

FOSSIL ODONATES IN TERTIARY AMBER

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Dragonflies and damselflies are one of the most spectacular, but also one of the rarest, insect inclusions in Tertiary amber. Up to now there are no odonates known from any Mesozoic amber. Because of this rarity dragonflies are not even mentioned in a recent book on insects in amber (KRZEMINSKA & KRZEMINSKI, 1992). This paper is a short review and preliminary revision of all currently known specimens, based on a revised and amended version of BECHLY (1993). LARSSON (1978) explained the presence of odonate larvae or exuviae in Baltic amber. The fact that nearly all amber preserved odonates are damselflies, can be explained by the conditions of fossilisation: Damselflies (Zygoptera) get easier trapped and enclosed in resin than dragonflies (Anisoptera). Thus it is evident that Anisoptera preserved in amber will always be extremely rare and consequently of course also very expensive fossils (see ORR, 1993).

The following damselfly-fossils from the Dominican amber are located in the paleontological "Museum am Löwentor des Staatlichen Museums für Naturkunde" in Stuttgart / Germany (SCHLEE, 1990 and pers. comm.1993):

- **1.)** A complete damselfly, which is not very well visible, because the insect is surrounded by dirt.
- **2.-4.)** A relatively large piece of amber, containing three (!) damselflies.
- **5.)** A fragmentary damselfly-wing.
- **6.)** A fine preserved distal half of a damselfly-wing in very clear amber.
- **7.)** A damselfly (head, thorax, legs, proximal abdomen and wing bases) in excellent condition, preserved in clear, polished amber!

Colour-photos of the last two mentioned specimens, probably Coenagrionidae, have been published in SCHLEE (1990: 83) (see [fig. 1](#) and [fig. 2](#)). Unfortunately the magnificent amber collection of the Stuttgart museum is presently (fall 1996, probably till end of 1997) not open for scientific studies, because of the unexpected retirement of Dr. Schlee.



fig. 1

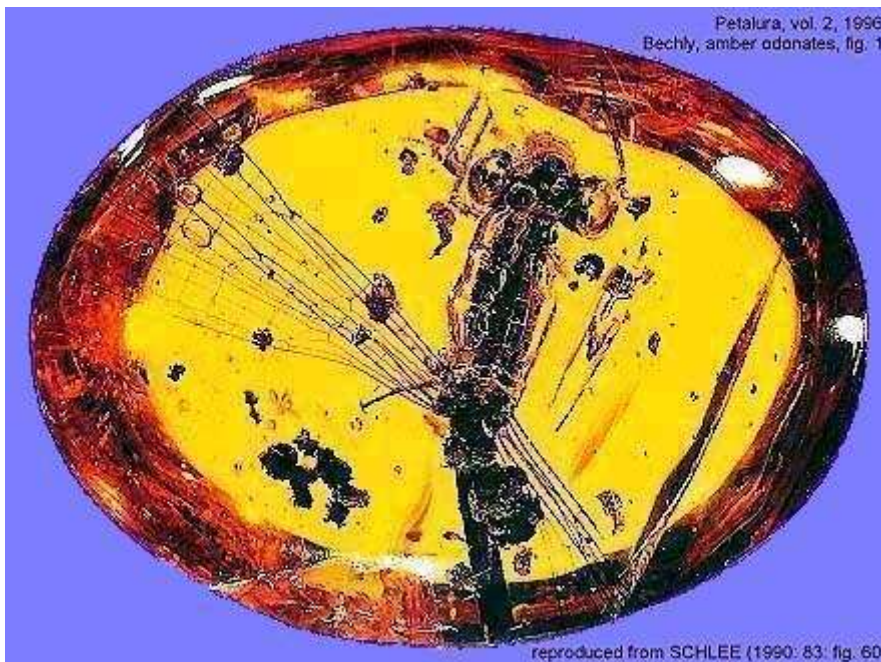


fig. 2

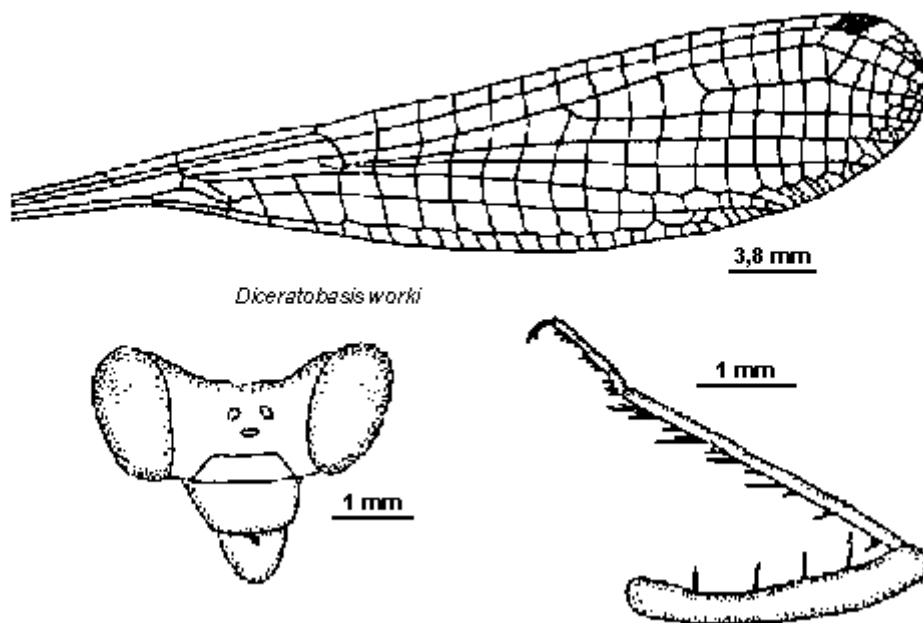
There are only three other records of odonate specimens from Dominican amber:

- **8.)** ORR (1993) reported about a libelluloid-like dragonfly completely preserved in Miocene amber, certainly from the Dominican Republic. Its present location unfortunately is unknown and it has apparently never been illustrated or described (ORR, pers. comm. 11/96). It would be very important to find out its present location (if any of the readers should know something about it, I would be most grateful for a

short information by email to: bechly.smns@naturkundemuseum-bw.de), and to check if this remarkable specimen indeed represents a genuine Tertiary amber fossil or maybe just a more recent copal inclusion.

- 9.) DONNELLY (1993; and pers. comm. 11/96) has a damselfly wing (similar to *Telebasis*) in amber from the Dominican Republic too. It is still in his private collection, but has never been illustrated or described yet.
- 10.) POINAR (1996) described a new species of the recent coenagrionid genus *Diceratobasis* (see [fig. 16](#)) from a piece of Dominican amber that is located in the private collection of Jim Work (Ashland, Oregon, USA). The larvae of this species probably lived in phytotelmata of tank bromeliads.
 - POINAR (1996: 382-383): "*Diceratobasis worki* sp. nov."

Petalura, vol. 2, 1996
Bechly, amber odonates, fig. 16



redrawn from POINAR (1996: 383, fig. 1-2, 4)

fig. 16

The Dominican amber originated in the Middle Eocene to Upper Oligocene (45-25 Mio. years b.p.), maybe even to the Lower and Middle Miocene (15 Mio. years b.p.). The Dominican "amber-tree" most probably has been a member of the Recent genus *Hymenaea*, a neotropical leguminous that is known for its high production of resin (SCHLEE, 1986). Amber from the Dominican Republic is extraordinary for the following reasons:

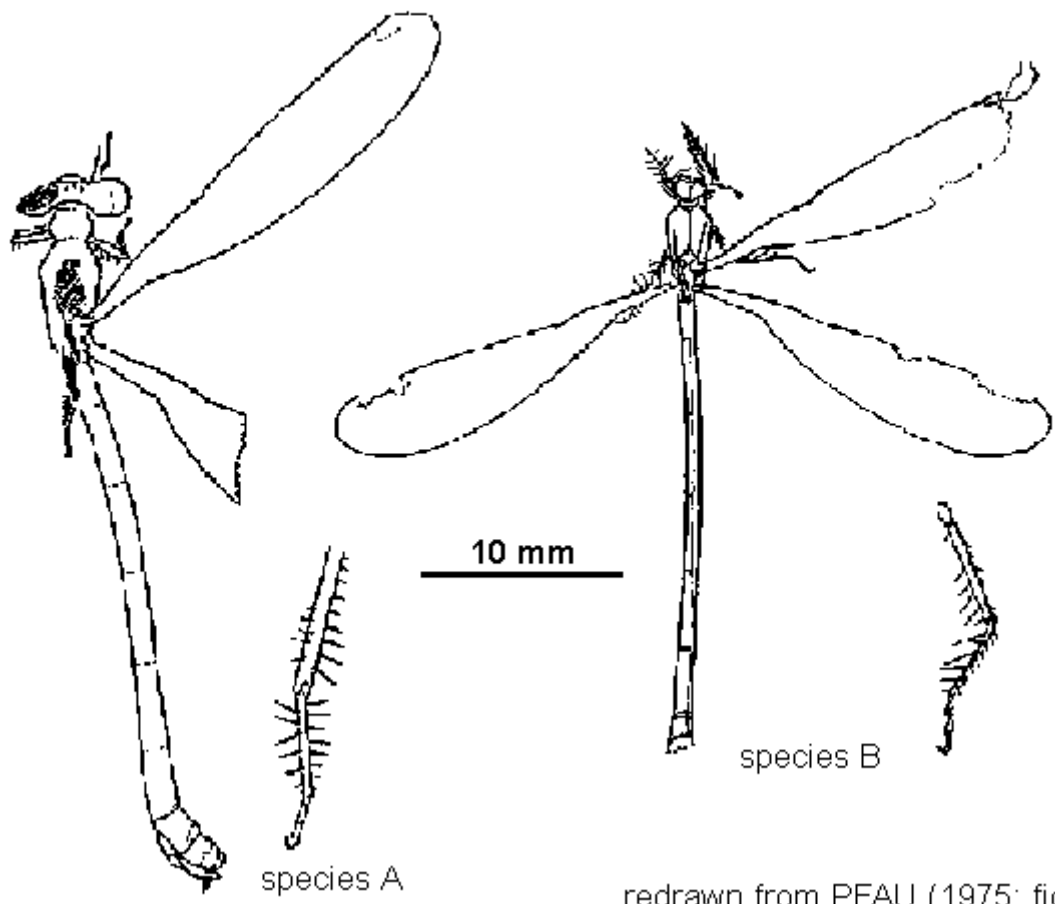
- numerous places of discovery, with a large output of high-quality amber.
- regular findings of large pieces of amber, up to 13 kg!
- frequent and diverse fossils in excellent condition: Plants (blossoms, leaves and bark), arachnids (incl. scorpions, amblypigids and pseudoscorpions), insects (incl. odonates, mantids, membracids, strepsipteres and fleas) and even vertebrates (mammal bones and bird feathers, as well as complete small frogs, gekkos and anolis-iguanas)! There are also single pieces of amber with mass-catches of insects, e.g. containing 2000 ants, or 1000 dolichopodid flies, or 15 moths etc.

Therefore it is certainly not over-optimistic to expect further odonates from Dominican amber in the future, but there are also some fossil odonates known from the Baltic amber of eastern Europe, which originated in the Upper Eocene (ca. 40-50 Mio. years b.p.) of Scandinavia, but is found in secondary deposits of glauconitic sands ("blue earth") of the Lower Oligocene (ca. 30-35 Mio. year b.p.) at the Baltic coast. Based on the monograph of CONWENTZ (1890) the Baltic "amber-tree" has long been assumed to be an extinct conifer, which has been named *Pinus* (or *Pinites*) *succinifera* Goepp., although this taxon is still undefined and could include five different species (SCHLEE, 1986), however since the studies of KATINAS (1971) it is regarded as more likely that the Baltic amber was produced by a cedar (close to the Recent species *Cedrus atlanticus*) and maybe also an araucaria of the genus *Agathis* (= kauri-pine).

HAGEN (1854) mentioned five odonates and HANDLIRSCH (1906-1980) mentioned six odonates from Baltic amber. Handlirsch's list was incomplete and contained several errors, which unfortunately have been frequently perpetuated, even recently by the author himself (BECHLY, 1993), although they had been corrected already by ANDER (1942).

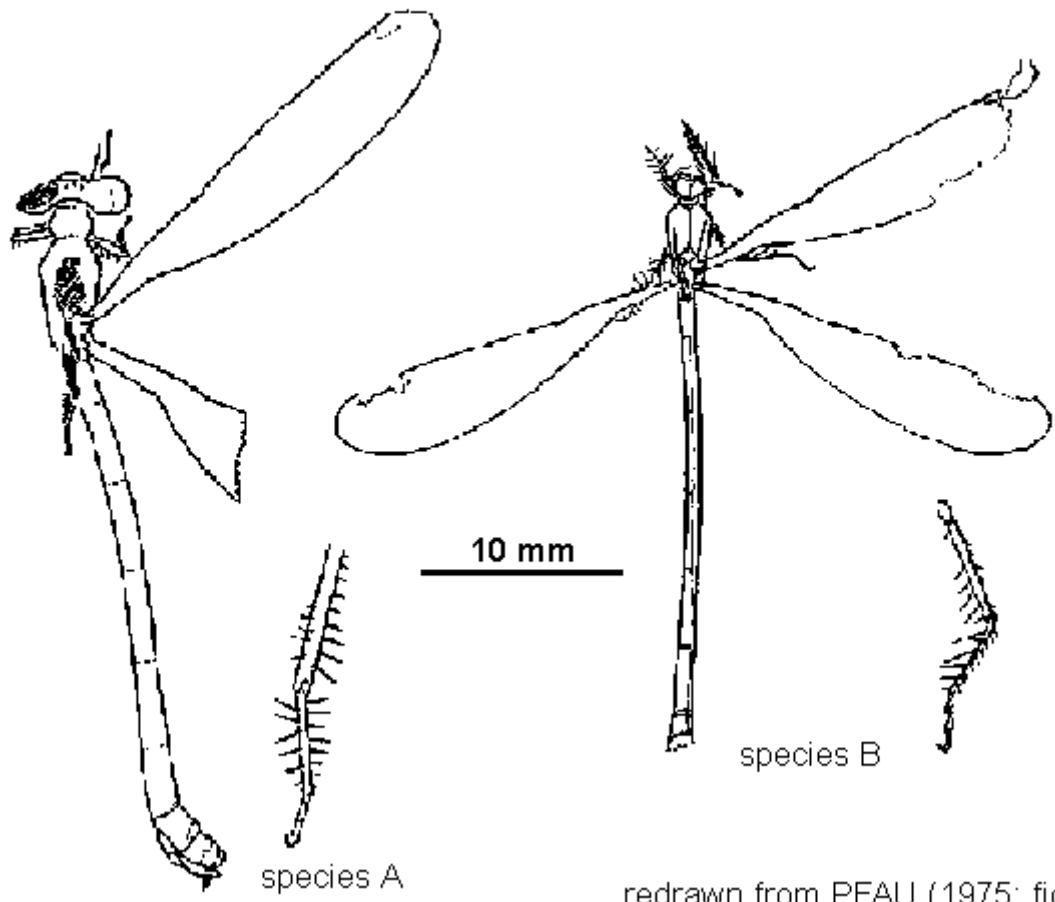
Unfortunately the Odonata chapter in the well known catalogue of amber fossils by KEILBACH (1982: 208-209) is likewise incomplete and incorrect, and furthermore even contains some additional errors too. The following new list will hopefully be rather complete and error-free:

- **11.-12.)** Two fossil damselflies of the famous "Koenigsberg amber collection" are now located in the "Geologisch-Paläontologisches Institut der Universität" Göttingen / Germany (species A: no. 3 B 696; and species B: no. K 8088). These specimens were described and figured by PFAU (1975) (see [fig. 3](#), [fig. 4](#) and [fig. 5](#)). They are remarkably well preserved and seem to represent female specimens of two different Coenagrionoidea species of the Upper Eocene, which are still unnamed. Pfau's suggestion that these fossils might belong to the Recent family Platycnemididae is not really supported by the available evidence, so that these fossils should rather be regarded as Coenagrionoidea incertae sedis. According to Pfau one of the species might be conspecific with "*Agrion antiquum*" Hagen.
 - PFAU (1975: 1): "..., Zygoptera - möglicherweise Platycnemididae"
 - KEILBACH (1982: 209): "Platycnemididae spec. A. u. spec. B."
 - NEL & PAPA ZIAN (1990: 254): "Platycnemididae, genre incertae sedis (Pfau, 1975)"
 - BECHLY (1993: 14): "... seem to represent two different platycnemidid species, which are still unnamed."



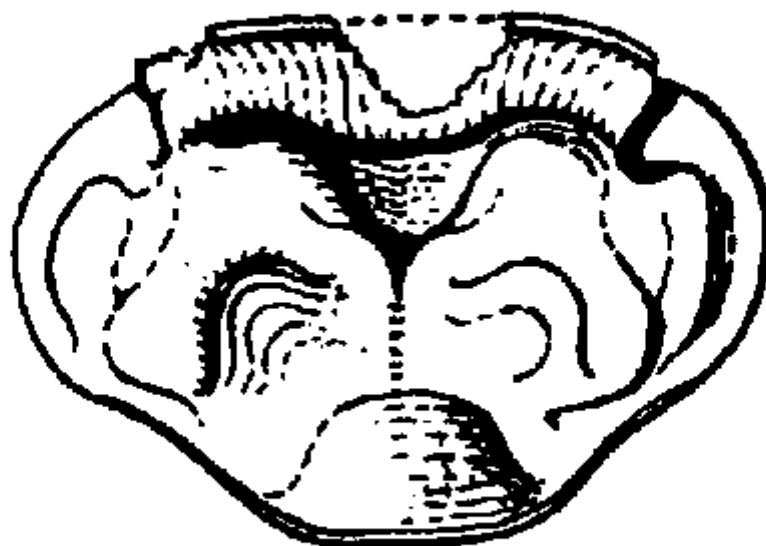
redrawn from PFAU (1975: fig. 1)

fig. 3



redrawn from PFAU (1975: fig. 1)

fig 4



protergum of species B

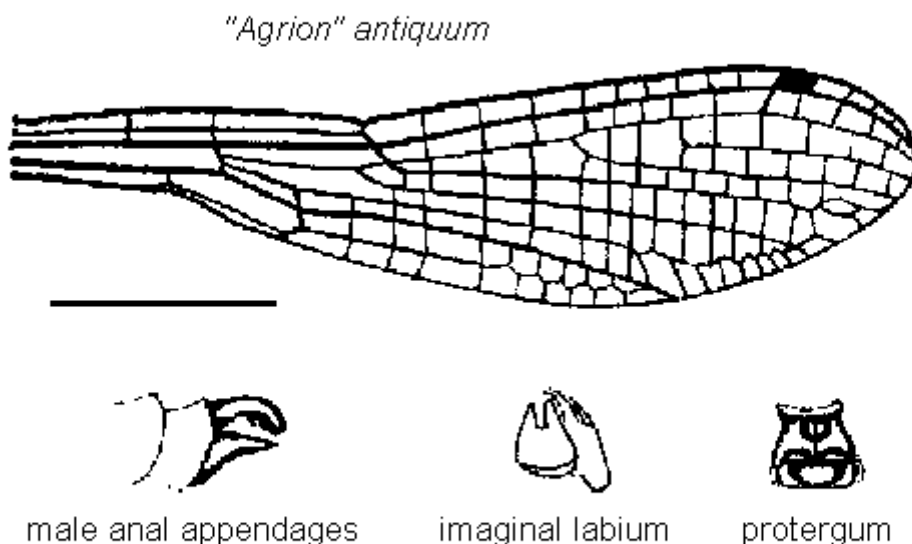
redrawn from PFAU (1975: fig. 3)

fig 5

- **13.-17.)** Four pieces of amber (with remains of five specimens of damselflies), of which three have been located in the "Collection Berendt" of the "Paläontologisches Museum des Museums für Naturkunde der Humboldt-Universität" in Berlin / Germany. PFAU (1975) could only locate the two of these pieces in the Berlin museum (see [fig. 6](#) and [fig. 7](#)). The location of the fourth specimen is unknown. One of the two remaining specimens is one piece (no. 16) with a basal wing fragment and a male and a female abdomen ([fig. 8](#)). It probably represents the remains of a trapped pair, and the appendices of the male abdomen indicate that they belong to the same species as the second specimen (PFAU, 1975). The second piece contains a wing fragment without base and apex ([fig. 9](#)), head ([fig. 10](#)), all 6 legs but without coxae and tarsi ([fig. 11](#)), and the apex of a male abdomen. The labels for both pieces are marked with a red spot, which is indicating a status as original and/or type, and by the description there is no doubt that both pieces represent originals of HAGEN & PICTET (1856), so that these two pieces seem to represent syntypes of "*Agrion antiquum*". The female specimen described by PICTET (1856: 79) is apparently lost, as already supposed by PFAU (1975). Therefore I decided to designate the second specimen (original of HAGEN, 1856: 79) as lectotype of "*Agrion antiquum*", since even PICTET (1856: 79) already mentioned that the specific identity of piece no. 16 can not be decided.

- HAGEN (1848: 7): "*Agrion antiquum* Pictet" (nomen nudum; knows 2 specimens)
- HAGEN in SELYS (1850: 357-358): "*Agrion ? antiquum* Pictet"
- SELYS (1850: 366): "*Platycnemis ? antiquum*"
- HAGEN (1854: 227): "*Agrion antiquum* P. 3."
- GIEBEL (1856: 273): "*Agrion antiquum*"
- PICTET in BERENDT (1856: 78-79, fig. 4a-d & 5 on tab. vi): "*Agrion antiquum*" (first description; knows 3 specimens)
- HAGEN in BERENDT (1856: 79-80, fig. 11a-c on tab. viii): "*Agrion antiquum*" (supplementary description; knows 4 specimens)
- KIRBY (1890: 175): "*Coenagrion antiquum* Hag."
- SCUDDER (1890: 127): "*Platycnemis antiquum*"
- HANDLIRSCH (1908: 899): "*Platycnemis antiqua* Hagen"
- ANDER (1942: 76): "*Agrion antiquum* Pictet et Hagen 1856 ... Die systematische Stellung dieser Art ist noch nicht entschieden"
- WEIDNER (1958: 52-53): "*Platycnemis ? antiqua ?*" (see no. 23.)
- PFAU (1975: 4): "*Agrion antiquum* Pictet (= *Platycnemis antiqua* Hagen)"
- LARSSON (1978: 83): "*Platycnemis antiqua*"
- KEILBACH (1982: 209): "*Platycnemis antiqua* (Pictet & Hagen, 1856)"
- NEL & PAPA ZIAN (1990: 254): "*Platycnemis antiqua* (Pictet & Hagen, 1856)"
- BRIDGES (1993: VII.15): "*Platycnemis antiquum* (Pictet & Hagen), 1856"
- BECHLY (1993: 14): "Three *Platycnemis*-like damselflies, described by Hagen (1848, 1856) as *Platycnemis antiqua*."
- BRIDGES (1994: VII.16): "*Platycnemis antiquum* (Pictet & Hagen), 1856"

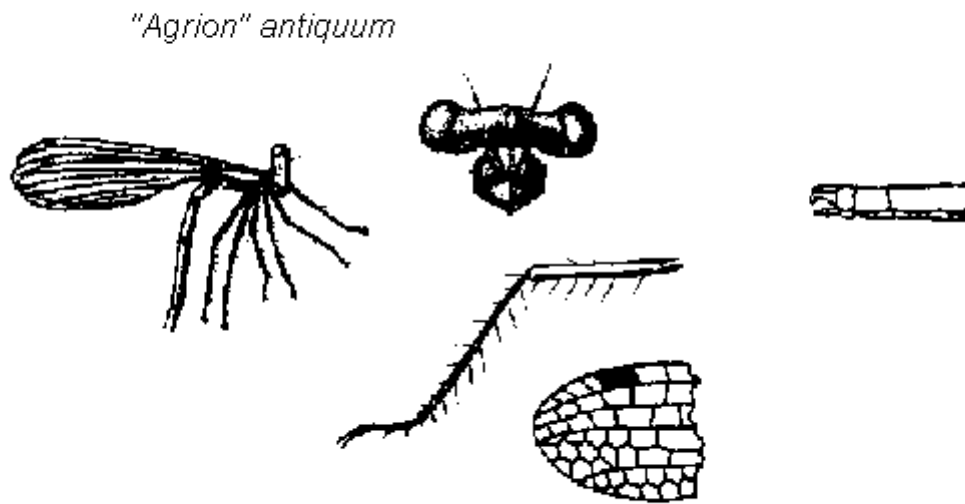
Petalura, vol. 2, 1996
 Bechly, amber odonates, fig. 6



redrawn from Hagen in BERENDT (1856: pl. viii, fig. 11)

fig 6

Petalura, vol. 2, 1996
Bechly, amber odonates, fig. 7



redrawn from Pictet in BERENDT (1856: pl. vi, fig. 4 & 5)

fig 7

Petalura, vol. 2, 1996
Bechly, amber odonates, fig. 8
original

"Agrion" antiquum
paratype, Coll. Berendt / Berlin

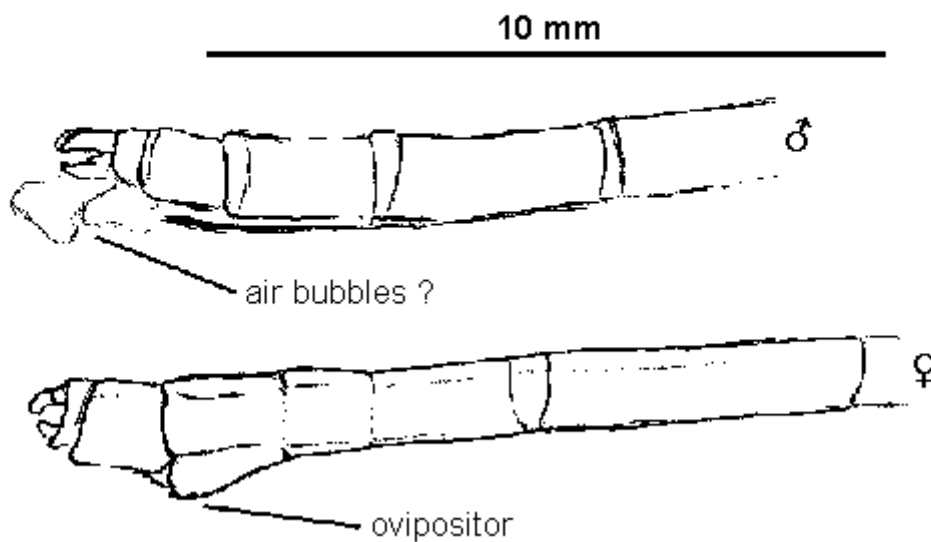


fig 8

Petalura, vol. 2, 1996
Bechly, amber odonates, fig. 9
original

"Agrion" antiquum
lectotype, Coll. Berendt / Berlin

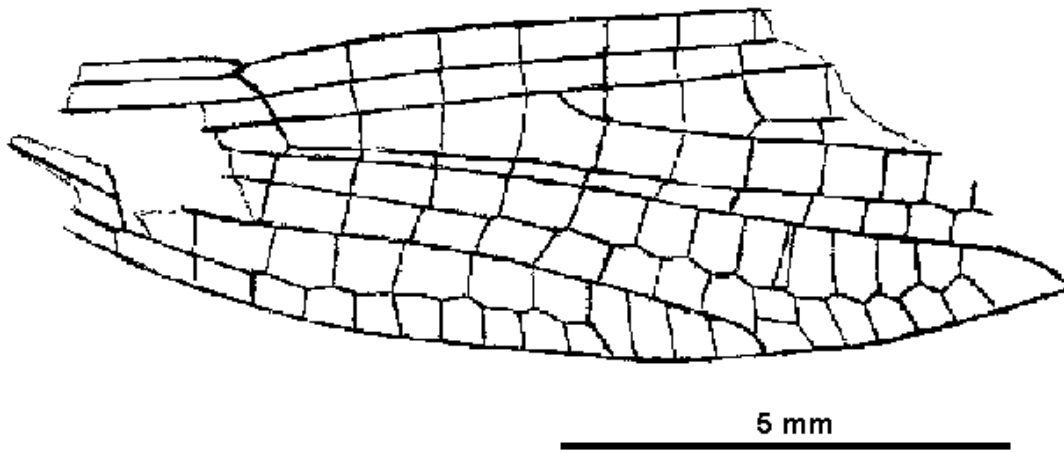
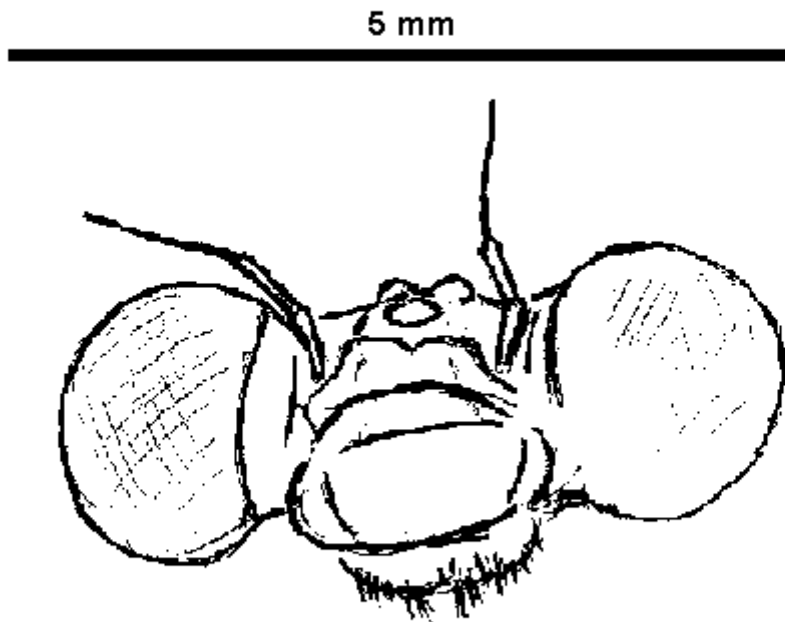


fig 9

Petalura, vol. 2, 1996
Bechly, amber odonates, fig. 10
original



"Agrion" antiquum
lectotype, Coll. Berendt / Berlin

fig 10

"Agrion" antiquum
lectotype, Coll. Berendt / Berlin

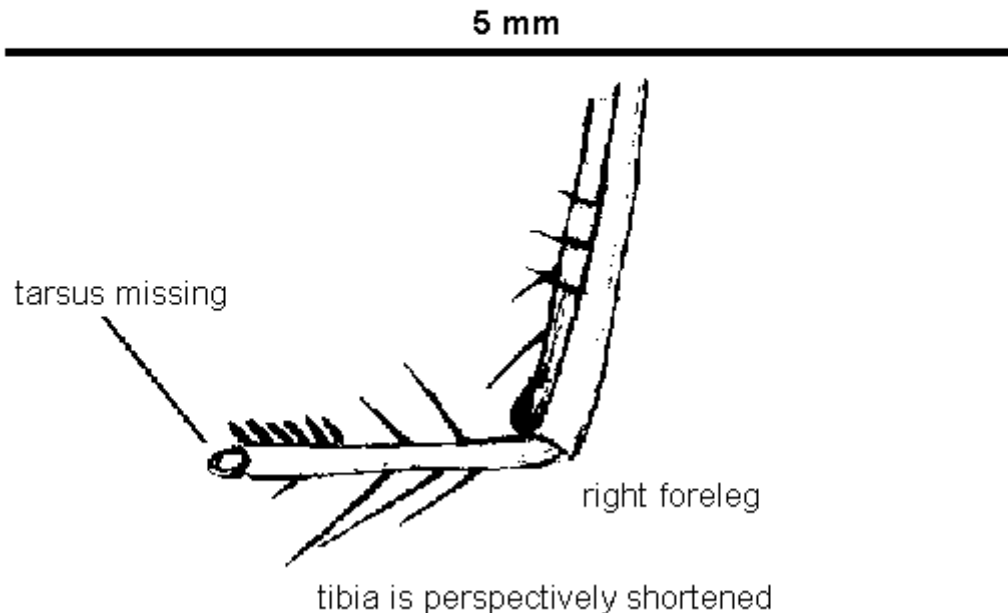


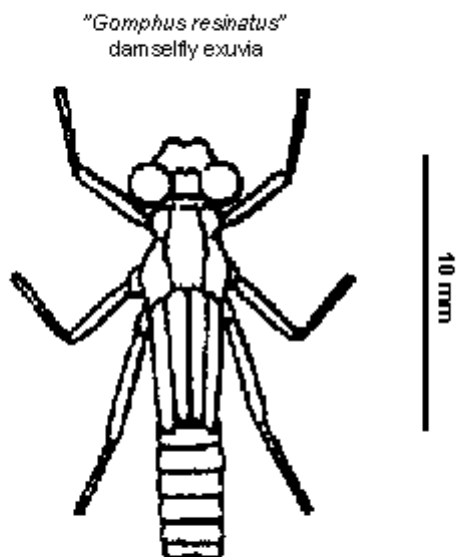
fig 11

- **18.)** A piece of amber with one basal and two apical fragments of the wings of a relatively large dragonfly (wing span ca. 3 inches according to Hagen) in the "Collection Menge". The present location is unknown.
 - HAGEN (1854: 227): "*Aeschna. Flügelspitzen.* - ... wahrscheinlich zu *Gomphoides*"
 - HAGEN in BERENDT (1856: 81): "*Gomphoides occulta* Hagen" (nomen nudum; no valid description)
 - KIRBY (1890: 168): "*Gomphoides occulta* Hag."
 - HANDLIRSCH (1908: 900): "*Gomphoides occulta* Hagen"
 - HANDLIRSCH (1921: 217): "*Gomphoides* Selys"
 - ANDER (1942: 77): "*Aeschnidae* s.ll."
 - FRASER (1957: 94): "... *Gomphoides* ... have also been reported from Bavarian amber and the Miocene."
 - LARSSON (1978: 83): "*Gomphoides occultus*"
 - KEILBACH (1982: 209): "*Gomphoides occultus* Hagen, 1856"
 - CARPENTER (1992: 81): "*Gomphoides* SELYS-LONGCHAMPS in SELYS-LONGCHAMPS & HAGEN, 1850, p. 360 [Generic assignment of fossil doubtful.] PICTET & HAGEN, 1856."
 - BRIDGES (1993: VII.167): "*Gomphoides occulta* Hagen, 1856"
 - BECHLY (1993: 14): "An adult dragonfly, described by Hagen (1854, 1856) as *Gomphus resinatus*."

- NEL & PAICHELER (1994: 60): "*Gomphoides occultus* Hagen, 1856 (in Berendt : 81)"
- BRIDGES (1994: VII.170): "*Gomphoides occulta* Hagen, 1856"
- **19.)** A damselfly exuvia (Zygoptera) in the "Collection Berendt". My recent (November 1996) examination of the fossil, which is still preserved in the Coll. Berendt at the Natural History Museum (Paleontological Museum) in Berlin / Germany, basically confirmed the redescription and conclusion of HAGEN (1856) (see [fig. 12](#) and [fig. 13](#)). It is most probably an exuvia of a Coenagrionoidea incertae sedis. If this fossil is conspecific with *Agrion antiquum* can neither be confirmed by positive evidence nor discarded by conflicting evidence. It seems to be very unlikely that this exuvia was embedded at the original site of emergence, because of the following reasons: The first evidence is the reasonable assumption that the conifer trees that produced the resin for the Baltic amber most probably were adapted for dry soils just like Recent conifers too, while damselfly larvae almost exclusively emerge on small plants that are very close to their breeding waters. The second evidence is the circumstance that all tarsi as well as the end of the abdomen with the caudal gills are missing. The most likely explanation seems to be, that an old exuvia was blown during a storm on a blotch of resin and became embedded. On the other hand it should be noted that two specimens of Gammaridae (Crustacea) are known from Baltic amber (BACHOFEN-ECHE, 1949 (reprinted 1996): 42-44), of which at least one was embedded when it was still alive. Some aquatic habitats thus must have been close enough to the amber trees that such purely aquatic animals could become embedded.
 - HAGEN (1848: 8): "*Gomphus resinatus*" (nomen nudum; no description)
 - HAGEN in SELYS (1850: 358): "*Gomphus resinatus* Hagen, Nymphe"
 - GIEBEL (1852: 639): "*Gomphus resinatus* Hagen"
 - HAGEN (1854: 227): "*Calopteryx* ?, Nymphenhaut."
 - GIEBEL (1856: 284): "*Libellula resinata*"
 - PICTET in BERENDT (1856: 78 and 80, fig. 6 on tab. vi): "*Gomphus* - (larva)" (first description)
 - HAGEN in BERENDT (1856: 80, fig. 12 on tab. viii): "Agrionide" (supplementary description; the term "Larva" in the explanation of fig. 12 refers to *Agrion antiquum*)
 - KIRBY (1890: 168): "*Aeschna resinata* Hag."
 - HANDLIRSCH (1908: 896): "*Calopteryx* ? (larva) Hagen"
 - HANDLIRSCH (1908: 900): "*Gomphus resinatus* Hagen"
 - HANDLIRSCH (1908: 900): "*Gomphus* - (larva) Hagen"
 - HANDLIRSCH (1921: 217): "Calopterygidae, zweifelhafte Larve"
 - HANDLIRSCH (1921: 217): "2 als Gomphus bezeichnete Formen"
 - ANDER (1942: 76): "Agrioniden-Larve 1"
 - FRASER (1957: 94): "... *Gomphus* ... have also been reported from Bavarian amber and the Miocene."
 - KEILBACH (1982: 209): "*Agrion spec.* Hagen in Berendt 1856, p. 80"
 - KEILBACH (1982: 209): "*Gomphus* Larva Hagen in Berendt 1856, p. 80"
 - KEILBACH (1982: 209): "*Gomphus resinatus* Pictet, 1856 in Berendt, p. 81"
 - CARPENTER (1992: 81): "*Gomphus* LEACH, 1815, p. 37. [Generic assignment of fossil (nymph) doubtful.] HAGEN, 1848."
 - CARPENTER (1992: 87): "*Calopteryx* LEACH, 1815, p. 137. HAGEN, 1848, Oligo., Europe (Baltic), ..."
 - BRIDGES (1993: VII.196): "*Gomphus resinatus* Hagen, 1848"

- BECHLY (1993: 14): "A damselfly-larva (!) described by Hagen (1854) as *Calopteryx*."
- BECHLY (1993: 14): "Another adult dragonfly, described by Hagen (1848, 1856) as *Gomphus resinatus*."
- BECHLY (1993: 14): "A dragonfly larva (!), described by Hagen (1856) as *Gomphus*."
- NEL & PAICHELER (1994: 57): "*Gomphus resinatus* Pictet, 1856 (*in* Berendt, 1856: 81) (d'après Keilbach, 1982) ... Elle doit être considérée comme un Odonata Gomphidae (?) de position incertaine."
- NEL & PAICHELER (1994: 57): "*Gomphus* "larva" Hagen, 1856 (*in* Berendt) ... Son attribution est très douteuse."
- BRIDGES (1994: VII.200): "*Gomphus resinatus* Hagen, 1848"

Petalura, vol. 2, 1996
 Bechly, amber odonates, fig. 12

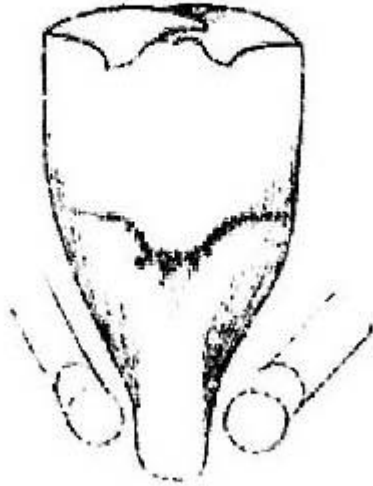


redrawn from Pictet in BERENDT (1856: pl. vi, fig. 6)

Pictet's original drawing is rather imprecise, e.g. showing all tarsi although none of them is actually preserved, and not showing the ecdysial sutures although they are clearly visible in the fossil!

fig 12

"*Gomphus resinatus*"
damselfly exuvia



reproduced from Hagen
in BERENDT (1856: pl. viii, fig. 12)

fig 13

- **20.)** Another Zygoptera-larva in the "Collection Hagen". The author could not find this specimen in the amber collections of the Museum of Comparative Zoology in Cambridge (laboratory of late F.M. Carpenter), although the complete Coll. Hagen is presently located in this institution.
 - HAGEN in SELYS (1850: 357): "Agrion Une petite nymphe, ou plutôt l'étui vide."
 - GIEBEL (1856: 273): "Eine unvollständige kleine Larve"
 - ANDER (1942: 76): "Agrioniden-Larve 2"
- **21.)** An odonate "larva" (certainly an exuvia) of uncertain affinities (location: unknown; lost according to ANDER, 1942):
 - HAGEN in BERENDT (1856: 78): "Libellenlarve"
 - ANDER (1942: 77): "Odonaten-Larve incert. sedis"

This specimen might be identical with the specimen cited by HANDLIRSCH (1906-1908) as Odonata incertae sedis:

- BERENDT (1830): "*Libellula* -"
 - HANDLIRSCH (1906-1908: 904): "Odonata incertae sedis. (*Libellula*) - Berendt."
 - BECHLY (1993: 14): "A specimen classified by Handlirsch as Odonata incertae sedis, wa described by Berendt (1830) as *Libellula* spec."
- **22.)** An undescribed abdomen of a female damselfly (completely preserved, incl. ovipositor) in the collection Bachofen-Echt (Fach 2 L1A) at the "Bayerische

Staatssammlung für Paläontologie und historische Geologie" in Munich / Germany ([fig. 14](#)).

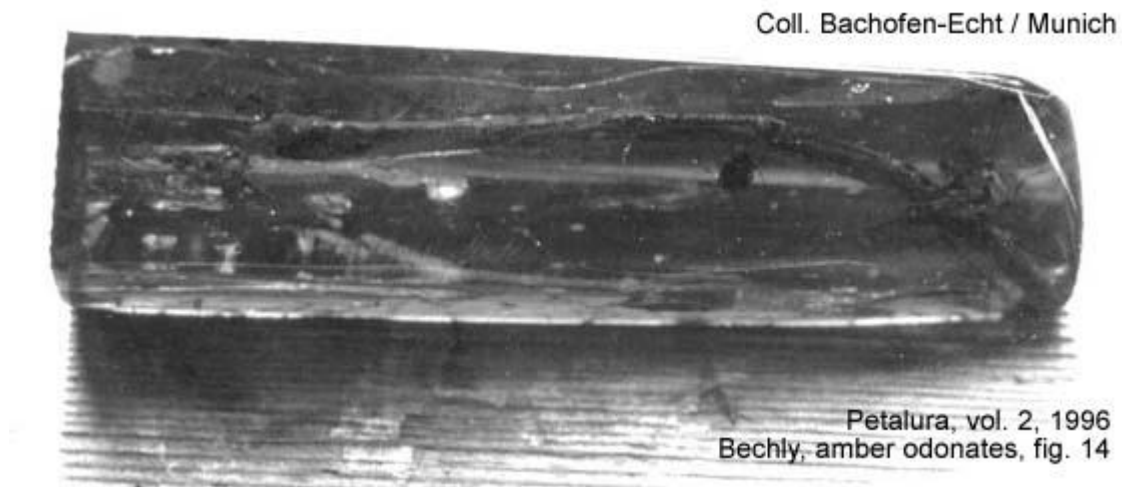


fig 14

- **23.)** A completely preserved damselfly in clear amber which is mentioned and figured by BACHOFEN-ECHT (1949 (reprinted 1996): p. 78 and fig. 63) (see [fig. 15](#)). The specimen is cited as Agrionidae, but without doubt represents the only known Lestidae in amber, since the specimen has wings with an oblique vein and two cells beneath the distinctly braced pterostigma (clearly visible in the illustration of the original edition, but not well visible in the reprint). I could not find the specimen in the collection Bachofen-Echt in Munich (BSGPM), thus its present deposition unfortunately has to be regarded as unknown.

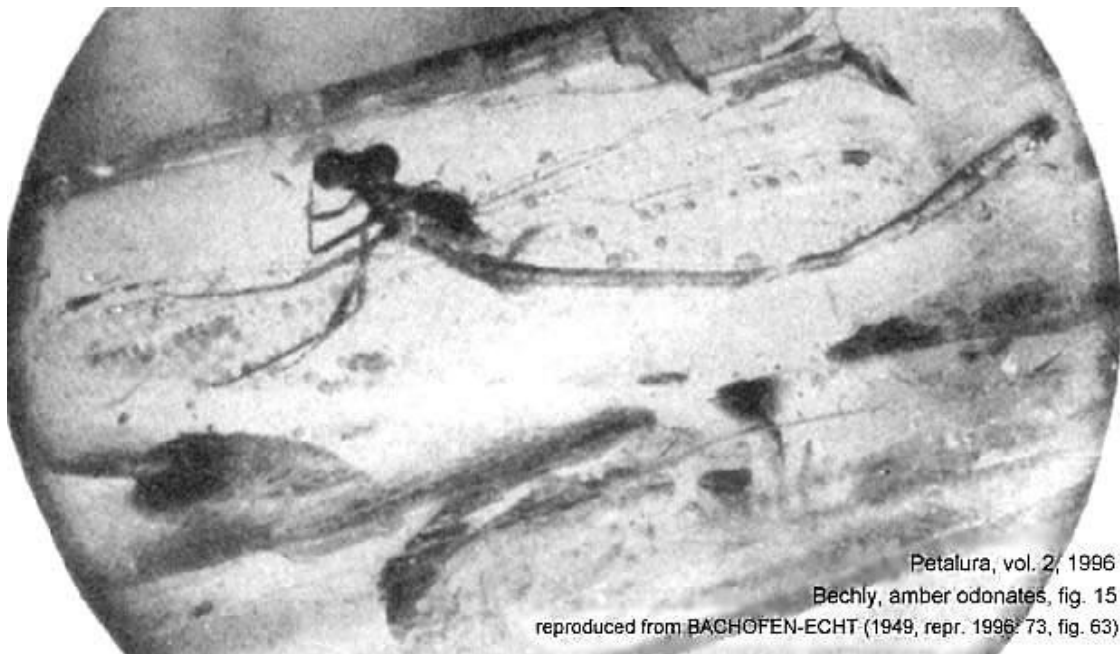


fig 15

- **24.)** WEIDNER (1953) reports about a Zygoptera "larva" (*Platycnemis ? antiqua ?*) in a piece of Tertiary Baltic amber in the Coll. Scheele (Nr. 1082. Typ. Kat. Nr. 45.) of the "Geologisches Staatsinstitut Hamburg" / Germany.
- **25.-29.)** Mr. Walter Ludwig (Berlin, Germany) reported (pers. comm. 1996) about a damselfly wing in a piece of Saxonian amber from Bitterfeld in the private collection of Mr. Hoffeins Tiperas (Hamburg), and a complete damselfly in Baltic amber in the collection of a fossil trader in Berlin. Furthermore he has 3 specimens in his private collection (Coll. Ludwig, Berlin). One specimen is a fragment of a damselfly thorax (open so that one can see inside!) with two wing bases and a nearly complete wing of a stem-group representative of Euphaeidae. It is very similar to the genera *Parazacallites* and *Litheuphaea*, and is sharing with the latter the complete suppression of any secondary antenodals between ScP and RA (contrary to the original description of *Litheuphaea*). Another specimen is absolutely unique, since it shows a damselfly that is just emerging from its exuvia, both completely preserved in a "Schlaube". The wings of the imago are not yet unfolded and the apex of the abdomen is still inside the exuvia. The exuvia has saccoid gills with a long filamentous apex, very similar to the neotropical genus *Palaemnema* (Platystictidae). Both mentioned specimens are from Baltic amber and will be formally described by the author. The third specimen is a piece of amber with head (with deeply fissured labium) and one fore leg (with cleaning "brush") of a damselfly from the Saxonian amber of Bitterfeld (Eastern Germany, Miocene, ca. 22 mybp).
- **30.)** Mr. Hans Lüdicke (Kronberg, Germany) has a well preserved and nearly complete damselfly (about 4 cm long) from the Baltic amber in his private collection. This specimen is currently studied by Prof. Rainer Rudolph (Münster, Germany).
- **31.-32.)** Two damselflies from the Baltic amber are present in the collection of the amber-museum at Ribnitz-Damgarten (East Germany). According to Mr. Ulf Erichson (pers. comm. 1997) one specimen is a wing and a body fragment in a piece of amber that was later manufactured as piece of jewellery. The second specimen is a rather complete damselfly, however the piece of amber contains some dirt and unfortunately had to be glued after it was accidentally broken.

All these fossils together make a total of 32 different specimens. The present location of 25 specimens is known to me, and except two, all others are preserved in Germany, which therefore can be considered as "El Dorado" for researches on amber dragonflies. Anyway my enumeration will probably still be somewhat incomplete, since it is quite likely that at least a few specimens have disappeared in private collections without having been noticed by scientists. A few small damselflies are rumoured to be present in local collections in the Dominican Republic. HAGEN (1856: 78) mentions the existence of a further imaginal damselfly (Coll. Saturnus / Königsberg) and an odonate larva (Kabinett physik.-oekonom. Gesellschaft zu Königsberg), both from Baltic amber of course. Nevertheless it can not be excluded that these two specimens might be identical with specimens already mentioned in this enumeration. Even all the known specimens are in need of a thorough revision, because their taxonomic and phylogenetic status seems to be more or less unsettled. Such a revision is projected by the author.

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