On morphology of *Tanyderus pictus* (Diptera: Tanyderidae) pupa and adult from Chile

О морфологии куколки и имаго *Tanyderus pictus* (Diptera: Tanyderidae) из Чили

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ABSTRACT. The male and female pupae of *Tanyderus pictus* Philippi, 1865 are described, diagnosed, and illustrated for the first time from the specimens collected in Chile. The pupa is distinct from the others known for this family in the cylindrical thoracic horns with the cup-shaped plastron plate at apex, middle leg sheaths shortest, and pairs of protuberances with one central seta surrounded by numerous shorter chaetoids on tergites II–VII. The pupation always occurs inside a log or branch, in the same chamber where larva resided and at least sometimes adult emerges inside the trunk, just where pupation occurred. Several larvae pupated in laboratory and two females emerged, confirming our earlier identification of the larvae as *T. pictus* and their xylophagy. Photographs of live pupae and female of *T. pictus* are included. The female mandibles of *T. pictus* are well developed, sclerotized, and finely toothed along apical margin. The halter of *T. pictus* and some other tanyderids is provided with a short anterobasal projection corresponding to the prehalter of Ptychopteridae.

Introduction

The family Tanyderidae, or primitive crane flies, is an ancient and archaic nematoceran group, known since the Early Jurassic [Ansorge, 1994; Skibińska et al., 2014]. Tanyderids have an amphitropical distribution with higher diversity in the Southern Hemisphere, and were even more widespread in the Mesozoic [Eskov, Lukashevich, 2015]. The family includes 38 extant species in 10 genera. Only three monotypic genera are known in South America, all in the temperate zone and all described from Chile: *Tanyderus* Philippi, 1865, *Neoderus* Alexander, 1927 and *Araucoderus* Alexander, 1929.

Knowledge of tanyderid immatures is sparse (for larvae see a review in [Lukashevich, Shcherbakov, 2014]). The larvae were first discovered and reared to pupa and adult in *Protoplasa flockii* Osten-Sacken, 1860 by Crampton [1930] and Alexander [1930a]. Later the pupae collected together with larvae were described for *Peringueyomyina barnardi* Alexander, 1921 and *Prospanyda margarita* Alexander, 1948 [Wood, 1952; Knight, 1964]. However, larvae are usually found without pupae [Exner, Craig, 1976; Podeniene, Gelhaus, 2013] and only sometimes successfully reared to adults [Pilgrim, 1990]. To date, larvae are not described for the genera *Araucoderus*, *Neoderus* and *Nothoderus* Alexander, 1927, and pupae for these three plus *Tanyderus*, *Radinoderus* Handlirsch, 1909, *Eutanyderus* Alexander, 1928, and *Mischoderus* Handlirsch, 1909 (pupae of *Eutanyderus wilsoni* Alexander, 1928 and *Mischoderus* sp. were obtained but remain undescribed [Hinton, 1966; Pilgrim, 1990]). Tanyderid larvae, but...
The larvae of all three genera, which pupae are described, *Protoplasa* Osten-Sacken, 1860, *Protanyderus* Handlirsch, 1909 and *Peringueyomymina* Alexander, 1921, occur in the hyporheic zone of sand- and cobble-bottom rivers and streams; these pupae were found in drier ridges above the water, to where larvae migrate prior to pupation. No one pupa of xylobiotic genera was described yet.

The type genus of the family Tanyderidae was described a century and a half ago [Philippi, 1865], however up to now this monotypic genus is very rare in collections and only a dozen of adults is known [Alexander, 1936; I.R. Madriz, pers. comm., 2014]. In 2014 we discovered and described tanyderid larvae from logs submerged in streams among *Nothofagus* forests in the national parks Alerce Andino and Nahuelbuta, Los Lagos and Araucania regions, Chile [Lukashevich, Shcherbakov, 2014]. The larvae were identified as *Tanyderus pictus* based on their COI gene sequences being strongly different from those of adult *Araucoderus gloriosus* (Alexander, 1920), the only other tanyderid species known from the region. However no adults or pupae of *T. pictus* were collected by us in 2014. In January 2015 in the national parks Alerce Andino and Alerce Costero, Los Lagos and Los Ríos regions we again collected many larvae and also in the former park a pupal cast and a mature pupa of *T. pictus*. Of numerous larvae from the latter park four pupated in laboratory, one very soon and three several months later, and two *T. pictus* females emerged (Figs 1–4). Our new data confirm the earlier identification of the larvae as *T. pictus* and their xylophagy.

**Material examined**

*Tanyderus pictus* Philippi, 1865


**PUPAE**: Alerce Andino National Park, sector Sargazo, Lenca River, 340 masl, 1 male pupal exuvium #1 and 1 female pupa #2, 17.01.2015, E. Lukashevich; Alerce Costero National Park, sector Chaihuin, 2 km E Chaihuin, 20 masl, 1 male pupa #3, 25.01.2015 (larva pupated in laboratory); 2 female pupal exuvia #4 and #5, 8.03.2015, 12.03.2015 (larvae pupated in laboratory); 1 female pupa #6, 1.05.2015 (larva pupated in laboratory), E. Lukashevich.

**ADULTS**: Alerce Costero National Park, sector Chaihuin, 2 km E Chaihuin, 20 masl, 2 females #4 and #5, 15.03.2015 and 19.03.2015 (emerged as adults from larvae pupated 8.03.2015 and 12.03.2015 in laboratory).

**Methods**

All field-sampled and reared specimens were put in 70% ethanol, one reared female was pinned.

The larvae were transferred to the laboratory along with their native substrate. They were kept in plastic boxes with *Nothofagus* branches (10–20 cm long and 2–6 cm in diameter, with or without bark); the water covered only the container bottom, without any circulation; most part of branches were wet, but out of water. We maintained containers at ambient room temperature of the laboratory at day and kept cool at night (15º C); the containers were checked daily for pupated larvae (later for reared adults) and misted with water.

Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera, Z-stacked using Helicon Focus 4.10 Pro and adjusted in Adobe Photoshop® CS3 10.0. For scanning electron microscopy (SEM) two pupal exuvia were dehydrated in graded alcohols, soaked in hexamethyldisilazane, and dried. Scanning electron micrographs of uncoated and gold-coated specimens were taken with a Tescan Vega microscope using backscattered electron (BSE) and secondary electron (SE) detectors.

The morphological terminology generally follows that of Crampton [1930] and Wood [1952].

**Abbreviations used in the figures**

al anterior lateral or pleural setae and seta-bearing processes
ant antenna
apa anterior parietal setae and processes
as antesternite
asp postabdominal spiracle
at antetergite
atg anterior tergal seta
b bubbles
ba raised basalar area and setae
bc basi cercus
dc disticerus
es epistomal setae
fl hind leg
fp frontal setae and processes
ge gonocoxite
gs gonostyle
h thoracic horn
hl hind leg
hp hypopharynx
l labrum
lp labial palpus
lpr lateral processes
md mandible
ml middle leg
mn metanotum
mp maxillary palpus
mx maxilla
pf prefrontal setae
ph prehalteral setae
pl posterior lateral or pleural setae and processes
po precocular setae
pp posterior parietal setae and processes
ps posterior sternal setae
pt posterior tergal setae
sc scutal setae
gs genal or subgenal setae
sp rudimentary spiracle
tg tegular region and setae
vp verriculate protuberance
Localities, habitats and behaviour

The larvae were collected in the national parks Alerce Andino and Alerce Costero (Figs 5–6), in Nothofagus-dominated forests containing other broadleaved trees and rare conifers (Fitzroya). The site in Alerce Andino, the same one as in 2014, was the forested fast-flowing Lenca River, at 340 masl, with a shingle bottom, abundant detrital material, most of which is woody and probably originates from abrasion of drifting trees during high water levels, and almost whole dead Nothofagus trees, occasionally with preserved bark. The river in that area is about 10 m wide and 0.4–1 m deep, with occasional diagonal and mid-channel bars. Some logs with larvae laid on the fast-flowing midstream, some in the quiet backwater, all logs possessed bark, and some of them were out of the water when its level dropped. About 20 larvae were collected from 8 logs in three sites (two extreme sites approximately 1 km apart) during one week. In all three sites several adults of Araucoderus gloriosus were captured, and again no adult Tanyderus pictus though a male pupal cast and a mature female pupa were found, so adults of the latter genus were already “on wing” in mid-January.

In 2014 we have found only two logs with larvae in Alerce Andino, and in both larvae lived without chambers crawling under the bark in a smell semi-liquid pulp. Such conditions turned out to be optional: in 2015 we discovered larvae in deep straight chambers under the surface of wood as well as in branched chambers just under the bark with numerous crushed wood fragments inside. The larvae collected in Alerce Andino in 2015 are similar in size to those collected there a year before [Lukashevich, Shcherbakov, 2014].

The Nothofagus branch (0.8 m long and 8 cm in diameter) which yielded the male pupal cast #1 and mature female pupa #2 laid on the horizontal support of the old wooden bridge (clearly brought by spring flood, being absent one year before, Fig. 5), with pupal cast #1 occurring in the dry part of the branch and pupa #2 in a narrow chamber under a knot near the boundary of dry part (Fig.1, pupa #2 in situ, bark removed). The pupal cast #1 didn’t protrude from the branch surface as one can see in various limoniid pupae, and was found near a larval exuvium retaining the head capsule in a narrow chamber under the bark. Besides tanyderids, only numerous red larvae of Chironominae and pupae of Coleoptera were found in this branch.

The sector Chaihuín of Alerce Costero National Park is about 40 km from Los Ulmos, Valdivia where the holotype of T. pictus was captured in March 1865. In January 2015 no adult Tanyderidae was collected by us, only numerous larvae. Almost two dozen of logs with larvae were found during one week in two small forested creeks (sandy bottom, 0.1–0.2 m deep, 2 km apart) and in shallow backwaters of the large Chaihuín River and its tributary (sand-mud substrate at the water’s margin near gravel-cobble main bed, <0.5 m deep). Some of these branches were with bark and some without, some were solid and some saturated, decomposed, easily disintegrating into whitish fibres. The most productive log (1.5 m long, 25 cm in diameter) that yielded more than 70 larvae of second to forth instars was without bark, with very soft, decomposing outer layers. Numerous larvae and pupae of non-aquatic Coleoptera, Neuroptera and Diptera were found together with tanyderid larvae, some of the latter dwelling in the beetle galleries partly filled with frass but always near the solid wood still light in colour.

Larvae from Alerce Costero are clearly larger then those from Alerce Andino and on average larger than those from the Nahuelbuta National Park [Lukashevich, Shcherbakov, 2014]: Alerce Costero: 4th instar (n=7): head length 2.45–3.10 (mean 2.84) mm, width 2.1–2.55 (mean 2.4) mm, maximum total body length 55 mm including 8.5 mm tail filaments; 3rd instar (n=16): head length 1.65–1.90 (mean 1.75) mm, width 1.4–1.65 (mean 1.47) mm; 2nd instar (n=5): head length 1.00–1.65 (mean 1.35) mm, width 0.9–1.45 (mean 1.2) mm.

We tried to rear one dozen of large larvae of forth instar just in Alerce Costero, but only one #3 found on 23 January in a narrow chamber, situated under a knot of short branch (25 cm long, 5 cm in diameter), pupated very soon, on 25 January in the same chamber (Fig. 2). The male pupa #3 maturated for a week, with adult colouration and setation becoming visible (Fig. 29), but died on 1 February occasionally damaged by another larva. Three larvae pupated in laboratory inside the branches: #4 and #5 probably on 8 and 12 March (pupae were seen on 11 and 16 March, respectively), and #6 on 1 May. The pupae #4 and #5 were reared into females of T. pictus on 15 and 19 March, respectively (Figs 3, 4, 7–11); the female pupa #6 died on 11 May. The larva #4 escaped into chambers existing under the bark on 1 February and dwelt inside up to the pupation (probably on 8 March); the larva was checked once per two weeks by removing the bark (was found in a fresh self-dug chamber near a knot) or outer layer of wood (was found in an old long chamber directed into empty middle part of the branch); when disturbed, the larva retreated into another chamber and never returned to the previous one in spite of putting back the bark or piece of wood. The larva #5 was inside the branch since the end of January in Alerce Costero and wasn’t seen before pupation: the pupa occurred on the surface of the branch on 16 March already with dark pattern on the wings, therefore several days after pupation. The larva #6 crawled in the water layer under the branch and wood fragments six weeks (with dark gut content), sometimes hided under the bark partly or entirely and later crawled outside. This larva hid inside finally only in the middle of March, six weeks before its pupation on 1 May, and almost every day a new portion of crushed wood fragments appeared at the exit of its self-dug chamber, which was situated near a knot and later extended around the knot, subparallel and close to the surface (the light of illuminator fibres from outside was visible inside). During a month one can see the head of larva directed to the chamber exit, and later
Figs 1–6. Live *Tanyderus pictus* and their habitats: 1 — female pupa #2 *in situ* (Alerce Andino, 17.01.2015); 2 — freshly moulted male pupa #3 (Alerce Costero, 25.01.2015); 3–4 — female #5 (photographs by R. Rakitov) and its pupa (Alerce Costero, reared from larva in laboratory, 19.03 and 18.03.2015); 5 — Lenca River, Alerce Andino; 6 — tributary of Chaihuin River, Alerce Costero; arrows, location of finds of larvae and pupae.

Рис. 1–6. Живые *Tanyderus pictus* и их местообитания: 1 — куколка самки #2 *in situ* (Алерсе Андино, 17.01.2015); 2 — свежевылупившаяся куколка самца #3 (Алерсе Костеро, 25.01.2015); 3–4 — самка #5 (фото Р. Ракитова) и ее куколка (Алерсе Костеро, выведены из личинки в лаборатории, 19.03 и 18.03.2015); 5 — р. Ленка, Алерсе Андино; 6 — приток р. Чайун, Алерсе Костеро; стрелки, места находок личинок и куколок.
the thoracic horn and part of cephalothorax of the pupa at depth 2 cm, whereas the major part of the larva or pupa was situated “behind the corner”, beyond the knot and was invisible. When disturbed (e.g. by the light of illuminator), the larva as well as pupa #6 retreated “behind the corner” becoming invisible through the chamber exit.

The pupation in all three cases occurred in the same chamber where the larva dwelt (as a result, the larval exuvium was always found nearby). The pupa #4 quickly reared in the same place where larva and pupa resided and pupal and larval exuvia were found nearby. The pupa #5 crawled onto the side saw cut of the branch and was positioned with the cauda up anchoring by cephalothorax. The pupa #6 crawled out of the chamber on the tenth day, was positioned with the cauda up, however in the night returned into its chamber and died inside.

Summarizing, T. pictus, once considered quite rare, can be abundant (about one hundred larvae of various instars in a single 1.5 m log) in suitable lotic habitats, including rivers and streams in Nothofagus-dominated forests, with trees growing close to the water. Like in many other xylobiotic Diptera [Krivosheina, Mamajev, 1967] several females may lay eggs into the same part of a fallen rotting log, so a colony is formed; females probably oviposit for a long time, not simultaneously, as a result the colony consists of larvae of various ages. The larvae dwell in logs (more than 20 cm in diameter) and small branches (3–5 cm in diameter) with and without bark, at various stages of wood decay (solid or saturated, decomposed, easily disintegrating into whitish fibres). Larvae move easily not only in semiliquid pulp just under the bark but also through self-dug narrow chambers in the solid wood, sometimes with the abdominal apex forwards. As we can conclude based on laboratory rearing, larvae are semiaquatic but can survive for a long time outside the branch, in the water, provided with abundant decaying wood fragments on the bottom, though we didn’t find any larvae outside the logs. Probably at least a month before pupation the larva hides inside the log and in this case its relatively short chamber is positioned not far from its surface. However usually larvae live inside logs during the whole larval life, and their chambers become longer (sometimes branched) and much deeper into the wood with the age. Larvae push debris out of their chambers, from a short chamber just onto the outside surface of the log lacking bark, or in the more usual long gallery just behind the larva, nearer to the gallery exit (in Fig. 1 numerous crushed wood fragments puddled by larva are visible all round the pupa). Pupation always occurs in the wood, in the same chamber where the larva resided, and at least sometimes the adult emerges inside, where pupation occurred. Duration of pupal stage is no less than 7, probably 8–10 days. Probably larvae never pupate in underwater logs, only in drier parts of partly submerged logs or after the water level dropping in summer.

Most of behaviour peculiarities noted here, are similar to those described recently in detail for another wood-inhabiting, semiaquatic fly Axymyia furcata McA-
te, 1921 [Wihlm, Courtney, 2011]. It is worth to mention that when tanyderid larvae were still unknown, it was the axymyiid larvae found in saturated logs were mistakenly referred to Tanyderidae [Alexander, 1927], therefore Alexander and Crampton “began a critical survey of all saturated logs, stranded and imbedded in the earth at the stream margin” where a large swarm of Protoplasa was seen earlier [Alexander, 1930a]. However the first tanyderid larvae were discovered there in sandy gravel at the water’s margin, and only many years later it became obvious that saturated logs indeed are a suitable habitat for semiaquatic larvae of several genera of Tanyderidae [Colless, McAAlpine, 1970; Krzeminski, Judd, 1997; Judd, 2004].

Kovalev [1984] supposed the dwelling deep in the submerged wood or bottom substrate to be the oldest mode for dipteran larvae, and explained the absence of the fossil Late Triassic and Early Jurassic dipteran larvae by such mode of life unfavourable for burial. Now in spite of their real rarity the immatures of Diptera are known since the Middle Triassic [Lukashevich et al., 2010], however larvae of Tanyderidae are exceptionally rare in the fossil record—so far only two larvae in one Late Jurassic locality [Lukashevich, Krzeminski, 2009].

Morphology of Tanyderus pictus

**Adult.** Two reared females from Alerce Costero (Figs 3, 7–11) fit the descriptions of the holotype (male?) from nearby Los Ulmos [Philipi, 1865; Alexander, 1913] and allotype female from Concepción [Alexander, 1929, 1930b], their wing venation and colour pattern being as figured by Williams [1933; fig. 34], but their size smaller than in historical specimens: total length 23–24 mm, wing length 21–22 mm, compared to 35 mm and 31.5 mm in the allotype. Description of the adult is supplemented with several characters:

- Short hairs between ommatidia (as in all Tanyderidae [Alexander, 1927]). Female dichoptic, interocular distance about two diameters of ommatidia; posterior part of cranium with long dense setae (Figs 12, 15). Clypeus cl very strong, with several dozen of marginal and distal setae (Figs 12, 14). Antenna with 22–25 flagellomeres (22 in female #5; Fig. 11). Mouthparts moderately elongate. Labrum l sclerotized, subequal to clypeus, with apertures of unclear nature at base (Figs 13–14). Mandibles md and maxillae mx rather broad blades obliquely truncate apically; mandibles overlapped, sclerotized, apex acute, inner apical margin dark and minutely denticulate; maxillae with sclerotized shaft near outer margin and weakly sclerotized inner area, apex narrowly rounded, inner apical margin translucent with submarginal row of minute, short, spaced ridges; hypopharynx hp trough-like, sclerotized, microscopically denticulate on margin, with dark salivary canal. Maxillary palpai mp elongate, densely pubescent; labial palpi, or labellae lp large, two-segmented; mandibles and maxillae slightly shorter than labrum and hypopharynx, two latter somewhat protruding between labellae in repose (Figs 13, 20–21). Wing venation: usually Rs forked into R5 and R2+3+4, but in our specimens origin of R5 very close to origin of R4+5, and sometimes even just beyond it (in the case R4 shorter than crossvein r-m—in both wings of female #5; Figs 3, 16). Halter with short anterobasal projection (Figs 22–24). Claws simple, arolium, empodium and pulvilli ab-

Рис. 7–11. Живая самка *T. pictus* #5 (Алерсе Костеро, фото Р. Ракитова, 19.03.2015): 7 — общий вид сверху; 8 — голова сбоку; 9 — конец брюшка сверху; 10 — брюшко, сбоку; 11 — общий вид, сбоку.
Figs 12–19. Female T. pictus #5 (Alerce Costero; SEM, uncoated, BSE): 12–14 — head and mouthparts frontally; 15 — eye; 16 — part of wing (inset, female #4, photograph, part of wing); 17–18 — claws dorsally and ventrally; 19 — cerci dorsolaterally.

Рис. 12–19. Cамка T. pictus #5 (Алерсе Костеро, СЭМ, без напыления, BSE): 12–14 — голова и ротовые части спереди; 15 — глаза; 16 — часть крыла (врезка, самка #4, фото, часть крыла); 17–18 — коготки сверху и снизу; 19 — церки сверху-сбоку.
Figs 20–27. Details of adult: 20–24 — T. pictus; 25 — Araucoderus gloriosus; 26 — Macrochile spectrum; 27 — Ptychoptera handlirschi (Czizek, 1919); 20–21 — female #4, mouthparts; 22–24 — female #5: 22 — head and thorax laterally; 23 — rudimentary prehalter; 24–27 — base of halter with (rudimentary) prehalter; 23–24, 27 — SEM, uncoated, BSE; arrow, rudimentary prehalter; homologous parts numbered.

Рис. 20–27. Детали строения имаго: 20–24 — T. pictus; 25 — Araucoderus gloriosus; 26 — Macrochile spectrum; 27 — Ptychoptera handlirschi (Czizek, 1919); 20–21 — самка #4, ротовые части; 22–24 — самка #5: 22 — голова и грудь сбоку; 23 — зачаточный прехальтер; 24–27 — основание жужжалца с (зачаточным) прехальтером; 23–24, 27 — СЭМ, без напыления, BSE; стрелка — зачаточный прехальтер; гомологичные части пронумерованы.
sent (Figs 17–18). Female cercus orange, of two segments, basicercus $bc$ and disticercus $dc$, both relatively large and elongated (Figs 9–10, 19); in female #5 one basicercus with abnormal narrow projection (Figs 9, 19).

In the mature pupa (with pharate adult inside) some details of adult habitus, colouration and setation characteristic of $T. pictus$ are visible (Figs 4, 28–39): 22–25 flagellomeres (probably 26 in male); peculiar dark spots on yellow tergites and sternites; venation with Rs forking into $R_1$, $R_2$, and $R_3$ with base of $R_1$ very close to nearest fork and two supernumerary veins in r4 and r5 cells; peculiar dark pattern on wing with pale distal triangle whereas the other pale areas of adult wing being grey and separated by pale stripes from dark distal Y-shaped and middle X-shaped bands and the base of wing; dark knob and pale stem of halter; dark femur and dark ring on tibia below pale knee, pale lower part of tibia and tarsus; yellow female cerci (orange in adult).

**Pupa.** The following characters, common to all the described tanyderid pupae, appear to be of the family level and thus are not repeated below: Thoracic horns equal in size. Sheaths of maxillary palpi very stout, five-segmented, bent upward (directed laterad and then cephalad). Abdominal tergites I–VII each with transverse row of strong setae on prominent tubercles near posterior margin, tergites VIII–IX each with transverse row of strong setae at the posterior margin.

**DESCRIPTION.** Prominent setation on cephalothorax and abdominal tergites; no frontal horns or epistomal processes; thoracic horns small, almost cylindrical, with comparatively small, cup-shaped plastron plate at apex; tergites I–VII in middle part with pair of verruculose protuberances with one central seta surrounded by numerous shorter parallel chaetoids; leg sheaths overlapping, unequal in length, middle pair shortest, hind longest.

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**COMPARISON.** Distinct from the other described pupae of Tanyderidae (i.e. from *Protoplasa*, *Protanyderus* and *Peringueyomyina*) in the presence of paired verruculose protuberances on tergites II–VII, cylindrical thoracic horns with a cup-shaped plastron plate at apex, and the middle leg sheaths shortest. Similar to African *Peringueyomyina* in the absence of frontal horns, presence of three uniform tuberculate setae dorsad of antennal base, and overlapping leg sheaths, but the latter genus is distinct in the shorter leg sheaths reaching only abdominal segment III and sclerotized cauda. It is unknown

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**DESCRIPTION.** Prominent setation on cephalothorax and abdominal tergites; no frontal horns or epistomal processes; thoracic horns small, almost cylindrical, with comparatively small, cup-shaped plastron plate at apex; tergites I–VII in middle part with pair of verruculose protuberances with one central seta surrounded by numerous shorter parallel chaetoids; leg sheaths overlapping, unequal in length, middle pair shortest, hind longest.

**DIAGNOSIS.** Prominent setation on cephalothorax and abdominal tergites; no frontal horns or epistomal processes; thoracic horns small, almost cylindrical, with comparatively small, cup-shaped plastron plate at apex; tergites I–VII in middle part with pair of verruculose protuberances with one central seta surrounded by numerous shorter parallel chaetoids; leg sheaths overlapping, unequal in length, middle pair shortest, hind longest.

**COMPARISON.** Distinct from the other described pupae of Tanyderidae ([i.e. from *Protoplasa*, *Protanyderus* and *Peringueyomyina*]) in the presence of paired verruculose protuberances on tergites II–VII, cylindrical thoracic horns with a cup-shaped plastron plate at apex, and the middle leg sheaths shortest. Similar to African *Peringueyomyina* in the absence of frontal horns, presence of three uniform tuberculate setae dorsad of antennal base, and overlapping leg sheaths, but the latter genus is distinct in the shorter leg sheaths reaching only abdominal segment III and sclerotized cauda. It is unknown
whether *Peringueyomyina* has apical plastron plate in thoracic horn or sheaths of cerci on segment X in male.

In its larval characters *Tanyderus* is similar to but distinct from *Mischoderus*, *Radinoderus* and *Eutanyderus*, and some species of these genera also have xylobiotic larvae. The pupae of three latter genera remain undescribed, except for the structure of thoracic horns in *Eutanyderus* [Hinton, 1966] which differs markedly from that of *Tanyderus*. Since the pupa of *T. pictus* is the first xylobiotic pupa known, one can expect to find significant differences from hyporheic pupae. However

Figs 41–49. Details of male pupal exuvium of *T. pictus* #1 (Alerce Andino; SEM, uncoated, BSE): 41 — face; 42 — thoracic horn; 43 — scutal setae (fore pair abnormal); 44 — middle group of additional spinules on tergite V; 45 — tergites VI–VII; 46–47 — cauda dorsally and caudally; 48 — distal part of lateral process on tergite VIII; 49 — lateral process on tergite IX.

Рис. 41–49. Детали строения экзувиев куколки самца *T. pictus* #1 (Алерсе Андино; СЭМ, без напыления, BSE): 41 — лицо, 42 — торакальный рог; 43 — скутальные хеты (первая пара — аберрантная); 44 — срединная группа шипиков на тергите V; 45 — тергиты VI–VII; 46–47 — конец брюшка сверху и сзади; 48 — конец бокового выроста на тергите VIII; 49 — боковой вырост на тергите IX.
we failed to find such difference e.g. from *Protoplasa* described in detail by Crampton, except for unique verriculate protuberances and the absence of frontal horns (the latter shared with hyporheic *Peringueyomyina*); the unique leg sheath pattern with the shortest middle pair is apparently associated with life mode of adults rather than that of immatures.

Discussion

**Mandibles.** Crampton [1930] discovered the small and rather indistinct processes on the pupal exuvium of *Protoplasa* and supposed that they probably are mandible sheaths, Knight [1964] also noted these small pro-

Figs 50–55. Details of female pupal exuvium of *T. pictus* #5 (Alerce Costero; SEM, coated, BSE): 50 — face; 51 — mouthparts; 52 — distal part of thoracic horn with plastron; 53 — part of plastron; 54 — cauda ventrally; 55 — postabdominal spiracle dorsally.

Рис. 50–55. Детали строения экзувия куколки самки *T. pictus* #5 (Алерсе Костеро, СЭМ, напылено золотом, BSE): 50 — лицо; 51 — ротовые части; 52 — дистальная часть торакального рога с пластроном; 53 — часть пластрона; 54 — конец брюшка снизу; 55 — заднее дыхальное сверху.
Figs 56–64. Chaetotaxy of female pupal exuvium of *T. pictus* #5 (Alerce Costero; SEM, coated, BSE): 56 — tergite I; 57 — antetergite II; 58 — tergite II; 59 — middle group of additional spinules on tergite II; 60 — pleurite V; 61 — middle group of additional spinules on tergite VI; 62 — verruculate protuberance on tergite V; 63 — posterior part of sternite V; 64 — antesternite VI.

Рис. 56–64. Хетотаксия экзувия куколки самки *T. pictus* #5 (Алерсе Костеро, СЭМ, напылено золотом, BSE): 56 — тергит I; 57 — антетергит II; 58 — тергит II; 59 — срединная группа шипиков на тергите II; 60 — плеврит V; 61 — срединная группа шипиков на тергите VI; 62 — щетконосный вырост на тергите V; 63 — задняя часть стернита V; 64 — антестернит VI.
cesses, however no mandibles were found in a morphological study of the adult [Williams, 1933]. Later Downes, Colless [1967] briefly noted that in the adult Protoplasa mandibles are clearly developed, but small and unarmed, whereas the adult Radinoderus occidentalis (Alexander, 1925) possesses fully developed mouthparts, both mandibles and maxillae being broad thin blades and mandibles armed with very fine closely set teeth down the inner margin. Until now the adult mandibles were not illustrated or described in detail in any living Tanyderidae. However, in the minute, sandfly-teeth down the inner margin. In the pupa of Tanyderus the outer anterior tergal seta weakened and the inner one shifted mediad, strengthened and complicated. We failed to find the structures similar to verruculate protuberances in other dipteran pupae, in any case they are uncommon.

In the pupa of Protoplasa Crampton described 1 anterior lateral seta al just behind the spiracle and 3 subeuqal posterolateral setae pl in the posterior row on pleurites I–VII. The similar pattern was found by us in Tanyderus larvae (also with subequal setae) [Lukashchevich, Shecherbakov, 2014: figs 16, 18] and herein in its pupa, where both outer setae pl are much stronger than the middle one (Figs 36, 60). The arrangement of posterior tergal setae on the pupal tergites I–VII just before the posterior margin with a transverse row of 4 large tubercles on each side, 1 medial pt, and 3 lateral pl_{2,4} (Figs 39, 45, 58), also follows the larval pattern. Conformity of larval and pupal chaetotaxy was demonstrated e.g. for abdominal setae in Ceratopogonidae [Lawson, 1951; Urbane et al., 2015].

**Legs of pupa.** Fore legs of the adult Tanyderus are the longest due to the longest tarsi (fore leg/tarsus length 36/14 mm compared to 33/12 mm for middle and 34/11 mm for hind legs in female #4), so that in its pupa the fore leg sheaths surpass the middle, but not the hind sheaths (in pupae the length of leg sheaths is compared by the position of their tips). Such pupal pattern with the sheaths of middle legs shortest is extremly rare in Diptera and described in Tanyderidae for the first time. Oosterbroek, Theobald [1991] considered the pattern with shortest middle sheaths (and all leg sheaths lying side by side as usual in Tipulomorpha) as a synapomorphy of Eriopterinae (Limoniiidae) noting that it “apparently does not occur in other Nematocera.”

The leg sheaths are longer in the Tanyderus male pupa (reaching to the abdominal segment VI) than in the female pupa (only to the base of V segment), and this cannot be attributed to variable extension of the abdomen, because the male pupa and one of two female pupae were fixed dead and another female pupa alive.

**Cauda of pupa.** Crampton [1930] compared the pupa of Protoplasa with that of limoniid Eriocera Macquart, 1838 (now a subgenus of Hexatoma Lateille, 1809) and found a great similarity in their cephalothorax. It is interesting that the processes of abdominal apex are also widespread in Limoniidae Limnophilinae (former Hexatomenae) often possessing three pairs of robust dorsal spines [Savchenko, 1986; Podeniene, Gelhaus, 2010]. Probably, the most similar pattern of abdominal apex with similar proportions of parts one can find in the pupa of Leptotarsus Guérin-Méneville, 1831, one of the basal genera of Tipulidae and the oldest known member of the family [Ribeiro, Lukashchevich, 2014]. In male pupal exuvia of Leptotarsus (Longius) testaceus (Loew, 1869) tergites VIII–IX likewise bear lateral processes (= dorsal lobes), all with small spines along length and “two dome-like protuberances between genital sheaths and dorsal lobes, each protuberance with distinct papillae at apex” [Gelhaus, Young,
compared halters of extinct be a precursor of the prehalter—a peculiar appendage 1850 (Baltic amber, Eocene) and supposed that it may opposite to tarsal claws (present in Chilean was suggested as a synapomorphy linking Tanyderidae Sinclair, 2012]. Indeed up to now only one character teridae with Culicomorpha and Bibionomorpha [Borkent, deridae lacking the synapomorphy grouping Ptychop- tion” was discovered in the male genital tract of Tany- infraorders. Recently “no evidence of sister group rela- but some authors place them even into the different Oosterbroek, Courtney, 1995; Shcherbakov et al., 1995], closely related [Hennig, 1973; Wood, Borkent, 1989; Shcherbakov et al., 1995], but some authors place them even into the different infraorders. Recently “no evidence of sister group relation” was discovered in the male genital tract of Tanyderidae lacking the synapomorphy grouping Ptychopteridae with Culicomorpha and Bibionomorpha [Borkent, Sinclair, 2012]. Indeed up to now only one character was suggested as a synapomorphy linking Tanyderidae and Ptychopeteridae, the claspers organ on male tarsi — tarsomere IV with basal swelling bearing tufts of setae opposite to tarsal claws (present in Chilean Araucoderus, pers. obs.).

Crampton [1926] discovered a projection on the halter of fossil tanyderid Macrochile spectrum Loew, 1850 (Baltic amber, Eocene) and supposed that it may be a precursor of the prehalter—a peculiar appendage from the halter base in Ptychopeteridae, considered to be unique within the Diptera [Wood, Borkent, 1989]. We compared halters of extinct Macrochile and extant Tanyderus and Araucoderus and have found very similar short projections, positioned at the same place as prehalters of Ptychoptera (Figs 22–27), but tanyderid projections are not so well developed, so we agree with Crampton’s suggestion. In the case the presence of the prehalter in Tanyderidae can be considered a synapomorphy with Ptychopeteridae.

**Tanyderidae and Ptychopeteridae.** Traditionally Tanyderidae and Ptychopeteridae are considered to be closely related [Hennig, 1973; Wood, Borkent, 1989; Oosterbroek, Courtney, 1995; Shcherbakov et al., 1995], but some authors place them even into the different

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**References**


On morphology of Tanyderus pictus pupa and adult from Chile


