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HAEMOLYMPH COAGULATION IN INSECTS AND TAXONOMY

BY

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(With 59 figures)

CONTENTS

ABSTRACT

Grégoire, Ch. Haemolymph Coagulation in Insects and Taxonomy. — The distribution of patterns of haemolymph coagulation in vitro has been recorded in 580 Neotropical, Palearctic, African and Australian species of insects, not previously investigated. Finding of an exclusive pattern in certain taxonomical categories of insects suggests that this pattern might represent a stable taxonomic character for these categories. This situation has been found at different levels of the taxonomic hierarchy. Including previous observations, 1650 species of insects from 14 orders and about 150 families and subfamilies have been examined.

Pattern I is a stable character in the whole orthopteroid complex (Dictyoptera, Mantodea, Isoptera, Phasmoptera, Orthoptera and Dermaptera), in the *Nepidae-Ranatridae* and *Belostomatidae* (a remarkable exception among Heteroptera), in *Cicadidae, Dictyopharidae* and *Fulgoridae* (Homoptera), in *Oedemeridae*, *Cerambycidae*, the genera *Cybister* (*Dytiscidae*), *Meloe* (*Meloidae*), *Necrophorus* (*Silphidae*), *Pimelia* (*Tenebrionidae*), *Chrysolina* and *Timarcha* (*Chrysomelidae*) (*Coleoptera*), in *Corydalidae* (Megaloptera) and in *Vespidae*, *Formicidae* and *Pompilidae* (Hymenoptera).

Pattern II is representative or predominant in *Histeridae*, some subfamilies of *Scarabaeidae* (*Rutelinae*, *Aphodiinae*, *Dynastinae*, *Trichiinae*, *Valginae*, *Cetoniinae*), in *Erotylidae* (Coleoptera Polyphaga), in larval Lepidoptera (except *Saturniidae*) and in *Araneae* (Arachnida).

Pattern III is representative of *Cercopidae*, *Cicadellidae*, possibly *Membracidae* (Homoptera), *Elateridae*, *Tenebrionidae*, the genus *Carabus* (Coleoptera), larval *Tenthredinidae* (Hymenoptera), possibly larval Odonaptera.

Extremely rapid reactions of the coagulocytes and considerable amounts of clotting material were observed in *Belostomatidae* (Heteroptera), *Fulgoridae* (Homoptera), *Prioninae* (Coleoptera, *Cerambycidae*) and *Corydalidae* (Neuroptera- Megaloptera).

No haemolymph coagulation (pattern IV) could be found in adult Ephemeroidea, in most *Reduviidae*, in *Coreidae*, *Pyrrhocoridae*, *Pentatomidae* (Heteroptera), *Hydrophilidae*, *Staphylinidae*, *Cantharidae*, most *Curculionidae*, *Brenthidae* (Coleoptera), adult Diptera and *Apidae* (Hymenoptera).

Under the technical conditions of this study, the results support former conclusions that the coagulocytes play an exclusive part in initiation of haemolymph coagulation in insects.

INTRODUCTION

A category of haemocytes (coagulocytes) initiate haemolymph coagulation in insects. Observed in thin films under a phase contrast microscope, the reactions of these cells to contact with foreign surfaces and those of the surrounding plasma are not identical in all the insects. On the basis of these differences, four patterns of morphological reactions have been suggested. As previously recognized, insects belonging to a taxonomic group frequently show the same pattern, whereas in insects from other groups another pattern was predominant. The present paper reports original data about distribution of patterns of haemolymph coagulation in 393 species of Neotropical insects and 187 species of insects from other parts of the world.

MATERIAL AND METHOD

The insects were collected and studied, when possible, immediately after capture, during visits to Trinidad (West Indies, 1959), to the Smithsonian Institution's Tropical Preserve on Barro Colorado Island (Canal Zone Biological Area, third stay 1959), to Ecuador (El Oriente: El Puyo, Shell Mera, Limoncocha: 1964) and to Peru (Iquitos, 1971). Other insects were sent by airmail: Australian (Prof. Dr. D. F. Waterhouse and Dr. F. J. Gay: C.S.I.R.O.) and African Termites, Carabidae and Tenebrionidae (Prof. G. Goffinet, Lubumbashi, Congo)*.

A drop of haemolymph issuing from a leg or antenna severed directly at the edge of a coverglass lying on a slide, was allowed to spread out into a thin film. Under these conditions, the haemolymph has been in short contact with air before spreading. As the changes in coagulocytes are instantaneous or occur within one or two seconds, the conditions do not differ from the natural ones (note 1).

OBSERVATIONS

The patterns of Haemolymph Coagulation in Insects

The coagulocyte, an haemocyte highly sensitive to foreign surfaces and physical interfaces, is selectively involved in initiation of clotting of the plasma in insects (Grégoire and Florkin, 1950). The differences in the microscopical reactions in vitro of the coagulocyte have been ranged into four patterns (Grégoire, 1951). These patterns were recorded by microci-

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* 509 specimens from 361 species of Neotropical Insects used in this and previous studies are deposited in the collections of the Department of Entomology of the Smithsonian Institution.

nematography in phase contrast (Ch. Abel and Ch. Grégoire, 1949-1951)

Pattern I (Figs 1-21). Irreversible, selective structural alterations of the coagulocyte produce exudation or explosive discharge (without cell disintegration: Fig. 38) of small amounts of cytoplasmic substance into the surrounding plasma. This plasma rapidly or instantaneously becomes a gel in the form of progressively extending, circular, granular fogs (islets of coagulation) around the coagulocyte. In some species (Figs. 6 and 16), the clot appears densely hyaline in the immediate vicinity of the coagulocyte and becomes more loosely granular in the distance. In the channels which separate the circular islets, the fluid plasma progressively clots into granular substance, which is organized into networks of granular fibrils (Fig. 20). After its alterations, the coagulocyte appears, in many insects, in the form of a congealed, rounded vesicle, swollen by imbibition (Figs 1-21). This vesicle contains a relatively small, sharply outlined nucleus and scattered granules. In certain insects (e.g. Termites, Fig. 6 and *Timarcha*, Fig. 12), the coagulocyte may occasionally show bubble- or club-like cytoplasmic expansions.

Pattern II (Figs 22-25,42)

On contacting the glass or foreign bodies, coagulocytes extrude long, straight threadlike expansions, carrying cytoplasmic granules. These expansions are highly adhesive to solid particles, to other haemocytes and to physical interfaces (air bubbles). These expansions form loose meshworks with similar expansions produced by other coagulocytes. The other categories of haemocytes, including the granulocytes, are passively agglutinated on these meshworks. Confined to these systems of cytoplasmic meshworks, the reaction of the plasma develops in the form of transparent or granular elastic veils.

Pattern III (Figs 26-41, 43, 44, 45, 47-50).

Coagulocytes send cytoplasmic expansions, forming meshworks, within which plasma veils develop, as in pattern II. As in pattern I, clots of greater density appear around coagulocytes, free or already involved in cytoplasmic systems (note 2). The two phases develop simultaneously or in succession in the same or different samples or haemolymph. Coagulation islets may appear first, before extrusion of pseudopodial systems, or alternatively. In some samples, the double reaction is incomplete: one of the phases appears alone (note 2).

Pattern IV (Figs 52-59).

Coagulocytes appear inert or become hyaline after ejection of cell substance. The consistency of the surrounding plasma does not show visible change, at least under PCM conditions.

Distribution of the patterns of haemolymph coagulation.

The results on distribution of patterns in the species investigated are reported in Table 1. In this Table, the name of the species (adults, unless otherwise stated), the number of specimens investigated, and the site of capture are ranged in the first column. In this column, the terms « Former data » refer to the average pattern recorded in previous observations on corresponding families and genera (Neotropical material: Grégoire, 1957, 1959 ab; Palearctic material: Grégoire, 1951, 1955ab; African material: Grégoire, 1955a, Grégoire and Jolivet, 1957). In the second column, the pattern of coagulation representative or predominant is indicated by the following symbols: ●: pattern I; ○: pattern II; ⦵: pattern II incomplete, emission of cytoplasmic expansions by coagulocytes, as in pattern II, but unaccompanied by formation of veils in the plasma; ⊙ : pattern III; —: pattern IV; ● ⊙ , ○ ⊙ : pattern III dissociated into its components in parts of the samples or in different samples of the same specimen or species; (): pattern inconstantly or exceptionally recorded in films exhibiting predominantly another pattern; (?): microscopical reactions of a pattern not clear-cut or equivocal. Artifacts possibly involved.

Abbreviations used: BCI: Barro Colorado Island; Tri(nidad); Ec(uador); Iqu(itos), Peru; v.r. : varied individual reactions; spm: specimen. Asterisks (*) indicate gradations in the intensity of the clotting reaction around the coagulocytes, especially with regard to pattern I, from fringes around coagulocytes to general clotting of the haemolymph film and reorganization into abundant meshworks of granular fibrils: The film appears then as a bluish, opalescent jelly.

TABLE 1. Patterns of Coagulation

Material	Patterns representative or predominant
THYSANURA	
Former data, two species (Paleartic and African), 6 spms	—
Neotropical ODONAPTERA	
Former data: *Libellulidae* sp., 1 species, adult; *Agrionidae* sp., 1 species, adult	—
Palearctic	
Coenagrion sp., larvae, 5 spms	—(○)
Aeschna sp., larvae, 19 spms	vr. ○(● ⊙)
Cordulegaster sp., larva	—(○)
Libellulidae sp., larva	● ⊙
Former data	
Genera *Anax, Aeschna*, *Libellula*, larvae, 36 spms	● ⊙
Libellulidae sp., adults, 2 species	—
Palearctic EPHEMEROPTERA	
Ephemera danica Müller, adults, 9 spms, larvae, 14 spms; *Ephemera lineata* Eaton, adults, 17 hours after hatching, 35 spms; *Ephemeridae* sp., adult; *Ecdyonurus* sp., larvae, 2 spms (*Heptageniidae*); *Ephemerella ignita* Poda, 2 spms (*Ephemerellidae*); *Baetis rhodani* Pictet (*Baetidae*)	—
Neotropical PLECOPTERA Nr *Chloroperlidae*, Ec., adult	⦵
Palearctic *Perlidae* (Figure 8) *Perla* sp., larvae, 2 spms, Unid. *Perlidae*, 4 spms	●✻
Former data, 1 species, 11 spms	●
ORTHOPTEROID Complex	
Neotropical DICTYOPTERA [BLATTODEA, 3 unid. species, Iqu.	●✻✻
Neotropical MANTODEA	
Liturgousa sp. *peruviana* G.-T. or near, E.c; *Tithone roseipennis* Saussure-Zehntner, Tri.; *Choeradodis rhombicollis* Latr., BCI; *Stagmatoptera* sp. (Vatinae), Iqu.; *Catamusonia* sp. (*Thespinae*), Iqu., 4 spms; Unid. *Mantidae* Iqu.	●✻✻✻

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Neotropical PHASMOPTERA *Geoxylus spinosus* Fabr., Tri.; *Libethra regularis* Br. v. W., Tri., 2 spms; *Calynda bicuspis* Stål, Tri., 3 spms; 5 unid. *Phasmidae*, Tri. and Ec.	● * *
Neotropical ISOPTERA *Nasutitermes* corniger, BCI, 5 workers; *Nasutitermes nigriceps* (Hald), BCI, 3 winged nymphs	●
Australian *Neotermes insularis*, 2 winged spms, 4 soldiers, 25 workers; *Bifiditermes condonensis*, 15 winged spms, 4 soldiers, 18 workers; *Porotermes adamsoni*, 7 soldiers, 8 workers	● * * *
African *Cusitermes* sp., 2 queens, Congo, (Figure 6)	● * *
Former data: 3 species, including *Calotermes flavicollis* Fabricius.	●
Neotropical ORTHOPTERA TETTIGONIIDAE *Oxyprorella gregoirea* nov. sp. (*Phaneropterinae*), BCI; *Peucestes championi* Pictet & Saussure, M., BCI; *Eupeucestes crassifolius* de Haan, Tri.; *Copiphora brevirostris* Stål, M., BCI; *Acanthodis aquilina* L., BCI, 2 spms; *Neoconocephalus maxillosus* Fabr. (*Conocephalidae*), BCI; Cocconotur degeeri Stål, BCI.	● * *
GRYLLIDAE *Stenaphorus macilentus* Stål, BCI; *Oecanthus* sp., Tri.; *Hapithes* (Apithes) sp., Tri..	● * *
Rhipipteryx rivularia Sauss., Tri., 3spms; *Neoxabea bipunctata* de Geer, BCI (note 4).	—
GRYLLOTALPIDAE *Gryllotalpa hexadactyla* (Perty), Tri, Ec., 3 spms; *Scapteriscus didactylus* (Latr.), 3 spms, Iqu.	● * *
GRYLLACRIDAE *Ablona salvini* Sauss., *Brachybaenus* sp., BCI	● *

TABLE 1. *(continued)*

Material	Patterns representative or predominant
ACRIDIDAE *Paurotarsus amazonicus* Hancock (Tetrigoidea) Iqu.; *Paurotarsus rugosus* Brunner, Tri.; *Omura congrua* Walker (*Pyrgomorphidae*), Iqu.; *Tetrataenia* sp. (*surinama* L. ?) (*Oxyinae*), Iqu.; *Osmilia flavo-lineata* de Geer, M. & F., Tri. BCI; *Tropidacris latreillei* Perty, Tri., 2 spms; unid. *Catantopidae* (larva, first stage) Tri.	●(**)
DERMAPTERA (Fig. 9) *Doru lineare* (Esch.) (*Forficulidae*), Ec.; *Carcinophora percheron* (Guérin) (*Labiduridae*)Tri., 17 spms; *Carcinophora* sp., Ec.; genus near *Carcinophora*, Tri., 5 spms; *Spongiphora buprestoides* Kirby, F., Tingo Maria, 2 spms; *Spongiphora croceipennis* (Serv.), F., BCI; 2 unid. Dermapteroidea, Tri., Iqu.	● **
Former data on Neotropical DICTYOPTERA, ISOPTERA, PHASMOPTERA, ORTHOPTERA, DERMAPTERA, 116 species	● **
Palearctic and African material (Orthopteroid Complex). *Pyrgomorpha conica* (Olivier), larvae, 2spms; *Locusta* sp.; *Acrida bicolor* (Thunb.), larva; *Gryllotalpa* sp., 5 spms, Congo; unid. *Phasmidae*, Madagascar, *Euborellia annulipes* Luc., F. Congo.	● **
Former data (Palearctic: 34 species; African: 29 species).	● **
HEMIPTERA-HETEROPTERA Neotropical *REDUVIIDAE* *Panstrongylus geniculatus* (Latr.), 4 spms, BCI; (G., 1957 a: same reaction); *Harpactocorinae*, gen. sp. ? Tri; *Zelus* sp., nymph, Iqui.; *Zelus* sp. (different from above), Iqu.; *Zelus* sp. (another form) Iqu.; *Apiomerus* sp. ? Ec.; *Heniartes* sp. ? (possibly *putumayo* Wygodzinsky) Ique., 7 spms; *Zelurus* sp. ? near *luteispinus* Stål, Ec.; *Montina lobata* (Stål) Ec. (G. 1959, same reaction, Tingo Maria); *Montina* sp., Iqu., 10 spms (see note 3); subfamily *Ectrichodiinae*, gen. ? sp. ?, Ec.; *Zirta* sp., near *hirticornis* (Fabricius) Iqu., 3 spms; 5 unid. species, Tri, BCI	—
Apiomerus luctuosus Lima, Seabra & Hathaway, Iqu.; *Montina confusa* Stål, Ec.	—(⊖)
Zelus sp., Iqu. (note 4)	⊖ ○
Former data: 28 species	—

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Palearctic *REDUVIIDAE*	
Reduvius personatus L. (larva and adult)	—(⊖)
Former data: Palearctic, 3 species; African, 7 species	—
Tentative generalization, Reduviidae, 58 species	—
Single specimens of *Apiomerus*, *Rasahus*, *Ploegaster* (Neotropical), *Ectrichodia* and *Rhinocoris* (African) (note 4)	(●?)
Palearctic *Gerridae*	
Gerris sp., 18 spms	—(⊖)
Former data, 1 species	—
Neotropical *COREIDAE*	
Acanthocoris sp., Ec., 4 spms; *Leptocorisa*? sp. (*Abydidae*) Ec.; *Paryphes* sp., Ec.; *Zoreva spinifera* Stål, Ec (G 1959, Tingo Maria, same reaction; *Leptoglossus* sp., Iqu.; 5 unid. (different) sp. of *Coreidae*, Iqu. 9 spms; *Hypselonotus aberrans* Horvath, M. & F., Ec., 3 spms.	—
Former data, 14 species	—
Palearctic and African *Coreidae*	
Former data, 5 species	—
Neotropical *Gelastocoridae*	
Nerthra tenebrosa Todd, Ec., 3 spms	—(⊖)
Former data, 1 species	—
Neotropical *PYRRHOCORIDAE*	
Dysdercus bimaculatus Stål, BCI, 2 spms; *Dysdercus ruficollis* (Linn.), Tri.; *Dysdercus mimus* SAY, M. & F., Ec; 3 unid. species, Iqu. 9 spms	—
Dysdercus mimus (Say), 1 spm	—(○ ***)

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Former data, 4 species	—(⊖)
Palearctic *Pyrrhocoridae*	
Former data, 1 species	—(○)
Neotropical *Largidae* *Largus* sp., Ec., 2 spms (G. 1959, Tingo Maria, same reaction).	—
Neotropical *Lygaeidae* *Oncopeltus varicolor* (Fabr.), Tri; unid. *Lygaeinae*, Iqu.	—
Palearctic and African *Lygaeidae* *Oncopeltus famelicus* Fabricius (African)	—(●?)
Former data, 3 species	—
Neotropical *PENTATOMIDAE* *Arocera elongata* Schowalter, Ec.; *Edessa patricia* Stål, BCI; *Edessa leucoryx* Breddin, Ec.; *Edessa* sp.? Iqu.; *Edessa* sp., Ec.; *Oplomus marginalis* (Westwood), Ec.; *Prolobobes gigas* (Sign.), BCI; *Proxys victor* (Fabr.) Tri., 2 spms; *Sphyrocoris elongatus* Dist., BCI, 2 spms; *Antiteuchus sepulchralis* (Fabricius), Iqu.; *Acrosternum marginatum* (Beauvois), Iqu.; *Euschistus* sp.? (near *acutus* Stål), Iqu.; 4 unid. species of *Pentatomidae*, BCI, Tri.	—
Former data; 25 species	—
Palearctic and African *Pentatomidae* Former data, 18 species	—
Other families of HETEROPTERA Former data: *Cydnidae* (1 species), *Nabidae* (1 species); *Scutellerinae* (7 species); *Tesseratominae* (1 species); *Plataspididae* (1 species); *Miridae* (1 species); *Naucoridae* (2 species); Corixidae (1 species);	—
Cryptacrus (Scutellerinae); *Notonecta* (*Notonectidae*)	—(○)
BELOSTOMATIDAE (5 species); *NEPIDAE-RANATRIDAE* (4 species) (Fig. 21)	● * * *

TABLE 1 *(continued)*

Material	Patterns representative or predominant
HEMIPTERA-HOMOPTERA	
Neotropical *CICADIDAE* (Fig. 2).	
Carineta sp., Tri.; *Dorisiana semilata* (Walker), Ec.; *Pacarina puella* Davis, BCI, 5 spms; genus? species; nymph, Ec.	● * *
Former data, 7 species	● * * *
Neotropical CERCOPIDAE (Figs. 27, 28, 29, 33)	
Aeneolamia astralis (Distant), Ec.; *Aeneolamia* sp.? -A, Ec., 3 spms; *Aeneolamia* sp. ? -B, Ec. (note 7); *Delassor tristis* (Fabricius) Ec., 4 spms; *Delassor andigenus* (Jacobi), Ec., 3 spms; *Tomaspis aequinoctialis* Jacobi, Ec., 2 spms; *Tomaspis melanoptera* (Germar), Ec.; *Tomaspis galbana* Jacobi, Ec., 3 spms; *Tomaspis* sp. near *rubra* (L.), Tri., 7 spms; *Tomaspis* (sens. lat.), (A, -A5, BCDEF), 7 species, Ec.; *Sphenorhina rubra* (Linnaeus) var?, 7 spms, Ec. (note 7); *Sphenorhina* sp. ?-A, Ec., 5 spms; *Sphenorhina* sp., ?-B Ec., 2 spms; *Sphenorhina* sp. ?-4, 2 species, 3 spms, Ec.; *Sphenorhina* sp. ;-4, Ec.	⊙ * * * ● * * * ● ⊙ * * *
Sphenorhina latifascia Walker, Ec. (note 4)	—
Cephisus siccifolius (Wlk.), BCI, 2 spms, (note 4) (G. 1959, Tingo Maria, Peru: pattern I); *Cephisus sanguisugus* Jacobi, Ec., 2 spms; *Cephisus* sp., Ec., 3 spms.	— ○ ⊙
Zulia pubescens (Fabricius), Ec., Iqu., 20 spms; *Zulia* sp. (1), Tri.; *Zulia* sp. (2), Ec.; unid. sp., BCI.	● ⊙ * * *
Former data, 12 species (*Tomaspis*, 11 species)	● * * * (⊙)
Palearctic	
Philaenus spumarius Linné, M. & F., 15 spms, Fig. 39; *Neophilaenus lineatus* Linné. M. & F.; *Cercopis sanguinea* Geoffroy; *Aphrophora alni* Fall, 32 spms (Figs. 38-40).	● ⊙ * *
Former data, 3 species.	● ⊙
Tentative generalization, Cercopidae, 46 species.	● ⊙ * * *
MEMBRACIDAE (Fig. 32)	
Amastris elevata Funkhouser, Ec.; *Enchenopa lanceolata* (Stoll) Ec.; *Enchenopa lateralis* (Stoll), Ec.; *Gelastogonia chrysura* (Fairmaire), Ec.;	● ⊙
Ceresa (sensu strict. of Caldwell 1949) species; *Stictopelta acutula* Fairmaire, 2 spms, Ec.;	○ * * (⊙)

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Tribe *Ceresini*, Gen. sp. ? Iqu.; *Membracis lefebvrei* (Fairmaire) Ec.	—
Former data, 1 species	●
Neotropical *CICADELLIDAE* (Figs. 3, 6, 26, 30)	
Baleja flavoguttata (Latr.), BCI (G. 1959, BCI, same reaction); *Cicadellà (Poeciloscarta) bisellata* (Signoret), Ec., Iqu., 14 spms; *Cicadella miniaticeps* (Fowler) Ec.; Sp. of *Cicadellinae*, Gen. ? Ec.; *Diestostemma* sp., 10 spms (G 1959, 4 species, same reaction); *Gypona* sp., BCI, 2 spms (G. 1959, 4 species of Gypona, same reaction); *Oncometopia expansa* Melichar, Ec.	● *** (⊙)
Megacoelidia splendida Kramer and Linnavuori, Ec., 2 spms; *Oncometopia venosula* Distant, Ec., 3 spms; *Pseudoscarta* sp., *obliquatula* (Jacobi), Ec., 3 spms; *Rhaphirrhinus phosphoreus* (L.), Ec., 4 spms; *Tretogonia* sp., Iqu., 22 spms.	● ⊙ ***
Evacanthus interruptus Linné, Ec.; *Pseudometopia phalaesia* (Distant), Ec; *Amblyscarta moesta* (Fab.), Ec., 2 spms; *Agrosoma* new species, 6 spms, Ec.; *Baleja* sp. ?, Tri.; *Diestostemma stesilea* Distant, Ec.; *Erythrogonia jumaca* Medlar, Ec., 2 spms; *Sphaeropogonia* sp. near *aureatula* Breddin, Ec.; *Tretogonia punctatissima* (Melichar), Ec., 3pms.	⊙ *** (●)
Amblydiscus sp. near *variabilis* (Signoret), Ec., 2 spms; *Amblyscarta* new species, near *partitula* Jacobi, Ec.	○ (⊙ prob)
Cardioscarta quadrifasciata (L.), Ec.; *Molomea virescens* (Distant), Ec. (note 4)	—
Former data, 19 species.	●
Palearctic CICADELLIDAE	
Cicadella (Tettigella) viridis Linné (*Jassus lanio* L., Jassidae), 17 spms; *Aphrodes bicinctus* Schrk; *Graphocephala coccinea*, 26 spms.	● ⊙ ***
Former data, 1 species	● ** ⊙ ***
Tentative generalization, CICADELLIDAE, 49 species	● ⊙ ***
Neotropical *Cixiidae* *Oliarus* sp., F., Ec.	—

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Former data, 1 species	——
Neotropical *Derbidae* *Derbe* Sp., F., Ec.	——
Neotropical *DICTYOPHARIDAE* (Figure 1)	
Hyalodictyon brachyrhinum (Walker), BCI, 2 spms; *Hyalodictyon obtusifrons* (Walker), BCI; *Hyalodictyon* sp., F., Ec.; *Nersia florens* Stål, BCI, 5 spms (G. 1959, same reaction).	● * *
Mitrops noctivida (L.) M., Ec.; *Trimedia sp., F., Ec. (note 4).*	——
Former data, 4 species	●
Tentative generalization, *Dictyopharidae*, 10 species	● * * *
FULGORIDAE	
Cyrpoptus obscurus Metcalf (?), BCI; *Calyptoproctus elegans* (Oliver), BCI, 3 spms (G. 1957: same reaction); *Enchophora prasina* Gerst., BCI; 2 unid. *Fulgoridae*, BCI; *Odontoptera carreñoi* Signoret BCI (G. 1957, 1959: same reaction)	● * * * *
Former data, 10 species	● * * * *
Neotropical *NOGODINIDAE*	
Bladina rudis (Walker), 3 spms., Tri.	——
Vutina, sp. nova, M., Ec.	● * *
Former data, 1 species	——
Neotropical *FLATIDAE* (Fig. 52).	
Anormenis sp., BCI, 8 spms; *Carthaeomorpha rufipes* Melichar, BCI, Ec., 5 spms (G. 1957: same reaction); *Flatidae* sp., bci; *Epormenis roscida* (Germ.), BCI, Ec., 9 spms; Gen. & sp. (a), BCI; Gen. & sp. (b), BCI.	——
Flatoidinus occidentalis (Walker), BCI	——(● ?)
Former data, 5 species	——(● ?)

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Neotropical *Issidae*	
Former data, 1 species	——?
COLEOPTERA	
Adephaga	
Neotropical *CICINDELIDAE*	
Former data, 3 species	●(⊙ ?)
Palearctic	
Former data, 1 species	⊖——
Neotropical *CARABIDAE*	
Genus *Agra* Fabr., Tri.; Genus *Pachyteles* Perty (?), BCI, 2 spms (*Ozaenaidae*)	⊙ (○)
Genus *Galerita* Fabricius sp. (found in cocoa pods), Tri.; unid. larva (found in cocoa pods), Tri.	——(⊖)
Former data, 18 species	v.r.
Palearctic and African (Figs. 41, 42)	
Carabus auronitens Fabri., 2 spms; *Carabus violaceus* (*purpurascens*), 3 spms; *Carabus* sp.; *Hadrocarabus problematicus* Hbst	⊙ * * *(●)
Abax ater; *Abax* sp.; *Dichaetochilus incrassatus* Boh. (Congo), 2 spms; *Pterostichus* sp.	○ * *(——)
Nebria brevicollis F., 3 spms; *Amblygenius validicornis* Boh., 2 spms; *Hyparpalus tomentosus* Deg., Congo	——
Former data Palearctic *Carabidae*, 18 species	v.r.
African *Carabidae*, 7 species	v.r. ● ⊙
Tentative generalization, *Carabidae*, 55 species	v.r.
Predominance of a pattern at the genus level	
gen. *Carabus*	⊙ * * *
gen. *Agra*	● ⊙
Palearctic *Hygrobiidae*	
Former data, 1 species	——(○ ?)

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Palearctic and African *DYTISCIDAE*	
Agabus bipustulatus, 2 spms	○ * *
Agabus melanarius L., *Agabus* sp. (Figure 54)	—
Dytiscus marginalis L.,M. &F., adults, 8 spms	○ ⊙ * *
larvae, 3 spms	○ (—)
Tentative generalization, *Dytiscidae*, 19 Species	v.r.
genus *Cybister*	● * * *
.. *Dytiscus*	⊙
(Fig. 53) ..*Hydaticus*	—?
Polyphaga	
Palearctic and African *HYDROPHILIDAE*	
Former data, 5 species	—
Palearctic *SILPHIDAE*	
Oeceoptoma (*Silpha*) *thoracica* Linnaeus, 3 spms; Byrrhus ductinus Steff.	—
Necrophorus sp.; *Necrophorus investigator* Zett.	● * * *
Tentative generalization, *Silphidae*, 11 species	v.r.
(Fig. 34) genus *Necrophorus*, 4 species	● * * * (⊙)
Neotropical *HISTERIDAE*	
Hololepta sp., Tri.; *Hololepta* sp., Tri.;, 3 spms; *Omalodes bifoveolatus* Mars, Tri.; *Omalodes gagatinus* Er., Tri.	○
Former data, Palearctic *Histeridae, 2 species*	○
African *Histeridae*, 4 species	○ (v.r.)

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Neotropical *STAPHYLINIDAE* (Fig. 55) Unid, spm, Tri.; Genus sp. ?, Tri. (found in cocoa pods); Genus sp. ?, Ec.	—
Former data, 1 species	—
Palearctic *Staphylinus caesareus* Cederb, 2 spms; 7 unid. spms; Quedius mesomelinus Mrsh	—
Former data, Palearctic and African, 10 species	—
SCARABAEOIDEA *PASSALIDAE* Neotropical *Passalus interruptus* Linn., Tri., 6 spms; *Passalus morio* (Subsp. ?) Perch., Tri.; *Passalus interstitialis* subsp., Tri., 2 spms; *Passalus sp.*, Tri.; Gen. sp. ?, Iqu., 4 spms; Gen. sp. ?, Ec., 3 spms; Gen. sp. ?Iqu;Gen.sp. ?Ec.,	○ (**)
Former data	
Neotropical, 6 species	v.r. ⊖
African, 5 species	● ⊙
SCARABAEIDAE COPRINAE (SCARABAEINAE) Neotropical *Onthophagus rhinophyllus* Har., Tri; *Canthon triangulare* Drury, Tri., Ec., 10 spms; *Uroxys* gordon Arrow, BCI	○**
Former data, 4 species	○ (—)
Palearctic *Copris* sp., *Copris* sp.	○ (⊙ ?)
Former data, African, 17 species	●* ⊙*
Tentative generalization, *Coprinae*, 28 species (see discussion)	

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Neotropical *Rutelinae*	
Macraspis chalcea Burm., Tri.	○
Former data, 8 species	○
African *Rutelinae*, 3 species	○
Palearctic *Aphodiinae*	
Aphodius (Teuchestes) rufipes; unid. sp., 9 spms	○ *
Former data, 2 species	○
Palearctic *Geotrupinae*	
Scarabaeus sacer Linné, 2 spms; *Typhoeus* sp., 3 spms	⊙ (●)
Scarabaeus cicatricosus Lucas (note 4)	(——?)
Former data, 5 species	⊙
Neotropical *MELOLONTHINAE*	
Ancistroma sp., Tri; *Ancistroma* sp., Tri.; *Phyllophaga* sp. BCI; *Phyllophaga rorulenta* Burm.	○ * *
Former data, 1 species	○
Former data, Palearctic *Melolonthinae*, 3 species, including *Melolontha melolontha.* (Fig. 46)	○ (⊙ ?)
African *Melolonthinae*, 2 species	⊙
Tentative generalization, *Melolonthinae.* 10 species	○ (⊙)
African *Hybosorinae*, 1 species	⊙
Neotropical *DYNASTINAE* (Fig. 22.)	
Bothynus sp., Iqu., 2 spms; *Cyclocephala* sp., Tri.; *Cyclocephala* sp., Tri.; *Cyclocephala* sp., Tri., BCI; *Oryctes* sp., Ec.	○
Former data, 6 species	○
Palearctic and African *Dynastinae*, 10 species (note 5)	○ * * * (⊙)
Former data. Palearctic (9 species) and African (14 species) *Trichiinae*, *Valginae* and *Cetoniidae*	○ * *

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Palearctic *LUCANIDAE*	
Lucanus cervus Linnaeus, M.; unid. larva	○
Dorcus parallelipipedus Linnaeus, M. & F., adults, 10 spms	●**(⊙ **)
larvae, 9 spms	○(⊙)
near pupation	—
Former data, Palearctic and African *Lucanidae* 3 species.	○(⊙)
Neotropical *Cebrionidae*, Former data, 1 species	●*
Neotropical *Sandalidae*, Former data, 1 species	—?(●?)
ELATERIDAE	
Neotropical (Figure 35)	
Unid. spm, Tri.; unid. spms, Tikal, 2 spms; *Chalcolepidius porcatus* Linnaeus, Ec. (G. 1957 pattern II); *Pyrophorus* sp., Tri.; *Dicrepidius corvinus* Dejean, F., BCI; *Dicrepidius palmatus* Dejean, M., BCI; *Achrestus* sp., Ec.; genus? Tri., larva, 2 spms	●**(⊙ **) ⊙ ●** ⊙ **
Former data, 6 species	⊙
Palearctic	
Lacon punctatus Herbst; *Ctenicera* (*Corymbites*) *cuprea* Fabr. (var. *aeruginosa* Fabr., F., 3 spms; *Athous obscurus* L.	○
Ampedius sanguineus L.	—
Former data, Palearctic (6 species)	⊙ (○)
African, 4 species	⊙
Tentative generalization, *Elateridae*, 27 species	⊙ **
Neotropical *CANTHARIDAE*	
Aspidoma sp., Tri.; *Discodon* sp. near *birubronotatus* Pic., Ec.; 2 gen. sp. unid., Tri.	—
Palearctic *Cantharidae*	
Former data, 7 species	—(○)

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Palearctic *Malachiidae*	
Former data, 1 species	—
Neotropical *LYCIDAE* (note 6)	
Calopteron serratum (L.), Ec.; *Calopteron* spp., Tri., 7 spms; *Calopteron* sp., Tri., 2 spms	—
Former data, Neotropical, 1 species	?(○ ?)
African, 1 species	—
Neotropical *Lampyridae* (notes 6 & 7)	
Photinus sp., Tri.; *Phaenolis* sp., Ec.; *Phaenolis* sp., Ec.; *Aspisoma* sp., Iqu.	—
Phaenolis sp., Ec.	?(● * * ?)
Former data: *Photinus* sp. and 2 unid. species	— ?
Palearctic *Lampyridae*	
Lampyris noctiluca Linnaeus	—(⊖ ?)
Neotropical *Lymexilidae*	
Former data, 1 species	● ⊙
Endomychidae	
Former data: Neotropical, 1 species	⊖
African, 1 species	—
Palearctic Buprestidae,former data, 3 species	○ *
Neotropical *Ostomidae*	
Tenebriodes sp., BCI	⊖
Former data, Palearctic, 1 species	● * ⊙ *
Coccinellidae (note 6)	
Former data Neotropical, 2 species	—
Palearctic and African, 2 species	○ ?

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Neotropical *Nilionidae* *Nilio* sp., Ec. (Fig. 11)	●*
Neotropical *Eucharitidae* *Kapala furcata* (F.), 4 spms	—
Erotylidae (Figs 23, 24).	
Brachysphaenus (*Megaprotus*) *octopunctatus* Kirsch, Ec.; *Brachysphaenus* (*Saccomorphus*) *interruptus* Kuhnt., Ec.; *Brachysphaenus quinquefasciatus* Lacordaire, Iqu., 2 spms; *Aegithus punctatissimus* F., Iqu., 2 spms; *Cypherotylus* sp., Ec.; *Cypherotylus* sp., near *debauvei* De May, Iqu., 2 spms; *Erotylina maculiventris* (Lec.) Ec.; *Erotylus spectrum* Thomson, Ec., Iqu.; *Homoeotelus orbignyanus* Lac., Ec., 4 spms; *Homoeotelus umbonatus* Lacordaire, Iqu.; *Lybas atripennis* Erichson, Ec.: *Priotelus detrahens* Crotch, Ec.; *Scaphidomorphus* bosci Guérin, Ec.	○**
Inconstant reactions in samples of *Brachysphaenus quinquefasciatus*, *Cypherotylus* near debauvei and *Erotylus spectrum.*	(⊙)
Erotylus flavopunctatus Kuhnt, Ec.	○(⊙)
Brachysphaenus (*Saccomorphus*) *glyptoderus* Lac.; Ec.; *Prepopharus* sp., Ec. (note 4)	—
Former data, 4 species	○(⊙?)
Tentative generalization, Erotylidae, 21 species	○(⊙?)
Former Heteromera (*TENEBRIONIDAE*, *MELOIDAE*, *LAGRIIDAE*, *OEDEMERIDAE*).	
TENEBRIONIDAE	
Neotropical	
Zophobas sp., BCI; *Alegoria dilatata* Laporte, Tri.; *Nyctobates gigas* (Guérin), M. & F., Iqu., 3 spms; *Paroeatus nitidus* Gebien, Iqu.; *Anaedus* sp., Ec.; *Opatrinus* sp., BCI, 2 spms	●(⊙) ●** ⊙***
Former data, 4 species	⊙(●)
Palearctic and African (Figs 43, 44, 47)	
Akis granulifera (Sahlb.) F., 2 spms; *Akis* sp.; *Ancophtalmus clathratus* Gerst, 4 sms; *Erodius tibialis* L., 3 spms; *Gonocephalum simplex* F., 5 spms; *Helops striatus* L.; *Pimelia incerta* Sol.; *Pogonobasis seriepilosus* Gebien, 3 spms; *Tenebrio* sp. (Greece), 2 spms; 3 unid. spms; *Zophosis fartula* Chat.	⊙***
Pimelia (*Amblyptera*) *fornicata* Herbst; *Pimelia* sp.	●***(⊙)

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Former data, Palearctic, 14 species	● * ⊙ *
African, 14 species	⊙ * * * (●)
Tentative generalization, *Tenebrionidae*, 52 species	⊙ (●)
Lagriidae	
Former data, Palearctic, 1 species	⊙
African, 2 species	●(⊙)
Palearctic *Oedemeridae*	
Former data, 4 species	● * *
MELOIDAE	
Neotropical	
Epicauta grammica Fischer von Waldheim, BCI (G. 1957, same reaction)	● * * ⊙ * *
Palearctic	
Former data, 6 species	● * * (⊙ * *)
African *MONOMMIDAE*	
Former data, 2 species	⊙ *
Neotropical *THROSCIDAE*	
Drapetes sp., Tri., 2 spms	○
CERAMBYCIDAE	
Neotropical	
PRIONINAE (Figure 10) *Stenodontes* sp., BCI	● * * * *
Former data, 5 species	● * * * *
African *Prioninae*, 3 species	● * * * *
LAMIINAE	
Estola sp., BCI, Iqu., 3 spms; *Oreodera glaucus* L. BCI; *Acanthoderes sp.*, BCI; *Colobothea* sp., BCI; gen. not ascert., BCI; *Hippopsis* sp., Tri., 3 spms; *Esthlogena porosa* (Bates), BCI; *Alcidion* sp., Tri.; prob. *Leptostylus* sp., BCI; *Polyraphis* sp., BCI, 2 spms	● * *

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Leptostylus sp., BCI; *Steirostoma* sp., Tri., Ec., 3 spms	●**(⊙**)
Former data, 16 species	●***(⊙)
Palearctic and African Lamiinae, 4 species	●** ⊙**
CERAMBYCINAE	
Eburia sp., poss. *pedestris* White, BCI; *Stenygra* sp., Ec.; *Brasilianus*, prob. *mexicanus* (Thoms.) Tri.; *Xestia* sp., BCI, 2 spms; *Oxymerus* sp., M., Iqu., 2 spms; *Malacopterus tenellus* Fabricius, BCI	●**(⊙***)
Former data, 4 species	●(⊙)
Palearctic *Cerambycinae* and *Lepturinae* *Ergates faber* Linn., larva and adult, 4 spms; *Leptura* sp. (maculata ?); *Leptura rubra* L.	●***
Former data, Palearctic and African, 9 species	●(⊙)
Tentative generalization, Cerambycidae, 63 species	●***(⊙)
Neotropical CHRYSOMELIDAE (broad sense)	
Neotropical *EUMOLPIDAE* *Eumolpus* sp., Iqu.	●***
Typophorus sp., Ec.	⊖
Colaspis sp., Tr.; *Podoxenus* sp., Iqu..	—?
Former data, Neotropical, 3 species	○—
Palearctic, 1 species	—
African, 1 species	—(○?)
Neotropical *CHRYSOMELIDAE* (s.s.) (Fig. 25)	
Calligrapha sp., Ec., 6 spms; *Desogramma* sp., Ec.; *Doryphora* sp., Ec., 2 spms; *Doryphora* sp. Ec.	○
Former data, 3 species	v.r.
genus *Stilodes*	⊙
Palearctic *Chrysomelidae* s.s. Unid. sp.	●

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Former data, 18 species	● ⊙
Genus *Chrysolina* (9 species), Genus *Timarcha* (5 species)	●**
Neotropical *GALERUCIDAE* (note 6)	
Diabrotica brevilineata Jac., BCI, 2 spms; *Diabrotica* sp., Tri., 2 spms; *Dircema* sp. or near, Ec.; *Dircema* sp., Ec., 2 spms; *Galerucinae*, gen. sp. ? Iqu.	○*
Monocesta sp., Ec., 2 spms; *Dircema* sp. or near, Ec.; *Dircema* sp. or near, Ec.; *Coelomera cajennensis* Fabr., Iqu., 2 spms	—(⊖)
Former data, *Galerucidae*, Neotropical, 2 species	—
Palearctic, 2 species	⊙ (○)
African, 3 species	v.r.
Genus *Hyperacantha flavodorsata*	●**
Neotropical *Alticidae*	
Altica sp., Ec., 5 spms	● ⊙
Former data, 3 species	—
African, 1 species	⊙
Neotropical *Hispidae*	
Arescus sp., Ec	⊙
Former data, 1 species	—
Neotropical *CASSIDIDAE* (Fig. 13) (note 6)	
Agenysa sp., near amazonica Spaeth, Iqu.	● ⊙ ****
Stolas sp., Ec.; *Stolas* sp., Ec., 2 spms; *Stolas sermus* Er., or near, Ec.; *Mesomphalia* sp., Ec.; *Stolas* sp., Ec., 2 spms *Stolas* sp., Ec.; *Stolas sermus* Fabr., or near, Ec., 4 spms; prob. *Mesomphalia* sp., Ec.	○ (—)
Former data, Neotropical, 2 species	⊖—
African, 5 species	v.r. ○ —
Sagridae	
Former data, African, 1 species	—(● ?)

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Crioceridae	
Former data, Palearctic, 3 species	v.r.
genus *Lema*	⊙
African, 2 species	—
Clytridae	
Former data, Palearctic, 1 species	●
Donacidae	
Former data, Palearctic, 2 species	● (—)
Neotropical *Bruchidae*	
Amblycerus sp., BCI	—
Former data, 1 species	—
Neotropical *Brenthidae*	
Brenthus sp., Ec; *Arrhenodes* sp., Ec.; unid. sp., Ec.	—
Former data, African, 1 species, 20 spms	—
Palearctic *Scolytidae*	
Dendroctonus micans Kugel, 7 spms, larvae	⊖
CURCULIONIDAE	
Neotropical (note 8)	
Brachyomus tuberculatus (Boh.) Tri.; *Cholus* spp. Ec., 3 spms; *Exorides* sp., Ec.; *Heilipus bellicosus* (Hbst) Ec.; *Heilipus* sp., BCI; *Heilipus* sp., BCI; *Heilipus* sp., BCI; *Heilipus* sp., Ec.; *Hilipinus*. sp. BCI; Hilipinus sp., BCI; *Metamasius* sp., prob. *hemipterus* (Linnaeus) Ec,: *Metamasius*. sp., Tri., 3 spms; *Metamasius* sp., Tri.; *Rhinostomus barbirostris* (F.), Ec.; *Rhodobaenus* sp. near *subcristatus* Champ., Ec.	—
Former data, 10 species	—
Palearctic and African	
Phyllobius urticae de Geer, M. & F., 3 spms; *Otiorrhynchus veterator* Uyttberg; *Phytonomus fasciculatus* L. or *Hypera zoilus* Scop.	—
Former data, Palearctic and African, 22 species	—

TABLE 1 *(continued)*

Material	Patterns representative or predominant
Tentative generalization, *Curculionidae*, 51 species (note 8)	—— (○)
PANORPOID COMPLEX (NEUROPTERA-PLANIPENNIA, MEGALOPTERA-SIALODEA, MECOPTERA, TRICHOPTERA, LEPIDOPTERA, DIPTERA).	
Neotropical Neuroptera- Planipennia	
Chrysopa sp., near *tetrastica* Navas, Bci, 25 spms	——
Palearctic material	
Chrysopa sp., 18 spms	——
Former data. *Chrysopa vulgaris* Linnaeus	●
Neotropical *Myrmeleontidae*	
Former data, 1 species	●
Palearctic *Myrmeleontidae* *Myrmeleon formicarius* larva	●
African *Myrmeleontidae*, 2 species (note 4)	——
Neotropical *Ascalaphidae*	
Former data, 1 species	○ (⊙ ?)
Neotropical *Mantispidae*	
Former data, 2 species	—— (⊖ ?)
Palearctic *Hemerobiidae* (Neuroptera s.s.)	
Drepanepteryx phalaenoides L.	——
Megaloptera-Sialodea	
Neotropical *Corydalidae*	
Corydalus, prob. armatus (Hag.), Ec.; *Corydalus* sp., Ec. (Figure 18ab)	● ✲ ✲ ✲ ✲
Former data, *Corydalidae*, 3 species, BCI	● ✲ ✲ ✲ ✲

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Palearctic Sialodea	
Sialis sp.; *Sialis* sp.; *Sialis* sp., 6 spms, adults	●(⊙)
Sialis sp., larvae, 2 spms	○ * *(⊙ ?)
Former data, *Sialidae*, 1 species	●
TRICHOPTERA	
Neotropical	
Leptonema dissimile Mos (*Hydropsychidae*), 3 spms, Ec.	—(○)
Former data, 1 species, probably *Leptonema*	●
Palearctic (note 9) (Figs. 56, 57, 59)	
Potamophylax cingulatus (Stephens), M. & F., adults, 6 spms shortly hatched; *Grammotaulius submaculatus* (Rambur), F., adult; *Stenophylax* sp., larva, 7 spms.	—(● ?)
Potamophylax cingulatus (Stephens), larvae, 5 spms; *Potamophylax* sp., nymphs, 5 spms; *Potamophylax* sp., larvae, 3 spms; *Rhyacophila* sp. or *Stenophylax* sp., larvae, 14 spms; unid. *Phryganea or Limnophilidae*, larva, 3 spms; *Phryganea grandis* Linnaeus, larva.	—(○)
Chaetopteryx sp., larva; unid. adult *Limnophilidae*; *Potamophylax latipennis* Curtis, M. adult; *Rhyacophila fasciata* Hagen, larva	—
Prob. *Limnophilus flavicornis*, adult, 2 spms; *Phryganea grandis* Linnaeus, adult; *Plectronemia conspersa* Curtis (*Polycentropidae*), larva, 3 spms; unid. Trichoptera, adult, 8 spms	⊙ (●)(—)
Former data, Trichoptera, 2 species, including *Anabolia nervosa* Leach.	● * ⊙ *
Palearctic MECOPTERA	
Panorpa sp., adults, 33 spms	—(● ?)
Panorpa vulgaris Imh. & Labri, adults, 4 spms	○(●)
Former data, 3 species of *Panorpa*	●

TABLE 1 *(continued)*

Material	Patterns representative or predominant
LEPIDOPTERA	
Neotropical (late larval stages)	
Former data, 5 species	○
Palearctic	
Lycophotia praecox L.; *Noctuidae* sp.; *Geometridae* sp.; *Lymantriidae* sp.; *Phalera bucephala, Bombycidae*; *Sphingidae* sp.	○
Former data, 20 families, 92 species	○
Spms of African Saturniidae, 9 species ; Sphingidae, 2 species, Cossus (Palearctic Cossidae)	⊙
DIPTERA	
Neotropical	
Sarcophaga sp., F., adult, Tri.; *Dermatobia cyaneiventris* Macquart, larva, BCI, *Oestridae*; *Psilops petrolei*, larvae, 22 spms (G. 1975) (Fig. 58)	—
Former data, 2 species	—
Palearctic	
Eristalis arbustorum L. (*Syrphidae*)	—
Former data, 13 families, 31 species, adults	—
Larval *Tipulidae*	○ **
HYMENOPTERA	
Palearctic *TENTHREDINIDAE* (Figs. 36, 48, 49, 50)	
Athalia cornubiae Benson, larvae, 12 spms; *Athalia rosae*, L. (*Athalia coliBri* Christ.) M. & F. adults; *Neodiprion sertifer* Geoffr., M. & F., larvae, 12 spms and adults, 26 spms, *Tenthredopsis sordida* Klug, adults, 2 spms; *Selandria serva*, F., adult; unid. adult;	● ** ⊙ **
Neodiprion sertifer Geoffr., nymphs, 3 spms	○
Former data, 14 species	● * ⊙ *

TABLE 1. *(continued)*

Material	Patterns representative or predominant
Palearctic *Siricidae* (Figure 14) *Sirex juvencus* L., adult F.	●✻✻✻
Neotropical *Braconidae*	
Former data, 1 species	——?
ICHNEUMONIDAE	
Neotropical	
Eiphosoma sp., BCI (note 4)	○
Former data, 1 species	●
Palearctic	
Amblyteles armatorius Förster, M. & F., 4 spms; *Apistephialtes punctulatus* Ratzeburg, F.	●✻✻(⊙)
Former data, 2 species	●(⊙)
FORMICIDAE	
Neotropical (Figs. 15, 16)	
Paraponera clavata (Fabricius) F., BCI, 10 spms Ec., 4 workers (G. 1957: same reaction); *Cephalotes atratus* (Linnaeus), F., BCI.	●
Atta cephalotes (Linnaeus), workers, 12 spms, Tri., Ec.; *Atta* sp., Iqu., 3 spms	●✻(⊙ ✻)
Cephalotes atratus, Workers, Ec., 3 spms; *Labidus praedator sedulus* (Menozzi), M., BCI, 8 spms; *Azteca* sp., F., BCI, 3 spms; *Neivamyrmex pilosus mexicanus* (F. Sm.), M., BCI, 4 spms; *Nomamyrmex esenbecki crassicornis* (F. Sm.), M., BCI, 4 spms (note 4)	○
Former data, 13 species	●
Palearctic and African	
Former data, 3 species	● ⊙ ✻✻
Tentative generalization, Formicidae, 23 species	●✻✻(⊙)
Neotropical *Mutillidae*	
Former data, 3 species	⊙

TABLE 1 *(continued)*

Material	Patterns representative or predominant
VESPIDAE	
Neotropical	
Unid. spm, Iqu.; *Polistes* sp., Iqu.; *Apoica pallida*, var. pallens (F.), F., Tri., BCI (G. 1957: pattern III); *Polistes canadensis* (L.), F., Tri. (G. 1957: pattern III)	●(**)
Apoica pallida (Oliv.) (note 4), Tri.; *Mischocittarus melanius* (Cam.), F., Tri., BCI, 2 spms (G. 1957: patterns I and IV)	—(●?)
Former data, 8 species	v.r.(⊙ —)
Paleartic	
Dolichovespula media De Geer, F., 35 spms, larvae (10-12 mm), nymphs, near hatching, adults	● ●* ●**
Larvae (4-8 mm)	—
Vespula rufa L., 15 spms, larvae (12 mm up), nymphs (near hatching), adults, M. & F. and workers	⊙ **(●)
Larvae (4-8 mm) and nymphs, early stages	—
Ancistrocerus nigricornis Curtis, F.	⊙
Vespula germanica. L. (10 spms); *Vespula vulgaris* L, F. 17 spms	⊙ ** ● **
Vespula saxonica L., M. & F., 6 spms	●**(⊙)
Former data, Palearctic, 2 species	● ⊙
African, 1 species (note 4).	⊖
Tentative generalization, Vespidae, 18 species	●**(⊙ **)
POMPILIDAE	
Neotropical	
Priochilus seriseifrons (Fox), F. BCI; *Pepsis* subg. Gigantopepsis cf, plutus Klug, F., Iqu.	●**(⊙)
Palearctic	
Former data: *Anoplius viaticus* L.	●

TABLE 1. *(continued)*

Material	Patterns representative or predominant
SPHECIDAE	
Neotropical	
Trypoxylon palliditarse Sauss., 1 M., 2 F., Tri. BCI (note 4)	○ —
Former data, 6 species	● * * (⊙)
HALICTIDAE	
Neotropical	
Megaloptera genalis M.-W.,F.,BCI	⊖ (—)
Palearctic	
Former data, *Halictus* sp., M.	—
Neotropical *Colletidae*	
Former data, 1 species	○ (—)
APIDAE	
Neotropical	
Xylocopa frontalis (Oliv.) F., Tri.	—(● ?)
Former data, 2 species	—(⊖)
Palearctic	
Bombus agrorum F., M. & F., 10 spms; *Andrena clarkella* Kirby, F., 3 spms (G. 1955a : pattern II); *Andrena flavipes* Panzer, F., 5 spms.	—(○ *)
Former data, 9 species	—(⊖)
Nomada flava Panzer	● ⊙
Tentative generalization, Apidae, 15 species	—(⊖)

TABLE 1 *(continued)*

Material	Patterns representative or predominant
ARACHNIDA	
ARANEAE	
Neotropical	
Brachypelma sp. (*Theraphosidae*); *Gasteracantha servillei* (Guérin), F. Ec., 2 spms; *Micrathena sexspinosa* (Hahn), F., Ec; *Argiope argentata* L., BCI (*Araneidae*, *Argiopidae*); 4 unid. sp., BCI, Tri.	○
Palearctic	
Araneus diadematus, 4 spms (*Argiopidae*) (G. 1955b: pattern II)	○(●?)
Tegenaria sp., M. subadult; *Tegenaria jarietina* M., 2F.; *Tegenaria sp.*, juvenile and adult, 5 spms; *Agelena labyrinthica*, M. subadult; *Coelotes terrestris* F. (*Agelenidae*); *Scothophagus scutulatus* L. Koch (*Gnaphosidae*)	○
Former data on Neotropical, Palearctic and African *Araneae* (including the genera *Brachypelma*, *Eurypelma*, *Meta*, *Argiope*, *Nephila*, *Lycosa*, *Ctenus*, *Heteropoda* and *Torania*), 53 species from 18 families	○(* *)
Neotropical Scorpionidae	
Unid. sp. Tri.	—
Former data, Neotropical and African, 3 species	—
Amblypygae	
Former data, 1 Neotropical species	—(○)
MYRIAPODA	
Neotropical	
2 gen. sp. unid. (Diplopoda), Ec.	—
1 gen. sp. unid. (Chilopoda), Ec.	○
Palearctic *Schendyla* sp. (*Geophyllidae*)	—
Former data, Neotropical, Palearctic and African Myriapoda, 20 species	—(○)

TABLE 1. *(continued and end)*

Material	Patterns representative or predominant
Neotropical Opiliones	
Opilion sp., Ec.	—
Former data, Palearctic, 1 species	—
Neotropical Pedipalpida	
Former data, 1 species	—
Neotropical Ixodidae	
Former data, 1 species	—

DISCUSSION AND CONCLUSIONS

The present results and illustrations support the selective role of the insect coagulocyte in initiating haemolymph coagulation, (note 10). The controversies about the coagulocyte, a relatively newcomer in the hemograms, have been reviewed elsewhere (Grégoire, 1974; Crossley, 1975; Grégoire and Goffinet, 1979; Ravindranath, 1980). (note 11).

Preferential clustering of the coagulocytes around foreign bodies, such as fragments of cuticle, and air bubbles, illustrated in Figs 26, 27, 31, 34, 51, 53, 59, simulates the environmental conditions encountered at wound sites, where the coagulocytes floating in the haemolymph issuing from the body, immediately adhere to the wound edges and start clotting the plasma (note 12).

On the basis of new data from 580 species of insects, some belonging to families poorly or not represented in previous investigations, the present state of the relations between pattern of coagulation and taxonomy in insects may be summarized as follows.

Several taxonomic groups, at different levels of the classification, are remarkably homogeneous as regards the morphological aspect of their haemolymph coagulation. In these groups, listed below, the pattern of coagulation may be considered as a stable taxonomic character.

In other taxonomic groups, also listed below, predominance of one or other pattern could not be recognized because of great differences in reaction between different samples of a species or between different species of a family.

Ephemeroptera — No plasma reaction (pattern IV) occurred in the 6 species (larvae and adults) investigated.

Odonata — The reactions varied greatly. Pattern III seemed predominant in the genus *Agrion* (larvae).

Plecoptera — pattern I was recorded in the few specimens studied.

Orthopteroid Complex (Dictyoptera, Mantodea, Phasmoptera, Isoptera, Orthoptera, Dermaptera) (242 species). — Pattern I, with an abundant clotting reaction, is highly representative of these six orders.

Hemiptera-Heteroptera — In this order (204 species investigated), homogeneous results were obtained at the family level: Pattern IV characterized or was predominant in 15 families, including *Reduviidae*, *Coreidae*, *Pentatomidae*, *Pyrrhocoridae*. In striking contrast with these families, the *Nepidae-Ranatridae* and *Belostomatidae* consistently exhibited pattern I, with a high proportion of coagulocytes and an abundant clot.

Homoptera — In 11 families (159 species investigated), pattern I alone or associated with pattern II (= pattern III), with a substantial amount of clotting material in several families, was representative in *Cicadidae*, *Cercopidae*, *Membracidae*, *Cicadellidae*, *Dictyopharidae* and *Fulgoridae*. Pattern I constitutes a stable character in these families, especially in *Cicadidae* and *Fulgoridae*. In the latter group, the clotting process was instantaneous and extremely abundant.

In *Nogodinidae* (3 species), an abundant pattern I was found in *Vutina* sp. nova, Ecuador (Figure 7).

Haemolymph did not clot (pattern IV) in several samples from species of *Issidae*, *Cixiidae*, *Derbidae* and *Flatidae*. However, in *Flatidae*, pattern I appeared incidentally in a few species (e.g. *Carthaeomorpha rufipes*: Grégoire, 1957, 1959).

Coleoptera

Adephaga — In the 79 species investigated, specific and individual variations in the haemolymph reactions were of such extent that the pattern representative or predominant could not be established in many genera. However, the reactions seemed to be consistent at the genus level in *Carabus* (*Carabidae*) (pattern I or III) and in *Cybister* (*Dytiscidae*) (Substantial pattern I).

Polyphaga — Among the 56 families and subfamilies investigated (540 species), some showed consistent reactions of the same pattern in all or most of the species. In these groups, listed below, the pattern of coagulation of the haemolymph can be considered as a stable taxonomic character.

Pattern I: *Oedemeridae* (4 species); *Meloidae* (7 species, especially genus *Meloe*); genus *Pimelia* (*Tenebrionidae*); genus *Necrophorus* (*Silphidae*); genus *Dorcus* (*Lucanidae*); the whole family *Cerambycidae* (63 species) (*Prioninae*, *Lamiinae*, *Cerambycinae*), with one of the most abundant clotting reactions recorded among the insects in the *Prioninae*; genus *Timarcha* (5 species), genus *Chrysolina* (7 species) (*Chrysomelidae* s.s.).

Pattern II: *Histeridae*, several subfamilies of *Scarabaeidae* s.1. (71 species) (*Rutelinae*, *Aphodiinae*, *Melolonthinae*, *Dynastinae*, *Trichiinae*, *Valginae*, *Cetoniinae*).

Pattern IV: *Hydrophilidae*, *Staphylinidae*, *Cantharidae*, most *Curculionidae* (51 species) (note 3); *Brenthidae* (3 species).

In other families, listed below, one of the patterns was predominant at the family level and the reactions differed at the generic and specific levels. This situation especially concerns the taxonomic groups in which the reactions of pattern III, association of patterns I and II, are predominant: the reaction may be incomplete and one of the two phases of pattern III occurs alone.

In the subfamily *Scarabaeinae* (*Coprinae*) (28 species), the present results confirm the divergence previously recorded between Neotropical (predominance of pattern II) and African (patterns I and III) materials.

In *Geotrupinae* (8 species), in spite of individual variations, Pattern III seemed to be representative.

Pattern II was recorded in *Lucanidae*, with the exception of the genus *Dorcus* (see above).

In *Silphidae* (11 species), a representative pattern could not be established at the family level. Coagulation was scarce or not visible. However, the genus *Necrophorus* was remarkable by the stability of its pattern I and abundance of the clot.

In *Passalidae* (19 species), the divergence previously noted (Gregoire and Jolivet, 1959) between African (pattern I/III) and Neotropical (pattern II frequently incomplete) subsist in the present material.

In *Elateridae* (27 species), Pattern III, frequently dissociated in patterns I and II, seems to be representative of this family.

In *Erotylidae* (21 species), the predominant pattern II might be an incomplete reaction of pattern III, which was recorded in *Erotylus flavopunctatus* Kuhnt (Ecuador).

In the former group Heteromera, pattern III was predominant over pattern I in *Tenebrionidae* (52 species), *Lagriidae* (3 species) and *Monommidae* (2 species).

In 9 families of *Chrysomelidae* s.l. (74 species), the reactions varied greatly at the genus, species and individual levels. Substantial patterns I/III occurred in specimens of *Eumolpus* sp. (*Eumolpidae*, Iquitos), *Hyperacanthus flavodorsata* (African *Galerucidae*) and *Agenysa* near *amazonica* (Cassididae, Iquitos).

In 16 other families of Polyphaga, the material was too scarce and the representative pattern of haemolymph coagulation could not be established. However, pattern I alone or associated with pattern II (= pattern III) occurred in specimens of *Cebrionidae* and *Lymexilidae*.

Panorpoid Complex.

Pattern I is a highly significant character in *Corydalidae* (Fig. 18ab). In this family, the reactions of the coagulocytes and of the plasma were instantaneous. The clot was one of the most considerable so far observed in insects.

In Trichoptera and Mecoptera (22 species), the haemolymph reactions in vitro varied greatly, even in different specimens of a same species. Patterns I and III occurred inconstantly (note 9).

Hymenoptera — Among the 12 families investigated, pattern I (and subsidiarily pattern III) seems to be predominant in *Tenthredinidae*, *Formicidae*, *Vespidae*, *Pompilidae*, *Sphecidae*, and possibly in *Ichneumonidae*. In *Formicidae*, differences between genera were recorded. For example, pattern I appeared in all the specimens of the genus *Paraponera*, whereas no coagulation could be observed in the genus *Azteca*.

With the exception of the Palearctic *Nomada flava* (pattern I: Grégoire, 1955a), pattern IV was consistently predominant in 15 species of *Apidae*.

Arachnida — As previously reported (Grégoire, 1955b, reviewed in Grégoire and Goffinet, 1979), the reactions in vitro of the spider haemolymph (70 species) resembled those of pattern II in insects, especially of lepidopteran larvae.

NOTES

1. The validity of this procedure has been discussed in previous papers and still recently reexamined (Grégoire and Goffinet, 1979). In insects, haemolymph coagulation is a rapid, or an instantaneous process. Intermediary manipulations, used by several authors, between emission and spreading out of an haemolymph film, such as transfer of the haemolymph onto slides through pipettes and syringes, and mechanical agitation of the drop of haemolymph, thoroughly destroy the relationships between coagulocytes and the surrounding clotting plasma. Under these conditions, it is not possible to observe the selective part played by the coagulocytes in initiation of the plasma coagulation. In addition, many highly adhesive coagulocytes, sticked to the wall of pipettes, syringes and needles, disappear from the collected haemolymph and are absent in the hemograms.

2. As previously noted (Grégoire, 1951), in insects characterized by a rapid coagulation of the shed haemolymph, mechanical streaming of the plasma clotting around the coagulocyte (pattern I) can simulate cytoplasmic expansions of coagulocytes which develop in pattern II and may cause confusion with pattern III. However the filamentous, granular expansions of the stretched clot are mainly unipolar (Figs 5, 8, 12, 18), and run in direction of the stream. Actual cytoplasmic expansions (pattern II) are generally bipolar (Figs. 23-25, 26, 28, 29, 32-35, 39-45, 47). In the transmission electron microscope (TEM), the cytoplasmic expansions of pattern II appear as tubular structures (Grégoire, 1964, Plate III c). Threadlike stretched clots are formed by linear aggregations of microflocs (Grégoire and Jolivet, 1957, Plate 6, figure 3; Grégoire, 1959b, Plate IV, figure 2), or chains of corpuscular units.

3. In *Montina* sp. (*Reduviidae*, Iquitos), the colour of the issuing haemolymph was intensely azure-blue. An identical coloration of the haemolymph has been found in the Palearctic *Athalia lineolata* and *Athalia cornubiae* (*Tenthredinidae*: Grégoire, 1955a).

4. In insects collected at random, the factors of the divergences from the pattern predominant in, or representative of their taxonomic group, have been previously reviewed (Grégoire, 1974). Stage of development, season, starvation, infection and parasitism, environmental pollution are among these factors. They produce fluctuations in the amount and composition of the coagulable material and might alter the selective permeability of the coagulocyte membrane. In the present material (Table 1), divergent reactions were recorded in « dry » specimens (e.g. *Cephisus*

siccifolius (Wlk.), *Cercopidae*; *Formicidae*, *Sphecidae*, *Vespidae*), starved specimens (e.g. *Scarabaeus cicatricosus*, some *Elateridae*), and infected specimens. In other insects, such as *Rhipipterix* and *Neoxabea* (*Gryllidae*), the divergences could not be explained. There is not enough basis to safely consider the divergences in the reactions observed at the species level as specific stable characters.

5. Association of pattern I with pattern II (pattern III) was incidentally found in samples of the African *Dynastinae Oryctes boas* Fabr., and *Temnorrhynchus stormsi* Duv. (Grégoire, 1955a).

6. In *Lycidae*, *Lampyridae*, *Cantharidae* (Aspidoma), *Coccinellidae*, *Galerucidae* (*Monocesta*, *Dircema*, *Coelomera*) and *Cassididae*, dense suspensions in the milky haemolymph of small, oval, refractile particles concealed the haemocyte reactions (Grégoire, 1951; 1955a, 1957).

7. In the present material, reflex bleeding occurred in *Aeneolamia* sp., *Sphenorhina rubra* (*Cercopidae*), *Photinus* (*Lampyridae*), *Erotylus spectrum* (*Erotylidae*), *Dircema* sp. (*Galerucidae*), all from Ecuador. In *Photinus pyralis*. (*Lampyridae*) (Blum and Sannasi, 1974), the blood exuded by the reflex bleeding coagulates instantaneously (pattern I) and assumes a resinous consistency, when exposed to air. Under the conditions used in this and previous studies, this reaction could only be observed in our material at the edge of the coverglass, in contact with air. However, it could not be established whether this reaction was a true coagulation. The parts of the films protected from air remained fluid, and the floating particles remained in motion for hours.

8. Cytoplasmic expansions, sent by a few coagulocytes, and veils (pattern II) occurred in a few samples of the Neotropical *Exorides*, *Cholus*, *Heilipus*, from Ecuador, and of the African weevils *Brachycerus kumbanensis* Quedenfeld, *Rhynchophorus phoenicis* Fabricius (Grégoire, 1959b) and *Sipalinus squalidus* Kolbe (Grégoire and Jolivet, 1957). In these samples, the haemolymph became viscous after shedding.

As previously reported (Grégoire, 1955a, 1959; Mac Laughin and Allen, 1965), plastic, pleomorphic haemocytes developed cytoplasmic expansions of considerable lengths, forming arborizations in the haemolymph of all the Curculionidae. The literature on the role of identical structures in Diptera has been reviewed elsewhere (Grégoire, 1974; Grégoire and Goffinet, 1979). These pleomorphic haemocytes were redescribed in 1972 by Zachary, Hoffman and Porte, who called them thrombocytoids.

9. In *Potamophylax* (Trichoptera), many coagulocytes sent short bubble-or club-like, radiating cytoplasmic expansions. Some of these cells expelled coarse granules without disintegrating. A diffuse granular reaction sometimes appeared in the plasma at some distance of the coagulocyte. This reaction did not present the clear-cut aspect of pattern I.

10. The prohaemocytes, plasmatocytes and granulocytes, which, under the Phase Contrast Microscope, differ from the coagulocytes by a

distinctly larger nucleus and a darker cytoplasm, do not take part in initiation of plasma coagulation. Surrounded by a bright diffraction halo, these cells are obviously inert, passively embedded in the clots or clustered along the highly adhesive expansions already sent by the coagylocytes (Figs 7, 8, 18ab, 28, 33, 37, 38). Degranulation of the granular haemocytes, reported in literature as the cause of the plasma coagulation, is a later process, which occurs when the bulk of the clot has already developed (see discussion in Grégoire, 1951; Grégoire and Goffinet, 1979, Goffinet and Grégoire, 1978). In agreement with these observations, Rowley (1977) reported in the stick insect *Clitumnus extradentatus* that release of granules, which causes coagulation of the haemolymph, is extremely rapid in the coagulocytes and much slower in the granulocytes. Rowley suggested that the coagulocytes produce the bulk of the coagulation whereas the granulocytes are more concerned with the melanization of wounds and production of antibacterial factors (see also Brehélin, Zachary and Hoffmann, 1978).

In one winged specimen of *Bifiditermes condonensis* and in one worker of *Neotermes insularis* (Australian Termites), a pale, diffuse, lately developed and limited reaction in the plasma around a few granular haemocytes appeared to be superimposed on the considerable clotting reaction already produced by the coagulocytes (pattern I). Such a plasma reaction around haemocytes other than coagulocytes has been observed only in two among several thousands of haemolymph samples. On the other hand, in the present material, in areas of haemolymph films which did not contain coagulocytes, dissolution of the granules within granular haemocytes did not produce any change in the surrounding plasma.

As all cells contain thromboplastic substances (Heilbrunn, 1961), the functional selectivity of coagulocytes in haemolymph coagulation might be variously explained. TEM observations (Goffinet and Grégoire, 1975, 1978) of multiple microruptures in the plasma membrane of the reacting coagulocyte and simultaneously of intact plasma membranes in the other categories of haemocytes, suggest that differences in permeability of the cell membranes might be an important factor of the coagulocyte selectivity in initiation of haemolymph coagulation in insects.

11. Additional information has been obtained in the present material as regards the high percentage of coagulocytes in the hemograms (Grégoire, 1955a, 1971): 100 % in *Oncometopia venosula* (*Cicadellidae*), in *Oryctes* sp. (*Dynastinae*); 90 to 100 % in *Necrophorus investigator* (*Silphidae*), in *Athalia rosae* (*Tenthredinidae*); 84-100 % in Termites; 80-90 % in *Bombus agrorum* (*Apidae*); 83 % in *Neodiprion sertifer* (*Tenthredinidae*); 74 % in *Osmilia flavolineata* (*Acrididae*); 70 % in *Forficula* sp. (*Dermaptera*); 66 % in *Phyllophaga* sp. (*Melolonthinae*: Fig. 46; 45-67 % in *Panorpa* (Mecoptera); 50 % in *Aphrophora alni* (*Cercopidae*) and in *Carabus auronitens* (*Carabidae*); 34-54 % in *Dytiscus marginalis* (*Dytiscidae*); 39 % in *Pterostichus* (*Carabidae*). The high

figure recorded in *Bombus*, in which haemolymph coagulation could not be observed, seems to be an exception to the correlation between percentage of coagulocytes and haemolymph coagulability. Such a correlation has been reported on the basis of experimental data and of observations (see review of literature in Grégoire and Goffinet, 1979).

12. According to Jones (1977), no one seems to have demonstrated that the coagulocytes (cystocytes) specifically cause solidification of the haemolymph at the wound. However, previous data of litterature seemed to answer this objection. In insects (pattern I), the clot plug formed at the end of a sectioned leg or antenna appears first in the form of a transparent pearl, in which the islets of coagulation are discernible as bright glistening spots (Figure 10). The role, in the arrest of haemorrhage, of the explosive cells of Hardy, functionally homologous to the coagulocytes, has been first observed by Tait (1910), in the stump of sectioned antennae of the Crustacean *Gammarus*, in the form of a chain reaction, consisting of successive explosions of Hardy's corpuscles, followed by development around these cells of globular masses (islets of coagulation) which grow like soap bubbles and cling to the end of the stump. Other haemocytes cluster to these masses. The whole process induces obstruction of the wound.

Addition on galley proofs

The rapid or immediate, selective clustering, without lysis, of the highly sensitive coagulocytes, to foreign bodies, inorganic surfaces or physical interfaces (« non self surfaces ») illustrated in FIg. 51 and in previous studies (Grégoire, 1953, Figs 18 and 19; 1955a, Figs 4, 7, 11, 12, 20, 39; 1957, Fig. 9; 1970, Fig. 17; 1971, Fig. 23; 1971. Fig. 4; Grégoire and Jolivet, Pl. III, Fig. 4, Pl. V, Figs. 1, 2, 3) simulates in vitro the earliest phase of the cell defense mechanism of insects.

In descriptions of the processes of nodule formation and encapsulation, the role of the coagulocyte in the initial phase has been reported by several authors.

In *Carausius morosus* (Reik, 1968), the initial reaction to an implant was the contact and lysis of coagulocytes. Crossley (1975) has obtained evidence that disrupted labile hemocytes (coagulocytes ?) accumulate at wound sites, locally releasing their cytoplasmic contents which are rich in phenoloxidizing enzymes. Introduction of cellophane fragments into the body cavity of *Locusta* induced an immediate but limited plasma coagulation around the implant, involving only the coagulocytes. These coagulocytes do not participate in the formation of capsules (Brehélin, Hoffmann, Matz and Porte, 1975). Clustering of hemocytes, predominantly coagulocytes (60 per cent), occurred around foreign objects introduced into *Thermobia* (François, 1975).

Participation of the granulocytes, alone or associated with the coagulocytes, to the initial phase has been reported by other authors.

According to Ratner and Vinson (1983), ultrastructural evidence indicates that extremely fragile granulocytes rupture upon encountering a foreign surface. Bohn, Barwig and Bohn (1981) also report that the granulocytes are the most sensitive cells. In their review on the role of hemocytes in defense against biological agents, Ratcliffe and Rowley (1979) write (p. 399) that the first «recognition» phase appears to be mediated «by coagulocytes/granulocytes... which lyse in contact with foreign surfaces...». In the two-step processes of wound healing, nodule formation and encapsulation, the first stage is initiated by the lysis of granule-containing hemocytes (granulocytes and/or coagulocytes) and hemolymph coagulation on the surface of the foreign body. In their conclusions, Ratcliffe and Rowley note (p. 400) that «we are still unable to explain why coagulocytes/granulocytes behave so violently toward non-self surfaces».

Our present and previous observations are at variance with some points of these conclusions. Some divergences have been previously considered (Grégoire and Goffinet, 1979). As shown in the illustrations listed above, the coagulocytes were not lysed in contact with foreign material in our preparations. After undergoing the alterations described in many previous papers, they appeared in the form of irreversibly congealed vesicles, frequently swollen by imbibition.

As regards the granulocytes, we never observed the violent disruption reported by Ratcliffe and Rowley. In striking contrast with the coagulocytes, the granulocytes, many of them surrounded by bright diffraction halos, remained inert for hours in thin films of haemolymph in vitro. They passively attached to the coagulocytes and to their highly adhesive cytoplasmic expansions. The transmission electron microscope has revealed the exclusive, consistent and immediate development of multiple micro-ruptures in the plasma membranes of the coagulocytes (Moran, 1971; Goffinet and Grégoire, 1975, 1978), whereas the plasma membranes of granulocytes and plasmatocytes remained intact. This difference between coagulocytes and granulocytes suggests that the coagulocyte may be considered, according to the recent terminology, as the haemocyte which realizes the initial recognition of foreignness, and that the immunological reactions start in or around its plasma membrane.

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LEGENDS

Fig. 1. — a. *Hyalodictyon* sp., Homoptera, *Dictyopharidae*, Ecuador. Pattern I: a slight granular reaction of the plasma is seen around two coagulocytes attached to an air bubble. Another coagulocyte is surrounded by an abundant, circular coagulation islet.

Fig. 2. — *Dorisiana semilata.* (Walker), Homoptera, *Cicadidae*, Ecuador. Pattern I.

Fig. 3. — *Oncometopia venosula* Distant, Homoptera, *Cicadellidae,* Ecuador, Pattern I. Confluence of islets of plasma coagulation produced by five coagulocytes is shown.

Fig. 4. — *Cicadella* (*Poeciloscarta*) *bisellata* (Signoret), Homoptera, *Cicadellidae*, . Pattern I.

Fig. 5. — *Elateridae* sp., Tikal. Pattern I.

Fig. 6. — *Cusitermes* sp., queen, Isoptera, African. Pattern I. Club-like, radial expansions of the cytoplasm have been previously observed in Termites'coagulocytes (Grégoire, 1955a). In the immediate vicinity of the cell, the first wave of the clot appears dense and glassy. The more peripheral, second wave of coagulation is coarsely granular.

Fig. 7. — *Vutina,* sp. nova, Homoptera, *Nogodinidae*, Ecuador. Pattern I. Plasma coagulation starts around a coagulocyte (above). No plasma reaction appeared around the four other (outlined) haemocytes (below).

Fig. 8. — *Perla* sp. Palearctic Plecoptera. Pattern I. A coagulocyte, surrounded by an islet of plasma coagulation, is seen in the vicinity of an inert plasmatocyte

Fig. 9. — *Carcinophora percheron* (Guérin), Dermaptera, Trinidad, Pattern I.

Fig. 10. — *Mallodon downesi* Hope, Coleoptera, *Cerambycidae*, *Prioninae*, African. Pattern I. In the drop of haemolymph shown lying onto a piece of cellophane, a number of islets of plasma coagulation centered by coagulocytes appear in the form of scattered shining spots. Extension of the clot to the entire drop has not yet occurred. Identical picture is shown in the drops of clotting haemolymph detached from the edges of wounds.

Fig. 11. — *Nilio* sp., Coleoptera, *Nilionidae*, Ecuador. Pattern I.

Fig. 12. — *Timarcha* sp., Coleoptera, Palearctic *Chrysomelidae* s.s. Pattern I. Club-like, radial expansions of the coagulocyte cytoplasm are shown.

Fig. 13. — *Agenysa* sp., near *amazonica* Spaeth, Coleoptera, *Cassididae*, Iquitos. Pattern I.

Fig. 14. — *Sirex juvencus L.*, adult, Hymenoptera, Palearctic *Siricidae*. Pattern I.

Fig. 15. — *Formica rufa*, Hymenoptera, Palearctic *Formicidae*. Reaction of pattern I developed around a coagulocyte in contact with a fragment of cuticle.

Fig. 16. — *Paraponera clavata* (Fabricius), Hymenoptera, *Formicidae*, Barro Colorado Island. Pattern I. Two waves of plasma coagulation are shown around a coagulocyte in the form of a first, dense clot directly around the cell, and of a second, peripheral, less dense wave.

Fig. 17. — *Stenophylax* sp., larva, or *Limnophilidae*, Palearctic Trichoptera. In the film of haemolymph, kept 24 hours in a moist chamber, a pale reaction of pattern I was detected around a coagulocyte and its club-like expansions.

Figs 18ab. — *Corydalus* sp., Megaloptera, Sialodea, Ecuador. Pattern I. Instantaneous haemolymph coagulation, one of the most considerable reactions recorded among all the insects. Multiple waves of clotted plasma are composed of clustered islets of coagulation, centered by coagulocytes, and their areas of extension. Other kinds of haemocytes and among them granulocytes (schematically represented in the diagram with a dark cytoplasm), obviously did not take part in coagulation. Their stock of granules was still intact when the clotting process had stopped. Streaming of the clot appears in the form of granular pseudofilaments. The whole film is a bluish jelly.

Figs 19 and 20. — *Saga pedo* Pallas, Orthoptera, *Tettigoniidae*. Pattern I. Plasma coagulation is shown around four coagulocytes (asterisk). Extension of the clot is visible in the form of granular pseudofibrils. In *Tettigoniidae* and in *Acrididae*, the nucleus of the coagulocyte undergoes considerable swelling, before appearing congealed. The chromatin structures become suddenly highly refractile during a few seconds (Grégoire, 1951). Three other hemocytes (prohaemocyte and granulocytes) appear shrunk and surrounded by refractile halos. These haemocytes did not take part in the coagulation process and remained inert. × 800.

Fig. 21. — *Laccotrephes vicinus* SIGNORET s.l. Heteroptera, *Nepidae*. Pattern I. An intense reaction of plasma coagulation occurred around two coagulocytes. x 800

Fig. 22. — *Oryctes* sp., Coleoptera, *Dynastinae*, Ecuador. Pattern II. The cytoplasmic expansions of 35 coagulocytes are embedded (together with four other inert haemocytes surrounded by a bright diffraction halo) in a plasma clot in the form of a diffuse wave-like veil, which conceals a part of the cytoplasmic expansions.

Fig. 23. — *Lybas atripennis* Erichson, Coleoptera, *Erotylidae*, Ecuador. Systems of pattern II developed between two air bubbles. A scarce veil, delimited by cytoplasmic expansions of coagulocytes, is the plasma reaction. No condensation of the clot takes place around any of these coagulocytes. Above, outline of an inert granulocyte is shown

Fig. 24. — *Erotylus flavopunctatus* Kuhnt, Coleoptera, *Erotylidae*, Ecuador. Pattern II. Cytoplasmic expansions sent by coagulocytes (asterisk) are seen. A pale islet of plasma coagulation has lately developed around another coagulocyte (incidental pattern III) in this Sample.

Fig. 25. — *Doryphora* sp.., Coleoptera, *Chrysomelidae*, Ecuador. Pattern II. A system of cytoplasmic expansions sent by coagulocytes (asterisks) is shown. Reaction of the plasma occurs in the form of a thin veil. Six coagulocytes and a prohaemocyte are clustered around an air bubble. Three other haemocytes are attached to the threadlike, adhesive expansions. Pattern I had been previously recorded in the Palearctic *Leptinotarsa decemlineata* (Grégoire, 1951, Figs 19- 22).

Fig. 26. — *Pseudoscarta obliquatula* (Jacobi), Homoptera, *Cicadellidae*, Ecuador. Pattern III (patterns I and II combined). Reactions observed immediately after haemolymph withdrawal. Twelve coagulocytes are the only haemocytes seen in this field. Eleven of them, several swollen by imbibition, are scattered along adhesive, cytoplasmic expansions sent by other coagulocytes (small asterisk). Agglutination of six of these coagulocytes to splinters of cuticle (large asterisk) simulates the clustering of coagulocytes, which takes place at the wound sites. Plasma coagulation is starting around six of these coagulocytes and has already developed a circular islet around one of them.

Fig. 27. — *Sphenorhina* sp., Homoptera, *Cercopidae*. Ecuador, Pattern III. The confluence, near a foreign body, of islets of coagulation produced by fifteen coagulocytes, appears in the form of a veil-like granular clot. Cytoplasmic expansions of coagulocytes are seen at the top of the diagram. Other expansions and the cytoplasm of several coagulocytes are concealed in the veil.

Fig. 28. — *Sphenorhina* sp. (different from 27), Ecuador. Another aspect of pattern III. Left : inert haemocytes (outlined) are attached to the cytoplasmic expansions of coagulocytes.

LEGENDS

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Fig. 28. — *Sphenorhina* sp. (different from 27), Ecuador. Another aspect of pattern III. Left : inert haemocytes (outlined) are attached to the cytoplasmic expansions of coagulocytes.

Fig. 29. — *Tomaspis galbana* Jacobi, Homoptera, *Cercopidae*, Ecuador. Pattern III. Meshworks of straight cytoplasmic expansions sent by coagulocytes (small asterisks) delimit a plasma reaction in the form of a granular veil (pattern II). Islets of coagulation at different stages of development appear around eight coagulocytes (pattern I). Some of these coagulocytes are swollen by imbibition. Others have expanded cytoplasmic blisters (below). Others, after emission of cytoplasmic expansions, are reduced to the nucleus (small asterisk). Reorganization of the clot into granular fibrils begins in one area (large asterisk).

Figs 30, 31. — *Cicadella viridis* Linné, Homoptera, Palearctic *Cicadellidae*. Two parts of a coagulation system of pattern III are shown. In Fig. 31, coagulocytes embedded in a coagulation islet are clustered around a foreign body. Four of these coagulocytes have sent threadlike expansions and their cell body appears to be reduced to the nucleus. An inert, immature granulocyte is seen in the vicinity. In Fig. 30, seven coagulocytes, surrounded by coagulation islets, adhere to cytoplasmic expansions sent by other coagulocytes lying outside the depicted field.

Fig. 32. — *Ceresa* (s.s.), Homoptera, *Membracidae*, Ecuador. Pattern III. Nine Coagulocytes appear clustered around a cuticle splinter. Other scattered coagulocytes have sent cytoplasmic expansions and are reduced to their nucleus and a small amount of cytoplasm. Islets of coagulation have developed around two of these cells. Two other haemocytes with a large nucleus do not take part in the reactions.

Fig. 33. — *Delassor tristis* (Fabricius), Homoptera, *Cercopidae*, Ecuador. Pattern III. Cytoplasmic expansions sent by coagulocytes and an islet of coagulation around another coagulocyte are seen. Two passive plasmatocytes adhere to the threadlike expansions.

Fig. 34. — *Necrophorus vespilloides* Herbst, Coleoptera, Palearctic *Silphidae*. Pattern III. Coagulocytes, the only kind of haemocytes seen in this field, are clustered around a bubble and along cytoplasmic expansions of other coagulocytes (asterisk). Around the air bubble, confluence of islets of plasma coagulation. In most species and specimens of the genus, pattern I was consistently observed.

Fig. 35. — unid. *Elateridae*, Trinidad. Pattern III, with predominance of pattern I. Eight islets of coagulation are seen. Cytoplasmic expansions of other coagulocytes are anchored to a small debris of cuticle (left). Two inert haemocytes adhere to the cytoplasmic expansions of a coagulocyte.

Fig. 36. — *Athalia rosae* L., Hymenoptera, Palearctic *Tenthredinidae*. Pattern III. Many coagulocytes of small size appear agglutinated around a large air bubble. Some of them have sent straight cytoplasmic expansions. Confluence of the islets of plasma coagulation is seen around the bubble.

Fig. 37. — *Athalia cornubiae* Benson, Hymenoptera, Palearctic *Tenthredinidae* Pattern III. A wave-like limit of the plasma clot is bordered inside by clusters of coagulocytes of very small size (asterisks). The cytoplasmic expansions of these coagulocytes and the islets of coagulation (centre) (see Figs 48 and 50) are concealed in part by the general clotting reaction. Seven other large haemocytes (including granulocytes), encircled by bright diffraction halos (not shown in the diagram) were inactive in the clotting process.

Fig. 38. — *Aphrophora alni* Fall, Homoptera, *Cercopidae*. The steam-throw-like granular material shown is composed of clotting plasma and of very small amounts only of cytoplasmic coagulation-inducing substances, including granules, of the coagulocyte. The form of the clot suggests an explosive discharge of coagulins, followed by a sudden and considerable gelation of the plasma. Two granulocytes (top left), surrounded by diffraction halos, are not involved in the coagulation process. Their stock of granules was still intact 20 minutes and a few hours after haemolymph withdrawal, × 800.

Fig. 39. — *Philaenus spumarius* and Fig. 40. — *Aphrophora alni*, Homoptera, *Cercopidae*. Pattern III. Altered coagulocytes, (asterisks in Fig. 39, C in Fig. 40), expanding spherical blisters and threadlike cytoplasmic pseudopods, are shown. In Fig. 40, nine inert

other haemocytes (including plasmatocytes and granulocytes) surrounded by diffraction halos, and with their stock of granules still intact, are scattered along the adhesive pseudopods of the coagulocytes. Fig. 39: × 800; Fig. 40: × 1000.

Figs. 41, 43, 44. — Reactions of Pattern III are shown in *Carabus violaceus* (Coleoptera, *Carabidae*) Fig. 41: × 800), *Ancophtalmus clathratus* (Fig. 43: × 800), and *Blaps gigas* (Fig. 44: × 1080) (Coleoptera, *Tenebrionidae*). Threadlike cytoplasmic expansions of coagulocytes (small asterisks), carrying along granules, are anchored to air bubbles or foreign bodies and delimit fibrillar or amorphous veils (Figs 41, 44). Areas of greater density in the plasma around coagulocytes (islets of coagulation) (Fig. 44) appear reorganized into meshworks of fibrils (Fig. 41: large asterisks). The other categories of haemocytes appear shrunk, surrounded by diffraction halos, and passively attached to the strands (arrows in Figs. 41 and 43).

Fig. 42. — shows in *Abax ater* (Coleoptera, *Carabidae*) a typical reaction of pattern II: systems of cytoplasmic expansions of coagulocytes (asterisks) form loose meshworks. × 800.

Fig. 45. — Unidentified aquatic coleopteran larva. Pattern III. Bipolar, straight cytoplasmic expansions from a cluster of coagulocytes (top), recorded 20 minutes after haemolymph withdrawal. These expansions are attached to other coagulocytes (bottom). Note the inert plasmatocyte and granulocytes anchored to the cytoplasmic expansions. × 800.

Fig. 46. — *Melolontha melolontha* L., Coleoptera, *Melolonthinae*. Coagulocytes of distinctly smaller size than the other categories of haemocytes (bottom left) are shown. 60 of these coagulocytes are clustered at the limit of a substantial veil-like clot (on the right). As in Figs 22, 37 and 49, the cytoplasmic expansions of these coagulocytes are concealed in the veil. × 800

Fig. 47. — *Erodius tibialis*, Coleoptera, Heteromera, *Tenebrionidae*, Pattern III (patterns I and II combined). In this starving specimen, the reaction was incomplete. The threadlike cytoplasmic expansions, carrying along granules, produced by six coagulocytes (small asterisks) (pattern II), are shown. The reaction in the plasma (pattern I) is only faintly visible (veil delimited by the cytoplasmic expansions and granular substance coating some of these cytoplasmic expansions). × 960.

Figs 48. and 50. — *Athalia cornubiae*, larva, Hymenoptera, *Tenthredinidae*. Pattern III. In larvae of this family, the process of haemolymph coagulation is instantaneous and considerable. As shown diagrammatically in Fig. 37, a substantial veil of plasma coagulation embeds many coagulocytes of small size (asterisks) and their cytoplasmic expansions (arrow). These coagulocytes are especially numerous at the boundary of the clot. Figure 50. shows that the veil is produced by coalescence of many islets of coagulation (asterisks). Seven granulocytes, surrounded by bright diffraction halos, have not yet discharged their granular content 15 minutes after haemolymph withdrawal. × 800.

Fig. 49. — *Athalia cornubiae*, larva. Four hours after mixture of the haemolymph with a 1 per cent solution of potassium oxalate, a powerful anticoagulant of insect blood (Grégoire, 1953). The Figure confirms the small size of the coagulocytes (asterisks) in this species, which are seen floating in the fluid plasma.

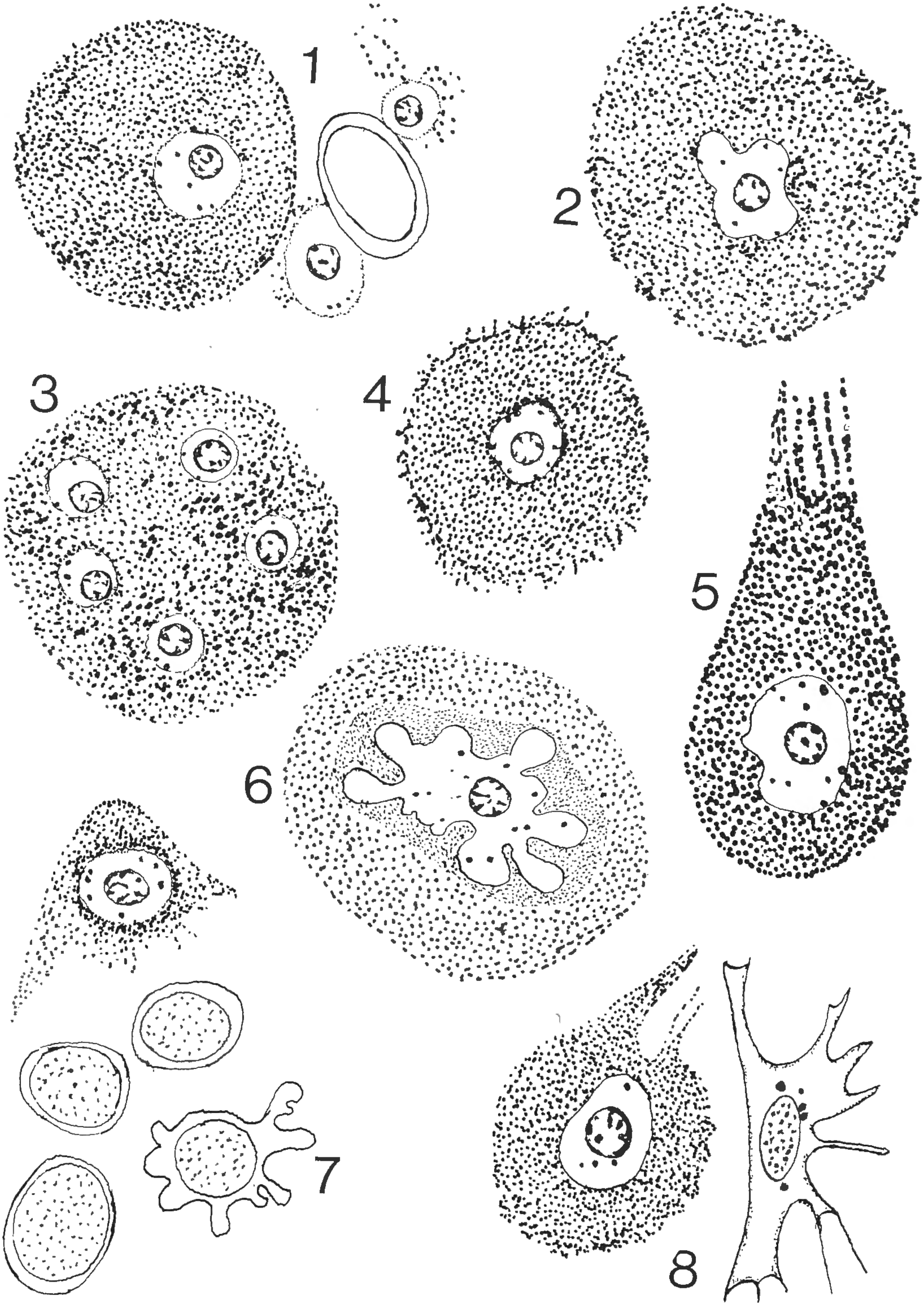
Fig. 51. — *Dytiscus marginalis* L. (Coleoptera, Palearctic *Dytiscidae*). Clustering of coagulocytes around a fragment of cuticle simulates the reaction of haemolymph at the wound sites × 800.

Fig. 52. — *Epormenis roscida* (Germ.), Homoptera, *Flatidae*, Barro Colorado Island. The outlines of five haemocytes are seen: prohaemocyte, granulocyte, plasmatocyte and two coagulocytes (small asterisks), around which no plasma coagulation takes place: pattern IV.

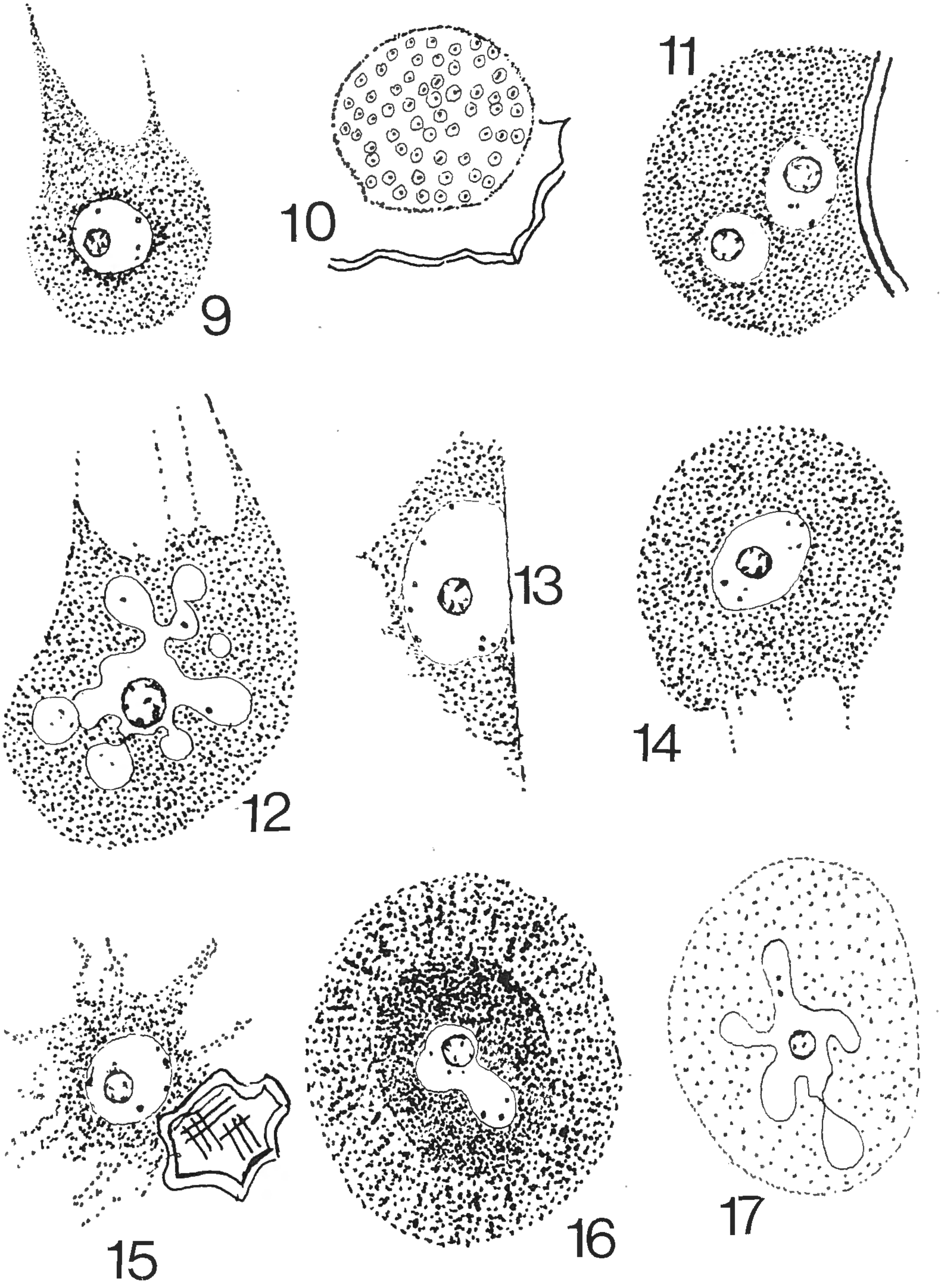
Fig. 53. *Hydaticus arcuatus* Régimbart, Coleoptera, African *Dytiscidae*; Fig. 54. *Agabus melanarius* L., Coleoptera, Palearctic *Dytiscidae*; Fig. 55. unidentified *Staphylinidae*, Coleoptera, Ecuador. In these three specimens, no plasma coagulation is detected around the coagulocytes (asterisks), free or attached to fragments of cuticle (pattern IV); Fig. 56. *Limnophilidae* sp., Palearctic Trichoptera; Fig. 57. *Grammopterus submaculatus* (Rambur). Palearctic Trichoptera. Pattern IV. In these two specimens, no plasma reaction could be observed around the coagulocytes and their blisters.

Fig. 58. — *Psilopa petrolei*, larva, Diptera, Ephydridae, Trinidad (from Grégoire, 1975: 127). Pattern IV. No plasma reaction appeared around this coagulocyte swollen by imbibition (enlarged by comparison with the other diagrams). (Courtesy editor of Arch. intern. Physiol. Bioch.).

Fig. 59. — *Chaetopteryx* sp., larva, Palearctic Trichoptera, *Limnophilidae*. A coagulocyte, adhering to fragments of cuticle, has extruded a few granules. Pattern IV, pattern I questionable (see discussion).



Figs. 1 à 8



Figs. 9 à 17

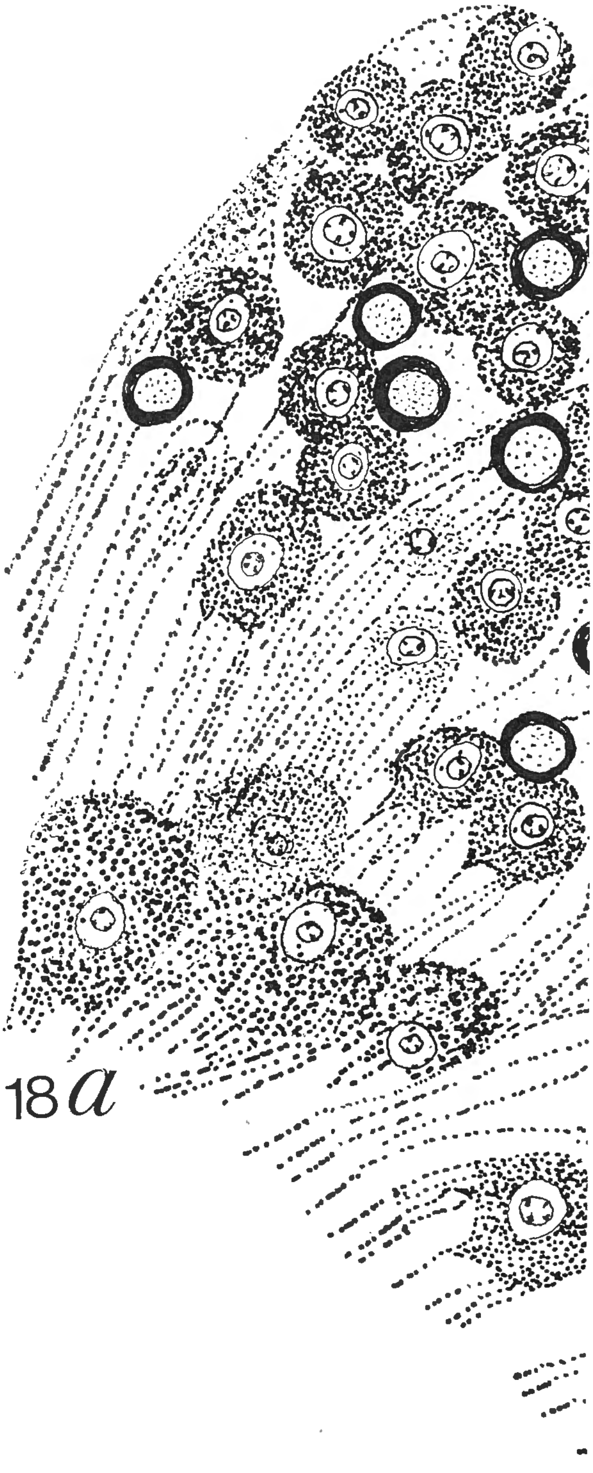


Fig. 18a

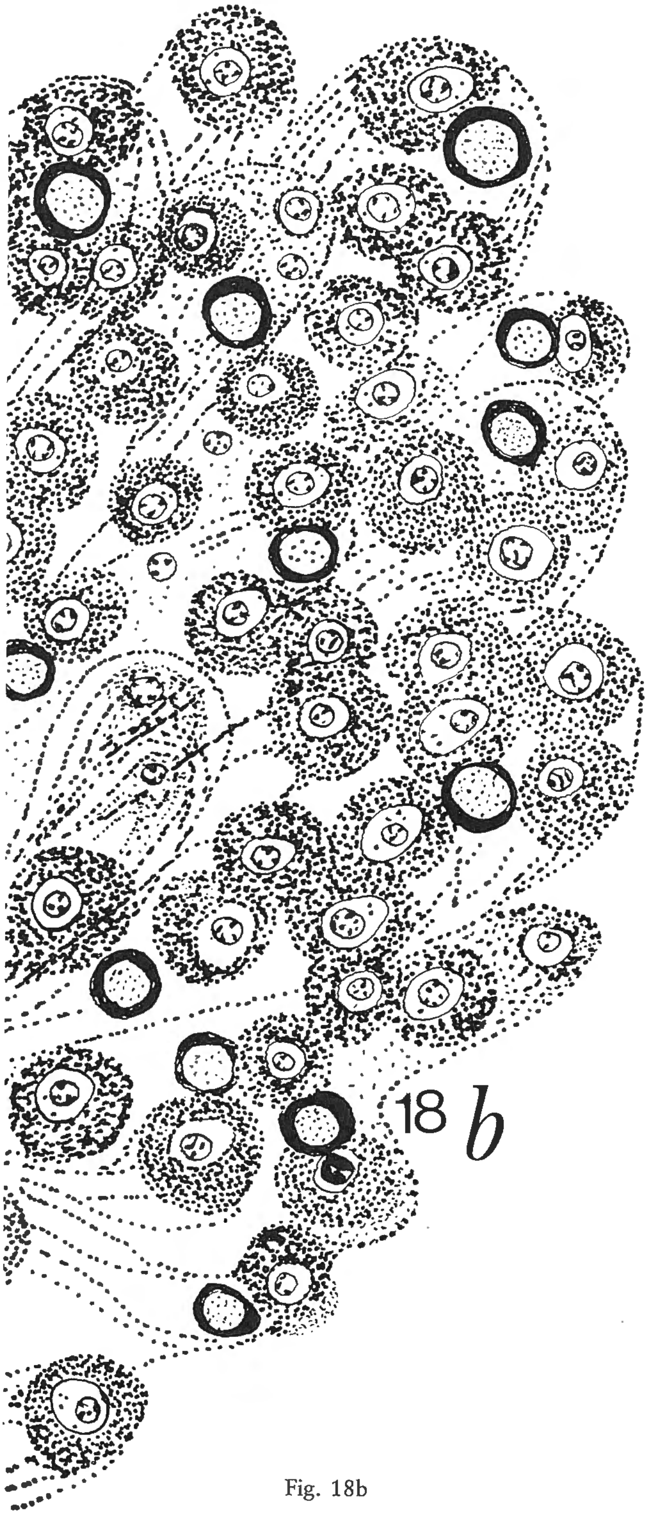
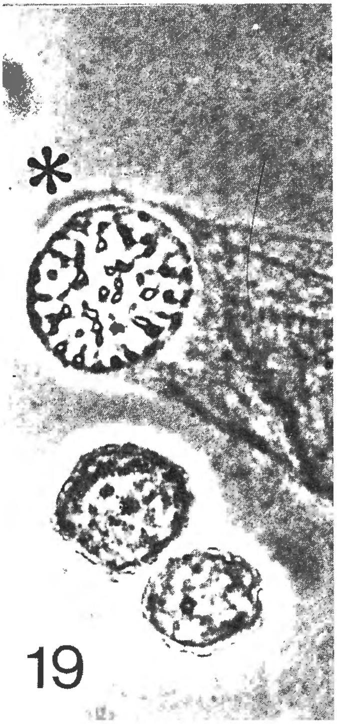
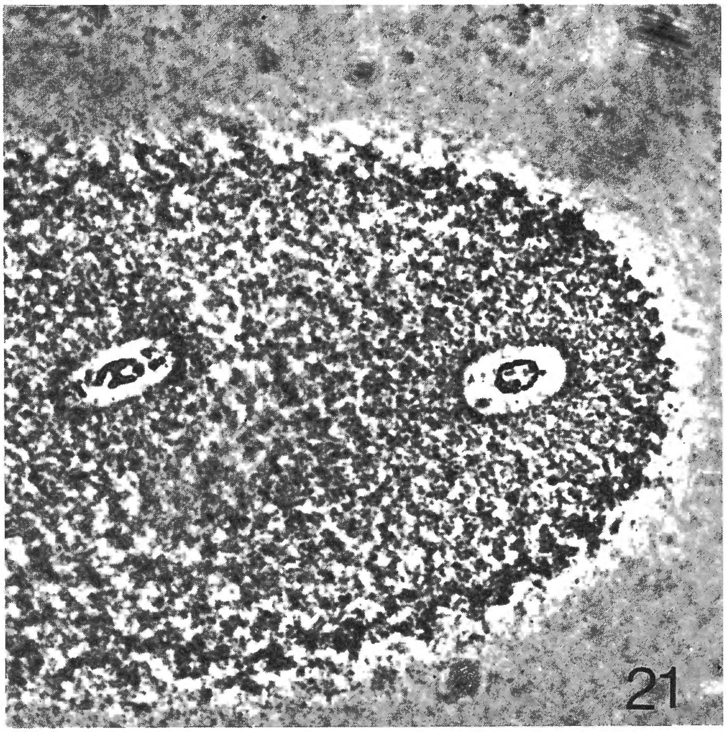
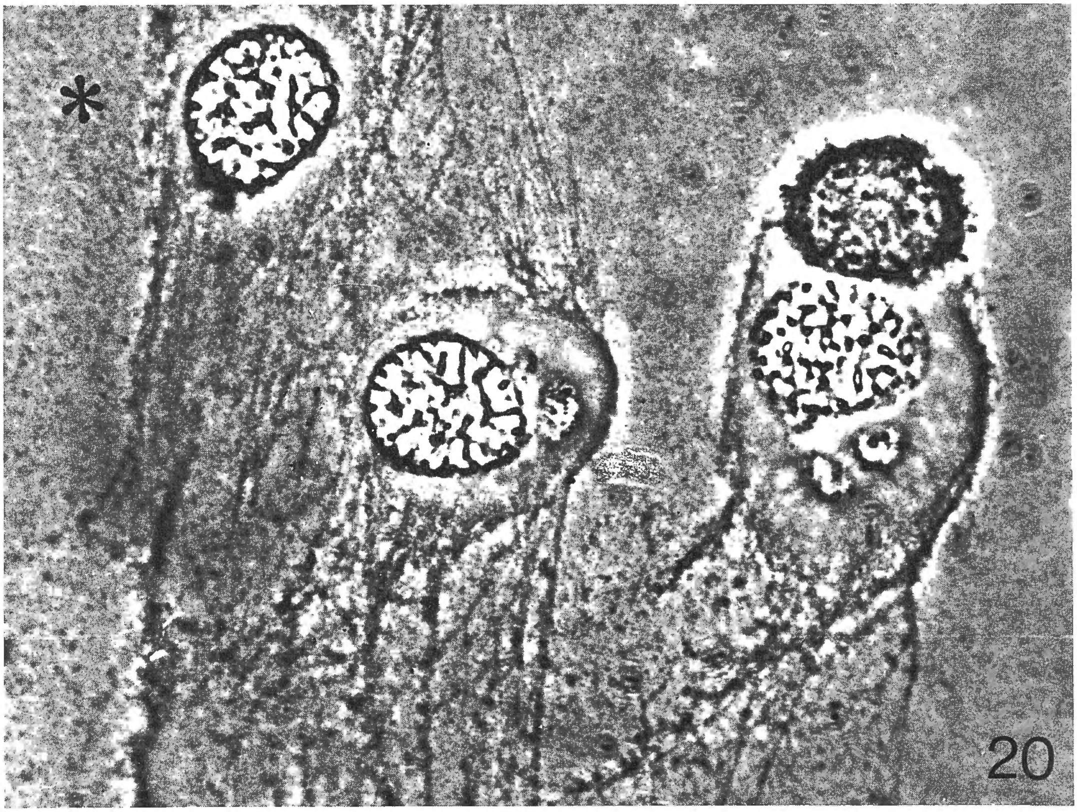


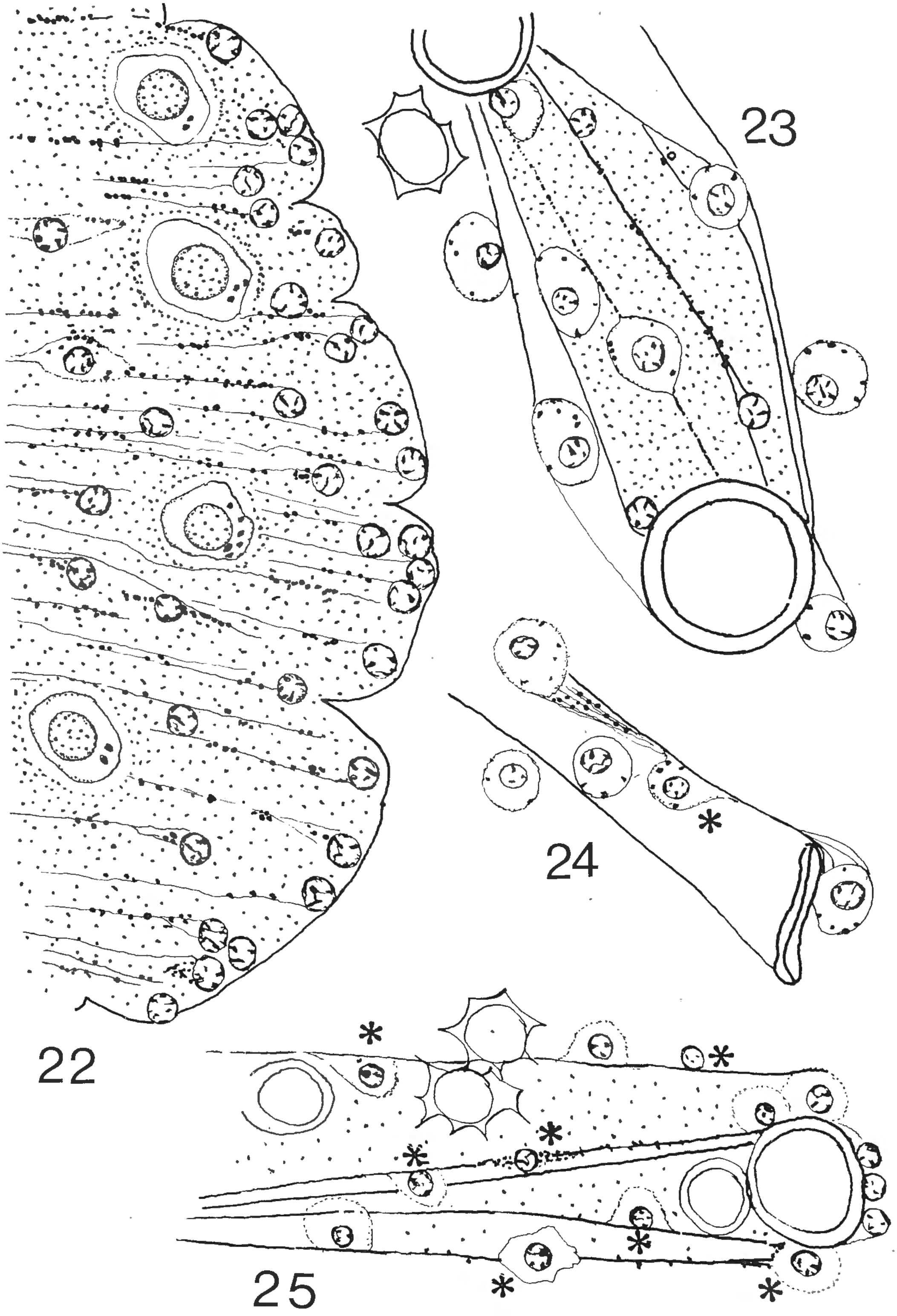
Fig. 18b



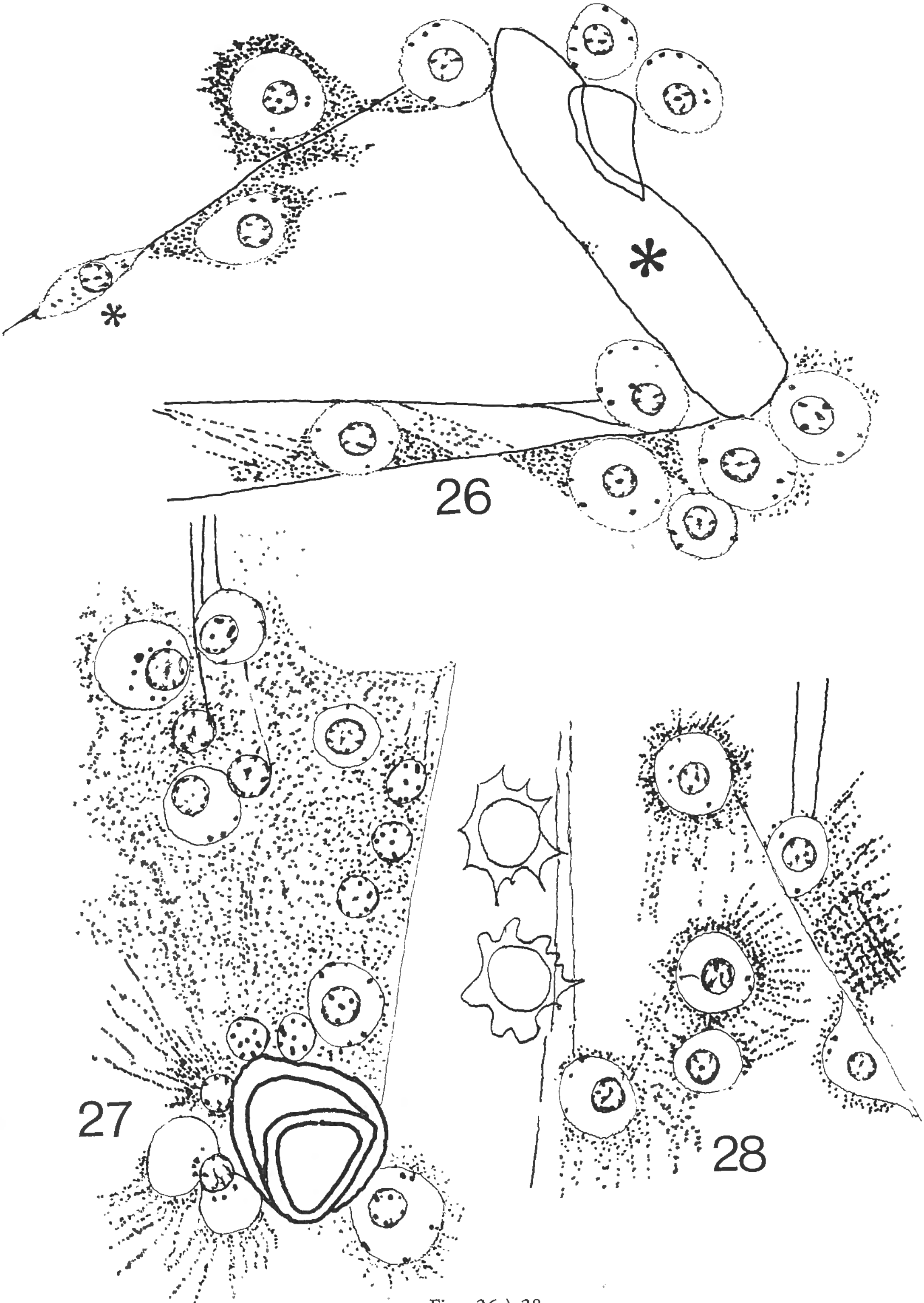




Figs. 19 à 21



Figs. 22 à 25



Figs. 26 à 28

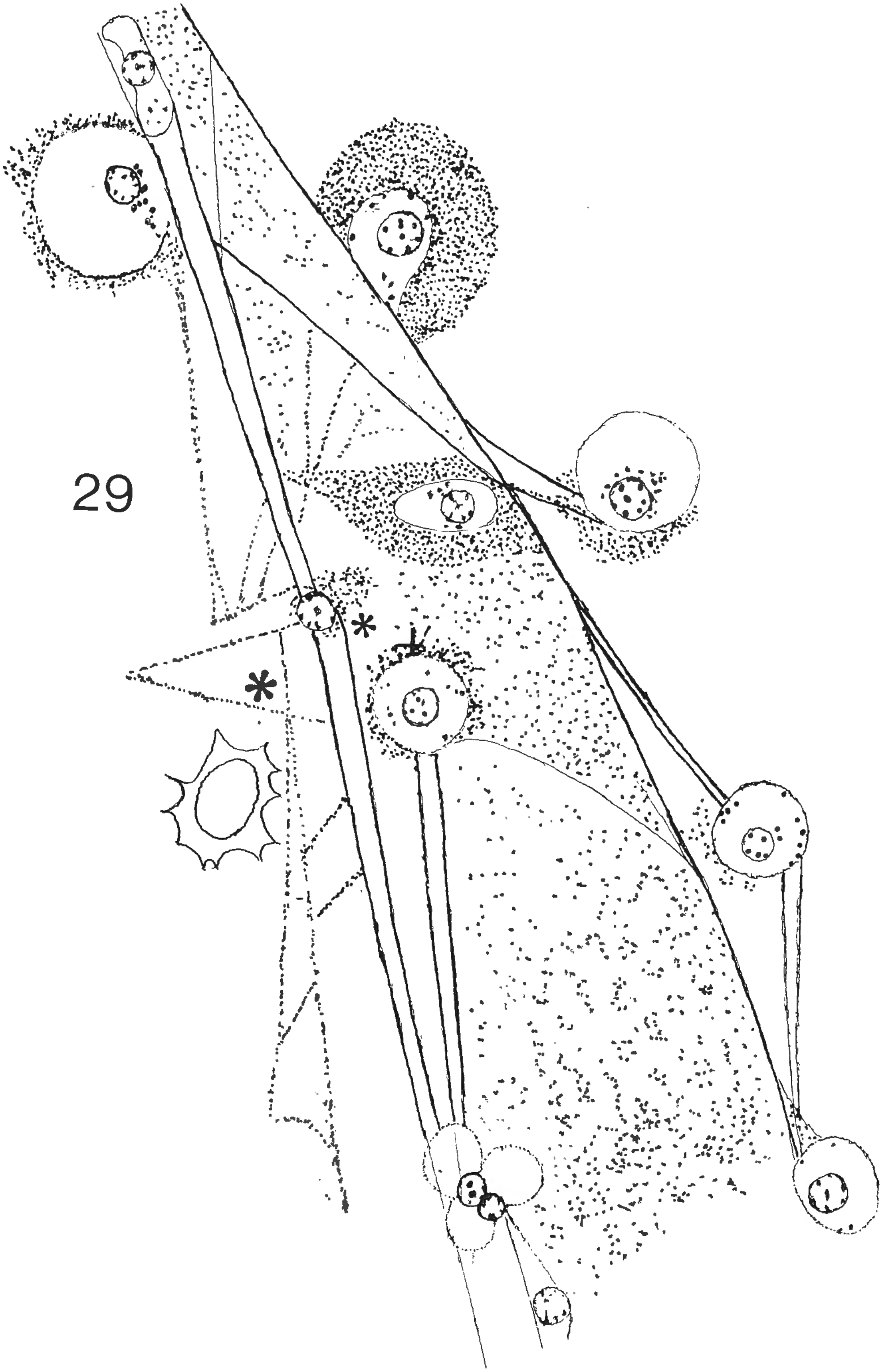


Fig. 29

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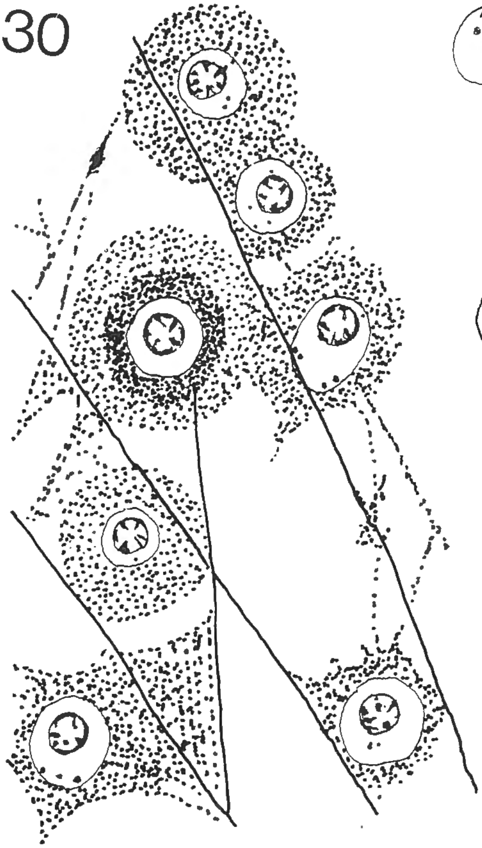

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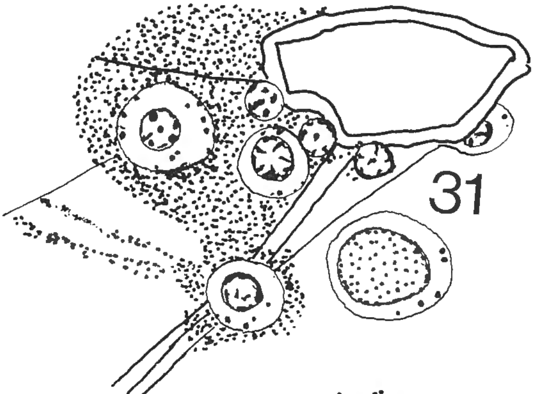

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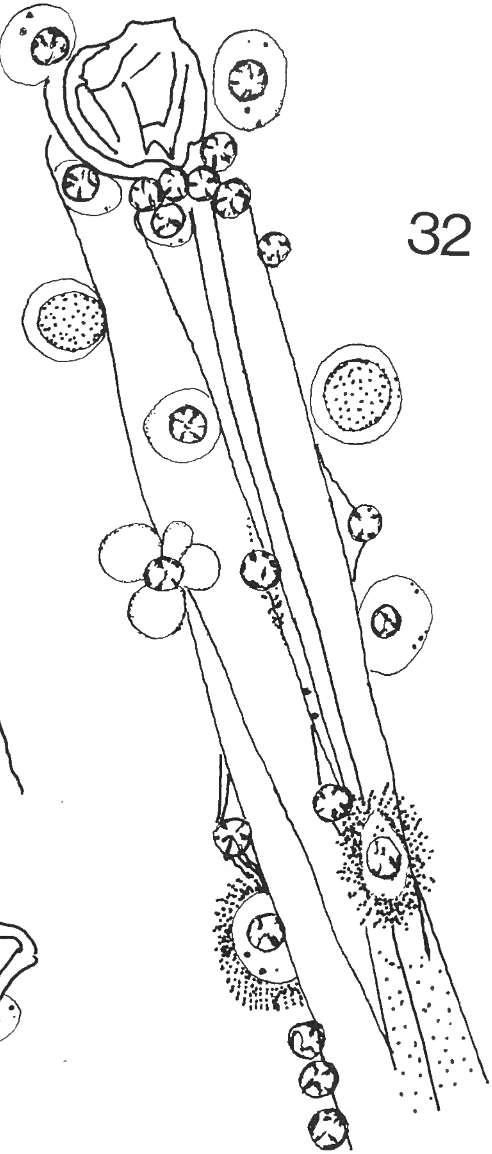

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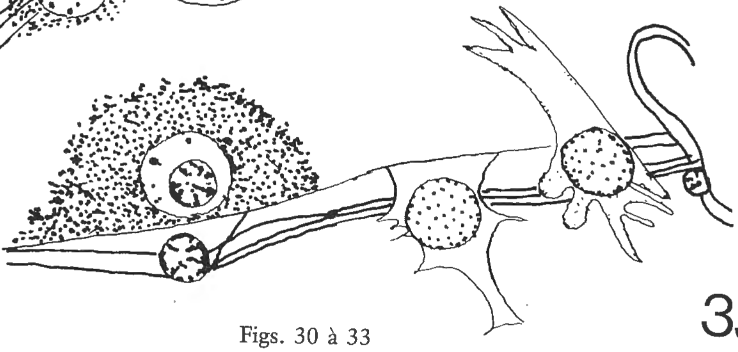
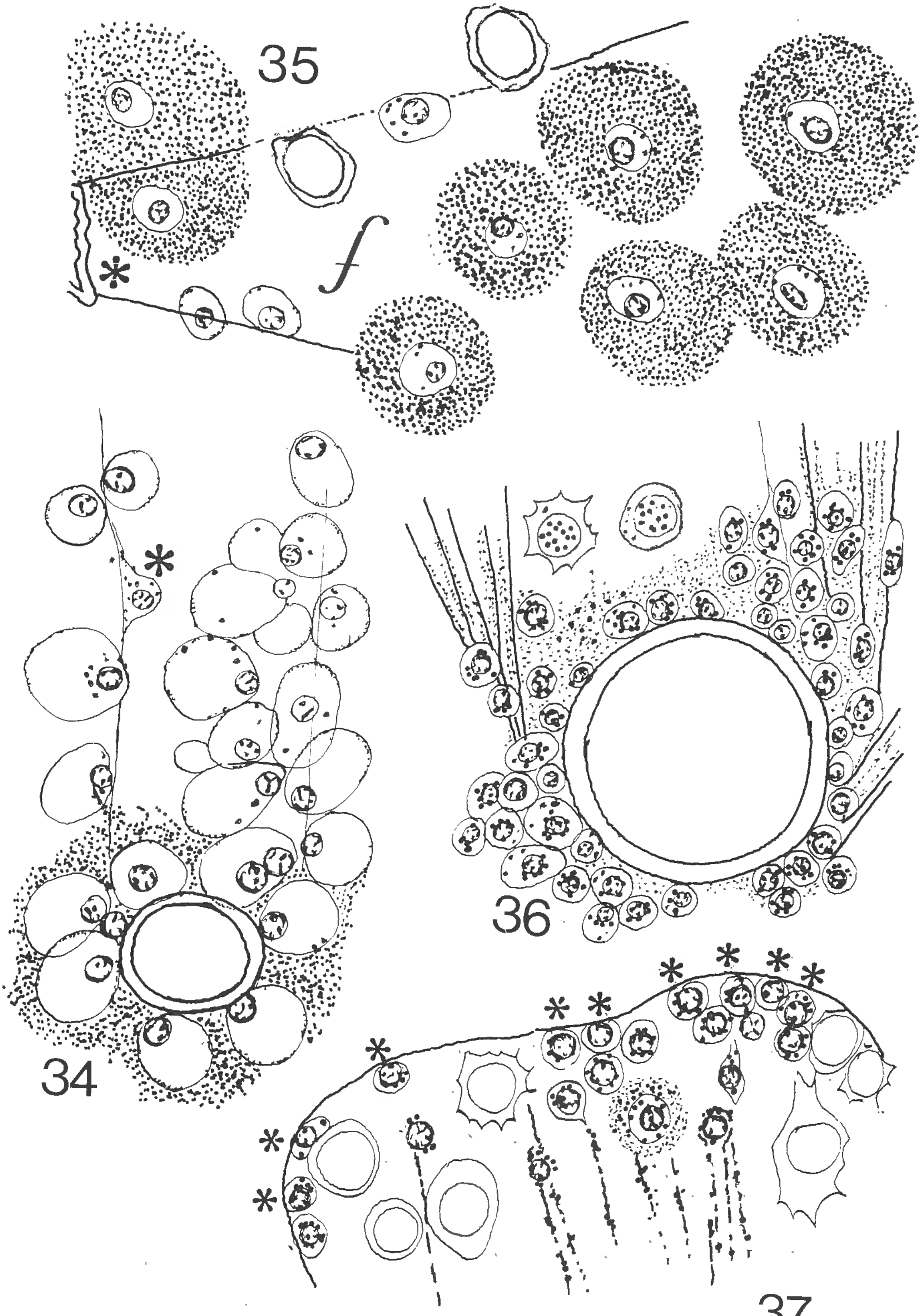
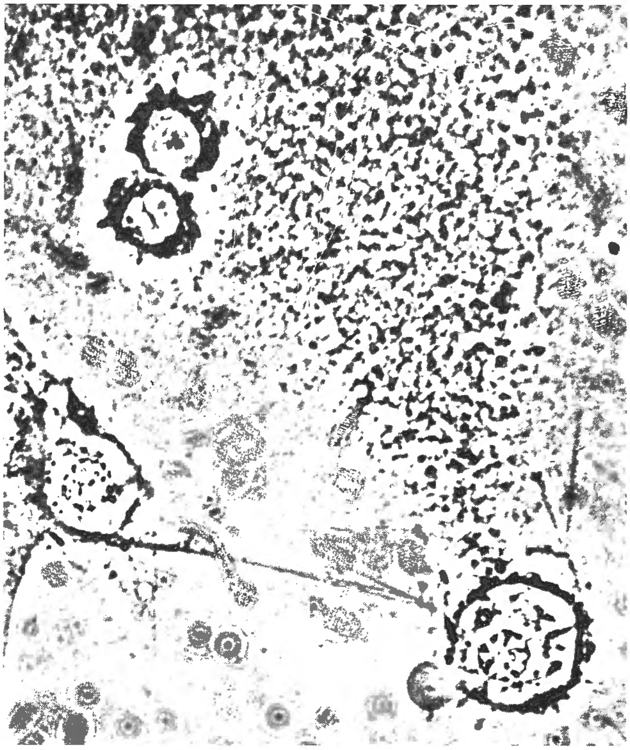


Figs. 30 à 33



Figs. 34 à 37



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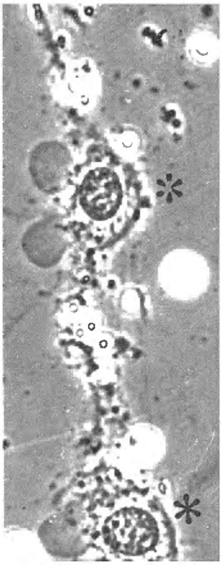

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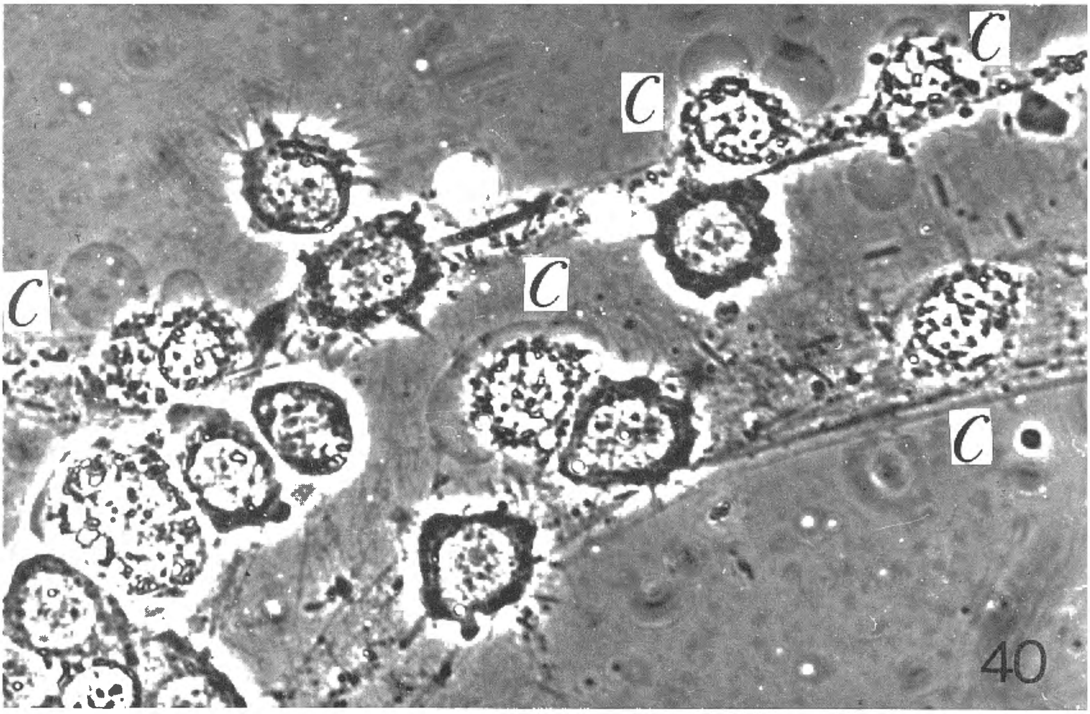

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Figs. 38 à 40

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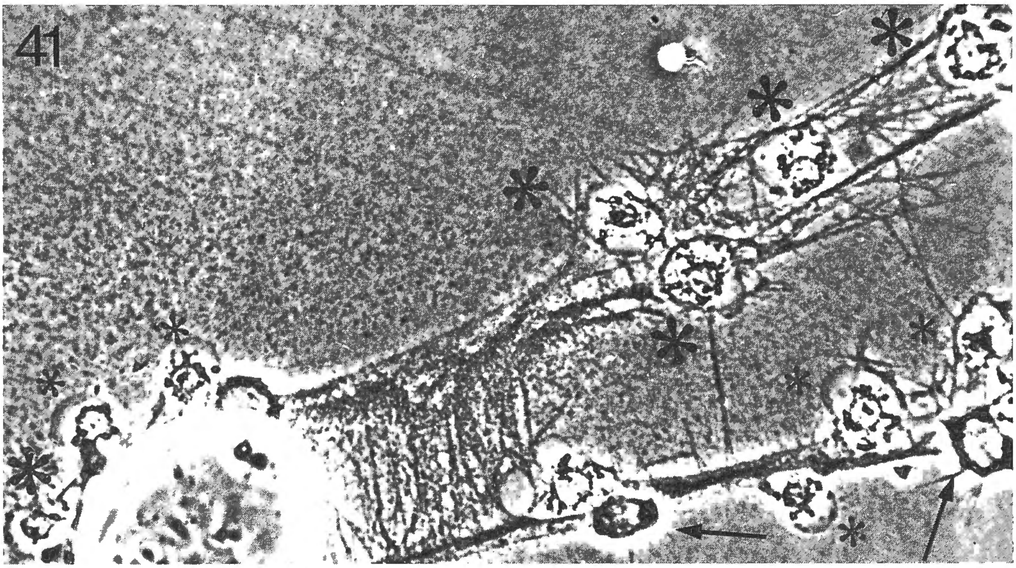

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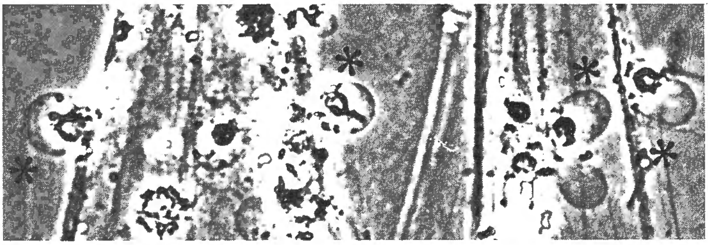

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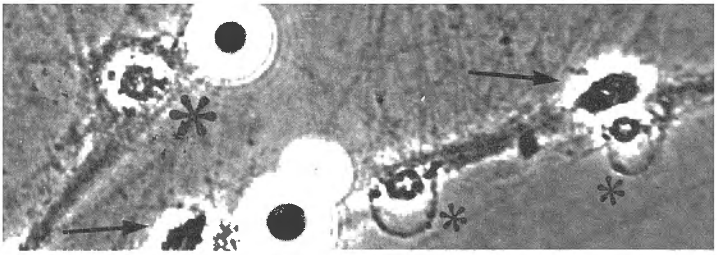

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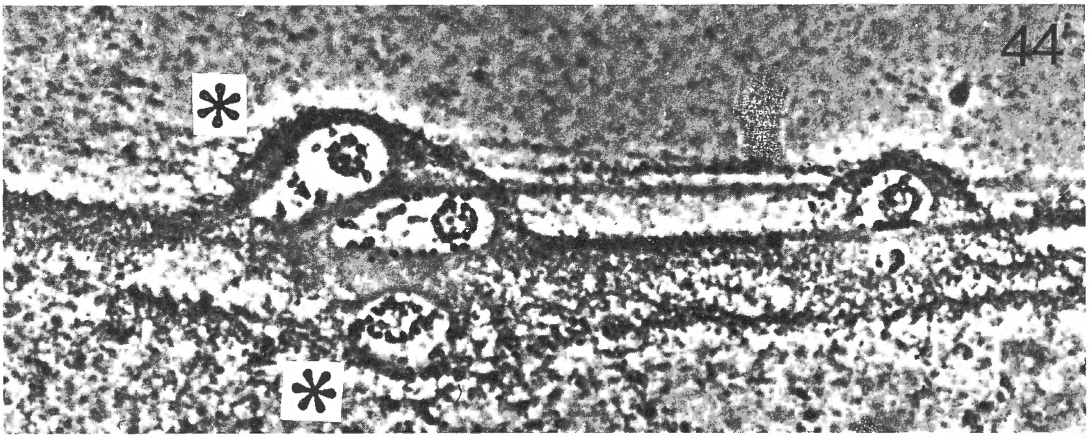
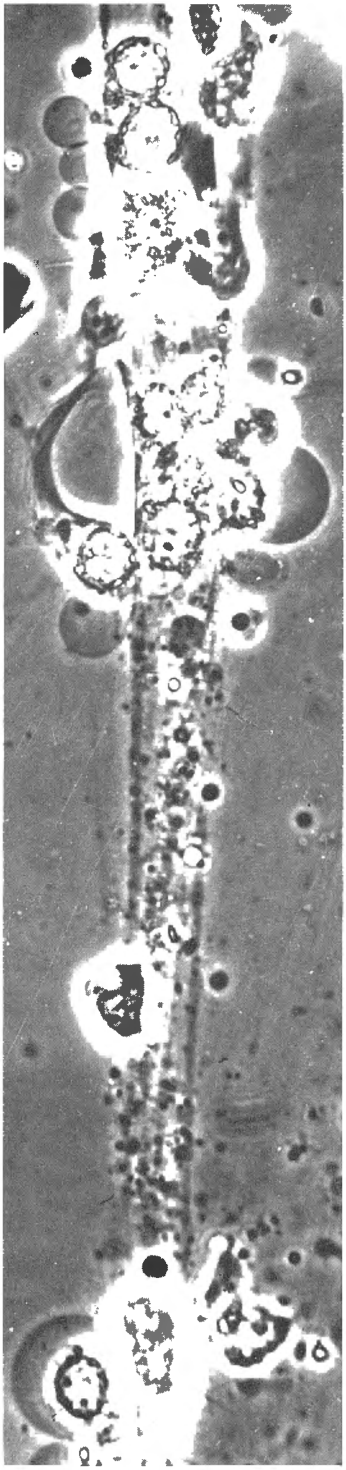


Figs. 41 à 44



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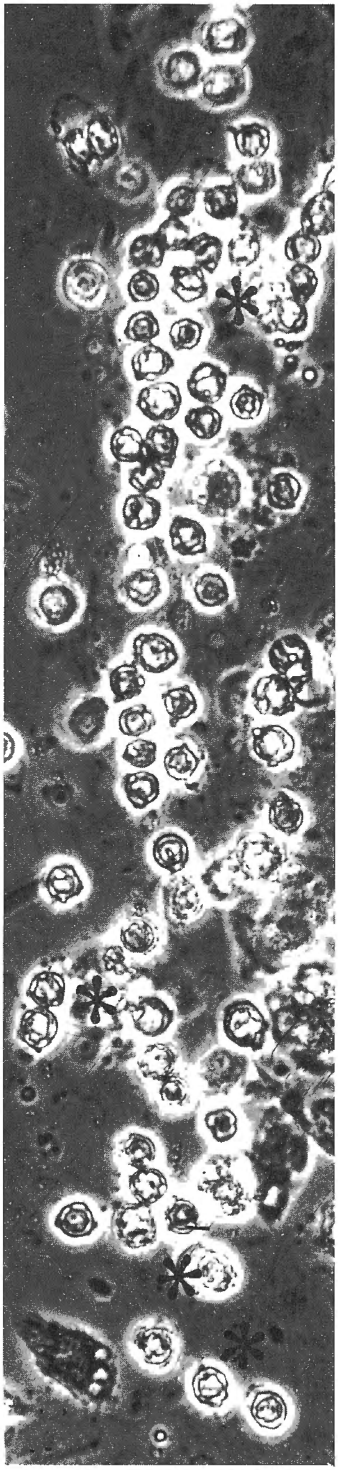

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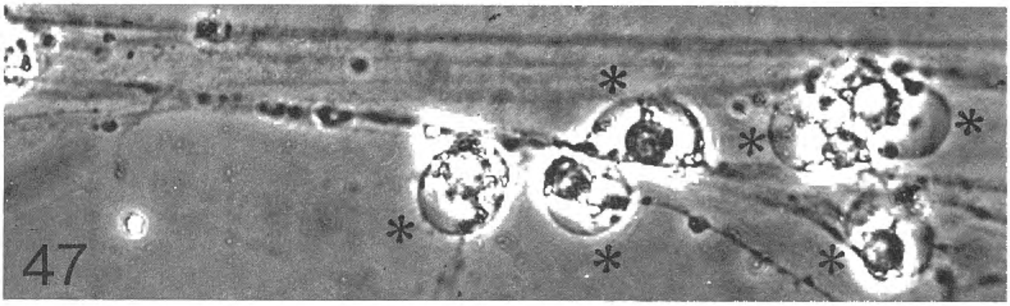
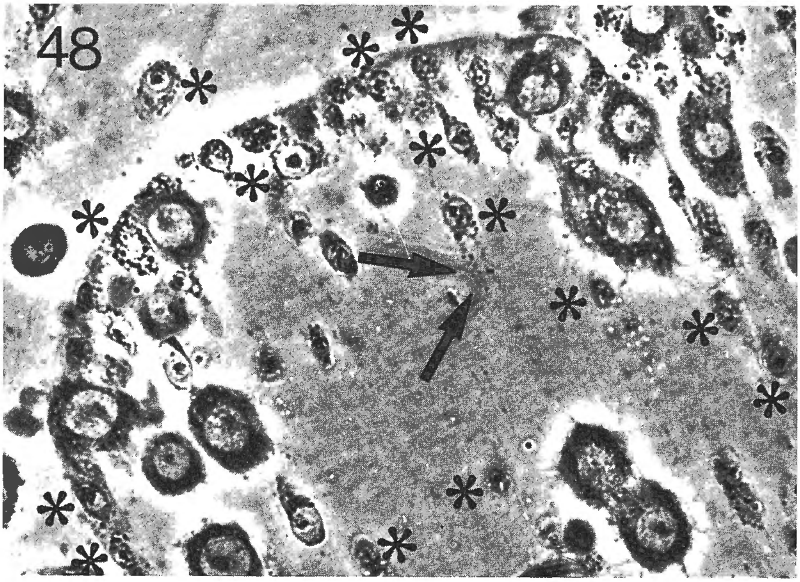
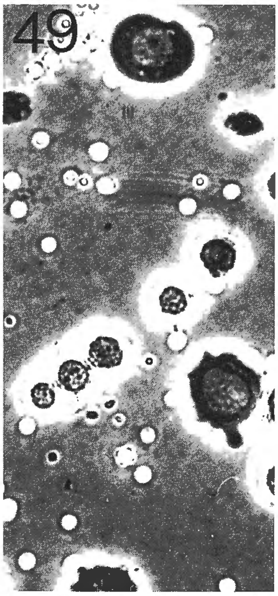
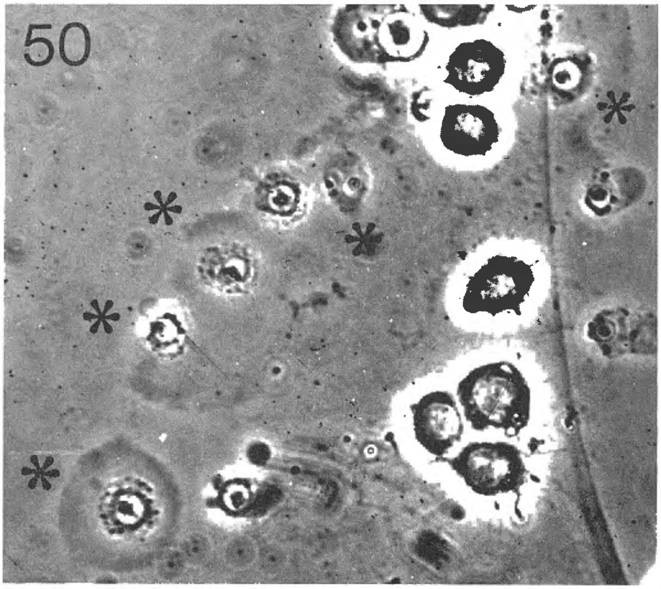
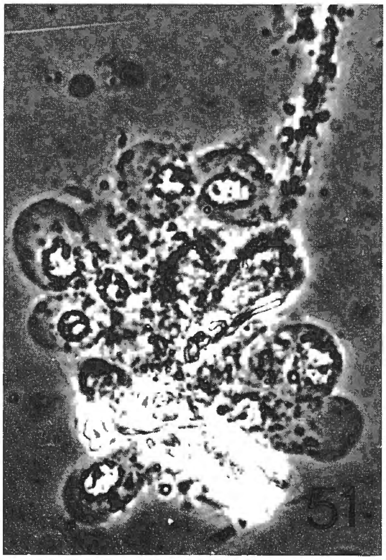
Figs. 45 à 46



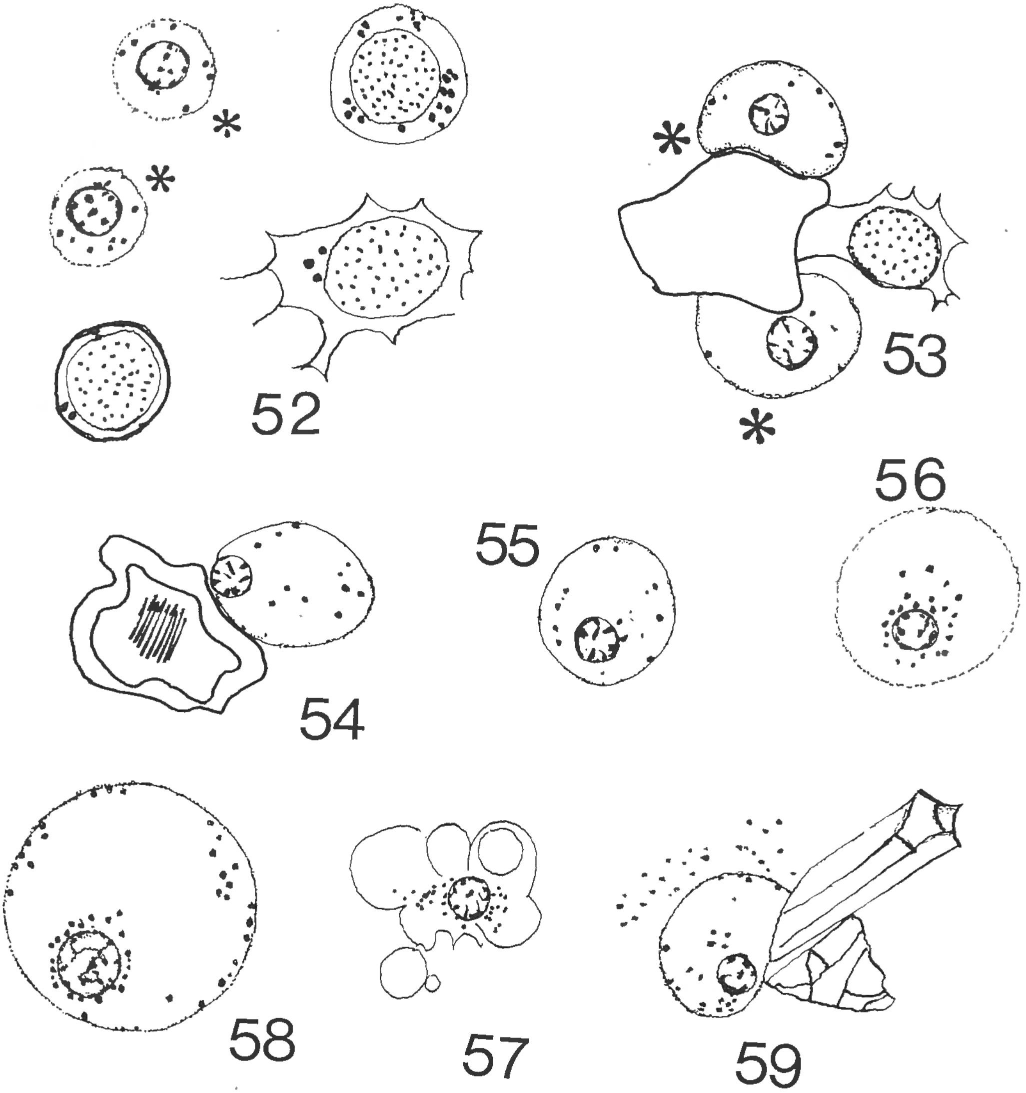








Figs. 47 à 51



Figs. 52 à 59