F. Paris

METHODS OF INVESTIGATION

USE OF INFRARED LIGHT FOR THE STUDY OF CHITINOZOA

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ABSTRACT: Certain methods of studying the surface of Chitinozoa and their internal structure are briefly described. A compressed account is given of the classification of Jansonius based on the structure of the prosomal complex and the tegument. Mention is made of the structural complexity and diversity of the prosomal complex in certain genera, and of the possibilities which the use of infrared light affords for study of the internal structure and the role of such study for correct identification of genera and establishment of their stratigraphic importance.

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The Chitinozoa are a group of extinct microorganisms of which only the exoskeleton, consisting of chitinous, usually opaque matter, is preserved in the fossil state. These remains are of great stratigraphic importance for Lower Paleozoic deposits and since they are found both in calcareous and in terrigenous rocks they may serve for the correlation of different facies.

The Chitinozoa were first studied by Eisenack (1931), who isolated and described numerous genera and species from Baltic material, solely on the basis of the morphological characters of the opaque exoskeletons (Eisenack, 1931, 1934, 1939, 1955, 1958, 1962). Beginning with the sixties investigation of the Chitinoza developed widely in connection with oil prospecting; many of these fossils were found in Ordovician-Devonian deposits in many countries and new genera were isolated and described. There are now descriptions of approximately 40 genera of the Chitinozoa based as previously on the shape of the body, the proportions of the body and the neck, and the ornamentation. In most instances study of the Chitinozoa is carried out only in ordinary incident light, which greatly limits the investigator and may lead to serious errors in determination of the species and even the genus to which individuals belong. As Taugourdeau has correctly noted (1966), the use of reflected light with a dark field is far more useful for recognition of the external characteristics of the exoskeleton. Characteristic features of the surface become apparent: the distribution of elements of the ornamentation - uniform or as distinct longitudinal rows, the presence of longitudinal or transverse ridges, and the structure of the base: the latter is particularly important since, for example, in Conochitina the copula or basal callus may be located in the center of a dome-like concave base and may then be completely invisible in incident light, but excellently revealed in reflected light. In Cyathochitina it is frequently only in reflected light that it is possible to see the structure of the basal edge, ornamented by a thickened ridge or a thin frill; in incident light they may appear the same. Therefore, the use of reflected light becomes a completely essential element in investigation of the Chitinozoa.

In a paper published in 1966 Taugourdeau described a further method for investigation of the Chitinozoa in reflected light directly in the bedding planes of schistose rocks. The bedding surface moistened with water is examined under a binocular lens. Taugourdeau regards this method as highly promising, since it makes it possible to detect brittle parts of the exoskeleton which do not withstand ordinary chemical processing of the rock and are destroyed. However, this method is extremely laborious and the scope for its use is limited, since it is rare to find surfaces of schistose rocks rich in Chitinozoa.

In view of the great variability of species of the Chitinozoa and the comparatively limited number of characters which may be used to discriminate them, Taugourdeau and Jekhowsky (1964) attempted to apply biometrics to supplement ordinary quantitative analysis. They took exoskeletons of the genus Conochitina for the attempt. Measurements were made of three parameters: the overall length of the vesicle, the maximum width, and the minimum width (around the aperture). The results were plotted on the diagrams separately for each specimen, after which a "gross" specimen was summed on a single diagram. Fairly clearly delineated "concentration fields," each of which corresponded to a definite species, were revealed in this way. This method is a useful objective addition to the ordinary study and description of the characters of the Chitinozoa.

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All the methods enumerated make possible a fairly complete description of the external habit of the Chitinozoa, their shape and ornamentation.

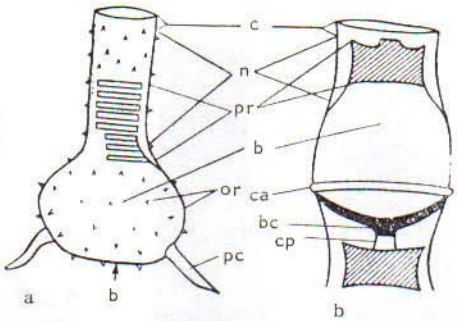

FIGURE 1. Structural diagram of the exoskeletons in Chitinozoa.

a - detached vesicles; b - colonial forms.

c - collarette; n - neck; pr - prosome; b - body chamber; or - ornamentation; b - base (aboral pole); pc - processes; ca - carina; bc - basal callus; cp - copula (Combaz and Poumot, 1962).

The discovery of Chitinozoa with semitransparent exoskeletons in an investigation of Silurian deposits in North Africa in 1962 enabled Combaz and Poumot (1962) to describe not only the external habit, but also some internal structural elements (fig. 1). They noted that in some forms the aperture was closed by a lid or operculum. Within the neck a distinctive structure was seen which Combaz and Poumot called the "prosome." These authors considered that the prosome was made up of rings of different thickness; the upper part of the prosome was capable of compression and extension, like an accordion, and when compressed it resembled an opaque plug which could be located at different levels in the neck and even emerge beyond the edge of the aperture. In some forms the authors observed an opaque round body in place of a rectangular plug. In the lower part of the body chamber Combaz and Poumot discovered a dark, frequently filiform body with sharp contours, which they called the opisthosoma. This element appears either as an independent "utriculus," most often with its convexity facing upward, or as a spherical form, sometimes split and invariably located around the greatest diameter of the body chamber. An opisthosoma is sometimes present in far from all specimens.

Taugourdeau (1966) makes quite a detailed examination of the structure of the prosome, which he also refers to as the "inner annulated tube." He writes that the tube is most often dilated at the base of the neck and becomes lost in the inner wall of the body and that less frequently no dilation is observed. The tube is more often compressed and sometimes has an operculum with its convex surface upward. Most rarely the tube broadens as a funnel toward the aperture. Taugourdeau also observed the presence of an opisthosoma, but in no case were an annulated tube and an opisthosoma encountered simultaneously in one specimen.

It is essential to note that Combaz and Poumot and also Taugourdeau observed internal structures only in naturally translucent exoskeletons.

Jansonius (1967) used photography in infrared light to investigate the Chitinozoa. Infrared rays pass through the chitinous wall, which is nontransparent to ordinary light, and the internal structure of Chitinozoa becomes apparent when photographed on infrared film. This investigator (Jansonius, 1970) proposed a new classification of the Chitinozoa based on the structure of the prosomal complex and of the tegument. According to Jansonius, the structures developed in the neck may be represented as a simple operculum, external or submerged, and a more intricately formed prosome including a thin-walled tube, frequently with transverse grooves ("annulated tube"), continued at the end as the operculum proper. In conformity with this he proposed that the Chitinozoa should be combined into two major groups: Complexoperculati - with intricate recessed operculum-prosome (fig. 2a-d) and Simplexoperculati - with simple operculum, external or recessed (fig. 2e-h). Each of these groups comprises two families. The first contains forms with a simple prosome and usually without differentiation of the aboral pole (Sphaerochitinidae; fig. 2a) and forms with an intricate prosomal complex and more or less complex differentiation of the aboral pole (Tanuchitinidae; fig. 2b-d). The second group contains forms with an external operculum (Desmochitinidae; fig. 2g, h) and with a recessed operculum (Conochitinidae; fig. 2e, f). It is essential to note that, despite the fact that these families were distinguished on the basis of differences in the structure and arrangement of the prosomal complex and the operculum, far from all the genera included in these families have the characteristics of this organ. Jansonius gives brief descriptions of 42 genera, in 17 of which this characteristic is not recorded at all, since it is unknown, in 5 of which it is recorded with the comment "possibly" or "probably," and in only 20 genera is it present.

In the MIK infrared microscope designed in the Soviet Union the infrared image is transformed into a visible image by an electron-optical image converter. This microscope makes it possible to observe the internal structure of the Chitinozoa and the walls directly in the slides, which makes possible detailed investigation of the structure of the prosomal complex, the operculum and the wall. We were given the opportunity of examining a small number of slides under the MIK-1 microscope

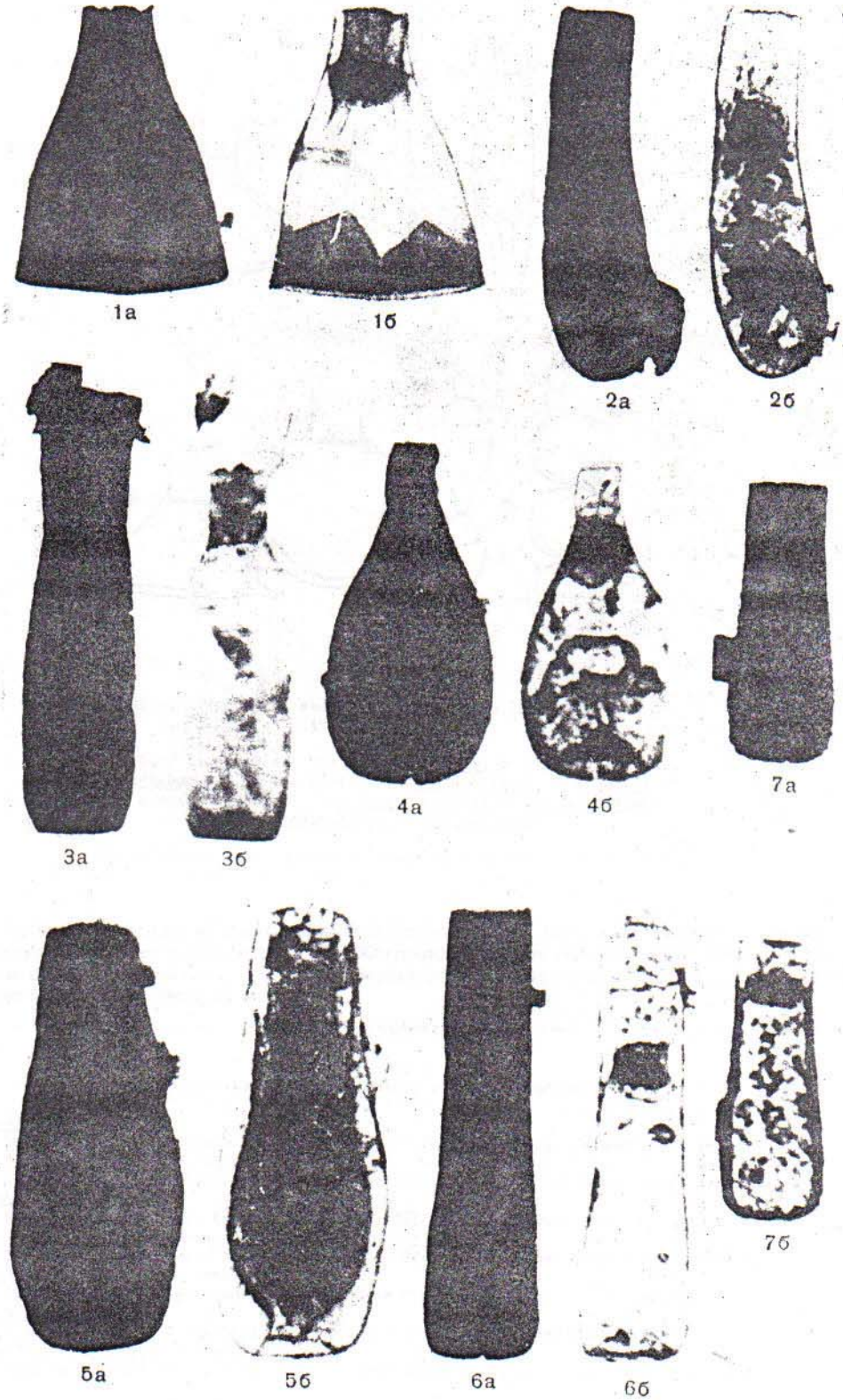

PLATE XII

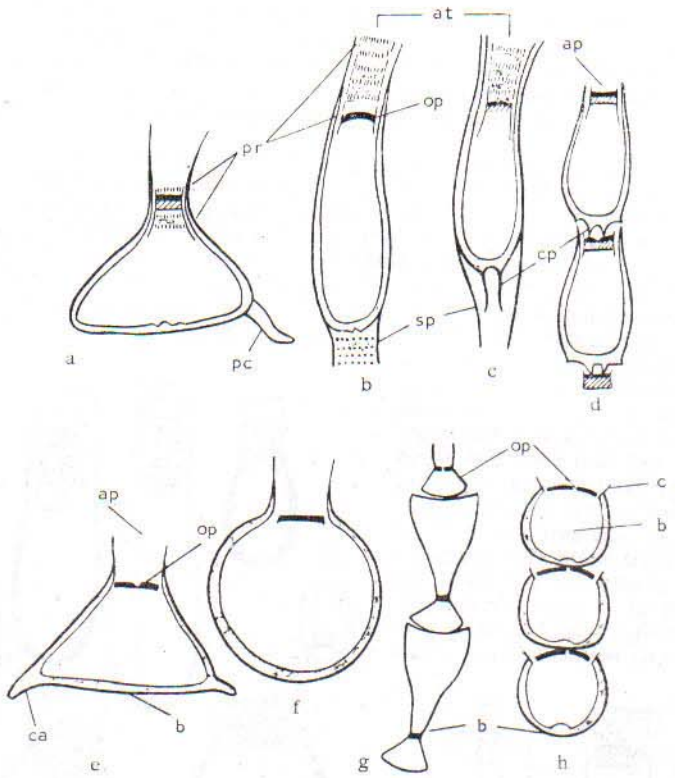

FIGURE 2. Diagram of exoskeleton structure in some genera of the Chitinozoa.

a-d - Complexoperculati: a) Ancyrochitina, b) Tanuchitina and Rhabdochitina (in part), c) Velatachitina, d) Linochitina
e-h - Simplexoperculati: e) Cyathochitina, f) Lagenochitina, g) Margachitina, h) Desmochitina.

at - annulated tube; op - operculum; ap - aperture; sp - siphon; otherwise as in fig. 1 (Jansonius, 1967).

in the N.F. Gamaleya Institute of Microbiology and Epidemiology. We should like to take the occasion of expressing our deep gratitude to M. Ya. Korn and N.I. Solov'yev, scientific officers at the Institute, for their kind cooperation and for assistance in mastering the procedure for using this microscope and for photomicrography with it.

KEY TO PLATE XII
Magnification approximately x 145 throughout

Cyathochitina sp.:
1 - Specimen 1/5039; Talsi bore, 897 m; Upper Ordovician, Upper Caradocian substage;
Lagenochitina pervulgata N. Umnova:
2 - Specimen 1/2387; Rybinsk 5-R bore, 1758-1762 m; Lower Ordivician, Llanvirnian stage;
Euconochitina sp.:
3 - Specimen 1/6214; Danilovskaya 3-D bore, 1923-1927 m; Ordovician;
Lagenochitina tumida N. Umnova:
4 - Specimen 1/5038; Talsi bore, 895 m; Upper Ordovician, Upper Caradocian substage;
Lagenochitina magnifica N. Umnova:
5 - Specimen 1/5051; Talsi bore, 934 m; Lower Ordovician, Llanvirnian stage;
Euconochitina sp.:
6 - Specimen 1/5051; Talsi bore, 934 m; Lower Ordovician, Llanvirnian stage;
Euconochitina subbrevis (N. Umnova):
7 - Specimen 1/5039; Talsi bore, 897 m; Upper Ordovician, Upper Caradocian substage.

In all instances: a - in ordinary light; b - in infrared light.

When approximately 200 exoskeletons of Chitinozoa in which the prosomal complex was preserved were examined it was found that the complex was considerably more varied and intricate in structure than had been noted by Jansonius and, moreover, we observed different structure of the prosomal complex in forms placed in the same genus. Let us take as an example several forms from Lower Paleozoic deposits of the northern part of the Russian Platform.

The prosome is seen in exoskeletons of the genus Lagenochitina as a compact homogeneous plug of the same width as the width of the neck or slightly narrower, approximately half the length of the neck, with flat or convex upper and lower surfaces (fig. 3d, e, g). This plug may terminate below in a fine frill (pl. XII, illus. 4) or a hemisphere (fig. 3f). In addition to a prosome of such simple structure, exoskeletons of the same genus are found to have a very complicated prosome consisting of a flat disc slightly upward concave, on which there is a fine tube with weakly apparent annulation and with a compact nucleus in the lower half. A spherical body with a compact dark membrane is attached to the concave face of the disc below (pl. XII, illus. 2). Sometimes the fairly compact annulated tube is crowned above by a compact homogeneous spherical body (fig. 3a) and the annulated tube is frequently located on a plug consisting of parts of different density and terminating below in a finer frill (fig. 3c). Varied types of prosome, ranging from very small, consisting of a small compact nucleus with a fine frill below (fig. 4a), to a very large plug of intricate structure with broad frills above and below (pl. XII, illus. 3), are seen in Euconochitina. A prosome is also seen in the form of a plug with a more compact central part, a fine frill below and an annulated tube above extending to the

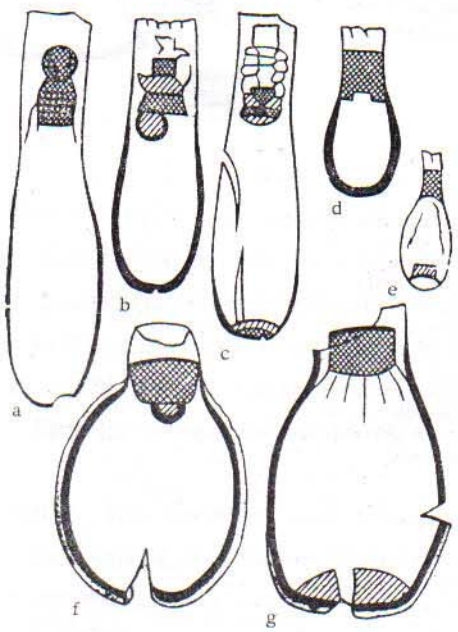

Fig. 3

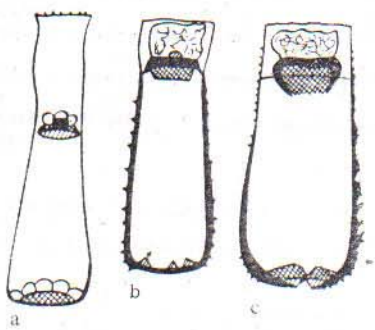

Fig. 4

FIGURE 3. Structure of the operculum and prosomal complex in some species of the genus Lagenochitina.

a - L. ovoidea Taugourdeau; Specimen 1/2387a; Ryabinskaya 5-R bore, 1758-1762 m; Lower Ordovician, Llanvirnian stage
b - L. pervulgata N. Umnova; Specimen 1/2387a; same site
c - Lagenochitina sp.; Specimen 1/5051; Talsi bore, 934 m; Lower Ordovician, Llanvirnian stage
d - L. curta N. Umnova; Specimen 1/2900; Rybinskaya 5-R bore, 1755-1758 m; Lower Ordovician, Llanvirnian stage
e - L. curta N. Umnova; Specimen 1/5044, Talsi bore, 912.2 m; Middle Ordovician, Lower Caradocian substage
f - Lagenochitina sp.; Specimen 1/4348; Edole bore, 865 m; Upper Ordovician, Upper Caradocian substage
g - Lagenochitina sp.; Specimen 1/5038; Talsi bore, 895 m; Upper Ordovician, Upper Caradocian substage.

FIGURE 4. Structure of operculum and prosome in some species of the genus Euconochitina.

a - Euconochitina sp.; Specimen 1/5051; Talsi bore, 934 m; Lower Ordovician, Llanvirnian stage
b - E. subbrevis (N. Umnova); Specimen 1/5039; Talsi bore, 897 m; Upper Ordovician, Upper Caradocian substage
c - E. subbrevis (N. Umnova); Specimen 1/5039; same site.

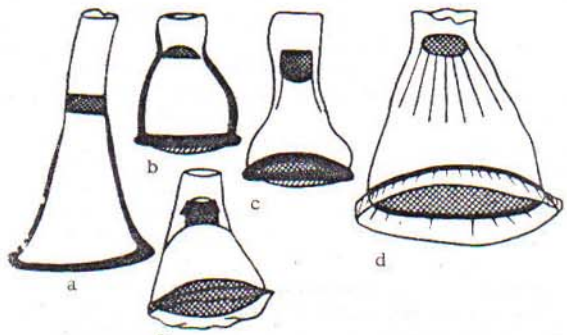

Fig. 5

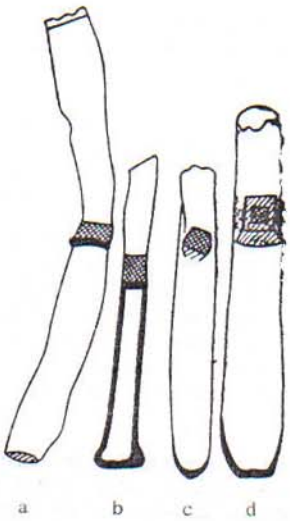

Fig. 6

FIGURE 5. Structure of operculum and prosome in some species of the genus Cyathochitina.

a - Cyathochitina sp.; Specimen 1/2900; Rybinskaya 5-R bore, 1755-1758 m; Lower Ordovician, Llanvirnian stage
b - C. granulata Taugourdeau; Specimen 1/5039; Talsi bore, 897 m; Upper Ordovician, Upper Caradocian substage
c - Cyathochitina sp.; Specimen 1/5058; Talsi bore, 961 m; Lower Ordovician, Llanvirnian stage
d - Cyathochitina sp.; Specimen 1/5036; Talsi bore, 891 m; Upper Ordovician, Upper Caradocian substage
e - Cyathochitina sp.; Specimen 1/5109; Kustinskaya bore, 906-910.1 m; Middle Ordovician, Caradocian stage.

FIGURE 6. Structure of operculum in some species of the genus Rhabdochitina.

a - Rhabdochitina sp.; Specimen 1/5058; Talsi bore, 961 m; Lower Ordovician, Llanvirnian stage
b - Rhabdochitina sp.; Specimen 1/5058; same site
c - Rhabdochitina sp.; Specimen 1/6214; Danilovskaya bore, 3-D, 1923-1927 m; Ordovician
d - Rh. gallica Taugourdeau; Specimen 1/2902; Rybinskaya 5-R bore, 1745-1748 m; Lower Ordovician, Llanvirnian stage.

aperture (pl. XII, illus. 6). A prosome of completely different structure is observed in exoskeletons with a spiny surface (pl. XII, illus. 7; fig. 4b). Some other types of prosome are also known in Cyathochitina and Rhabdochitina (pl. XII, illus. 1; figs. 5, 6).

It is evident from the foregoing few examples that the prosome is of very intricate structure and it is therefore premature, in our view, to create new classifications based on the structural nature of this organ.

Apart from study of the prosomal complex, infrared light makes it possible to observe the wall structure of the Chitinozoa exoskeletons and the presence and nature of the opisthosoma (?).

There is at present no unambiguous opinion on the structure of the tegument in the Chitinozoa. Combaz and Poumot (1962) note that it is double in some Ordovician forms: the basic thick wall is covered by a fine outer layer. Some authors regard the tegument as three-layered, but Taugourdeau (1966) notes that three layers have never been found simultaneously and that therefore the presence or absence of a third layer is open to dispute. In a large compilation on the Chitinozoa, Combaz et al. (1967) distinguish three clear layers in the wall: periderm (investing tegument layer), ectoderm or tegument proper, exhibiting superficial differences (ornamentation), and endoderm (inner tegument layer). Jansonius (1970) considers that the tegument appears to be two-layered and that the outer granular layer usually forms the ornamentation. Observations in infrared light have shown that a three-layered wall really does exist. The outer layer (periderm), which is slender and

transparent and invests the entire vesicle, apart from the neck, or only its lower part, is very rarely observed. It is possible that it is simply destroyed during processing, but the possibility has not been excluded that it is characteristic only for certain species of the Chitinozoa. We have as yet found it only in some Lagenochitina (fig. 3f, g), but Combaz et al. (1967) note its presence in Eremochitina and Velatachitina. The middle layer (ectoderm), or the chitinous tegument proper, is almost invariably opaque and frequently ornamented on the surface. The inner layer (endoderm), which is very fine, extends from the aboral end of the prosome and then merges with the ectoderm (fig. 3g; fig. 5e). Like the outer layer it is rarely observed. The ectoderm, or middle layer, is distinguished both by the ornamentation of its outer surface and by thickness. It may be uniformly thin (fig. 5e; fig. 6a) or uniformly thick all over the vesicle, thicken in a regular manner from the neck to the base or form abrupt thickenings on the basal edge and base (fig. 5a-c). The opisthosoma (?) is observed fairly infrequently and is almost invariably split (pl. XII, illus. 1, 3, 4, 6; fig. 3g; fig. 4a, c), most probably it is simply a concave base. Membranes enclosing an element of intricate configuration in the middle part of the body chamber joined by a slender tube through the opisthosoma (?) to the aboral pole (pl. XII, illus. 4) have been found in (as yet) isolated specimens and also Lagenochitina with a fairly fine exoskeleton in which there is a thick ovoid vesicle (pl. XII, illus. 5). An intricate prosome with an annulated tube is developed in this inner vesicle.

How complex is the internal structure of the Chitinozoa is evident even from the few examples given, as is its importance for classification and the great scope which the use of infrared light offers for the solution of these questions. Investigators are now faced with the task of accumulating data on the structure of the prosome and the prosomal complex and with establishing the causes of their modification. These modifications may probably have occurred not only during the existence of a given species, but may also have been dependent on the age stage of its separate individuals, which may be established only on the basis of a large amount of material. Solution of these questions in parallel with study of the other internal structural elements, the structure of the wall, and the ornamentation is important for understanding the development of the Chitinozoa and to correctly identify the species. This, in its turn, should make it possible to establish precisely the vertical range of the Chitinozoa and, consequently, to make correct use of this group of fossils for the stratification of the deposits containing them.

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