

A survey of fossil Oonopidae (Arachnida: Aranei)

Обзор ископаемых пауков семейства Oonopidae (Arachnida: Aranei)

Yuri M. Marusik¹ & Jörg Wunderlich²
Ю.М. Марусик¹, Й. Вундерлих²

¹Institute for Biological Problems of the North, Portovaya Str. 18, Magadan 685000 Russia. Email: yurmar@mail.ru
ИБПС ДВО РАН, Портовая 18, Магадан 685000 Россия.

²Oberer Häuselbergweg 24, 69493 Hirschberg, Germany. Email: JoergWunderlich@t-online.de

KEY WORDS: Amber, inclusion, spiders, new combination

КЛЮЧЕВЫЕ СЛОВА: янтарь, инклюзы, пауки, новая комбинация

ABSTRACT. Fossil oonopids are known only from amber inclusions. The fossils are found in Baltic, Burmese, Canadian, Chinese, Colombian, Dominican, French (Paris), Japanese, Kenyan, Lebanese, Madagascan, Mexican, New Jersey and Ukrainian (Rovno) ambers. At present, 35 oonopid species belonging to six genera are reported from resins: *Fossilopaea* (1); *Heteroonops* (1); *?Oopaea* (1); *Orchestina* (27); and *Stenops* (3). Of these, 27 are identified to species level, six to generic level, and two to family level. All species and records of these fossil oonopids are commented on, their age, type deposition, and morphological features are discussed briefly. The oldest oonopid was found in 120–130 Ma Lebanese amber. Two new combinations are established: *Stenops seldeni* (Penny, 2000) comb.n., ex. *Oonops s.*; and *Orchestina pusilla* (Menge, 1854) comb.n., ex. *Segestria p.* Four species groups are recognized among fossil *Orchestina*.

РЕЗЮМЕ. Ископаемые Oonopidae известны исключительно из янтарных инклюзов. Пауки этого семейства обнаружены в балтийских, бирманских, канадских, китайских, колумбийских, доминиканских, французских, японских, кенийских, мадагаскарских, мексиканских, ньюджерсийских и украинских янтарях. К настоящему времени известно 35 видов относимых к 6 родам *Fossilopaea* (1), *Heteroonops* (1), *?Oopaea* (1), *Orchestina* (27) и *Stenoonops* (3). Из них 27 имеют видовые названия, 6 видов определены лишь до уровня рода, а два вида определены только до семейства. Для всех видов найденных в янтарях даны краткие комментарии относительно места хранения типовых экземпляров, возраста, морфологических особенностей. Самые древние представители семейства найдены в ливанских янтарях, возраст которых 120–130 млн лет. Предложено две новые комбинации: *Stenoonops seldeni* (Penney, 2000) comb.n., ex. *Oonops s.* и *Orchestina pusilla* (Menge, 1854) comb.n., ex. *Segestria p.* На основании строения пальпы самцов ископаемые виды *Orchestina* разбиты на четыре группы видов.

Introduction

Oonopidae is a relatively small family of haplogyne spiders with 491 extant species distributed worldwide [Platnick, 2008]. Most species of this family are restricted to the tropics and subtropics. In terms of species number, it is the third largest of the haplogyne families [cf. Platnick, 2008], with only Pholcidae and Dysderidae encompassing more species, 986 and 494 respectively. However, it seems that the species diversity of this family is expected to be much greater, perhaps including at least five times as many species [Platnick, 2006]. Considerable progress in the study of this family was achieved during last decade thanks to Michael I. Saaristo, who described alone or with coauthors 42 species and ten of the 73 known genera [Saaristo, 2001, 2002, 2007; Saaristo & van Harten, 2002, 2006; Saaristo & Marusik, 2004]. In addition to the extant species, many oonopids are known as fossils. All described fossil species were found as inclusions in amber. Although the number of described extant (recent) oonopid species comprises only 1.2% of the whole order [4024 species, Platnick, 2008], the ratio for extinct Oonopidae is higher and comprises 3.5% (of about 1000 fossil species). While the number of fossil oonopids is relatively high, information about them is spread among more than a dozen different publications. The main goal of this paper is to survey the described species and recorded specimens, and also the distributions and ages of oonopid fossils.

History

The first extant oonopid spider, *Oonops pulcher*, was described by Templeton (1835), and the first fossil oonopid was described soon after from the Baltic amber, as *Segestria pusilla* Menge, 1854 (= *Orchestina* sp., cf. Wunderlich [1981, 2004]). Two species, *O. baltica* and *O. imperialis*, were described by Petrunkévitch [1942, 1963], also from Baltic amber. Most of the fossil oonopid species were described by Wunder-

lich in three publications [1981, 1988, 2004]. Fossil oonopids were known exclusively from Baltic ambers for more than a century. Then, Petrunkevitch [1971] described *Orchestina mortua* from Mexican (Chiapas) amber, and few years later another species was reported from Japanese copal *sub. Orchestina* sp. by Nishikawa [1974]. The first large-scale research on fossil Oonopidae was made by Wunderlich [1981], who described 18 species of *Orchestina* from Baltic, Dominican and Kenyan fossil and subfossil resins. A later revision of Dominican ambers and copals [Wunderlich, 1988] revealed five more species, four of which were described. The first survey of all Oonopidae described or reported from resins was provided by Penney [2000]. This publication contained data on 24 species of Oonopidae, most of which (16) belong to *Orchestina*. More recent publications by Penney [2002a, 2004, 2006, 2007] and Wunderlich [2004] added 11 species, some of which came from new deposits (Canada, China, Colombia, France, Madagascar and Ukraine). Up to now, fossil oonopids are known from almost all well studied amber and resin deposits, namely: Baltic, Burmese, Canadian, Chinese, Colombian, Dominican, French, Japanese, Kenyan, Lebanese, Madagascan, Mexican, New Jersey and Ukraine (Rovno), but were not found in Taimyr ambers [Eskov & Wunderlich, 1995]. In fact, Oonopidae are known from more fossil deposits than any other spider family [Penney, 2006]. It is worth mentioning that Oonopidae together with Segestriidae are the oldest haplogyne spiders found as fossils, as both families are known from Lebanese amber (120–130 Ma) [Penney, 2006].

Material and methods

This paper is based partly on literature and partly on the study of types and comparative specimens from personal (JW) and museum collections. Morphological terminology was adopted from Saaristo & van Harten [2006].

Abbreviations used for specimen depositories: AMNH — American Museum of Natural History, New York; BPHGM — The Bayer City Collection for Palaeontology and Historical Geology, Munich; GPIMUH — Geological-Palaeontological Institute and Museum of the University of Hamburg; MCZ — Museum of Comparative Zoology, Harvard; CJW — Personal collection of Jörg Wunderlich.

Survey of species

Oonopidae indet. gen. sp.

Unidentified specimens, new record: Penney, 2000: 244.

Two specimens (AMNH 3 and L-AE-148 (AMNH) from Lebanese amber were just reported in the table I in which all fossil oonopids were surveyed. In the table legend Penney [2000] wrote that “These specimens will be described in papers dealing with the total spider faunas of these Cretaceous deposits”. Unidentified specimens from New Jersey and Burmese ambers were described in subsequent papers [Penney, 2002a,b, 2004]. Detailed studies of two specimens

revealed that the Lebanese amber specimen (AMNH no. 3) belongs in Segestriidae and AMNH L-AE-148 is a juvenile and somewhat poorly preserved and cannot be placed in a genus. However, it was correctly placed in Oonopidae, based on the habitus, spineless legs, two tarsal claws on an onychium and the arrangement of the six eyes [Penney, 2006].

Oonopidae indet. gen. sp.

Fig. 26.

Gen. et sp. indet.: Penney, 2002a: 712, f. 3, pl. 2. f. 1 (juv. or ♀)

Report of this species from the Cretaceous amber of New Jersey is based on a female or juvenile specimen. The specimen is deposited in AMNH (NJ-13) but is not well preserved and cannot be placed with certainty in any genus. However, it lacks a dorsal scutum, has spines on legs I and II (like *Oonops* s.l. or *Oonopinus*), lacks a swollen femur IV (unlike *Orchestina*) and formally can be placed in extant *Stenoonops* (which includes fossil species), a genus known from the new World.

Gen. *Fossilopaea* Wunderlich, 1988

Fossilopaea Wunderlich, 1988: 58. Type species *Fossilopaea sulci* Wunderlich, 1988.

This is a single extinct oonopid genus. Diagnosis same as for species.

Fossilopaea sulci Wunderlich, 1988

Fig. 1.

F. s. Wunderlich, 1988: 59, f. 55–60 (♂).

This species and genus was described on the basis of the holotype male from Dominican amber in GPIUH. Palpal patella swollen, thicker than femur and bulbus. Tibia swollen, shorter than patella and femur. Cymbium fused with bulbus (cymbiobulbus). Psempolus with stylus and spine-like outgrowth, stylus long, gradually tapering. Among known extinct oonopids only one species *?Opopaea* sp. (♀) from Dominican amber also have cymbiobulbus. Among extant oonopids a cymbiobulbus is known from several unrelated genera of Oonopidae-molles and Oonopidae-loricatae.

Gen. *Heteroonops* Dalmás, 1916

This genus is known from two extant species and both only from females. *Heteroonops* is weakly diagnosed and its status is unclear. Two species are present in Caribbean.

?Heteroonops sp.

?H. sp.: Wunderlich, 1988: 56.

One female (in GPIUH) from Dominican amber was mentioned in the text and brief description without illustration was provided.

Comments Lack of the male and absence of generic revision of Oonopidae do not allow placement of this specimen in *Heteroonops* with certainty.

Gen. *Opopaea* Simon, 1891

?Opopaea sp.

?O. sp.: Wunderlich, 1988: 58.

One female (in GPIUH) from Dominican amber was mentioned in the text and briefly described, but not supplied with illustrations. Lack of male does not allow placement of

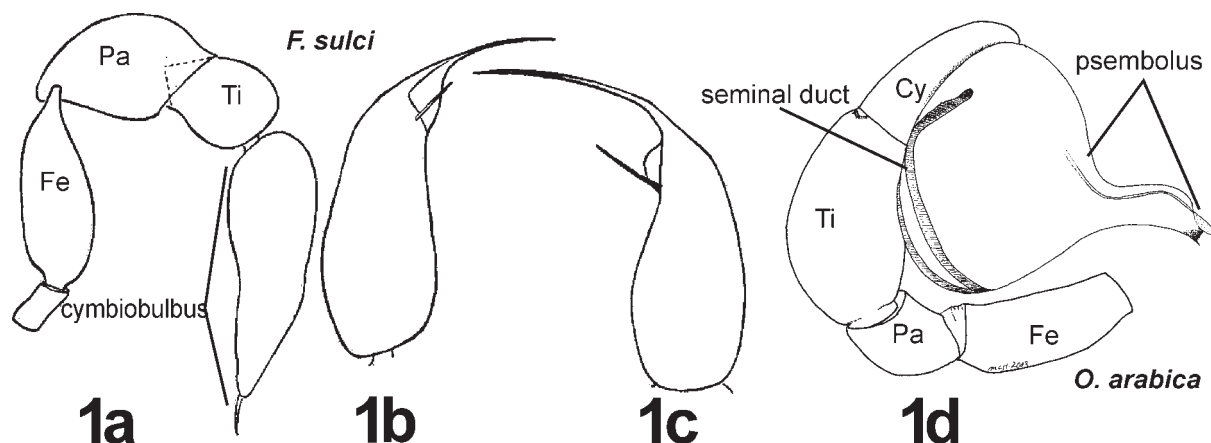


Fig. 1. Male palps of *Fossilopaea sulci* (a–c, after Wunderlich [1988]) and *Orchestina arabica* (d, after Saaristo & van Harten [2006]): a & d — whole palp; b–c — cymbiobulbus, different views. Abbreviations: Cy — cymbium, Fe — femur, Pa — patella, Ti — tibia.

Рис. 1. Пальпус *Fossilopaea sulci* (a–c, по Wunderlich [1988]) и *Orchestina arabica* (d, по Saaristo & van Harten [2006]): a & d — весь пальпус; b–c — цимбиобульбус, под разными углами. Сокращения: Cy — цимбиум, Fe — бедро, Pa — колено, Ti — голень.

this specimen in *Opopaea* with certainty. This specimen can not be conspecific with *Fossilopaea sulci* because it has smaller size and different eye arrangement.

COMMENTS. When this specimen was reported from Dominican amber and until now *Opopaea*, which has pan-tropical distribution, remains unknown in recent fauna of Hispaniola.

Gen. *Orchestina* Simon, 1882

This genus is clearly diagnosed, as compared with other Oonopidae, and has even been placed in a separate subfamily, namely Orchestinae by Chamberlin & Ivie (1942: 6). The subfamily and genus were diagnosed as: “abdomen high and rounded; bulb of the male palp distinct from the cymbium; hind femora swollen; behavior of jumping backwards when disturbed”. An unfused cymbium and bulb is common for most oonopid genera, but the other diagnostic characters well describe the affinities of the genus. Additionally, members of *Orchestina* have a rounded abdomen (more elongate in other Oonopidae), and the male has a seminal duct in the bulb (absent in all other known Oonopidae, and a swollen (in most species) palpal tibia, which is wider and often larger than the femur. The latter character seems absent in other oonopid genera. Another character of *Orchestina* is an abdominal pattern with one or more U-shaped pale stripes [cf. Fig. 6, Hickman, 1932; Fig. 5, Oi, 1958; Fig. 49, Saaristo & van Harten, 2006]. At the same time the genus is very polymorphic in the form of the embolus, which can be tapering, blunt, or bifurcate.

Orchestina albertensis Penney, 2006

Fig. 25.

O. a. Penney, 2006: 231, f. 1, pl. 1, f. 1 (♂).

This species was described on the basis of the holotype male (RTMP 96.9.627) from Canadian amber of Cretaceous (Campanian) age, dating about 78 Ma. Male palpal joints are not modified, being equal in diameter, while most of *Orchestina* have a swollen tibia (thicker than femur). Psem-

bolus large and bifurcate, with sigmoid edge at the embolic tip. Both arms of psemبولus unusually thick. Judging from not modified palpal tibia it may belong to a separate undescribed genus.

Orchestina baltica Petrunkevitch, 1942

Fig. 2.

O. b. Petrunkevitch, 1942: 444, Pl.7, f.55–56, Pl. 59, f. 548 (♂)

O. b.: Petrunkevitch, 1946: 17.

O. b.: Petrunkevitch, 1950: 336.

O. b.: Petrunkevitch, 1958: 354–58, f. 578–587.

O. b.: Wunderlich, 1981: 88, f. 3–5 (♂).

O. b.: Wunderlich, 2004: 695, f. 8k–m, photo 32 (♂).

Described from Baltic amber and known from the holotype (BMNH, In. 18138) and several other specimens. Petrunkevitch [1950] briefly mentioned thirteen specimens in MCZ, eight mature males, one mature female and four females of indeterminate age, while an additional 6 specimens were mentioned in a subsequent paper [Petrunkevitch, 1958]. Later, Petrunkevitch [1963] selected one male from this series as the holotype of *O. imperialis*. It is very likely that additional specimens may also be misidentified. The holotype was redescribed by Wunderlich [1981]. Males of this species have simple, long, gradually tapering psemبولus, which is longer than the tegulum. Some specimens have a bifurcated tip of the psemبولus (Fig. 2d). Similar bifurcation is present also in *O. parisiensis* (Fig. 7).

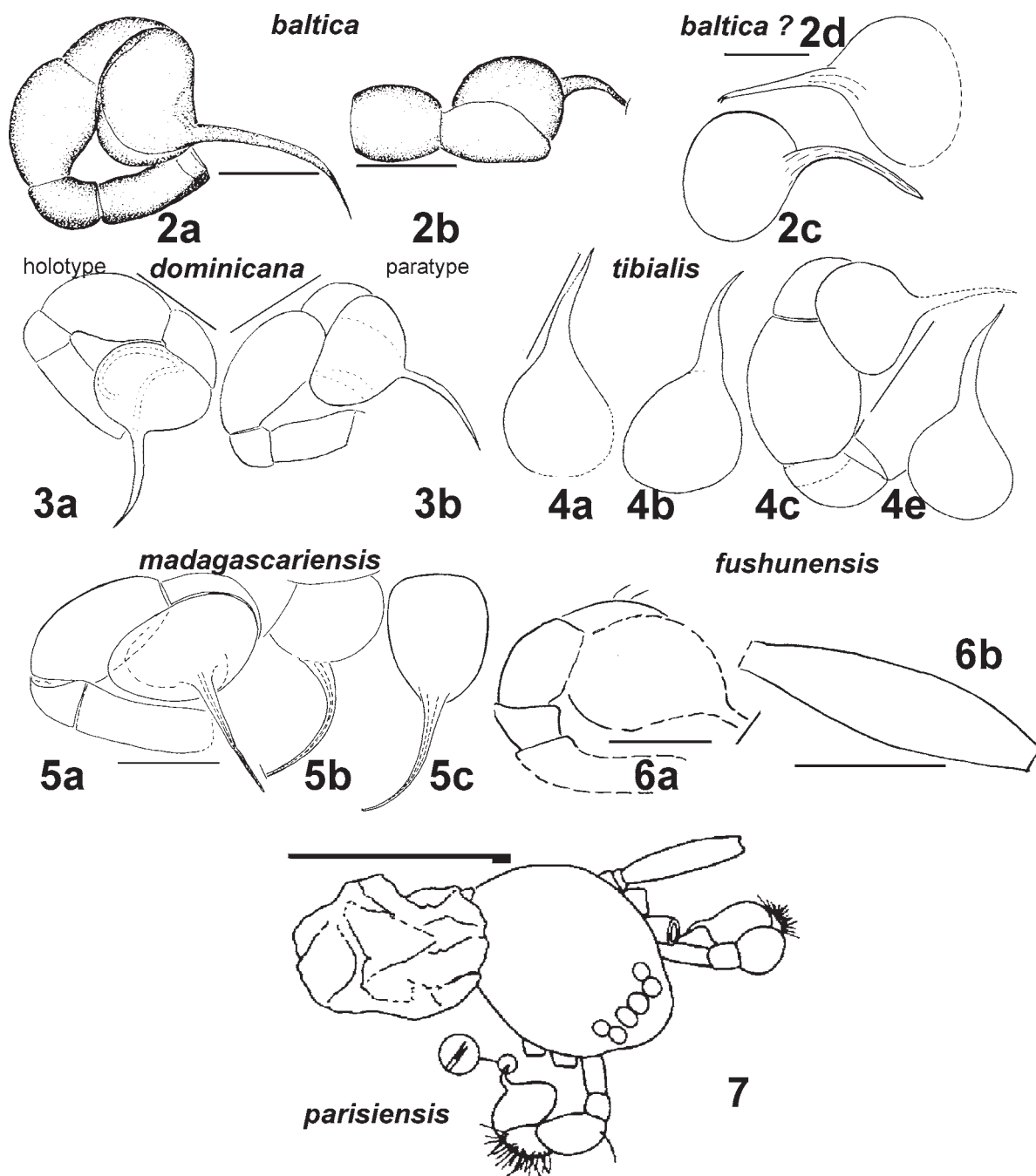
Orchestina breviembolus Wunderlich 1981

Fig. 17.

O. b. Wunderlich 1981: 88, f. 6–8 (♂)

O. b.: Wunderlich, 2004: 695, f. 8n–p (♂).

Described on the basis of the holotype (GPIMUH, No. 2526) and 5 paratypes (2 in CJW, 2 in GPIMUH, Nos. 2501 and 2518 and 1 in BMNH, No. 18714) from Baltic ambers. This species has a simple blunt psemبولus, which is shorter than the diameter of the tegulum. In general appearance, the male palp is rather similar to that of the extant *O. algerica* Dalmas, 1916.



Figs 2–7. Male palps of *Orchestina baltica* (2), *O. dominicana* (3), *O. tibialis* (4), *O. madagascariensis* (5) and *O. fushunensis* (6) and habitus of *O. parisiensis* (7). After Wunderlich [1981, 1988, 2004] and Penney [2007].

Рис. 2–7. Пальпс *Orchestina baltica* (2), *O. dominicana* (3), *O. tibialis* (4), *O. madagascariensis* (5), *O. fushunensis* (6) и *O. parisiensis* (7). По Wunderlich [1981, 1988, 2004] и Penney [2007].

Orchestina cochlembolus Wunderlich, 1981

Fig. 11.

O. c. Wunderlich, 1981: 93, f. 14a–b (♂).

O. c.: Wunderlich, 2004: 695, f. 8q–s (♂).

This species was described on the basis of two males from Baltic amber (GPIMUH: holotype No. 2522, paratype in GPIUH). This species has a modified psempolus, a tapering embolic part and a short triangle-shaped outgrowth in

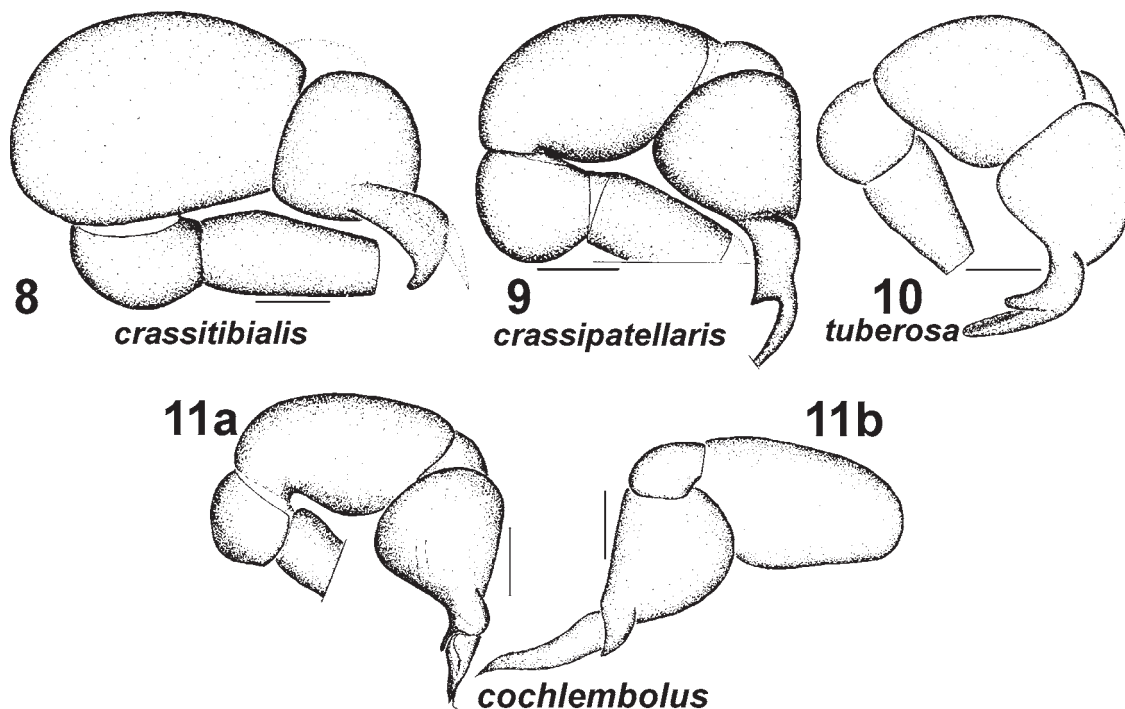
the base. The cymbium is very small, but the palpal tibia is enlarged, being larger than the tegulum.

Orchestina colombiensis Wunderlich, 2004

Fig. 16.

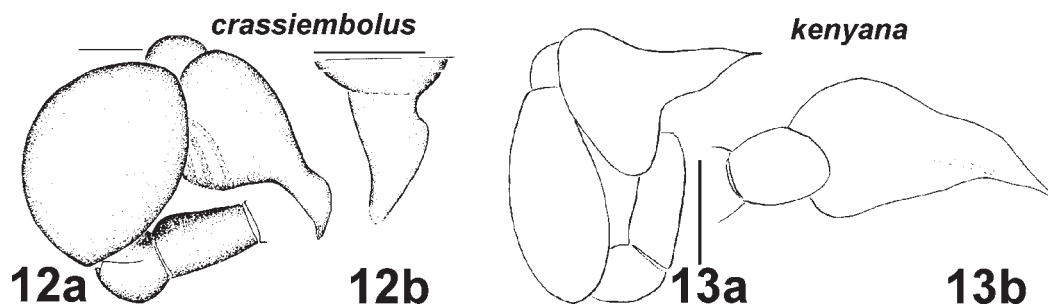
O. c. Wunderlich, 2004: 1855, f. 1–4 (♂).

This species described on the basis of the male holotype (F953/CC/AR/OON?CJW) from Colombian (Simatara) co-



Figs 8–11. Male palpi of *Orchestina crassitibialis* (8), *O. crassipatellaris* (9), *O. tuberosa* (10), *O. cochlembolus* (11). After Wunderlich [1981].

Рис. 8–11. Пальпус *Orchestina crassitibialis* (8), *O. crassipatellaris* (9), *O. tuberosa* (10), *O. cochlembolus* (11). По Wunderlich [1981].



Figs 12–13. Male palps of *Orchestina crassiembolus* (12) and *O. kenyana* (13). After Wunderlich [1981].

Рис. 12–13. Пальпус *Orchestina crassiembolus* (12) и *O. kenyana* (13). По Wunderlich [1981].

pal. Male palp with swollen tibia, tegulum almost round, psemboles with bifurcated tip.

Orchestina crassiembolus Wunderlich, 1981
Fig. 12.

O. c. Wunderlich, 1981: 92, f. 1, 12–13 (♂).
O. c.: Wunderlich, 2004: 695, f. 8t (♂).

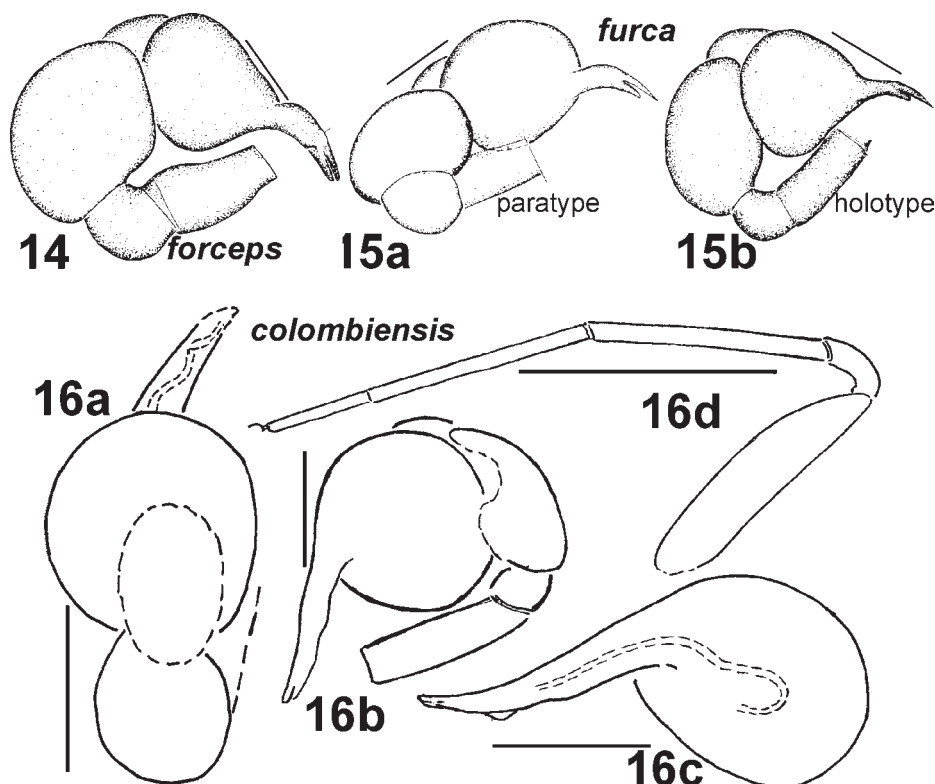
This species was described on the basis of two males from a single piece of Baltic amber (GPIMUH, Specimen No. 2521). The psemboles in this species are relatively small (about the size of tegulum) but thick with parallel margins near the base, and tapering in terminal half. Tibia strongly

swollen, thicker and larger than tegulum. Seminal duct thin and long with at least three coils.

Orchestina crassipatellaris Wunderlich, 1981
Fig. 9.

O. c. Wunderlich, 1981: 95, f. 16b (♂).
O. c.: Wunderlich, 2004: 695, f. 8u (♂).

This species was described on the basis of one male (BPH-GM, 1958 VIII 71) from Baltic amber. Psemboles are modified, being well separated from the tegulum, with two arms, gradually tapering embolic part and short sharply pointed ventral outgrowth. The palpal tibia is larger than the tegulum.



Figs 14–16. Male palps *Orchestina forceps* (14), *O. furca* (15) and *O. colombiensis* (16). After Wunderlich [1981, 2004].

Рис. 14–16. Пальпус *Orchestina forceps* (14), *O. furca* (15) и *O. colombiensis* (16). По Wunderlich [1981, 2004].

Orchestina crassitibialis Wunderlich, 1981

Fig. 8.

O. c. Wunderlich, 1981: 96, f. 16c (♂).

O. c.: Wunderlich, 2004: 695, f. 8v–w (♂).

This species was described on the basis of one male (GPIMUH, Specimen No. 2533) from Baltic amber. Psembo-
lus modified, palpal tibia about two times larger than tegulum.

Orchestina dominicana Wunderlich, 1981

Fig. 3.

O. d. Wunderlich, 1981: 104, f. 19–20 (♂, ♀).

O. ?dominicana Wunderlich, 1981: 105–106 (♀).

O. d.: Wunderlich, 1986 65, f. 55 (♂).

O. d.: Wunderlich, 1988: 56, f. 48 (♂).

O. d.: Penney, 2000: 348.

This species was described on the basis on four males (holotype in GPIMUH, Specimen No. 2525) and two questionable females from Dominican amber. The psembo-
lus is long and gradually tapering, slightly longer than tegulum, palpal tibia longer but thinner than tegulum, seminal duct forming one coil. Figures 105–106 of *O. ?dominicana* in Wunderlich [1981] may belong to *O. tibialis* [cf. Wunderlich, 1988, p. 57].

Orchestina forceps Wunderlich, 1981

Fig. 14.

O. f. Wunderlich, 1981: 94, f. 16a (♂).

O. f.: Wunderlich, 2004: 695, f. 8x (♂).

This species was described on the basis of one male (GPIMUH, No. 2524) from Baltic amber. The psembo-
lus is modified, relatively short (shorter than tegulum), well separated from tegulum, with bifurcate tip having two arms equal in length and resembling forceps. The palpal tibia is globular, slightly larger than tegulum.

Orchestina furca Wunderlich, 1981

Fig. 15.

O. f. Wunderlich, 1981: 90, f. 9–10 (♂).

O. f.: Wunderlich, 2004: 695, f. 8y (♂).

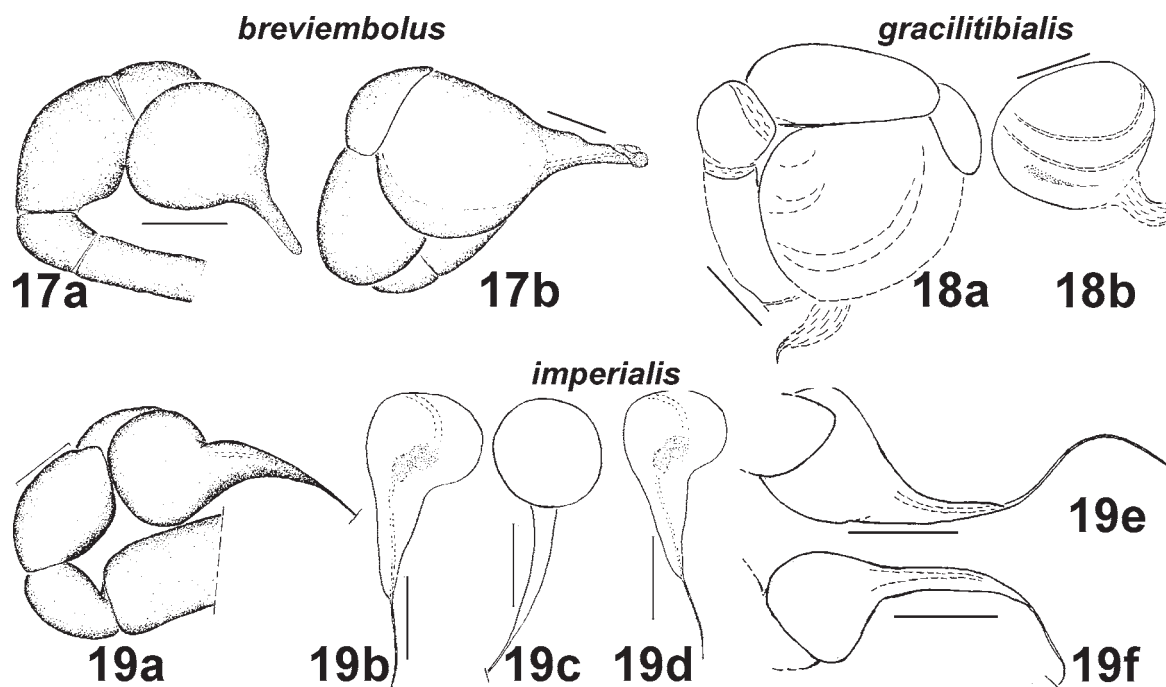
This species was described on the basis of the holotype male (GPIMUH, No. 2519) and paratypes, one female and 3 males, from Baltic amber. The psembo-
lus is modified, relatively short (shorter than tegulum), well separated from tegulum, with bifurcate tip having upper arm longer than ventral. The palpal tibia is globular, about the size of tegulum.

Orchestina fushunensis Wunderlich, 2004

Fig. 6.

O. f.: Wunderlich, 2004: 1862, f. 1–2, photo 28 (♂♀).

This species was described on the basis of the holotype male (F956/CB/AR/OON/CJW) and paratypes, ♂ (F957/CB/AR/OON/CJW) and ♀ (F958/CB/AR/OON/CJW), from the Chinese amber from Fu Shun locality in Liaoning, NE China. Age of this deposit is Early Tertiary. Male palpal tibia slightly swollen, tegulum ovoid, psembo-
lus thin and long (terminal part is not visible).



Figs 17–19. Male palps of *Orchestina breviembolus* (17), *O. gracilitibialis* (18) and *O. imperialis* (19). After Wunderlich [1981, 2004].
 Рис. 17–19. Пальпус *Orchestina breviembolus* (17), *O. gracilitibialis* (18) и *O. imperialis* (19). По Wunderlich [1981, 2004].

Orchestina gracilitibialis Wunderlich, 2004
 Fig. 18.

O. g.: Wunderlich, 2004: 696, f. 8z1–8z2 (♂).

Described on the basis of two males from Baltic amber (Holotype F510/BB/AE/OON/CJW, paratype in Copenhagen Museum). Patpal tibia swollen and strongly elongate, tegulum globular with short (about 1/3 of tegulum diameter) and broad psembo- and embolus. Seminal duct long, making several large coils.

Orchestina imperialis Petrunkevitch, 1963
 Fig. 19.

O. baltica: Petrunkevitch, 1958: 356, f. 583–507 . 357, f. 588. (♂).

O. imperialis Petrunkevitch, 1963: 27 (description with reference to the figures in Petrunkevitch, 1958).

O. imperialis: Wunderlich, 1981: 91, f. 11a–d (♂).

O. sp. (? imperialis): Wunderlich, 1981: 91, f. 11e–f (♂).

O. i.: Wunderlich, 2004: 696, f. 8z3–8z5, photo 34 (♂).

This species was described on the basis of two males from Baltic ambers. One female that possibly belongs here was also described. The male palp differs significantly from all other fossil and extant *Orchestina* species in having a long and thick femur, longer than the tibia, and about its width. Another difference is the modified tapering psembo- and embolus with stylus (filamentous extension) So far stylus is not known in other *Orchestina* but in *Oonops*, *Oonopinus* and several other genera. Presence of stylus, and enlarged palpal femur, do not allow to consider this species in *Orchestina*.

Orchestina kenyana Wunderlich, 1981
 Fig. 13.

O. k. Wunderlich, 1981: 107, f. 22–24 (♂).

This species was described on the basis of the holotype male (GPIMUH, Specimen No. 2528) from Kenyan copal.

The male palp has a very long tibia which is only about 2 times thicker than the femur, and a psembo- and embolus that is short and thick.

Orchestina longimana Wunderlich, 1981
 Fig. 22.

O. l. Wunderlich, 1981: 106, f. 21 (♂).

This species was described on the basis of the holotype male (GPIMUH, Specimen No. 2527) from Kenyan copal. The male palp has a very long tibia which is only about 1.8 times thicker than the femur, and a psembo- and embolus longer than the tegulum, with parallel sides and bifurcate in upper 1/4, with arms diverging and sharply pointed.

Orchestina madagascariensis Wunderlich, 2004
 Fig. 5.

O. m. Wunderlich, 2004: 1836, f. 4–6, photos 29–31, 431 (♂♀).

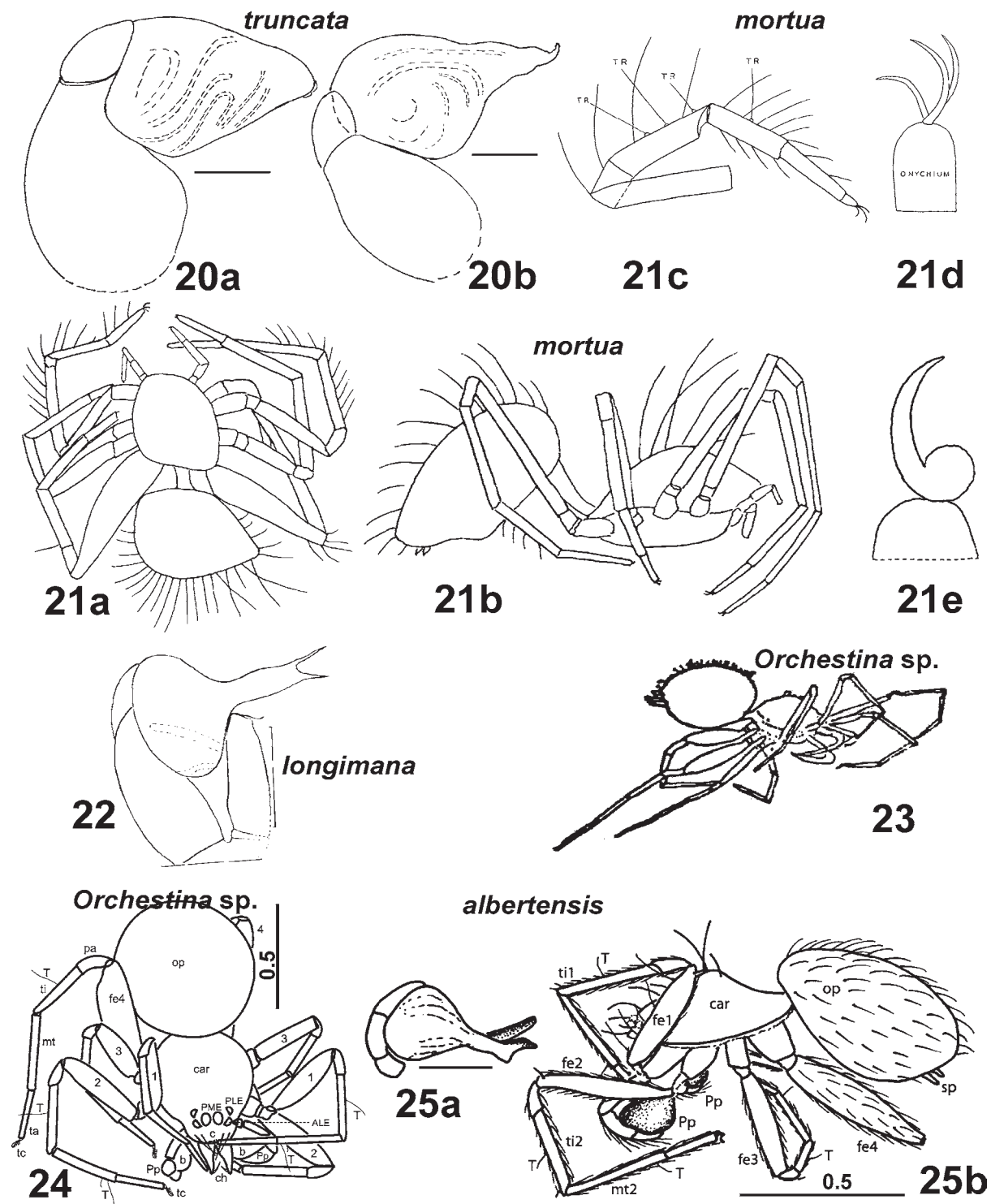
This species was described on the basis of 5♂ (Holotype F1119/CMAR/OON/CJW) and 2♀ in copal from Madagascar. It was the first record of Oonopidae from Madagascar, while there are about 100 undescribed recent species on the island [Platnick, 2006].

Orchestina mortua Petrunkevitch, 1971
 Fig. 21.

O. m. Petrunkevitch, 1971: 33, f. 81–90, T. 1b (♀♂).

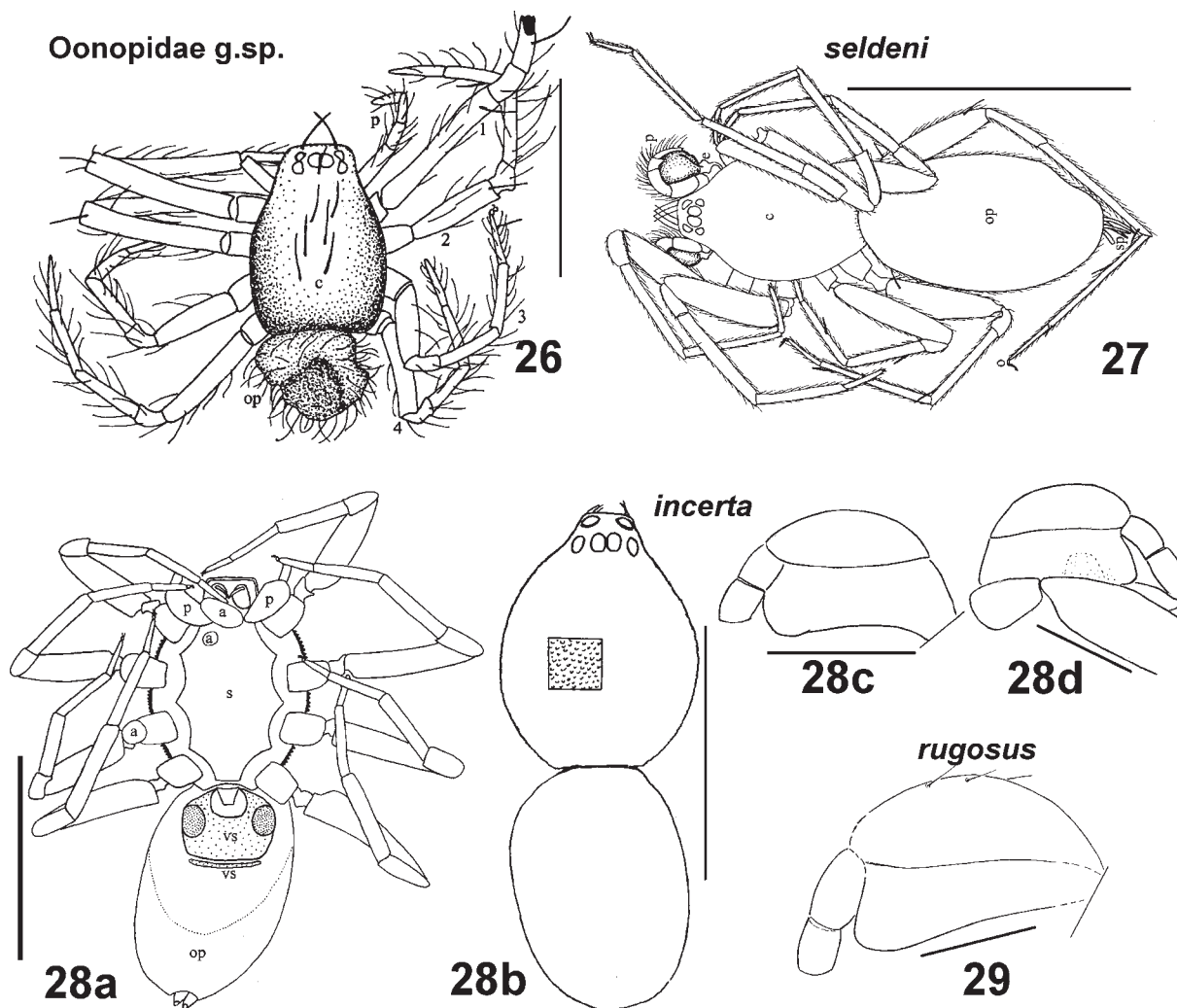
O. m.: Wunderlich, 1981: 107.

This species was described from the holotype ♀ (MPUC, No. 13543, Loc. B-4119.) and distorted paratype ♂ (MPUC, No. 13068, Loc. B-7461) from Mexican (Chiapas) amber. The female is very small, about 0.7 mm in the length. Legs



Figs 20–25. Male palps and habitus of *Orchestina truncata* (20), *O. mortua* (21), *O. longimana* (22), *Orchestina* spp. (23–24) and *O. albertensis* (25): 20a–b — palp, different turns; 21b — swollenness of femur IV in lateral view invisible; 21c — leg II with trichobothria shorter than hairs; 21d — “onychium and claws of second right leg”; 21e — “palpus”. 20 — after Wunderlich [2004]; 21 — after Petrukevitch [1971]; 22 — after Wunderlich [1981], 23 — after Nishikawa [1974], 25 — after Penney [2006].

Рис. 20–25. Пальпус и габитус *Orchestina truncata* (20), *O. mortua* (21), *O. longimana* (22), *Orchestina* spp. (23–24) и *O. albertensis* (25): 20a–b — пальпус под разными углами; 21b — вздутость бедра IV при виде сбоку не видна; 21c — нога II с трихоботриями короче чем волоски; 21d — “onychium и claws of second right leg”; 21e — “palpus”. 20 — по Wunderlich [2004]; 21 — по Petrukevitch [1971]; 22 — по Wunderlich [1981], 23 — по Nishikawa [1974], 25 — по Penney [2006].



Figs 26–29. Oonopidae gen. sp. (26, after Penney [2002]), *Stenoconops seldeni* (27, after Penney, [2002]) *S. incerta* (28a–b, after Penney [2000]; 28c–d, after Wunderlich [1988]) and *S. rugosus* (29, after Wunderlich [2004]).

Рис. 26–29. Oonopidae gen. sp. (26, no Penney [2002]), *Stenoconops seldeni* (27, no Penney, [2002]) *S. incerta* (28a–b, no Penney [2000]; 28c–d, no Wunderlich [1988]) и *S. rugosus* (29, no Wunderlich [2004]).

and body are covered with unusually long (for Oonopidae) hairs, longer than trichobothria. The ocular area was not illustrated. The male palp is not clearly visible, but does not resemble an oonopid palp (Fig. 21e). In addition, Petrunkevitch [1971] mentioned and illustrated (Fig. 21d) 3 tarsal claws on leg II, and claws have no teeth. So far, all known oonopids have only two claws [Jocqué & Dippenaar-Schoeman, 2006] which are biserial (bipectinate) [Forster & Platnick, 1985]. If interpretation of the specimens (holotype and paratype) is correct, this species cannot be placed in *Orchestina*, nor even Oonopidae.

Orchestina parisiensis Penney, 2007

Fig. 7.

O. parisiensis Penney, 2007: 2, f. 1a–b (♂).

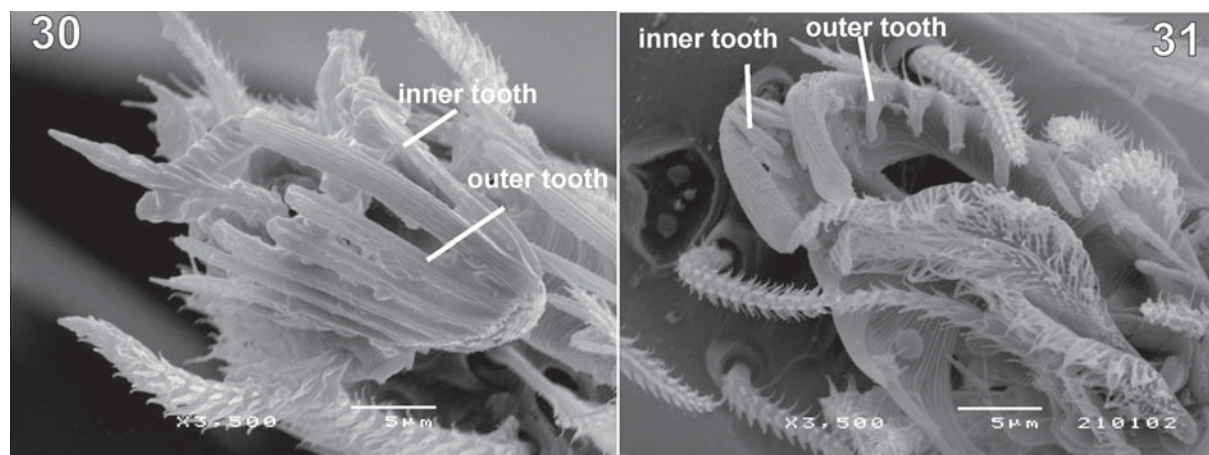
The species description is based on the holotype (PA 759) and paratype (PA 1909) males from French (Paris) amber, of lowermost Eocene. The palp is well visible and

illustrated. the palpal tibia is slightly swollen, about 1.5 times wider than femur, cymbium fairly large, psemبولus simple but bifurcated on the tip, psemبولus shorter than tegulum. As was stated by Penney [2007], the bifurcation of the psemبولus tip is similar to the bifurcation of *O. ?baltica* (cf. Fig. 2d).

Orchestina pusilla (Menge, 1854) **comb.n.**

Segestria pusilla Menge, 1854 in Koch & Berendt, 1854: 74.

The description of this species is very brief (rounded and hairy opisthosoma) and not supported by any figure and without information about sex of holotype. Petrunkevitch [1942] treated this species as *nomen nudum*, but later [Petrunkevitch, 1950] listed it as a valid species. Wunderlich [1981] recognized that this species belongs to *Orchestina*, but did not suggest a new combination. Here we make a formal new combination, although the species remains unrecognizable.



Figs 30–31. Biserial claws of the leg I of *Orchestina manicata*: 30 — male; 31 — female. Scale: 5 µm.

Рис. 30–31. Коготки ноги I *Orchestina manicata*: 30 — самец; 31 — самка. Масштаб: 5 µm.

Orchestina tibialis Wunderlich, 1988

Fig. 4.

O. t. Wunderlich, 1988: 57, f. 51–54.

This species was described on the basis of two males (in GPIUH) from Dominican amber. The palpal tibia is swollen, thicker than femur, psemبولus simple, gradually tapering.

Orchestina truncata Wunderlich, 2004

Fig. 20.

O. t. Wunderlich, 2004: 1856, f. 5–6 (♂)

This species was described on the basis of one male holotype (F1113/CC/AR/OON/CJW) from Colombian copal derived from Pena Blanca. The palp has a strongly swollen tibia, bulbus large, droplet shaped, about the size of tibia, psemبولus not separated from tegulum, bulbus with long seminal duct which makes several loops within tegulum and psemبولic part.

Orchestina tuberosa Wunderlich, 1981

Fig. 10.

O. t. Wunderlich, 1981: 93, f. 15 (♂).

O. t.: Wunderlich, 2004: 696, f. 8z7 (♂).

This species was described on the basis of the holotype male (GPIMUH, Specimen No. 2523) and one additional doubtful male from Baltic amber. The psemبولus is modified: bifurcate with two blunt arms, ventral arm is shorter than dorsal. Palpal tibia strongly swollen, almost globular, slightly larger than tegulum. Palp is similar to those in *O. crassipatellaris* and *O. crassitibialis*.

Orchestina sp.

Fig. 23.

O. sp.: Nishikawa, 1974: 401, f. XX-4-1A (♀?)

A detailed description of a specimen from Japanese copal was written in Japanese. Judging from the figure it is a female or subadult. Total length is 0.85. Femur IV swollen.

Orchestina sp.

O. sp. Wunderlich, 2004: 1822.

This record is based on 2 males and 1 female from Rovno amber and which no doubt represents a new species.

Orchestina spp.

Oonopidae sp.: Rasnitsyn & Ross, 2000: 24 (2 specimens).

Oonopidae sp.: Grimaldi et al., 2002: 29 (juvenile and ♂?)

Oonopidae sp. indet.: Penney, 2006: 232, pl. 1, f. 2 (juvenile or ♀).

Penney's record is based on a juvenile specimen or adult female from late Cretaceous (Cenomanian or Albian age) Burmese amber belonging to the American Museum of Natural History. While Grimaldi et al. [2002] mentioned two specimens (Bu-706 juvenile and Bu-708 ♂?) Penney [2006] studied only one specimen. Generic placement of the presumably adult specimen is unknown. Two specimens of Oonopidae reported by Rasnitsyn and Ross [2000] belong to the Natural History Museum in London. The sex and stage of these specimens are unknown. As they may belong to the same undescribed species or another, the number of species and genera in Burmese amber remain unclear.

Orchestina sp.

Fig. 24.

O. sp.: Penney, 2002b: 4, f. 3 (♂)

O. sp.: Penney, 2004: 368, f. 1, Pl. 1: f. 1–2 (♂).

The tip of the palp of a the single specimen from New Jersey amber is invisible and therefore this specimen was not named. Age of the specimen is upper Cretaceous (90–94Ma).

Comparison of species

Study of the fossil and extant *Orchestina* s.l. reveals one additional diagnostic character of this group. In addition to swollen palp and presence of seminal duct inside the palp, a swollen male palpal tibia larger or at least thicker in diameter than femur can be used as a key and diagnostic character

of *Orchestina* s.l. Only one fossil species, *O. albertensis*, and two extant *O. simoni* Dalmas, 1916 and *O. longipes* Dalmas, 1922 have no swollen tibia, and another species, *O. imperialis*, has swollen tibia smaller than enlarged femur.

Based on the shape of the male palp, four species groups can be discerned among fossil *Orchestina*:

I. *O. crassitibialis*, *O. crassipatellaris*, *O. cochlembolus* and *O. tuberosa*

II. *O. crassimbolus* and *O. kenya*

III. *O. baltica*, *O. dominicana*, *O. fushunensis*, *O. madagascariensis*, *O. parisiensis* and *O. tibialis*.

IV. *O. forceps*, *O. furca* and ?*O. columbiensis*.

Other species *O. albertensis*, *O. breviembolus*, *O. gracilitibialis*, *O. imperialis*, *O. longimana*, *O. mortua* and *O. truncata* either form monotypic groups among fossil *Orchestina* or their placement is unclear.

Comparison with extant species reveals that group IV is similar to the generotype *O. pavesii* in having a bifurcate tip of the psembolus, and this group can be called *O. pavesii*-group. Besides the mentioned species, it contains *O. arabica* Dalmas, 1916, *O. pavesiiformis* Saaristo, 2007, *O. manicata* Simon, 1893, and four questionable species ?*O. bedu* Saaristo & van Harten, 2002, ?*O. mirabilis* Saaristo & van Harten, 2006, ?*O. hammamali* Saaristo & van Harten, 2006 and *O. lahj* Saaristo & van Harten, 2006.

Male palp in group III of fossil *Orchestina* with an unmodified psembolus has the same conformation as the palp in extant *O. dentifera* Simon, 1893, *O. flagella* Saaristo & van Harten, 2006, *O. foa* Saaristo & van Harten, 2002, *O. moaba* Chamberlin & Ivie, 1935, *O. minutissima* Denis, 1937, *O. obscura* Chamberlin & Ivie, 1942, *O. pilifera* Dalmas, 1916, *O. sedomnikha* Saaristo, 2007, ?*O. justini* Saaristo, 2001, ?*O. saltitans* Banks, 1894, and this group can be called *O. pilifera*-group. *O. okitsuni* Oi, 1958 from Japan may belong to the same group, or to *O. pavesii*-group. Figures provided for this species are not good enough to see details of the psembolus.

Group I of fossil *Orchestina* has no similar species among extant congeners and seems extinct.

Group II has a similar type of palp as in extant *O. sechellorum* Benoit, 1979, *O. ebriola* Brignoli, 1972, and the three species can provisionally be placed in the *O. sechellorum*-group. An important difference between fossil and recent species is the undivided psembolus in *O. crassimbolus* and *O. kenya* and bifurcate one in *O. sechellorum*.

O. sechellorum- and *O. pilifera*-groups are close to each other and have no clear distinguishing characters as in the other groups. *O. sechellorum*-group have massive base of psembolus, while *O. pilifera*-group have thin spine-like psembolus. *O. foa* have intermediate type, thick base of psembolus and spine-like terminal half.

Among ungrouped fossil Oonopidae, *O. breviembolus* is very similar to the extant *O. algerica* Dalmas, 1916, and these species can be placed in the *O. algerica*-group.

O. truncata has a palp similar to *O. sinensis* Xu, 1987, *O. thoracica* Xu, 1987 and *O. flava* Ono, 2005. All four species form *O. sinensis*-group, which can be diagnosed by a thick psembolus.

Among extant *Orchestina* only two species (*O. simoni* and *O. longipes*) have atypical male palp with unswollen tibia, which is just only elongate. Bulbus in these species are also very different from all extant and extinct species. *O. tubifera* Simon, 1893 from Sri Lanka known by female only is also remarkably different from other *Orchestina* and all oonopids by having elongate abdomen with tail-like outgrowth carrying spinnerets.

Gen. *Stenoonops* Simon, 1891

Diagnosis of this genus is very obscure and it is not based on revisional study. Some species included here have a normal male palp, while some have cymbiobulbus [cymbium fused totally with bulbus, Wunderlich, 2004].

Stenoonops incerta (Wunderlich, 1988)

Fig. 28.

Gamasomorpha i. Wunderlich, 1988: 60, f. 61–63 (♂)

S. i.: Wunderlich, 2004: 692, f. 8a (♂).

S. i.: Penney, 2000: 348, f. 2, pl. 2 (♂) redescription of holotype.

This species was described on the basis of the male holotype from Miocene Dominican amber. It evidently does not belong to *Gamasomorpha*, but placement in *Stenoonops* (poorly diagnosed and studied) is also highly questionable. Cymbium is very large, larger than tibia and patella together. Tibia slightly longer than patella. Details of psembolus are invisible.

?*Stenoonops rugosus* Wunderlich, 2004

Fig. 29.

?*S. r.* Wunderlich, 2004: 692, f. 8b, photo 35 (♂).

Description of this species is based on the male holotype (F28/BB/AR/OON/CJW) from Baltic amber from Bitterfeld deposit. Placement of this species in *Stenoonops* is not certain because this genus lacks clear diagnosis and was never revised. General appearance of palp is similar to those in *S. incerta*, while base of psembolus seems thinner.

Stenoonops seldeni (Penney, 2000) new comb.

Fig. 27.

Oonops seldeni Penney, 2000: 345, f. 1, pl. 1. (♂).

This species is described in *Oonops* Templeton, 1835 on the basis of one male from Dominican amber. Genus *Oonops* is poorly diagnosed. While 73 species from West Palaearctic, African, S and N America are placed in this genus [cf. Platnick, 2008], it seems that only one species belongs to this taxon [Saaristo & Marusik, personal data]. By no means can *O. seldeni* be placed in *Oonops sensu lato* because it lacks spines on legs I and II. Habitus, male palp and eye pattern of *O. seldeni* is also different from *O. pulcher* (the generotype) and other European species assigned to *Oonops*. Judging from the formal diagnosis (lack of dorsal scutum, lack of spines on legs I and II) *O. seldeni* should be transferred to *Stenoonops*.

Misplaced record

Poinar and Milki [2001: 33, pl. 23] listed and figured one specimen attributed to Oonopidae from Lebanese amber. Study of this specimen revealed that it belongs to a new subfamily of Segestriidae, but not to Oonopidae.

Discussion

So far at least 35 species of oonopids belonging to six genera: *Fossilopaea* (1), *Heteroonops* (1), ?*Opo-paea* (1), *Orchestina* (27) and *Stenoonops* (3) have been reported from the resins. Generic placement of



Map. Distribution of the amber deposits which contain inclusions of Oonopidae. Large dot corresponds to Baltic amber deposits.

Карта. Места находок янтарей с инклюзами Оопориде. Наиболее крупный кружок указывает местонахождения балтийских янтарей.

the oldest amber inclusions remains unknown. The number of extinct oonopid species is rather high in comparison to 491 extant species [Platnick, 2008] and comprises 7.1%. The ratio of extinct species in the whole order is about 2.5%, with about 1000 fossil species [Penney, 1995; Wunderlich, 2004] and 40024 extant ones [Platnick, 2008]. It seems that among extant families only Archaeidae is better represented in ambers than Oonopidae (25 extant and 10 fossil species).

As was mentioned earlier, most of the fossil species belong to *Orchestina* (27 species). Three species are tentatively placed in *Stenoonops*, and three other genera are known by a single fossil species. Among fossil oonopids, only one genus, *Fossilopaea*, is known solely from ambers, all others being represented in the recent fauna.

Most of the oonopids found in resins belong to Oonopidae-molles (sometime treated as subfamily Oonopinae) and have no dorsal abdominal scutum. Only two species ?*Opopaea* sp. and *Fossilopaea* belong to Oonopidae-loricatae (sometime treated as subfamily Gamasomorphinae) and have dorsal abdominal scutum. The oldest fossil oonopids belongs to Oonopidae-molles.

With the exception of most *Orchestina* species, the placement of fossil oonopids into extant genera is doubtful or incorrect. *Oonops seldeni* does not fit the diagnosis of the genus (lacks spines on leg I–II, has no stylus) and was transferred to *Stenoonops* (although its placement there is not convincing). *Stenoonops* and *Heteroonops* are poorly studied and diagnosed genera. Correctness of the placement of *Opopaea* sp. cannot be checked, because single specimen is female, while this

genus can be recognized with certainty only on the base of male palp which has fenestra [Saaristo & van Harten, 2006].

Oonopidae is one of the two oldest haplogyne families known in palaeorecords [cf. Penney, 2006]. Among extant araneomorph spider families only two are known from older deposits than Oonopidae: Archaeidae and Uloboridae. Four families have the same age as Oonopidae (upper Cretaceous, 120–130 Ma): Segestriidae, Oecobiidae, Deinopidae and Araneidae. The record of Linyphiidae from that period [cf. Penney, 2006, f. 3] was based on misidentification [Wunderlich, 2004: 1299]. Segestriidae a second haplogyne family known from the upper Cretaceous, was represented in Lebanese ambers by a separate extinct subfamily known only from one locality.

The oldest identified and reported oonopid genus is *Orchestina*. It was reported from Burmese and New Jersey amber which is of middle Cretaceous age (90–97 Ma) [Penney, 2000]. There are no other extant spider genera that are known from such old fossils, with the exception to *Ariadna* (Segestriidae) [Wunderlich, in press]. All Cretaceous described and undescribed species of *Orchestina*, judging from the morphology, are very different from Cenozoic *Orchestina*, and can be treated in a separate genera. *Orchestina* is not only an oldest araneomorph genus, but it is also most speciose (23 described and at least 4 unnamed species) and most widespread genus in the past and now. At present, *Orchestina* is known from Tasmania, Samoa, SE Asia, Seychelles, Venezuela, South Africa, Gabon, and south Holarctic [cf. Platnick, 2008]. Other than these mentioned countries, it is also known from

Table 1. List of described or recorded fossil Oonopidae.
Таблица 1. Список ископаемых Oonopidae.

	Species name	Source	Age
1.	Oonopidae indet. g.sp. (not loricatini)	Lebanese amber	120–130 Ma
2.	Oonopidae indet. g.sp. (not loricatini)	New Jersey amber	90–94 Ma
3.	<i>Fossilopaea sulci</i> Wunderlich, 1988	Dominican amber	15–20 Ma
4.	? <i>Heteroonops</i> sp. Wunderlich, 1988	Dominican amber	15–20 Ma
5.	? <i>Opopaea</i> sp. Wunderlich, 1988	Dominican amber	15–20 Ma
6.	<i>Orchestina albertensis</i> Penney, 2006	Canadian amber	78.2 Ma
7.	<i>O. baltica</i> Petrunkevitch, 1942	Baltic amber	40–50 Ma
8.	<i>O. breviembolus</i> (Petrunkevitch, 1942)	Baltic amber	40–50 Ma
9.	<i>O. cochlembolus</i> Wunderlich, 1981	Baltic amber	40–50 Ma
10.	<i>O. colombiensis</i> Wunderlich, 2004	Colombian copal*	?
11.	<i>O. crassimbolus</i> Wunderlich, 1981	Baltic amber	40–50 Ma
12.	<i>O. crassipatellaris</i> Wunderlich, 1981	Baltic amber	40–50 Ma
13.	<i>O. crassitibialis</i> Wunderlich, 1981	Baltic amber	40–50 Ma
14.	<i>O. dominicana</i> Wunderlich, 1981	Dominican amber	15–20 Ma
15.	<i>O. forceps</i> Wunderlich, 1981	Baltic amber	40–50 Ma
16.	<i>O. furca</i> Wunderlich, 1981	Baltic amber	40–50 Ma
17.	<i>O. fushunensis</i> Wunderlich, 2004	Early Tertiary Chinese amber	55–65 Ma
18.	<i>O. gracilitibialis</i> Wunderlich, 2004	Baltic amber	40–50 Ma
19.	<i>O. imperialis</i> Petrunkevitch, 1963	Baltic amber	40–50 Ma
20.	<i>O. kenya</i> Wunderlich, 1981	Kenyan amber (copal?)	?
21.	<i>O. longimana</i> Wunderlich, 1981	Kenyan amber (copal?)	?
22.	<i>O. madagascariensis</i> Wunderlich, 2004	Madagascar copal	?
23.	<i>O. mortua</i> Petrunkevitch, 1971	Mexican amber	20–30 Ma
24.	<i>O. parisensis</i> Penney, 2007.	French (Paris) amber	53 Ma
25.	<i>O. pusilla</i> (Menge, 1854)	Baltic amber	40–50 Ma
26.	<i>O. tibialis</i> Wunderlich, 1988	Dominican amber	15–20 Ma
27.	<i>O. truncata</i> Wunderlich, 2004	Colombian copal	?
28.	<i>O. tuberosa</i> Wunderlich, 1981	Baltic amber	40–50 Ma
29.	<i>O. sp.</i> [Nishikawa, 1974]	Japanese amber (copal?)	?
30.	<i>O. sp.</i> [Wunderlich, 2004]	Rovno amber	40–50 Ma
31.	<i>O. spp.</i> [Rasnitsyn & Ross, 2000; Grimaldi et al., 2002]	Burmese amber	90–100 Ma
32.	<i>O. sp.</i> [Penney, 2002b, 2004]	New Jersey	90–94 Ma
33.	<i>Stenoonops incerta</i> Wunderlich, 1988	Dominican amber	15–20 Ma
34.	? <i>Stenoonops rugosus</i> Wunderlich, 2005	Baltic amber	40–50 Ma
35.	<i>Stenoonops seldeni</i> Penney, 2000	Dominican Amber	15–20 Ma

* Copal – from recent to several thousand years

Ecuador (personal data). In the Palaearctic the northernmost records of *Orchestina* are from Slovakia [Platnick, 2008], Azerbaijan [Marusik & Guseinov, 2003] and Hokkaido [Yaginuma, 1977]. In addition, the diversity of fossil *Orchestina* (at least 27 species) is amazingly high in comparison to number of described extant species [43, Platnick, 2008]. Judging from the variation in copulatory organs, *Orchestina*, seems not to be a monophyletic genus [Saaristo, 2001]. All species, extinct and extant, were attributed to this genus only because of one somatic character, swollen femur IV.

Orchestina is not only one of the oldest araneomorph genus, it is also rather morphologically primitive in several respects. It has several plesiomorphic characters such as presence of seminal ducts within the bul-

bus (present in all spiders, exception all other oonopidas and several other haplogyne genera, it has no dorsal abdominal scutum (present in many oonopid genera), cymbium never fused with bulb like in all other spiders (cymbiobulbus present in many unrelated oonopid genera) and unmodified biserial claws (Figs 30–31). Biserial (bipectinate) claws are known in several related haplogyne spider families such as Orsolobidae, Oonopidae and few Dysderidae [Forster & Platnick, 1985]. In most of the oonopids studied by Forster & Platnick [1985] one of the rows can be reduced to one tooth or absent completely. In *Gamasomorpha* sp. [fig. 838, Forster & Platnick, 1985] teeth on inner row are much smaller than those on outer row. In *Orchestina manicata* Simon, 1893 both rows of teeth are equal

in size. Another two species examined, type species *O. pavesii* (Simon, 1873) and *O. pilifera* Dalmas, 1916 have also typical biserial claws.

It is worth mentioning that the distribution of oonopids, at least in recent northern hemisphere, in the past was significantly wider than now. For example first oonopid from Madagascar was described on the basis of a specimen found in copal [Wunderlich, 2004] when none of the extant species has been known from the island. Actually oonopids are present in Madagascar and are highly diverse there [Platnick, 2006]. Presently, oonopids are absent in Rovno Area of Ukraine and from Alberta (Canada). There are no free living Oonopidae in Baltic states (exception – *Oonops pulcher* from south Poland [Woźny, 1984]).

Moreover, diversity of oonopids at whole European (Baltic, Ukraine, France) ambers (15 species) or only in Baltic ambers (13 species) is higher than diversity of Oonopidae in whole Europe north of 45°N (4 species). The number of oonopids in Europe [19 species, cf. Platnick, 2008] is subequal to the number of fossils. Diversity of *Orchestina* s.l. in European ambers (14 species) is higher than the diversity of *Orchestina* s.l. in whole West Palaearctic (9 species).

It is easy to assume that *Orchestina* s.l. is easily trapped by resin, because many species live on tree trunks. *Oonops* (*O. domesticus*) also lives on tree trunks, but *Oonops* s.l. and even Oonopinae are not known from European ambers at all.

All groups of Oonopidae, molles and loricatae, live in the tree canopy in Ecuador (personal data). In tropical rain forest in south China in tree-trunk traps among 42 adult oonopids 9 specimens or almost ¼ were loricatae. So, if some scutate or Oonopidae-molles existed in Baltic Eocene forests, they should have been trapped from time to time, but only one species and specimen of Oonopidae-loricatae is known from Baltic amber (*Fossilopaea*) and one from Dominican amber. On the other hand, not all extant *Orchestinina* live on trees, but in litter as well (personal observation in India, Iran, Azerbaijan, south China).

So it seems that Oonopidae-loricatae are younger than *Orchestina* s.l. and Oonopidae-molles and not known before Eocene. If to suggest that scutate Oonopidae evolved earlier, they should avoid forests. Comparison of value of scutate and not scutate oonopids in Baltic ambers and tree-trunk traps in recent rain forest reveals that Oonopidae-loricatae were not living on tree trunks and in canopy.

ACKNOWLEDGEMENTS. We wish to thank the following persons for helping in this review. David Penney generously made his unpublished catalogue of spiders found in fossil resins available to us. He also greatly helped us with literature and supplied an early draft of our manuscript with very important comments. We are obligated to the late Michael I. Saaristo for fruitful discussions on different topics of oonopid taxonomy and to Seppo Koponen for his help in arranging work space for YM at Turku University. Dmitry

Logunov, Sarah Crews helped us with some literature and Darrell Ubick provided us with illustrations of extant *Orchestina* and other oonopid genera. D. Ubick provided numerous helpful comments and suggestions for the final draft of the manuscript.

References

- Chamberlin R.V., Ivie W. 1942. A hundred new species of American spiders // Bull. Univ. Utah. Vol.32. No.13. P.1–117.
- Eskov K.Y., Wunderlich J. 1995. On the spiders from Taimyr ambers, Siberia, with the description of new family and with general notes on the spiders from the cretaceous resins (Arachnida: Araneae) // Beitr. araneol. Bd.4. P. 95–108.
- Forster R.R., Platnick N.I. 1985. A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea // Bull. Am. Mus. nat. Hist. No.181. P.1–230.
- Grimaldi D., Engel M.S., Nascimbene P.C. 2002. Fossiliferous Cretaceous amber from Burma (Myanmar): its rediscovery, biotic diversity, and paleontological significance // Amer. mus. Novit. No.3361. P.1–72.
- Hickman V.V. 1932. Studies in Tasmanian spiders. Part 5 // Pap. Proc. Roy. Soc. Tasman. 1931. P.20–31.
- Jocqué R., Dippenaar-Schoeman A. 2006. Spider families of the world. Musée Royal de l'Afrique Centrale. Tervuren. 336 pp.
- Marusik Yu.M., Guseinov E.F. 2003. Spiders (Arachnida, Aranei) of Azerbaijan. I. New families and genera records // Arthropoda Selecta. Vol.12. No.1. P.29–46.
- Menge A. 1854. Footnotes in Koch, C.L. & Berendt, G.C. Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. Berlin (1854). 124 S. 17 pls.
- Nishikawa Y. 1974. XX–4. Amber spiders from Mizunami, Japan // Bulletin Mizunami Fossil Museum. Vol.1. P.401–406.
- Oi R. 1958. Three new species of the six eyed spider // Acta arachn. Tokyo. Vol.15. P.31–36.
- Penney D. 1995. Spiders in amber and the potential use of amber inclusions for measuring The biodiversity of palaeoecosystems. [unpublished report]
- Penney D. 2000. Miocene spiders in Dominican amber (Oonopidae, Mysmenidae) // Palaeontology. Vol.43. P.343–357.
- Penney D. 2002a. Spiders in upper Cretaceous amber from New Jersey (Arthropoda: Araneae) // Palaeontology. Vol.45. Part 4 P.709–724.
- Penney D. 2002b. Arachnological gems: spiders in amber // Newsletter of the British Arachnological Society. No.94. P.2–5.
- Penney D. 2004. New spiders in Upper Cretaceous amber from New Jersey in the American Museum of Natural History (Arthropoda: Araneae) // Palaeontology. Vol.47. P.367–375.
- Penney D. 2006. Fossil oonopid spiders in Cretaceous ambers from Canada and Myanmar // Palaeontology. Vol.49. P.229–235.
- Penney D. 2007. A new fossil oonopid spider in lowermost Eocene amber from the Paris Basin, with comments on the fossil spider assemblage // African Invertebrates. Vol.47. No.1. P.71–75.
- Petrunkovitch A. 1942. A study of amber spiders // Trans. Connect. Acad. Arts Sci. Vol.34. P. 119–464.
- Petrunkovitch A. 1946. Fossil spiders in the collection of the American Museum of Natural History // American Museum Novitates. No.1328. P.1–36.
- Petrunkovitch A. 1950. Baltic amber spiders in the Museum of Comparative Zoology // Bulletin of the Museum of Comparative Zoology. Vol.103. No.5. P.259–337.
- Petrunkovitch A. 1958. Amber spiders in European collections // Transactions of the Connecticut Academy of Arts and Sciences. Vol.41. P.97–400.
- Petrunkovitch A. 1963. Chiapas amber spiders // University of California Publications in Entomology. Vol.31. P.1–40.
- Petrunkovitch A. 1971. Chiapas amber spiders, II // University of California Publications in Entomology. Vol.63. P.1–44.
- Platnick N.I. 2008. The world spider catalog, version 8.5. American Museum of Natural History, online at <http://research.amnh.org>.

- amnh.org/entomology/spiders/catalog/index.html (Accessed at April 8, 2008).
- Platnick N.I. 2006. PBI: The megadiverse, microdistributed spider family Oonopidae <http://research.amnh.org/oonopidae/project-description/projectdescription.php>. (Accessed at April 8, 2008).
- Poinar G.O., Jr., Milki R. 2001. Lebanese amber: the oldest insect ecosystem in fossilized resin. Corvallis: Oregon State University Press. 96 pp.
- Rasnitsyn A.P., Ross A.J. 2000. A preliminary list of arthropod families present in the Burmese amber collection at The Natural History Museum, London // Bull. nat. Hist. mus., London (Geology). Vol.56. P.21–24.
- Saaristo M.I. 2001. Dwarf hunting spiders or Oonopidae (Arachnida, Araneae) of the Seychelles // Insect Syst. Evol. Vol.32. P.307–358.
- Saaristo M.I. 2002. New species and interesting new records of spiders from Seychelles (Arachnida, Araneae) // Phelsuma. Vol.10(suppl. A). P.1–31.
- Saaristo M.I. 2007. The Oonopid spiders (Araneae: Oonopidae) of Israel // Arthropoda Selecta Vol.15. No.2. P.119–140.
- Saaristo M.I., Marusik Yu.M. 2004. *Ferchestina*, a new genus of oonopid spiders from Russian Far East (Aranei, Oonopidae) // Arthropoda Selecta. Vol.13. No.1–2. P.51–54.
- Saaristo M.I., van Harten A. 2002. The oonopid spiders (Arachnida: Araneae: Oonopidae) of Socotra, Yemen // Fauna Arabia. Vol.19. P.311–319.
- Saaristo M.I., van Harten A. 2006. The oonopid spiders (Araneae: Oonopidae) of mainland Yemen // Fauna of Arabia. Vol.21. P.127–157.
- Woźny M. 1984. *Oonops pulcher* Templeton, 1834 (Oonopidae, Aranei) nowy gatunek pająka dla fauny Polski // Przegląd zool. Vol.28. No.2. S.205–206.
- Wunderlich J. 1981. Fossile Zwerg-Sechsaugenspinnen (Oonopidae) der Gattung *Orchestina* Simon, 1882 im Bernstein, mit Anmerkungen zur Sexual-Biologie (Arachnida: Araneae) // Mitt. geol.-paläont. Inst. Univ. Hamburg. Bd.51. S.83–113.
- Wunderlich J. 1986. Spinnenfauna gestern und heute: Fossile Spinnen in Bernstein und ihre heute lebenden Verwandten. Wiesbaden: Quelle & Meyer. 283 S.
- Wunderlich J. 1988. Die Fossilen Spinnen im Dominikanischen Bernstein. Published by the author. Straubenhardt, West Germany. 378 pp.
- Wunderlich J. 2004. Fossil spiders in amber and copal // Beitr. Araneol. Bd.3(A–B). 1908 pp.
- Yaginuma T. 1977. A list of Japanese spiders (revised in 1977) // Acta arachn. Tokyo. Vol.27 (Spec. No.). P.367–406.