The Role of Cuticular Strata Nomenclature in the Systematics of Nemata

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Abstract: A system of cuticular nomenclature based on the strata observed in Enoplia is proposed. Nematode cuticle is divided into four fundamental strata: epicuticle, exocuticle, mesocuticle, and endocuticle. Application of this system allows the correlation of complementary strata throughout Nemata. The major taxonomic categories within Nemata are differentiated on the basis of their cuticular strata as compared with the Enoplia model cuticle. *Key Words:* cuticle, Enoplia, classification.

Systematists have long utilized external modifications and specialized organs of the cuticle to separate species, genera, families, etc. Even today, with our improved knowledge of internal structures and organs, the external cuticle remains a basic character to the taxonomist. Perhaps the importance given cuticle in taxonomy is justified by the fact that the hypodermis is a remnant of embryological ectoderm, retaining the primitive potential of the tissue. That potential is shown in diverse integumental organs functioning in secretion, excretion, and sensation. Furthermore, the glands of the body and the cuticle of body invaginations are appreciated more fully if they are recognized as derivitives of ectoderm.

Since the external modifications and manifestations of the cuticle have played a major role in our systematic concepts, it seems plausible that the internal structuring of nema integument could be useful in examination of current systematic concepts.

Nematode cuticle is commonly described as a laminated noncellular elastic secretion of the hypodermis. Although numerous studies have been conducted with light microscopy, TEM, and SEM, we continue to have little understanding of this complex organ that interfaces the nema with its external environment.

Studies of ascarid cuticle with the light microscope and TEM (3, 6, 10, 22) serve as the basis for contemporary interpretations of nematode cuticle. The model ascarid cuticle has nine layers distributed among three strata designated as the cortical, matrix (median), and basal layers. It has been assumed that these same strata occur in all Nemata and the terms have been used in a manner that implies they have chemical or functional relationships that prove them homologous within Nemata. In fact, such relationships have not been proved, and superimposition of this terminology throughout is misleading. Bird (3) pointed out that "the diversity in Nomenclature of the various layers of the nematode cuticle has resulted in some confusion."

After a review of cuticular studies I believe that the laminated strata and their sequential order can have significance and correlation throughout Nemata if an enoplid cuticle model is used. There is little purpose in attempting any understanding of cuticular strata following current nomenclature. One simply cannot talk about or see an orderly sequence among Nemata for the "so-called" median (homogeneous matrix) layer or the basal layer. Recent reviews attempting to do that have broken down because current concepts based on *Ascaris* do not allow for comparison, primarily because of the assumption that all nema cuticles have the complete complement of cortical, median, and basal layers (3, 4). It is my premise that continuing to view cuticle on that basis will impede correlation of cuticular characteristics with our understanding of nematode systematics. Furthermore, Hinz (9) finds no justification for designating the cortical, fibril, and homogeneous (= median) layers in *Parascaris equorum* as separate strata, and he treats them as substrata of the cortical layer.

A topographic system of nomenclature utilizing an enoplid for reference is presented here. Of the nematodes studied, *Denontostoma* of Enoplia offers the most complete sequence of cuticular strata. The toponyms are all based on the noun 'cuticle' modified by adjectives connoting relative positions and, as such, the integument is divided into four fundamental strata:

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epicuticle, exocuticle, mesocuticle, and endocuticle.

Fig. 1 applies the toponyms to the recognized strata in *Deontostoma* (21). This concept correlates cuticular strata throughout Nemata with an Enoplia model and allows for the absence of certain strata depending upon the cuticle under consideration. For example, in the cuticle of *Ascaris* only three strata are recognized: epicuticle, exocuticle and mesocuticle; current studies show no evidence of endocuticle.

Applying this system, based on Enoplia, to the Nemata we can recognize differences between Adenophorean and Secernentean cuticle. We can further differentiate, on the basis of the nature of the strata, Enoplia from Chromadoria. In Secernentea it is possible to distinguish among Rhabditida, Spirurida, Strongylida, and Tylenchida. Therefore, our major taxonomic divisions and phylogenetic concept are confirmable by this system. That cannot be done with systems based on cortical, median, and basal layers. For instance, the "basal" layer of *Ascaris* (22) is not the same stratum as the "basal" layer of *Meloidogyne* (2) or the "basal" layer of *Xiphinema* (19). In fact, those are different strata in each of the genera named. In the system proposed here, the "basal" layers of those genera are recognized as exocuticle in *Meloidogyne,* mesocuticle in *Ascaris,* and endocuticle in *Xiphinema.*

Fig. 1, utilizing diagrams based on TEM studies, illustrates the application of this concept and its conformity to our current taxonomic concepts. To show strata identifications the diagrams are scaled, where feasible, to Enoplia; the thicknesses of strata do not represent actual measurements. For purpose of simplification the cuticles diagrammed are based on main body cuticle studies; anterior and caudal cuticles are excluded.

The characteristics of the four fundamental strata derived from an enoploid model are as follows:

Epicuticle: The outermost stratum, typically tri-laminate and consisting of two electron-dense layers separated by an electron-transparent zone. In at least two nematodes, *Meloidogyne javanica* and *Trichinella spiralis* (4), the outer electron-dense layer appears also to be triple-layered.

Exocuticle: This stratum is subdivisible into two or more sublayers. In Enoplida it contains two substrata: an outer lamination composed of a finely granular dense substance. The inner substratum, common to much of Nemata, consists of fine radially oriented striae, which at higher resolution appear to be formed from two electron-dense plates separated by an electron-transparent core. Body wall canals may extend through the exocuticle.

Mesocuticle: This stratum is composed of organized rods, fibers, plates, or struts. In the enoplid model this stratum consists of fibrous layers arranged obliquely at 45 to 55° from each other. The number of substrata is variable.

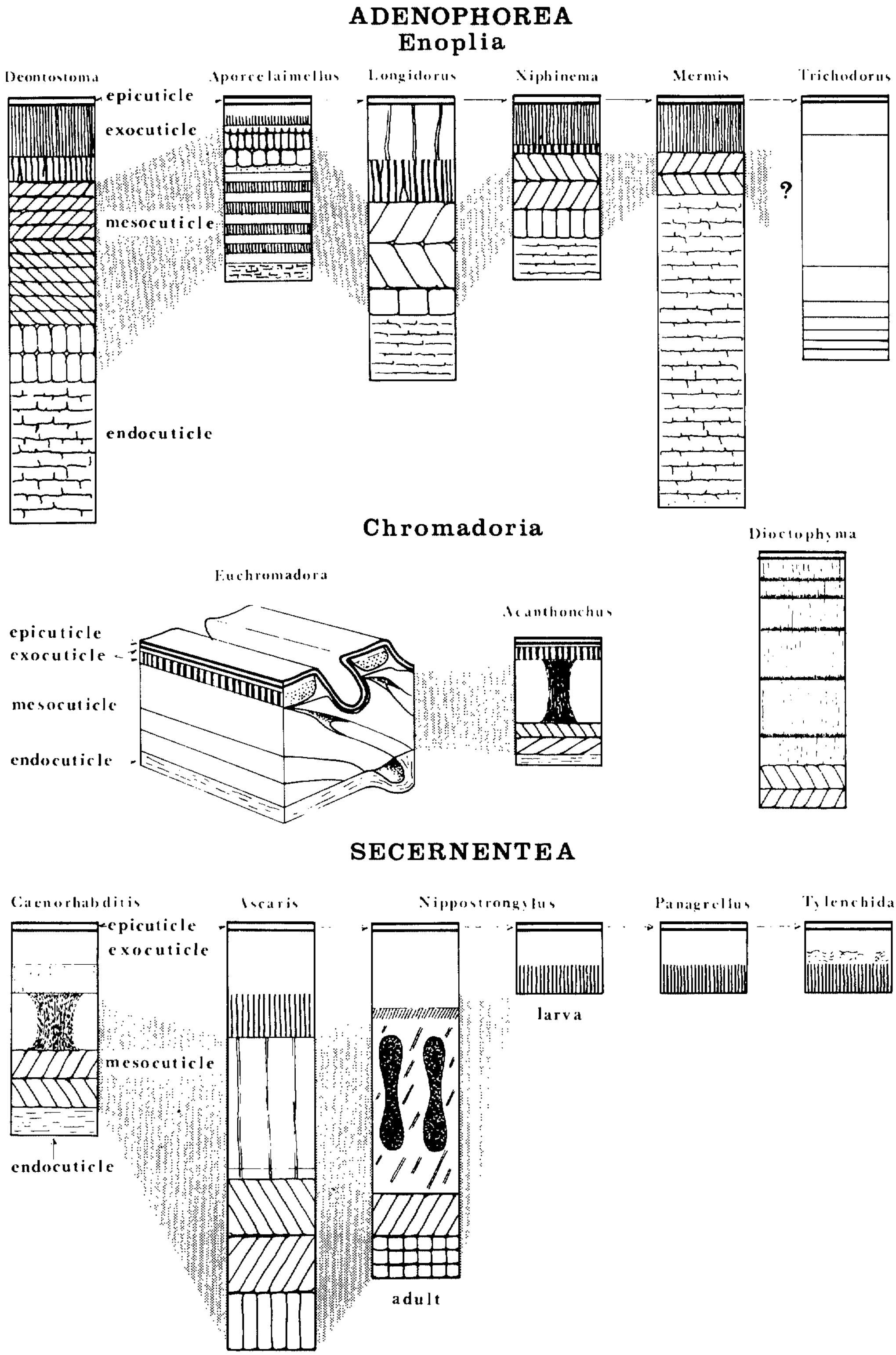
Endocuticle: The substrate of this layer is poorly defined. The substratum often appears to be penetrated by hypodermal extensions and muscle attachment. In TEM photos and reconstructions of the endocuticle it sometimes appears to have a feathery fibroidal consistency.

Among Enoplia the presence of all strata is remarkably constant. The mesocuticle varies by the number of fiber layers, their direction, and angular relationship. The evolutionary trend (Fig. 1) seems to be reflected in a reduction of the number of substrata and oblique fibers (1, 8, 11, 15, 17, 18, 19, 21). The thickness of endocuticle is also variable, showing strong development in the insect parasite *Mermis* (15). The structure of the cuticle of *Trichodorus* (18) has been poorly resolved and currently has as a distinct stratum only the epicuticle.

Chromadoria are distinguished by the striking modifications of the mesocuticle (16, 23, 24), which may be platelike or a combination of oblique fibers and a "fluid" substratum with structural struts.

The similarity in cuticular structure of *Acanthonchus* (24), *Chromadorina* (16), and *Caenorhabditis* (7, 25) lends circumstantial evidence to the hypothesis that Secernentea arose from chromadorid-like ancestors. The literature indicates that the endocuticle occurs only in Rhabditida (7, 25). Filarids, Ascarida, Spirurida, and Strongylida are characterized by the presence of only three strata: epicuticle, exocuticle, and mesocuticle (10, 12, 14, 22).

In the larvae and adults of Cephalobidae


ADENOPHOREA
Enoplia
Deontostoma
Aporcelaimellus
Longidorus
Xiphinema
Mermis
Trichodorus
epicuticle
exocuticle
mesocuticle
endocuticle
?
Chromadoria
Dioctophyma
Euchromadora
Acanthonchus
epicuticle
exocuticle
mesocuticle
endocuticle
SECERNENTEA
Caenorhabditis
Ascaris
Nippostrongylus
Panagrellus
Tylenchida
epicuticle
exocuticle
mesocuticle
endocuticle
larva
adult

(20) and Tylenchida (2, 3, 4, 5, 13) and larval Rhabditida (7, 25) and Strongylida (12, 14) the cuticle is limited to two strata: epicuticle and exocuticle.

It also appears that when the endocuticle and mesocuticle are present the entire cuticle is shed without layer resorption. That observation should be carefully checked for endocuticle resorption, however. It seems that the endocuticle, mesocuticle or both act as a barrier to the molting fluids. In Tylenchida, which lack these strata, the exocuticle is dissolved and "resorbed" with only the epicuticle being shed (3). When all layers are present, as in chromadorids, the entire cuticle is reported to shed (3).

Taxonomically, an area of particular interest is the ambiguity of the placement of *Dioctophyma renale*. Its taxonomic characters are in some measure inconsistent with its placement in Adenophorea near Dorylaimida or *Mermis*. Characters such as a male reproductive system with single testis, spicule elongate and single, and a bursalike extension around male cloaca (= "sucker") are associated more typically with Secernentea rather than with Adenophorea (17). In Fig. 1 the schematic illustration would also support a Secernentean relationship. No endocuticle is evident; in fact, the cuticle is very similar to that of *Ascaris*. It is thus apparent that this nematode requires closer study. At any rate, the current hypothesis tends to confirm the ambiguity of the placement of *Dioctophyma* as an Adenophorean.

Consideration of cuticle in this light indicates that there is a relationship of cuticular strata among nematodes. The hypothesis presented here allows for meaningful comparison of nematode cuticles. The traditional application of similar names to dissimilar strata hinders our understanding of strata and their chemistry and function. More attention needs to be directed to internal cuticle as well as to the secondary deposition of "infracuticle" seen in the anterior of such widely divergent groups as Dorylaimida and Tylenchida. Studies indicate that the nature of anterior and caudal cuticle may well be highly significant. Grootaert and Lippens (8) point out that in Dorylaimida anterior infracuticle appears to be a secondary formation which may be valuable in evaluating the categories of Dorylaimida. Such a view is complementary to the system presented here and clearly indicates why we should discard the old nomenclature which does not have the flexibility to incorporate or utilize valuable observations such as those suggested by Grootaert and Lippens.

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FIG. 1. Schematic representation of nematode cuticles and strata relationships to a *Deontostoma* model. Mesocuticle comparisons are shown by shaded connections. *Deontostoma*, based on TEM, Siddiqui and Viglierchio, 1977; *Aporcelaimellus*, based on Grootaert and Lippens, 1974; *Longidorus*, based on Aboul-Eid, 1969; *Xiphinema*, based on Roggen et al., 1967; *Mermis* and *Dioctophyma* based on Chitwood and Chitwood, 1950; *Trichodorus* based on TEM, Raski et al., 1969; *Euchromadora*, based on Watson, 1965; *Acanthonchus*, based on Wright and Hope, 1968; *Caenorhabditis*, based on Zuckerman et al., 1973; *Ascaris*, based on TEM, Watson, 1965; *Nippostrongylus*, based on TEM, Jamuar, 1966; *Panagrellus*, based on TEM, Samoiloff, 1973.

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