Bisonicola sedecimdecembrii (Phthiraptera: Trichodectidae) from European bison – redescription of adults and description of juvenile stages

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Bisonicola sedecimdecembrii is a specific parasite of the genus *Bison*. The European bison became completely extinct in natural conditions at the beginning of the 20th century, and the currently existing wild populations are a result of successful restitution and reintroduction. Only three European bison-specific parasites have survived until now, including the chewing louse *B. sedecimdecembrii*, described from the female by Eichler (1946). This paper redescribes the adults and describes the juvenile stages for the first time, based on the analysis of 1,203 specimens of *B. sedecimdecembrii* from 115 bison from Poland.

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1. Introduction

Chewing lice are obligatory parasites of birds and mammals that developed high host specificity. Among European mammals, specific chewing lice species dwell in carnivores and ungulates, including the European bison *Bison bonasus* (Linnaeus, 1758). It is the biggest living European animal and a relic of the Pleistocene megafauna, occurring across almost the whole forested area of the west, central and south-east part of the continent after the last glaciation. The species became completely extinct in natural conditions at the beginning of the 20th century, and the currently existing wild populations are a result of successful restitution and reintroduction. Lowland European bison (Lowland Wisent) *B. b. bonasus* survived the longest in the wild in Poland in the Białowieża Primeval Forest. The Białowieża European bison population included 350–1,900 individuals until the World War I, and the last European bison died in the wild in 1919. On the other hand, highland European bison (Caucasian bison, Caucasian Wisent) *B. b. caucasicus* died in 1927 in the Caucasus. In 1929 in the Białowieża Primeval Forest, reintroduction of the species has been started in a closed breeding facility on the basis of few individuals that survived in zoological gardens and breeding centres. In 1952 a release programme of European bison was launched; the bison were also transferred to other places in Poland and Europe (Krasińska & Krasiński 2007). At present, representatives of two genetic lines – the Lowland line (*B. b. bonasus*) and the Lowland-Caucasian line, occur in the wild (*B. b. bonasus* x *B. b. caucasicus*).

In the composition of European bison parasitic fauna, only three European bison-specific species survive – the blood parasite *Trypano-*

soma wrublewskii Wladimiroff & Yakimoff, 1909, the chewing lice *Bisonicola sedecimdecembrii* (Eichler, 1946) and the skin mite *Demodex bisonianus* Kadulski & Izdebska, 1996. The parasites survived a breakdown of the size of the host population, extinction of free-ranging herds and the time of reintroduction on the basis of individuals obtained from breeding. At present they commonly occur in the populations of European bison. However, the infestations are usually asymptomatic, which presumably results from the perfect adaptation acquired during the long-term coevolution of the host-parasite system (Izdebska 2006). Hence they are an extremely interesting subject of research, although they are very difficult to obtain, as European bison are animals subject to strict species protection in their areas of occurrence, listed in the IUCN Red List of Threatened Species.

The chewing louse was described as *Bovicola sedecimdecembrii* by Eichler (1946) on the basis of several museum preparations obtained from specimens from Białowieża European bison in 1918, and the laconic description published at that time applied only to a female. That material lacked males, which the author accounted for by the possibility of parthenogenesis, which is founding some other Trichodectidae with rare occurrence of males. In 1960 Hopkins completed the description with characterization of a male and a female obtained from American bison. The name *Damalinia sedecimdecembrii* was used in the studies on the parasitic fauna of *Bison bison* (Hopkins 1960, Fuller 1966, McHugh 1972), sometimes also for *B. bonasus* (Hopkins & Clay 1952).

Furthermore, Blagoveshtchensky (1967) regarded American bison chewing lice as a separate subspecies (*Bovicola sedecimdecembrii bison*), and thus forms deriving from European bison were named as a nominotypic subspecies. During the systematic revision of Trichodectidae based on the cladistic analysis, Lyal (1985), on the basis of the specimens of Eichler and Blagoveshtchensky, classified chewing lice of this species into a separate genus – *Bisonicola*. In turn, Price *et al.* (2003) regard *Bisonicola* as a subgenus of *Bovicola* and they do not regard the subspecies *Bisonicola sedecimdecembrii bison* as a valid taxon but as a junior synonym of *Bisonicola sedecimdecembrii sensu stricto*. However, this paper (Price *et al.* 2003) does not introduce weighty facts, so it seems appropriate to use a name previously used in European literature (Mey 1988, Złotorzycka 1994, Izdebska 2003).

From the time of discovery of chewing lice, it was not until the 1970s – 1980s that the parasites were found for the second time during a study on the parasitic fauna of more than a dozen European bison from the Białowieża Primeval Forest (Kadulski 1977, 1989). Then some studies at the turn of the centuries on almost half of the Białowieża population and European bison from other free-ranging herds and closed breeding facilities in Poland demonstrated that chewing lice are common at least in half of the hosts, however, they usually exhibit low intensity of infestation and rarely cause mallophagosis (Izdebska 2003). Chewing lice were found in the European bison of the both genetic lines (Izdebska 2001a, 2001b, 2001c).

So far, the only data on the occurrence of *B. sedecimdecembrii* in European bison from wild populations, breeding centres and zoological gardens are from Poland. Parasitological parameters of chewing lice infestation of host populations, host site preference, dynamics of occurrence, and population structure were described by Izdebska (2003). However, so far there is no detailed morphological characterisation of the lice, as the existing characterisation performed on the basis of only a few specimens does not take into account either the individual variation or the description of juvenile stages.

2. Material and methods

The material collected within the fourteen years (1992–2005) was used for the multi-directional analysis of European bison parasitic arthropods. The study included almost one-third of the Polish bison population (about 250 individuals). The European bison came from free-ranging herds (from Białowieża Primeval Forest and Bieszczady Moutains), closed breeding facilities (Niepołomice, Smardzewice, reserve in Białowieża Forest) and zoological gardens (Gdańsk Oliwa). The material was collected during autopsies of European bison from selective and reduc-

Table 1. Means, ranges and standard deviations of different features of *Bisonicola sedecimdecembrii* (100 specimens of each group).

Features*	Nymph I	Nymph II	Nymph III	Male	Female
Head-L	0.31 [0.25–0.39] *SD* 0.04	0.36 [0.30–0.46] *SD* 0.05	0.42 [0.32–0.50] *SD* 0.07	0.42 [0.38–0.47] *SD* 0.03	0.45 [0.36–0.51] *SD* 0.04
Head-W	0.32 [0.26–0.45] *SD* 0.13	0.37 [0.26–0.51] *SD* 0.09	0.44 [0.27–0.58] *SD* 0.12	0.46 [0.35–0.50] *SD* 0.04	0.52 [0.47–0.59] *SD* 0.04
Thorax-L	0.17 [0.11–0.28] *SD* 0.05	0.22 [0.14–0.28] *SD* 0.05	0.26 [0.16–0.37] *SD* 0.08	0.30 [0.19–0.38] *SD* 0.07	0.33 [0.23–0.42] *SD* 0.07
Thorax-W	0.29 [0.23–0.39] *SD* 0.05	0.34 [0.27–0.47] *SD* 0.06	0.40 [0.28–0.48] *SD* 0.08	0.43 [0.36–0.50] *SD* 0.03	0.47 [0.40–0.54] *SD* 0.05
Abdomen-L	0.63 [0.45–0.83] *SD* 0.12	0.87 [0.50–1.14] *SD* 0.25	1.09 [0.69–1.33] *SD* 0.22	1.20 [0.74–1.41] *SD* 0.19	1.35 [0.98–1.53] *SD* 0.15
Abdomen-W	0.45 [0.32–0.64] *SD* 0.10	0.60 [0.47–0.74] *SD* 0.10	0.75 [0.55–0.98] *SD* 0.16	0.70 [0.59–0.81] *SD* 0.08	0.87 [0.65–1.04] *SD* 0.08
Body-L	1.15 [0.87–1.43] *SD* 0.17	1.50 [1.10–1.84] *SD* 0.22	1.74 [1.39–2.09] *SD* 0.22	1.92 [1.59–2.23] *SD* 0.21	2.16 [1.82–2.39] *SD* 0.16

* L: length, W: width

ing culling performed in the Białowieża Primeval Forest and other centres with the approval of the Polish Ministry of the Environment.

Skin surface and hair of dead European bison were examined an hour after their death at the latest; the hair was investigated in strips every 5 cm; adults and nymphs were picked with tweezers, and eggs were collected with hair. Such method, despite its high labour intensity, enabled the determination of parasite distribution over the body of its host. The collected specimens were preserved in 70% ethanol, and then used to make permanent polyvinyl-lactophenol preparations.

The study included 1,203 chewing lice specimens (from 115 European bison), consisting of 319 males, 416 females and 468 nymphs. The following measurements of the best-preserved specimens (100 from each group) were carried out: body length, length and width of particular tagmata. The terminology used by Lyal (1985) were adopted.in the present paper. Specimens are deposited in the Department of Invertebrate Zoology, University of Gdańsk.

3. Redescriptions of adults of *Bisonicola sedecimdecembrii*

Male. Body light, average body length: 1.92 mm (Table 1, Figs.1a and 2a). Head transverse (wider than long); anterior margin cone-shaped, osculum absent; temple margins rounded. Dorsal preantennal sulcus present; clypeal marginal carina slightly widened in the middle. Clypeus strengthened with lateral ridge interrupted in the middle. In the middle and posterior part of head sclerites visible in the form of dark lines separating temples from occiput on dorsal side and temples from area gularis on ventral side; additional reinforcements along posterior margin of temples and occiput. Mandibles with six ribs, dark-coloured; pulvinus clearly evident. Antennae massive, bent at an angle towards back; scape barrel-shaped, longer and wider than other segments – its length is similar to the sum of lengths of other segments. Tuber-like clavus at base of pedicel on internal side. Small setae and 6–7 cones located at the end of flagellum on ventral side; 2 or 3 posterolateral spines. Uniform head chetotaxy – on dorsal side two lines of setae along anterior

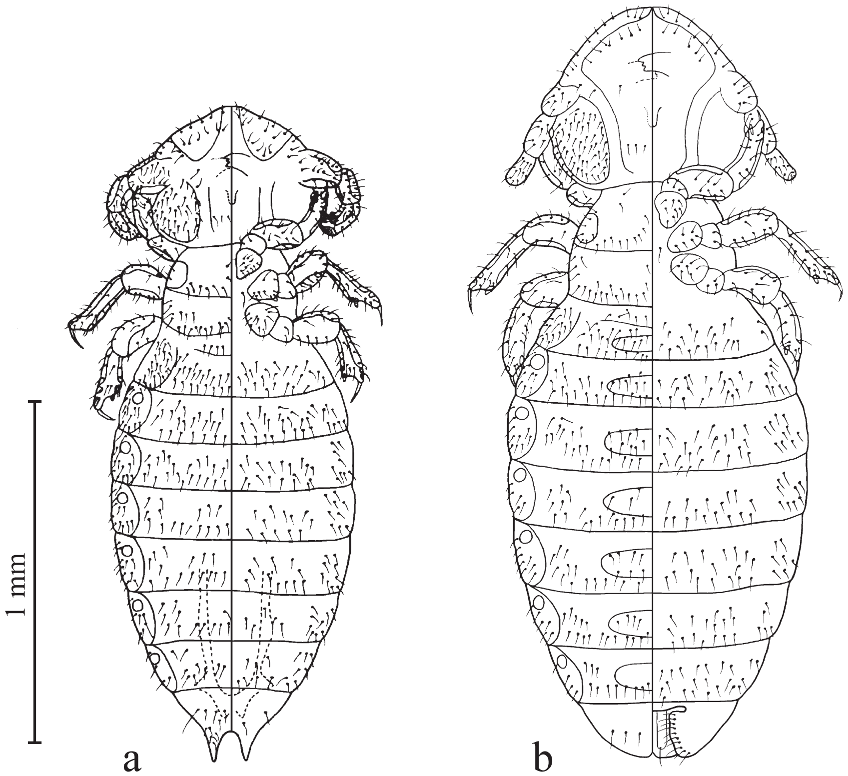

Fig. 1. Adults of *Bisonicola sedecimdecembrii* (dorsal/ventral view). – a. Male. – b. Female.

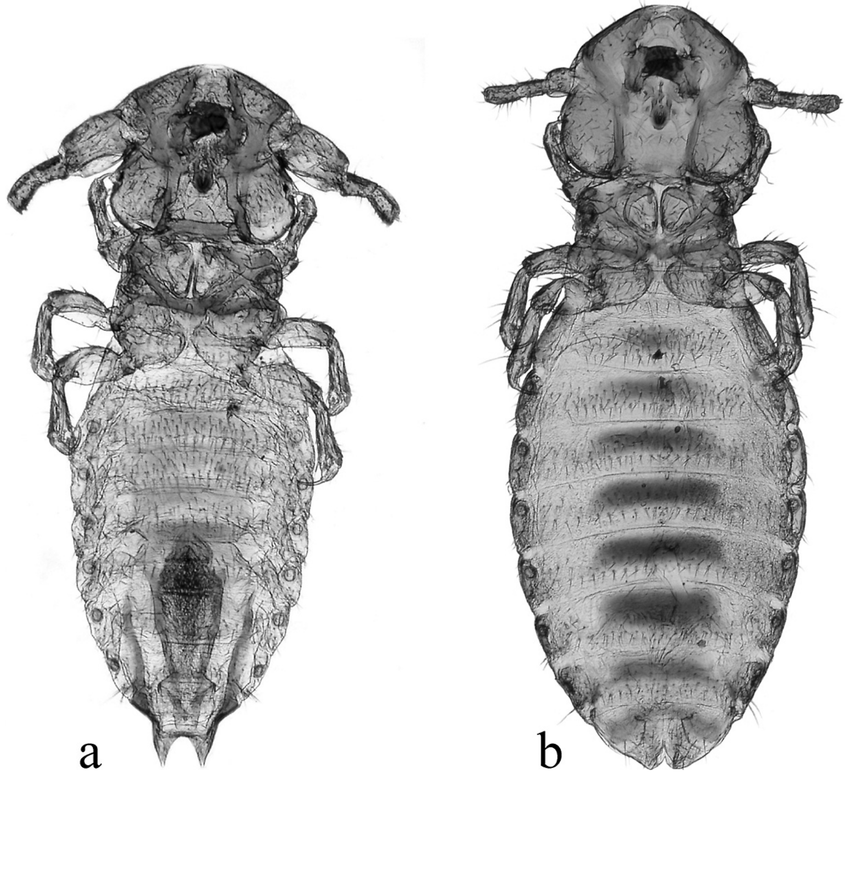

Fig. 2. Adults of *Bisonicola sedecimdecembrii* (dorsal view): – a. Male. – b. Female.

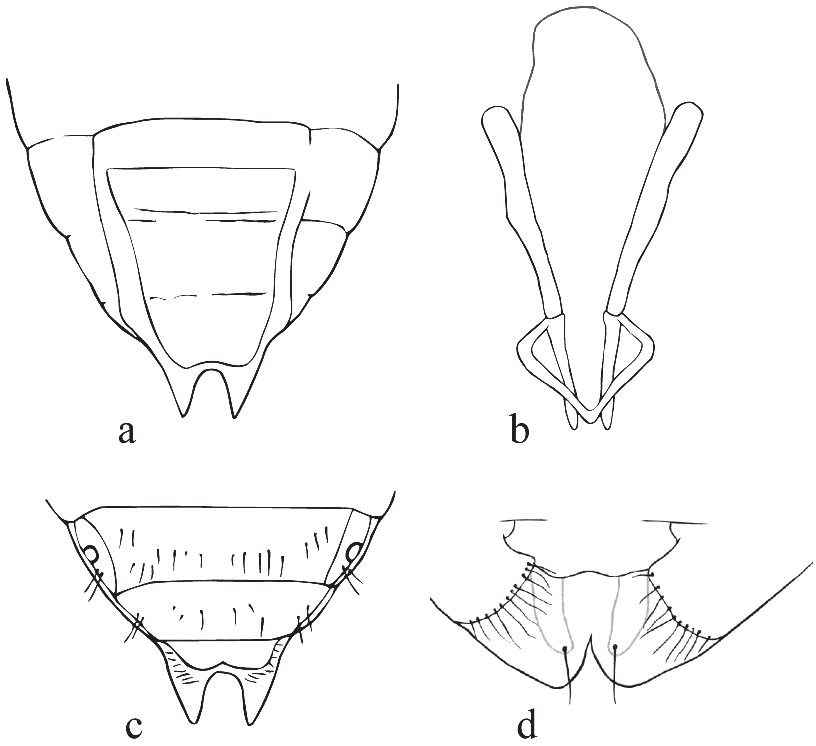

Fig. 3. Adults of *Bisonicola sedecimdecembrii*. – a. Shape of male subgenital plate. – b. Male genitalia. – c. Male terminalia. – d. Female terminalia.

margin of clypeus, a single line of setae on occiput and on average 32 setae on each temple. Ventral setae unevenly located along anterior margin of clypeus. Numerous setae also on scape and within sensory field of flagellum.

Thorax transverse with lateral and dorsal setae, long and moderately long, along margins on prothorax and pterothorax. Posterior margin of thorax bordering on dorsal side with the first tergum of abdomen, slightly concave in the middle. Atria of thoracic spiracles very large. Legs I shorter and more stocky than legs II and III, with massive coxa and covered with a small number of setae. Single spine present at distal end of tibia. Single chelae on tarsi; chela of first leg I is smaller than the others.

The first abdominal segment with 6–9 setae. Male subgenital plate with sternites VII and X fused to lateral rods of subgenital plate. Sternite VIII present but not fused to lateral rods of subgenital plate which are heavily scterotized, widest sternum VIII. Copulatory apparatus sclerotised, visible in central part of segments VI–VIII; parameres separate, attached to mesomeral arch. Basiparameral sclerites absent. Two sharp clavi, cone-shaped, arising from posterior margin of sternum XI, separated with U-shaped hollow, forming so-called pseudostyli, usually equipped with 6–7 setae on dorsal side (Figs. 3a–c). Chetotaxy of somatic part of abdomen monomorphic, abdomen covered only with setae. Setae located in clusters – centrally and laterally (Table 2).

Female. Body light beige, average body length: 2.16 mm (Table 1, Figs. 1b and 2b). Head transverse, pentagonal; anterior head margin rounded, temple margins rounded. Exoskeleton and mandibles similar to those of male. Antennae bent at an angle towards back, shaped differently to those of male – scape thicker, covered with clavus at base, flagellum is the longest segment, with small setae and 6–9 cones at the end, forming terminal sensory organ. Head covered with microchaetae; dorsally two lines of setae along margin of clypeus and a single line of about 6 setae on occiput and on average 40 setae on each temple. Ventral setae are unevenly located, along anterior margin of clypeus.

Thorax and legs similar to those of male; posterior margin, bordering on dorsal side with the

Table 2. Number of setae of abdomen of *Bisonicola sedecimdecembrii* (based on 1,203 specimens, consisting of 123 NI, 151 NII, 194 NIII, 319 males and 416 females).

Segment of abdomen	Nymph I dorsal/ventral	Nymph II dorsal/ventral	Nymph III dorsal/ventral	Male dorsal/ventral	Female dorsal/ventral
I	2–4/–	4–7/–	5–10/–	5–9/–	6–11/–
II	5–9/5–7	11–17/9–16	21–37/19–30	28–49/21–49	35–64/33–59
III	5–10/6–8	12–20/12–19	26–40/24–34	31–58/31–61	41–68/39–65
IV	8–11/6–9	13–19/11–19	24–40/24–35	31–55/29–51	32–66/37–63
V	5–12/6–8	14–19/10–16	22–33/18–33	25–44/30–37	33–60/21–54
VI	7–11/6–12	11–16/10–21	13–34/17–29	16–34/19–30	33–50/21–54
VII	9–11/8–12	11–17/9–23	16–31/18–30	20–42/10–24	30–47/23–51
VIII	4–8/6–8	9–16/10–20	14–24/13–29	15–26/10–35	16–33/23–45
IX	5–8/5–10	6–10/5–10	7–11/5–10	8–13/8–10	6–13/45–69

first tergum of abdomen, slightly concave in the middle. Abdomen oval; 6–9 setae on tergum. On ventral side two truncate, wide gonapophyses; setae present along postero-median margin; ventral lobe absent; ventral margin of vulva not sclerotised, very short, more or less straight; subgenital lobe absent. The last segment with narrow V-shaped notch medially (Fig. 3d). Chetotaxy of somatic part of abdomen monomorphic, and abdomen covered only with setae. Setae located in clusters centrally and laterally. Eight to thirteen setae on gonapophysis, located along internal margins (Table 2).

4. Description of juvenile stages of *Bisonicola sedecimdecembrii*

Nymph I. Body milk-white, average body length: about 1.15 mm (Table 1, Fig. 4a). Head almost as wide as long; anterior head margin arch-shaped, straight on a short section in the middle. External skeleton forms arched ridge along clypeus and list in central and posterior part of head. Mandibles bluntly ended and well coloured, pulvinus clearly evident. Antennae set almost perpendicularly to head axis; scape barrel-like, wider than other segments, of similar length to pedicel; clavus small, sheet-shaped at base of scape. Fla-

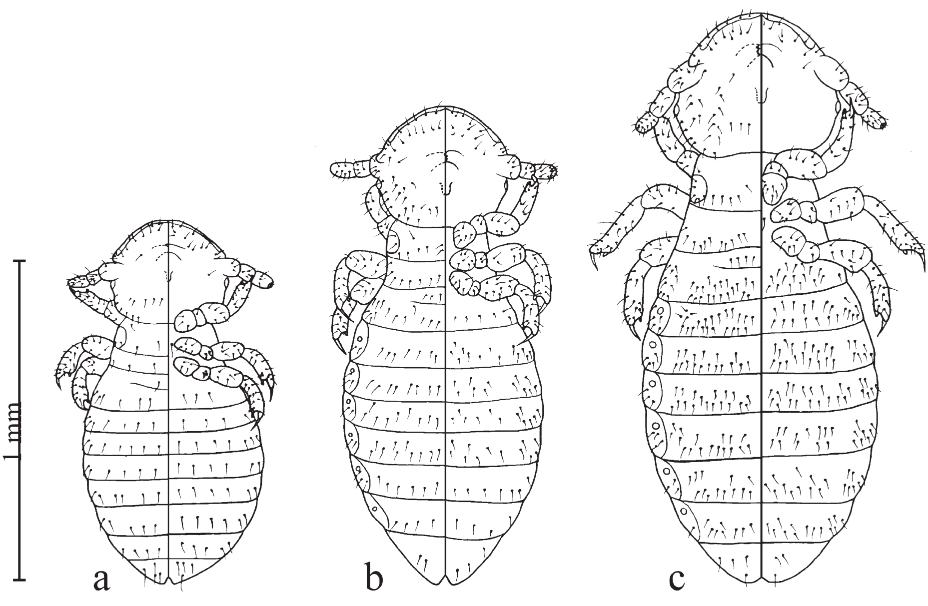

Fig. 4. Juvenile stages of *Bisonicola sedecimdecembrii* (dorsal/ventral view). – a. Nymph I. – b. Nymph II. – c. Nymph III.

Table 3. Comparision of nymphal (NI, NII, NIII) and adult (M: males, F: females) stages of *Bisonicola sedecimdecembrii*.

Features	NI	NII	NIII	M	F
Ratio of body length to width	2.6	2.5	2.3	2.7	2.5
Ratio of head length to total length	0.27	0.24	0.24	0.22	0.21
Ratio of abdomen length to total length	0.55	0.58	0.63	0.63	0.63
Ratio of head length to head width	0.97	0.97	0.96	0.91	0.87
Number of setae on tergum	2–4	4–7	5–10	6–11	6–9
Number of setae on II segment of abdomen	5–9	11–17	21–37	28–49	35–64
Abdominal spiracles*	–	+	+	+	+

* – = absent, + = present

gellum is the longest segment, its end bearing ventral terminal setae of various size and on average 4 cones. Head chetotaxy scarce; dorsal setae located in two lines along anterior margin of clypeus, in a single line on occiput, consisting of 6 setae and on average 9 setae per each temple. Ventral setae unevenly located along anterior margin of clypeus.

Thorax transverse, on dorsal side a single line of setae along lower margin of each segment; on ventral side one pair of setae as long as height of coxae II; leg segments covered with sparse setae. Tibia with a spine at the end. Abdomen oval, with 2–4 setae; the last segment cut in the middle. Scarce chetotaxy; setae located in single lines on the whole width of individual segments (Table 2).

Nymph II. Body light beige, average body length: 1.50 mm (Table 1, Fig. 4b). Head almost as wide as long, similar to that of NI. Mandibles and pulvinus well developed. Antennae set almost perpendicularly to head axis; scape barrel-shaped, wider than other segments, at base restricted with triangular clavus. Trichoid sensilla and 5–7 cones forming a sensory organ at the end of flagellum. Setae on head and antennae are more numerous than in NI but similarly located; 18 setae per each temple. Thorax composed similarly to NI, with a greater number of setae on dorsal side. Legs I shorter than the others, with massive femur; setae on tibiae are grouped at distal margin near a spine. Abdomen oval, 4–7 setae on tergum. Abdominal pleurae poorly evident; abdominal spiracles within them, visible from segment III to VIII, on dorsal side; the last segment cut in the middle. Abdominal setae form single lines on both sides along other segments and within pleurae (Table 2).

Nymph III. Body light beige, average body length: about 1.74 mm (Table 1, Fig. 4c). Anterior margin of head rounded, slightly concave in the middle on a short section; temple margins rounded. Mandibles strongly pigmented, with distinct ribs; pulvinus well developed. Antennae bent at an angle towards back; scape is the widest segment and flagellum is the longest segment; 6–8 cones within sensory field. Setae on head and antennae more numerous than in other nymphs, similarly located; on average 24 setae on each temple. Thorax similarly composed to that of earlier stages, with a greater number of setae on dorsal side. Legs I are shorter than the others, with massive femur; tibia distally widened, with a spine. Abdomen oval, 5–10 setae on tergum. Pleurae more distinct than in NII, with similarly located spiracles. Visible cut in the middle of the last segment. Uniform chetotaxy, abdominal setae form two distinct groups on both sides – central (1–3 uneven lines) and lateral, within pleurae. No rudiments of copulatory organs and gonopophyses were found (Table 2).

5. Discussion

The following changes in the development of *B. sedecimdecembrii* are observed: changes in the proportions between body tagmata (especially head size in comparison to other tagmata), differences in the arrangement of antennae, enrichment of chetotaxy, visible especially on the dorsal side (Table 3). Similar relationships seem to be typical of the development of this group of insects and have been described also in other Phthiraptera (e.g., Piotrowski & Kadulski 1970, Kadulski &

Fryderyk 1996, Modrzejewska & Złotorzycka 1987). Undoubtedly, nymph I is the easiest stage to distinguish due to the lack of abdominal spiracles. Chetotaxy of the abdomen is of particular importance in the taxonomic diagnostics. Hence the number of setae of segment II of abdomen on the dorsal side may be one of markers for distinguishing the developmental stages of *B. sedecimdecembrii*. For other species (e.g. *Damalinia meyeri*, *Rhabdopedilion longicornis*), the number of setae on the tergum are used for this purpose (Piotrowski & Kadulski 1970), however, European bison chewing lice exhibit too much variation in the number of these setae in the particular stages (Table 3). Some traits are constant in the subsequent nymph and adult stages, such as the number of setae on occiput or the pair of setae on the ventral side at the height of legs II.

Adults exhibit clearly evident sexual dimorphism including the shape of head, antennae and abdomen ending (Figs. 1 and 2). Similar differences occur also in other Trichodectidae (Złotorzycka 1994). In male chewing lice of European bison the clypeus is cone-shaped, while in a female it is rounded. On average females are slightly larger and have slightly different body proportions (Tables 1 and 3). Although the male head is on average a little smaller than that of the female, the scape of the male antennae is twice as long and at least 1.5 times wider. In addition, tuber-like clavus at the base of pedicel and three spines at the terminal end of flagellum are found on male antennae. On the other hand, females are usually characterized by more extensive chetotaxy. Even though so far there are no observations on the primordia of copulatory organs and gonopods in nymph III, and there are no differences in the number and arrangement of setae on the last abdominal segment, it is possible to distinguish male specimens already at this developmental stage on the basis of differences in the structure and size of antennae.

B. sedecimdecembrii from European bison exhibits relatively little morphological and morphometric variation. According to Clay (1958), chewing lice, compared to other insects, are characterized by rather low individual variation. However, this variation seems to be smaller in *B. sedecimdecembrii* also in comparison to other chewing lice from large ungulates. Presumably the reason is that the current population derives from the small founding group – the present world population of European bison has its origin in merely 12 individuals, and probably only some of the animals obtained from *in vitro* conditions were infested with chewing lice.

It is difficult to follow through the whole dynamics of chewing lice population in European bison, since the material can be obtained only during scheduled European bison eliminations (selective and reducing culling), i.e. mainly in winter, from December to March. In the material collected during a dozen or so years of studies, the ratio of males to females was 1:2. In many species of Trichodectidae, males are scarce, e.g. in research on *Bovicola bovis* from cattle, no male was found in the material that included a few thousand specimens (Eichler 1963). The lack or a rarity of males in 11 species of trichodectid lice almost certainly confirms obligatory parthenogenesis as the dominant method of reproduction within the Phthiraptera (Mey & González-Acuña 2007). However, a high share of males in the population of *B. sedecimdecembrii* suggests bisexual reproduction.

High prevalence of chewing lice with the usually asymptomatic infestation in the contemporary natural populations of European bison suggests that as a result of the long-term coevolution, perfect adaptation occurred in the host-parasite system of its both components. Host specificity, related to the evolution of the host-parasite system, has developed by the adaptation of all developmental stages to managing on the skin and hair coat of a host, which on the other hand forced stabilization of host specificity within such narrow borderlines that a given species/subspecies of chewing lice is on principle loyal to one host species. The occurrence of closely related forms of chewing lice in European and American bison suggests a close relationship between the mammals, or even a common ancestor. However, the issue of their origin remains contentious in the light of both palaeontological and molecular research.

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