

PALAEONTOLOGICAL COLLECTIONS OF LILLE UNIVERSITY – SCIENCES AND TECHNOLOGIES. II — DIPLOSTRACA (TYPES AND FIGURED SPECIMENS)

Collections paléontologiques de l'Université de Lille – Sciences et Technologies. II — Diplostraca (types et figurés)

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Abstract. – An exceptional collection of Diplostraca (Spinicaudata, Leaiina) from various geographic localities all around the world and from Devonian to Jurassic beds, is re-described in this catalogue. Despite some imperfections due to the geopolitical climate of the epoch (the Cold War), the great value of the Defretin's and Novozhilov's work is confirmed. New interpretations are provided about discussed taxa: *Estheriina*, *Pseudoasmussia*, *Taimyrites*, *Fernandoalmeidium*, *Pseudestheria*, and *Teixeirium*. Used as a reference work, this catalogue might permit these taxa to be reviewed in light of new methodologies and taxonomic schemes currently employed. Some species remain enigmatic, "*Estheria*" *destombesi*, "*Lioestheria*" *toricata*, "*Lioestheria*" *propinqua* and "*Pseudoasmussia*" *striata*, but offer a great possibility of revision by means of the data of this catalogue. The early record of Devonian-Carboniferous spinicaudatans in our collection is noteworthy, and provides important information on the early diversification of this group.

Résumé. – Une collection exceptionnelle de Diplostraca (Spinicaudata, Leaiina), provenant de nombreux gisements mondiaux et d'une période géologique s'étendant du Dévonien au Jurassique, est révisée dans ce catalogue. Le travail des deux chercheurs, S. Defretin et N. Novozhilov, ayant contribué à constituer cette collection durant une période difficile (la guerre froide), conserve sa pleine importance scientifique, moyennant quelques précisions que ce catalogue tente d'apporter. Notre compilation permet aussi d'alimenter les discussions actuelles sur plusieurs taxons : *Estheriina*, *Pseudoasmussia*, *Taimyrites*, *Fernandoalmeidium*, *Pseudestheria*, et *Teixeirium*. Notre travail devrait déboucher sur des révisions, fondées sur les méthodes modernes de la taxinomie, d'espèces encore incomplètement élucidées : "*Estheria*" *destombesi*, "*Lioestheria*" *toricata*, "*Lioestheria*" *propinqua* et "*Pseudoasmussia*" *striata*. Le point scientifique le plus intéressant, abordé dans ce catalogue, concerne l'ordre des Spinicaudata, que notre matériel permet de suivre depuis ses premières formes du Dévonien-Carbonifère.

Keywords. – Diplostraca, Conchostraca, Europe, Russia, Devonian, Jurassic.
Mots-clés. – Diplostraca, Conchostraca, Europe, Russie, Dévonien, Jurassique.

I. — INTRODUCTION

The palaeontological collection of the Lille University – Sciences and Technologies comprises 50,000 specimens, more than 3,000 of which are "types and figured" (Cuvelier *et al.*, 2011). In majority, they are represented by fossil plants and micropalaeontologic materials. The first catalogue devoted on to the Lille's collection described the eurypterids (Blieck *et al.*, 2013)⁽¹⁾. This second catalogue inventories the diplostracans (formerly conchostracans). The diplostracan material of Lille was mainly investigated by S. Defretin-Lefranc (Defretin, 1950a, 1950b, 1953; Defretin-Lefranc, 1963, 1965, 1970; Defretin & Fauvelet, 1951), who studied her first *Estheria* in 1948 under Professor Pruvost's guidance. She collaborated with the Russian specialist

N. Novozhilov (whose name was previously transliterated as Novojilov), and published a general synthesis (Defretin-Lefranc, 1965) about materials collected in the former USSR during the Cold War, and partly described by Novozhilov (1958a, b, c, d). The diplostracan material of Lille is represented by 95 types and figured specimens, the original labels of which indicated 22 holotypes, 4 neotypes, 1 syntype, 16 paratypes, 4 homotypes, 2 metatypes, and 46 figured specimens. The terms holotype, neotype or paratype are well known in taxonomy; the definitions of the less known terms, homotype and metatype, may be found for example in the Webster's Dictionary (Anonyme, 1971). Homotypes (or more exactly homeotypes) are specimens determined by a revisor author (i.e., plesiotypes) which strongly resemble the type material whereas

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(¹) Since the publication Blieck *et al.* in 2013, University of Lille 1 became Lille University – Sciences and Technologies.

metatypes are homeotypes or topotypes more dissimilar to the type-material. Since five years, the first author (J.C.) compiles and presents the types and figured specimens of the Lille University on the French national database TransTyfipal. All the specimens described hereafter are available on the website <http://transtyfipal.u-bourgogne.fr/>, searching the following site: Order: “Diplostraca” / Establishment keeper: “Lille - Université Lille 1”.

II. — PRELIMINARY REMARKS

1) Abbreviations

The following abbreviations are used across this catalogue: USTL (Lille University – Sciences and Technologies; because, as formerly called Université des Sciences et Technologies de Lille, its acronym was USTL); Loc. (Locality); Lithos. (Lithostratigraphy); Biost. (Biostratigraphy); Chronost. (Chronostratigraphy); ill. (illustrated).

2) Editorial remarks

The principal lithostratigraphic, geographic and toponymic terms, traditionally used in the French coal basins, are translated as follows: *Assise* – Formation; “*Bowette*” – intersecting horizontal gallery; *Faisceau* – Member; *Passée* – parasequence; *Puits, fosse* – pit. We have transliterated the Russian names according to the current phonetic rules based on the English phonetics; e.g., Novozhilov for Novojilov or Nechaev for Netschajev. For practical reasons, we have kept the original numbering of the specimens of Russia (without prefix) while all other specimens were re-numbered with the prefix “USTL”.

3) Systematic classification of Diplostraca

The classification used in this catalogue was established by one of the authors (O.G.). It is based on an original synthesis of the work of Novozhilov (1958a, b, c, d), Defretin-Lefranc (1965, 1970), Tasch (1969, 1987), Chen & Shen (1985), Shen (1985), Jones & Chen (2000), and Martin & Davis (2001). The same classification was followed for the catalogue of Diplostraca of the Natural History Museum of Lille (Hennion *et al.*, this volume). Some of the catalogue specimens have not received clear systematic placements, because they lack the main diagnostic characters adopted in our classification. Similarly, in the absence of sufficient information, the status of some species treated in this catalogue has not been definitively fixed. All these taxa need further studies.

4) Stratigraphic and geographic distributions of specimens

As mentioned above, we have re-found 95 specimens of Diplostraca. They belong to 40 species. More than half of these specimens (61) come from Russia; 25 other specimens come from different regions of France (Nord – Pas-de-Calais, 9; Languedoc–Roussillon, 5; Lorraine, 4; Alsace, 2; Franche-Comté, 2; Rhône–Alpes, 2; and Centre, 1); 4 from Germany; 4 from Morocco, and 1 from Switzerland. Furthermore, these 95 diplostracan specimens are stratigraphically distributed from the Devonian to the Jurassic (Devonian, 2; Carboniferous, 11; Permian, 36; Triassic, 33; Jurassic, 13).

III. — SYSTEMATIC CATALOGUE

Authors of taxon names are indicated in small capital letters followed by year of authorship. The corresponding bibliographical references are not listed here in the bibliography section; they can be found in the papers of Novozhilov (1958a, b, c, d), Defretin-Lefranc (1965, 1970), Tasch (1969, 1987), Chen & Shen (1985), Jones & Chen (2000), and Martin & Davis (2001). All other cited papers are in the bibliography section.

Phylum ARTHROPODA VON SIEBOLD, 1848
 Subphylum CRUSTACEA BRÜNNICH, 1772
 Class BRANCHIOPODA LATREILLE, 1817
 Subclass PHYLLOPODA PREUSS, 1951
 Order DIPLOSTRACA GERSTAECKER, 1866
 Suborder SPINICAUDATA LINDER, 1945
 Superfamily VERTEXIOIDEA KOBAYASHI, 1954
 (*sensu* ZHANG *ET AL.*, 1976)
 Family PALAEOLIMNADIIDAE TASCH, 1956
 Subfamily ESTHERIININAE KOBAYASHI, 1954
 Genus *ESTHERIINA* JONES, 1897

Preliminary comments. (1) For a detailed analysis and discussion of the family Palaeolimnadiidae, see Astrop & Hegna (2015). (2) Estheriiniins are part of a complex group of diplostracans having a strong convex umbonal region. This particularity involves a relationship with the Lioestherioidea (*sensu* Holub & Kozur, 1981); nevertheless, the estheriiniins received various systematic assignments. The placement of *Estheriina* in the family Palaeolimnadiidae is admitted here, in agreement with Kobayashi (1954) and Tasch (1969, 1987); nevertheless, Chen & Shen (1985) included this genus in the family Euestheriidae, because they inferred the presence of a reticular ornamentation. However, we concede that this group needs a thorough revision because, even if the type species *Estheriina bresiliensis* Jones, 1897 shows a punctate ornamentation between the growth bands, the convex umbonal area is known in other families or superfamilies.

Estheriina bethunensis (DEFRETIN, 1953)

USTL 1064: Left and right valves (Syntype of *Estheria* (*Estheriina*) *bethunensis* Defretin, 1953, pl. X, figs. 1-6).

Loc.: Roof of the parasequence encountered at the depth -530 m, Pit 5bis, Concession of Bully, Group of Béthune (Pas-de-Calais, France).

Lithost.: Probably sampled at the base of the Six-Sillons Member (see Hennion *et al.*, this volume).

Chronost.: Carboniferous, Westphalian (now Moscovian).

Remarks. The counterprint of the *Estheriina bethunensis* type (fig. 2 of Defretin, 1953) was not re-found in the course of our investigation.

Comments. Apparently, the combination *Estheria* (*Estheriina*) was proposed by Defretin (1953), because she mentioned that, after the description of Jones (1897), no species were described, and that this latter author did not provide any justifications. We agree with this assignment to *Estheriina bethunensis*, but we cannot provide additional systematic comments, due to the absence of ornamentation characters. The binomen is validly published here for the first time (see also below the comments about the use of the name “*Estheria*”).

Genus *PALAEOLIMNADIA* RAYMOND, 1946
? *Palaeolimnadia rogeri* NOVOZHILOV, 1958b

401-21: Left valve (holotype of *Eulimnadia rogeri* Novozhilov, 1958b, pl. IV, fig. 59).

Loc.: Littoral of Laptev Sea, Tigian river, core of borehole K-202, depth 372.5-375.7 m (Arctic regions of Russia).

Chronost.: Middle Triassic, Anisian or Carnian? (Novozhilov, 1958b, p. 17, 52).

Comments. According to Gallego (2010) and Astrop & Hegna (2015), the Novozhilov's original assignment of this fossil species to an extant genus is to revise. Also the present assignment to the fossil family and genus is tentative.

Family PALAEOLIMNADIOPSIDAE DEFRETIN-LEFRANC, 1965

Preliminary comments. Astrop & Hegna (2015) indicated that this family was initially recorded from the Devonian of Russia and based on the presence of a curvature in the postero-dorsal angle of the carapace, even if this character only appears in the last growth stages. Such a character is however mentioned in extant and fossil taxa having different hierarchical taxonomic levels, e.g., *Leaia*, *Limnadiopsis* and *Leptestheria*. Hence, Astrop & Hegna (2015, p. 8) suggest that "... [due to] the presence of this character in multiple lineages, it seems unwise that this feature alone should be used to sustain an entire family". We believe that this hypothesis needs to be examined thoroughly, as well as other proposals of Astrop & Hegna (2015) about this family.

Subfamily PALAEOLIMNADIOPSINAE DEFRETIN-LEFRANC,
1965 (*sensu* SHEN, 1985)

Genus *PALAEOLIMNADIOPSIS* RAYMOND, 1946
Palaeolimnadiopsis brevis NOVOZHILOV, 1958a

1126-6: Right valve (holotype of *Palaeolimnadiopsis brevis* Novozhilov, 1958a, pl. I, fig. 12).

Loc.: Right bank of Vetluga (which is a right bank tributary of Volga River); upper part of rapids between Spass and Kostliv villages (High-Volga Basin, Russia).

Lithost.: Spasskien Member (= Vetlugian 4).

Chronost.: Early Triassic, Vetlugian (i.e., a continental regional stage equivalent of Induan-Olenekian).

Palaeolimnadiopsis kouznetskensis DEFRETIN-LEFRANC, 1965

950-54/5: Right valve (ill. as *Palaeolimnadiopsis albertii* Voltz, 1837 in Novozhilov, 1958a, pl. I, fig. 10; paratype of *Palaeolimnadiopsis kouznetskensis* Defretin-Lefranc, 1965, pl. III, fig. 2).

Loc.: Right bank of Tom river, 0.5 km upstream for Babii Kamen (western Siberia, Russia).

Lithost.: Maltsevo Group.

Chronost.: Early Triassic, upper zone.

1126-4: Left valve (ill. as *Palaeolimnadiopsis albertii* Voltz, 1837 in Novozhilov 1958a, pl. I, fig. 9; paratype of *Palaeolimnadiopsis kouznetskensis* Defretin-Lefranc, 1965, pl. III, fig. 1).

Locality, lithost., chronost.: As for the specimen 1126-6.

Genus *BELGOLIMNADIOPSIS* NOVOZHILOV, 1958a
Belgolimnadiopsis stockmansii (MAILLIEUX, 1939)
emend. NOVOZHILOV, 1958a

USTL 1065: Right valve (ill. as *Estheria stockmansii* Maillieux, 1939 in Defretin, 1950a, pl. I, fig. 7).

Loc.: Vincly (Pas-de-Calais, France).

Lithost.: Matringhem Sandstone.

Biostr. and chronost.: "Fish beds" – *Rhinopteraspis dunensis* biozone, Pragian-Emsian (Early Devonian) according to Blicek & Janvier (1989).

USTL 1066: Left valve (ill. as *Estheria stockmansii* Maillieux, 1939 in Defretin, 1950a, pl. I, fig. 6).

Loc., lithost., biostr., chronost.: As for the specimen USTL 1065.

Comments. Being one of the oldest taxa of this group, this species informs about the origin and diversification of the Spinicaudata.

Genus *ROSSOLIMNADIOPSIS* NOVOZHILOV, 1958a
Rossolimnadiopsis marlierei NOVOZHILOV, 1958a

1106-3: Left valve (holotype of *Rossolimnadiopsis marlierei* Novozhilov, 1958a, pl. I, fig. 1).

Loc.: Vyazniki town (Vladimir oblast, Russia).

Chronost.: Late Permian, Kazanian (now Middle Permian, and probably Wordian).

Comments. Another interesting species informing about the early diversification of Spinicaudata.

Subfamily ASIOLIMNADIOPSEINAE LIU, 1982

Genus *ENDOLIMNADIOPSIS* SHEN, 1985
Endolimnadiopsis eichwaldi (NECHAEV, 1894) emend. SHEN, 1985

818-7: Right valve (homotype of *Palaeolimnadiopsis eichwaldi* (Nechaev, 1894) in Novozhilov, 1958a, pl. I, fig. 8).

Loc.: Tatarstan, Kitiak river, near Akbatyrov village (Volga region, Russia).

Chronost.: Late Permian, Kazanian (now Middle Permian, Wordian).

Comments. This is the type species of a genus which is also recorded from the Late Triassic strata from Argentina with *Endolimnadiopsis rusconi* (Gallego, 2005).

Subfamily ANOMALONEMATINAE NOVOZHILOV, 1958d

Genus *ANOMALONEMA* RAYMOND, 1946
Anomalonema reumauxi (PRUVOST, 1911)

Fig. 1A

USTL 1336: Right valve (Defretin-Lefranc, 1970, pl. XIII, fig. 8).
Loc.: Northern "bowette" 4 at the depth 754 m, distance 170 m, Concession of Crespin, Group of Valenciennes (Nord, France).

Lithost.: Bruay Formation.

Chronost.: Carboniferous, Westphalian C (now late Moscovian).

Comments. Due to its particular morphology and restricted stratigraphic distribution, this interesting species constitutes an excellent fossil guide of the Westphalian C-D *Anomalonema reumauxi-Pseudestheria simoni* Assemblage-Zone (Schneider *et al.*, 2005).

Family IPSILONIIDAE NOVOZHILOV, 1958a
Genus *KERATESTHERIA* CHERNYSHEV, 1948

Preliminary comments. According to Y.B. Shen (pers. comm., 2015) “*Keratestheria* is very much similar to *Nestoria* in the stout and prominent growth lines and broad growth bands ornamented with large hexagonal reticulation, except for spine-type projections in the different position along the dorsal margin. *Keratestheria* possibly is an aberrant form of the *Nestoria*. So it should be attributed to *Nestoriidae* rather than *Ipsiloniidae*”. Taking into account this situation and the consideration brings on such matter by Astrop and Hegna (2015), we consider to maintain the original assignation to prevent further systematic confusions. On the other hand, this important fossil marker for the Jurassic-Cretaceous from Asia, is an important component of the Kimmeridgian *Nestoria-Keratestheria* fauna (Chen *et al.*, 2007).

Keratestheria bukaczacziensis CHERNYSHEV, 1948

903-19: Left valve (Novozhilov, 1958a, pl. II, fig. 21; Defretin-Lefranc, 1965, pl. III, fig. 6).

Loc.: Rossyp rapids, right bank of Kuenga river, left bank tributary of Shilka river, itself tributary of Amur River, in front of the Utany village, Chita area (Transbaikalia, Russia).

Chronost.: Middle Jurassic.

903-25: Right valve (neotype of *Keratestheria bukaczacziensis* Chernyshev, 1948 in Novozhilov, 1958a, pl. II, fig. 19; Defretin-Lefranc, 1965, pl. III, fig. 5).

Loc., chronost.: As for the specimen 903-19.

903-31: Right valve (homotype of *Keratestheria bukaczacziensis* Chernyshev, 1948 in Novozhilov, 1958a, pl. II, fig. 20).

Loc., chronost.: As for the specimen 903-19.

Comments. As already suggested by Novozhilov (1958a) and Defretin-Lefranc (1965), the three specimens assigned to *Keratestheria bukaczacziensis* have no preserved “winglike” process (*sensu* Astrop & Hegna, 2015).

Keratestheria magna CHERNYSHEV, 1948
Fig. 1B-C

903-21: Right valve (neotype of *Keratestheria magna* Chernyshev, 1948 in Novozhilov, 1958a, pl. II, fig. 16).

Loc., chronost.: As for the specimen 903-19.

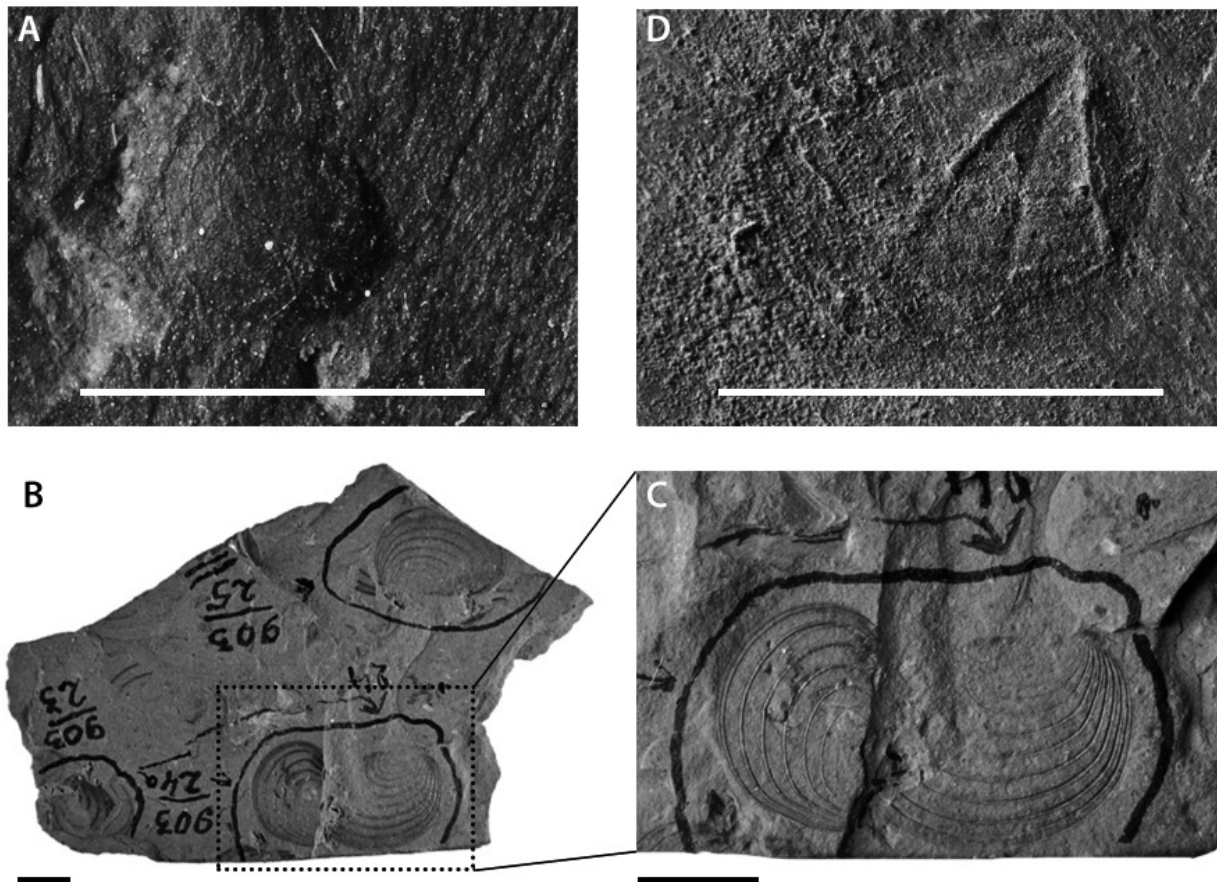


Fig. 1. — A- *Anomalonema reumauxi*, specimen USTL 1336, Westphalian; B-C- *Keratestheria magna* and *Keratestheria rugosa*, specimen 903-24, Middle Jurassic; D- *Hemicycloleia baentschiana*, specimen USTL 1094, Lower Stephanian. Scale bar represents 5 mm.

Fig. 1. — A- *Anomalonema reumauxi*, spécimen USTL 1336, Westphalien; B-C- *Keratestheria magna* et *Keratestheria rugosa*, spécimen 903-24, Jurassique moyen; D- *Hemicycloleia baentschiana*, spécimen USTL 1094, Stéphanien inférieur. L'échelle représente 5 mm.

903-24a: Right valve (paratype of *Keratesthesia magna* Chernyshev, 1948 in Defretin-Lefranc, 1965, pl. III, fig. 7).

Loc., chronost.: As for the specimen 903-19.

903-32: Left valve (homotype of *Keratesthesia magna* Chernyshev, 1948 in Novozhilov, 1958a, pl. II, fig. 17).

Loc., chronost.: As for the specimen 903-19.

Comments. The specimen 903-32 is very difficult to compare with the other representatives of this species.

Keratesthesia rugosa CHERNYSHEV, 1948

903-24: Right valve (ill. as *Keratesthesia magna* Chernyshev, 1948 in Novozhilov, 1958a, pl. II, fig. 18; Defretin-Lefranc, 1965, pl. III, fig. 7).

Loc., chronost.: As for the specimen 903-19.

Remarks. This specimen was identified by Novozhilov (1958a) as *Keratesthesia magna*; in contrast, Defretin-Lefranc (1965) assigned the illustrated specimen to *K. rugosa* (but not listed in the synonymy list), and the other specimen, located just to the left, to *K. magna*. Due to this initial discrepancy, both species remain hard to discriminate (Fig. 1B-C).

903-30: Left valve (holotype of *Keratesthesia kusumii* Novozhilov, 1958a, pl. II, fig. 23; Defretin-Lefranc, 1965, pl. III, fig. 4).

Loc., chronost.: As for the specimen 903-19.

903-32a: Left valve (Defretin-Lefranc, 1965, pl. III, fig. 3).

Loc., chronost.: As for the specimen 903-19.

903-33: Left valve (homotype of *Keratesthesia rugosa* Chernyshev, 1948 in Novozhilov, 1958a, pl. II, fig. 14).

Loc., chronost.: As for the specimen 903-19.

903-35: Left valve (neotype of *Keratesthesia rugosa* Chernyshev, 1948 in Novozhilov, 1958a, pl. II, fig. 15).

Loc., chronost.: As for the specimen 903-19.

903-34: Left valve (neotype of *Keratesthesia tumida* Chernyshev, 1948 in Novozhilov, 1958a, pl. II, fig. 22).

Loc., chronost.: As for the specimen 903-19.

Comments. The specimen 903-33 is very difficult to compare with the other specimens of this species. Defretin-Lefranc (1965) suggested the specimen 903-34 as a synonym of *K. rugosa*. We agree with this proposal based on the similar morphology of the antero-dorsal recurvature.

Family LIOESTHERIIDAE RAYMOND, 1946 emend. HOLUB & KOZUR, 1981

Subfamily VERTEXIIDAE KOBAYASHI, 1954

Genus *CORNIA* LYUTKEVICH, 1937

Cornia sibirica (NOVOZHILOV, 1958a) emend. DEFRETIN-LEFRANC, 1965

950-17/18: Right valves (paratype of *Gabonestheria sibirica* Novozhilov, 1958a, pl. II, figs. 31-32; Defretin-Lefranc, 1965, pl. II, fig. 9).

Loc., lithost., chronost.: As for the specimen 950-54/5 (see p. 121).

950-19: Right valve (paratype of *Gabonestheria sibirica* Novozhilov, 1958a, pl. II, fig. 33).

Loc., lithost., chronost.: As for the specimen 950-54/5.

950-21: Left valve (holotype of *Gabonestheria sibirica* Novozhilov, 1958a, pl. II, fig. 30; Defretin-Lefranc, 1965, pl. II, fig. 10).

Loc., lithost., chronost.: As for the specimen 950-54/5.

950-21b: Right valve (paratype of *Cornia sibirica* Novozhilov, 1958 in Defretin-Lefranc, 1965, pl. II, fig. 8).

Loc., lithost., chronost.: As for the specimen 950-54/5.

Comments. For a detailed discussion on the genus assignment of this species, see Defretin-Lefranc (1965), but briefly we can note that she argued against and finally rejected the erection of the genus *Gabonestheria* Novozhilov (1958a). This proposal is to revise, taking into account that this genus is considered valid by different authors as Tasch (1969, 1987) and Chen & Shen (1985).

Superfamily EOESTHERIOIDEA ZHANG & CHEN, 1976 IN ZHANG *et al.*, 1976

Family ULUGKEMIIDAE NOVOZHILOV, 1958

Genus *ULUGKEMIA* NOVOZHILOV, 1955

Ulugkemia borisi NOVOZHILOV, 1959

1342c-120: Left valve (Defretin-Lefranc, 1965, pl. I, fig. 10).

Loc.: Left bank of Kitiak stream right bank tributary of Viatka river, itself tributary of Volga River, near the Bolchoi Kitiak village, Malmyzh district, Kirov province (High-Volga Basin, Russia).

Lithost.: Belebei Formation.

Biostr.: Lower beds with conchostracans and insects.

Chronost.: Late Permian, Kazanian (now Middle Permian, Wordian).

1342c-121/1: Left valve (Defretin-Lefranc, 1965, pl. I, fig. 11).

Loc., lithost., biostrat., chronost.: As for the specimen 1342c-120.

1342c-134: Right valve (Defretin-Lefranc, 1965, pl. I, fig. 9).

Loc., lithost., biostrat., chronost.: As for the specimen 1342c-120.

Family EUESTHERIIDAE DEFRETIN-LEFRANC, 1965

Genus indet.

“Estheria” destombesi DEFRETIN, 1950b

Preliminary comments. For this species, we retain the original designation of Defretin (1950b) and agree with her arguments implying an absence of ornamentation, which consequently prevents the assignment to any other known genera. Definitely, *“Estheria”* cannot be used as a genus of diplostracans because it is homonym and pre-occupied by the insect (parasite flies) name *Estheria* Robineau-Desvoidy, 1830 (see Raymond, 1946 and Gallego, 2010).

USTL 1073: Right valve (paratype of *Estheria destombesi* Defretin, 1950b, pl. IX, fig. 2).

Loc.: Saint-Menge, mine waste (Vosges, France).

Chronost.: Triassic.

USTL 1076: Left valve (paratype of *Estheria destombesi* Defretin, 1950b, pl. IX, fig. 4).

Loc., chronost.: As for the specimen USTL 1073.

USTL 1078: Right valve (paratype of *Estheria destombesi* Defretin, 1950b, pl. IX, figs. 5-6).

Loc.: Borehole of Lacoste, depth 155 m (Gard, France).

Chronost.: Triassic, Middle Keuper.

USTL 1079: Left valve of a juvenile specimen (holotype of *Estheria destombesi* Defretin, 1950b, pl. IX, fig. 7; Defretin-Lefranc, 1963, pl. I, fig. 16).

Loc., chronost.: As for the specimen USTL 1078.

USTL 1089: Right valve (Defretin & Fauvelet, 1951, pl. I, fig. 6).

Loc.: Argana-Bigoudine area (western High-Atlas, Morocco).

Lithost.: Ait Khtab Group (Ait Khtab is now written Ait Khattab).

Chronost.: Triassic.

USTL 1090: Right valve (Defretin & Fauvelet, 1951, pl. I, fig. 5).

Loc., lithost., chronost.: As for the specimen USTL 1089.

Genus indet.

“*Lioestheria*” *toricata* (NOVOZHILOV, 1946)

401-47: Left valve (holotype of *Lioestheria toricata* (Novozhilov, 1946) in Novozhilov, 1958b, pl. III, fig. 28).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

Comments. Novozhilov (1958b) included this species in *Lioestheria*, because of its alveolar ornamentation. However, the current ideas on the lioestheriid taxonomy lead us to doubt this genus assignment.

“*Lioestheria*” *propinqua* NOVOZHILOV, 1958b

400-9: Right valve (holotype of *Lioestheria propinqua* Novozhilov, 1958b, pl. III, fig. 29).

Loc., chronost.: As for the specimen 400-4 (see p. 126).

Comments. See above.

Genus *EUESTHERIA* DÉPERET & MAZERAN, 1912

Euestheria bourozi DEFRETIN-LEFRANC, 1970

Preliminary comments. Defretin-Lefranc (1970, p. 125) mentioned that the reticular ornamentation is conformed by areola having 0.05 mm in diameter; therefore, we think that this species belongs to the family Loxomegaglyptidae.

USTL 1337: Left valve (holotype of *Euestheria bourozi* Defretin-Lefranc, 1970, pl. XIII, fig. 4).

Loc.: Borehole 23 at the depth 650.22 m, Pit 6 South, Concession of Courrières, Group of Hénin-Liétard (Pas-de-Calais, France).

Lithost.: Bruay Formation, Six-Sillons Member.

Chronost.: Carboniferous, Westphalian C (now late Moscovian).

Euestheria evenkiensis (LYUTKEVICH, 1938)

Preliminary comments. This species was originally designated by Lyutkevich (1938) as “*Estheria*” *evenkiensis*, and subsequently emplaced in the genus *Lioestheria* by Novozhilov (1958b), or *Palaeostheria* by Defretin-Lefranc (1965). According to Raymond (1946), *Palaeostheria* was never validly described, even if it was mentioned in several publications (e.g., Daday de Déés, 1914; Barnard, 1929; Rennie, 1934). Daday de Déés (1914) suggested to use preferentially the names *Palaeostheria* and Palaeostheriidae for the fossil *Estheria* (spinicaudatans), and to restrict the name *Estheria* (see

comments on “*Estheria*” *destombesi* below) to modern species; however, neither particular species nor genotype were formally designed by Daday de Déés (1914). Raymond (1946) regarded *Palaeostheria* as a *nomen nudum*. Despite this, Barnard (1929) had used this genus, and described five species, *P. anomala* Barnard, *P. draperi* Barnard, *P. greyi* Barnard and two innominate species, from different localities and stratigraphic levels; but again no genus diagnosis was provided by Barnard. That is probably why Raymond (1946) proposed to attribute the genus to Barnard and Daday de Déés. Meanwhile, Rennie (1934) described (but still without any diagnosis) and illustrated a poorly preserved Devonian-Carboniferous species that he named according to Daday de Déés (1914) as *Palaeostheria* sp.. Consequently, Raymond (1946) proposed *Palaeostheria anomala* as type species, and introduced the following genus diagnosis: “*Carapace oval, umbonal region smooth, the remainder bearing numerous narrow, sharp costellae, between which there is no ornament.*” Raymond explained also that: “*This genus is in many respects similar to Pseudestheria, but differs in having more numerous and more close-set costellae, and particularly in having a larger smooth area at the umbo.*” Defretin-Lefranc (1967) described the species, and emphasized the presence of a rounded or elongate tubercle in the umbonal area. Then, Busnardo (1969) described four Late Triassic species from Spain and accurately revised and discussed the genus diagnosis. He noticed also that Novozhilov (1960) omitted the genus in his work, probably because he previously synonymized it with *Ovjurium* Novozhilov & Varentsov (1956). On the other hand, Kobayashi (1954) synonymized it with *Lioestheria*, because of its smooth umbonal area. Furthermore, due to the presence of a tubercle (*sensu* Defretin-Lefranc, 1967), Chen & Shen (1985, p. 70) included this genus (erroneously written as *Palaeostheria*) in the family Palaeolimnadiidae. Contrary to these interpretations, Tasch (1969, 1987) did not agree with the large smooth or even nodal structures of the umbonal area and transferred all the species of *Palaeostheria* to the genus *Cyzicium* and subgenus *Euestheria* or *Lioestheria*. Kozur & Weems (2007) highlighted the taxonomic incongruence of this proposal, since *Euestheria* Depéret & Mazeran, 1912 being the junior synonym of *Palaeostheria* Barnard, 1929, *Euestheria* is necessarily the priority name of the taxon. In this paper, we included *E. evenkiensis* in *Euestheria*, due to 1) the reticular ornamentation (Defretin-Lefranc, 1965), 2) the absence of a node in the umbonal area (this latter is present in *Lioestheria sensu* Kozur *et al.*, 1981), and 3) the absence of a smooth umbonal region (as in *Palaeostheria* Barnard *sensu* Raymond, 1946).

815-25/1: Right valve (ill. as *Palaeostheria evenkiensis* Novozhilov, 1958b in Defretin-Lefranc, 1965, pl. I, fig. 2).

Loc.: Right bank of Lower Tunguska River, left bank tributary of Yenisey River, 271 km downstream from the confluence of the Ilmpeia River or 6 km upstream from the confluence of the Khovorkili River (Central Siberia, Russia).

Lithost.: Khovorkili Zone = Tatarian 4 Zone.

Chronost.: Late Permian, late Tatarian (now Changhsingian).

815-25/2: Right valve (holotype of *Palaeostheria evenkiensis* Novozhilov, 1958b in Defretin-Lefranc, 1965, pl. I, fig. 1).

Loc., lithost., chronost.: As for the specimen 815-25/1.

Remarks. There is a *lapsus calami* in the original publication; the holotype has not the number 915, valve n°25-2 as written, but the number 815, valve n°25-2.

Euestheria minuta (VON ZIETEN, 1833) RAYMOND, 1946

USTL 1072: Right valves (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin, 1950b, pl. VIII, fig. 5).

Loc.: Lacoste borehole, 149 m depth (Gard, France).

Chronost.: Late Triassic, Middle Keuper.

USTL 1074: Fragments of shell (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin, 1950b, pl. VIII, fig. 6).

Loc.: Lacoste borehole, 156 m depth (Gard, France).

Chronost.: Late Triassic, Middle Keuper.

USTL 1075: Right valve (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin, 1950b, pl. VIII, fig. 3).

Loc.: Vouhenans; x = 406.15, y = 96.1 (Haute-Saône, France).

Chronost.: Late Triassic, Middle Keuper.

USTL 1077: Left valve (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin, 1950b, pl. VIII, fig. 2; Defretin-Lefranc, 1963, pl. I, fig. 14).

Loc., chronost.: As for the specimen USTL 1073 (see p. 123).

USTL 1079: Left valve (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin, 1950b, pl. IX, fig. 1).

Loc., chronost.: As for the specimen USTL 1078 (see p. 123).

USTL 1081: Left valve (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin, 1950b, pl. VIII, fig. 1).

Loc.: Gemmelaincourt mine, borehole near the Cracco pit, x = 369.12, y = 166.51 (Vosges, France).

Chronost.: Late Triassic, Middle Keuper.

USTL 1082: Group of valves (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin, 1950b, pl. VIII, fig. 4).

Loc.: Conliège borehole, depth 371.4 m (Jura, France).

Chronost.: Triassic.

USTL 1085: Right and left valves (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin-Lefranc, 1963, pl. I, fig. 15).

Loc.: Bex (Switzerland).

Chronost.: Triassic.

USTL 1087: Right valve (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin-Lefranc, 1963, pl. I, fig. 12).

Loc.: Pechelbronn, borehole 4617, depth 1515-1516 m (Bas-Rhin, France).

Lithost.: Keuper, bed Ku 2.

Chronost.: Late Triassic.

Remarks. This other misinterpreted specimen comes in reality from the depth 1515-1516 m, as written in the legend and on the label associated with the specimen, and not from 1915-1916 m as written in the publication.

USTL 1088: Group of valves (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin & Fauvelet, 1951, pl. I, figs. 1-2).

Loc.: Argana-Bigoudine area, borehole 14 (western High-Atlas, Morocco).

Lithost.: Bed A2.

Chronost.: Triassic.

USTL 1090: Left and right valves (ill. as *Estheria minuta* Alberti in von Zieten, 1833 in Defretin & Fauvelet, 1951, pl. I, figs. 3-4).

Loc., lithost., chronost.: As for the specimen USTL 1089 (see p. 124).

Comments. This species displays large variations in morphology and outline, probably related to geographic and stratigraphic varieties; the Lille's collection will permit a detailed population analysis. Due to its restricted stratigraphic distribution (Middle to Late Triassic) and cosmopolitanism, this species is an interesting palaeontologic tool.

Euestheria ricouri (DEFRETIN, 1950b)

USTL 1080: Left valve (holotype of *Estheria ricouri* Defretin, 1950b, pl. IX, fig. 8).

Loc.: Montgivray (Indre, France).

Chronost.: Early Jurassic, Hettangian.

Comments. Defretin (1950b) assigned this species to the genus and subgenus *Estheria* (*Euestheria*) *ricouri*. We modified the binomen, since we consider now *Euestheria* as a genus, based on the revised spinicaudatan taxonomy. Defretin (1950b) compared *Euestheria ricouri* with *E. brodieana* Jones. This latter species was interpreted by Kozur & Weems (2010) as a Rhaetian (latest Triassic) fossil guide in Germany and the USA, even if it subsists up to the early Hettangian (earliest Jurassic) in the USA.

Euestheria simoni (PRUVOST, 1911) PRUVOST, 1919

USTL 1338: Right valve (ill. as *Cycladestheria simoni* (Pruvost, 1911) in Defretin-Lefranc, 1970, pl. XIII, fig. 3).

Loc.: Borehole 11F, depth 136.75 m, Douai Group (Nord, France).

Lithost.: Bruay Formation.

Chronost.: Carboniferous, Westphalian C (now late Moscovian).

Comments. This species is assigned to *Euestheria* taking into account the synonymy of Defretin-Lefranc (1970) who mentioned that Feys (1953) designated this species as *Estheria* (*Euestheria*) *simoni*. Defretin-Lefranc (1970) described also a reticular ornamentation measuring 0.02 to 0.05 mm. The validity of the genus *Cycladestheria* Defretin-Lefranc, 1970 will be analyzed in the future with detailed population studies. Finally, we consider that this species, which possibly belongs to Loxomegaglyptidae, needs a detailed revision. *E. simoni* is an important biostratigraphic species, being characteristic of the Westphalian C-D *Anomalonema reumauxi-Pseudestheria simoni* Assemblage-Zone (Schneider *et al.*, 2005).

Family LOXOMEGAGLYPTIDAE NOVOZHILOV, 1958d

Preliminary comments. This family was defined by Zhang *et al.* (1976) and Astrop & Hegna (2015) as follows: "Growth bands wide and flat with large, irregular 'mesh' ornament, the walls of which are shallow and thin. Ornament elongates transversely with ontogeny. (...) Generally with cycliciform-cycladiform carapace shapes". Notwithstanding, a more detailed diagnosis was published later by Chen & Shen (1982) as: "Carapace valve elliptical to obliquely oval in outline; growth band broad and flattened, few in number, ornamented with variant moderate to large reticulations or caverns; each mesh 0.02-0.2 mm in size".

Genus LAXITEXTELLA KOZUR, 1982

Preliminary comments. The genus *Laxitextella* Kozur, according to Kozur & Weems (2007, 2010), comprises forms with ornamentation ranging from reticulate, polygonal to elongate parallel to the growth lines patterns. This genus was placed by Chen & Shen (1985) in the Eosestherioidea Loxomegaglyptidae, while Kozur & Weems (2005) included

it in their new family Shipingiidae composed of *Shipingia* Shen, *Anyuanestheria* Zhang & Chen, *Laxitextella* Kozur and *Redondestheria* Kozur, Weems & Lucas. These Shipingiidae were found in China, Germany and along the United States East Coast (in the Newark Supergroup). According to Kozur & Weems (2005), the Loxomegalyptidae differ from the Shipingiidae by their small dimensions and their umbo located at middle of the dorsal margin. Moreover, the Loxomegalyptidae are Early Triassic in age, whereas the Shipingiidae are Late Triassic. Kozur & Weems (2005) did not mention the systematic placement of Shipingiidae within a pre-existing superfamily; in our opinion, the Shipingiidae encompass some spinicaudatans with different fundamental morphologic features, as the genus *Laxitextella* Kozur, that lacks the radial lirae in the ventral growth bands (see Kozur & Weems, 2005).

Laxitextella laxitexta (JONES, 1878) emend. KOZUR, 1982

USTL 1083: Left valve (ill. as *Estheria laxitexta* (Jones, 1878) in Defretin-Lefranc, 1963, pl. I, fig. 11).

Loc.: Saint-Lattier, borehole S.P.V. 2734 (Isère, France).

Chronost.: Triassic.

USTL 1084: Right and left valves (ill. as *Estheria laxitexta* (Jones, 1878) in Defretin-Lefranc, 1963, pl. I, figs. 8-9).

Loc.: Pechelbronn, borehole 4653, depth 837 m (Bas-Rhin, France).

Lithost.: Bed assigned to the Lettenkohle (unit Ku 1).

Chronost.: Triassic.

USTL 1086: Group of valves (ill. as *Estheria laxitexta* (Jones, 1878) in Defretin-Lefranc, 1963, pl. I, fig. 10).

Loc., chronost.: As for the specimen USTL 1083.

Comments. Evolutionarily and biostratigraphically, this species is important, because 1) it is a clue species to clarify the relationship between the Euestheriidae, Loxomegalyptidae and Shipingiidae and 2) it is an important component of the Carnian *Gregoriusella fimbriata*–*Laxitextella laxitexta* Zone (Kozur & Weems, 2010).

Family ORTHOTHEMOSIIDAE DEFRETIN-LEFRANC, 1965

Preliminary comments. Astrop & Hegna (2015), based on Defretin-Lefranc (1965), defined this family as follows: “*Valves are relatively short and the ventral anterior and posterior edges regularly rounded. The umbo is approximately 2/5 of the hinge. Ornamentation punctuated or smooth*”. These authors add that they are “*Cycladiform-telliniform in shape*”, and discuss that “*Defretin-Lefranc (1965) erected Orthothemosiinae with the above diagnosis. Zhang et al. (1976), and Chen and Shen (1985) elevated it to family rank. It is not very diverse and, like Aquilonoglyptidae discussed above, may ultimately be more fruitfully considered a part of the euestheriids.*” Defretin-Lefranc (1965) and Tasch (1987) interpreted Orthothemosiinae at the subfamily level, and included it in the family Asmusiidae (see next comments; and those about the genus *Glyptoasmussia*, below). The family Asmusiidae is a particularly controversial taxon, which is defined by its straight long dorsal margin and its strong angles at both ends and subcentral umbo. The diagnosis (Kobayashi, 1954 emended by Tasch, 1969) mentioned an ornamentation ranging from smooth, punctuate, with radial lirae, to alveolar. Chen & Shen (1985) assigned this family to the superfamily Estheriteoidea, due to its radial ornamentation. Nevertheless, Raymond (1946) mentioned that the type genus (*Asmusia*) and its type species (*A. membranacea* Pacht) both display a reticulate ornamentation. Defretin (1950a)

described this species with a striated ornamentation. Astrop & Hegna (2015) thinks to a translation of the emended diagnosis of Zhang *et al.* (1976), stated that this species has: “*Growth lines adorned with fine fiber-like ornament (described as ‘hachure’ by Tasch (1969))*” and added the following diagnostic criterion: “*Cyziciform in carapace shape, often with umbo situated in the center of the dorsal margin*”.

Genus *GLYPTOASMUSSIA* NOVOZHILOV & VARENTSOV, 1956

Preliminary comments. The diagnosis, translated by Defretin-Lefranc (1965) and emended by Tasch (1987), is: “*Anterior and posterior margin narrowly or broadly rounded; the dorsal margin in front of the umbo is two-thirds or more the length of the margin behind the umbo, except where umbo is submedial. Valve height less than or almost equal to the length. Ornamentation fine and alveolar (i.e., with small depressions or pits).*” There is an inconsistency in the type of ornamentation between the diagnosis of family (punctuated or smooth) and genus (fine and alveolar). The comments on the family Asmusiidae (above) and the present comment on the alveolar ornamentation of the genus *Glyptoasmussia*, permit to devise why Novozhilov (1958b, p. 37) erected the family Glyptoasmussiidae, but we do not use this latter family here.

Glyptoasmussia quadrata NOVOZHILOV, 1958b

400-4: Right valve? (holotype of *Glyptoasmussia quadrata* Novozhilov, 1958b, pl. III, fig. 36).

Loc.: Eastern Taimyr, near Cape Tsvetkov (Russia).

Chronost.: Early Triassic (upper zone).

Remarks. Even though the specimen in the collection has exactly the numbering indicated in the Novozhilov’s publication, it might be different; the insufficient photographs of the publication do not permit indeed its precise identification.

400-5: Left valve (Defretin-Lefranc, 1965, pl. II, fig. 6).

Loc., chronost.: As for the specimen 400-4.

400-10: Right valve (holotype of *Concherisma tomensis* Novozhilov, 1958b, pl. IV, fig. 50; synonymized by Defretin-Lefranc, 1965, pl. II, fig. 7).

Loc., chronost.: As for the specimen 400-4.

Remarks. As indicated above for sample 400-4, this specimen, although having the number indicated in the Novozhilov’s publication, probably differs from the illustrated individual.

Genus *TAIMYRITES* NOVOZHILOV, 1958b

Preliminary comments. Chen & Shen (1985, p. 178-179) placed this genus among their chapter of questionable taxa. Due to its particular morphological outline, we consider that this taxon is well characterized; and following the Novozhilov’s (1958b) placement, we include it in the family Orthothemosiidae.

Taimyrites strachovi NOVOZHILOV, 1958b

400-16: a specimen with the two valves (holotype of *Taimyrites strachovi* Novozhilov, 1958b, pl. IV, fig. 47).

Loc., chronost.: As for the specimen 400-4 (see p. 126).

Remarks. This specimen has effectively the collection number mentioned in the Novozhilov's publication, but probably does not correspond the illustrated specimen; but once again, the poor quality of the photographs of the publication does not permit to conclude with certainty.

Family unknown (probably Orthothemosiidae, see below)
Genus *PSEUDESTERIA* RAYMOND, 1946

Preliminary comments. This genus was created by Raymond (1946), as a group of morphospecies without stratigraphic significance. Raymond (1946) recognized that this taxon "... must inevitably become a sort of dumping ground for not too well preserved fossils." Raymond (1946) defined this genus as: "*Lioestheriidae* with oval carapace, engirdled by concentric lirae or costellae separated by spaces equal or greater than their own width. No sculpture, except punctuation, is present in the intervals." The last sentence reflects either the complete absence of ornamentation between the growth lines, or the presence of a punctuated ornamentation that is related with the Eoestherioidea-Euestheriidae complex and more precisely with the family Orthothemosiidae.

Pseudestheria borisi DEFRETIN-LEFRANC, 1965

1342c-151a: Left valve (holotype of *Pseudestheria borisi* Defretin-Lefranc, 1965, pl. I, fig. 7).

Loc., lithost., biostrat., chronost.: As for the specimen 1342c-120 (see p. 123).

1342c-155/1: Right valve? (paratype of *Pseudestheria borisi* Defretin-Lefranc, 1965, pl. I, fig. 8).

Loc., lithost., biostrat., chronost.: As for the specimen 1342c-120 (see p. 123).

Pseudestheria hersinensis DEFRETIN-LEFRANC, 1970

USTL 1333: Right valve (paratype of *Pseudestheria hersinensis* Defretin-Lefranc, 1970, pl. XIII, fig. 2).

Loc.: Borehole 031 at the depth 386.90 m, level - 482, Pit 3 west, Concession of Courrières, Group of Hénin-Liétard (Pas-de-Calais, France).

Lithost., chronost.: As for the specimen USTL 1337 (see p. 124).

USTL 1335: Right valve (holotype of *Pseudestheria hersinensis* Defretin-Lefranc, 1970, pl. XIII, fig. 1).

Loc.: Parasequence at 128 m, "bowette" Nord 555, Pit 7, Concession of L'Escarpelle, Group of Douai (Nord, France).

Lithost., chronost.: As for the specimen USTL 1337 (see p. 124).

Pseudestheria tatarimensis DEFRETIN-LEFRANC, 1965

1342c-159: Left valve (Defretin-Lefranc, 1965, pl. I, fig. 5).

Loc., lithost., biostrat., chronost.: As for the specimen 1342c-120 (see p. 123).

1342c-161: Left valve (Defretin-Lefranc, 1965, pl. I, fig. 6).

Loc., lithost., biostrat., chronost.: As for the specimen 1342c-120 (see p. 123).

Pseudestheria tungussensis (LYUTKEVICH, 1938) emend.
DEFRETIN-LEFRANC, 1965

815-2b: Left valve (Defretin-Lefranc, 1965, pl. I, fig. 3).

Loc., lithost., chronost.: As for the specimen 815-25/1 (see p. 124).

815-27/3: Left valve (Defretin-Lefranc, 1965, pl. I, fig. 4).

Loc., lithost., chronost.: As for the specimen 815-25/1 (see p. 124).

Family AQUILONOGLYPTIDAE NOVOZHILOV, 1958b

Preliminary comments. According to Astrop & Hegna (2015), "*Aquilonoglyptidae* was originally a family based on a single genus (*Aquilonoglypta* Novozhilov, 1958b), which was in turn based on a single species, which was in turn based on a single specimen." These authors stated that: "*Novozhilov (1958b) regarded the features present distinctive enough to warrant such an isolated placement*". These authors also mentioned that: "*Additional species have since been described from China (Wang and Liu, 1980)*", and concluded that: "*the small size of this family almost guarantees that it is monophyletic, but it probably renders Euestheriidae paraphyletic as well*".

Genus *AQUILONOGLYPTA* NOVOZHILOV, 1958b
Aquilonoglypta ardua NOVOZHILOV, 1958b

401-30: Right valve (holotype of *Aquilonoglypta ardua* Novozhilov, 1958b, pl. IV, figs. 54-54a).

Loc.: Cape Ilya, on the southern bank of Khatanga Gulf, borehole P-2, depth 1274-1280 m (Arctic regions of Russia).

Lithost.: Misailap Formation, Khatanga zone = Tatarian 2 zone.

Chronost.: Late Permian, Kazanian (now Middle Permian, Wordian).

Family POLYGRAPTIDAE NOVOZHILOV, 1954
Genus *POLYGRAPTA* NOVOZHILOV, 1946

Preliminary comments. *Polygrapta* was defined as subgenus of *Estheria* by Novozhilov (1946), with *P. chatangensis* as type species, and included in the family Limnadiidae. Then, Novozhilov (1954) created the subfamily Polygraptinae, included in the family Bairdestheriidae, but he did not include this subgenus in this new subfamily, while Novozhilov (1958b) included the genus *Polygrapta* in the family Bairdestheriidae. Zhang *et al.* (1976) and Chen & Shen (1985) included this genus in the family Euestheriidae (see Astrop & Hegna, 2015). Tasch (1987) synonymized this genus with *Cyzicus (Lioestheria)*. Polygraptidae is considered here as a group of estheriteoid spinicaudatan.

Polygrapta chatangensis NOVOZHILOV, 1946

401-2: Group of valves (paratype of *Polygrapta chatangensis* Novozhilov, 1946 in Novozhilov, 1958b, pl. I, fig. 2; Defretin-Lefranc, 1965, pl. II, fig. 2).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

401-4: Right valve? (paratype of *Sphaerograptia dechaseauxae* Novozhilov 1958b, pl. III, fig. 18; Defretin-Lefranc, 1965, pl. II, fig. 1).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

401-5: Left valve (Defretin-Lefranc, 1965, pl. II, fig. 1).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

401-6: Left valve (paratype of *Sphaerograptia dechaseauxae* Novozhilov, 1958b, pl. III, fig. 17).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

401-9: Right valve (metatype of *Polygrapta chatangensis* Novozhilov, 1946 in Novozhilov, 1958b, pl. I, fig. 3).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

401-13/1: Right valve (Defretin-Lefranc, 1965, pl. II, figs. 2 et 5).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

401-50: Right valve (Novozhilov, 1958b, pl. I, fig. 1).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

Comments. Defretin-Lefranc (1965) subsequently designed this specimen as the holotype.

Polygrapta laptevi NOVOZHILOV, 1946

401-58: Left valve (holotype of *Polygrapta laptevi* Novozhilov, 1946 in Novozhilov, 1958b, pl. II, fig. 9).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

Comments. Defretin (1953) rather considered this specimen as a representative of *P. chatangensis*.

Polygrapta multinstita NOVOZHILOV, 1946

401-3: Right valve (holotype of *Polygrapta multinstita* Novozhilov, 1946 in Novozhilov, 1958b, pl. II, fig. 10).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

401-48: Left valve (holotype of *Pemphicyclus arngastachi* Novozhilov, 1946 in Novozhilov 1958b, pl. II, fig. 13; Defretin-Lefranc, 1965, pl. II, fig. 4).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

401-55/55a: Left valve (metatype of *Polygrapta multinstita* Novozhilov, 1946 in Novozhilov, 1958b, pl. II, fig. 12).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

Comments. Although Defretin-Lefranc included both specimens in *P. chatangensis*, they were probably well identified because they are similar to the specimen 401-3.

401-116: Right valve (Defretin-Lefranc, 1965, pl. II, fig. 3).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

Comments. The specimen 401-48 has got a subcircular outline with strong postero-dorsal angle (cycladiform to limnadopsiform) and umbo placed anteriorly; while the specimen 401-116 reflects another morphotype with ovate outline and subcentral umbo probably due to sexual dimorphism.

Polygrapta necta NOVOZHILOV, 1946

401-17: Left valve (paratype of *Polygrapta necta* Novozhilov, 1946 in Novozhilov, 1958b, pl. I, fig. 7).

Loc., lithost., chronost.: As for the specimen 401-30 (see p. 127).

Comments. Defretin (1953) include this specimen in *P. chatangensis* but we think that *P. necta* is a better identification.

Superfamily ESTHERITEOIDEA ZHANG &
CHEN IN ZHANG *et al.*, 1976

Family FUSHUNOGRAPTIDAE WANG IN HONG *et al.*,
1974 Genus indet.

Preliminary comments. The name *Pseudoasmussia* Defretin-Lefranc, 1969 was changed by Tasch (1987) into *Pseudoasmussiata*, due to the homonymy with *Pseudoasmussia* Novozhilov, 1954; even if many species of this genus (including the type species *Pseudoasmussia grassmuecki* Defretin-Lefranc, 1969; corrected spelling here for *grassmückeri*), show a reticulate ornamentation, not consistent with the family diagnosis. Furthermore, Tasch (1969, 1987) synonymized *Pseudoasmussia* Novozhilov, 1954 with *Cyzicus* (*Euestheria*), due to its reticular ornamentation. Therefore, the status and name of the genus described here will remain in open nomenclature as “*Pseudoasmussia*”.

“*Pseudoasmussia*” *striata* (MÜNSTER IN GOLDFUSS, 1826)
emend. DEFRETIN-LEFRANC, 1970

USTL 1334: Left valve (ill. as *Pseudoasmussia striata* (Münster in Goldfuss, 1826) in Defretin-Lefranc, 1970, pl. XIII, fig. 9).

Loc.: Borehole 14F; depth 163.75 m, Douai Group (Nord, France).

Chronost.: Carboniferous, Westphalian (now Moscovian).

Comments. See comments on “*Lioestheria*” *striata* (Hennion *et al.*, this volume).

Suborder LEAIINA KOBAYASHI, 1972
Superfamily LEAIOIDEA RAYMOND, 1946
Family MONOLEIOLOPHIDAE NOVOZHILOV, 1954

Preliminary comments. Our species *Teixeirium rossicum* Novozhilov was previously assigned to the family Estheriellidae (Estheriellina sensu Shen, 2003), but due to the presence of a unique antero-ventral carina, it is transferred to the suborder Leaiina. According to Jones & Chen (2000), and based on the revision of the type species of *Estheriella* Weiss and *Pseudestheriella* from the Early Triassic of Germany, the Estheriellidae is to exclude from Diplostraca and even from Crustacea, and perhaps to assign to Bivalvia. That might confirm the hypothesis of Giebel (1857). Later, according to Shen (2003), the suborder Estheriellina is considered valid. However, Kozur & Weems (2010) did not admit the hypothesis of Jones & Chen (2000), and argued that these materials, being preserved as taphonomic impressions, do not display any structure comparable with bivalve hinges. Our dubious material of *Teixeirium rossicum* Novozhilov might belong to the subfamily Karagandiinae (Estheriellidae) defined by Tasch (1961). However, no further work (Tasch, 1969; Chen & Shen, 1985) has confirmed the validity of this subfamily.

Genus *TEIXEIRIUM* NOVOZHILOV, 1958c

Preliminary comments. Chen & Shen (1985, p. 186) listed, without discussion, this taxon in their chapter of the invalid genus names.

Teixeirium rossicum NOVOZHILOV, 1958c

1321-2: Right valve (holotype of *Teixeirium rossicum* Novozhilov, 1958c, pl. I, fig. 2).

Loc.: Left bank tributary of the Kerzhenets river (itself right bank tributary of the Volga river), 25 km southeast of Ilyinsky-Zaborsky village, Gorkovsk area (Russia).

Chronost.: Late Permian, Tatarian (now Changhsingian).

Comments. The revised material confirms the validity of this genus and species due to its uncommon morphology. Even if these genus and species are not based on only one specimen (contrary to the assertion of Astrop & Hegna, 2015), an additional material is necessary to interpret the real systematic affinities of *Teixeirium rossicum* because its morphology more evokes the suborder Leaiina than the suborder Estheriellina originally assigned by Novozhilov (1958c).

Family LEAIIIDAE RAYMOND, 1946

Genus *HEMICYCLOLEAIA* RAYMOND, 1946

Hemicycloleaia baentschiana (BEYRICH, 1864) RAYMOND, 1946
Fig. 1D

Preliminary comments. Although Waterlot (1934) used the binomen *L. baentschi*, the original name *L. baentschiana* is perfectly valid according to the rules of the International Code of Zoological Nomenclature; hence, we re-use the specific name *baentschiana* and consider *L. baentschi* as a *nomen vanum*.

USTL 1093: Right valve (ill. as *Leaia baentschi* Beyrich, 1864 in Waterlot, 1934, pl. VII, fig. 11).

Loc.: Registered office of Götteborn, 2d floor, at 1 576 m of well II (Saarland, Germany).

Lithost.: Sarrelouis Formation.

Biost.: *Leaia* beds.

Chronost.: Carboniferous, Lower Stephanian (now Kasimovian).

USTL 1094: Right valve (ill. as *Leaia baentschi* Beyrich, 1864 in Waterlot, 1934, pl. VII, fig. 10).

Loc., lithost., biost., chronost.: As for the specimen USTL 1093.

Comments. This sample includes two specimens, the larger of which corresponds to a right valve illustrated by Waterlot (1934) and a small second specimen that corresponds to a left valve; both have got the same distinct character that probably is a taphonomic feature that corresponds to a less marked fourth rib, between the anterior and the posterior ones. Hence, this material needs further studies to clarify its systematics.

USTL 1095: Group of valves (ill. as *Leaia baentschi* Beyrich, 1864 in Waterlot, 1934, pl. VII, fig. 1).

Loc.: Entry of the Frankenholz pit (Saarland, Germany).

Lithost.: Sarrelouis Formation.

Biost.: Shales with *Leaia baentschi*.

Chronost.: Carboniferous, Early Stephanian, Ottweiler subdivision (now Kasimovian).

USTL 1096: Left valve (ill. as *Leaia baentschi* Beyrich, 1864 in Waterlot, 1934, pl. VII, fig. 3).

Loc., lithost., biost., chronost.: As for the specimen USTL 1095.

Comments. This important spinicaudatan species is a secondary biostratigraphic marker of the Stephanian B-C *Pseudestheria* Form Schadewalde-*Lioestheria* Form Frenswegen-*Palaeolimnadiopsis* Form Jessen Assemblage-Zone (Schneider *et al.*, 2005).

Hemicycloleaia kuzedeica NOVOZHILOV, 1956

1198-4: Right valve (Defretin-Lefranc, 1965, pl. III, fig. 8).

Loc.: Right bank of Kondoma river, left bank tributary of Tom river, near Verkhniy Kaltan village (western Siberia, Russia).

Lithost.: Kuznetsk Formation.

Chronost.: Early Permian.

1198-5: Left valve (Defretin-Lefranc, 1965, pl. III, fig. 9).

Loc., lithost., chronost.: As for the specimen 1198-4.

Comments. Both forms probably represent two distinct morphotypes, 1198-4 with a subquadrate outline and 1198-5 with an ovate outline and a ventral margin strongly inclined postero-dorsally.

Hemicycloleaia kamaensis NOVOZHILOV, 1956

1342a-19: Right valve (Defretin-Lefranc, 1965, pl. III, fig. 12).

Loc.: Left bank of Kitiak stream, right bank tributary of Viatka river, itself tributary of Volga river, near Bolchoi Kitiak village, Malmyzh district, Kirov province (High-Volga Basin, Russia).

Lithost.: Belebei Formation.

Biost.: Lower levels with conchostracans and insects.

Chronost.: Late Permian, late Kazanian (now Middle Permian, Wordian).

1342a-37: Right valve (Defretin-Lefranc, 1965, pl. III, fig. 13).

Loc., lithost., biost., chronost.: As for the specimen 1342a-19.

Comments. Both specimens mentioned here have got a subovate or elliptical outline and a convex dorsal margin, curved downward (postero-ventrally) behind the umbonal area. These characters are not illustrated in the specimens of Novozhilov (1956, fig. 27) and Defretin-Lefranc (1965, fig. 19), which exhibit a subcircular outline and a straight dorsal margin not curved downward. However, as mentioned above, the specimens here considered were presented as microphotographs by Defretin-Lefranc (1965, pl. III, figs. 12-13). The specimens, re-drawn by Novozhilov as well as Defretin-Lefranc, probably differ from these photographed specimens. Perhaps, the morphologic variation might indicate a sexual dimorphism or different subspecies.

Hemicycloleaia securiformis NOVOZHILOV, 1956

1342a-11: Right valve (Defretin-Lefranc, 1965, pl. III, fig. 10).

Loc., lithost., biost., chronost.: As for the specimen 1342a-19 (see p. 129).

1342a-23: Right valve (Defretin-Lefranc, 1965, pl. III, fig. 11).

Loc., lithost., biost., chronost.: As for the specimen 1342a-19 (see p. 129).

Comments. This species was also mentioned in synonymy lists of Defretin-Lefranc (1965) as *Leaia securiformis*.

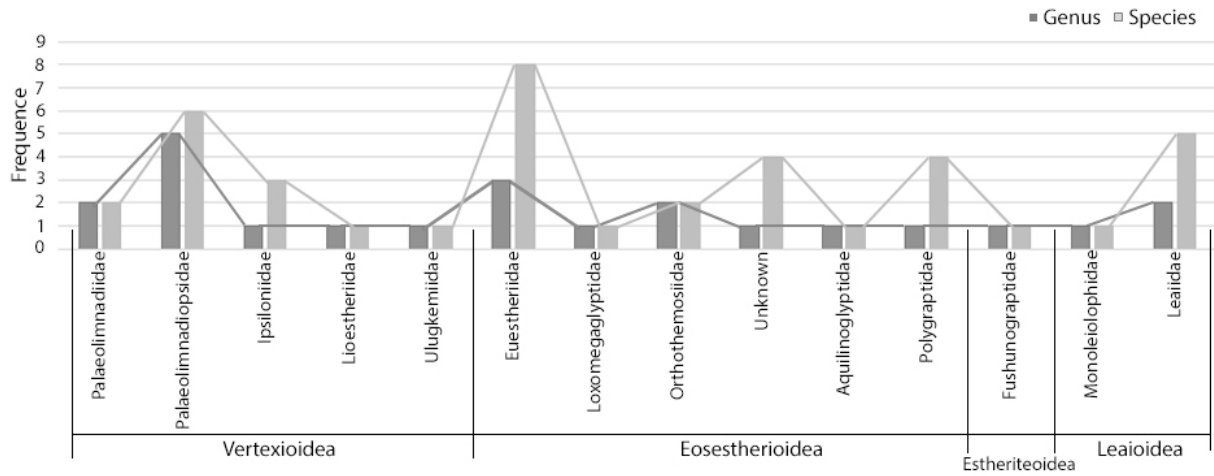


Fig. 3. — Histogram of Diplostraca genera and species corresponding to families housed in Lille University.

Fig. 3.— Histogramme de fréquence des genres et des espèces correspondant aux familles de Diplostraca conservées à l'Université de Lille.

species of *Keratestheria* and four species of *Polygrapta* come from the same locality and stratigraphic level. However, our catalogue demonstrates the great value of the Defretin's and Novozhilov's work. Some taxa, like *Estheriina*, *Taimyrites*, *Fernandoalmeidium*, *Pseudestheria*, and *Teixeirium*, are considered as dubious by different authors. It appears clearly, after our preliminary work, that these taxa should be reviewed in light of new methodologies and taxonomic schemes currently employed. Some species are left in open nomenclature due to the poor diagnoses of some genera, e.g., "*Estheria*" *destombesi*, "*Lioestheria*" *toricata*, "*Lioestheria*" *propinqua* and "*Pseudoasmussia*" *striata*. Another interesting point is that we have eight species of the family Euestheriidae, including in particular five belonging to the genus *Euestheria* and ranging from Carboniferous to Cretaceous. That allows to planify future evolutionary studies on this group. The doubtful family Orthothemosiidae is represented by six species (four of which belongs to the problematic genus *Pseudestheria*, included here for the first time in that family) that ranged from Carboniferous to Middle Jurassic. *Pseudestheria* as well as *Estheria*, *Lioestheria* and *Euestheria* are heterogeneous taxa that include many different species and even, different genera.

The presence of five genera of the family Palaeolimnadiopsidae plus one Ipsiloneidae, that range from

Devonian to Jurassic, brings a large amount of data on the diversification of the group and permits to clarify the real affinities of the limnadopsiform spinicaudatans (as mentioned by Astrop & Hegna, 2015). Furthermore, it is remarkable that we have seen 21 species belonging to the superfamily Eosestherioidea. Inversely, we remarked the low number of representatives of the superfamily Estheriteoidea (1), and these of the suborder Leaiina (6), in addition to two palaeolimnadiids and one Lioestheriidae (Fig. 3). This large amount of materials, ranged from the Devonian to the Jurassic, brings a great possibility of development for different studies on the collection. The early record of Devonian-Carboniferous spinicaudatans provides important information on the early diversification of the group, whereas the Jurassic record informs on their decline.

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ANNEX: SYSTEMATIC INDEX (in alphabetical order)

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