

Taxonomy and morphology of *Dasyleptus* Brongniart, 1885, with description of a new species (Insecta: Machilida: Dasyleptidae)

Систематика и морфология *Dasyleptus* Brongniart, 1885, с описанием нового вида (Insecta: Machilida: Dasyleptidae)

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КЛЮЧЕВЫЕ СЛОВА: *Dasyleptus*, Monura, Machilida, Archaeognatha, ювенилизация.

ABSTRACT: *Dasyleptus lucasi* Brongniart, 1885, from the Upper Carboniferous of France, *D. sharovi* (Durden, 1978), from the Lower Permian of Kansas, USA, and *D. brongniarti* Sharov, 1957, from the lower Upper Permian of SW Siberia, are redescribed, and *D. nolisp.n.*, is described basing on one paralectotype of *D. lucasi*. Further evidence is presented in favour of the hypothesis that *Dasyleptus* represents a juvenilised group of the order Machilida (= Archaeognatha).

РЕЗЮМЕ. Переизучены *Dasyleptus lucasi* Brongniart, 1885, из верхнего карбона Франции и *D. brongniarti* Sharov, 1957, из низов верхней перми ЮЗ Сибири, *D. sharovi* (Durden, 1978) из нижней перми Канзаса, США. Один из паралектотипов *D. lucasi* выделен в *D. nolisp.n.* Представлены дополнительные свидетельства в пользу гипотезы, что *Dasyleptus* представляет ювенилизированных щетинохвосток Machilida (= Archaeognatha).

History of the case

The genus *Dasyleptus* and species *D. lucasi* have been established by Brongniart [1885] for several fossils from the Upper Carboniferous (Stephanian) of the Commeny Basin in Allier, France. Brongniart has described the fossil as a member of the order Thysanura. The description has been accompanied with neither illustrations nor indication of the housing family.

The type material has been re-studied in part by Handlirsch [1906-08] who has misinterpreted it as belonging to several non-insect groups. His short descriptions and low quality drawings are not much informative.

The next attempt of restudy of the Brongniart's material has been made by the late Frank M. Carpenter. Unfortunately, it remains unfinished and unpublished, except for the very concise description of the genus and higher rank taxa, as well as the good photograph, appeared in Carpenter [1992, fig. 11a].

Very recently, Bitsch & Nel [1999] in their revision of the fossil Archaeognatha have redescribed *D. lucasi* and selected the lectotype and paralectotypes.

Meanwhile, during about a decade since 1949, a number of related and much better preserved fossils have been collected in the Kaltan locality (Kuznetsk Basin in the SW Siberia), in deposits of the Kuznetsk Formation [Sharov, 1957, 1959, 1961]. That time the age of the deposits was considered as the Early Permian [Rohdendorf et al., 1961]; now its dating is changed as the earliest Late Permian (Ufimian, Zhuravleva & Ilyina 1988). The Kuznetsk material has been described by Sharov [1957] as representing one more species, *D. brongniarti* Sharov, within the Brongniart's genus. To harbour the latter, a new family Dasyleptidae Sharov and new order Monura have been proposed, basing on the combination of numerous plesiomorphic characters in the head, trunk, and appendages, and of the apomorphic loss of cerci (Sharov, 1957, 1959, 1961, 1966; I have used the modern hennigian terminology here to express the precise Sharov idea).

The related genus and species, *Lepidodasypus sharovi* Durden was described from the Lower Permian Wellington Formation of Elmo, Kansas, USA [Durden, 1978]. Study of the type specimen reveals it as just one more species of *Dasyleptus* (see below). Further Carboniferous and Permian fossils from Czechia, France and USA are referred to as either belonging or related to *Dasyleptus* reviewed by Rowland [1997] and Bitsch and Nel [1999]. Of them, I was able to study only those from the uppermost Carboniferous or lowermost Permian deposits in Carrizo Arroyo (New Mexico, USA). These are mostly poorly preserved exuvia of early instars of a new species of *Dasyleptus* (to be described later on).

Additionally, the trace fossils have been described recently from the Upper Carboniferous of Kansas, USA [Mángano et al., 1997] as possibly made over a tide affected sedimental plane by an animal related or belonging to *Dasyleptus*.

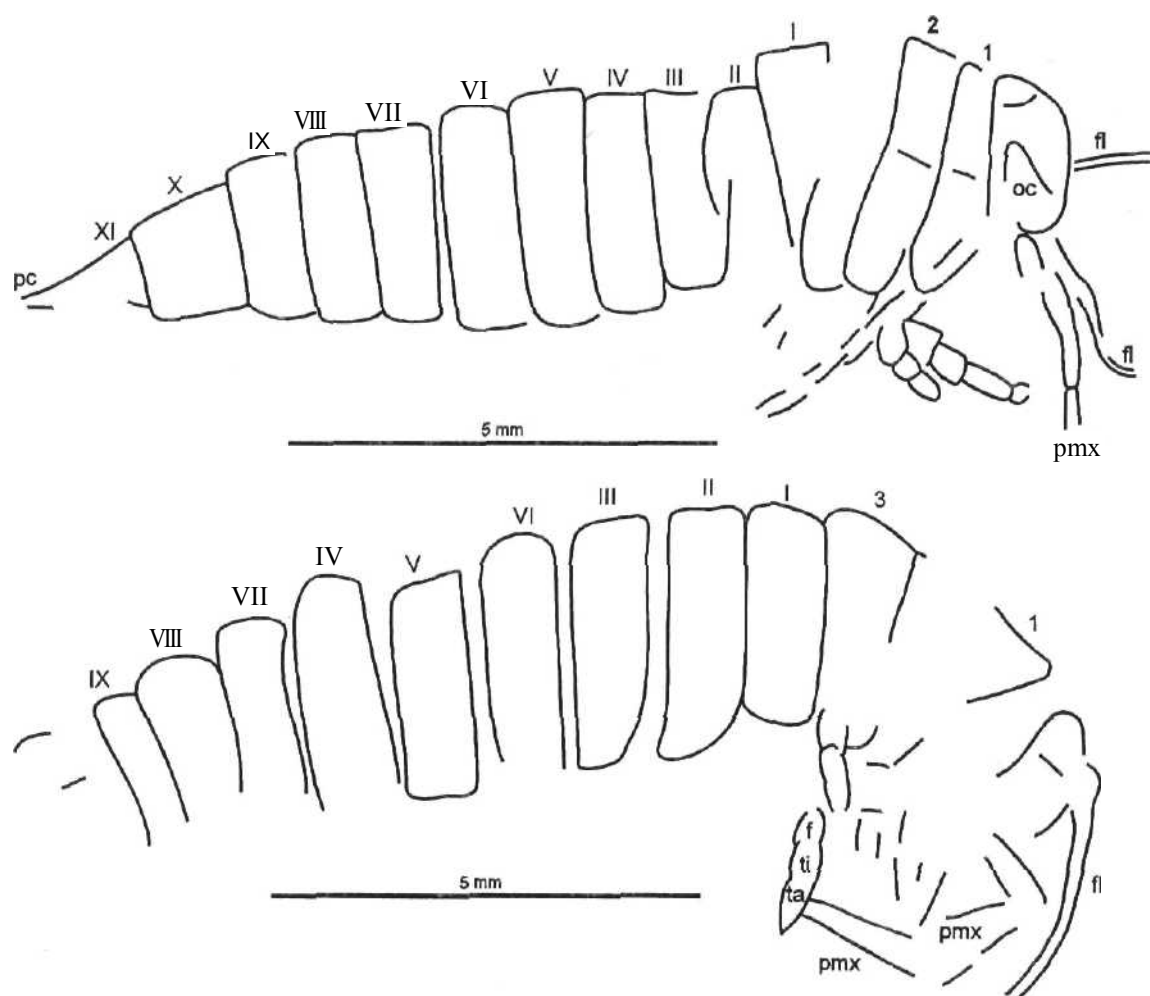


Fig. 1—2. *Dasyleptus lucasi* Brongniart: 1—lectotype, 2—paralectotype MNHN-LP-R. 55215. Abbreviations for all figures: ap — apodem, cv — cervical sclerite, ex — coxa, f — femur, fc — frontoclypeus, fi — antennal flagellum, ga₈ — gonapophysis of abdominal segment 8, ic — mandibular incisor, lr — labrum, md — mandible, mo — mandibular mola, oc — eye, ol — ocellus, pc — paracercus, pd — pedicell!, pmx — maxillary palp, pt — pretarsus (claw), s₁₁ — sternum of abdominal segment 11, sc — scape, sy — stylus, sx — subcoxa, ta — tarsus, ti — tibia, tlb — tergum of labial segment, tmd — tergum of mandibular segment, tmx — tergum of maxillary segment, tr — trochanter; Arabian figures denote thoracic terga, Roman — abdominal ones.

Рис. 1–2. *Dasyleptus lucasi* Brongniart 1 — лектотип, 2 — паралектогип MNHN-LP-R. 55215. Условные обозначения для всех рисунков: ар — аподема, св — цервикальный склерит, сх — тазик, f — бедро, fc — фронтотипеус, fl — жгутик антенны, ga₈ — гонапофизы 8-го брюшного сегмента, ic — инцизор мандибулы, lr — верхняя губа, md — мандибула, то — мола мандибулы, oc — сложный глаз, ol — глазок, pc — парацерк, pd — педицеллус, pmx — челюстной щупик, pt — претарз (коготок), s₁₁ — стернит 11-го брюшного сегмента, sc — скапус, sy — стилус, sx — субкокка, ta — лапка, ti — голень, tlb — тергит лабиального сегмента, tmd — тергит мандибулярного сегмента, tmx — тергит максиллярного сегмента, tr — вертлуг; арабскими цифрами обозначены грудные, римскими — брюшные тергиты.

The Siberian fossils have been later restudied by Rasnitsyn [1980], Kukalová-Peck [1985, 1998], and Carpenter [1992]. Carpenter's study was a part of the project also covering *D. lucasi* and various undescribed fossils from the North America (personal communication, 1989). Like in the case of *D. lucasi*, the only published result was a good photo in Carpenter [1992, fig. 11,b]. Rasnitsyn [1980] presents some corrections of the reconstruction by Sharov, as well as a new hypothesis that *Dasyleptus* does not represent any independent order: instead, it is considered to be a juvenilised (foe-

talised, pedomorphic) representative of the order Machilida (= Archaeognatha). In contrast, Jarmila Kukalová-Peck has concluded that Monura represents the sister-group of Zygentoma + Pterygota, and not of Archaeognatha [Kukalová-Peck, 1985, 1987, 1991]. However, the fossils that she relays on (undescribed material from the Carbondale Formation, Westphalian D, Upper Carboniferous of Mazon Creek, Illinois, USA) differ from *Dasyleptus* so radically that it cannot be related to *Dasyleptus* [Kristensen, 1998; Kukalová-Peck, 1998; Bitsch & Nel, 1999]. According to her

descriptions and illustrations [Kukalová-Peck, 1985, 1987, 1991, 1998], these insects have double claws, sclerotised, stick-like styli, leg-like cerci, and paracercus which is thin basally, thus reminding *Zygentoma* rather than *Monura*. Indication of *D. brongniarti* specimens as having cercal legs as well [Kukalová-Peck, 1985: 944] is a mistake.

Since Sharov's publications, *Dasyleptus* and *Monura* are referred to regularly in the literature. Some students accept Sharov's idea that they represent an early off-shoot of Ectognatha [Kristensen, 1975; Boudreaux, 1979]. Others either include *Dasyleptus* into Archaeognatha or their stem group [Tiegs & Manton, 1958; Tuxen, 1960; Hennig, 1969; Carpenter, 1977, 1992; Rasnitsyn, 1980; Carpenter & Bumham, 1985; Bitsch & Nel, 1999], or, as mentioned above, relate it to *Zygentoma* + *Pterygota* [Kukalová-Peck, 1998].

The lucky opportunities to study the Brongniart material kept at the Museum National d'Histoire Naturelle in Paris, and the Durden's type, currently on loan to J. Mark Rowland, New Mexico Museum of Natural History, Albuquerque, USA, have stimulated me to continue my old and clearly insufficient study [Rasnitsyn, 1980] and so prepare a revision of the types studied. For photographs of the fossils under revision, see Sharov [1957, 1959, 1961], Durden [1978] and Carpenter [1992].

Taxonomy

Order Machilida Grassi, 1888 (= Archaeognatha Burner, 1904 = Microcoriphia Verhoeff, 1904; + Monura Sharov, 1957)

Family Dasyleptidae Sharov, 1957

DIAGNOSIS. Elder immatures (adults probably unknown) differing from those and adult of Machilidae and Meunertellidae in antenna relatively short, filiform (not bristle-shaped), with pedicell long; head with gnathal lerga delimited, eyes not contiguous, straight dorsally, arching ventrally, frontoclypeus almost reaching eye level dorsally; pronotum much shorter than following terga, without cephalic lobes, furrowed transversally, laterally; meso- and metatergum alike abdominal terga; legs weakly movable in tibiotarsal articulation, tarsus entire, pretarsus daw-like; abdominal leglets short, fleshy, subsegmented; cerci absent.

GENERA INCLUDED. *Dasyleptus* Brongniart, 1885 from the Carboniferous and Permian of Eurasia and North America.

Genus *Dasyleptus* Brongniart, 1885

Dasyleptus: Brongniart, 1885: 58;

Dasyleptus: Handlirsch, 1906: 343;

Dasyleptus: Sharov, 1957: 797; 1959: 177-185; 1961: 66;

Dasyleptus: Carpenter, 1992: 16;

Lepidodasypus: Durden, 1978: 1 (type species, *L. sharovi* Durden, 1978, by monotypy and original designation), **syn.n**;

Lepidodasypus: Bitsch & Nel, 1999: 23.

Type species *D. lucasi* Brongniart, 1885 (original designation).

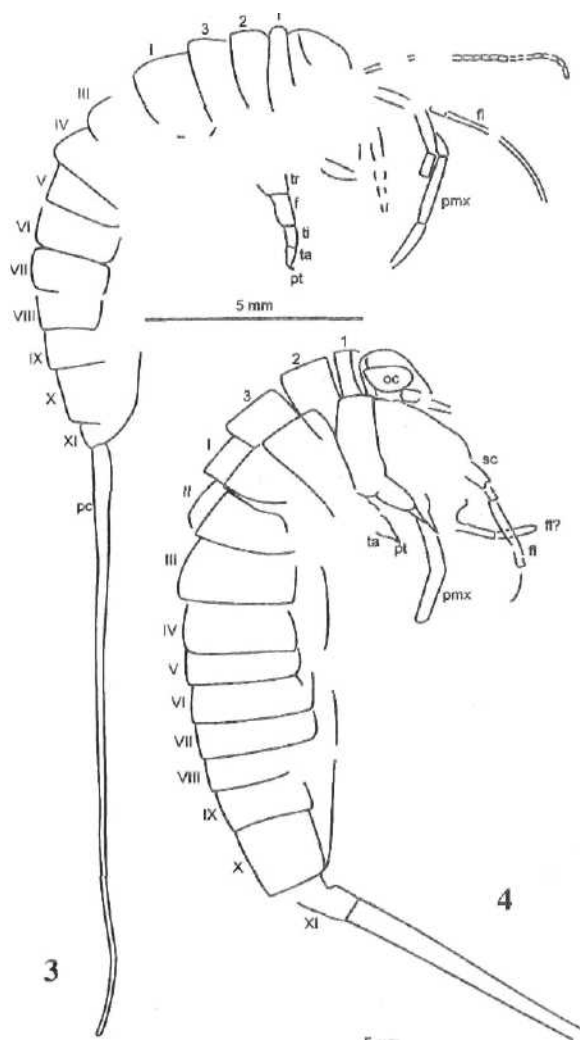


Fig. 3-4. *Dasyleptus lucasi* Brongniart: 3 — paralectotype MNHN-LP-R. 55216, 4 — Carpenter's specimen.

Рис. 3—4. *Dasyleptus lucasi* Brongniart: 3 — паралектотип MNHN-LP-R. 55216, 4 — экземпляр, изображенный Карпентером.

SPECIES INCLUDED. The type species from the Upper Carboniferous (Upper Coal Measures, Stephanian) of the Commentry Basin in Allier, France, *D. brongniarti* Sharov, 1957, from the the earliest Late Permian (Ufimian) Kaltan locality in the Kuznetsk Formation, Kuznetsk Basin in Southwest Siberia, *D. sharovi* (Durden, 1978), *D. noli* sp.n. based on a part of the type series of the type species, and several undescribed species from the Carboniferous and Permian of Europe and North America.

Dasyleptus lucasi Brongniart, 1885

Figs. 1-4.

Dasyleptus lucasi: Brongniart, 1885: 58 (partim);

Dasyleptus lucasi: Handlirsch, 1906: 343, pi. 34, figs. 30-32;

Dasyleptus lucasi: Carpenter, 1992: fig. 11a;

Dasyleptus lucasi: Bitsch & Nel, 1999: 21, fig. 1.

LECTOTYPE. MNHN-LP-R.55214, from the Upper Carboniferous (Upper Coal Measures, Stephanian) of the Commentry

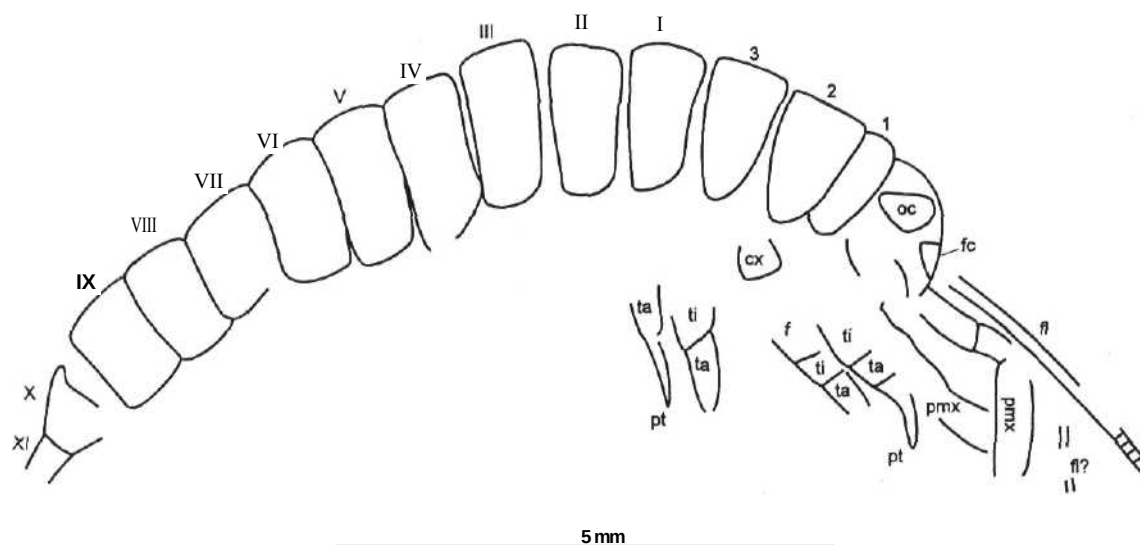


Fig. 5. *Dasyleptus noli* sp.n., holotype.

Рис. 5. *Dasyleptus noli* sp.n., голотип.

Basin in Allier, France, kept at the Museum National d'Histoire Naturelle, Paris, France, designated by Bitsch & Nel [1999].

PARALECTOTYPES. R55215, R55216, R55217 from the same deposits as lectotype (designated by Bitsch & Nel, 1999).

ADDITIONAL MATERIAL. Specimen figured by Carpenter (1992, fig. 11a; presumably the syntype not appreciated as such yet but coming from the same deposits as lectotype, and kept at the same museum; however, by the time of submitting of the manuscript, the specimen has not been located and so was studied after the published photograph).

DIAGNOSIS. The species differs from all other described species in that the antenna is distinctly longer than the head and thorax combined and with the flagellar segments elongate (penultimate segments at least 1.5 times as long as wide, subbasal ones about twice as long as wide), in that all four apical (large) segments of the maxillary palp are narrow (less than half as wide as eye), and possibly in that the caudal filament is much longer than the body (length of the caudal filament is unknown for *D. noli*). It differs additionally from *D. noli* in that the claw (pretarsus) is short (less than half as long as eye) and the penultimate abdominal segment is much longer than the preceding one. It differs from *D. brongniarti* in that the basal large segment (the fourth from apex) of the maxillary palp is subequal in width to the following segments.

DESCRIPTION. The following complement the above characteristics. No coarse sculpture is discernible, and nothing but simple hairs are found to cover the body and legs. Antenna is about as long, or longer than, the head, thorax and the first abdominal segment combined, and not much shorter than the maxillary palp, flagellum with at least about 20 segments, with subbasal segments about twice as long as wide. Caudal filament is about 2.5 times as long as antenna. Holotype: length of body without caudal filament 9 (paratypes 9-13) mm, of antenna ca. 5.5 mm, of penultimate and ultimate segments of maxillary palp ca. 1.7 and 1.3 mm, respectively, of mesonotum and abdominal segments 5-9 0.9-1.0 mm (0.7-0.9 in paratypes, 12-13 mm long, mesonotum length 0.7 in Carpenter's paratype 9 mm long), tergum 10 1.2 mm (same in larger paratypes, 1.0 mm in Carpenter's one), caudal filament ca. 14 mm.

REMARKS. The specimens studied by Handlirsch [1906-1908], judging from his figures, belong to this species rather than to *D. noli*. The specimen appearing as Handlirsch's fig.

31 well may be the lectotype, and that one shown as fig. 32 there — the Carpenter's specimen. The fossil figured as fig. 33 is not among those I had a chance to study, so its tentative identification as *D. lucasi* is simply because it is this species which is dominating in the fossil assemblage.

The present study shows considerable variation of the proportions of various parts of body and appendages in the specimens examined. Presumably this is the result of incomplete preservation state and various postmortem modification of the fossils: the latter is particularly likely, because the material consists in part of exuvia rather than the bodies fossilised, evident in case of the Carpenter's specimen (Fig. 3). The possibility cannot be ruled out as well that the species might deserve further splitting. The reliable re-study of the Commeny species depends on study of the entire material kept at the Museum National d'Histoire Naturelle: unfortunately, my stay there was not long enough to make this possible.

Dasyleptus noli Rasnitsyn, sp. n.

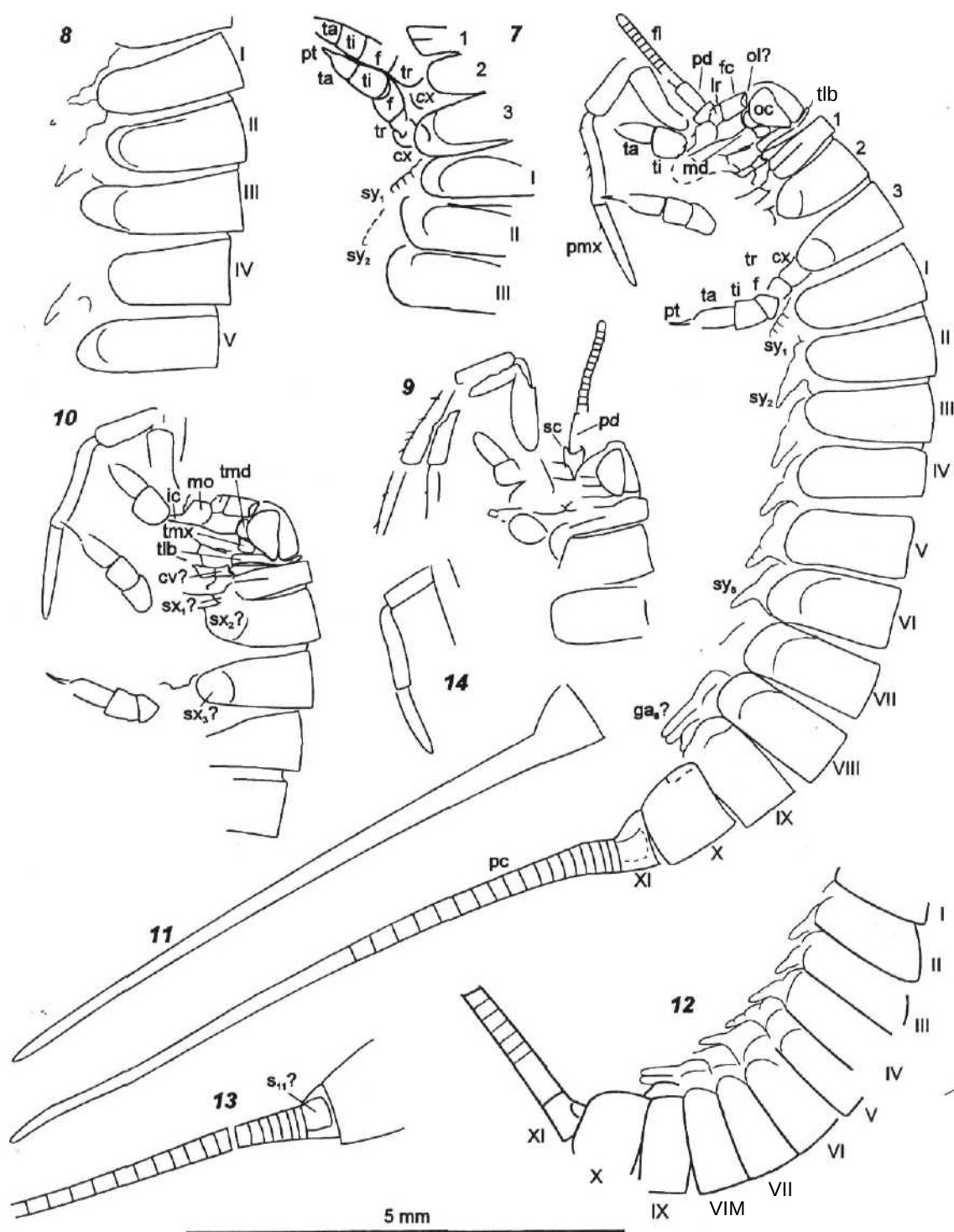
Fig. 5,

Dasyleptus lucasi: Brongniart, 1885, p. cii (partim).

HOLOTYPE. R55212 (paralectotype of *Dasyleptus lucasi* Brongniart, 1885, designated by Bitsch & Nel, 1999), from the Upper Carboniferous (Upper Coal Measures, Stephanian) of the Commeny Basin in Allier, France, kept at the Museum National d'Histoire Naturelle, Paris, France.

DIAGNOSIS. The holotype differs from other described species, in that the antenna is about as long as the head and thorax combined and with several penultimate segments subquadrate, the largest seen (probably penultimate) segment of the maxillary palp is very wide (as wide as eye) and much wider than the short previous segment, the claw (pretarsus) very long (hind claw about 1.5 times as long as eye), and the penultimate abdominal segment is not much longer than the preceding one.

DESCRIPTION. The following complement the above characteristics. Length of body, as preserved, 9.5 mm, of antenna ca. 3 mm, length and width of the largest segment of the maxillary palp ca. 1.3 and 0.4 mm, respectively, length of



Figs. 6—14. *Dasyleptus brongniarti* Sharov: 6 — reconstruction based on the holotype PIN 1197/595, with some structures added from figs. 7—14; 7 — paratype PIN 966/19, thorax and base of abdomen; 8 — paratype PIN 1197/594, part of abdomen with styli; 9 — paratype PIN 1197/585, head and thorax with appendages; 10 — paratype PIN 1197/594 (counterpart), head and thorax with appendages; 11 — paratype PIN 1197/592, abdominal segment 11 with paracercus; 12 — paratype PIN 1197/602, abdomen with appendages; 13 — paratype PIN 504/231, abdominal apex with partial paracercus; 14 — maxillary palp of holotype.

Рис. 6-14. *Dasyleptus brongniarti* Sharov: 6 — реконструкция на основе голотипа ПИН 1197/595, с добавлением ряда структур с рис 7 — 14; 7 — паратип ПИН 966/19, грудь и основание брюшка; 8 — паратип ПИН 1197/594, часть брюшка со стиллями; 9 — паратип ПИН 1197/585, голова и грудь с придатками; 10 — паратип ПИН 1197/594 (протоотпечаток), голова и грудь с придатками; 11 — паратип ПИН 1197/592, 11-й сегмент брюшка с парацерком; 12 — паратип ПИН 1197/602, брюшко с придатками; 13 — паратип ПИН 504/231, вершина брюшка с парацерком; 14 — голотип: челюстной щупик.

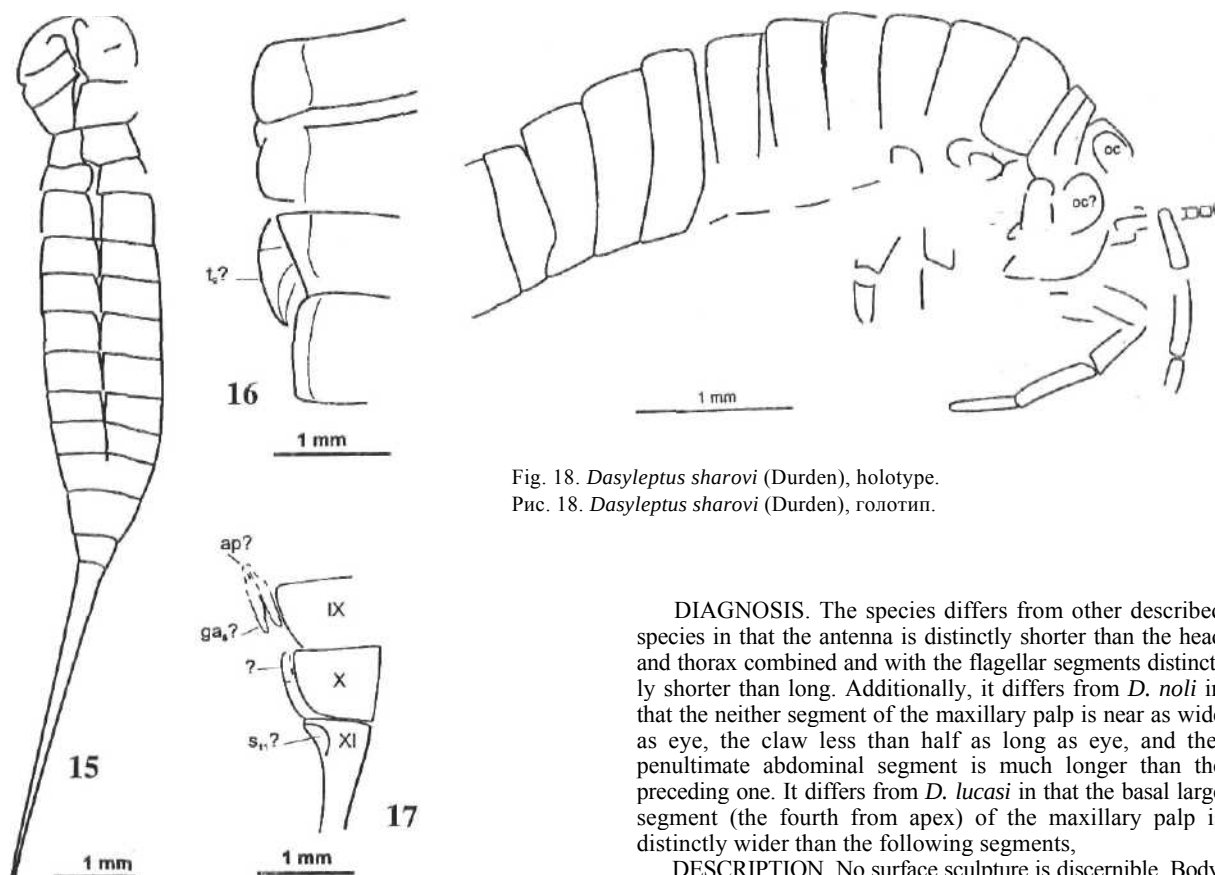
Fig. 18. *Dasyleptus sharovi* (Durden), holotype.Рис. 18. *Dasyleptus sharovi* (Дурден), голотип.

Fig. 15—17. *Dasyleptus brongniarti* Sharov: 15 — paratype PIN 1197/610, molting cast seen from above; 16 — paratype PIN 1197/601, partial abdomen showing a structure (t_9 ?) taken by Sharov [1958] for gonopods: probably a broken and damaged contralateral paranotum; 17 — paratype PIN 1197/598, partial abdomen with supposed gonopod rudiments (gas_8 ?, ?).

Рис 15-17. *Dasyleptus brongniarti* Шаров: 15 — паратип ПИН 1197/610, линочная шкурка (вид сверху); 16 — паратип ПИН 1197/601, часть брюшка со структурой (t_9 ?), принятой Шаровым [1958] за гоноподы (вероятно, отломанная и поврежденная паранота протоположного полутергита); 17 — паратип ПИН 1197/598, часть брюшка с предполагаемыми зачатками гонопод (gas_8 ?, ?).

hindleg claw 0.7 mm, of mesonotum 0.8 mm, of abdominal terga 1-9 ca. 0.7 mm.

ETYMOLOGY. The species name is the Latin for undesirable ("I don't wish it").

Dasyleptus brongniarti Sharov, 1957

Fig. 6-17.

Dasyleptus brongniarti: Sharov, 1957: 797-798, figs. 1-3; 1959: 177-185, figs. 2, 3, 5, 7, 8; 1961: 66-68, figs. 24-26. pi. 1;

Dasyleptus brongniarti: Rasnitsyn, 1980: fig. 2;

Dasyleptus brongniarti: Carpenter, 1992: figs. 11b, c;

Dasyleptus brongniarti: Bitsch & Nel, 1999: 22, fig. 2.

MATERIAL EXAMINED. The type series of *Dasyleptus brongniarti* as recorded by Sharov [1957], except paratypes PIN, 1197/589, 590, 591, 600, 606, which represent fragments of some other arthropods, and specimen PIN, 1424/4, mentioned by Sharov [1959], all kept at the Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

DIAGNOSIS. The species differs from other described species in that the antenna is distinctly shorter than the head and thorax combined and with the flagellar segments distinctly shorter than long. Additionally, it differs from *D. noli* in that the neither segment of the maxillary palp is near as wide as eye, the claw less than half as long as eye, and the, penultimate abdominal segment is much longer than the preceding one. It differs from *D. lucasi* in that the basal large segment (the fourth from apex) of the maxillary palp is distinctly wider than the following segments,

DESCRIPTION. No surface sculpture is discernible. Body and appendages covered with more or less uniformly small hairs, except for several (2-4) longer and thicker hairs seen along dorsal margin of two apical segments of the maxillary palp. On the body segments, pubescence displays distinct orientation best expressed on pronotum: hairs directed fan-like from the point opposite hind eye corner, and with upper half or so of tergum densely pubescent, lower part sparsely so, and with the borderline between them rather distinct. Antenna with scape rather short though not necessary much shorter than long, pedicell long, cylindrical, about 0.33-0.4 as long as flagellum, flagellum with about 12-13 segments which are shorter than long except the apical and, possibly, one or more basal segments which are slightly longer than wide. Eye contour half-circular, close to fore and hind head contours, its dorsal margin nearly straight, ventral one convex. Among four apical segments of maxillary palp, basal the most thick (almost as wide as eye), apical least thick (about as wide as pedicell), the second segment the shortest; the longest is basal segment in some specimens, distal one in some other. Pronotum shorter than other body segments, particularly near midline, with suture running at tergum midlength subparallel its fore margin, from near eye level downward. Meso- and. Metanotum and abdominal terga 1-9 little differ in length, tergum 10 about 1.5 times as long as these, tergum 11 longer than pronotum but shorter than other terga. Abdominal terga with paranoia comprising about 0.25 width of half-tergum (the lines seen on meso- and metanotum laterally may represent some pleural structure rather than paranotum boundary, because they are arching medially and not laterally, as in case of abdominal terga). Form of leg segments somewhat varies, possibly depending in part on details of burial and fossilisation processes, and their proportions cannot be appreciated very precisely. Claw about as long as tibia, shorter than eye wide, narrow, gently curved; tarsus about twice as long as

Table 1. *Dasyleptus brongniarti*, measurements (length, mm; body — without caudal filament; pmx s/a — maxillary palp: subapical segment; pmx a — same: apical segment; $N_2/*N_3$ — mesonotum or (*) metanotum; at₆ — abdominal tergum 6, or (*) tergum 3, or (**) tergum 5, or (***) tergum 9; at₁₀ — tergum 10; cf — caudal filament).

Таблица 1. *Dasyleptus brongniarti*, промеры (длина в мм; тело — без хвостовой нити; pmx s/a — предпоследний членик челюстного жгутика; pmx a — последний членик челюстного жгутика; $N_2/*N$ — среднеспинка или (*) заднеспинка; at₆ — 6-й или (*) 3-й или (**) 5-й или (***) 9-й тергит брюшка; at₁₀ — 10-й тергит брюшка; cf — хвостовая нить).

Specimen	body	antenna	pmx s/a	pmx a	$N_2/*N_3$		at ₆	Cf
holotype	10.3	1.7	1.0	0.8	0.6	0.7	0.85	7.7
679/75	~5	~1			0.35	**0.4		
966/14	10.3				0.6	0.7	0.85	
966/15	9.0				0.6	0.7	1.0	
966/16	~10				-0.7	0.65	0.85	
966/17	~4.5				-2.5	0.3	0.4	
966/18	~10-11			1.0	0.65	*0.65		
966/19	~10				*0.65	0.75	0.9	
966/20	~5.5				*0.4	0.35	0.5	
1197/585	~11	2.1	1.35		0.65	0.75		
1197/586	~7.5				0.6	***0.6	0.8	
1197/587	~7				0.45	0.45	0.55	
1197/592	~7.7					0.75	0.85	7.1
1197/594	12		1.15	1.0	0.6	0.75	0.9	
1197/596	5.5				0.4	0.4	0.55	4.4
1197/597	~4				0.3	0.3		
1197/598	9.5				0.6	0.75	0.9	
1197/601	~9	1.9	0.9	0.9	0.6	0.6	0.8	
1197/602	8				0.5	0.55	0.7	
1197/603	8.7				0.55	0.5	0.75	
1197/605	~4				0.3	*0.3		
1197/608	5.8		0.6	0.55	*0.35	0.4	0.5	
1197/609	~5.5				0.45	0.45		
1197/610	~3.5					0.2	0.25	1.8
1424/4	~5.5	~1.2	0.7		0.37	0.4	~0.5	

wide; tibia and femur slightly or not at all longer than wide, tibia distinctly tapering apicad, femur and, probably, trochanter, tapering basad. Abdominal appendages other than caudal filament seen on segments 1-8 (for details, see Morphology). Caudal filament is about as long as abdomen (shorter than that in small fossils), with basal segments very short, those near basal 0.4 length distinctly longer than wide. Colour probably uniform dark (most fossils are light more or less, possibly because these may represent shed exuvia rather than insects themselves). For measurements, see Table 1.

Dasyleptus sharovi (Durdin, 1978), **comb.n.**

Fig. 18.

Lepidodasypus sharovi: Durdin, 1978: 3, figs. 1-3.

MATERIAL EXAMINED. Holotype YPM 28152, from the Lower Permian (Elmo Limestone, Wellington Formation, Artinskian) near Elmo, Kansas, USA, kept at the Yale Peabody Museum of Natural History (currently on loan to J.M. Rowland, University of New Mexico, Albuquerque, New Mexico, LISA).

DIAGNOSIS. The species possibly differs from younger immatures of *D. brongniarti* in the weakly expressed (possibly thin or even soft) lateral tergal margins and in paler ground colour (young immatures of *D. lucasi* and *D. noli* are unknown).

DESCRIPTION. No surface sculpture is discernible. Uniform small hairs discernable on darker parts of tergums, on antenna and maxillary palp. Basal flagellar segments very slightly longer than wide. 4 apical segments of maxillary palp becoming gradually narrower from the basal to apical one, the longest penultimate segment about 5.5 times as long as wide. Clypeus looking more convex than in other species, though head is damaged and interpretation of its structure is difficult. Pronotum of typical form for genus, following terga also ordinary except their lower (lateral) boundaries rarely traceable (possibly weakly sclerotised). Preserved leg segments ordinary (no claw found preserved). Visible ventral parts of abdominal segments (sterna?) somewhat slanting backward. Upper (tergal) part of body, femoral and tibial apices, (hind) tarsus entirely, and maxillary palp segments dorsally infuscated. Length of body, as preserved, 4.3 mm, length and width of penultimate segment of the maxillary palp ca. 0.55 and 0.1 mm, respectively, of ultimate segment ca. 0.45 and 0.08 mm, length of mesonotum 0.5 mm, of abdominal terga 2-4 ca. 0.33-0.35 mm.

REMARKS. My study of the holotype surprisingly reveals nothing of the intriguing morphological details described and figured in the original description, viz. abdominal leglets, spiracles, scale-like hairs, etc. I was able to see an ordinary young immature of *Dasyleptus* hardly

distinguishable from *D. brongniarti*. That is why I dare to synonymise *Lepidodasypus* under *Dasyleptus*.

Dasyleptus sp.

Dasyleptus sp.: Rowland, 1997: 3, fig. 3.

REMARKS. I was able to study the material referred to this taxon in the above publication. The material (some 20 young immatures, mostly exuvia, of the mean preservation state) comes from the Red Tanks Member (probably the uppermost Carboniferous or earliest Permian) at Carrizo Aroyo in the Sierra Lucero, Valencia County, New Mexico, USA. It is kept in the New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA. The material deserves careful description which would be labourous be-

cause of the imperfect preservation state. For the present, it is possible to conclude that the species closely reminds *D. brongniarti* and *D. sharovi* but differs from their young immatures in having the basal flagellar segments distinctly elongate, and the two ultimate segments of maxillary palp slightly more wide.

Morphology

This section is based primarily on the better preserved material of *D. brongniarti*, and deals with the characters concerning the phylogenetic and taxonomic position of monurans in respect to other insects, rather than interrelationships of their lower rank taxa.

Head capsule. The eyes are clearly separated (Figs. 1, 3, 4, 6, 9, 10), in contrast to be in wide contact in Archaeognatha. Lateral ocellus is almost squeezed between the eye and frontoclypeus (Fig. 6, 10); no medial ocellus is found, most probably because all heads of the better preservation states are buried in lateral position. Frontoclypeus is entire, separated by a suture from the labrum which may be subdivided (Fig. 6, 10), though the evidence is not conclusive. Mandibular and maxillary terga form independent sclerites below eye (Figs. 6, 9, 10). Labial segment delimited from the rest of the head at least dorsally and laterally (Fig. 6, 9, 10). No exceptional structures illustrated by Kukalová-Peck [1998, fig. 19.5c,d] (supernumerary ocelli, dorsal section of the maxillary tergum, multiple subdivision of the frontoclypeus and labrum) is found possible to confirm.

Head appendages. Monuran antenna is unusual in having long pedicell and sometimes oligomeric flagellum (Fig. 6, 9). Mandible is possibly of typical archaeognath form (elongate, with large mola and slender incisor), though it is not well seen in fossils (Fig. 6, 10). For maxilla, only four distal palp segments are known which are all large and apparently correspond to the same of living archaeognaths (Figs. 1-6, 9, 10, 14). No claw-like structure mounts the palp apex. Contrary to Sharov [1959], labial palp is not discernible with any certainty.

Thorax. Pronotum short throughout (without lobes covering head sides). Meso- and metanotum similar in form and size. Pleura] and ventral structures are essentially unknown. In side view, the thoracic tagmadoes not seem apparent, except for the legs present there, but the exuvia buried in the dorsoventral position show a very distinct constriction toward thoracic hind margin (Fig. 15). This constriction may be exaggerated in exuvium, and nevertheless it should reflect a real difference in organisation of the two tagmata.

Legs. Legs are short and uniform in their structure (Figs. 1, 6, 7, 10). Subcoxa and coxa are poorly preserved, if at all, in the fossils available, otherwise Sharov's [1957, 1959] description is correct: leg segments are short, tarsus one-segmented, pretarsus claw-like, intersegmental articulations weakly movable except probably coxal-trochantal one, with the postcoxal leg forming an arch which reaches the ground with the claw tip (Figs. 1-7, 10).

Abdomen. Abdominal terga are apparently simple plate-like, with the faint arching lines delimiting rather narrow paranoia (Fig. 6-8), and with the mid-dorsal molting line (the line of fusion of the embryonic half-terga) extending probably from the epicranial suture in the head and via the thoracic terga till at least the eighth tergum (Fig. 3, 15). The terga are uniform except for the small subconical tergum 11, and tergum 10 which is often elongate. Pleural and ventral structures insufficiently known. Spiracles are described by Durden [1978] to open extratergally: dark dots can be seen in similar position in some abdominal segments in *D. brongniarti* (paratype 1197/602) as well, though without enough certainty. Segment 11 shows a somewhat bent plate-like structure inside or, rather, on its lower surface: this might be either sternum 11 or a structure associated with the anus (Figs. 6, 13, 17).

Abdominal appendages. Those other than the caudal filament (paracercus), when rarely preserved, are pale and weakly outlined (Fig. 6, 7, 12, 17). Most probably they are fleshy (weakly sclerotised) structures. In segments 1-6, these appendages are 3- or 4-segmented, short, directed obliquely backward (possibly slightly outward as well), and reaching to about the midlength of the following segment. In segment 7 and 8, they are more elongate. For the abdominal limb 9, observations are somewhat contradictory. In *D. brongniarti*, the genital structures described by Sharov [1958] probably represent a crushed part of the contralateral half-tergum (Fig. 16). Instead, a double structure is sometimes seen under the tergum 9 (Figs. 6, 12, 17): this might be either entirely the limb 8 of unusual form, or a pair of limbs 8 shifted mesad and aligned each other (unlike the pregenitalic limbs placed sublaterally), or else these might be a short limb 9 aligned to the longer limb 8. The limbs 8 (and 9?) are not sclerotised enough to act as a functional ovipositor or copulatory device. This indicates, contrary to Sharov's inference, that even the largest specimens of *Dasyteptus* were immature. No appendages are found on the segment 10. Likewise, cerci are most probably entirely suppressed, in agreement with Sharov (1957-1966) and contrary to my earlier claim [Rasnitsyn, 1980]: the structure I have taken for the cercus rudiment is most probably a part of broken tergum 11. No possible cereal articulation foramen is found in (the fossils studied).

Discussion

The above account of the monuran morphology is well compatible with the hypothesis that the most striking of their differences from the living archaeognaths are characteristic of the mid-age and late embryos of the machilids, as described by Larink [1969] and Machida [1981]. These are the separated gnathal terga, short antenna, simple (not bifid) leg apex, simple (not subsegmented) tarsus, fleshy abdominal limbs directed backward rather than obliquely forward, and suppressed cerci.

Besides these, there are differences not easily ascribed to the different developmental timing in *Dasyteptus*.

tidae and Machilidae + Meunertellidae¹. These are separated eyes, frontoclypeus attaining the eye level basally, long pedicell, short pronotum in *Dasyleptidae*, vs. adjoining eyes, low position of the frontoclypeus, short pedicell, and pronotum with cephalic lobes in the living archaeognaths. These differences are probably of moderate taxonomic importance suggesting a familial rather than ordinal level of distinction of the taxa involved. The alternative set of differences considered above appears to be of high importance. However, as it was demonstrated by Tikhomirova [1991], the processes of juvenilisation and adultisation like these are highly flexible evolutionary. Unless independent evidence appears that these modifications have been successfully stabilised (e.g., gave rise to a large, successful group), these characters are not to be taken for evidence of the high rank of the taxon concerned. This was my reason to discard the Order Monura and to consider *Dasyleptidae* simply the third archaeognath family [Rasnitsyn, 1980]. Carpenter [1992] considers Monura as a suborder within Archaeognatha; to my mind, it is redundant to introduce a suborder to separate one family in the order from two others. So I feel my reason as not seriously affected.

The present observations may have implications to the habits of *Dasyleptus* as well. It is not to question the inference by Sharov [1957, 1959] that these insects lived at least near water: otherwise wingless insects cannot be so common in freshwater deposits. *Dasyleptus* could even be true aquatic insect despite it have no evident aquatic adaptations. Although the fleshy abdominal limbs might be used as gills, they are neither elongate, nor branched, nor leaf-like flattened, as is characteristic of the insect gills. The supposed immature nature of all numerous fossils of *Dasyleptus* implies the different habits of their adults: for instance, they might differ from their immatures in being non-aquatic.

Another problem concerning the dasyleptid habits arises because of their lack of stiff styli. Living archaeognaths, like dasyleptids and in contrast to all other insects, have thick paracercus that forms a smooth continuation of their body, reminding tail of reptiles and some of more primitive mammals. Similarly to these, it works as a body support and a device that secures the direction control in fast locomotion. In the machiloids, their paracercus additionally participates, jointly with styli, in the characteristic escape behavior by leaping. Dasyleptids lack styli stiff enough to render necessary support, so their leaping ability needs further evidence.

The very interesting observations by Mángano et al. [1997] on the Upper Carboniferous fossil traces, which are comparable to what *Dasyleptus* might make, are contradictory. The general appearance of the traces, their size variability (from 6.4 to 21.4 mm without appendages), absence of any traces of genitalic structures, and their preservation on the sedimentation plane which is of intermittent subaerial/subaquatic origin, all are

in agreement with our above inferences. However, the supposed thoracic leg imprints [Mángano et al., 1997: fig. 2, A2-A4] are admedian in position and can be left by nothing but coxa and/or trochanter, while the rest legs, including their apices, should escape any contact with substrate — in sharp contrast with what the known *Dasyleptus* morphology suggests [Sharov, 1958]. Also, the traces demonstrate the caudal appendage (paracercus) attached directly to the eighth abdominal segment, while in *Dasyleptus* (Figs. 1-15) ninth and tenth segments combined are about as long as, or longer than, two previous segments taken together, and so hardly can be missed (the 11th segment in not considered here being small and possible to form an apparent 'tail' base of the fossil trace). And the last though not the least: contrary to Mángano et al. [1997], the very jump moment is either not reflected in the traces documented, or is different considerably from what is known for Machilidae and ascribed to *Dasyleptus*. Indeed, a sharp downstroke by the paracercus should result in the impression in the substrate which is deeper than those of body and other appendages, and be accompanied with signs of disturbed soft sediments alongside, and scars of body and appendages trailed over surface for a short distance due to the stroke. Nothing of these is seen in the good illustrations of the trace fossils. Contrary, the tail impression is widely interrupted subbasally there. Evidently, the very important observations by Mángano et al. [1997] deserve further considerations.

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¹ The fourth archaeognath family cited by Carpenter [1992] and Bitsch & Nel [1999], the extinct monotypic Triassomachilidae, was found based on the mayfly (Ephemeroidea) nymphal fossils [Rasnitsyn, 1980].

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