genitoconia, Forcepimenia,* etc.) which prey on and attack solitary Cnidaria; their number will be greatly increased after numerous still undetermined animals have been examined.

The Gastropoda-Nudibranchia are generally known to be enemies of Coelenterates, and numerous epizoan species are especially characteristic of the Aeolidiacea (Table 2) which store the nematocysts in their cerata (1). This group also includes the pelagic *Glaucus*-species and *Fiona pinnata* already mentioned, as well as the minute interstitial, mesopsammobiotic Pseudovermidae (comp. Challis 1969).

The problem of nematocysts in the cerata of Nudibranchs has not yet been cleared up satisfactorily. Whereas it was until recently believed that the ingested nematocysts function as active weapons (cleptocnids) against enemies (comp. Grosvenor 1903, Glaser 1910), modern researchers tend to the opinion that the discharge in the cerata occurs only occasionally (comp. Haefelfinger 1969): by protective contraction of the body which causes pressure in the cerata, or by the bite of enemies.

Streble (1968) concludes in his examinations that the cnidosacs are used only for storage of nematocysts which are subsequently eliminated through facultative pores, so that the nematocyst-storing cerata would function as kinds of excretory organs.

Much less notice was given earlier to further, smaller groups of the Gastropoda-Streptoneura, even through they must be categorized as just as characteristic. In addition to the above-mentioned Heteropoda, the Epitoniidae (e.g. *Clathrus clathrus* (L.) = *Scala c., Opalia crenimarginata* (Dall), *Alexania inazawai* (Kuroda), *Amaea* sp., and many others) as well as the Janthinidae (*Janthina* spp., *Reluzia* spp.) —both of which are closely related (Ptenoglossa)—devour Coelenterates (comp. Thorson 1958; Ankel 1962; Bayer 1963; Robertson 1963, 1966, 1970); nevertheless, ecologically conditioned they differ anatomically greatly from each other. The Epitoniidae go in search of Actinaria as well as of other animals, while the Janthinidae, driven along on their pelagic mucus float, depend primarily on jellyfish and specialize on *Velella, Porpita,* and *Porpema* (Chondrophora).

Another group of related Cnidaria-eaters within the Streptoneura includes the Cypraeacea, of which special emphasis must be placed on the Ovulidae (with all European species; comp. Robertson 1966, 1970; Nordsieck 1968), feeding mainly on Gorgonaria; some, such as *Simnia spelta* (L.), tend to assume protective colouring (Theodor 1967; over the period of approximately one month) by utilizing the prey's pigments (e.g. *Simnia patula* (Pennant) on *Alcyonium, Eunicella,* and *Tubularia*; *Simnia* (*Neosimnia*) *spelta* on *Parerythropodium, Eunicella, Paramuricea,* and *Leptogorgia sarmentosa*; *S.* (*N.*) *uniplicatum* Sowerby on *Leptogorgia virgulata* and *L. hebes*; *Pseudosimnia carnea* (Poiret) on *Corallium rubrum* and *Eunicella*; *Pedicularia sicula* Swainson on *Corallium* and Gorgonaria; *P. californica* Newcomb on *Allopora*; *Cyphoma* spp. on *Pseudogorgia, Plexaura, Plexaurella* and others; etc.). Yet Cypraeidae, too, e.g. *Zonaria zonata* (Chemnitz), devour Actinaria or colonial Coelenterates, and species of Lamellariidae and numerous Eratoidae graze on colonial Hydroidea or on corals (e.g. *Velutina flexilis* (Montagu) = *V. plicatilis* on *Tubularia*; *Erato voluta* (Montagu) mainly on Synascidiae but also on hexamerous corals).

(1) The Saccoglossa, however, although provided with Cerata, feed exclusively on algae (comp. Streble 1968; Thompson et all. 1970).

TABLE 2

List of Gastropoda-Nudibranchia which feed on Cnidaria (comp. Graham 1955, Miller 1961, Thompson 1964, and others).

Species	Prey
Doridacea:	
Phyllidia bourgini Risbec	*Acropora* sp., *Millepora* sp.
Dendronotacea:	
Tritonia bayeri Marcus et Marcus	*Briareum asbestinum*, *Pseudopterogorgia* sp.
Tritonia hombergi Cuvier	*Alcyonium digitatum*
Tritonia manicata Deshayes	*Cornularia* sp.
Tritonia pickensi Marcus et Marcus	Gorgonaria
Tritonia plebeia Johnston	*Alcyonium digitatum*, *Eunicella* sp.
Tritonia striata Haefelfinger	*Paralcyonium elegans*
Tritonia wellsi Marcus	*Leptogorgia virgulata*, Gorgonaria
Lomanotus genei Verany	*Nemertesia antennina*, *Tubularia indivisa*
Scyllea pelagica (Linné)	medusae variae, Siphonophora
Hancockia uncinata (Hesse)	*Campanularia* sp.
Dendronotus frondosus (Amphitrite) = *D. arborescens*	*Tubularia* spp., *Dynamena* sp., *Hydrallmania* sp., *Sertularia* sp.
Doto coronata (Gmelin)	Hydroidea varia
Doto cuspidata (Alder et Hancock)	*Nemertesia ramosa*
Doto fragilis (Forbes)	*Nemertesia antennina*, *N. ramosa*
Doto lancei Marcus et Marcus	*Aglaophenia* sp.
Doto paulinea Trinchese	*Obelia* sp.
Doto pinnatifida (Montagu)	*Nemertesia antennina*, *Obelia* sp.
Phyllirrhoe spp.	*Zanclea* (= *Mnestra*) ; medusae variae, Siphonophora
Arminacea:	
Armina spp.	corals
Janolus hyalinus (Alder & Hancock)	Hydroidea
Antiopella cristata (Delle Chiaje)	Hydroidea
Hero formosa (Loven)	*Abietinaria abietina*, *Hydrallmania falcata*, *Tubularia indivisa*
Dirona picta (Cockerell & Eliot)	*Aglaophenia* sp.
Aeolidiacea:	
Coryphella lineata (Loven)	*Tubularia indivisa*, *Sarsia eximia*, *Hydrallmania falcata*, *Nemertesia antennina*, *N. ramosa*
Coryphella pedata (Montagu)	*Tubularia indivisa*, *T. larynx*, *Eudendrium ramosum*, *Abietinaria abietina*, *Hydrallmania falcata*, *Bougainvillea*,
Coryphella pellucida (Alder et Hancock)	*Tubularia indivisa*, *Hydrallmania falcata*
Coryphella stimsoni (Verrill)	*Tubularia* sp., *Halcampa duodecimcirrata*, *Edwardsia elegans*
Coryphella verrucosa (Sars)	*Tubularia larynx*, *Sarsia eximia*, *Clythia johnstoni*, *Obelia flexuosa*, *Dynamena pumila*, *Hydrallmania falcata*
Coryphella pellucida (Alder & Hancock)	*Kirchenpaueria pinnata*, *Tubularia* sp.
Eubranchus farrani (Alder & Hancock)	*Tubularia indivisa*, *Obelia geniculata*
Eubranchus pallidus (Alder & Hancock)	*Cordylophora caspia*, *Tubularia indivisa*, *Obelia geniculata*, *O. longissima*, *Hydrallmania falcata*
Eubranchus tricolor Forbes	*Tubularia indivisa*, *Obelia dichotoma*, *Abietinaria abietina*, *Hydrallmania falcata*, *Nemertesia antennina*, *N. ramosa*
Capellinia exigua (Alder & Hancock)	*Obelia geniculata*, *O. flexuosa*, *Hydrallmania falcata*, *Plumularia catharina*, *Halecium* sp., *Coryne* sp., *Bougainvillea* sp.
Cuthona amoena (Alder & Hancock)	*Halecium beani*, *H. halecinum*
Cuthona concinna (Alder & Hancock)	*Sertularia argentea*
Trinchesia coerulea (Montagu)	*Halecium halecinum*, *Sertularella polyzonas*, *Hydrallmania falcata*

Species	Prey
Trinchesia foliata (Forbes & Goodsir)	*Tubularia* spp., *Nemertesia* spp., *Obelia geniculata, Sertularella polyzonas, Hydrallmania falcata, Coryne* sp. *Dynamena* sp.
Trinchesia granosa Schmekel	*Podocoryne* sp.
Trinchesia ocellata Schmekel	*Halecium* sp.
Catriona aurantia (Alder & Hancock)	*Tubularia indivisa, T. larynx, Sarsia eximia, Bougainvillea ramosa*
Tergipes despectus (Johnston)	*Sarsia eximia, Clava multicornis, Aglaophenia pluma Obelia geniculata, O. flexuosa,*
Phestilla melanobrachia Bergh	Dendrophyllidae spp.
Phestilla sibogae Bergh	*Porites compressa*
Embletonia pulchra (Alder & Hancock)	Thecaphora varia
Tenellia ventilabrum (Dalyell) = *Embletonia pallida*	*Obelia* sp., *Podocoryne* sp.
Fiona pinnata (Eschscholtz)	*Velella, Porpita*
Pseudovermis boadeni Salvini-Plawen & Sterrer	*Halammohydra vermiformis ?*
Pseudovermis hancocki Challis	*Heterostephanus* sp. ?
Flabellina affinis (Gmelin)	*Eudendrium ramosum*
Calmella cavolinii (Verany)	*Eudendrium ramosum*
Facelina drummondi (Thompson)	Thecaphora, *Tubularia indivisa*
Facelina fusca Schmekel	*Eudendrium* sp.
Facelina longicornis (Montagu)	*Tubularia larynx*
Facelina punctata (Alder & Hancock)	*Eudendrium* sp.
Facelina rubrovittata Costa	*Eudendrium* sp.
Antonietta luteorufa Schmekel	*Podocoryne carnea*
Hervia costai Haefelfinger	*Eudendrium ramosum*
Hervia peregrina (Gmelin)	*Eudendrium ramosum*
Caloria maculata Trinchese	*Perigonimus* sp.
Favorinus branchialis (Rathke)	Thecaphora varia
Cratena kaoruae Marcus	Hydroidea
Aeolidia papillosa (Linné)	Actiniaria varia ; *Tubularia indivisa*
Aeolidiella glauca (Alder & Hancock)	*Sagartia elegans, Stomphia coccinea*
Aeolidiella takanosimensis Baba	*Sagartia* sp.
Spurilla neapolitana (Delle Chiaje)	*Aiptasia mutabilis, Actinia equina, Anemona sulcata, Bunodeopsis* sp.
Berghia coerulescens (Laurillard)	*Aiptasia mutabilis, Sagartia* sp.
Glaucus spp.	*Velella, Porpita, Porpema ; Physalia*

The radula-less Coralliophilidae (Stenoglossa-Muricacea) are to be found as a unified group on or in corals which extensively form their food (*Rhizochilus antipathicus* Steenstrup on *Antipathes ericoidea, Quoyula madreporarum* (Sowerby) as well as numerous *Coralliophila* spp. and *Magilus antiquus* Montfort on Madreporaria, *Rapa rapa* (L.) on soft corals, *Leptoconchus* spp. in the tissue of corals, etc.). Finally, *Philippia radiata* Röding and the various *Heliacus*-species (Architectonicidae = Solariidae; Cerithiacea) must be mentioned which eat the body tissues of the stony coral *Porites lobata* and of Zoantharia respectively (comp. Robertson 1967, 1970).

The fourth class under consideration here, the Pantopoda (=Pycnogonida), consists—as we know—largely of cnidaria-vorous representatives; the spider-like, seemingly aberrant Chelicerata have four to nine pairs of extremities, a greatly reduced abdomen and a strong proboscis. Consequently, these sucking animals are well-adapted to prey specifically (comp. Fry 1965) on most forms of Cnidaria (as well as on Algae, sponges, and Bryozoa) which they capture by using their sense of touch. Occasionally even the larvae (= Protonymphon) appear as parasites, e.g. *Pycnogonum litorale* Ström on *Clava, Sertularia,* and Actinaria, *Halosoma exiguum* (Dohrn) on *Podocoryna, Phoxichilidium femoratum* Rathke on further Hydroidea, or a juvenile *Ascorhynchus* sp. which causes gall-like swellings on *Chrysogorgia papillosa* (comp. Stock 1953).

DISCUSSION

In contrast to the food specialists mentioned in the first section, we are considerably better informed about the cnidaria-vorous groups. All those animals coming into question have either a pharynx which functions as a sucking apparatus (Turbellaria; Solenogastres; Gastropoda-Epitoniidae, -Coralliophilidae, -Architectonicidae; Pantopoda), or they are equipped with an expandable buccal cavity (Nudibranchia and others); therefore, the prey can be imbibed or swallowed alive. The predominantly unexploded nematocysts are ingested and then partly stored in the predator's tissue (Turbellaria, Nudibranchia) during feeding as so-called cleptocnids (1). These are ingested in an undestroyed condition and most of them remain entirely intact. Until now, however, the question has been unanswered *how* the animals are able to protect themselves against the stinging of the nematocysts when the prey is devoured, as well as *how* the predators are able to prevent the nettle capsules from exploding during absorption.

A Pantopode which is "mit seinen Schreitbeinen auf der lebhaft zuckenden und heftig nesselnden Meduse festgeklammert" (Prell 1911, p. 26), is protected by its cuticula, as shrimps and other Crustaceans are; the Solenogastres possess externally a protective shield in their spicula-bearing integument (comp. Salvini-Plawen 1969 a, p. 66). Some Turbellaria-species (*Archimonocelis*) seem to be protected by the cuticule lining of the extremely long proboscis and, in the Streptoneura, we meet with a similar situation, for their buccal cavity is equipped with a cuticule. These anatomical features, however, are only of value against already exploded nematocysts but offer the devouring animals no protection against the poisonous explosion of the nematocyst itself. This principal question, "auf welche Art und Weise kann die Nesselzellenentladung verhindert werden" (Schlichter 1969, p. 327), does not seem to have been solved until now.

With respect to the anemone-fish *Amphiprion,* Eibl-Eibesfeldt (1960, p. 9) assumes that the animals "apparently produce a substance in their skin which protects them from their anemone by inhibiting the discharge of nematocysts"; Graham (1938, p. 229) surmises "that the copious secretion of mucus which is a normal preliminary to feeding has great value in preventing too harsh a treatment of the food during the process of feeding" on Coelenterates by Aeolidiacea, and Karling (1966, p. 14) points to a similar function in Turbellarians, "which possess in their rhabdites a protective slimy substance".

Schlichter's research (1967, 1969) seems to offer a solution for the anemone-fish, but there is no real evidence concerning the cnidaria-vores in general. In *Amphiprion,* in the mediterranean *Gobius bucchichii* Steind., and in other fishes symbiotic with specific

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(1) Cleptocnids, of course, have nothing to do with the pseudocnids formed in Dinoflagellata ("nematocysts"), in Turbellaria (paracnids and rhabdites), in some Nemertini "nematocysts") in Lineidae: *Cerebratulus utricans* (Müller), *Micrura purpurea* (Dalyell), *M. delle chiajei* (Hubrecht), *Lineus geniculatus* (Delle Chiaje); and rhabdites in *Lineus ruber* Müller, *Emplectonema echinoderma* (Marion), *Hubrechtella dubia* Bergendal, *H. indica* Kirsteuer, *Zygonemertes* spp., *Amphiporus* sp., and others, and in Tunicata-Appendicularia ("cellulae urticantes")!

Anthozoans, the protection against an explosion of the nematocysts rests on the layer of anemone mucus with which the fish successively covers its body, getting therefore a protective lining. One could assume a comparable situation in Turbellarians and most Nudibranchs epizoic on Cnidarians, but not in such animals as Solenogastres or those Aeolidiacea such as *Aeolidia papillosa* (L.), where we know that nematocysts are shot at the animal's body itself (comp. Edmunds 1966, Salvini-Plawen 1969a). As the Cnidaria have to possess an immunizing mechanism to prevent the nematocysts from exploding (in most species at least for self-protection, except for example in *Actinia equina* or in the different varieties of *Cerianthus membranaceus* (comp. Abel 1954), two general possibilities came into consideration:

a) the animals acquire a protective substance from their hosts (as in anemone-fishes);

b) the animals themselves produce a substance which prevents the explosion of the nettlecapsule.

According to the circumstances observed within Solenogastres and in some Aeolidiacea (see above), and with respect to the manifold Cnidaria-species which might not have a real body secretion as do anemones, only the second possibility seems to be correct for most epizoans on Cnidaria. Therefore, the immunity of Nudibranchs "is probably due largely to the secretion of mucus, which either acts simply as a shield or actually prevents the discharge of nematocysts" (Grosvenor 1903 : p. 485), so that the prey « is crawled over and lavishly covered with mucus before any attempt at eating it is begun » (Graham 1938: p. 299), or the "epidermal vesicles probably protect the animal from explosions of nematocysts whilst feeding" (Edmunds 1966, p. 69). Similarly in Turbellarians "the pharyngeal secretion is evidently protective during ingestion" (Karling 1966, p. 14). The ability to produce within the foregut glands a specific secretion which prevents the nervously, hormonally or mechanically effected discharge of the respective nematocysts has also been concluded for Solenogastres (Baba 1940; Salvini-Plawen 1967a, b). Robson's statement (1953, p. 233) that the discharge of nematocysts obviously depends on their property as osmometers —on the viscosity of the surrounding medium (e.g. five-molecular sucrose and olive oil prevent the discharge, which is very slow in one-molecular sucrose)— may point to a simple hyper-viscosity of the predator's mucus; this may also be the reason why the ingested nematocysts do not explode during transport within the gut: i.e. due to the digestive secretion (as guessed by Grosvenor 1903, p. 484). Lentz & Barrnett (1962) were able to prove that, except for cholesterinase, all decomposing enzymes inhibit the discharge of nematocysts, which lends force to the above supposition. Consequently, the immunizing effect of the predator's secretion need not be adapted to the prey very specifically since almost every (!) hyper-viscous or enzymatic secretion prevents a discharge (1); therefore the enormous number of cnidaria-vorous representatives would be explicable.

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(1) Accordingly, personal observations made on hydras touching *Planorbis planorbis* (L.) and other, partly juvenile Planorbidae (Basommatophora) did not effect the snails to react because of their mucous body-lining (comp. also Kothbauer 1971).

A protective mucus lining apparently isolates the mechanism for inducing the explosion of the nematocysts, but does not impair the ability to discharge: in Turbellaria, as well as in Aeolidiacea, the nematocysts can be shot out mechanically (by means of muscular pressure or by the bite of an enemy), and the same has also been proved within the Solenogastres (e.g. *Genitoconia*, Plate I, 4), in which the nematocysts and spirocysts found in the intestine hurl forth the cnidonema by mechanical manipulation (1) (Salvini-Plawen 1968; comp. also Lentz & Barrnett 1962).

Whether the secretion of the hypobranchial gland in gastropods is toxic as in some Muricidae (*Murex, Thais, Urosalpinx;* comp. Keyl & al. 1957, Nicil 1964, Franc 1968), or anesthetic as in some Epitoniidae (*Epitonium, Opalia*) to permit penetration of the proboscis in the prey's tissue, has not yet been generally proved. But some Coralliophilidae (comp. Ward 1965) as well as many species of Solenogastres seem to be able to use secretions of the foregut glands also for extrapharyngeal etching and maceration; this allows the forms without radula (or those species equipped with an obviously unsuitable radula, as *Alexandromenia* with scarcely-structured plates) to ingest the prey's tissue by sucking it up. This proteolytic manner of feeding has been partially proved for some Solenogastres (*Drepanomenia vampyrella* and *D. tenuitecta, Strophomenia* spp., *Nematomenia* spp.) where the prey's tissue was found dissolved in the rostral part of the foregut — as proved experimentally in *Epimenia verrucosa* by Baba (1940), and as for example in the radula-bearing *Ocheyoherpia lituifera*. The same can be assumed, too, for all the Solenogastres without radula and the Gastropoda-Coralliophilidae, as well as for Turbellaria and, perhaps, for Pantopoda.

Summary

1. A review of those representatives which—either as predators or as parasites—nourish themselves on Cnidaria, shows that the Coelenterates form a widespread source of food, and according to our knowledge there are neither systematic-anatomical nor ecological limits to exploit this resource in spite of the stinging nettle-weapons.

2. In comparing all these animals, the avoidance of the poisonous effect of the nematocysts seems to take place either by mechanical protection (cuticule lining of the pharynx, etc.) or by glandular action (of the integument or the gut).

3. As hyper-viscosity of the surrounding medium prevents the discharge of nematocyts, most mucous and enzymatic secretions principally show an immunizing effect. The specificity of the predator's secretion to the prey therefore would not need to be very profound, and the enormous number of cnidaria-vores would be explicable.

4. Some experimental findings and other evidence in Solenogastres (which have been dealt with in detail) as well as in Turbellaria and Gastropoda show that secretions of the gut, in reality, immunize the prey's tissue before it is devoured.

Zusammenfassung

1. Ein Überblick über alle jene Vertreter, welche sich — sei es als Räuber oder sei es als Parasiten — von Cnidaria ernähren, zeigt, daß die Nesseltiere eine weitverbreitete Nahrungsquelle darstellen und daß nach den bisherigen Kenntnissen

(1) Whereby ability to explode obtained only by a developmental process of ingested "immature" nematocysts—as Haefelfinger (1969) discusses within the Aeolidiacea—can here be excluded unequivocally.

weder anatomische noch ökologische Grenzen gesetzt sind, um diese Nahrung trotz der nesselnden Bewaffnung zu erschließen.

2. In Gegenüberstellung all dieser Konsumenten ergibt sich, daß die Auswirkung der Nesselkapseln entweder durch mechanischen Schutz (cuticularisierter Vorderdarm, etc.) oder durch Drüsentätigkeit (des Integumentes oder des Darmtraktes) umgangen zu werden scheint.

3. Da eine Hyper-Viscosität des umgebenden Mediums eine Explosion der Nesselkapseln unterbindet, ist prinzipiell fast jedes mucöse oder Ferment-hältige Sekret zur Immunisierung geeignet. Die Spezifität des benützten Sekretes hinsichtlich des Cnidoms der Beute bräuchte daher nicht sehr tiefgreifend sein, womit auch die große Anzahl der Cnidaria-Fresser erklärbar würde.

4. Etliche Befunde und einige experimentelle Belege bei den eingehender behandelten Solenogastres und bei Turbellaria wie Gastropoda zeigen, daß (Vorder-) Darm-Sekrete tatsächlich das Beute-Gewebe immunisieren, bevor es aufgenommen und verschlungen wird.

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