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Searching for palaeontological evidence of viruses that multiply in Insecta and Acarina

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Abstract. Viruses are known to be agents of important diseases of Insecta and Acarina, and many vertebrate and plant viruses have arthropods as propagative vectors. There is fossil evidence of arthropod pathogens for some micro-organisms, but not for viruses. Isolated virions would be hard to detect but, in fossil material, it could be easier to find traces of virus infection, mainly virus-induced cellular structures (VICS), easily recognisable by electron microscopy, such as virions encapsulated in protein occlusion bodies, aggregates of membrane-bounded virus particles and crystalline arrays of numerous virus particles. The following main taxa of viruses that multiply in arthropods are discussed both for some of their evolutionary aspects and for the VICS they cause in arthropods: A. dsDNA *Poxviridae, Asfarviridae, Baculoviridae, Iridoviridae, Polydnaviridae* and *Ascoviridae,* infecting mainly Lepidoptera, Hymenoptera, Coleoptera, Diptera and Acarina; B. ssDNA *Parvoviridae,* infecting mainly Diptera and Lepidoptera; C. dsRNA *Reoviridae* and *Birnaviridae,* infecting mainly Diptera, Hymenoptera and Acarina, and plant viruses also multiplying in Hemiptera; D. Amb.-ssRNA *Bunyaviridae* and *Tenuivirus,* that multiply in Diptera and Hemiptera (animal viruses) and in Thysanoptera and Hemiptera (plant viruses); E. -ssRNA *Rhabdoviridae,* multiplying in Diptera and Acarina (vertebrate viruses), and mainly in Hemiptera (plant viruses); F. +ssRNA *Togaviridae, Nodaviridae, Tetraviridae, Flaviviridae* and *Picornaviridae,* multiplying mainly in Lepidoptera, Hymenoptera, Diptera and Acarina (animal viruses), and in Hemiptera the plant Marafiviruses; G. RNA-RT *Metaviridae* and *Pseudoviridae,* multiplying in Diptera and Lepidoptera.
Fossil arthropods included in amber or similar material derived from plant resins, that had the ultrastructure preserved, would be the best material for viral palaeontological studies. Volcanic ash and carbon deposits could also give good preservation.

Key words: arthropods, plant and animal viruses, virus-induced inclusions, electron microscopy.

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I. INTRODUCTION

Fossil evidence of pathogens or symbionts of arthropod such as rickettsiae, bacteria, cyanobacteria, protozoa, algae and fungi are known (cf. POINAR et al. 1993; POINAR 1996; POINAR & POINAR

1998; POINAR & POINAR 1999), but not yet for viruses. POINAR & POINAR (1999), referring to *Polydnaviridae,* wrote: "It is probable that entombed braconid wasps also possess such viruses". Molecular studies of viruses are shedding light on the possible common origin of some animal and plant viruses, but palaeontological confirmation is lacking, mainly because it is very difficult to recognise virus particles in fossilised material. LOVISOLO & BOCCARDO (1996) suggested that, in spite of the difficulties, palaeontology might help in checking some hypotheses on origin and evolution of viruses, searching typical virus-induced cellular structures (VICS) caused by virus infection, which are much larger and more likely to be preserved in fossil tissues than virus particles.

The evolution and possible palaeontology of viruses with emphasis on those of plants was treated in a previous paper (LOVISOLO & RÖSLER 2001). Here we deal with viruses that multiply in arthropods. The main aim of this paper is to point out to palaeontologists doing microscopy on fossil arthropods the possibility to detect traces of virus infections. Several viruses are known to be agents of diseases of insects, quite often severe and leading to death. Some virus diseases of mites are also known, but little is known of their properties (POINAR & POINAR 1998; VAN DER GEEST et al. 2000). Arthropod viruses have mainly dsDNA and +ssRNA genomes, while other groups are less represented if compared to the viruses infecting vertebrates and plants, and no *Retroviridae* is known to infect insects. Some "orphan viruses", apparently not causing disease, are also present in arthropods.

Arthropoda is the phylum with the most important relationships with viruses, vertebrates and plants, although a lower number of arthropod virus species is known than for vertebrates, plants and bacteria (cf. LOVISOLO & RÖSLER 2001). Insecta, with almost a million species described, represent about 90% of all arthropod species, and Arachnida (to which Acarina belong) represent about 7%. More than 75% of all living animal species are arthropods (GOULD 1989). JARZEMBOWSKI (2001) observed that "If biodiversity is the measure of success, then insects (hexapods) are the most successful arthropods of all time".

Some Insecta and Acarina species are major vectors of viruses of both plants and animals. They are very diversified in the way they transmit viruses. The most complex relationships are between insects and plant viruses. It is generally recognised that insects have played an important role in the evolution of angiosperms, mainly for their involvement in pollination, which became widespread during the Cretaceous period (cf. LOVISOLO & RÖSLER 2001). According to LABANDEIRA (1999), "significant insect herbivory began during the Late Carboniferous to Early Permian". These relationships have certainly favoured the evolution of viruses that infect plants. After such a long coevolution, we now have three main categories of arthropod-plant virus relationships:

1. Viruses that do not replicate and do not circulate in their vectors ("non-persistent" and "semipersistent", which are mainly +ssRNA viruses);

2. Viruses that do not replicate but circulate in the vectors ("non-propagative circulative viruses", which are mainly +ssRNA and ssDNA viruses);

3. Viruses that circulate and replicate in their vectors ("persistent propagative viruses"), mainly dsRNA and -ssRNA, but also some +ssRNA and negative – ambisense RNA viruses. In this paper, we will deal only with persistent propagative viruses because they could be more easily detected in fossil arthropods.

Most of the viruses of vertebrates transmitted by arthropods replicate and circulate in their vectors, being "propagative viruses". "Non-circulative transmission" is not widely associated with animal viruses (cf. MURPHY 1999), even if there are numerous vertebrate-infecting viruses that are transmitted by arthropod vectors but do not replicate in the vector (cf. GRAY & BANERJEE 1999). MARAMOROSCH (1955) remarked that plant viruses that multiply in arthropods probably were originally arthropod viruses. More recently, several authors have agreed that the oldest virus-host-vector relationships are those of the arboviruses (arthropod-borne viruses). According to MURPHY (1999) over 500 arboviruses are known, which infect mainly humans and replicate in their blood-sucking arthropod hosts, mainly the Diptera and Acarina. Many +ssRNA (*Toga-* and *Flaviviridae*), dsRNA (*Reoviridae),* -ssRNA (*Rhabdoviridae),* and negative and ambisense RNA (*Bunyaviridae)* viruses are arboviruses. The most important plant viruses that multiply in arthropods (Hemiptera, Thysanoptera and Acarina) possess dsRNA, -ssRNA, negative and ambisense RNA genomes.

The viruses that are propagative in arthropods played a role in the evolution of viruses not only of arthropods but also of vertebrates and plants (NUTTAL et al. 1991). Dealing with *Iridoviridae*, which have only been isolated from poikilothermic animals (amphibians, fishes and insects), WEBBY & KALMAKOFF (1999) suggested that insect viruses were the first ones and "that they later adapted to life in vertebrates which fed on the insects". CALISHER (1999) pointed out that "mosquitoes belonging to some of the species that transmit alphaviruses typically feed on plants as well as on vertebrates", and according to JOLIVET (1998), "it seems that at the beginning all of those hematophagous bloodsucking insects were phytophagous or nectariphagous, as males mosquitoes still are". In the course of evolution, viruses that multiply in arthropods, in addition to adaptation of some to vertebrates and plants as vectors or pathogens, could have passed from vertebrates to plants, and vice-versa. At present there is no evidence that any plant virus affects mammals and vice-versa, but that could have happened in the remote past. At present, viruses of plants and poikilothermic animals have optimal replication rates mainly at temperatures lower than 30°C, while homoiothermic animal viruses have replication optimum higher than 30°C (cf. LOVISOLO & RÖSLER 2001).

The main families and genera of viruses known to include species that multiply in arthropods are listed in Table I, and the virus groups that could be detected in fossil material because of their VICS, are indicated with asterisks. Most of the information on the taxonomy of viruses, when not specifically mentioned, was taken from the 7th Report of the International Committee on Taxonomy of Viruses, ICTV (VAN REGENMORTEL et al. 2000). According to the new rules of the "International Code of Virus Classification and Nomenclature", the names of orders, families, subfamilies, genera and species are always printed in italics, as an indication that the names had been approved. When the taxonomic status of a putative species is uncertain, it will be considered a "tentative" or "unassigned species" and its name will not be given in italics.

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II. VIRUS-INDUCED CELLULAR STRUCTURES (VICS) AS TOOLS FOR DETECTION OF VIRUS INFECTIONS IN FOSSIL ARTHROPODS

Virus infection of plant and animal cells often causes VICS, which are distinctive for some types of virus and easily recognised by electron microscopy and sometimes even by light microscopy. The main VICS are: a. different types of inclusion bodies (protein structures staining abnormally, visible by light microscopy); b. occlusion bodies (virions encapsulated in protein, sometime large proteinaceous polyhedra); c. membrane-bound enclaves of virions; d. crystalline arrays of numerous virions (Fig. 1); e. viroplasms (amorphous cytoplasm inclusions associated to virus synthesis, without a surrounding membrane); f. protein tubular or lamellar structures.

The most suitable material for these investigations is embedded in amber or similar material derived from plant resins that permitted good ultrastructural preservation. The existence of amber of ancient origin, till 135 millions years ago, is known. Volcanic ash, carbon deposits and gypsum crystals could also give good preservation. According to POINAR (1993), amberization gives the most complete type of fossilisation of insects, a gentle process inducive to the preservation not only of cells and tissues, but also of organelles like mitochondria and ribosomes. POINAR & HESS (1982, 1985) investigated the ultrastructure of 40 million years old fossil fly tissues included in Baltic amber showing a good preservation of cell structures including muscle fibrils, mitochondria cristae (Fig. 2) and endoplasmic reticulum cisternae.

Table I

Families and genera of viruses that replicate within members of the indicated arthropod (Insecta and Acarina) taxonomic groups

Nucleic Acids	Families and genera of viruses	Taxonomic groups of arthropods that contain members in which viruses of the groups indicated with asterisks may replicate																														
		Plant viruses (1)								Invertebrate and vertebrate viruses (1)																							
		Aphididae	Cicadellidae	Delphacidae	Piesmidae	Thripidae	*Eriophyidae*	*Tenuipalpidae*	Blattodea	Coleoptera	Diptera	Ephemeoptera	Hemiptera	Hymenoptera	Isoptera	Lepidoptera	Mallophaga	Neuroptera	Odonata	Orthoptera	Thysanura	Trichoptera	*Argasidae*	*Ixodidae*	*Laelaptidae*	*Tetranychidae*	*Varroidae*					
dsDNA:	Poxviridae:																															
	Entomopoxvirinae									*	*					*				*												
	Asfarviridae																						*									
	Baculoviridae:																															
	Granulovirus															*																
	Nucleopolyhedrov.									*	*		*	*		*		*			*	*										
	Unassigned animal									*						*											*					
	Iridoviridae:																															
	Iridovirus									*	*	*	*	*	*	*				*												
	Chloriridovirus										*																					
	Polydnaviridae													*																		
	Ascoviridae															*																
ssDNA:	Parvoviridae:																															
	Densovirinae								*		*			*		*			*	*												
dsRNA	Reoviridae:																															
	Cypovirus									*	*			*		*		*														
	Orbivirus										*												*	*								
	Coltivirus										*												*	*								
	Fijivirus and Oryzavirus			*																												
	Phytoreovirus		*																													
	Unassig. Animal & plant Reo		*	*						*	*		*	*						*			*								
	Birnaviridae:																															
	Entomobirnavirus										*																					
Negative, ambisense RNA	Bunyaviridae:																															
	Animal Bunya										*		*											*								
	Plant Bunya					*																										
	Tenuivirus		*	*																												
-ssRNA	Rhabdoviridae:																															
	Lyssavirus										*																					
	Ephemerovirus										*													*								
	Vesiculovirus										*													*	*							
	Sigma rhabdovir.										*																					
	Cytorhabdovirus	*	*	*																												
	Nucleorhabdovir.	*	*	*																												
	Unassign. animal										*																					
	Unassign. plant	*	*	*	*		*	*																								
	Orthomixoviridae:																															
	Thogotovirus										*													*								
	Unassign. Animal										*													*								

Nucleic Acids	Families and genera of viruses	Taxonomic groups of arthropods that contain members in which viruses of the groups indicated with asterisks may replicate																												
		Plant viruses (1)							Invertebrate and vertebrate viruses (1)																						
		Aphididae	Cicadellidae	Delphacidae	Piesmidae	Thripidae	*Eriophyidae*	*Tenuipalpidae*	Blattodea	Coleoptera	Diptera	Ephemeroptera	Hemiptera	Hymenoptera	Isoptera	Lepidoptera	Mallophaga	Neuroptera	Odonata	Orthoptera	Thysanura	Trichoptera	*Argasidae*	*Ixodidae*	*Laelaptidae*	*Tetranychidae*	*Varroidae*
	Togaviridae:																													
	Alphavirus									*	*		*	*			*							*					
	Nodaviridae:																													
	Alphanodavirus									*	*			*		*													
	Tetraviridae															*													
+ssRNA	Marafivirus		*																											
	Flaviviridae:																													
	Flavivirus										*																			
	Picornaviridae:																													
	Cardiovirus										*																			
	Arthrop. Picorna-like & unassigned									*	*		*	*	*	*				*								*	*
	Metaviridae:																													
	Metavirus										*					*													
RNA-RT	Errantivirus										*					*													
	Pseudoviridae:																													
	Hemivirus										*																			

1) Insect taxonomic groups are in straight characters, those of Acarina in italics.

Plant virus inclusions that may permit recognition of virus infections in fossil material were discussed by LOVISOLO & RÖSLER (2001), while arthropod virus inclusions are treated in this paper. Arthropods more frequently infected by viruses, or the ones in which viruses multiply, belong mainly to Lepidoptera, Diptera, Hymenoptera, Coleoptera and Hemiptera for insect viruses; Diptera and Acarina for vertebrate viruses; Hemiptera, Thysanoptera and Acarina for plant viruses (Table I). Table II lists the taxonomic groups of arthropods which members may be hosts of propagative viruses, including in addition to insect and acari also some Scorpionida and Crustacea. Table II also indicates the earliest palaeontological records of the listed arthropod groups. It would be important for palaeontologists that detect VICS in fossil samples of arthropods to discuss their findings with virologists in order to check possible traces of antique virus infections. Several illustrations of VICS can be found, in addition to the mentioned ones, in "The Atlas of Insect and Plant Viruses" (MARAMOROSCH 1977).

IIA. Double stranded DNA (dsDNA) viruses are present mainly in animals, and prokaryotes. Ten of a total of 61 genera infect invertebrates, mainly insects, belonging to Coleoptera, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Neuroptera, Orthoptera, Thysanura, Trichoptera, some Acari (Argasidae and Tetranychidae) and some Crustacea (Decapoda and Isopoda). The dsDNA viruses able to infect arthropods belong to *Poxviridae* (*Entomopoxvirinae*), *Baculoviridae* (*Granulo-*, *Nucleopolyhedrovirus*, Nonoccluded baculoviruses), *Iridoviridae* (*Irido-*, *Chloriridovirus*), *Polydnaviridae*, *Ascoviridae* and *Asfarviridae*.

Entomopoxvirinae (EPV) is one of the two subfamilies of the *Poxviridae* that infect mainly Orthoptera, Diptera, Coleoptera, Lepidoptera and Hymenoptera (MOYER 1999). EPV members have an optimal growth temperature at 26-28°C as compared to about 37°C for vertebrate's poxviruses. The *Entomopoxvirinae* have quite large, brick- or oval-shaped virions, with lengths of 150 to 470 nm and widths from 165 to 300 nm. Virions are easily recognised in adipose tissues of infected insects,

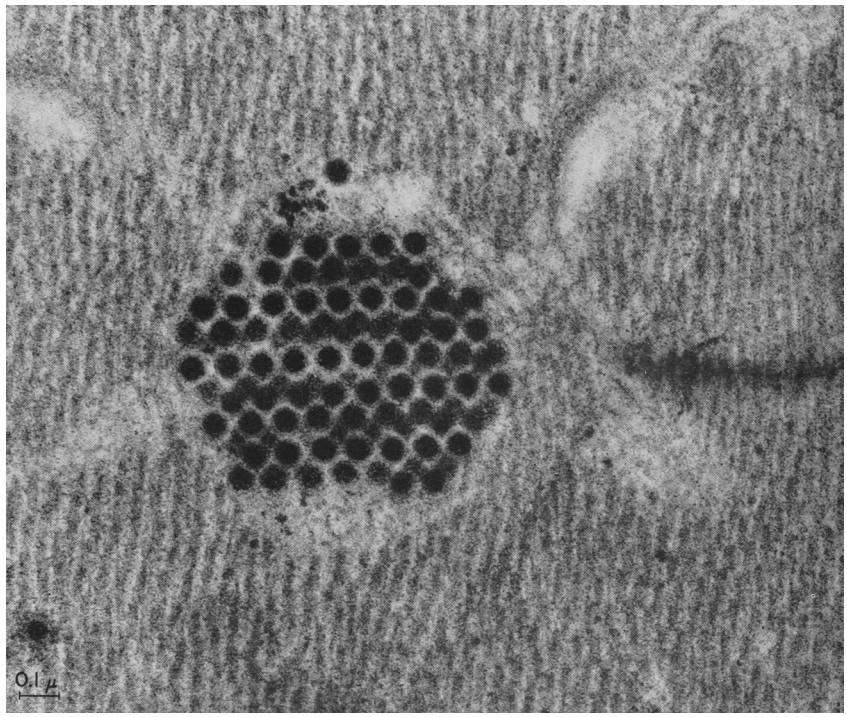

Fig. 1. A microcrystal of *Wound tumour virus* (*Phytoreovirus*) in a muscle cell of *Agalliota constricta.* Scale bar is 0.1 μm. Reprinted by permission from SHIKATA and MARAMOROSCH Nature, 208: 507-508, 1965, Copyright 1965 Macmillan Magazines Ltd.

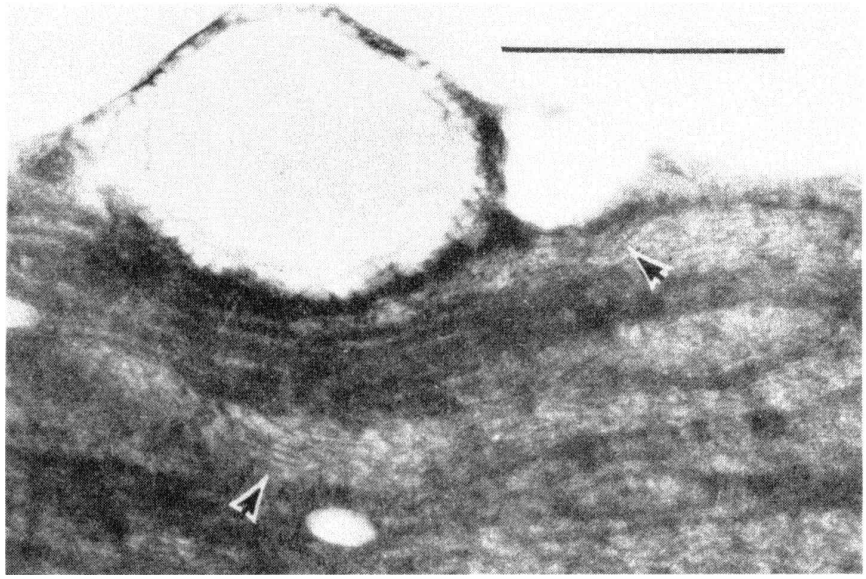

Fig. 2. Electron micrograph of a fossilised 40 million-year-old muscle fly tissue. Tracheoles, muscle fibrils, mitochondria and cristae (arrows) are clearly defined. Scale bar is 0.5 μm. Reprinted with permission from POINAR and HESS, Science, 215: 1241-1242, 1982, Copyright 1982 American Association for the Advancement of Science.

Table II

Taxonomic groups of arthropods that contain members in which viruses of the indicated nucleic acid type may replicate, and their earliest palaeontological records (1)

Taxonomic groups of arthropods	Nucleic acid of susceptible viruses	Earliest palaeontological records
INSECTA		
Coleoptera	dsDNA, dsRNA, ssRNA	PERMIAN, Sakmarian
Blattodea	ssDNA	CARBONIFEROUS, Bashkirian
Diptera	dsDNA, ssDNA, dsRNA, amb. –RNA, -ssRNA, +ssRNA, RNA-RT	?PERMIAN, Ufimian
Hemiptera		
Aleyrodidae	dsDNA, +ssRNA	Early CRETACEOUS
Aphididae	-ssRNA, +ssRNA	CARBONIFEROUS, Moscovian
Cicadellidae	dsRNA, -ssRNA, amb. –RNA, +ssRNA	CRETACEOUS, Berriasian
Cimicidae	dsDNA, dsRNA, +ssRNA, amb.-RNA	CARBONIFEROUS, Moscovian
Delphacidae	dsRNA, -ssRNA, amb.-RNA	CRETACEOUS, Aptian
Piesmatidae	-ssRNA	TERTIARY, Late Miocene
Hymenoptera	dsDNA, dsRNA, +ssRNA	TRIASSIC, Ladinian
Isoptera	dsDNA, +ssRNA	CRETACEOUS, Valanginian
Lepidoptera	dsDNA, ssDNA, dsRNA +ssRNA, RNA-RT	JURASSIC, Sinemurian
Neuroptera	dsDNA, dsRNA	PERMIAN, Sakmarian
Odonata	ssDNA,	CARBONIFEROUS, Bashkirian
Orthoptera	dsDNA, ssDNA	CARBONIFEROUS, Moscovian
Thysanoptera	amb. –RNA	PERMIAN, Sakmarian
Trichoptera	dsDNA	TRIASSIC, Ladinian
ARACHNIDA ACARINA: Argasidae, Eriophyidae, Ixodidae, Laelaptidae, Tenuipalpidae, Tetranychidae, Varroidae	dsDNA, dsRNA, -ssRNA, +ssRNA	Late CRETACEOUS
SCORPIONIDA	dsRNA	Late SILURIAN
CRUSTACEA Cladocera, Decapoda, Isopoda	dsDNA, dsRNA	PERMIAN

Data on insects are taken mainly from HAMILTON (1990), ROSS & JARZEMBOWSKI (1993) and LABANDEIRA (1999); those on Acarina are taken mainly from KLOMPEN & GRIMALDI (2001).

especially when occluded within a proteinaceous mass forming occlusion bodies (KURSTAK & GARZON 1977).

Baculoviridae have been isolated from arthropods only, mainly from Lepidoptera, but also other arthropods listed in Table I. Many Baculoviruses are highly virulent causing widespread epizootics. *Nucleopolyhedrovirus* (NPV) members produced in infected cells roughly polyhedral proteinaceous occlusion bodies containing numerous virions. These occlusion bodies, occurring within the nuclei of the midgut epithelium and fat bodies, are up to 5 μm in diameter and easily visible with a light microscope (cf. MILLER 1996; ROHRMANN 1999). Enlarged nuclei packed with polyhedra can be seen in fat body cells of a NPV of *Heliothis virescens* FABRICIUS 1781 (Noctuidae, Lepidoptera). Typical occlusion bodies of *Autographa californica multiple nucleopolyhedrovirus* have also been illustrated (cf. GRANADOS & FEDERICI 1986). Larvae killed by NPVs hang head downward in a

characteristic manner (SMITH 1967). The members of the genus *Granulovirus* (cf. WINSTANLEY & O'REILLY 1999), isolated only from Lepidoptera, have ovicylindrical occlusion bodies (crystallised proteins) containing a single virion, occurring in the cytoplasm after the rupture of the nuclear membrane. Fat bodies are the main organ attacked. A number of oval-spherical vesicles containing numerous occlusion bodies are present in infected cells, first found and called "boules hyalines" by PAILLOT (cf. SMITH 1967; SUMMERS 1977). All these structures could easily be recognised if present in fossil arthropods. Infected larvae may have internal tissues in a state of disintegration with a large number of polyhedra that can be observed with a light microscope. In the case of *Cydia pomonella granulovirus* infections can be easily recognised in fat bodies during the late stages of infections, when the nuclear membrane disintegrates and the cells fill with occluded virus particles. The unassigned *Oryctes rhinoceros* virus and *Heliothis zea* virus 1 were previously classified as non-occluded *Baculoviridae*. Possible non-occluded *Baculoviridae* (cf. POINAR & POINAR 1998; VAN DER GEEST et al. 2000) are the agents of diseases of the Tetranychidae *Panonychus citri* McGREGOR 1916 and *P. ulmi* KOCH 1836, and of the Phytoseiidae *Phytoseiulus persimilis* ATHIAS-HENRIOT 1957 and *Amblyseius* (=*Neoseiulus*) *cucumeris* OUDEMANS 1930. The *Invertebrate iridescent virus 6* (Iridovirus) infected *Bemisia argentifolii* (BELLOWS & PERRING), 1994) nymphs when experimentally inoculated (FUNK et al. 2000).

Iridoviridae have only been reported from poikilothermic animals including a wide range of arthropods of taxonomic groups listed in Table I, particularly of aquatic and damp habitats. Infected larvae of Diptera, Lepidoptera and Coleoptera produce closely packed paracrystalline arrays of virus particles (120 x 200 nm), mainly in the cytoplasm of fat bodies and of haemocytes. Such paracrystalline arrays (cf. WILLIAMS 1996; WEBBY & KALMAKOFF 1999) could be easily recognised if present in fossil samples. A characteristic of Iridoviruses is the blue to purple iridescence of masses of virus particles that gave the name to the genus.

Within *Polydnaviridae, Bracovirus* members infect parasitic Hymenoptera of the Braconidae family and *Ichnovirus* members infect only Ichneumonidae wasps. A typical viral envelope, enclosing several nucleocapsids, occurs in the infected wasp ovary (cf. STOLTZ 1999).

Ascoviridae is a family of enveloped viruses that has only lepidopterous insects as hosts, mechanically vectored by endoparasitic wasps. *Ascovirus* members are present mainly in fat bodies but also, according to the different species, in epidermis, tracheal matrix and midgut. Their unusual cytopathology leads to the formation of virion-containing vesicles (VCVs). The nucleus of infected cells undergoes hypertrophy and lyses, with invagination of the plasmalemma and formation of VCVs ranging in size from 5 to 10 μm. The VCVs, which migrate to the haemolymph, are recognisable by optical microscopy. In the electron microscope, the VCVs appear full of large virus particles, 200-400 x 130 nm. Ultrathin sections through viral vesicles produced by *Trichoplusia* and *Spodoptera* ascoviruses are illustrated by FEDERICI (1999).

African swine fever virus (*Asfarviridae*) is the only known DNA arbovirus that propagates in soft tick vectors, the Argasidae *Ornithodoros* spp. (SALAS 1999).

IIB. Single stranded DNA (ssDNA) viruses are mainly present in bacteria, mycoplasmas and plants. Only the *Parvoviridae (Densovirinae*) are known to infect members of Blattodea, Diptera, Hymenoptera, Lepidoptera, Odonata and Orthoptera. Denso-like viruses multiply also in crabs and shrimps (Decapoda).

IIC. Double stranded RNA (dsRNA) viruses. The non-enveloped dsRNA are present in all host phyla except bacteria. *Reoviridae* have 5 genera of viruses infecting vertebrates (*Orthoreovirus, Orbivirus*, *Rotavirus, Coltivirus* and *Aquareovirus*), one genus infecting only arthropods (*Cypovirus*), and 3 genera infecting plants (*Fijivirus, Phytoreovirus* and *Oryzavirus*). Most *Orbivirus* members replicate in Diptera and some in ticks (Argasidae and Ixodidae, Acarina), with little or no evident effect. Most *Coltivirus* members replicate in ticks (Argasidae and Ixodidae) and some in Diptera. Information on their replication in arthropods is limited. It is believed (MERTENS 1999) that *Bluetongue virus* (*Orbivirus*) initiates infection via the cells of the midgut wall, and that progeny virus particles are released into the insect hemocele. Orphan or-

biviruses of arthropods are also known. Some unassigned and incompletely characterised *Reoviridae* have been found infecting mainly members of Diptera, Hemiptera and Hymenoptera and also the other arthropod groups listed in Table I (cf. NODA & NAKASHIMA 1995).

Within dsRNA viruses the evolution of plant reoviruses (*Fijivirus*, *Oryzavirus* and *Phytoreovirus*) could have been connected with the divergence of the major taxonomic groups of Hemiptera during the middle Jurassic (cf. HENNIG 1981; NAULT & AMMAR 1989). Thus phytoreoviruses may have evolved with the Cicadellidae, while Fijiviruses and Oryzaviruses evolved with the Delphacidae. *Wound tumour virus* (*Phytoreovirus*), first found in *Agalliopsis novella* SAY 1830 (Hemiptera, Cicadellidae), was found in plants only after 47 years (cf. LOVISOLO & RÖSLER 2001). Indirect confirmation of the view that plant reoviruses are of insect origin is given by two Fiji- or Fiji-like viruses, the leafhopper A virus (LAV), and the *Niloparvata lugens reovirus* (NLRV). LAV was first thought to be the causative agent of a maize disease, but OFORI & FRANCKI (1985) proved that LAV multiplies in *Cicadulina bimaculata* EVANS 1940 (Cicadellidae, Hemiptera), and not in maize. The virus is injected into the plant and circulates transiently, permitting horizontal transmission among the leafhoppers. Similar behaviour has been reported for NLRV and rice plants (cf. NODA & NAKASHIMA 1995). A few Fijiviruses are orphans in Delphacidae, such the ones found in *Peregrinus maidis* ASHMEAD 1890 (Delphacidae, Hemiptera) by HEROLD & MUNZ (1967) and FALK et al. (1988). In the case of plant Reoviruses, neoplastic plant tissues are often full of virus particles, sometimes arranged in big crystals, viroplasms and other virus induced structures like the tubules (cf. LOVISOLO & RÖSLER 2001). Plant *Reoviridae* multiply also in their insect vectors, and produce in several of their organs the majority of the structures found in infected plants. Investigations may discover such abnormal structures in fossil insects. SHIKATA & MARAMOROSCH (1965) published an electron micrograph of a muscle of *Agalliota* (=*Agallia*) *constricta* VAN DUZEE 1849 (Hemiptera, Cicadellidae) infected with *Wound tumor virus.* Numerous virus particles arranged in crystals of about 1 μm diameter were present among muscle fibrils (Fig. 1). Muscle ultrastructure of a 40 million years old fossil fly (Mycetophilidae: Diptera) embedded in amber was illustrated (Fig. 2) by POINAR & HESS (1982).

VICS have been found in several organs and in the mycetome of the Hemiptera vectors of both *Fijivirus* and *Phytoreovirus* members (cf. MATSUI & YAMAGUCHI 1966; SHIKATA & MARAMOROSCH 1967; VIDANO 1970; WOOD 1973).

Cypovirus (cytoplasmic polyhedrosis viruses) members have been isolated from more than 250 species belonging to Lepidoptera, Diptera, Hymenoptera, Coleoptera, Neuroptera and to a cladoceran crustacean (BELLONCIK 1999). *Cypovirus* replication, inhibited above 35°C, generally starts in the midgut and produces large numbers of proteinaceous polyhedral occlusion bodies. *Bombyx mori Cypovirus 1* produces polyhedra composed of a large number of isometric virus particles embedded in the matrix protein (polyhedrin). Polyhedra produced by *Trichoplusia ni Cypovirus 5* in cell lines established from ovarian cells of *T. ni* have been photographed in phase contrast light microscopy (PAYNE & HARRAP 1977; BELLONCIK 1999). Well recognisable crystallised virus-like particles, tubules filled with aligned particles and viroplasms of an orphan virus have been found (MAILLET & FOLLIOT 1967) in the testicles, trachea and fat body tissues of the *Fagocyba* (=*Typhlocyba*) *douglasi* EDWARDS 1878 (Cicadellidae, Hemiptera). HEROLD & MUNZ (1967) and FALK et al. (1988) found many crystallised virus-like particles in salivary glands, intestine cells, muscle fibrils, ovaries, spermatocytes and mycetome of apparently healthy *Peregrinus maidis*.

Other non-enveloped dsRNA viruses infecting animals are the *Birnaviridae* with 3 genera. Entomobirnaviruses infect only insects, mainly *Drosophila* spp. (Drosophilidae, Diptera), but also *Culicoides* spp. (Ceratopogonidae, Diptera,). Aquabirnaviruses infect fishes, molluscs and crustaceans and Avibirnaviruses infects only birds. An unassigned Rotifer birnavirus is known.

IID. Negative and ambisense RNA (amb.-RNA) viruses. The *Bunyaviridae* have 4 genera infecting vertebrates (*Bunyavirus*, *Hantavirus*, *Nairovirus* and *Phlebovirus*) and one genus infecting plants (*Tospovirus*). Members of the genera *Bunyavirus*, *Nairovirus*, and *Phlebovirus* replicate in vertebrates and arthropods (Diptera, Hemiptera and Ixodidae).

Generally they are cytolytic for vertebrates, but cause little or no cytopathogenicity in the arthropod hosts. *Tospovirus* members replicate in plants and in Thripidae (Thysanoptera) vectors. Tospoviruses could have evolved as plant viruses within the *Bunyaviridae* through insects or Acari (ROGGERO et al. 1995). Thrips attacking man are known (BAILEY 1936) and one species was identified (ARNAUD 1970) as *Frankliniella occidentalis* PERGANDE 1895, an important vector of Tospoviruses. *Tenuivirus* is another genus of negative and ambisense RNA viruses that has similarities with Phleboviruses. Its members replicate in Graminae and in their insect vectors (Delphacidae and Cicadellidae).

IIE. Negative single stranded RNA (-ssRNA) viruses are of great interest for virus evolution because most of them replicate both in their plant or animal hosts and in their vectors (arthropods). They are present in vertebrates (22 genera), invertebrates (6 genera) and plants (5 genera), but not in bacteria, algae, fungi and protozoa.

One of the few orders accepted by ICTV (VAN REGENMORTEL et al. 2000) is that of the *Mononegavirales,* that comprises 4 families of enveloped viruses (*Borna-*, *Paramyxo-*, *Filo-* and *Rhabdoviridae*). The first two families infect only vertebrates, while the *Rhabdoviridae* have 4 genera of viruses infecting animals (*Vesiculo-*, *Lyssa-*, *Ephemero- and Novirhabdovirus*) and 2 genera infecting plants (*Cyto- and Nucleorhabdovirus*). *Filoviridae* are the closest relatives to *Rhabdoviridae* and *Paramyxoviridae* (KLENK et al. 1999). LUNDSGAARD (1996) detected filovirus-like particles in extracts from the leafhopper *Psammotettix alienus* DAHLBOM 1851 (Cicadellidae, Hemiptera).

Among the animal Rhabdoviruses two Lyssaviruses distantly related to rabies viruses, but with unknown vertebrate hosts, have been isolated from Diptera. *Vesiculovirus* members have mainly Diptera, but also ticks (Ixodidae and Laelaptidae), as vectors. Transovarial transmission in sand flies is known for 4 of them (SHOPE & TESH 1987). Vesicular stomatitis virus multiplies efficiently when inoculated in *Peregrinus maidis* (LASTRA & ESPARZA 1976). *Ephemerovirus* members have vertebrates as host and Diptera as propagative vectors. Some Ephemeroviruses and Vesiculoviruses are orphans in Diptera and Ixodidae.

Unassigned animal Rhabdoviruses include *Sigma virus*, a harmless virus transmitted vertically through the germinal cells of *Drosophila* spp.

No *Rhabdovirus* is known to be transmitted vertically in vertebrates or plants, an indication that probably they did not originate in vertebrates and plants.

Both *Cytorhabdovirus* and *Nucleorhabdovirus* members have as propagative vector members of three families of Hemiptera: Cicadellidae, Delphacidae and Aphididae. Numerous unassigned plant *Rhabdovirus* members have as propagative vectors members of Hemiptera (Cicadellidae, Delphacidae, Aphididae, Piesmatidae) and of Acarina (Eriophyidae, Tenuipalpidae). The present situation is that the animal-infecting rhabdoviruses diverged more than the plant ones. Rabies virus and rabies-related lyssaviruses are not transmitted by arthropods. The cell wall around the plant cell may be the constraint by which the plant rhabdoviruses did not lose their close association with insects (PETERS 1991). Also the fact that plant rhabdoviruses have an envelope may be an indication of their animal origin, because of the ability of enveloped viruses to recognise and c ross the plasma membrane, an important step for infection of animal cells but not for plant cells. Some plant rhabdo-like viruses, mainly the *citrus leprosis virus*, propagative in *Brevipalpus* spp. (Tenuipalpidae, Acarina), may have lost their envelope during passage from mites to plants (cf. LOVISOLO 2001). *Rhabdoviridae* can be easily recognised not only in plants and animals hosts, but also in their arthropod vectors. In the case of plant *Rhabdoviridae* there are several investigations. CONTI & PLUMB (1977) illustrated aggregates of *Barley yellow striate mosaic virus* particles and membrane-bound enclaves of particles and tubules in the cytoplasm of salivary gland cell of *Laodelphax striatellus* FALLÉN 1826 (Hemiptera, Delphacidae). JACKSON et al. (1987) illustrated large groups of virions (230 x 63 nm) of *cereal chlorotic mottle virus*, sometime in palisade arrays and in a granular matrix, in salivary glands and brain cells of the vector *Nesoclutha pallida* EVANS 1942 (Hemiptera, Cicadellidae). The virions were associated with the lamellae of the nuclear membrane. AMMAR (1991) illustrated the assembly sites of *Maize mosaic virus* in the vector *Peregrinus maidis* salivary

gland and brain cells. Virus particles (240 x 48 nm) accumulate in intercellular and extracellular spaces, budding through the inner nuclear membrane.

Other -ssRNA viruses are the *Orthomyxoviridae,* in which only vertebrate *Thogotovirus* members have as propagative vectors members of the Ixodidae. Orphan Thogotoviruses have been isolated from Acarina and Diptera.

IIF. Positive single stranded RNA (+ssRNA) viruses. The alpha-like virus supergroup (not yet accepted by the ICTV) includes animal and plant viruses (cf. LOVISOLO & RÖSLER 2001). Within the *Togaviridae,* vertebrate-infecting *Alphavirus* members replicate mainly in and are transmitted horizontally by mosquitoes. *Fort Morgan virus* is transmitted by Cimicidae (Hemiptera). *Sindbis virus* is known to be transovarially transmitted, and has also been isolated from some species of Acarina. *Alphavirus* is usually noncytolytic in mosquito cells, but ultrastructural studies of *Eastern equine encephalitis virus*-infected *Culiseta melanura* COQUILLET 1902 (Culicidae, Diptera) have shown cytopathological lesions in the mosquito midgut and accumulation of numerous virus particles within membranous cytoplasm inclusions in salivary gland acinar cells (WEAVER et al. 1998). Characteristic aggregates of the unassigned chronic bee-paralysis virus (CBPV) have been described in hind-gut of an adult honey bee (BAILEY & WOODS 1977), while crystalline aggregates of virions have been found in the midbrain of infected paralysed bees (BAILEY & MILNE 1969). CBPV virions can also be found in densely packed groups, free or within vesicles, in the cytoplasm of thoracic and abdominal ganglia, gut, mandibular and hypopharyngeal glands (cf. BAILEY & WOOD 1977). Large crystals of cloudy wing virus particles (unassigned ssRNA virus) were found by BAILEY et al. (1980) between sarcolemmae of fibres of infected bee muscles. *Tetraviridae* and *Nodaviridae,* which probably have a common ancestor, belong to the alpha-like supergroup. All the *Tetraviridae,* belonging to the genera *Betatetravirus* and *Omegatetravirus,* were isolated from Lepidoptera species. Virus particles arranged in crystalline arrays within cytoplasm vesicles have been found in the midgut of Lepidoptera affected by members of the *Tetraviridae* (LEE & FURGALA 1965). All species of *Alphanodavirus* (*Nodaviridae*) were isolated from insects, but the type species (*Nodamura virus*) also infects mammals, and Flock *house virus* RNA replicates not only in insects (Table I) and vertebrate cells, but also in yeast and plant cells (BALL 1999). Virus particles arranged in crystalline arrays within cytoplasmic vesicles have been found in fat-body cells of *Apis* spp. (Apidae, Hymenoptera) affected by sacbrood virus (cf. SMITH 1967), an unclassified small RNA virus similar to *Nodoviridae*. The plant-infecting *Marafivirus* members, very distantly related to alpha-like viruses, are propagative in their vectors. *Alphavirus* and *Marafivirus* could be the survivors of viruses that were arthropod-viruses before coming to infect their extant hosts (cf. LOVISOLO & RÖSLER 2001). Micrographs of membrane-bounded and crystalline aggregates of *Oat blue dwarf virus* (*Marafivirus*) in the cytoplasm of cells of the neural lamella surrounding the supraesophageal ganglia of adult *Macrosteles fasciifrons* STÅL 1858 (Cicadellidae, Hemiptera) were shown by BANTTARI & ZEYEN (1976).

In the *Flaviviridae*, most vertebrate *Flavivirus* members are transmitted and multiply in a wide range of mosquitoes (50 % of the virus species) and ticks (28 %). Dengue viruses, according to GUBLER (1999), were most likely mosquito viruses prior to becoming adapted to lower primates and humans. According to PORTERFIELD (1999), it is supposed that Flaviviruses evolved from a common, primitive precursor, possibly a virus infecting arthropods and that the cell-fusing agent virus, isolated from mosquitoes, may be the present day survivor of the primeval Flaviviruses. There is some evidence that the Flaviviruses originated within the past 10 000-20 000 years, and that the evolution has been gradual for tick-borne viruses, and much more rapid for mosquito-borne members, but at present several Flaviviruses have no known vectors. GOULD (1999) assumes an African origin of the *Tick-borne encephalitis virus* complex and a dispersal pattern across Southeast Asia during the past 5000-10 000 years.

The *Picornaviridae* and *Caliciviridae* have no known arthropod propagative vectors, but the *Cardiovirus Encephalomyocarditis virus* has been isolated from mosquitoes and ticks, and an unassigned calicivirus (*Amyelosis chronic stunt virus*) is an insect virus. All members of the "Cricket

paralysis-like viruses", genus with phylogenetic relationships to *Picornaviridae,* have been isolated from invertebrate species, belonging to Orthoptera, Hymenoptera, Lepidoptera, Hemiptera and Diptera. Numerous other +ssRNA viruses, mainly arthropod picorna-like (SCOTTI & CHRISTIAN 1999) have been isolated from insects (Orthoptera, Hymenoptera, Lepidoptera, Hemiptera, Diptera, Isoptera) and Acari (*Panonychus* spp., Tetranychidae and *Varroa jacobsoni* OUDEMANS 1904, Varroidae). The Hemiptera *Myzus persicae* SULZER 1776, *Rhopalosiphum maidis* FITCH 1856*, R. padi* LINNAEUS 1758 and *Bemisia tabaci* GENNADIUS 1899, in addition to be host of picorna-like viruses are well known vectors of plant viruses.

IIG. RNA Reverse-Transcribing (RNA-RT) viruses. *Retroviridae* are not known to multiply in arthropods, but in the *Metaviridae* and *Pseudoviridae,* related *to Retroviridae,* some virus species do, while others infect fungi, plants and nematodes. Some Metaviruses infect *Drosophila* spp., *Bombyx mori* LINNAEUS 1758 (Bombycidae, Lepidoptera) and *Tribolium castaneum* HERBST 1797 (Tenebrionidae, Coleoptera). Some Errantiviruses (*Metaviridae*) infect *Drosophila* spp. and *Trichoplusia ni* HÜBNER 1802 (Lepidoptera, Noctuidae) and *Drosophila melanogaster gypsy virus* produce recognisable ultrastructure in follicle cells of *D. melanogaster* (BUCHETON et al. 1999). Within the *Pseudoviridae,* infecting mainly fungi and plants, two Hemiviruses infect *Drosophila melanogaster* MEIGEN 1830.

REFERENCES

AMMAR E. D. 1991. Mechanisms of plant virus transmission by Homoptera insects. [In:] K. MENDGEN D. R., LESEMANN (Eds) – Electron Microscopy of Plant Pathogens*,* Springer -Verlag, Berlin. Pp: 133-146.

ARNAUD P. H. 1970. Thrips "biting" man. *The Pan-Pacific Entomologist*, **46** (1): 76.

BAILEY S. F. 1936. Thrips attacking man. *The Canadian Entomologist*, **69**(5): 95-98.

BAILEY S. F., BALL B. V., CARPENTER J. M., WOOD R. D. 1980. Small virus-like particles in honey bees associated with chronic paralysis virus and a previously undescribed disease: *Journal of General Virology*, **46:** 149-155.

BAILEY L., MILNE R. G. 1969. The multiplication regions and interaction of acute and chronic bee-paralysis viruses in adult honey bees. *Journal of General Virology*, **4**: 9-14.

BAILEY L., WOODS R. D. 1977. Bee Viruses. [In:] K. MARAMOROSCH (Ed.) – The Atlas of Insect and Plant Viruses*,* Academic Press, New York. Pp: 141-147.

BALL L. A. 1999. Nodaviruses (*Nodaviridae*). [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp.1026-1031.

BANTTARI E. E., ZEYEN R. J. 1976. Multiplication of the oat blue dwarf virus in the aster leafhopper. *Phytopathology*, **66**: 896-900

BELLONCIK S. 1999. Cypoviruses (*Reoviridae*). [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, San Diego, Academic Press, San Diego. Pp. 332-339.

BUCHETON A., PÉLISSON A., TERZIAN C. 1999. Retroviruses of drosophila: The gypsy paradigm. [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition. Academic Press, San Diego. Pp. 1526-1530.

CALISHER C. H. 1999. Chikungunya, O'nyong Nyong and Mayaro viruses (*Togaviridae*). [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp 262-268.

CONTI M., PLUMB R. T. 1977. Barley yellow striate mosaic virus in the salivary glands of its planthopper vector *Laodelphax striatellus* Fallén. *Journal of General Virology*, **34**: 107-114.

FALK B. W., KIM K. S., TSAI J. H. 1988. Electron microscopic and physicochemical analysis of a reo-like virus of the planthopper *Peregrinus maidis. Intervirology*, **29**: 195-206.

FEDERICI B. A. 1999. Ascoviruses (*Ascoviridae*) [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition. Academic Press, San Diego. Pp. 97-103.

FUNK J., DAVIDSON E. W., HUNTER W. 2000. Infection of whitefly (*Bemisia argentifolii*) nymphs and cultured cells with the Chilo iridovirus. XIIIth International Poxvirus and Iridovirus Symposium*,* Montpellier, FR, p. 148.

GOULD E. A. 1999. Tick-borne encephalitis and Wasselsbron viruses [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition. Academic Press, San Diego. Pp. 430-437.

GOULD S. J. 1989. Wonderful Life, Norton & Co, New York.

GRANADOS R. R., FEDERICI B. A. (Eds) 1986. The Biology of Baculoviruses. CRC Press Boca Raton, FL.

GRAY S. M., BANERJEE N. 1999. Mechanisms of arthropod transmission of plant and animal viruses. *Microbiology and Molecular Biology Reviews*, **63**: 128-148.

GUBLER D. J. 1999. Dengue viruses (*Flaviviridae*). [In:] A. GRANOFF, R. G. WEBSTER (Eds – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 375-379.

HAMILTON K. G. A. 1990. Chapter 6. Homoptera. [In:] D. GRIMALDI, J. MAISEY (Eds) – Insects from the Santana formation, Lower Cretaceous, of Brazil. *Bulletin American Museum of Natural History,* **195:** 82-122.

HENNIG W. 1981. Insect Phylogeny. WILEY, New York.

HEROLD F., MUNZ K. 1967. Virus particles in apparently healthy *Peregrinus maidis. Journal of Virology*, **1**: 1028-1036.

JACKSON A. O., FRANCKI R. I. B., ZUIDEMA D. 1987. Biology, structure, and replication of plant rhabdoviruses. [In:] R. R. WAGNER (Ed.) – The Rhabdoviruses, Plenum Press, New York and London. Pp.427-508.

JARZEMBOWSKI A. 2001. The phanerozoic record of insects. *Acta Geologica Leopoldensia*, **24** (52/53): 73-79.

JOLIVET P. 1998. Interrelationship between Insects and Plants. CRC Press, Boca Raton, FL.

KLOMPEN H., GRIMALDI D. 2001. First Mesozoic record of a parasitiform mite: a larval argasid tick in Cretaceous amber (Acari: Ixodida: Argasidae). *Annals of the Entomological Society of America*, **94:** 10-15.

KLENK H-D., SLENCZKA W., FELDMANN H. 1999. Marburg and Ebola viruses (*Filoviridae*). [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 939-945.

KURSTAK E., GARZON S. 1977. Entomopoxviruses (Poxviruses of Invertebrates) [In:] K. MARAMOROSCH (Ed.) – The Atlas of Insect and Plant Viruses*,* Academic Press, New York. Pp: 29-66.

LABANDEIRA C. C. 1999. Insects and other hexapods. [In:] R. SINGER (Ed.) – Encyclopedia of Paleontology*,* volume 1, Fitzry Dearborn, London. Pp: 603-624.

LASTRA J. R., ESPARZA J. 1976. Multiplication of vesicular stomatitis virus in the leafhopper *Peregrinus maidis* (ASHM.), a vector of a plant rhabdovirus. *Journal of General Virology*, **32**: 139-142.

LEE P. E., FURGALA B. 1965. Electron microscopy of sacbrood virus *in situ. Virology*, **25**: 387-392.

LOVISOLO O. 2001. Citrus leprosis virus (CiLV): Properties, diagnosis, agro-ecology and quarantine. *Bulletin OEPP/EPPO Bulletin*, **31**: 79-89.

LOVISOLO O., BOCCARDO G. 1996. Considerazioni su evoluzione, biodiversitŕ, origini e possibili indagini paleontologiche sui virus. *Museologia scientifica*, **13**-Suppl.: 93-112.

LOVISOLO O., RÖSLER O. 2001. Evolution and possible palaeontology of viruses. *Acta Geologica Leopoldensia*, **24** (52/53): 181-205.

LUNDSGAARD T. 1996. Filovirus-like particles detected in extracts from the leafhopper *Psammotettix alienus.* 10th International Congress of Virology, PW64-1, p.266.

MAILLET P.-L., FOLLIOT R. 1967. Sur la présence d'un virus dans le testicule chez un Insecte Homoptére. *Comptes Rendus Académie de Science, Paris, Série D*, **264**: 2828-2831.

MARAMOROSCH K. 1955. Multiplication of plant viruses in insect vectors*. Advances in Virus Research,* **3:** 221-249.

MARAMOROSCH K. (Ed.) 1977. The Atlas of Insect and Plant Viruses". Volume 8 of Ultrastructure in Biological Systems, Academic Press, New York.

MATSUI C., YAMAGUCHI A. 1966. Some aspects of plant viruses *in situ. Advances in Virus Research*, **12**: 127-174.

MERTENS P. P. C. 1999. Orbiviruses and Coltiviruses (*Reoviridae*) – General features. [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 1043–1061.

MILLER L. K. 1996. Insect viruses. [In:] B. N. FIELDS, D. M. KNIPE, P. M. HOWLEY (Eds in Chief) – Fundamental Virology, Third Edition, Philadelphia, LIPPINCOTT-RAVEN Publ. Pp. 401-424.

MOYER R. W. 1999. Entomopoxviruses (*Poxviridae*). [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 474–481.

MURPHY F. A. 1999. Epidemiology of viral diseases. [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 482-487.

NAULT L. R., AMMAR E. D. 1989. Leafhopper and planthopper transmission of plant viruses. *Annual Review of Entomology*, **34**: 5O3-529.

NODA H., NAKASHIMA N. 1995. Non-pathogenic reoviruses of leafhoppers and planthoppers. *Seminars in Virology*, **6**: 109-116.

NUTTAL P. A., JONES L. D., DAVIES C. R. 1991. The role of arthropod vectors in arbovirus evolution. [In:] K. F. HARRIS (Ed.) *Advances in Disease Vector Research*, **8:** 15-45.

OFORI F. A., FRANCKI R. I. B. 1985. Transmission of leafhopper A virus, vertically through eggs and horizontally through maize in which it does not multiply. *Virology*, **144**: 152-157.

PAYNE C. C., HARRAP K. A. 1977. Cytoplasmic polyhedrosis virus [In:] K. MARAMOROSCH (Ed.) – The Atlas of Insect and Plant Viruses, New York, Academic Press, Pp: 105-129.

PETERS D. 1991. Divergent evolution of Rhabdoviridae and Bunyaviridae in plants and animals. *Seminars in Virology*, **2**: 27-37.

POINAR G. O. Jr. 1993. Insects in amber. *Annual Review of Entomology*, **38**: 145-159.

POINAR G. O. Jr. 1996. Bacteria. [In:] McGRAW-HILL Yearbook of Science & Technology, McGRAW-HILL, Inc., New York. Pp.27-29.

POINAR G. O. Jr., HESS R. 1982. Ultrastructure of 40-million-year-old insect tissue. *Science*, **215**: 1241-1242.

POINAR G. O. Jr., HESS R. 1985. Preservative qualities of recent and fossil resins: electron micrograph studies on tissue preserved in Baltic amber. *Journal of Baltic Studies*, **16**: 222-230.

POINAR G. Jr., POINAR R. 1998. Parasites and Pathogens of Mites. *Annual Review of Entomology*, **43**: 449-469.

POINAR G. Jr., POINAR R. 1999. The Amber Forest, Princeton University Press, Princeton, New Jersey. Pp.137-167.

POINAR G. O. Jr., WAGGONER B. M., BAUER U. C. 1993. Terrestrial soft-bodied protists and other microorganisms in triassic amber. *Science*, **259**: 222-224.

PORTERFIELD J. S. 1999. Encephalitis viruses and related viruses causing hemorrhagic disease. [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 424-430.

ROGGERO P., LISA V., LUISONI E. 1995. I fitovirus del genere tospovirus (Bunyaviridae)**.** *La Difesa delle Piante,* **18**(3): 163-187.

ROHRMANN G. F. 1999. Baculoviruses (*Baculoviridae*): Nucleopolyhedrovirus. [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp.146-152.

ROSS A. J., JARZEMBOWSKI A. J. 1993. Arthropoda (Hexapoda; Insecta). [In:] M. J. BENTON – The Fossil Record 2, CHAPMAN & HALL, London. Pp. 363-426.

SALAS M. L. 1999. African swine fever virus (*Asfarviridae*) [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 30-38.

SCOTTI P. D., CHRISTIAN P. D. 1999. Picornaviruses – insect (*Picornaviridae*). [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 1267-1275.

SHIKATA E., MARAMOROSCH K. 1965. Plant tumour virus in arthropod host: Microcrystal formation. *Nature*, **208**: 507-508.

SHIKATA E., MARAMOROSCH K. 1967. Electron microscopy of wound tumor virus assembly sites in insect vectors and plants. *Virology*, **32**: 363-377.

SHOPE R. E., TESH R. B. 1987. The ecology of rhabdoviruses that infect vertebrates. [In:] R. R. WAGNER (Ed.) – The Rhabdoviruses, Plenum Press, New York and London. Pp.509-553.

SMITH K. M. 1967. Insect Virology, Academic Press, New York-London.

STOLTZ D. 1999. Polydnaviruses (*Polydnaviridae*), [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, San Diego, Academic Press, p.1349-1351.

SUMMERS M. D. 1977. Baculoviruses (Baculoviridae) [In:] K. MARAMOROSCH (Ed.) – The Atlas of Insect and Plant Viruses, Academic Press, New York. Pp: 3-27.

VAN DER GEEST L. P. S., ELLIOT S. L., BREEUWER J. A. J., BEERLING E. A. M. 2000. Diseases of mites. *Experimental and Applied Acarology*, **24**: 497-560.

VAN REGENMORTEL M. H. V., FAUQUET C. M., BISHOP D. H. L., CARSTENS E. B., ESTES M. K., LEMON S. M., MANILOFF J., MAYO M. A., McGEOCH D. J., PRINGLE C. R., WICKNER R. B. 2000. Virus Taxonomy. Seventh Report of the International Committee on Taxonomy of Viruses, Academic Press, San Diego.

VIDANO C. 1970. Phases of maize rough dwarf virus multiplication in the vector *Laodelphax striatellus* (FALLÉN). *Virology*, **41:** 218-232.

WEAVER S. C., SCOTT T. W., LORENZ L. H., LERDTHUSNEE K., ROMOSER W. S. 1988. Togavirus-associated pathologic changes in the midgut of a natural mosquito vector. *Journal of Virology*, **62**: 2083-2090.

WEBBY R., KALMAKOFF J. 1999. *Iridoviridae* – Invertebrate. [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp. 862-869.

WILLIAMS T. 1996. The Iridoviruses. *Advances in Virus Research*, **46**: 345-412.

WINSTANLEY D., O'REILLY D. 1999. Baculoviruses (*Baculoviridae*): Granuloviruses. [In:] A. GRANOFF, R. G. WEBSTER (Eds) – Encyclopedia of Virology, Second edition, Academic Press, San Diego. Pp.140-146.

WOOD H. A. 1973. Viruses with double-stranded RNA genomes. *Journal of general Virology*, **20**: 61-85.