Fig. 1. *Neadelphus protae* n. sp. Dorsal aspect of holotype.
THE NEUROPTERA OF THE BALTIC AMBER.
I. ASCALAPHIDAE, NYMPHIDAE, AND PSYCHOPSIDAE

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INTRODUCTION
Along with the related Megaloptera and Raphidiodea, fossils representing the Neuroptera (Planipennia) are known from the Permian of Russia (Martynova, 1962), Australia (Riek, 1953), and Kansas. Several of these early fossils, such as those of the Palaemerobiidae and Permithonidae, have a decidedly modern aspect and by the mid-Mesozoic the living families Chrysopidae (Adams, 1967), Nymphidae (Adams, 1958), and Psychopsidae were already in existence. Other than the Baltic amber, Tertiary deposits have yielded a disappointingly small number of Neuroptera. Among these the Chrysopidae are relatively the most numerous, although in fact they are actually represented by only a small number of fossils from the Florissant shales of Colorado and a few additional specimens from Europe.

Both the Megaloptera and Raphidiodea are known from the Baltic amber (Hagen, 1856; Carpenter, 1956) from a very limited number of specimens, whereas the Neuroptera are much more com-
THE NEUROPTEROUS LARVAE OF THE BALTIC AMBER

Without formally naming them, Hagen (1836) provided detailed descriptions of two larval specimens which he felt belonged to the Neuroptera. The first of these, designated as “Larva Hemerobii”, was described as possessing long, scimitar-shaped jaws, a broad head, and round, strongly constricted setigerous tubercles on the thorax. The remains of a trash packet, consisting of stellate plant hairs, was noted to be present in the vicinity of the larva. It has proved impossible to learn of the present whereabouts of this larva and this is unfortunate since it is quite likely that this specimen is a chrysopid, a family, as noted above, otherwise curiously unrepresented in the Baltic amber. Hagen suggested that this “Larva Hemerobii” might possibly belong to one or another of his several species of amber Hemerobiidae, but our knowledge of present-day hemerobiids rules this out as their larvae are now known to be non-trash carrying forms lacking tubercles and with unspecialized setae. The idea that hemerobiid larvae were trash carriers was wide-spread in the last century and for its time Hagen’s suggestion, though incorrect, was reasonable. I have seen several specimens of trash-carrying coleopterous larvae from several amber collections, and it might seem possible that Hagen misidentified one of these as a neuropteran. The mouthparts of these beetle larvae, however, are small and typically coleopterous, whereas Hagen describes the jaws of his larva as “... etwa noch einmal so long als der Kopf, säbelförmig mit scharfer Spitze, glatt und zahnlos, und zangenförmig gestalt wie bei Hemerobius und Chrysopa.” Various species of Ascalaphidae, Myrmeleontidae, and Nymphidae are also known to construct dorsal trash packets, but the larvae of none of these families really have globular, strongly constructed tubercles and, of course, all have toothed mandibles.

Hagen’s second larval specimen, designated by him simply as “Larva”, has been located in the portion of the Berendt collection now residing in the Museum of Humboldt University, Berlin. It is a member of the Psychopsidae, a family which at the time was unknown to Hagen in the larval stage. This specimen is redescribed below.

In addition to these specimens, larvae, apparently of a myrmeleontoid facies, were mentioned on a number of occasions in the early literature dealing with the Baltic amber (Berendt, 1830, 1845; Burmeister, 1832; Hope, 1834). Upon study, it emerges that only Berendt claimed to have actually seen such a specimen,
the notations of Burmeister and Hope being obviously secondary sources. Such a larva was, curiously, not mentioned by Hagen and, aside from the later bibliographic compilations of Scudder (1886, 1891), which do not note that the earlier references pertained to a larva, this larval type was not mentioned again until 1910. In that year Klebs, again without formal description, mentioned the existence of this type of larva in his extensive personal collection and, without reaching any final conclusions, discussed the opinions of several persons whom he had contacted as to whether it was an ascalaphid or a myrmeleontid. Klebs' collection was subsequently acquired by Albertus University, Königsberg (Andréé, 1937), while, as noted above, portions of Berendt's collection are now located in Berlin; however, a recent search of the remains of these collections has failed to produce any specimens on which these records might have been based. Both Handlirsch (1906, 1925) and Bachofen-Echt (1949), again apparently misled by the earlier references of the nineteenth century, have also dutifully recorded the existence of a myrmeleontid from the amber.5

Weidner (1958) has finally given a formal description of a myrmeleontoid larva and his specimen has been available to me for restudy. In addition, a magnificent specimen of an ascalaphid larva from the Haren Collection of the Museum of Comparative Zoology will also be described. As noted below, it is possible that this latter specimen is the one which was once owned by Klebs.

**FAMILY ASCALAPHIDAE SCHNEIDER, 1845**

The present distribution of this small family includes all major zoogeographic regions, although there is a pronounced concentration of the major taxa in the tropical and subtropical regions of the New and, particularly, the Old World. Two fossil ascalaphids, both adults, have been described from Tertiary deposits of Europe: *Ascalaphus proavus* Hagen (1858), from the brown coal near Linz, West Germany, and *A. edwardsi* Oustalet (1870) from Saint-
Fig. 2. *Neadelphus protae* n. sp. Dorsal aspect of holotype. The body, which is slightly curved in the specimen, is here depicted as straightened out.
Gerand le Puy, France. Both of these deposits are referred to Upper Oligocene horizons. Navás (1913) has erected a new genus for each of the fossil species, Borgia and Ricartus respectively, but this treatment, as well as their original assignment to Ascalaphus, has no present value as the fossils have never been restudied in the light of the modern classification of the family. Weidner (1958) described a larva from the Baltic amber which he felt was an ascalaphid. My study of this specimen had indicated that it is actually a nymphid and it is dealt with below under that family.

The collection of the Museum of Comparative Zoology contains a beautifully preserved small larva which is without question an ascalaphid. Because this specimen provides the earliest geological record for a member of this family, a formal description of the larva is presented here.

**Neadelphus** new genus

*(figs. 1-4)*

**Description.** Head capsule: quadrate, parallel-sided, with cor- date postero-lateral margins; surface generally smooth, raised bases of setae imparting only a slightly rugose texture to surface. Ocular tubercles large, prominent, approximately parallel-sided, each with the usual seven stemmata, six visible in dorsal view, the seventh located ventrally. Antennal tubercle very small. Jaws very long and slender, nearly straight for most of their length, with the three true teeth of the medial mandibular surface beyond the mid-point of the mandible. Labial palpi short, slender.

Body: prothorax approximately elliptical, with a bilateral pair of small, globular setigerous tubercles antero-laterally; prothoracic spiracles only slightly produced as a low cone, elliptical in outline. Meso- and metathorax broader and shorter, each with two elongate setigerous scoli on each lateral margin, the posterior member of each pair distinctly smaller than the anterior one. Legs as in fig. 4, the tarsi quite distinct from the tibiae on the pro- and mesothoracic segments, the metathoracic tarsi fused to their tibiae and showing no indication of a line of fusion.

Abdominal segments I-VIII with a bilateral pair of elongate, unflattened, setigerous scoli, the pairs located on segments I-VII

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6The specimen upon which these descriptions are based has previously been illustrated, as a color photograph, on p. 21, of the volume of the *Life Nature Library* entitled *The Insects* (1962. New York: Time Inc.).
subequal in length, the pair on segment VIII much shorter; with no trace of a ventral series of scoli. Only abdominal spiracles I-II visible in fossil, these located ventrally, directly beneath base of corresponding scolus (fig. 4, sp 1, sp 2). Posterior margin of ninth sternum lacking short, stout, "digging" setae.

Head and body covered with short black setae which are longer along the lateral margins of the head capsule, down the midline of the thorax and abdomen and, particularly, on the scoli; longer setae narrowly lanceolate in shape.

Type species, the following —

**Neadelphus protae** new species

*Description.* Setae along lateral margins of head only moderately elongated; central mandibular tooth the largest of the three, distinctly nearer the anterior tooth than the posterior tooth, the posterior tooth the smallest; right antenna with 14 sub-segments distal to the scape, the left antenna with 12.

Maximum width of head capsule immediately behind ocular areas — 1.40 mm. Body length from anterior-most clypeal margin to tip of IX abdominal segment — 3.6 mm.

Holotype: No. 5848, in the Haren Collection of Baltic amber of the Museum of Comparative Zoology. The name for this insect is derived from the Greek Phaëthon myth and translates literally as "Prota's new brother".

The specimen, undoubtedly a first-instar larva, is contained in a nearly square block of pale-yellow amber with all important taxonomic details easily visible. The block has been mounted on an oblong piece of glass by some previous owner. This glass bears a label with the printed notation "Coll. Dr. Klebs", to which someone has added in India ink "N27-." To this I have added the MCZ type number in blue ink and a new label with the designations "*Neadelphus protae* MacLeod" and "Holotype". It seems certain that this was the larva mentioned by Klebs in 1910, and it is possible that the references to a larva from the early nineteenth century also pertain to this specimen. The route by which it finally reached the Haren Collection is not known.

*Generic diagnosis and discussion.* The cordate posterior margins of the head capsule and large ocular tubercles with seven stemmata combined with the distinct fusion of the tibia and tarsus of the metathoracic leg show, without question, that this larva belongs to the Ascalaphidae.
From the time of Hagen's pioneering synthesis of 1873, a number of different types of larval ascalaphids have been described (summarized in MacLeod, 1964 and MS in preparation). A careful reading of this literature, however, reveals few cases in which larvae have been associated with their adults either through rearing or by hatching from eggs laid by a captive female. Most often these associations have been made by a loose, deductive process of elimination from a list of the species which are known as adults from the general area from which the larva was obtained. In view of the continuing poor state of our knowledge concerning the distribution of the species of the Ascalaphidae, this procedure is of no real value. Larval-adult associations which I believe to be reliable have only been achieved for the genera Ascalaphus, Helicomitus, Pseudoptynx, Suhpalacsa, and Ululodes, all of which belong to the subfamily Ascalaphinae. One might add to these the description by Froggatt (1902) of the rearing of a species now placed in the genus Acmonotus, but his unillustrated account is too general to be of any present use. In addition to the genera just noted, I can add to the list of associated forms the larvae of the genus Ascaloptynx, representing the subfamily Ascaloptyninae, which I have reared. For strictly nomenclatorial reasons, the larvae of the genera Neulatus
Figs. 4, 5. Larvae of Nymphidae and Ascalaphidae.

Fig. 4. *Neadelphus protae* n. sp. Ventral view of holotype showing position of first two abdominal spiracles (sp1, sp2) and leg segmentation, setae omitted.

Fig. 5. Larvae of *Pronymphes mengeanus* (Hagen), dorsal view, showing details of lateral scoli; setae of dorsal head capsule and of body proper omitted.
and *Sodirus*, which Navás (1913) erected for two unassociated larval forms, must also be noted here. Although long experience with Navás' taxonomic methods teaches one to anticipate novel procedures, I am hard put to understand this particular action since I believe that there is every reason to anticipate the discovery that these larvae produce adults which belong to long-established genera.

By comparison with these larvae and with a number of additional, unassociated forms available to me for study or described by previous workers, *Neadelphus* appears to differ by the following combination of characters: 1) the quadrate, parallel-sided head capsule; 2) the relatively narrow, produced jaws which are curved only near their tips and which bear the three mandibular teeth distal to the midpoint of the jaw; 3) the elongate, unflattened shape of the twelve pairs of lateral scoli which are unaccompanied by the development of small, additional anterior or ventral scoli or tubercles on the abdominal segments; 4) the ventral position of the first two pairs of abdominal spiracles (and presumably of the remaining six posterior pairs). Various larvae of living species show one or a few of these features, but none show this unique combination. With particular respect to the larval-based genera *Neulatus* and *Sodirus*, *Neadelphus* differs in the form of its prominent, parallel-sided ocular tubercles. These are small and distally narrowed in *Neulatus* and rather short and hemispherical in *Sodirus*. In addition, this latter genus has flattened scoli and a small tubercle on several of the abdominal segments, immediately anterior to the scolus, which are features lacking in *Neadelphus*.

The ventral location of all eight pairs of abdominal spiracles, which *Neadelphus* shares with several living genera including *Ululodes*, is presumably a generalized feature derived from the lateral position of these openings in unflattened ancestral nymphids. Such additional features of *Neadelphus* as the cylindrical shape of the scoli and the non-falcate development of the jaws, though also shared with some living forms, are probably additional examples of generalized character states. In contrast, the presence of only a dorsal series of abdominal scoli must be considered as a specialization from the nymphid double series (see below). Thus, in this respect, the Oligocene *Neadelphus* appears already specialized by comparison to several living larval forms which retain a trace of the ventral series of scoli either as short projections beneath the main dorsal series on abdominal segments I and II (as in an un-
associated larva which I have seen from Tanzania), or perhaps as the small tubercles anterior to the main scoli on abdominal segments III-VII (as in Ascaloptynx and several unassociated forms from Central and South America which I have studied). Other than these general observations, I do not believe that the inadequate state of our knowledge of the larvae of this family permits any more definite taxonomic assignment of N. protae at this time.

**FAMILY NYMPHIDAE Rambur, 1842**

This phylogenetically important family is presently confined to the Australian Region where a small number of species, classified into six genera, are known. The group is obviously of great antiquity as the very closely related Nymphitidae is known from Triassic strata of Russia (Martynova, 1949) and the species Mesonymphes hageni Carpenter from the Bavarian Jurassic is already so similar to the living forms that Adams (1958) concluded that it should be included in the Nymphidae itself.

The only apparent Tertiary record of the family has been an adult specimen described from the Baltic amber by Hagen (1856) as Nymphes mengeanus and redescribed as representing a new genus, Pronymphes, by Krüger (1923). This specimen, originally from Menge's collection, retained only the basal portion of the wings and was missing its abdomen. Krüger's reexamination of the specimen provided a few additional details and corrected several minor errors in Hagen's drawing of the wings. Krüger noted that the specimen was at that time contained in the collections of the Danzig Provincial Museum and, as it has proven impossible to locate, it may not have survived World War II. My redescriptions of the genus Pronymphes is, then, derived from the accounts of Hagen and Krüger and may require future corrections.

I will also here redescribe the larval specimen which Weidner (1958) has treated as a member of the Ascalaphidae. For reasons to be given shortly, I am convinced that the specimen is actually a nymphid, which I will tentatively refer to Pronymphes.

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1In my treatment of this family I am tentatively following the conclusions of Adams (1958) who presented important reasons against the separation of the Myiodactylidae from their close relatives in the Nymphidae. I have previously suggested (1964 and MS in preparation) that a fuller knowledge of the structure and ecology of the larvae of this group may force a reevaluation of this idea.

Bachofen-Echt (1949) notes seven species as having been described from the Baltic amber. I am unable to determine the origin of this error.
Pronymphes Krüger


**Description.** Wings narrowly elongate. Fore wing: costal space narrow, not abruptly widened at base, costal crossveins unforked; Rs+MA originating near base of wing, fused for a rather long distance before separation of MA; MP deeply forked at a level which is distinctly proximal to separation of MA from Rs, the two branches of MP running nearly parallel, the posterior branch separate from CuA; basal branches of Cu running close together and nearly parallel, CuA unforked in portion preserved, CuP with pectinate branches to hind margin of wing, lacking crossveins between branches basally, perhaps with a series of irregular crossveins distally.

Hind wing: costal space and crossveins as in fore wing; origin of Rs+MA much further distal than in fore wing; MP deeply forked to base of wing, MP2 with wide fork slightly distal to origin of Rs+MA; Cu very short, with only a few pectinate branches to hind margin of wing, unconnected by crossveins.

**Discussion.** The elongate, narrow form of the wings of *Pronymphes* is quite unlike the short, broad wings with abrupt basal dilations of the costal space to be found in the living genera *Myiodactylus* and *Nymphidrion* and I believe that these genera bear no close phylogenetic relationship to the fossil genus. There are such additional differences in venational details as the unforked MP in the fore wing of *Myiodactylus* to reinforce this conclusion. The wings of the species of *Osmylops*, though somewhat narrower in proportion to their width, are still distinctly broader than those of *Pronymphes* and the costal space of *Osmylops* also has a pronounced dilation near the base.

In terms of their overall similarity in wing shape and venation, *Pronymphes* is obviously close to the living genera *Nymphes*, *Australonymphes*, and, particularly, *Nesydrion*. Unfortunately, attempts to infer the probable details of the interesting phylogenetic interrelationship of these four genera, from which I believe their phenetic similarities derive, will be somewhat frustrated until specimens showing the complete wings of *Pronymphes* are discovered. It is especially critical to learn the detailed structure of CuA in the fore wing and, particularly, whether this vein was forked or not. Certain similarities
Fig. 6. Larva of *Pronymphes mengeanus* (Hagen), dorsal view.
and differences between Pronymphes and these living genera are, however, obvious.

Thus, in the fore wing, the rather far distal separation of MA from Rs is a feature common to all of these genera, while Pronymphes shares the deep, basal fork of MP in this wing with both Nymphes and Nesydron. In both Nymphes and some of the species of Nesydron this forking is distal to the separation of MA from Rs but in other species of Nesydron the fork of MA is as far proximal as it is in Pronymphes. Austronymphes differs from the other three genera in having MP unforked in the fore wing. The three living genera show various stages in the evolution of the prominent fork of CuA in the fore wing, which is characteristic of all the higher myrmeleontoid families, with this fork nearly marginal in Nesydron, just proximal to the middle of the wing in Austronymphes and far proximal to mid wing in Nymphes where it is closer to the base than the fork of MP or the separation of MA from Rs. The exact development of this important venational feature cannot yet be determined in Pronymphes, although it is obvious that if a fork of CuA was present it certainly was considerably more distal than in Nymphes and, probably, Austronymphes. The rather distal point of origin of Rs+MA in the hind wing of Pronymphes is quite like the condition of this vein in Nesydron and this feature contrasts sharply with the distinctly more basal origin of this vein in all other living genera of the family. Finally, in the weak, submarginal development of the fork of MP₂ in the hind wing, Pronymphes is similar to the condition found in Austronymphes and Nesydron and quite distinct from Nymphes where a deep fork is developed which mimics the appearance of the fork of CuA of the fore wing.

Krüger, who was also impressed with the similarity of Pronymphes and Nesydron, felt that these genera could be differentiated by the fact that the fork of CuA of the fore wing is at about the level of the separation of MA from Rs in Nesydron, while in Pronymphes no such fork in CuA is developed at this level. The fore wing of Pronymphes is preserved for only a very short distance beyond this region and if, with the discovery of additional specimens, a fork in CuA is found to be present just distal to the region preserved in Hagen’s specimen, I doubt if a generic distinction will be possible. Krüger suggested that there were additional differences to be found in the hind wings of Pronymphes and Nesydron, although he did not stipulate what these might be. I am unable to discover any important differences in the hind wings of these two genera. It will
Fig. 7. Detail of left jaw of larva of ?Pronymphes mengeanus (Hagen) showing the small setae at the tips of the three proximal mandibular teeth and the globular tips of additional setae. Setae elsewhere on the body proper have these same modified tips. (Photographed with a Zeiss compound microscope using Nomarski interference contrast optics.)

be interesting to see if the larvae of the species of Nesydrion, when they are discovered, will throw any light on this question when they are compared to the presumptive larva of Pronymphes described below.

**Pronymphes mengeanus** (Hagen)


?*Pronymphes* sp. (Larva)

(figs. 5-7)


*Description.* Head: somewhat quadrate, with broadly rounded occipital margins which are not, however, cordate; surface some-
what rugose; clypeal margin with two bilateral pairs of setae with large, blunt bases. Ocular area not borne on raised tubercle. Antenna arising from small antennal tubercle; scape large, prominent, dilated distally, diameter much larger than remainder of antenna. Jaws longer than head, curving inwardly for distal one-third of length; with four apparent teeth on medial surfaces of each mandible, the three proximal teeth with a seta at tip (fig. 7). Undersurface of head with the usual myrmeleontoid specializations of maxillae and labium (MacLeod, 1964). Anterior margin of postlabium very broad; divided pieces of prelabium (apparent basal palpimere) subequal in length to basal palpimere; second palpimere 3/4 length of basal palpimere, distal palpimere lanceolate, about as long as basal palpimere. Maximum head width 0.65 mm.

Body: thorax with an elongate, finger-like scolus at sides of meso- and metathorax. All legs with tibia and tarsus unfused. Abdominal segments I-VII each with two lateral scoli on each side, placed to form a dorsal series along edges of terga and a ventral series along edges of sterna; scoli of dorsal series shortest anteriorly, gradually increasing in length posteriorly; those of ventral series longest anteriorly, gradually decreasing in length posteriorly (fig. 5). Scoli of both thorax and abdomen simple tubular projections, not pedunculate.

Both head and body, including scoli, clothed with smooth-sided setae of varying lengths, many with globular tips (figs. 5, 7).

Judging from its size, the specimen is almost certainly in its first larval stadium. The material studied comprises a thin, triangular piece of clear yellow amber, numbered “25”, from the collection of the Geologisches Staatsinstitut of Hamburg, Germany. The piece also contains a thysanuran and a small nematocerous dipteran.

Discussion. The few known larvae of the living species of Nymphidae have been poorly described and as a result the exact features by which they differ from those of other families of the Myrmeleontoidea have remained rather vague. Tillyard (1926) figured a form identified as Osmylops pallidus Banks which he may have reared and this illustration has been widely copied. Although the larva of Nymphes myrmeleonoides Leach has apparently been known to several Australian entomologists (Froggatt, 1902; Tillyard, 1926; Gallard, 1935) it has never been properly described.8

8Froggatt has given a poor figure of the larva of what is probably this species as fig. 36 in his book Australian Insects (1907) under the misidentification of Porismus strigatus, a member of the Osmylidae.
In connection with a general study of the larvae of the Neuroptera (MacLeod, 1964), I have examined the known larvae of the Nymphidae, including authentic material of *Nymphes* hatched from eggs from a captive female, and larvae identified as *Osmylops* and *Nymphidrion* from Tillyard's collection. The results of this more general study are now in preparation for publication, but the relevant information relating to the unique features of larval nymphids will be noted here.

Nymphid and nemopterid larvae differ from other members of the Myrmeleontoidea in the lack of any fusion of the tibia and tarsus in any of their legs. In contrast, other myrmeleontoids have these segments fused in the metathoracic leg. In addition to a single scolus on each side of the meso- and metathorax, nymphids characteristically have two elongate lateral scoli on each side of the first seven abdominal segments, either arranged above each other as in the larva described here and in *Nymphes*, or else with these tubercles placed one behind the other as in the very flattened type of larva figured by Tillyard as *Osmylops*. In contrast, wherever elongate scoli are developed on the abdomen in the larvae of the Ascalaphidae and Myrmeleontidae these are present dorsally on segments I-VIII (figs. 1, 2) and if any portion of a ventral series is present, as they are in a few ascalaphids, these are confined to the first two abdominal segments. As noted above, in a few ascalaphid larvae from the New World there is, in addition to the usual scoli on the first eight abdominal segments, a very small setigerous tubercle on segments III-VII just anterior to the scolus of the segment. The known larvae of the Nemopteridae lack any real traces of scoli.

The larvae of the Ascalaphidae, Stilbopterygidae, and most Myrmeleontidae also differ from those of the Nymphidae in the shape of the ocular area formed by the aggregated lateral stemmata. This area is produced into a distinctly raised ocular tubercle (fig. 3, OT) in these three families (secondarily reduced only in some specialized myrmeleontids), rather than having the stemmata organized as a nearly sessile lateral group as occurs in the Nymphidae. With respect to this feature, the larvae of the Nemopteridae are similar to nymphids.

Nymphid larvae have been presumed to differ from those of the

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*Actually most myrmeleontids (and Stilbopteryx) have only setigerous swellings on the abdomen and elongate scoli do not occur; however, a few generalized Myrmeleontidae have moderately developed scoli and, with their somewhat quadrate heads, they look surprisingly like ascalaphids.*
Myrmeleontidae and Ascalaphidae in their possession of a single mandibular tooth, as opposed to three or four in these other two families. All ascalaphid larvae with which I am familiar do have three mandibular teeth, but the number varies from one to four in the Myrmeleontidae (MacLeod, 1964). In addition, this generalization is now further weakened by the very large setal bases along the inner surface of the mandible in the larva of ?Pronymphes sp. which approximate true teeth very closely. In my opinion the size of these bases in this fossil larva, combined with Baba's (1953) experimental demonstration that such enlarged setal bases are the probable precursors of the true mandibular teeth, robs this character of whatever residual value it might have had in identifying nymphid larvae. Very likely the number of teeth in the larvae of this family has varied during its evolutionary history.

The amber larva is quite similar to the larva of the living Nymphes myrmeleonoides in such important regards as its unspecialized body shape, in the somewhat rugose texture of the cuticle of the head, in the presence of distinct dorsal and ventral rows of lateral scoli on the abdomen, and in the vestiture of setae with globular tips. Differences, probably of generic importance, occur in the details of the lateral abdominal scoli, which are longer and, in the dorsal series, distinctly pedunculate in N. myrmeleonoides. In addition, N. myrmeleonoides shows no traces of tooth-like, enlarged setal bases along the medial mandibular surface.

FAMILY PSYCHOPSIDAE HANDLIRSCH, 1906

Of the living families of Neuroptera, the family Psychopsidae is among the earliest to appear in the fossil record, since species, apparently little different from some recent forms, are known from Mesozoic horizons as old as the Upper Triassic of Australia (Tillyard, 1922; Riek, 1956) and the Jurassic of Russia (Martynova, 1949). Apparently related species, presently classified as the families Kalligrammatidae, Osmylopsychopsidae, and Prohemerobiidae, are also known from Triassic and Jurassic strata and there appears to have been a rather extensive radiation of this group in the early Mesozoic from which only the approximately two dozen species of living psychopsids remain as descendants. Other than Krüger's (1923) description of a species from the Baltic amber, Tertiary records of this family have seemed to be lacking. Carpenter (1943b), however, concluded that Cockerell's species Polystoechotes piperatus (Cockerell, 1908) from the Oligocene (Florissant) of Colorado is probably a psychopsid
and my recent restudy of this specimen has substantiated this view, so a rather wide Tertiary distribution of these insects is indicated.

At the present time the family is restricted to southern Africa, Asia (Burma, China, Formosa), and Australia. In the most recent revision, Kimmins (1939) treated the living species as representing eight genera which are distinguished principally on the basis of rather small differences in such details as the pattern of anastomoses between M and Cu in the fore wing, the pattern of maculation of the wings, and in the relative widths of the fore and hind wings.

In the Baltic amber the family has, until now, been known only from the single specimen described as *Propsychopsis helmi* by Krüger (1923), although as noted above one of Hagen’s larval specimens turns out to have been a psychopsid. A total of six specimens, including two larvae, is available for the present study. The four adults seem to fit Krüger’s description of *Propsychopsis* and although these specimens show a number of similarities to several living genera, the differences between the living and fossil forms are sufficient to retain Krüger’s generic name. I shall here redescribe, and somewhat redefine, *Propsychopsis* based on Krüger’s account and on the new material now available.

*Propsychopsis* Krüger

(figs. 8-11)


Description. Head lacking ocelli, but vertex with three raised, wart-like protuberances bearing long setae, the median protuberance smaller than the lateral two; head with a trace of a median sulcus posteriorly. Pronotum about as long as broad, anterior margin nearly straight, rounded at lateral corners. Male: prothoracic tibiae not swollen; ectoprocts posteriorly produced (figs. 10, 11); mediuncus elongate. Female: ninth gonocoxites with a stylus.

Fore wing (figs. 8, 9): 30-40 costal veinlets, mostly single forked, a few twice or unforked. Rs with 12-18 branches, mostly unforked before marginal twiggings. Basal piece of MA (fig. 8, b) oblique, fusing with stem of R for a very short distance and separating from stem of Rs near its base; a nygma present in small cell basad of basal piece of MA (fig. 8, n). MP (fig. 8, MP) with basal fork
Fig. 8. Left fore wing (drawn as right fore wing) of paratype ♀ of *Propsychopsis lapicidae* n. sp.

Abbreviations: 1A, 2A, 3A — 1st, 2nd, 3rd anal veins; b — basal free piece of MA; CuA, CuP — anterior, posterior cubitus; MA, MP — anterior, posterior median; n — nygma; R₁ — anterior branch of radius.

Far proximal and with no additional forkings before vicinity of wing margin, the two main forks connected to each other only by cross veins, the posterior fork not touching or anastomosing with CuA. Cu forking very near wing base; CuA with several series of dichotomous forkings slightly proximal to marginal forks; CuP with several pectinate forkings nearer wing base. 1A well developed, with a number of pectinate branchings; 2A and 3A smaller, with fewer branches. Costal space with an interrupted series of gradate veins; three series of gradate veins elsewhere on wing, the outer series somewhat interrupted or nearly complete; elsewhere only a few irregularly spaced cross veins between Sc and R₁, between R₁ and the axis of Rs, and between the branches of MP and Cu. Pattern consisting of a series of distinct, separated dark spots and with a paler, more diffuse series of separate and fusing irrorations scattered uniformly over wing; transverse fasciate patterns absent.

Hind wing: slightly fewer costal veinlets than in fore wing,
mostly once forked; 8-12 branches to Rs, unforked before terminal branchings at margin; free basal piece of MA longitudinal but not sinuate, not fusing with R but connected to base of Rs by a short cross vein; MP forking somewhat more distally than in fore wing, at about the level of first forking of Rs beyond cross vein to MA, without further branches before forks at margin; Cu forked very near wing base, neither CuA nor CuP with further forks until just before margin. Cross veins present only as an interrupted costal gradate series and two somewhat interrupted gradate series behind vena triplica. Wing membrane nearly clear, with a very faint irrorated pattern, lacking the darker spotings of fore wing and without any trace of a circular dark mark distally behind the terminal anastomosis of the vena triplica.

Discussion. The species of Propsychopsis possess a number of features which, by comparison to the Mesozoic fossils and to the magnificent living Megapsychops illedgi (Froggatt)11 of Australia, I judge to be somewhat generalized. These include the retention of all three raised vertex protuberances, the lack of any anastomoses between the branches of MP or between the posterior branch of MP and CuA in the fore wing, the longitudinal orientation of the free basal piece of MA in the hind wing, and in the relatively broad hind wing. In this combination of features Propsychopsis is unique.

Various living genera retain one or more of these generalized character states, and I would judge that Propsychopsis is only slightly more unspecialized than several of these living groups and is clearly more specialized than Megapsychops. Thus Silveira possesses the full complement of three vertex tubercles and the two lateral tubercles are retained in Balmes, Cabralis, and Notopsychops. In the strictly Australian Magallanes and Psychopsis, at most only a small vestige of these structures remains and in Wernzia they are totally absent. In the fore wing, some degree of fusion between the branches of MP or between MP and CuA occurs in all living genera of the family (including Megapsychops) with the exception of Balmes, Magallanes, and Wernzia, and in this last genus MP2 and CuA usually touch at a point and in some specimens are actually fused for a short distance. With respect to the orientation of the basal piece of MA in the hind wing, only Notopsychops (and

11The ensuing discussion is derived from an examination of species of all living genera with the exception of Megapsychops. My knowledge of this insect is based on the account of Tillyard (1918a).
Figs. 9-11. Adults of Propychopsis spp.

Fig. 9. Paratype ♀ (MCZ) of Propychopsis lapicidae n. sp. illustrating venation and maculation pattern of fore wing.

Fig. 10. Holotype ♂ (Berlin Mus.) of Propychopsis lapicidae n. sp. showing detail of ectoprocts, latero-dorsal view.

Fig. 11. Holotype ♂ (Berlin Mus.) of Propychopsis hageni n. sp. showing detail of abdomen and ectoprocts, latero-ventral view.
possibly *Megapsychops*, Tillyard's account does not mention or figure this vein) retains a longitudinal orientation of this vein although in *Magallanes*, *Silveira*, and *Wernzia* it is distinctly oblique in its placement. In *Psychopsis* the transverse orientation of the basal piece is so pronounced that it resembles a cross vein and in *Balmes* it is absent altogether. Finally, a number of living forms retain relatively broad hind wings, although a reduction in width has occurred in the species of *Silveira* and in the Australian *Balmes gallardi* Tillyard.

Contrary to Krüger's belief in a close similarity between *Propyschopsis* and *Psychopsis*, I believe that the species of this latter genus are the quite specialized products of a long, isolated evolutionary history of their own and are only distantly related to the living species outside of Australia and to *Propyschopsis*. In addition to the specialized structural features of *Psychopsis* noted above, the complex, colorful, and very beautiful transverse fasciate patterns of the fore wing and the large dark spot behind the terminal anastomosis of the vena triplica of the hind wing of these species should also be noted. Both of these features are shared with *Megapsychops* and the hind-wing spot also occurs in *Magallanes* and *Wernzia*. These patterns are quite unlike the mottled, splotched, or irrorated wing patterns of the living species outside of the Australian Region and of *Propyschopsis*.

In its pattern, small size, unspecialized condition of MP and CuA in the fore wing and in its broad hind wing, *Propyschopsis* approaches the Asiatic species of *Balmes* very closely, although, as I have noted, *Balmes* shows the specializations of the loss of the median vertex tubercle and the base of MA in the hind wing neither of which are found in *Propyschopsis*. The African genera *Noto-psychops* and *Silveira* show the more generalized state of these two features, but these genera have such additional specializations as anastomoses between the branches of MP (or between MP2 and CuA in *Noto-psychops*) and, in *Silveira*, a reduction in the width of the hind wing. Barring the discovery of additional fossils or annexant living forms, I do not believe that a more precise conclusion as to the phylogenetic relationship between *Propyschopsis* and the living species is now possible.

The four adult specimens now before me clearly comprise two species. I am, however, unable to identify either of these as Krüger's *P. helmi* from his very general description and, as I have been unable to locate his type specimen for restudy, I am describing each
of these as new. Following these descriptions I will present a general account of the two larval specimens.

**Propsychopsis helmi** Krüger

*Propsychopsis helmi* Krüger, 1923, Stett. Ent. Zeit. 84: 84-85. Type specimen stated to be in the Danzig Museum, not examined.

Discussion. Krüger mentions the presence of about 40 costal cross veins and about 25 cross veins in each of the cells between Sc and R1 and between R1 and Rs. All of these counts are higher than in the specimens now at hand and it is possible that these characters may provide the means of subsequently identifying *P. helmi* when additional material is discovered. These particular venational features, however, are quite variable and new material could also show these characters to have no taxonomic importance in *Propsychopsis*. Krüger made no mention of any wing pattern in his description, but as he seldom mentioned any features other than the venation in his treatment of any species, living or fossil, his omission in this case is probably of no significance.

**Propsychopsis lapicidae** n. sp.

*(figs. 8-10)*

Description. Antenna with about 30 flagellomeres distal to pedicel. Fore wing with 33-35 costals proximal to end of vena triplica; 16-17 branches to Rs (not including MA); terminal (outer) gradate series complete; with a pattern (fig. 9) of two large spots along length of Cu and a third across MP distally, with additional similar-sized dark spots in the middle of the discal gradate series and along vena triplica, elsewhere smaller, paler spots and blotches. Hind wing with 10-11 branches to Rs, two gradate series; membrane patterned with faint irrorations. Male genitalia (fig. 10) with the ectoprocts produced posteriorly, presenting a rounded triangular outline in lateral view; mediuncus (arcessus of Tjeder, 1960) elongate, parallel sided basally, then tapering to a long triangular point.

Holotype, male: right fore wing with 33 costal veinlets, 17 branches to Rs; length approximately 13 mm (tip missing); right hind wing with 10 branches to Rs. The specimen is oriented with all four wings spread in a thin piece of yellow amber which, except for one rounded corner, is rectangular in shape. This insect was apparently subject to some decay before complete entombment, as the ventral half of the head and thorax, including the legs, are missing. In addition much of the tip of the left fore wing is gone.

Fig. 12. Detail of head, dorsal view, of Berlin larval psychopsid.

Fig. 13. Berlin larval psychopsid.

Fig. 14. MCZ larval psychopsid. The small projections visible at the sides of the thorax and abdomen are dolichasters.
along with a small piece of the right fore wing tip. The type is contained in the amber collection of the Institut für Paläontologie und Museum der Humboldt Universität, Berlin. The specimen is in mineral oil in a vial along with its original labels reading “Fam. Megaloptera” and “Hemero bius resinatus” in black ink and “B-8” in blue ink to which I have added my determination label. Paratypes comprise one male and one female in the collection of the Museum of Comparative Zoology.

This species is named in honor of Professor F. M. Carpenter of Harvard University, whose concern and efforts, extending over many years, are primarily responsible for the development of the collection of fossil insects of the Museum of Comparative Zoology.

**Propyschopsis hageni** n. sp. *(fig. II)*

*Description.* 29 flagellomeres distal to pedicel. Fore wing with 28 costals proximal to end of vena triplica; 13 branches to Rs (not including MA); terminal (outer) gradate series interrupted; pattern indistinct, but consisting at least of faint irrorations. Hind wing indistinct. Fore wing length — 12 mm. Male *(fig. II)*: 9th tergite with a pronounced lobe postero-ventrally; ectoprocts very narrowed posteriorly and curving ventro-medially; mediuncus with a broad trapezoidal base from which the remaining portion extends as an elongate ligulate structure with a blunt, triangular tip.

Holotype, male: from the amber collection of the Institut für Paläontologie und Museum der Humboldt Universität, Berlin. The type specimen is contained in a flat block of dark orange amber and is preserved in mineral oil along with labels reading “Fam. Megaloptera” and “Hemero bius resinous” in black ink and “B-7” in blue ink along with my determination label. I have seen no additional specimens of this species.

This species is named in honor of Hermann Hagen whose thread of life is so richly interwoven with the Neuroptera, the Baltic amber, and the Museum of Comparative Zoology.

*Discussion.* *P. hageni* differs strikingly from *P. lapicidae* in the form of the ectoprocts which in lateral view are quite narrow with a distinct medioventral curvature in *P. hageni* in contrast to their broader, rounded triangular outline in *P. lapicidae*. The mediunci of the two species are also quite distinct, the tip having a ligulate shape, in dorsal view, in *P. hageni* rather than the produced, triangular shape seen in *P. lapicidae*. Comparable differences between
the male genitalia of closely related species of living psychopsids occur in Silveira judging from Tjeder's (1960) revision of these species. It is possible that additional material may show other important differences in such non-sexual features as the fore wing pattern and may reveal whether the apparent difference in the degree of development of the terminal gradate series of the fore wing is real or not.

The two psychopsid larvae are rather poorly preserved and show no important differences from each other. As noted above, Hagen's specimen is now contained in the Museum of Humboldt University, Berlin, while the second specimen is from the collection of the Museum of Comparative Zoology. As our knowledge of the taxonomy of the larvae of this family is so scanty, being confined to the brief accounts of Froggatt (1902, 1907), Gallard (1914, 1922, 1923), and Tillyard's more extensive study of 1918b, there is no real reason for referring the amber larvae to the amber genus, and I do so here only as a bookkeeping measure.

?Proopsychopsis sp. (Larvae)
(figs. 12-14)


Description. Head capsule: nearly quadrate in dorsal view, widest at about level of antennal bases, narrowing somewhat anteriorly to jaw bases and much more gradually posteriorly to distinct occipital corners, beyond occipital corners head abruptly constricted to form short tubular section anterior to cervix; anterior margin with a distinct, triangular labrum-like projection between jaw bases; ventral surface (best seen in Berlin specimen) with sclerites of maxillary bases and labium small, confined to anterior portion of head capsule; surface of head capsule covered with small papillae, imparting a rugose texture to cuticle. Appendages: antennae slender, with flagellomeres much longer than wide, length of antennae about equal to jaws; jaws smoothly curved throughout length, straight-line length from base to tip slightly shorter than length of head capsule; labial palpi short, slender, segmentation indistinct but with at least three palpimeres.

Body: widest at methathorax (approximately twice as wide as head in Berlin specimen, narrower in MCZ specimen), parallel
sided for abdominal segments I-IV then narrowing gradually to tip of abdomen; prothorax much narrower than remainder of thorax, somewhat trapezoidal in shape, widest posteriorly, dorsal surface with dolichasterine setae which are somewhat more slender than elsewhere on body (best seen in MCZ specimen); meso- and metaterga with small, triangular, smooth latero-dorsal sclerites (pinacula of Tillyard, 1918b) above corresponding coxae, each bearing a few small dolichasters, these sclerites equal sized on the two segments (not visible in Berlin specimen); body surface posterior to prothorax (and ventrally on prothorax) covered with numerous small, broad, cup-shaped dolichasters; legs rather short, stout (tips missing in Berlin specimen).

Head width — 0.98 mm (both specimens); head length (base of labral extension to level of occipital corner) — 1.0 mm (both specimens); total length from tip of closed jaws to tip of abdomen — 6.1 mm (MCZ specimen).

Discussion. While recognizing his larva as a neuropteran, Hagen was understandably perplexed as to its relationships and after rejecting any association with the Coniopterygidae, Hemerobiidae, and Sisyridae, he left open the possibility that it might be a nymphid or perhaps an unusual osmylid. Larvae of living species of the Psychopsidae were not described until the early years of this century, so Hagen’s perplexity is quite understandable.

Hagen indicated some concern over the apparent shortness of the legs of his specimen and suggested the possibility that they had been mutilated. The amber piece containing his specimen was evidently once a faceted bead as it has a nearly circular outline and has been pierced through the center. In addition, traces of facets are still visible around its circumference. The original bead was not a single unit, however, as two separate pieces of amber have been joined together and, probably in preparation for this joining, the piece containing the larva was planed down to the point where portions of the legs and the ventral surface of the body were removed. The composite bead itself has been subsequently ground down, probably so as to better examine the larva, and the double piece now has the form of a round flat disc. The portions of the legs remaining in Hagen’s specimen, and the intact legs of the MCZ specimen, show that the legs of these amber larvae are normally proportioned for psychopsids.

Judging from the size of the amber specimens they are both second-instar larvae. They differ in no important regard from a
series of unidentified, field-collected larvae of one or more living Australian species which I have studied, and it would be difficult to separate the amber specimens from these living forms. Although the mature-sized larvae of my Australian series have heads which are distinctly longer than broad, the smaller larvae of this series, presumably second-instar, have more quadrate head capsules like the two amber specimens. Whether this is a feature of taxonomic importance or is simply a reflection of a pattern of ontogenetic allometry occurring in the Psychopsidae cannot now be known.

Tillyard (1918b) reports that the larvae of Australian forms are to be found in the deep crevices of the bark of living trees of a number of species and that they are especially frequent in the vicinity of sap flows where they presumably seize, as prey, other insects visiting the fermenting sap. Similar habits in the larvae of the amber species should have made them especially liable to entrapment in the resin which produced the amber and this perhaps accounts for the capture of the larvae discussed here.

Recent classifications of the families of living Neuroptera have usually treated the Psychopsidae as belonging to the same superfamily as the Hemerobiidae (Withycombe, 1925; Tillyard, 1926; Handlirsch, 1936; Killington, 1936; Riek, 1970), although Withycombe and Riek realized that such a classification of this odd family was an oversimplification. The Psychopsidae and its close Mesozoic relatives have also been placed in the Hemerobioida by Martynova (1962) in her classification of the fossil forms. In Tillyard's final statement on the question (1932) he considered the Psychopsidae to comprise a very specialized side branch of their own.

I have elsewhere (1964 and MS in preparation) noted that the larvae of the Psychopsidae are structurally of the same, unique form as are those of the families of the Myrmeleontoidea, complete to such details as the very unusual specializations of the tentorium, maxillae, and labium. It would seem that these specializations rule out any close evolutionary relationship of the Hemerobiidae, or its true allies, to the Psychopsidae. Future attempts to trace the origins of the Psychopsidae and its Mesozoic relatives, or the origins of such phylogenetically important myrmeleontoids as the Nymphidae, must take these distinctive features of larval morphology into account.

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