Ephemera, 1999, Vol. **1** (1) : 61-73

Pseudokageronia thomasi gen. nov., sp. nov. from the Upper Miocene of Murat (France) [Ephemeroptera : Heptageniidae]

by Gérard MASSELOT & André NEL*

Laboratoire d'Entomologie, Muséum National d'Histoire Naturelle, 45, rue Buffon, F-75005 Paris
e-mail: gm@invfrm.org and anel@mnhn.fr
* adresse de correspondance

Keywords : Ephemeroptera, Heptageniidae, *Pseudokageronia thomasi* gen. sp. nov., fossil, Upper Miocene, France, phylogeny, palaeoecology.

We describe a new fossil heptageniid genus and species *Pseudokageronia thomasi* (Upper Miocene, France). It is considered as the sister genus of the Recent group [*Dacnogenia* + (*Heptagenia* + [*Afronurus* + (*Ecdyonurus* + *Electrogena*)])]. The palaeoecological implications of the presence of this Heptageniidae in a diatom palaeolake are discussed.

Nouvel Heptageniidae de l'Eocene supérieur de Murat (France) : *Pseudokageronia thomasi* gen. nov., sp. nov. [Ephemeroptera : Heptageniidae]

Mots clés : Ephemeroptera, Heptageniidae, *Pseudokageronia thomasi* gen. sp. nov., fossile, Miocène supérieur, France, phylogénie, paleoécologie.

Un nouvel Heptageniidae fossile, *Pseudokageronia thomasi*, est décrit du Miocène supérieur français. Il est considéré comme le genre-frère du groupe [*Dacnogenia* + (*Heptagenia* + [*Afronurus* + (*Ecdyonurus* + *Electrogena*)])]. Les implications paléoécologiques de la présence de cet Heptageniidae dans un paléolac à diatomées sont discutées.

1. Introduction

The only known fossil Heptageniidae larvae are *Miocoenogia gorbunovi* TSHERNOVA, 1962 (Oligocene, West Siberia, Russia), *Heptagenia* sp. from the Upper Miocene (Shanwang, Shandong Province, China, ZHANG, 1989), *Succinogenia larssoni* DEMOULIN, 1965 from the Upper Eocene (Baltic amber), and an Heptageniidae gen. et sp. undetermined (Eocene, Klondike Mountain Formation, Republic, Washington State, U.S.A., LEWIS, 1992). The systematic position of *Heptagenia shanwangensis* (HONG, 1983) (Upper Miocene, Shanwang, Shandong Province, China) is rather uncertain. After the original photography of the holotype by HONG (1983), this larva looks like an Ephemerellidae, rather than a Heptageniidae, because of its legs with non-broadened femora. A direct revision of the holotype is necessary to have an accurate familial attribution of this species.

Seven larvae of Heptageniidae (with the body distinctly depressed, the prognathous head, and the eyes and antennae dorsal), one of them being very well preserved (specimen MNHN-LP-R.

55196, figure 1, photo 1), have been collected from diatom deposits in a Late Miocene paleolake near Murat (Massif Central, France). These fossils belong to a new genus and species of a great interest for the knowledge of the palaeocology and palaeobiodiversity of this family.

The outcrop of Faufouilloux near Murat is a lacustrine diatom bed (maar) dated from the Uppermost Miocene (- 5.3 ± 0.3 M.y., ROIRON, 1991). The insect fauna is very rich and diverse and has affinities both with the Palaearctic and Afrotropical Recent faunas (NEL, 1988, 1992, 1996 ; NEL & PAICHELER, 1993 ; NEL, ARILLO & MARTINEZ-DELCLOS, 1996, NEL & JARZEMBOWSKI, 1997 ; MARTINEZ-DELCLOS, PAPIER & OUDARD, 1997 ; NEL, ARILLO & ORTUÑO, 1997). Unlike ROIRON (1991), the aquatic entomofauna is highly diversified, with many Odonata and Ephemeroptera larvae, Megaloptera Sialidae, Heteroptera Notonectidae, Corixidae and Naucoridae.

2. Systematic palaeontology

Family Heptageniidae Needham (in Needham & Betten, 1901)

***Pseudokageronia* gen. nov.**

Etymology

After pseudo and the Recent genus *Kageronia*.

Type species

Pseudokageronia thomasi sp. nov.

Diagnosis.

Larvae : head more or less quadrangular, eye in a postero-dorsal position, posterior margin of the head with a small but distinct median concavity (notch). Lateral margins of the pronotum regularly rounded without latero-posterior expansions. Inner margins of the wingbuds not fused together. Presence of long setae on the distal 2/3 of the hind margin of the femora, the anterior margin being glabrous. Pointed phanerae, not densely disposed on the upper surface of the femora. Tibia glabrous and without phanera, nearly as long as the femora. Tarsi as long as half of the tibias. Posterior margin of the abdominal segments bearing sharp teethes, all similar. Two cerci and a paracercus, without setae. Gills not preserved.

Adults and eggs : unknown.

Pseudokageronia thomasi sp. nov.

Material

Holotype specimen MNHN-LP-R. 55196, a larvae (gut visible). Paratypes specimens MNHN-LP-R. 55197, 55198 and 55199 (exuvial skins). Three more exuvial skins have been recently discovered. Deposited in the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris.

Etymology

After Dr. Alain Thomas, Université Paul Sabatier, Toulouse, a great ephemeropterologist, and a friend.

Stratum typicum and locus typicus. Uppermost Miocene, - 5.3 M.y., outcrop Les Faufouilloux, Sainte-Reine, near Murat, alt. 1100 m.

Description

Larvae :

Dimensions : width of head capsule 2.2 mm, length 1.4 mm, more or less quadrangular, eye in a postero-dorsal position, antenna not conserved. Pronotum width 1.8 mm, length 0.8 mm, lateral

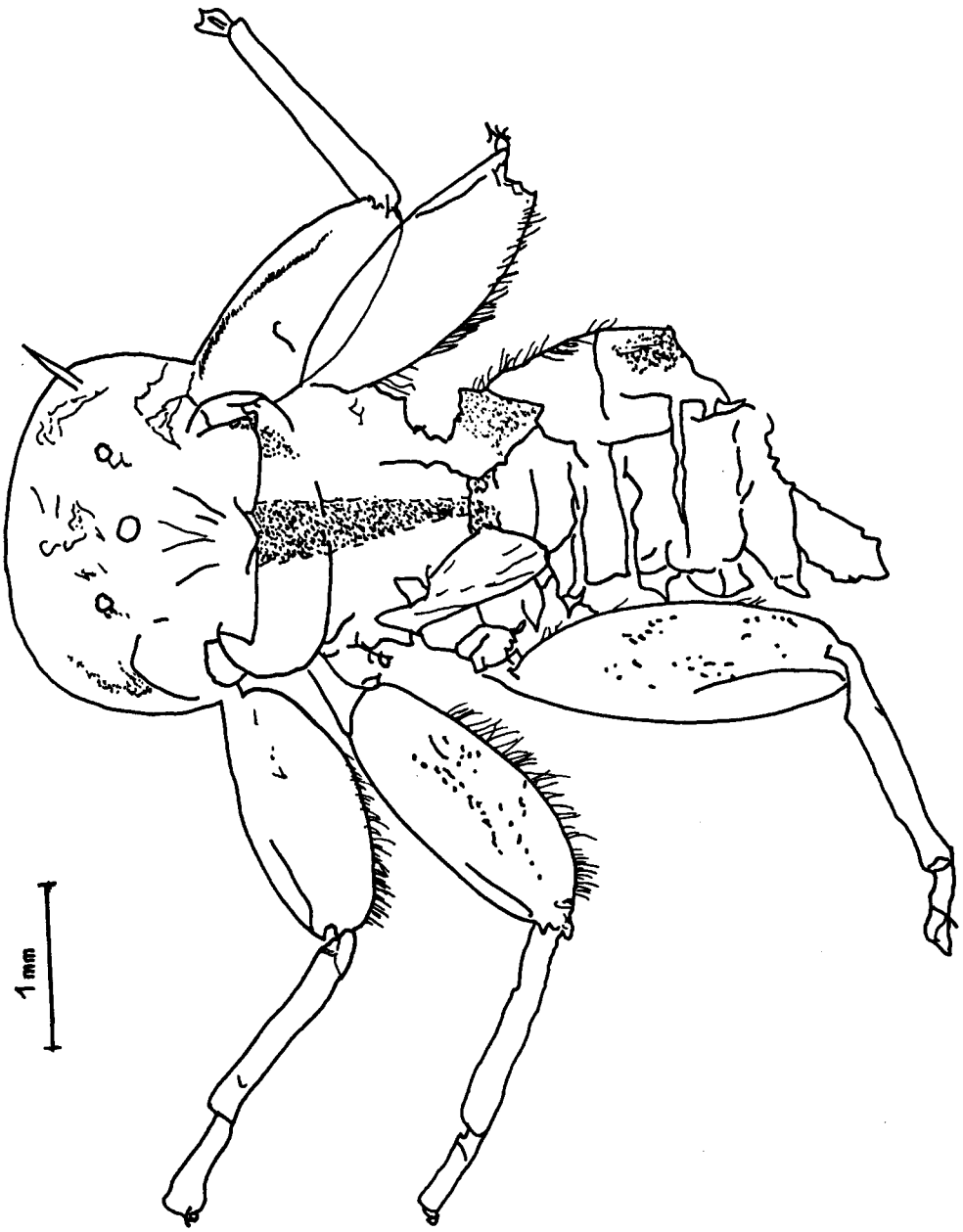

Figure 1. — Habitus holotype specimen MNHN-LP-R. 55196

margins regularly rounded, without expansions. Wing-buds : length 1.4 mm, internal margin non-fused together. Gills not conserved. Length of femora : fore 1.6 mm, middle 1.8 mm, hind 2.0 mm. widths 0.7 mm, 0.8 mm and 0.7 respectively. Long setae along the distal 2/3 of hind margin of femora, fore margin glabrous (phoot 2). Pointed phanerae not densely disposed on the upper surface of the femora (photo 3). Tibias length 1.4 mm. Fore and middle tarsus 0.6 mm long. Abdominal segments bearing sharp teeth, all similar (photo 4). Cerci and terminal filament not preserved on holotype (figure 1), 2 cerci and a terminal filament, without any setae on paratypes.

3. Discussion

Pseudokageronia gen. nov. has three caudal filaments. So, are excluded the genera *Acanthomola* WHITING & LEHMKYHL, 1987, *Epeorus* EATON, 1881, *Iron* EATON, 1883 (treated both as synonym and subgenus of *Epeorus*), *Ironodes* TRAVER, 1935, *Ironopsis* TRAVERS, 1935, *Belovius* TSHERNOVA, 1981, genera described on the sole basis of the adults, and closely related to *Epeorus*. *Pseudokageronia* has no pronotal processes. Because of this character, are excluded *Miocoenogia* TSHERNOVA, 1962 (Neogene of Siberia) which has latero-anterior pronotal processes, *Stenacron* JENSEN, 1974 (having lateral expansions of the pronotum), *Ecdyonurus* EATON, 1868 (having postero-lateral expansions of the pronotum). The absence of lateral expansions on the abdominal segments of *Pseudokageronia* excludes *Compsoneuria* EATON 1881 (= *Notonurus* CRASS, 1947, see GILLIES, 1984 ; = *Compsoneuriella* ULMER, 1939). The frontal margin of the head capsule of *Cinygmula* MCDUNNOUGH, 1933 is emarginate along the median area, unlike *Pseudokageronia*. The head of *Cinygma* is 1.25 times as wide as long, unlike *Pseudokageronia* (1.6 times as wide as long). *Pseudokageronia* differs from *Stenacron* JENSEN, 1974 in having no spine on the femora but rather dense setae and no lateral expansions of the pronotum. The femora of *Pseudokageronia* bear a series of relatively short setae (less long than half width of the femora) along the hindmargin. These setae are absent in the proximal part of the margin but they increase in length distally. After KLUGE (1988), this character excludes the genera *Ecdyonurus, Cinygma, Rhithrogena*, and *Epeorus*. *Bleptus* EATON, 1885 is also excluded because it has short strong setae but no long setae on posterodorsal margin, unlike *Pseudokageronia* (UENO, 1931 ; KLUGE, 1988). The pronotum and the head capsule of *Stenonema* are emarginate on the posterior margin, unlike *Pseudokageronia*. Unlike the larvae of *Atopopus* EATON, 1881, which has 'femora, tibiae, and tarsi with row of long setae along posterior margin, surface of femora with scattered spatulate setae' (WANG & MACCAFFERTY, 1995). *Pseudokageronia* possesses long setae on 2/3 of femora, and the phanerae on the surface of femora are sharp, not spatulate. *Pseudokageronia* differs from *Macdunnoa* LEHMKUHL, 1979 in the absence of spine on its femora and tibias, unlike the latter, which has spines of two kinds and marginal fine hairs on the femora. *Raptoheptagenia* WHITING & LEHMKUHL, 1987 has a dense setation on the dorsum of the abdomen, unlike *Pseudokageronia*. *Succinogenia* DEMOULIN, 1965 has distinctly narrower femora than the new *Pseudokageronia*.

Within *Heptagenia* (*sensu* KLUGE, 1988), the absence of setae in the proximal part of the hind margin of the femora would exclude all subgenera, except *Kageronia* MATSUMURA, 1931 described on the basis of adults. Nevertheless, MATSUMURA (1933) synonymised the type species *Kageronia suzukiella* with *Heptagenia kihada* two years after he created the genus *Kageronia*. After OMANISHI (1935), the larvae of *Heptagenia kihada*. has 'tibia slightly shorter than the femur, tarsus about one-third of the tibia (...) each of the tergites 1-9 with a spine on its postero-lateral corner'. *Pseudokageronia* has no spine on the postero-lateral corner.

The genus *Afronurus* LESTAGE, 1924 is discussed by BELFIORE (1994, 1996) for European species, who considers that KLUGE (1988) has too rapidly synonymised the genera having 'triangular gills' with *Ecdyonurus*, underestimating the morphological characters of larvae. *Afronurus* has

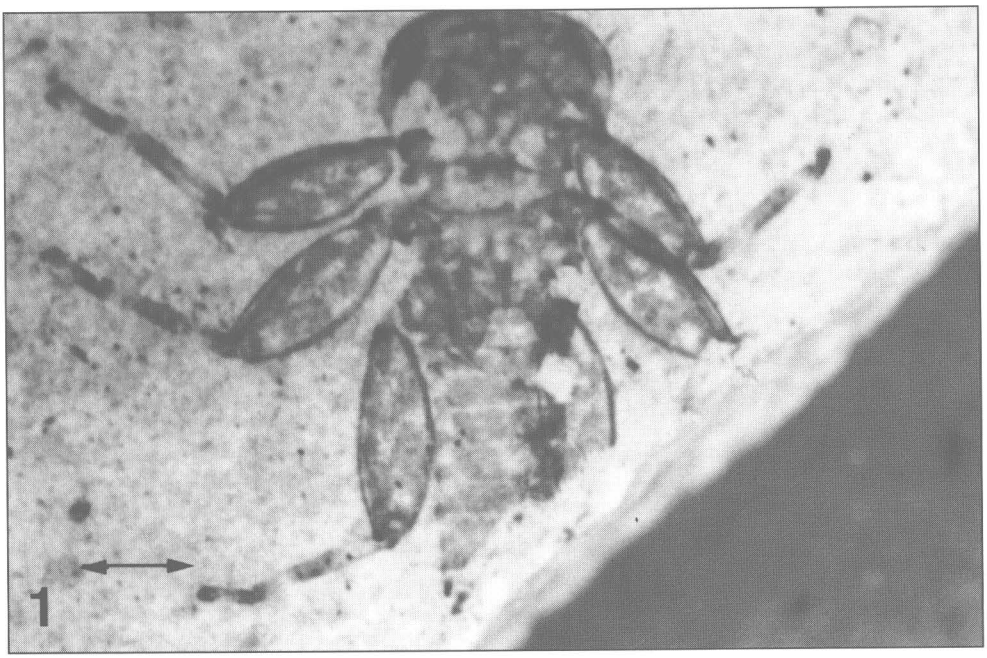

Photo 1. — Habitus holotype.

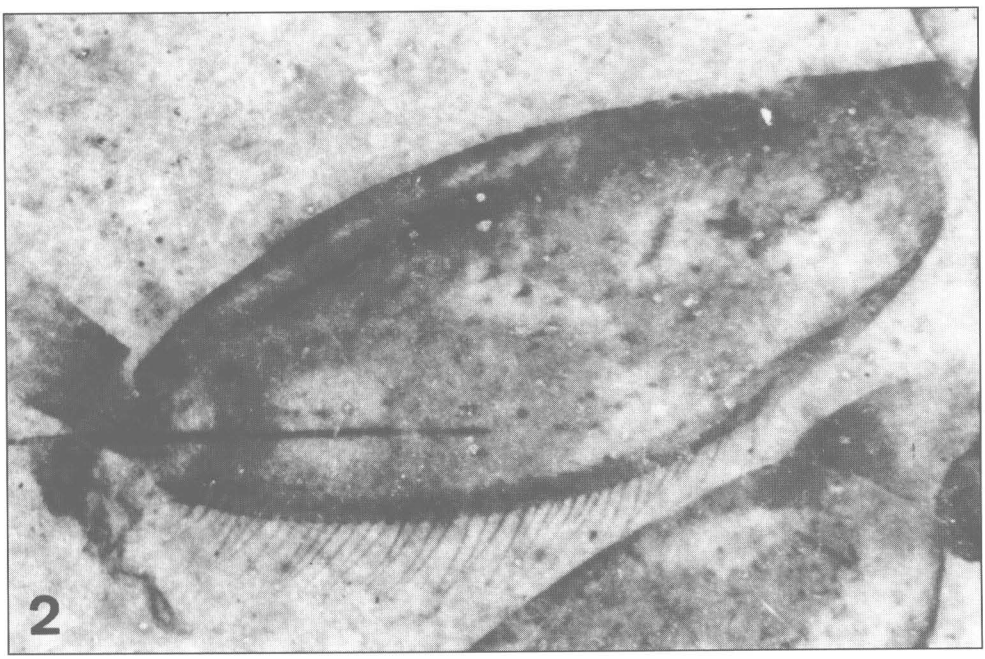

Photo 2. — Fore femora.

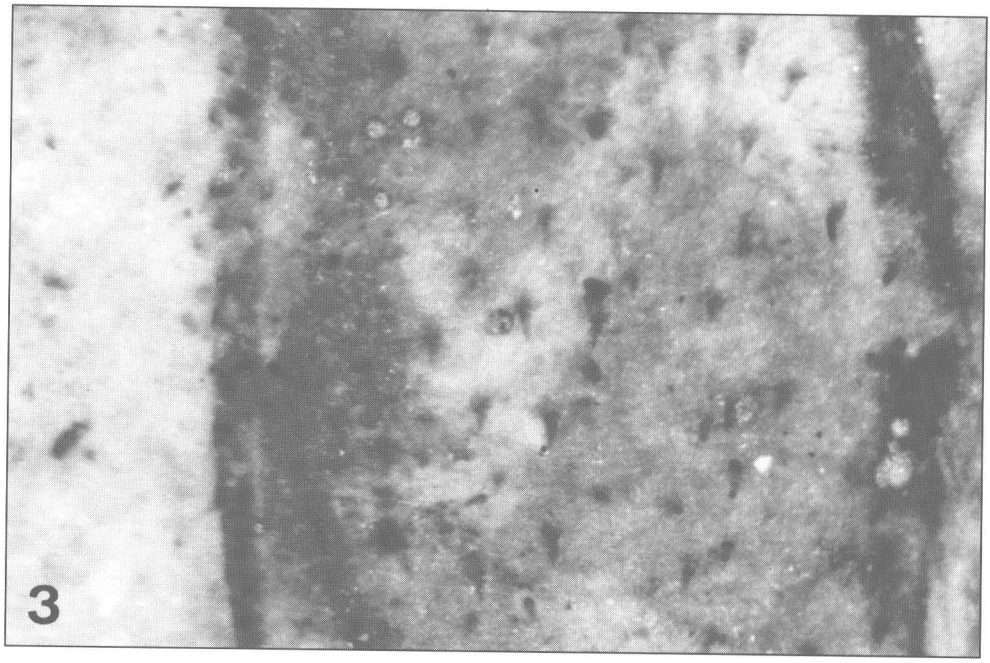

Photo 3. — Phanerae on fore femora.

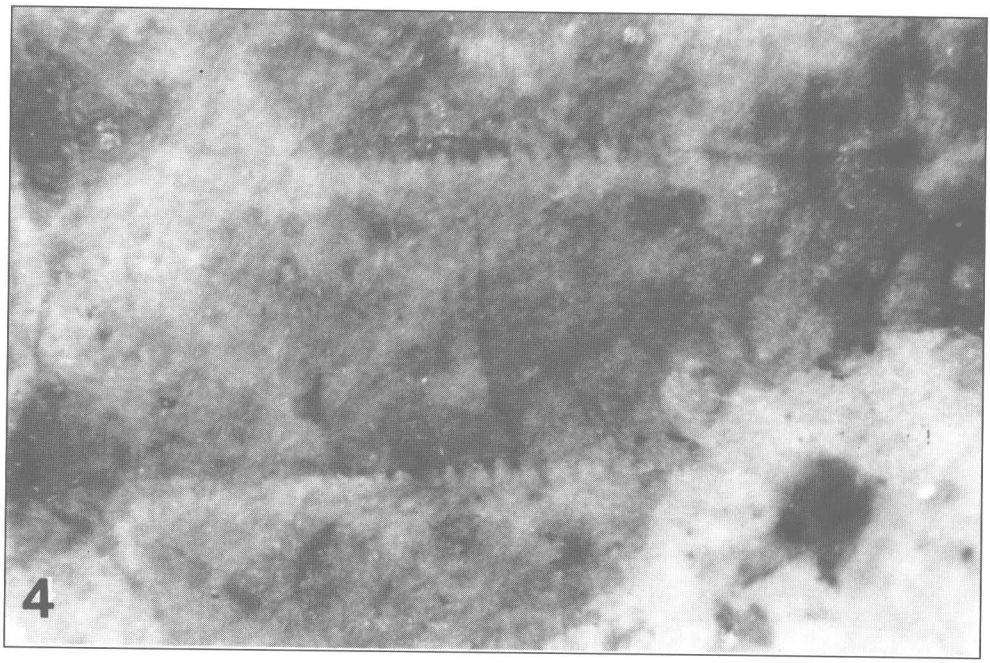

Photo 4. — Spines on hind margin of tergites.

long setae on the whole posterior margin of the femora and the setae on the surface of femora are not sharp, unlike in *Pseudokageronia*.

None of the characters used by ZURWERRA & TOMKA (1985) for the original description of *Electrogena* are preserved in *Pseudokageronia*. Thus, the comparison between the two taxa is based on the following characters : *Electrogena* bears setae on the whole length of the hind margin of the femora, mainly the median and posterior, these setae being shorter on the fore femora, unlike in *Pseudokageronia*. Posterior femora of *Electrogena* are more pilose than others.

Lastly, the Upper Miocene larva attributed to *Ecdyonurus* by ZHANG (1989) has a distinctly transverse head, unlike *Pseudokageronia*. The fossil larvae attributed to *Heptagenia* by ZHANG (1989) have distinctly narrower femora than *Pseudokageronia*.

4. Phylogenetic analysis

Sainte-Reine is a relatively recent outcrop, with an entomofauna related to the recent faunas of the Palaearctic and Afrotropical regions. Furthermore, the Heptageniidae are supposed to be a rather modern family (KLUGE, 1993), thus it is highly probable that *Pseudokageronia* is more closely related to the recent genera from the Western Palaearctic region : *Afronurus, Ecdyonurus, Electrogena, Heptagenia*, and *Kageronia*. MACCAFFERTY (1991b) has shown that the Oligoneuriidae is the sister-group of Heptageniidae. Thus, we have tried to make a phylogenetic analysis of these genera.

The genus *Oligoneuriella* ULMER, 1924, is considered as outgroup for the present attempt of cladistic analysis. The software Hennig86 version 1.5 (FARRIS, 1988) with the help of the matrix and tree editor Tree Gardener version 2.2.1 (RAMOS, 1998) have been used, with the implicit enumeration option ('ie'), without any weighting of characters. 16 characters are used, 12 being both visible in *Pseudokageronia* and on the type species of Recent genera. The last four characters are coded '?' for *Pseudokageronia*. Nevertheless, the recent genera are mainly characterised on the basis of the mouthparts and gills structures, not visible in *Pseudokageronia*. In order to minimise the number of undetermined states of characters in *Pseudokageronia*, we have chosen to introduce only the characters most discriminant for the other genera. Neither *Rhithrogena* nor *Epeorus* have been integrated in the study because : 1) the problem we want to solve concerns the subgenera of *Heptagenia* (*Dacnogenia, Kageronia*, and *Heptagenia* sensu stricto), *Ecdyonurus* (*Electrogena, Afronurus*, and *Ecdyonurus* sensu stricto), and the position of the new genus *Pseudokageronia* ; 2) *Epeorus* and *Rhithrogena* are strictly rheophilous genera, while *Heptagenia* and *Ecdyonurus* sensu lato are found indifferently in lentic (even in standing waters) or lotic environments ; 3) the characters necessary to the integration of *Epeorus* and *Rhithrogena* in the analysis would have concerned the mouthparts and gills, not visible in the fossil. Thus, this option would have introduced too numerous biases in the analysis.

Only one minimal tree was obtained (length 30 ; CI 0.60 ; RI 0.58) showing :

1) a monophyletic group [*Ecdyonurus+Electrogena*]+ *Afronurus*. If *Electrogena* (raised to genera rank for several *Ecdyonurus* species by ZURWERRA & TOMKA, 1985) is without any doubt a genus, the occurrence of *Afronurus* in West-palaearctic region remains doubtful (see BELFIORE, 1994, 1996). It is highly probable that *Afronurus zebratus* from Corsica should be retransfered to *Electrogena*.

2) another monophyletic group, (([*Ecdyonurus+Electrogena*]+ *Afronurus*) + *Heptagenia*) + *Dacnogenia*. *Dacnogenia* appears as a valid genus, more basal than *Heptagenia*, after the present analysis. This result will need confirmation after a future analysis including imaginal characters.

Character		
1	**Head capsule**	
	Width equal or larger than 1.5 time its length	0
	Width less than 1.5 time its length	1
2	**Pronotum**	
	Without lateral expansions	0
	With lateral expansions	1
3	**Pronotum**	
	Width of fore margin inferior or equal to width of hind margin	0
	Width of fore margin superior to width of hind margin	1
4	**Fore tarsus**	
	Presence of setae on the hind margin	0
	Absence of setae on the hind margin	1
5	**Fore femora**	
	Width less or equal to 0.4 length	0
	Width superior to 0.4 length	1
6	**Fore femora**	
	Length inferior or equal to length of tibia	0
	Length superior to length of tibia	1
7	**Fore femora**	
	Setae on only a part of hind margin	0
	Setae all along hind margin	1
8	**Fore femora**	
	Numerous phanerae on dorsal side	0
	No, or few phanerae on dorsal side	1
9	**Shape of phanerae on femora**	
	Sharpened	0
	Other shapes, or no phanerae	1
10	**Length of fore tarsus**	
	Equal or inferior to ¼ of the length of tibia	0
	Between ¼to ½ of the length of tibia	1
11	**Hind corners on posterior abdominal segments**	
	Sharp	0
	Blunt	1
12	**Tergites**	
	No spines on posterior margin	0
	Presence of spines, of only one size	1
	Presence of spines of several sizes	2
13	**Shape of glossae**	
	Elongated	0
	Square	1
	Pyramidal	2
14	**7th gill**	
	Always with a filamentous tuff	0
	Generally without filamentous tuff	1
15	**Small denticles on claws**	
	Yes	0
	No	1
16	**Galea and lacinia**	
	With a row of setae on the ventral side	0
	Other	1

Table 1. — List of characters.
Tableau 1. — Liste des caractères.

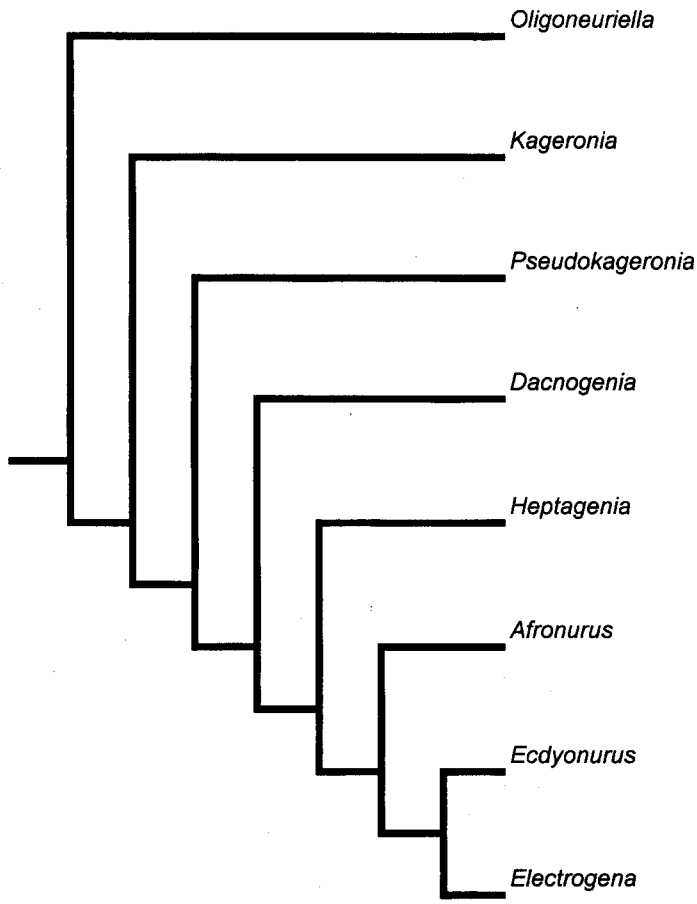

Figure 2. — Minimal tree (Length : 30 ; CI : 0,60 ; RI : 0,57).
Figure 2. — Arbre minimal (Longueur : 30 ; IC : 0,60 ; IR : 0,57).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Oligoneuriella	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Afronurus	1	0	1	1	0	0	1	0	1	1	1	2	1	1	1	1
Ecdyonurus	0	1	1	1	0	1	1	0	0	0	0	2	1	1	0	1
Electrogena	1	0	1	0	0	1	1	1	0	1	1	2	1	1	0	1
Heptagenia	1	0	1	1	0	0	1	1	1	1	1	2	0	0	1	0
Kageronia	0	0	0	1	?	0	0	1	0	1	0	?	0	1	0	0
Pseudokageronia	1	0	0	0	1	0	0	1	0	1	1	1	?	?	?	?
Dacnogenia	1	0	0	1	1	0	1	1	1	0	1	1	2	0	1	0

Table 2. — Matrix of characters.
Tableau 2. — Matrice de caractères.

3) The basal position of *Pseudokageronia* and *Kageronia* confirms the results of KLUGE (1993) who said that *Kageronia* might be considered as the most primitive 'group' among the Recent Heptageniinae. Further, together with the presence of an adult attributed to this genus in the Upper Eocene Baltic amber (KLUGE, 1986), it supports the hypothesis of a Palaearctic origin for *Kageronia*. As for *Dacnogenia*, and according to JACOB et al. (1995), we propose to raise *Kageronia* as a genus.

5. Ecological and ethological remarks

The phylogenetic affinities between *Pseudokageronia* and *Kageronia* are supported by ecological data. *Kageronia fuscogrisea* is known to live exclusively in the aquatic vegetation and is never found on the stones or gravel (MADSEN, 1968). MACAN (1960) has reported this species from two Recent lakes. A comparison of morphological features of *Heptagenia sulphurea* and *Kageronia fuscogrisea* shows that the presence of a dense fringe of hairs along the hind edge of the femora would be an adaptation to lotic habitats (MADSEN, 1968). *Kageronia fuscogrisea* has not such a dense fringe. Nevertheless, *K. fuscogrisea* has a dense fringe of hairs along the hind edge of the tibia, interpreted by MADSEN (1968) as an adaptation to swimming. *Pseudokageronia* has not such a fringe of hairs.

The presence of fossilised exuvial skins suggests that emergence occurred beneath or upon the surface of water, as in Recent Baetidae, and not climbing on macrophytes or stones, as *Ecdyonurus dispar*, for example.

The paleolake of Faufouilloux, near Murat was a very peculiar environment : lack of large stones, or pebbles, or even gravel in the layers where the Ephemeroptera larvae have been found (laminated beds of fine diatomite, green diatom mud, near the base of the series, corresponding to a palustrine palaeoenvironment). In the standing water, the aquatic macrophyte Ceratophyllaceae *Ceratophyllum demersum* L. was present (ROIRON, 1991). This species is typical of standing waters, where it can proliferate. Numerous species of diatoms have been, studied of SERIEYSSOL & GASSE (1991) who show that the diatom flora is constituted of 90-95 % by pennate diatoms, of poor chronological value, and centric diatoms (*Cyclotella kutzingiana, C. meneghiniana, Stephanodiscus dispar* for example). ROIRON (1991) thinks that salinity of water and gas releases excluded all animal life, because these diatom species are found in brackish water. GERMAIN (1981) says that *Cyclotella meneghiniana* is very frequent on macrophytes, among littoral deposits. It seems to tolerate salinity as much as 10 %. DESCY (1984) shows that *C. meneghiniana* tolerates temperature variations between 2.1 to 26.0 °C ; O_2 from 1.2 to 13.7 mg/L ; pH from 6.2 to 10 ; Sulphates from 5.5 to 160 mg/L ; Sodium from 2.0 to 159 mg/L. GALLIK (1932) mentions the presence of *Stephanodiscus* in Hungarian sulphur thermae and HUBER-PESTALOZZI (1942) writes it occurs in oligotrophic Alpine lakes. For SLADECEK (1956), this species would be a α-ß mesosaprobe. The very large spectrum of tolerance of these diatoms to various chemical conditions does not allow asserting anything about the quality of the water where *Pseudokageronia thomasi* lived. Yet, it is highly probable it fed on this microflora. ROIRON (1991) writes that the climate was probably temperate or cold with relatively temperate winters. This assumption, based on the low abundance of thermophilous macroflora, and the greater abundance of alleged temperate or cold floristic elements, is to be compared with the presence of a diverse Isoptera fauna (NEL & PAICHELER, 1993) and Odonata Megapodagrionidae (NEL *et al.*, 1997), which occur in Recent hot and wet climates.

ROIRON (1991) quoted that FOURNIE (1965) and MAURIZOT-BLANC (1974) have observed fluviatile deposits in the series of Sainte-Reine. A hypothesis could be that *Kageronia*, initially occurred in the streams. It colonised the nearby lake, with adaptations (*Pseudokageronia*) to its special ecological conditions. *Pseudokageronia* extincted as this special environment disappeared. There is no more maar, with secondary volcanic activity in the Massif Central (France).

References

BELFIORE, C. 1994. Taxonomic characters for species identification in the genus *Electrogena* Zurwerra and Tomka, with a description of *Electrogena hyblaea*, sp. n. from Sicily (Ephemeroptera : Heptageniidae). Aquatic Insects, **16** (4) : 193-199.

BELFIORE, C. 1996. Identification and discrimination of *Electrogena* species by numerical methods (Ephemeroptera : Heptageniidae). Systematic Entomology, **21** : 1-13.

BRAASCH, D. & T. SOLDAN. 1984. Beitrag zur Kenntnis der Gattung *Thalerosphyrus* Eaton, 1881 im Hinglick auf die Gattung *Ecdyonuroides* Thanh, 1967 (Ephemeroptera, Heptageniidae). *Reichenbachia*, **22** : 201-206.

CRASS, R.S. 1947. Mayflies (Ephemeroptera) collected by J. Omer-Cooper in the Eastern Cape Province, South Africa, with a description of a new genus and species (*Notonurus cooperi*). *Proceeding of the Royal entomological Society of London*, **17** : 124-128.

DEMOULIN, G. 1965. Contribution à la connaissance des Ephéméroptères de l'ambre oligocène de la Baltique. *Entomologiske Meddelelser*, **34** : 143-153.

DESCY, J.P. 1984. Ecologie et distribution de diatomées benthiques dans le bassin belge de la Meuse. *Institut Royal des Sciences naturelles de Belgique*. Documents de travail N° 18.

EATON, A.E. 1868. An outline of a re-arrangement of the genera of Ephemeridae. *Entomologist's Monthly Magazine*, **5** : 82-91.

Eaton, A.E. 1881. An announcement of new genera of the Ephemeridae. *Entomologist's Monthly Magazine*, **18** : 21-27.

EATON, A.E. 1883-1888. A revisional monograph of recent Ephemeridae or mayflies. *Transactions of the Linnean Society of London*, Second Series, Zoology, **3** : 1-352, 65 pl.

FARRIS, J.S. 1988. *Hennig86 version 1.5 manual.*

FOURNIER, F. 1965. *Etude de quelques gisements diatomifères d'Auvergne*. DES. Orsay, 80 p.

GALLIK, O. 1932. Enumeratio Diatomacearum in Thermis Hadjuszoboozlo Inventarum. *Archiv Protistenk.*, **76** : 306-308.

GERMAIN, H. 1981. *Flore des Diatomées Diatomophycées. Eaux douces et saumâtres du Massif Armoricain et des contrées voisines d'Europe Occidentale*. Editions Boubée Paris, 444 pp.

GILLIES, M.T. 1984. On the synonymy of *Notonurus* Crass with *Compsoneuriella* Ulmer (Heptageniidae *in V. Landa, T. Soldan & T. Tonner, eds. Proceedings of the Fourth International Conference on Ephemeroptera. Czechoslovak Academy of Sciences, Ceske Budejovice*, p. 21-25.

HONG, Y.C. 1983. Fossil insects in the diatoms of Shanwang. *Bulletin of the Tianjin Institute, Geology and Mineral Resources*, **8** : 1-11.

HUBER-PESTALOZZI, G. 1942. Das Phytoplankton des Sübwassers. Diatomeen Teil II. **2** : 549 pp. *in Thienemann. Die Binnenwässer 16.*

IMANISHI, K. 1935. Mayflies from Japanese torrents VI. Notes on the genera *Ecdyonurus* and *Rhithrogena. Annotationes Zoologicae Japoneses*, **15** : 538-549.

JACOB, U., A. DORN & A. HAYBACH. 1995. Systematik und Verbreitung der gattung *Heptagenia* und nahestehender Taxa in Europa. *Verh. Westd. Entom. Tag.*, **S.8** : 93-105.

JENSEN, S.L. 1974. A new genus of mayflies from North America (Ephemeroptera : Heptageniidae). *Proceedings of the entomological Society of Washington*, **76** (6) : 225-228.

KLUGE, N. Yu. 1986. [Contributions to the knowledge of mayfly species (Ephemeroptera, Heptageniidae) from Baltic amber]. *Paleontologicheskii Zhurnal*, **1986** (2) : 111-112.

KLUGE, N. Yu. 1988. Revision of genera of the family Heptageniidae (Ephemeroptera) I. Diagnoses of tribes, genera and subgenera of the subfamily Heptageniinae. *Entomologicheskoe Obozrenie*, **67** (2) : 291-313 (in russian) translated in *Entomological Review*, **68** : 1-25 (1989).

KLUGE, N. Yu. 1993. Revision of the genera of the family Heptageniidae (Ephemeroptera) II. Phylogeny. *Entomologicheskoe Obozrenie*, **72** (1) : 39-57 (in Russian) [translated in *Entomological Review*, 1994, **73** (1) : 1-16].

LESTAGE, J.A. 1924. Les Ephémères de l'Afrique du Sud. Catalogue critique & systématique des espèces connues et description de trois genres nouveaux et de sept espèces nouvelles. *Revue Zoologique Africaine*, **12** : 316-352.

MACAN, T.T. 1960. A key to the nymphs of the British species of Ephemeroptera. *Scientific publications. Freshwater Biological Association*, **20** : 1-64.

MADSEN, B.L. 1968. A comparative ecological investigation of two related mayfly nymphs. *Hydrobiologia*, **31** : 337-349.

MATSUMURA, S. 1931. [*Ephemerida*] (in Japanese). 6000 Illustrated Insects of the Japanese Empire : 1465-1480.

MATSUMURA, S. 1933. [*Ephemerida*] (in Japanese). 6000 Illustrated Insects of the Japan, vol 5.

MAURIZOT-BLANC, C. 1974. Etude des formations volcaniques de la cuvette de Murat et de la Vallée de la Chevade. *Thèse 3ème cycle, Grenoble.*

McCAFFERTY, W.P. 1991. The cladistics, classification, and evolution of the Heptagenioidae (Ephemeroptera) *in Alba-Tercedor J. & Sanchez-Ortega A. (Eds). Overview and Strategies of Ephemeroptera and Plecoptera. Sandhill Crane Press, Gainesville, Florida* : 87-102.

McCAFFERTY, W.P. 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta) : A commentary on systematics. *Annals of the entomological Society of America*, **84** : 343-360.

McCAFFERTY, W.P. & A. PROVONSHA 1985. Systematics of *Anepeorus* (Ephemeroptera : Heptageniidae). *Great Lakes Entomologist*, **18** : 1-6.

McDUNNOUGH, J. 1933. The nymph of *Cinygma integrum* and description of a new Heptagenine genus. *The Canadian Entomologist*, **65** : 73-76.

NEL, A. 1988. Les Sialidae (Megaloptera) fossiles des diatomites de Murat (Cantal, France) et de Bes-Konak (Anatolie, Turquie). *Neuroptera International*, **5** (1) : 39-44.

NEL, A. 1992. Nouveaux Tingidae fossiles du Cénozoïque de France (Heteroptera). E.P.H.E., *Travaux du laboratoire de Biologie et Evolution des Insectes*, **5** : 97-104.

NEL, A. & J.-C. Paicheler. 1993. Les Isoptera fossiles. Etat actuel des connaissances, implications paléoécologiques et paléoclimatiques. *Cahiers de Paléontologie*, C.N.R.S. (ed.) : 102-179.

NEL, A, A. ARILLO & X. MARTINEZ-DELCLOS. 1996. New fossil Odonata from the Upper Miocene of France and Spain. (Insecta, Odonata, Anisoptera, Zygoptera). *Neue Jarbuch Pal. Geol., Abhandlungen*, **199** (2) : 167-219.

NEL, A. 1996. Le premier représentant fossile du genre *Ibalia* dans le Miocène supérieur du Cantal (France) (Hymenoptera : Cynipoidea : Ibaliidae). *Bulletin de la Société entomologique de France*, **101** (2) : 141-143.

NEL, A. & A.E. JARZEMBOWSKI. 1997. New fossil Sisyridae and Neurorthidae from Eocene Baltic amber and Upper Miocene of France (Insecta : Neuroptera). *European Journal of entomology*, **94** : 287-294.

NEL, A., X. MARTINEZ-DELCLOS, F. PAPIER & J. OUDARD. 1997. New fossil Odonata from the Cenozoic of France. (Sieblosiidae, Lestidae, Coenagrioniidae, Megapodagrionidae, Libellulidae). *Deutsche Entomologische Zeitschrift*, **44** (2) : 231-258.

NEL, A., A. ARILLO & V. ORTUÑO. 1997. New Western Palaearctic Cenozoic Odonata. (Insecta : Odonata : Zygoptera and Anisoptera). *Bulletin de la Société Entomologique de France*, **102** (3) : 265-270.

RAMOS, T.C. 1998. *Tree Gardener. Version 2.2 Manual.*

ROIRON, P. 1991. La macroflore d'âge miocène supérieur des diatomites de Murat (Cantal, France). Implications paléoclimatiques. *Palaeontographica*, (B), **223** : 169-203.

SERIEYSSOL, K. & F. GASSE. 1991. Diatomées néogènes du Massif Central Français : quelques faits biostratigraphiques. *C.R. Acad. Sci. Paris*, t 312, Série II : 957-964.

TRAVER, J.R. 1933. Mayflies of North Carolina part III the Heptageniidae. *Journal of the Elisha Mitchell Scientific Society*, **48** : 141-207.

TRAVER, J.R. 1935. Two new genera of North American Heptageniidae (Ephemerida). *The Canadian Entomologist*, **67** : 31-38.

TRAVER, J.R. 1939. Himalayan mayflies (Ephemeroptera). *Annals and Magazine of Natural History*, **11** (4) : 32-56.

TSHERNOVA, O.A. 1962. Litchinki podenok iz neogena zapadnoy Sibiri (Ephemeroptera, Heptageniidae). [Ephemeroptera larvae from the Neogene of West Siberia (Ephemeroptera, Heptageniidae)] (in Russian). *Zoologicheskii Zhurnal*, **41** : 943-945.

TSHERNOVA, O.A. 1981. [On the systematics of adult mayflies of the genus *Epeorus* Eaton, 1881 (Ephemeroptera, Heptageniidae)] (in Russian). *Entomologicheskoe Obozrenie*, **60** : 323-336.

UENO, M. 1931. Contribution to the knowledge of Japanese Ephemeroptera. *Annotationes Zoologicae Japoneses*, **13** : 189-226, pl. 12-13.

ULMER, G. 1924. *Oligoneuriella* gen. n. for *Oligoneuria* auct (part) type *rhenana* Imh. *Konowia*, **3** : 31.

ULMER, G. 1939-1940. Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln. *Archiv für Hydrobiologie*, Supplement **16** : 443-692, figs. 1-469, 4 tab.

VENKATAMARAN, K. & K.G. SIVARAMAKRISHNAN. 1987. A new species of *Thalerosphyrus* from South India (Ephemeroptera : Heptageniidae). *Current Science*, **56** (21) : 1126-1129.

WANG, T.Q. & W.P. MCCAFFERTY. 1995. First larval descriptions, new species, and evaluation of the Southeast Asian genus *Atopopus* (Ephemeroptera : Heptageniidae). *Bulletin de la Société d'Histoire naturelle de Toulouse*, **131** : 19-25.

WANG, T.Q. & W.P. MCCAFFERTY. 1995. Relationships of the Arthropleidae, Heptageniidae, and Pseudodironidae (Ephemeroptera : Heptagenioidea). *Entomological News*, **106** (5) : 251-256.

WHITING, E.R. & D.M. LEHMKUHL. 1987. *Acanthomola pubescens*, a new genus and species of Heptageniidae (Ephemeroptera) from western Canada. *The Canadian Entomologist*, **119** : 409-417.

WHITING, E.R. & D.M. LEHMKUHL. 1987. *Raptoheptagenia cruentata*, gen. nov. (Ephemeroptera : Heptageniidae), new association of the larvae previously thought to be *Anepeorus* with the adult of *Heptagenia cruentata* Walsh. *The Canadian Entomologist*, **118** : 405-407.

ZHANG, JUNFENG. 1989. *Fossil insects from Shanwang, Shandong, China*. Shandong Science and Technology Publishing House, Jinan : 459 pp. [in Chinese with abstract in English].

ZURWERRA, A. & I. TOMKA. 1985. *Electrogena* gen. nova (sic), eine neue Gattung der Heptageniidae (Ephemeroptera). *Entomologische Berichte Luzern*, **13** : 99-104.