The Skeletal Anatomy of the Heads of Adult Mnesarchaeidae and Neopseustidae (Lep., Dacnonypha).

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The lepidopterous suborder Dacnonypha Hinton, 1946 (superfamily Eriocranoidea auct.) is generally recognized as being a group of primary importance for the understanding of the early evolution of the order. However, the literature contains relatively few facts about the anatomy of the families constituting the suborder. A somewhat detailed description of the head and the alimentary canal of the family Eriocraniidae (of which fresh material may readily be obtained) has just been completed (Kristensen, 1968). The condition of the scanty material existing of the remaining families, viz., the Agathiphagidae, the Mnesarchaeidae and the Neopseustidae, only permits examination of the skeleton. The head of Agathiphagidae was described by Dumbleton (1952, supplementary details in Kristensen, 1967) and no further information on this family seems to be available at present. The mouthparts of Mnesarchaeidae were described by Tillyard (1923); this description, however, is not very detailed and partly incorrect. The Neopseustidae are stated by Hering (1925) to have distinct but unfunctional mandibles and a short proboscis, but otherwise nothing is known about their head structure. New information on the two last-mentioned families is thus of obvious interest.

Material and methods.

One of the two specimens of *Neopseustis meyricki* Hering preserved in the British Museum (Nat. Hist.), one specimen of *Mnesarchaea loxoscia* Meyrick and one specimen of *M. hamadelpha* Meyrick were placed at the author's disposal by Mr. P. E. S. Whalley whose generous help is hereby gratefully acknowledged. The heads were macerated in KOH, dissected, cleared and finally mounted in balsam. It should be stressed that even for the study of details in the skeleton, e.g., the relation between the head-capsule and the stipes, examination and sectioning of fresh material is needed.

Mnesarchaea loxoscia and M. hamadelpha.

The head-capsule (Figs. 1—2). The head is hypognathous, the anterior surface arched, the posterior surface flattened. The contour of the head-capsule is dorsally quite even. Subgenal processes are but slightly developed.

The compound eyes are relatively large; the ratio between their diameter and height of head-capsule is about 1 : 1.6. Ocelli are lacking.

The antennal sockets are situated between the eyes and are connected by a weak transverse sulcus. In M. loxoscia there is a weakly sclerotized line immediately above this sulcus. The scapus articulates with the ordinary ventral condyle and with a dorsal projection from the head-capsule.

Apart from the above-mentioned interantennal sulcus the head is entirely devoid of distinct sulci, and only vestiges of the temporal sulci from the upper corners of the occipital foramen may be recognized. The occipital condyli are bent posteriorly. The frontal and dorsal portions of the head are densely covered by upright narrow scales.

The endoskeleton. Occipital sclerites are well developed. The anterior tentorial arms are strongly sclerotized throughout the head. Posteriorly they fuse with the inner side of the occipital condyli, thus no posterior arms are present. Dorsal arms are well developed, arising with a broad basis from the anterior arm (Fig. 3). They are not attached to the head-wall. Posteromedially on the corporotentorium is a short process.

The antennae. The antennae are filiform, covered with narrow brown scales. The scapus is of moderate size, thickest at mid-length; dorsally on its base is a small hair-plate. There is a triangular sclerite in the membrane between scapus and pedicellus.

The mouthparts. The labrum is much reduced and not distinctly demarcated form the clypeus. Its epipharyngeal surface is furnished with a single sensillum basiconicum in each side (Fig. 13).



Figs. 1—2. *Mnesarchaea loxoscia*, head: 1, anterior view, left antenna removed; 2, posterior view. Hairs and scales omitted. Alveoles of cranial scale-groups indicated. Scale 0,3 mm. (Lettering, see p. 149).



Fig. 3. *Mnesarchaea hamadelpha*, anterior (aa) and dorsal (da) tentorial arm. Scale 0,1 mm.

The mandibles, stated by Tillyard (1923) to be absent, are present as small, rounded, inwardly tapering lobes without articulations (Fig. 12).

The maxillae are inserted in a membranous area ventrad of the genae (Fig. 2). The cardo is an arched sclerite, having the lateral and distal margins thickened. The stipes is tubular, weakly sclerotized except for the ventromedial area. The maxillary palp, as described by Tillyard (1923), is short, 3-segmented and covered with narrow scales. The two galeae together form a proboscis about 1.3 mm long. The wall of the medial food-groove is made from a series of plates each having a fine vertical striation. The anterior edge of each plate extends ventrally as an anteriorlyinwardly directed process. These processes constitute the ventral linking mechanism. The dorsal linking is brought about through narrow anteriorly-inwardly directed processes from the dorsal galea-wall. This structure of the food-canal closely resembles that of Eriocraniidae (see Kristensen, 1968), which only differs in having two or three ventral projections from each plate. Externally the galea is furnished with numerous microtrichia and seta-like sensilla (presumably chemoreceptors). No lacinia-vestiges could be identified.

The labium (Fig. 2) has only a narrow prementum with the palp distinctly developed. On the postmental region is a large Eltringham's organ, separated from the prementum by a membranous area. The prementum extends laterally and is shaped like a palp segment. The palp is 3-segmented, very densely covered with narrow scales. The apical segment is without sensory in-

vagination, but with a small group of presumably chemoreceptiveseta-like sensilla.

The hypopharynx forms a short blunt projection in front of the prementum; laterally it is connected to the head-capsule through a hypostomal bridge (Fig. 13). Its dorsal surface is continued into the head as a triangular sclerite (tapering inwardly) forming the floor of the sucking pump. This sclerite is furnished with several sensilla. The salivary opening, as far as could be ascertained from the material available, is located apically on the hypopharynx.

Nepseustis meyricki.

The head-capsule (Figs. 4—6). The head is hypognathous, the anterior surface somewhat arched, the posterior surface flattened. Dorsally the head-capsule has a medial impression. Lateroventrally it extends as very well-developed subgenal processes.

The compound eyes are relatively large; the ratio between their vertical diameter and height of head-capsule (subgenal process not included) being about 1 : 1.4. Ocelli are lacking.

The antennal sockets are situated adjacent to the anterodorsal corners of the eyes. Along the margin of the wide articular membrane the head-wall is strengthened by a thickened cuticular rim. Anteriorly this rim is produced into a condyle with which the scapus articulates. The antennal sockets are connected by a transfrontal sulcus.

Immediately ventrad of the antennal bases is a pair of arched Eltringham's organs bearing ordinary setae and raised, narrow scales. A pair of similar, but smaller organs occurs behind the transfrontal sulcus.

The anterior tentorial pits are located ventrad of the firstmentioned Eltringham's organs.

The frontoclypeus is laterally bounded by the large Eltringham's organs and the laterofacial sulci extending from the labral corners to the anterior tentorial pits. Ventrally the frontoclypeus bulges somewhat over the clypeolabral suture. No obvious boundary between clypeus and frons is present.

The occipital sulcus is well developed, dorsally it curves anteriorly. It gives off two branches which extend to the compound eye; the anterior is interpreted as the continuation of the laterofacial sulcus, the posterior is termed the postfrontal sulcus. A few N. P. Kristensen



Entomologiske Meddelelser 36 (1968)



Figs. 4—6. *Neopseustis meyricki*, head: 4, anterior view; 5, posterior view; 6, lateral view. Most hairs, sensilla and scales omitted. Alveoles on Eltringham's organs indicated. Scale 1 mm. (Lettering, see p. 149).

Ent. Medd. 36

143



Fig. 7. Neopseustis meyricki, anterior (aa) and dorsal (da) tentorial arm. Scale 0,5 mm.

rows of narrow, brown scales are present in front of the occipital sulcus on the vertex and on the genae behind the eyes; on the vertex broad silvery white scales are present as well. The occiput is naked.

The postoccipital sulcus is distinct; dorsolaterally it is connected with the occipital sulcus by a temporal sulcus. The occipital condyli are well developed and point inward. Immediately ventrad of the occipital condyli are the posterior tentorial invaginations. The occipital foramen is ventrally bounded by a hypostomal bridge. The subgenal sulcus is distinct only on the posterior surface of the head and near the labral corners where it forms a pair of small blunt projections (possibly the remnants of the anterior mandibular articulations). The subgenal processes are heavily sclerotized.

A distinct mid-cranial sulcus is present dorsally, extending from the foramen to the occipital sulcus.

The endoskeleton. Ocular sclerites are well developed. The anterior tentorial arms are strongly sclerotized throughout the head. Dorsal arms are well developed, curving backwards and terminating near the dorsal hind-corners of the eyes. They are not attached to the head-wall. The corporotentorium is a stout bar transversing the occipital foramen; it is furnished with a posteromedian process. The bar fuses with the anterior arms at its origins at the head-capsule; no posterior arms can therefore be distinguished (Fig. 5).

The antennae. The antennae are submoniliform and covered with narrow brown scales. The scapus is large, apically widened. A well developed condylus on the scapus articulates



Figs. 8—10. *Neopseustis meyricki:* 8, basal antennal segments, scales and hairs omitted; 9, section of galea, very diagramatic, striation in bars of food-groove omitted; arrow indicates anterior; 10, hypopharynx (asymmetry an artifact in preparation). Scale in figs. 8 and 10, 0,2 mm; in fig. 9, 0,05 mm. (Lettering, see p. 149).

N. P. Kristensen

with a ginglymus on the pedicellus (Fig. 8). There is a narrow sclerite laterally in the membrane between scapus and pedicellus. Two diametrically opposed hair-plates (proprioceptors) are present on the basal edge of the pedicellus.

The mouthparts. The labrum is elongated, trapezoidal; distally it is membranous. The epipharyngeal surface is even; its medioproximal area is membranous and furnished with two groups of sensilla basiconica.

The mandibles (Fig. 11) are present as relatively large, but unspecialized lobes, medially tapering. Their apical portion is flattened and unsclerotized. Basally the mandibles are weakly sclerotized; no distinct articulations are developed. Presumably their only function is moving the pupal mandibles in the pharate adult stage.

The maxillae originate in indentations in the hypostomal bridge (Fig. 5). The cardo is an arched sclerite having the distal margin thickened. Dorsally the stipes is weakly sclerotized. Its proximal edge is thickened and its ventral wall is strengthened by a longitudinal costa terminating between the palp and the galea. The palp is 5-segmented. The first segment is short and stout, and only medially is it distinctly delimited from the stipes; the plane of articulation with segment two is almost parallel to the long axes of the segments. The relative lengths of the segments are approximately 0.7:1:2.1:5.7:4.7. Apparently there is a marked bend at the joint between segments 3-4. The two galeae together form a proboscis about 3 mm long. The medial food-groove of each galea is relatively narrow (Fig. 9). Its wall is composed by bars separated by irregular vertical grooves. In each bar an extremely fine vertical striation is visible; possible these bars consist of closely packed lamellae similar to the arrangement described in Pieris by Eastham and Eassa (1955). The dorsal linking mechanism consists of broad, rounded, scale-like, finely striated projections from the medial wall immediately above the food-groove. The long axes of the scales are almost perpendicular to that of the galea; each scale is overlapping that in front. The ventral linking is brought about through a series of sclerotized projections originating some distance below the food-groove. These projections have the upper edge dentate; they are somewhat anteriorly directed. At the ventral edge of the food-groove above the projections the wall is transversely grooved. The external galeal wall is furnished with numerous microtrichia. Dorsally two kinds of sensilla basiconica occur, a short, stout type and a longer, setalike type. No lacinia-vestiges were found.

The labium only has the prementum and the palp well developed, the entire postmental area being membranous. The prementum is deeply intended medially. The long, scale-covered palp is 3-segmented. The apical segment bears a group of seta-like basiconic sensilla.

The hypopharynx (Fig. 10) is laterally connected with the headcapsule through a hypostomal bridge; distally it is a free tapering lobe, richly provided with microtrichia. A pair of elongate sclerotizations in its lateral walls may represent the suspensoria. The salivary orifice is situated on its anterior (dorsal) surface. The proximal part of the anterior hypopharyngeal surface is an approximately quadratic sclerite forming the floor of the sucking pump. It is furnished with a pair of lateral sensilla-groups. From the anterolateral corners of this cibarial plate arises a pair of slender arms. They appear to be directed towards the mandibular bases and could possibly be homologous with the "ligament" between the hypopharynx and mandible in Micropterygidae, described by Tillyard (1923) and Hannemann (1956). However, their identity could not be definately ascertained from the material available.

Discussion.

The results obtained seem to confirm the view that the Mnesarchaeidae and the Neopseustidae are the most advanced dacnonyphous families. The loss of ocelli and sensory invagination on the distal segment of the labial palp in both families are probably true synapomorphies (terminology of Hennig, e.g., 1965); the two families then constitute the sister-grops of a monophyletic group within the suborder.

The Mnesarchaeidae have retained many features of the Eriocraniid-like ancestor; notable similarities (symplesiomorphies) being the simple scapus-pedicellus joint, the postmental Eltringham's organ (considered a plesiomorph character since it occurs in some Micropterygidae, Busck and Böving 1914, Fig. 36) and the structure of the galeal food-groove and the ventral linking mechanism. The derivation of the Mnesarchaeid head-structure from an Eriocraniid type has otherwise been achieved through a process of overall simplification and reduction (obliteration of sulci, loss of ocelli, loss of movable labrum, reduction of mandibles and maxillary palp, shortening of hypopharynx, loss of sensory pit on labial palp).

The Neopseustidae anatomically appear to be a rather more isolated group as already suggested by Hering (1925). They possess several plesiomorph characters (very complete sulcus-pattern, large labrum and mandibles, 5-segmented maxillary palp, long hypopharynx-lobe) but the structure of the proboscis is fundamentally similar to that of higher Lepidoptera, having no distinct, uniform plates in the wall of the food-groove and having the ventral linking brought about through processes under the groove; the serrated processes in *Neopseustis*, however, are rather different from the various hooks described from higher Lepidoptera (Charlanes, 1960). The monocondyle articulation between scapus and pedicellus is a specialization which does not appear to be known from other primitive Lepidoptera.

Summary.

1. The head-capsule in Mnesarchaeidae is almost devoid of sulci whereas in Neopseustidae it has a very complete sulcus-pattern. Dorsal tentorial arms are present in both families. The labrum is large in Neopseustidae, hardly recognizible in Mnesarchaeidae. Ocelli are absent in both families.

2. Mandibles are present in both families but are quite small in Mnesarchaeidae. The maxillary palp is 5-segmented in Neopseustidae, 3-segmented in Mnesarchaeidae. The galeae in both families are haustellate; the medial food-groove and ventral linking mechanism of Mnesarchaeidae resembles that of Eriocraniidae whereas that of Neopseustidae is more similar to that of higher Lepidoptera. The labium in both families is of the typical lepidopterous structure except for the absence of a sensory pit on the apical palp segment. A long free hypopharynx-lobe with dorsal salivary opening is present in Neopseustidae, in Mnesarchaeidae the hypopharynx is much shortened.

3. The Mnesarchaeidae and the Neopseustidae possibly constitute an advanced monophyletic group within the suborder Dacnonypha. The Mnesarchaeidae are rather easily derived from an Eriocraniid-like ancestor; the Neopseustidae are somewhat more isolated within the suborder.

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Explanation of figure lettering.

| aa | anterior tentorial arm | hy | hypopharynx |
|---------------|-------------------------|------------------|-----------------------|
| ar | arm of cibarial plate | la | labrum |
| ant | antenna | lf | laterofacial sulcus |
| at | anterior tentorial pit | lp | labial palp |
| ca | cardo | ma | maxillary palp |
| ci | cibarial plate | md | mandible |
| co | condylus | mi | mid-cranial sulcus |
| da | dorsal tentorial arm | oc | occipital condylus |
| ds | dorsal linking scales | os | occipital sulcus |
| Eo | Eltringham's organ | pe | pedicellus |
| ep | epipharynx | \mathbf{pf} | postfrontal sulcus |
| es | epipharyngeal sensilla | \mathbf{pm} | prementum |
| ey | compound eye | po | postoccipital sulcus |
| fcl | frontoclypeus | sb | sensillum basiconicum |
| \mathbf{fg} | galeal food-groove | sc | scapus |
| ga | galea | sg | subgenal sulcus |
| hb | hypostomal bridge | so | salivary opening |
| hs | hypopharyngeal sensilla | $^{\mathrm{sp}}$ | subgenal process |
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N. P. Kristensen

| st | stipes | te | temporal sulcus |
|----|--|----|-------------------------|
| su | hypopharyngeal | tf | transfrontal sulcus |
| | suspensorium | ts | triangular sclerite |
| tb | tentorial bridge (corporotentorium) | vp | ventral linking process |

Fig. 11. Neopseustis meyricki, mandible. Scale 0,1 mm. Phasecontrast. — Fig. 12. Mnesarchaea hamadelpha, mandible. Scale 0,05 mm. Phasecontrast. — Fig. 13. Mnesarchaea loxoscia, hypopharynx. Scale 0,1 mm. Phasecontrast. (Lettering, see above).

