

Fossil Ant Nest Beetles

(Coleoptera, Carabidae, Paussinae)

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Abstract

Fossil Ant Nest Beetles (Coleoptera, Carabidae, Paussinae)

For the first time, fossil neotropical Paussinae in Dominican amber are described, i. e. *Eobomopterus paulmuelleri* sp. n. and *Homopterus hispaniolensis* sp. n., which are both representatives of the only two recent neotropical genera. Furthermore, new specimens of Baltic amber Paussinae are described. The most prominent characteristics of the fossil specimens are dealt with in relation to the living forms, and all fossil forms hitherto described are listed and discussed. The genus *Arthropterillus* Wasmann is placed synonymous with the genus *Succinarthropterus* Kolbe. The genus name *Arthropterus* which has hitherto been used for most of the fossil Baltic amber forms can no longer be used, since there is no generic identity between the fossils and the recent species of this genus (which occur exclusively in the Australian Region). The name *Pleurarthropterus* Wasm., subgen. *Balticarthropterus* nom. nov. is introduced to replace *Arthropterus* s. str. Wasmann, nec MacLeay.

1. Fossil Ant Nest Beetles hitherto known

The only fossil ant nest beetles hitherto known originate from the Baltic amber and have been studied monographically by Wasmann (1929b) who also included previous publications in his study (Menge, 1856, Motschulsky 1856, Stein 1877, Schaufuss 1896, Klebs 1910, Quiel 1910, Wasmann 1906, 1919a, 1919b, 1925, 1926a, 1926b, 1926c, 1926d, 1927, 1928a, 1928b, 1929a, 1929c, Handlirsch 1925, Kolbe 1925, 1927).

Supplementary observations especially on the shape of the coxae can be found in Wasmann (1929a), whereas Kolbe's (1926) work in which he established a new subgenus (*Succinarthropterus*) on the basis of an amber specimen escaped Wasmann's notice, as did the allusion to the fossils by Scudder (1885) and Reitter (1882). After that, only Bachofen-Echt (1949, p. 104, f. 100, 101)¹ and Weidner (1952, p. 66)² reported the occurrence

¹ Fig. 100 definitely represents an ant nest beetle (with distinctly separate front coxae!) whereas I cannot find a similarity with Paussinae in the specimen shown in Fig. 101.

² These six Paussinae mentioned by Weidner have kindly been made available to me for investigation by Dr. Weitschat from the Geological-Palaeontological Institute at Hamburg.

of fossil ant nest beetles in Baltic amber pieces unknown to that date, whereas other authors only refer to publications already existing (ANDREE 1937, DARLINGTON 1950, LUNA DE CARVALHO 1961 a, 1961 b, 1963, 1983, MÜLLER, A. H. 1963, 1978, LARSSON 1978, WEITSCHAT 1978, NAGEL 1980). LUNA DE CARVALHO (1965, p. 7) mentions a fossil *Paussus* (teste BASILEWSKY) from the geological collection of Paris, which, however, was not traceable.

No ant nest beetle have so far become known from the insect-rich Mexican amber (from Chiapas) (PETRUNKEVITCH et al. 1963, 1971); the same goes for the Canadian amber (especially from the Cedar Lake) (cf. MACALPINE & MARTIN 1969)³ as well as other amber finds from the cretaceous and the tertiary (comp. SPAHR 1981; BARTHEL & HETZER 1982).

DALMAN (1825) described a *Paussus cruciatus* from Kopal (subfossil resin) which, as early as 1830 had been assigned by WESTWOOD to his newly created genus *Trochoideus* (WESTWOOD 1833, pp. 673), which KLUG (1834, p. 284) recognized as a member of the Endomychinae (comp. also WASMANN 1919b, 1926 a, 1929b, 1929c).

From North America, the genus *Paussopsis* has been described with two species (COCKERELL 1911, WICKHAM 1912) from the Oligocene (not Miocene as originally supposed, comp. WILSON et al. 1967) lake deposits near Florissant, Colorado; this genus, however, has nothing in common with ant nest beetles, but belongs most probably to the Rhynchophora in the broadest sense which show "a remarkable preponderance" (WICKHAM 1912, p. 4, comp. also WASMANN 1929b, p. 10, 11) within the Florissant fauna. I share this view with WASMANN (1929b) and DARLINGTON (1950, p. 84).

I also fully agree with DARLINGTON (1950, p. 84) in that *Paussoides menzei* MOTSCHULSKY which WASMANN (1929b) still regarded as a "genuine" paussid beetle is definitely not an ant nest beetle. Apart from a vaguely similar habitus, there is not one single typical ant nest beetle characteristic; on the contrary, the structures encountered cannot be found in any of the ant nest beetles hitherto known.

2. New contributions on amber Paussinae

Our knowledge of the constitutive characteristics of fossil ant nest beetles is so insufficient that a complete revision would be urgently required. The following survey will be restricted to a summary description of the Baltic amber Paussinae from the Geological-Palaeontological Institute of Hamburg as well as from my own collection, in order to allow an evaluation of the characteristics as they have been described by WASMANN (1929b). Furthermore, Paussinae from Dominican amber are available for the first time and will be described; these specimens could be closely investigated and hence exactly defined due to the frequently mentioned clearness of the trapped material (e. g. SCHLEE and GLÖCKNER 1978).

³ Dr. CAMPBELL from the Biosystematics Research Institute in Ottawa confirmed in 1982 (pers. com.) that there are no fossil Paussinae in their collection.



Fig. 1. Distribution of the neotropical Paussinae; circles: *Homopterus* (recent); squares: *Eobomopterus* (recent); F: fossil forms; white, thin lined: continent in the late oligocene (cf. THENIUS 1980).

2.1 Dominican amber

The Dominican amber mainly originates from Oligocene strata of the Cordillera Septentrional north of the city of Santiago in the eastern part of the Hispaniola island in the state territory of the Dominican Republic (SANDERSON & FARR 1960, p. 324, Fig. 36, 37; SCHLEE & GLÖCKNER 1978). Other localities are known especially from the area of the eastern Cordillera (SCHLEE 1980). However, the Oligocene age of the amber itself is not considered to be certain (SANDERSON & FARR 1960, SCHLEE & GLÖCKNER 1978). It may well be that some of the amber finds can be ascribed to the Miocene so that the Dominican amber must altogether be assumed to be approximately 20 to 35 million years old (SCHLEE 1980). From additional investigations, a period of 15 to 38 million years can be inferred (BARONI URBANI 1980).

A survey of the palaeogeographical development of the West Indies and Central America is given by WEYL (1966, pp. 330, 1970, pp. 295, 1980, e. g. pp. 116). According to this survey, a land-solid connection between Central America and the West Indies has no longer existed at least since the Eocene. Obviously, parts of Hispaniola represent the oldest permanent land-solid regions in the area of the Caribbean Islands (Fig. 1).

The recent neotropical ant nest beetles are rare throughout, yet relatively well investigated (Fig. 1). In this context, the monographic studies by KOLBE (1920), REICHENSPERGER (1938) and LUNA DE CARVALHO (1963) deserve particular attention. Additional contributions can be found in DARLINGTON (1964), MARTINEZ & JIMINEZ-ASUA (1965), LUNA DE CARVALHO (1966, 1967), REICHARDT (1977), ERWIN (1974, 1979 a, 1979 b, 1981) and ERWIN et al. (1977). ERWIN (1979 c) gives a survey of the West Indian carabides.

2.2 Paussinae in Dominican amber

Eobomopterus paulmuelleri sp. n.

(Fig. 2–7)

Holotype: sex. indet.; in Dominican amber; coll. NAGEL in BGSS⁴

Derivatio nominis: The above name is given to this species in honour of my teacher Prof. Dr. rer. nat. Paul MÜLLER, professorial chairholder at the Institute of Biogeography of the University of the Saarland, Saarbrücken. I am indebted to him for my biogeographical training and especially the possibility to work on ant nest beetles on a taxonomic and historic-zoogeographical level. The relationship to the Neotropical Region follows from his biogeographical studies in and works on this area such as his analysis of the dispersal centres of the vertebrate fauna (MÜLLER, P. 1973).

Diagnosis: Tarsal joints 2 and 3 dilated laterally and pilose underneath; pronotum with lateral margins unidirectionally rounded and straight towards basis; first flagellum joint transversal, acutely rhombic; epistome sharp-edged (shrinkage?).

⁴ Biogeographische Sammlung der Universität des Saarlandes

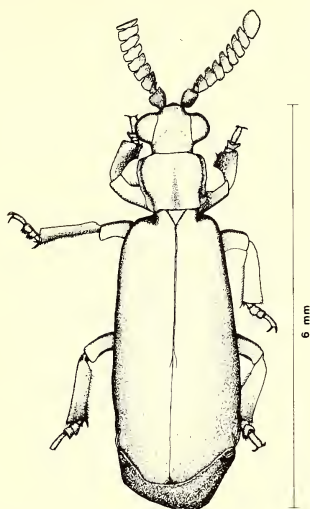


Fig. 2. *Eohomopterus paulmuelleri* sp. n., habitus in originally fixed position.

Description:

Total length: 5.6 mm (from epistome to apex of elytra); amber piece: $10 \times 6.5 \times 3$ mm.

Colour: Uniformly light-brown, tibiae and antennae somewhat darker.

Head 1.6 times larger than long with markedly protruding semicircular eyes; frons and vertex between the eyes weakly concave, with two small flat median pits; the temples, which are not visible from dorsally, form flat, nonprotruding, semicircular lobes, directly clinging to the eyes; anterior part of the head laterally sloping to the mandibular basis within the range of the two inner margins of the eyes and forming a right angle with the frontal surface in this area; in the middle of the anterior head margin, this front side (clypeus) sloping to base of labrum is even concave, which makes the anterior margin of the front (epistome) sharp-edged and even somewhat projecting (shrinkage?); the antennae are inserted right under the rectangular edge within the two inner eye margins; looked upon from above, this projecting central part of the anterior margin of the head (epistome) is sharp-edged and very faintly raised.

Antennae longer than head and pronotum together, in a turned-back position they would reach the humerus; club inserted at right angle to scapus; scapus laterally heavily compressed with its broadside positioned dorsally due to a twist as a result of the embedding; this compression has most probably been caused by shrinking; upper (in present position interior) apical corner of scapus acute (shrinkage!); occasional obliquely projecting setae (the longest being as long as the scapus is wide), scattered over the lower broadside and the interior narrow margin of scapus; pedicellus ring recognizable; antennal club (flagellum) nine-segmented, parallel; 1. club segment (3. antennal segment)

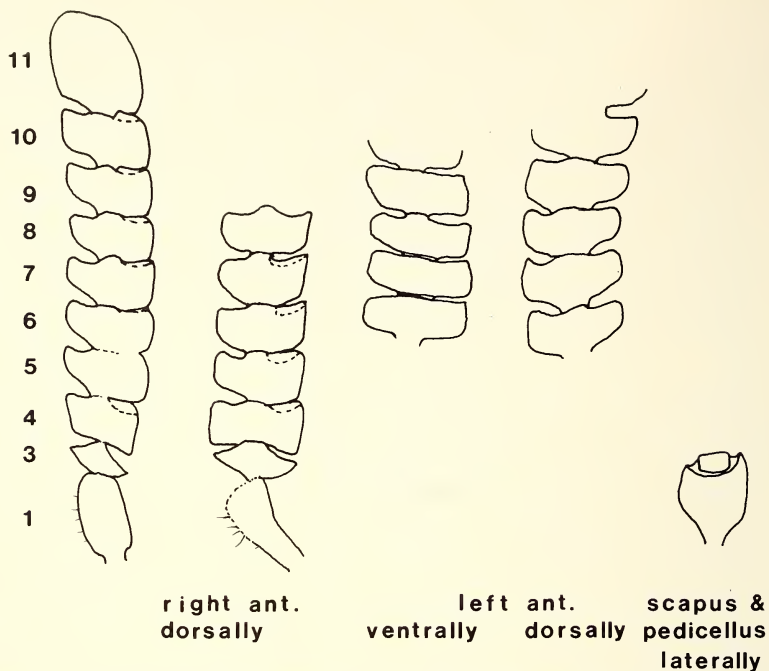


Fig. 3. *Eobomopterus paumuelleri* sp. n., antenna from different angles of distortion.

transversally rhombic, 2. to 8. segments transversally rectangular, of equal size, somewhat more than double as broad as long; last antenna segment semicircularly rounded at the apex, three quarters of the length of the two preceding segments; exterior apical corners of the 2. to 9. club segments with weak tooth-shaped prolongations, interior apical corners less distinctly marked; the individual club segments show a forward rounding in the middle of their distal margins; the antennal club is markedly flattened, the individual club segments are flat; the observed disengagement of the individual club segments seems to be caused by shrinking processes.

Mouth parts: maxillary palpi with four non-enlarged segments; last segment hardly tapering to the apex, apically rounded, 1.5 times as long as the preceding one; antepenultimate segment with few setae, hardly longer than the following one; the first segment is not clearly visible, but seems to be a very short segment inserted on the palpifer (coštipes), with the palpifer itself projecting and simulating a free segment; labial palpi with three visible end segments, the last being markedly enlarged and plate-shaped (broadly "hatchet-shaped") with a very flat dish-shaped depression; truncate apical margin of this last segment of the labial palpi with a band-like spongy looking sensory field; first and second segments of the labial palpi with some single obliquely projecting setae; ligula (= fused glossae) ("languette" according to RAFFRAY, LUNA DE CARVALHO, "labium" according to WESTWOOD and DARLINGTON) projecting as far as the pointed, relatively thin

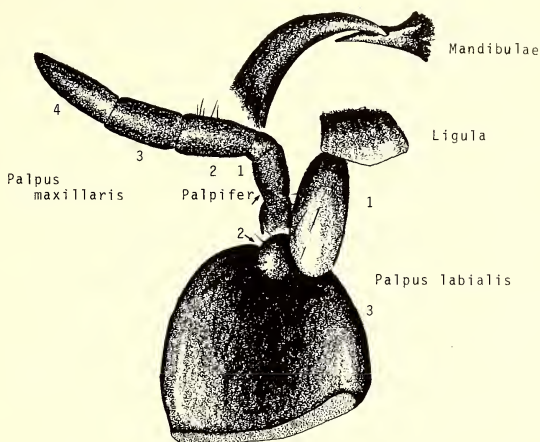


Fig. 4. *Eohomopterus paulmuelleri* sp. n., mouth-parts.

mandibles, with which it forms a short “beak” in the sense of DARLINGTON (1950, p. 66); mandibles and parallel to them ligula not projecting forward straight in line with the body axis, but slightly extending forward-downward; mandibles markedly projecting freely: with the scapus aligned parallel to the mandibles, both would roughly be equally long; mandibles not covered by labrum dorsally; although labrum is not visible, it can neither be large nor considerably protruding.

Pronotum 1.2 times wider than long, with lateral marginal edge, with lateral margin dorsally narrowly set off and bent upwards; weakly marked median longitudinal furrow existing, which ends far before the anterior and posterior margins and is flatter and broader caudal; anterior and posterior corners rounded, lateral margin running in a unidirectionally convex flat curve, almost straight in the posterior half; lateral marginal furrow distinct, subbasally more enlarged inwardly in the shape of a pit; in this area on the right somewhat defect and displaced probably as a result of the embedding; no punctuation of pronotum discernible.

Elytra almost flat on the disc, more distinctly vaulted towards the lateral margins, especially in the posterior half; lateral marginal edge very sharp in the humeral area (shrinkage?), from here running possibly as a blunt edge as far as the middle, posterior half without trace of the marginal edge; subapical fold long and narrow; scutellum equilaterally triangular; suture present in the form of true elytral engagement only as far as just behind the centre; shoulders accentuated by depressions in the area of the elytral insertions; elytra smooth and presumably not punctuated; setae of the “series umbilicata” not discernible.

Front coxae separated by a narrow prosternal process, middle and hind coxae contiguous; front coxae level with the middle pleurosternum (“prosternum”) as well as the prosternal process; metasternum with transversal praecoxal suture (postmetasternum

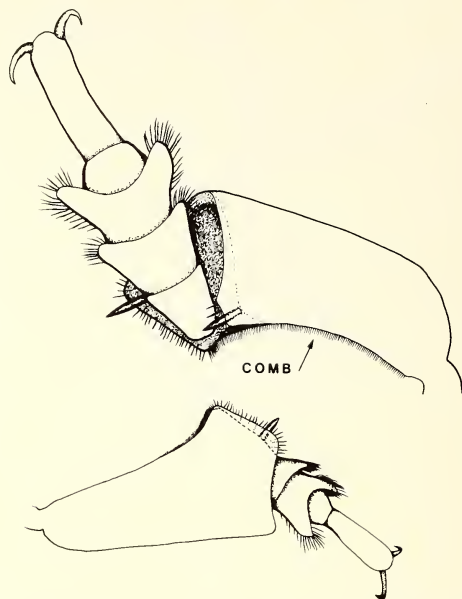


Fig. 5. *Eohomopterus paulmuelleri* sp. n., left protarsus and protibia (oblique position!) ventrally (top), right protarsus and protibia dorsally (bottom).

distinctly set off); notopleural suture (tergopleural suture in BAEHR 1979) at prothorax present; "pleurosternal suture" not distinctly visible; the pleural lamellae which may be encompassing the front coxae posteriorly are not visible because of the position of the specimen; if existing, however, they can only be very narrow.

Mesotibiae and metatibiae flattened, each with two final spurs standing closely together, the apical $\frac{3}{4}$ of the tibial length with parallel lateral margins, interior margin set with one row of loosely standing short setae; front tibiae also enlarged, apically dilated and slightly thickened with two very distinctly separated final spurs; comb organ at the concave inner edge consisting of very fine regularly short setae; 2. and especially 3. tarsal segment dilated in all three leg pairs; only in the mesotarsae and metatarsae the first segment is also visible from above, whereas in the front legs, it remains hidden under the dilated apical margin of the tibiae; 4. tarsal segment short, not enlarged, hardly protruding beyond the lobes of the third segment; the underside of the 2. and 3. tarsal segments of all three leg pairs with dense, regular, brushlike pilosity; claws simple, distinctly bent; all femora in the distal third with a deep furrow to receive the retractile tibiae; all femora appear to have a faint and loosely scattered granulation; this observation could point to the insertions of short setae.

Pygidium not exactly discernible, but obviously without any conspicuous features.

The surface structure cannot be precisely recognized, because the whole specimen appears to be somewhat shrunk, which has caused longitudinal and transversal cracks in

the directly superadjacent resin layer, yet a distinct pilosity is definitely lacking from all parts of the body other than those described above as showing setae; some small areas, for instance the eyes, are surrounded by a strongly reflecting (air) layer.

The colour of the amber is a vivid ochrous yellow; 8–10 laminated structures as a result of several resin flows (“Schlauben”) are clearly visible; furthermore quite a large number of differently sized air bubbles are also included.

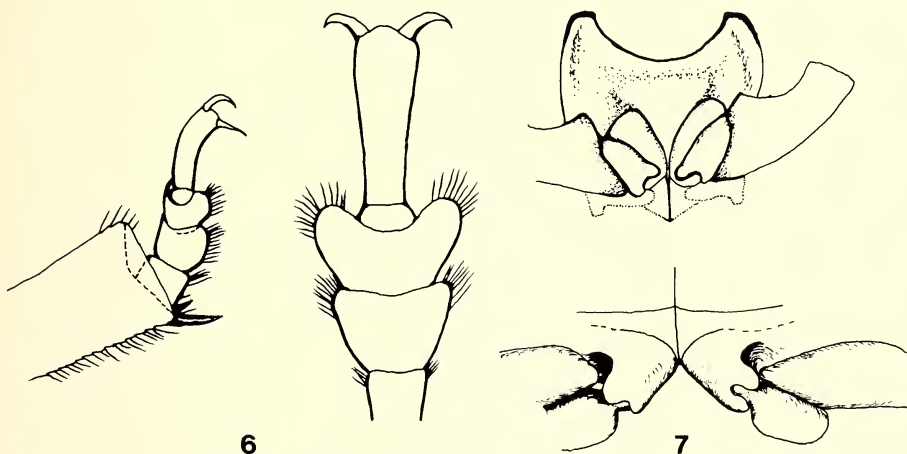


Fig. 6–7. *Eohomopterus paulmuelleri* sp. n., 6 right mesotarsus in original oblique position (left) and reconstruction of dorsal view (right), 7 prothorax and metacoxae ventrally.

Differential diagnosis:

The genus *Eohomopterus* has so far only been known from the two type specimens of the only two representatives, i. e. *E. aequatoriensis* (WASMANN, 1899) from Ecuador and *E. centenarius* LUNA DE CARVALHO, 1960, from Brasil. In addition to his new species, LUNA DE CARVALHO (1960) also studied, redescribed and illustrated the holotype of *E. aequatoriensis* (which was badly needed in view of the faulty presentation by WASMANN, 1899; cf. e. g. DARLINGTON 1950, p. 69). At a later date, he repeated these descriptions and figures in a work on the Paussinae of South America (LUNA DE CARVALHO 1963). Neither WASMANN (1899) nor LUNA DE CARVALHO (1960, 1963) points to the structure of the front coxae, the shape of the lateral margin of the elytrae or the size of the ligula.

The diagnostic character of the second and third tarsal segments which are dilated and pilose underneath definitely characterizes the species as pertaining to the genus *Eohomopterus*. Apart from the position of the aedeagus, this genus differs from *Carabidomemmus* only by this characteristic. In view of the creation of new genera as hitherto practised, the sharp-edged epistome (unless caused by a shrinking process) by which *E. paulmuelleri* differs from the two *Eohomopterus* species, would also support the establishment of a new genus on the basis of this new species: An epistome structure of

this kind is typical of all tribes with a one-segmented antennal club (Platyrhopalini, Ceratoderini, Paussini), yet has never been described so far in genera with a higher number of club segments. In *E. aequatoriensis* the edge of the epistome is distinct and blunt, whereas in *E. centenarius* it is distinctly rounded. In two as yet undescribed *Carabidomemnus* species from Cameroon (leg. DE MIRE), the epistome is not sharp-edged, but in any case it has a distinct blunt edge. In view of the fact that these species are clearly identified as belonging to the genus *Carabidomemnus* (s. l.) by the aedeagus showing to the right, it must either be assumed that the above characteristic is a plesiomorphic sign or has developed several times independently. Since it cannot be decided at the moment which of either assumption is true, the creation of a new genus does not appear to be justified.

The holotypes of *Eohomopterus centenarius* and *aequatoriensis* are available to me, so that it can be clarified that the structure of the front coxae does not differ from that of the fossil species.

The structure of the labial palpi and the ligula is also identical in *E. paulmuelleri* sp. n. and *E. centenarius*. As against this, in *E. centenarius* and *aequatoriensis* the penultimate segment of the maxillary palpi is only $\frac{1}{2}$ of the preceding segment and only $\frac{1}{3}$ of the length of the apical segment, whereas in *paulmuelleri* sp. n. the three apical segments of the maxillary palpi are approximately equally long.

Another diagnostic character of *E. paulmuelleri* sp. n. is the transversal rhombic shape of the first club segment. It is the shape of this segment which is the most decisive criterion for the separation of the species within the genus *Carabidomemnus*. In the amber species, this segment has a unique structure never encountered so far in any other member of the Paussinae (including the genus *Eohomopterus*).

A marginal edge of the elytra (as it is typical of the noncylindrical genera of the Ozaeninae) cannot be found in any known member of the Paussinae in its original carabidoid structure. Only in *Paussus* subgen. *Amphipaussus* and *Hyperpentarthrus* does the lateral margin end in a blunt longitudinal outward fold. Both recent *Eohomopterus* species do not have a similar structure of the elytral margin. The reduced lateral marginal edge at least in the humeral area of *E. paulmuelleri* sp. n. can therefore also be considered a distinguishing character, although it cannot be completely excluded that it has been caused by shrinking processes.

The length of the suture has not been taken into account so far, but it can be clearly said that the recent species are also characterized by a shortening of the elytral engagement.

The structure of the tarsi of *E. paulmuelleri* is identical to that of *E. centenarius*, whereas in *E. aequatoriensis*, the 2. and 3. tarsal segments are extremely strongly lobed. *E. aequatoriensis* is also distinguished from *E. centenarius* and *E. paulmuelleri* by the distinctly cordiform pronotum. On the other hand, *E. paulmuelleri* is much more slender than the two recent species. *E. paulmuelleri* sp. n. and *aequatoriensis* are similar in that they both show the regular overall pilose tarsal pilosity, whereas the tarsi of *centenarius* are set with two rows of hairs.

In summary, *E. paulmuelleri* is distinguished from the two recent species by the following characteristics: 1. club segment transversally rhombic, the 3 apical segments of the maxillary palpi of approximately the same length, slender body shape and possibly (unless caused by shrinkage) epistome sharp-edged and elytra with marginal edge formation in the humeral area.

Homopterus hispaniolensis sp. n.

(figs. 8–10, 12–13)

Holotype: ♀; in Dominican amber, coll. NAGEL in BGSS

Derivatio nominis: The species name refers to the locus typicus, i. e. the Caribbean island of Hispaniola.

Diagnosis:

Legs extremely enlarged, tibiae obtuse-angled at interior distal corner, broadly rounded off at the exterior distal corner; tarsi much shorter than width of tibiae; margin of pronotum regularly convexely rounded; 2. to 8. antennal club segments completely simple and conspicuously transversally rectangular; 1. club segment 1.1 times longer than the following one, tapering to the basis.

Description:

Total length: 5.9 mm (from epistome to apex of elytra), amber piece: $10 \times 5 \times 6$ mm.

Colour: uniformly black-brown.

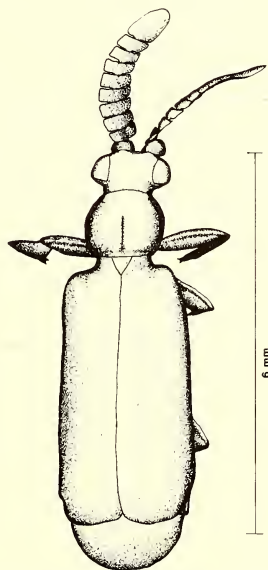


Fig. 8. *Homopterus hispaniolensis* sp. n., habitus in originally fixed position.

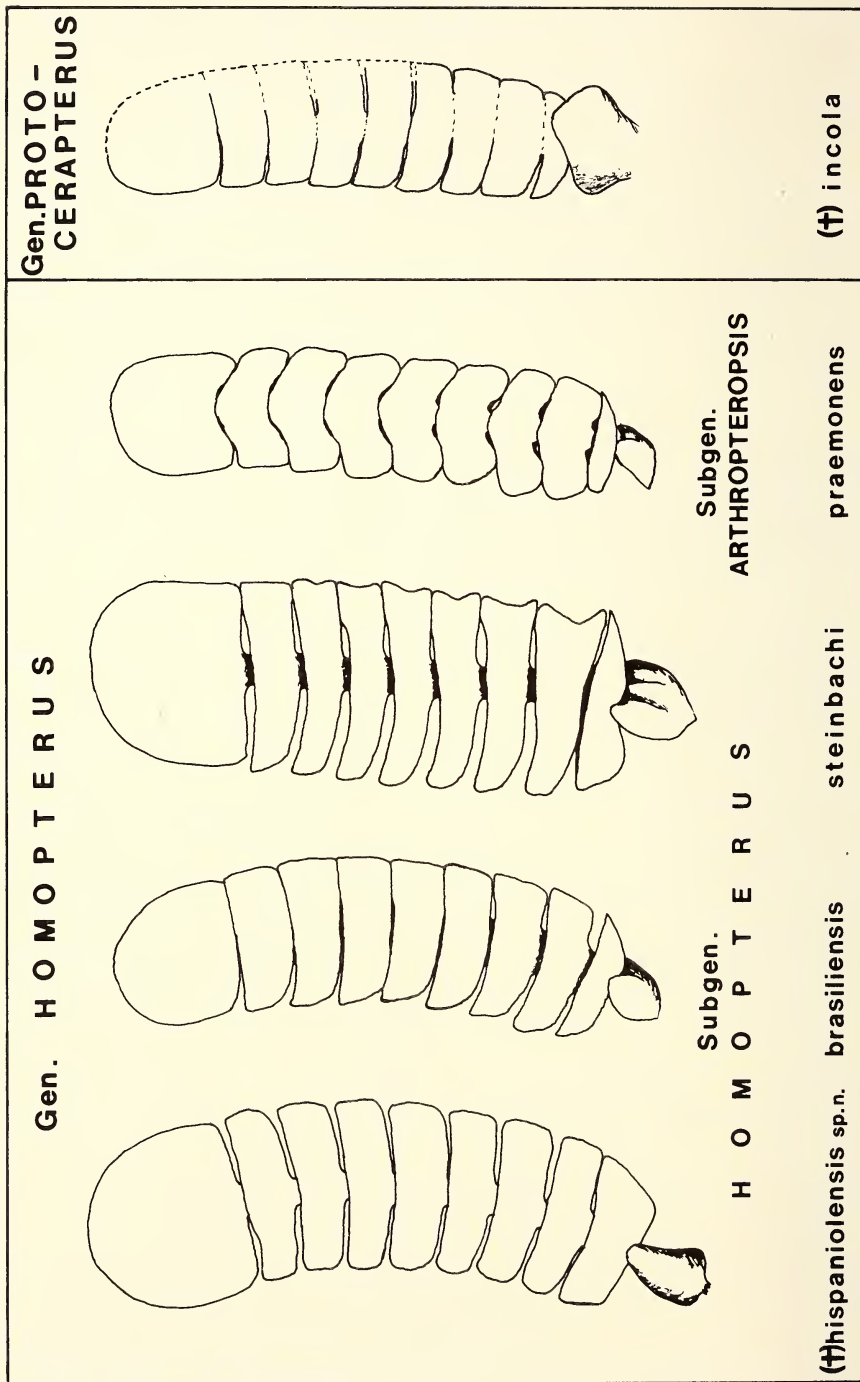


Fig. 9. Antennal shape of *Homopterus* and *Protocerapterus* (convergence!) (original, acc. to REICHENSPERGER 1938c, and acc. to WÄSMANN 1929b).

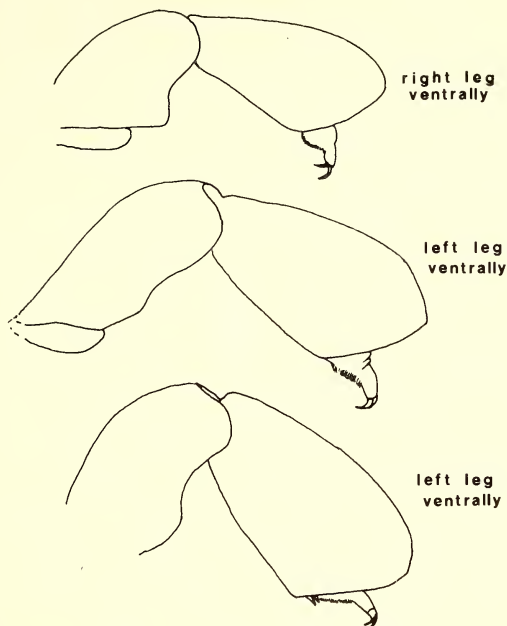


Fig. 10. *Homopterus hispaniolensis* sp. n., front, middle and hind leg (from top to bottom).

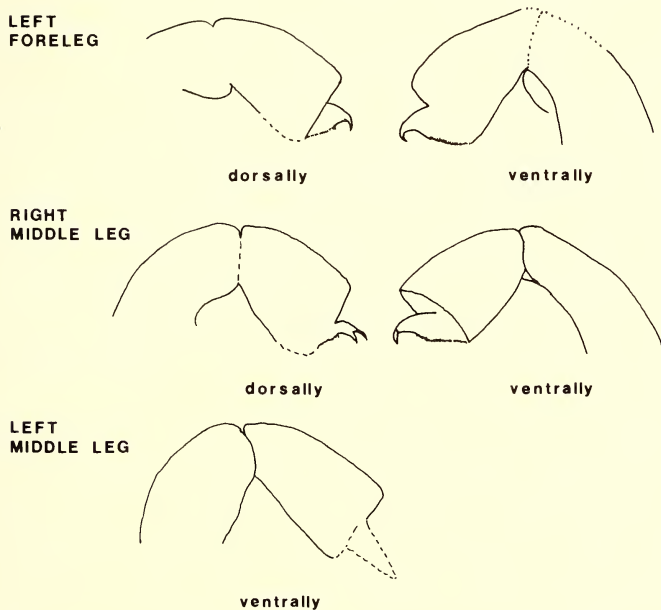


Fig. 11. *Protocerapterus primigenius* Wasm., front and middle legs according to Wasmann (1929b, pl. 3, fig. 27, 28): convergent dilatation of the tibiae as compared to Homopterus.

Head with the semicircularly protruding eyes 1.7 times broader than long; frons and vertex flat, anterior margin of head not straightly truncate, but faintly concave; frons passing to vertical clypeus over a short rounding; temples forming eye cups which extend over $\frac{1}{5}$ of the eyes, but are completely adjacent and not protruding laterally.

Antennae much longer than head and prothorax together, in turned-back position reaching the first quarter of the elytra; scape compressed, ratio of broadside to narrow side 2:1, at a right angle to the flagellum; pedicellus ring not visible because of the deep insertion in the scape; antennal club with parallel sides, nine-segmented, flat, very broad. 1. club segment (3. antennal segment) 1.1 times longer than each of the following 7 completely identical club segments; 1. club segment transversal, in the middle 1.4 times broader than long, margins diverging outwardly and distally reaching the width of the subsequent segments; 2.–8. club segment transversally rectangular with acutely rounded corners, each 3.6 times wider than long; last segment 1.1 times wider than long, semicircularly rounded; each antennal club segment very flat.

Mouth-parts identical to those of the recent *Homopterus* species; the subapical segment of the labial palpus shows the enlargement typical of the genus; the apical segment is very large, rotund, plate-shaped (broadly "hatchetshaped"); maxillary palpi distinctly shorter than labial palpi, only reaching $\frac{2}{3}$ of the last segment of the labial palpi; the two subapical segments of the labial palpi of equal length, apical segment also cylindrical, bluntly rounded at the top; ligula narrow, projecting as far as the subapical maxillary palp segment, bristled at the top; labrum not visible because of a position of the specimen unfavourable for its identification.

Pronotum strongly and regularly rounded laterally; anterior corners completely rounded-off, posterior corners very faintly marked by almost straight posterior margin, anterior margin with a weak forward rounding; pronotum 1.2 times wider than long; disc but little vaulted, with short, flat middle furrow on the posterior half; suddenly and rather steeply sloping towards the narrowly set-off, much deeper lying, sharp-edged lateral margins (shrinkage?).

Elytra double as long as wide; scutellum acutely triangular; suture present as true interlocking of the elytra, reaching almost as far as the apex; elytral disc flat, regularly rounded towards margins; from shoulder to middle of elytra a very blunt, ever flattening lateral marginal edge is indicated; subapical fold on either side only very faintly suggested because of streaks and air cushions.

Front coxae conically projecting (hanging), contiguous, without visible prosternal process in between; the lobularly protruding pleura forms the lateral margin of the coxa; the middle coxae contiguous, slightly spherically projecting; hind coxae also contiguous; notopleural suture (tergosternal suture) and "pleurosternal suture" at prothorax existing; the pleural lamellae encompass the cavities of the front coxae posterially; the shape of the median ends of the former in the middle behind the front coxae is not clearly visible, yet they seem to be broadly contiguous; ventral side of the prothorax in front of and behind the coxal cavities of equal length.

Femora and tibiae large, broad, flat; femora in the basal part with an additional, likewise flat inward enlargement which ends in an almost dentate shape in the front femur, whereas in the two hind legs it is bluntly rounded at the site where it merges into the apical part; trochanters large, in the two hind legs reaching $\frac{1}{3}$ of the femoral length, in the frontal femora almost as long as $\frac{1}{2}$ of the femur; tibiae distally markedly dilated and rounded with a very obtuse interior apical angle causing the exterior apical corner to look prolonged distad and the distal tibial end to be bevelled; tarsi only half as long as the width of the tibiae; the two terminal spurs are only visible in the middle and hind tibiae; the individual tarsal segments are not clearly visible, but at least two of the subapical tarsal segments are densely set with fine, short brush-like pilosity on the underside.

Pygidium semicircular, vaulted on the disc, without any conspicuous characteristics; the sclerosed styles of the female genitalia are projected and are in principle identical to those described for *Homopterus* by DARLINGTON (1950a, p. 95, 140, f. 186) (palmate, with tuft of setae); styles are basally very broad, apically very pointed and three-edged over the whole visible length: the normal dorsal and ventral edges of the plate and an additional exterior one which runs from the apex parallel to the lower edge; this lateral marginal keel ends distally in a large bent terminal tooth with one additional smaller tooth in front of it on the keel; a thin tuft of setae is inserted on the lower side of the apex of the plate at the level of the large terminal tooth of the lateral keel and does not project beyond the apex.

Surface structure not discernible, apart from a tiny little part on the frons which is distinctly shagreened; however, any coarse punctuation or long pilosity are definitely lacking.

Differential diagnosis:

Today, the exclusively Neotropical genus *Homopterus* comprises eleven species distributed from Argentina to Mexico. A summarizing description of the Neotropical Pausinae including figures of the relevant characteristics can be found e. g. in REICHENSPERGER (1938) and LUNA DE CARVALHO (1963). The assignment of the new amber species to the genus *Homopterus* is unequivocally justified by the following characteristics: last labial palp segment plate-shaped with simultaneously enlarged subapical segment; legs extremely enlarged and flattened with tarsi only half as long as width of tibiae, the latter with a bevelled distal margin; styles of the female genitalia bi-palmate; antennal club nine-segmented, very large and broad.

Within the genus, the two subgenera *Homopterus* s. str. and *Arthropteropsis* have been described, the latter being represented only by the species *H. praemonens* from Bolivia. The middle club segments of this latter species show double-arcuate distal and proximal margins due to the distad prolonged centre of the individual segments. The subgenus *Homopterus* s. str. is characterized by its simply transversal middle club segments. Within this subgenus, the *H. steinbachi*-group is characterized by the fact that its middle antennal segments are concave at the exterior narrow lateral edge, whereas in the *H. brasiliensis*-group, the middle club segments have a straight external margin. For this reason,

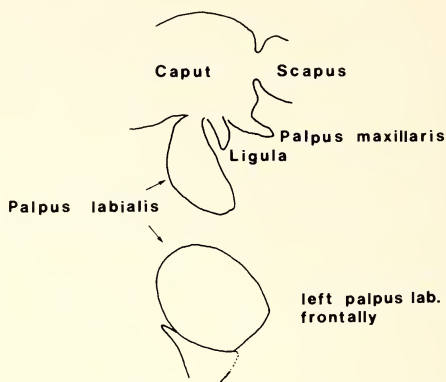


Fig. 12. *Homopterus hispaniolensis* sp. n., mouth-parts.

H. hispaniolensis sp. n. must be assigned to the subgenus *Homopterus* on the basis of the defined diagnostic characteristics. Within this subgenus however, it cannot readily be assigned to any of the established species groups. It does not have the concave external margins of the middle club segments and for this reason can by no means be assigned to the species group *steinbachi*. On the other hand, it differs from the species group *brasiliensis* as well as from all remaining *Homopterus* species so far known by its prolonged first club segment which, moreover, is wider at its exterior margin than at the interior edge, where as in all species of the genus so far known, the exterior margin of the first club segment tapers to a narrow point.

In the extremely dilated tibiae *H. hispaniolensis* sp. n. resembles the *steinbachi* group, whereas the tibiae of the remaining species of the *brasiliensis* group are more slender. The pronotum is more slender than in the recent species. The conspicuously sloping lateral parts of the disc of the pronotum may indicate that this shape is probably caused by shrinkage. In the unidirectional rounding of the margins of the pronotum *H. hispa-*

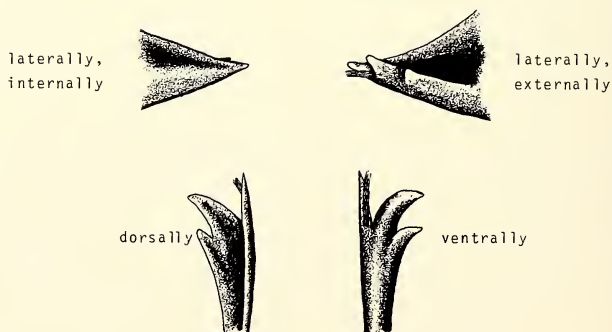


Fig. 13. *Homopterus hispaniolensis* sp. n., ♀, retractile styles.

niolensis sp. n. resembles e. g. *H. brasiliensis*, *H. praemonens* and *H. steinbachi*, whereas e. g. *H. amplificatus* and *H. subcordatus* are characterized by distinctly cordate shape. In its laterally non-protruding temples *H. hispaniolensis* sp. n. resembles *H. brasiliensis* and others, whereas in *H. subcordatus* for instance, the temples form a conspicuous angle together with the eyes. Finally, *H. hispaniolensis* sp. n. and *H. brasiliensis* resemble each other in the slender habitus.

Unfortunately, the female genitalia of *Homopterus* (*H. steinbachi*) have so far only been described and figured by DARLINGTON (1950). Whereas it cannot be doubted on the basis of this description that the styles of *H. hispaniolensis* sp. n. and *H. steinbachi* do resemble each other in the basic type by which they are distinguished from all remaining Paussinae, they can nevertheless be well distinguished: in *H. hispaniolensis* sp. n. the interior apex is very narrow and sharp-edged and clearly projects posteriorly beyond the level of the marginal teeth, whereas in *H. steinbachi* this part is truncate and ends at the level of the middle of the lateral tooth. Due to the lack of more ample material it cannot be decided whether these are specific or subgeneric differences.

In summary, it can be said that *H. hispaniolensis* sp. n. differs from all recent species of the genus by the special shape of its first antennal club segment, whereas other characteristics also occur in some other species.

It also results clearly from the present investigation that the *Protocerapterus* described from the Baltic amber does not show any close relationship to *Homopterus*, as had been postulated by LUNA DE CARVALHO (1961 a). The dilatation of the antennae and tibiae is based on convergence (figs. 9–11), a fact which can also clearly be recognized from the completely different shape of the distal area of the tibiae (cf. NAGEL 1987).

2.3 Baltic amber

The majority of finds of Baltic amber originate from the Samland peninsula, where amber has been used commercially as early as from early historical times onward. The literature available about Baltic amber is very abundant; for this reason, only a few publications shall be mentioned here and are referred to for more detailed references: HENNIG 1969, LARSSON 1978, SCHLEE & GLÖCKNER 1978, WEITSCHAT 1978, SCHLEE 1980. These publications also contain distribution maps of fossil resin in general and of Baltic amber in particular. The main deposits of the Baltic amber are ascribed to the early Oligocene, but it is now assumed that it arrived there only by redeposition, so that the period of origin is considered to be the late Eocene (40 million years ago). The climatic conditions prevailing at that time have to be considered tropical—at least there is no mention of seasonal changes anywhere (LARSSON 1978).

In contrast to the Dominican amber, the specimens embedded in Baltic amber very often show white opacities on one side of the body caused by emulsions of excreted body fluids with the still liquid resin. Light and the associated warming up of the material can cause this opacity to disappear, so that at least the light-exposed side of the specimen turns clear again (cf. SCHLÜTER & KÜHNE 1974, SCHLEE & GLÖCKLER 1978).

2.4 Description of new Paussinae inclusions in Baltic amber

Six inclusions are available, of which the five inclusions from the Geological-Palaeontological Museum of Hamburg had already been investigated and partly given names by REICHENSBERGER, Bonn. REICHENSBERGER made these names known in a letter in 1957, however, he could not publish his results any more. The sixth ant nest beetle mentioned by WEIDNER (1952) is a Rhipiphorid. The sixth ant nest beetle dealt with in the present paper is from my own collection.

Unfortunately, all specimens are covered by white opacities so that essential structures could not be recognized. The animals have been investigated for all visible structural characteristics; however, the following list will be restricted to a summary of the clearly visible relevant features. In order to allow comparisons with the data on lengths as given by WASMANN (1929b), the total length as measured in these fossils refers to the area from the epistome to the posterior margin of the pygidium.

No. BB 45 (Geol. Pal. Inst. Hamburg):

The specimen is accompanied by the following labels: "II A 28, *Cerapterus* Sw., KORSCH det. 1933, Coll. A. SCHEELE, Berlin-Lichterfelde" and "*Cerapterites* sp.? nach A. REICHENSBERGER, briefl. Mitt. Aug. 1957".

Pronotum slightly cordate, towards basis with almost straight sides, with a sharp lateral marginal edge, front coxae and popleurosternum on the same level, prosternal process narrow, visible between the coxae, pleural lamellae encompassing the coxal cavities posteriorly, ventral side of prothorax anterior to the coxae double as long as posteriorly, notopleural suture (tergosternal suture) visible over the whole length.

Head with eyes somewhat narrower than pronotum; maxillary palpi with 3 terminal segments, one additional segment (? possibly part of the palpifer) visible; apical segment cylindrical, apically rounded, double as long as each of the equally sized preceding segments; maxillary and labial palpi of same length; the latter with three visible terminal segments, the antepenultimate of which (first visible one) spherical, the penultimate also short, but already cylindrically dilated distad, apical segment as long as the two preceding ones together, thick-cylindric, somewhat flattened with transversally truncate apex (weakly hatchet-shaped); ligula very short, only reaching half of the first segment of the labial palpi, concavely truncate at apex; mandibles thin, projecting as usual, bent inward in the apical area.

Antennae short, hardly reaching the shoulder in turned-back position, parallel, club nine-segmented, elytra slender, more than double as long as wide; subapical fold distinct; apex not truncate, but rounded; lateral marginal edge missing.

Middle and hind coxae contiguous; tibiae short and broad, approx. 2.4 times longer than wide; tarsi with long claw and small fourth segment, the first three with two rows of loose short setae underneath.

Aedeagus (in dorsal view of the animal with head directed forward) protruding to

the left, lower paramere narrower than in *Carabidomemnus*, without conspicuous pilosity, apex of the central part not visible.

Body not longitudinally vaulted; black; TL 7.8 mm, BW 2.2 mm, "K" 3.5⁵.

If one tries to classify this specimen in the sense of W_{ASMANN} (1929b), it would have to be assigned to his "*Arthropterus* s. str." because of its slender body. The shape of the pronotum and the tibiae identifies it as standing close to "*A. str.*" *aterrimus*.

No. BB 1503 (Geol. Pal. Inst. Hamburg):

Accompanying label: "*Arthropterus aterrimus* W_{ASM.} (det. REICHENSBERGER 1957)".

Pronotum transversal, faintly cordate, with sharp, set-off lateral marginal edge; tergo-pleural suture (notopleural suture) distinct over whole length.

Antennae short, only reaching basis of pronotum in turnedback position; club nine-segmented, parallel.

Head with eyes somewhat narrower than pronotum; elytra behind the scutellum in prolongation of the posterior corners of the pronotum each with one very large bristle-bearing pore; lateral marginal edge not present; elytral suture not visible, however, the weak vaulting of the left elytron shortly behind the middle is interpreted by me as suggesting that at least from there, a true engagement of the elytra is missing.

TL 6.7 mm, BW 1.8 mm, "K" = 3.7.

In view of the shape of its body, pronotum, tibiae and antennae, this specimen must also be placed close to "*A. str.*" *aterrimus*, just like No. 45, however, it is not identical with it because of its shorter antennae.

No. 1494 BB (Geol.-Pal. Inst. Hamburg):

Antennal club nine-segmented, parallel, very short, not reaching the posterior margin of the pronotum in turnedback position.

Head with eyes somewhat narrower than pronotum, eyes not markedly protruding; mouth open, terminal segment of labial palpi thick, terminal segment of maxillary palpi slender, obtusely rounded; because of a dense white opacity over the mouth parts the latter cannot be described in more detail.

Pronotum with a sharp, narrowly set-off lateral marginal edge, towards basis slightly concavely narrowed; most probably not transversal but at best as long as wide.

Tibiae short, broad, compressed, hind tibiae approx. 2.1 times longer than wide; tarsi hardly longer than width of tibiae.

Elytra without a suture engagement at least in the last third; without a lateral marginal edge; from humerus to the first third of the elytral margins numerous large bristle-

⁵ TL = total length, BW = body width, "K" = "Formkonstante" in the sense of W_{ASMANN} (1929b), i. e. TL : BW

bearing pores (series umbilicata); turned-down elytral part (epipleura) in humeral area rather densely set with short, very thick protruding setae; elytra rounded apically, not truncate.

Body slender; TL 6.7 mm, BW 2.1 mm, "K" 3.1.

This specimen must likewise be assigned to WASMANN'S subgenus "*Arthropterus* s. str.". Due to the shape of its body, pronotum, tibiae and antennae, it must most probably be classified as standing close to „*A. balticus*“.

No. BB 1600 (Geol.-Pal. Inst. Hamburg):

Label: "*Arthropterus* sp.? (det. REICHENSPERGER 1957) (briefl. Mitt.)"

Antennae club nine-segmented, parallel, reaching the shoulder in a turned-back position; head with the strongly vaulted eyes somewhat narrower than pronotum.

Pronotum transversal, faintly cordate; with sharp lateral marginal edge; elytra apically rounded; behind the middle with a simple red patch; tibiae very short and broad, approx. double as long as wide; tarsi hardly longer than width of tibiae; 4. tarsal segment small, basal segments with two rows of bristles underneath; protibia interiorly with comb-organ running obliquely from outside to the inner edge-middle; without protibial emargination.

Habitus slender; TL 7.8 mm, BW 2.9 mm, "K" 2.6.

Due to the shape of the body and the tibiae as well as the red marking of the elytrae, this specimen is identified as belonging most probably to the genus *Cerapterites*; however, it is distinguished from the only species hitherto described, *C. primaevus*, by the weakly cordate pronotum, which has completely straight margins in *C. primaevus*.

No. BB 388 (Geol.-Pal. Inst. Hamburg):

Label: "*Protocerapterus* (n. sp.?) det. REICHENSPERGER 1957 (briefl. Mitteilung)"

Antennal club nine-segmented, only reaching the basis of the pronotum in a turned-back position; head with normally protruding eyes clearly narrower than pronotum; frons sloping shortly rounded to the vertical clypeus.

Terminal segments of labial palpi large, thick-oval cylindrical, broadly truncate at apex; terminal segments of maxillary palpi thinly cylindrical, obtusely rounded at apex; ligula not visible because of cracks in the amber, in no case, however, can it be of large size; labrum narrow, transversal, straightly truncate; mandibles thin, curved, little projecting.

Pronotum transversal, tapering to basis, faintly cordate; with sharp lateral marginal edge; tergopleural suture (notopleural suture) visible over whole length; cavities of front coxae close posteriorly, prosternal process between coxae distinct, but narrow; coxal cavities dividing the ventral side of the prothorax into two equally short anterior and posterior parts.

Elytra without lateral marginal edge, with subapical fold; suture existing as elytral engagement presumably only as far as close to the middle; apex of elytra not truncate but rounded; posterior half of each elytron with an indistinctly delineated reddish patch directed obliquely to the posterior outer margin.

Middle and hind coxae contiguous, antecostal suture closely before hind coxae; tibiae and femora markedly dilated and shortened; both tibiae and femora approx. double as long as wide; femora at interior margins with a deep furrow as far as the basal third for receiving the tibiae; interior and exterior margins of the femora slightly unidirectionally curved; tibiae with parallel interior and exterior edges; tibiae straightly truncate; tarsi hardly longer than width of tibiae.

Styles of the female genitalia projected, close; from a lateral view triangularly plate-shaped, ending in a very pointed apex; the apex itself narrowly truncate with a slight outward bevel; from this tiny surface, which looks like a large pore, rises a thin long tuft of setae.

TL 8.9 mm, BW 3.2 mm, "K" 2.7

According to WASMANN'S (1929b) key, this specimen would also have to be assigned to *Cerapterites*. Its essential features are in conformity with this: body relatively slender (not double as long as wide as in *Protocerapterus*), tibiae parallel (not dilated to the apex as in P.), tibiae relatively slender (not only slightly longer than wide apically as in P.), elytral marking present.

This specimen is distinguished from the preceding species No. 1600 by its greater total length, the somewhat longer antennae, the almost completely pilose tarsi and the differently shaped elytral markings. From the described *C. primaevus*, both specimens mentioned are distinguished by the shape of the pronotum.

No. BB 1 (coll. NAGEL in BGSS) (figs. 14–15)

Antennal club nine-segmented, parallel, reaching the basis of the pronotum in turned-back position.

Head with the semicircularly protruding eyes distinctly narrower than pronotum; labrum transversal, narrow, straightly truncate anteriorly; mandibles thin, somewhat projecting, curved to the apex; terminal segment of maxillary palpi cylindrical, distally obtusely rounded, double as long as the preceding segment; labial palpi with three visible segments; first segment small, spherical; 2. segment just as short but clearly dilated distad and forming a transition to the thick, weakly compressed cylindrical and apically broadly truncate terminal segment; ligula short, transversally truncate in an obtuse angle, projecting at best as far as the first quarter of the antepenultimate segment of the labial palpi.

Pronotum transversal, weakly cordate, with sharp-edged lateral margin; prosternal process between coxae distinctly visible.

Hind tibiae more than 2.5 times longer than wide, distally truncate in a straight bevel, which causes the exterior apical corner to look somewhat prolonged; tarsi markedly longer than width of tibiae.



Fig. 14. *Pleurarthropterus (Balticarthropterus)* spec., Coll. NAGEL in BGSS; left: dorsal view with white opacity, right: ventral view.

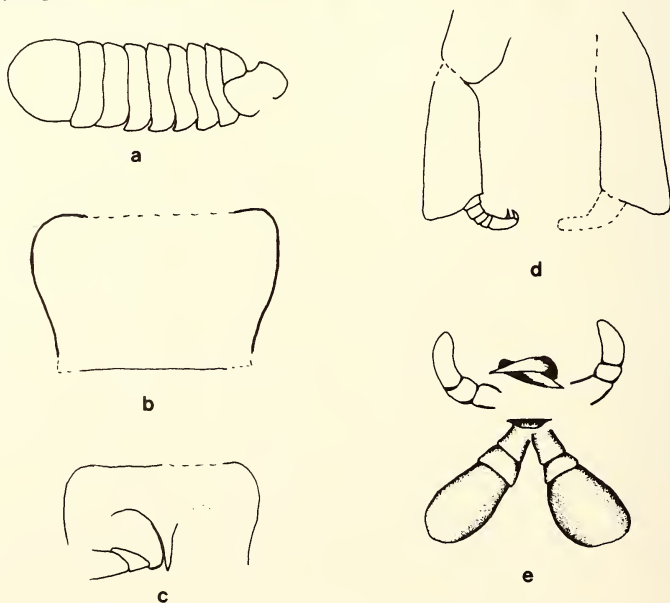


Fig. 15 *Pleurarthropterus (Balticarthropterus)* spec., Coll. NAGEL in BGSS; a: antennal club, b: pronotum, c: prothorax ventrally, d: right hind leg dorsally and ventrally, e: mouth-parts.

Elytra without lateral marginal edge; $\frac{3}{4}$ of the elytra and complete abdomen missing due to grinding.

The shape of the antennal club and the tibiae characterize this species as belonging to "*Arthropteris* s. str." sensu Wasmann. It is, however, not possible to assign this specimen to any of the described forms because of the missing posterior body half.

3. Characteristics of the Baltic amber Paussinae

1. Gen. *Succinarthropteris* Kolbe, 1926

Syn.: Gen. *Arthropteris* auct., nec Macleay, 1838

Gen. *Arthropterillus* Wasmann, 1926b

Diagnosis:

Body small (4.5–5.5 mm), longitudinally and transversally vaulted; pronotum pulviniform; legs very short and broad, tibiae only double as long as wide (according to Wasmann 1929b).

No specimens have been available to me which would conform to this description, but on the basis of Wasmann's (1929b) figures and species descriptions the following characteristics can be added: apex of elytra rounded, not truncate; exterior and interior tibial margins weakly diverging distad; antennae parallel; terminal segments of labial palpi grossly enlarged (Wasmann 1929b, pl. I, f. 3).

I strongly doubt the necessity of separating this genus from the following on the basis of the above characteristics, because the longitudinal vaulting of the animals which Wasmann (1929b) draws upon as the main reason for separating the two genera and which "is otherwise unusual in Paussids" also occurs more or less distinctly in the recent species of the genera with nine-segmented antennal clubs. The front coxae could not be recognized in any of the specimens (Wasmann 1929a).

2. Gen. *Pleurarthropteris* Wasmann, 1927

Syn.: Gen. *Arthropteris* Wasmann, nec Macleay, 1838

Diagnosis:

Body size 4.9–8.5 mm, only weakly transversally vaulted; pronotum scutiform; legs moderately long and broad, tibiae mostly with distinctly diverging margins distad (according to Wasmann 1929b).

Stein (1877) and Schaufuss (1896) assigned the first amber Paussinae that were found to the recent genus *Arthropteris* which is distributed in Australia. This classification was taken over by Kolbe and Wasmann; at a later date, the latter placed these two first described species into his new genus *Arthropterillus*. In spite of this, the original misjudgement obviously sufficed for all others to place most of the specimens known from am-

ber in this genus on the basis of their superficial similarity, although W_{AS}MANN (1926 b) had already pointed to a principle difference to *Arthropterus*, i. e. the fact that the elytral apex of the fossils is rounded. Besides all Baltic amber Paussinae the only taxa to have non-truncate elytra are the above described fossil *Eohomopterus*, the two recent *Eohomopterus* species and the recent genera *Hexaplatarthrus* and *Carabidomemnus* (s. l.). Another principal difference is the shape of the front coxae which is discussed in detail in NAGEL (1987). W_{AS}MANN (1929 a) says of the four "*Arthropterus* s. str." species *antiquus*, *aterrimus*, *subtilis*, and *hagedorni* that their front coxae are contiguous. However, two of the above amber specimens investigated by me, of which at least one must be placed in the immediate neighbourhood of *aterrimus*, definitely have separate coxae which are lying on the same level as the middle pleurosternum and which do not project as pegs. I therefore must assume that W_{AS}MANN (1929 a) only paid attention to whether the coxae are lying close to each other or not, since in three out of the four cases, the photographs in W_{AS}MANN (1929 b) show the white opacity at the crucial sites, so that a prosternal keel could not be recognized at all. In addition, W_{AS}MANN's (1929 a) description of the coxal shapes is wrong in at least two other cases in that he described the front coxae of *Carabidodoxus* (= *Carabidomemnus* s. l.) also as being contiguous, which is definitely wrong (the holotypes of 3 species are available to me), and the middle coxae of *Homopterus* as being separate, which is wrong again. Even if the coxae are close to each other, this does not permit any inference to be made on whether the coxae project conically or not, a fact which was not observed by W_{AS}MANN either.

The third diagnostic characteristic which proves that the fossils cannot belong to the recent genus *Arthropterus* is the fact that the elytra are only engaged over a short distance along the suture. All Australian *Arthropterus* species show a true suture almost as far as the apex. The only other taxa to have short sutures are the recent *Carabidomemnus* species and the fossil as well as the recent *Eohomopterus*.

For the above mentioned reasons, the genus name *Arthropterus* which has so far been used for the amber specimens has to be replaced by the oldest available name of the same species group, i. e. *Pleurarthropterus* W_{AS}M. (cf. Int. R Zool. Nom., Art. 23(e) (III)).

2.1 Subgen. *Balticarthropterus* nomen novum⁶

Syn.: Subgen. *Arthropterus* W_{AS}MANN, nec. MACLEAY, 1838

Diagnosis:

Antennae parallel; lateral sides of the pronotum with simple margin; body at least three times longer than wide; head and pronotum without any particular characteristics; front coxae separated by prosternal process.

⁶ Deriv. nom.: the subgenus first described as *Arthropterus* from the Baltic amber

Most of the species described by Wasmann (1929b) as well as four of the six specimens available to me fall into this category. This is a very heterogeneous grouping which is most probably not monophyletic.

2.2 Subgen. *Pleurarthropterus* Wasmann, 1927

Diagnosis:

7.6 mm; antennae strongly dilated distad; body three times longer than wide; lateral margin of the pronotum set-off and raised, in the posterior angles with a pit-like depression each, the latter with exsudate organs; head without any particular characteristics.

The figure of the only species of this subgenus so far described in Wasmann (1929b, pl. II, f. 20) is not inconsistent with Wasmann's opinion that there is an exsudate opening each in the posterior corners of the pronotum. In conjunction with the distad enlarged antennae, which can also be found in some *Carabidomemnus* forms, this subgenus is well marked off against other taxa. On the other hand, lateral pronotal margins which are narrowly raised and bounded by marginal grooves can also be found in other species of the subgenus *Balticarthropterus* nom. nov. The mouth-parts are not described and are obviously hardly visible because of the heavy white opacity in this area. However, the photograph (Wasmann 1929b, pl. II, f. 21) shows at least that the terminal segments of the labial palpi are conspicuously enlarged.

2.3 Subgen. *Acmarthropterus* Wasmann, 1929b

Diagnosis:

7.6 mm; body cylindrical (approx. 3 times longer than wide); vertex prolonged posteriorly spine-like; anterior margin of the markedly vaulted pronotum with a notch in the middle and a longitudinal furrow; elytra subapically probably with a red patch each; antennae parallel.

The special structure of the vertex and the associated shape of the anterior margin of the pronotum characterize the type specimen unmistakably. Within the genera with nine-segmented antennal clubs, this structure is unique, however, within the genus *Pausus* numerous vertex structures can be found which may e. g. also be prolonged caudad.

3. Gen. *Cerapterites* Wasmann, 1925

Diagnosis:

6.6–8.9 mm; body 2.5 times longer than wide; tibiae with parallel sides not diverging distad; each elytron with an ill-defined red subapical patch; antennae parallel; maxillary palpi with cylindrical terminal segment which is obtusely rounded at apex, three times longer than wide, each of the two preceding basal segments as long as wide; terminal segment of labial palpi thick, long-oval, hardly double as long as wide, truncate at apex (n. b.: Wasmann, 1929b, confounded the maxillary palpi with the labial palpi!); front coxae separated by prosternal process.

These forms also seem to be quite frequent (like *Balticarthropterus* nom. nov.), because three specimens were already available to Wasmann (1929b), and two others are available to me. Due to the combined characteristics of a “stout body”, “parallel antennae” and “relatively short tibiae with parallel lateral margins”, these forms can well be distinguished from *Balticarthropterus* nom. nov.

4. Gen. *Protocerapterus* Wasmann, 1926a

Diagnosis:

9–10.5 mm; body little more than double as long as wide; pronotum transversal, with rounded lateral margins and clearly visible posterior corners; antennae parallel; tibiae conspicuously dilated distad, only little longer than wide at apex; terminal segment of the labial palpi only little longer than wide, almost rectangular; front coxae separated by prosternal process.

This genus is distinguished from the preceding one by the apically dilated short tibiae, the even more pronouncedly stout shape of the body and the markedly enlarged terminal segment of the labial palpi. The structure of the terminal segment of the labial palpi seems to show a similarity with some species of the recent genus *Carabidomemnus*.

5. Gen. *Arthropterites* Wasmann, 1925

Diagnosis:

7 mm; antennal club nine-segmented, dilated only from 3. club segment onwards, heavily dilated distad; body slender; pronotum not transversal; tibiae parallel, approx. double as long as wide, dilated to the apex; maxillary palpi unobscured, slender; terminal segment of labial palpi very thick (Wasmann, 1929b, confounded the maxillary palpi and the labial palpi).

Wasmann (1926a, 1929b) was not completely sure about the number of antennal segments, however, he did not exclude the possibility that the first visible segment following the scapus (according to Wasmann the second, however, because of the hidden pedicellus, the third antennal segment) consists in fact of two individual segments. I personally believe that this is the most probable interpretation, because a flagellum with only eight segments would be absolutely unusual. Within the recent genus *Carabidomemnus* s. l. there is a tendency to a narrowing also of the second club segment, which, in some species, results in an increasing width of the antennae towards the apex. Whereas a flagellum with but eight segments in *Arthropterites* cannot be excluded with absolute certainty—the type specimen nor any similar one was available to me—, I consider this extremely unlikely in view of the photographs in Wasmann (1926a, 1929b).

The genus can therefore be distinguished from all other known fossil genera by the fact that a distinct broadening of the antennae only starts from the 3. club segment and that they are generally increasing in width distad. The second discriminating feature is the slender pronotum.

6. Gen. *Eopaussus* Wasmann, 1926a

Diagnosis:

5.7 mm; front coxae widely separate; antennal club onesegmented, reaching the first third of the elytra in a turned-back position; with an oblong, boat-shaped excavation, with two basal exudate trichomes; head with protruding eyes; apex of antennal club with disc-shaped chitin papilla; palpi relatively short and thick, cylindrical; terminal segment of the labial palpi three times longer than wide, rounded at the apex; penultimate segment of the labial palpi ring-shaped, short, basal segment double as long as penultimate segment but still transversal; terminal segment of maxillary palpi cylindrical, double as long as penultimate segment, ending in a rounded eggshaped apex; antepenultimate segment somewhat longer than penultimate segment, the segment preceding the antepenultimate one only half as long as the latter; ligula projecting almost to the apex of the labial palpi, deeply split in two lobes; pronotum transversal, wider than the head; presumably without exudate organs, possibly with a short medial longitudinal furrow at the anterior margin; elytral apex rounded; femora slender, tibiae long, cylindrical, tarsi almost half as long as tibiae, not dilated.

This is doubtlessly the most interesting amber ant nest beetle species, even though practically all conclusions drawn by Wasmann about its relationship to recent species are completely untenable, as already pointed out by Darlington (1950). The one-segmented antennal club and the slender tibiae characterize this genus unequivocally within the Paussinae with flat front coxae and rounded elytral apices. The maxillary palpi have a similar structure than those of the *Carabidomemmus* species as well as those of the Ozaeninae. Very simply structured labial palpi can also be found in the Pentaplatarthrinae and Heteropaussinae as well as the Ozaeninae. The two-lobed ligula is unique within the Paussinae.

4. Listing of the described fossil ant nest beetles

In spite of Wasmann's (1929b) comprehensive publication about the ant nest beetles of the Baltic amber, the following list of the forms hitherto described pretends a high standard of knowledge which has by far not been reached. I have nothing to add to the following two statements by Darlington (1950, p. 85): "A better taxonomist than Wasmann might have made fewer genera and species of the amber Paussids" and "I doubt almost everything that Wasmann says about relationships of genera [which he also underlined by his naming of the genera, P. Nagel]". In all probability, all fossil forms have the following two characteristics in common: 1. elytral apex rounded (established in all forms) (cf. Wasmann 1929c), 2. front coxae flat, separated by prosternal process, lying in the middle of the underside of the prothorax (established in numerous forms, not recognizable in the remaining species). The position of the fossil forms in the phylogenetic system of the Paussinae as well as data on the distribution history of the ant nest beetles are published in Nagel (1987).

In view of the insufficient knowledge of the Baltic amber Paussinae and the associated uncertain (fossil) generic standing, I refrain from making any status changes against the monography by Wasmann (1929b). Although there are sound reasons for uniting some of Wasmann's genera, I would not like to do so without having studied the types myself. Yet, what proved to be necessary because of the priority rule was the modification of the generic name *Arthropterillus* into *Succinarthropterus*. The most essential alteration is the abolition of the generic name *Arthropterus* for the fossil species; this name, which is based on recent Australian species was replaced by the name for the subgenus *Pleurarthropterus* which had been incorporated by Wasmann (1929b) in the same genus. In view of this change it was necessary to create a name to substitute *Arthropterus* s. str. in the sense of Wasmann, which I decided to be *Balticarthropterus* nom. nov. Unfortunately, before publishing his monography (1929b), Wasmann had already published most of the species and genus names in what were partly semi-scientific journals so that the following listing, besides stating the date of the initial publication, also includes the date of the first detailed description. The abbreviations have the following meaning: + = fossil, r = recent, BB = Baltic amber, DB = Dominican amber.

1. + (BB) Gen. *Succinarthropterus* KOLBE, 1926 (Sept. 30th, cf. LUCHT 1984)
Arthropterus subg. *Succinarthropterus* KOLBE, 1926
 Type species: *Arthropterus küblii* KOLBE, 1925, nec STEIN, 1877 (cf. KOLBE 1926) = *Arthropterillus kolbei* Wasmann, 1926 b
 Syn.: Gen. *Arthropterillus* Wasmann, 1926 b (Oct. 5th), **syn. nov.** (cf. Wasmann 1927, 1928 a, 1928 b, 1929 a, 1929 b, 1929 c)
 Type species: *Arthropterus helmi* SCHAUFUSS, 1896 (cf. Wasmann 1926 b)
 Syn.: Gen. *Arthropterus* auct., nec MACLEAY, 1838, **syn. nov.** (cf. STEIN 1877, SCHAUFUSS 1896, KOLBE 1925, Wasmann 1925 partim)
 - 1.1 *Succinarthropterus helmi* (SCHAUFUSS, 1896)
Arthropterus helmi SCHAUFUSS, 1896
Arthropterillus helmi (SCHAUFUSS, 1896) Wasmann, 1926 b (cf. Wasmann 1929 b, 1929 c)
 - 1.2 *Succinarthropterus küblii* (STEIN, 1877)
Arthropterus küblii STEIN, 1877
Arthropterillus küblii (STEIN, 1877) Wasmann, 1926 b (cf. Wasmann 1929 b, 1929 c)
 - 1.3 *Succinarthropterus kolbei* (Wasmann, 1926 b)
Arthropterus küblii KOLBE, 1925, nec STEIN, 1877
Arthropterus (Succinarthropterus) küblii KOLBE, 1926, nec STEIN, 1877
Arthropterillus kolbei Wasmann, 1926 b (cf. Wasmann 1929 b, 1929 c)
2. + (BB) Gen. *Pleurarthropterus* Wasmann, 1927
 Type species: *Arthropterus hermenau* Wasmann, 1926 b (cf. Wasmann 1928 b)
 Syn.: *Arthropterus* auct., nec MACLEAY, 1838, **syn. nov.**
 - 2.1 Subgen. *Pleurarthropterus* Wasmann, 1927 (cf. Wasmann 1928 b, 1929 b, 1929 c)
 Type species: *Arthropterus hermenau* Wasmann, 1926 b (cf. Wasmann 1928 b)
 - 2.1.1 *Pleurarthropterus (Pleurarthropterus) hermenau* (Wasmann, 1926 b)
Arthropterus hermenau Wasmann, 1926 b
Arthropterus (Pleurarthropterus) hermenau Wasmann, 1928 b (cf. Wasmann 1929 b, 1929 c)
 - 2.2 Subgen. *Balticarthropterus* **nom. nov.**
 Syn.: *Arthropterus* Wasmann, 1925 partim, nec MACLEAY, 1838 (cf. Wasmann 1926 b)

Arthropterus s. str. Wasmann, 1928 b, nec Macleay, 1838 (cf. Wasmann 1929 b, 1929 c)
Type species: *Arthropterus antiquus* Wasmann, 1925 (cf. Wasmann 1929 b)

2.2.1 *Pleurarthropterus (Balticarthropterus) andreei* (Wasmann, 1928 a)
Arthropterus andreei Wasmann, 1928 a

Arthropterus (s. str.) *andreei* Wasmann 1928 b (cf. Wasmann 1928 a, 1929 b, 1929 c)

2.2.2 *Pleurarthropterus (Balticarthropterus) skwarrae* (Wasmann, 1929 b)

Arthropterus (s. str.) *skwarrae* Wasmann, 1929 b

2.2.3 *Pleurarthropterus (Balticarthropterus) balticus* (Wasmann, 1926 b)

Arthropterus balticus Wasmann, 1926 b

Arthropterus (s. str.) *balticus* Wasmann, 1928 b (cf. Wasmann 1926 b, 1929 b, 1929 c)

2.2.4 *Pleurarthropterus (Balticarthropterus) spec. aff. balticus* Wasm.

(No. 1494 BB, Geol. Pal. Inst. Hamburg) (Nagel)

2.2.5 *Pleurarthropterus (Balticarthropterus) subtilis* (Wasmann, 1926 b)

Arthropterus helmi Quiel, 1910, partim, nec Schaufuss, 1896

Arthropterus subtilis Wasmann, 1926 b

Arthropterus (s. str.) *subtilis* Wasmann, 1929 b (cf. Wasmann 1926 b, 1929 c)

2.2.6 *Pleurarthropterus (Balticarthropterus) hagedorni* (Wasmann, 1926 b)

Arthropterus helmi Quiel, 1910, partim, nec Schaufuss, 1896

Arthropterus hagedorni Wasmann, 1926 b

Arthropterus (s. str.) *hagedorni* Wasmann, 1929 b (cf. Wasmann 1926 b)

2.2.7 *Pleurarthropterus (Balticarthropterus) antiquus* (Wasmann, 1925)

Arthropterus antiquus Wasmann, 1925 (cf. Wasmann 1926 b)

Arthropterus (s. str.) *antiquus* Wasmann 1929 b (cf. Wasmann 1925)

2.2.8 *Pleurarthropterus (Balticarthropterus) aterrimus* (Wasmann, 1929 b)

Arthropterus (s. str.) *aterrimus* Wasmann, 1929 b

2.2.9 *Pleurarthropterus (Balticarthropterus) spec. aff. aterrimus* Wasm.

(No. BB 45, Geol. Pal. Inst. Hamburg) (Nagel)

2.2.10 *Pleurarthropterus (Balticarthropterus) spec. aff. aterrimus* Wasm.

(No. BB 1503, Geol. Pal. Inst. Hamburg) (Nagel)

2.2.11 *Pleurarthropterus (Balticarthropterus) simoni* (Wasmann, 1926 b)

Arthropterus helmi Quiel, 1910, partim, nec Schaufuss, 1896

Arthropterus simoni Wasmann, 1926 b

Arthropterus (s. str.) *simoni* Wasmann, 1929 b (cf. Wasmann, 1926 b)

2.2.12 *Pleurarthropterus (Balticarthropterus) schaufussi* (Wasmann, 1926 b)

Arthropterus helmi Quiel, 1910, partim, nec Schaufuss, 1896

Arthropterus schaufussi Wasmann, 1926 b

Arthropterus (s. str.) *schaufussi* Wasmann, 1929 b (cf. Wasmann 1926 b)

2.2.13 *Pleurarthropterus (Balticarthropterus) frittschi* (Wasmann, 1929 b)

Arthropterus (s. str.) *frittschi* Wasmann, 1929 b

2.2.14 *Pleurarthropterus (Balticarthropterus) spec.*

(No. BB 1, Coll. Nagel in BGSS) (Nagel)

2.3 Subgen. *Acmarthropterus* Wasmann, 1929 b (cf. Wasmann 1929 c)

Type species: *Arthropterus kuntzeni* Wasmann, 1927 (Wasmann 1929 b)

2.3.1 *Pleurarthropterus (Acmarthropterus) kuntzeni* (Wasmann, 1927)

Arthropterus kuntzeni Wasmann, 1927

Arthropterus (Acmarthropterus) kuntzeni (Wasmann, 1929 b, 1929 c)

3. + (BB) Gen. *Cerapterites* Wasmann, 1925 (cf. Wasmann 1926a, 1927, 1928b, 1929a, 1929b, 1929c)
Type species: *Cerapterites primaevus* Wasmann, 1925 (Wasmann 1926a)
 - 3.1 *Cerapterites primaevus* Wasmann, 1925 (cf. Wasmann 1926a, 1929b, 1929c)
Pleuropterus spec. Reitter, nec Lacordaire, in Kleps, 1910
Cerapterus spec. Reitter, nec Svederus, in Klebs, 1910
 - 3.2 *Cerapterites* spec. (No. BB 1600, Geol. Pal. Inst. Hamburg) (Nagel)
 - 3.3 *Cerapterites*? spec. (No. BB 388, Geol. Pal. Inst. Hamburg) (Nagel)
4. + (BB) Gen. *Protocerapterus* Wasmann, 1926a (cf. Wasmann 1927, 1928b, 1929a, 1929b, 1929c)
Type species: *Protocerapterus primigenius* Wasmann, 1926a
 - 4.1 *Protocerapterus primigenius* Wasmann, 1926a (cf. Wasmann 1929b, 1929c)
 - 4.2 *Protocerapterus incola* Wasmann, 1927 (cf. Wasmann 1929b, 1929c)
5. + (BB) Gen. *Arthropterites* Wasmann, 1925 (cf. Wasmann 1926a, 1927, 1928b, 1929a, 1929b, 1929c)
Type species: *Arthropterites klebsi* Wasmann, 1925 (Wasmann 1926a)
 - 5.1 *Arthropterites klebsi* Wasmann, 1925 (cf. Wasmann 1926a, 1929b, 1929c)
"gen. nov." Reitter, in Klebs, 1910
6. + (BB) Gen. *Eopaussus* Wasmann, 1926a (cf. Wasmann 1926c, 1927, 1928b, 1929a, 1929b, 1929c)
Type species: *Eopaussus balticus* Wasmann, 1926a
 - 6.1 *Eopaussus balticus* Wasmann, 1926a (cf. Wasmann 1926c, 1927, 1928b, 1929a, 1929b, 1929c)
Paussus spec. Quiel, 1910
7. +/r (DB/Neotropis) Gen. *Eohomopterus* Wasmann, 1919a
Homopterus subg. *Eohomopterus* Wasmann, 1919a
Type species: r *Homopterus aequatoriensis* Wasmann, 1899 (Wasmann 1919a)
 - 7.1 *Eohomopterus paulmuelleri* sp. n.
8. +/r (DB/Neotropis) Gen. *Homopterus* Westwood, 1841
Cerapterus subg. *Homopterus* Westwood, 1841
Type species: *Cerapterus brasiliensis* Westwood, 1841
 - 8.1 *Homopterus hispaniolensis* sp. n.

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Zusammenfassung

Erstmals werden fossile neotropische Paussinae in Dominikanischem Bernstein beschrieben, die je einen Vertreter der beiden einzigen auch rezent in der Neotropis lebenden Genera repräsentie-

ren: *Eohomopterus paulmuelleri* sp. n. und *Homopterus hispaniolensis* sp. n. Weiterhin werden neue Exemplare von Paussinae in Baltischem Bernstein bekannt gemacht. Die wesentlichen Charakteristika der Fossilien werden in ihrer Relation zu den rezenten Formen herausgestellt sowie sämtliche bisher beschriebenen fossilen Formen zusammengestellt und diskutiert. Die Gattung *Arthropterillus* Wasmann wird in die Synonymie von Gen. *Succinarthropterus* Kolbe gestellt. Der bisher für die meisten fossilen Formen des Baltischen Bernsteins benutzte Gattungsname *Arthropterus* kann nicht weiter verwendet werden, da zwischen den Fossilien und den rezenten Arten dieser Gattung (die ausschließlich die Australis besiedeln) keine Identität besteht. Für *Arthropterus* s. str. Wasmann, nec. Macleay, wird die Bezeichnung *Pleuarthropterus* Wasm. subgen. *Balticarthropterus* nom. nov. eingeführt.

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