CADDISFLY PUPAE FROM THE MIOCENE INDUSIAL LIMESTONE OF SAINT-GÉRAND-LE-PUY, FRANCE

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ABSTRACT. Trichoptera pupae are described for the first time in the Indusial Limestone Formation of Saint-Gérand-le-Puy, Allier, France. The caddisfly pupal cases, named *Indusia tubulosa*, constitute this limestone. The relationships of these pupae to extant families are analysed and they are placed in the Limnephilinae. Fossil preservation and palaeoenvironment are discussed.

BOSC(1805) was the first author to mention the Indusial Limestone of Saint-Gérand-le-Puy and to describe the tubes of which it is composed as consisting 'de très-petits hélices fossiles agglutinés, tantôt en masse irrégulière, tantôt en forme de cylindres ouverts par un bout et fermés par l'autre, ou mieux, de cônes creux d'environ un pouce et demi de long sur cinq lignes de diamètre total, et un peu plus d'une ligne d'épaisseur'. He gave them the name of *Indusia tubulosa*, but was not able to establish if they were made by polychaete annelids or by caddisflies (Insecta: Trichoptera). Brongniart (1810) demonstrated the freshwater origin of the limestone and assigned a caddisfly larval origin to the tubes. As the knowledge on extant Trichoptera progressed, Oustalet (1870) classified these cases in the genus *Phryganea*; he even recognized two new species: *P. gerandiana* for the cases from Saint-Gérand and *P. corentiana* for those found in Gergovie (Puy-de-Dôme).

Up to now, no body part of Trichoptera had ever been described from Saint-Gérand, but recently two fossil pupae were found which prove that the tubes are really caddisfly cases. This study presents these new finds and provides evidence for systematic assignment and taphonomy, taking into account that much progress has been made in the taxonomical and biological knowledge of the Trichoptera since the first record.

GEOLOGICAL SETTING

The fossils were found at Le Vendant limestone quarry, Boucé commune, Allier Department, France, which is situated in the Limagne d'Allier basin in the Massif Central.

The Limagne d'Allier cuts a north–south furrow in the Hercynian basement of the Massif Central. The Allier River runs through this basin, which is 180 km long and roughly 35 km wide. Geophysical studies and boreholes demonstrate that, from the Eocene to the beginning of the Miocene, a series of small sedimentary basins, isolated from each other by tectonic or volcanic thresholds, opened from north to south in a plateau area and contained lakes of various sizes. Rapid subsidence led to the deposition of more or less thick sequences of clastic and carbonate sediments (Donsimoni and Giot 1977). Progressive migration from south to north during the Oligocene restricted the upper sequence (Upper Oligocene–Aquitanian) to the Vichy area; here, the fluvio-lacustrine sediments are characterized by the widespread development of stromatolitic limestones, which reached a maximum in the Saint-Gérand-le-Puy area. Algal growths in various shapes and sizes, from small ooliths and pisoliths to large spheroidal and columnar concretions, coalesced to form a limestone reef more than 20 m thick. This limestone often encloses an aggregate of tubes 3 or 4 cm long and 1 cm wide, generally covered by small mollusc shells and bound together by a

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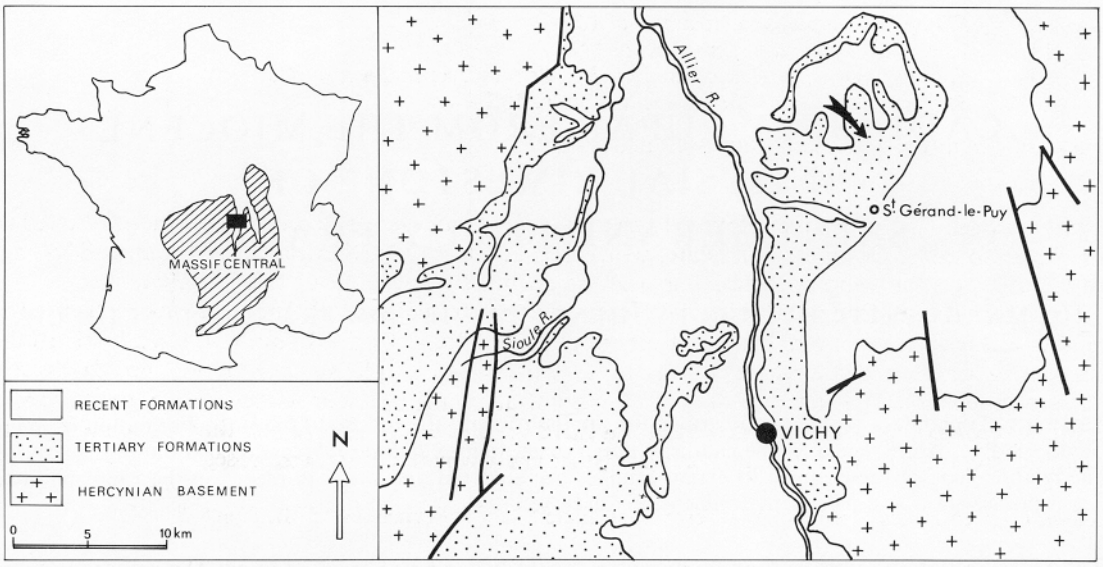


TEXT-FIG. 1. Location map: Le Vendant quarry is indicated by an arrow.

calcareous crust: since the tubes resemble caddis larvae cases, the limestone is known as the 'Calcaire à Phryganes' or the 'Indusial Limestone'.

The oldest bioherms are contemporaneous with the fossil mammal site of Cournon (Puy-de-Dôme), which is dated at about 30 Ma; the youngest correlate with the mammalian fauna of Marcoin (Puy-de-Dôme), which is older than the marine Burdigalian (> 21·9 Ma). Favourable conditions for caddises lasted for 8 million years. Later on, the lake progressively filled and the swamps dried up.

Le Vendant quarry belongs to the quarry group known since 1833 as Saint-Gérand-le-Puy, when Geoffroy-Saint-Hilaire recorded fossil vertebrate-bearing deposits there. These quarries have been exploited for more than 150 years, and the large and small mammals recovered are so numerous and important that these localities have been selected as a reference level for the fossil mammal biozonation of Europe (Mein 1976). They have also yielded an exceptional variety and abundance of fossil bird remains, mostly aquatic forms (Cheneval 1984), and are internationally recognized fossil bird localities, having no equivalent within or outside Europe. Nevertheless, caddisflies have never before been described from there.

SYSTEMATIC PALAEONTOLOGY

Class INSECTA Linnaeus, 1758
Order TRICHOPTERA, Kirby, 1813
Family LIMNEPHILIDAE Kolenati, 1848
Subfamily LIMNEPHILINAE Kolenati, 1859
Genus INDUSIA Bosc, 1805

Indusia tubulosa Bosc, 1805

Plate 1, figs. 1–4; Text-fig. 2A

1805 *Indusia tubulosa* Bosc, pp. 397–400, pl. 7, figs A–E.
1810 *Indusia tubulata* Bosc; Brongniart, p. 357.
1829 *Indusia tubulosa* Bosc; de Serres, p. 208.
1833 *Indusia tubulata*; Geoffroy-Saint-Hilaire, p. 77.

?1871 *Phryganea Gerandiana* Oustalet, p. 102.
?1871 *Phryganea Corentiana* Oustalet, p. 101.
1969 *Indusia tubulosa* de Serres, *non tubulata* Brongniart; Fischer, p. 326.
1973 *Boscindusia tabulata* (*sic*) Bosc; Vialov, p. 586.

Emended diagnosis. See Vialov and Sukatsheva 1976.

Remarks. Bosc (1805) always referred to the fossils as 'Indusie tubuleuse'; the name of the taxon is latinized only in the title of his plate, which is placed much farther on in the volume. This fact led to errors on the valid specific name and the author's attribution of this binomial.

The International Code of Zoological Nomenclature (3rd edition, 1985) makes a clear distinction between the work of an animal (art. 23 f-iii) and its traces (art. 23 g-iii). In our opinion a fossil caddis case corresponds to the work of an animal and is not a trace fossil: normally, trace fossils are features independent of their producers; this is not at all the case for a caddis case, for the larva cannot live without it. So we consider that we have to refer to art. 23 f-iii and that the name *Indusia tubulosa*, created for the cases, is valid for the animals which made these cases.

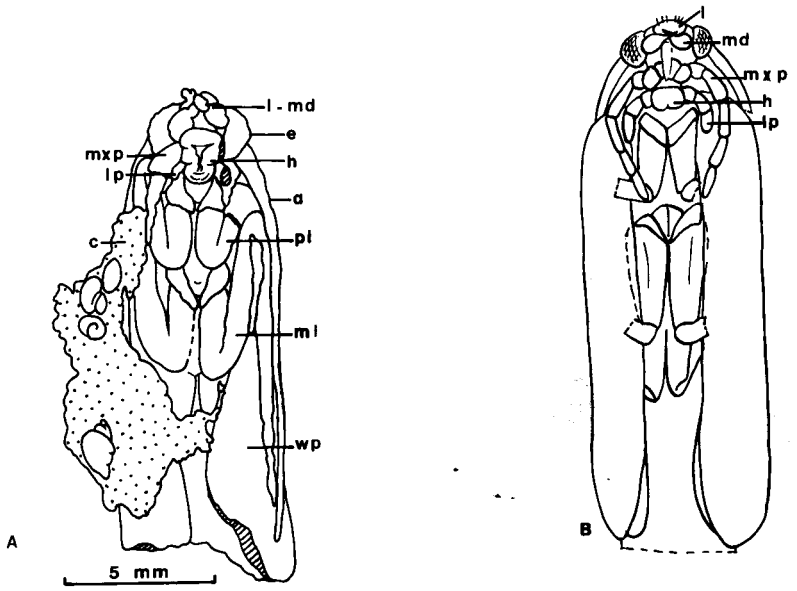
Repository. Centre des Sciences de la Terre, Université Lyon I, France; No. FSL 97698–97701.

Description. One of the two specimens is lying in its case and only its back is exposed. The other is free, but fragments of the case remain attached to it and only the ventral face can be observed clearly.

Head: eyes, antennae, labial and maxillary palpi and haustellum are well preserved. In front of the maxillary palpi, the head shows a bifid structure interpreted as the mandibulae spread out and joined to the labrum. The dimensions and the relative position of the labial and maxillary palpi are characteristic for pupae of the families Phryganeidae or Limnephilidae. Thorax: coxae and femora of the prothoracic legs and coxae of the mesothoracic ones are easily recognizable. The entire left mesothoracic leg, with all its distinct segments, is lying on the wing pad as in Recent Trichoptera pupae. Dorsal face: similar in shape and ornamentation to those of Phryganeidae and Limnephilidae.

Discussion. The pupae and the cases (indusia of the earlier authors) identify this form as a member either of the Phryganeidae or of the Limnephilidae. In these two families there exist genera whose larvae construct large cylindrical cases. In the extant Phryganeidae, the cases are constructed exclusively from plant material arranged in a spiral. The pupae of *Indusia tubulosa* are closer to those of the family Limnephilidae and even to the subfamily Limnephilinae. In the genus *Limnephilus*, the larvae build their cases from more diverse materials: owing to the availability of construction materials and behavioural preferences, they choose vegetable or mineral matter, or mollusc shells, or a mixture of these components. The fossil forms of Saint-Gérand seem to have preferred mollusc shells, ostracod carapaces or ooliths (Donsimoni 1975; Guillot 1979), but we observed also, in some fossil cases, vegetable fragments mixed with mollusc shells exactly as in the extant *Limnephilus*. In the Limnephilinae, different species can build similar cases but, reciprocally, different cases can be built by the larvae of a single species. So it is impossible to determine if the Saint-Gérand Limnephilinae represent one or more species and, without adult specimens, to decide whether the genus *Indusia* is a synonym of the genus *Limnephilus*, the cases of which are very similar to those of *Indusia*.

The author of the taxon *Indusia tubulosa* is Bosc (1805) and not Brongniart (1810) or de Serres (1829) as indicated by Fischer (1969) and Vialov and Sukatsheva (1976). The genus *Indusia* includes several fossil species (often only cases) from the Cretaceous and the Tertiary of Mongolia, Siberia and North America (Fischer 1969, Vialov and Sukatsheva 1976). As far as true Limnephilidae are concerned, the genus name *Phryganea* given by Oustalet (1871) to his new species is not correct, but as different species of Limnephilidae can build similar cases, it is impossible to decide if *I. gerandiana* and *I. corentiana* are synonyms of *I. tubulosa*.



TEXT-FIG. 2. A, *Indusia tubulosa* Bosc, 1805. FSL 97699. Ventral aspect of body. a, antenna; c, case; e, eye; h, haustellum; l-md, mandibulae joined to the labrum; lp, labial palp; ml, mesothoracic leg; mxp, maxillary palp; pl, prothoracic leg; wp, wing pad. The left maxillary and labial palpi and part of the left prothoracic leg are broken. B, *Limnephilus* sp. Ventral aspect of the anterior part of an extant pupa showing especially the masticatory apparatus.

TAPHONOMY AND PALAEOENVIRONMENT

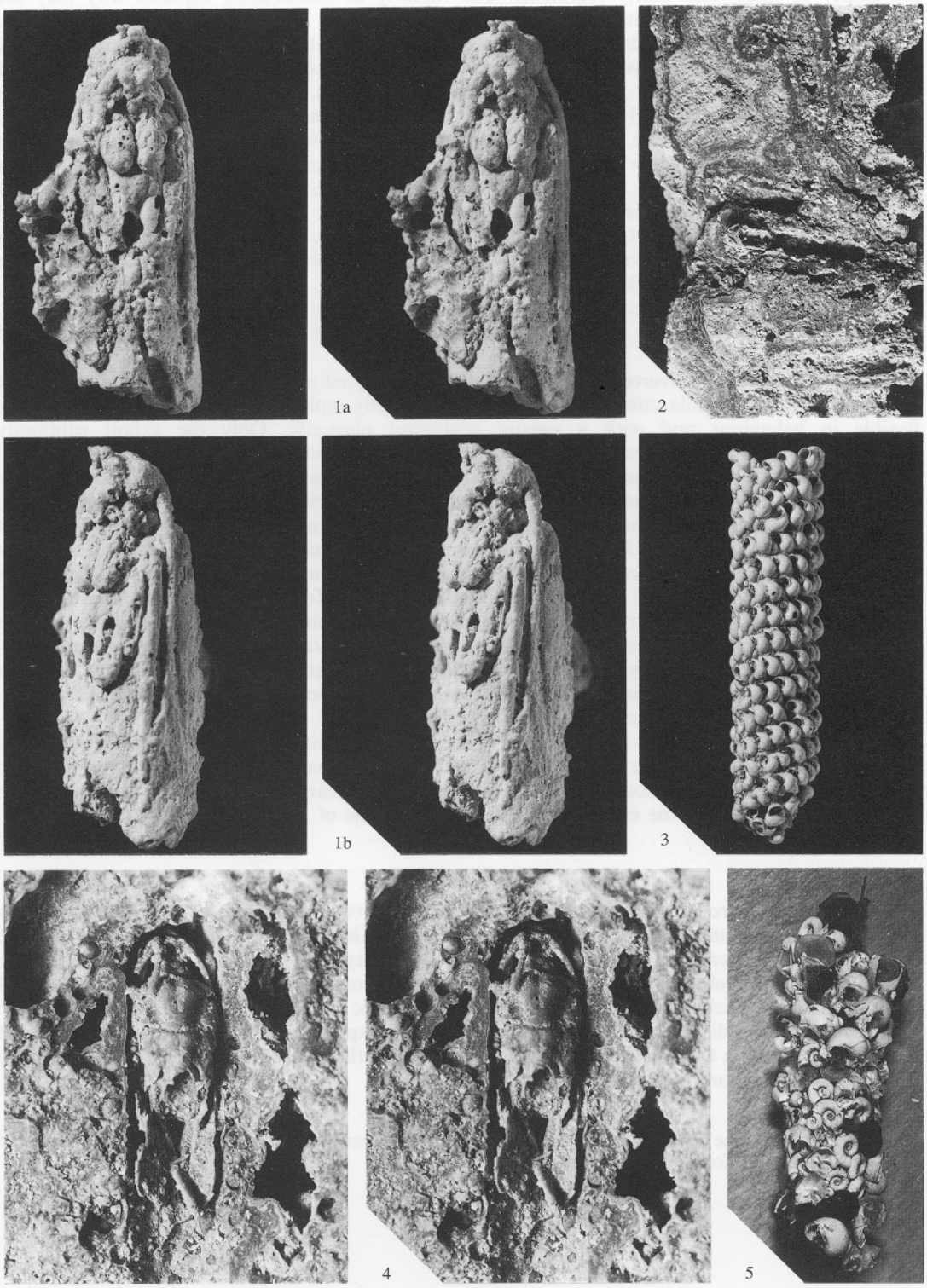
This find of fossil caddis pupae is quite remarkable, considering this stage lasts only about two weeks in the trichopteran life cycle, and how fragile the animals are at that precise moment when the most intensive histolysis of the larval tissues takes place. When natural mortality of the pupa occurs, the dead tissues decay rapidly (in a few days) and only an empty, floppy pupal cuticle remains in the case. Evidently, the caddisflies were encrusted very rapidly, just before emergence, at the precise moment when the tissues became firm; but the tissues themselves are not preserved and the two specimens are natural moulds of external surfaces of the pupae.

On the other hand, since all the cases are the same size, Donsimoni (1975) believed, rightly in our opinion, that they are pupal case concentrations. It is unlikely that these concentrations are due to water currents because, just before the metamorphosis and even in stagnant conditions, the Trichopteran larvae fasten their cases on the substrate (here, rocky substrate or other cases) with silk threads. Under natural conditions, bacterial decay destroys the silk threads that bind the constitutive elements of the cases together in just a few months. In Saint-Gérand, most of the cases

EXPLANATION OF PLATE 1

Figs. 1–4. *Indusia tubulosa* Bosc, 1805. Indusial limestone of Saint-Gérand-le-Puy (Le Vendant quarry), Aquitanian. 1*a*, *b*, FSL 97699, isolated pupa, ×3·6; 1*a*, stereo-pair of ventral side; 1*b*, stereo-pair of lateral side. 2, FSL 97698, section of an indusial bioherm showing the caddisfly tubes, transversely or longitudinally cut, encrusted by repeated algal laminations, ×1. 3, FSL 97700, isolated and non-incrusted tube from another more sandy part of the same quarry; this exceptional tube differs from the others by the helicoidal and regular arrangement of the *Pseudamnicola gerannensis* (Rey, 1974) shells, ×1·6. 4, FSL 97701, pupa preserved in its case, stereo-pair of dorsal side, ×2·5.

Fig. 5. *Limnephilus* sp., extant larval case made from mollusc shells, ×2·2.



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are empty or filled with marly sediments. The rapidity of fossilization explains why they are preserved in such large quantities.

Virtually all the older records of Trichoptera, from Upper Cretaceous to Tertiary (the last partly contemporary with the Indusial Limestone fauna), are based on small adult remains from worldwide amber (Ulmer 1912; Botosaneanu and Wichard 1983), while *Indusia* are large. In amber, the case-makers are generally represented by extant genera of the families Phryganeidae, Calamoceratidae, Molannidae and Sericostomatidae. But the family Limnephilidae has not yet been reported. In Laurentiaux's opinion (1953) families recovered from amber could indicate a tropical or subtropical climate. Even if the lack of Limnephilidae in amber is due more to the adult way of life than to a real absence of the family at that time, we can suppose that the exceptional accumulation of the Limagne Indusial Limestone could be related to the Tertiary climatic changes (in particular progressive cooling). Indeed, whilst tropical or subtropical forms are represented in the rich vertebrate fauna of Saint-Gérand (crocodile, anhinga, secretary bird, parrot, pangolin, tapir), palynology suggests the temperate deciduous forest region (*Ulmus*, *Alnus*, etc.: Gorin 1975). At present the Limnephilinae are characteristic of holarctic temperate or cold habitats (Schmid 1955).

Most of the species recovered from amber, certainly adapted to higher temperatures, must have disappeared from the holarctic region and have been partly replaced by the Limnephilidae, more flexible in behaviour and with a greater ecological plasticity. Only the extant subfamily Limnephilinae includes species able to survive in temporary pools (Wichard and Reichel 1970; Wiggins 1973) due to an imaginal diapause. Moreover, the larvae of some species of this subfamily are the only Trichoptera to occur in brackish water (Sutcliff 1960; Leader 1971; Malicky 1974; Colburn 1983). In Saint-Gérand, skeletal elements of fossil flamingoes (*Phoenicopterus croizeti*, not very different from the extant *Phoenicopterus ruber*) are commonly found, and modern flamingoes are known to exploit food sources available only in brackish water, therefore salinity tolerance is also suggested by Donsimoni (1975) for the fossil *Indusia*. The fossil assemblage of Saint-Gérand, and especially the flamingoes, remind us of the modern community of the brackish Natron Lake in Africa, since one or two million *Phoeniconaias minor* and several thousand *Phoenicopterus ruber roseus* live there. Sedimentary conditions are strikingly similar (Hillaire-Marcel and Casanova 1987) but, as the distributional range of the Limnephilinae does not reach Africa, there is no opportunity for the development of trichopteran bioherms.

Due to the drying up of the lakes, the one or more Limnephilinae species of Saint-Gérand, with most probably a high degree of dependence on particular habitat features (salinity, volcanic particles supply, high algal productivity), have certainly disappeared, and this explains why we have no modern equivalent of the exceptional Indusial Limestone of Limagne.

CONCLUSION

Several taxonomic problems remain to be settled, since the two specimens lack crucial features. As the extant adult Limnephilinae, which show considerable flying ability, leave the aquatic environment just after emergence and return to it only to lay their eggs, it is very unlikely that we would find adult *Indusia* that would permit a more accurate determination; the discovery of prepupae is more likely and should complete the systematic information provided by the pupae.

Nevertheless, this discovery emphasizes the remarkable expansion of a trichopteran family which (certainly in response to Tertiary climatic changes) invaded the whole Northern Hemisphere, where it grew more and more numerous and diversified.

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REFERENCES

BOSC, L. 1805. Note sur un fossile remarquable de la montagne de Saint-Gérand-le-Puy, entre Moulins et Roane, Département de l'Allier, appelé l'Indusie tubuleuse. *Journal des Mines*, **17**, 397–400, pl. 7.

BOTOSANEANU, L. and WICHARD, W. 1983. Upper Cretaceous Siberian and Canadian amber caddisflies (*Insecta*: *Trichoptera*). *Bijdragen tot de Dierkunde*, **53**, 187–217.

BRONGNIART, A. 1810. Sur des terrains qui paraissent avoir été formés sous l'eau douce. *Annales du Muséum d'Histoire naturelle de Paris*, **15**, 357–405.

CHENEVAL, J. 1984. Les oiseaux aquatiques (Gruiformes à Ansériformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France): révision systématique. *Palaeovertebrata*, **14**, 33–115.

COLBURN, E. A. 1983. Effect of elevated temperature on osmotic and ionic regulation in a salt-tolerant caddisfly from Death Valley, California. *Journal of Insect Physiology*, **29**, 363–369.

DONSIMONI, M. 1975. Etude des calcaires concrétionnés lacustres de l'Oligocène supérieur et de l'Aquitanien du bassin de Limagne (Massif Central, France). Thèse 3e cycle (unpublished), Université de Paris VI.

—— and GIOT, D. 1977. Les calcaires concrétionnés lacustres de l'Oligocène supérieur et de l'Aquitanien de Limagne (Massif Central). *Bulletin du Bureau de Recherches géologiques et minières*, **2**, 131–169.

FISCHER, F. C. J. 1969. *Trichopterorum Catalogus. Pars 3. Limnephilidae*, **X**, Nederlandsche entomologische Vereeniging, Amsterdam, 332 pp.

GEOFFROY-SAINT-HILAIRE, E. 1833. Considération sur des ossemens fossiles la plupart inconnus, trouvés et observés dans les bassins d'Auvergne. *Revue encyclopédique*, **59**, 76–95.

GORIN, G. 1975. Etude palynostratigraphique des sédiments paléogènes de la Grande Limagne (Massif Central). *Bulletin du Bureau de Recherches géologiques et minières*, **1**, 147–182.

GUILLOT, L. 1979. Recherches sur les Phryganes de la Limagne tertiaire. *Revue scientifique du Bourbonnais*, 18–31.

HILLAIRE-MARCEL, C. and CASANOVA, J. 1987. Isotopic hydrology and palaeohydrology of the Magadi (Kenya)–Natron (Tanzania) basin during the Late Quaternary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **58**, 155–181.

INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE. 1985. International trust for zoological nomenclature and British Museum (Natural History), London, 338 pp.

KIRBY, W. 1813. Strepsiptera, a new order of insects proposed; and the characters of the order with those of its genera laid down. *Transactions of the Linnean Society of London*, **11**, 86–122.

KOLENATI, F. 1848. *Genera et species Trichopterorum*, **1**, Moscou, 108 pp.

—— 1859. *Genera et species Trichopterorum*, **2**, Moscou, 143–296.

LAURENTIAUX, D. 1953. Classe des Insects. *In* Piveteau, J. (ed.), *Traité de paléontologie*, **III**, 397–527. Masson, Paris, 1063 pp.

LEADER, J. P. 1971. Effect of temperature, salinity, and dissolved oxygen concentration upon respiratory activity of the larva of *Philanisus plebejus* (Trichoptera). *Journal of Insect Physiology*, **17**, 1917–1924.

LINNAEUS, C. 1758. *Systema naturae, sive regna tria naturae systematice proposita per classes, ordinis, genera et species*. I: Regnum animale, 824 pp. Laurentii Salvii, Holmiae.

MALICKY, H. 1974. Eine im marinen Gezeitenbereich lebende europäische Trichopterenlarve. *Archiv für Hydrobiologie*, **73**, 266–269.

MEIN, P. 1976. Biozonation du Néogène méditerranéen à partir des Mammifères. *Proceedings of the VIth Congress of the Regional Committee on Mediterranean Neogene Stratigraphy* (Bratislava 1975), **2**, 18.

OUSTALET, E. 1870. Recherches sur les Insectes fossiles des terrains tertiaires de la France. *Annales des Sciences géologiques*, **II**, 1–178.

SCHMID, F. 1955. *Contribution à l'étude des Limnophilidae* (*Trichoptera*). La Concorde, Lausanne, 245 pp.

SERRES, M. DE 1829. *Géognosie des terrains tertiaires*, Pomathio-Durville, Montpellier and Paris, 277 pp.

SUTCLIFF, D. W. 1960. Observation on the salinity tolerance and habits of a euryhaline caddis larva, *Limnephilus affinis* Curtis (Trichoptera: Limnephilidae). *Proceedings of the Royal Entomological Society of London*, **35**, 156–162.

ULMER, G. 1912. Die Trichopteren des baltischen Bernsteins. *Beiträge zur Naturkunde Preussens*, **10**, 1–380.

VIALOV, O. S. 1973. Classification of fossil larval tubes (Trichoptera). *Academy of Sciences of the Ukrainian Soviet Socialist Republic*, **7**, 585–588. [In Russian].

—— and SUKATSHEVA, I. D. 1976. Fossil caddisfly cases (Insecta, Trichoptera) and their stratigraphical value. In *Paleontology and Biostratigraphy of Mongolia. The Joint Soviet-Mongolian Paleontological Expedition* (*Transactions*). Nauka, Moscow, **3**, 169–232. [In Russian].

WICHARD, W. and REICHEL, H. 1970. Zur Trichopterenfauna periodischer Gewässer; Trichopterenstudien zur Duisburger Sechs-Seen-Platte, II. *Nachrichtenblatt der Bayerischen Entomologen*, **18**, 57–58.

WIGGINS, G. B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary pools. *Life Sciences Contributions of the Royal Ontario Museum*, **88**, 1–28.

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