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A fossil head of an enicocephalomorphan (Hemiptera: Heteroptera) from England revisited: Identity of the first fossil species of Enicocephalidae from Europe

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Abstract. † *Pyrenicocephalus jarzembowskii*, gen. et sp. n. (Hemiptera: Heteroptera: Enicocephalomorpha: Enicocephalidae: Enicocephalinae) from Early Eocene, London Clay, England, Isle of Sheppey, is described and illustrated according to the unique pyritized adult head reported as a larval enicocephalid head by Jarzembowski (1986). The head anatomy of similar and related genera of Enicocephalinae is compared and the close relationship of the new genus to a clade including the extant genera *Oncylocotis, Embolorrhinus* and *Hoplitocoris* is suggested, most probably as the sister genus to *Hoplitocoris* (presently with Afrotropical, East Palaearctic and Oriental range).

INTRODUCTION

Occurrence of a minute enicocephalid head capsule in early Eocene deposits of London Clay formation was reported by Jarzembowski (1986). He described and illustrated the head, considered it as belonging to an unidentifiable larva of the Enicocephalidae and, for this reason, left the fossil unclassified. He also reviewed the insect fauna and taphonomy of the fossil site, the eroding cliffs on the Isle of Sheppey situated off the Kent coast in Southern England, and summarized the data on the Sheppey palaeoenvironment (Jarzembowski, 1992). The London Clay deposits are marine, 51–53 MY old (Jarzembowski, pers. comm.; see also King, 1981), and their insect fossils are mineralised, having undergone the process of pyritization (Allison, 1988).

The record of the head capsule concerned is so far the only published evidence of the past occurrence of the Enicocephalomorpha in Europe but both the Enicocephalidae and Aenictopecheidae are represented in European ambers and will soon be investigated (Štys, Popov and Heisss, in prep.). Only one individual of an extant species of an enicocephalid was ever found in Europe, namely the holotype of a then new genus and species, *Henschiella pellucida* Horváth, 1888, in Bileća (Bosnia and Herzegovina).

The Enicocephalomorpha (for review see Štys, 1995) is the sister-group to Euheteroptera that contains the rest of true bugs (e.g., Schuh & Slater, 1995). Consequently, the rare fossils of the group are always of a high phylogenetic, morphological and biogeographical interest. The fossil Enicocephalomorpha were reviewed in a now outdated revision by Štys (1969), surveyed subsequently by Azar et al. (1999), and discussed within a broader context of evolution of the Hexapoda by Shcherbakov & Popov (2002) and Grimaldi & Engel (2005).

I have re-examined the head concerned, found it to belong to an adult individual of a new genus and species that are described and formally classified in the present paper jointly with a discussion of the relevant diagnostic characters and comparison with the head anatomy of similar and related taxa.

MATERIAL AND METHODS

The fossil is only represented by the exoskeleton of its head capsule, and only this specimen is referred to in the description. Owing to fragility and vulnerability of the pyritized (iron sulphide) fossil that should only be exposed to the urban atmosphere for the shortest possible time, the photographs from views documented sufficiently by Jarzembowski (1986) were not repeated. These photographs are referred to as J-fig.a (= Jarzembowski 1986: fig. 1a = ventrolateral view), J-fig.b (ibidem, fig. 1b = lateral view), J-fig.c (ibidem, fig. 1c = compound eye and surrounding cuticle in lateral view), respectively.

A new photograph (Fig. 1 = dorsal view) was taken in the Department of Palaeontology of the Natural History Museum, London, using a Canon EOS 450D camera attached to a Zeiss Axioshop 20 microscope, and the composite photographs were focus stacked using the program Helicon Focus. Measurements were taken from scaled photographs (J-b,c; Fig. 1).

The cylindrical part of the head between the compound eyes and the antenniferous tubercles is called "gena" although the true genae are only forming a part of this region. The ocular index has been calculated as "(diatone – synthlipsis): (2 × synthlipsis)" – see Štys et al. (2010). The comparative data from other genera of Enicocephalidae may be found mainly in Villiers (1969), Wygodzinsky & Schmidt (1991) and Štys (2002), or result from an unpublished research (Štys & Baňař, unpubl.).

Abbreviations: ALH – anterior lobe of head; CON (in Discussion) – dissimilar character states; L – length; max – maximum; min – minimum; PLH – posterior lobe of head; PRO (in Discussion) – similar character states; W – width.

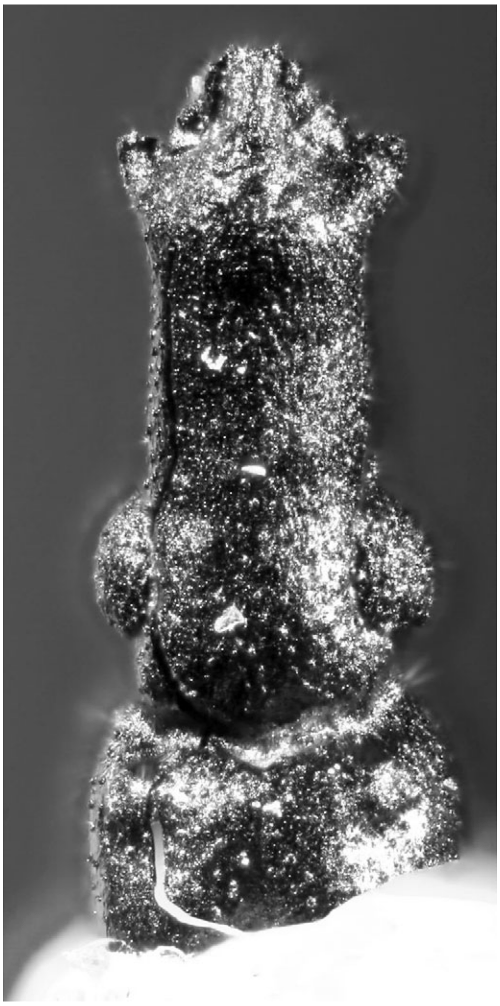

Fig. 1. † *Pyrenicocephalus jarzembowskii*, gen. et sp. n., holotype head. Dorsal view, slightly tilted. Focus stacked (see Material and Methods). Maximum total length 0.85 mm.

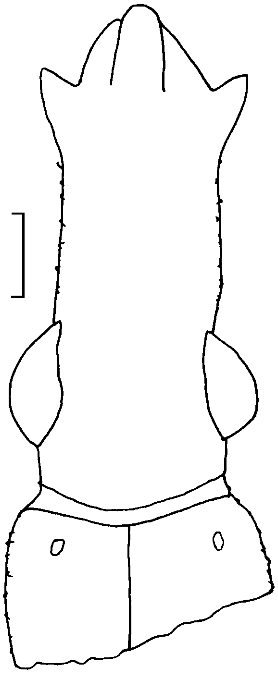

Fig. 2. † *Pyrenicocephalus jarzembowskii*, gen. et sp. n., holotype head. Dorsal view, slightly tilted. Drawn from the photograph (Fig. 1) to show apical structures and ocelli. Scale 100 µm.

HEMIPTERA: HETEROPTERA: ENICOCEPHALOMORPHA: ENICOCEPHALIDAE: ENICOCEPHALINAE

† *Pyrenicocephalus* gen.n.

Type species. *Pyrenicocephalus jarzembowskii* sp. n. by present designation**.**

Etymology. Derived from *Pyr*ite (= iron sulphide), alluding to type of mineralisation of the fossil, and *Enicocephalus* (name of a type genus of Enicocephalidae); masculine.

Diagnosis. Head strongly elongate, without any processes or paired tubercles, covered by small setigerous tubercles all over, no other conspicuous microelements present. Apex of anteclypeus bent ventrad, slightly exceeding mandibular plates, ventrally connected with head capsule; transclypeal sulcus absent. Antenniferous tubercles strongly protruding; antennal insertions subapical. Genae narrow, cylindrical, nearly twice as long as eye. Eyes medium-sized, multifaceted, situated in dorsal part of head, in lateral view distant from both dorsal and ventral margins of head, about 0.3 times as wide as vertex, remote from a deep postocular constriction; postocular lateral margin of anterior cephalic lobe (“tempus”) straight, nearly half as long as eye (dorsal view). Posterior lobe of head transverse, with median linear impression, lateral sides rounded. Ocelli small, flat, remote from posterior lobe margins (dorsal view), aligned with inner eye margins, interocellar distance longer than distance ocellus – eye, ocellar tubercles absent. Total body length estimated at 2.8–4.2 mm (see Discussion).

Comparative diagnosis. See Discussion sub (3) and (4).

† *Pyrenicocephalus jarzembowskii* sp.n.

Enicocephalid juv. indet.: Jarzembowski, 1986: 2, Plate 1: figs 1a-c.

Holotype. A head. England, Kent, Isle of Sheppey, Paddy’s Point (National grid reference TQ 971734); C. King 1983 lgt; Registration number In. 64680, Department of Palaeontology, Natural History Museum, London.

Horizon. Early Eocene. Upper London Clay, Division E, unit SH-12c (fide Jarzembowski, 1986).

Holotype condition. Head glued horizontally to a triangular card on a pin. Carbon-coated, black specimen. Appendages missing, all the vestiture abraded. The very posterior part of PLH and neck broken off and missing, posterior part of PLH covered by glue. Anterior edge of buccular bridge damaged; the area between antennal insertion and apex of anteclypeus either partly damaged or not fully cleaned, consequently its details not visible.

Measurements. All in µm; ventral synthlipsis not measurable. Total length of the fossil (max, lateral view) 850.

Dorsal view. ALH, max L (apex – mid constriction) 597, L eye 122, L postocular margin of head

(= “tempus”) 58, median L of that part of ALH exceeding antennifers 86, medial L postocular constriction 31. Distances eye – basis of antennifer (= L gena) 223, eye – apex antennifer 315, max transocular W (= diatone) 300, min interocular W (= min W “vertex” = dorsal synthlipsis). Gena, W max 196, W min 184. PLH, max L ?, max W 327; distances, interocellar 174, ocellus – eye 125.

Lateral view. Height, min. gena 200, max transocular 279, max PLH 319, Eye, max height 160, max L 132 min posterior distance to postocular constriction 32, distance of upper margin from dorsal outline of head 51, of lower margin from ventral outline of head 68. Postocular constriction, dorsal depth 43, average lateral L 34, max dorsal distance between ALH and PLH beginning to form slopes of the constriction 102.

Ratios. Dorsal ocular index 0.36 (ventral one not measurable). L gena: L eye (dorsal) 1.83. L (distance eye – apex antennifer) : L eye (dorsal) 2.58. Diatone : min W gena 1.63. Interocellar distance: (distance ocellus-eye) 1.39. Height eye: L eye (lateral view) 1.21.

General facies of the head. Strongly elongate, with particularly long tubular genae.

Microsculpture (J-figs b, c; Fig. 1). Cuticle with extremely minute granulation and small, sharp, setigerous tubercles all over; tubercles particularly dense on ventral part of ALH, scarcer on PLH, surface of gular area and PLH appearing somewhat microdentate; setigerous tubercles smaller and little prominent in lateral preocular regions of ALH and anterolateral parts of PLH. Postocular constriction separating ALH from PLH with very fine longitudinal striation.

ALH. Dorsal outline in lateral view (J-fig.b) very shallowly concave, with two moderate convexities between antennifers (postclypeal region?) and between eyes, respectively. Anteclypeus subequal in length to mandibular plates, slightly exceeding those (Fig. 2) and buccular bridge, but contiguous with head capsule throughout; narrow, its distal half arcuate, moderately bent ventrad; transclypeal sulcus absent. Antennifers situated in ventral half of ALH (J-fig.b), strongly protruding, tooth-like, apices acute (Fig. 1) and slightly bent ventrad, posterior margins slightly convex, antennal insertions subapical. Genae (Fig. 1) long and rather narrow, more than twice as long as eye; parallel-sided with nearly straight lateral margins in dorsal view, only margins near antennifers and eyes slightly concave; an extensive low bulge not reaching ventral margin of head present in front of lower half of eye.

Eyes moderately sized, nearly hemispherical with posterior margin slightly flattened (J-fig.c; Fig. 1); subdorsal, remote from both dorsal and ventral margins of head in lateral view (J-fig.b); in dorsal view slightly sunken within head capsule (more precisely: situated within depression of head capsule), inner margins moderately convex; eyes far remote from postocular constriction in dorsal view (Fig. 1), only slightly remote from the latter in lateral view (J-fig.b); facets separately convex, eye multifaceted (J-fig.c). Ventral outline of eyes slightly margined, ventral interocular space bulged. Interocular areas strongly convex on both dorsum and venter.

Buccular bridge long and broad, not delimited by a sulcus.

Postocular constriction (Fig. 1) sharply marked, its dorsal sector arcuate, deep; lateral and ventral sectors shallow but constriction distinct even ventrally on head (J-figs a, b), lateroventral part slightly sinuate. Anterior wall of constriction (on ALH) convex in lateral view (J-fig.b), posterior wall (on PLH) oblique, straight. Deepest part of constriction levelling with upper margins of eyes in lateral view.

PLH (the extant part; Fig. 1) with sides moderately rounded. Dorsum convex, with a percurrent linear median**. Ocelli** (see Discussion; Figs 1, 2) small and rather flat, situated at anterolateral part of PLH, directed anterolaterad, aligned with inner eye margins, not well visible and not situated on ocellar tubercles, more distant mutually than from eyes.

DISCUSSION AND CONCLUSIONS

(1) Presence and absence of ocelli: adult or larval stage?

Presence or absence of ocelli is in many paurometabolous insects a critical diagnostic character to discriminate between adult and larval stages because the presence of ocelli is usually associated with presence of articulated wings in adults. However, this rule of thumb is equivocal, particularly in Heteroptera. Many adult heteropterans have wings reduced or absent, and a concomitant loss or reduction of ocelli is frequent in all major clades, being often sex- or morph-limited. However, this situation is not universal; for instance, brachypterous or micropterous adults of some species of the Enicocephalidae possess ocelli, while others do not. On the other hand, many clades of Heteroptera do consistently lack ocelli in their adult stage even in macropterous flying morphs (e.g., many Nepomorpha, all the Pyrrhocoridae, Largidae, Tingidae (s. str.), and all the Miridae except for Isometopinae; individual subfamilies and genera in many families). Consequently, absence of ocelli is not decisive for diagnosing an isolated head of a true bug as larval.

On the other hand some 5th instar larvae of Heteroptera do possess ocelli owing to heterochronic predisplacement (some Enicocephalomorpha and Dipsocoromorpha, the Gelastocoridae, Corixidae: Diaprepocorinae, some Anthocoridae and others; Štys, unpubl.). The ocelli may be externally represented by a simple red-pigmented spot each (not to be confused with a reddish rudiment of ocellus of a developing pharate adult instar, often visible through semitransparent larval cuticle) up to adult-like structures with external lens each (e.g., many Gelastocoridae). However, the latter condition is rare, and it is parsimonious to regard the presence of an ocellus with lens on an isolated non-gelastocorid head as evidence that the adult stage is involved.

The head of *Pyrenicocephalus jarzembowskii* was supposed to lack the ocelli and was therefore assessed as larval (Jarzembowski, 1986). The generality of such a conclusion is false; moreover, the ocelli are present on the specimen. They are visible and their lenses are clearly delimited on the actual fossil, but they are difficult to see on the photograph (Fig. 1) because of flatness of lens and absence of ocellar tubercles on one hand, and artificial charging of the image on the other. I cannot estimate what influence on the visibility of a transparent ocellar lens was exerted by the natural process of pyritization and the subsequent artificial carbon coating.

The larval ocelli of the Enicocephalomorpha, if present, usually take the form of pigment spots. However, those of the larvae of the Madagascar and Seychelles endemic genus *Cocles* Bergroth, 1905, possess sharply delimited lens (Štys, unpubl.) occurring in association with hypertrophied compound eyes. Consequently, we may safely assume that the ocelli-bearing English fossil head belonged to an adult individual.

(2) Body length of *Pyrenicocephalus jarzembowskii*

Length of the head (excluding its neck, often telescoped into the pronotum) takes 20–30% of the total body length of a macropterous individual of the Enicocephalidae. Therefore the total body length of *P. jarzembowskii* is likely to range between 2.8–4.2 mm. (Data calculated from illustrations and measurements provided by Villiers (1969) and Wygodzinsky & Smith (1991) for those species-rich genera discussed below in detail.)

(3) Comparative notes

The London Clay head belonged undoubtedly to a species of the Enicocephalomorpha (general shape, position of antennifers, subdivision in two cephalic lobes, character of microsculpture, position of ocelli). Can it be accommodated (does it cladistically belong) into any of the established genera? We have to falsify this possibility prior to suggesting the establishment of a new genus for the species. However, the head of enicocephalomorphans is rather unsuitable source of characters for comparison and diagnostics. Most of the salient generic characters concern the sculpture and architecture of pronotum, armature of fore legs and tarsus, middle and hind apicitibial combs, forewing venation and male terminalia; there is no comparative study of head available; most characters, particularly in species-rich genera, are greatly diverse, neither exclusive nor inclusive in individual clades; the stable character states are usually autapomorphic or convergent.

Only the higher taxa and genera that share (or include species that do so) with *P. jarzembowskii* at least some of the character states listed below have been considered, regardless of their present distribution. (1) Anteclypeus at least slightly extending in front of mandibular plates ("protruding") retaining at the same time ventral connection with the head capsule; (2) antennifers subapical, outstanding; (3) genae long, narrow, cylindndrical to subcylindrical, strikingly longer than eye; (4) eyes modally developed, moderately large, multifaceted, not too deeply sunken within head capsule; (5) ALH distinctly separated from PLH by a deep postocular constriction; (6) setigerous tubercles present over a large area; (7) size compatible with † *P. jarzembowskii* (i.e. species neither considerably smaller or larger than the estimated length 2.8–4.2 mm). Usually striking similarities or dissimilarities are only emphasized, and a few additional characters compared as well.

The two genera with ranges geographically closest are quite dissimilar. (a) The only genus occurring in Europe, the modern *Henschiella* Horváth, 1888 (Enicocephalinae), with species all over E Hemisphere (excl. New Zealand and Pacific islands) does meet none of the above criteria except the size (genae absent, antennifers adjoining the eyes, etc.). (b) † *Enicocephalinus acragrimaldii* Azar, Fleck, Nel & Solignac, 1999 (Lower Cretaceous amber, Lebanon; Enicocephalidae: subfam. inc. sed.) is of the same size (head 0.5–0.6 mm long, total L 2.5–2.8 mm) and its gena is long and tubular, but antennifers are apical and not protruding, there is no postocular region of ALH, the setigerous tubercles are absent, and, moreover, the ocellar tubercles are distinct.

The above criteria exclude all the † Disphaerocephalinae (cf. Štys, 1969 – fam. inc. sed.), Aenictopecheidae, and Enicocephalidae: Phthirocorinae, Alienatinae and Megenicocephalinae, and of the Enicocephalinae all the endemic American, Australian (mostly undescribed) and New Zealand (all undescribed) genera. The Phallopiratinae (inclusive undescribed genera; Oriental region) do not have anteclypeus protruding and antennifers, outstanding, their gena is thicker, eyes are distinctly sunken within the head capsule, and all are larger. The only striking similarity is the presence of continuously distributed, conspicuous setigerous tubercles all over the head. Only few genera of the Enicocephalinae merit comparison; in the species-rich ones the length of gena, size of eyes, distribution of setigerous tubercles and body size usually vary at the species level.

Heads of some endemic Malagasy genera may in some aspects resemble that of *P. jarzembowskii*, but none qualifies for its inclusion**.** *Euchelichir* Jeannel, 1942 (incl. subg. *Desystellores* Villiers, 1958) – PRO: antennifers, insertion of antennae and position of compound eyes relative to the postocular constriction as in *P. jarzembowskii;* gena tubular and long; eyes large and not sunken; CON: anteclypeus not protruding; no setigerous tubercles; larger size (usually much over 6.5 mm); PLH always strongly elongate, with no median. *Henicocorinus* Štys, 1988 – PRO: G extremely long and narrow, parallel-sided; fine setigerous tubercles present though with discontinuous distribution; PLH transverse, with a linear median; CON: anteclypeus not protruding, eyes far too distant from the postocular constriction (by more than length of eye); ocelli in anterolateral position at PLH, not aligned with inner margins of eyes but situated mesad to them. *Proboscidopirates* Villiers, 1958 – PRO: gena long and tubular in some species; CON: anteclypeus not protruding; eyes sunken and much smaller; if setigerous tubercles are present at all, their distribution is discontinuous, or the tubercles are much larger and head irregularly rugulose. PLH elongate. *Trichopirates* Villiers, 1958 – PRO: one of the three species, *T. imaitsoensis* Villiers, 1969, with long, tubular G, more than twice longer than eye. CON: in all other respects different from *P. jarzembowskii.*

Only the five most species-rich genera remain now for comparison, namely a cosmopolitan *Systelloderes* Blanchard, 1852, and the Eastern Hemisphere *Embolorrhinus* Jeannel, 1942 (Afrotropical and Madagascar), *Hoplitocoris* Jeannel, 1942 (Afrotropical, Oriental, E Palaearctic), *Oncylocotis* Stål, 1855 (Palaeotropical and Australian, excl. New Zealand), and *Stenopirates* Walker, 1873 (Oriental, E Palaearctic).

Systelloderes – PRO: gena diverse, long, tubular, parallel-sided in some species (e.g., *S. kivuensis* Villiers, 1960) to absent; eyes often distant from the postocular constriction. CON: anteclypeus not protruding; all species possessing long gena with minute eyes, reduced postocular constriction and elongate PLH; setigerous tubercles absent or localized. The modern range of *Systelloderes* is not overly distant from Europe since an undescribed species is available from Israel (Štys, in prep.).

Embolorrhinus – PRO: anteclypeus strongly exceeding apex of head, straight or arching ventrad in the subgenus *Ceratotrachelus* Usinger, 1945, slightly protruding and often arching ventrad also in some species of *Embolorrhinus* s.str.; setigerous tubercles present continuously all over the head surface, ranging from small, fine, mutually distant (as in *P. jarzembowskii*) up to high, rough, contacting each other. CON: anteclypeus, if produced, very narrow; gena always very short and thick; total length over 8 mm; eyes situated in ventral part of head, outstanding to partly sunken within head capsule.

Hoplitocoris – PRO: anteclypeus narrow, slightly arching ventrad, probably always slightly protruding; antennal insertion subapical, antennifers strongly outstanding; gena always cylindrical, very long, sometimes several times longer than eye; eyes small to large, multifaceted; sculpture of cuticle usually as in *P. jarzembowskii* (continuous region of dense, minute setigerous tubercles) up to continuously granular; CON: eyes shifted posterad, covering dorsolateral parts of the postocular constriction, never remote from the latter, ALH with no postocular lateral margins.

Stenopirates – most species undescribed, hence also comparative data mostly unpublished (Štys, in prep.); head with no particular diagnostic features. PRO: general shape of ALH, eyes, postocular constriction, and PLH in many species resembling *P. jarzembowskii*. CON: anteclypeus not protruding; setigerous tubercles, if present, minute and not giving the head the characteristic rather rough appearance characteristic of *P. jarzembowskii*; most species larger than estimated for *P. jarzembowskii.*

Oncylocotis – most species undescribed and head architecture diverse, without an obvious common ground plan. PRO: gena in some Afrotropical species and in a set of undescribed Oriental and Malesian species long and cylindrical, 2.0 times or more as long as the length of eye; some species with postocular part of ALH well developed; some species with continuously distributed setigerous tubercles. CON: anteclypeus not protruding and proximally delimited by transclypeal sulcus (cf. Štys et al., 2010 – all species?); gena usually broad and short, mostly less than 1.5 length of eye; those Afrotropical species possessing long gena with eyes small and size over 5.5 mm (usually much longer), only *O.* (*Lococytonis*) *bruneaui* Villiers, 1969 (Cameroon) possessing eyes large and distant from a deep postocular constriction but combined with body length 9.8 mm; the set of undescribed Oriental and Malesian species with long gena and very large eyes all large, about 8–10 mm long, all lacking continuously distributed setigerous tubercles; eyes usually slightly sunken; if setigerous tubercles present, then not continuously distributed, less dense and inconspicuous (exc. some undescribed species from Australia); PLH usually more rounded.

(4) Relationships and classification

The above comparisons suggest that the English Clay fossil head does not fit any modern genus of the Enicocephalinae and that establishment of *Pyrenicocephalus jarzembowskii*, gen. et sp. n., is warranted.

In the text below only the unique characters of *P. jarzembowskii, Systelloderes, Embolorrhinus, Hoplitocoris, Stenopirates*, and *Oncylocotis* are identified and the shared similarities assessed.

Protruding anteclypeus (apomorphy) is shared by *P. jarzembowskii, Hoplitocoris* and some *Embolorrhinus* species (extreme protrusion of even ventrally individualized anteclypeus in the subgenus *Ceratotrachelus* is autapomorphic). It is not clear whether synapomorphy or convergences are involved.

Strikingly long gena (undoubtedly an apomorphy) is another inclusive character state shared by *P. jarzembowskii* and *Hoplitocoris* but it occurs in some species of *Systelloderes, Oncylocotis* and *Stenopirates,* and in some Madagascan genera as well; consequently, an overall distribution of this character state must be convergent. Very short gena is frequent in some species of *Systelloderes* and *Oncylocotis*, but it occurs inclusively in *Embolorrhinus* only.

Position of eyes relative to the postocular constriction (constriction situated either just behind the eyes or close to them, or far posteriorly to eyes that were shifted antead) is mostly dependent on the length of genae – the longer the genae the longer usually is the distance eye – postocular constriction. However, the long and rounded "tempora" of *P. jarzembowskii* are probably autapomorphic. *Hoplitocoris* does not fit this rule – its genae are always long but the eyes are invariably situated at the constriction, exceeding it laterally (an autapomorphy).

The occurrence of setigerous tubercles all over the head capsule is apomorphic, occurring convergently in some species or species-groups in *Systelloderes*, *Stenopirates* and *Oncylocotis*, and inclusively in *Hoplitocoris* (the tubercles being sometimes replaced by their granular homologues), *Embolorrhinus* and *P. jarzembowskii.*

Transclypeal sulcus (a symplesiomorphy with "Auchenorrhyncha"?) has only recently been ascertained in *Oncylocotis* (cf. Štys et al., 2010) and I do not know whether its occurrence is inclusive in the genus and cannot assess its polarity and distribution; it is definitely absent in *P. jarzembowskii.*

Flat ocelli and a seeming lack of ocellar tubercles in *P. jarzembowskii* are autapomorphic unless they are taphonomic artifacts.

Some of the genera considered seem to be well identifiable on basis of head characters by their inclusive autapomorphies, namely † *Pyrenicocephalus, Hoplitocoris* and *Embolorrhinus,* the others, namely *Systelloderes*, *Stenopirates* and *Oncylocotis*, do not possess exclusive diagnostic characters (are polythetic respective to cephalic character states), with the possible exception of the presence of a transclypeal sulcus in *Oncylocotis. Systelloderes* is possibly a sister group to the rest of the Enicocephalinae (cf. Wygodzinsky & Schmidt, 1991), *Stenopirates* fall within the group of enicocephaline genera characterized by complete forewing venation and simple midlobe of pronotum (cf. Štys, 2002), while *Onylocotis, Embolorrhinus* and *Hoplitocoris* share complex sculpture of the midlobe, derived from basic *Oncylocotis*-like condition with paired lateral Y-shaped impressions and a medial inversely T-shaped impression. Because *Pyrenicocephalus* shares most of its character states (mostly apomorphic: protruding anteclypeus, excessively long genae, microsculpture) with *Hoplitocoris* (except for different autapomorphic positions of eyes in both, and possibly flat ocelli without ocellar tubercles in † *Pyrenicocephalus*), these two genera are probably sister-groups. Consequently, I dare to predict that † *Pyrenicocephalus jarzembowskii* will also possess a similarly complex architecture of the midlobe of pronotum as *Oncylocotis*-related group of genera.

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