PLANT – ARTHROPOD INTERACTIONS IN THE EARLY ANGIOSPERM HISTORY

Evidence from the Cretaceous of Israel

Editors

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Evidence from the Cretaceous of Israel

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Contents

PART I

Traumas on Fossil Leaves from the Cretaceous of Israel

PART II

Fossil Insects in the Cretaceous Mangrove Facies of Southern Negev, Israel

PART I

Traumas on Fossil Leaves from the Cretaceous of Israel

by

Valentin Krassilov

in cooperation with

Natalia Silantieva
&
Zeev Lewy

TRAUMAS ON FOSSIL LEAVES FROM THE CRETACEOUS OF ISRAEL

by

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1. Introduction

Plant – arthropod interactions are generally recognized as a major force under the evolutionary developments in both plants and arthropods, as well as of the terrestrial ecosystems as a whole. Yet surprisingly little was made for exploring the fossil record for documentation and understanding of these fruitful interactions over times. To enlist fossil plants and arthropods coming from one and the same locality or to depict insect traces on fossil leaves is the first step requiring an analytical procedure for further advancements.

Since in Israel even the first step had been but timidly made, it was our task, after describing the fossil flora from the richest Cretaceous locality (Krassilov *et al.*, 2005), to provide an inventory of insect body fossils and of the mite and insect traces on fossil plants. Yet we attempted a step further into the realm of structural and functional relationships linking morphology to ecosystem evolution.

The Cretaceous of Negev provides the richest regional material of arthropod traces on fossil leaves (phyllostigmas) at the time of a major restructuring stage in the history of terrestrial ecosystems brought about by the advent and rise of angiosperms. In the middle of Cretaceous period already, these newcomers have surpassed all the other groups of higher plants in the diversity of their foliar and floral structures, as well as in the plasticity of their life forms. These developments were matched, and perhaps enhanced, by the burst of adaptive radiation in the leaf parasites providing ample evidence of plant – arthropod co-evolution. The material is favorably preserved for developing morphological classification of fossil traces, which is necessary for further accumulation and processing of the data.

The insect body fossil fauna of Negev is not so rich, but of general interest on account of its paleogeographic situation and paleoecological settings, in particular, the early angiosperm mangrove habitats. Some insect taxa appear surprisingly modern in comparison with their contemporaries north of the Tethys having their closest relatives in the younger Cretaceous and Tertiary assemblage elsewhere. Fortunately, stratigraphic control is rigorous enough for all the insect localities in Israel, and the modern-looking faunistic elements are just evidence of high rate morphological evolution in the insect groups directly or indirectly linked to the explosive angiosperm radiation.

Traces of arthropod feeding and habitation on fossil leaves may add to the diversity of contemporaneous fossil faunas, because the trace makers (both miners and gall inducers) are rarely if at all represented in the body fossil assemblages. Yet classification of traces primarily reflects the diversity of habits, being indirectly, and sometimes ambiguously, related to taxonomic diversity. In the trace studies, parasitic habits are inferred from the structures these habits induced or produced. It must be said from the very beginning that our comparison with phyllostigmas of modern arthropods do not imply taxonomic affinities, but indicate similarity of behavioral traits that has an evolutionary history of their own.

Moreover, since parasitic behavior is regulated by the host responses on the one hand, and by the secondary parasites (parasitoids) and predators on the other, and insofar as we can infer the effectiveness of regulation from such structural features as selectivity of predation marks, or the marks of temporary mining, as well as form the co-occurrence of various phyllostigmas and their on leaf diversity, the paleoecological dream of observing extinct ecosystems in action nearly comes true.

2. Acknowledgements

This work is a contribution to the German Israeli Science Foundation project no. 1–888–159.8/2005. We acknowledge the support by the University of Haifa where the main part of the research was conducted. The field works were on several occasions assisted by Israeli Geological Survey. Dr Sophia Barinova has participated both in the field studies and in preparing graphs for the mine and gall distribution analysis. Our thanks are due to Professor Eviatar Nevo for his encouragement and advice, to Alexander Rasnitsyn, Conrad Labandeira and Carlos Herrera for their helpful comments on publications related to this study, to Meinolf Hellmund and Winfried Hellmund, who were involved in the study of Odonata egg sets from the Albian of Makhtesh Ramon, as well as to all the colleagues from the Institute of Evolution, University of Haifa and Paleontological Institute, Russian Academy of Sciences for their interest in our research.

3. Material and methods

Materials of this study came mainly from the lower – middle Albian Upper Hatira Formation of erosional depressions ('craters") Makhtesh Ramon and Makhtesh Hatira in the central – northern Negev and from the mid-Turonian Ora Formation of Arava Rift Valley (Fig. 1). The bulk of the material has been collected in 2001–2006 by Valentin Krassilov assisted by Natalia Silantieva and Sofia Barinova, partly in collaboration with Zeev Lewy and Shelomo Ashkenazi from Geological Survey of Israel, Jerusalem. Alexander Rasnitsyn took part in the field work in Arava in 2004. Additional materials were loaned from Yaakov Lorch's collections deposited in the Hebrew University, Jerusalem.

Fossil plants are collected from five localities at two fossiliferous horizons in the lower and upper parts of the Upper Hatira Formation, altogether about 500 fossil plant specimens preserved as the bedding plane impressions coated with pinkish to brick red ferruginous films showing microscopic details of leaf surface topography, including the traumatic structures, or *phyllostigmas* (on preservation of phyllostigmas see Chapter 5). The flora consists of ferns, ginkgophytes, conifers and angiosperms forming several plant communities (Silantieva & Krassilov, 2006). A number of gymnosperm leaves are stigmatized with marginal and apical cut-outs, and a few narrow-leaved angiosperms (or possibly pro-angiosperms) of *Acaciaephyllum* type bear sets of inserted eggs.

No arthropod traces were found in the Cenomanian of Israel, but a few occurred in the material collected by Flavio Bacchia form the Nammoura locality in the Mont-Liban district of Lebanon (Krassilov & Bacchia, 2000; see also Dalla Vecchia *et al*., 2002). The flora is essentially angiospermous, with few ferns and gymnosperms. A leaf of gymnospermous *Pseudotorrelia* is mined and occasional angiosperm leaves show marginal cut-outs.

The mid-Turonian plants and insects of Arava Valley, southern Negev are collected form two localities at the mouth of Gerofit Wadi about 60 km north of Eilat and in the Qetura Wadi 2.2 km further north, 4 km before the mouth. Both represent one and the same plant-bearing horizon in the Upper Shale Member of Ora Formation (Krassilov *et al*., 2005). The flora comprises about 50 species of angiosperms representing coastal as well as inland plant communities. The locality is remarkable in abundance of oviposition, surface feeding, mining, and gall construction (Krassilov, 2007 and Chapter 12). The insect body fossils are relatively rare, representing 16 species (Dobruskina *et al*., 1997 and this book Part II).

The lithofacies and preservation of Turonian plant remains from Arava are similar to those of the Albian material from central Negev. The leaf impressions on gray siltstones in the lower part of fossiliferous sequence are coated with clay films with dispersed organic matter, those from the upper variegate claystones are ferruginous incrustations and subcrustations (mineralized beneath the cuticle that is not preserved but imprinted upon the mineral film). The phyllostigmas were studied and photographed under stereomicroscope

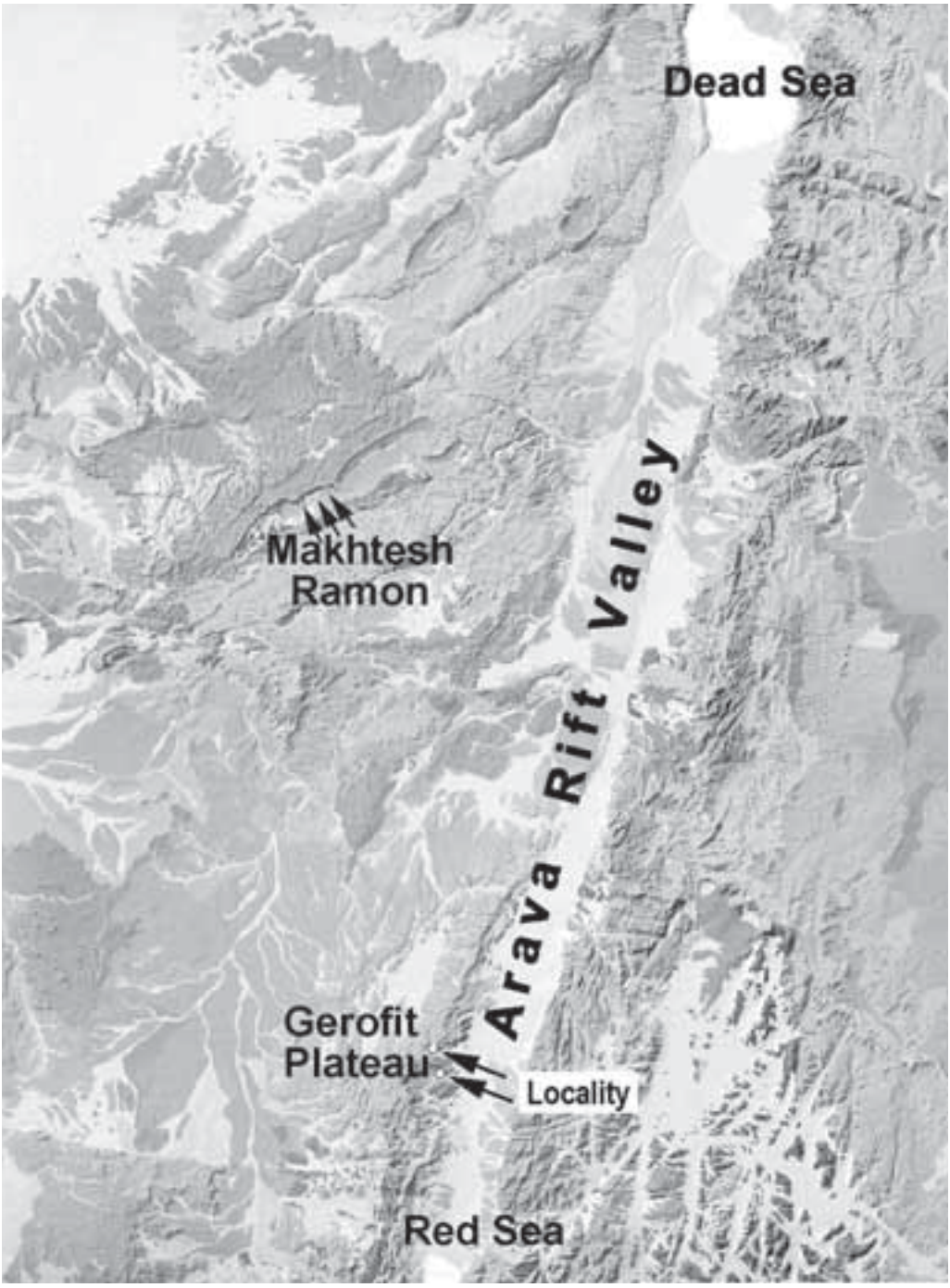

Fig.1. Map of Negev and Arava showing plant and insect localities of Makhtesh Ramon and Gerofit (arrows).

LEICA MZ6 and digital camera LEICA DFC320. Transfer preparations, successful in a few cases of structurally preserved insect eggs and mite galls, were studied in transmitted light and under SEM.

The collection is deposited in the Institute of Evolution, University of Haifa, Israel, depository numbers IMR and IG1.

4. Stratigraphic overview of Cretaceous fossil plant/insect localities in Israel and adjacent countries

The Arabo-Nubian landmass of the northern Gondwana realm was periodically inundated by the Tethys. However, for a considerable part of geological history, it was an area of continental deposition. The great thicknesses of the "Nubian Sandstones" consist of alternating non-marine and marginal marine clastic sediments of the time span from the mid-Paleozoic to Eocene. The Cretaceous deposition was prevailingly non-marine prior to the late Albian transgression and a carbonate platform build-up afterwards, with episodic influxes of terrestrial material from the south.

Jurassic – Neocomian

In southern Israel, the non-marine and paralic deposits containing the plant/insect localities are known from the erosional windows (locally known as craters or circuses) of central Negev, as well as from the Dead Sea and Arava Rift valleys. In the larger circuses, Makhtesh Ramon and Makhtesh Hatira, the Cretaceous is unconformable on the mid-Jurassic Mahmal Formation with the mid-Jurassic flora of ferns, cycadophytes and conifers sharing a number of species with contemporaneous European localities (Lorch, 1959, 1967, 1968; Chaloner & Lorch, 1960). Similar plant assemblages are described from Sinai (Van Konijnenburg-van Cittert & Bandel, 2001) and South Tunisia (Barale *et al*., 2000). The Late Jurassic plants from Kidod Formation, Early Oxfordian of Mt. Hermon and from Kidod 2 borehole west of the Dead Sea are the cheirolepidiaceous brachyphylls (Conway, 1996; Raab *et al*., 1986).

A Hauterivian – Barremian locality in the Tayasir volcanite of Samaria (Mimran, 1971) contains few ferns and gymnosperms, as well as insects *Cretosperchus medievalis* Ponomarenko (Coleoptera: Hydrophilidae), *Gondwablatta abrahami* Vršanský (Blattellidae), and a poorly preserved dragonfly nymph (Estes *et al*., 1978; Dobruskina *et al*., 1997; Vršanský, 2004 b).

The Neocomian of Lebanon contains diverse insect remains in amber (Azar, 2000). Plant remains, probably of the amber producers, are presently under study. The Late Jurassic – Early Cretaceous flora of Libya (El Chair *et al*., 1995) is also non-angiospermous, evidencing a gradual transition from the Jurassic to Neocomian assemblages. The Neocomian locality Quehmez/Beskintaa near Beirut contains coniferous wood and leafy shoot remains (Barale *et al*., 2003).

Aptian

In the Makhtesh Ramon and Makhtesh Hatira of central Negev, the Cretaceous Lower Hatira sequence (Fig. 2) begins with conglomerates and fluvial sandstones followed by the Zuweira Marine Tongue sandstone/siltstone/dolomite alternation with bivalves (Mytilidae), naticid and cerethid gastropods, *Lingula*, crustaceans and plant remains. This marine ingres-

sion is traced in the outcrops and boreholes over the southern and central Negev and is correlated with the marginal marine horizons of the Abu Ballas Formation in southern Egypt and with gastropod shales ("Coches à Gasteropodes") of Lebanon. It ended with basaltic flows, pyroclastics and their covering lateritic red beds.

On magnetostratigraphic evidence and on isotopic dating of the basalts, the Lower Hatira Formation is assigned to the Barremian (?) – Early Aptian (Gwitzman *et al*. 1996) and more recently to the Aptian – early Albian (Segev *et al*., 2005). First angiospermoid pollen appeared at this level (Schrank, 1992; Brenner, 1996), but plant macrofossils are mostly ferns *Weichselia* in the marine deposits and gymnosperms in the basaltic member (Lorch, 1963; Nevo, 1968; Krassilov *et al*., 2004). The fruit-like *Afrasita lejalnicoliae* Krassilov et Lewy, first described from the Abu Ballas Formation of Dakhla Basin, southern Egypt, as the earliest angiosperm macrofossils (Lejal-Nicol, 1981) was re-interpreted as proangiospermous of gnetophytic affinities, representing the same evolutionary grade as those found in the Lower Cretaceous of Central Asia (Krassilov *et al*., 2004).

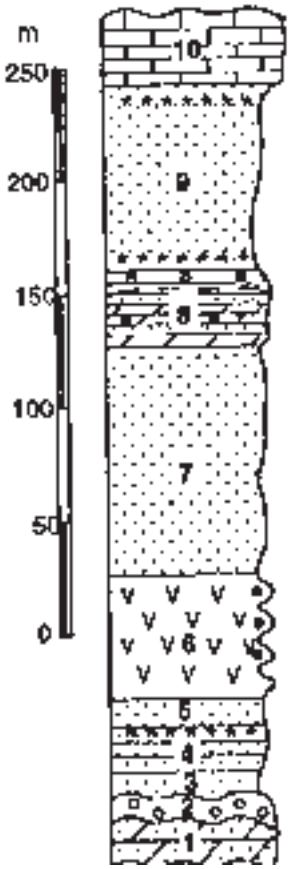

Fig. 2. Cretaceous section of Makhtesh Ramon (after Gwirzman *et al*., 1996): 2–6, Lower Hatira Formation, 7–9, Upper Hatira Formation; plant-bearing horizons are marked by asterisks.

The Sabaya Formation of Dakhla Basin, deposited after retreat of the Aptian sea, contains a diverse assemblage of conifers, *Araucaria* among them, but still lacking angiosperm macrofossils (Barthel & Böttcher, 1978; Klitzsch & Lejal-Nicol, 1984). The Asfer Group of southern Tunisia, although of a wider stratigraphic range (Tithonian – Aptian), is of a similar aspect (Barale & Ouaja 2002).

Albian

In Makhtesh Hatira, the Lower Aptian marine intercalation is overlain by a sandy sequence comprising terrestrial plant remains in the lower part and shallow water marine mollusks in the upper part. It is followed by the marl and argillaceous limestone horizon rich in ferruginous inclusions, in which the Albian ammonite genus *Knemiceras* Böhm first appears. The sandstone, siltstone and clayey sequence above contains two fossil plant-bearing horizons and grades upward into a carbonate unit with *Knemiceras dubertreti* Basse of the Late Albian age. Variegated sandstones separate this marine intercalation from the limestones and dolomites of the Upper Albian – Upper Cenomanian Hazera Formation with abundant marine invertebrates. Fossil plants were reported by Lorch (in Nevo, 1968) and Glikson (MSc Thesis, unpublished). Recently a more extensive collecting by Silantieva & Krassilov (2006) revealed a diverse flora of ferns, ginkgophytes, conifers and angiosperms, taxonomically a mixture of Mesozoic survivors, such as the ferns *Cladophlebis*, *Weichselia* and *Piazopteris*, ginkgophytes *Sphenobaiera* and *Ginkgodium*, bennettites *Otozamites*, and conifers *Brachyphyllum* and *Podozamites*, with newcomers represented by the ferns *Onoclea*, modern-type Araucariaceae, and angiosperms of several morphological groups including both narrow leaved and broadleaved morphotypes, as well as aquatic forms with floating leaves.

Barale & Ouaja (2001) described from the Upper Aptian – Lower Albian of South Tunisia two localities with "mixed" floras of the Upper Hatira aspect, consisting of *Weichselia*, *Podozamites* and brachyphyllous conifers, as well as of the narrow-leaved angiosperms and aquatic forms (Barale & Ouaja, 2001).

No insect body fossils are found in the Hatira Formation, but a few gymnosperm leaves show apical cut-outs, while the well-preserved egg sets of Odonata occur on the angiosperm (or angiospermoid) *Acaciaephyllum*-type leaves.

Cenomanian

Plant macrofossils are rare in the marly interbeds of the upper Albian – Cenomanian platform carbonates of Judean Mountains and are almost exclusively represented by *Sapindopsis*, the compound angiosperm leaf morphotype with narrow leaflets. This genus is also important in the Batn al Ghul locality of southwestern Jordan, collected by Zeev Lewy and Inna Dobruskina (unpublished), and from Nammoura locality, Mont-Liban district of Lebanon (Dilcher & Basson, 1990; Krassilov & Bacchia, 2000). The flora is essentially angiospermous, with few ferns and gymnosperms. Occasional angiosperm leaves show insect cut-outs and a gymnospermous leaf *Pseudotorrelia* is mined.

A well-dated Cenomanian flora is known from the Bahariya Formation of southwestern Egypt (Lejal-Nicol & Dominik, 1990). It consists of *Weichselia* and angiosperms, assigned to

the extant families Magnoliaceae, Lauraceae, Cornaceae, Vitaceae, and Proteaceae. An angiospermous flora of Jordan, with a single gymnospermous species *Nilssoniophyllum benderi* Mädler (Bender & Mädler, 1969), apparently represents the same evolutionary level.

Turonian

The Turonian plants and insect localities Qetura and Gerofit (GIS coordinates 29° 59' 32" N, 35° 04' 32" E) of Arava Valley, southern Negev are confined in the Upper Shale Member of the Ora Formation. Their age assignments are based on the mid-Turonian ammonites from the underlying Vroman Bank carbonates (T-5–6; Freund & Raab, 1969) and the latest Middle Turonian ammonites (*Collignoniceras woollgari* Zone) found at the base of the overlying marine Gerofit Formation (Bartov *et al*., 1972; Lewy, 1989; Krassilov *et al*., 2005). The plant-bearing sequence starts with the cross-bedded sandstones followed by gray siltstones/claystones and then by red (crimson) claystones. It is overlain by an alternation of dolomites and variegate shales with an oyster bed near the base and with gypsum and anhydrite above (Fig. 3). The uppermost Ora deposits are black shales and carbonates with a brackish-water invertebrate assemblage.

Plant and insect remains from Gerofit were collected and preliminary studied by Lorch (1965) and Dobruskina (1996, 1997). Six insect species were reported by Dobruskina et al. (1997). The largest collection form Gerofit and Qetura was build-up during several field trips in 2004–2006 by Krassilov in collaboration with Zeev Lewy, Shelomo Ashkenazi, Sophia Barinova, Natalia Silantieva and Alexander Rasnitsyn (Krassilov *et al*., 2005; Krassilov & Silantieva, 2005). The flora is presently the most representative not only for Israel but for the northern Gondwana realm as a whole. It comprises about 50 species of angiosperms belonging to the orders of modern dicotyledons Ranunculales, Nymphaeales, Nelumbonales, Trochodendrales, Hamamelidales, Juglandales, Rosales, Myrtales, and Sapindales, monocotyledons Najadales, Pontederiales, Arales, Cyclanthales, Arecales, and Typhales, and an extinct *Gerofitia* group, probably proangiospermous. The insect body fossils are assigned to 16 species of nine extant and one extinct family (Dobruskina *et al*., 1997; this book Pt. II). The phyllostigmas constitute perhaps the most diverse regional trace assemblage (preliminary reported in Krassilov, 2007 and *in press*; Krassilov & Shuklina, *in press*).

The comparable angiosperm floras, although perhaps somewhat younger, are described from Egypt and Sudan (Vaudois-Miéja & Lejal-Nicol, 1987, 1988; Schrank & Rüffle, 2003).

It follows from the above overview that the Aptian – Turonian succession of macrofossil plant assemblages in Israel is potentially the most complete in the northern Africa – Middle East region and with additions from adjacent countries documents the most significant stage of angiosperm evolution starting with occasional entries in the fern/gymnosperm dominated communities and culminating in the unraveled angiosperm dominance over a wide range of habitats. By that time, not only new high rank taxa, but also new plant communities had appeared, betraying a close correlation between morphological diversity and ecosystem evolution. Arthropods, constituting the next trophic level of terrestrial ecosystems, are so far rather patchily recorded, but their body and trace fossils combined reveal chronological parallelism of diversification trends with those of their contemporaneous vegetation.

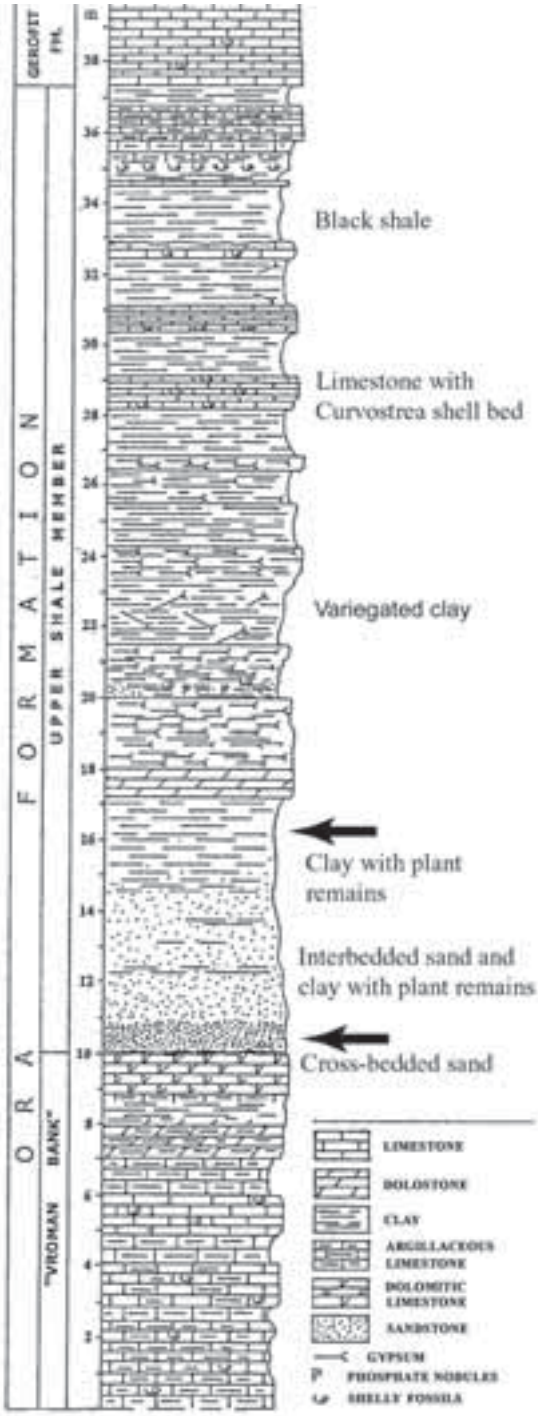

Fig. 3. Section of the Ora Formation at Gerofit, arrows mark the plant-bearing interval.

5. Plant communities

Terrestrial arthropods are components of biotic communities conventionally defined on the basis of their vegetation components. Therefore, a brief discussion of plant communities may serve as a framework for paleoecology of fossil arthropods and their traces. Classification of plant communities is not the topic of this work. It would suffice our purposes to define fossil plant communities as distinctive assemblages of plant remains recognized on account of their taxonomic composition and the numerically dominant forms (Krassilov, 1975, 2004).

Reconstruction of plants communities is based primarily on sedimentological and taphonomic evidence, i.e. the lithofacies of plant deposition, quantitative representation of plant species, and preservational features related to transportation or lack of such. This information allows distinguishing between autochtonous (hypoautochtonous) elements representing lowland vegetation adjacent to deposition site, and allochtonous elements transported from distant sources. A sequence of communities from lowland (coastal, wetland) to upland (inland, dryland) sites constitutes a catenic system of basinal vegetation.

The Neocomian and Aptian floras are insufficiently known for reconstruction of plant communities. It can be noted however that in the Hatira Formation of Makhtesh Ramon and Makhtesh Hatira, the basal cross-bedded sandstones with ripple marks, representing tidal sand flat deposits, contain almost exclusively the ferruginous remains of root system, stems, sterile and fertile leaves, and spore-bearing structures of *Weichselia*. These remains were found in a range of lithofacies grading from the sandy/silty channel deposits to ferruginous marsh soil. The taphonomy suggests deposition at or near the growth site. The sclerophytic habit of *Weichselia* might have been related to a water-logged habitat, probably under the influence of marine tides. Through the early Aptian transgressive phase, *Weichselia*t was dominant, or locally the only, species of a coastal (intertidal ?) arboreal fern community, sometimes interpreted as mangrove, but perhaps ecologically closer to the back-mangrove supratidal growths of extant "mangrove fern" *Acrostichum aureum* (Tomlinson, 1994).

The fruit-like gnetophyte cones *Afrasita lejalnicoliae* Krassilov et Lewy are locally abundant in the littoral gastropod shales of marine Zuweira tongue, probably representing an alternative type of coastal plant communities. That such proangiospermous communities were source of angiospermoid pollen is a possibility, as yet unexplored.

The overlying clayey horizon of the tidal mud flat, covered with Ramon basalts, contains abundant remains of scale-leaved cheirolepidiaceous gymnosperms. These also represent a coastal plant community, supposedly the cheirolepidiaceous marshes (Watson, 1988) growing at the fringe of the tidal flat, monospecific, but contaminated with allochtonous material from inland sources (fragmentary cycadophytes and araucariaceous conifers).

The extrusions of alkalic Ramon basalts mark a general uplift phase in the central Negev causing a radical change of vegetation cover. The interbasaltic playa lake deposits with

amphibian remains (Nevo, 1968) are conspicuous by the absence of *Weichselia* that retreated with the early Aptian sea. Fossil plant assemblages of this level represent a dryland coniferous – cycadophyte vegetation with occasional and fragmentary angiospermoid remains.

A brief ingression of the early Albian *Knemiceras* sea brought back *Weichselia* that is numerically dominant in all the Albian localities indicating a rapid recovery of pre-basaltic wetland communities. Yet *Weichselia* beds now contain numerous remains of angiosperms that penetrated coastal vegetation in the course of recovery. Prominent among them is the narrow-leaved *Acaciaephyllum* morphotype. Judging by the abundance and relatively complete preservation, this leaf material came from a wetland source intruding *Weichselia* wetlands or forming an adjacent zone of angiosperm marshes. The egg sets of Odonata confirm their proximity to the water sources (Krassilov *et al*., 2007). Few remains of peltate nymphaeoid leaves may belong to aquatic angiosperm community of the same coastal complex.

A quite different, mesomorphic, group of broadleaves is represented by platanophyllous *Credneria*, as well as by the variably dissected *Cissites* – *Vitiphyllum* morphotypes. Their constant associates are the araucariaceous conifers represented by leaves and about as numerous winged cone scales, a situation suggesting selective preservation of transportable organs from a distant source. Such allochtonous remains are numerically subordinate and fragmentary, but found over a wide range of depositional environments.

As a whole, the Albian succession of coastal to dry-land communities (paleocatena) included the following elements:

1. *Weichselia* tidal flat pre-mangrove vegetation with a possible participation of narrow-leaved angiosperms;
2. Marsh-like community of narrow-leaved angiosperms;
3. Aquatic macrophytes with peltate floating leaves;
4. Dry-land araucarian forests with a broad-leaved angiosperm understorey.

Narrow-leaved angiosperms prevailed in the Cenomanian of Judean mountains, Bath al Ghul in Jordan and Nammoura in Lebanon (Krassilov & Bacchia, 2000) attesting to the rise of angiosperm marshlands at the expense of *Weichselia* pre-mangroves, although the latter still survived in the Cenomanian of Egypt (Smith *et al*., 2001; Schweitzer *et al*, 2003) and elsewhere. The allochtonous remains of upland vegetation represent a diversity of small-leaved angiosperms in association with pinaceous conifers.

The Turonian flora is much more diverse and modern looking, the rise of morphological diversity being accompanied by a rapid ecological differentiation. The shoreline to inland sequence of mangroves, marshes, back-mangrove freshwater macrophytes, riparian trees or shrubs, and dryland broadleaved forests has been reconstructed on the basis of quantitative representation, preservation and sedimentary facies of the fossil plant remains (Krassilov *et al*., 2005; Silantieva & Krassilov, 2006).

The transported remains of broadleaved arboreal vegetation and aquatic macrophytes are abundantly represented in the lower part of Gerofit and Qetura sections indicating a massive influx of terrestrial plant material. The inland broadleaved zone is represented by genera that are taxonomically close to the extant broadleaves growing together in central China, but

some are represented by the wind-borne samaras alone. The wetland to dryland transition must have been gradual, with mesic broadleaves intruding the platanoid riparian zone. The aquatic community was exceptionally rich and productive, developing a voluminous biomass of floating leaf mats.

In the upper red clay horizon, the extensive root mats, with horizontal cable roots, root knees and pneumatophores, betray a tidal flat vegetation of mangrove aspect confirmed by the leaf morphological and reproductive features, such as the cryptoviviparous seedlings (Krassilov *et al*., 2005). This was perhaps the earliest mangrove community on the Tethys shores (Figs. 4, 5).

The Turonian paleocatena (Fig. 6) based on the parallel successions at Gerofit and Qetura localities, might have included:

1. *Dewalquea – Eudebeya* mangroves;
2. Back-mangrove palm zone;
3. *Gerofitia* marshes;

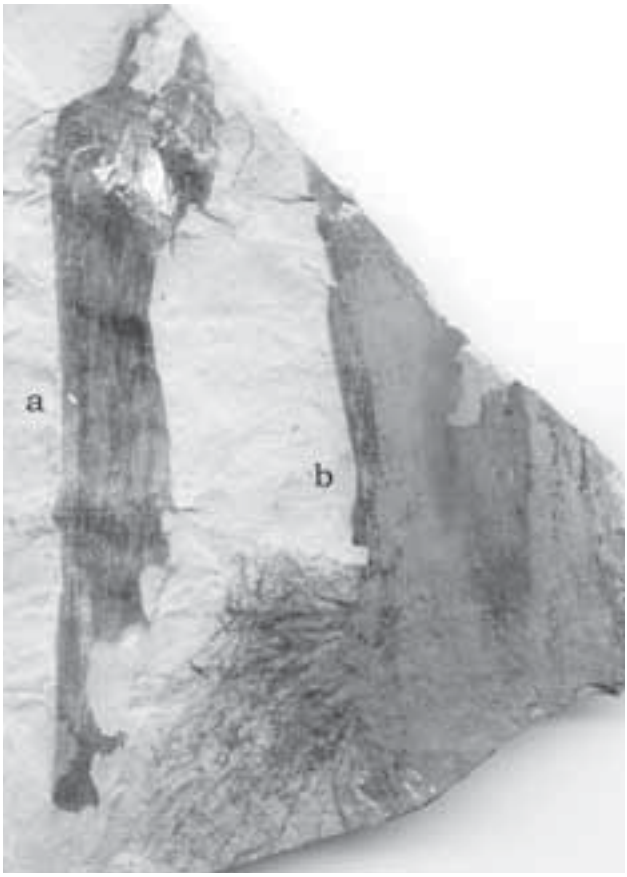

Fig. 4. Roots of the Turonian root-bed at Gerofit (a) knee-root, (b) columnar root with a tuft of branches with capillary rootlets (Krassilov et al., 2005).

4. Back-marsh *Nelumbites – Brasipelta* aquatic vegetation;
5. Back-marsh riparian *Platanervia – Platydebeya* forest;
6. Broadleaved *Eocercidiphyllites – Dicarperonia* dryland forest.

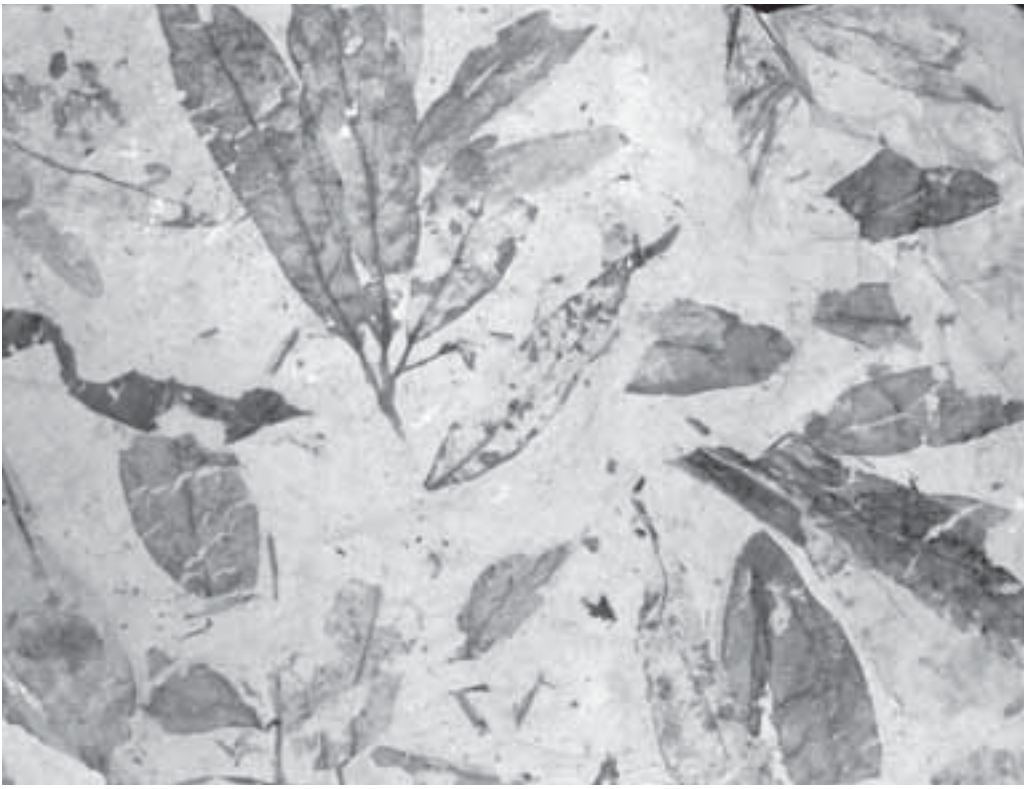

Fig. 5. *Dewalquea gerofitica* on a bedding plane, Gerofit (Krassilov, 2005).

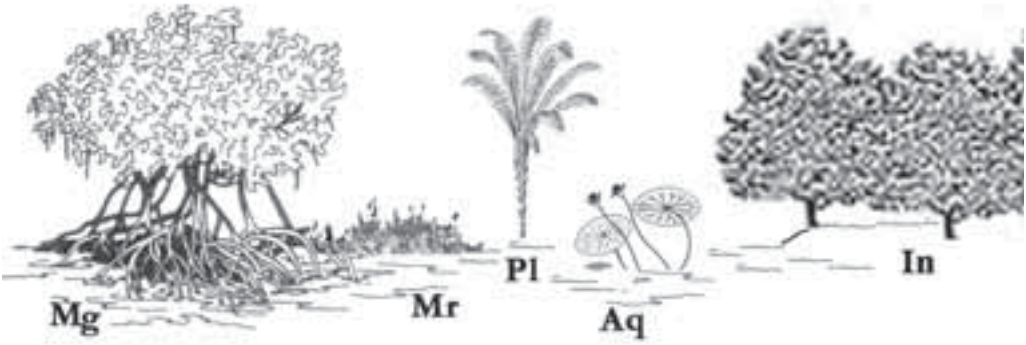

Fig. 6. Succession of Turonian plant communities at Gerofit – Qetura: Mg, *Dewalquea* mangroves, Mr, *Gerofitia* marshes, Pl, *Queturea* palm zone, Aq, *Nelumbites* wetlands, In, *Eocercidiphyllites* inland forest.

In comparison with the Albian – Cenomanian stage, the Turonian paleocatena is further differentiated, with a few more zonal members intercalating between the wetland and dryland communities. Major changes occurred in the coastal zone, where the fern pre-mangroves with *Weichselia* and narrow-leaved marshy angiosperms were replaced by true mangroves, and a new type of coastal marshes appeared. The Turonian freshwater community gives evidence of a rapid advancement since the Albian both in terms of morphological evolution and diversity of aquatic/semiaquatic dicots and monocots. Major changes in the upland vegetation consisted in the replacement of the dominant coniferous (araucariaceous) element by new groups of broadleaved angiosperms assignable to Cercidiphyllaceae and Celastraceae, which might have derived from the understorey broadleaves of the Albian mixed forests.

According to the climax cut-off model (Krassilov, 2003 and elsewhere), long-term stressful conditions impose abbreviation of seral sequences eventually undermining their climax stages. In distinction, the pioneer replacement model requires a brief, but devastating impact upon the stress-tolerant early seral stages having far-reached consequences for the ecosystem as a whole. Both models seem applicable to the entries of angiosperms in the Mesozoic plant communities, first as the pioneer plants of coastal wetlands and later as ecological dominants of the regional climax vegetation.

During the transitional period, leaf parasites have switched from the declining gymnosperm hosts to the rapidly expanding angiosperms, benefiting from and in turn contributing to the build up of their host diversity by the burst of new habits.

6. Taphonomy of phyllostigmas

In principle, all kinds of phyllostigmas, from unicellular epidermal emergences to sophisticated gall constructions, have fair chances to be preserved and recognized on fossils leaves, recording traumatic structures that can be translated into parasitic life habits. However, when interpreting the fossil record of parasitarian communities, it has to be taken into account, that preservation chances are unequal for different kinds of phyllostigmas, their diversity and numerical ratios being, to various degrees, but inevitably, biased by taphonomic processes.

Preservation forms

Preservation of foliar egg scars, mine tracks and galls depends, in the first place, on the taphonomy of their bearing leaves that are brought to the deposition site, buried in the sediment and transformed by mechanical pressure, dehydration, decay and mineralization into the durable impressions or inclusions that retain recognizable features of the leaf morphology. In the permineralized leaves, phyllostigmas are sometimes preserved in the molds of epidermis, parenchyma or vascular tissues, but this preservation form is relatively rare (more frequent in three-dimensional plant organs). The most common leaf fossils are the organically preserved compressions and inorganic impressions, which are not so the mechanical imprints, as the mineral precipitates deposited on the leaf surface or beneath the cuticle.

Leaf impressions are thereby produced by chemical interaction between the buried organic matter and its depositional environment. Before the fluid sediment is diagenetically transformed into a solid rock, the decaying plant material imposes a redox gradient that inflicts migration of chemical elements precipitating on or infiltrated into the leaf tissues. Mineral films commonly consist of iron carbonates or oxides in combination with clay minerals.

In the leaf compressions, epidermal structures and their traumas are replicated and preserved on the durable cuticles. On the leaf impressions, the leaf surface micromorphology is replicated by the external mineral films, whereas subcutaneous mineral films infiltrated under the cuticle (which is pilled off the decaying mesophyll beneath) is the most favorable preservation form for both epidermal structures and the near-surface parenchymal phyllostigmas. Fine details of phyllostigmatic structures are preserved in this way (Figs. 7, 8).

The conspicuousness of phyllostigmas against their bearing leaf impressions depends on their morphological and/or biochemical distinctness Thus, insertive oviposition inflicts plant cell death and wound reaction that can be further enhanced by the subsequent mining or gall inducing activities of the hatching larva. Both mines and galls inflict traumatic cell hypertrophy and hyperplasy in the surrounding tissues. An alien organic material (the egg bound and larval metabolic substances) is introduced into the leaf creating a distinctive microclimatic and biochemical environment. An increased humidity (sap concentration), gas pressure, greenhouse effect (of decaying reaped cells and frass accumulations), and acidity

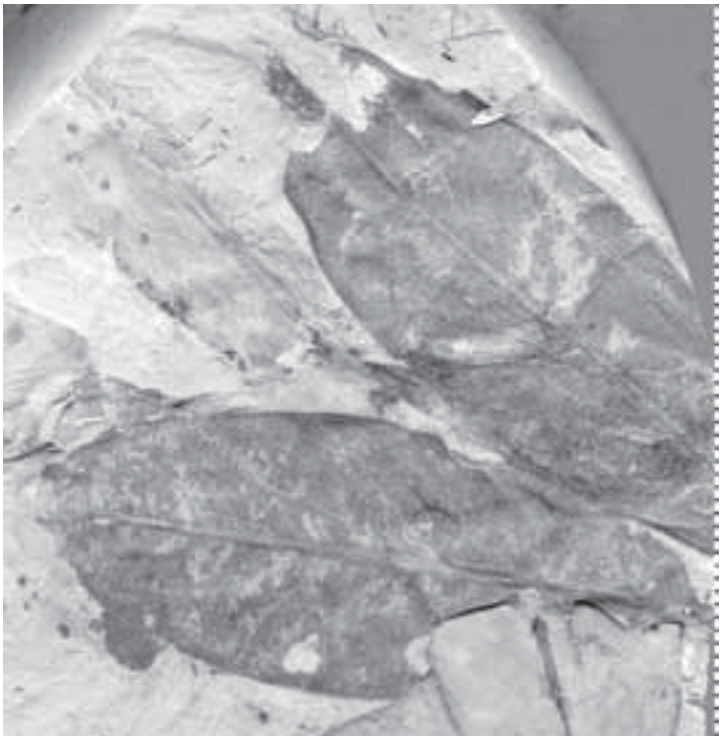

Fig. 7. Eriophyid emergent gall on *Dewalquea gerofitica*, IG1-31 (details on Pl. XIV, figs. 1, 2).

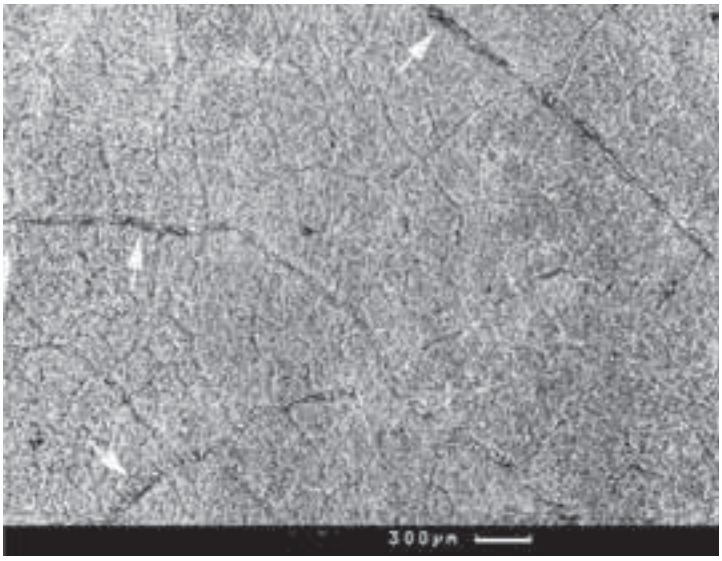

Fig. 8. Impression (subcrustation) of fine venation with a histoid gall causing hypertrophic swelling of tertiary veins on *Platanervia integrifolia* (arrows); SEM.

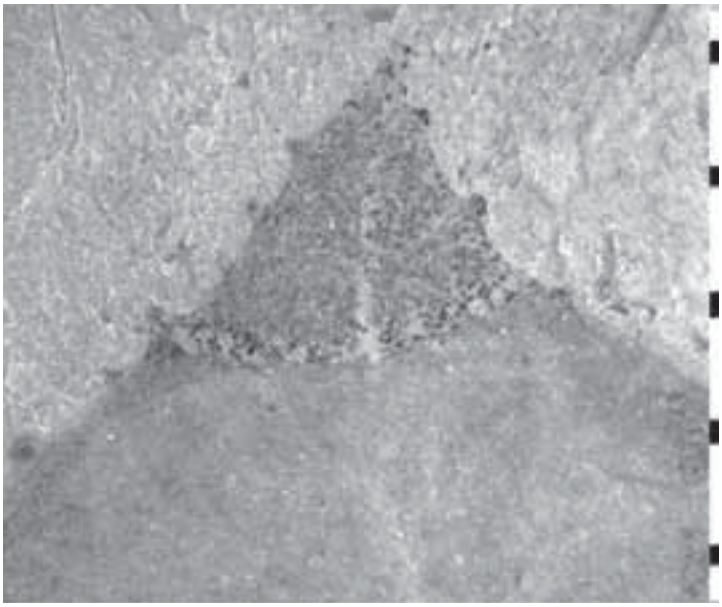

Fig. 9. "Ringing" of leaf apex cut off by a transverse mine track on *Platydebeya papilionacea*, IG1-1261, Gerofit.

of the mine add to the mechanical damage resulting in necrosis, ringing (undernourishment of cells next to severed vascular bundles), discoloration or aberrant coloration owing to local degradation of chlorophyll or accumulation of anthocyanine (Hering, 1951).

Discoloration during life is responsible for the lighter colors of fossil mines and the ringed areas (Fig. 9), whereas the bright red to purple anthocyanine coloration is often retained in the fossils by the substituting iron oxides. Callus is marked on fossil leaves by the darker corrugate fringes of traumatic structures, over which the contours of hypertrophic cells are often discernible. These effects enhance visibility of phyllostigmas against the differently colored leaf impressions.

Preservation chances and biases

Leaves make abundant fossils giving their phyllostigmas a fair chance of being fossilized. Phyllostigmas are discernible on fossil leaves owing to their morphological and/or biochemical distinctness. It appears self-evident that durable phyllostigmas should be better preserved. Durability may in turn depend on the life habits. Thus gall midges produce either fairly durable or rapidly degrading galls depending on whether they pupate in the gall or elsewhere. Yet numerical representation of a phyllostigmatic morphotype depends in the first place on selective representation of its host species in the fossil leaf assemblage.

As is well known, the bulk of plant debris comes from lowland vegetation proximal to deposition site. This means that the lowland communities of plant-dwelling organisms are notoriously overrepresented relative to the distal (inland) communities. The pioneer riverside

communities of willows and poplars bear a distinctive fauna of sawfly and psyllid gall inducers that has better chances of entering the fossil record than the inland fauna of cecidogenous cynipids on oaks, for example. However, the enormous bias in favor of lowland plants can be less significant for polyphagous leaf parasites spreading over a wide range of plant habitats. Insofar as preservation chances are concerned, polyphagy is advantageous over the mono- and oligopahgy.

The host plant growth forms are likewise important. Terrestrial and aquatic, arboreal and herbaceous, evergreen and deciduous forms widely differ in the amount of leaves they produce and shed, and therefore have different chances of being adequately represented in the fossil leaf assemblages. Their leaf parasite records are similarly biased. Thus, in the species-rich genus *Agromyza* (Diptera: Agromyzidae), the majority of species mine herbaceous plants, and only few, as *A. ulmi*, are found on trees. Yet these proportions are likely to be reversed in the fossil record because of the taphonomic bias in favor of arboreal plants.

The last taphonomic problem to be mentioned here is the influence of leaf parasites on their host's taphonomy. By interfering with leaf production, functioning and longevity, leaf parasites affect both quantity and quality of plant material available for preservation as well the chances of this material being selectively preserved and collected. Epidemic attacks of phytophagous insects may cause defoliation – an abundant, although accidental, source of leaf material.

Seasonal leaf shedding is variously affected by leaf parasites, being enhanced in some cases and retarded in the other. Insects that mine fallen leaves, e.g., *Coenorhhinus pauxillus* (Coleoptera: Curculionidae) tend to accelerate leaf shedding by ovipositing at petiole insertion or midrib (Hering, 1951). On the other hand, insects that complete their development in the mine would rather prevent premature leaf shedding and are even capable of retarding chlorophyll degradation over the "green islands" sustained by the excessive moisture of the mine.

Certain galls regularly cause abscission of leaves, as well as floral organs (Ionescu & Neacşu, 1969), thus increasing their availability for preservation. This can be counterbalanced by a lower preservation quality of parasitized leaves that become too fragile or brittle to make good fossils. Leaves infected in bud may wilt before time scarcely making a good fossil.

7. Functional morphology of phyllostigmas

Phyllostigmas are studied as a source of taxonomic inference adding to the body fossil diversity, as a factor of plant evolution or in relation to phytomass utilization in the terrestrial carbon cycle (Labandeira, 2002 a,b; Labandeira *et al*., 2002; Wilf *et al*., 2005, 2006). A rich fauna of leaf inhabitants is poorly if at all recorded in the body fossil material, until know our major source of information on arthropod evolution. In effect, the chronology of first appearances for many groups of phytophagous arthropods might have been heavily biased, their appearances in the body fossil assemblages being drastically belated in respect of their feeding marks on leaves.

The main focus of the present study is plant – arthropod co-evolution as conveyed by evolution of parasitic habits. In this chapter, functional morphology of structures caused by egg insertion, gall induction and mining will be considered from this viewpoint.

Eggs and procecidia

Insect eggs very in size, shape, sculpture, shell structure, the chorionic aeration systems of several complexity grades (Hinton, 1981), and, even more importantly for the fossil trace studies, in the mode of deposition leaving recognizable marks on the leaf impressions. The egg set patterns are sometimes indicative of oviposition habits as in the case of "attended" oviposition in damselflies (Odonata), when the egg-laying female is guided by her male partner. Laid in this way, the egg pattern is fairly regular, "die niedlichste Nadelarbeit die mann sich denken kann" (Wesenberg-Lund, 1943, p. 70), whereas the "unattended" mode, in which the female keeps changing her position while moving against the current, usually generates a less orderly arrangement (Kumar & Prasad, 1977). At the same time, the froth covered egg masses of these non-phytophagous insects are similar to those of the mining flies and Lepidoptera.

In Lepidoptera, eggs are laid flat on leaf surface or inserted in punctures, bored in, singly or in small clusters, into midrib furrows (Tischeriidae) or epidermal pockets (Eriocraniidae), but never persist on the mine. In Hemiptera: Homoptera: Cicadoididae, Delphacidae, and in Heteroptera: Nabidae, Tingidae, Pleidae and some other families (Hinton, 1981), eggs are inserted in slits made (sawed) by ovipositor, sometimes in long rows. In sawflies (Hymenoptera: Tenthredinidae), slits or pockets are sawed into the midribs or leaf margins, with the egg scars often seen on the borders of the mines. In Coleoptera, they are coated with frass (Buprestidae) or laid in cavities gnawed by the beak (Curculionidae) on the flanks of midribs or in the leaf margins, sometimes occurring among the nearly identical feeding holes. In Diptera: Trypetidae, Agromyzidae, Cecidomyiidae, and Drosophilidae, with long ovipositors, eggs are inserted in punctures (that look like feeding punctures in agromyzids), preferably over the leaf margins or in the leaf tips, sometimes in transverse rows or small clusters.

Egg insertion inflicts wound reaction causing abrasion or hyperplasy and a transient or persistent swelling of surrounding leaf tissues. The morphological effect varies in respect

to oviposition techniques and the associated biochemical effects of pheromones secreted by gravid female and/or by the egg itself (Quiring & McNell, 1984).

Callous swellings around inserted eggs are known as egg-galls, but far not all their producers are gall-makers and some (*Lestes*, Odonata: Pierre, 1902) are not phytophagous at all (Ross, 1932). The conspicuous annular outgrowths around inserted eggs, as in *Cystiphora taraxaci* or *Monarthropalpus buxi*, Cecidomyiidae, are considered as pustular galls (Mani, 1964; Skuhravá *et al*., 1984) or sometimes as mines (Hering, 1951). Yet, insofar as cecidogenesis is a specialized form of phytophagy, the gall-like structures formed around inserted eggs before hatching are not galls in this restricted sense. A more appropriate designation "procecidia" is ascribed to F. Thomas (1902) and A. Pierre (1902). The typical procecidia are low parenchymal egg cupules that may or may not give rise to gall development.

The wound effect is prominent in sawflies that inflict cleavage fissures by sawing with their serrate ovipositors, and is relatively persistent in genera with free-living larvae (Ross, 1932). In the cecidogenous *Pontania*, it is modified by the growth substances secreted into the slit and by subsequent cecidogenous activity of the hatching larva.

In cynipids, the direct injury by endophytic oviposition is less obvious, although a callus border can be formed. The egg itself exudes lysigenous enzymes preparing a chamber that is further expanded by the larva.

In beetles, the wound effect of oviposition is sometimes accompanied by morphological deformities, such as vein bending at egg insertion by *Orchestes*, Curculionidae, a mining beetle primarily (Needham *et al*., 1928).

Except in cynipid galls, the preparatory stage of which is performed by oviposition, the role of eggs in preconditioning cecidogenesis is insufficiently studied, but appears significant in aphids with cecidogenous nymphs (gallicolae) hatching from parthenogenetic eggs, in Psylloidea: Triozidae with the egg-induced leaf margin roll, and in both tephritid (with the first larval instar sometimes developing inside the egg shell) and cecidomyiid flies producing a variety of primordial gall-like structures.

Galls

Despite the long history of gall studies (cecidology) going back to the ancient Greek times, there is no agreement on definition of gall. Traditionally, galls are understood as enclosures induced by plant parasites for securing their development. By this restricted definition, galls (cecidia) do not comprise the associated (cecidogenous) plant deformations. Many aphids, for instance, "cause leaf or stem deformations which in the older literature are referred to as galls, even when all the aphids are not enclosed within the plant structure. The term "pseudogalls" is used in such cases by some authors" (Wool, 1984: 12). Such a strict definition would exclude from the "true galls" even such manifestly adaptive cecidogenous structures as eriophyid erinea and the other fitzgalls. The term "pseudogall' is more often applied for the gall-like enclosures, such as domatia, produced without parasitic induction (Monod & Schmitt, 1968).

In contrast, a broad definition of galls comprises "all manifestations of growth, whether positive or negative, and of abnormal differentiation induced on a plant by animal or plant

parasites" (Meyer, 1987: 1). However, cecidogenous abnormalities have to be discriminated from regeneration structures associated with oviposition, external feeding and mining.

Gall production is a peculiar form of parasitism, in which not only the gall inducers obtain the mechanisms of altering programmed development of their hosts, but also the induced organisms are capable of specific responses. In this sense, cecidogenesis is related to carcinogenesis, bearing on the general problems of neoplasm origins (Wittlake, 1981). The mechanisms of gall induction are not as yet fully understood and may be many. In certain cases at least, gene insertion in the plant genome took place (Manulis, 1992), mediated by a plasmid in saliva of the larvae.

It seems therefore appropriate for the scope of cecidological studies to define galls as *a systemic plant disease induced by parasitic organisms, the etiology of which includes both specific and non-specific symptoms, partly beneficial to the inducer*. It is the etiology of cecidogenesis that is revealed in the course of gall studies. The symptoms comprise all developmental abnormalities that can be ascribed, by direct observation or analogy, to parasitic induction. This would allow the term gall being used for the fossil phyllostigmas that find their analogies among extant cecidogenous structures, whatever their adaptive meaning.

For the cecidogenous and gallicolous organisms, galls serve as food, shelter or both. Some are external feeders, as eriophyid mites and Thysanoptera, the other find their food inside the gall and remain there during certain developmental stages or through the entire life. Such galls produce nutritive tissue, although no evidence of such can be found in some primitive (or reduced) gall forms (examples in Meyer, 1987).

Perhaps all higher plants are susceptible to gall induction, although there are great differences both in cecidogenic intensity of parasites and susceptibility of their host plants. The former vaguely correlates with the method of induction, such as piercing, ovipositon or larval feeding. It is known that young plant tissues are more susceptible than the old ones, which justifies separation of the growth point galls, or *acrocecidia*, from the rest, or *pleurocecidia* (Thomas, 1873; Houard, 1904).

Galls develop on all plant organs, from roots to fruits, but each species of cecidogenous organisms has its more or less definite preferences for certain plant organs and the plant responses are also organ-specific, variously affecting the gall morphology. It therefore makes sense to distinguish between the root galls, stem galls, bark galls, shoot galls and leaf galls, etc. (*radicecidia, caulicecidia, corticecidia, ramicecidia, foliocecidi*, etc.). Leaf galls can be induced in bud or develop on fully grown leaves, which partly determines the intensity of leaf deformation. The symptoms include both histological and morphological abnormalities, as well as specific enclosures for parasitic feeding and habitation. Their relative significance for the gall etiology is reflected in the recognition of *histoid* (typically induced by attacking a single cell, as in eriophyid mites), *organoid*, and *neoplasmatic* (the vaguely defined *cataplasmatic* or distinctive *prosoplasmatic*) galls (Küster, 1911; Meyer, 1987).

The leaf gall topography pertains to the habits of cecidogenous organisms, the majority of which are epiphyllous. Many galls are evident, though differently, on both side of the leaf. The main targets of cecidogenous transformation are meristematic cells in general and

cambial cells in particular. Moreover, in certain kammergalls, the nutritive tissue is poorly if at all developed and the larvae are feeding directly from nearby vascular bundles, as in the pustular galls of a cecidomyiid *Monarthropalpus buxi* (Meyer, 1887) – another reason for making them close to the veins.

Gall morphology is the issue of cecidogenous morphogenetic processes, such as hypertrophy, hyperplasy, lysis, inhibition of cell differentiation, neoplastic differentiation and combinations of these, accompanied by various forms of trichomes, excessive or reduced lignification and cutinization, suppression or abnormal development of stomata, depletion of chlorophyll and accumulation of melanin, xanthophyll or anthocyanine. Gall topology (*epi-* or *hypophyllous, petiolar, apical, marginal, costal*, etc.) and the gall shape designations, such as *trichomate, agglomerate, solid, hollow, stalked, sessile, pustular, lenticular, nodular, pock-like, pellet-like, horn-like, drumstick-like*, etc. are descriptive terms of certain classification utility, combined with morphogenetic types, in which the major distinction is made between the exogenous and endogenous initiation and their morphological correlates.

The descriptive terminology of gall structures have been developed by generations of European cecidologists. The etymology is rooted in the French and German languages mainly, transliterated or translated into English, and the meanings may vary from one linguistic domain to another. The following designations correspond to the more common practical usage of the terms (based on Houard, 1904; Ross, 1932; Mani, 1964; Meyer, 1987):

Blister galls are sac-like bulges of various internal structures.

Cover galls are enclosures formed by covering growth or out-pocketing of leaf tissues over the cecidogenous organism, typically the fundatrix of aphids (e.g., the petiole gall of *Pemphigus* on *Populus*) or gall-midge larva;

Deciduous galls are the pouches and other gall structures shed from a persistent basal disc or platform detached over the annular separation tissue, exemplified by the well known *Mikiola fagi* (Diptera: Cecidomyiidae) (some jump by the motions of the larva inside, as in the "*jumping galls*" of *Neuroterus sallans*).

Emergence galls (*fitzgalls*) are epidermal or parenchymal blisters, papillate, hairy emergences and their aggregates on the leaf surface, typically caused by eriophyid mites, also by thrips (Thysanoptera) that are external feeders essentially, but can be enclosed in the gall. *Erinea* of nutritive hairs are histoid fitzgalls that develop on the leaf surface or inside the mite galls, or *acarocecidia*.

Fold galls are essentially primordial leaves that failed to unfold, transformed into a sealed or unsealed pod-like or bag-like structure, as those produced by Thysanoptera.

Kammergalls are endogenous closed hollow fleshy lenticels as of cynipids *Neuroterus* on *Quercus*, some vascularized as in *Pontania* (Hymenoptera: Tenthredinoidae) on *Salix*.

Krebsgalls are thick irregular globose or grape-like hyperplastic swellings over an external inducer, typically an aphid or coccid (Homoptera).

Lenticular galls are flattened hemispherical or discoid lenticels, often shortly stalked and broadly rimmed, with the larval cavity delineated with sclerenchyma, developing as *markgalls* or *kammergalls* within the mesophyll and erupted to the surface, typically of sawflies and cynipids (*Neuroterus*), also of gall-midges.

Lysenchyme galls are heteromorphic swellings over a cavity formed by lysis of leaf mesophyll in contact with cecidogenous organism, typically caused by cynipids (Hymenoptera: Cynipoidea).

Mantle galls are thin cover growths over exogenous cecidozoa causing insignificant swelling of leaf blade.

Margin roll galls are the locally or continuously thickened leaf margins rolled upwards or downwards, with histological differentiation suppressed or variously altered, some with parenchymal extrusions (outpocketings), produced by all kinds of cecidozoa, including mites, thrips, psyllids, coccids, and gall midges.

Mark-galls are the lenticular, cylindrical, bowl-shaped or clavate, often spiny hyperplastic enclosures around a hard sometimes detachable larval cavity (the "*inner gall*"), some with a simple or multichamber atrium, mostly of cynipids (Hymenoptera: Cynipoidea), known as oak-apple, pine-apple, sea-urchin, Knospengalle, Zapfengalle, cerebra, rosettes, etc.

Midrib roll galls are the subcylindrical infolding of leaf midribs, typically caused by *Gynaikothrips*, Thysanoptera.

Nodular galls of eriophyids are here considered as a variety of *pock galls*.

Operculate galls or *pyxidiocecidia* are the cup-shaped to bottle-like structures topped with a dehiscent lid or stopper.

Pellet galls are minute globular swelling with the inner cavity underdeveloped or reduced, some basally oscillate, typically of eriophyids, also primordial galls of gall midges.

Pit (basin) galls are smallish, shallow, widely open invaginations of leaf blade.

Pock galls (*Pockengalls*) are mm-sized solid biconvex swellings expressed on both sides of the leaf, involving both palisade and spongy tissue, some ostiolate, typically produced by eriophyids, but also by gall midges.

Pouch galls are mm- to cm-sized hollow invaginations, bulges or combinations of such, widely open, ostiolate or exostiolate, stalked or sessile, of various, typically utricular, conical-truncate, globose or horn-like shapes, some deciduous on a discoid platform, with histological differentiation inhibited or abnormal, some thickly cutinized and with an inner cuticle lining the cavity. *Cephaloneons* are pouch galls of a head-like, globose or hemispheric shape. *Ceratoneons* are horn-like or pyriform pouch galls. The latter terms typically refer to eriophyid galls, but are applicable to insect galls as well.

Pustular galls are parenchymal pustules formed around inserted eggs, typically of sawflies (Hymenoptera: Tenthredinoidea), also of Odonata (see under *procecidia*).

Ridge and wrinkle galls are linear cecidogenous structures of leaf surface, mostly of eriophyid mites (*Faltengalls* of the German language literature, not to be confused with *foldgalls*).

Roll galls are the whole-leaf tubular structures, some spirally twisted, as the galls of *Eothrips* (Thysanoptera) and some gall midges (*Dasineura*, Cecidomyiidae) on broadleaved plants.

Among them, the emergence (fitz), wrinkle and ridge galls are essentially histoid, the various fold and roll galls are organoid, the pustular, pock, pellet or nodular structures are cataplasmatic microgalls, primordial galls or procecidia, whereas the lenticular mark- and

kammergalls, krebsgalls, cover and pouch galls are prosoplasmatic. These distinctions will be reflected in the formal classification of fossil gall structures (Chapter 12).

Mines

Mining is an adaptation of insect larvae to endophytic life, in which the habitat is created by consuming epidermal cell contents or excavating from under the epidermis. Mine construction conforms to the growth, metabolic activity and developmental stages of the larva by adjusting the breadth, depth and configuration of the track and by providing for breathing and frass disposal. For the larva, mining is a temporary habit or extends from hatching to pupation, which takes place in a pupation chamber or outside the mine. Traces of external feeding are occasionally similar to mines, but they give no evidence of habitation.

Mines are commonly considered as mechanical wounds merely, to which the host plant reacts by producing callus tissue along the track. However, the traumatic effects of mining are not only mechanical, but also biochemical. Mine differs from the surrounding plant tissue in both humidity and temperature elevated by greenhouse effect of accumulated organic matter. Respiration of the larva, remnants of reaped cells and, in particular, frass deposition inflict functional disturbances that are manifested in aberrant pigmentation, anthocyanine accumulation or chlorophyll "islands" in the vicinity of the mine (Hering, 1951). Such traumatic effects are produced by mines and galls alike, which led some researchers to believe that mining is just a primitive, and in the evolutionary sense precursory, form of cecidogenesis (reviewed in Hering, 1951). However, not only insects, but also mites, nematodes, fungi and even prokaryotic organisms induce plant galls: a wider spread and seemingly less specialized parasitic habit. Perhaps our idea of what is simple and what is elaborate, based on our engineering experience, does conform to that of the plant parasites. Yet it is for paleotraumatology to discover the actual evolutionary sequence of cecidogenesis and the mining.

Taxonomic mine types

Mines of certain insect species are readily recognizable, but this is far not the typical situation. More often they are not assignable to one or the other taxonomic group of miners otherwise than by breeding experiment. Yet it is commonly assumed that at least the orders of miners are distinguishable by the structures they produce. Mine types corresponding to the major orders of mining insects are *lepidopteronomes, dipteronomes, hymenopteronomes, and coleopteronomes* (Hering, 1951). Each of them includes various mine track configurations, histologies, frass deposition modes, and associated cut-outs, some of which are characteristic, although maybe not unique, for the group. Thus, certain behavioral features of moth miners, such as the permanent epidermal sap feeding or spinning over the mine track before construction of puparia, allow recognition as lepidopteronomes the following types:

- long epidermal mines;
- frass-less mines;
- mines with minute, less than 5 mm in diameter, circular exit holes;
- linear mines with frass deposited in a continuous median line;

- silk-lined mines, in particular the tentiform mines with the covering epidermis fastened by silk threads;
- cut-outs for case construction in the temporary miners, as well as association with attached cases or traces of external larval feeding.

These types embrace a relatively small fraction of lepidopteronomes, and even for these the distinctions are not absolute. For instance, in *Eriocrania*, *Stigmella* and some other Lepidoptera the exit holes are semicircular (Needham *et al*., 1928) as in the Diptera. Linear mines with a continuous median frass line are produced by *Phytomyza* (Diptera: Agromyzidae), while in the Tendipedidae silk is spread over the track. Yet these habits are atypical of the dipteronomes that are recognizable owing to such larval habits as lying on its side and thrusting sideways during feeding. The corresponding structures are:

- secondary feeding tracks on both sides of the primary track, forming a "herring bone pattern";
- double rows of frass pellets (occasionally mimicked by the nepticulid and gracilariid Lepidoptera);
- straight linear mines with circular entrance and exit holes (as in chironomid mines on aquatic plants).

The hymenopteronomes (sawfly mines) are mostly blotches with a short linear part, if any. Frass is scattered or sometimes piled near the entrance. The leaf venation is typically intact over the blotch. However, these features occur outside the group (e.g., in Lepidoptera: Eriocraniidae,) and are valid only in the absence of characters typical of the other groups. In *Phyllotoma*, the cut-outs for pupal cases are like in the mines of Lepidoptera.

The coleopteronomes likewise have very few recognizable features of their own, although the persistent egg shells (also in the Tischeriidae, Lepidoptera), as well as the egg nests and the confluent or communal blotches are more common here than in the other mining groups. The globular cocoons constructed inside the mine are rather typical of weevils (Coleoptera: Curculionidae), but are also produced by Lepidoptera: Gracilariidae and *Tischeria*.

The host plant taxonomy may help in recognition of the mine when it is known, for example, that conifer needles are mined by Lepidoptera, while the mines on aquatic plants and grasses are most commonly made by Diptera. Such criteria are scarcely helpful in the taxonomy of pre-Tertiary mines.

Mine types related to leaf topography

Mine location against the host leaf topography is related to availability of palatable tissue, longevity of mining period and protection of the mine. The assimilating palisade parenchyma is more often mined than the spongy mesophyll. Young meristematic tissues are preferable over the older and sclerotic ones, which explain why leaf tips and marginal areas are often mined. However, these areas are less reliable in terms of protection, unless a rolling of leaf blade is caused by the mining.

A better protection combined with a higher concentration of nutrients can be found in the vicinity of stronger veins. Midrib mines are fairly common, in particular when mining

starts in the petiole (and is often derived form the stem mining). However, for many species, strong veins are impediment to mining.

Thus, the choice of one or the other strategy depends on the balance of forces and can be species- or stage-specific, as well as depending on the plant host. Both linear and blotch mines can be designated as *costal*, *inercostal* and *transcostal*, that is transcurrent to the stronger veins. To avoid running into a vein, the intercostal mines may take parallel to the adjacent veins. Yet their paths are seldom unidirectional, except in the parallelodromous grass leaves. Coiled and sinuous tracks provide for increasing the mining area without transgressing the veins. Stronger veins are commonly avoided in the early instars when the mouth parts are not yet fully developed, but can be surmounted later in development. In such cases the early ophionome runs parallel to the lateral veins, but later turns along the margin or midrib.

Morphological mine types

A typical mine has both leaf epidermises intact, although there can be epidermal holes and even larger "windows". If epidermis is removed, than it is a *trench*, rather than mine, although a roof of frass fastened with silk threads is sometimes built over it. *Epidermal mines* are typically made by sap-feeders, whereas *parenchymal mines* involve subepidermal tissues or these only in the case of *intraparenchymal mines*. Mines restricted to either spongy or palisade tissue are called the *epiphyllous* and *hypophyllous* parenchymal mines, respectively. *Full-depth mine* removes all the tissue between the upper and lower epidermal sheets. If mesophyll is taken between the veins that remain intact, the leaf patch so affected appears skeletonized forming a *skeletal mine*.

Hering (1971) has distinguished the following types of mine configurations:

Ophionome, or linear track;

Stigmatonome, or blotch mine;

Heliconome, or serpentine mine of tight coils;

Visceronome, or loosely ("intestinally") coiled mine;

Asteronome, or digitate mine with arms spreading from a central spot;

Physonome, or blister mine forming a conspicuous swelling on the leaf;

Ptychonome, or tentiforme mine with epidermal roof over the blotch silk padded and folded.

A few additional types recognized in this work are:

Eustigmonome, or small blotch mine commensing at an egg scar and with pupation cocoon or an exit hole, suggesting an early transition to ectophytic life;

Retractonome, or mine retracting its former tunnel;

Troponome, or mine track forming close loops;

Holostigmonome, or mine blotch extending the whole leaf breadth;

Symphyenome, or communal mine made by several larvae;

Distigmonome, or mine-in-mine structure formed by consecutive instars;

Apostigmonome, or mine with one epidermis removed as a "window";

Stomonome, or mine with leaf (epidermal) pieces cut out for case construction.

The transitional or combinatorial types are designated as *ophistigmatonome*, *ophiphysonome*, *ophiptychonome*, etc. Many miners produce linear track that, with a change of feeding habit, expands into a blotch or a series of blotches. If the initial track is short it can be consumed by the blotch appearing as a typical stigmatonome in this case. On the other hand, blotch mine sometimes gives off a linear arm before pupation.

Miners shear plant cells horizontally, sometimes leaving recognizable arched feeding marks over the blotch or a sinuous line along the margin. Mottled mines are formed by the larvae that occasionally bite vertically into the underling parenchyma.

If feeding habits change over development, the construction of the mine may vary from one instar to the other, an early mine appearing quite different from the fully developed in shape, depth, and coloration. Mine in mine structures, or distigmonomes, can be formed when a late instar expands the initial mine after a callous border is formed around it or when a deeper mine is excavated inside the shallowly mined area. Temporary mining is a change from endophytic to ectophytic life during development leaving small eustigmonomes or apostigmonomes with epidermal windows or else the mines with a leaf piece cut out (stomonomes).

For secondary parasites, predators and scavengers, mines are accumulations of organic matter to be used as substrates or to be eaten. Not infrequently, the mined areas are repeatedly mined by the same or different species or used by non-mining organisms, sometimes in a specific way bearing on recognition of the original miner. Predation traces on mines, or *trophostigmata*, are important as evidence of trophic cascades and the top-down regulation in the leaf parasite communities.

8. Morphological classification of phyllostigmas

Even extant parasitic structures pose certain recognition problems that in dealing with fossils are aggravated by the lack of experimental approach and because the habits can only be inferred from structural remains. Too many parasitic organisms produce similar phyllostigmas for the latter being confidently assigned to one or another taxonomic group. Leaf rolls, pit gals, lenticels, pustules and even more complex forms, such as horn-like poach galls are produced by virtually all the major groups of cecidogenous organisms: the eriophyids, thrips, aphids, psyllids, coccids, cynipids, and cecidomyiids.

Organoid effects, such as leaf rolling, midrib swelling, vein twisting, etc., and even leaf fusion (pair-wise needle fusion in pines induced by such taxonomically remote cecidozoa as scale insects, Coccidoidea, and gall midges, Cecidomyiidae) are of a low specificity *per se*. The cataplasmatic microgalls, such as pocks, pits, pustules or pellets, are scarcely specific either, their affinities being mainly established by experimental breeding studies. The amazing parallelism of eriophyid acarocecidia on one hand and the insect galls of Thysanoptera and Psylloidea on the other are amply commented upon in the literature (see under Ananthakrishnan, 1984).

Homeomorphy is no less important in construction of mines. The well known cases are the "mimicry" of mines in *Bacculatrix* and *Stigmella* or a striking similarity of mining habits and the issuing structures in Lepidoptera: Eriocraniidae, and Hymenoptera: Tenthredinidae (Needham *et al*., 1928; Hering, 1951).

Even if analogous parasitic structures differ in their typical design, the ranges of their variation often overlap. Though analogous gall forms of cecidomyiids (Diptera) and cynipids (Hymenoptera) typically differ in their expressiveness and complexity, some lenticular cecidomyiid galls are scarcely distinguishable from those of a cynipid *Neuroterus* (Ross, 1932). Tubular galls on grasses are commonly caused by gall-midges, but occasionally also by chalcids, Hymenoptera.

The fossil record preserves common rather than rare forms. Yet it must be kept in mind that the ranges and patterns of variation change through times.

Another set of recognition problems are related to polymorphism of phyllostigmas produced by one and the same species at different developmental stages or on different plant hosts, as well as sexually dimorphic (in coccid galls). When two forms of galls are produced during the life cycle they are, as a rule, dissimilar, as in heterogonic cynipids (that are sometimes more readily recognized by their galls than by their own external morphology), with alternating agamic and bisexual generations, each producing galls on one and the same or different plant organs (roots and leaves). In Homoptera: Aphidoidea: Pemphigidae, the fundatrix nymphs make a small primordial midrib gall, the typical gall being produced, at a different location on the leaf, by their parthenogenetic offsprings, the fundatrigeniae, whereas in

the Adelgidae, galls are prepared by the feeding fundatrix, but are further developed, later in the year, by the nymphs (gallicolae) emerging from parthenogenetic eggs. Even experienced cecidologists have assigned such forms to different species or even genera evoking a lasting taxonomic confusion (Wool, 1984). In paleocecidology, dissimilar conspecific forms are bound to be assigned to different morphotypes.

Mines seem to present a lesser problem in this respect, because developmental changes are recorded by configuration of mine track and the mode of frass deposition. Developmental transitions from linear mines to blotches and/or from epidermal to parenchymal feeding can be fairly obvious in the fossil mines as well. However, consecutive generations of mining species may differ in their habits, which depend on the season (hardening of leaf tissues over the growing season) and, in polyphagous miners, also on the choice of plant host. In temporary miners, the larva may leave its mine, feed on the leaf surface for some time and then re-enter the leaf forming a different type mine. Such feeding behavior is considered as the least specialized, which implies that it might have been wider spread in the past, yet evading recognition by paleontologist.

Morphotypes of fossil phyllostigmas

On account of widespread homeomorphy, classification of arthropod phyllostigmas reflects the diversity of feeding habits not infrequently evolving in more than one phylogenetic lineage. The nomenclature of pyllostigmatic morphotypes, both the nomomorphes and cecidomorphs (Krassilov, 2007), need not depend on our judgments of affinities that can be commented upon and revised without renaming the taxa. A vast experience of such formal classification is accumulated in paleopalynology and can be adopted in paleotraumatology as well. Yet, to be useful for evolutionary studies *formal classification units have to be the distinctive phyllostigmatic morphotypes pertaining to the functional morphology of extant phyllostigmas* (Chapter 7).

Few attempts of morphological classifications were made in respect to extant galls. Eriophyid fitzgalls resemble fungal structures and were initially described as such under the names *Phyllarium* and *Erineum* (see Mani, 1964), that have been later used as cecidological terms. A morphological classification by Bremi divided gall shapes into the head-like, *Cephaloneon*, and horn-like, *Cerathoneon*, each with a number of specific binominals (Nalepa, 1929; Ross, 1932). These morphological divisions were for several decades used as informal descriptive designations (e.g., Ross, 1932; Mani, 1964). Formal names, but based on taxonomic affinities rather than morphology, are sometimes applied to extant mine forms, for which an ordinal or supraordinal assignment only is feasible (e.g., *Lepidopterion*: Hering, 1957).

In the early paleobotanical literature of 1870s – 1880s, gall-like remains were commonly ascribed to fungi of extant genera *Sphaeria* or *Hysterium* (Ettingshausen, 1868; Heer, 1868; Lesquereux, 1878). Taxonomic status of the derived fossil genera *Sphaerites* Unger, 1950 and *Sclerotites* Meschinelli, 1892, remains uncertain. Though intended for fossil fungi, they might have been the first generic names of fossil leaf galls.

Since 1880s, galls and mines form Tertiary deposits have been conventionally assigned to extant arthropod taxa. Few nomomorphs from the Late Cretaceous and Tertiary were

named after extant genera that produce similar mines (Frič, 1882; Kernbach, 1967; Kozlov, 1988), and a number of new species of mites and insects were based on gall remains alone, e.g., *Eriophyes daphnogene* Ambrus et Hubly from the Oligocene of Hungary (Ambrus & Hably, 1979), or *Contarinia* spp. and *Mikiola pontiensis* Villalta form the Miocene of Spain (Villalta, 1957). In exceptional examples, as in the cecidomyiid remains from the Miocene lignites of Germany, the supposed extant affinities were confirmed by the larval and pupal remains (Mohn, 1960).

The above considerations suggest, however, that, despite the sometimes striking evolutionary conservatism of gall producers, such as cecidomyiids (Roskam, 1993), taxonomic assignments of fossil galls and mines to generic and even suprageneric taxa of extant gall-makers are dubious even for the Tertiary remains and are scarcely acceptable for pre-Tertiary records.

The first generic name intended for fossil galls was *Galla* (Ludwig, 1957 ex Lesquereux, 1892) and the first binominal applied specifically for fossil galls was *Galla quercinea* Lesquereux from the Cenomanian of Kansas (Lesquereux, 1892). Van Amerom (1973) introduced *Acrobulbilites* for the supposed acrocecidia on the Carboniferous asterophylls. Morphological classification of Neogene galls was discussed in Brooks (1955) and Strauss (1977). Waggoner & Poteet (1996) gave start to the form genus approach to fossil gall classification by introducing *Antronoides* Waggoner et Poteet. Recently Vassilenko (2007) has erected *Paleogallus* for all fossil galls (actually corresponding to *Galla* Lesquereux) and *Paleoovoidus* for fossil egg sets with a definite scar pattern, perhaps a too broad category to be practically useful.

A formal classification worked out for description of Cretaceous phyllostigmas from Negev (Chapter 12) is based on the functional morphology of egg scars, procecidia, galls and mines, outlined in Chapter 7, thus primarily pertaining to the diversity of parasitic habits producing distinctive, albeit conceivably homomorphous, structures.

9. Diversity of Cretaceous phyllostigmatc structures

In the Albian, phyllostigmas caused by non-phytophagous insects, such as the egg sets of Odonata, are more prominent then through the later ages. As in the present day *Lestes*, the egg scars are procecidial in the Albian set (Pl. I, figs. 2–5). The traumatic apical cut-outs (Fig. 10, a, b) might have been caused by a non-folivorous insect as well, using leaf material for nest construction as is the habit in the megachilid bees known since the Eocene (Brooks, 1955), whereas beetles constructing pupal cases for their leaf-born cocoons seem to have been responsible for the marginal cut-outs on both the Albian and Cenomanian angiosperm leaves (Fig. 10, c). This form of phyllostigmas declined in the Turonian, perhaps with the mainly tropical buprestids or their extinct ecological equivalents.

More than 80 morphological species (exact figure depending on the numbers of morphospecies lumped under spp.) of phyllostigmas are recognized in the trace assemblage of Gerofit. Their tentative taxonomic assignments suggest domination of cecidomyiids among the gall-makers, with aphids second in abundance, sawflies the third and the rest far less prominent (Fig. 11). Lepidoptera prevail in the mining community comprising more than half of all morphotypes, followed by Diptera and Hymenoptera, with Coleoptera as minor contributors (Fig. 12). Climatic aspects of such distribution are discussed in Chapter 11.

From evolutionary point of view, the paucity of cynipid galls, fairly common under similar climatic conditions now, may indicate a relatively recent acquisition of gall-making habits in this group. The same may pertain to the ratios of Lepidoptera to Diptera miners, although in this case a climatic influence might have been more significant.

For this parasitic community, evidence of evolutionary status comes from the morphological grouping in the first place. Numerical data given in Table 1 can be summarized as follows.

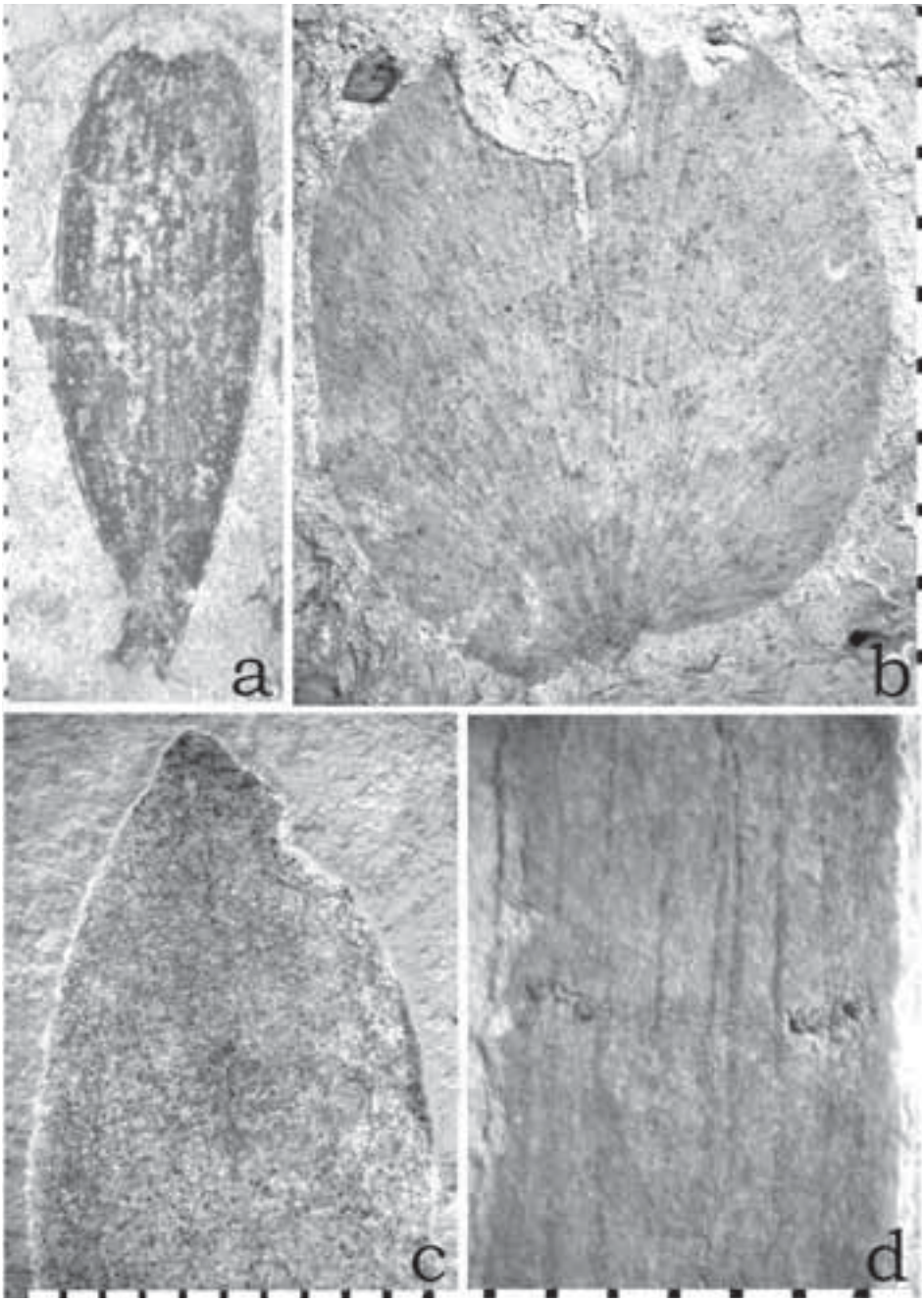

Fig. 10. Insect traces on the Albian and Cenomanian plants: apical cut-outs on (a) ginkgophyte leaf and (b) pinnule of bennettitalean leaf, Makhtesh Ramon, Albian; (c) marginal cut-out on *Parvileguminophyllum* sp. and (d) a transverse mine track on *Pseudotorellia* sp., Nammoura (Krassilov & Bacchia, 2000).

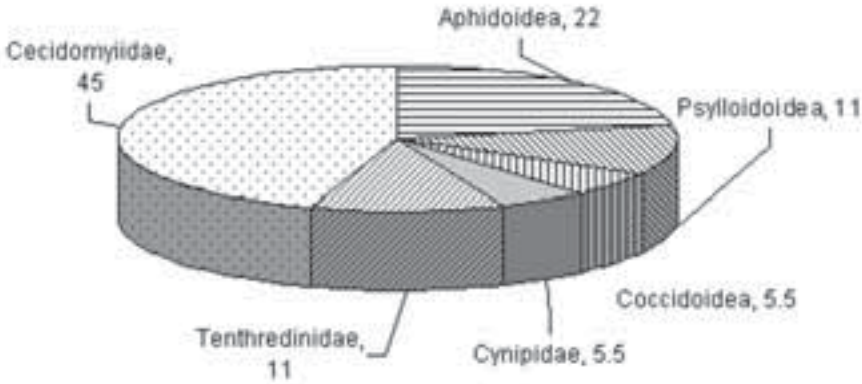

Fig. 11. Numerical representation of tentatively recognized taxonomic groups (percents of the total insect gall occurrences) in Gerofit assemblage.

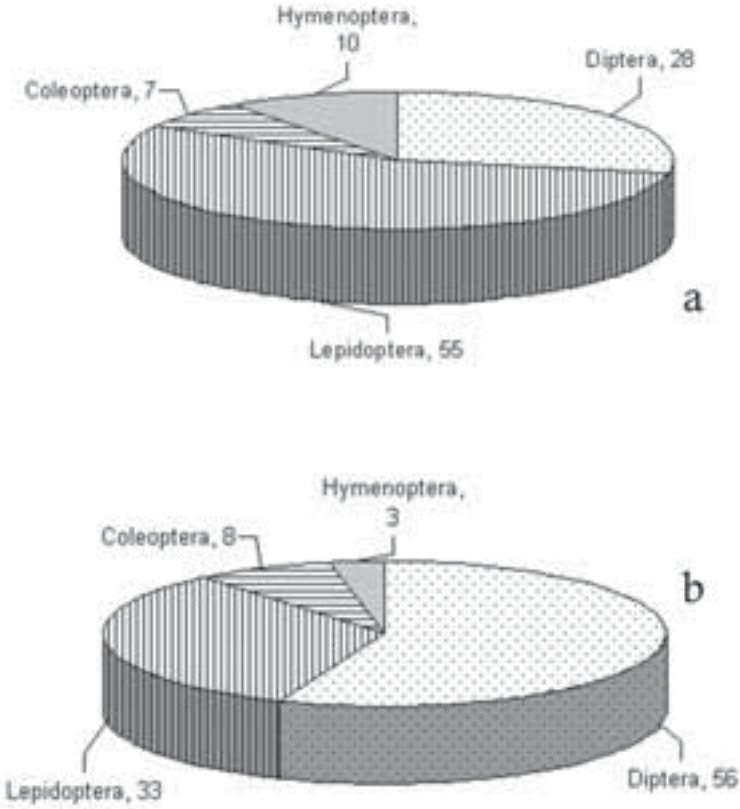

Fig. 12. (a) Numerical representation of tentatively recognized taxonomic groups (percents of the total mine occurrences) in Gerofit assemblage, compared with (b) representation of extant taxa in the mining fauna of England (data from Hespenheide, 1991).

Table 1. Occurrnces of phylostigmas on the main host plants: s – single, r – rare, c – common

	Phyllostigmas / Host	*Dewalquea gerofitica (Dg)*	*Eocercidiphyllites glandulosus (Eg)*	*Eudebeya angusta (Ea)*	*Menispermites cuspidentatus (Mc)*	*Nelumbites aravensis (Na)*	*Platanervia integrifolia (Pi)*	*Platydebeya papilionacea (Pp)*	*Retrodewalquea pendens (Rp)*	*Typhacites negevensis (Tn)*	*Yammelechia superba (Ys)*
1	*Sertoveon arcuatum*	S									
2	*Sertoveon cribellum*							S			
3	*Sertoveon scalarum*					S					
4	*Sertoveon moniliforme*					S					
5	*Costoveon transfixum*					S					
6	*Costoveon vergens*					S					
7	*Costoveon adnatum*	R									
8	*Margoveon incisum*							R			
9	*Margoveon* sp.						S				
10	*Massoveon globulosum*	S				S					
11	*Transpiroveon polygonatum*		S								
12	*Cupuleon caveum*	C		R							
13	*Cupuleon nodulosum*					C					
14	*Cupuleon craterellum*	S		R							
15	*Foveon patellatum*	S?				R					
16	*Foveon astrellum*		S			R					
17	*Emergeon scabratum*	S							S		
18	*Emergeon catenulatum*	S									
19	*Emergeon* sp.	C					C	S			
20	*Pustuleon gregarium*	S									
21	*Lenticeon minusculum*	C						R			
22	*Lenticeon agglomeratum*	S									
23	*Lenticeon nervosum*							R			
24	*Cephaloneon squamosum*				C						
25	*Ceratoneon ovatum*	R									
26	*Ceratoneon mucronatum*	R						S			
27	*Ceratoneon (?) sp.*							S			
28	*Petioleon inflatum*	C									
29	*Petioleon ostiolatum*								S		
30	*Costaeon flexum*	R					C	C			
31	*Costaeon foveum*			R			S				
32	*Costaeon capsulatum*						S				
33	*Costaeon schizmatum*	C		S							

34	*Costaeon blastoides*	R						C			
35	*Costaeon* sp.						S				
36	*Involuteon compressum*	C		S							
37	*Ophionoma paradroma*									S	
38	*Ophionoma serranoides*					S		S			
39	*Ophionoma digitata*	S	S								
40	*Ophionoma arcuata*	S									
41	*Ophionoma* spp.	C	S			S					
42	*Ophistigmtonoma rectiserialis*	C									
43	*Ophistigmonoma crassa*		S	R		S		R			
44	*Ophiheliconoma resupinata*	S									
45	*Troponoma crucitracta*						S				
46	*Troponoma curvitracta*	C									
47	*Troponoma festunata*	S									
48	*Eustigmonoma amoeboides*	S									
49	*Eustigmonoma ochrea*	S									
50	*Eustigmonoma alternans*	S									
51	*Distigmonoma fimbriata*						S				
52	*Distigmonoma variegata*	C	C					S			
53	*Distigmonoma oculata*	C									
54	*Asteronoma arachnoides*	S						C			
55	*Asteronoma expansa*					C		C			
56	*Asteronoma helicoides*					S					
57	*Symphyenoma adcostalis*	R									
58	*Holostigmonoma zebrina*	S									
59	*Holostigmonoma fenestrata*	R									
60	*Apostigmonoma fibrosa*										R
61	*Stomonoma dimorpha*	S				C					
62	*Stomonoma spinulata*					S					
63	*Stomonoma crenulata*	C	C			R	C				
64	*Stomonoma multiforata*		R			S					
65	*Folicasa cuspidata*							S			
66	*Folicasa tubularis*	S									
67	*Folicasa inflata*						S				
68	*Stigmatophaga lobata*							R			
69	*Stigmatophaga perforata*	S			R	S					
70	*Stigmatophaga punctata*							R			
71	*Trophoglypha diffusa*	C			S		C	S			
72	*Trophoglypha* spp.	C		S		C	R	R			

Egg remains

Nearly all egg scars are insertions with more or less prominently raised, apparently callous, margins implying a wound reaction. Solitary insertions are much more frequent at this evolutionary stage than nest insertions, which were found in two occasions only. This latter oviposition habit is common in Coleoptera, but occurs also in Lepidoptera, such as Eriocraniidae.

A single instance of structurally preserved egg shells, *Transpiroveon polygonum*, shows a simple, with incipient differentiation, intrachorionic transpiration meshwork, which is commonly considered as primitive relative to the complex intrachorionic and plastronic systems (Hinton, 1981).

Six egg set patterns are recognized in respect of the leaf topography: (a) arches or zigzag lines over the leaf blade, (b) rows along the primary veins or (c) leaf margins, (d) rows along and between the lateral veins, (e) scattered arrangement over the leaf blade, and (f) dense egg masses. Pattern (a) may represent egg sets of Odonata resulting from the "attended" oviposition by the mating pairs, (b) is common among both miners and gall-makers, indicating, above all, a defensive significance of costal oviposition. The costal egg scars show procecidial developments (*Cupuleon craterrelum.*). They also give rise to the communal midrib mines (*Symphyenoma adcostalis*).

Pattern (c) may inflict a rolling of leaf margins as a preparation to, or even consequence of ovipositon, as in psyllids, but also in cecidomyiids (Chapter 12). Pattern (d) is characteristic of mining Diptera (*Pegomyia*, Anthomyiidae). Egg masses are laid on leaves of waterside plants by Odonata, as well as Homoptera (*Lachnodius*, Coccidoidea), some Lepidoptera (*Yponomeuta*, Yponomeutidae, *Arzama*, Noctuidae), in the case of small globose eggs of *Massoveon globulosum* probably the latter. Scattered egg deposition occurs in various groups of insects. For the lager scattered egg scars, a curculionid affinity (Coleoptera: Curculionidae) is prompted by the association with the feeding holes that in this group are inflicted in much the same way as their oviposition holes.

Procecidial remains

Examples from various groups of gall-makers (Chapter 7) show that cecidogenesis is a two-stage process starting with non-specific wound responses which alert the defensive system of the host to specific plasmatic responses. Procecidia expressed as bulging of leaf tissue around the egg scar forming a more or less distinctive cupule rank among the most widespread phyllostigmas of Gerofit assemblage suggesting even greater than now significance of preparatory stage triggered by oviposition.

Gall remains

A remarkable feature of Gerofit gall community is the paucity of prosoplasmatic cecidia, represented by a relatively complex monophagous cephaloneon species assigned to Aphidoidea and by two rare species of small ceratoneons comparable to those produced by eriophyids, thrips, psyllids and other cecidozoa, but tentatively ascribed to gall midges (Diptera: Cecidomyiidae) on evidence of their deciduousness.

The cataplasmatic microgalls are much more abundant, including lenticular, foveal and open-top cupular forms. Insofar as such forms are produced by all major groups of cecidogenous Homoptera, as well as by gall midges and other cecidozoa, their taxonomic assignments are problematic, inferred primarily from topological evidence of gall development. Thus, an aggregation of a larger central bulge and the radially arranged smaller bulges in *Lenticeon agglomeratum* suggests a fundtrix gall surrounded by a crop of smaller galls produced by the gallicolae. For *Foveon minusculum*, a psyllid affinity is inferred from the association of the pits with hypertrophied smaller veins.

Organoid galls are the most prominent in Gerofit assemblage in terms of their abundance (about 40% of all gall occurrences), diversity, and morphological conspicuousness. The most widespread organoid effects are the inflation of leaf petioles, webbing of petiolules in the palmate compound leaves, twisting, fasciculation, and splitting of the stronger veins, as well as rolling of the leaf margins. Their localized cataplasmatic expressions are pits, fusiform swellings or pockets, sometimes associated with a slender adventitious branching of the costae.

The inconspicuous bulges at the base of sinuous veins (*Costaeon flexum*), might have been caused by eriophyid mites, whereas the more expressive organoid effects find their morphological analogies in the work of extant gall midges. In the case of *Costaeon schizmatum*, recognized by its organoid effect alone, it is an extensive dissociation of vascular bundles that betrays a cecidomyiid gall-maker.

Insofar as cecidogenesis is considered as a co-adaptive interaction allowing the host plants to localize the damage (Mani, 1964; Wool, 1984), the prevalence of organoid effects over prosoplasmatic constructions in Gerofit assemblage (Fig. 13) signifies a low grade co-evolutionary development, perhaps typical of the early angiosperm – arthropod systems.

Species-specificity of cecidogenous effects is commonly held as an advanced feature of such systems, and it is scarcely a co-incidence that the only prosoplasmatically advanced form, *Cephaloneon squamosum*, is also the one of a few strictly monophagous galls. At the same time, the most destructive organoid form, *Costaeon schizmatum*, is also monophagous, or nearly so, on the most abundant leaf species, *Dewalquea gerofitica*. An explanation of this unusual phenomenon must be sought in the ecology of its host plant, an incipient angiosperm mangrove species (Chapter 5).

Mine remains

The mine types of morphological classification correspond to distinctive feeding habits such as the two-stage mine development (*Distigmonoma*) in association with peripheral frass deposition, characteristic of gracilariform mines (Lepidoptera: Gracilariidae) or the remnants of fibrovascular system and frass scattered around the mine indicating a sawfly miner (Hymenoptera: Tenthredinoidea). The coleopteronomes are recognized by their adherence to the stronger mines and by persistent egg remains, a rare feature in the other mining groups (except in Lepidoptera: Tischeriidae, in which it is associated with the trumpet shape of the mine).

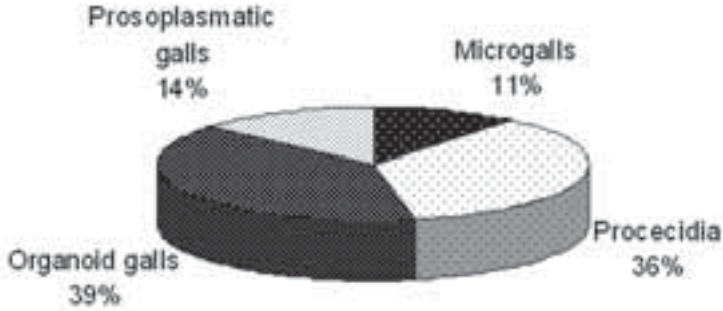

Fig. 13. Contributions of morphological groups to the gall assemblage of Gerofit.

The digitate asteronomes with double rows of frass pellets are quite similar to those of extant Agromyzidae, Diptera, supposedly a younger group of higher flies. However, some evolutionary conservative genera (*Phytoliriomyza*) are miners of bryophytes and ferns, of which *Cyathea* appeared before angiosperms (Spencer, 1990). The whole-leaf mines with epidermal windows are also assigned to dipteronomes, of Anthomyiidae probably. Stomonomes with a leaf pieces cut out for case construction are convincing evidence of temporary moth miners (Chapter 10).

With exclusion of occasional one-time occurrences, few mine types represent the monophagous habit. Notable among them is a modern-looking *Troponoma curvitracta*. Here, as in the Cretaceous gall forms, monophagy associates with morphological advancement.

Irrespective of the provisional taxonomic assignments, the Cretaceous mine assemblage of Gerofit exhibits both strategies of the present day mine construction, blotch mining and linear mining. Blotches prevail over linear tracks in terms of abundance and diversify of both the miners and their host plants (Fig. 14). This situation is opposite to what is typical of the present day mining communities (e.g., Hering, 1957).

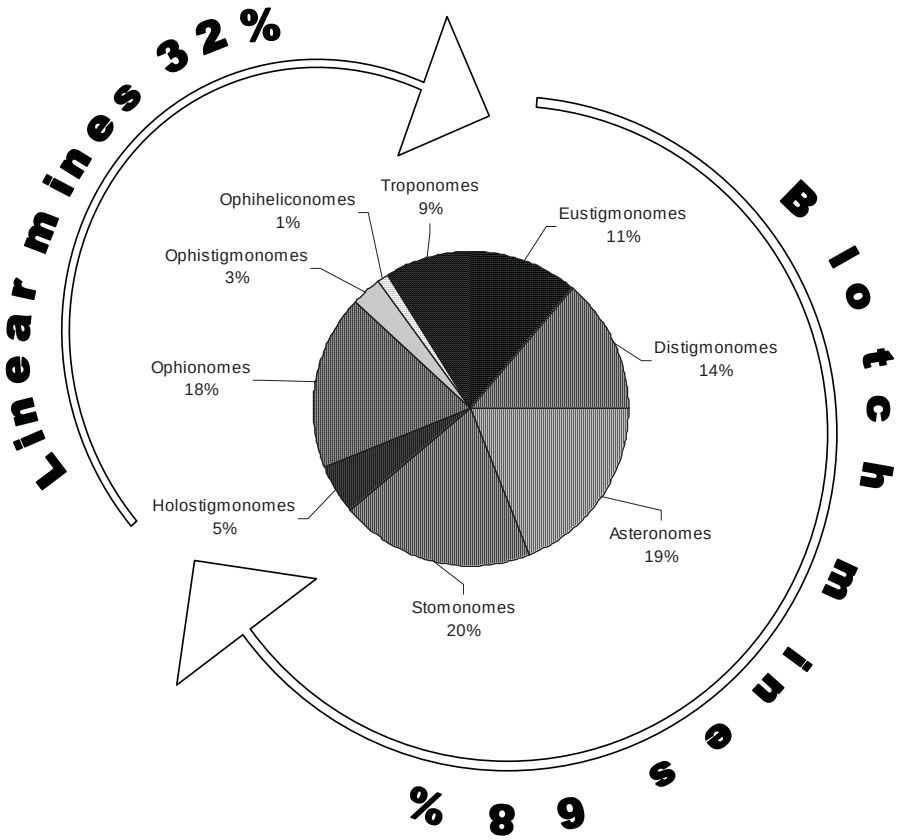

Fig. 14. Contributions of morphological groups to the mine assemblage of Gerofit.

Another distinction is that the combined linear-blotch mines (ophistigmatonomes) are exceedingly rare in the Cretaceous assemblage, the linear segment being either negligibly short or altogether lacking, which means that the hatching larvae immediately took to blotch feeding, whereas in the present day ophistigmatonomes, the blotches typically mark developmental changes in the feeding habits. The area and depth of the blotches increase at the later stages of mine construction, their expansion being related to the growth and mandibular development of the larva on the one hand and to the lower nutritive quality, compensated by the quantity, of the ageing leaf tissues on the other.

Insofar as blotches are more destructive for leaf functions than linear tracks, a high ratio of stigmatonomes to ophionomes in the Cretaceous trace assemblage is evidence of a low co-adaptive status in the same way as the prevalence of organoplastic gall effects (above). This complies with such features as:

(1) The whole leaf area – whole depth mines (*Holostigmonoma zebrina*), some with epidermal windows (*Holostigmonoma fenestrata*).
(2) The incidents of petiole to midrib (primary vein) mining causing leaf stunting and deformity (*Ophionoma digitata* on *Eocercidiphyllites glandulosus*).
(3) The rarity of frass-less mines representative of epidermal sap feeders, in conjunction with
(4) The absence of typical serpentine tracks, the most parsimonious mine construction in terms of the track length/area ratio (approached, but not typically represented by *Ophiheliconoma resupinata* and *Troponoma curvitracta*).

A number of mine remains bear unequivocal evidence of mine predation witnessing top-down regulation of the leaf miner community (Chapter 10)

10. Host plant – arthropod interactions

Egg sets on the Albian leaves, although belonging to non-phytophagous insects (Odonata), are nevertheless of some bearing on paleoecology of early angiosperms. The pre-Cretaceous records of the kind represent eggs inserted in stems of equisetalean plants or in drifted plant remains. The habit of ovipositing on leaves might have been acquired with the advent of angiosperms (reviewed in Krassilov *et al*., 2007). In Odonata, larvae hatching on leaves fall in water or on wet ground or they perish. In view of controversial interpretations of early angiosperm habitats, it may be significant that, as configuration of the scars suggests, the eggs were inserted in still growing, rather than shed leaves, thus unambiguously indicating a waterside habitat of Albian angiosperms.

The apical cut-outs on the Albian gymnosperms are the most damaging form of leaf handling that was not found later in the history of the regional plant – arthropod communities. They might have been inflicted by some unknown non-folivorous insects. The marginal cut-outs are like those of buprestid beetles, in which the habit of cutting leaf pieces with pupation cocoons is presently widespread in the tropics. This traumatic form had appeared on angiosperm leaves in the Cenomanian and was still present, although scarcely prominent, in the Turonian.

Although almost each leaf in the collection of 1500 fossil plant specimens from Gerofit bears traces of arthropod feeding and/or habitation, the identifiable phyllostigmas occur on 10 leaf species only, eight of which are abundant (*Dewalquea gerofitica, Nelumbites aravensis*) or common (*Eocercidiphyllites glandulosus, Eudebeya angusta, Menispermites cuspidentatus, Platanervia integrifolia, Platydebeya papilionacea, Typhacites negevensis*) and two are rare (*Retrodewalquea pendens, Yammelechia superba*).

The immediately evident regularity of plant – arthropod interaction in the Turonian is that the leaf parasites attacked the common plants species in the first place. At the same time, mine morphotypes on the rare leaf species (e. g., *Apostigmonoma fibrosa* on *Yammelechia superba*) are different from those on the common plant species.

Another striking feature is the ubiquitous co-occurrence of different type phyllostigmas, with up to five morphotypes co-occurring on leaves of *Dewalquea gerofitica*. In the present day mine communities, this feature is regulated in a complex way, first of all by competition between the mining larvae and between them and external feeders, as well as by the bottom-up and top-down regulations (Faeth, 1980; Hawkins, 1988). As a rule, crowding increases competition between the mining larvae and their interference with the externally feeding larvae. However, larval interactions vary from cannibalism to cooperative gregariousness and synchronization of developmental stages (Hespenheide, 1991). Mine gregariousness decreases the host photosynthetic area, but also confers advantage by deterring external feeders that avoid mined leaves on account of their decreased palatability. In Gerofit the latter effect is obvious: the copiously mined leaves seldom show traces of external feeding, such as feeding

holes, hieroglyphic marks, etching marks, scratches, skeletonization, etc. Either the miners avoided ectophyllous feeding grounds, or the surface feeders avoided mined leaves because of their lower nutritional qualities, more probably the latter.

The bottom up regulation is administered by the plant host defense reaction, which either increases with the impact of miners, thus preventing their further crowding, or decreases, thereby allowing more parasites to join. The latter phenomenon is known as "weakness parasitism". It appears to have been widespread in Gerofit attesting to a relatively low level of co-adaptive interaction.

On account of their host specificity, parasitic arthropods are monophagous (on a single host species), oligophagous (on taxonomically related host species) or polyphagous (on unrelated host species). Taxonomic affinities of Cretaceous plants are based on both leaf and reproductive morphologies and seem confidently defined in the case of *Nelumbites* (Nelumbonales: Nelumbonaceae) and *Eocercidiphyllites* (Cercidiphyllales: Cercidiphyllaceae), both representing relict monotypic orders of extant angiosperms (Fig. 15). The leaf morphologies are fairly distinctive in *Menispermites* (Ranunculales: Menispermaceae) and *Platanervia* (Hamamelidales: Platanaceae). The *Debeya – Dewalquea* group of compound leaves is controversial, with putative affinities in the Menispermaceae, Platanaceae or Myrtaceae (reviewed in Kvaček *et al*., 2001; Krassilov *et al*., 2005) and possibly heterogeneous. For *Platydebeya*, the nearest morphological equivalents are found in the Sargentodoxacea, a small family related to Menispermaceae, whereas both *Dewalquea gerofitica* and *Eudebeya angusta*, apparently related, are found in association with flowers and fruits of myrtalean affinities. *Yammelechia* is provisionally assigned to the Myrtales as well on the basis of its distinctive leaf venation. *Typhacites* definitely represents a monocot with parallelodromous leaves of a reedmace aspect (Typhales: Typhaceae).

It must be taken into consideration that archaic extant families, presently assigned to separate, albeit related, orders, might have been less diverged in the Cretaceous, forming relatively close generic groups. Thus *Menispermites*, Menispermaceae seems closely related to *Nelumbites*, Nelumbonaceae, the latter family showing both foliar (broad peltate leaves with palmate venation) and floral (apocarpous heads, sunken carpels, peltate stamens) similarities to the Cretaceous platanoids. The Cercidiphyllaceae is akin to both Nelumbonaceae and Platanaceae on account of leaf venation, ochreic prophylls, apocarpy, and pollen morphology. These comparisons suggest that *Eocercidiphyllites, Nelumbites, Menispermites, Platanervia,* and *Platydebeya* might have belonged to a broad stem group of lineages evolving in the direction of respective families. The myrtoid group (*Dewalquea, Eudebeya, Retrodewalquea, Yammelechia*) is fairly distinct, although perhaps remotely related to the platanoids.

Insect traces may help in revealing affinities of their host plants in the case of oligophagous co-adaptations. Yet distinctions between oligophagy and polyphagy depend on the current concepts in plant phylogeny, controversial as they are. Leaf parasites may know better than plant taxonomists, but their pragmatic knowledge is concerned with a few morphological and a wider range of biochemical traits that are acquired in the course of plant – insect interaction and are potentially as homoplastic as any others. Still it may turn out significant

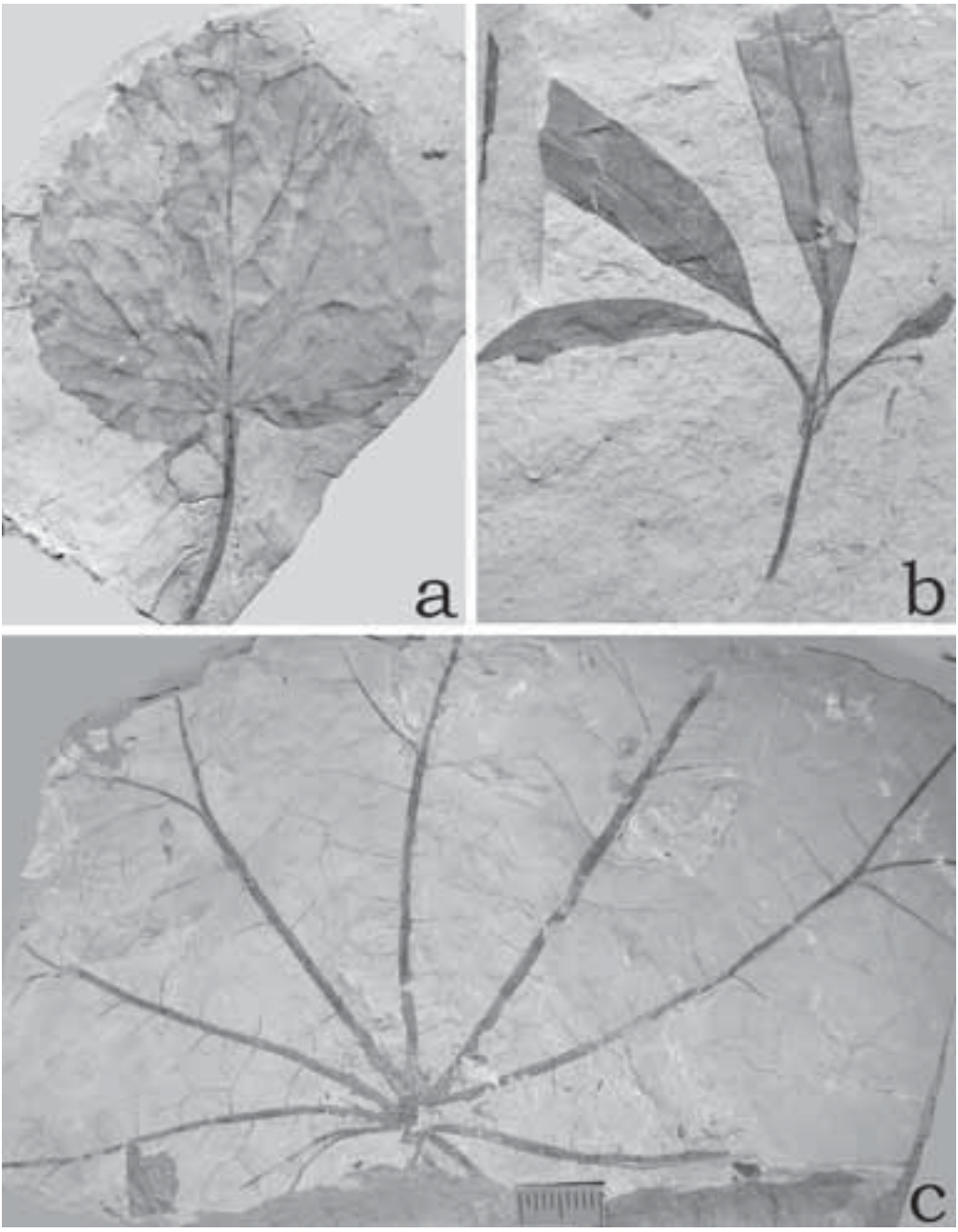

Fig. 15. Host leaf types: (a) deciduous *Eocercidiphyllites glandulosus* of an inland plant community, IG1-999; (b) compound *Dewalquea gerofitica*, IG1-861, representing the incipient mangrove wetlands, and (c) peltate *Nelumbites aravensis*, IG1-29, of freshwater wetlands.

in this respect that, in our material, leaf genera of the ranunculoid – platanoid group share commonly occurring conspecific phyllostigmas between themselves mainly, while sharing occasional phyllostigmas only with members of the myrtoid group (Table 1). The instructive occurrences of supposedly oligophagous phyllostigmas occurring and equally common on two plant hosts only involve *Platanervia* and *Platydebeya* in two cases (*Costaeon flexum* and *Asteronoma expansa*). Such trace occurrences strengthen morphological arguments for phylogenetic relatedness. Yet for the leaf parasites, ecological relatedness of their host plants might have been as mandatory as the phylogeny.

Ecologically, *Nelumbites* and *Typhacites* definitely came from aquatic/wetland communities of quite modern aspect (Chapter 5). *N. aravensis* had two types of leaves, floating and emergent, on rhizomes with ochreic prophylls, as in extant *Nelumbo nucifera*. *Eocercidiphyllites glandulosus* represents typical long-petiolate aspen-like leaf morphology typical of temperate deciduous trees and similar to those of extant *Cercidiphyllum japonicum*, a canopy tree in the mountain forests of eastern China and Japan. Platanoids apparently maintained their ecological niche of deciduous riparian trees from the Cretaceous to the present. Large peltate *Menispermites cuspidentatus* and the broadly trifoliate *Platydebeya papilionacea* might have been shed by understorey shrubs or climbers of the riparian community. For the xeromorphic *Dewalquea – Eudebeya* group, ecological inference is based on taphonomic, rather than morphological, clues. These leaves are abundantly preserved in the root zone, accompanied by the cryptoviviparous fruit remains. This assemblage is interpreted as a species-poor primordial angiosperm mangrove.

It can be inferred from the data presented in Table 1 that trace assemblages were different in the mangrove and inland plant communities. The total number of phyllostigmas is much higher on *Dewalquea gerofitica* than on any other host species, yet the numbers of shared phyllostigmas is only slightly higher, indicating a large proportion of phyllostigmas occurring on this species alone (either monophagous, or occasional). Also more types of phyllostigmas common on *D. gerofitica* are shared with *Eudebeya angusta*, putatively a member of the same plant community, and with *Nelumbites aravensis* of a back-mangrove wetland community than with any host species from the inland terrestrial community. Other noteworthy features of the phyllostigmatic assemblage on *D. gerofitica* are:

(1) Despite the abundance of phyllostigmas found on this plant only, evidence of monophagous adaptation is slim (except for *Costaeon schizmatum*, the midrib splitting gall), because the majority of phyllostigmas are occasional (one-time occurrences); the common occurrences constitute only ¼ of all phyllostigmas found on this leaf type;

(2) Each parasitized leaf bears more than one, and not infrequently up to five different types of phyllostigmas (Figs. 16, 17), which indicates a high tolerance for co-occurring parasites. This in turn suggests that (a) the plant resistance had not appreciably increased, maybe decreased even, with the increasing impact of leaf parasites, witnessing a weak bottom-up regulation of parasitic community on the part of the host (the “weakness parasitism”), and (b) the co-occurrences of para-

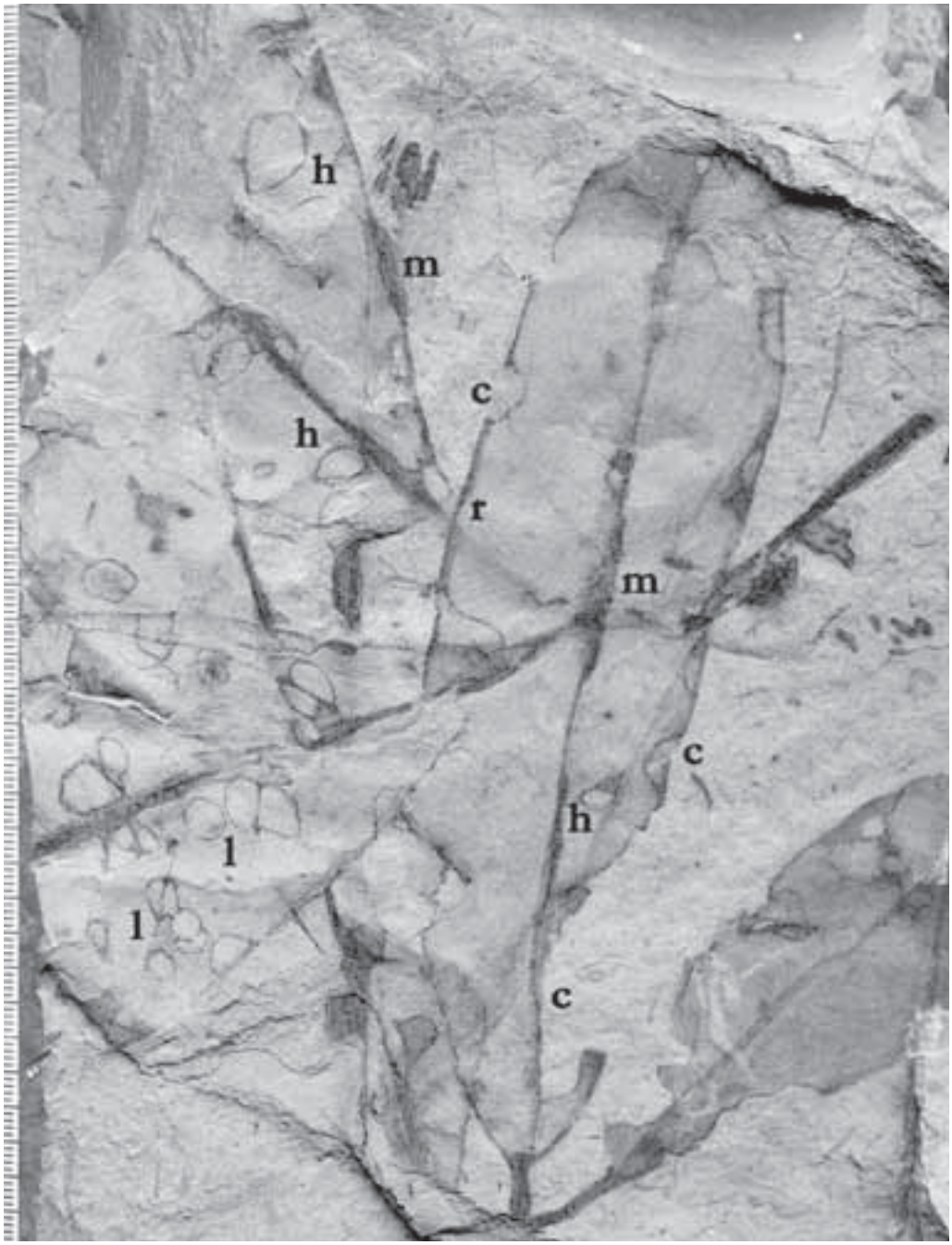

Fig. 16. Co-occurrence of (l) lenticular, (m) midrib swelling, and (r) margin roll galls with (h) rounded –elliptical feeding holes, and (c) marginal semicircular and irregular half-blade deep cut-outs on the amassed leaves of *Dewalquea gerofitica*, IG1-642, Gerofit.

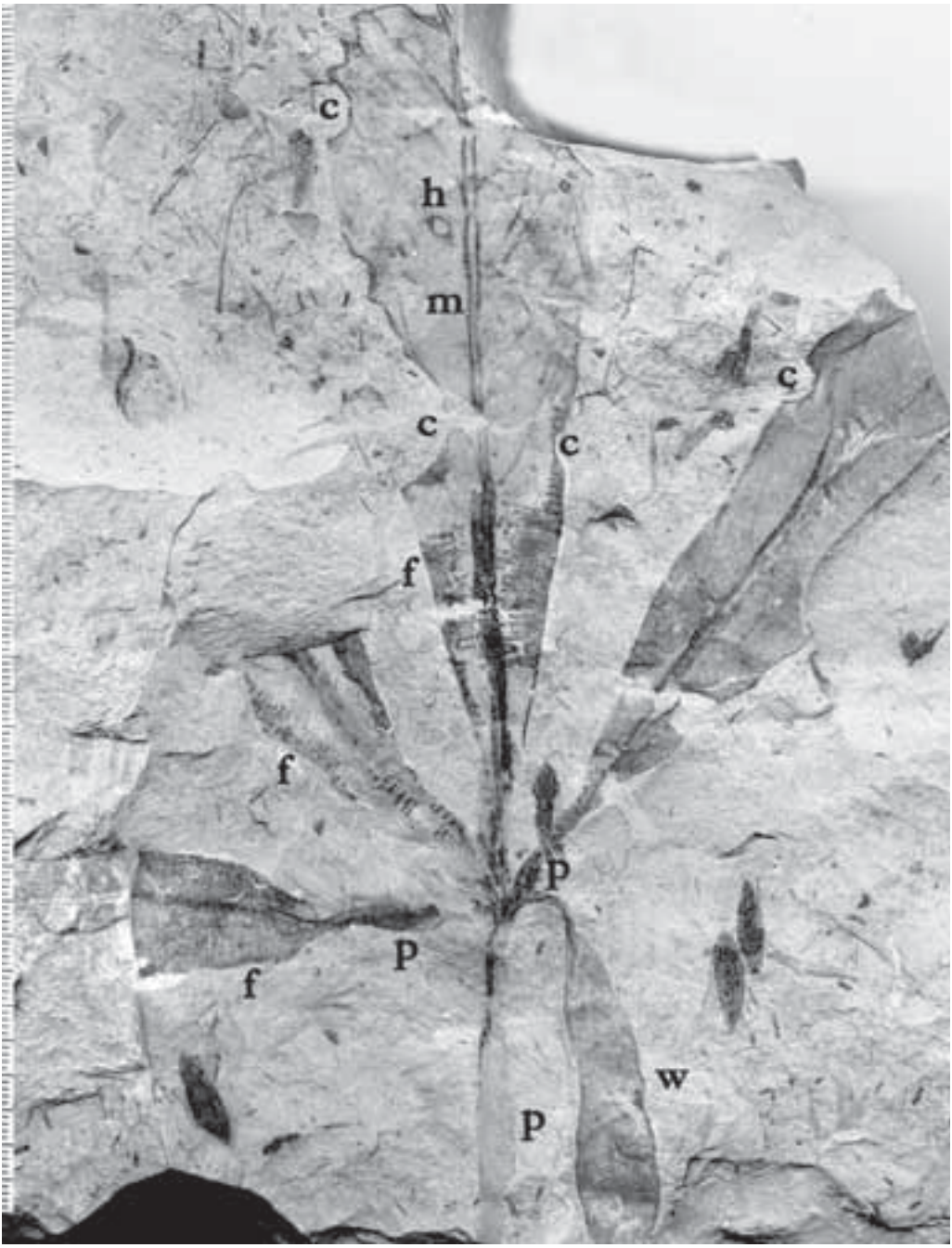

Fig. 17. Co-occurrence of (p) petiolar gall extending to petiolules, with (w) one leaflet wilting, (m) midrib-splitting gall, (f) whole-leaf dipteronome marked by transverse strings of frass pellets, (h) feeding holes, and (c) marginal cut-outs on *Dewalquea gerofitica*, IG1-539, Gerofit.

sites was not effectively constrained by their joint attractiveness to predators and parasitoids, indicating a likewise ineffective top-down regulation;

(3) Traces of mine predation are relatively rare on *D. gerofitica* confirming that predators and parasitoids had not exercised any significant top-down regulative role;

(4) A relatively high frequency of systemic damages, such as midrib splitting, affecting vital leaf functions, as well as the whole-leaf mine blotches *Holostigmonoma fenestrata* and *H. zebrina* comply with the other features of ineffective host – parasite feedbacks;

(5) Mass accumulation of heavily damaged leaves on a few bedding planes may indicate periodic defoliation of *D. gerofitica* plant.

A general impression is that of a low degree co-adaptive constrains over the leaf parasite community on mangrove plants. One of the reasons might have been the overdominance of a single species, *D. gerofitica*, in the low-diversity community of incipient angiosperm mangroves still poorly adapted to the physical stresses of their recently colonized littoral habitats. It must be mentioned, however, that defoliation induced by phytophagous Lepidoptera sometimes occurs in the present day mangroves as well (Hogarth, 1999).

In contrast, the phyllostigmatic assemblage on the inland broadleaves, *Eocercidiphyllites, Menispermites, Platanervia, and Platydebeya*, exhibits certain features of a more advanced and better co-adapted plant – arthropod community. These are:

(1) Evidence of specialized monophagous (*Cephaloneon squamosum* on *Menispermites*) or nearly monophagous (*Asteronoma arachnoids* on *Platydebeya papilionacea*) and oligophagus (the common occurrences of *Stomonoma crenulata* on both *Eocercidiphyllites globulosus* and *Platanervia integrifolia*) feeding habits;

(2) A complex prosoplasmatic gall form *Cephaloneon squamosum* and the likewise complex communal mine forms, *Symphyenoma* spp.;

(3) The relatively frequent traces of mine and gall predation (*Stigmatophaga perforata* on *Cephaloneon squamosum*, *S. digitata* on *Asteronoma arachnoids*, *S. punctata* on *Ophionoma* sp.), correlated with a relatively low on leaf co-occurrence of different phyllostigmatic types indicating an appreciable effect of top-down regulation;

(4) A relatively high incidence of temporary mining consummated with case construction (*Stomonoma crenulata*, *Folicasa cuspidata* on *Platydebeya papilionacea*, *F. inflata* on *Platanervia integrifolia*), here considered as a specialization for both endophytic and ectophytic feeding developing under the joint constrains of the bottom–up and top – down regulation.

More mine types, including those of temporary mining, are shared by the dryland broadleaves with *Nelumbites aravensis*, an aquatic species with above-water broadleaves, than with *Dewalquea gerofitica* and the other mangrove species.

Temporary mining

In distinction from the permanent mining from hatching until pupation, the temporary mining is restricted to a certain (early, with few exceptions) developmental stage, after which the larva lives openly or under a shelter of folded leaf margin or else in the leaf cases

constructed for this purpose. Such life styles are commonly considered as less specialized than permanent mining (Hering, 1951). However, temporary mining is a complex behavior, including larval adaptations to both endophytic and ectophytic environments.

Generally, mining habit is advantageous for herbivorous insects in terms of food availability and protection, but, like other parasitic habits, it incapacitates defense responses making the larva most vulnerable to both internally and externally induced changes of foliar environments, such as suppression by the host plant wound response, ageing (hardening) of leaf tissues, leaf abscission, predation or parasitoid attacks. Temporary mining opens a way out of this controversy, sheltering young larva at the most sensitive stage and skipping the adverse effects of protracted mining afterwards.

Plant injury from a short-time mining is minimal (unless mine density per leaf is too high), at the same time eliciting the systemic defense response against parasite attacks (Zhu-Salzman *et al*., 2005). In this sense, short-time mining can be seen as a co-adaptive plant – insect interaction.

Temporary mining is far less common than permanent mining, mostly occurring in Lepidoptera and, in this order of specialized miners, confined to a few families alone (the Incurvariidae, Coleophoridae, Heliozelidae, and Gelechiidae mainly). In *Parornix* and some other temporary miners the caterpillar occasionally goes on mining until pupation (Hering, 1951). The origin of temporary mining from the permanent is as problematic as the other way round. Such pending problems in evolution of behavior require chronological information.

The Gerofit material provides abundant evidence of temporary mining, both the cut-outs for case construction in the mining areas and the attached larval cases. The most spectacular example is *Stomonoma dimorpha*, a set of small blotches on *Nelumbites aravensis* (Pl. XLVI). The blotches vary in size and frass deposition, but are certainly the work of one and the same mining species. The smaller blotches, occupying central part of the leaf blade, are of irregular shape, with abundant frass grains scattered over the blotch or occasionally concentrated in the folded peripheral zone. In all such mines, a leaf piece is cut out, leaving a curvilinear, sharply outlined hole. The larger blotches are rounded-polygonal, consisting of a broad elliptical or somewhat angular central cell encircled by an incomplete ring of smaller meshes marked by deeply impressed higher order venation. The central cell is flat, smooth, clean of frass that is collected over the marginal fringe. Fine radial striation over the folded fringe apparently represents the spinning silk threads.

A comparison with the mining habit in *Coleophora* (Lepidoptera: Coleophoridae) suggests, that the first type blotches are constructed by young larvae (corresponding to the first instar larva in *Coleophora*) cutting their first case out of them. As in *Coleophora*, the early cut-outs occur in the central part of the leaf blade (Needham *et al*., 1928). Later in development, the larva resided to mining producing larger blotches (devoid of frass in *Coleophora*, but with peripheral frass deposits in *Stomonoma dimorpha*) around the previously mined area and delineating their second case. In our material, the larger blotches with a marked out central cell may correspond to this stage.

Gregarious case-constructing miners make cut-outs the configurations of which are sometimes typical of a genus or a family, such as *Stomonoma multiforata* on *Eocercidiphyllites glandulosus*

(Pl. XLIX, figs. 1, 2). perforated by numerous elliptical holes marked out by minutely dentate borderlines, which look exactly as the leaf pieces cut out for case construction from the mine epidermis of broadleaved plant species by extant *Antispilina*, Heliozelidae (Hering, 1957). *Stomonoma crenulata*, the curvilinear crenulate-cuspate cut-outs on the same leaf species (Pl. XLVIII, figs. 1–4), appear exactly as birch leaves after incurvariid case construction (Hering, 1951, 1957).

Larval cases attached to the same or different leaves are also found in Gerofit collection. Remarkably, one case type, *Folicasa cuspidata*, is constructed of cuspate leaf stripes like the cut-outs of *Stomonoma crenulata*. The case is attached at about 30° to the leaf margin, which implies the mouth plane inclined at about 15° to the leaf margin ("mouth type II") and is comparable to the "pupa type" coleophorid cases (Hering, 1951), but with no close equivalents among the living species as far as the arrangement of the leaf pieces is concerned. *Folicasa inflata* and *F. tubularis* represent different types of coleophorid cases, one attached at the petiole insertion of *Platanervia integrifolia*, the other apically on *Dewalquea gerofitica* (Pl. L, figs. 1–3).

Folicasa spinulata on *Nelumbites aravensis* (Pl. X, Figs. 1, 2) shows three distinct angular contours in line across the leaf blade marked out by a thin sharply angular thread-like borderline with staple-like dents at the angles, exhibiting a faint venation tracery. They resemble early cases of *Paraclemensia* (Lepidoptera: Incurvariidae) that are spun to the leaf allowing the larva to feed under the cover (Needham *et al*., 1928).

Altogether, the traces of temporary mining constitute 22% of all mine occurrences in Gerofit assemblage, thus attesting to a considerable diversity of temporary miners. Although taxonomic affinities of Cretaceous temporary miners are problematic, their behavior characters appear quite modern. Extant equivalents can be found for all types of temporary mining and case construction found in the Cretaceous, indicating that evolution of the trait has been essentially accomplished during the mid-Cretaceous. This in turn attests to a high adaptive value of the temporary mining habit in the leaf parasite communities on the early angiosperms.

In Gerofit, traces of case construction occur on plants of two ecological groups: (1) the broadleaved plants of deciduous leaf aspects as *Platanervia inegrifolia* and *Eocercidiphyllites glandulosus*, inhabiting the riparian to dry land sites back of the more abundantly represented coastal plants (*Dewalquea*, *Eodebeya*) that are heavily mined, yet providing no evidence of temporary mining, except a tubular larval case, possibly cut out from a different leaf, and (2) the wetland – aquatic plants with emergent leaves (*Nelumbites*).

Just such habitats might have promoted (although for different reasons) a short-time mining habit that in deciduous plants is advantageous on account of rapid leaf ageing (making leaf tissues hard and less palatable for a miner operating over a restricted area of a single leaf). Early leaf shedding cause high rate mortality of miners (reviewed in Hespenheide, 1991) conceivably conferring a selection pressure for abbreviation of mining stage. Temporary mining is likewise advantageous under high risk of being chocked in the mine by flooding water on emergent leaves of aquatic plants.

In addition to the bottom-up regulation by the host plant – mining insect interaction, mine predation also impels a shorter mining life, because early mines are less conspicuous for the visually attracted predators. A number of leaf mines form Gerofit locality bear traces of preda-

tion, suggesting that this factor might have come into play already (below). Remarkably, both temporary mine and predation traces come form the inland broadleaved and freshwater aquatic plant communities mainly, being exceedingly rare in the coastal mangrove community.

Predation

The plant – parasite interaction is a two-level trophic system superimposed by the third level of mine predators and parasitoids. The system is regulated from bottom up, by plant responses, and from top down, by predation (Faeth, 1985).

Mines are opened for larvae mainly (although mines are sometimes opened by the free living folivorous larvae, the mined leaf tissue is nutritionally inferior to the leaf itself), whereas galls can be taken out also for the sake of their nutritive tissue. Mine predators are ants and birds mainly, but also mites, lacewings, wasps, bugs, and beetles. Predators seem to affect mining strategies in different ways, such as reduction of mine densities (because predation increases with the number of mines per leaf), restriction of mining to early developmental stages, at which the mines are less conspicuous for the visually attracted predators, such as birds, or mining over stronger veins that conceal the channels (reviewed in Hering, 1951; Hespenheide, 1991).

Unequivocal evidence of mine predation in the Gerofit community are predation traces on the asteronomes, in particular, the whole mine cut-outs (*Stigmatphaga digitata* on *Asteronoma arachnoids*) and the large feeding holes with crenulate margins on both *A. digitata* and *A. arachnoids*, as well as on the densely coiled linear mine *Troponoma festunata* and on the gall *Cephaloneon squamosum*. A different type of small peck-like perforations are found on long linear tracks winding over the leaf blade.

Asteronomes seem to have been especially attractive for predators, because about half of them are cut out or perforated. In specimen IG1-138, an irregularly lobed hole on *A. arachnoides* retains configuration of the mine, taking out the whole central part and extending over the arms, the tips of which, with characteristic arrangement of frass pellets, are left on the leaf Pl. LI, fig. 2). The lobes over the arms of the mine vary from low arches to broad wedges tapered into narrow slits up the arm. The predator might have worked from the middle into the arms, failing, however, to cut them out as precisely as the modern mine predators, ants or birds, would by excavating the entire mine.

Another asteronome, IG1-600, also on *Platydebeya papilionacea*, shows a bunch of digitate arms with frass pellets, the rest of the mine being cut out leaving an irregularly lobed hole between lateral veins. The holes are bordered by the sinuous series of smooth arcuate bites about 1 mm long, 0.2 mm deep. A larger *A. digitata* is cut in the middle by a large nearly circular hole with microcrenulate margin of the kind produced by a predator with hooked mandibles. Three smaller holes mark additional cut-outs over the radial arms indicating that there were several larvae in the mine (as in the communal mines of *Pegomyia*, Diptera: Anthomyiidae) picked out by the predator.

The angular holes on a broad subpeltate leaf of *Menispermites cuspidentatus* Krassilov, specimen IG1-753, mark the sites of cut-out cephaloneon galls occurring on many specimens of such leaves ((Pl. LII, fig3 ; Fig. 25). The galls are surrounded by the dark pitted callus

fringes of large hypertrophied cells that remain intact around the holes when the whole body of the gall is taken out.

Troponoma festoonata on *Dewalquea gerofitica* has its middle part cut out leaving a rounded elliptical hole surrounded by the radial festoons of the looping filiform tracks ((Pl. XXVI, fig. 1). The borders of the central hole are broad arches, about 2 mm long, 0.2 mm wide, divided by shallow notches, with minute crenulations on the callus fringe.

A different kind of predation activities is represented by small rounded or elliptical holes over the winding linear mines on *Platydebeya papilionacea*. The mine tracks are sinuous, marked by discontinuous frass lines. The holes are solitary, rather evenly spaced over the track coils, or paired, occasionally contiguous, about 0.4 mm in diameter, with thick patchy borders (Fig. 25). Another leaf on the same hand specimen is mined over the whole surface by the tortuously coiled tracks that are more densely pecked or punctured, with the holes mostly elliptical, oblique to the mine, concatenate or contiguous, cutting an arcuate slit over an entire coil of the track (Pl. LII, figs. 1–3).

The following considerations pertain to the role of mine/gall predation as a factor of top-down regulation in Gerofit community. On account of gall etiology, the essence of co-adaptation in the plant – cecidozoan systems is restriction of gall effects, ideally to the gall body (the prosoplasmatic expression) itself. The logic of the system dictates that in the course of evolution the prominence of gall body would increase at the expense of organoid effects. As a consequence, the gall bodies are becoming more conspicuous to predators, and the top down regulation of plant – cecidozoan systems gains in importance. Since organoid galls strongly prevail in the Cretaceous Gerofit assemblage, gall predation should be rare, which is actually the case. However, the morphologically most advanced of a few prosoplasmatic galls, the scaly cephaloneon on the broadleaved *Menispermites cuspidentatus,* is often predated.

In contrast, the proportion of mines bearing unequivocal predation traces, about 9 percent, is by no means trifle. Both blotches and linear tracks are predated with a notable preference of the former (in extant mines, the adaptive advantages of blotch *vs.* linear configurations are uncertain in this respect). The most frequently attacked asteronomes are fairly conspicuous on fossil leaves and must have been so on the living leaves as well owing to the great spatial extent of their digitate arms speckled with frass pellets. That such mines have been preferred may indicate a predominantly visual detection. The spidery mines are cut-out in the middle and at various extents over the arms, with narrow slits reaching to the tips. Such slits are observed on the holes of cut-out cephaloneon galls as well (Fig. 25). Ants and birds are the most widespread present day mine predators, taking out the whole mine. Yet extant ants would more precisely follow the perimeter. The marginal slits may indicate shearing with the beak.

The symmetrically disposed holes on the supposedly communal asteronomes with several larvae simultaneously at work likewise attest to visual orientation of the predator. Bite marks preserved as crenulations at the border of the holes are of diverse shapes and dimensions indicating that this type mines were cut-out by more than one predatory species, some unrecognized orthopteran or coleopteran insects probably, differing from each other in their mouth part morphologies.

Among the linear mines, only those winding over large leaf areas are predated, which may indicate a visual detection from flight. The mines were pecked, punctured or thrust open by miniature beaks or rostra. Relative rarity of such mines indicates that predation selection for mine track configurations might have been at work already.

Predation traces may indicate top down regulation in the system of plant – insect interaction, but only indirect evidence is available for provisional assessment of its relative efficiency in conjunction with the other regulation circuits. The following features of the mine trace assemblages are potentially informative in this respect:

(1) In the plant collection of about 1500 specimens about 70 percent bear traces of incipient to advanced mine construction. In living plants, such abundance of mine traces would mean an outbreak of leaf mining that can be experimentally invoked by elimination of mine predators (Hickley, 1963). Since mine predators were there in the Turonian assemblages, we have to surmise that their efficiency as top down regulators must have been inferior to what it is now. At the same time, the frequencies of the mine traces are considerably higher in the coastal narrow-leaved *Dewalquea – Eudebeya* assemblage than in the inland broadleaved *Eocercidiphyllum – Platanervia – Platydebeya* assemblage, being negatively correlated with the occurrences of predation marks in these assemblages.

(2) Leaf morphological evidence of ant attraction, such as marginal glands, exists for the inland leaf assemblage (the prominent marginal glands in *Eocercidiphyllum* and *Platydebeya*), but was not hitherto recorded in the coastal assemblage.

(3) Mine morphological evidence of protection against visual detection is a restriction of mined area by the tight helical coiling of the mine track that is rare in Gerofit assemblage relative to its present day ubiquity in all the major groups of mining insects. In the inland broadleaved community, the individual blotch mines are rather small, but a whole leaf (leaflet) mining with abundant frass deposition in the mine (making it conspicuous when most of the leaf tissue is excavated) is recorded in the coastal assemblage.

(4) The proportion of midrib miners in Gerofit, about 30 % of all mine types, is exceptionally high by the present-day standards. Strong veins are impediments for the majority of invertebrate predators (but not for *Chrysopa*: Hering, 1951) and they scarcely protect from acoustic detection guided by the sounds of feeding larva (Sugimoto *et al*., 1988), unless the larva resided to the midrib when not feeding.

(5) Early transition from endophytic to ectophytic life is adaptive as an escape from predation, the risk of which increases with the size of mine and to the end of the season when the free leaving prey is scarce. In the case of the most frequently predated arachnoid asteronomes, the smaller ones (Pl. LI, fig. 1) more often escape predation than the larger, suggesting selection for smaller size – shorter mining period.

We conclude that, on account of indirect evidence, the role of predation as a factor of top-down regulation might have been significant in the Turonian plant – arthropod communities already. Leaf parasitism in the more stable inland communities was more effectively constrained in this way than in the incipient mangroves, but generally the regulation efficiency was much lower than in the present day communities.

11. Environmental variables

Our comparison of the coastal and inland plant – arthropod assemblages (Chapter 5) has shown significant differences in the diversity and on leaf density of phyllostigmatic morphotypes, as well as in the instances of different mine co-occurrence, being appreciably higher in the coastal community. These features suggest "weakness parasitism", or a deficiency of resistance feedback on the part of the host plant, while the instances of mine predation, implying a top-down regulation of parasitic community, are exceedingly rare. The most damaging leaf galls causing dissociation of midrib bundles, occurs on the dominant plant species of this assemblage, *Dewalquea gerofitica*, representing an incipient angiosperm mangrove community inhabiting the unstable intertidal zone at the time of large-scale sea level fluctuations.

At the same time, the advanced types of galls, such as the scaly cephaloneons, and the majority of symphyenomes come from the inland assemblage that also excels in the instances of mono- and oligophagy, as well as temporary mining. Such co-adaptive features are accompanied by the diverse traces of mine and gall predation. A higher plant species and life form diversity of the inland assemblage indicates a complex vegetation structure of relatively stable physical environments. The dominant species most frequently attacked by the leaf parasites, had leaves of a typical deciduous aspect.

We conclude that the more stable inland communities might have been more effectively constrained by both bottom-up and top-down regulation mechanisms and were relatively advanced in terms of plant – arthropod co-adaptation. Deciduousness of the broadleaved inland vegetation made a vital distinction from the evergreenness of the mangroves, for which occasional traumatic defoliation is suspected on taphonomic evidence.

Climatic conditions are inferred from paleobotanical data (Krassilov *et al*., 2007) revealing a catenic succession of evergreen and deciduous plant communities (Chapter 5), as in the present day warm temperate – subtropical vegetation of southern Mediterranean or the northern Gulf of Mexico embankments. The coastal community of Gerofit is comparable with the stunted extratropical rather than the fully developed tropical extant mangroves. The association of mangroves and marshes is likewise atypical of the tropical sea-shore vegetation, but occurs in northern Florida at about 30°N. The back-mangrove aquatic vegetation was species rich and immensely productive, as in northern Israel today. The inland broadleaves (in particular, *Eocercidiphyllites globulosus* and *Dicarperonia inaequiloba*) have their ecological equivalents in the deciduous broadleaved forests of warm-temperate to subtropical lowlands and in tropical highlands of eastern Asia. Yet, in Gerofit locality, such plant remains are too common among the transported plant material to be brought from distant highlands. More realistically, they can be assigned to a lower slope vegetation locally intruding the riparian platanophyllous wetlands.

Since behavior is more dynamically related to climate than species ranges, trace assemblages are potentially more informative as climate indicators than taxonomic compositions of ether plant or insect body fossil assemblages. However, for these potentials being realized, much more must be learned of climatic influence upon the plant – insect interactions. Generally, the geography of phytophagous parasites is determined by the chorology of their plant hosts. Observations show, however, that parasite ranges tend to be narrower than their host plant ranges. For the "weakness parasites" the reason may be that they are spread over stressed habitats where their host plants are not in their prime, whereas for the "health parasites" the contrary may be the case.

The leaf surface environments are as critical for the leaf parasites, as the ambient environments of their host plants. The major variables of leaf environments are the leaf longevity, phenology, including the timing of leaf unfolding, chlorophyll degradation and leaf shedding, as well as the leaf growth patterns, venation, stomatography, distribution of trichomes, and nitrogen content. On arboreal plants, parasites are to a different extent affected by the crown shape. Hard sclerotic and hairy leaves are usually detested by the miners, many of which prefer shade leaves to sun leaves, but such preferences vary among species. With trophic conditions deteriorating towards the periphery of the host plant ranges, the leaves tend to become smaller and stronger sclerified, which makes them less palatable for the miners.

The discrepancies of host plant and parasite ranges are enhanced by the parasitoid and predation pressures inflicting radical behavioral changes. The higher rates of predation (in particular, by ants) in the tropics may encourage transition from surface feeding to mining (as in the southern representatives of ectophytic species in the Gelechiidae: Hering, 1951). A far greater diversity of buprestid beetles constructing pupal cases in the tropics is ascribed to the same factor (Hespeheide, 1991).

Geographic differentiation of leaf parasite communities is commonly discussed in terms of relative diversity and abundances of taxonomic groups. A widely accepted generalization of such analyses is that both diversity and abundance of mining Coleoptera, in particular, the buprestids and hispines, considerably increase down the latitudes (Hespenheide, 1991). The tropical hispines (Coleoptera: Chrysomelidae) mine over the wide range of plant growth forms in the tropics, whereas in the temperate zone they are confined to grasses mostly. Conversely, weevils of subfamily Rhynchaeninae are important miners in the northern temperate realm, but decrease to the south Contribution of sawflies (Tenthredinidae, Hymenoptera) likewise decreases with latitude being considerably reduced in the Mediterranean region relative to the central Europe.

The relative abundances of Lepidoptera and Diptera, each infesting the largest and nearly equal numbers of plant host families in Europe (Hering, 1951), strongly correlates with distribution of arboreal and non-arboreal vegetation. The sap-feeding gracilariids, in particular, *Phyllocnistis* strongly dominate the mining communities in the tropics, exploiting an increasingly wider ranges of host plants down the latitudes. Agromyzids, the major mining family in Europe, decline to the south in parallel with replacement of *Phytomyza*, a major

mining genus in the temperate realm, by *Melanagromyza* and *Ophiomya* in the tropics (Hering, 1951).

Prominent in the Albian and Cenomanian phyllostigmatic assemblages are the marginal cut-outs for pupal case construction characteristic of tropical buprestids in the first place. Such phyllostigmas are becoming far less common in the Turonian assemblage of Gerofit, for which our tentative taxonomic assignments suggest the leading role of cecidomyiids and aphids among the gall inducers, with a much lesser cynipid contribution (Fig. 11). The cecidozoan community thus appears temperate rather than tropical, in particular, on account of cecidogenous aphids, in which the succession of primary and secondary hosts betrays temperate heritage (Wool, 1984).

The diagram for a mining assemblage of northern Europe, based on numerical estimates in Hespenheide (1991), shows a significant prevalence of Diptera, with Lepidoptera second in abundance (Fig. 12b). In distinction, in Gerofit assemblage, about one half of the mines are lepidopteronomes, which is different from both temperate and tropical present day mining communities, the latter being typically dominated by Coleoptera (Hespenheide, 1981). Even if we underestimated coleopteronomes by order of magnitude, their occurrences are far too low for a tropical assemblage. Argomyzid mines prevail among the dipteronomes, whereas the occurrences of incurvariid mines is somewhat higher than those ascribed to gracilariids. The traces of temporary mining in our material are associated with temperate floristic elements, thus strengthening the conclusions based on paleobotanical evidence alone (Krassilov et al., 2005; Silantieva and Krassilov, 2006).

12. Systematic description of phyllostigmas

Morphological genera of phyllostigmas are distinguished on the basis of the functional morphology of traumatic leaf structures discussed in Chapter 7. Morphological species are the distinctive phyllostigmatic morphotypes under the morphogenera. Since phyllostigmas are preserved as fossil leaf structures, the botanical nomenclature seems more appropriate for them than the zoological, although the differences are unessential. The following genera and species of egg remains, procecidia, galls, mines, and secondary structures related to temporary mining and external feeding, including predation marks, are described in this chapter:

Group Ovisignata

Genus *Catenoveon* **Krassilov et Silantieva, gen. nov.**

Catenoveon undulatum Krassilov et Silantieva, sp. nov.

Genus *Sertoveon* **Krassilov, gen. nov.**

Sertoveon arcuatum Krassilov, sp. nov.

Sertoveon cribellum Krassilov, sp. nov.

Sertoveon scalarum Krassilov, sp. nov.

Sertoveon moniliforme Krassilov, sp. nov.

Genus Costoveon Krassilov, gen. nov.

Costoveon transfixum Krassilov, sp. nov.

Costoveon vergens Krassilov, sp. nov.

Costoveon adnatum Krassilov, sp. nov.

Genus *Margoveon* **Krassilov, gen. nov.**

Margoveon incisum Krassilov, sp. nov.

Margoveon sp.

Genus *Massoveon* **Krassilov, gen. nov.**

Massoveon globulosum Krassilov, sp. nov.

Genus *Transpiroveon* **Krassilov, gen. nov.**

Transpiroveon polygonatum Krassilov, sp. nov.

Ovisignata spp.

Group Procecidimorpha

Genus *Cupuleon* **Krassilov, gen. nov.**

Cupuleon caveum Krassilov, sp. nov.

Cupuleon nodulosum Krassilov, sp. nov.

Cupuleon craterellum Krassilov, sp. nov.

Genus *Foveon* **Krassilov, gen. nov.**

Foveon patellatum Krassilov, sp. nov.

Foveon astrellum Krassilov, sp. nov.

Group Cecidimorpha

Subgroup Catacecidimorpha

Genus *Emergeon* **Krassilov, gen. nov.**

Emergeon scabratum Krassilov, sp. nov.
Emergeon catenulatum Krassilov, sp. nov.
Emergeon spp.

Genus *Pustuleon* **Krassilov, gen. nov.**

Pustuleon gregarium Krassilov, sp. nov.

Genus *Lenticeon* **Krassilov, gen. nov.**

Lenticeon minusculum Krassilov, sp. nov.
Lenticeon agglomeratum Krassilov, sp. nov.
Lenticeon nervosum Krassilov, sp. nov.

Subgroup Prosocecidimorpha

Genus *Cephaloneon* **Bremi**

Cephaloneon squamosum Krassilov, sp. nov.

Genus Ceratoneon Bremi

Ceratoneon ovatum Krassilov, sp. nov.
Ceratoneon mucronatum Krassilov, sp. nov.
Ceratoneon (?) sp.

Subgroup Organocecidimorpha

Genus *Petioleon* **Krassilov, gen. nov.**

Petioleon inflatum Krassilov, sp. nov.
Petioleon ostiolatum Krassilov, sp. nov.

Genus *Costaeon* **Krassilov, gen nov.**

Costaeon flexum Krassilov, sp. nov.
Costaeon foveum Krassilov, sp. nov.
Costaeon capsulatum Krassilov, sp. nov.
Costaeon schizmatum Krassilov, sp. nov.
Costaeon blastoides Krassilov, sp. nov.
Costaeon sp.

Genus *Involuteon* **Krassilov, gen. nov.**

Involuteon compressum Krassilov, sp. nov.

Group Nomomorpha, leaf mines

Subgroup Ophionomata

Genus *Ophionoma* **Krassilov, gen. nov.**

Ophionoma paradroma Krassilov, sp. nov.
Ophionoma serranoides Krassilov, sp. nov.
Ophionoma digitata Krassilov, sp. nov.
Ophionoma arcuata Krassilov, sp. nov.
Ophionoma spp.

Genus *Ophistigmonoma* **Krassilov, gen. nov.**
Ophistigmonoma rectiserialis Krassilov, sp. nov.
Ophistigmonoma crassa Krassilov, sp. nov.
Genus *Ophiheliconoma* **Krassilov, gen. nov.**
Ophiheliconoma resupinata Krassilov, sp. nov.
Genus *Troponoma* **Krassilov, gen. nov.**
Troponoma crucitracta Krassilov, sp. nov.
Troponoma curvitracta Krassilov, sp. nov.
Troponoma festunata Krassilov, sp. nov.
Subgroup Stigmonomata
Genus *Eustigmonoma* **Krassilov, gen nov.**
Eustigmonoma amoeboides Krassilov, sp. nov.
Eustigmonoma ochrea Krassilov, sp. nov.
Eustigmonoma alternans Krassilov, sp. nov.
Genus *Distigmonoma* **Krassilov, gen nov.**
Distigmonoma fimbriata Krassilov, sp. nov.
Distigmonoma variegata Krassilov, sp. nov.
Distigmonoma oculata Krassilov, sp. nov.
Genus *Asteronoma* **Krassilov, gen. nov.**
Asteronoma arachnoides Krassilov, sp. nov.
Asteronoma expansa Krassilov, sp. nov.
Asteronoma helicoides Krassilov, sp. nov.
Genus *Symphyenoma* **Krassilov, gen. nov.**
Symphyenoma adcostalis Krassilov sp. nov.
Genus *Holostigmonoma* **Krassilov, sp. nov.**
Holostigmonoma zebrina Krassilov, sp. nov.
Holostigmonoma fenestrata Krassilov, sp. nov.
Genus *Apostigmonoma* Krassilov, gen. et sp. nov.
Apostigmonoma fibrosa Krassilov, sp. nov.
Genus *Stomonoma* **Krassilov, gen. nov.**
Stomonoma dimorpha Krassilov, sp. nov.
Stomonoma spinulata Krassilov, sp. nov.
Stomonoma crenulata Krassilov, sp. nov.
Stomonoma multiforata Krassilov, sp. nov.
Group Casasignata
Genus *Folicasa* **Krassilov, gen. nov.**
Folicasa cuspidata Krassilov, sp. nov.
Folicasa tubularis Krassilov, sp. nov.
Folicasa inflata Krassilov, sp. nov.

Group Trophostigmata

Genus *Stigmatophaga* Krassilov, gen. nov.

Stigmatophaga lobata Krassilov, sp. nov.

Stigmatophaga perforata Krassilov, sp. nov.

Stigmatophaga punctata Krassilov, sp. nov.

Genus *Trophoglypha* **Krassilov, sp. nov.**

Trophoglypha diffusa Krassilov, sp. nov.

Trophoglypha spp.

Group Ovisignata

Arthropod eggs and oviposition scars

Name. L. *ovum*, egg, *signum*, sign.

Genus *Catenoveon* Krasslov et Silantieva, gen. nov.

Name. L. *catena*, chain, *ovum*, egg.

Type. Holotype of *Catenoveon undulatum* sp. nov.

Diagnosis. Egg sets oriented in the direction of stronger veins.

Comments. This type of egg sets corresponds to oviposition mode, in which the midrib and/or stronger veins are used for orientation by the gravid female or, in the "assisted mode", by the mating couple, as in extant damselflies (Odonata).

Species content. *Catenoveon undulatum* sp. nov.

Catenoveon undulatum Krassilov et Silantieva, sp. nov.

Pl. I, figs. 1–5

Name. L. *unda*, wave.

Holotype. IMR-A2-303a, Makhtesh Ramon (Pl. I, figs. 1, 2, 4, 5).

Diagnosis. Whole-leaf set of elliptical to fusiform egg pits in undulate (zigzag) chains on both sides of the midrib.

Host. "*Acaciaephyllum*" sp.

Description. The egg set covers the whole surface of leaf blade, nearly parallel or, more commonly, oblique to the veins, somewhat spreading before the leaf margin, avoiding midrib and the stronger secondary veins, although occasionally placed quite near the latter. Scar density is 18–20 per 5 sq. mm of leaf surface and the whole number of eggs per leaf fragment (about one fifth of the whole leaf) is about 250. Occasional punctures between the egg scars probably mark failed egg-laying attempts.

At the first glance, the scar pattern appears chaotic, but, at closer inspection, short arches or S-figures of 4–7 scars are discernible (Pl. I, figs. 2, 4). The egg files are wobbling in zigzag manner across the path, usually well-spaced, but occasionally closely approaching each other. The distances between consecutive scars of a file are highly variable within the range of 0.1–0.5 mm. A coulisse-like arrangement of adjacent scars is quite common. Occasional scars are paired.

Individual egg scars are elongate to fusiform pits, 1.0–1.1 mm long, deeply engraved with irregularly swollen borders, transversely plicate, symmetrically pointed to both ends or with one end bluntly, the other acutely pointed, occasionally with a discernible mucro – a stich mark pointing toward the leaf apex. Few egg impressions show a slender twisted dark band inside (Fig. 5), probably representing a dried yolk or exuvium of embryonic larva (compare with the organically preserved prolarval exuvia figured in Hellmund & Hellmund, 1996: figs. 6, 13).

Comments. The egg pattern conforms to the coenagrionid zigzag type (Hellmund & Hellmund, 1991), although less regular than in the Tertiary examples.

Material. Whole-leaf egg sets on "*Acaciaephyllum*", IMR-A2-303a, b.

Genus *Sertoveon* Krassilov, gen. nov.

Name. From L. *sertum*, girdle, *ovum*, egg.

Type. Holotype of *Sertoveon arcuatum* sp. nov.

Diagnosis. Egg scars in transverse rows or arches, inserted at about right angle to the direction of the row.

Comments. The genus comprises egg sets laid in girdles across the leaf, with their long axis longitudinally oriented, as is the case in the Odonata, as well as Diptera.

Species content. *Sertoveon arcuatum* sp. nov., *S. cribellum* sp. nov., *S. scalarum* sp. nov., *S. moniliforme* sp. nov.

Sertoveon arcuatum Krassilov, sp. nov.

Pl. II, figs. 1–5

Name. L. *arcus*, bow.

Holotype. IG1-1118, Gerofit (Pl. II, figs. 1–5).

Diagnosis. Eggs elliptical, inserted in long curved rows across the leaf blade.

Host. *Dewalquea gerofitica* (Dobruskina) Krassilov.

Description. Egg scars appear as white spots against the grayish-brown leaf impression, disposed in broad arches across the leaflet, becoming irregularly scattered in small groups near the leaf margins (Pl. II, figs. 4, 5). Individual scars are stretched longitudinally or somewhat obliquely to the leaf axis, rotating with the bent of the row to conserve the angle of about 90° to the arch, nearly equidistant; those in small groups occasionally paired (Pl. II, fig. 5). A few eggs impressed parallel to the leaf surface are of a perfect elliptical shape, 0.5 x 0.25 mm, but typically they are inserted at a steep angle to the leaf surface, showing a triangular to hemispherical cross-section. Occasional egg scars are thickly contoured and irregularly expanded through erosion of surrounding leaf tissue.

Comments. The egg rows stretching the entire width of the leaf blade are typically deposited by the Odonata. Although these insects use plants merely as oviposition substrate, the eggs may have a cecidogenous effect on the surrounding plant tissue (Ross, 1932).

Material. Egg rows across the leaf blade on *Dewalquea gerofitica*, IG1-1118.

Sertoveon cribellum Krassilov, sp. nov.
Pl. III, figs. 1–4.

N a m e. L. *cribrum*, cribble.

H o l o t y p e. IG1-128, Gerofit (Pl. III, figs. 1–4).

D i a g n o s i s. Egg sets in cribbled rows across leaf, egg scars oblique to the rows, saggitate, pointed down the leaf.

H o s t. *Platydebeya papilionacea* Krassilov.

D e s c r i p t i o n. The egg sets are preserved on a leaflet with well-marked venation (hypophyllous), extending in broad arches of cribbled scars across the leaf blade, locally forming dense masses across the lateral veins. The crowded eggs are stuck vertically or almost so, appearing as irregular dots or minute points. Those dispersed in a cribble pattern are flatly impressed upon the leaf blade. Such scars might have been left by the eggs glued to the leaf surface when their covering froth dried out. They are well-marked black arrowheads about 0.3 mm long, mostly directed down, occasionally up, the leaflet, rather uniformly spaced, only rarely paired or contiguous. The peripheral scars are slightly spreading toward the leaf margins. There is no evidence of procecidial developments around the eggs scars.

C o m m e n t s. The cribbled arrangement is a variant of "coenagrionid" pattern in the Odonata (Hellmund & Hellmund, 1991).

M a t e r i a l. Egg masses on *Platydebeya papilionacea*, IG1-128 (counterpart IG1-123).

Sertoveon scalarum Krassilov, sp. nov.
Pl. IV, figs. 1–4

N a m e. L. *scala*, ladder.

H o l o t y p e. IG1-503, Gerofit (Pl. IV, figs. 1–4).

D i a g n o s i s. Eggs fusiform, in short parallel rows across the leaf blade.

H o s t. *Nelumbites aravensis* Krassilov.

D e s c r i p t i o n. Egg scars are arranged in short transverse rows resembling rungs of a rope ladder, stretching in disregard of the prominent tertiary vein network and across the strong primary veins that are also scarred. However, at least in one occasion, a tertiary vein is severed at the egg scar (Pl. IV, fig. 1). The rows are straight, parallel to each other, emplaced at variable distances about 1.2 (0.6–1.7) mm, but never overlapping. The egg scars are fully exposed on the leaf surface, 4–10 per row, inserted parallel to each other at 0.3–0,5 mm, fusiform, 0.7–0.9 mm long, acutely pointed down the leaf. They are preserved as empty pits with thick, elevated transversely striate borderlines. Some pits harbor a glistening filmy body, probably a chorion membrane (Pl. IV, fig. 3).

C o m m e n t s. Short transverse rows of fusiform eggs are typically oviposited by flies. Similar egg set pattern occurs in *Pegomyia* (Diptera: Anthomyiidae).

M a t e r i a l. Egg rows on *Nelumbites aravensis*, IG1-503 (counterpart IG1-504).

Sertoveon moniliforme Krassilov, sp. nov.
Pl. V, figs. 1–3

N a m e. L. *monile*, necklace.
H o l o t y p e. IG1-891, Gerofit (Pl. V, figs. 1–3).
D i a g n o s i s. Moniliform egg rows of dozens dense egg scars, straight, undulate or arched, with punctuate marks opposite the eggs. Egg scars about 0.3 mm long, deeply engraved, transverse or somewhat oblique to the row, with micropylar ends pointing to one direction.
H o s t. *Nelumbites aravensis* Krassilov.
D e s c r i p t i o n. The holotype shows two egg sets, one of straight or undulate rows of several dozens egg scars each, tending parallel to a primary vein of palmate leaf, the other at an open angle to the first, straight or gently arched. The egg scars are engraved upon the leaf impression as small, but prominent pits marked by a thick borderline, as if obliquely inserted in the leaf blade, but some appear as black streaks on the surface. Not all, but most of the rows show minute punctuate marks opposite to the egg scars.

The eggs seem to have had an erosional effect on the surrounding leaf tissue, some of the scars expanding into broad irregular pits that are occasionally confluent. In addition, there are irregular islands of dark, conceivably necrous cells adjacent to the egg rows.
C o m m e n t s. A characteristic feature of this egg sets, the punctae opposite the egg scars, might have been left by a spine on the end of ovipositor, variably developed in the Cecidomyiidae: Diptera (e.g. *Lasioptera*: Skuhravá *et al*., 1984).
M a t e r i a l. Holotype.

Genus Costoveon Krassilov, gen. nov.

N a m e. L. *costa*, rib, *ovum*, egg.
T y p e. Holotype of *Costoveon transfixum* sp. nov.
D i a g n o s i s. Egg scars over leaf midribs or primary veins.
C o m m e n t s. Oviposition in leaf midribs and primary veins of palmate venation is common among the Coleoptera (buprestid beetles, the curculionid genera *Prionomerus, Orchestes*), Hymenoptera (*Phyllotoma, Euura, Pontania*), and Diptera (*Dasineura*), as well as in the Eriocraniidae and Coleophoridae: Lepidoptera.
S p e c i e s c o n t e n t. *Costoveon transfixum* sp. nov., *C. abcostale* sp. nov, and *C. adnatum* sp. nov.

Costoveon transfixum Krassilov, sp. nov.
Pl. VI, figs. 1–3

N a m e. L. *trans*- across, *fixus*, to fix.
H o l o t y p e. IG1-1030, Gerofit (Pl. VI, figs. 1–3).
D i a g n o s i s. Eggs in long costal rows of transversely decurrent incision marks.
H o s t. *Platanervia integrifolia* Krassilov.
D e s c r i p t i o n. Holotype is a long coastal row of more than 20 eggs appearing as knob-like swellings, rounded-ovate in outline, about 0.3–0.4 mm long, uniformly spaced, protruding

on one side or occasionally on both sides of the vein, inserted singly or occasionally in pairs upon the obliquely transverse incision marks. The series of straight or arched, punctuate decurrent lines are also seen on the veins with no or indistinct egg impressions (Pl. IV, fig. 1).
Comments. The incision marks may indicate oviposition in a sawed slit on primary veins, as is the habit in sawflies (e.g., *Phyllotoma*, *Kaliofenusa*, *Metallus rubi*).
Material. Coastal egg rows on *Nelumbites aravensis*, IG1-1030, IG1-1031.

Costoveon vergens Krassilov, sp. nov.
Pl. VII, figs. 3–5

Name. L. *vergens*, bent aside.
Holotype. IG1-114, Gerofit (Pl. figs. 3–5).
Diagnosis. Egg scars in long one-sided costal row, obliquely spreading from the costae.
Host. *Nelumbites aravensis* Krassilov.
Description. The eggs are pointed at the micropylar end, 0.7–0.8 mm long, irregularly punctuate, showing a faintly marked inner body, some crumpled, with micropyle turned up. Their spacing and the angle of departure are uniform, determined by the departing tertiary veins. However, in the basal part of the leaf, the egg rows are less regular, with occasional gaps where oviposition failed or the eggs were detached (Pl. VII, fig. 5).
Comments. Ovipositing over the stronger leaf veins is a common habit in *Eriocrania* (inserting at the base of lateral veins) and *Coleophora*: Lepidoptera, as well as in the Curculionidae: Coleoptera. The latter, however, gnaw oviposition holes that cause the leaf tissue swell around the eggs. Such a procecidial effect is not observed in *C. vergens*.
Material. Costal egg rows on *Nelumbites aravensis*, IG1-114.

Costoveon adnatum Krassilov, sp. nov.
Pl. VI, fig. 4a; Pl. VII, figs. 1, 2

Name. L. *adnatus*, adnate.
Holotype. IG1-111, Gerofit (Pl. VII, figs. 1. 2).
Diagnosis. Egg scars in rows laterally adnate to the midrib, longitudinally oriented.
Host. *Dewalquea gerofitica* (Dobruskina) Krassilov.
Description. The egg scars are oblong to elongate, bluntly or acutely pointed, about 0.8 mm long, marked by a thick, somewhat irregular borderline, punctuate, deposited in a one-sided row parallel and adnate to the midrib. Features that can be seen as abnormalities are the occasional contiguous scars, their local deviation from the midrib, and a solitary scar on the opposite side of it (Pl. VII, fig. 1). Similar egg scars on split midribs sometimes cause spiral coiling of dissociated vascular strands (Pl. VI, fig. 4a).
Comments. The irregularly thickened borderlines, as well as occasional confluence of egg scars, indicate a wound reaction commonly inflicted by egg insertion in excavated holes, as in weevils (Coleoptera: Curculionidae).
Material. Costal egg scars on *Dewalquea gerofitica*, IG1-111, IG1-1110a.

Genus *Margoveon* **Krassilov, gen. nov.**

N a m e. L. *margo*, margin.
T y p e. Holotype of *Margoveon incisum* sp. nov.
D i a g n o s i s. Egg insertions into or close to leaf margin.
S p e c i e s c o n t e n t. Type species.

Margoveon incisum Krassilov, sp. nov.
Pl. VIII, figs. 1, 2, 5

N a m e. L. *margo*, margin.
H o l o t y p e. IG1-45. Gerofit (Pl. VIII, figs 1. 2).
D i a g n o s i s. Egg insertions into slits or pockets at the leaf margin.
H o s t. *Platydebeya papilionacea* Krassilov.
D e s c r i p t i o n. On the leaflets with glandulate marginal serrations, eggs are typically inserted into the marginal glands, occasionally between the glands, at the right angle or somewhat obliquely to the margin. The slits are about 0.8 mm deep, containing from one to three eggs. Frass pellets are preserved both outside and inside the slits. The procecidial development causes distortion of intramarginal veins clearly seen in Pl. VIII, fig. 2, where they are looping away from the egg pocket.
C o m m e n t s. Oviposition in marginal slits occurs in Lepidoptera; Eriocraniidae, Hymenoptera: Tenthredinoidea: Schizoceratinae, and Coleoptera: Buprestidae. In *Pachyscchelus*, Buprestidae, marginal egg capsules swell as ovate blisters on both sides of the leaves (Needham *et al*., 1928). The habit of covering egg lumps with frass occurs in various groups of Coleoptera.

Interdental incisions, as those shown in Pl. VIII, fig 5, are probably related to the same oviposition method. When cut in young leaves they are stretched with subsequent marginal growth, appearing as deep sinuses between the marginal serrations (Pl. VIII, fig. 3).

A looping mine on *Platydebeya papilionacea*, IG1-142 (Pl. VIII, fig. 3) is associated with the marginal ovipositon marks, probably representing a larval track of the same or related species. The track starts from a marginal egg scar, extends for about 5 cm inside the leaf blade then arching back towards the margin. The exit hole is situated between two marginal glands that are pushed apart. The nearly continuous frass line along the track is shortly interrupted when passing, evidently without eating, the lateral veins.
M a t e r i a l. Marginal oviposition slits on *Platydebeya papilionacea*, IG1-45, IG1-142.

Margoveon sp.
Pl. IX, fig. 3

D e s c r i p t i o n. The upper surface of *Platanervia integrifolia*, IG1-449, shows strains of well-spaced circular eggs attached to the leaf edge and filed over the frass stained area between the leaf margin and a ridge gall running parallel to it. The scars are procecidial, increasing up the leaf to 0.5 in diameter.

Comments. In Psilloidea: Triozidae, marginal oviposition is associated with the margin rolls. Oviposition onto flat leaf edge or at some distance from it commonly occurs in Diptera: Agromyzidae (e. g., *Agromyza melampyga*, *Ceratodonta femoralis* (Needham *et al*., 1928).
Material. Marginal egg scars on *Platanervia integrifolia*, IG1-886.

Genus *Massoveon* Krassilov, gen. nov.

Name. L. *massa*, lump.
Type species. *Massoveon densum* sp. nov.
Diagnosis. Dense egg masses attached to leaves.
Comments. It is supposed that stripes and patches of dense eggs masses represent slime or froth deposits over the egg lumps. Such hypophyllous egg masses occur in the Perlida, Ephemrida, Trichoptera, Odonata, Diptera (chironomids) and some Lepidoptera, such as the Noctuidae (Wesenberg-Lund, 1943). Their shapes and position on leaves are scarcely distinctive and the inferences of taxonomic affinities are based on morphology of the eggs, as well as on circumstantial evidence.
Species content. *Massoveon globulosum* sp. nov.

Massoveon globulosum Krassilov, sp. nov.
Pl. X, figs. 1–3

Name. L. *globulus*, small globe.
Holotype. IG1-676A, Gerofit (Pl. X , figs. 1–3).
Diagnosis. Patchy stripes of dense minute (0.15 mm) globose eggs spread downleaf over the primary veins.
Host. *Nelumbites aravensis* Krassilov.
Description. The egg mass is spread from near the margin in the upper part of leaf blade down the primary vein splitting into three long arms of undulate egg patches. Individual eggs appear as dark globules about 0.15 mm in diameter. Their density is about 20 per sq. mm. Short files of contiguous globules are discernible over the patches, whereas between them the eggs are irregularly scattered.
Comments. Similar egg masses from the Triassic deposits of central Europe have been assigned to Odonata (Grauvogel-Stamm & Kelber, 1996.). In our case, the egg masses are associated with incurvarioid leaf cases (see under *Folicasa spinulata* below).
Material. Egg masses on *Dewalquea gerofitica*, IG1-480 and *Nelumbites aravensis*, IG1-676.

Genus *Transpiroveon* Krassilov, gen. nov.

Name. L. *spirare*, to breath, *ovum*, egg.
Type. Holotype of *Transpiroveon polygonatum* sp. nov.
Diagnosis. Structurally preserved egg shells with an intrachorionic transpiration system.

Comments. The genus comprises structurally preserved egg shell remains with a simple intrachorionic transpiration meshwork. Such transpiration structures occur in various groups of terrestrial insects, in particular, the Hemiptera, Coleoptera, and Diptera. Simple intrachorionic meshworks are commonly considered less advanced than the complex intrachorionic and plastronic systems (Hinton, 1981).
Species content. *Transpiroveon polygonatum* sp. nov. is the first record of respiration system in the Mesozoic egg remains.

Transpiroveon polygonatum Krassilov, sp. nov.
Pl. X1, figs. 1–5

Name. Gr. *poly*, many, *gonia*, angle.
Holotype. Slide IG1-249, Gerofit (Pl. X1, figs. 1–5).
Diagnosis. Eggs elliptical, about 1 mm long, with intrachorionic transpiration system of anisomerous polygonal meshes.
Host. *Eocercidiphyllites glandulosus* Krassilov.
Description. Egg remains are short strains of overlapping or dissociated eggs about 1 mm long studied in transmitted light on a leaf impression transferred to varnish film. They are elliptical or oblong, rounded on both ends, with a micropyle vaguely if at all marked by an apical depression. The egg shell appears delicate, showing minute surface pits, evidently corresponding to the aeropyles, and a polygonal meshwork seen at a lower focus. The polygons are of variable dimensions, large and small in a disorderly pattern, isometric over the shell valves, constricted over the hatching suture.
Comments. The irregular meshwork of larger and smaller polygons is a rather unusual feature indicating an incipient differentiation of a complex intrachorionic system.
Material. Eggs on *Eocercidiphyllites glandulosus*, IG1-74.

Ovisignata spp.
Pl. IX, figs 1, 2, 4, 5

Description and comments. Relatively large, about 1,5 mm long, ovate scars scattered on the upper surface of *Platanervia integrifolia* are marked by a minutely cogged borderline with occasional longer protuberances (Pl. IX, fig 1). They are similar to the feeding marks on the same plant species ascribed to Coleoptera: Curculionidae (Pl. LIII, fig. 2). Similar scars on *Dewalquea gerofitica* are specked with frass grains and also show the faint radial prominences. However these structures may represent more than one species of procecidial egg scars, because oviposition punctures are similar to feeding punctures not only in beetles, but also in the Agromyzidae: Diptera.
Material. Egg remains on *Dewalquea gerofitica*, IG1-41, IG1-78, IG1-596, on *Platanervia integrifolia*, IG1-400, IG1-588, IG1-886.

Group Procecidimorpha

Emergent structures at egg insertion

Name. L. *pro-*, for, *cecidium*, gall, *morphe*, form.

Genus *Cupuleon* Krassilov, gen. nov.

Name. L. *cupula*, cupule.

Type. Holotype of *Cupuleon caveum* sp. nov.

Diagnosis. Cupulate scars encircled by an elevated callous rim.

Comments. This morphological genus is intended for pustular or cupulate egg scars produced by various groups of cecidozoa, such as psyllids, aphids, coccids and cecidomyiids. Although such structures do not look like any mycocecidia, they can be confused with ascogenous apothecia. However, In the case of *Cupuleon caveum* and similar structures, no traces of mycelium or stromata on the one hand and the rim of hypertrophied epidermal cells on the other seem to rule out a mycological interpretation.

Species content. *Cupuleon caveum* sp. nov., *C. nodulosum* sp. nov., C. *craterellum* sp. nov.

Cupuleon caveum Krassilov, sp. nov.

Pl. XII, figs. 1–4

Name. L. *cavus*, hollow.

Holotype. IG1-887, Gerofit (Pl. XII, figs. 2, 4).

Diagnosis. Scattered, mainly intercostal, cupulate egg scars with a thick elevated rim, fringed with hypertrophied leaf tissue.

Host. *Dewalquea gerofitica* (Dobruskina) Krassilov, *Eudebeya angusta* Krassilov.

Description. This is a widespread form of scattered egg scars showing different stages of procecidial developments, at an advanced stage appearing as cupules 0.9 mm in diameter framing a circular or elliptical cavity 0.5 mm wide. The cupular rim is radially striate, concentric with the cavity. Epidermal cells in the vicinity of the cupule are large, with distinctly marked sinuous walls. Other cupuleons of the same intercostal group emerge obliquely to the leaf surface and appear elliptical, with elongate, almost slit-like cavity. Paratype IG1-600 on a leaf fragment with 22 cupules, some at a less advanced stage of procecidial development than the holotype, irregularly scattered, solitary or in small groups of two – three between the lateral veins, less frequently set upon a lateral vein.

Comments. The well-known egg cupules of *Cystiphora taraxaci* Kieff. and *Monarthropalpus buxi* Laboulb., Cecidomyiidae: Diptera (Mani, 1964; Meyer, 1987) are extant examples of similar egg gall structures.

Material. Scattered egg cupules on *Dewalquea gerofitica*, the holotype and paratypes IG1-76, IG1-79, IG1-240, IG1-325, IG1-870, IG1-887, IG1-1111, IG1-1119, IG1-1123, on *Eudebeya angusta*, IG1-892, IG1-896.

Cupuleon nodulosum Krassilov, sp. nov.
Pl. XIII, figs. 1–6

N a m e. L. *nodus*, node.

H o l o t y p e. IG1-501, Gerofit (Pl. XIII, figs. 1, 2, 6).

D i a g n o s i s. Hypophyllous nodular swellings, ovate, glabrous, about 1.5 mm long; cavity rounded or elliptical with a low rim of small isometric concentrically aligned thick-walled cells.

H o s t. *Nelumites aravensis* Krassilov.

D e s c r i p t i o n. The nodules occur on the lower leaf surface with prominent vein ridges, over the callus of the ridges, singly or in groups or short files of 3–5. They are flattened in the plane of leaf impression, ovate, from 1 to 2 mm, on average 1.5 mm long. The cavity is elliptical 0.6–0.8 mm long, marked by a thick borderline, surrounded by a broad rim of concentric cell layers (Pl. XIII, fig. 3). The nodules appear as light specks against the dark callus fringes of primary veins extending as narrow processes over the transverse tertiary veins. The callus shows outlines of large thick-walled polygonal and elliptical cells. The higher order veins traversing the callus fringe are marked by sinuous cell files (Pl. XIII, fig. 2).

C o m m e n t s. The cupules vary from a low rim around the egg scar to elongate depressions considerably exceeding the egg pit inside and conceivably formed by abrasion of adjacent leaf tissue. Persistence of the procecidial structures over the callus of the mined costal areas may indicate a coleopteran miner.

M a t e r i a l. Procecidial cupules on *Nelumbites aravensis*, IG1-48, IG1-474, IG1-501, IG1-755.

Cupuleon craterellum Krassilov, sp. nov.
Pl. XIV, figs. 1–4

Name. L. *crater*, bowl.

H o l o t y p e. I G 1 - 155 (Pl. XIV, fig. 1).

D i a g n o s i s. Crater-shaped thick-walled open-top cupules with a wall of several cell layer, developed in the callous midrib zone.

H o s t. *Eudebeya angusta* Krassilov, *Dewalquea gerofitica* (Dobruskina) Krassilov.

D e s c r i p t i o n. The cupules develop on a leaflet of *Eudebeya angusta* within the callus fringe that is symmetrically spreading on both sides of the midrib, with teeth-like projections over the lateral veins. The most prominent cupule swells sideways from the midrib to the edge of the callous fringe, its long axis parallel to the lateral veins, elliptical, 4 x 2 mm, with a stalk-like extension towards the midrib. It exposes a relatively large, 2 x1 mm, oblong cavity, which is sharply delineated, strongly convex on the upper side of the leaf. The wall increases in thickness away from the midrib, showing outlines of radial elongate medullar cells surrounded by the smaller concentrically aligned cortex cells.

Two probably conspecific galls on *Eudebeya angusta*, IG1-691 (Pl. XIV, figs 3, 4) occupy a similar position in respect to the midrib and its meandering callus fringe on the lower side of leaflet sitting on the adjacent lobes of the callus. They appear as nearly circular craters or

basins bordered by a thick knotty rim. On *Dewalquea gerofitica*, IG1-1120 (Pl. XIV, fig. 2), two circular craters occur on a lobe of the similarly developed midrib callus.

Comments. These structures are here interpreted as open-top cupular procecidia differing from *C. nodulosum* in being larger and more gall-like, with differentiated wall, comparable also to basin galls of coccids, e.g., of *Capulinia crateraformans* (Beardsley, 1984).

Material. Cupular swelling on midrib callus of *Eudebeya angusta*, IG1-155, IG1-691, and *Dewalquea gerofitica*, IG1-1120.

Genus *Foveon* Krassilov, gen. nov.

Name. L. *fovea*, pit.

Type. Holotype of *Foveon patellatum* sp. nov.

Diagnosis. Egg scar depressions or primordial open pit galls developing from such, fringed with stellar processes.

Comments. Small open-top pit galls are induced mainly by eriophyids, aphids and psyllids, but also by gall midges (Meyer, 1987; Wool, 1984, Hodkinson, 1984; Skuhravá *et al.*, 1984). Pit galls with a conspicuous organoplastic effect, developing on stronger veins, are assigned to the organoid genus *Costaeon* (below).

Species content. *Foveon patellatum* sp. nov., *F. astrellum* sp. nov.

Foveon patellatum Krassilov, sp. nov.

Pl. XV, figs. 1

Name. L. *patella*, little pan.

Holotype. IG1-754, Gerofit (Pl. XV, fig. 1).

Diagnosis. Costal row of flat discoid to pan-shaped or cog-wheel shaped cupules about 1–1.5 mm wide.

Host. *Nelumbites aravensis* Krassilov, probably also *Dewalquea gerofitica* (Dobruskina) Krassilov.

Description. The scars are flat or slightly concave on the lower surface of *Nelumbites aravensis*, darker then the leaf impression and marked out by distinct, somewhat thickened borderlines. They alternate on both sides of a primary vein, increasing up the vein from the minutely cogged disks 1 mm in diameter to a slightly lobed cog-wheel 1.6 mm in diameter. A single specimen of *Dewalquea gerofitica*, IG1-481, shows numerous eggs over the midrib, the incipient procecidial structures of which suggest an early developmental stage of *C. patellatum* (Pl. XV, figs. 3, 4).

Comments. The fovea might have been developed from procecidial eggs inserted in the midrib, as is the case in *Dasineura* and some other cecidomyiids.

Material. Egg galls on *Nelumbites aravensis*, IG1-154, IG1-872, probably also on *Dewalquea gerofitica* IG1-481.

Foveon astrellum Krassilov, sp. nov.
Pl. XV, fig. 2

N a m e. Gr. *aster*, star.
H o l o t y p e. IG1- 755, Gerofit (Pl. XV, fig.2).
D i a g n o s i s. Scattered stellate or echinate scars fringed with slender radial processes.
Host. *Nelumbites aravensis* Krassilov, *Eocercidiphyllites glandulosus* Krassilov.
D e s c r i p t i o n. Stellate scars occur on the upper surface of *Nelumbites aravensis*, rather evenly spaced irrespective of venation. They are of uniform size, about 0.5 mm in diameter, surrounded by a somewhat irregular fringe of minute slightly hooked processes. Pl. XV, fig. 3 shows a scar on the same leaf evidently at an early stage of procecidial development. The similarly scattered echinate scars on *Eocercidiphyllites*, IG1-746 (Pl. IX, figs. 4, 5) may represent an early stage of this type procecidia.
C o m m e n t s. These structures resemble pit galls of *Trioza*, Psilloidea: Triozidae, and may represent procecidial egg scars of psyllids, in which oviposition can be to a various extent procecidial.
M a t e r i a l. Stellate foveons on *Nelumbites aravensis*, IG1-755 IG1-754, on *Eocercidiphyllites globulosus*, IG1-746 (?).

Group Cecidimorpha

Leaf galls

N a m e. Gr. – L. *kekis*, *cecidium*, gall, *morphe*, form.

Subgroup Catacecidimorpha

Cataplasmatic galls, microgalls

N a m e. **Gr.** *cata*, low.

Genus *Emergeon* Krassilov, gen. nov.

N a m e. L. *emergere*, out of.
T y p e. Holotype of *Emergeon scabratum* sp. nov.
D i a g n o s i s. Scabrate, pitted and densely trichomate leaf areas representing emergent histoid galls.
C o m m e n t s. The genus is intended for leaf surface emergent structures of the type produced by Acari: Eriophyidae (e.g., Buhr, 1965; Jeppson *et al.*, 1975; Keifer *et al.*, 1982; Westphal, 1977; Meyer, 1987).
S p e c i e s c o n t e n t. *Emergeon scabratum* sp. nov., *E. catenulatum* sp. nov. and *E.* spp.

Emergeon scabratum Krassilov, sp. nov.
Pl. XVI, figs. 1, 2; Figs. 7, 18d

N a m e. L. *scabratum*, scabrate.
H o l o t y p e. IG1-31, Gerofit (Pl. XVI, fig. 1).

D i a g n o s i s . Patchy microtrichomate areas on flanks of midrib, penetrated by irregular pit clusters and abraded stripes over the lateral veins.

H o s t . *Retrodewalquea pendens* Krassilov, *Dewalquea gerofitica* (Dobruskina) Krassilov.

D e s c r i p t i o n . In the holotype, a dark patch of scabrate epidermis about 5 mm wide, densely covered with minute emergences, is traversed by the lateral venation discernible as white lines, and is penetrated by a cluster of the lightly colored irregularly lobbed, horse-shoe shaped or vermiculate speckles. The surrounding leaf area shows outlines of hypertrophied sinuous cells (Pl. XVI, fig. 1). Similar pits occur on *Dewalquea gerofitica*, IG1-796 near the midrib splitting gall *Castaeon schizmatum* (Pl. XXIX, fig. 1).

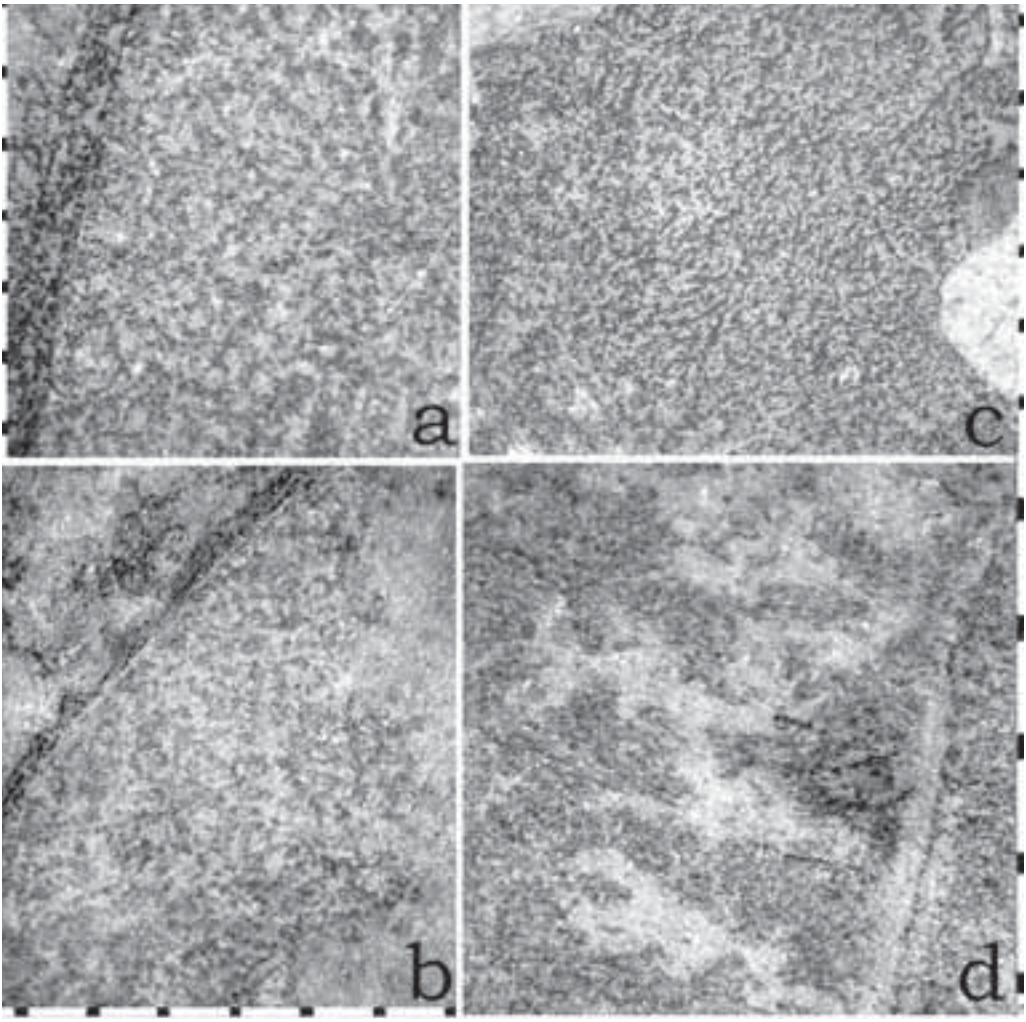

Fig. 18. Histoid galls: (a-c) *Emergeon* spp. on *Dewalquea gerofitica*, IG1-596 and IG1-588, and on *Platanervia integrifolia*; IG1-620; *Emergeon scabratum* gen. et sp. nov, (d) paratype IG1-81 on *Dewalquea gerofitica*.

In paratype IG1-81, a larger scabrate areas on both sides of the midrib are traversed by the lighter stripes with irregularly spreading arms extending over the lateral veins and their branches (Fig. 7). The stripes appear as etchings or abrasions against the darker trichomate area, conceivably marking paths of feeding larvae (Pl. XVI, fig. 2, Fig. 18, d).
Comments. Extant eriophyids produce similar patches of microtrichomate epidermis swathed by the larvae. The pits might have been inhabited by the same gall-inducers.
Material. On *Retrodewalquea pendens*, IG1-31, on *Dewalquea gerofitica*, IG1-81.

Emergeon catenulatum Krassilov, sp. nov.
Pl. XVI, fig. 3

Name. L. *catenula*, small chain.
Holotype. IG1-221, Gerofit (Pl. XVI, fig. 3).
Diagnosis. Minute catenulate intumescences over transverse epidermal cell rows.
Host. *Dewalquea gerofitica* (Dobruskina) Krassilov.
Description. The bead-like, concatenate and partly confluent tumuli are developed in the marginal area of large, thick-walled, apparently hypertrophic cells and are arranged parallel to the cell rows transverse to the leaf margin. The area is also dotted with microscopic frass pellets.
Comments. The area of catenulate emergences is here interpreted as a histoid gall of obscure modern affinities.
Material. On *Dewalquea gerofitica*, IG1-81.

Emergeon spp.
Figs. 8, 18 a-c

Material and comments. Also ascribable to histoid acarocecidia are the leaf areas of punctuate emergences forming different, polygonal and vermiculate patterns over the hypertrophied cell areas in *Dewalquea gerofitica*, IG1-59, IG1-239, IG1-588, IG1-596 (Fig. 18 a, b), *Platanervia integrifolia*, IG1-589, IG1-603, IG1-620 (Fig. 18 c), and *Platydebeya papilionacea*, IG1-196. SEM studies of leaf impressions revealed such cecidogenous histoid features as the twisted minor veins with punctuate swellings of hypertrophied vascular tissue (Fig. 8).

For comparable Tertiary acarocecidia see Brooks (1955); Ambrus & Hably (1979); Diéguez *et al.* (1996).

Genus *Pustuleon* Krassilov, gen. nov.

Name. L. *pustule*, hollow swelling, pustule.
Type. Holotype of *Pustuleon gregarium* sp. nov.
Diagnosis. Dense aggregates of minute distinct ostiolate pustules on or near the stronger veins.
Comments. Aggregates of minute pustules are induced and then used for egg emplacement by eriophyid mites (further comments under *Pustuleon gregarium*).
Species content. *Pustuleon gregarium* sp. nov.

Pustuleon gregarium Krassilov, sp. nov.
Figs. 19, 20

N a m e. L. *grex*, flock.

H o l o t y p e. IG1-180, Gerofit (Figs. 19, 20 a-c). Counterpart of the holotype was covered with gold and studied under SEM (Figs. 20 a-c, 21 a, b).

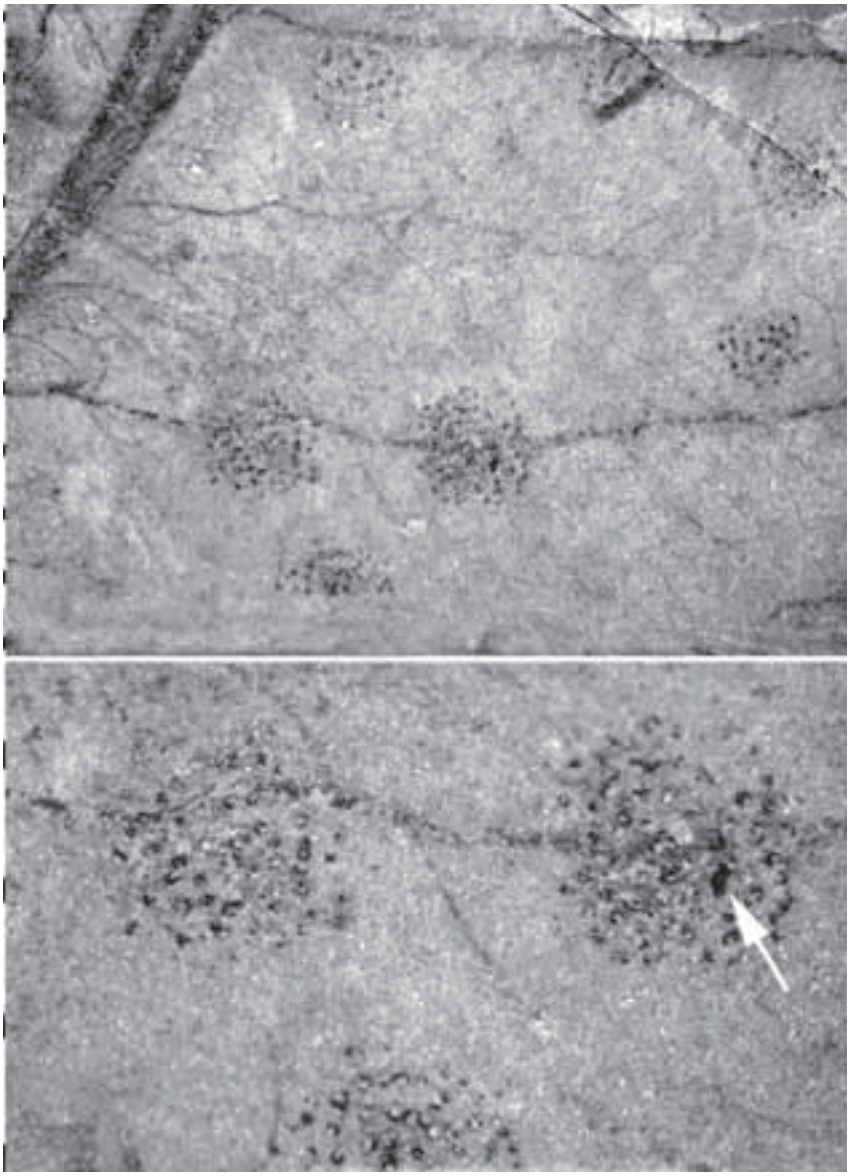

Fig. 19. *Pustuleon gregarium* gen. et sp. nov., holotype IG1-180, circular groups of minute pustules, arrow on a supposed compression of adult eriophyid mite.

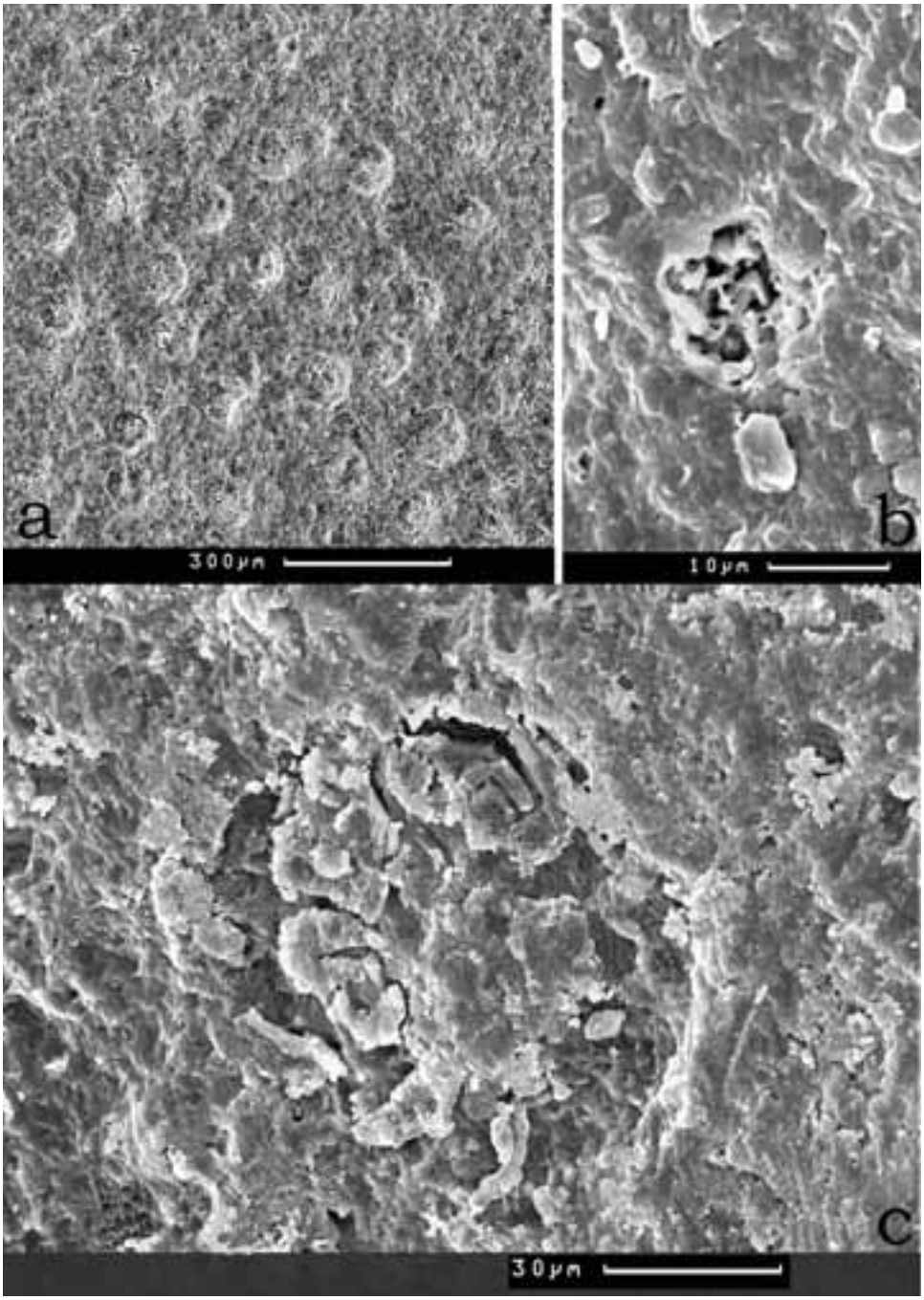

Fig. 20. *Pustuleon gregarium* gen. et sp. nov., counterpart of holotype IG1-180: (a) pustules, (b) open pustule with the larval appendages emerging, (c) open pustule with coiled structures (larval remains ?) iinsude; SEM.

H o s t . *Dewalquea gerofitica* (Dobruskina) Krassilov.
D i a g n o s i s . Minute pustules in dense circular aggregates, hemispherical, with punctate ostioles, containing coiled larval remains and trichomate outgrowths.
D e s c r i p t i o n . The hemispherical pustular swellings about 0.2 mm in diameter are aggregated in circular clusters about 1.5 mm in diameter, situated on, or at a short distance from, the lateral veins. The costal aggregates are somewhat larger, containing 30–40 individual pustules. An apical pit is discernible on the pustules under SEM (Fig. 20 a). Cuticle around the pustules reveals circular basal cells of large trichomes (Fig. 20 a). Several pustules are laid open by irregular apical holes or crevasses with converging marginal lobes. One such pustule (Fig. 20 b) shows four pointed appendages protruding through the apical hole. A wider open pustule (Fig. 20 c) contains several coiled, transversely striate warm-like bodies about 30 µm long.
C o m m e n t s . In extant eriophyid mites, a sting by fundatrix may induce a similar cluster of numerous pustules. Vein twisting by the gall is also typical of cecidogenous eriophyid effects. Occasional black fusiform bodies among the pustules (arrow on Fig. 19) may represent an adult mite (compare Fig. 2 c in Westphal, 1977). However it must be admitted that interpretation of the interior structures remains ambiguous because of insufficient preservation of the scanned material.
M a t e r i a l . The holotype.

Genus *Lenticeon* Krassilov, gen. nov.

N a m e . L. *lens*, lentil.
T y p e . Holotype of *Lenticeon minusculum* sp. nov.
D i a g n o s i s . Microcecidian lenticular swellings, blisters or freckles scattered or concatenate and contiguous over leaf.
C o m m e n t s . The genus comprises small lenticular galls that typically develop as kammergalls and arise as subepidermal swelling. Producers of such galls are known among the Tenthredinoidea, Cynipoidea and Cecidomyiidae.
S p e c i e s c o n t e n t . *Lenticeon minusculum* sp. nov., *L. agglomeratum* sp. nov., *L. nervosum* sp. nov.

Lenticeon minusculum sp. nov.

Pl. XVII, figs. 1–4

N a m e . *L. minusculus*, tiny.
H o l o t y p e . IG1-893, Gerofit (Pl. XVII, fig. 1).
D i a g n o s i s . Lenticels angular-elliptical, fusiform, 2–3.5 mm across, flat, thickly bordered, with puncture marks over the border or in the middle, solitary scattered, paired or concatenate, transverse to the midrib or aligned with lateral veins, filling the meshes of tertiary venation.
H o s t . *Eodebeya angusta* Krassilov, *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n . Holotype represents dark solid lenticels on the lower side of two leaflets, about 20–25 per leaflet, scattered or in groups of 3–4, some contiguous. In the median zone,

the lenticels are predominantly transverse, some crossing the midrib. Closer to the margins, most of the lenticels are oblique, set upon the secondary (lateral) veins or aligned with them. Individual lenticels are ovate, elliptical, fusiform, hemispherical or rounded-polygonal, about 3–3.5 mm long, contoured by thick smooth borderlines. The straighter segments of the border are formed by the thickened secondary or intersecondary veins, apparently hypertrophied by the gall. Groups of contiguous lenticels are dumbbell-shaped or beed-like. Outlines of sinuous epidermal cells are far more distinct over the lenticels than on the leaf impression. Piercing marks usually occur on the border, rarely inside the border (Pl. XVII, fig. 2) and are scattered over the leaf blade (Pl. XVII, fig. 3), sometimes showing early stages of gall development as irregular swellings around the puncture. There are numerous oviposition marks and primordial pellet galls over the leaf blade, occasionally causing a slight sinuosity of lateral veins.

This type lenticels also occur on *Dewalquea gerofitica* where they can be as dense as 50 per leaflet (Pl. XVII, fig. 4), somewhat smaller, 2–3 mm across, lighter, with prominent borders and with distinct puncture marks. Their shapes correspond to the meshes of the tertiary vein network, and the bordering veins are appreciably thickened. On *Dewalquea gerofitica*, IG1-80b (Pl. XVIII, figs 2, 3), there are only two lenticels adjacent to a lateral vein, one elongate-ovate, 3 mm long, the other trapezoid, conformable with the tertiary meshes and thickly contoured. The lateral vein is thickened at the site of the gall.

Comments. Critical features for interpretation of this type lenticels are their association with veins that are punctured and hypertrophied on the sides of and short distance beyond the lenticel. Such lenicels might have been formed by nymphs of triozid psyllids that feed on sap from vascular bundles.

Material. Lenticels on *Platydebeya papilionacea*, IG1-646, IG1-893 on *Dewalquea gerofitica* IG1-128, IG1-80, IG1-484, IG1-1150.

Lenticeon agglomeratum Krassilov, sp. nov.
Pl. XIX, figs. 1–3

Name. L. *agglomerare*, to glue.

Holotype. IG1-479, Gerofit (Pl. XIX, figs. 1–3).

Diagnosis. Low bulges agglomerated over leaf veins and along the margin, rounded-elliptical, ostiolate, minutely pitted, solitary or in radial clusters of a larger central bulge surrounded by smaller swelling.

Host. *Dewalquea gerofitica* (Dobruskina) Krassilov.

Description. The gall develops in series of solitary or more often agglomerated low swellings, 1–2 mm wide, occasionally in groups of a central larger and the radially arranged about twice smaller bulges (Pl. XIX, fig. 3) or strained over the lateral veins and along the margin roll. They are only slightly darker than the leaf impression, but distinct owing to their well-marked borderlines and punctuate, probably microtrichomate, external walls. A circular pit in the middle marks a prominent ostiole. The leaf margins are callous, discontinuously rolled over the intramarginal swellings intruding the callus.

C o m m e n t s . This gall might have been induced by a "weakness parasite" attacking leaf affected by the midrib-splitting gall, *Costaeon schizmatum*. In the Homoptera, margin rolls (over fundatrix) and pustular swellings are sometimes induced by one and the same gall maker. The radially arranged larger and smaller swellings suggest a fundatrix surrounded by a corona of eggs developing into the gallicolae, as in the: Aphidoidea: Phylloxeridae.

Eriophyid mites produce similar agglomerated pustules described as *Cephalonen pustulatum* Bremi (Ross, 1932), but these are both sessile and shortly stalked, lacking ostiole.

M a t e r i a l . Agglomerations on *Dewalquea gerofitica*, IGI-479.

Lenticeon nervosum sp. nov.

Pl. XX, figs. 1–3

N a m e . L. *nervosus*, with abundant veins.

H o l o t y p e IG1-244, Gerofit (Pl. XX, figs. 1–3).

D i a g n o s i s . Lenticels discoid, intercostal and intramarginal, covered with a fine venation network, minutely pitted (microtrichomate). Ostiole faintly marked or obliterated.

H o s t . *Platydebeya papilionacea* Krassilov.

D e s c r i p t i o n . The disks are scattered over the lower surface, solitary, occasionally paired, about ten per leaflet, rounded-elliptical, about 5 x 4 mm, arising between and slightly onlapping the lateral veins that are appreciably reduced after the gall (Pl. XX, fig. 1). The intramarginal lenticels are hemispherical, widely spaced, approached by the lateral veins that ascend and loop before the margin. The disk impressions are prominent due to their reddish-brown color and a thick border marked by double line with occasional minute prominences. They are covered with a fine vein tracery indiscernible on the leaf impression. The disk surface is minutely pitted, with a larger central pit or irregular depression probably representing an ostiole that is only feebly marked or obliterated. The leaf cuticle is irregularly torn off the disk margin that must have been raised before compression.

The leaf surface around is speckled with smaller dark swelling, perhaps primordial galls of the same species. Even at this developmental stage they affect the course of the lateral veins (see under *Costaeon blastoides* below).

C o m m e n t s . The disks appear as low surface bulges of endophytic kammergalls typically produced by sawflies (*Pontania*) or cynipids (*Neuroterus*), but also by *Millettia* and other gall midges. The tracery of vascular network rather indicates a sawfly inducer (Hymenoptera: Tenthredinoidea).

M a t e r i a l . Lenicels on *Platydebeya papilionacea*, IG1-178, IG1-244.

Subgroup Prosocecidimorpha

Prosoplasmatic galls.

Name. L. *prosus*, straightforward.

Genus *Cephaloneon* Bremi

Comments. Morphological genus *Cephaloneon* has been intended for all kinds of isometric bulges, but in practice the name was applied to spheroid and pustular galls, mostly, but not only, of mites (e.g., an eriophyid gall *Cephaloneon pustulatum* Bremi, see Ross, 1932). Prosoplasmatically less distinctive microcephaloneons can be better defined by their organoid effects (described under Organocecidimorpha).

Cephaloneon squamosum Krassilov, sp. nov.

Pl. XXI, figs 1–3; Pl. XXII, figs 1–4

Name. L. *squama*, small scale.

Holotype. IG1-403, Gerofit (Pl. XXI, figs. 1–3).

Diagnosis. Leaf gall hemispherical, scaly, about 4 mm in diameter, sessile on strong leaf veins, surrounded by irregular callous fringe. Inner chamber spherical, well-marked. Scales about 10–20, triangular, bluntly pointed, imbricate, separated at dehiscence.

Host. *Menispermites cuspidentatus* Krassilov.

Description. The gall develops on the upper side of leaf blade (with prominent vein network) on lateral veins and their stronger branches, singly at the distal forking points, nearly equidistant from the leaf margin. In the holotype, the galls are at about the same developmental stage, hemispherical, of appressed or slightly spreading scales (Pl. XXI, figs 1–3), Some galls of a series are shed or more probably cut out, leaving a hole surrounded by the distinctive callous fringe. A larger gall closer to the leaf base disintegrated into a mass of scales (Pl. XXII, fig. 4). The galls are surrounded by the concentric or irregular dark fringes of radially striate callous tissue. (Pl. XXII, figs. 2, 3). The stronger veins are scarcely affected by the gall, but the smaller veins are flexed and produce minute hair-like processes that were not observed anywhere outside the gall callus.

Smaller scaly structures on this and conspecific leaves probably represent primordial galls showing a thick-walled rounded-elliptical central chamber 0,7 mm wide encircled by a few petal-like scales (Pl. XXII, fig. 3).

Comments. The gall apparently consisted of a larger central chamber and a number of smaller peripheral chambers of a miniature pine-apple type (Aphidoidea: Adelgidae).

Material. Costal gall on *Menispermites cuspidentatus*, IG1-48, IG1-51, IG1-379, IG1-403, IG1-753, IG1- 768.

Genus *Ceratoneon* Bremi

Comments. This morphological genus was introduced by Bremi for the horn-like and conical galls of mites, later applied also to the similar poach galls of thrips (e.g., of *Liothrips* on

Schefflera: Raman & Ananthakrishna, 1984) and other insects (Ross, 1932). Ceratoid galls of eriophyid mites, thrips, aphids and gall midges are scarcely distinguishable by their shapes. However, deciduous galls detached from their basal disk at a neat abscission scar are relatively advanced, typically produced by gall wasps and gall midges (e.g., the well-known *Mikiola fagi*).

Ceratoneon ovatum Krassilov, sp. nov.
Pl. XXIII, fig. 3

N a m e. L. *ovum*, egg.
H o l o t y p e. IG1-201, Gerofit (Pl. XXIII, fig. 3).
D i a g n o s i s. Leaf gall elongate-ovate, few mm long, bluntly pointed, ostiolate, constricted above the attachment disk.
H o s t. *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n. A solitary gall arises at about 75°to the leaf margin that is narrowly rolled above. The gall body is elongate-ovate, erect, 2.2 mm long, with a well-defined circular ostiole, conspicuously constricted at the base and then expanded into attachment disk. The gall surface appears scabrate and hairy, with minute pointed trichomes increasing toward the apex. An attachment disk impression nearby may belong to a gall developed on the opposite side of the leaf blade. It is circular, 1.3 mm in diameter, with a thick knotty margin and small central pit.
C o m m e n t s. This gall form might have been deciduous, shed from a persistent basal disk, as in Diptera: Cecidomyiidae, such as *Mikiola fagi*. Unlike *C. mucronatum* (below) it is definitely ostiolate and trichomate.
M a t e r i a l. Horn and disks on *Dewalquea gerofitica*, IG1-20, IG1-201.

Ceratoneon mucronatum Krassilov, sp. nov.
Pl. XXIII, fig. 4

N a m e. L. *mucro*, sharp point.
H o l o t y p e. IG1-277, Gerofit, Pl. XXIII, fig. 4.
D i a g n o s i s. Horn-like outgrowths, 3 mm long, smooth, straight or slightly crescentic, acutely pointed, without ostiole, detachable from the basal disk.
H o s t. *Platydebeya papilionacea* Krassilov, probably also *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n. On leaflet of *Platydebeya papilionacea*, a series of horn-like structures arise form discoid swellings of the leaf margin, which is appreciably thickened around the horn bases. Discoid marks scattered over the blade suggest more such structures being shed form the leaf.
C o m m e n t s. The gall shapes are rather like in *Hormaphis hamamelidis* Frich (Thelaxidae: Aphidoidea) on *Hamamelis* (Lewis & Walton, 1958). However, the gall body might have been deciduous, as in *C. ovatum*. Rather similar ceratoneons on the Miocene oak leaves are described by Waggoner & Poteet (1996) as a form genus and species *Antronoides shorni* Waggoner et Poteet. In this form, assigned to Hymenoptera: Cynipidae, the fusiform gall bodies develop in clusters between the lateral veins leaving annulate scars when detached.
M a t e r i a l. Intact horns on *Platydebeya papilionacea*, IG1-227 (counterpart IG1-220); basal disks on *Dewalquea gerofitica* IG1-160, IG1-201.

Ceratoneon (?) sp.
Pl. XXIII, fig. 1

C o m m e n t s . Peculiar marginal outgrowths on *Platydebeya papilionacea*, of unequal length, crescent-shaped, forwarded toward the leaf apex, acute, decurrent, some constricted at base, appearing as hypertrophied marginal teeth of the type shown for comparison in Pl. XXIII, fig. 2. Whether such problematic structures are cecidogenous remains an open question, but they are rather similar to the ceratoneons of the same assemblage.

Group Organocecidimorpha

Cecidogenous organoid structures

Genus *Petioleon* Krassilov, gen. nov.

N a m e . L. *petiolus.*
T y p e . H o l o t y p e o f *Petioleon inflatum* sp. nov.
D i a g n o s i s . Localized or whole length inflation and/or cohesion of leaf petioles (leaflet petiolules in compound leaves).
C o m m e n t s . Superficially similar petiolar galls are produced by psyllids, aphids, sawflies, tephritid and cecidomyiid flies, and less frequently by the other groups of cecidogenous insects.
S p e c i e s c o n t e n t . *Petioleon inflatum* sp. nov., *Petioleon ostiolatum* sp. nov.

Petioleon inflatum Krassilov, sp. nov.
Pl. XXIV, figs. 1–3; Fig. 17

N a m e . L. *inflatus*, swollen.
H o l o t y p e . IG1- 601, Gerofit (Pl. XXIV, fig. 2).
D i a g n o s i s . Fusiform swelling, webbing or coalescence of petiolules in palmate compound leaves, variously extended up the midribs or decurrent upon the leaf petiole.
H o s t . *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n . Holotype represents a fusiform thick-walled swelling extending the whole length of a petiolule (4 mm) and intruding a short distance up the midrib of a strongly asymmetrical leaflet. A circular orifice is discernible in the middle of the swelling. In adjacent leaflet, the petiolule is inflated and twisted sideways, showing the planiconvex profile of the gall. This is a typical condition met in a number of *Dewalquea* leaves. Less frequently, the swelling involves basal parts of leaflets causing strong asymmetry of leaf blade (Pl. XXIV, fig. 3) or the petiolules are webbed and coalescent, the web extending down the petiole (Pl. XXIV, fig. 1).
C o m m e n t s . Extensive webbing of petioles is caused by gall midges (*Perrisia fraxini:* Mani, 1964), the most probable producers of the petiole galls on *Dewalquea*.
M a t e r i a l . Petiolule gall on *Dewalquea gerofitica*, IG1-36, IG1-557, IG1-539, IG1-601, IG1- 1003.

Petioleon ostiolatum Krassilov, sp. nov.
Pl. XXIV, fig. 4

N a m e. L. *ostiole*, opening.
H o l o t y p e. IG1-539. Gerofit (Pl. XXIV, fig. 4).
D i a g n o s i s. Elongate decurrent distinctly ostiolate swelling over the petiole insertion.
Host. *Retrodewalquea pendens* Krassilov.
D e s c r i p t i o n. Petiole of a compound palmate leaf is markedly inflated before the point of insertion, 4.6 mm wide, gradually decreasing down the petiole. Gall cavity is marked by an elongate light yellow area inside the dark brown, slightly undulate walls. A prominent transverse elliptical pit in the middle of the swelling apparently represents an ostiole.
C o m m e n t s. Of many comparable petiole galls, those of gall midges *Harmandia* on *Populus* and *Xestophanes* on *Potentilla* are most similar in affecting the area just before petiole insertion, prominent ostiole and in the larval chamber situated within the medulla (Mani, 1964).
M a t e r i a l. Petiole gall on *Retrodewalquea pendens*, IG1- 539.

Genus *Costaeon* Krassilov, gen. nov.

N a m e. L. *costa*, rib.
T y p e. Holotype of *Costaeon flexum* sp. nov.
D i a g n o s i s. Localized costal swellings variously affecting the course and branching of the veins.
C o m m e n t s. Well-known extant examples of costal (midrib) galls are those produced by *Eriophyes* (Eriophyidae), *Ginaikothris*, Thysanoptera, *Pemphygus*, Aphidoidea, *Pontania* and *Euura*, Tenthredinoidea, *Dasineura* and *Monarthropalpus*, Cecidomyiidae. Most of them would not be readily distinguishable as fossils by their prosoplasmatic expression alone, being more distinctive organoplastically.
S p e c i e s c o n t e n t. *Costaeon flexum* sp. nov., *C. capsulatum* sp. nov, C. *foveum* sp. nov., *C. schizmatum* sp. nov., *C. blastemum*, *C*. sp.

Costaeon flexum Krassilov, sp. nov.
Pl. XXV, figs. 1–4.

N a m e. L. *flexus*, bend.
H o l o t y p e. IG1-123d, Gerofit (Pl. XXV, fig. 3).
D i a g n o s i s. Low nodular or knob-like costal swellings associated with flexuous deformation of the veins.
H o s t. *Platydebeya papilionacea* Krassilov, *Platanervia integrifolia* Krassilov, *Dewalquea gerofitica* Dobruskina) Krassilov.
D e s c r i p t i o n. In the holotype, a larger swelling about 1 mm wide occurs on the midrib before a conspicuous flexure, followed by a small nodule at the base of a tortuously winding lateral vein. The midrib is further twisted above.

On *Platanervia integrifolia*, IG1-606, an elliptical nodular swelling 1.5 mm wide occurs opposite a sharp flexure of the midrib (Pl. XXV, fig. 2). Minute dots around the swelling may represent trichome bases.

Paratype IG1-447 is an example of sinuous lateral vein in *Platanervia integrifolia*, associated with an inconspicuous nodular swelling at the base of it (Pl. XXV, fig. 1).

On *Dewalquea gerofitica*, IG1-597, sinuosity of midrib is apparently related to a knob-like swelling in the middle of it (Pl. XXV, fig. 4), which, does not cause dissociation of vascular bundles as in the case of the more conspicuous *Costaeon schizmatum* (below).

Comments. The holotype and paratypes of *C. flexum* may well belong to different biological species, but they all share the etiology of an inconspicuous knob-like adcostal swelling of a generalized *Cephaloneon* type associated with conspicuous twisting of the costae, characteristic of eriophyid galls.

Material. Vein-twisting gall on *Platydebeya papilionacea*, IG1-123d, IG1-239, IG1-1026 *Platanervia integrifolia*, IG1-34, IG1-36, IG1-444, IG1-447, IG1-606, IG1-798, on *Dewalquea gerofitica*, IG1-239, IG1-597.

Costaeon foveum Krassilov, sp. nov.
Pl. XXVI, figs 1–4

Name. L. *fovea*, depression.

Holotype IG1-1125 (Pl. XXVI, figs. 1, 2).

Diagnosis. Small costal pit galls causing swelling and fasciculation of the veins.

Host. *Eudebeya angusta* Krassilov, *Platanervia integrifolia* Krassilov.

Description. In trifoliate *Eudebeya angusta*, small pit galls occur on all three leaflets, singly or several per midrib, better developed in the distal parts of the leaflets. The pits are elliptical, about 2 mm long, bright red against the gray-brown leaf impression, surrounded by a narrow fringe of callous cells. An elongate black body in one of them (Pl. XXVI, fig. 1) may represent a larval imprint. The midrib does not change its course above the gall, but is markedly thickened and produces a bush-like fascicle of short down-curved and longer up-curved branches. These cecidogenous branches are slightly sinuous and/or knotted.

A midrib pit gall in paratype IG1-1126 (Pl. XXV, fig 3) is somewhat larger, associated with a sharp twisting and irregular branching few millimeters below it. Callus develops around the pit and over the knee of the midrib.

In *Platanervia integrifolia*, IG1-444 (Pl. XXVI, fig. 4), the midrib is likewise divided distally into three irregularly diverging arms, each bearing a pit gall near, or some distance above, the branching node. Here also a dark elongate body 1–1.3 mm long inside the cavity may represent a larval imprint.

Comments. The pit galls are assignable to the morphological genus *Foveon*, but their organoplastic effect on the leaf veins is more conspicuous than their prosoplasmatic expression. Pit galls of comparably simplified morphology are known in *Dasineura* and other gall midges, in which the gallicolus larva feeds directly from the vascular bundle (Meyer, 1967).

Material. Vein-twisting *Foveon* on *Eudebeya angusta*, IG1-1125, IG1-1126, and *Platanervia integrifolia*, IG1-444.

Costaeon capsulatum Krassilov, sp. nov.

N a m e . L. *capsule*, small case.

H o l o t y p e IG1-589 (Pl. XXVII, figs. 1–3).

D i a g n o s i s . Elliptical thick-walled capsulate gall on stronger veins that are reduced after the gall body site.

H o s t . *Platanervia integrifolia* Krassilov.

D e s c r i p t i o n . The gall bodies occur on two successive branches of a strong basal vein at about midway to the margin. They are elliptical, bright red against the pale reddish brown leaf impression, the lower 5 mm long, obliquely spreading from the vein and shortly decurrent, the upper 4.2 mm long, traversed by the vein, rounded on top and asymmetrically decurrent. The larger gall body is bulging inside out (outpocketed) over a longitudinal slit in the wall, showing dense transverse striation, apparently representing parallel cell rows, on the inner cortex.

The difference in size apparently correlates with the relative thickness of the veins, the lower of which is interrupted after the gall, the upper taking a sinuous course shortly before and after the gall, fading out distally. The scalariform tertiary veins are somewhat crowded over the gall spreading away from it.

C o m m e n t s . *Pontania* and *Yuura*, Tenthredinidae, produce rather similar, if but larger, costal pocket galls and outpocketings on *Salix*, whereas *Parapergandea caryaevenae* (Phylloxeridae: Aphidoidea) on *Carya* and *Dasineura*, Cecidomyiidae on *Urtica* produce superficially similar costal cover galls (Meyer, 1987).

M a t e r i a l . Costal pocket gall on *Platanervia integrifolia*, IG1-589.

Costaeon schizmatum Krassilov, sp. nov.

Pl. XXVIII, figs. 1–4; Pl. XXXIX, figs. 1–3; Fig. 17

N a m e . Gr. *schizein*, to cleave.

H o l o t y p e . IG1- 796, Gerofit (Pl. XXVIII, fig. 1, Pl. XXIX, fig. 1).

D i a g n o s i s . Coastal gall causing dissociation of vascular bundles and extensive lengthwise splitting of the midribs.

H o s t . *Dewalquea gerofitica* (Dobruskina) Krassilov.

D e s c r i p t i o n . Midrib splitting is a common phenomenon in *Dewalquea gerofitica* (Dobruskina) Krassilov. It varies from a narrowly crevassed groove to a wide separation of dissociated vascular strands. Splitting is accompanied by hypertrophy and undulation of the midrib that can be divided for its whole length or nearly so. The splitting is symmetrical, into equal strands, or asymmetrical, with one strand considerably thicker than the other. Slender parallel or anastomosing strands sometimes intervene between the diverging arms. Usually, the symmetrically split strands run parallel and close to each other for a considerable distance (Pl. XXVII, figs. 2, 3), whereas, in asymmetrical splitting, the weaker arm is meandering in broad irregular loops, while the stronger arm takes a more direct course to the apex (Pl. XXVIII, figs. 1, 4).

Midrib splitting is the main and for the most part the only etiological feature of the gall, whereas its prosoplasmatic manifestations are relatively inconspicuous. In the holotype, a tu-

bular swelling 4.5 mm long, 1.2 mm broad occurs on the midrib just below the split (Pl. XXIX, fig. 1). The swelling is deeply longitudinally grooved and densely minutely worsted, giving rise to dissociation of vascular bundles. A lateral vein departing form the gall site is markedly swollen at the base. A peculiar feature of the midrib-splitting gall is a cluster of fine repeatedly forking striae on both sides of it, conceivably representing a cecidogenous venation.

Other features associated with midrib splitting in *Dewalquea* are (1) the variably developed flanking zones of callus, (2) undulation, irregular thickening and occasional splitting of lateral veins, (3) slender interstitial veins arising on both sides of the midrib or on the outside of the split arms and traceable for a short distance beyond the callus zone, and (4) narrow, but sharp and apparently rigid ridges running parallel, or meandering parallel, to the arms of split midribs, representing an etiological feature of the same or co-occurring gall (Pl. XXVIII, figs. 2, 3).

Comments. The gall apparently affected not only vascular tissue of the midrib, but also mesophyll on flanks of it, thus producing the effect of a "gouty-vein gall". Such galls are induced by a number of taxonomically unrelated organisms (Mani, 1964). In particular, the fusiform midrib gall of *Pipaldiopsis*, Cecidomyiidae may cause dissociation of vascular bundles. Similar cecidogenous effects are conferred by *Perrisia* and other gall midges. However, the extent of midrib splitting in the fossil gall is unprecedented, indicating an early gall induction in juvenile leaves, in which the dissociated midrib bundles were pulled apart by expansion of leaf blade between them.

Midrib splitting may or may not associate with margin rolls (Pl. XXVIII, fig. 1) Eggs, attached in beed-like strains to the split midribs are described under *Costoveon adnatum* (Pl. VI, fig. 4).

The fusiform swellings on the midrib of *Dewalquea gerofitica* IG1-559 (Pl. XXIX, fig. 2), and on a primary vein of *Nelumbites aravensis,* IG1-901 (pl. XXIX, fig. 3) resemble *Costaeon schizmatum* and are likewise surrounded by callus, yet not inflicting an appreciable splitting of the midrib. These galls are comparable with the midrib galls of extant sawflies (*Euura* on Salix: Ross, 1932).

Material. Midrib-splitting gall affected most of the leaves in *Dewalquea gerofitica*, conspicuously IG1- 81, IG1-110, IG1-232, IG1-414, IG1-479, IG1-481, IG1-539, IG1-557, IG1-575, IG1-590, IG1-597, IG1-796, IG1-849, IG1-870, IG1-1002.

Costaeon blastoides Krassilov, sp. nov.

Pl. XII, fig. 3; Pl. XVIII, fig. 2d; Pl. XX, fig. 2; Fig. 21

Host. Gr. *blastos*, sprout.

Holotype.. IG1-557, Gerofit (Pl. XII, fig. 3).

Diagnosis. Primordial gall pellets occurring at the sites of vein deformation.

Host. *Dewalquea gerofitica* (Dobruskina) Krassilov, *Platydebeya papilionacea* Krassilov.

Description and comments. The holotype is a spherical blister causing deviation and radial branching of a lateral vein in *Dewalquea gerofitica*. Pellets on bending veins of *Platydebeya papilionacea*, IG1-244, are associated with *Lenticeon nervosum*, possibly representing procecidia or primordial galls of the same species. Elongate blisters on the flexed veins of

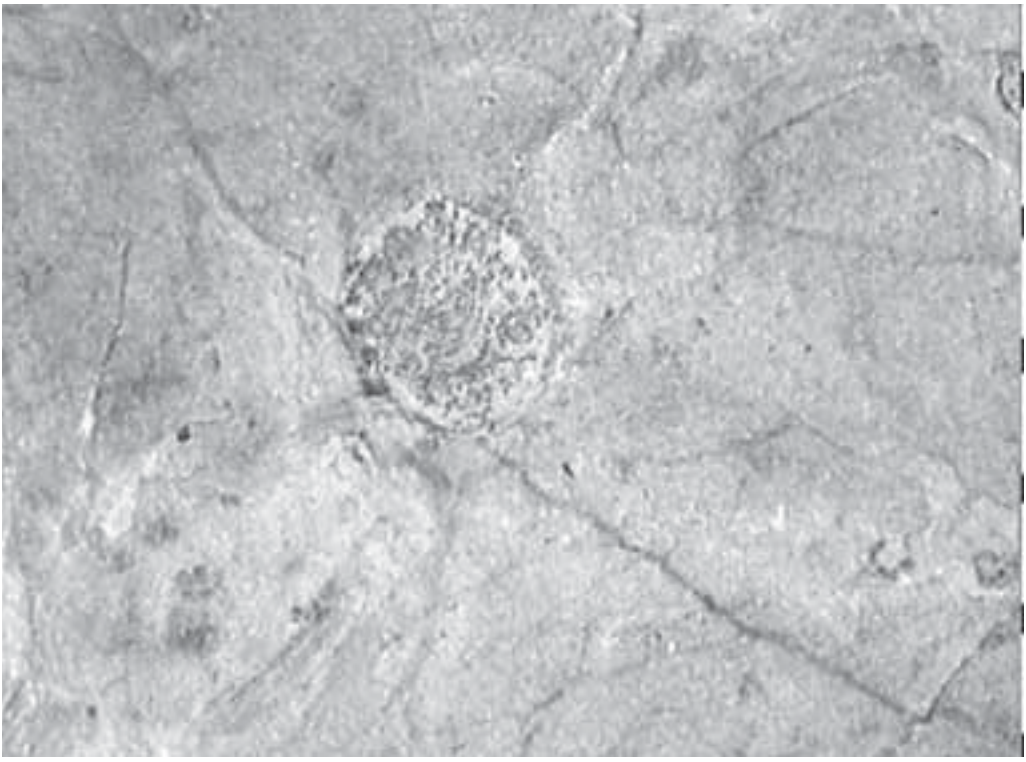

Fig. 21. *Costaeon blastoides* gen. et sp. nov., paratype IG1-1236, primordial pellet gall on lateral vein of *Platydebeya papilionacea*; the gall body is minutely punctuate (microtrichomate), and the vein is bent and hypertrophied at the contact with the gall.

Platydebeya papilionacea, IG1-128 and *Dewalquea gerofitica*, IG1-80 are associated with *Lenticeon minusculum*, apparently developing from cecidogenous punctures into the veins.
M a t e r i a l . Primordial vein-twisting galls on *Dewalquea gerofitica*, IG1-80, IG1-557 and *Platydebeya papilionacea*, IG1-123b, IG1-128, IG1-244.

Costaeon sp.
Pl. XXVII, figs. 4, 5

H o s t . *Platanervia integrifolia* Krassilov.
D e s c r i p t i o n a n d c o m m e n t s . A costal gall associated with *Costaeon capsulatum*, but of a different morphology, occurs on the midrib and lateral veins of *Platanervia integrifolia*, IG1-567. The midrib is slightly hypertrophied all over its length showing a narrow elongate swelling in the proximal part and a larger more prominent swelling distally (Pl. XXVII, fig. 4). The latter is fusiform, reddish brown, 6 mm long, and the midrib is appreciably thickened for another 10 mm above it, then dividing into three slender sinuous arms. Fine striation develops over the gall borders. The tertiary veins are crowded, irregularly looping alongside

the swelling. The gall on the lateral vein is somewhat smaller, but the pattern of tertiary veins about it are similarly disorganized (Pl. XXVII, fig. 5).
M a t e r i a l . Fusiform costal gall on *Platanervia integrifolia*, IG1-567.

Genus *Involuteon* Krassilov, gen. nov.

N a m e . L. *involutus*, rolled.
T y p e . Holotype of *Involuteon compressum* sp. nov.
D i a g n o s i s . Solid continuous, intermittent or folded leaf margin rolls.
C o m m e n t s . Margin rolls are the most widespread feature of gall etiology in taxonomically unrelated cecidogenous organisms (fungi, eriophyids, thrips, psyllids, aphids, sawflies, gall midges), providing a few distinguishing features, such as the epiphyllous or hypophyllous direction of coiling, number of turns and their spacing, hollow or solid structure, coriaceous or fleshy texture, continuity, plication, hypertrophy of the marginal tissue, pubescence or lack of such, etc., not all of which are discernible in fossil material. Lumping of different gall forms under one morphological species is unavoidable in such cases.
S p e c i e s c o n t e n t . *Involuteon compressum* sp. nov.

Involuteon compressum Krassilov, sp. nov.

Pl. XVIII, figs. 1, 2; Pl. XIX, figs. 1, 3; Pl. XXV, fig. 4b; Pl. XXVIII, fig. 1, Pl. XLIV, fig. 3

N a m e . L. *compressum*, pressed together.
H o l o t y p e . IG1-887, Gerofit (Pl. XLIV, fig. 3).
D i a g n o s i s . Leaf (leaflet) margin roll marked as prominent bulge or double ridge along the margin, narrow and intermittently developed near the leaf base, continuous above, with smooth parallel edges, occasionally folded.
H o s t . *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n . The margin roll is most distinct on leaflets of *Dewalquea gerofitica*, IG1-887, considerable areas of which are cut out along the margin, but leaving the rolls intact (Pl. XLIV, fig. 2). Here the rolls are uniformly thick from base to near the apex. In paratype IG1-80 (Pl. XVIII, figs. 1, 2), the margin roll is epiphyllous on three leaflets of *Dewalquea*, about 1 mm thick, continuous from base to at least ¾ of the length, extending over the marginal folds and fading out short distance before the apex. Outlines of large sinuous hypertrophied epidermal cells are locally discernible over the rolls. On one of the leaflets, the roll is less callous, marked by a ridge over its inner edge, onlapped by intramarginal cut-outs. In some instances, IG1-796b, the gall is extended from narrow intermittent folds near leaf base to a continuous parallel-sided roll above (XXVIII, fig. 1).
C o m m e n t s . Simple continuous uniformly thick rolls extending the whole or most of the leaf and accompanied by insignificant swelling of leaf tissue, as in the holotype, are produced by both eriophyids and thrips. Those associated with lenticular galls, such as *Lenticeon agglomeratum* (above), which are onlapped by the roll (Pl. XIX, fig. 3), might have been the

work of fundatrix or fundatrigeniae of the same species, as in the Aphidoidea. The rolls by psyllids and gall midges are stronger developed, but the distinctions can hardly be used as diagnostic features so far.

Material. Margin rolls are fairly common on *Dewalquea gerofitica*, the best preserved are IG1-80, IG1-597, IG1-796, IG1-833, IG1-887, also on *Eudebeya angusta*, IG1-479.

Group Nomomorpha

Leaf mines

Subgroup Ophionomata

Linear mines

Name. Gr. *ophis*, snake, *nomas*, wanderer.

Genus *Ophionoma* Krassilov, gen. nov.

Name. As above.

Type. Holotype of *Ophionoma paradroma sp. nov.*

Diagnosis. Linear mines (ophionomes: Hering, 1951) with no or insignificant blotch component.

Species content. *Ophionoma paradroma* sp. nov., *O. serranoides* sp. nov., *O. digitata* sp. nov.

Ophionoma paradroma Krassilov, sp. nov.

Pl. XXX, figs. 3, 4

Name. Gr. *parallelos*, parallel, *dromos*, running.

Holotype. IG1-639, Gerofit (PL. XXX, figs. 3, 4).

Diagnosis. Rectilinear mines running along the veins of a parallelodromous leaf.

Host. *Typhacites negevensis* Krassilov.

Description. The mine extends the entire length or a considerable part of ribbon-shaped leaf with paralellodromous system of stronger primary veins and two or four slender veins between them. The track is marked by a thick black frass line, interrupted, with acute point, in the middle of the leaf where the veins are slightly flexed.

Comments. Linear mines of the kind are constructed by *Arzama* (Noctuidae, Lepidoptera) on *Typha*, as well as by agromyzid flies, such as *Agromyza* or *Cerodonta*, on graminoid leaves.

Material. Linear mine on *Typhacites negevensis*, IG1-639

Ophionoma serranoides Krassilov, sp. nov.

Pl. XXX, fig. 2

Name. L. *serra*, saw.

Holotype. IG1-121, Gerofit (Pl. XXX, fig. 2).

Diagnosis. Sinuous saw line track over leaf margin.

Host. *Platydebeya papilionacea* Krassilov, *Nelumbites aravensis* Krassilov.

D e s c r i p t i o n . Leaflets of *Platydebeya papilionacea* with minute marginal glands are mined over the margin with sinuous track appearing as a sharp irregularly serrate-crenulate saw line notched at the marginal glands. When incised in juvenile leaves, the notches increase with leaf growth producing false serration of leaf margin.
C o m m e n t s . Miners of leaf margins occur in all major groups of mining insects, but similar sawline marginal mines are typically made by the Fenusinae: Tenthredinidae: Hymenoptera.
M a t e r i a l . *Platydebeya papilionacea*. IG1-121a, *Nelumbites aravensis*, IG1-1026.

Ophionoma digitata Krassilov, sp. nov.
Pl. XXXI, figs. 1–3

N a m e . L. *digitus*, finger.
H o l o t y p e . IG1-1003, Gerofit (Pl. XXXI, figs. 1, 2).
D i a g n o s i s . Linear mines entering leaf blade from petiole and extending as diverging tracks over the primary veins.
H o s t . *Dewalquea gerofitica* (Dobruskina) Krassilov, *Eocercidiphyllites glandulosus* Krassilov.
D e s c r i p t i o n . On *Dewalquea*, the linear tracks are well-marked, nearly straight and relatively broad (0.5 mm) over the long petiole, flexed and considerably constricted over the transition to the midribs of the palmately spreading leaflets. The leaf as a whole is rather small, perhaps stunted, and the leaflets are impressed at various angles to the bedding plane, which suggests their torsion before burial, possibly caused by the mine. The track does not show any frass remains but is prominent owing to its reddish hew probably caused by anthocyanine accumulation in the mine.

On a small, immature or stunted, reniform leaf of *Eocercidiphyllites glandulosus*, the mine tracks are discernible as slender slightly undulating lines over the petiole and the primary veins that in the host leaf species are but vaguely differentiated into the midrib and the equally strong basal laterals. The leaf margin is mined above the end of the basal vein and over the apex that appears folded. The mine does not cause an appreciable thickening or deviation of the primary veins, yet the leaf is deformed as a result of the marginal mining (Pl. XXXI, fig. 3).
C o m m e n t s . Mining through petiole into the leaf blade is rather widespread in all major groups of leaf miners representing a primitive mine strategy that can be most damaging to the leaf. The comparable digitate mines of *Marmara*, Gracilariidae, may extend down the leaf to stem and back up the petiole and primary veins, eventually folding the leaf margin to construct their cocoon under it (Hering, 1951), which might have been also the case in the Cretaceous miner on the folded leaf of *Eocercidiphyllum*.
M a t e r i a l . On *Dewalquea gerofitica*, IG1-1003, *Eocercidiphyllites glandulosus*, IG1-747.

Ophionoma arcuata Krassilov, sp. nov.
Pl. XXXII, fig. 1.

N a m e . From L. *arcus*, bow.
H o l o t y p e . IG1-598, Gerofit (Pl. XXXII, fig. 1).
H o s t . *Dewalquea gerofitica* (Dobruskina) Krassilov.

D i a g n o s i s. Linear mine arching along the margin, with an elliptical exit hole about 0.5 mm wide. Frass in discontinuous median line.
D e s c r i p t i o n. The mine starts near the midrib as a thin, rapidly increasing frass line taking a nearly straight course between the lateral veins, then turning up across the laterals a short distance before the margin. The frass line is interrupted over the lower of the crossed laterals (evidently passed without eating), but is continuous above. The track is only slightly expanded near the elliptical exit hole, which is only 0.5 mm wide.
C o m m e n t s. This is an example of mining strategy, in which the stronger veins are avoided until they decrease closer to the leaf margin. The mine presents few diagnostic features, but a combination of a median frass line and minute exit hole indicates a lepidopteronome. Similar track configurations can be found in lyonetid mines, but the frass lines are less conspicuous. Mines of *Phytomyza*, Agromyzidae can be similar on account of frass line, but their exit holes are considerably larger.
M a t e r i a l. Linear mine on *Dewalquea gerofitica*, IG1-598.

Ophionoma spp.

M a t e r i a l. Less distinctive linear mines are represented as filiform tracks or slender frass lines on *Dewalquea gerofitica*, IG1-315, IG1-388, IG1-480, IG1-633, IG1-822, IG1-826, *Nelumbites aravensis*, IG1-755, *Eocercidiphyllites glandulosus*, IG1-1000. The winding ophionomes punctured by feeding holes, IG1-192, IG1- 192a are described under *Stigmophaga punctata* sp. nov. (Pl. LII, figs. 1–3; Fig. 26).

Genus *Ophistigmonoma* Krassilov, gen. nov.

N a m e. Gr. *ophis*, snake, *stigma*, mark.
T y p e. Holotype of *Ophistigmonoma rectiserialis* sp. nov.
D i a g n o s i s. Linear track expanding into blotch or series of blotches.
C o m m e n t s. The genus comprises linear-blotch mines, or ophistigmatonomes (Hering, 1951), with both components considerably developed.
S p e c i e s c o n t e n t. *Ophistigmonoma rectiserialis* sp. nov.

Ophistigmonoma rectiserialis Krassilov, sp. nov.
Pl. XXXII, figs. 2–4

N a m e. L. *rectus*, straight, *series*, row.
H o l o t y p e. IG1-633, Gerofit (Pl. XXXII, figs. 2–4).
D i a g n o s i s. Rectilinear leaf mine forming a series of consecutively increasing blotches.
H o s t. *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n. The holotype is a hypophyllous stigmatonome extending up the leaf blade across lateral veins midway between the leaf margin and midrib, parallel to the latter. Another obviously conspecific ophistigmatonome takes a somewhat oblique course in the same direction closer to the leaf margin. Each commences as a thread-like frass line proceeding as

a narrow straight, occasionally slightly winding track with minute frass grains, occasionally fused into continuous line, on both sides of it. A series of three nearly equidistant small irregular blotches are formed before the track is expanded into a larger blotch, elongate, 10 x 3 mm, followed up by another such blotch that is incompletely preserved.

C o m m e n t s . Rectilinear mines are commonly produced on parallelodromous leaves. When crossing the laterals, they tend to trace the leaf margin (e.g., in *Dicranomyia foliocuniculator*: Needham, 1928). Anyway, the abrupt expansion of linear track into a blotch is a feature of dipteronomes, as is also the double frass line.

M a t e r i a l . Linear – blotch mines on *Dewalquea gerofitica*, IG1-633, IG1-850, IG1-1110.

Ophistigmonoma crassa Krassilov, sp. nov.
Pl. XXXIII, figs. 1–4

N a m e . L. *crassus*, thick, *nomos*, domain.

H o l o t y p e IG1-6, Gerofit (Pl. XXXIII, figs. 1–4).

D i a g n o s i s . Small isometric blotches with rudimentary linear part, scattered over the midrib zone and leaf margins, marked by thick cogged contours. Frass pellets in peripheral girdles inside the blotch.

H o s t . *Eudebeya angusta* Krassilov, *Platydebeya papilionacea* Krassilov, *Eocercidiphyllites glandulosus* Krassilov, and *Nelumbites aravensis* Krassilov.

D e s c r i p t i o n . On the upper side of a compound trifoliate leaf of *Eudebeya angusta* (Pl. XXX, fig. 1), small blotches are scattered, about ten per leaflet, over the midrib zone and along the margins. The blotches are of the shape of rain droplets on a flat surface, irregularly rounded-ovate, semicircular along the margin, 2–2.5 mm wide, fairly distinct on account of their disproportionately thick deeply engraved cogged borderlines. Some of them show frass grains in line along the border, whereas the central part is clean, in the others the central part is covered with irregular patches of dark callous tissue. The linear part, if at all represented, is tortuous, with a thickened knot before the main blotch (Pl. XXXIII, fig. 2). More often it is obliterated or reduced to a short proximal appendage on the blotch border.

C o m m e n t s . These blotches might have been the work of young larvae hatching from eggs deposited over the respective leaf zones. The peripheral deposition of frass pellets indicates a gracilariid miner that started with a linear track leading away from the midrib and rapidly expanding into a blotch. However, the blotches are too small for a long mining period, and the conspicuously thickened callous borders suggest that they remained on leaf long after being abandoned by the larva. This implies a temporary miner with a short endophytic stage, as in *Bucculatrix*, Tineoidea: Bucculatricidae that typically makes slender serpentine mines, but also small scattered blotches.

M a t e r i a l . Small ophistigmatonomes on *Eudebeya angusta*, IG1-6, IG1-1120, *Platydebeya papilionacea*, IG1-129, IG1-130, *Eocercidiphyllites glandulosus*, IG1-212, and *Nelumbites aravensis*, IG1-191.

Genus *Ophiheliconoma* Krassilov, gen. nov.

N a m e. Gr. *ophis*, snake, *helix*, spiral.
T y p e. Holotype of *Ophiheliconoma resupinata* sp. nov.
D i a g n o s i s. Leaf mine commencing as a helically coiled track, linear or blotched further on.
C o m m e n t s. The genus is here established for the mine tracks helically coiled at the beginning and linear later on, thus representing a combination of heliconome and ophionome. Coiling in early mines provides for extending their track without infringing the stronger veins and is quite common among extant miners, but rare in the Cretaceous.
S p e c i e s c o n t e n t. *Ophiheliconoma resupinata* sp. nov.

Ophiheliconoma resupinata Krassilov, sp. nov.
Pl. XXXIV, figs. 1, 2

N a m e. L. *resupinus*, turned backward.
H o l o t y p e. IG1-139, Gerofit (Pl. XXXIV, figs. 1, 2).
D i a g n o s i s. Mine track extending from midrib to leaf margin and back, coiled at both ends. Frass thread-like in the helical part, smeared over the channel at the later stages.
H o s t. *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n. The mine starts from an ovoid scar at the midrib and is initially apparent as a coiled thread of frass. It soon expands into a narrow coiled track with dense minute frass granules in it. Further on, the track turns up along the leaf margin as a dark band about 40 mm long, puffed out five times at irregular intervals. Eventually it turns back to the midrib, the distal coil terminating with an elliptical cut-out.
C o m m e n t s. The initial thread-like frass helix suggests a “nepticuliform” mine. Remarkably, if the puff-outs of the linear track correspond to consecutive developmental stages, then the mine was constructed by six instars, as in extant *Stigmella*.
M a t e r i a l. Helical – linear mine on *Dewalquea gerofitica*, IG1-139.

Genus *Troponoma* Krassilov, gen. nov.

N a m e. Gr. *tropos*, turn.
T y p e. Holotype of *Troponoma crucitracta* sp. nov.
D i a g n o s i s. Looping linear mines crossing their own tracks or wound in closed contours.
C o m m e n t s. Such mines would have been traditionally classified as looping ophionomes, yet crossing its own track or winding into a closed contour represent a peculiar mining habit that in the present day mines occurs as aberration mostly, developing under pressure in herbaria or under unfavorable natural conditions (Hering, 1951).
S p e c i e s c o n t e n t. *Troponoma crucitracta* sp. nov., *T. curvitracta* sp. nov., *Troponoma festunata* sp. nov.

Troponoma crucitracta Krassilov, sp. nov.
Pl. XXXIV, fig. 3

N a m e. L. *crus*, cross, *tractus*, trace.

H o l o t y p e. IG1-855, Gerofit (Pl. XXXIV, fig. 3).

D i a g n o s i s. Mine extending from near the midrib along the lateral vein, looping across its own track, terminating in a slit-like exit hole. Frass in pellets inside and on flanks of the mine.

H o s t: *Platanervia integrifolia* Krassilov.

D e s c r i p t i o n. The mine starts from a circular opening on flank of a lateral vein short distance from its departure from the midrib. The opening is surrounded by frass pellets. The track briefly loops sideways then continuing over the lateral vein. Before approaching the leaf margin, it makes 8-shaped figure that ends in a slit-like opening 1 mm long, marked by a thick callous borderline. The loop is puffed out above the crossing point, as if the miner shortly retracted it. Frass granules are scattered around the entrance hole and over the channel in its proximal part, notably increasing over the loop and strained on one side of it, but scarcely forming a double row.

C o m m e n t s. A habit of crossing and retracting the mine channel occurs in a number of lepidopteronomes (e.g., of *Marmara*, Gracilariidae, *Recurvaria*, Gelechiidae), in some of which frass is extruded from the entrance hole. Yet the shape and size of the exit hole rather suggest a dipteronome, as of *Phytomyza chrisanthemi* (Needham *et al.*, 1928).

M a t e r i a l. Looping mine on *Platanervia integrifolia*, IG1-447.

Troponoma curvitracta Krassilov, sp. nov.
Pl. VI, fig 4b; Pl. XXX, fig. 1; Pl. XXXV, figs. 1–5;

Name. L. *curvus*, bent, *tractus*, trace.

H o l o t y p e. IG1-160, Gerofit (Pl. XXXV, figs. 1–5).

D i a g n o s i s. Slender track starting from a persistent egg, typically wound into closed loops, occasionally rectilinear. Frass pellets powdery, dispersed over the track, partly in two side lines.

H o s t. *Dewalquea gerofitica* (Dobruskina) Krassilov.

D e s c r i p t i o n. The winding tracks are of various configuration, but assignable to one and the same species of mining insect on account of similar location, track dimensions and frass deposition. Of four better developed mines numbered in Pl. XXXV, number 1 is a straight linear track 15 mm long, starting from an obscure egg scar some distance from the midrib and extending nearly parallel to the lateral veins, shortly interrupted in the middle and terminated far before the leaf margin. It shows a double line of frass pellets appearing as dense dots arranged in slightly undulating side rows. Number 2 starts from a well-marked egg scar, taking a winding course towards the margin and then crossing a lateral vein to form two concentric loops. Frass deposition is like in number 1, but less distinctly double strained. A lump of larger frass grains at the crossing of the inner and outer loops probably marks an exit hole (arrow in Pl. XXXV, fig. 2). Number 3 is a peculiar narrowly looping track with a pair of eggs

on one end, on the opposite end entering the basal disk of a *Ceratoneon* type gall. The miner might have eaten the gall or inhabited it as an inquiline. Number 4 is a narrow, somewhat angular loop arching between two lateral veins. It makes angular points at intersection with the interstitial veins. An egg scar is preserved at one of such points. About 30 egg scars are scattered over the leaf surface some showing various stages of procecidial development.

In paratype IG1-563 (Pl. XXX, fig. 1), slender angular loops about 5 x 3 mm with a persistent egg scar on the bordering track are likewise wound into closed contours. No frass remains are discernible in or around these apparently superficial mines.

Comments. The mine configurations of the kind are sometimes produced by *Stigmella*. However, egg persistence on mines is a feature of coleopteronomes, and comparable looping mines are made by a weevil *Rhamphus pulicarium* on *Betula* (cf. Hering, 1957, Pl. 15, fig. 134). Hering explains small size of the mines by space limitations for the larvae simultaneously hatching from densely deposited eggs. Instances of gall eating are rare, but known in all orders of mining insects.

Material. Coiled mine on *Dewalquea gerofitica* Krassilov, IG1-160, IG1-81; IG1-563, IG1-496, IG1-599, IG1-1110b.

Troponoma festunata Krassilov, sp. nov.
Pl. XXXV, figs 1–3

Name. *L. festum*, feast.

Holotype. IG1-1001, Gerofit (Pl. XXXVI, figs. 1–3).

Diagnosis. Thread-like tracks wound into digitate intercrossing loops entangled into a solid mass in the centre.

Host. *Dewalquea gerofitica* (Dobruskina) Krassilov.

Description. The upper surface of a leaflet bears several mines consisting of a circular or elliptical central node and a loose network of radial festoons marked by the erratically winding, occasionally intercrossing filiform tracts. The whole structure is flat, about 5 mm in diameters or somewhat stretched in the direction of the lateral veins.

Except for the radial pattern of festoons, these structures scarcely stand out in either relief or coloration. In one of them, the central area is cut out giving it a flower-like outlook (Pl. XXXVI, fig. 1). Margins of the nearly circular cut-out piece are microcrenulate and slightly callous. Another irregular crenulate cut-out is seen on the opposite side of the midrib.

Comments. Similar mine configurations are known in *Stigmella*, Nepticulidae, although the radially spreading festoons may indicate a gracilariid miner similar in habits to the digitate miner *Parectopa robiniella* (Needham *et al*., 1928).

Material. Festooned mine on *Dewalquea gerofitica*, IG1-1001.

Subgroup Stigmonomata

Blotch mines

N a m e. Gr. *stigma*, scar, *nomas*, wanderer.

Genus *Eustigmonoma* Krassilov, gen. nov.

N a m e. Gr. *eu*, genuine, *stigma*, scar.

T y p e. Holotype of *Eustigmonoma amoeboides* sp. nov.

D i a g n o s i s. Small blotches commencing at persistent egg scar, with exit holes or cocoon scars opposite the entrance.

C o m m e n t s. The genus represents a distinctive habit, in which the hatching larva is engaged in blotch mining directly from under the egg skipping the linear advance. Egg persists on the mines produced by Coleoptera and a few Lepidoptera, such as Tischeriidae. Cocoons in the mine are more typical of Coleoptera, than the other mining groups. Smallish rounded cocoons, sometimes clustered at the end of communal mines, are made by *Prionomerus* and *Orchestres*, Chrysomelidae: Hallicinae. Among Lepidoptera, many species of *Lithocolletis* make their pupation, sometimes also hibernation, cocoons in the mine. Few Gelechiidae (*Cosmopteryx*) and Heliodinidae (*Cycloplasis*) cut out circular leaf (epidermal) pieces for making cocoon cases. Among Hymenoptera: Tenthredinidae this habit is known in *Phyllotoma* alone (Needham *et al.*, 1928).

S p e c i e s c o n t e n t. *Eustigmonoma amoeboides* sp. nov., *E. ochrea* sp. nov., *E. alternans* sp. nov.

Eustigmonoma amoeboides Krassilov, sp. nov.

Pl. XXXVIIII, fig. 3

N a m e. Gr. *amoibe*, change.

H o l o t y p e. IG1-363, Gerofit (Pl. XXXVIIII, fig. 3).

D i a g n o s i s. Small irregular blotch with an egg scar on the border and a circular exit (or cocoon) scar surrounded by frass pellets.

H o s t: *Dewalquea gerofitica* (Dobruskina) Krassilov.

D e s c r i p t i o n: The blotch is irregularly lobed, transversely oriented, 3.2 mm long, pink yellow against the paler leaf impression, marked out by a thick knotted borderline, the knots evidently corresponding to the larval bites along the margin. An elliptical marginal prominence 0.3 mm long represents an egg scar, whereas on the opposite end there is a prominent circular thick-bordered hole, surrounded by small black frass pellets.

C o m m e n t s. The persistent egg and the position of the exit (or cocoon) hole at the opposite end of the mine indicate a coleopteronome comparable to those of extant Hallicinae.

M a t e r i a l. Minute blotch on *Dewalquea gerofitica*, IG1-563.

Eustigmonoma ochrea Krassilov, sp. nov.

Pl. XVIII, figs. 1a, c, 2c, 4, 5

N a m e. Gr. *ochre*, funnel.

H o l o t y p e. IG1- 80a, Gerofit (Pl. XVII, fig. 4).

D i a g n o s i s. Funnel-shaped blotch with a fringed cocoon scar on end.

H o s t : *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n . The blotches commence from inconspicuous swellings at the leaf margin roll or marginal cutting, flare and then taper to the elliptical terminal body, supposedly a pupation cocoon, about 1 mm long, brick red, narrowly fringed by the blotch. Rows of black frass pellets are discernible over the reddish yellow blotch area. A supposedly conspecific mine, IG1-80c, extends short distance from the margin roll and ends in two elliptical cut-outs.
C o m m e n t s . This small blotch differs from the other eustigmonomes in being marginal rather than costal. The supposed affinities as in *E. amoeboides* above.
M a t e r i a l . Minute blotch with cocoon cut-outs on *Dewalquea gerofitica*. IG1- 70b.

Eustigmonoma alternans Krassilov, sp. nov.
Pl. XXXVII, figs. 1–5

N a m e . L. *alternare*, alternate.
H o l o t y p e . IG1-426, Gerofit (Pl. XXXVII, figs. 1–5).
D i a g n o s i s . Small blotches alternating on both sides of leaf midrib, clean of frass and traversed by leaf veins or filled with frass pellets. Rounded cocoon scars solitary or in clusters, some on a short out-pushing.
H o s t : *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n . Alternate series of blotches are aligned with the midrib on both sides of it or spread a short distance over the lateral veins. They evidently develop from the egg pockets discernible at their base on the midrib. The shapes of the blotches vary from elongate elliptical to wedge-shaped, distally flared (Pl. XXXVII, fig. 5), their edges are sharply delineated by thick knotted lines. The lighter blotches are 6–8 mm long, transparent, traversed by distinct traces of lateral veins that continue without changing their course beyond the mine. The darker blotches are filled with transversely oriented frass pellets, but with no vascular tracery discernible.

Small cut-outs, rounded, or occasionally concentric (Pl. XXXVII, fig. 5) are situated on the mine borders or on short outpushings, as in Pl. XXXVII, fig. 4. There seems to be three somewhat unequal swellings (cocoons?) clustered at the base of elongate blotch in Pl. XXXVII, fig 2.
C o m m e n t s . All the blotches on the holotype seem to be the work of one and the same miner, although they look somewhat different, perhaps representing various developmental stages. The costal egg pockets, frass disposition, and the position of cocoon bodies (holes) may indicate a coleopteronome of a chrysomelid beetle.
M a t e r i a l . Small adcostal eustigmonomes on *Dewalquea gerofitica*, IG1-426.

Genus *Distigmonoma* **Krassilov, gen. nov.**

N a m e . Gr. *di-*, double, *stigma*, scar.
T y p e . Holotype of *Distigmonoma fimbriata* sp. nov.
D i a g n o s i s . Mine-in-mine or mosaic structures of shallow and deep mines.
S p e c i e s c o n t e n t . *Disigmonoma fimbriata* sp. nov., *D. variegata* sp. nov., *D. oculata*, sp. nov.

Distigmonoma fimbriata Krassilov, sp. nov.
Pl. XXXVIII, figs. 1,2

N a m e. L. *fimbriatus*, fringed.
H o l o t y p e. IG1-588, Gerofit (Pl. XXXVIII, figs. 1, 2).
D i a g n o s i s. Reniform mine-in-mine blotches of prominent central part surrounded by a fringe of slender appendages.
H o s t. *Platanervia integrifolia* Krassilov.
D e s c r i p t i o n. The blotch occurs between lateral veins on the upper surface impression of a fully developed platanoid leaf. It starts from an elliptical acuminate egg 1 mm long laid close to a lateral vein. A short patchy track transverse to the lateral vein is suddenly puffed out into a reniform blotch 12 mm wide, consisting of a prominent dark central part marked off by a deeply engraved black wavy borderline, and a lighter 1.2–2.5 mm wide fringe with irregularly branched, anastomosing appendages. Tertiary venation, obscure on the leaf impression, is discernible over the darker part of the blotch. An elongate slit near the centre of the blotch may represent an exit hole.
C o m m e n t s. The blotch is a mine-in-mine construction comprising two consecutive stages: a shallow blotch made by an early instar and then expanded by cutting deeper in the parenchyma as in Lepidoptera: Gracilariidae.
M a t e r i a l. Large mine-in mine structure on *Platanervia integrifolia*, IG1-688.

Distigmonoma variegata Krassilov, sp. nov.
Pl. XXXIX, fig. 4

N a m e. L. *variegates*, variegate.
H o l o t y p e. IG1-644, Gerofit (Pl. XXXIX, fig. 4).
D i a g n o s i s. Whole-leaf variegate mosaic of orthogonal blotches, dark and light, with frass pellets in girdles over the periphery.
H o s t: *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n. The mined area extends the whole width of leaflet showing transverse series of contiguous blotches bound by lateral veins. The blotch shapes are elliptical, rectanguloid or irregular, about 4–5.5 mm wide, their sinuous lateral borders are defined by the transcurrent tertiary venation. The mosaic appears variegate, grading from pale beige to crimson or dark brown. Such color variations may correspond to the depth of blotches made by consecutive instars. The blotches appear perfectly flat, but the occasionally preserved fine striation across them may represent silk threads. Girdles of black rounded frass pellets are discernible over the periphery of the darker blotches, whereas their central parts are devoid of frass deposits. Bright red spots over the mosaic possibly represent hibernation cocoons at various developmental stages.
C o m m e n t s. The construction is typically lethicolletiform (described in detail in Needham et al., 1928), in which the first instar is a sap feeder mining lower leaf surface in large blotches between the lateral veins. After the third molt, the larva takes parenchyma first over the edges of an earlier blotch then moving inwards. Frass is deposited in girdles over the peripheral zone,

from which the parenchyma had been removed. In *Lithocolletis lucetiella*, the rectangular outlines of blotches are determined by scalariform tertiary venation of its host plant, *Tilia*, whereas the shapes of fossil mines reflect a far less regular network of tertiary veins in *Dewalquea*.
Material. On *Dewalquea gerofitica* IG1-201, IG1-478, IG1-600, IG1-644. IG1-645, IG1-646, IG1-821, IG1-855, on *Platydebeya papilionacea*, IG1-194, on *Eocercidiphyllites glandulosus*, IG1-9, IG1-740, IG1-743.

Distigmonoma oculata Krassilov sp. nov.
Pl. XXXIX, figs. 1, 2

Name. L. *oculus*, eye.
Holotype. IG1- 1110 (Pl. XXXIX, fig. 1).
Diagnosis. Costal mine-in mine construction of small concentric blotches.
Host. *Dewalquea gerofitica* (Dobruskina) Krassilov.
Description. The holotype is a double blotch on midrib between the lateral veins (also affected by the midrib splitting gall, *Costaeon schizmatum*), elliptical, somewhat obliquely transverse to the midrib, 5 mm wide, consisting of a dark, sharply delineated central part with peripheral frass dots and a lighter, slightly asymmetrically developed fringe, the latter showing an irregularly dentate margin, with acute points over the hypertrophied tertiary veins. Paratype IG1-600 represents two double blotches of similar shapes subopposite on both sides of the midrib. Here the inner blotch is only slightly darker than the fringe and the latter is marked out by a smooth or only minutely dentate borderline.
Comments. This is a rare type of mine traversing the midrib at an early, presumably sap-feeding stage already, but modern equivalents of it can be found among the lethicolletiform mines (e.g., *L. corylifoliella*: Mani, 1954, Fig. 108).
Material. Mine-in-mine structure on midrib of *Dewalquea gerofitica*, IG1-128, IG1- 600, IG1-1110.

Genus *Asteronoma* Krassilov, gen. nov.

Name. Gr. *aster*, star.
Type. Holotype of *Asteronoma arachnoides* sp. nov.
Diagnosis. Leaf blade mines digitate with double rows of frass pellets.
Comments. The genus comprises digitate blotch mines, or asteronomes (Hering, 1951) with distinct strains of frass pellets over the arms, as in the mines of agromyzid flies (Agromyzidae: Diptera).
Species content. *Asteronoma arachnoids* sp. nov., *A. expansa* sp. nov., *A. helicoides* sp. nov.

Asteronoma arachnoides Krassilov, sp. nov.
Pl. XL, figs. 1–3; Pl. XLI, figs. 1, 2, Pl. XLII, fig. 6; Pl. XLIII, fig. 3

Name. Gr. *arachne*, spider.
Holotype. IG1-138 (counterpart IG1-125), Gerofit (Pl. XL, fig. 1).

D i a g n o s i s . Digitate mine (asteronome) starting from a swelling on the leaf midrib, asymmetrically expanded on both sides of it. Rays radially spreading, ascending or recurved, of unequal length. Frass in double rows of minute rounded pellets.
H o s t . *Platydebeya papilionacea* Krassilov, occasionally *Dewalquea gerofitica* Krassilov.
D e s c r i p t i o n . This spidery asteronome starts from the midrib in the middle of the leaflet. The longer ray on one side of it ascends along the lateral vein and turns up before the margin. The rest of the rays are shorter, some cut across the laterals intersecting the ascending rays. On the opposite side, the rays are less distinct, cohering into a blotch. A smaller blotch at the leaf margin appears separate, but is actually linked to the main blotch by few strains of frass pellets. Frass pellets appear as distinct or locally confluent dots or minute pits, rounded or somewhat stretched obliquely to the rays.

Paratypes IG1-116 of shorter rays diverging from a relatively massive central blotch (Pl. XLII, fig. 6), IG1-128, a disorderly blotch with long and short arms twisted in opposite directions over a limited area among the other type mines (Pl. XLI, figs. 1, 2), and IG1-600, of unequal rays remained from a cut-out mine (Pl. XLIII, fig. 3), all have basically similar configurations of the spreading rays and frass pellets.
C o m m e n t s . The mine is closely comparable to those of agromyzid flies, in particular, of an extant European species *Phytomyza periclymeni* (Diptera: Agromyzidae) on *Lonicera* (Hering, 1957, fig. 376) that is also centered upon the midrib, but the rays are reflexed before the margin.
M a t e r i a l . Digitate blotch on *Platydebeya papilionacea*, IG1-138 (counterpart IG1-125), IG1-116, IG1-128 (counterpart IG1-45), IG1-600, on *Dewalquea gerofitica*, IG1-239.

Asteronoma expansa Krassilov, sp. nov.
Pl. XLII, figs. 3–5; Pl. XLIII, figs. 1, 2

N a m e . From L. *expansa*, spread.
H o l o t y p e . IG1-11, Gerofit (Pl. XLII, figs. 3, 4).
D i a g n o s i s . Digitate mine (asteronome) of half leaf-blade extension, with radial rays marked by double rows of elongate frass pellets transverse or slightly oblique to the ray mid-line.
H o s t . *Platydebeya papilionacea* Krassilov, *Nelumbites aravensis* Krassilov.
D e s c r i p t i o n . The holotype is a large asteronome 40 mm long on one side of the midrib, occupying most of the half-blade, which is much paler than the opposite unaffected (except quite locally across the midrib) deep purple half blade. Numerous rays, marked by double strains of frass pellets, are spreading from a pocket with several egg-like dark bodies adjacent to the midrib, turning down the leaf blade or ascending parallel to the lateral veins for some distance and reflexed before the margin. The frass strains are recurved on ends, the pellets are fairly distinct and evenly spaced, a few of them attached across the rays.

A marginal blotch of straight rays, IG1-9 (Pl. XVII, fig. 5) may belong to the same species, as well as a radially symmetrical mine on *Nelumbites*, IG1-868 (Pl. XLIII, fig. 1), the central part of which is a dark blotch streaked with faint strains of frass pellets, perforated by large feeding holes (see under *Stigmatophaga perforata*). Outside the dark area, the rays extend as double rows of frass pellets over the pale gray leaf impression.

Comments. Large size of the blotch involving the entire half-blade and a rather chaotic arrangement of the rays suggest a composite mine formed of two or several blotches simultaneously developing from a set of several eggs, as in *Chromatomyia gregaria* (Spencer, 1990: 240). Morphologically this species differs from *A. arachnoids* in its peculiar topography and in the frass pellets being longer and more regularly disposed over the rows.

A mine of the leaf apex, with looping branches down the blade (Pl. XLIII, fig. 2) may belong to this species on account of the similar elongate frass pellets transverse to the rows, although its general configuration is unknown. Anyway, mining of leaf apices is a specialized feature in extant Diptera, combining an advantage of feeding on young tissues with disadvantage of limited space for constructing the mine.

Material. Digitate mine on *Platydebeya papilionacea*, IG1-11, probably IG1-123, IG1-134, on *Nelumbites aravensis* IG1-9, IG1-868, IG1-872.

Asteronoma helicoides Krassilov, sp. nov.
Pl. XLII, figs. 1, 2

Name. From Gr. *helix*, spiral.

Holotype. IG1-675, Gerofit (Pl. XLII, figs. 1, 2).

Diagnosis. Digitate mine (asteronome) of helically coiled rays marked by discontinuous rows of dense minute frass pellets.

Host. *Nelumbites aravensis* Krassilov.

Description. The mine is prominent against the colorless leaf impression (the upper side with only vaguely marked venation pattern), radial, 37 mm across, of helically coiled rays marked by the broken and occasionally anastomosing strains of minute rounded or somewhat transversely stretched pellets that are unevenly spaced and locally confluent. A notable feature of the mine are irregular islands of callus onlapping the frass rows.

Comments. The mine is peculiar on account of the helically screwed egg rows, and the frass pellets are distinct in shapes and less regularly disposed than in the other asteronome species.

Material. Digitate mine on *Nelumbites aravensis*, IG1-675 (counterpart IG1-669).

Genus *Symphyenoma* Krassilov, gen. nov.

Name. Gr. *syn*, together, *phyein*, to grow.

Type. Holotype of *Symphyenoma adcostalis* sp. nov.

Diagnosis. Communal leaf blotch comprising a cluster of simultaneous blotches developed from persistent egg scars.

Comment. The genus is here erected for communal blotches consisting of several simultaneously developing partly or entirely confluent *Eusgtigmonoma* type blotches (above). In addition to the type species, communal blotches, distinctive on account of different features, are described under *Asteronoma expansa*, *Stomonoma crenulata* and *S. multiforata*.

Species content. *Symphyenoma adcostalis* sp. nov.

Symphyenoma adcostalis Krassilov sp. nov.
Pl. XLV, fig.4

N a m e. L *adcostalis*, rib bound.
H o l o t y p e. IG1-80e, Gerofit (Pl. XLV, fig. 4).
D i a g n o s i s. Composite midrib blotch comprising a transverse series of confluent blotches developing form a strain of eggs deposited off the midrib.
H o s t. *Dewalquea* gerofitica (Dobruskina) Krassilov.
D e s c r i p t i o n. An irregular strain of about ten small (0.2 mm) eggs, deposited about 1 mm off and parallel to the midrib, simultaneously develop into a series of transverse rib-bound blotches that become confluent over the midrib. Fewer eggs on the opposite side of it in their turn contribute to the composite blotch that acquires an asymmetrically lobed outline.
C o m m e n t s. Communal costal blotches developing from eggs deposited at or adjacently to the stronger veins and remaining on the mine surface are typically constructed by leaf beetles, such as *Prionomerus*, Chrysomelidae: Hallicinae (Needham *et al*., 1928).
M a t e r i a l. Communal blotch on *Dewalquea gerofitica*, IG1-80e, IG1-853.

Genus *Holostigmonoma* **Krassilov, sp. nov.**

N a m e. Gr. *holos*, whole, *stigma*, scar.
T y p e. Holotype of *Holostigmonoma zebrina* sp. nov.
D i a g n o s i s. Whole leaf blotches marked by frass pellets and callus patches extending from one leaf margin to the other.
C o m m e n t s. Close extant analogues of mines, involving compound leaf as a whole are not known, but extensive mined areas occupying most of the leaf blade as a continuous blotch are typically produced by Diptera: Anthomyiidae, and, among the Lepidoptera, by the coleophorid and nepticulid miners.
S p e c i e s c o n t e n t. *Holostigmonoma zebrina* sp. nov., *H. fenestrata* sp. nov.

Holostigmonoma zebrina Krassilov, sp. nov.
Pl. XLIV, figs. 1–3

N a m e. Afr. *zebra*, striped horse. In honor of paleontologist Zeev Lewy (nickname Zebra).
H o l o t y p e. IG1-539, Gerofit (Pl. XLIV, figs. 1–3).
D i a g n o s i s. Whole leaf mine marked by transverse strains of frass pellets extending over the midrib and reaching to the leaf margins.
H o s t. *Dewalquea gerofitica* (Dobruskina) Krassilov.
D e s c r i p t i o n. The mine occurs on two leaflets of an incomplete compound leaf. The mined areas are distinctive due to their dark color, mottled impression of callus cells, and transverse striping extending the whole width of leaflet across the midrib callus zone, but locally interrupted by irregular elongate holes, which are either epidermal windows, or external feeding marks. The transverse striping is dense, rectilinear, at 90° to the midrib or slightly flexed down the leaf blade. The stripes, about 0.2 mm thick, consist of distinct or confluent dot-like pellets.

Comments. Frass deposition in dark stripes with about equally wide white stripes in between is typical of trumpet mines (Lepidoptera: Tischeriidae), yet the whole leaf (or even half-blade) mining is uncommon in the Tischeriidae more often occurring in dipteronomes, like those of *Pegomyia*, Anthomyiidae.
Material Whole-leaf mine on *Dewalquea gerofitica*, IG1-123.

Holostigmonoma fenestrata Krassilov, sp. nov.
Pl. XLV, figs. 1a, 2

Name. L. *fenestra*, window.
Holotype. IG1-191, Gerofit (Pl. XLV, figs. 1a, 2).
Diagnosis. Whole-leaf (leaflet) blotches with a continuous or discontinuous median epidermal window.
Host. *Dewalquea gerofitica* (Dobruskina) Krassilov.
Description. On a 5-foliate compound leaf, the mine involves the whole width and most of the length of four elongate leaflets preserved. The mined areas are darker than the remaining patches of unaffected leaf surface and are densely speckled with small frass granules. The epidermis appears swollen over the mine and makes a mottled impression. On the central leaflet, it is removed in the middle, opening an elongate window 40 mm long with thick sinuous borders. A smaller second window occurs short distance above the first. The midrib is exposed in the windows, but mesophyll on both sides of it is excavated down to the lower epidermis that bears faint marks of frass granules. The lateral leaflets also show epidermal windows over their midribs.
Comments. The central window appears fairly transparent, all the tissue, except the vascular bundles of the midrib, being removed down to the lower epidermis. The leaf bearing this mine shows also several marginal cut-outs and an apically attached leaf case (described below under *Folicasa tubularis*). The habit of window eating in association with the larval case may suggest a moth miner with behavioral affinities to Lepidoptera: Coleophoridae.
Material. Whole leaf blade mine with epidermal windows on *Dewalquea gerofitica*, IG1-191, IG1-539.

Genus *Apostigmonoma* Krassilov, gen. et sp. nov.

Name. Gr. *apo*, from.
Type. Holotype of *Apostigmonoma fibrosa* sp. nov.
Diagnosis. Epidermal windows on mines exposing intact tracery of fibrovascular bundles.
Comments. The genus comprises structural evidence of "window feeding", in which pieces of epidermis are removed as "windows". Some holostigmonomas show windows, but their main distinguishing character is their whole-leaf extent and deep excavation of the leaf tissues. In *Apostigmonoma*, the epidermal windows are the most conspicuous feature of the mine, exposing the intact tracery of lateral venation. Among the mining insects, they are typically made by extant species of Coleophoridae, Buccularicidae, and Pyralidae (*Nausinoe*), the latter on aquatic plants.
Species content. *Apostigmonoma fibrosa* sp. nov.

Apostigmonoma fibrosa Krassilov, sp. nov.
Pl. XXXIII, fig. 5; Figs. 22, 23.

N a m e. L. *fibra*, fiber.

H o l o t y p e. IG1-331 (Pl. XXXIII, fig. 5; Figs. 22, 23).

D i a g n o s i s. Mottled mid-leaf areas with elongate epidermal windows traversed by traces of lateral veins.

H o s t. *Yammelechia superba*, sp. nov.

D e s c r i p t i o n. Two nearly identical blotches occur in the mid-blade area of a large leaf with dense parallel lateral venation, aligned with the tertiary network. The blotches are expressed as irregular mottled areas speckled with callus cells. Most of the veins are interrupted by the blotch or their traces are blurred by the callous epidermis. The elongate windows in the middle of the blotch are 5–8 mm long, extending obliquely to the midrib and expanding up the leaf to about 2 mm in width. The traces of lateral veins, but not the higher order venation, are distinctly marked across the window.

Fig. 22. *Apostigmonoma fibrosa* gen. et sp. nov., holotype, IG1-331, disposition of blotches (a, b) on *Yammelechia superba*, Gerofit.

C o m m e n t s . Except for the windows, the blotches are rather inconspicuous, and the speckles over them appear as scattered callous cells rather than frass pellets. It does not seem that they were inhabited for a long time by the miner, and the windows might have been made after the mine was abandoned. The feeding habit producing such constructions might have been as in *Bucculatrix* (Lepidoptera: Tineoidea: Bucculatricidae), which makes windows at an early free-leaving stage skeletonizing the leaf at the later stages.

M a t e r i a l . Two nearly identical blotches on *Yammelechia superba* sp. nov., IG1-331.

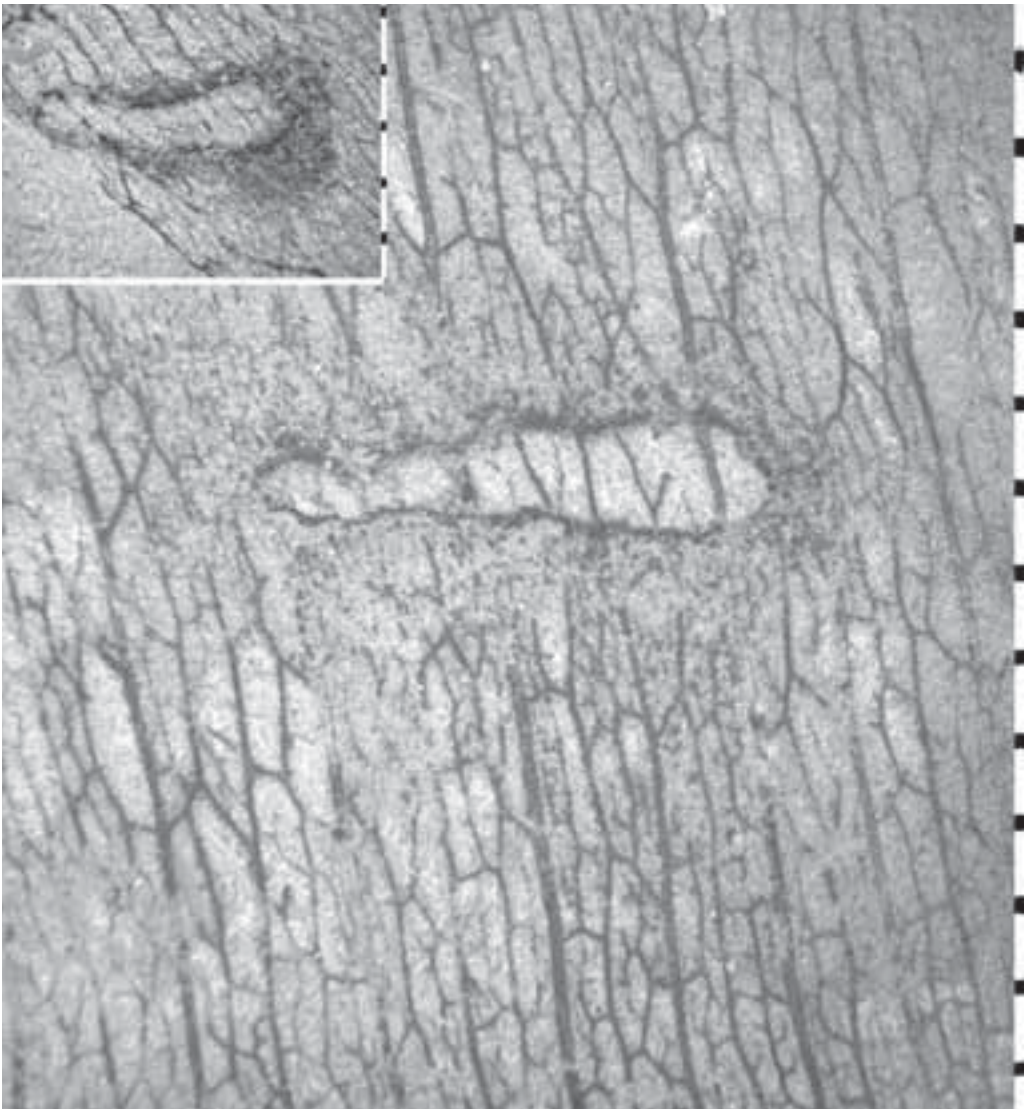

Fig. 23. *Apostigmonoma fibrosa* gen. et sp. nov., holotype IG1-331, two transparent blotches on *Yammelechia superba*, with the stronger fibrovascular strands extending across the windows.

Genus *Stomonoma* Krassilov, gen. nov.

N a m e. Gr. *stoma*, mouth.

T y p e. Holotype of *Stomonoma dimorpha* sp. nov.

D i a g n o s i s. Mines with whole leaf or epidermal cut-outs for larval or pupal case construction.

C o m m e n t s. Temporary miners cut-out epidermal or whole leaf pieces from (on the border of) the mines for constructing larval cases, sometimes two consecutive types of these. Cut-outs are also made for covering the pupation cocoons. Mines with such cut-outs are distinctive enough for being assigned to a separate form-genus.

S p e c i e s c o n t e n t. *Stomonoma dimorpha* sp. nov., *S. crenulata* sp. nov., *S. multiforata* sp. nov.

Stomonoma dimorpha Krassilov, sp. nov.

Pl. XLVI, figs. 1–6; Pl. XLVII, figs. 1–3

Name. Gr. *di*, twice, *morphe*, form.

H o l o t y p e. IG1-107 (counterpart IG1-108), Gerofit (Pl. XLVI, figs. 1–6; Pl. XLVII, figs. 1–3).

D i a g n o s i s. Gregarious irregular–polygonal blotches showing either curvilinear leaf piece cut-outs or radial meshes spun around a larger epidermal cut-out. Frass pellets collected in the peripheral folded areas, rarely scattered.

H o s t. *Nelumbites aravensis* Krassilov, occasional on *Dewalquea gerofitica* (Dobruskina) Krassilov.

D e s c r i p t i o n. In the holotype, the lower side impression of an incomplete peltate leaf is spotted all over with prominent irregular-polygonal blotches that are occasionally paired or contiguous (Pl. XLVI, fig. 1). The blotches avoid the primary veins and their stronger branches, but are often delineated and occasionally crossed by tertiary veins (Pl. XLVI, figs. 2–8).

There are two types of blotches, but they certainly are the work of one and the same mining species. The smaller blotches, occupying central position on the peltate leaf blade, are irregular, 4–5 mm wide, smooth or minutely dentate over the borders, with abundant frass grains scattered over the blotch or concentrated in the folded peripheral zone. All such mines show a curvilinear sharply outlined cut-out on the edge, occasionally in the middle (Pl. XLVII, figs. 1–3). Usually the cut-out leaf piece is at least four times smaller than the blotch, but in one occasion it is considerably larger than a diminutive blotch.

The second type blotches scattered around the first ones, are considerably larger, 5–7 mm wide, rounded-polygonal, consisting of a broad elliptical or somewhat angular central cell encircled by an incomplete ring of smaller meshes, or festoons. The central cell is flat, smooth, showing faint venation traces, free of frass pellets, only slightly if at all darker than the leaf impression around them. The encircling meshes corresponding to the forth order venation, are asymmetrically developed, forming a thick undulate contour, sometimes reduced to a narrow fringe, radially folded with cross fibers giving the blotch a bristled appearance. Fine striation over the marginal fringe (Pl. XLVI, fig. 6) evidently represents spinning silk threads. Frass in minute granules is collected over the folded margin of the blotch.

C o m m e n t s . The traces of spinning in association with case construction betray the work of a temporary mining Lepidoptera. A comparison with the mining habit of *Coleophora* suggests, that the first type blotches are constructed by young larvae (the first instar in *Coleophora*) that cut their first case out of them. As in *Coleophora*, these early blotches occur in the middle of the leaf. Later in development, the larva resided to mining producing larger blotches (devoid of frass in *Coleophora*) and outlining its second case. The later stage mines are less similar to those of *Coleophora*, however, having frass grains collected in the radially folded peripheral zone.
M a t e r i a l . Stomonomes on *Nelumbites aravensis*, IG1-62, IG1-107, IG1-145, IG1-247, on *Dewalquea gerofitica*, IG1-590.

Stomonoma spinulata Krassilov, sp. nov.
Pl. X, figs. 1. 2).

N a m e . L. *spina*, thorn.
H o l o t y p e . IG1-676, Gerofit (Pl. X, figs. 1, 2).
D i a g n o s i s . Angular-ovate or obovate minutely spinulate contours between, and aligned with, the primary veins.
H o s t . *Nelumbites aravensis* Krassilov.
D e s c r i p t i o n . A peltate leaf of *Nelumbites aravensis* with the primary veins mined by an inconspicuous filiform tracks, bears four blotches disposed in a slightly arched line across the central part of the leaf blade parallel to the primary veins, one slightly onlapping the adjacent vein. The larger body (Pl. X, fig. 2) is angular obovate, 17 mm long, somewhat darker than the leaf impression, showing faint venation traces. It is marked out by a sharp broken line with staple-like minutely spinulate dents at the angles, altogether 12 such staples over the contour. The other two contours are angular-ovate, likewise stapled, with few threads extending beyond the contoured area.
C o m m e n t s . These traces appear as leaf pieces marked for cutting out as larval cases, in particular, resembling the early cases of *Paraclemensia*, Incurvariidae (Needham *et al*., 1928). They co-occur on the leaf with the egg masses described above as *Massoveon globolosum*.
M a t e r i a l . Case plots on *Nelumbites aravensis*. IG1-676a.

Stomonoma crenulata Krassilov, sp. nov.
Pl. XLVIII, figs. 1–4

N a m e . L. *crena*, notch.
H o l o t y p e . IG1-739, Gerofit (Pl. XLVIII, fig. 1).
D i a g n o s i s . Blotches with curvilinear crenulate – cuspate cut-outs.
H o s t . *Eocercidphyllites glandulosus* Krassilov, *Platanervia integrifolia* Krassilov, *Dewalquea gerofitica* (Dobruskina) Krassilov, *Nelumbites aravensis* Krassilov.
D e s c r i p t i o n . The cut-outs occur in the broad mined areas with rows of egg scars over the border indicating a communal mine (Pl. XLVIII, fig. 2). The cut-out contours are elongate or orthogonal between the stronger veins, up to 10 mm long. Their edges are irregularly coarsely

crenulate with occasional pointed (cuspate) incisions (Pl. XLVIII, fig. 4). An intercostal cut-out, IG1-738 (Pl. XLVIII, fig. 3) is microcrenulate, possibly made by a different species.
Comments. Crenulate-cuspate cut-outs for case construction are typically made at the end of an early mining stage by the larvae of *Incurvaria* and the other incurvarioids (Lepidoptera: Incurvarioidea).
Material. Mines with case construction holes on *Eocercidphyllites glandulosus*, IG1-1110, IG1-733, IG1-738, IG1-739, IG1-743, IG1-745, *Platanervia integrifolia*, IG1-443, IG1-447, IG1-448, IG1-450, *Dewalquea gerofitica*, IG1-853, IG1-871, IG1-887, *Nelumbites aravensis*, IG1-523, IG1-752.

Stomonoma multiforata Krassilov, sp. nov.
Pl. XLIX, figs.1, 2

Name. L *multi-*, numerous, *foratus*, pierced.
Holotype. IG1-200, Gerofit (Pl. XLIX, fig. 2).
Diagnosis. Numerous elliptical cut-outs scattered or clustered over the leaf mine blotches.
Host. *Eocercidiphyllites glandulosus* Krassilov, *Nelumbites aravensis* Krassilov.
Description. Two adjacent clusters, of 6–7 elliptical holes each, occur on a broad ribbon-shaped blotch 3 mm wide, darker than the host leaf impression, contoured with sinuous borderlines, with longitudinal frass strains in the middle. The holes are distinct or in conjunctive pairs or trios, elongate-elliptical to rounded-elliptical or irregular, about 1 mm across, with distinct, probably callous, minutely crenulate borders. Paratype IG1-743 is an isometric irregularly rounded blotch 2 mm across, comprising elongate-elliptical cut-outs arranged in three conjunctive groups (Pl. XLVIII, fig. 1). Here the contours are less distinctly marked, as if cut out of one (upper) epidermis alone.
Comments. Multiple elliptical cut-outs on broad communal blotches of *Antispillina ludwigi* (Incurcvarioidae: Helizelidae) is an extant example of this type case constructing behavior (Hering, 1957, Fig. 480).
Material. Case construction holes over blotch mines on *Eocercidiphyllites glandulosus*, IG1-200, IG1-743 and *Nelumbites aravensis*, IG1-503.

Group Casasignata

Foliar larval cases

Name. L. *casa*, little house, *signum*, sign.

Genus *Folicasa* Krassilov, gen. nov.

Name. From L. *folium*, leaf, *casa*, little house.
Type species. *Folicasa cuspidata*, sp. nov. Gerofit.
Diagnosis. Larval cases constructed of leaf pieces and attached to leaves.
Comments. The genus comprises larval cases of various shapes and mouth types (Hering, 1951) attached to the leaf blades as well as to the leaf petioles, and constructed of leaf pieces

mainly. The species are differentiated on the basis of the case shapes, angles of attachment (corresponding to the mouth types), and arrangement of the leaf pieces.
Species content. *Folicasa cuspidata* sp. nov., *F. tubularis* sp. nov., *F. inflata* sp. nov.

Folicasa cuspidata, sp. nov.
Pl., L, figs. 2, 3

Name. L. *cuspis*, point.
Holotype. IG1-109, Gerofit, (Pl. L, figs. 2, 3).
Diagnosis. Case cylindrical about 2 mm long, constructed of coiled cuspate leaf pieces, attached at about 30° (mouth type 2).
Host: *Platydebeya papilionacea* Krassilov.
Description. The case is attached at a shallow marginal cut-out at about 30° to the leaf margin, which indicates the mouth plane inclined at about 15° to the case body (mouth type 2: Hering, 1951). It is 2,2 mm long, 0.5 mm broad, nearly straight, with slightly undulate contours, constructed of cuspate leaf stripes about 0.2 mm wide, which are darker than the leaf impression. The stripes are loosely coiled and criss-crossed, leaving a series of slit-like gaps traversed by elongate striation that probably represents spinning silk threads. The hind end is poorly impressed, with indication of a short mucronate appendage representing the primordial case.
Comments. The cuspate leaf stripes of which the case is composed imply a cuspate configuration of the case construction holes on the host leaf as those described above under *Stigmonoma crenulata* (Pl. XLVII, figs. 1, 4). In its shape and attachment the case is comparable to the "pupa type" coleophorid cases (Hering, 1951), but with no close equivalents among the living species as far as the arrangement of the leaf pieces is concerned.
Material. Foliar case attached to *Platydebeya papilionacea*, IG1-109.

Folicasa tubularis Krassilov, sp. nov.
Pl. L, fig. 1

Name. From L. *tubus* – pipe.
Holotype. IG1-877, Gerofit (Pl. L, fig.1).
Host. *Dewalquea gerofitica* (Dobruskina) Krassilov.
Diagnosis. Case tubular, about 3 mm long, ridged, incurved on the hind end, attached at about 15° (mouth type 2).
Description. The case is pendent on the tip of leaflet that is mined with a sinuous linear track along the margin vis-à-vis the case. The angle of the case attachment, about 15°, corresponds to the mouth type 2 (Hering, 1951). The tubular body of the case is 3 mm long, 0.5 mm broad, straight for 2/3 of its length, then smoothly curved toward the leaf margin. The hind end appears slightly notched, as if bilobed, but this can be inflicted by compression. Well-marked longitudinal ridges are traceable for the whole length of the tube.
Comments. The case shape is intermediate between the tubular type and, on account of the distal bent, the pistol type of coleophorid cases. (Hering, 1951). The leaf margin is mined

starting from the mouth of the case, which lends support to our suggestion that the mine was made by the owner of the case, as in coleophorids.
M a t e r i a l . Case attached to the leaf tip of *Dewalquea gerofitica*, IG1-877.

Folicasa inflata Krassilov, sp. nov.
Pl. XLIX, fig. 3

N a m e . L. *inflatio*, swelling.
H o l o t y p e . IG1-444, Gerofit (Pl. XLIX, fig. 3).
D i a g n o s i s . Case ovoid about 4 mm long, membranous, mucronate at the hind end, attached at the point of petiole insertion at about 60°, mouth type 4.
H o s t . *Platanervia integrifolia* Krassilov.
D e s c r i p t i o n . The case is attached near the petiole insertion at about 60° (mouth type 4, see Hering, 1951) fitting in the basal cut-out of the leaf blade that is marked by a callous margin. The case body appears flattened sac-like, convex on the upper (dorsal) side, nearly straight below. It is broadest before the mouth gradually tapering to the hind end which is shortly mucronate. The mouth is torn off by pressure and is partly seen on the bedding plane as an angular opening 0.7 mm wide, bordered by a concentric ridge. The case impression is brightly orange against the light yellow petiole and the purplish gray leaf impression, its surface is wrinkled, with minute warts scattered over it.
C o m m e n t s . The case body fits the marginal cut-out at the base of the leaf blade, under which it is attached to the petiole. The case itself corresponds to the homogeneous “sheath type” of coleophorid cases (Hering, 1971). It was apparently constructed of an upfolded leaf piece spun over the arcuate upper edge. A short mucronate appendage at the hind end probably represents a primordial case included in the later construction.
M a t e r i a l . Case attached at the base of *Platanervia integrifolia*, IG1-444.
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Group Trophostigmata

Ectophytic feeding marks

Name. Gr. *trophos*, eater, *stigma*, scar.

Genus *Stigmatophaga* Krassilov, gen. nov.

N a m e . Gr. *stigma*, scar, *phagein*, to eat.
T y p e . Holotype of *Stigmatophaga lobata* sp. nov.
D i a g n o s i s . Feeding holes on leaf mines and galls.
C o m m e n t s . Mines are targeted by predators for picking out the larvae, whereas galls can be taken out also for the sake of their nutritive tissue. Mine predators are ants and birds mainly, but also various groups of mites, lacewings, wasps, bugs, and beetles. Mines are sometimes opened by the free feeding larvae of phytophagous insects. The traces of mine/gall predation are the whole mine/gall cut-outs, as well as pecking or puncture marks upon the mine tracks.
S p e c i e s c o n t e n t . *Stigmatophaga lobata* sp. nov., *S. perforata* sp. nov., *S. punctata* sp. nov.

Stigmatophaga lobata Krassilov, sp. nov.
Pl. LI, figs. 1, 3.

N a m e. Gr. *lobos*, lobe.
H o l o t y p e. IG1-1150, Gerofit (Pl. LI, fig. 3).
D i a g n o s i s. Cut-outs conformous to the shape of digitate blotch mines (asteronomes).
H o s t. Leaf mine *Asteronoma arachnoides* sp. nov. on *Platydebeya papilionacea* Krassilov.
D e s c r i p t i o n. In holotype IG1-1150, an irregularly lobed hole reflects configuration of a digitate mine, taking out the whole central part and extending over the arms, the tips of which, with characteristic arrangement of frass pellets, are left on the leaf. Because of this, the asteronome can be easily recognized as *Asteronoma arachnoids* (above). The borders of the central hole are distinct, but scarcely callous. The mine arms are penetrated by the shallow rounded or the deeper wedge-shaped lobes, tapered into narrow slits up the arm.

Paratype IG1-600, on *Platydebeya papilionacea*, shows a bunch of digitate arms with frass pellets of *Asteronoma arachnoides* type, the rest of the mine being cut out leaving an irregularly lobed hole between lateral veins (Pl. LI, fig. 1) Similar holes on the opposite side of the mid-rib are also cut of the mined area bordered by the thickened (hypertrophied) lateral veins. The margins between the veins are sinuous series of smooth arcuate bites about 1 mm long, 0.2 mm deep.
C o m m e n t s. The predator might have worked from the middle into the arms, failing, however, to cut them out as precisely as the modern mine predators, ants or birds, would by excavating the entire mine.
M a t e r i a l. Feeding holes on digitate mines *Asteronoma arachnoids*, IG1-600, IG1- 1150.

Stigmatophaga perforata Krassilov, sp. nov.
XXXVI, fig. 1; Pl. XLIII, fig. 1; Pl. LI, fig. 2; Fig. 24

N a m e. L. *perforatus*, perforate.
H o l o t y p e. IG1-1101p, Gerofit (Pl. XXXVI, fig. 1).
D i a g n o s i s. Isometric cut-outs on mines and galls.
H o s t. *Troponoma festunata* sp. nov. on *Dewalquea gerofitica* (Dobruskina), *Asteronoma expansa* sp. nov. on *Nelumbites aravensis*, *Cephaloneon squamosum* sp. nov. on *Menispermites cuspidentatus* Krassilov.
D e s c r i p t i o n. In the holotype, a small erratically coiled mine on *Dewalquea gerofitica* has its middle part cut out leaving a rounded elliptical hole surrounded by the radial festoon-like filiform tracks (Pl. XXXVI, fig. 1). The borders of the central hole are broad arches, about 2 mm long, 0.2 mm wide, divided by shallow notches, with minute crenulations on the callus fringe.

A large radial asteronome of *A. expansa* type on *Nelumbites aravensis*, IG1-868, is cut in the middle by a large nearly circular hole with microcrenulate border. The smaller holes mark additional cut outs over the radial arms (XLIII, fig. 1). The angular holes on *Menispermites cuspidentatus* Krassilov, IG1-753 mark the sites of a cut-out gall *Cephaloneon squamosum* (Pl. LI, fig. 2; Fig. 25). They are surrounded by the dark pitted callus fringes of large hypertrophied cells that remain intact when the whole body of the gall is taken out.

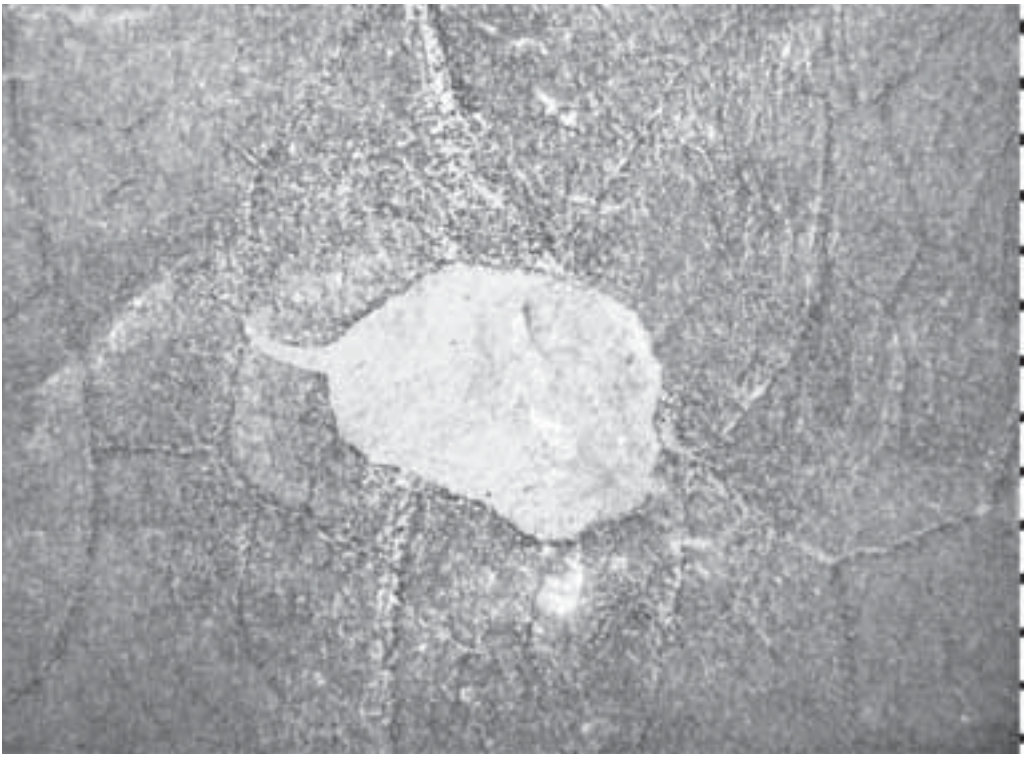

Fig. 24. *Stigmatophaga perforata* gen. et sp. nov., paratype IG1-494, a cut out cephaloneon gall on *Menispermites cuspidenntatus*, with a side slit as in *Stigmatophaga lobata* on asteronomes (Pl. LI, fig. 3).

C o m m e n t s . The cut-outs might have been inflicted by different mine predators, but their feeding habits must have been essentially similar. The cut-out borders are smooth, as if thrust open, or crenulate, as if produced by a predator with hooked mandibles. Different shapes and dimensions of marginal arches indicate more than one predatory species of diverse mouth part morphologies.

M a t e r i a l . Feeding holes on the mines *Troponoma festunata*, IG1-600, *Asteronoma expansa*, IG1-868, and on the gall *Cephaloneon squamosusm* IG1-753, IG1-494.

Stigmatophaga punctata Krassilov, sp. nov.
Pl. LII, figs. 1–3; Fig. 25

N a m e . L. *punctum*, point.

Holotype. IG1-192, Gerofit (Pl. LII, figs. 1–3).

Diagnosis. Isometric puncture marks and slits over linear mine tracks.

H o s t . *Platydebeya papilionacea* Krassilov.

D e s c r i p t i o n . A leaf of *Platydebeya papilionacea*, IG1-192 is mined over the whole surface by the tortuously coiled tracks that are densely pecked or punctured, with the holes mostly

elliptical, oblique to the track, concatenate or contiguous, cutting out arcuate slits over the coils of the track (Pl. LII, figs. 1–3).

Another linear mine on the same hand specimen, IG1-192a is sinuous, marked by a discontinuous frass line. The track is punctured with small rounded or elliptical holes that are less dense than in the holotype. The holes are solitary, rather evenly spaced over the track coils or paired, occasionally contiguous, about 0.4 mm in diameter, with thick patchy borders (Fig. 25).

Comments. Among the linear mines, only those winding over large leaf areas are predated, which may indicate a visual detection from flight. The mines might have been pecked or sheared by minute beaks or rostra, but the evidence is not enough for even preliminary identification of the predator.

Material. Punctured mine tracks on *Platydebeya papilionacea*, IG1-192, IG1-192a.

Genus *Trophoglypha* Krassilov, gen. nov.

Name. Gr. *trophos*, eater, *glyphein*, to carve.

Type. Holotype of *Trophoglypha diffusa* sp. nov.

Diagnosis. Feeding marks in the form of holes, punctures, specks (small callous patches), "etchings", hieroglyphic or scrip-like traces, mottling, and skeletonized areas.

Comments. The genus is broadly defined at present, to be split with accumulation of data for recording different feeding morphotypes. Trophoglyphes are evidence of feeding habits

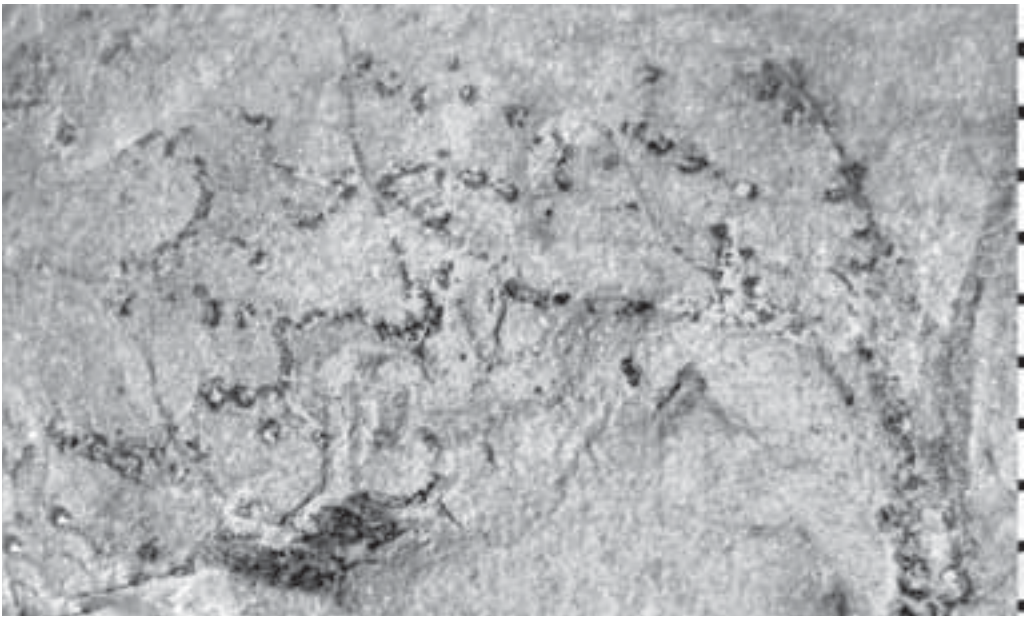

Fig. 25. *Stigmatophaga punctata* gen. et sp. nov., paratype IG1-192a, punctuate pecking marks on the winding track of a linear mine.

that can be widely spread over taxonomically unrelated groups or more narrowly confined. Thus similar feeding holes or punctures are made by *Bucculatrix*, Lepidoptera, *Microrhopala*, Coleoptera, *Agromyza*, Diptera, as well as mites and thrips. “Etchings” or script-like (“hieroglyphic”) marks represent curved swath lines made by the feeders with hooked mandibles, as in Diptera: Agromyzidae. Specks of callus develop over shallow patches gnawed out by chrysomelid beetles and weevils. Mottling results from horizontal shearing and occasional deeper bites into the parenchyma. Skeletonized network of fine venation can be the work of some gracilariid Lepidoptera, but also of *Bucculatrix*, Bucculaticidae, or behaviorally equivalent extinct forms. The diversity of feeding marks on angiosperm leaves of Gerofit assemblage includes all such and some other, by now poorly understood, morphotypes.

Species content. *Trophoglypha diffusa* sp. nov., *T*. spp.

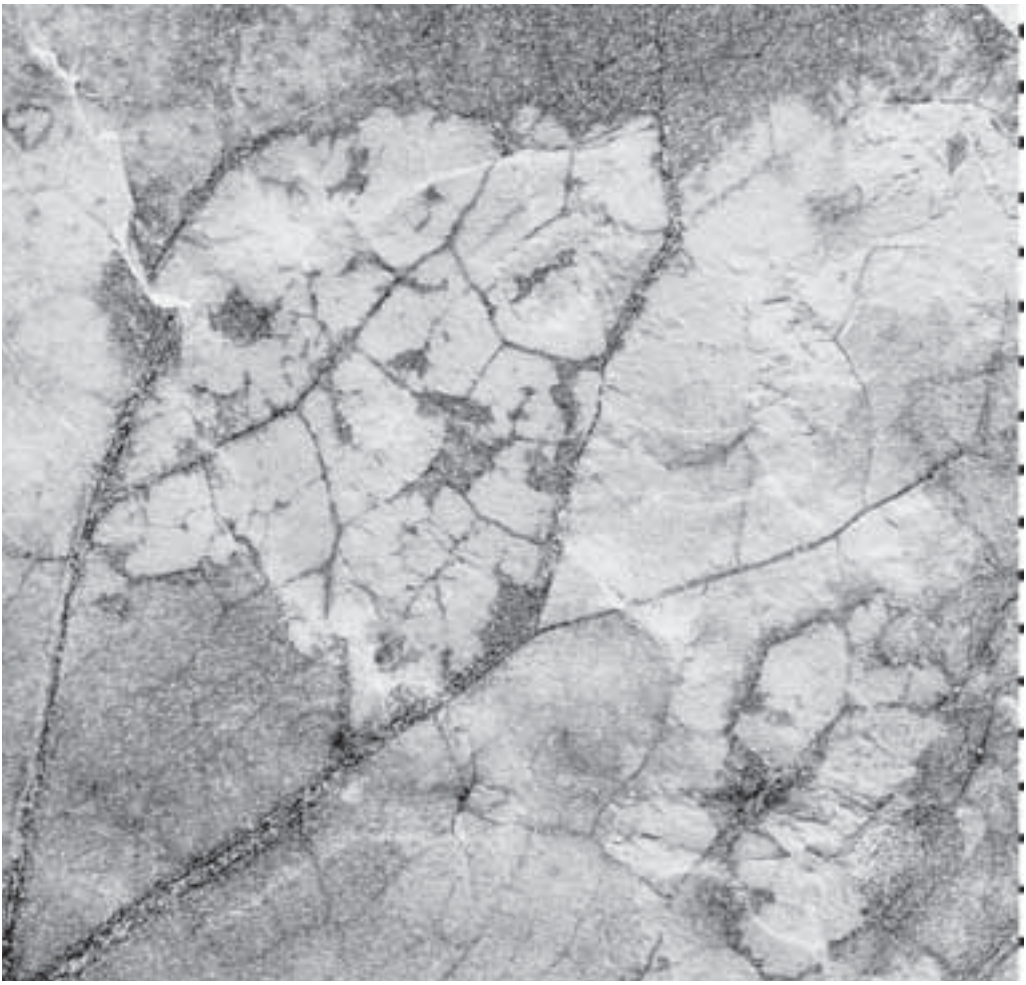

Fig. 26. Skeletonization on *Nelumbites aravensis*, IG1-506.

Trophoglypha diffusa Krassilov, sp. nov.
Pl. LIII, figs. 1, 2

N a m e. L. *diffusum*, scattered.
H o l o t y p e. IG1-1122, Gerofit (Pl. LIIL, fig. 2).
D i a g n o s i s. Feeding marks angular, less typically rounded specks, distinct or conjunctive, irregularly scattered over large leaf areas or clustered in small groups between the stronger veins.
H o s t. *Platanervia integrifolia* Krassilov, *Menispermites cuspidentatus* Krassilov, *Dewalquea gerofitica* (Dobruskina) Krassilov. *Platydebeya papilionacea* Krassilov.
D e s c r i p t i o n. On *Platanervia*, the specks are well-marked, much darker than the leaf impression and only rarely coherent. On *Menispermites*, IG1-563, they are denser and more frequently branched and anastomosing (Pl. LIII, fig.1). The co-occurring traces are the filiform linear mines and blotches with frass lines, sometimes encompassing the feeding specks, as well as the larger perforations.
C o m m e n t s. The irregularly branching and anastomosing patches (Pl. LIII, fig. 1) are like those excavated by *Baliosus*, Chrysomelidae. The more distinct, supposedly deeper, dark callous speckles are comparable to those left by feeding weevils, which make similar oviposition holes (compare with Pl. IX, fig. 1).
M a t e r i a l. Feeding marks on *Platanervia integrifolia*, IG1-200, IG1-442, IG1-588, IG1-563, IG1-1122, on *Menispermites cuspidentatus*, IG1-38, IG1-563, on *Dewalquea gerofitica*. IG1-79, IG1-180, IG1-245, IG1-252, *Platydebeya papilionacea*, IG1-310.

Trophoglypha spp.
Pl. XVIII, fig.1; Pl. XXXVI, fig. 1; (PL. XLV, fig. 3); Pl. LIII, figs. 3–6;
Figs. 10 a-c; 16; 17; 18c; 26

M a t e r i a l a n d c o m m e n t s. Specific names are not assigned at this stage to the parallel *scratches* on *Platanervia integrifolia*, IG1-36, IG1-444 (pl. LIII, fig. 3), *"etchings"* and *hierogliphic* feeding marks on *Platydebeya papilionacea*, IG1-345 (Pl. LIII, fig. 6) and *Dewalquea gerofitica*, IG1-825, supposedly of a fly feeder.
Feeding holes on *Nelumbites aravensis*, IG1-246 (Pl. LIII, fig. 4) and the similar holes on *Dewalquea gerofitica*, IG1-80 (Pl. XVIII, fig.1) and IG1-1101 (Pl. XXXVI, fig. 1) are circular to somewhat irregular, occasionally confluent cut-outs between lateral veins, with sinuous to irregularly crenulate margins that are slightly if at all callous. In IG1-887 (PL. XLV, fig. 3), long stripes are cut out on both sides of the midrib framed on the outside by the continuous marginal rolls. Distally such bilateral cut-outs converge, leaving patches of leaf blade densely pitted with the egg-gall pustules.

The marginal semicircular cut-outs with callous border, associating with mid-leaf holes of the same diameter, as in *Dewalquea* leaves IG1-642, IG1-539 (Figs. 16, 17) are here interpreted as feeding holes, although similar, if but somewhat more regular, scars are produced by megachilid bees for nest construction (Berry, 1916; Brooks, 1955). The apical and mar-

ginal cut-outs on the Albian and Cenomanian leaves (Fig. 10 a-c), occasionally showing a double-line border are comparable with those produced by buprestid beetles and some weevils (*Rhynchaenus*) cutting out leaf pieces with their pupation cocoons. The Turonian cut-outs on *Platanervia integrifolia* IG1-620 (Fig. 18c) may belong in the same category.

Skeletonization (Fig. 26) occurs on *Nelumbites aravensis*, IG1-245, IG1-506, IG1-872, IG1-1039, on *Platydebeya papilionacea*, IG1-125. on *Dewalquea gerofitica*, IG1-534, and *Eudebeya angusta*, IG1-155.

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PLATES

Scale ruler point 1mm for all figures

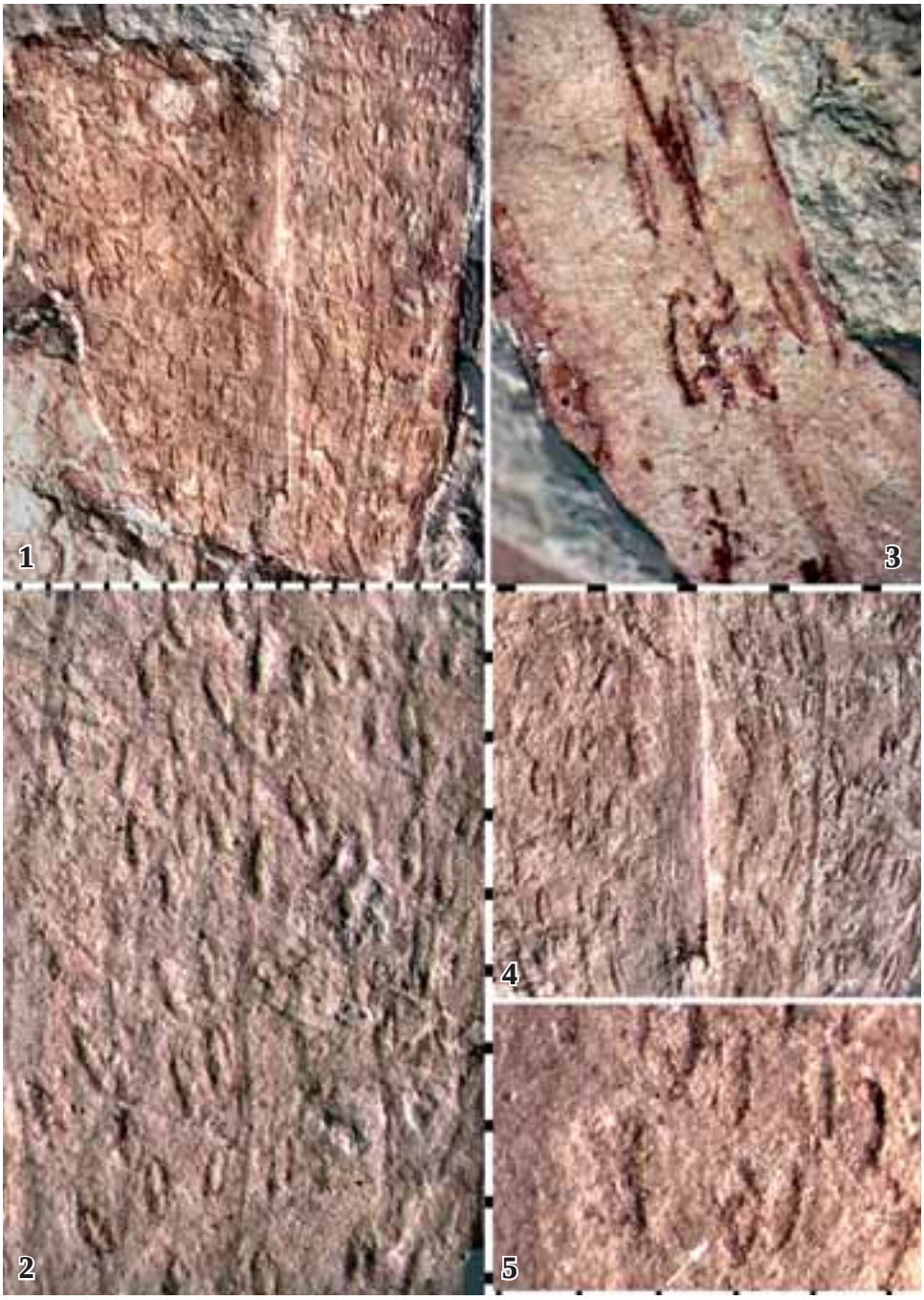

Plate I. *Catenoveon undulatum* gen. et sp. nov., Makhtesh Ramon: 1, 2,4, 5, holotype IMR-A2-303a., wobbling rows of egg scars showing callous border, 3, paratype IMRA2_303b, egg scars stretched and deformed by the leaf growth.

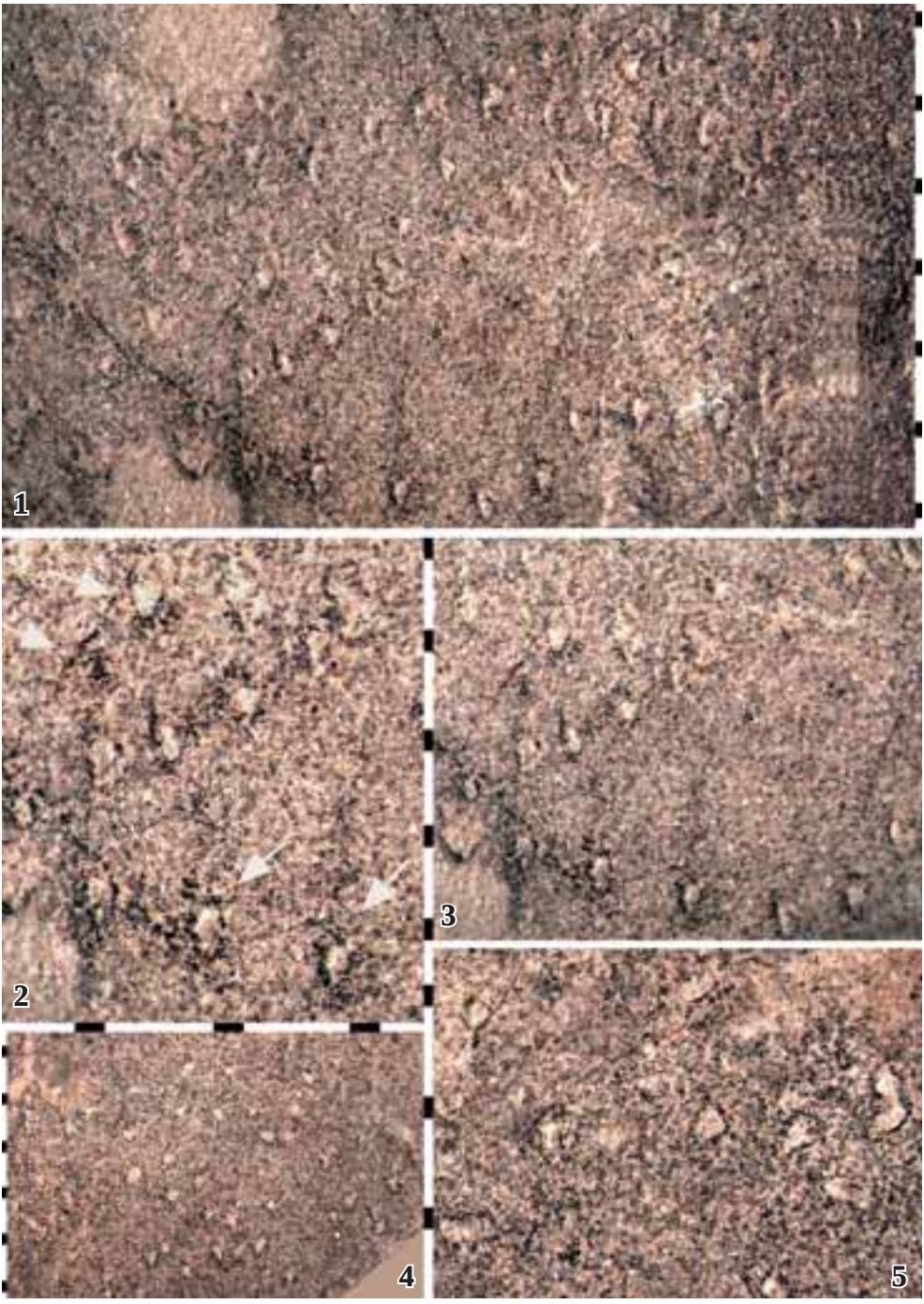

Plate II. *Sertoveon arcuatum* gen. et sp. nov., Gerofit: 1–5, holotype IG1-1118, transverse arches of egg scars, irregular and occasionally paired near the leaf margins (4), showing procecidial developments (5).

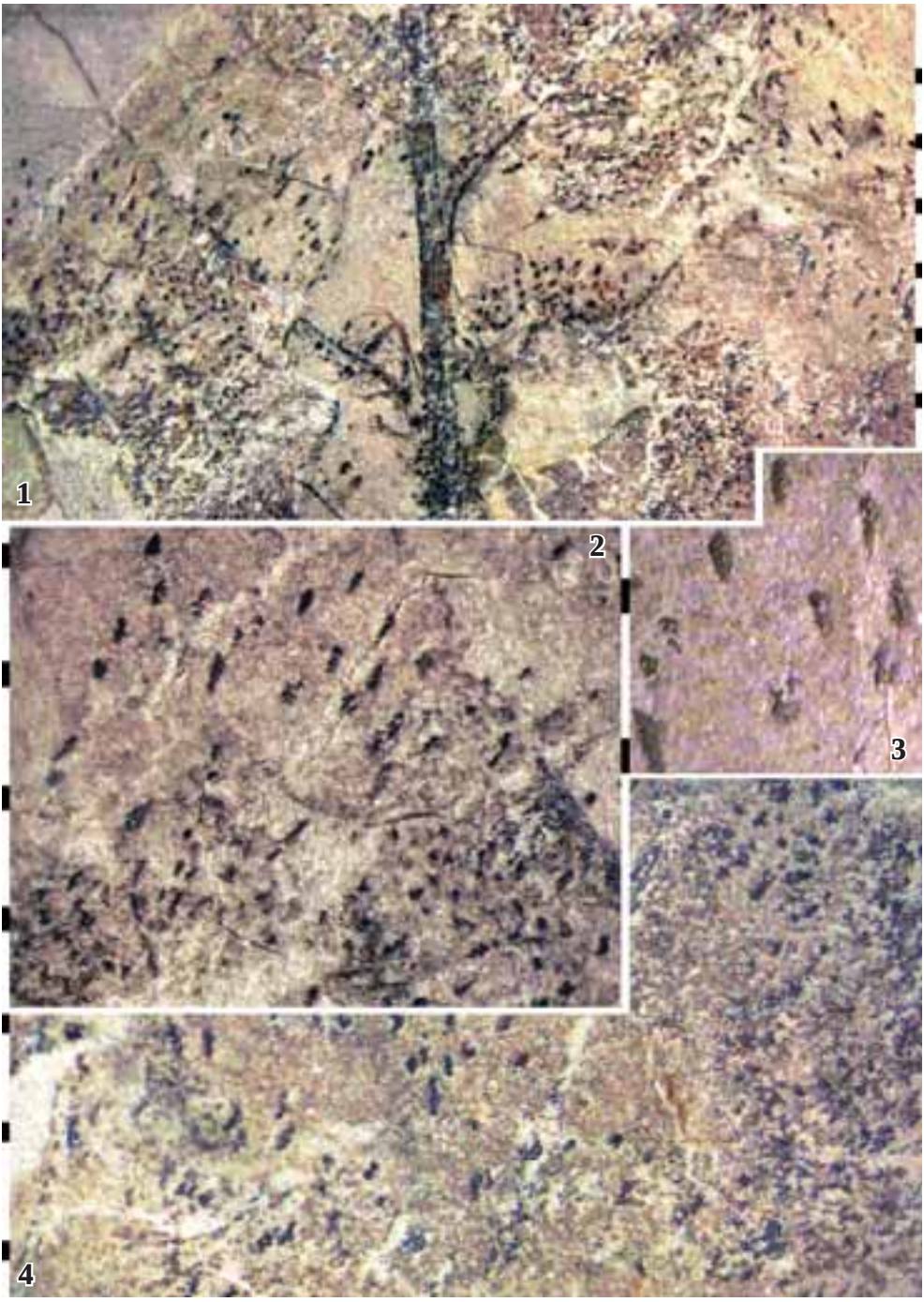

Plate III. *Sertoveon cribellum* gen. et sp. nov., Gerofit: 1–4, holotype IG1-128, amassed and scattered egg scar shapes (2, 3) and arrangement (1, 4).

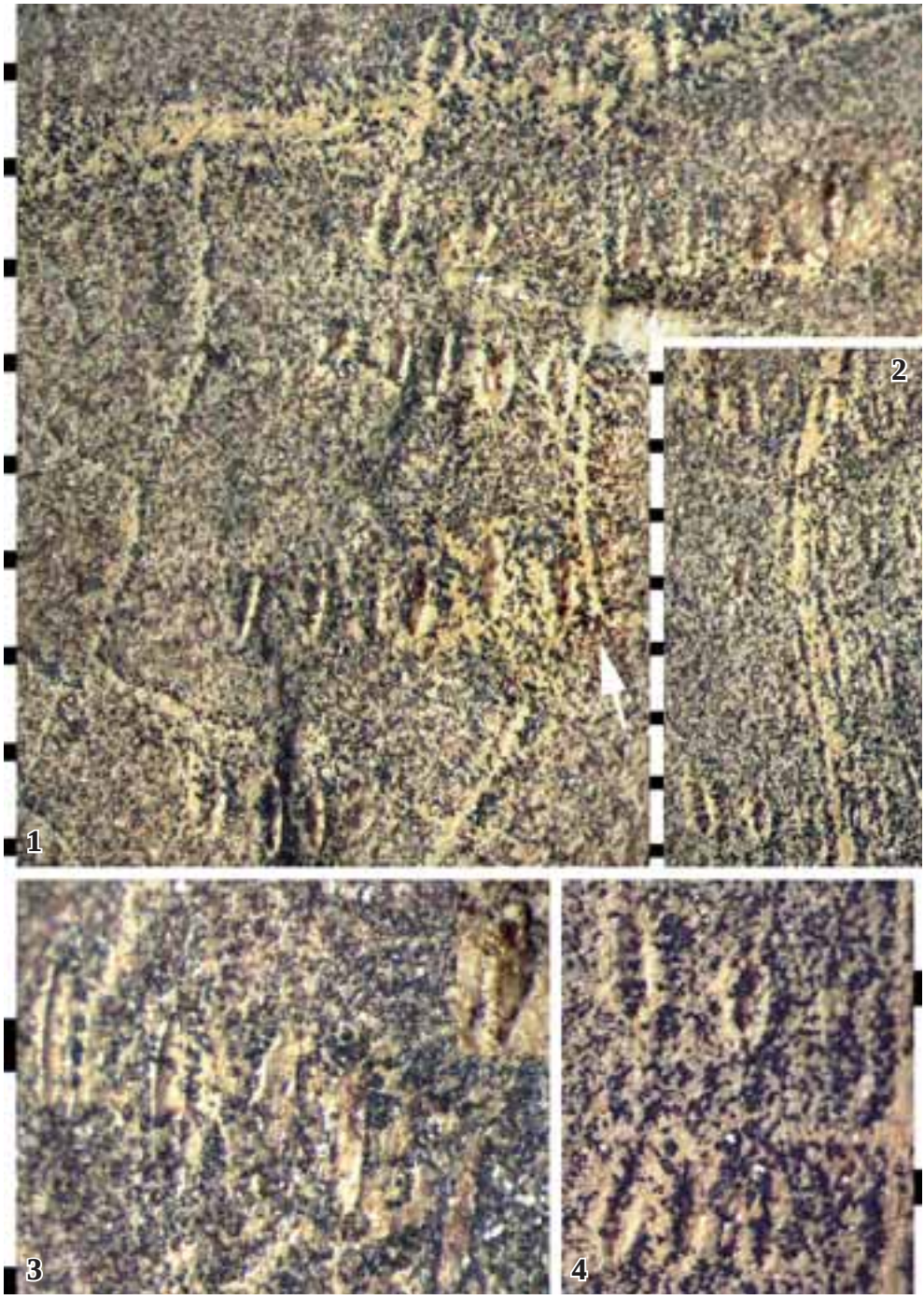

Plate IV. *Sertoveon scalarum* gen. et sp. nov., Gerofit: 1–4, holotype IG1-503, short parallel transverse rows of egg scars showing callous borders (4).

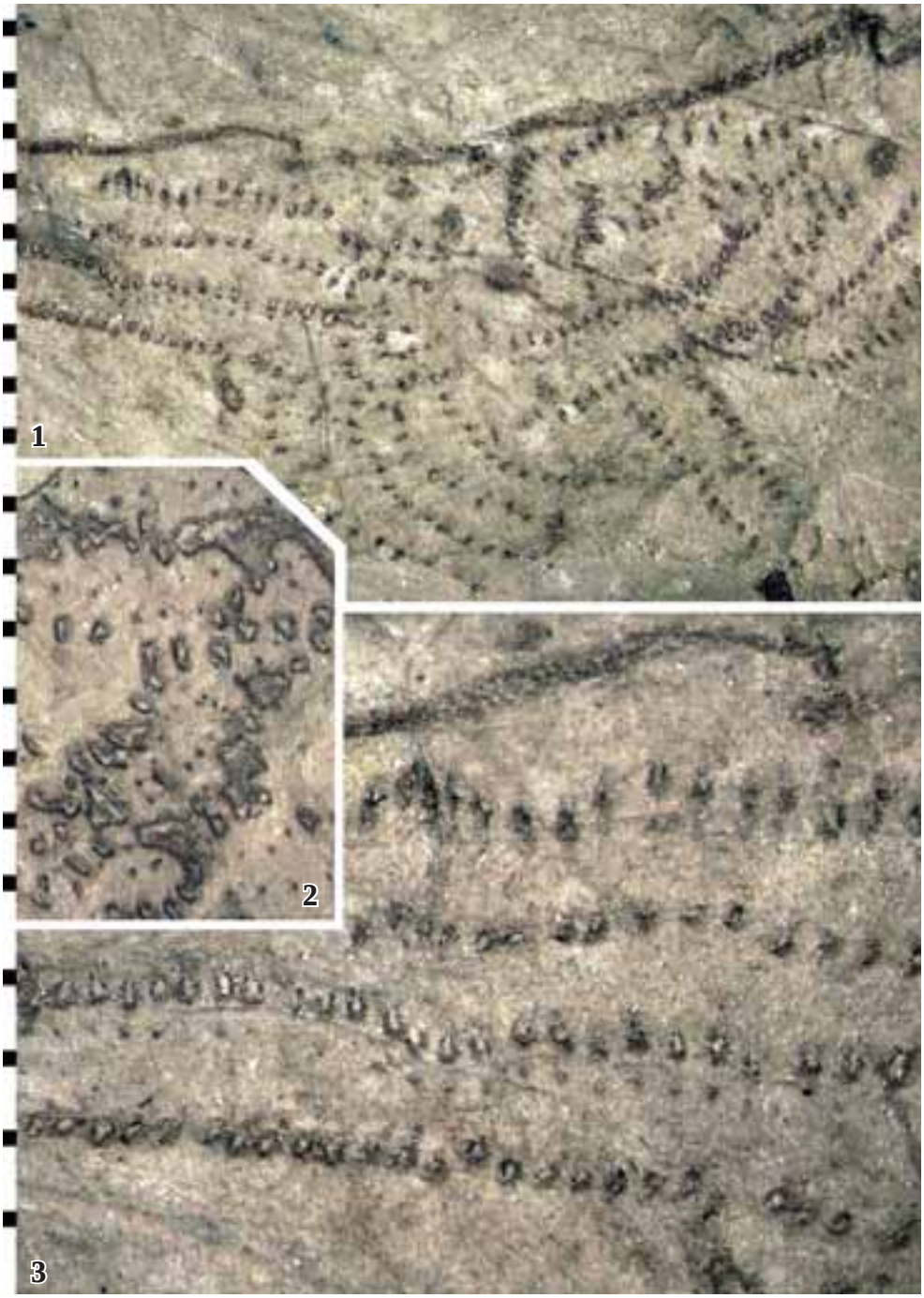

Plate V. *Sertoveon moniliforme* gen. et sp. nov., Gerofit: 1–3, holotype IG1-891, two sets of egg scars with punctuate marks (2, 3), some deformed by abrasion of surrounding leaf tissue (3).

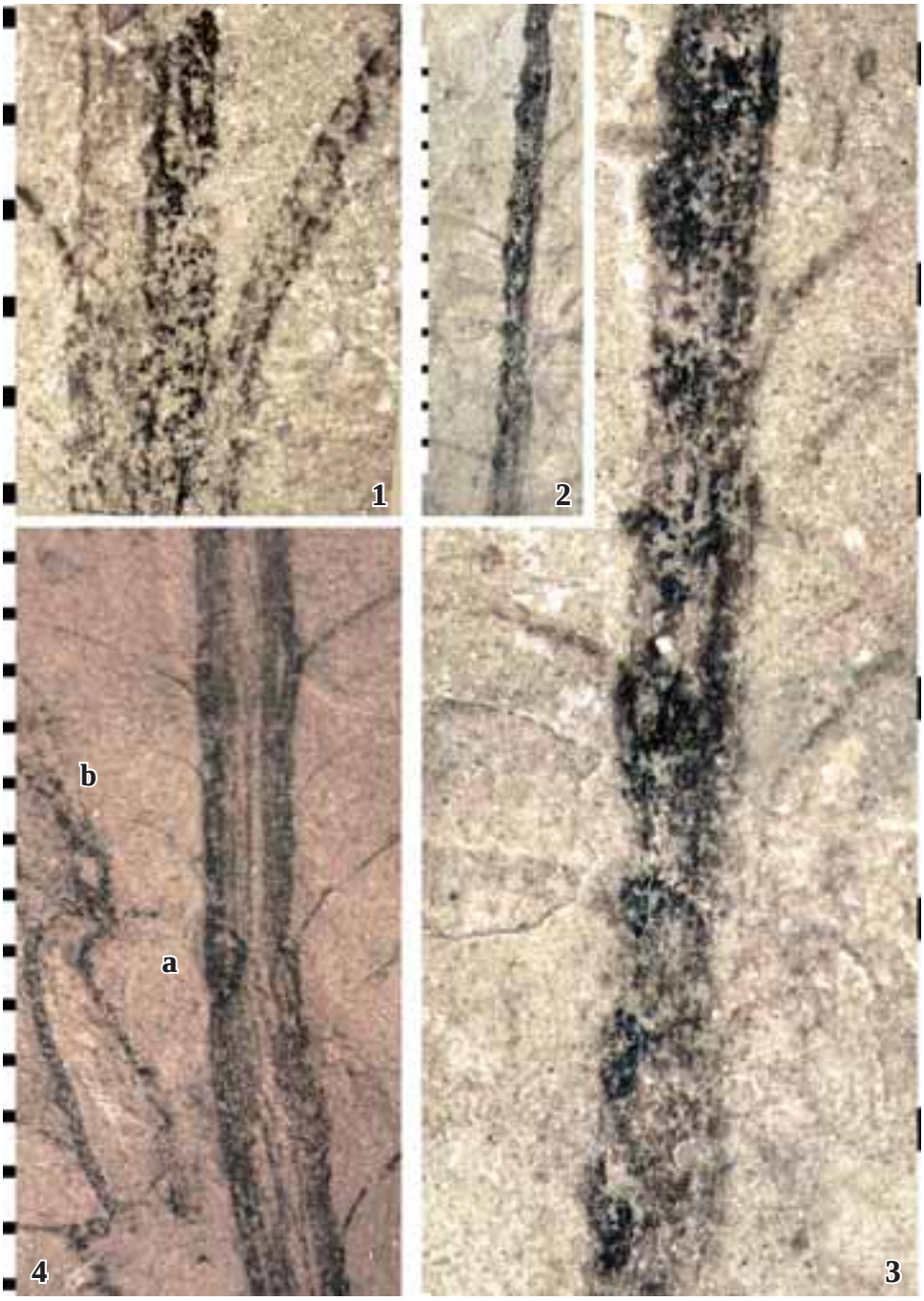

Plate VI. *Costoveon transfixum* gen. et sp. nov., Gerofit: 1 – 3, holotype IG1-1030, obliquely inserted egg scars and arcuate incision marks on lateral veins; *Costoveon adnatum* gen. et sp. nov., IG1-1110a, egg scars on split midrib, one on a spirally coiled strand; *Troponoma curvitracta* gen. et sp. nov., IG1-1110b, looping mine track.

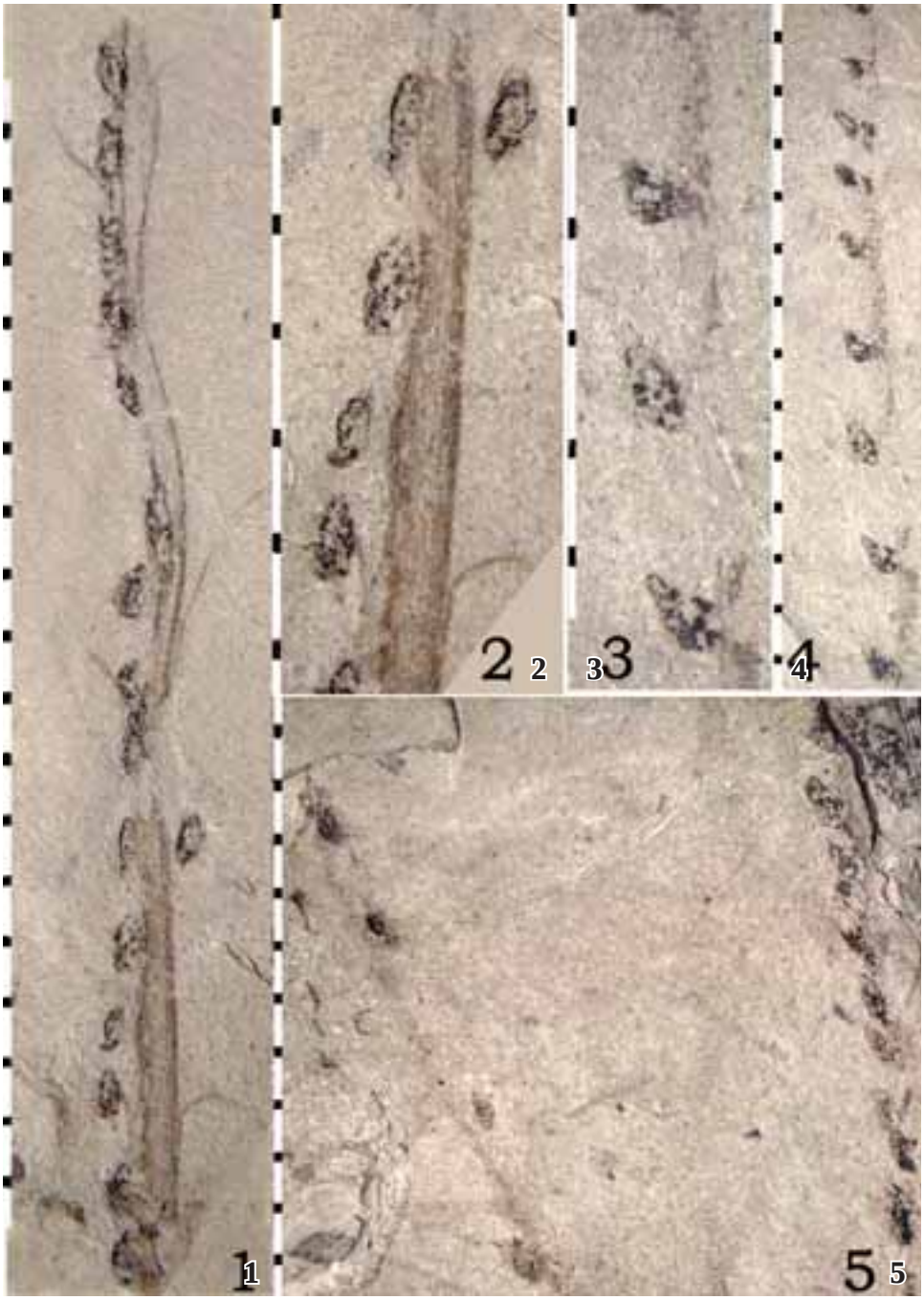

Plate VII. *Costoveon adnatum* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-111, egg scar files adnate to the midrib; *Costoveon vergens* gen. et sp. nov., Gerofit: 3–5, holotype IG1-114, egg scars diverging form the primary veins.

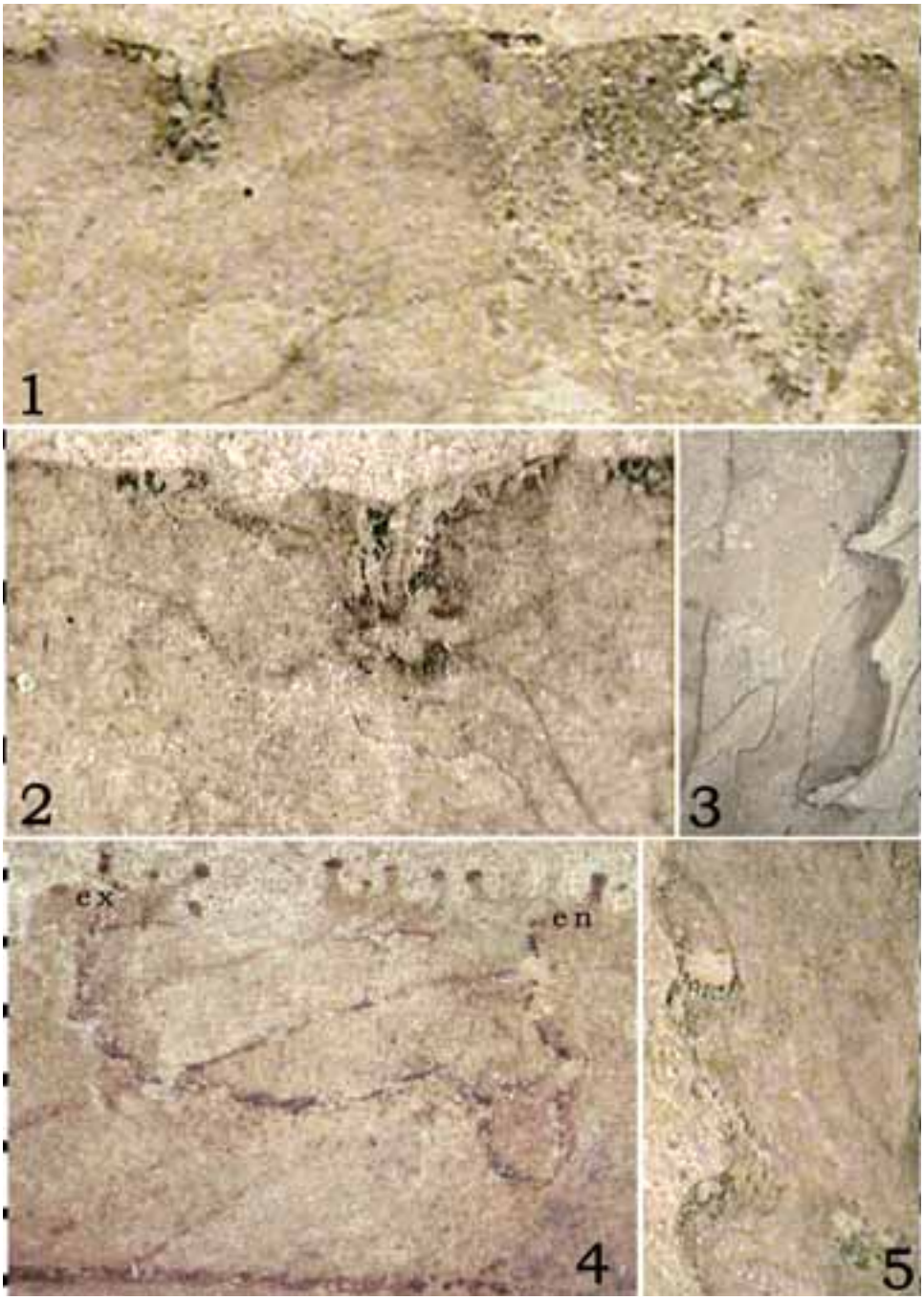

Plate VIII. *Margoveon incisum* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-45, marginal egg pockets, 3, IG1-242, leaf margin dentate by egg incisions, 4, IG1-4, looping mine starting at a marginal egg incision (en – entrance hole, ex – exit hole), 5, IG1-128, callus cells over the marginal egg pockets.

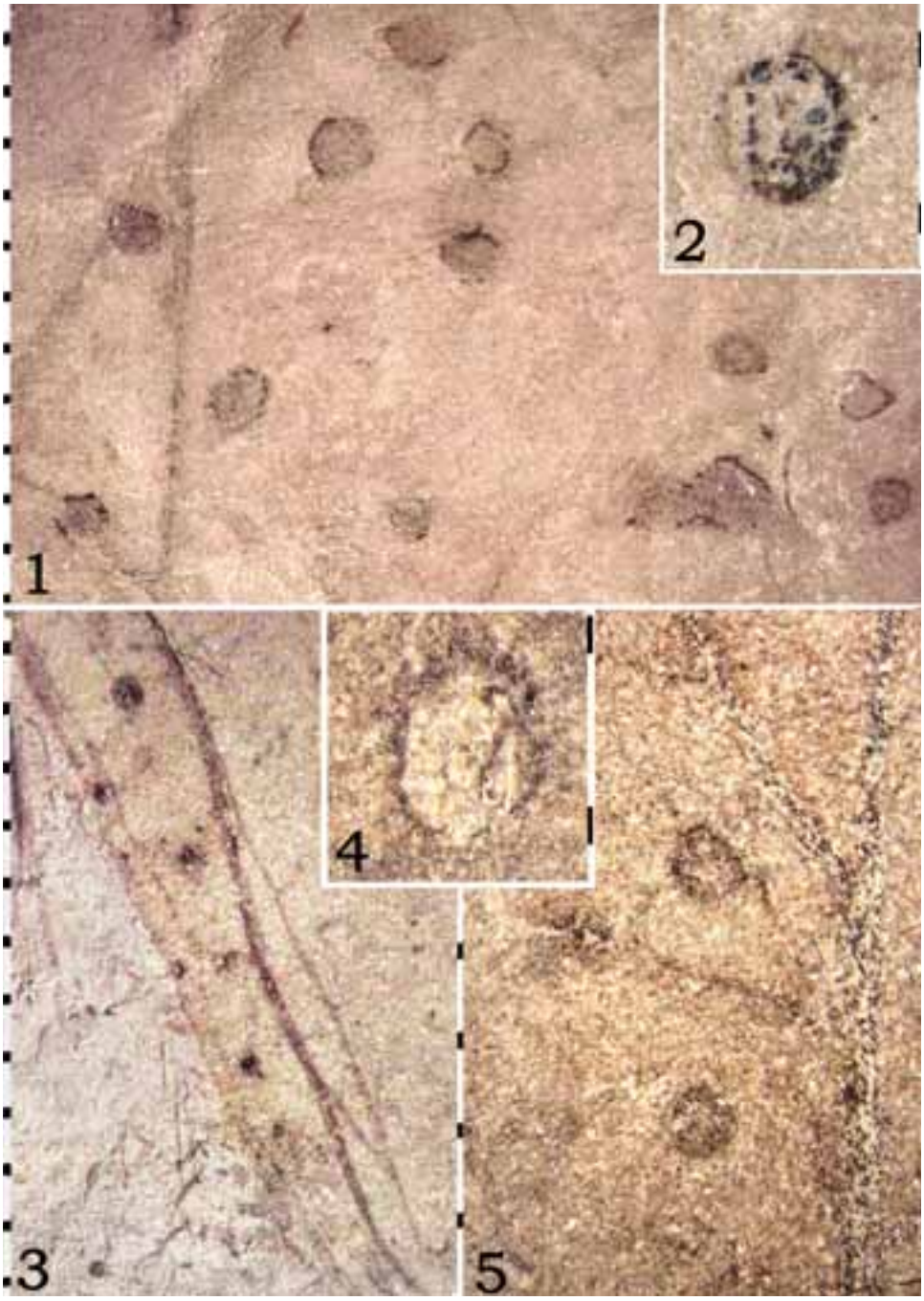

Plate IX. Ovisignata spp., Gerofit: 1, IG1-886, scattered egg holes resembling feeding holes on Pl. LIII, fig. 2; 2, IG1-178, impression of sculptured egg ; *Margoveon* sp., Gerofit: 3, IG1-449, intramarginal row of egg scars increasing up the leaf; 4, 5, IG1-746, egg scars with spiny protuberances (see *Foveon astrellum*, Pl. XV, fig. 2).

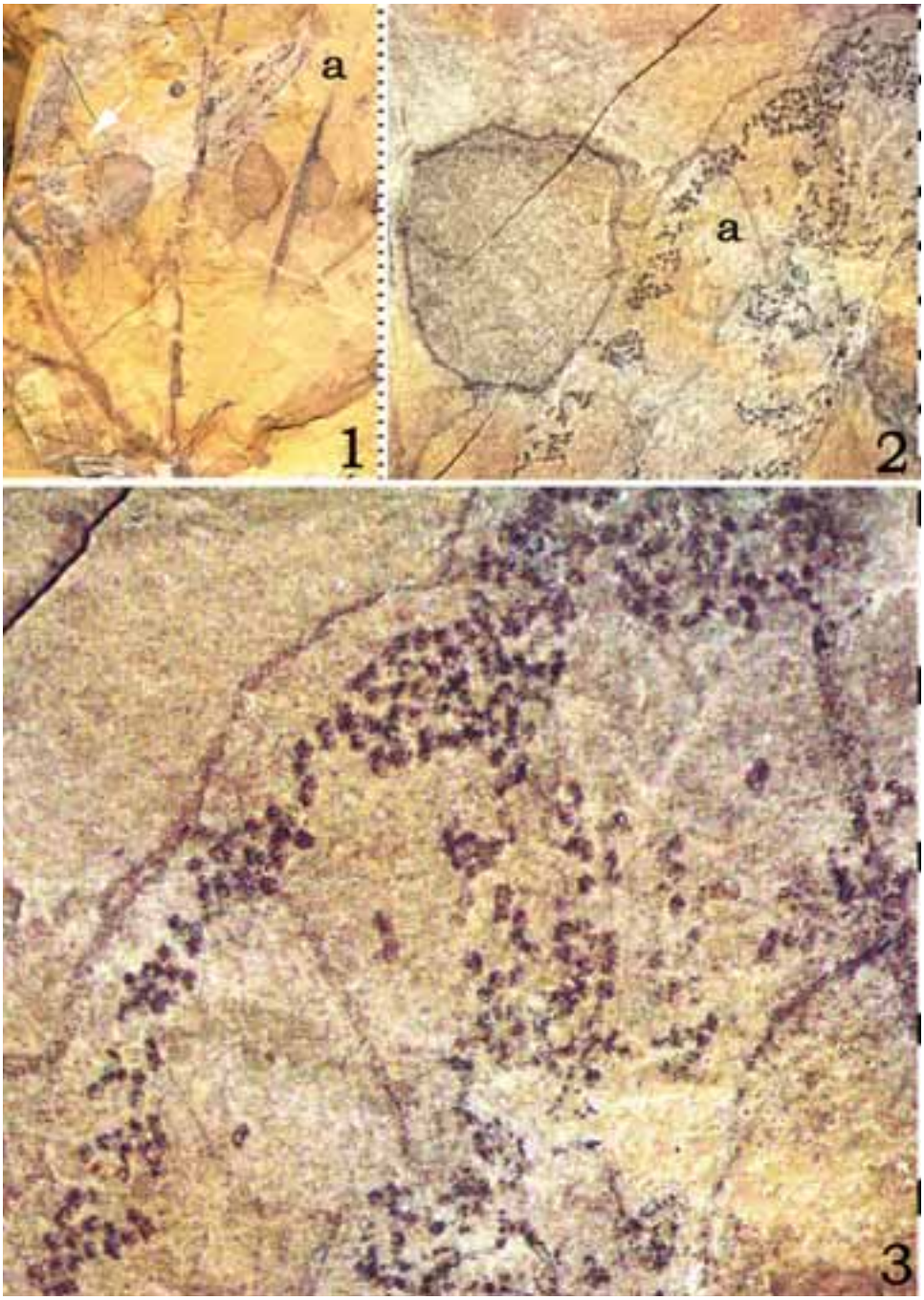

Plate X. *Folicasa spinullata* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-676, larval cases attached to the leaf blade; *Massoveon globulosum* gen. et sp. nov., Gerofit: 1a, 2a, 3, holotype IG1-676A, egg masses applied to the leaf surface.

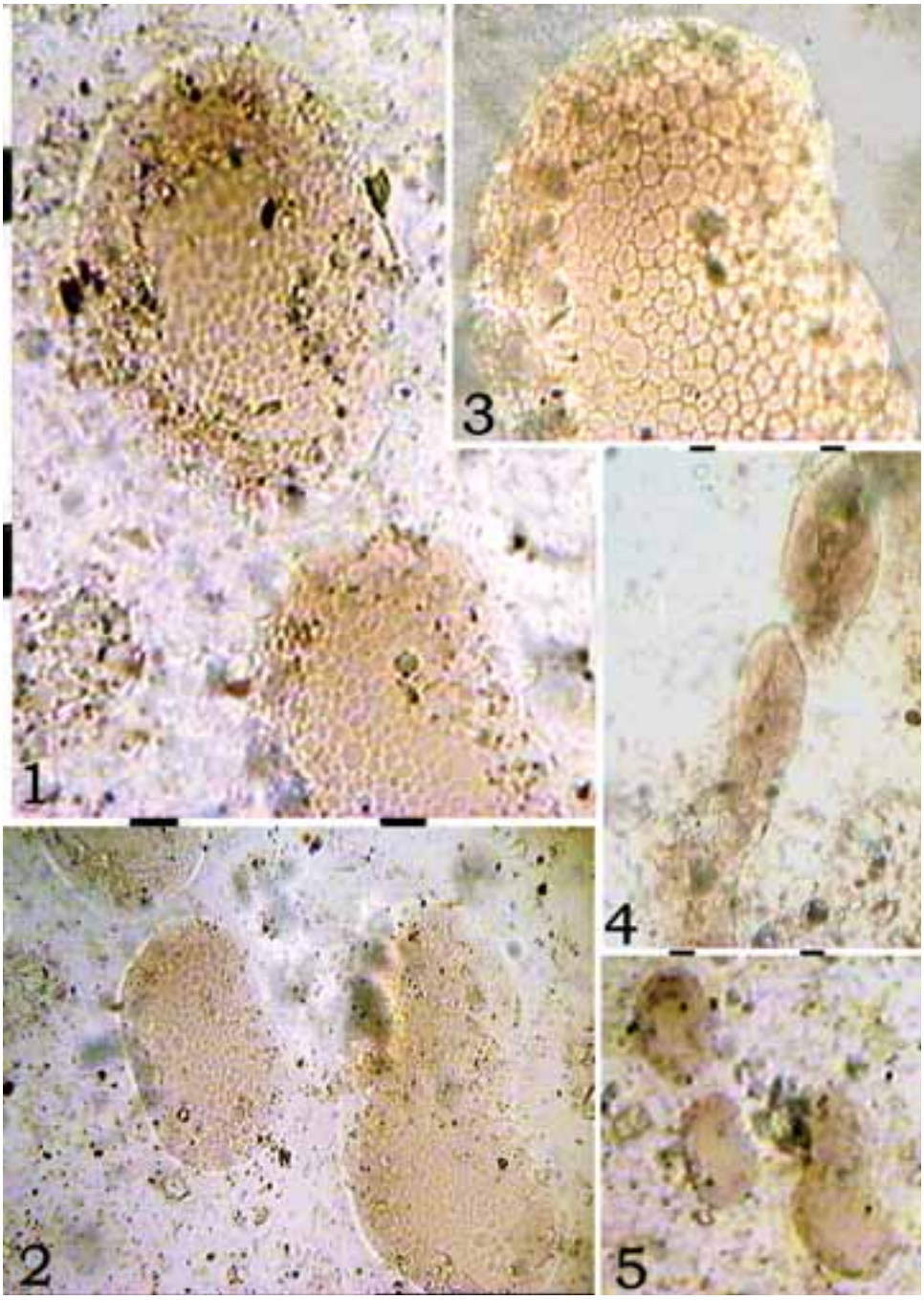

Plate XI. *Transpiroven polygonatum* gen. et sp. nov., Gerofit: 1–5, holotype IG1- 249, film transfer of catenate – irregular egg set with the egg shell showing polygonal transpiration meshwork.

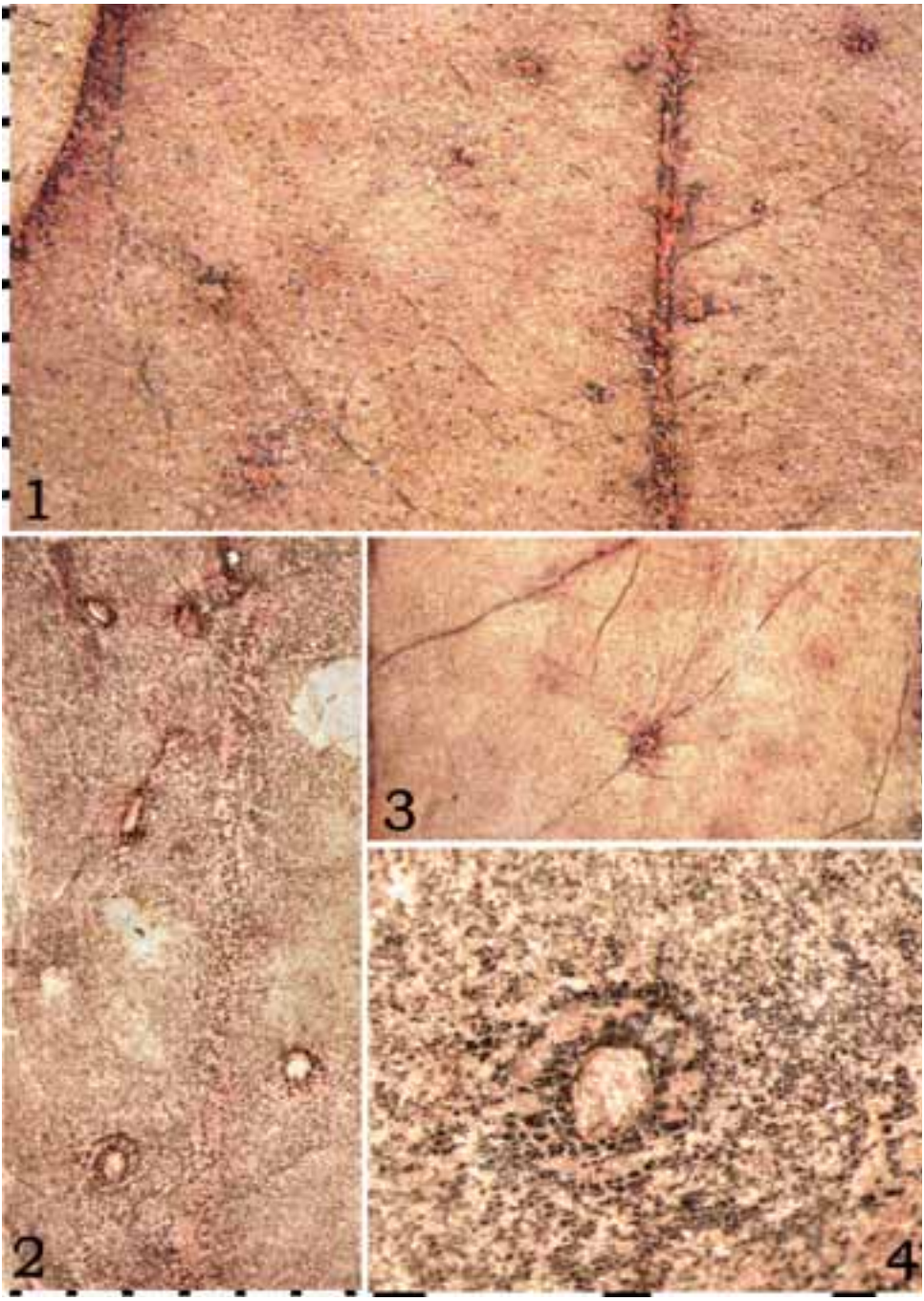

Plate XII. *Cupuleon caveum* gen. et sp. nov., Gerofit: 1, paratype IG1-600; 2, 4, holotype IG1-887, cupulate procecidia, 3, *Costeon blastoides* gen et sp. nov., holotype IG1-557, pellet gall associated with abnormal branching of lateral vein.

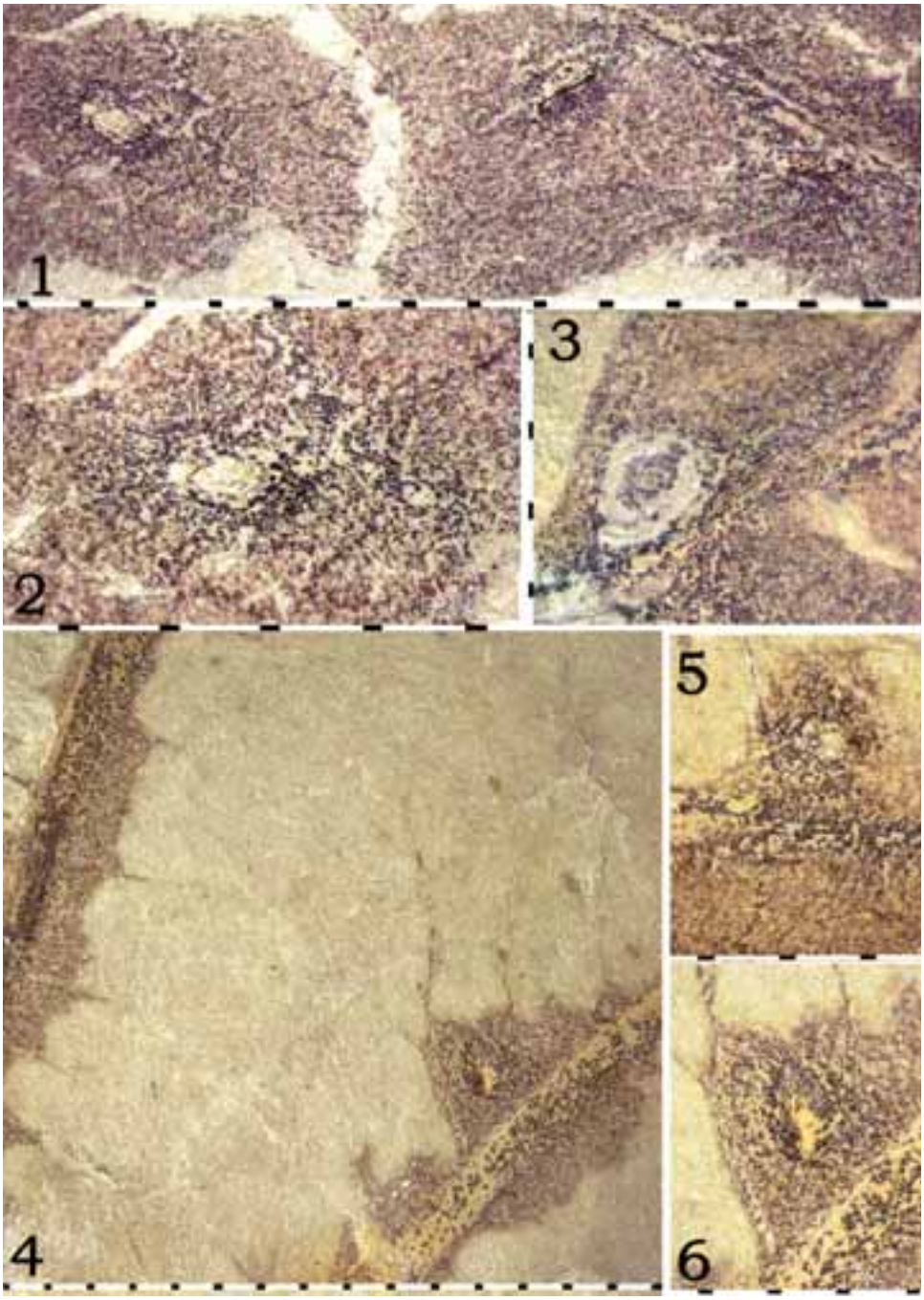

Plate XIII. *Cupuleon nodulosum* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-501, nodular procecidia surrounded by hypertrophic sinuous epidermal cells3, 4, paratype IG1-755; concentrically fringed nodules, 5, 6, paratype IG1-474, nodule in the callous costal zone.

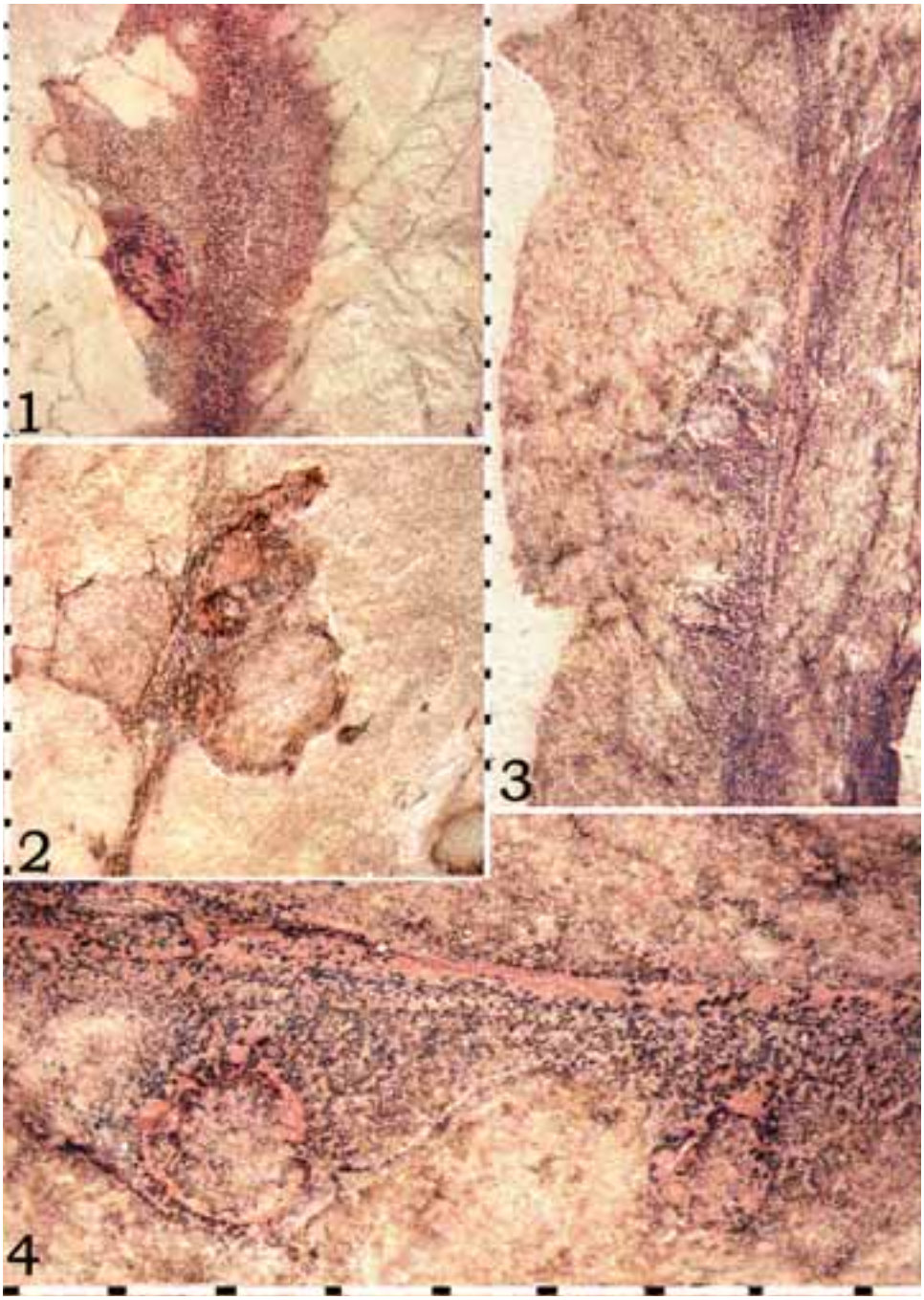

Plate XIV. *Cupuleon craterellum* gen. et sp. nov., Gerofit: 1, holotype IG1-155, a cupule in the callous midrib zone; 2, paratype IG1-1120, two cupules in the midrib zone; 3, 4, paratype IG1-691, cupules on the lobes of the midrib callus.

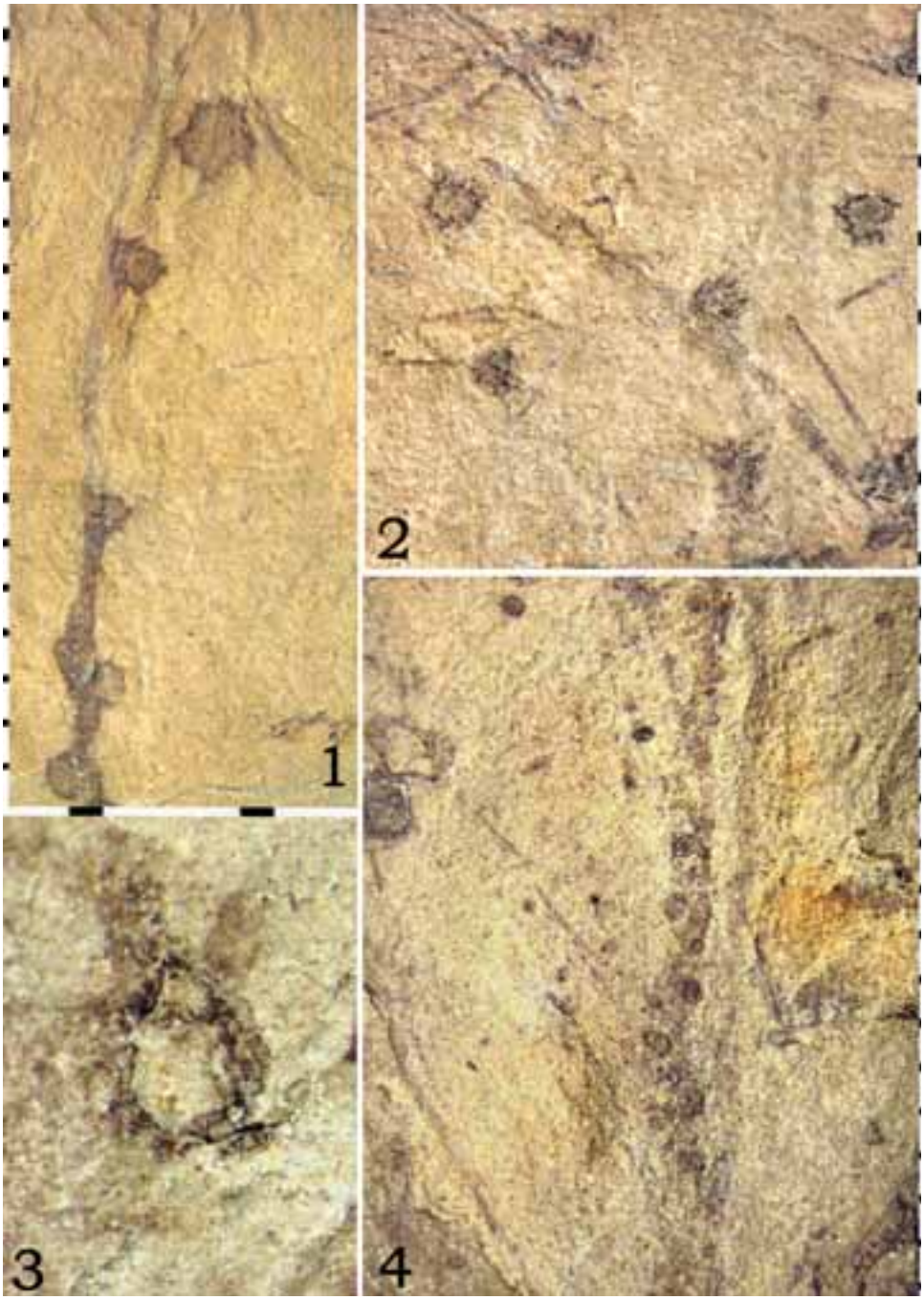

Plate XV. *Foveon patellatum* gen. et sp. nov., Gerofit: 1, holotype IG1-754, open procecidial cupules on and close to the leaf midrib; *Foveon astrellum* gen. et sp. nov., Gerofit: 2, holotype IG1-755, scattered cupules with radial protuberances; 3, 4, IG1-474, IG1-481, procecidial eggs probably related to *F. patellatum*.

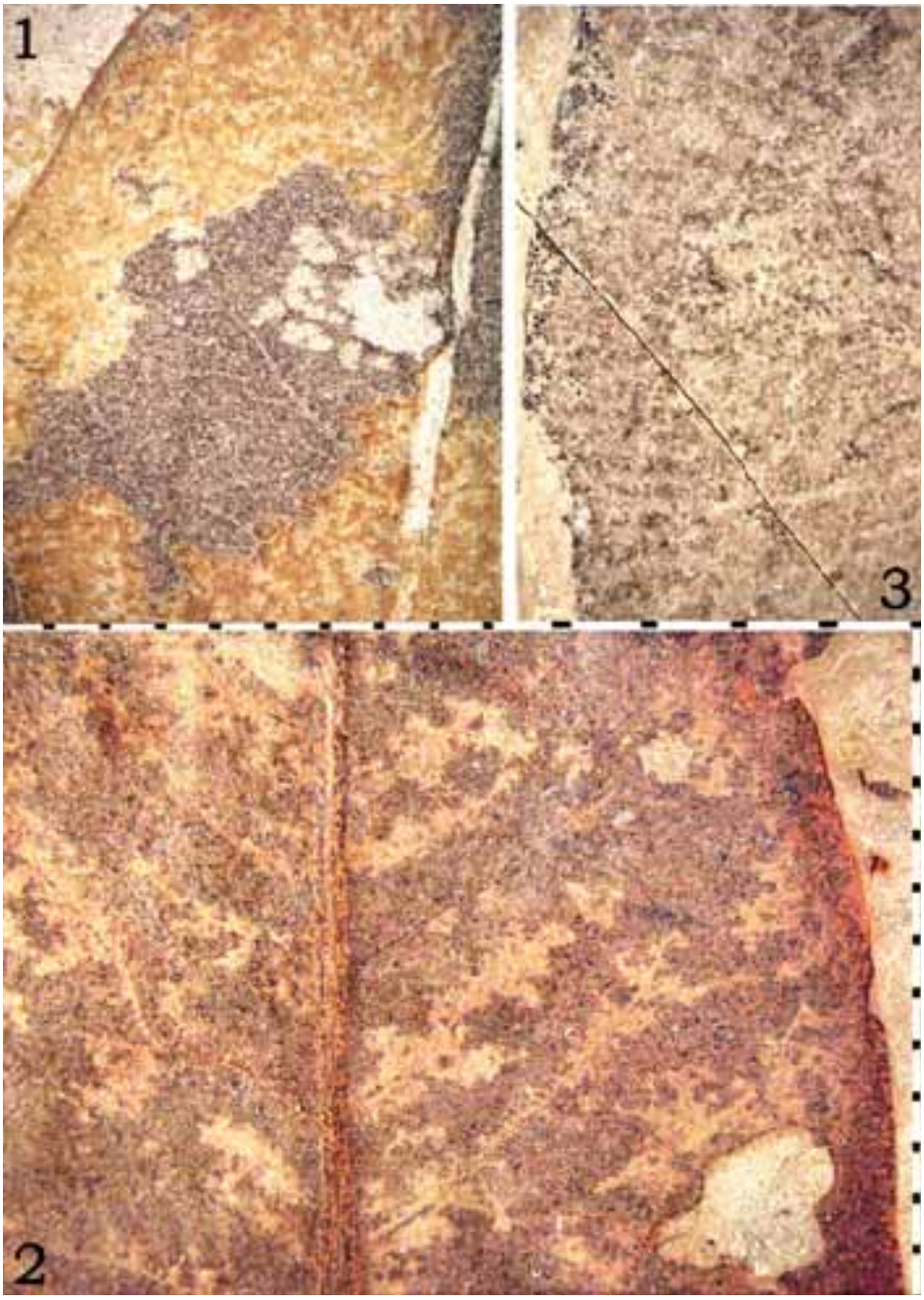

Plate XVI. *Emergeon scabratum* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-31 and paratype IG1-81, minutely pitted and trichomate areas of emergence gall, with irregular abrasions over the lateral veins; *Emergeon catenulatum* gen. et sp. nov., Gerofit: 3, holotype IG1-221, chains of single cell tumuli transverse to the thickened leaf margin.

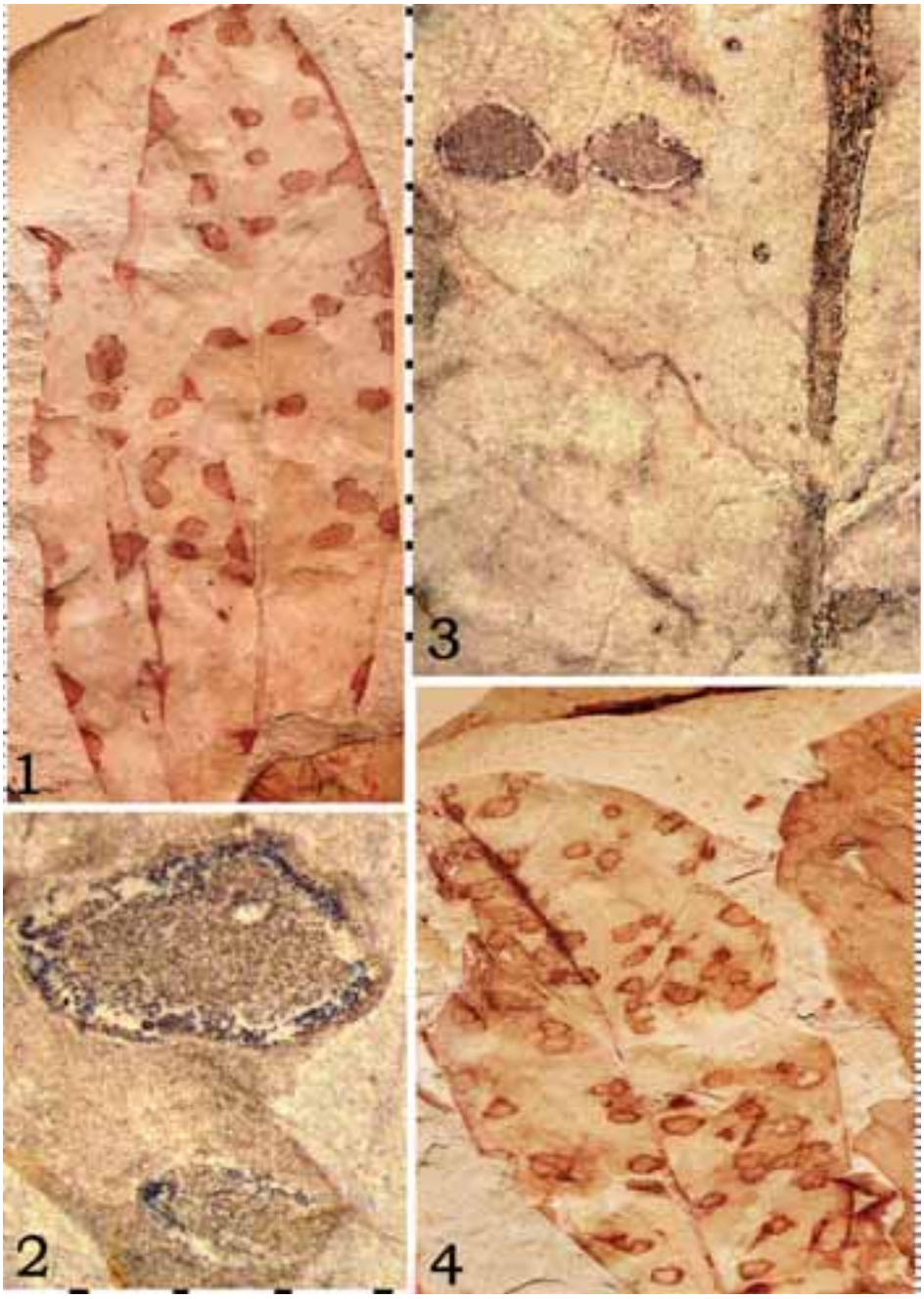

Plate XVII. *Lenticeon minusculum* gen. et sp. nov., Gerofit: 1, 4, holotype IG1-893 and paratype IG1-484 showing disposition of lenticels; 3, 4, paratype IG1-128, details of lenticels and associated primordial gall pellets, note local hypertrophy and twisting of lateral veins.

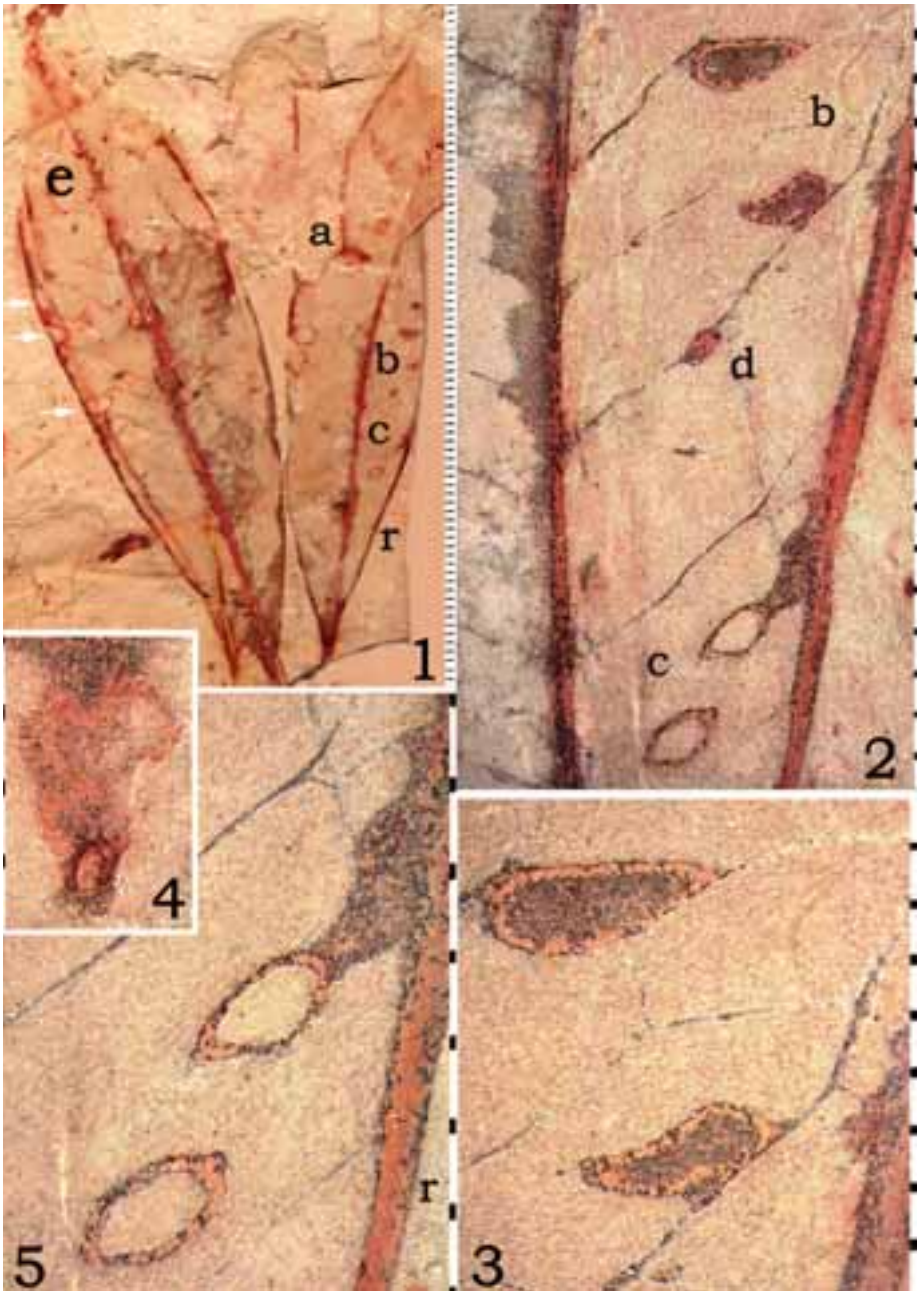

Plate XVIII. 1, Co-occurrence of phyllostigmas on *Dewalquea gerofitica*, IG1-80: 1a, 4, 2c, 5, *Eustigmonoma ochrea gen. et sp. nov., holotype* IG1-180a and paratype IG1-180c, mine with cocoon scars; *Lenticeon minusculum* gen. et sp. nov., Gerofit: 1b, 2b, 3, holotype IG1-80b, lenticels on the thickened lateral veins; 2d, *Costeon blastoides* gen et sp. nov., paratype IG1-180d, pellet gall on lateral vein; 1r, 2r, 5r, *Involuteon compressum* gen et sp. nov., paratype IG1-189r, margin roll gall.

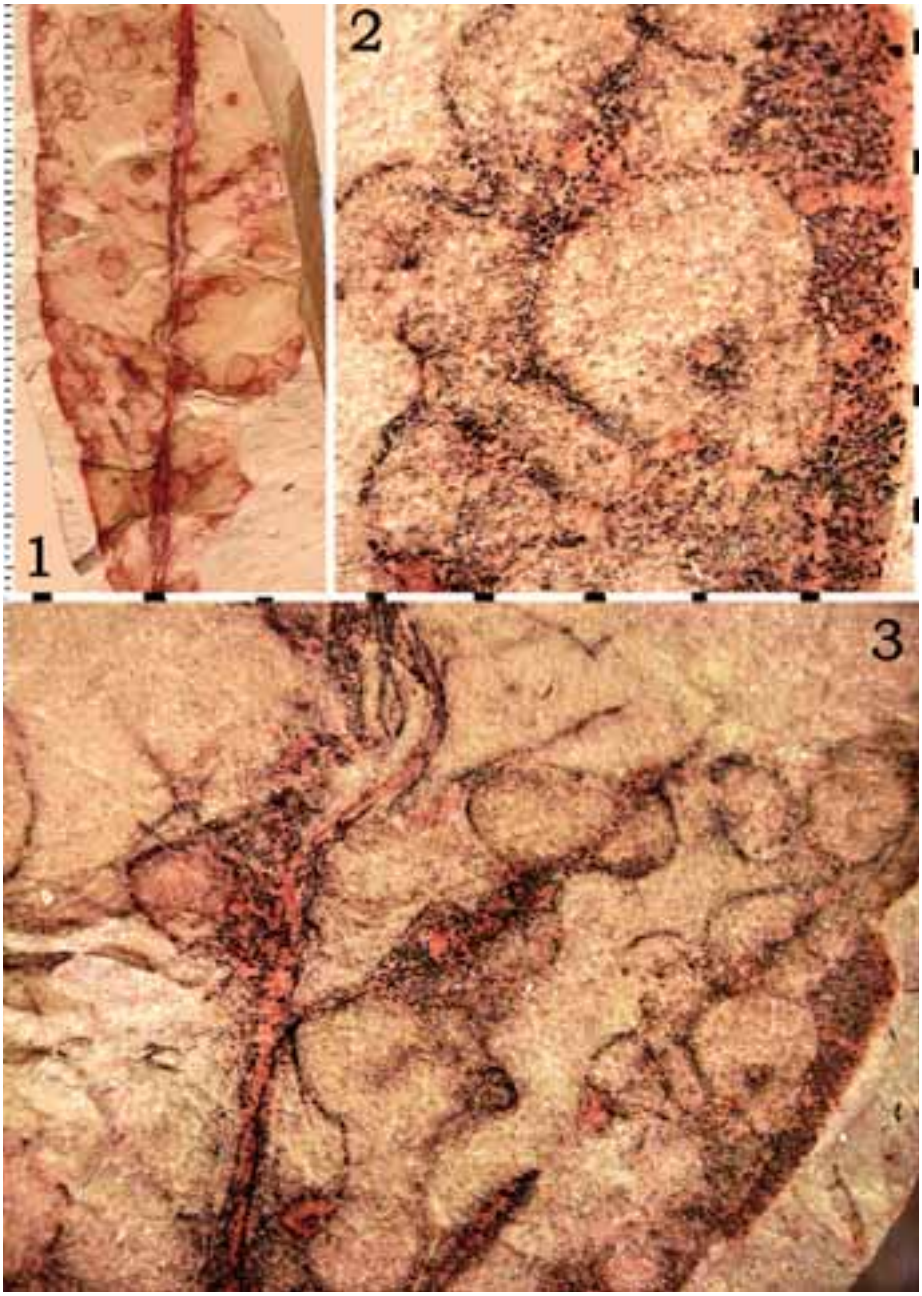

Plate XIX. *Lenticeon agglomeratum* gen. et sp. nov., Gerofit: 1–3, holotype IG1-479, on the lateral veins and in a radial cluster of a larger central and smaller peripheral bulges (3), associated with a margin roll.

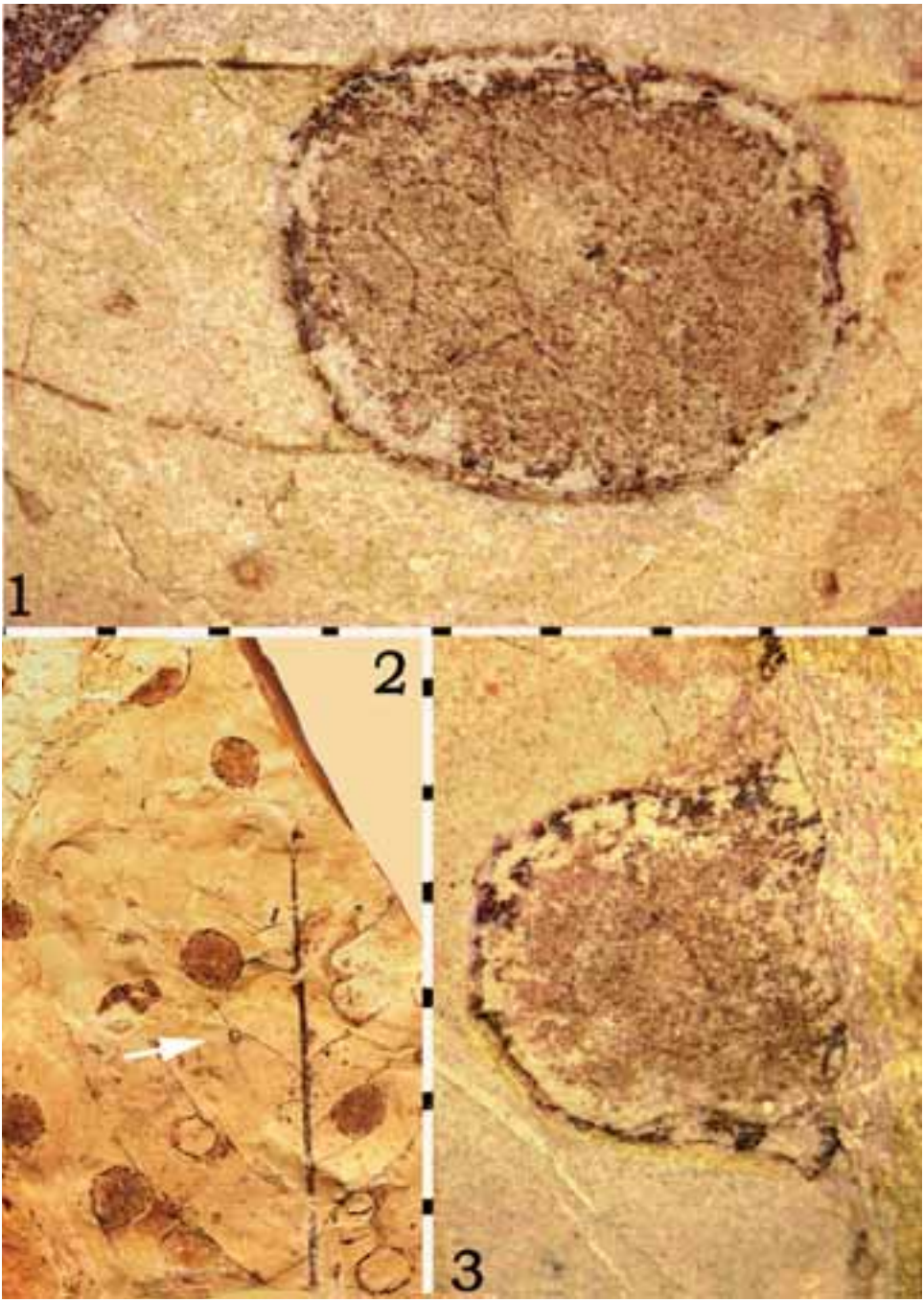

Plate XX. *Lenticeon nervosum* gen. et sp. nov., Gerofit: 1–3, holotype IG1-244, lenticel with fibrovascular tracery, stopping one of the lateral veins involved (1), on leaf disposition (2) showing also a primordial pellet gall *Costaeon blastoides* gen. et sp. nov. (arrow), and a marginal lenticel (3).

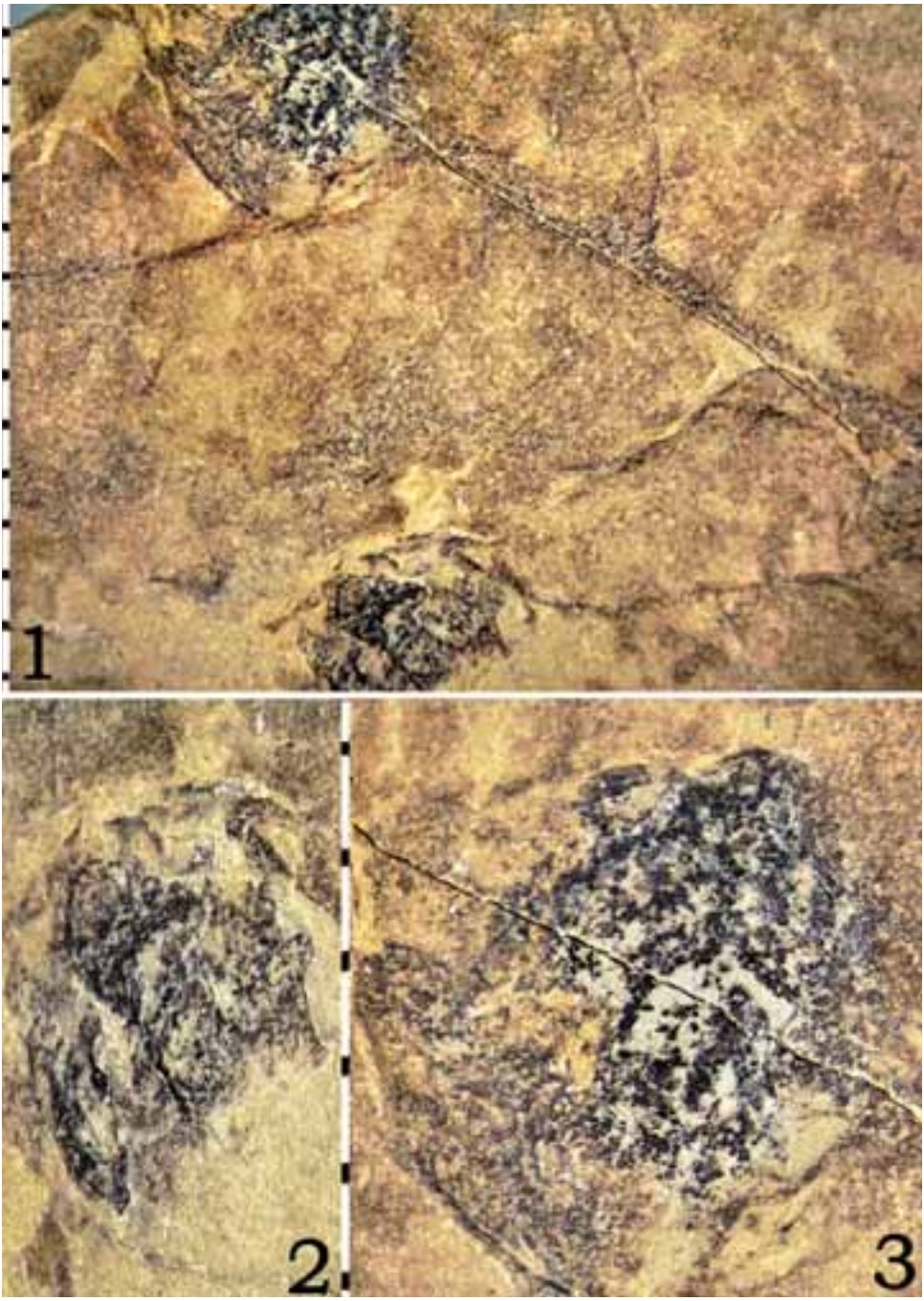

Plate XXI. *Cephaloneon squamosum* sp. nov., Gerofit: 1–3, holotype IG1-403, scaly gall on lateral veins, fig. 1 also showing a patchy emergence gall.

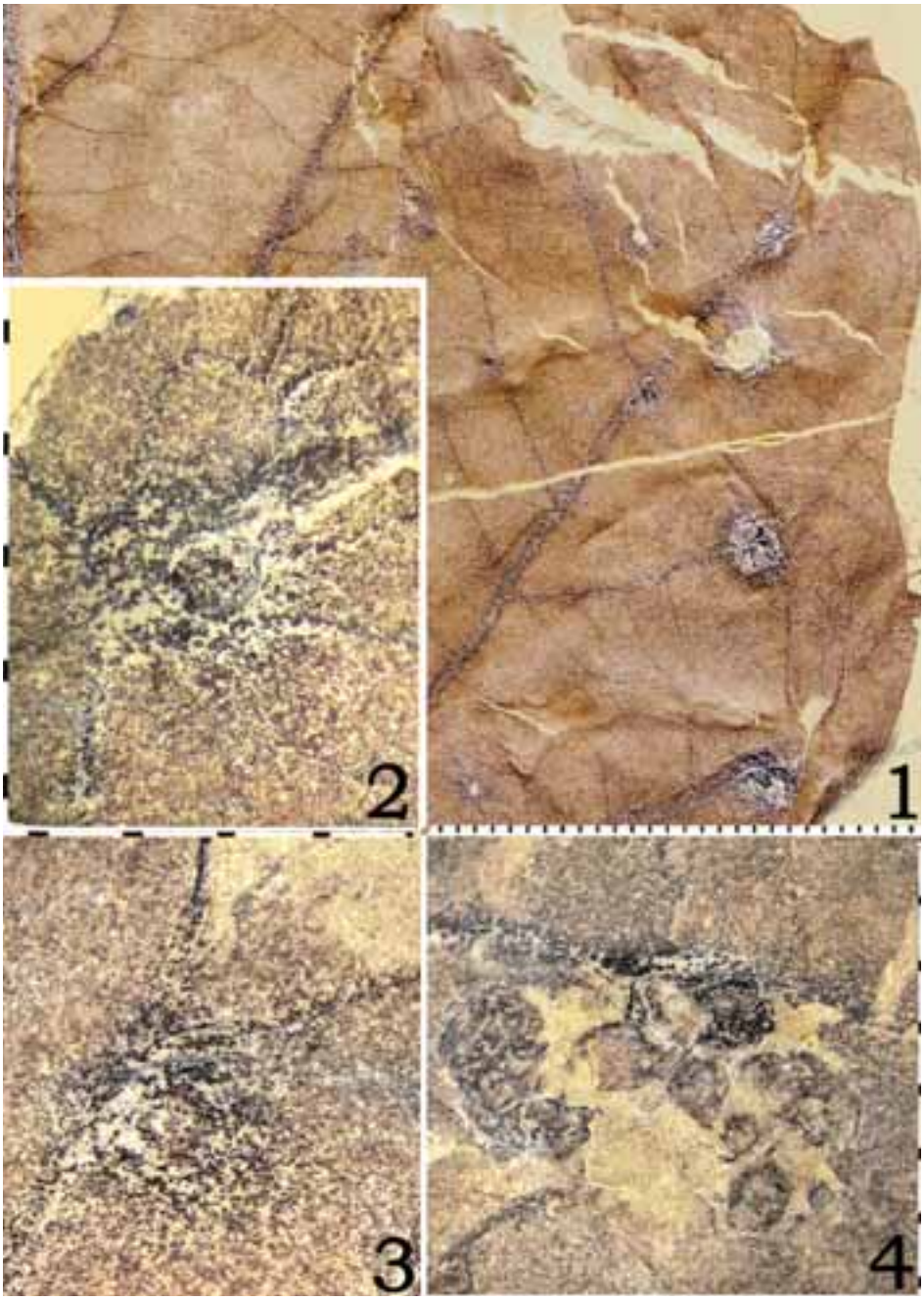

Plate XXII. *Cephaloneon squamosum* sp. nov., Gerofit: 1, paratype IG1-768, gall disposition on *Menispermites cuspidentatus*; 2, 3, paratypes IG1-753 and IG1-48, underdeveloped galls showing a larger central chamber, 4, holotype IG1-403, disintegrated gall.

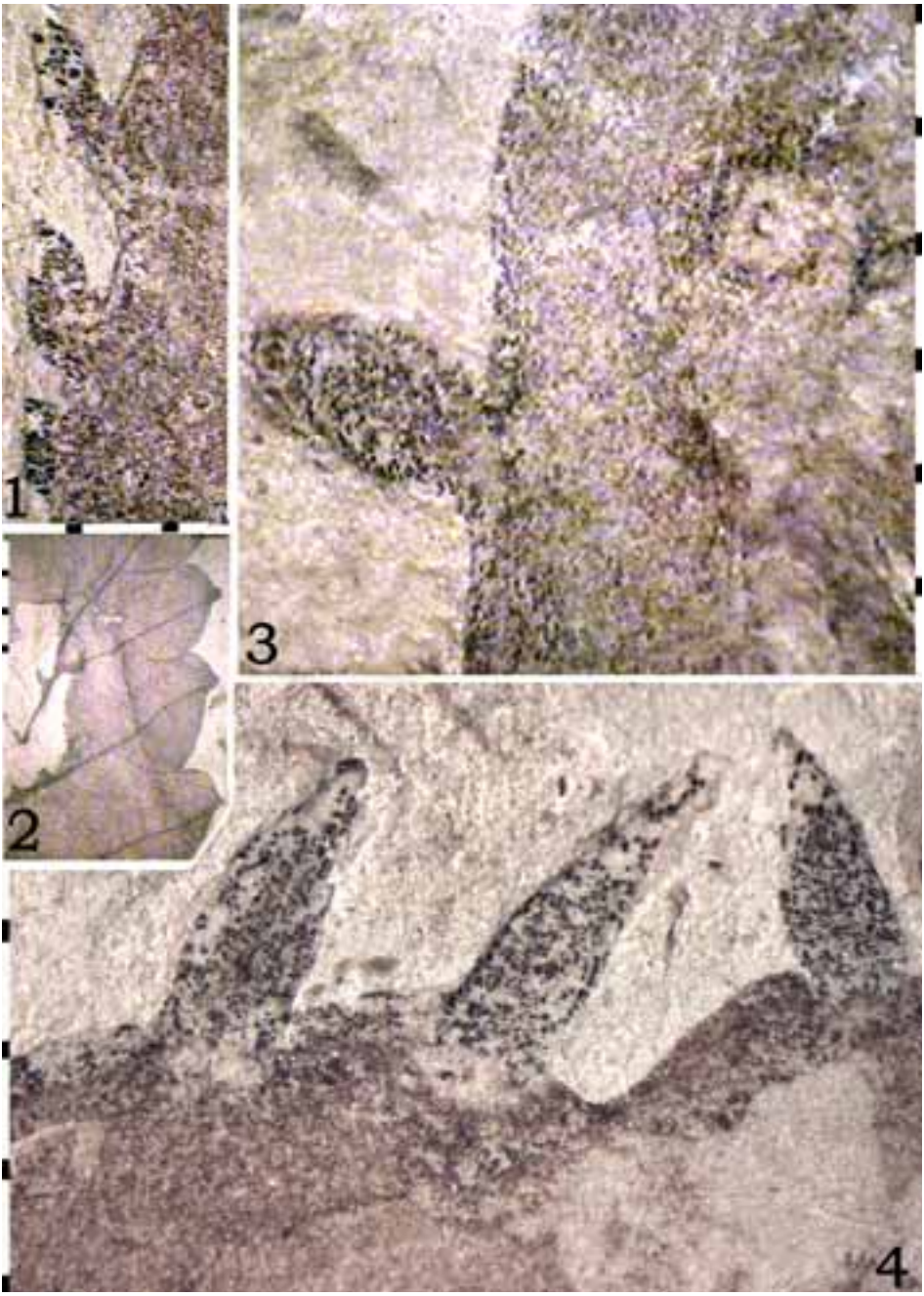

Plate XXIII. *Ceratoneon* (?) sp., Gerofit: leaf margin outgrowths positioned as marginal teeth, 2, glandulate marginal teeth of *Eocercidiphyllum glandulosum*, IG1-229; *Ceratoneon ovatum* sp. nov., Gerofit: 3, holotype IG1-201, marginal ceratoneon-type gall and a persistent attachment disk; *Ceratoneon mucronatum* sp. nov., Gerofit: 4, holotype IG1-277.

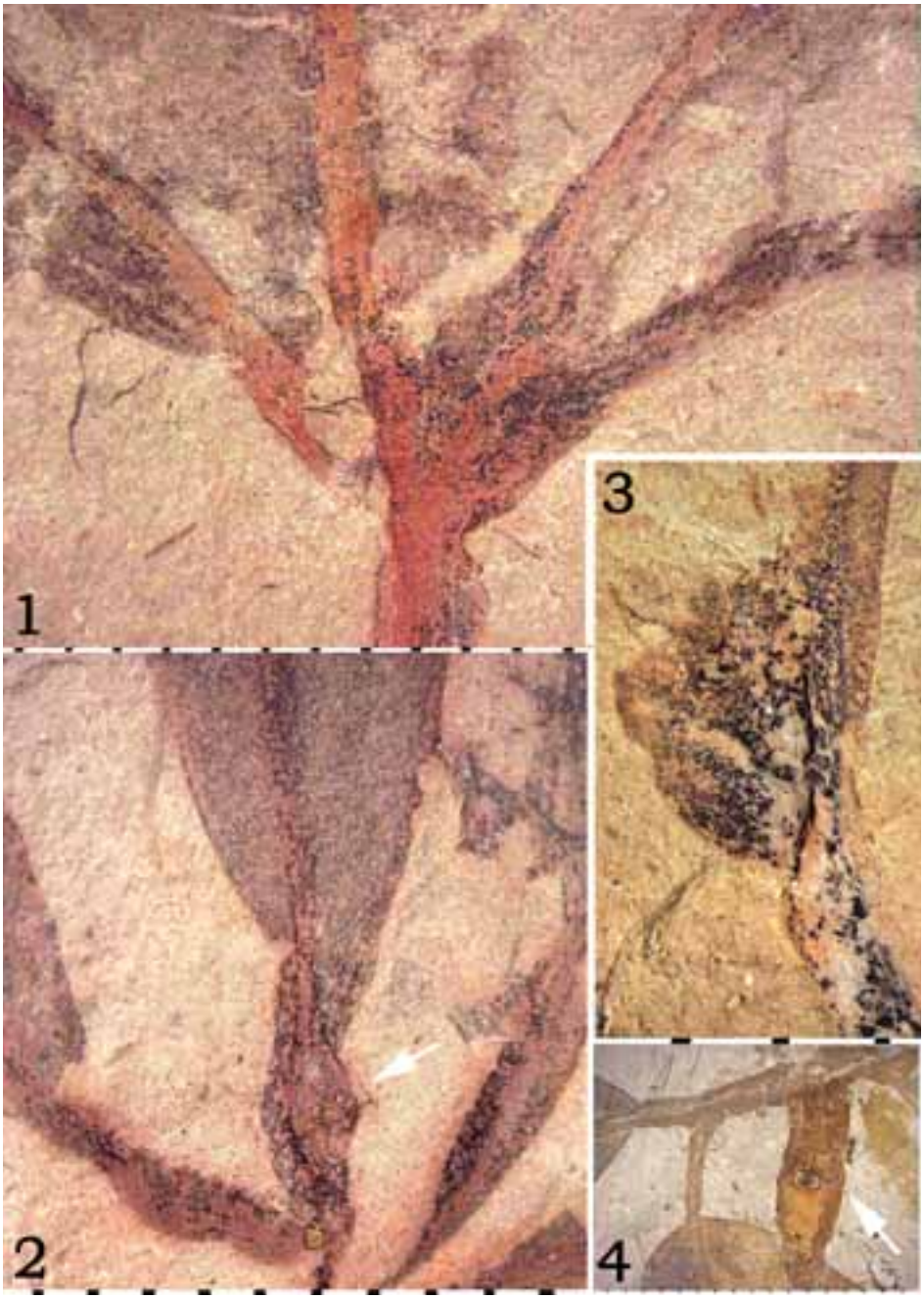

Plate XXIV. *Petioleon inflatum* gen. et sp. nov., Gerofit: 1, paratype IG1-36 showing webbing of petiolules in a compound leaf, 2, holotype IG1-601 showing elongate swellings of the petiolules, 3, paratype IG1-597, with the gall extending to the base of the leaflet; *Petioleon ostiolatum* gen. et sp. nov., Gerofit: 4, holotype IG1-539, ostiolate swelling of the petiole (arrow on ostiole).

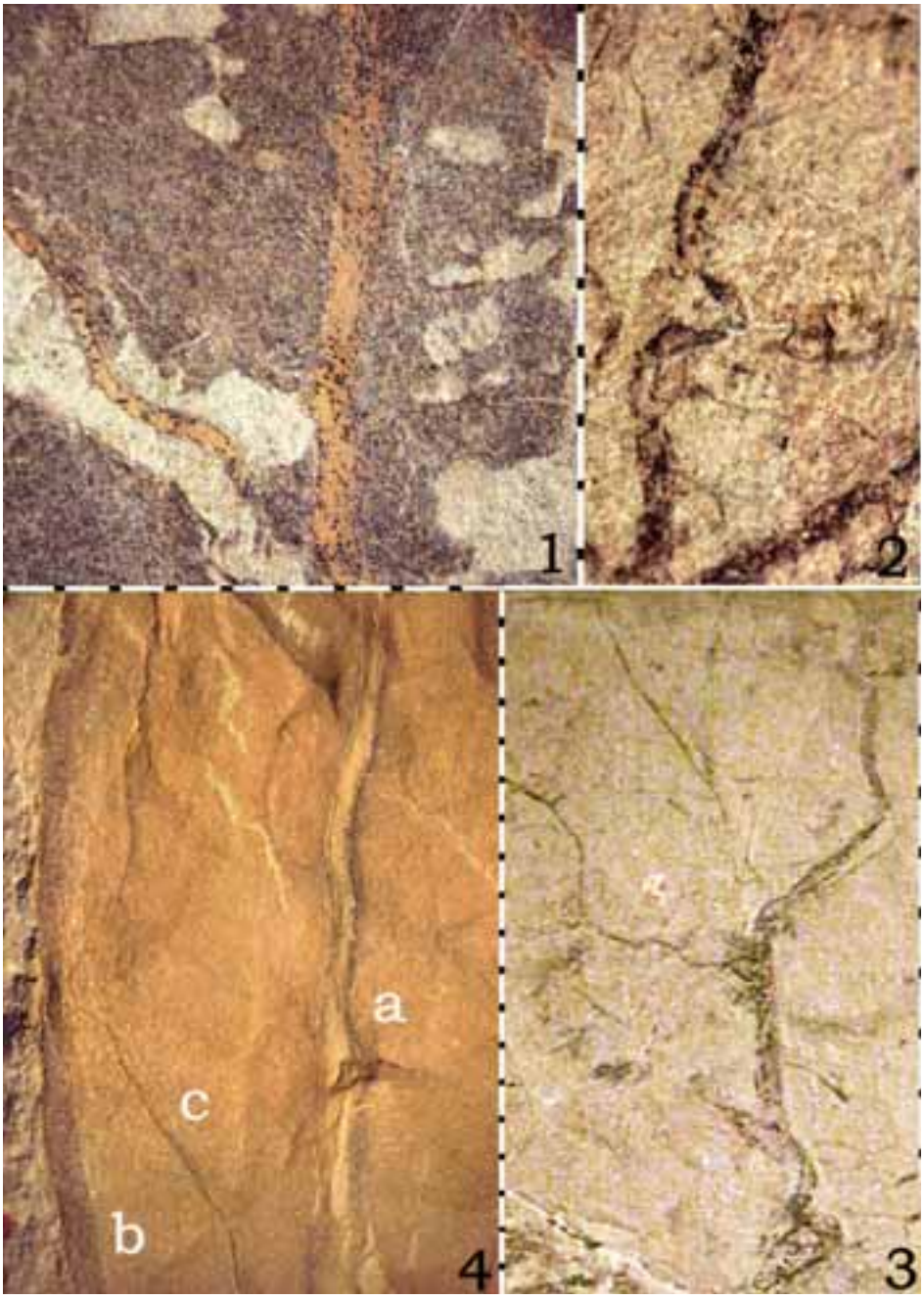

Plate XXV. *Costaeon flexum* gen. et sp. nov., Gerofit: 1, paratype IG1-447, 2, paratype IG1-606, 3, holotype IG1-123d, and 4a, paratype IG1-597, cataplasmatic swellings associated with extensive twisting of leaf midrib (2, 4) and/or lateral veins (1, 2), *Involuteon compressum* gen. et sp. nov., Gerofit: 4b, paratype IG1-597b, associated with a ridge gall (4c).

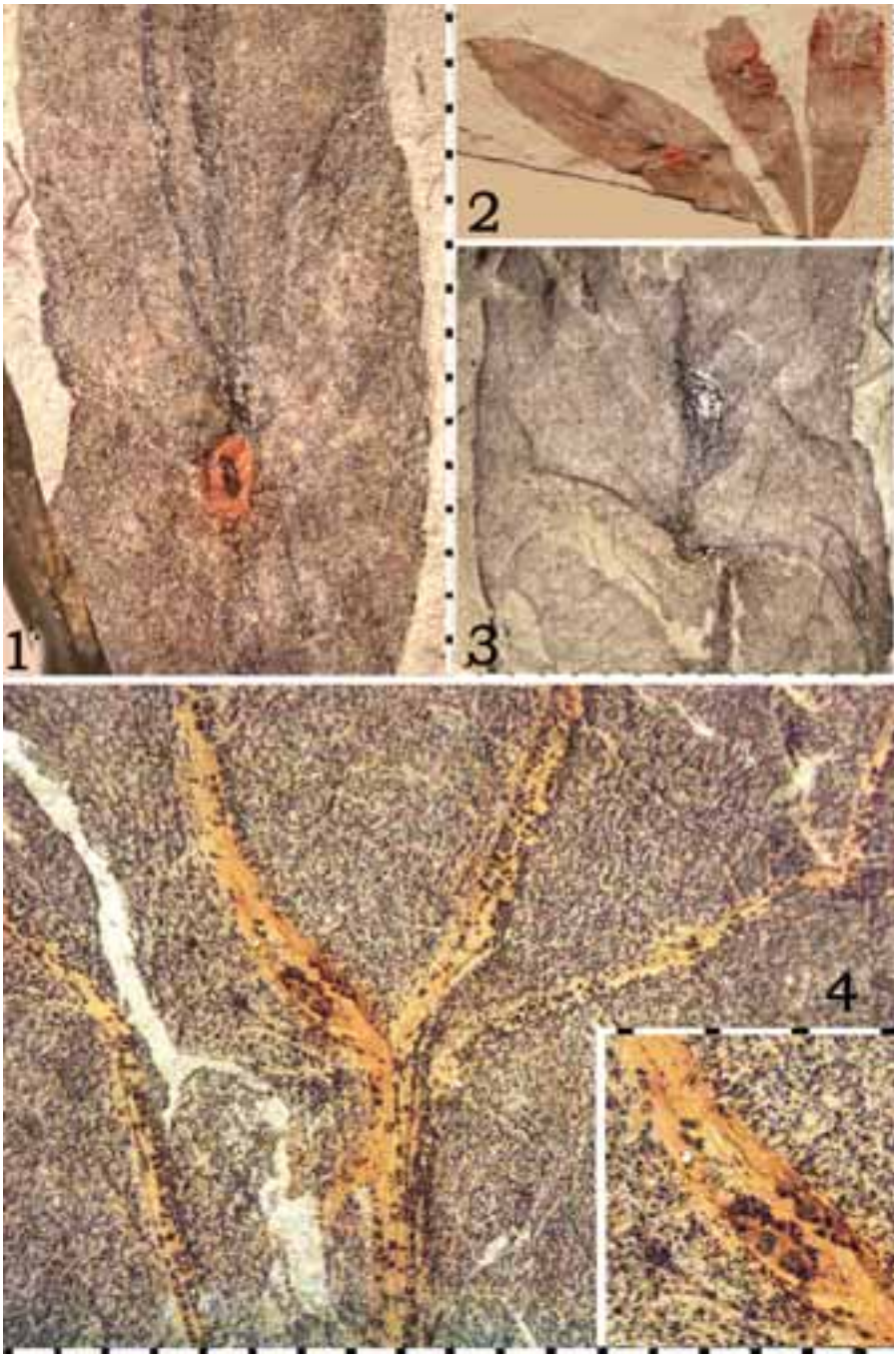

Plate XXVI. *Costaeon foveum* gen. et sp. nov., Gerofit: 1, 2 , holotype IG1-1125 and 3, paratype IG1-1126, showing gall pits on the leaflet midribs with fasciculate lateral veins, one with a dark (larval?) body inside (1), 4, paratype IG1-444, pits on fasciculate midrib branches.

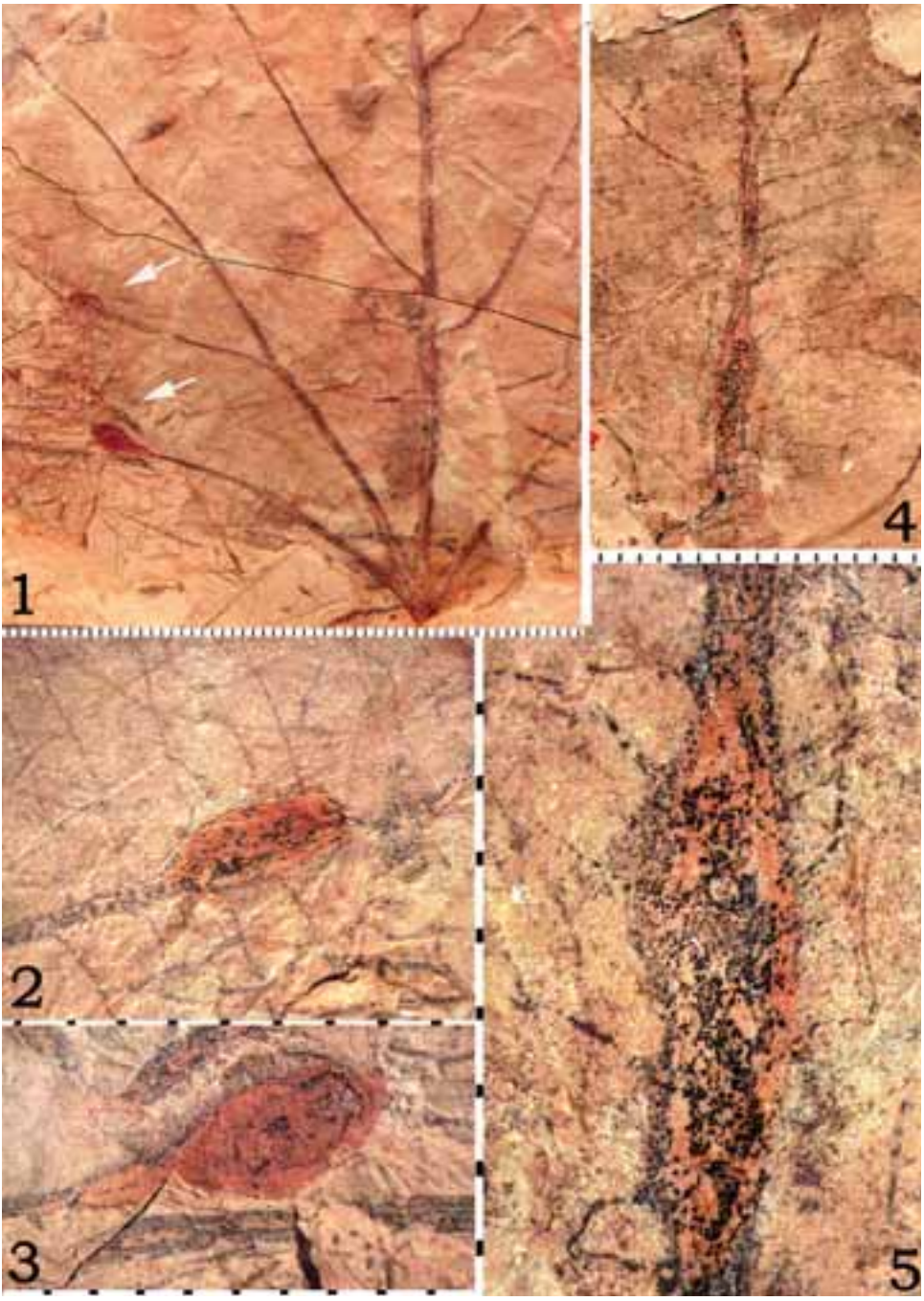

Plate XXVII. *Costaeon capsulatum* gen. et sp. nov., Gerofit: 1- 3, holotype IG1-589, disposition (1) and details (2, 3) of capsulate galls, the lateral veins decreasing and winding after the gall. *Costaeon* sp., Gerofit: 4, 5, IG1-457, fusiform gall bodies on lateral veins, associated with abnormal tertiary venation.

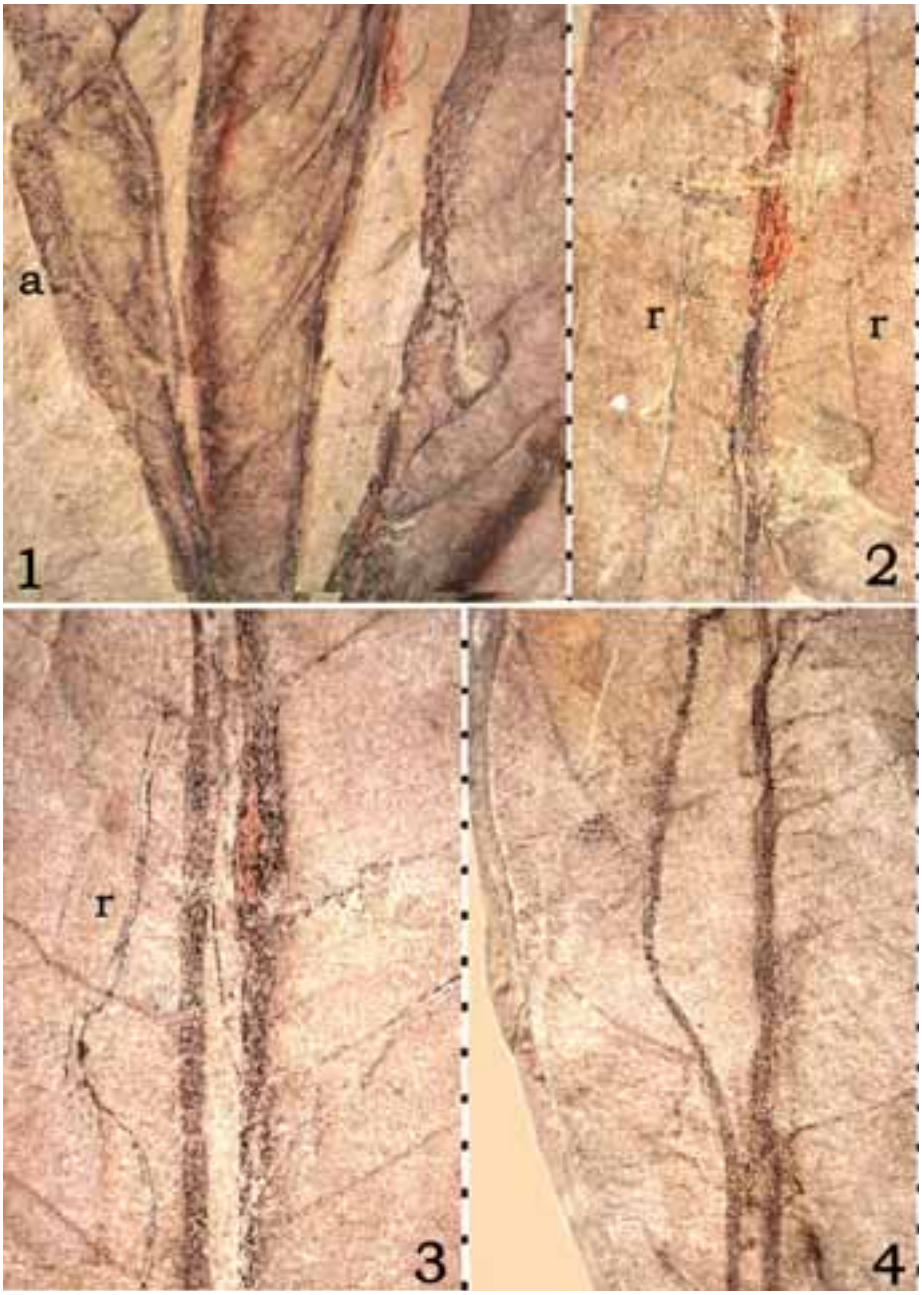

Plate XXVIII. *Costaeon schizmatum* gen. et sp. nov., Gerofit: 1–4, holotype IG1-796 (1) and paratypes IG1-1002 (2) and IG1-232 (3, 4), showing dissociation of vascular bundles, some accompanied by the ridge galls (r); *Involuteon compressum* gen. et sp. nov, paratype IG1-796a, margin roll gall.

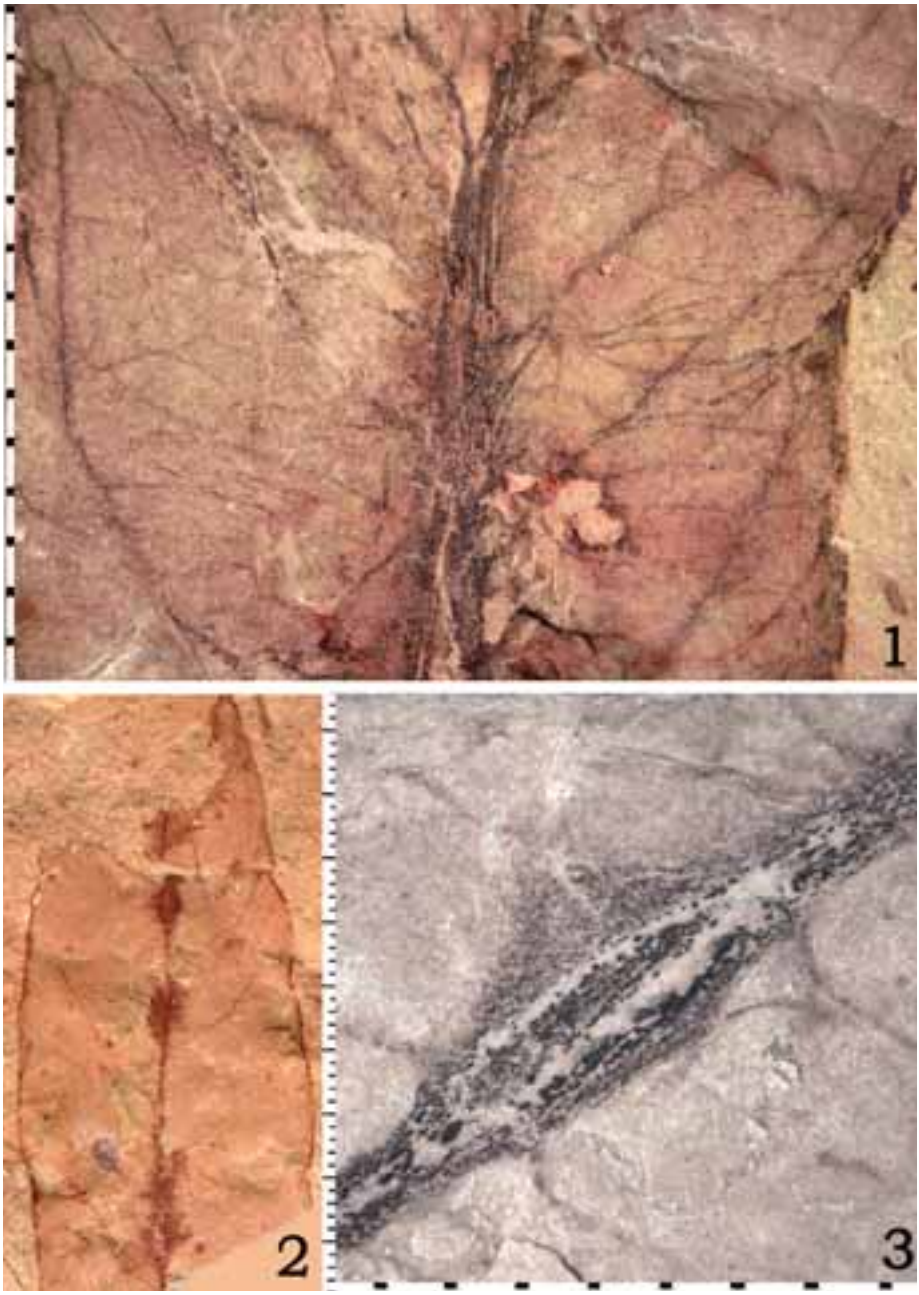

Plate XXIX. *Costaeon schizmatum* gen. et sp. nov., Gerofit: 1, holotype IG1-796, fusiform gall body associated with an incipient dissociation of vascular bundles and abundant cecidogenous venation; pits close to the midrib are probably caused by a mite gall, *Emergeon scabratum* sp. nov.. 2, 3, midrib swellings with callus fringes, probably belonging to *Costaeon schizmatum*, but scarcely inflicting dissociation of vascular bundles, IG1-559, IG1-901.

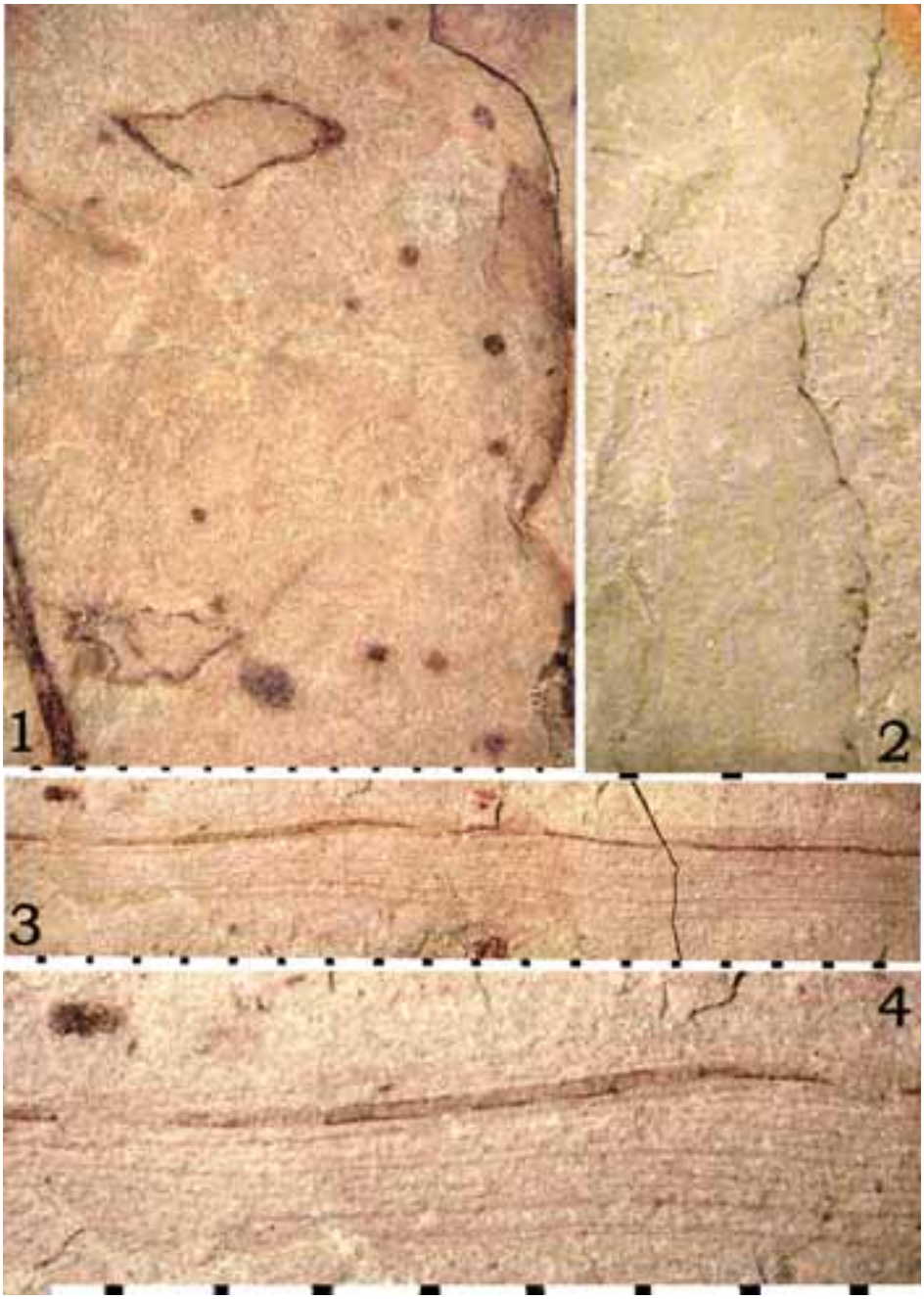

Plate XXX. *Troponoma curvitracta* gen. et sp. nov., Gerofit: 1, paratype IG1-563, close loop mines amid the egg scars, some on the borders of the mine tracks; *Ophionoma serranoides* gen. et sp. nov., Gerofit: 2, holotype IG1-121, marginal track with insertions; *Ophionoma paradroma* gen. et sp. nov., Gerofit: 3, 4, holotype iG1-639, linear track on monocot leaf.

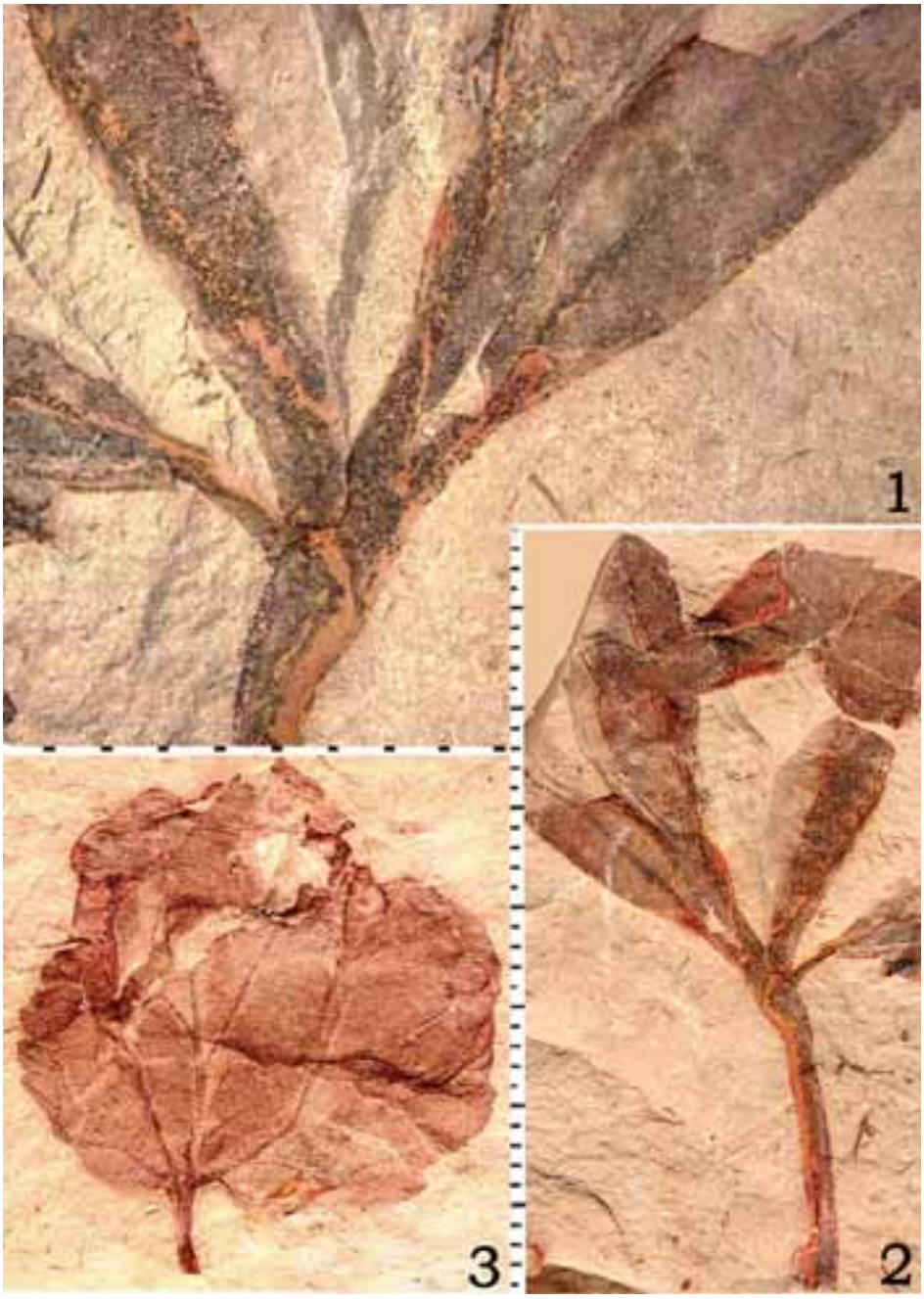

Plate XXXI. *Ophionoma digitata* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-1003, linear track extending over the leaf petiole into the midribs of the leaflets, 3, paratype IG1-747, petiole to primary vein mining on a deformed and stunted leaf.

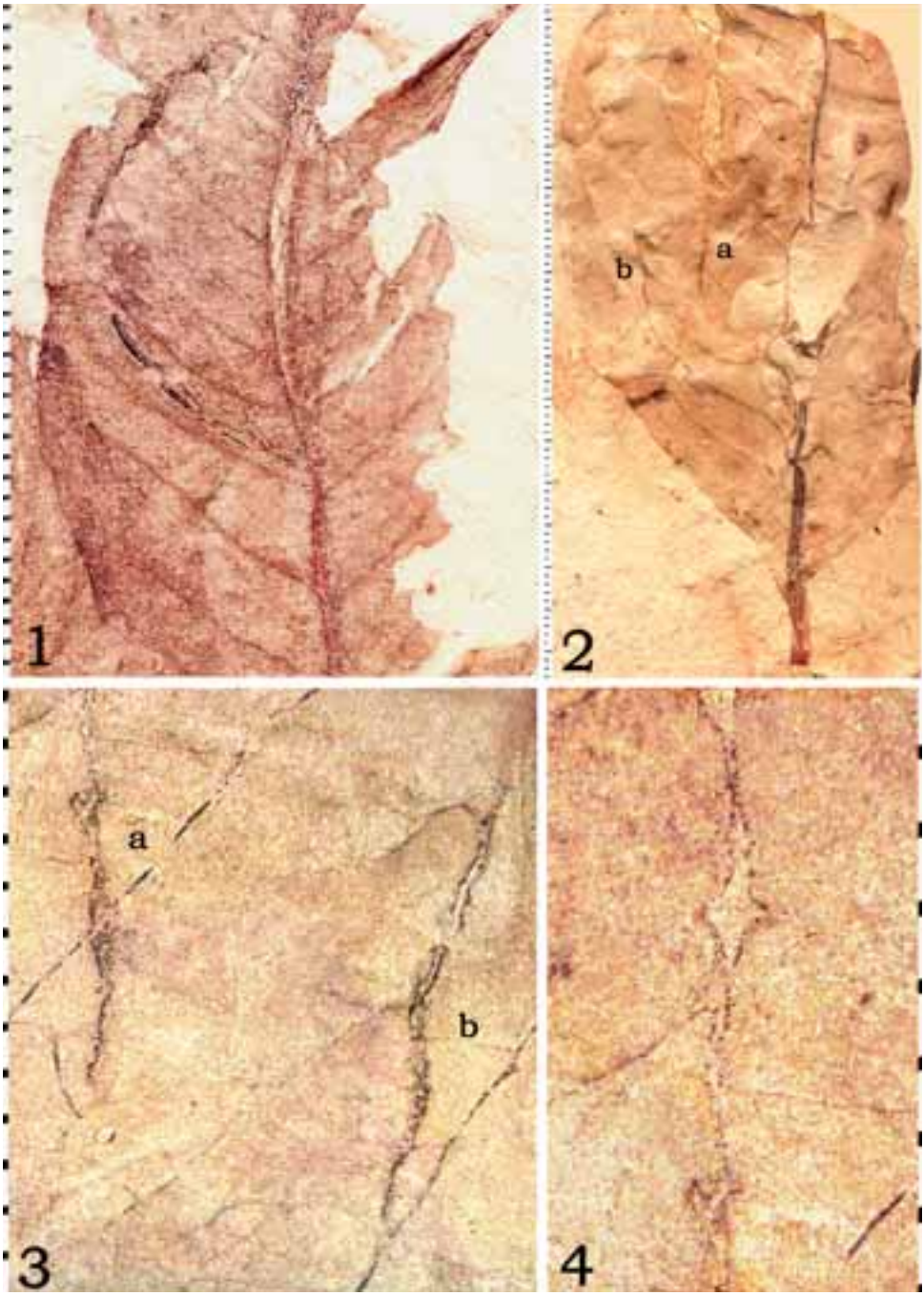

Plate XXXII. *Ophionoma arcuata* gen. et sp. nov., Gerofit: 1, holotype IG1-598, tracking between the lateral veins and along the margin; *Ophistigmonoma rectiserialis* gen. et sp. nov., Gerofit: 2–4, holotype IG1-633, parallel linear tracks expanding into series of blotches.

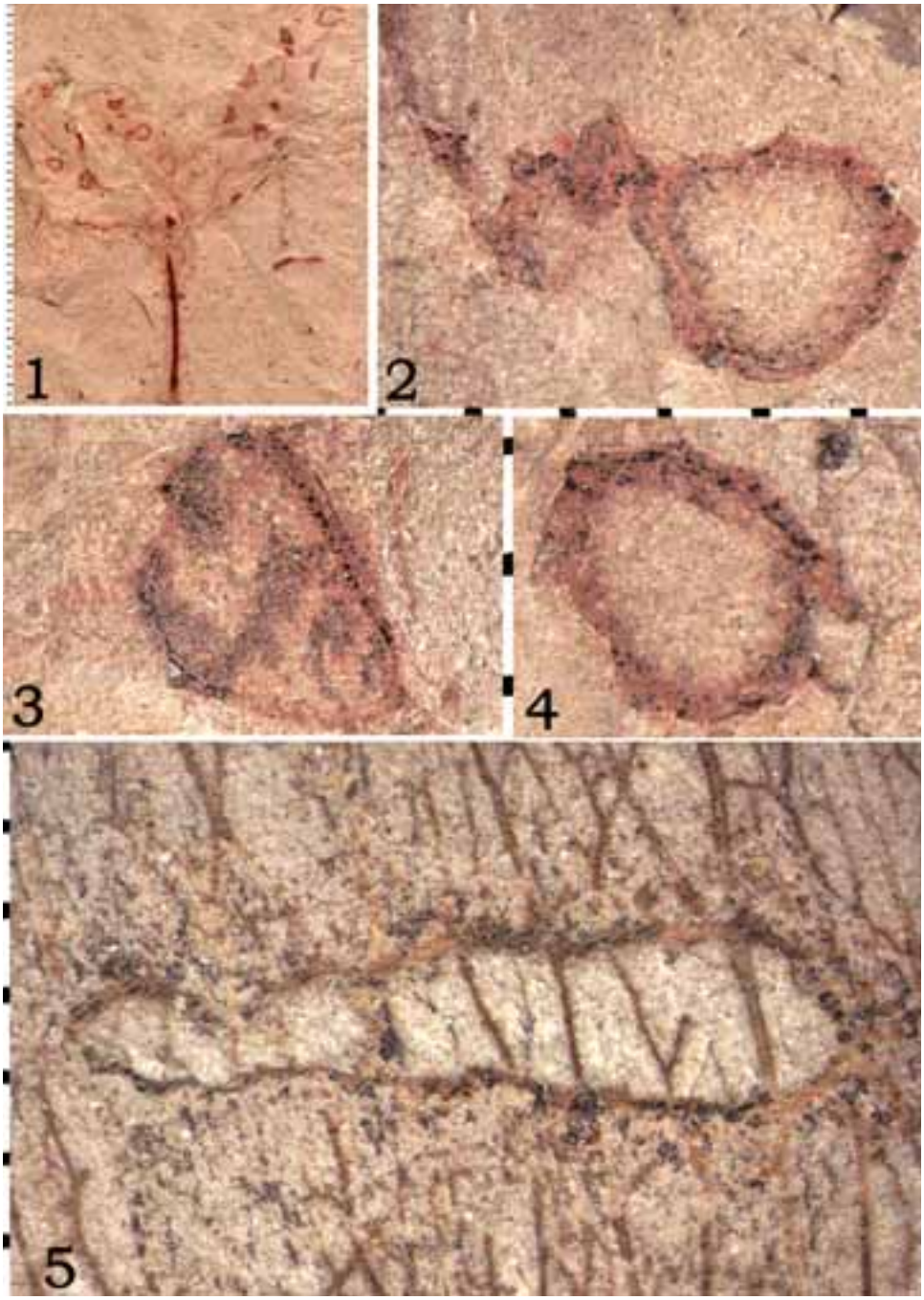

Plate XXXIII. *Ophistigmonoma crassa* gen. et sp. nov., Gerofit: 1–4, holotype IG1-6, disposition (1) and details of small (ophi)simooms with a thick cogged borderline, one with smeared frass inside (3); 4, *Apostigmonoma fibrosa* gen. et sp. nov., Gerofit: 4, holotype IG1-331, with tracery of the stronger veins intact.

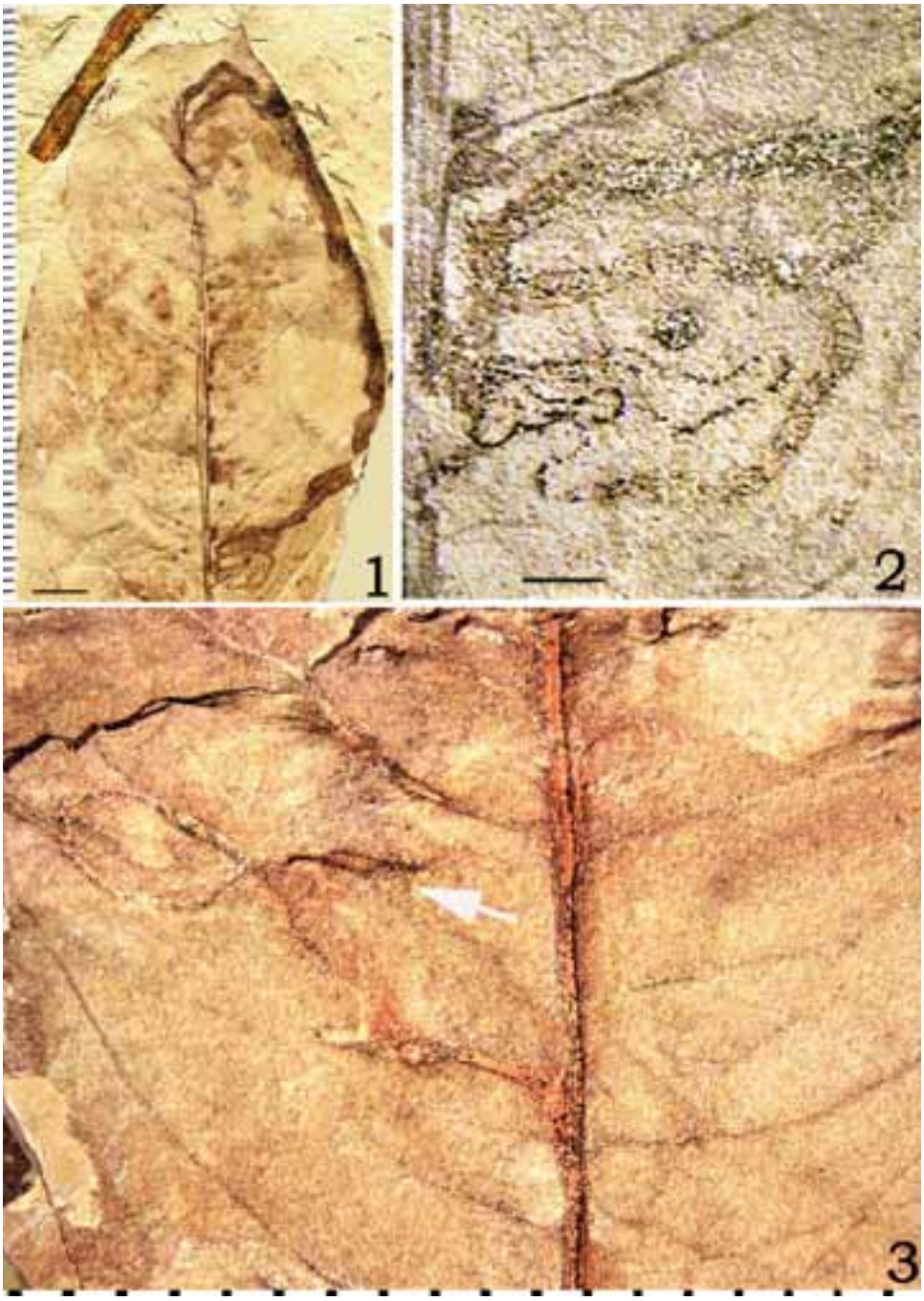

Plate XXXIV. *Ophiheliconoma resupinata* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-139, linear track helically coiled on ends; *Troponoma crucitracta* gen. et sp. nov., Gerofit: 3, holotype IG1-855, costal linear mine ending in a cross-track loop.

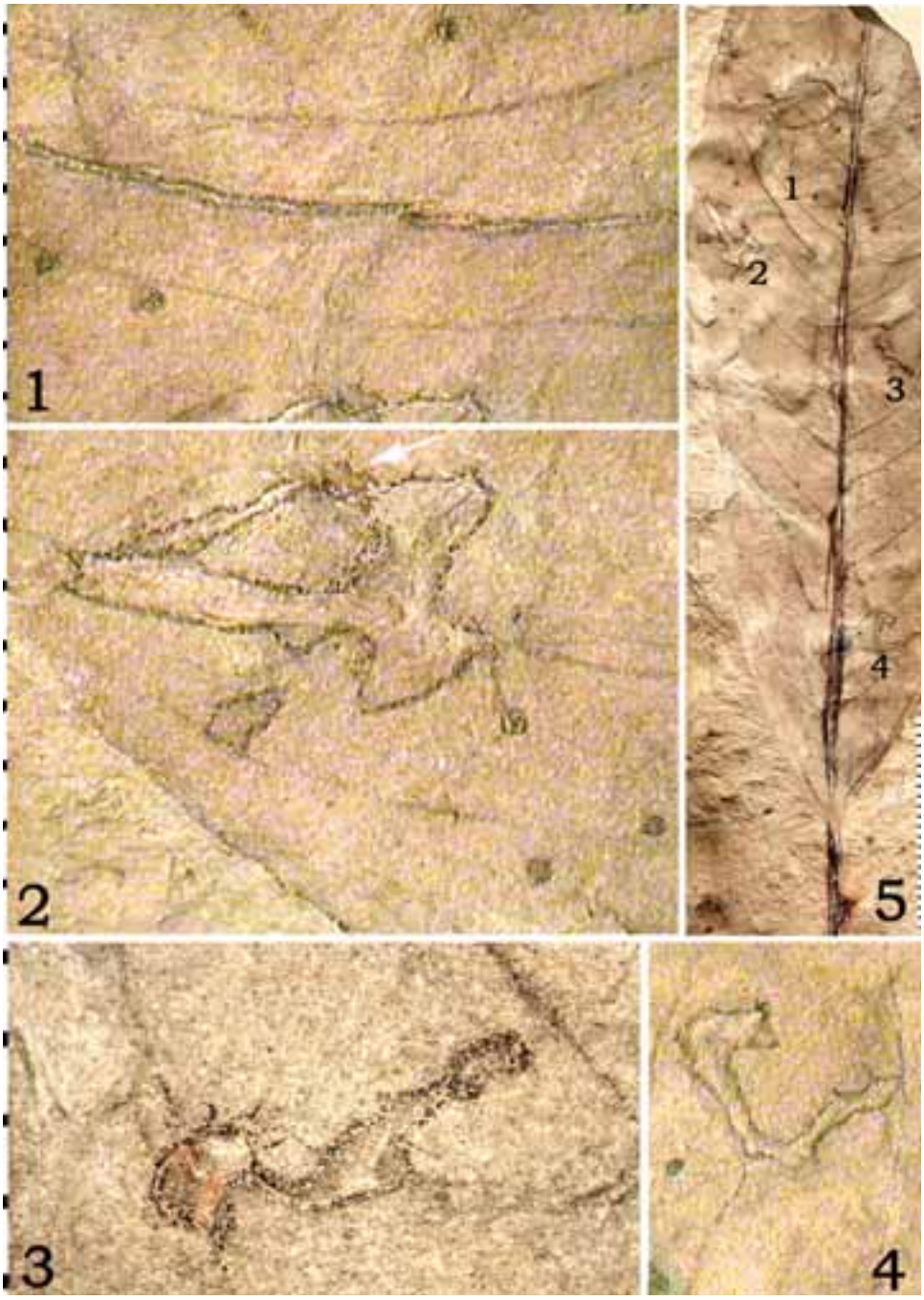

Plate XXXV. *Troponoma curvitracta* gen. et sp. nov., Gerofit: 1–4, holotype IG1-160, tracks wound into closed loops, their respective on leaf positions are numbered 1 to 4 in fig. 5.

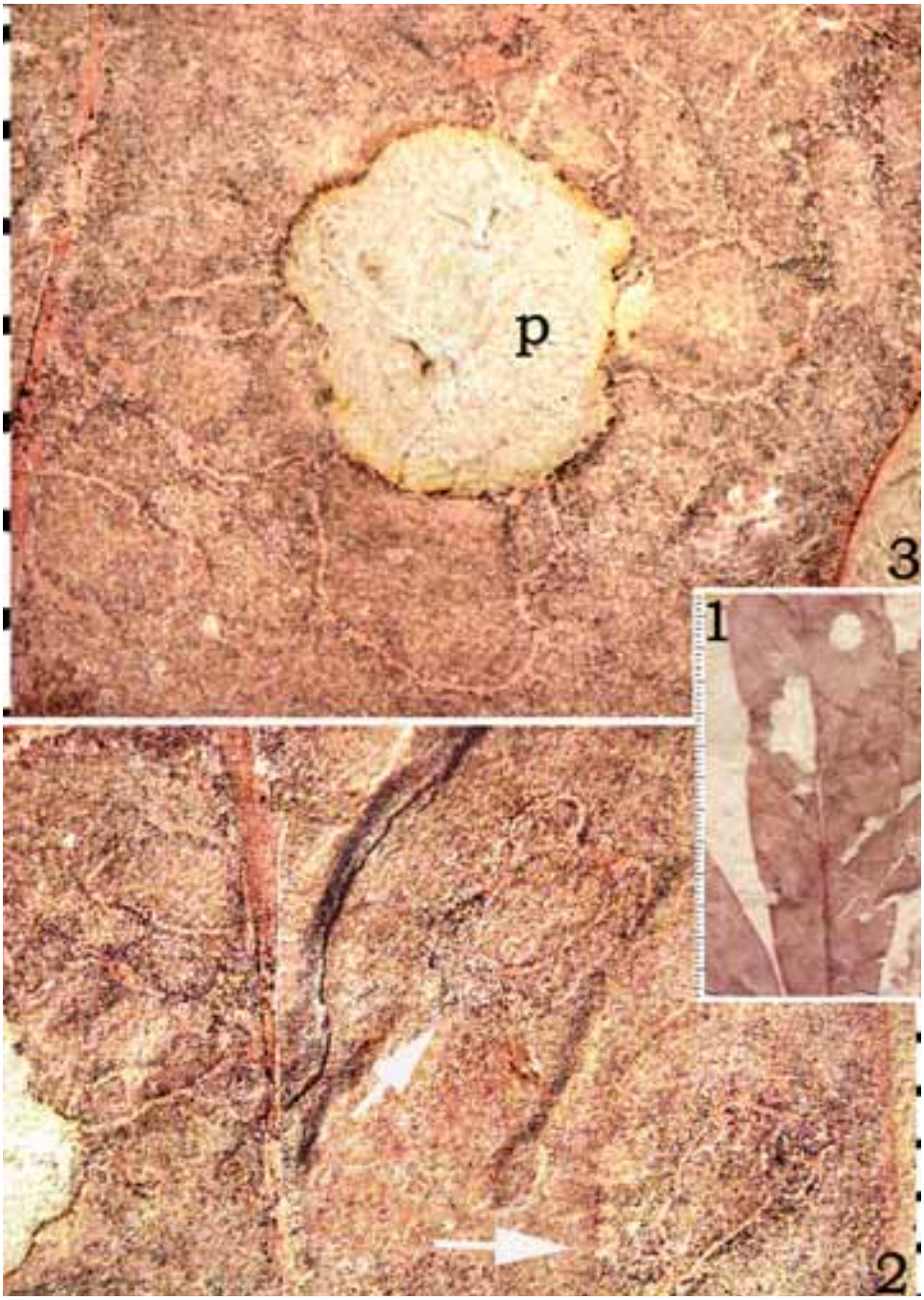

Plate XXXVI. *Troponoma festunata* gen. et sp. nov., Gerofit: 1–3, on leaf position (1) and configuration (2, 3) of the tightly coiled tracks; *Stigmatophaga perforata* gen. et sp. nov.: 3p, holotype IG1-1101p, a large predation hole (p) in the middle of a coiled mine *Troponoma festunata.*

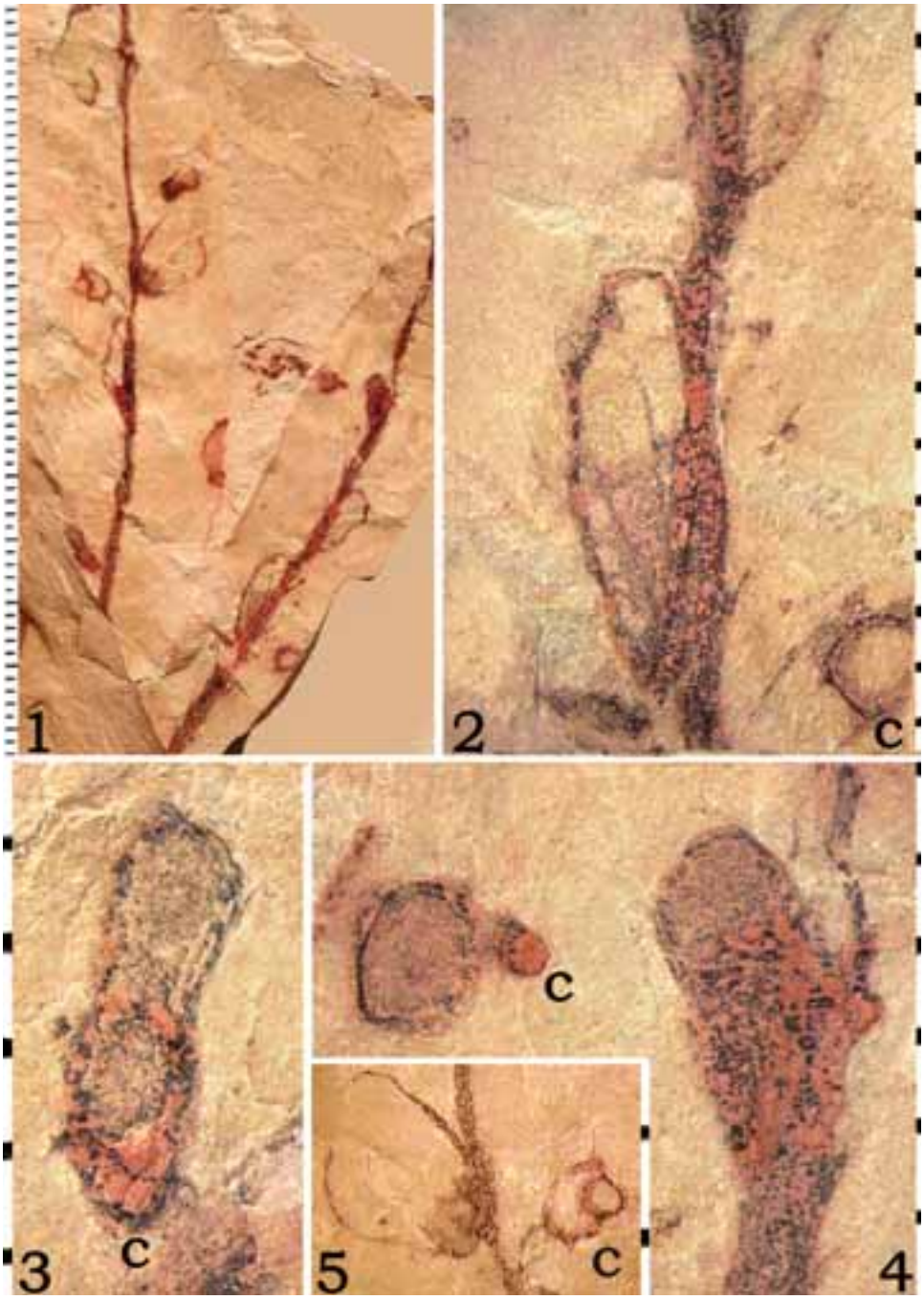

Plate XXXVII. *Eustigmonoma alternans* gen. et sp. nov., Gerofit: 1–4, holotype IG1-626, on leaf disposition (1) and details of blotches, some with cocoon scars (c).

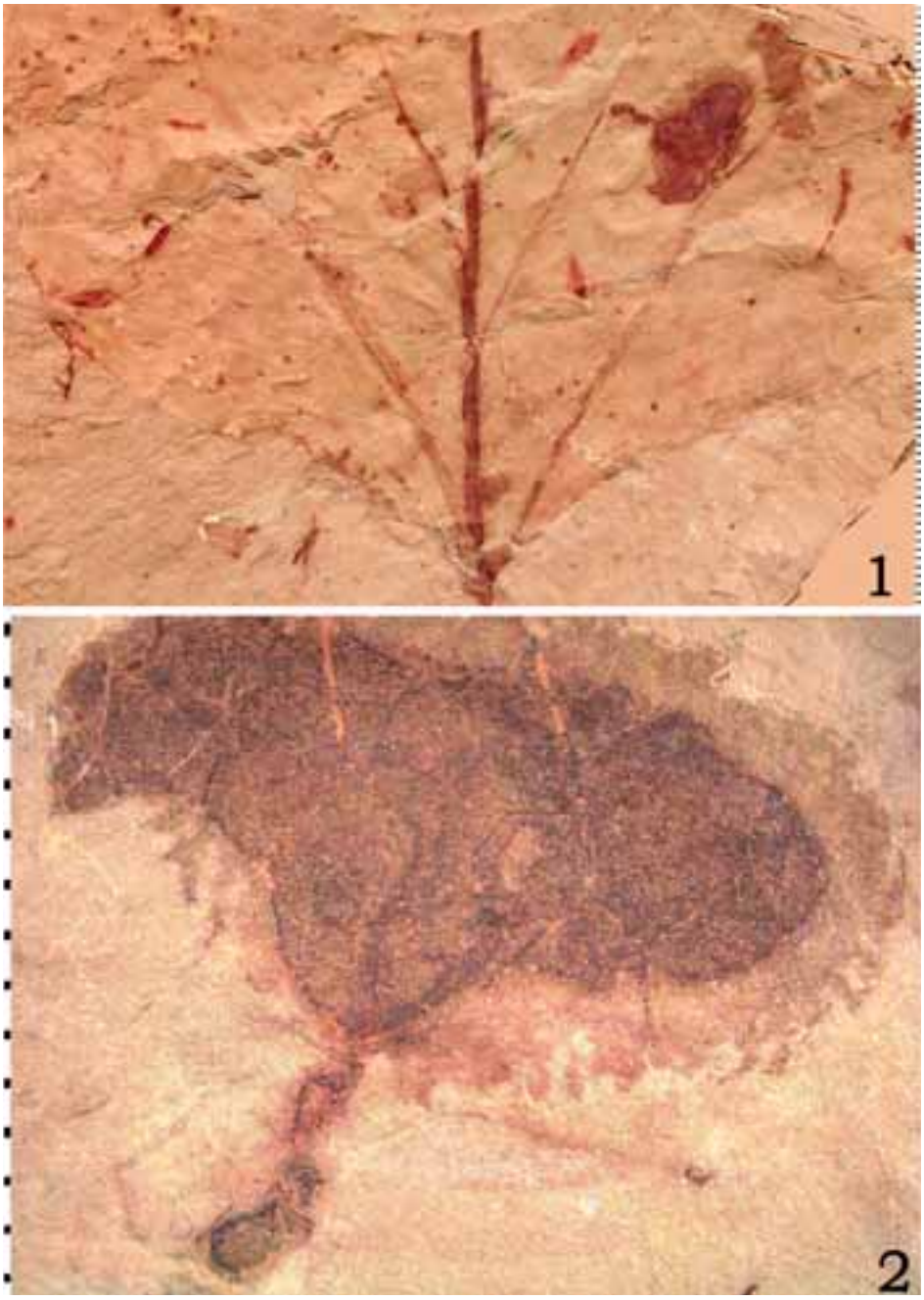

Plate XXXVIII. *Distigmonoma fimbriata* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-588, on leaf location and details of a large mine-in-mine structure.

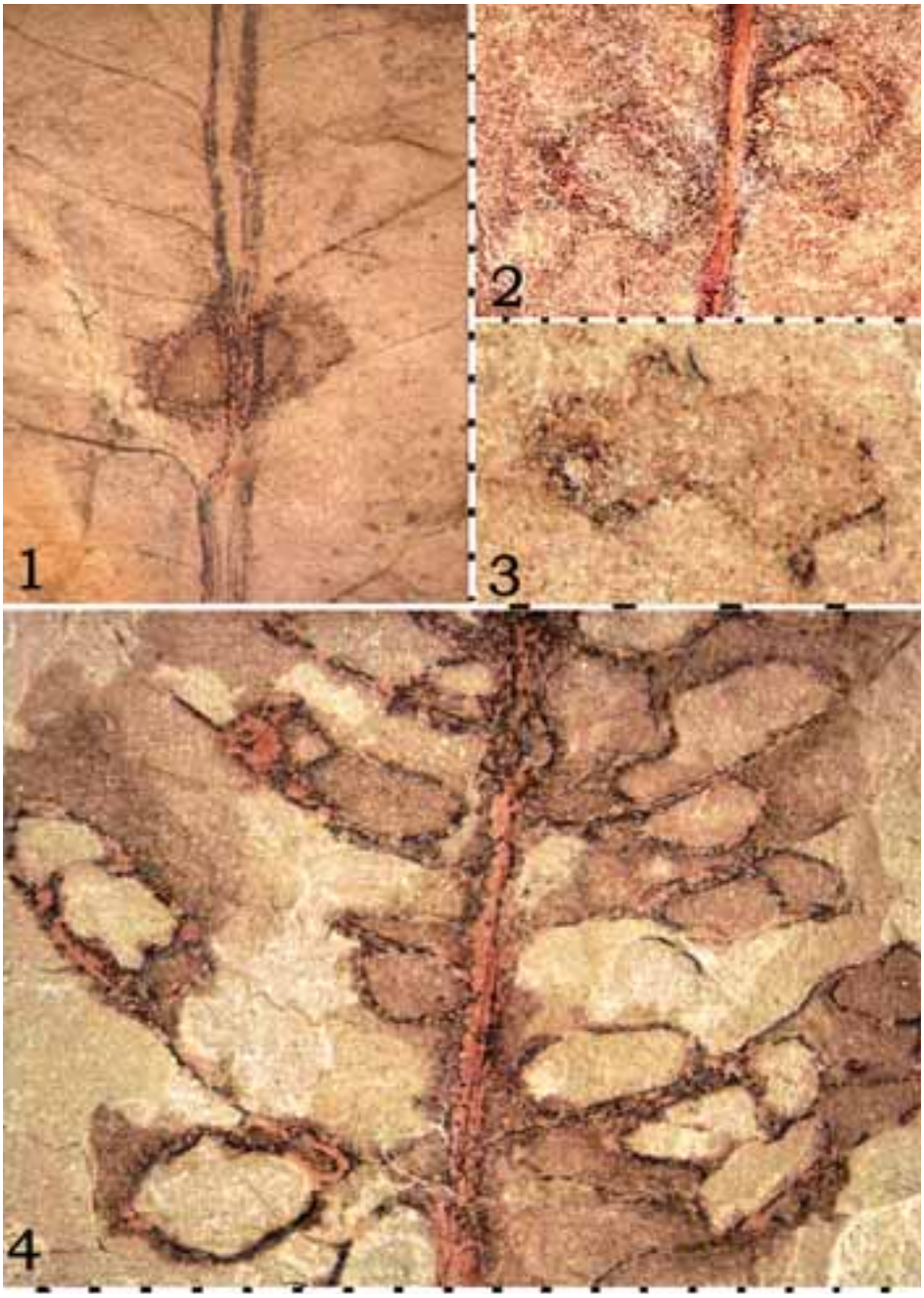

Plate XXXIX. *Distigmonoma oculata* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-1110 and paratype IG1-600, mine-in-mine structures; 3. *Eustigmonoma amaeboides* gen. et sp. nov., Gerofit: holotype IG1-363, small irregular mine with an egg scar on the border; 4. *Distigmonoma variegata* gen. et sp. nov., Gerofit: holotype IG1-644, a mosaic of two generations of blotches.

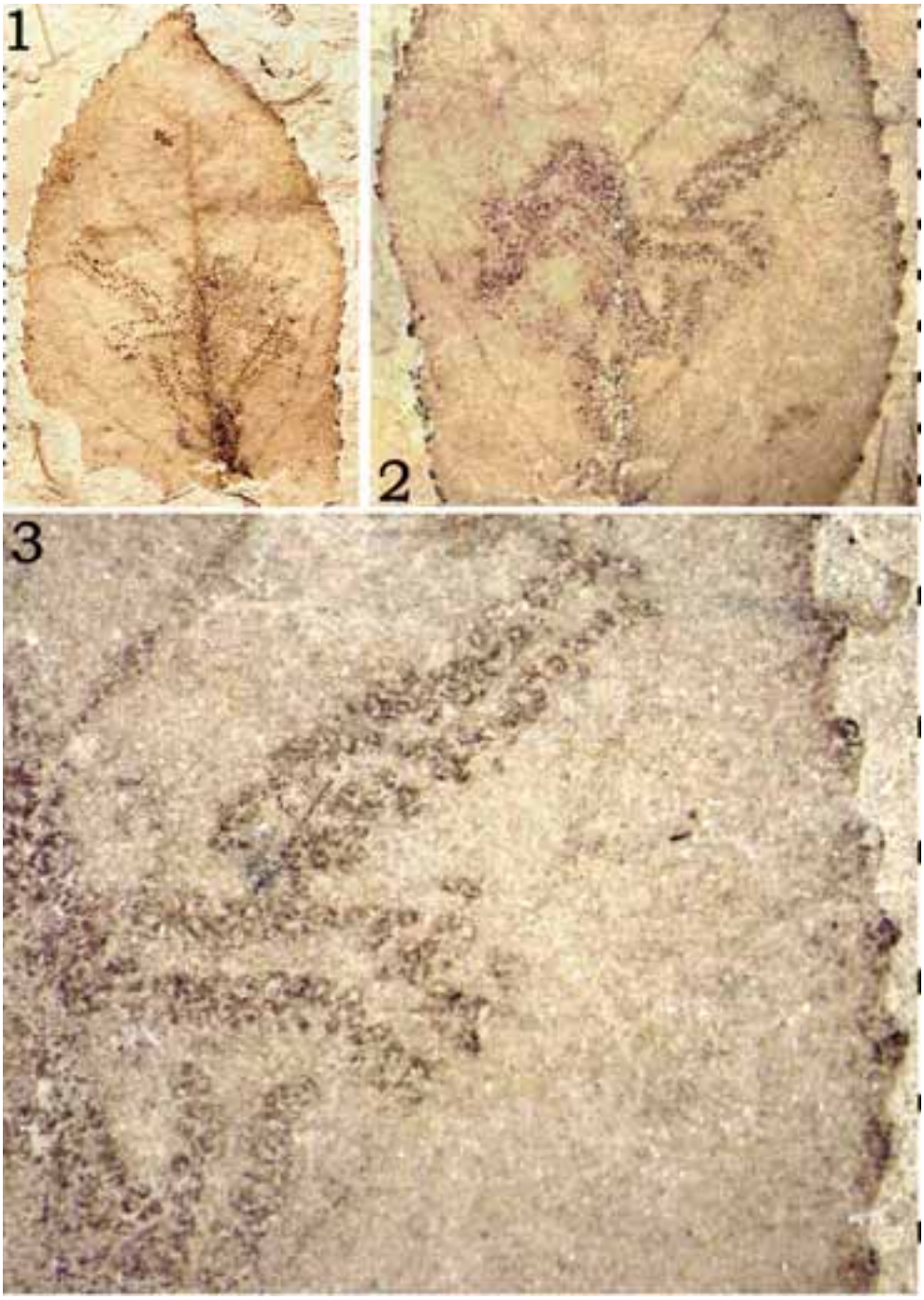

Plate XI. *Asteronoma arachnoides* gen. et sp. nov., Gerofit: 1, holotype IG1-138, 2, 3, counterpart IG1-125.

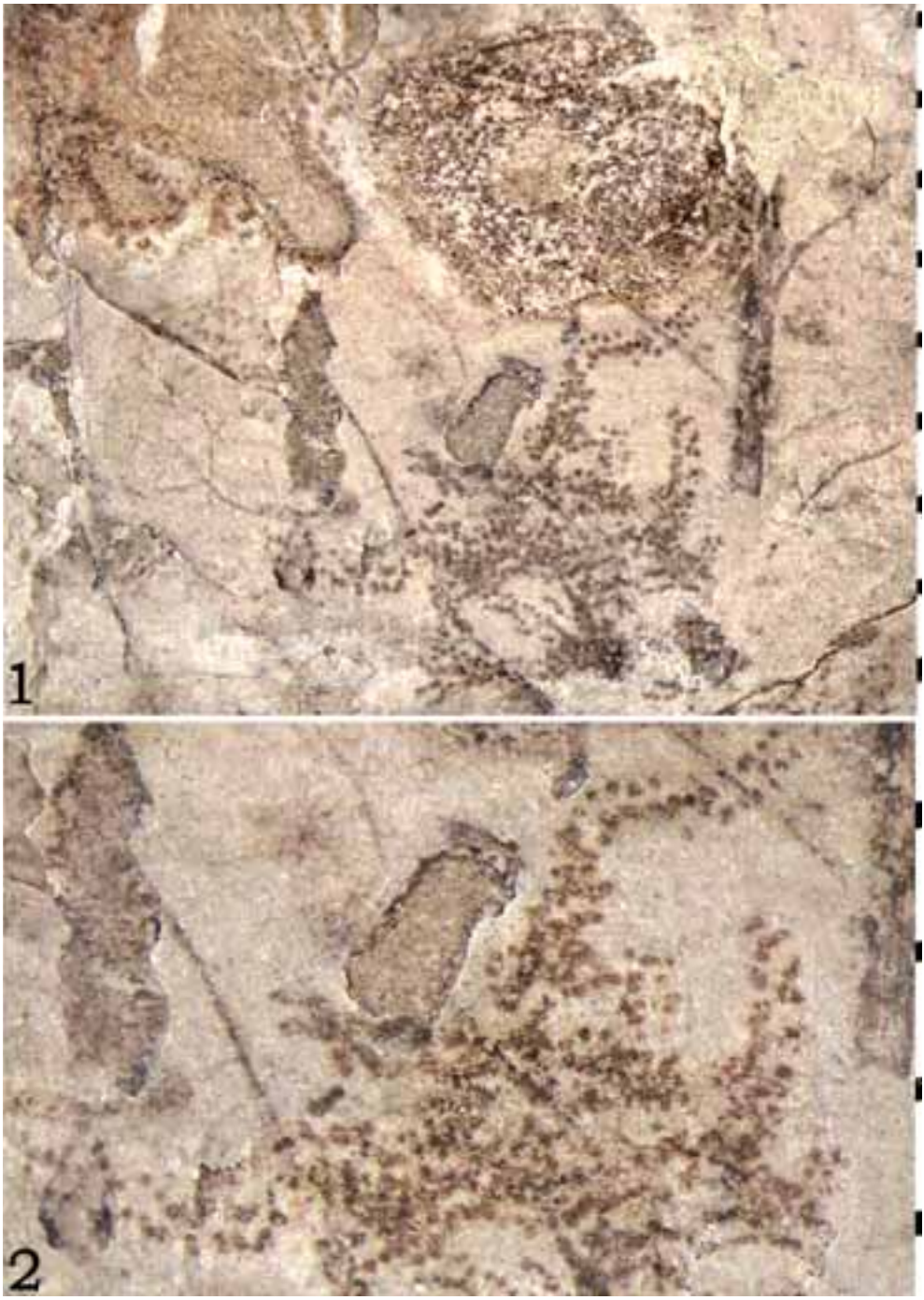

Plate XLI. *Asteronoma arachnoides* gen. et sp. nov., Gerofit: 1, 2, paratype IG1-128 and counterpart, small digitate mine surrounded by other type blotches.

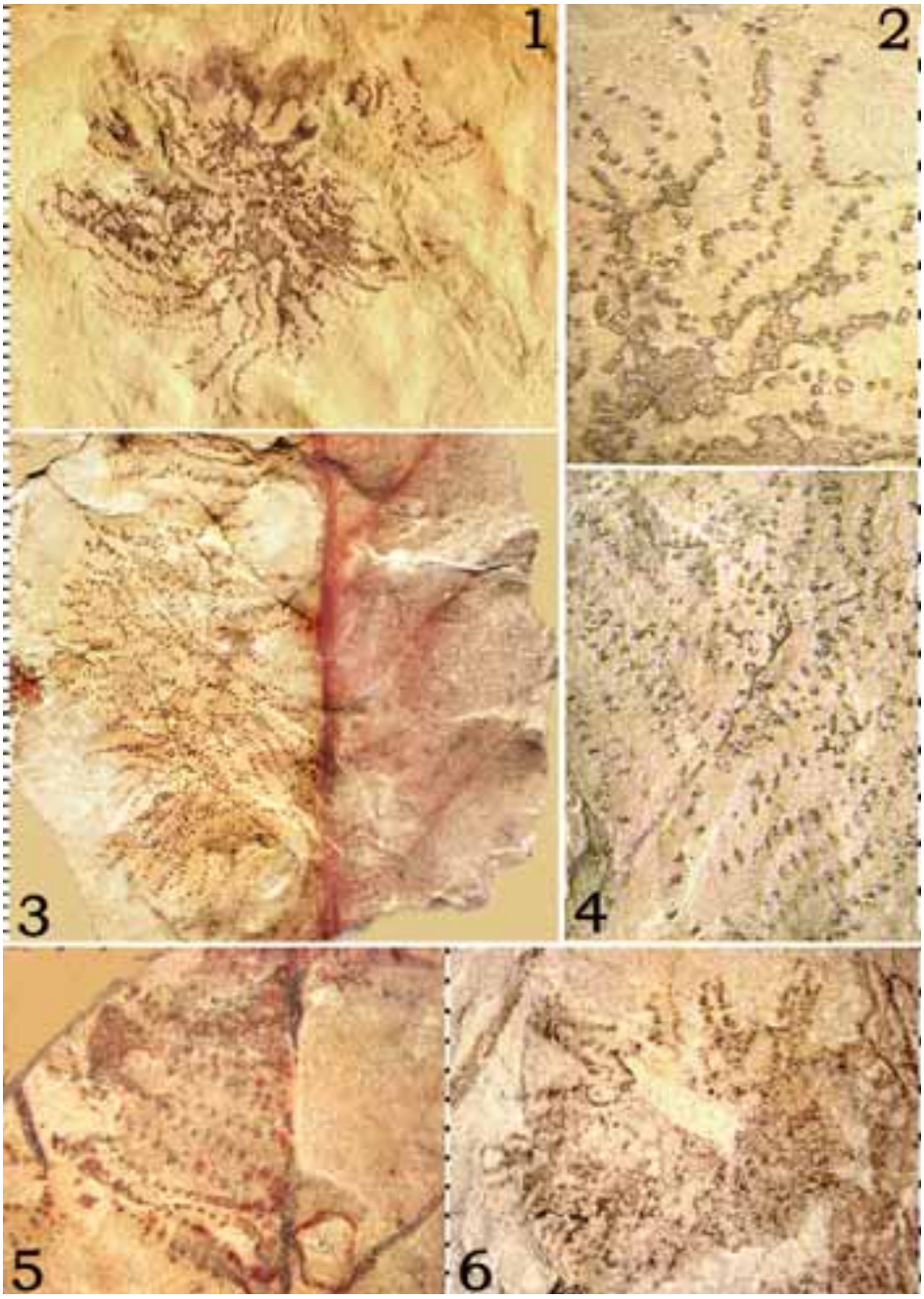

Plate XLII. *Asteronoma helicoids* gen. et sp. nov., Gerofit: 1, 2, holotype IG1-675, digitate mine with a whirlpool arrangement of arms; *Asteronoma expansa* gen. et sp. nov., Gerofit: 3, 4, holotype IG1-11, half-blade mine with double rows of elongate frass pellets, 5, paratype, IG1-9, double rows of frass pellets. *Asteronoma arachnoides* gen. et sp. nov., Gerofit: 6, paratype IG1-116, small irregular digitate mine.

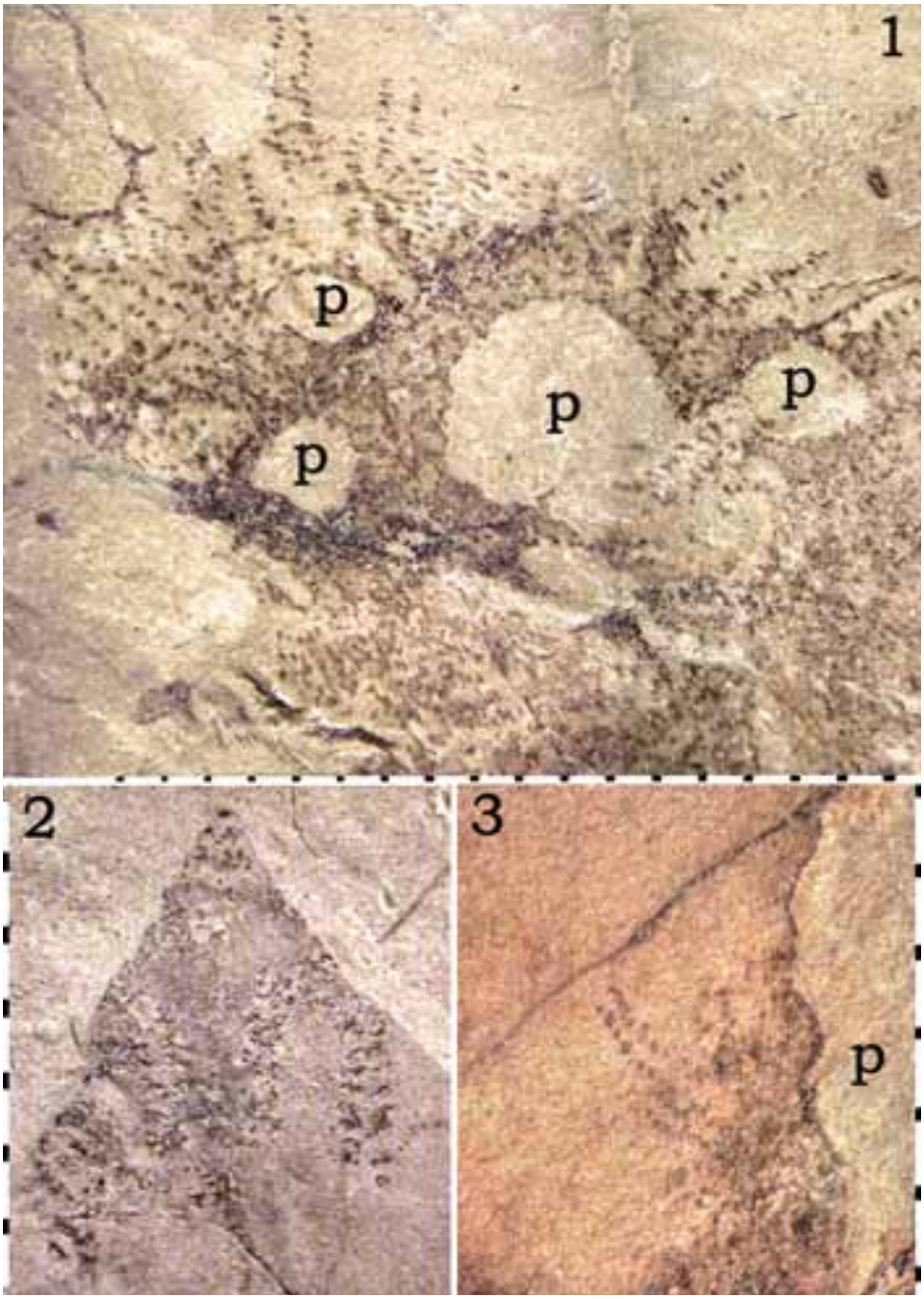

Plate XLIII. *Asteronoma expansa* gen. et sp. nov., Gerofit: 1, paratype IG1-868, digitate mine with symmetrically disposed predation holes *Stigmatophaga perforata* gen. et sp. nov., paratype IG1-868p, 2, paratype IG1-123, on the leaf tip; *Asteronoma arachnoides* gen. et sp. nov., Gerofit: 3, paratype IG1-600a, remnants of digitate mine consumed in the feeding hole of *Stigmatophaga perforata* (Pl. LI, fig. 1).

Plate XLIV. *Holostigmonoma zebrina* gen. et sp. nov., Gerofit: 1–3, holotype IG1-539, whole leaflet blotch with transverse rows of frass pellets.

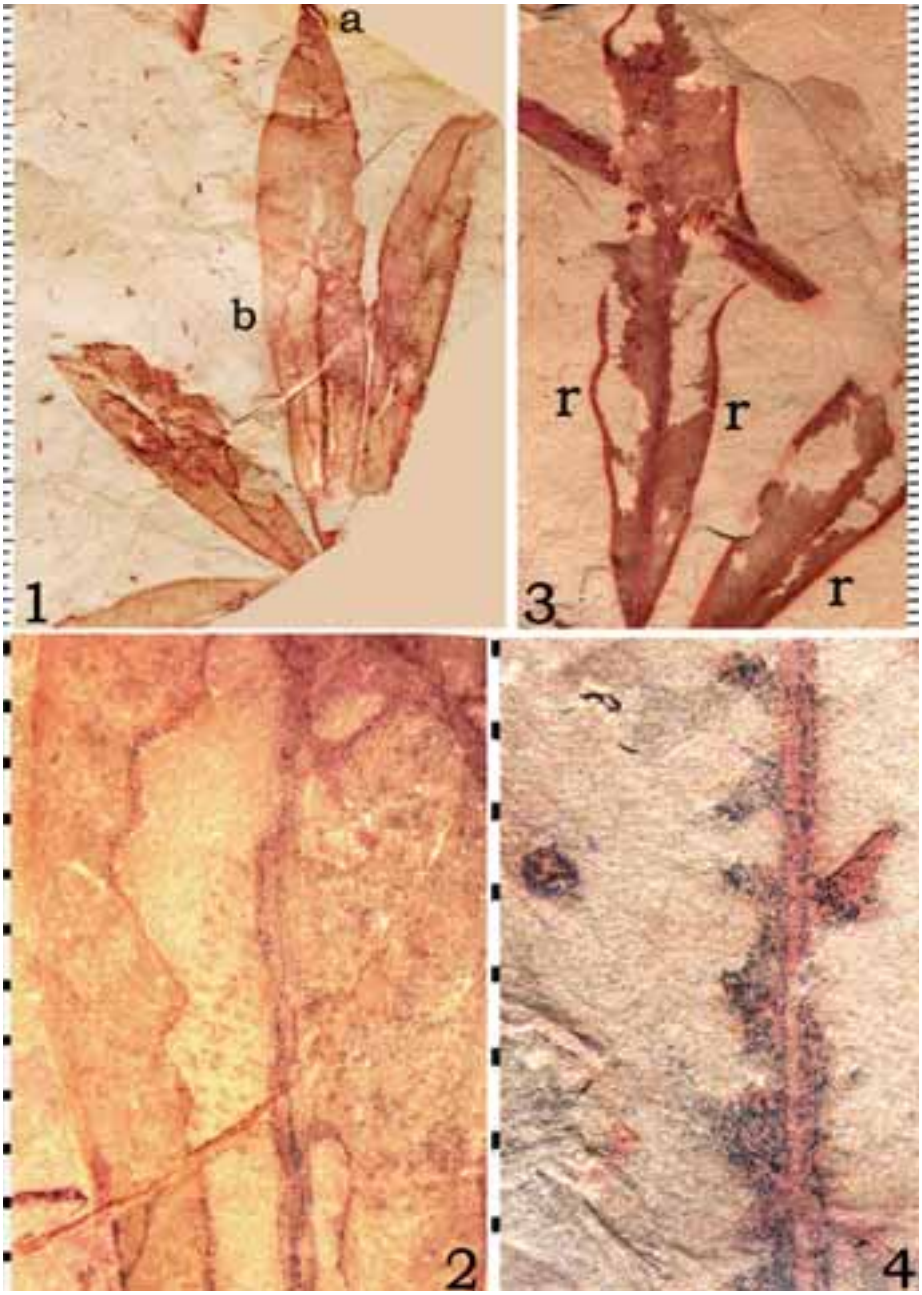

Plate XLV. *Holostigmonoma fenestrata* gen. et sp. nov., Gerofit: 1b, 2, holotype IG1-191, whole leaflet blotch with an elongate epidermal window and a marginal cut-out (arrow); *Involuteon compressum* gen. et sp. nov., Gerofit: holotype IG1-887r, continuous margin rolls, with cut-out areas next to it and a marginal cut-out (arrow); *Symphyenoma adcostalis* gen. et sp. nov., Gerofit: 4, holotype IG1-80e, blotch arms starting from egg scars, confluent over the midrib.

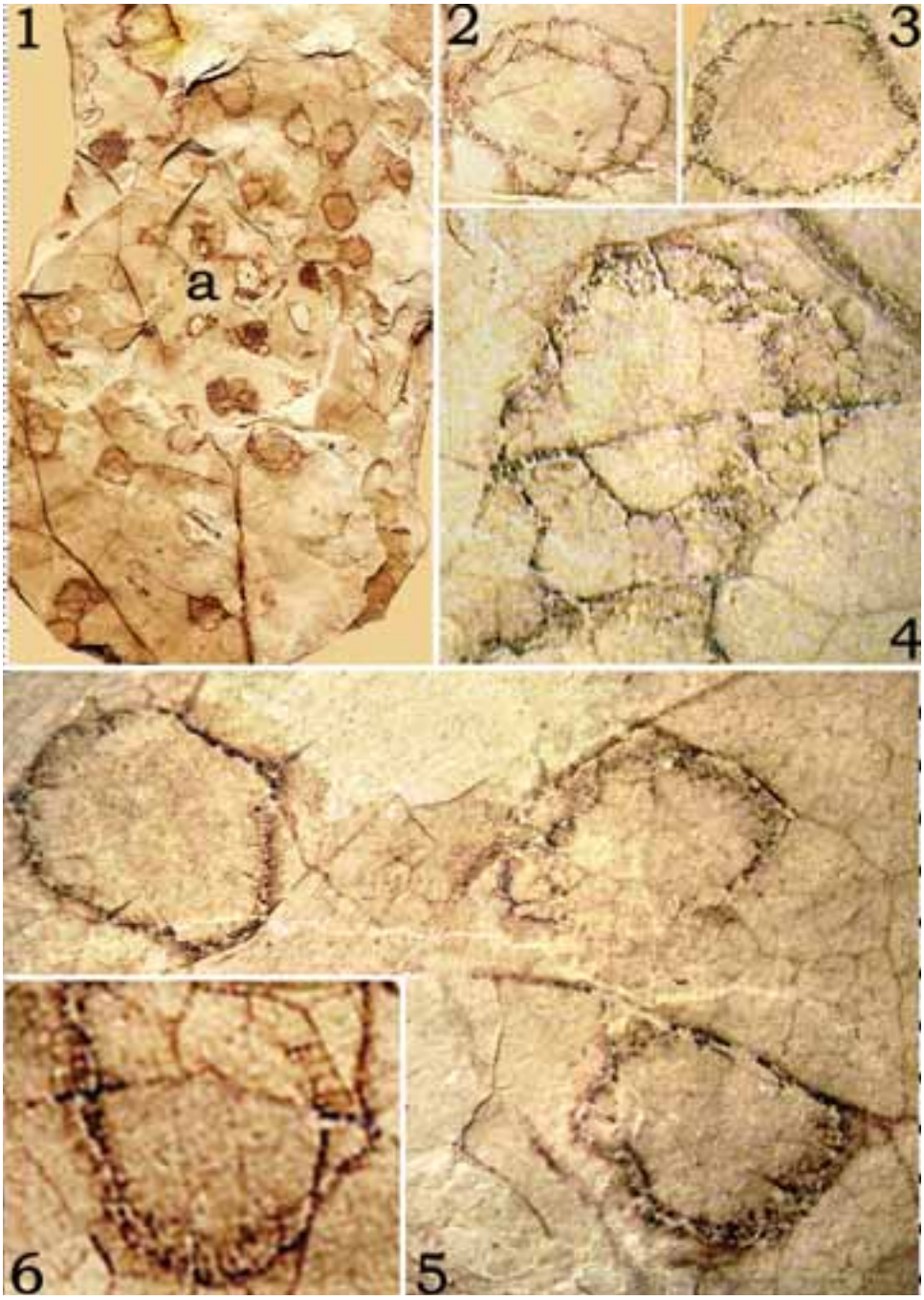

Plate XLVI. *Stomonoma dimorpha* gen. et sp. nov., Gerofit: 1–6, holotype IG1-107, small blotches with leaf pieces cut out in the middle of the leaf (a) and the larger ones over the periphery (2–6), showing spinning marks around the central cell.

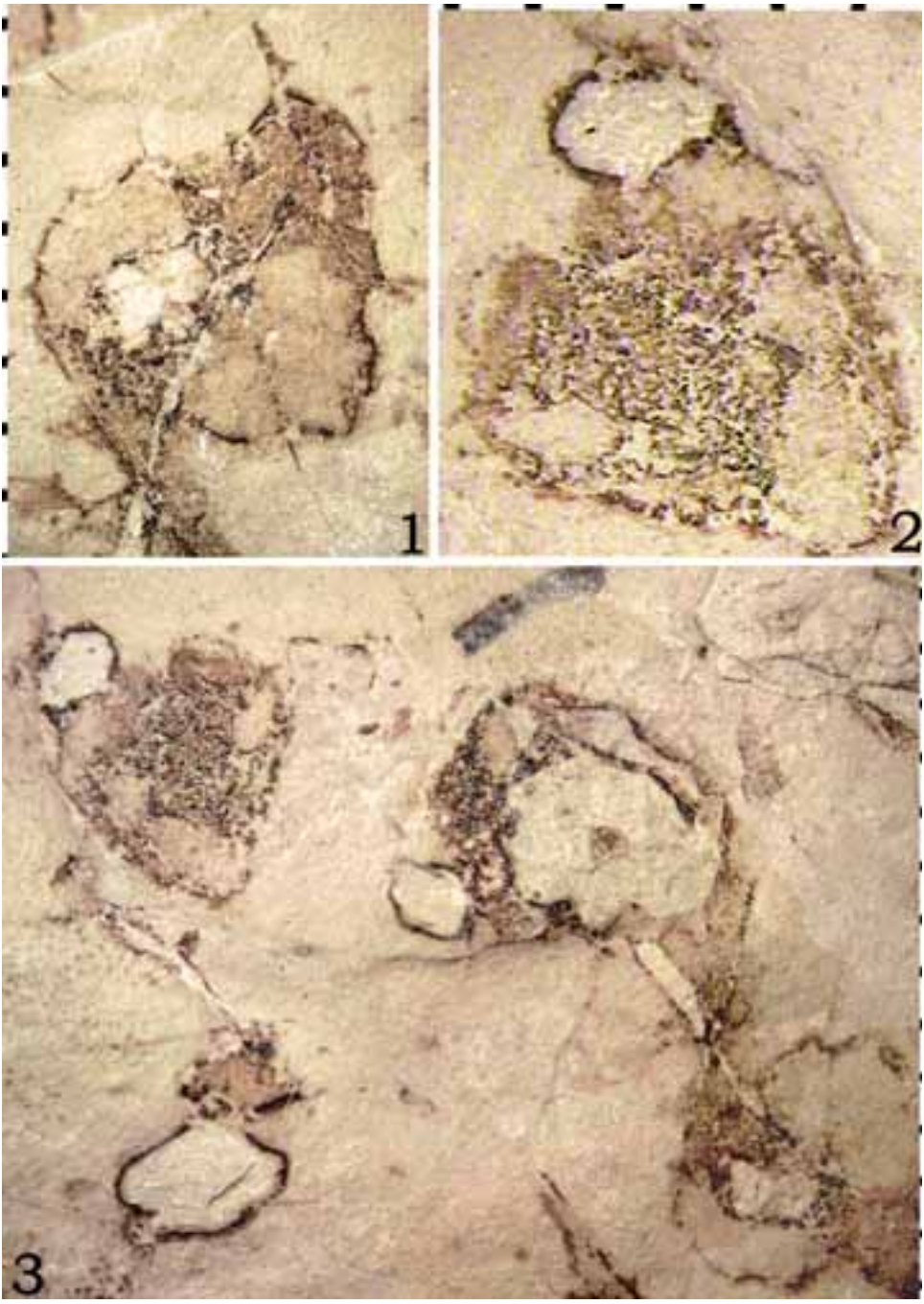

Plate XLVII. *Stomonoma dimorpha* gen. et sp. nov., Gerofit: 1–3, holotype IG1-107, small blotches with leaf pieces cut out for case construction.

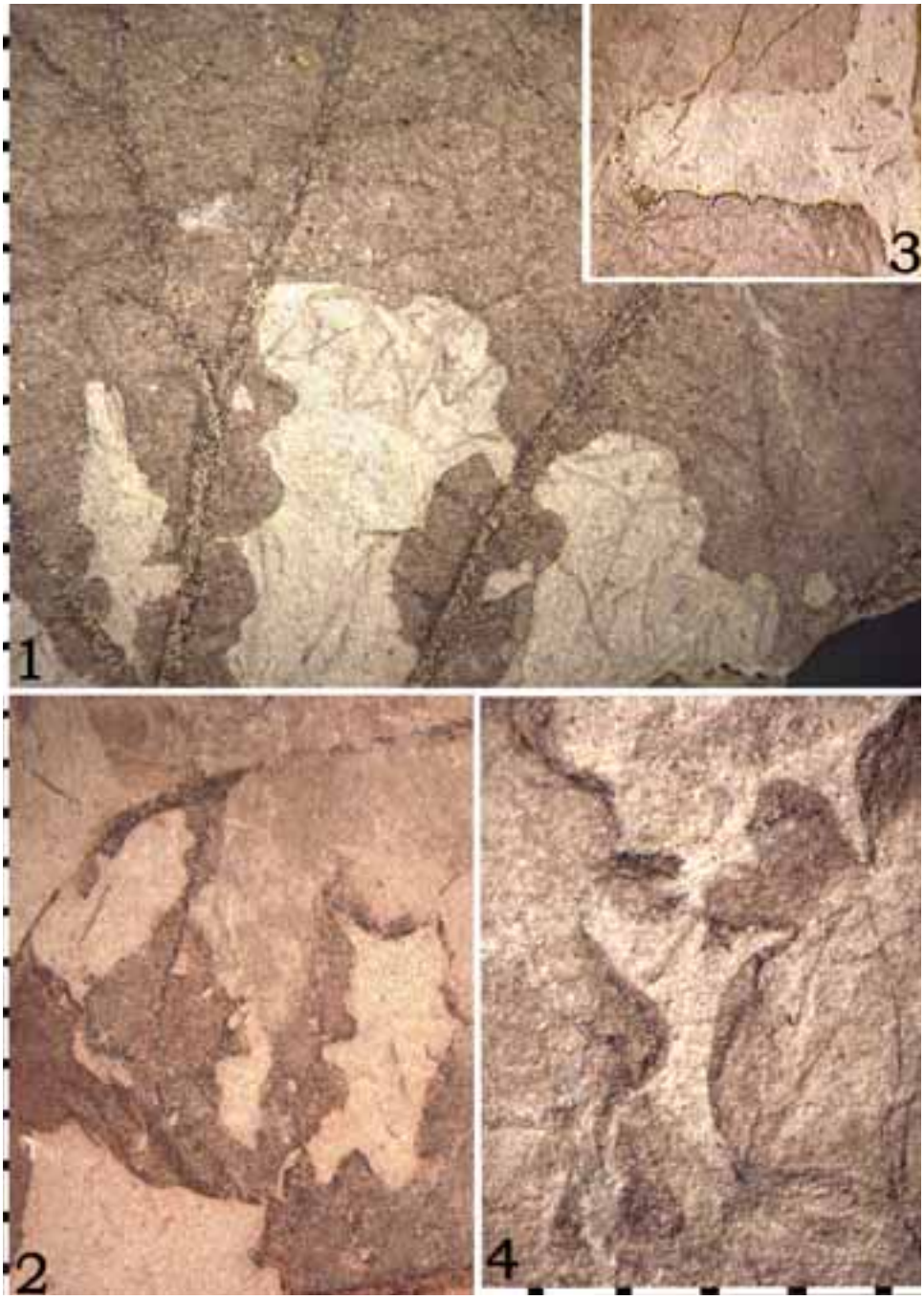

Plate XLVIII. *Stomonoma crenulata* gen. et sp. nov., Gerofit: 1–4, holotype IG1-739 (1), and paratypes IG1-238 (2), IG1-738(3), IG1-1101(4), crenulate cut-outs for case construction.

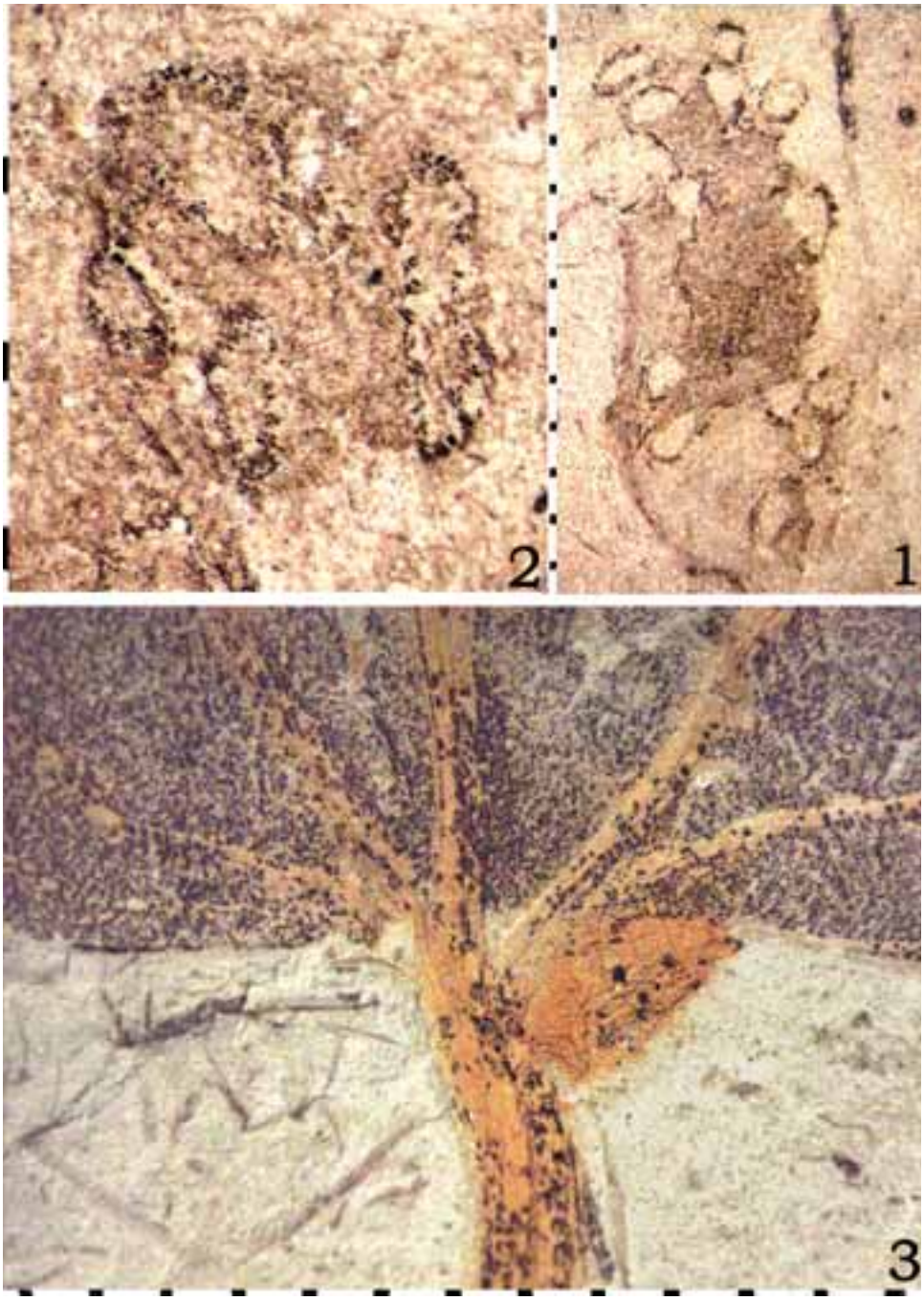

Plate XLIX. *Stomonoma multiforata* gen. et sp. nov., Gerofit: 1, holotype IG1-200, 2, paratype IG1-743, multiple epidermal cut-outs for case construction; *Folicasa inflata* gen. et sp. nov., Gerofit: 3, holotype IG1-444, larval case attached at the base of leaf blade.

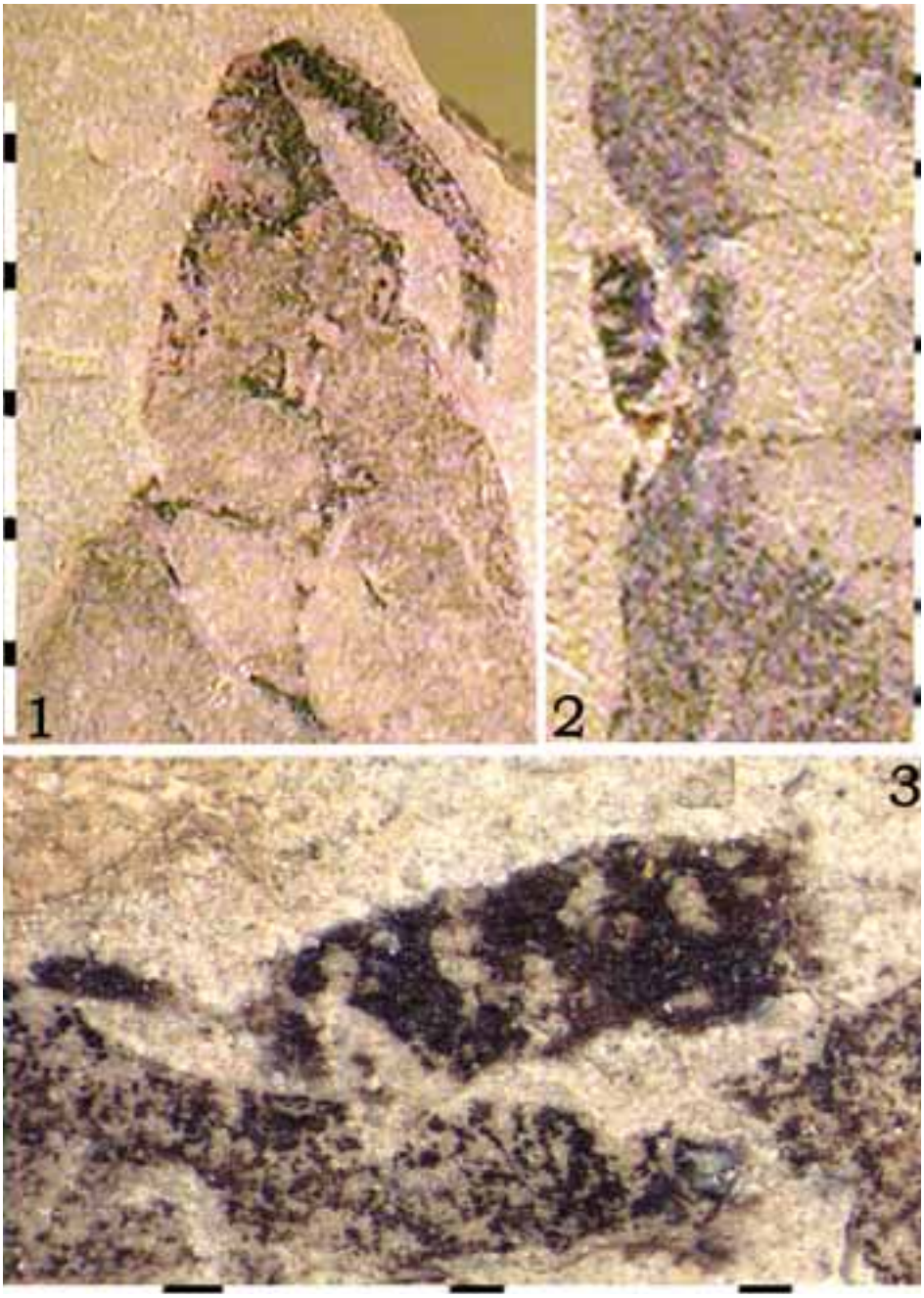

Plate L. *Folicasa tubularis* gen. et sp. nov., Gerofit: 1, holotype IG1-191, larval case attached at the leaf apex; *Folicasa cuspidata* gen. et sp. nov., Gerofit: 3, 4, holotype IG1-109, larval case of cuspate leaf pieces.

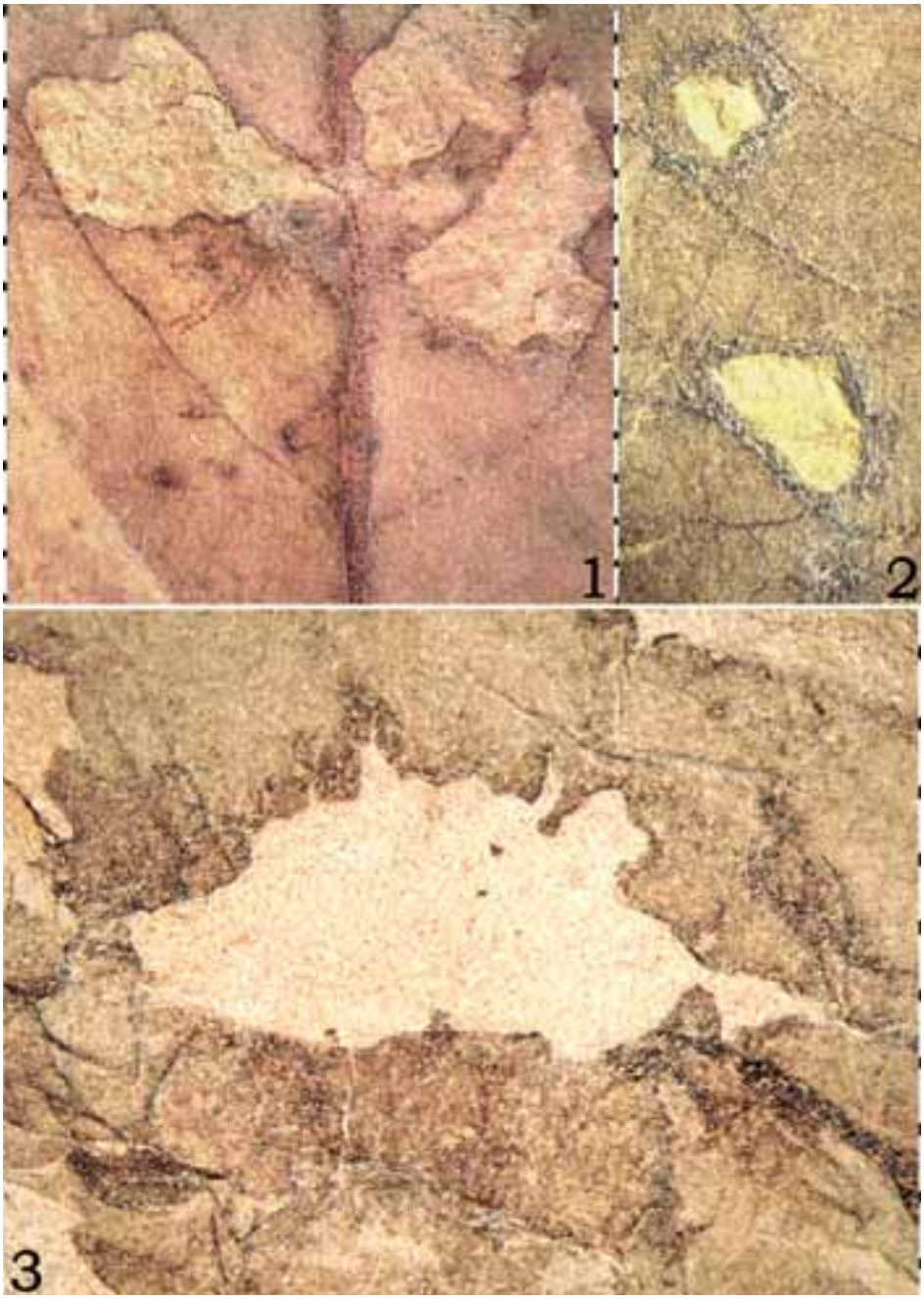

Plate LI. *Stigmatophaga lobata* gen. et sp. nov., Gerofit: 1, paratype IG1-600, lobed – crenulate predation hole on the mine *Asteronoma arachnoides* (Pl. XLIII, fig. 3); 3, holotype IG1-1150, digitate predation hole on the mine *Asteronoma arachnoides*; *Stigmatophaga perforata* gen. et sp. nov., Gerofit: 2, paratype IG1-753, predation holes on the gall *Cephaloneon squamosum*.

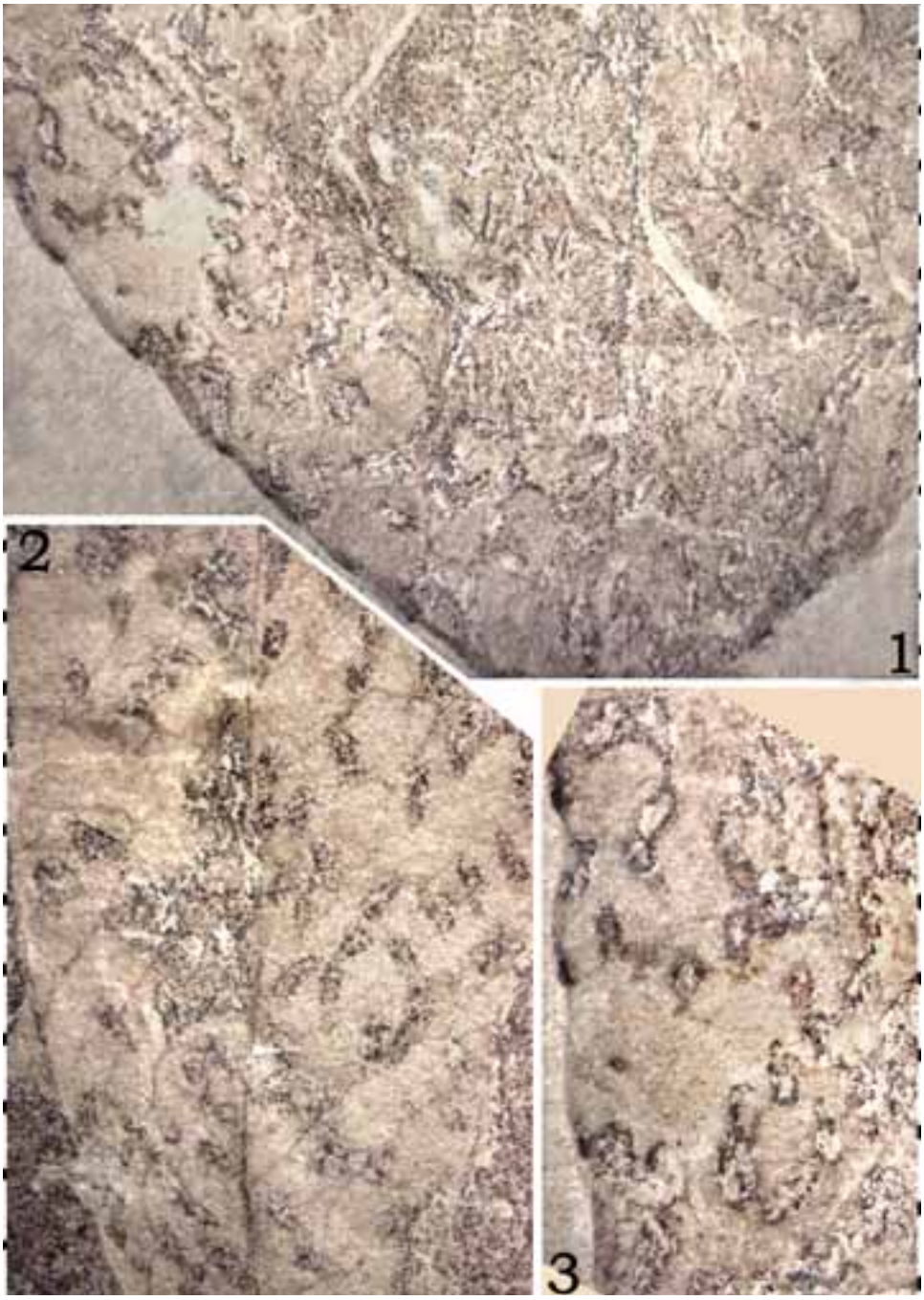

Plate LII. *Stigmatophaga punctata* gen. et sp. nov., Gerofit: 1-3, holotype IG1-192, predation punctures over a winding linear track.

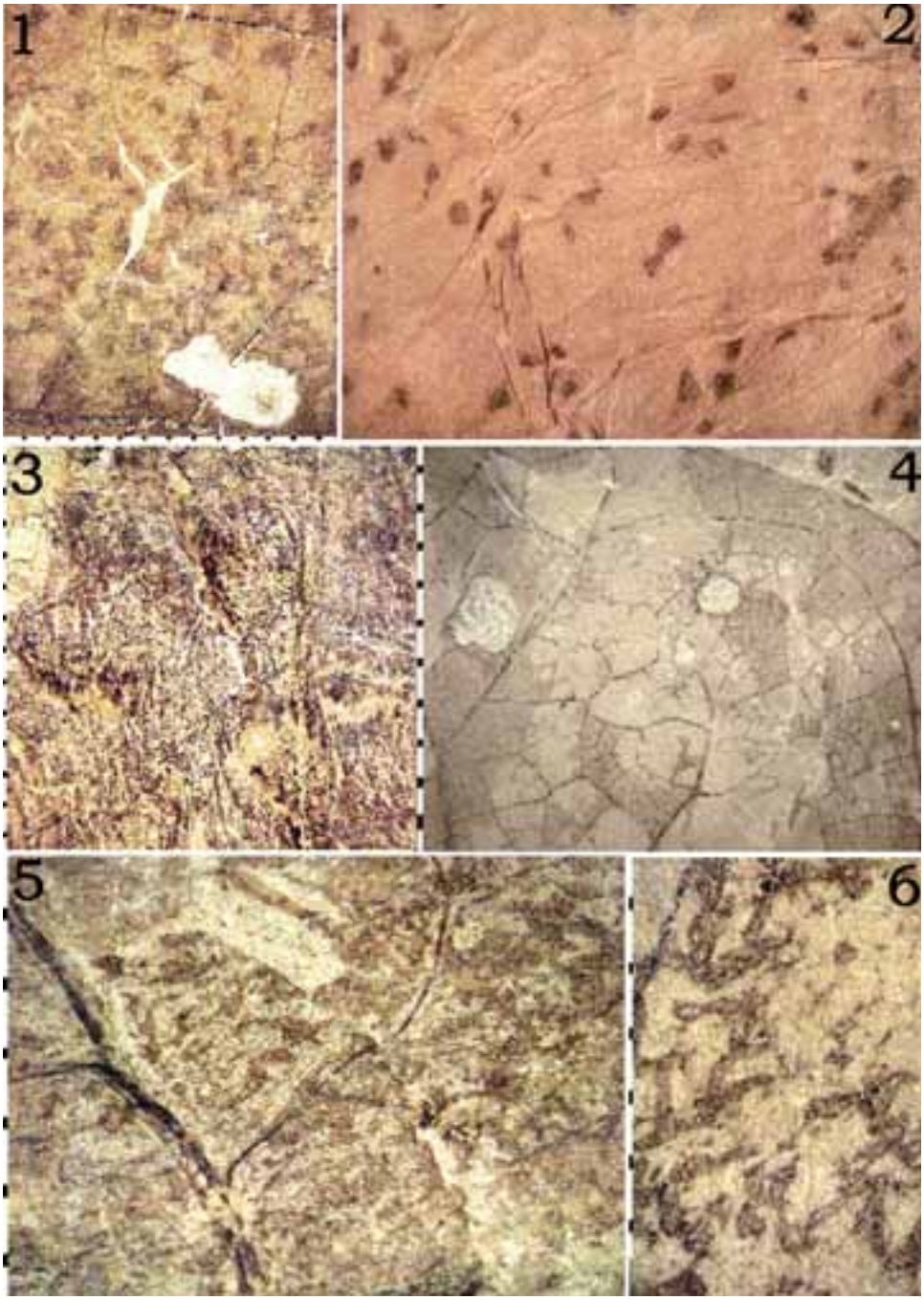

Plate LIII. *Trophoglypha diffusa* gen. et sp. nov., Gerofit: 1, paratype IG1-503, 2, holotype IG1-1122, leaf areas speckled with feeding marks; *Trophoglypha* spp.: 3, striation, IG1-444, 4, feeding holes, IG1-246; 5, 6, branching "hieroglyphic" marks, IG1-600a and IG1-345.

PART II

Fossil Insects in the Cretaceous Mangrove Facies of Southern Negev, Israel

by

L.N. Anisyutkin, V.G. Grachev,
A.G. Ponomarenko,
A.P. Rasnitsyn, P. Vršanský

FOSSIL INSECTS IN THE CRETACEOUS MANGROVE FACIES OF SOUTHERN NEGEV, ISRAEL

by

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1. Introduction

Until very recently, fossil insects were practically unknown in Israel. Before publication by Dobruskina *et al*. (1997), the only insect fossil has been figured in a paper on fossil plants (Lorch, 1965, fig. 13). Dobruskina *et a*l. (1997) have recorded and figured 6 fossil insects and provided species level description of two of them, including the one figured by Lorch (*Samsonileon medievalis* Ponomarenko, 1997, see below). Three more belonging to cockroaches have been later described by Vršanský (2004 b).

The Israel fossils come from two stratigraphic levels identified as the Lower and Upper Cretaceous (Chapter 4). The first assemblage from the Hauterivian - Barremian Tayasir volcanites in Shomron, North Israel, comprises *Cretosperchus medievalis* Ponomarenko, 1997 (Coleoptera: Hydrophilidae), *Gondwablatta abrahami* Vršanský, 2004 (Blattodea: Mesoblattinidae), and a poorly preserved dragonfly nymph (Odonata: Anisoptera).

The main insect assemblage comes from the Ora Formation in southern Negev (South Israel). The findings were made in the Gerofit locality by J. Lorch and his students in early 1960s (antlion *Samsonileon medievalis* Ponomarenko, 1997, Neuroptera: Myrmeleontidae, and cockroach *Turoniblatta israelica* Vršanský, 2004, Mesoblattinidae), followed by I.A. Dobruskina and A.P. Rasnitsyn in 1995 (cockroach *Nehevblattella grofitica* Vršanský, 2004, Blattellidae, an elytron possibly belonging to a diving beetle, Dytiscidae, and an unidentifiable, poorly preserved insect wing). More insects were collected in the Gerofit by V.A. Krassilov, in part jointly with A.P. Rasnitsyn, in 2003-2007, representing a cicad (Cicadellidae: ?Ledrinae indet.), two beetle elytra (*Memptus* sp., Adephaga *incertae sedis*, and Carabidae gen. sp.), a single elytron and three tegmina of roaches, and an ootheca (egg case) of a praying mantis or a roach. These are considered in more detail below. Another insect site Qetura has yielded only two beetle elytras belonging to one more species of *Memptus* and to *Echinocnemus*? sp., Curculionidae (see below).

The insect assemblage of Israel is of special interest in many aspects, such as: (1) Fossil insects are insufficiently known in the Near East and, in particular, of the critical period of their evolution in the Late Cretaceous when the major features of modern terrestrial biota have appeared. Morevover, the earlier information on the Near East insect world revealed an unexpected mixture of Gondwanan and Laurasian elements (Dobruskina et al., 1997).

(2) The plate tectonic reconstructions imply that the northern front of Gondwana (including Israel) approached Laurasia during the mid-Cretaceous. The fossil insect assemblage from Israel may help testifying this hypothesis, shedding light on relations of the northern and southern biotic realms at this time.

(3) Early evolution of the specific mangrove fauna are practically unknown, with a single insect fossil recorded so far from palaeomangal environments (Sukačeva et al. 2006; Vršanský 2007 a). Our study of the Cretaceous insect fauna of Gerofit, where an incipient

mangrove vegetation has been inferred from paleobotanical data (Krassilov *et al*., 2005) bears on this problem as well.

(4) And the most intriguing is the discrepancy between the advanced evolutionary aspect and the geological age of Gerofit assemblage, to be further discussed below.

The material considered is kept at the Paleontological Institute, Russian Academy of Sciences, Moscow (PIN), the Geological Museum, Institute of Earth Science, Hebrew University of Jerusalem (HU), and the Institute of Evolution, University of Haifa (IEUH).

2. Systematic description

Order Hemiptera (= Cimicida)

by A.P. Rasnitsyn

The only hemipteran fossil is found in the Gerofit locality (Pl.1, Fig. 1, 2). Because of its insufficient preservation state, it was very tentatively identified by D.E. Shcherbakov (Paleontological Institute, RAS, Moscow) as Ledrinae, a rather primitive subfamily of the advanced leafhopper family Cicadellidae. Shcherbakov (1992 and pers. com.) indicates the oldest record of Ledrinae as the Aptian (Santana Group of Brazil) and attests the extant Ledrinae as a termophilous group most abundant in the southern continents but entering the northern temperate zone as well, and feeding on tree trunks and branches rather than on leaves as majority of leafhoppers do.

The beetles. Order Coleoptera (= Scarabaeida)

by A.G. Ponomarenko

All beetle fossils encountered in Ora Formation so far represent isolated elytra, two being collected in Qetura locality, and six in Gerofit. Elytra of the post-Jurassic beetles are particularly difficult for identification: they belong to extant families but usually demonstrate deviant morphology. That is why all following considerations should be considered as preliminary.

One of the beetle fossils is the counterpart of right elytron from Gerofit of poor preservation and with part of the elytral base missing. The elytron (Pl. 2, Fig. 1) is 5.05 x 2.25 mm, the disc with 6 sharp impunctate striae meeting apically except for two external striae, adscutellar stria rather long, two adsutural striae roundly, subapically bent out of suture; setigerous pores not apparent. Striation pattern of the elytron is indicative of ground beetles (Carabidae). Similar elytra are known in majority of advanced extant subfamilies making impossible formal description of the fossil. Mesozoic carabid assemblages including the Turonian ones (e.g., Kzyl Zhar in Kazakhstan) lack elytra of this type.

Two other fossils, one from Qetura (Pl. 2, Fig. 2) and another from Gerofit (Pl. 2, Fig. 3-4), are small smooth elytra with all available characters being indicative of the widespread Mesozoic formal genus *Memptus* Handlirsch, 1906. In all cases when *Memptus* elytra were preserved with identifiable body remains, they show characters of the suborder Adephaga and apparently belong to aquatic beetles. Unfortunately in no case these elytra were possible to be associated with a particular beetle family. Specimen from Qetura is more typical for the genus in size (elytral dimension 2.2 x 1.0 mm) and general ap-

pearance but differs from other species in a wider elytron. Specimen from Gerofit is more distinct, with elytra larger (3.9 x 1.2 mm), convex and elongate. Scutellum is also larger than usual in the genus.

One more small (5.4 x 2.2 mm), smooth elytron from Gerofit (Text-fig. 1) considered in Dobruskina et al. (1997: Pl. X, Fig. 2), was questionably attributed by shape of elytra to a diving beetle (Dytiscidae).

The fourth small elytron from Gerofit (Pl. 2, Fig. 5-6) displays characters of the extant genus *Georissus* Latreille, 1809, although it is big comparing the living species (4.7 x 2.1). *Georissus* is now considered to form a monotypic subfamily of the water beetle family Hydrophilidae Latreille, 1802. Numerous extant species of *Georissus* live on muddy coasts of various fresh water bodies. All of them are under 2 mm long. They have two distinct types of elytral morphology: the present fossil displays a somewhat intermediate structure. The present record is the earliest for the genus and subfamily (the family Hydrophilidae is much older starting from the Early Jurassic).

The fifth elytron in the Gerofit locality is very small (2.4 x 1.0 mm), smooth, and with rounded apex (Pl. 3, Fig. 1). It represents few taxonomically important characters and cannot be attributed to a particular taxon; although it is likely belong to a terrestrial beetle.

The second elytron from Qetura (Pl. 3, Fig. 2; Text-fig. 2) and the fifth one from Gerofit (Pl. 3, Fig. 3; Text-fig. 3) belong to the huge family of weevils (Curculionidae) and also represent near-water beetle that most probably developed on helophytic monocot plants. They are considered in more detail below.

Text-fig. 1. Dytiscidae indet., HU 38331, left elytron, Gerofit (x 18) (Dobruskina et al., 1997: Pl. X, Fig. 2)

Thus the most part of beetle fossils found in the Ora Beds belong to aquatic and semi-aquatic beetles, a unique feature of the present fossil assemblage. Similar to an extent are only oryctocenoses in sediments of ancient oxbow lakes in alluvial series of the Siberian coal-bearing Jurassic deposits – the environment that hardly has much in common with that of Qetura and Gerofit. Composition of the present assemblage is unexpected also in that these hydro- and hygrophilous beetles are known as connected to fresh and not salt water characteristic of mangal environment. Noteworthy is that the only insect known from the Slovakian palaeomangal is a caddisfly developing in fresh water as well (Sukačeva et al. 2006).

Besides the weevil elytra, only the georissid-like one can be reliably assigned now. Concerning elytra of diving beetles, two generic names are available applicable to the Mesozoic Dytiscidae, viz. the Jurassic through Early Cretaceous genus *Palaeodytes* Ponomarenko, 1987, and the Turonian *Cretodytes* Ponomarenko, 1977. Unfortunately, elytral morphology is unknown for the latter genus, therefore selection of one of these names is impossible for the present.

Description of the Upper Cretaceous elytra in *Memptus* does not seem logical because all species attributed to this formal genus so far come from older deposits. Almost no beetle genera cross the Early/Late Cretaceous boundary, so a formal genus extending through that boundary would look impractical. That is why these two fossils are left undescribed until more material is accumulated.

A new morphgenus (as defined by Rasnitsyn, 2006) is introduced here for the *Georissus*-like elytron from Gerofit, which differs from numerous living species of *Georissus* only in its bigger size, so a meaningful comparison with these is impossible. For the same reason, *Georissus magnus* Haupt, 1956 from the Middle Eocene of Geiseltal in Germany is transferred to the new genus as well.

Family Hydrophilidae Latreille, 1802
Subfamily Georissinae Castelnau, 1819

Morphogenus *Georissites* Ponomarenko, morphogen. nov.

Name. From genus *Georissus*. Gender masculine.

Type species *Georissites negev* Ponomarenko, sp. nov.

Diagnosis. The formal genus is applicable to isolated fossil beetle elytra which are much convex, almost semiglobular when in pair, about twice as long as wide, with external margin much convex, with at least three external punctate striae starting there. Striae eight in number, bearing large punctures elongate longitudinally.

Species content. Type species and *Georissus magnus* Haupt, 1956 from the Middle Eocene of Geiseltal.

Georissites negev Ponomarenko, sp. nov.
Pl. 2, Fig. 5-6

N a m e. After the Negev Desert (noun in apposition).

H o l o t y p e. PIN 5068/7; isolate right elytron; Gerofit (Pl. 2, Fig. 5-6).

D i a g n o s i s. Differs from the only congener *G. magnus* Haupt, 1956 from the Middle Eocene of Geiseltal, Germany, in having interspaces rib-like and in larger size (*G. magnus* elytron is 2.5 mm long).

D e s c r i p t i o n. Elytron 4.7 mm long, with three external punctate striae starting at outer elytral margin, six striae ending there. External stria one third as long as medial ones. Strial punctures about as long as interstrial space. Interstrial space rib-like elevated, tuberculate. Elytral apex with flattened area.

M a t e r i a l. Holotype.

Family Curculionidae Latreille, 1802

by V.G. Grachev

Subfamily Erirhininae Schoenher, 1825

Genus *Echinocnemus* Schoenher, 1843

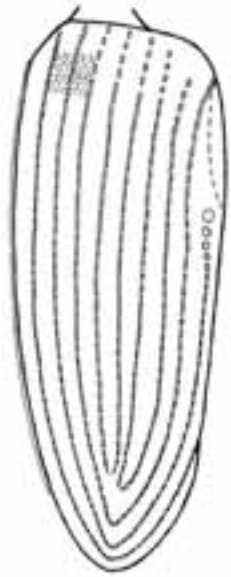
Echinocnemus qetura Grachev, sp. nov.
Text-fig. 2, Pl. 3, Fig. 2

N a m e. After locality Qetura.

H o l o t y p e. PIN 5067/2; right isolated elytron; Qetura (Text-fig. 2, Pl. 3, Fig. 2).

D i a g n o s i s. Differs from the only known other fossil *Echinocnemus* described below in larger size, uniform coloration, narrower internals, and punctured 10th stria.

D e s c r i p t i o n. Elytron 5.1 mm long, 2.0 mm wide, heavily sclerotized, densely covered with round scales, smoothly tapering from midlength to apex, 2.6 times as long as wide, entirely dark as preserved, lacking epipleura and adscutellar stria. Outer margin twisted downward between punctate striae 9 and 10, shoulder boss distinct, both preapical elevation and following depression smooth. Punctate striae thin, 10 in number, with punctures distant at least for their diameter. Intervals flat, weakly convex only beyond subapical knob, all of width subequal and about 3 times as wide as intervals. At elytral apex, stria 1 fusing with 10, 2 with 9, 3 with 8. At preapical knob, stria 4 fusing indistinctly with 5, 6 with 7. Striae 6, 7, and apparently 8 lost at shoulder boss not reaching elytral base. Striae 1-5 reaching elytral base. Stria 9 bearing enlarged punctures from elytral midlength baseward. Laterobasally in elytron, widened apical part of internal fold discernible, being weakly bent and probably long (judging from how the outer elytral margin is twisted down). Locking plate of elytral suture narrow, symmetrical, reaching at least apical quarter of elytron.



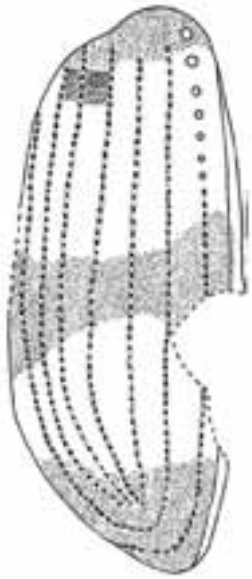
Text-fig. 2. *Echinocnemus qetura* Grachev, sp. nov., PIN 5067/2, right elytron, Qetura, line drawing (x 17).

Comments. The form and general appearance of the elytron are strongly indicative of weevils (Curculionidae), as evidenced by 10 punctate striae, presence of locking plate, and absence of both epipleuron and adscutellar stria. Structure of the internal lateral fold, shortened striae 6-8, character of subapical fusion of striae are all indicative of the subfamily Erirhininae. Dense scale cover is characteristic of the aquatic and semiaquatic Erirhininae and does not contradict to the above attribution of the fossil. The oldest undescribed Erirhininae are found in the Bon Tsagan (Lower Cretaceous, probably Aptian, of Mongolia). *Echinocnemus* is not known as fossil yet.

Comparison to extant Erirhininae has shown that the elytron under description is practically indistinguishable from those in the extant genus *Echinocnemus* Schoenher, 1843. Numerous extant representative of the genus are widespread over the Old World from tropics up to warm temperate regions, and are semiaquatic in habits, feeding on various monocots. Noteworthy is also similarity of the present fossil to some members of the tribes Stenopelmini and Bagoini which belong to the same subfamily and have similar habits. Unfortunately, there are no characters available from the fossil at hand to permit the species level comparison.
Material. Holotype.

Echinocnemus gerofiticus Grachev, sp. nov.
Text-fig. 3, Pl. 3, Fig. 3

Name. After locality Gerofit.
Holotype. PIN 5067/12; right isolated elytron; Gerofit (Text-fig. 3, Pl. 3, Fig. 3).
Diagnosis. Differs from the above species in having elytron of smaller size and with colour pattern, wider intervals, and stria 10 impunctate.



Text-fig. 3. *Echinocnemus gerofit* Grachev, sp. nov., PIN 5068/12, right elytron, Qetura, line drawing (x 20)

D e s c r i p t i o n . Elytron 4.5 mm long, 2.0 mm wide, heavily sclerotized, densely covered with round scales, tile-like overlaying each other, 2.6 times as long as wide, widest at its apical third, with dark base, apex, and medial oblique stripe (can be alternatively described as dark with two large pale spots). Shoulder boss distinct, both preapical elevation and following depression smooth. Punctate striae thin, 10 in number, with punctures distant at least for their diameter. Intervals flat, weakly convex only beyond subapical knob, intervals about 4 times as wide as striae, interwales 6, 7, 8, and 9 wider than others. At elytral apex, stria 1 fusing with 10, 2 with 9, 3 with 8. At preapical knob, stria 4 fusing indistinctly with 5, 6 with 7. Striae 6, 7, and 8 lost at shoulder boss not reaching elytral base. Striae 1-5 reaching elytral base. Stria 9 bearing enlarged punctures from elytral midlength baseward. Stria 10 thinner than others and lacking punctures.

C o m m e n t s . Similarity of the present fossil with *E. qetura* sp. nov. in all important characters justifies its attribution to the same genus.

M a t e r i a l . Holotype.

The antlions etc. Order Neuroptera

by A.G. Ponomarenko

Samsonileon medievalis Ponomarenko, 1997 (Text-fig. 4; Dobruskina et al., 1997: 93, Text-fig. 4, Pl. II, Fig. 1) belongs to the extinct antlion family Paleoleontidae whose typical representatives are known otherwise from near the mid-Cretaceous boundary of Labrador (North

America) and the Cretaceous/Paleogene boundary of Kuznetsk Basin (southern Siberia), while the questionable representatives are collected at various stratigraphic levels of the Lower Cretaceous in the eastern Asia (Transbaikalia, Mongolia) and Brazil (l.c.). Cretaceous antlions were most abundant and diverse in the Gondwana tropic zone (Santana, Brazil), and extant Myrmeleontoidea prefer warmer climate as well. However, the known distribution of Paleoleontidae gives no direct indication of their thermophily.

Cockroaches and mantises. Orders Blattodea (= Blattida) and Mantodea (= Mantida)

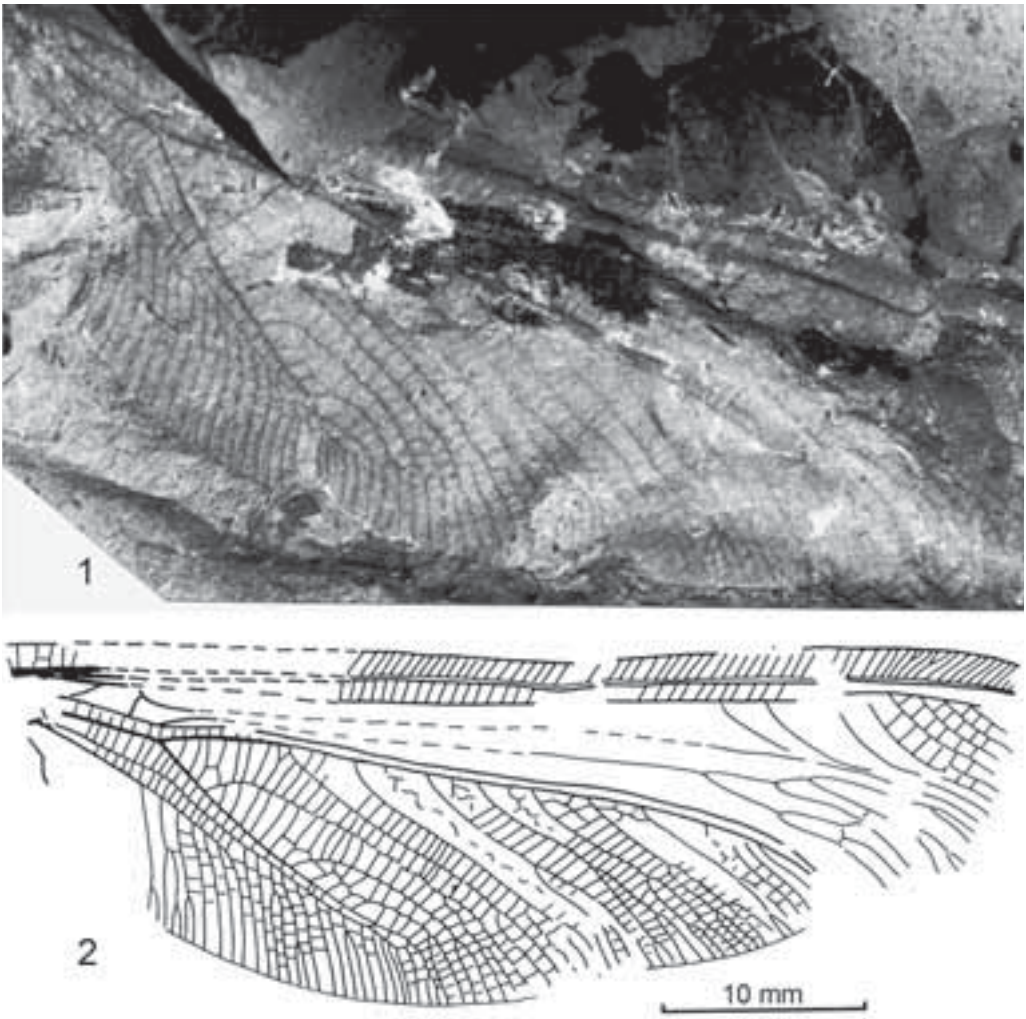
by L.N. Anisyutkin, A.P. Rasnitsyn, P. Vršanský

Cockroaches are found in the locality Gerofit. Two of them are already described (Vršanský, 2004 b).

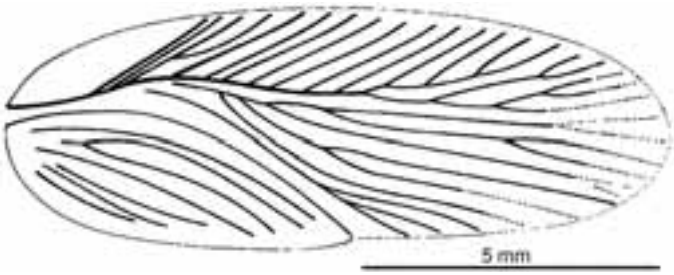
Nehevblattella Vršanský (Vršanský, 2004 b, p. 52) is an indigenous, monotypic genus advanced in the extant family Blattellidae, a widespread group known since the Early Cretaceous and embracing, among others, the common German cockroach. *N. grofitica* Vršanský (Vršanský, 2004 b, p. 52, fig. 2, 7) is known from nowhere but Gerofit yet (Text-fig. 5, Pl. 3, Fig. 4). One of the authors (Vršanský, l. c.) indicated an undescribed genus in the Santana fossil assemblage (the Aptian Crato Member or Formation, Santana Group, in Ceara State of Brazil) as the closest relative of *Nehevblattella*. At the same time, the following features of tegmina as the densely distributed posteriormost branches of R, CuA reduced to terminally branched single vein, and the long clavus are the character unknown in any Mesozoic taxa and closely remind the living genus *Parcoblatta* Hebard, 1917, e. g., the female of *P. pensylvanica* (De Geer, 1773) from the North America. *Parcoblatta* is a rather archaic member of the Blattellidae (although diverged only after *Euphylodromia* Shelford, 1908), but its deep sexual dimorphism is a phylogenetic novelty unknown in the Mesozoic (Vršanský, 2003 a), even though some Palaeozoic roaches were deeply dimorphic.

Another roach in the Gerofit assemblage (Text-fig. 6, Pl. 3, Fig. 5) also represents an indigenous, monotypic genus *Turoniblatta* Vršanský (Vršanský, 2004 b, p. 52). *T. israelica* Vršanský (Vršanský, 2004 b, p. 52, figs. 3, 8) belongs to the Mesoblattinidae s.str. (Vršanský, 2000). This new concept of the family restrict the latter to a few genera close to the previously misinterpreted type of *Mesoblattina* Geinitz, 1880, *M. protypa* Geinitz, 1880; while the vast majority of the former Mesoblattinidae are now considered as Caloblattinidae Vrsansky et Ansorge in Vršanský, 2000 (Vršanský, Ansorge, 2007). Mesoblattinidae *s.str.* is a rather advanced group of Mesozoic cockroaches possibly representing only a subfamily within Blattidae. Like *Nehevblattella*, *T. israelica* displays advanced characters unknown in the Mesozoic and shown by some living roaches, viz. irregular Sc and base of R, expanded R which overlaps the whole apex (probably including much of M, like in males of the above mentioned *Parcoblatta*), and unusually rich CuA.

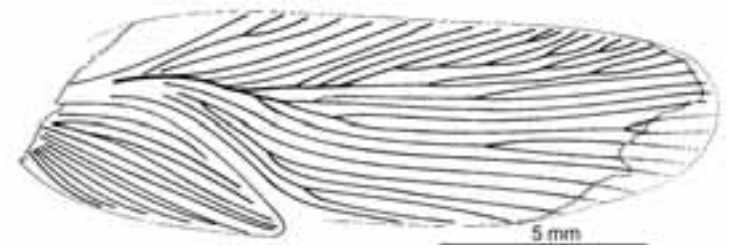
The next four fossils are still less expectable for the Mesozoic deposits, three of them being virtually indistinguishable by wing venation from the extant genera and hardly separable even from some advanced living species.



Text-fig. 4. *Samsonileon medievalis* Ponomarenko, 1997, HU 38330, Gerofit. 1 – holotype, 2 – same, line drawing (x 3.2) (Dobruskina et al., 1997: Pl. X, Fig. 1).



Text-fig. 5. *Nehevblattella grofitica* Vršanský, 2004, HU 38333, Gerofit (Vršanský, P. 2004 b, fig. 7)



Text-fig. 6. *Turoniblatta israelica* Vršanský, 2004, HU 38332, Gerofit (Vršanský, P. 2004 b, fig. 8)

Family Blaberidae Brunner von Wattenwyl, 1865
Subfamily Epilamprinae Brunner von Wattenwyl, 1865

Genus *Paratropes* Serville, 1839

Paratropes fossilis Vršanský et Anisyutkin, sp.nov.
Text-fig. 7, Pl. 4, Fig. 1

N a m e is the Latin for fossil.

H o l o t y p e. PIN 5068/10; isolate right tegmen; Gerofit (Text-fig. 7, Pl. 4, Fig. 1).

D i a g n o s i s. R not fused with M and CuA terminally. Anal venation complete, veins branched. Total number of veins at the margin about 60. Forewing length about 24 mm.

D e s c r i p t i o n. Wing shape with fore and hind margins almost straight except basally, approaching toward obliquely truncated apex. Venation regular. Costal space wide, Sc thick, with comb of branches rounded near base and directed obliquely to wing fore margin, and with one almost straight proximal branch. R free (partially separated from M and Cu), short, differentiated into R1 and RS, with about 25 more or less straight veins at the margin, the basalmost vein richly branched. Free part of M poorly branched, with 6 more or less straight branches; CuA rich, with about 16 veins at margin. Basalmost three branches of CuA separated. CuP sharply curved, reaching about one third of wing. Anal veins present in the whole clavus, A branched, with 11 veins at the margin. Total number of veins at the margin about 60. Forewing length about 24 mm.

C o m p a r i s o n. Except for R not fused with M and CuA which is a strong plesiomorphy (a partial separation of these branches is retained on a single studied exemplar of living *Paratropes* sp. as a subobsolete proximal parts of R, M and CuA), new species is a typical representative of the genus. *Paratropes* is unique within Blattaria in the shape of the forewing which is the widest at the level of distal clavus and with the fore and hind margins near straight, approaching to the obliquely truncated apex; in the wide costal area with Sc branches ascending and rounded basally; and in the last branches of CuA which are separated and running parallel to caudal margin of tegmen (the latter character is less distinct in the present species comparing the living *Paratropes*, that is, probably a plesiomorphy). Characteristic of the genus is also the sharply curved CuP. Except for the above-mentioned difference, the new species

looks similar with living species, e. g., *P. phalerata* Erichson, 1848 from Columbia. Size is essentially the same (tegmen length 24 mm *vs*. 23 mm in *P. phalerata*; cf. Rehn, 1951: fig. 44), but the forewing is probably without coloration. *P. elegans* (Burmeister, 1838) may reach the same size as well, but its venation is insufficiently known.

Comments. The living representatives of the genus are pictured, diurnal, characteristic of tropical forests in the South and Central America.

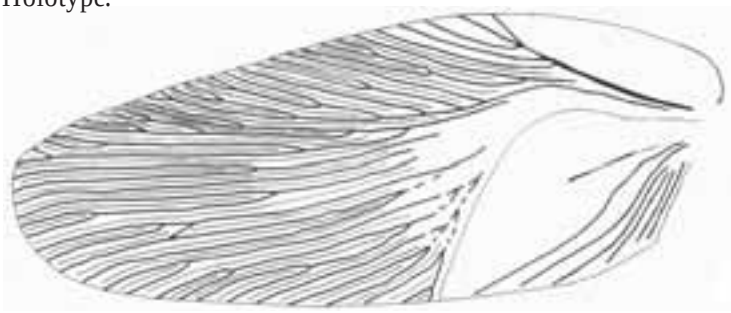
Paratropes was placed in Epilamprinae by Brunner von Wattenwyl (1865) and Rehn (1951). According to Maekawa et al. (2003), Epilamprinae is one of terminal taxa within Blaberidae which diverged only after Panchlorinae, Blaberinae, Perisphaerinae and also Oxyhaloinae. This appears to happen later in the Tertiary. In contrast, Roth (2003) and Princis (1960, 1967, 1971) have placed *Paratropes* within Nyctiborinae (Blattellidae). A placement of *Paratropes* into the ancestral Blattellidae indicates early diversification of the lineage leading to the genus. Our unpublished observations infer a kind of intermediate decision, viz., the basal position of Epilamprinae within Blaberidae. Moreover, the new species along with some undescribed Blaberidae fossils from the earliest Tertiary (Early Danian) of the Russian Far East show characters otherwise unique of some advanced Mesoblattinidae (similar character of branching, branched, tuberculated A, etc.). According to Vršanský (1997), Mesoblattinidae gave birth to Blattellidae. Therefore, according to this author it is possible that Blaberidae have actually evolved directly from the Mesoblattinidae and not from the Blattellidae. This is supported by the fact that the Blaberidae retain the branched A in tegmina which is lost already in the basalmost Blattellidae (Vršanský, Bolotsky, Bugdaeva, Anisyutkin, in preparation).

Paratropes spp. are apparently diurnal, and are thought to might pollinate certain plants in rainforests of Central America (Perry, 1978). Several species such as *Paratropes lycoides* Serville, 1839 (as well as *Eunyctibora* sp.) mimicks poison beetles of the family Lycidae.

Paratropes is specialized and comparatively advanced genus of the Blaberidae possessing numerous autapomorphies. Blaberidae itself is an advanced group unknown before the Tertiary which appears to evolve very rapidly. Therefore presence of the advanced living genus of the Blaberidae in the Cretaceous is unexpected (also see below).

The fusion of two branches of M with CuA in the new species is a teratological and not taxonomic character, as has been recently demonstrated for the Upper Jurassic cockroaches in Mongolia (Vršanský, 2004 a, 2005).

Material. Holotype.



Text-fig. 7. *Paratropes fossilis* Vršanský et Anisyutkin, sp. nov., PIN 5068/10; Gerofit (x 5.4)

Family Anaplectidae Walker, 1868

Genus *Pseudoplecta* Vršanský et Anisyutkin, gen. nov.

N a m e. Modified from *Anaplecta* and *Prosoplecta* Saussure, 1864, with *pseudo* being the Greek for false. Gender feminine.

T y p e s p e c i e s: *P. krassilovi* Vršanský et Anisyutkin, sp.nov.

S p e c i e s c o n t e n t. Type species.

D i a g n o s i s. Similar to *Areolaria fieberi* Brunner von Wattenwyl, 1865, the type species of genus *Areolaria*, in elongate shape and somewhat reduced venation of elytra (Brunner von Wattenwyl, 1865, Tab. 6, Fig. 27, B), but differs in branched and not sinuate Sc (Sc of *A. fieberi* is long, simple and sinuate, cf. Brunner von Wattenwyl, 1865, Tab. 6, Fig. 27, B). Differs from the living genus *Prosoplecta* Saussure, 1864, and particularly from the type species *P. coccinella* Saussure, 1864, in distinctly elongated elytron and greatly reduced venation (venation is apparent in *P. coccinella*, cf. Shelford, 1912, Pl. 48, Fig. 5). Differs from *Anaplecta lateralis* Burmeister, 1838, the type species of the genus *Anaplecta*, in poorly expressed venation (cf. Brunner von Wattenwyl, 1865, Tab. 1, Fig. 2, A, B).

D e s c r i p t i o n. Beetle-like cockroaches. Elytra (forewings) distinctly elongated and strongly sclerotized, with numerous cup-like structures called bunky, with anterior margin more or less prominent, posterior one nearly straight, with no color pattern preserved. Venation simplified, mostly obsolete; Sc short, secondarily branched, R secondarily branched, M and CuA reduced, with parallel, simple and straight veins (M+CuA together with only about 7 veins).

C o m m e n t s. McKittrick (1964) and Roth (2003) placed Anaplectinae into the Blattellidae (Anaplectinae). However, Anaplectinae sensu McKittrick, 1964 are found polyphyletic, with *Anaplecta* showing the polyphagoid type of male genitalia (Roth, 1996), while *Prosoplecta* (including *Areolaria*) displays the blattellid-type male genitalia (Roth, 1994). A special publication will be addressed to this problem (L. Anisyutkin, P. Vršanský, in preparation).

The new genus displays strong similarity to the Anaplectidae s.str. (the type genus *Anaplecta* Burmeister, 1838), such as elongated elytra with more extensive venation, and characteristic parallel simple straight branches.

The similarity of the terminalia of *Anaplecta* to those of the family Polyphagidae are actually in the concordance with the polyphagoid character of the venation, including the coloration which is virtually characteristic for the Jurassic Liberiblattinidae. In some species of *Anaplecta* this similarity is so apparent (and unusual) that it has been compared, and found (in "*Prosopleca cocareloides*" = *P. coccinelloides*) virtually identical to, the Umenocoleidae – another descentant of the Liberiblattinidae (Vršanský, 2003 b). Thus it appears very probable that Anaplectidae has originated directly from the Liberiblattinidae, or more probably from the early Polyphagidae (similar to *Eucorydia* Hebard, 1929) which probably retained the character of venation and coloration of the Liberiblattinidae such as *L. ihringovae* Vršanský, 2002.

The representatives of apparently related genera *Prosoplecta*, *Areolaria* and *Anaplecta* inhabit wet tropical regions, presumably primary rainforests of New and Old World.

Pseudoplecta krassilovi Vršanský et Anisyutkin, sp. nov.
Text-fig. 8, Pl. 4, Fig. 2-3

N a m e. After Professor Valentine A. Krassilov, collector of the material.

H o l o t y p e. PIN 5068/4; isolate right elytron; Gerofit (Text-fig. 8, Pl. 4, Fig. 2-3).

D e s c r i p t i o n. As for the genus. Elytra (forewings) distinctly elongate with venation simplified - secondarily branched R only with about 8 veins, M and CuA together with only about 7 veins. Forewing length about 13 mm.

M a t e r i a l. Holotype.

Family Polyphagidae Walker, 1868
Subfamily ?Polyphaginae Walker, 1868

Genus *Netherea* Vršanský et Anisyutkin, gen. nov.

N a m e. Genus name *Therea* with the prefix *ne-* (Slavic for *not*). Gender feminine.

T y p e s p e c i e s. *Netherea haatika* Vršanský et Anisyutkin, sp. nov.

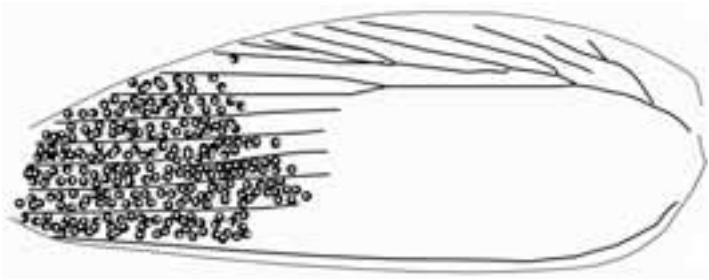
S p e c i e s c o n t e n t. Type species.

D i a g n o s i s. Forewing short and wide, costal space comparatively narrow, with most branches running longitudinally. M almost completely reduced. Intercalaries not visible. Anal veins apparent, branched. Wing apex not acute.

D e s c r i p t i o n. Forewing leathery, short and wide, with the posterior margin straight, anterior margin widening towards the medial part of the wing. Costal space long and narrow, with Sc branched terminally. R and M fused and extremely reduced. M shifted anterior; CuA S-shaped, expanded. CuA and M running parallel near the basis; CuP sharphly curved; A apparent, branched. Intercalaries not visible.

C o m m e n t s. The new genus appears to represent a lineage ancestral to *Therea* Billberg, 1820. Strong synapomorphies include the shape and leathery character of the forewing, with Sc richly branched, M and R reduced and fused, CuA expanded.

Netherea is plesiomorphic, when compared with *T. petiveriana* (Linne, 1758), the type species of *Therea*, and *T. nuptialis* (Gerstacker, 1861) from the Presidency Madras, India, in



Text-fig. 8. *Pseudoplecta krassilovi* Vršanský et Anisyutkin sp. nov., left tegmen, PIN 5068/4, part; Gerofit (x 9.5)

having costal space comparatively narrow and Sc less expanded and with branches running more longitudinally, and in apparent anal veins.

New genus is generally similar also to females of the dimorphic genus *Ergaula* Walker, 1868 in the wing structure, except that *Ergaula* has its wing apex characteristically acute.

Occurrence of a genus closely related to *Therea* in the fossil record supports the suggestion by Rehn (1951) that this branch has diverged from a basalmost branch of the Polyphagidae. This group appears plesiomorphic in respect to the Polyphagini in that females are alate, while the rest Polyphaginae are apomorphic in that they express profound sexual dimorphism, with males having developed tegmina and wings, while females have both shortened or lost. On the other hand, the genus *Therea* is also noticeably specialized, due to greatly sclerotized tegmina with reduction of its venation in most of representatives of the genus.

Representatives of the closely related genus *Therea* are forest species, which hastily hides in the roots when worried (Vidlička, 2001).

After Vršanský (2003 a) has recognised the family rank of the Holocompsidae and excluded Vitisminae from the Polyphagidae, the latter family in the new, restricted sense became an essentially Ceinozoic group, except the present fossil, the only possible Mesozoic record of the family. *Therea* is an early off-shoot of Polyphagidae (Rehn, 1951) *sensu stricto*. The new species assumes a basal position in respect to the genus *Therea*, so this find does not imply much earlier origin of the family and hence does not contradict its comparatively young age.

Unfortunately deep modification of the wing obscures phylogeny of the Polyphagidae and identification of its stem group: the most probable candidate for this appears to be the polyphagoid family Liberiblattinidae with branched Sc and A (unlike Blattellidae with these branches simple even in the oldest representatives and in the advanced Mesoblattinidae that have also simple A).

Liberiblattinidae are rare in the Cretaceous, but their descendants are present both in Laurasia (mantodeans since the Tithonian, Vitisminae since the Kimmeridgian and Euthyrrhaphidae since the Turonian) and Gondwana (the mantodeans since the Aptian).

These inferences together with the origin of the Anaplectidae (represented by *Pseudoplecta* gen. nov.) from the Liberiblattinidae or directly from the Polyphagidae implies that the Liberiblattinidae persisted during the Early and Late Cretaceous or, alternatively, the Polyphagidae originated before that time. The latter hypothesis is less likely because of the basal position of *Therea* within the Polyphagidae.

Netherea haatika Vršanský et Anisyutkin, sp.nov.
Text-fig. 9, Pl. 5, Fig. 1

N a m e. Heb. *haatika*, ancient.

H o l o t y p e. PIN 5068/6; isolate right elytron; Israel, S. Negev, left side of Vadi Gerofit next to its exit to Arava Valley; Ora Formation (Text-fig. 9, Pl. 5, Fig. 1).

D e s c r i p t i o n. Costal space narrow, Sc with 7 veins at the margin; R and M fused and extremely reduced (R with 4, M with only 2 branches). M shifted anterior; CuA S-shaped, expanded - with 8 branches. CuA and M running parallel near the basis; CuP sharphly curved; A apparent, branched. Intercalaries not visible. Forewing length ca. 10 mm.

Text-fig. 9. *Netherea haatika* Vršanský et Anisyutkin, sp. nov., right elytron, PIN 5068/6, Gerofit (x 13)

Comments. The representatives of the sister living genus *Therea* as well as the related (possibly ancestral) genus *Eucorydia* Hebard, 1929 are characterised by yellow spots on the dark blue tegmina and also short antennae characteristic of cryptobiotic cockroaches (e. g., many Panesthiinae). The spots are not apparent at the new fossil species.
Material. Holotype.

Genus *Ergaula* Walker, 1868

Type species: *Corydia carunculigera* Gerstaecker, 1861, living in Phillipines.
Comments. Living representatives of the genus are widely distributed. Besides the type species frequented Phillipines, there are species known from the Cambodia (*E. silphoides* Walker, 1868); Borneo (*E. funebris* Hanitsch, 1933); Myanmar (*E. capucina* Brunner von Wattenwill, 1893); Sumatra, Malacca and Borneo (*E. pilosa* Walker, 1868); Nepal and Myanmar (*E. nepalensis* Saussure, 1893). There are some additional, apparently new species from Thailand in the collection of the Zoological Institute SAS, Bratislava. Particularly distinctive is the wide distribution of *E. capensis* (Saussure, 1893) in Africa, namely in Nigeria, Cameroon, Kongo, Uganda, Kenia, Tanzania, Rhodesia and Angola (possibly a group of species, because such wide distribution is unusual for geophylous cockroaches), which have quite interesting ecology. According to Grandcolas (1997) this species inhabited tree holes or holes in termite nests at the bases of trees in the Gabonese rainforest. Populations are scattered in less than 16% of available treeholes and not very permanent over several years. As a mean, 8.8 nymphs and sometimes one adult female were aggregated and burrowed in the dry dust at the bottom of a cavity. The oothecae were deposited at the same place. Both the density of this species and the nymphal survival were very low. Males seem less sedentary than females, and one observation suggests that couples stay together before females found colonies in cavities.

The living *Ergaula* species display a considerable sexual dimorphism. The fossil descibed below apparently corresponds to the male type, while the females are brachypterous, with reduced hindwings, and notably similar to the fossil described above as *Netherea* gen. nov., except for the acute wing apex. The sexual dimorphism of *Ergaula* can be transitional to the Polyphagini whose females are apterous and the males fully winged.

Like in some other cases, the occurrence of the advanced living genus is anomalous for Cretaceous fauna.

Ergaula atica Vršanský et Anisyutkin, sp. nov.
Pl. 5, Fig. 2

N a m e . Heb. *atica*, ancient.
H o l o t y p e . PIN 5068/11; isolate right male elytron. Ora Formation. South Negev, left side of Vadi Gerofit next to its exit to Arava Valley, Israel (Pl. 5, Fig. 2).
D i a g n o s i s . Forewing fore margin distinctly arcuate, veins long, terminal bifurcations reduced except for Sc, which is rich. Intercalaries distinct. Length/width ca. 35 mm/12 mm.
D e s c r i p t i o n . Forewing transparent, long, with fore margin arcuate. Veins, intercalaries and numerous cross-veins distinct. Coloration as in Pl. 8, Fig. 3. Costal space long and wide, with subcosta branched terminally. R with dense venation, main veins often fused. M closely approximating R, with long, parallel, curved veins. Numerous CuA branches long, slightly curved. CuP sharply curved; A apparent, branched, ending at the anterior margin of CuA or in the posterior margin of the wing. Common vein fusions are present in radial field, where distances between veins are not constant, and in M and CuA with constant distances between veins.
C o m m e n t s . The new species differs from all living congeners only in having more distinct intercalaries (plesiomorphy).

Anterior part of the wing of new species shows vein fusions and varying distances between veins. These features are unknown in the Mesozoic cockroaches in this wing area. In contrast, both vein fusions and varying interveinal distances are characteristic of the anterior wing part of those living cockroaches which show lower flight ability. This is understandable because the anterior wing half is thought to be particularly aerodynamically controlled, so that reduction of the flight function can permit some extent of disorganization of the venation there.

General comment on Blattodea

Notably, from the six cockroach species in Gerofit, three are represented by very unusual taxa. Living *Paratropes* possess unique form and venation of elytra, and sophistically shaped pronotum; *Pseudoplecta* are beetle-like cockroaches, and all the known relatives of the *Netherea* are cockroaches with short antenna, unusual pronotum and blue-colored with yellow spots.

The roach fossils of Gerofit, like the majority of the other insect fossils including those inferred from many plant damages (see pt I of this book), show affinities mainly to living and not to known Early and Late Cretaceous cockroaches. At the same time, their Turonian age is hardly questionable being testified by ammonites found both in the underlying and overlying marine deposits. We cannot resolve this contradiction and have to leave it to future researches.

Dictyoptera incertae sedis

Trace fossils of an unidentified cockroach or praying mantis

Genus *Oothecichnus* Anisyutkin et Rasnitsyn, ichnogenus nov.

N a m e. A combination of *ootheca*, the Greek for egg case, and *ichnos*, the Greek for trace. Gender masculine.

T y p e g e n u s *O. negevianus* Anisyutkin et Rasnitsyn, ichnosp. nov.

C o m p o s i t i o n: Type species.

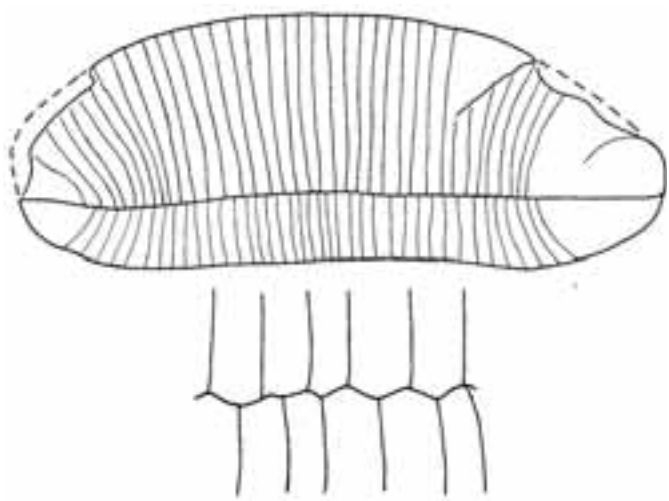
D i a g n o s i s. The new genus is proposed for fossil egg cases (oothecae) of roach-like insects, particularly of cockroaches and praying mantises.

Oothecichnus negevianus Anisyutkin et Rasnitsyn, ichnospecies nov.
Text-fig. 10, Pl. 5, Fig. 3

N a m e. After the Negev Desert.

H o l o t y p e. PIN 5068/9, slightly deformed ootheca; Gerofit (Text-fig. 10, Pl. 5, Fig. 3).

D e s c r i p t i o n. Irregularly elongate oval fossil 11.4 mm long, 4.4 mm wide, with rounded narrow ends, with one longer side (upper one as illustrated) widely rounded and another nearly straight, with longitudinal zigzag suture displaced toward straight side of impression and reaching lateral ends of fossil. Most part of fossil covered with numerous transverse lines more thin than zigzag suture and joining it, in imperfect alternating order from both sides of suture, to form Y-like figures at junctions. Thin lines really transverse over middle one third of fossil length, and increasingly slanting in opposite directions toward ends of fossil. Number of discernible transverse lines differing in different halves of fossils (about 34-36 preserved on convex side and 37-40 on straight one). Narrow ends of fossil roughly symmetrical and apparently crumpled as preserved, with transverse lines turning increasingly obsolete toward apices.



Text-fig. 10. *Oothecichnis negevianus* Anisyutkin et Rasnitsyn, ichnospecies nov., PIN 5068/9, Gerofit: general view (x 10.9) and fragment of the keel and transverse furrows, enlarged

Comments. The fossil could be interpreted as a slightly deformed ootheca of a certain representative of cockroaches or praying mantises. The ootheca was apparently fossilized in oblique dorso-ventral position. Accepting this hypothesis, the longitudinal suture can be interpreted as a weakly developed keel of ootheca, and the transverse lines as a striation of the ootheca surface or reflecting position of eggs inside ootheca.

Three types of oviposition can be distinguished in the superorder Dictyoptera (= Blattidea). The mainly Paleozoic cockroaches of the superfamilies Mylacridoidea, Phyloblattoidea, and a group of families related to the Mesozoic Caloblattidae, Blattulidae and Umenocoleidae (each probably deserving a superfamily rank) had long (medium-sized in Umenocoleidae and Blattulidae) external ovipositor and laid their eggs directly into substrate, that is with no ootheca (Vršanský, 1999, 2003 b; Anisyutkin, Gorochov, 2005).

The mantises, termites and the modern type roaches possess reduced, even if external, ovipositor and a primitive ootheca, that is the eggs aggregation covered with secretions of accessory glands of female (Vršanský, 1999, 2003 b; Anisyutkin, Gorochov, 2005). Origin of the primitive ootheca could be connected with transition to phytophylous habits (Gorochov, 2001, Anisyutkin, Gorochov, 2005). This type of ootheca is formed outside of the female abdomen using the shortened, but outer ovipositor. This type of oviposition is characteristic of mantises and some extinct cockroaches. It was suggested to consider cockroaches with such type of ovipositor as superfamily (or infraorder) Raphidiomimoidea (Gorochov, 2001; Anisyutkin, Gorochov, 2005). According to Nalepa and Lenz (2000), the synapomorphy of more specialized cockroaches and termites is an advanced type of ootheca. The ootheca of advanced type is formed within female abdomen, in the genital pouch which encloses the reduced ovipositor as an internal organ.

The fossil under description could be rather attributed to mantis type of ootheca for the following reasons. The comparatively weak keel is not a feature of less advanced roaches (Cryptocercidae, Blattidae, Polyphagidae) which have oothecae with well developed keel (Roth, 1968, 1971). Weak keel is common in specialized cockroaches (viviparous Blaberidae, some Blattellidae) like some of those found together with the present fossil. The mantis oothecae are variable in such structures (Shelford, 1909, Beier, 1968). Similarly, the dense transverse striation of ootheca wall is not uncommon in mantises (and, by inference, in primitive roach ootheca) and, as external reflection of numerous narrow eggs enclosed, in advanced Blaberidae and Blattellidae.

The assignment of above described ootheca to a representative of Blaberidae seems less probable because the internally incubated oothecae of blaberid type are usually more elongated, while ones of Blattellidae are relatively short (Roth, 1968). There is little probability for fossilization of blaberid ootheca due to a short time interval between the ootheca extraction from the brood sac of female and hatching of the larvae (although this might not be true for the ancient Blaberidae). The empty ootheca usually is eaten by the larvae directly after hatching. The abortive oothecae are rapidly destroyed after extraction, frequently by the female herself.

3. Conclusion

The insect assemblage of Gerofit, southern Israel, includes only 17 fossils, perhaps not enough for a comprehensive analysis. Nevertheless its composition shows some features of general interest.

Eleven insect families are recognized in the assemblage, two of them (Palaeoleontidae and Mesoblattinidae) extinct, and nine (Cicadellidae, Carabidae, Dytiscidae, Hydrophilidae, Curculionidae, Blaberidae, Polyphagidae, Blattellidae, and Anaplectidae) extant.

Taxonomic composition of the assemblage is strikingly unusual. The majority of the cockroaches found in the Ora Formation are highly advanced. They include at least two living genera (*Paratropes* and *Ergaula*) and some structures hitherto unknown in the Mesozoic roaches, hence being of a Cenozoic rather than Cretaceous aspect. The extant beetle genus *Echinocnemus*, and *Georissites negev* sp. nov. closest to *G. major* from the Eocene of Geiseltal, comply with this conclusion, as well as the ground beetle (Carabidae) of advanced (Cenozoic) affinities. In contrast, the antlion and one of cockroaches (*Turoniblatta israelica*) belong to extinct families of unambiguous Cretaceous affinities, although the latter shows similarity also with extant blattellid genus *Parcoblatta*.

The study of plant damages also revealed a number of structures characteristic of modern insect groups (Pt. I). The very abundance of the phyllostigmas is particularly characteristic of at least some Turonian deposits (e.g., Kzyl Zhar in Kazakhstan). However, some of their insect producers are compared by their habits with relatively modern, essentially Cenozoic, groups, such as the higher flies of the families Agromyzidae and Anthomyiidae. Also the revealed predators of the mining insect larvae are enigmatic, because their works most recall those of ants and birds. Ants are known in the Turonian (Dlussky in Rasnitsyn, 1975; Dlussky et al., 2004). However, they are rather archaic and rare there and so could be hardly responsible for the rather high proportion of the operated mines recorded. The passerine birds with sophisticated mine opening behavior are as yet unknown in the Turonian.

Geographic aspect of Gerofit insect assemblage is interesting as well. Few fossils at hand are geographically significant, and the available information is contradictory to an extent. Biogeographic affinities of the only leafhopper is with southern continents (without further specification), *Echinocnemus* weevil – with the Old World, antlion – apparently with northern Asia and both Americas, *Nehevblattella*, *Paratropes* – with South and Central America, *Pseudoplecta* – with the New and Old World tropics, and the descendants of *Netherea* – with India. Surprisingly, none has African affinities, although before Neogene the present day Near East was situated on the northernmost extremity of Africa (cf. Rasnitsyn & Quicke, 2002: figs. 501, 502).

Most of more precisely identified fossils belong to thermophilous (warm temperate to tropical) groups, viz., the Ledrinae leafhopper, the antlion, all roaches and probably a producer of the ootheca (either a praying mantis or a cockroach). At the same time, no exclu-

sively temperate or psychrophilous insects are found. This does not contradict mangrove habitats (there are extratropical mangroves), although no insect groups is presently confined to this type vegetation (ants, bees, mosquitoes, and lampyrid beetles are among the frequently recorded insects in the mangroves, cf. Hoggarth, 1999).

Insect life was very active in the extinct mangroves of Israel, as the abundance of leaf damage witnesses. In contrast, the insect fossils are found to be scanty in spite of rather intense collecting, and apparently include no one guilty of the damage observed. At least in part this results from the taphonomic conditions. All fossils are fragmentary and represented mainly by the most durable body parts – beetle elytra and roach tegmina, elytra and ootheca. The only fossil specimen represented by more than a single fragment is the leafhopper preserved as incomplete fore and hind wings buried about a centimeter apart. The only less durable fossils are the antlion wing and the leafhopper hind wing. In spite of undoubted abundance of the aphids and nematoceran Diptera in the source biota, as implied by the plant damages (pt. I), not a single of their delicate fossils is preserved. This indicates a taphonomically aggressive environment which prevents fossilization of less durable insect fossils. Insect corps might be dismembered, and their less durable parts destroyed either mechanically (by wave action), or biologically (providing quick decomposition and fragmentation of insect corpses). However, this hypothesis is limited in its explanatory power, for neither high energy of water, nor particularly intense biodegradation agents look consistent with the perfect preservation state of plant fossils both in Gerofit and Qetura localities. The observation that only mangrove leaves are perfectly preserved, which are known to possess resistance to excessive salt content (Pt. I), gives no complete explanation as well, because the insect fossils in marine deposits are not uncommon to display perfect preservation state. The only plausible alternative is action of a very specific biodegradation agent that would selectively prevent insect and not plant burial. Very hypothetically, it might be supposed, that mangal waters in contrast to fresh and non-mangal salt ones might be poor in bacteria which degrade the hydrophobous epicuticula of the insect corps and so open them way under the water surface toward the burial site (see Zherikhin, 2002, for details). This purely *ad hoc* hypothesis has no evidence thus far, but at least it is open for falsification, and hopefully it is not the only possible explanation of the puzzle observed. Evidently more research is necessary to resolve this contradiction.

Abundance of aquatic and subaquatic beetles, which are not known to be particularly adherent to salt water, is easier to explain. The belt of mangrove is normally fringed landward with marshes, ponds, and other freshwater-reach environments, and crossed with canals bringing freshwater at least at the low tide. These streams could easily bring dismembered and reworked insect corps to the burial sites in the mangal in precisely that state that we can see now in the material at hand, as well as in the case of the Slovakian mangal (Sukačeva et al., 2006). However, this raises another question: the contemporary mangal biotopes are rich in a variety of insects including those armed with durable skeleton such as beetles, wasps, bees, ants, and cockroaches (Hoggarth, 1999). Ants and bees were rare at best during the Cretaceous, but this was not the case of wasps, and yet not a single of them is found fossilised there. Comparatively many cockroach fossils are found in the Ora Beds, but we have no idea if any

of them was a mangal dweller: nothing is currently known about specifity of the roach fauna of mangroves (Hoggarth, 1999). There are many non-aquatic beetles that are common in mangals, including Chrysomelidae which were not very rare in the Late Cretaceous (the more so in Cenozoic) and yet completely absent from the assemblage at hand. Again, the observations suggest absence of the mangal resident insects from the assemblage at hand which might consist entirely of the allochthonous insects frequented farther landward environments.

The above considerations make us possible to conclude finally that the insect fossil assemblage of the Ora Formation, however small, is strikingly unusual and contradictory in its taxonomical, ecological and geographical composition. This utter originality is the only feature of the assemblage that stands in parallel with the equally original plant assemblage which is unique due to evidence of the oldest known angiosperm mangroves (Pt. I).

4. Acknowledgements

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PLATES

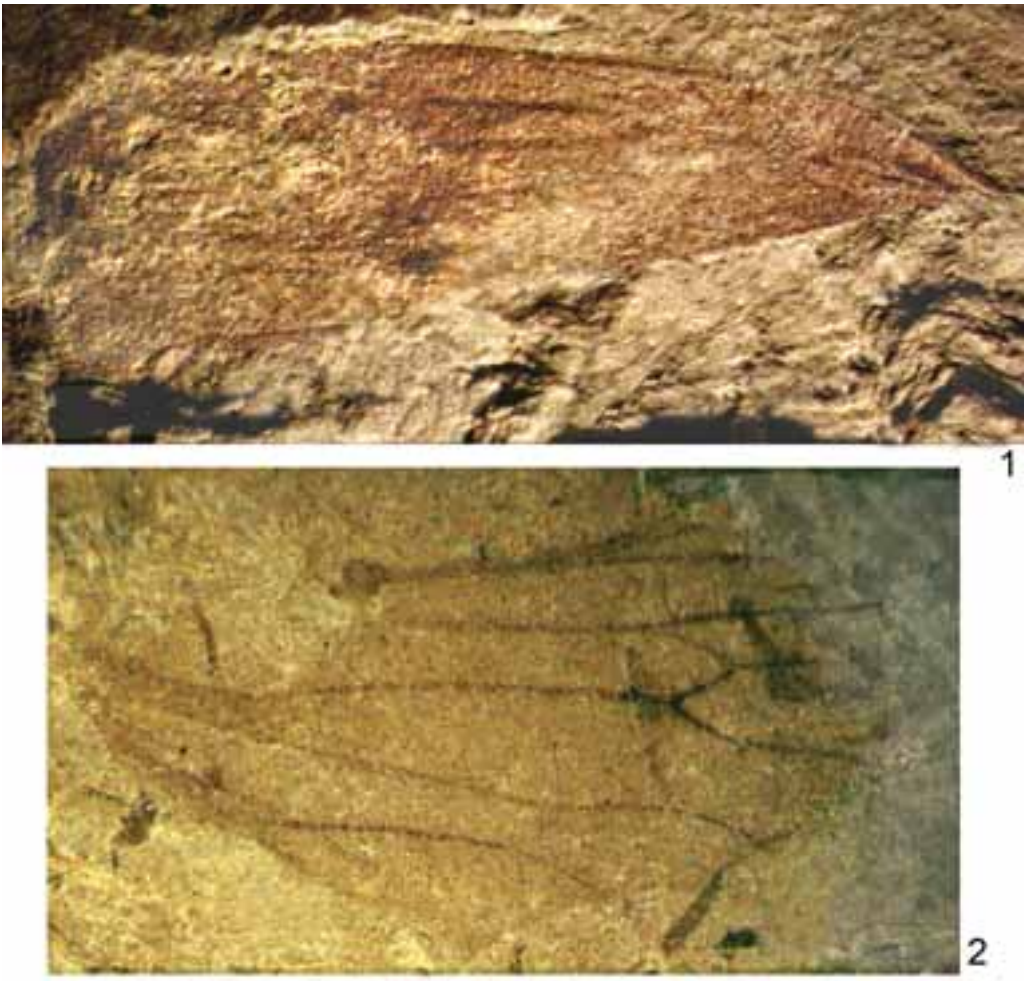

Plate 1. Fig. 1. Cicadellidae: Ledrinae? indet., PIN 5068/8, fore wing, Gerofit (x 8.5); Fig. 2. Same, hind wing.

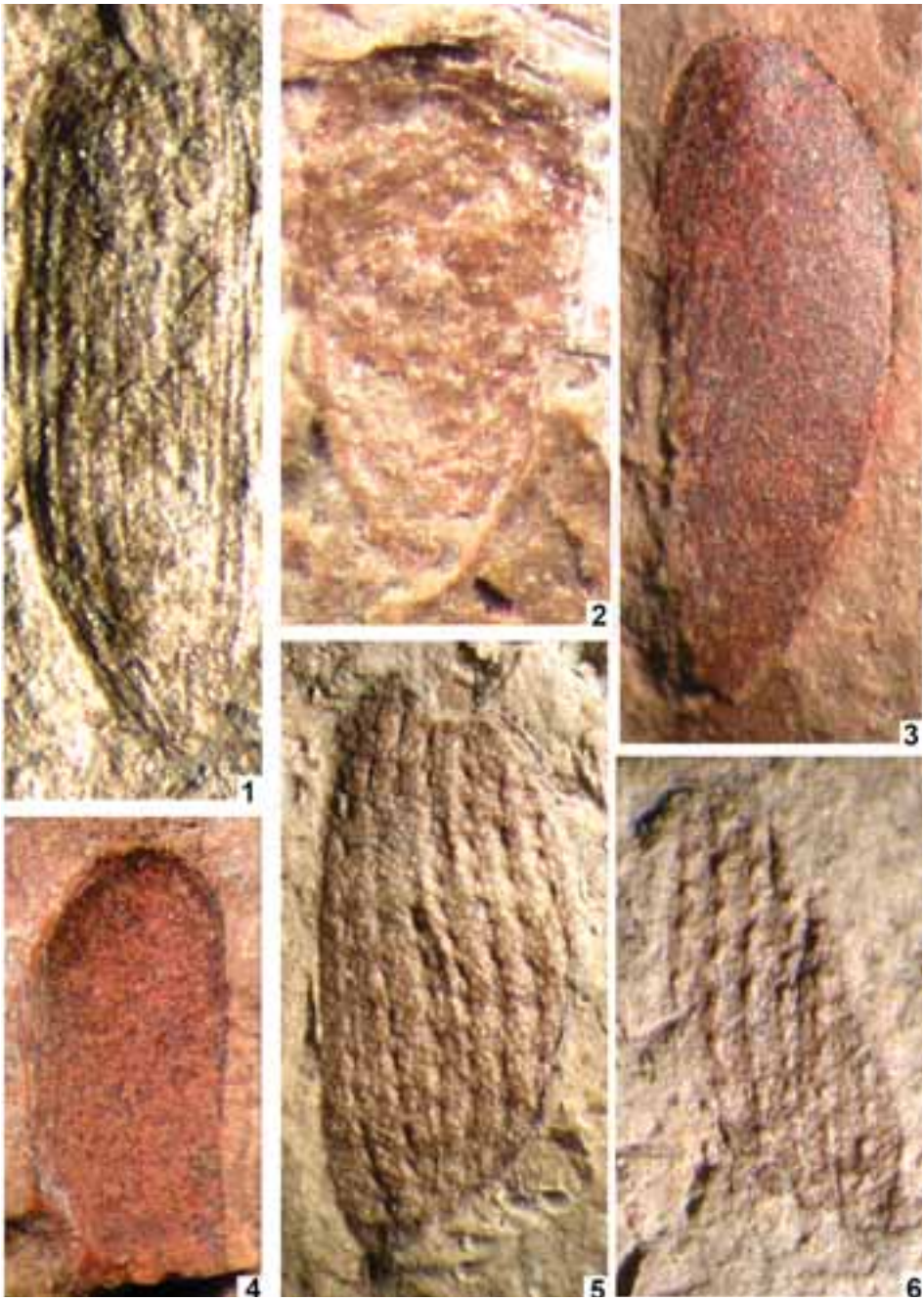

Plate 2. Fig. 1. Carabidae indet., IEUH 101-1311, right elytron, Gerofit, (x 21); Fig. 2. *Memptus* sp. 1, PIN 5067/1, right elytron, Qetura (x 40); Fig. 3. *Memptus* sp. 2, PIN 5068/5, right elytron, part; Gerofit (x 30); Fig. 4. Same, counterpart; Fig. 5. *Georyssites negev* sp. nov., PIN 5068/7, right elytron, part and counterpart; Gerofit (x 18); Fig. 6. Same, counterpart

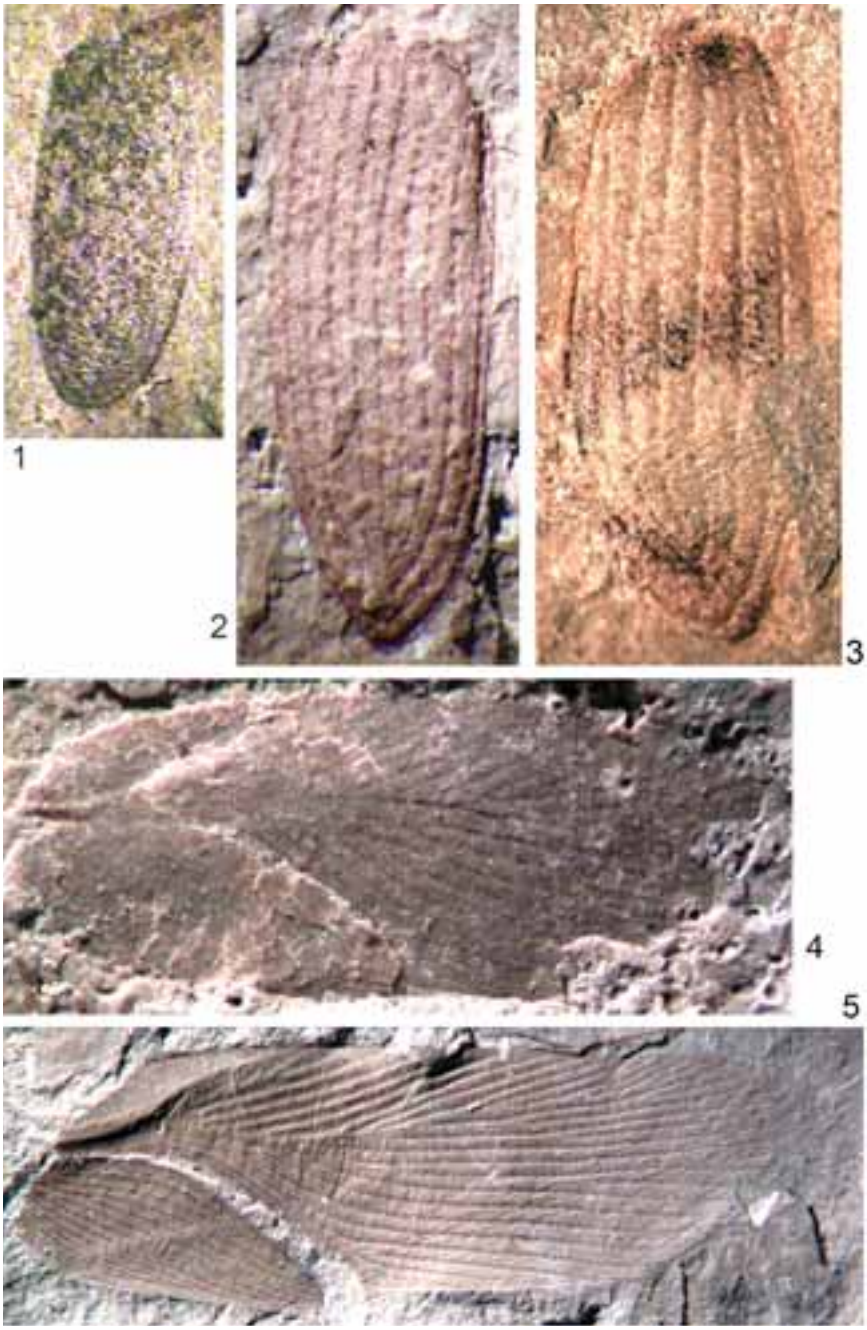

Plate 3. Fig. 1. Unidentified terrestrial beetle, IEUH 161-284C, left elytron, Gerofit (x 21); Fig. 2. *Echinocnemus qetura* Grachev, sp. nov., PIN 5067/2, right elytron, Qetura (x 17); Fig. 3. *Echinocnemus gerofit* Grachev, sp. nov., PIN 5068/12, right elytron, Gerofit (x 20); Fig. 4. *Nehevblattella grofitica* Vršanský, 2004, HU 38333, Gerofit (x 11); Fig. 5. *Turoniblatta israelica* Vršanský, 2004, HU 38332, Gerofit (x 7)

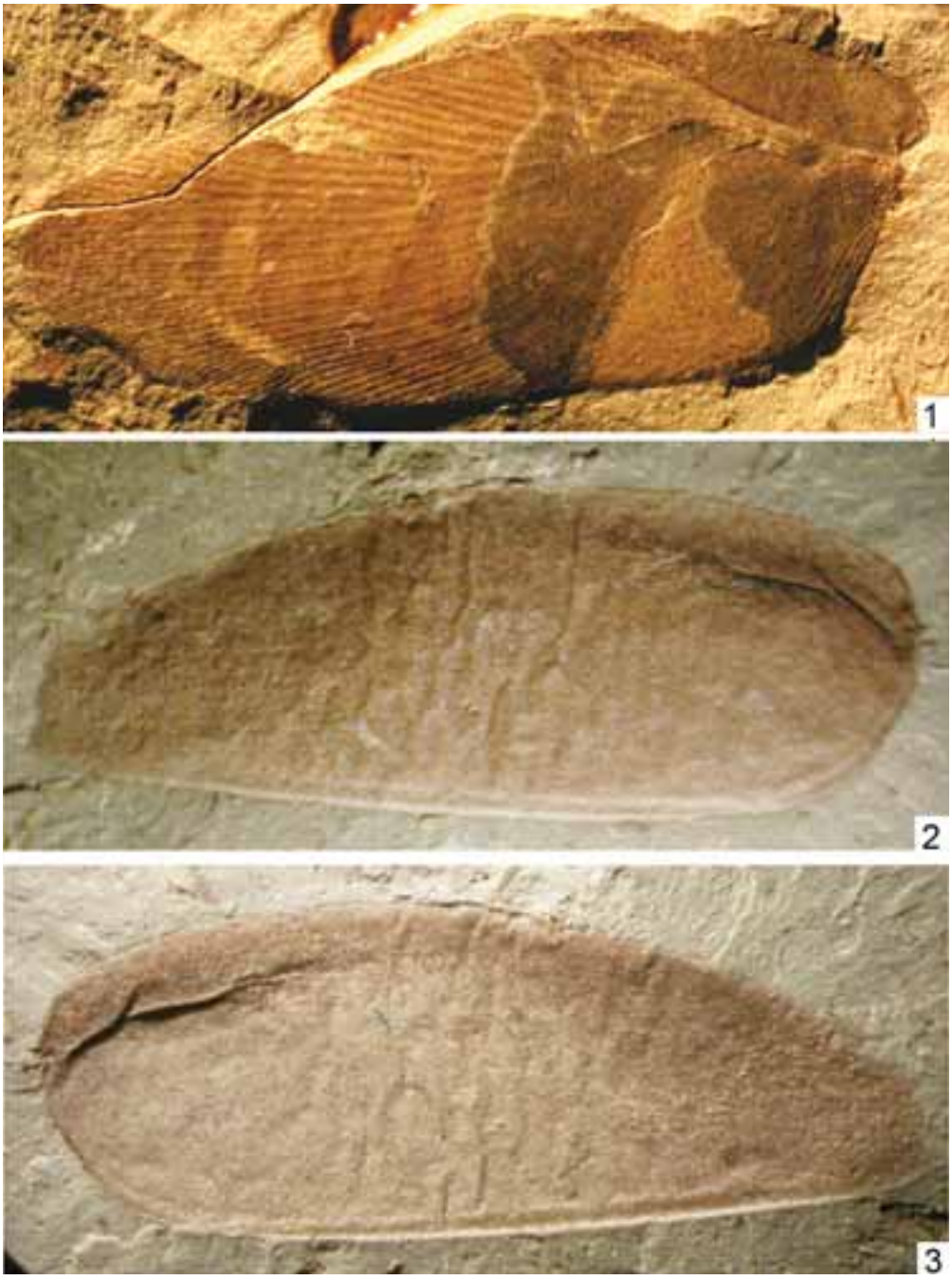

Plate 4. Fig. 1. *Paratropes fossilis* Vršanský et Anisyutkin, sp. nov., PIN 5068/10; Gerofit (x 5.4); Fig. 2. *Pseudoplecta krassilovi* Vršanský et Anisyutkin sp. nov., left tegmen, PIN 5068/4, part; Gerofit (x 9.5); Fig. 3. Same, counterpart.

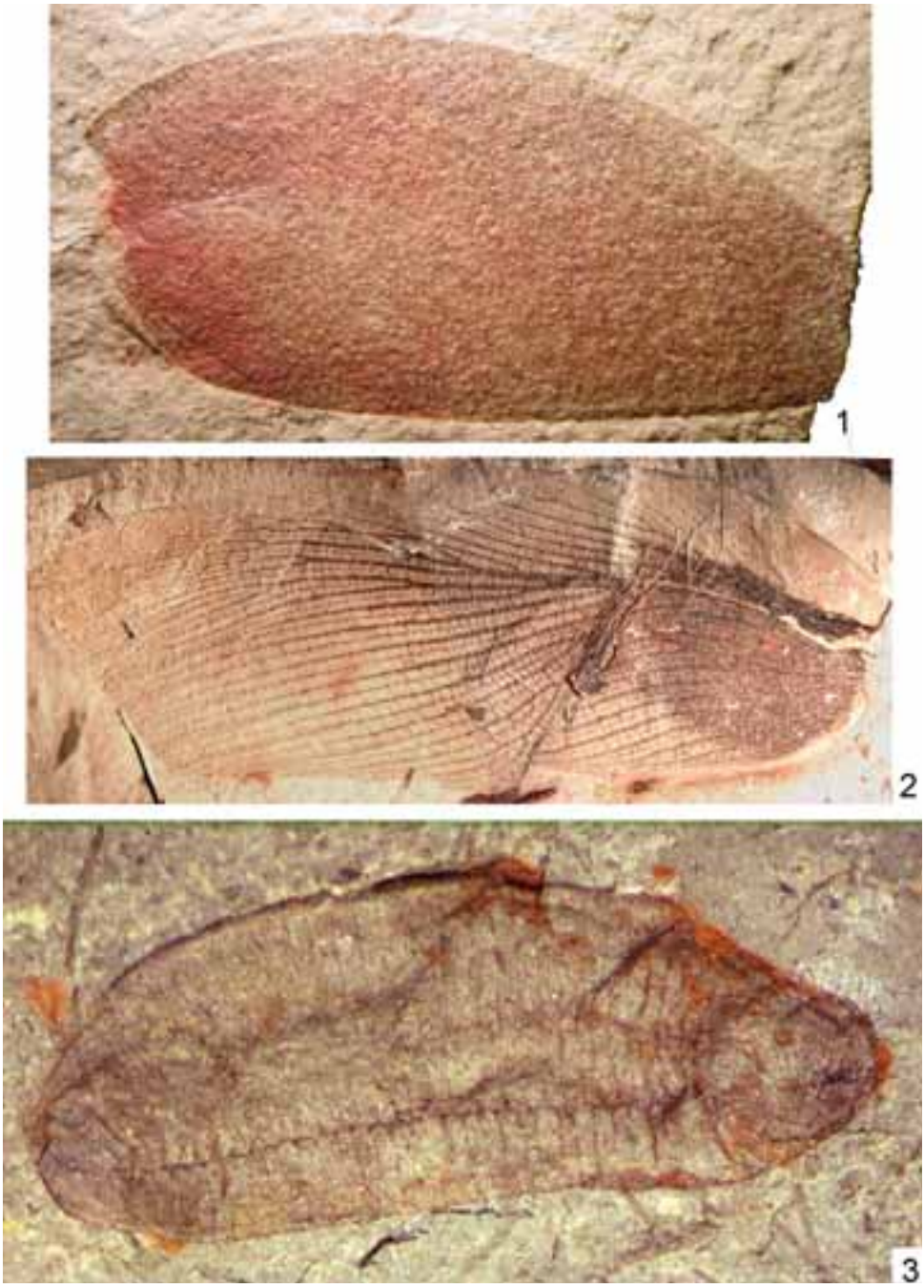

Plate 5. Fig. 1. *Netherea haatika* Vršanský et Anisyutkin, sp. nov., right elytron, PIN 5068/6, Gerofit (x 13); Fig. 2. *Ergaula atica* Vršanský et Anisyutkin, sp. nov., right elytron, PIN 5068/11, Gerofit (x 3.6); Fig. 3. *Oothecichnis negevianus* Anisyutkin et Rasnitsyn, ichnospecies nov., PIN 5068/9, Gerofit (x 10.9)