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Trinominal terminology for cephalic setose warts in Trichoptera (Insecta)

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Abstract: A trinominal nomenclature for all the setal warts on the head is introduced based primarily on localization on cranial regions delineated by grooves. The following terminology is suggested: labral setal warts (the warts usually present on the sclerotised dorsal part of the labrum), clypeal setal warts (the warts present above the labrum and below the frons, that is below the theoretical line connecting the anterior tentorial pits), frontal setal warts (the warts on the frontal area between the vertical frontogenal sutures), vertexal setal wart (warts present on the top of the cranium between and behind the compound eyes), occipital setal warts (warts found at the dorsal posterior region of the cranium), postoccipital setose lobe (the warts attached to the extreme posterior rim of the cranium behind the postoccipital suture, need confirmation), postgenal setal warts (the warts located behind the posterior and posteroventral part of the eyes), frontogenal setal warts (those warts located on the face laterally of the vertical grooves, on the gena and dorsally of the anterior tentorial pits), and the clypeogenal setal warts (located on the face laterally of the vertical grooves on the gena and ventrally of the anterior tentorial pits). Trinomen is given due to (1) the name of the listed cranial sclerites hosting them, (2) the name of nearest organs (antennae, ocellus) or directions on anatomical planes (anterior, posterior, median) to distinguish among them, if a sclerite holds more than one setal wart, and (3) the name of wart type (compact, fragmented, diffused).

Introduction

Despite the great importance in taxonomy and basic sensory function of the different forms of environmental energy, no nomenclatural agreement has been reached for the different forms of setal warts in Trichoptera. The cephalic and thoracic setal pattern has received less attention in taxonomic studies on the adult caddisflies compared to their wing venation and genital structure. However, significant progress in homologizing cephalic and thoracic setal wart patterns has been presented (WIGGINS 1984, IVANOV 1990). In general practice, the setal wart pattern of the entire head with all the anatomical planes are rarely described and figured. Instead, the abdomen is cleared for the detection, drawing and description of the genital structures, and examination of the head and thoracic features is only performed on intact animals. In many species the wart patterns are poorly visible and frequently indiscernible, especially if the warts have the same colour as the cranial sclerites, or if the setae on the warts are not detached the warts are covered by the setae. Clearing the entire wingless body would probably give us very useful information on the setal wart pattern for species descriptions. The number of dorsal setal warts on the head was counted for most of the hydropsychine species (OLÁH et al. 2007, OLÁH & JOHANSON 2007) but required clearing the entire body and usage of various incident light angles. Moreover, a standard terminology was not available on the names of the warts by their locations nor of the various wart types. Here we define a trinominal nomenclature system for all setal warts on the head. The names are given due to (1) the name of the cranial sclerites hosting them, (2) the name of nearest organs to distinguish among them, if a sclerite holds more than one setal wart, and (3) the name of wart type.

Background

A thorough survey of the literature revealed that the nomenclature used for the cephalic warts is confusing compared to the terminology applied for the thoracic setal warts. Especially evident were the conflicts when we compared the terminology used by various authors on the different Trichoptera families. We wanted to examine therefore the various families in the search for a general pattern which would be the basis for a general nomenclature for all families. During this survey, several names have been detected for the same wart on each of the cranial regions. For instance *posterior* (WIGGINS 1984), *occipital* (IVANOV 1990) and *cephalic* (SCHMID 1998) are names used in present day practice for the same pair of warts located on the posterior margin of the head dorsum. Moreover the description and drawing of dorsal warts on the epicranium dominate in recent studies while the facial and genal wart patterns have been neglected. There are few studies carried out or figures produced of the Trichoptera head in the anterior and posterior view. A standardised, formatted and template trinominal system of homologized setal wart terminology will be of great value in systematic and taxonomic studies in making descriptions more comparable. In order to produce a wart terminology we need to summarise the function of setal warts, as well as to review the terminology of cranial regions and the grooves delineating them.

The setal wart functions

This brief summary of the sensory functions of sensillae and the different kind of senses is prepared and presented here for those who are not involved in functional anatomy. Trichoptera have a plethora of peripheral sensors that enable the detection of different environmental energies: (1) the vibration energy of light (visual, thermal); (2) the moving (tactile) or vibrating (auditory) energy of matter; and (3) charged ionic energy of non-volatile (gustatory) and volatile molecules (olfactory). Insects sense and communicate the environmental energy mostly by using external structures of setal origin, including various *antennal sensilla* involved in the perception of pheromones (WELLS 1984). The male sex-linked pheromone dispersal (and sensory?) structures like alar, abdominal and appendage *androconia* are highly specialised organs in the stimuli-sensory complex. The majority of setae are associated with sensory nerve cells (SNODGRASS 1935). Most of the nerve cells are innervated setal external sense organs. The setal receptor complex and the sense cells function together as a *sensillum* and the setal external cuticular part is the *sensilla* having various forms like hairs, spines, scales and minute pegs located on the surface, elevated on a tubercle or sunken into a pit, or within deep cavities of the integument. In other invertebrates, millions of chemosensory neurons have been detected in the cephalic and thoracic appendages, as in the Decapoda (Crustacea) (DERBY & STEULLET 2001). The presence of multiple sensors has several advantages. The most important aspects of their surplus abundance are: (1) enlarging the sensory surface area; (2) diversity of sensor types; (3) compensation for non-functioning developmental stages; and (4) replacement of damaged ones. The different types of setal warts on the surface of the caddis fly body are concentrated loci of these sense organs (IVANOV 1990). Movable, hair-like setae (*sensilla trichodea*) and their modified varieties of the tactile and thick-walled, spine-like processes (*sensilla chaetica*), of the tactile and thick-walled, scale-like plates (*sensilla squamiformia*) and of the gustatory or olfactory, thin-walled or even membrane-capped, peg- or cone-like

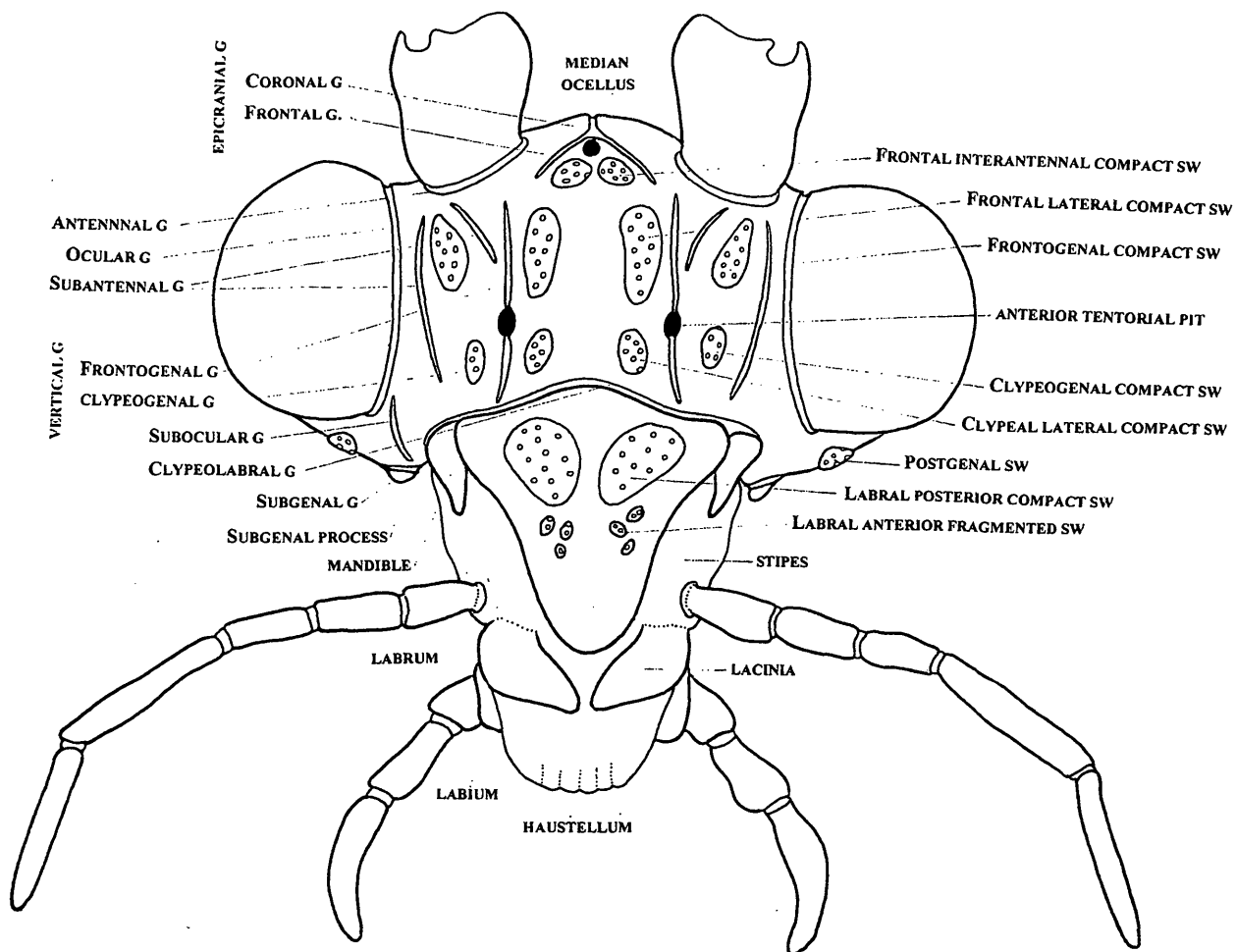


Figure 1.

A facial complex model of combined groove and setal wart patterns in Trichoptera. All the theoretically possible grooves and warts are integrated into the model.

Grooves:

Coronal groove+ frontal grooves=epicranial groove.
 Antennal grooves.
 Ocular grooves
 Subantennal grooves
 Frontogenal grooves+clypeogenel grooves=vertical grooves
 Subocular grooves
 Clypeolabral groove.
 Subgenal groove

Setal warts:

Frontal interantennal compact setal warts
 Frontal lateral compact setal warts
 Clypeal lateral compact setal warts
 Frontogenal compact setal warts
 Clypeogenel compact setal warts
 Labral posterior compact setal warts
 Labral anterior fragmented setal warts.
 Postgenal setal warts

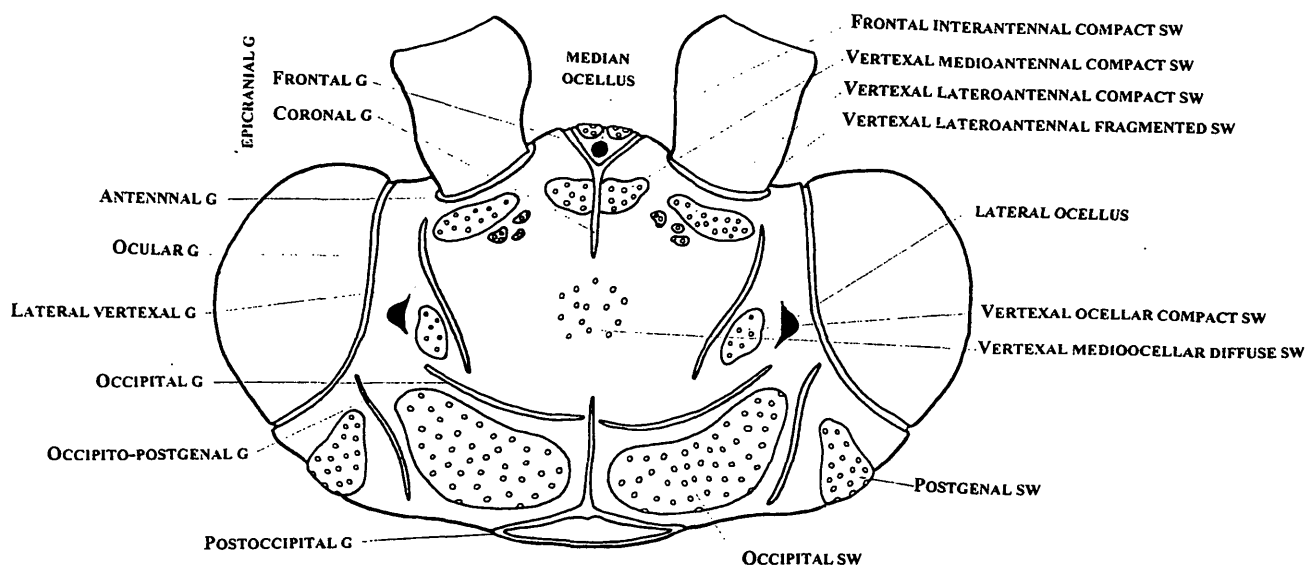


Figure 2.

A dorsal complex model of combined groove and setal wart patterns in Trichoptera. All the theoretically possible grooves and warts are integrated into the model.

Grooves:

Coronal groove+ frontal grooves=epicranial groove.
 Antennal grooves.
 Ocular grooves
 Lateral vertexal grooves
 Occipital grooves
 Occipito-postgenal grooves
 Postoccipital groove

Setal warts:

Frontal interantennal compact setal warts
 Vertexal lateroantennal compact setal warts
 Vertexal lateroantennal fragmented setal warts
 Vertexal medioantennal compact setal warts
 Vertexal ocellar compact setal warts
 Vertexal medioocellar diffuse setal warts
 Occipital setal warts
 Postgenal setal warts
 Postoccipital setal lobes of hydroptilids are not figured due to their dubious origin

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chemoreceptor structures (*sensilla basiconica*) are specifically receptive to certain energy forms: (1) sensation of contact or moving energy, orientation and movement including flight; (2) sensation of vibration energy in sound of various wavelengths; (3) sensation of vibration energy caused by temperature; (4) sensation of ionization energy of activated molecules (taste); (5) sensation of energy of volatile ions (smell); (6) sensation of energy of gravity in geotropic organs; and finally (7) the compound eyes senses the energy of electromagnetic vibration in light. The insects communicate the tactile, auditory, thermal, gustatory, olfactory, geotropic and visual stimuli to primary or secondary sense cells located in the epidermis or deeper in the sub-epidermis. The tactile setal sensillae in the cephalic and especially in the thoracic warts may be particularly important in the flight control of caddis flies. IVANOV (1990) demonstrated that blocking the thoracic warts for sensory capacity produced very visible flight disorders. The distribution and pattern of setal warts are important taxonomic criteria at family level, but the presence of certain wart types make evolutionary trends more detectable than does the pattern alone.

Head groove pattern

A trinominal nomenclatural system is here based on the cranial regions. The cranial regions are often delineated by grooves, but the primary grooves may disappear and secondary grooves may appear. The sclerites, the cranial areas, are also frequently fused without any visible borderline. In addition, the terminology for the different kinds of groove lines is also unsettled, leaving an unstandardized terminology of groove patterns. The types of grooves are not identified in most of the families and a better knowledge of the various lines of grooves, sulci and sutures may be helpful in delineating the head segmentation and the cranial regions, in order to name the head warts accordingly. Generally, grooves are the various sulci, depressions or fissures at the surface of an organ. Sulci are any of the narrow organ grooves, especially those marking the regions at the surface of the head, i.e. the lines of junction of two head regions. Insect cranial regions are usually delineated by sulci. In literature, sulci are termed grooves, crevices, furrows or trenches of the insect head and are of different origins and functions. There are three kinds of grooves on the insect head (SNODGRASS 1960): (1) true *sutures* with a seam produced by the union of two centres of sclerotization, sutures are the primary grooves of the original body segmentation; (2) *sulcus* with a surface groove incidental to the formation of a strengthening ridge at the inner surface of the cuticle, the secondary grooves of the functional ridges of the inner surface, developed secondarily; and (3) simple line of weakness, or *ecdysis cleavage line*, where the cuticle splits during ecdysis without an external groove and internal ridge. For a long time it has been disputed whether the *clypeolabral*, *frontoclypeal* and *postfrontal* grooves are sutures marking the positions of primary intersegmental lines on the insect head or secondary grooves, simple sulci of secondary functional origin, functional in term of skeletal strengthening or muscle attachment ridge at the internal surface. More and more work confirmed that these grooves are not primary segmentation lines (DUPORT, 1956; MATSUDA, 1965). For practical purposes, we conclude that most head grooves are assignable to the sulcus category. However, the dorsal, Y-shaped *epicranial* groove composed of the stem, the dorsal *coronal* groove, and of the branches, the *frontal* (ventral to antennae) or *postfrontal* (dorsal to antennae) groove is merely a line of weakness, representing the dorsal ecdysial cleavage line in most winged insects. The *postoccipital* groove is possibly the

only groove representing a true *suture* and the primary segmentation line, a line of fusion of maxilla and labium. All other grooves are sulci or simple cuticular weakening of ecdysial cleavage lines.

Since many grooves are frequently and variously imperfect, obsolete, suppressed or absent as experienced in many other insect orders, it naive at this stage to develop a detailed groove system for the Trichoptera. Our knowledge on the different Trichoptera groups is limited, and we are probably very far from a full knowledge of the homology of the groove morphology. In this paper, we therefore list the grooves that may have significance for the location of setal warts in delineating the cranial regions. These grooves are never present together and some of them have not been detected at all. However, their presence and homology have been studied only for a limited number of species, which are all listed below.

Clypeolabral groove. The anterior-most groove on the face, separates the labrum from the clypeus, and has various configurations. If present and visible, it is usually positioned well anterior of the theoretical lines connecting the anterior tentorial pits.

Frontoclypeal groove (epistomal suture). Rarely present and visible in the adult stage of Trichoptera. If present, it usually forms a horizontal line separating the clypeal and frontal cranial regions. If absent, the fused frontoclypeal cranial region can be divided into clypeus and frons by a theoretical epistomal suture between the two anterior tentorial pits. The anterior arms of the tentorium always arise near the subgenal or epistomal ridges. Their roots form external depressions in one of these sutures. Frontoclypeal sutures possibly form a primary intersegmental suture, the posterior boundary of the acronal clypeolabrum associated with the anterior tentorial pits on each ends, separating, if present, the preoral clypeus and the postoral frons.

Vertical groove of CRICHTON (1957), an integrated groove of the *clypeogenal* and *frontogenal* grooves. The central un-divided area of frontoclypeus usually bears a shallow vertical groove on each side associated with the anterior tentorial pits. The vertical groove posterior or above the anterior tentorial pits is regarded as the *frontogenal* groove, and its anterior continuation anterior and below the anterior tentorial pit is regarded as the *clypeogenal* groove. These lateral, vertical grooves separate the pregenal cranial sclerites from the frontoclypeal sclerite. All the three sclerites may have setal warts and specific configurations. *Frontogenal* and *clypeogenal* grooves are sulci separating *gena* (*pregena*) from the *frons* and from the *clypeus*. The integrated groove is formed by the *frontogenal* sutures and lies dorsally of the anterior tentorial pits and the *clypeogenal* suture that continues further vertical ventrally of the anterior tentorial pits. This groove is the *vertical groove* sensu CRICHTON (1957) and *laterofascial* groove sensu DUPORTE (1956).

Subantennal groove, a facial groove that extends downwardly from the antennal groove to the subgenal groove, seems additional to and associated with the vertical groove.

Subocular groove that extends from the lower angle of each compound eye to the subgenal suture and is possibly additional or rarely homologous with the vertical sutures.

Epicranial groove (dorsomedian, midcranial, mediocranial). Usually forming a Y-shaped ecdysial cleavage line, more or less developed on the vertex, i.e. on the head dorsally of the parietals. It may be variously developed or suppressed in the adults. The stem of the *coronal* groove runs medially and posterad on the vertex, and the two branches, the *frontal* or *postfrontal* grooves, run laterad and anterad,

delineating the frons posteriorly. The epicranial groove frequently disappears or is present only in variously reduced forms.

Frontal and postfrontal grooves. The facial arms or branches of the *epicranial* groove, embraces (if present) the frontal sclerite posteriorly. They diverge from the coronal groove above the median ocellus and proceed ventrally on the face mesally of the antennal bases. Mostly shortened or absent in the adults. Postfrontal grooves (if present) run posterad of the lateral ocelli. The two pairs of grooves do not occur in the same species.

Lateral vertexal groove. A pair of additional grooves visible on the vertex and running laterally of the coronal groove, for instance in many *Leptoceridae* genera.

Occipital suture. Rarely present or frequently imperfect in adults. The occipital and postgenal cranial areas can be defined only as the posterior region of the cranium. The suture possibly represents the primary intersegmental suture separating the mandibular and maxillary segments, usually absent in winged insects.

Occipito-postgenal grooves. Dorsally separating postgena from occiput in the occipital arch, frequently visible in Rhyacophilidae and Hydroptilidae.

Postoccipital suture is present at the extreme posterior part of the cranium surrounding the dorsal and lateral part of the *foramen magnum*. It is a primary intersegmental suture between the maxillary and labial segments. The posterior tentorial pits are associated with the postoccipital groove at the ventral ends of the postoccipital ridge. The pits are located in the lower extremities of the postoccipital suture.

Subgenal groove is located on each side of the head, close to the lower edge of the lateral cranial wall, and usually follows the contour of the cranial margin. Its anterior part is sometimes distinguished as the *pleurostomal groove* and its posterior part as the *hypostomal groove*.

Antennal grooves frequently encircle the antennae, forming an internal skeletal ridge around the edge of the membranous area of the antennal socket.

Ocular grooves frequently surround the compound eyes, forming an internal skeletal ridge around the edge of the retina.

Cranial areas

The insect head capsule has lost all semblance of the segmented structure. Most of its grooves are secondarily developed into sulci, the surface lines of the cuticular inflections that form endoskeletal ridges of head reinforcement. The cranial areas are delimited by the head grooves, when grooves are complete. If grooves are abbreviated or suppressed the limitations of the cranial areas become obscure. The cranial areas, the intersutural areas of the head, are sometimes termed sclerites. Setal warts are present on every cranial area.

Because the homologization of the setal warts is based on their association with cranial areas, the cranial areas hosting the warts also have to follow a homologous scheme of primary segmentation of the head. Several theories have been developed to explain the segmentation of the insect head (MATSUDA 1965). In the head, the external structures, musculature and innervation serve as supplementary criteria to establish the primary segmentation. The mesodermal coelomic cavities, the distribution of appendages, and the neuromeres in the insect embryo are primary criteria for detecting the segmentation on the fused cranium. The cranial regions of *frons*, *clypeus* and *labrum* develop from the outer wall of the prostomial lobulate plate, whereas the

epipharyngeal wall including the cibarial pump develops from its inner wall (DUPORTE 1957). The theory of head segmentation with prostomium, the unsegmented preoral piece of the acron, and with only four postoral somites, has been confirmed: (1) prostomium; (2) the antennal or antennocular segment; and the three gnathal segments (3) the mandibular segment; (4) the maxillary segment; and (5) the labial segment. It seems that the myth of intercalary segments has been refuted, i.e. the paired cephalic lobes belong to the prostomial segment rather than to an imaginary intercalary segment (SINGH 2005). The presence of an additional head segment anteriorly of the mandibular segments are clearly refuted by cell lineage analysis (Wolff & Scholtz 2006). At the same time the presence of the second antennal or intercalary segments has been demonstrated earlier by Hox gene analysis (DAMEN *et al.* 1998).

Primary areas of the insect cranium are the median *facial frontoclypeal area*, the *lateral parietals*, the *occipital arch*, the *postocciput*, and the narrow *subgenal areas* above the bases of the gnathal appendages.

Labrum. Prostomial in origin, acronal, non-segmental. Variously formed, elongated, triangular, usually with broad basal, flat lobe hanging downwardly and forming the anterior wall of the intergnathal preoral cavity. The external surface is attached and separated from the clypeus by the clypeolabral groove giving mobility to the labrum. The labrum shape varies greatly among families, but the essential structure forming a movable preoral lobe of the head is retained.

Frontoclypeal area. The typical facial region between the antennae, or between the frontal grooves and the labrum, if frontal grooves are present. If an epistomal groove is present the frontoclypeal area is divided into a dorsal or a posterior frons, and a ventral or an anterior clypeus. However the frontoclypeal area is mostly fused in Trichoptera. For their setal wart identity in our trinomial terminology below, we divide it by the theoretical line between the anterior tentorial pits. The frontal area is located above this line, and the clypeal area is located below this line. The frons bears the median ocellus on its upper part between the posterior corner of the frontal grooves. The antennae are never located on the true frontal area, however their bases, the scapes can be enlarged, or approximated medially, and constrict the frontal area between them. The frontal area is usually densely packed with setal warts, the clypeal area is less covered. The clypeus is often divided into postclypeus and anteclypeus, even though their limits may not be separated from the frons.

Parietal areas. The lateral areas of the insect head are separated above by the coronal suture. They are bounded anteriorly by the frontal and posteriorly by the occipital grooves. Each parietal area hosts an antenna, one lateral ocellus, and a compound eye.

Vertexal area. The dorsal surface of the two parietals, forming the top of the head, *vertex*. Vertex is usually fully packed with setal warts and divided by the medial or midcranial stem of the *epicranial groove*, however it is frequently shortened or even suppressed. Additional grooves, like the *lateral vertexal groove*, the dorsad shifted *occipito-postgenal groove*, the posteriorly shifted *frontal* or *postfrontal* groove, the enlarged *antennal* and *ocular grooves*, or the thickened rim of the skeletal rings of compact warts all may contribute to the various configurations of the vertexal setal pattern. These warts are usually not homologized.

Genal area. The lateral parts of the parietals beneath or behind the compound eyes are the genae.

Postgenal area. The posterior part of the genal area behind the eye on the occipital arch, separated from the occiput by the occipito-postgenal grooves only in the most

primitive families like the *Rhyacophilidae* and *Hydroptilidae*. This area is rarely delimited anteriorly and dorsally by grooves.

Pregenal area. This cranial area anteriorly to the eye is separated medially from the frontoclypeal area by the lateral vertical groove. This vertical groove, present on both sides of the face, is frequently visible only by the position of the anterior tentorial pits, or rarely visible by the frontogenal groove dorsally and by the clypeogenal groove ventrally of the anterior tentorial pits.

Occipital arch. Comprising the posterior narrow band of the head between the occipital and postoccipital sutures. The term occiput is given to the dorsal part of the arch, and to the lateral parts located posteriorly of the genae, called the postgenae. The arc is rarely present in the primitive members of the Trichoptera, in which the occiput and postgenae are separated by the occipito-postgenal groove. Since the occipital and occipito-postgenal grooves are frequently weakly developed or absent, the occipital and postgenal areas can generally be defined as the posterior region of the cranium.

Postoccipital area. The narrow posterior rim of the epicranium set off from the occipital arch by the postoccipital suture. The posterior margin of the postocciput may be produced ventrally into a small process, the occipital condyle, to which it is articulated with the anterior cervical sclerite.

Subgenal areas. The narrow marginal areas on the sides of the cranium below the subgenal grooves, to which the gnathal appendages are articulated. Its anterior corner is produced into a small lobe, the postgenal process.

Setal wart structure

The setal or setose warts generally form raised or elevated parts of the body surfaces encircled by a depressed skeletal ring with slightly thickened rim, and frequently, but not always of different colour than the surrounding body surface. This different colour makes the wart visible without mechanical and chemical clearing. If the wart colour is the same as the surrounding cranial surface or the dense setae are not detached, the wart pattern is almost indiscernible, not being visible on intact animals. In this case, clearing of the head is needed. The wart setae are large, usually easily detachable, but their alveolus or setal theca (IVANOV 1990) are well visible. The setal wart surfaces are identical to the surrounding areas in being covered with small, tapering, non-cellular cuticular processes, outgrowths or projections, the microtrichiae. These are arranged regularly, following the hexagonal or polygonal pattern of the epidermal cells. For that reason their proper name, although it has not come into general practice, is *acanthae* (RICHARDS & RICHARDS 1979). The seta itself is a slender hair-like process on the warts formed by a plasmatic outgrowth from a large epidermal cell. This unicellular process of the body wall emerges from a deep cylindrical internal cavity. This is the trichopore, or setal theca, and is surrounded by a thickened setal rim. Between the external hair-like apical part and the distal epidermal cell is a setal membrane depressed into a hair socket, representing the setal alveolus that may be elevated on a tubercle. In the setal theca a sense cell is associated with the seta, a bipolar neuron with a short curved dendrite, the distal process of the sense cell, the trichoid sensilla and a thin axon, or the sensory nerve. IVANOV (1990) distinguished three types of setose warts in Trichoptera:

(1) *Compact warts*, setose warts *sensu stricto*. Somehow elevated and surrounded by a skeletal ring formed by a depressed furrow with thickened rim. Sometimes the elevation is very significant or even could be developed into a tube or flap shaped unit (Johanson 1998).

(2) *Fragmented warts*. Setose wart which has undergone a disintegration into small warts with a restricted number (up to 20) of stronger setae without well-defined boundary. These small fragmented warts are arranged into scattered, irregular or regular patches, bands or in various lines.

(3) *Diffuse warts*. Setose surface of mostly individually scattered setae without a depressed skeletal ring and thickened rim. These individual setae can be also arranged in scattered irregular or regular patches, bands or in various lines.

Proposed terminology of cephalic setal warts

In coining names for the setal warts, two principles of nomenclature have been applied. Wiggins's principle (1984) relied upon the orientation on anatomical planes, and Ivanov's principle (1990) based either upon the cranial area (frons, occiput) or upon the functional organs (antennae, ocellus, compound eyes). JOHANSON (1998) has combined these two principles in his studies on the *Helicopsychidae* setae. We use exclusively the cranial regions for the primary name of the cephalic setal warts. However, if there are more warts within a region we use a secondary name. The primary name is the name of the cranial region bearing the warts. The secondary name is based either on Wiggins's principle of directions or on Ivanov's functional organs. The tertiary name refers to the type of setal wart involved. Two examples to explain our principle in practice are given below.

(1) A compact pair of warts, usually being well developed on the occiput, has the various names *occipital wart* (IVANOV 1990), *posterior wart* (WIGGINS 1996) or *cephalic wart* (SCHMID 1998) in the present day practice. We name it *occipital compact wart*, as primary cranial name without a secondary name because this is the only wart in this cranial region. This compact wart undergoes fragmentation only very seldom.

(2) A prominent setose wart on the posterior tip of the frontal area needs all the three names. It is primarily anterior of the median ocellus when the ocellus is present. It is on the tip between the anterior branches of the Y-shaped ecdysial cleavage line when present. It is also usually located between the antennae. This wart has the names of *frontal wart* (WIGGINS 1996) or *interantennal wart* (JOHANSON 1998) in the present day practice. This wart needs a trinomial nomenclature because there are more warts present on the cranial region of the frons. We name it *frontal interantennal compact wart*, where frontal is the primary cranial name and interantennal is the secondary functional organ-based name. The terminology listed below applies to the name of cranial sclerites, i.e. clypeus, frons, vertex, occiput, postocciput, and gena (pregena, postgena), hosting the warts for primary names; the name of orientation on anatomical plane, i.e. anterior, posterior, mesal, medial, lateral; and alternatively the name of the nearby functional organ, i.e. antennal, ocellar and ocular for secondary name and the type of warts, i.e. compact, fragmented and diffuse for tertiary name.

Labral setal warts

More or less compact setal warts could be present on the posterior basal, more sclerotised part of the labrum, usually fused.

Clypeal setal warts

This is a facial area above the labrum and below the frons. The epistomal or frontoclypeal suture that separates it from the frontal area is usually obsolete or suppressed. It is difficult to delineate its exact area. However, its boundary with the labrum is more pronounced. Warts, if present, are

those that are below the theoretical horizontal line connecting the anterior tentorial pits. Clypeal setose warts are paired or fused and usually diffused.

Frontal setal warts

There are various names for the frontal or clypeal setal warts: *warts on face between anterior tentorial pits*, (WIGGINS *et al.* 1985a), *median setal wart on the frons* (WIGGINS 1987), *frontal wart*, *anterolateral wart*, *hypomedial wart* (IVANOV 1990), *anteromedian wart* (WIGGINS 1985b), *anteromesal wart* (WIGGINS 1996), *interantennal wart* (JOHANSON 1998), and *frontal wart* (AREFINA *et al.* 2003).

The *frons* and the *clypeus* are not clearly defined or delimited cranial areas within Trichoptera because the *epistomal* (*frontoclypeal*) suture is frequently absent or usually suppressed. CRICHTON (1957) studied the *frontoclypeal* area in fifty-three species in thirteen caddisfly families and found only vertical groove present and associated with the *anterior tentorial pits* on each side of the anterior surface of the head capsule. This vertical groove is the *frontogenal* suture that is located dorsally of the anterior tentorial pit and continues below the pit as a *clypeogenal* suture. The central, undivided area between these grooves is the fused *frontoclypeal cranial area* as indicated by the separated dorsal and ventral attachments of the foregut muscles. The anterior tentorial pits and also the frontal ganglion lie at the level of separation between these two groups of muscles. The frontoclypeal area between the vertical frontogenal and clypeogenal sutures may develop rich setal warts, as in the Plectrotarsidae, Rossianidae, partly Brachycentridae, and Uenoidae. The frontoclypeal area is usually devoid of setal warts if the maxillary palps are upturning and covering the face, as in the males of many species of Lepidostomatidae, Goeridae, and Sericostomatidae. In these families, the frontal setal warts are absent on the face, but the *frontogenal* and *clypeogenal* warts (pregenal warts) are frequently present, like in *Gastrocentrella*. Although the frontoclypeal or epistomal suture is not developed between the two cranial sclerites, the boundary between frons and clypeus can be delineated by a hypothetical horizontal line connecting the two anterior tentorial pits. Thus even without a visible epistomal suture the frontal and clypeal setose warts can be differentiated by this hypothetical line.

The frontal setal wart pattern is rarely presented in taxonomic work, and we are therefore far from knowing the entire diversity of wart pattern on this cranial area. However, the presence of a *frontal interantennal compact wart* posteriad on the frons, between the converging frontal grooves, is rather stable between various groups. This prominent wart is usually fused, but could be approximated and even well separated. Moreover, it might be located anteriorly or posteriorly of the median ocellus. Occasionally the frontal grooves are obsolete and the frontal interantennal compact wart is coalescent with the *vertexal antennal median wart*. Other warts on the frons are located more anteriorly, one or two pairs of frontal lateral might be present, and sometimes the warts are fused into a large, central and circular setal wart, as in the genus *Lepnevaina* (Limnephilidae). Frontal warts located anteriorly of the frontal interantennal compact wart sometimes form diffuse bands, as in *Liapota* (Plectrotarsidae) and *Phryganopsyche* (Phryganopsychidae), or fragmented lines as in *Allomyia delicatula* (Apataniidae), or fragmented bands as in *Neophylax fuscus* (Uenoidae).

Vertexal setal wart

Various names for vertexal warts have been presented: *anteromesal and anterolateral* (NEBOISS 1975); *ocellar* (IVANOV 1990); *anterior* (WIGGINS 1996), *postantennal*

(JOHANSON 1998), *median postantennal* (JOHANSON 1998), *mediolateral*, *anteromedian* (ANDERSEN *et al.* 1999)

Vertexal warts are located on the vertex, on the top of the cranium between and behind the compound eyes. The vertex is the dorsal part of the parietals, separated by the coronal groove, or more frequently by the dorsal ecdysial cleavage line, which is merely a weak line and has no meaning as a morphological boundary. The vertex has the most diverse setal warts and their configurations are the most variable among and within families. The various vertexal setal warts are named after the nearby functional organs combined with an anatomical direction when required. There are a variety of *vertexal antennal* setal warts immediately behind the antennae: *vertexal lateroantennal compact* or *vertexal lateroantennal fragmented* as in many *Cheumatopsyche* species (*Hydropsychidae*), *vertexal medioantennal compact* are frequently fused. There are usually paired *vertexal ocellar compact*, *fragmented* or even frequently *diffused* warts present behind the lateral ocelli or around the hypothetical position of the ocelli when they are lacking.

Occipital setal warts

Various names for the occipital setal warts are presented in the literature: *occipital* (IVANOV 1990), *posterior* (WIGGINS 1996), *cephalic* (SCHMID 1998); and *cephalic/posterior* (JOHANSON 1998).

Since the occipital suture between the vertex and occiput is frequently weakly developed or absent, the occipital area can generally be defined only as the dorsal posterior region of the cranium, the dorsal region of the occipital arch. The occiput is a strongly setose area in almost all the caddisfly species which host this large compact wart. The occipital wart is rarely fragmented, as in *Phylloicus mexicanus* (Calamoceratidae).

Postoccipital setose lobe

Probably represents the dorsal *postoccipital* lobes or warts of the *Hydroptilidae* (MARSHALL 1979, KJAERANDSEN 2004), with or without hinged caps concealing an eversible scent dispersing organ (*Hydroptila*). The postocciput forms the extreme posterior narrow rim of the cranium behind the postoccipital suture, probably representing the sclerotic remnant of the labial somite. The identity of postoccipital setose warts or lobes is dubious, they could be of occipital origin (IVANOV, 2007, personal communication). Similar setal lobes on the occipital region of *Orinocotrichia* and *Tizatetrichia* (*Hydroptilidae*) are called posterolateral warts (HARRIS *et al.* 2002).

Postgenal setal warts

Different names for the postgenal setal warts are given in the literature: *postorbicular* (IVANOV 1990), *posterolateral* (WIGGINS 1996), *postocular* (JOHANSON 1998), *basolateral* (ANDERSEN *et al.* 1999).

Since the occipital suture is frequently imperfect or absent, the postgenal area is defined as the posterolateral region of the cranium. The postgena is a strongly setose area in most caddis fly species and the postgenal setal warts are an important and permanent pair of warts. The vertically elongated postgenal wart, curving along the posterior and posteroventral part of the eyes, are occasionally shortened or reduced and exhibiting only a small wart.

Frontogenal setal warts

The following names for the frontogenal setal wart are given in the literature: *warts on the front* (Wiggins 1974), *anterolateral* (IVANOV 1990); *lateral frontal* (JOHANSON 1998), *frontal* (HOLZENTHAL & PES 2004).

Frontogenal setal warts are located on the face laterally of the vertical grooves, on the gena and dorsally of the anterior tentorial pits.

Clypeogenal setal warts

The various names for clypeogenal setal warts presented in the literature are: *warts on the front* (WIGGINS 1974), *anterolateral* (IVANOV 1990); *lateral frontal* (JOHANSON 1998), *frontal* (HOLZENTHAL & PES 2004).

Clypeogenal setal warts are located on the face laterally of the vertical grooves on the gena and ventrally of the anterior tentorial pits.

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